Raznolikost, ekologija i vegetacija mahovina u hrvatskim kopnenim vodama

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DIVERSITY, ECOLOGY AND VEGETATION OF BRYOPHYTES IN THE FRESHWATERS OF CROATIA

DOCTORAL DISSERTATION

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Ovaj doktorski rad izrađen je u Botaničkom zavodu Prirodoslovno-matematičkog fakulteta pod vodstvom prof. dr. sc. Antuna Alegra, u sklopu Sveučilišnog poslijediplomskog doktorskog studija Biologije pri Biološkom odsjeku Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu.

MENTOR DOKTORSKE DISERTACIJE

prof. dr. sc. Antun Alegro

Rođen je u Karlovcu 10.12.1974. godine gdje je završio osnovnu školu i prirodoslovnu gimnaziju. Studij biologije na Prirodoslovno-matematičkom fakultetu u Zagrebu upisao je 1994. godine, a diplomirao 1998. godine na Botaničkom zavodu na kojem se iste godine zaposlio kao znanstveni novak. Magistrirao je 2002., a doktorirao 2007. Tokom 2000. boravio je na Institutu za botaniku Sveučilišta u Beču kao stipendist Republike Austrije. Od 2009. svake godine boravi nekoliko tjedana u Mađarskom prirodoslovnom muzeju radi usavršavanju u poznavanju mahovina i rada na mahovinskoj herbarijskoj zbirci. Usavršavao se i na nekoliko drugih tečajeva iz područja vegetacijske ekologije i matematičkih metoda u filogeniji. Kao znanstveni novak sudjelovao je u izvođenju praktikumske i terenske nastave iz kolegija Ekologija bilja, Geobotanika, Kormofita i Botanika. U zvanje docenta izabran je 2009., u zvanje izvanrednog profesora 2014., a u zvanje redovitog profesora 2019. godine. Na preddiplomskim i diplomskim studijima predaje kolegije Botanika, Primijenjena botanika, Nomenklatura i determinacija bilja i Vegetacijska ekologija, a na doktorskom studiju kolegij Biološko vrednovanje i zaštita kopnenih i slatkovodnih ekosistema. Sedam puta (2010., 2011., 2012., 2013., 2014., 2020. i 2021.) dobiva nagradu „Brdo“ Studentskog zbora PMF-a kao najbolji predavač na Biološkom odsjeku, a 2010. nagradu Biološkog odsjeka „Srećko Jelinić“, također kao najbolji predavač. Dosada su pod njegovim mentorstvom izrađena 24 diplomska rada te dvije doktorske disertacije. Njegova znanstvena djelatnost posvećena je florističkim, vegetacijskim i ekološkim istraživanjima koja su mahom vezana za područje Hrvatske te su uklopljena u širi kontekst jugoistočne Europe. U svojim istraživanjima obuhvatio je različite tipove vegetacije (šumska i travnjačka vegetacija, vegetacija pješčanih obala, slatkovodna i cretna vegetacija). Također se bavio sistematikom i biogeografijom trava koje grade suhe brdske i planinske travnjake, što je nadogradio istraživanjima vegetacijskih, ekoloških i fitogeografskih značajki tih travnjaka i njihove promjene u vremenu, osobito recentne, uzrokovane napuštanjem tradicionalnog gospodarenja. Pritom uvijek veliku pažnju poklanja općim florističkim istraživanjima, osobito u kontekstu proučavanja bioraznolikosti i njenih središta. Posljednjih godina intenzivno se bavi istraživanjima biogeografije i raznolikosti mahovina u Hrvatskoj. Nadalje, jedan od važnih fokusa istraživanja posljednjih godina su mu i makrofiti kopnenih voda, njihova raznolikost, rasprostranjenost i mogućnost upotrebe kao indikatora ekološkog stanja voda. Dosad je objavio 110 izvornih znanstvenih radova, dok je na znanstvenim skupovima sudjelovao sa 141 priopćenjem. Autor je i niza stručnih studija koje se bave travnjacima i njihovom sukcesijom, cretnom vegetacijom te florom i vegetacijom. Bio je voditelj i suvoditelj nekoliko međunarodnih projekata, te voditelj još dvadesetak projekata koji se bave florističkim i vegetacijskim istraživanjima različitih područja u Hrvatskoj. Član je uredničkih odbora časopisa Studia botanica hungarica te savjetničkog odbora časopisa Botanica Serbica. Bio je i član uredništva popularnog časopisa Priroda. Redoviti je recenzent u desetak botaničkih znanstvenih časopisa. Od 2010. do 2014. bio je predsjednik Hrvatskog botaničkog društva, dok je od 2020. do danas podpredsjednik Društva te je na tim funkcijama sudjelovao je u organizaciji četiri znanstvena skupa, „Evolucija bioraznolikosti na Balkanu“ održanog u Zagrebu 2012., „IV hrvatskog botaničkog simpozija“ održanog u Splitu 2013. godine, te X. simpozija Europskog društva za zaštitu mahovina i V. hrvatskog botaničkog simpozija, koji su održani 2022 godine u Zagrebu. Član je znanstvenih i stručnih udruga: Hrvatskog botaničkog društva, Hrvatskog udruženja slatkovodnih ekologa te međunarodnih društava Eastern Alpine and Dinaric Society for Vegetation Ecology and European Committee for Conservation of Bryophytes.

Sveučilište u Zagrebu Doktorski rad

Prirodoslovno-matematički fakultet

Biološki odsjek

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Tijekom istraživanja akvatičkih i semiakvatičkih mahovina na 786 lokaliteta na tekućicama i stajaćicama zabilježene su ukupno 83 vrste mahovina (68 pravih mahovina i 15 jeternjarki), što predstavlja 12 % dosad poznate raznolikosti mahovina u Hrvatskoj. Krške rijeke Dinaridske ekoregije podržavale su veću raznolikost u odnosu na rijeke Panonske ekoregije, na kojim su mahovine najvećim dijelom bile ograničene na obalna staništa, što je bilo podržano i razlikama u spektru životnih oblika i strategija između ekoregija. Većina mahovina preferirala je bistre, neutralne do bazične krške vodotoke s niskom razinom hranjivih tvari i organske tvari, odnosno neizmijenjene vodotoke s visokim udjelom prirodnog zemljišta u slivnom području. Među njima su se izdvojile vrste s vrlo uskim ekološkim nišama, koje se mogu smatrati dobrim i pouzdanim bioindikatorima. Međutim, najzastupljenije i široko rasprostranjene vrste imale su vrlo široke ekološke niše, dok su svega dvije, *Riccia fluitans* i *Leptodyctium riparium* preferirale hipereutrofne vodotoke s visokim udjelom intenzivne poljoprivrede u slivnom području. U prirodnim tekućicama Hrvatske, mahovine su bila dominantna komponenta vegetacije na svega 14,42 % istraživanih lokaliteta, prilikom čega je centar rasprostranjenosti bila Dinaridska ekoregija, tj. njeni hladni, brzi krški vodotoci s većim i stabilnijim supstratom. Ustanovljeno je ukupno pet mahovinskih zajednica, od čega su tri najzastupljenije bile karakteristične za krške rijeke Dinaridske ekoregije, a dvije za male Panonske tekućice. One su se razlikovale po bogatstvu i sastavu vrsta, udjelu mahovina u sastavu vrsta te njihovom afinitetu prema vodi te prema udjelu pojedinih životnih oblika. Ekološki su se ove zajednice odvojile duž gradijenata kemije vode (alkalitet i kakvoća vode), bioklimatskih parametara povezanih s dostupnosti vode i njenom raspodjelom tijekom godine te veličine slivnog područja.

(75 stranica, 154 literaturna navoda, jezik izvornika hrvatski)

Ključne riječi: slatkovodna staništa, reofiti, makrofiti, ekološki odgovori, bioindikatori, zajednice, kakvoća vode, bioklimatske značajke

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University of Zagreb Doctoral dissertation
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Diversity, ecology and vegetation of bryophytes in the freshwaters of Croatia

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During the research of aquatic and semi-aquatic mosses, which included 786 sites on watercourses and standing waters, 83 bryophyte species (68 mosses and 15 liverworts) were recorded. This amounted to 12% of the so-far-known bryophyte diversity in Croatia. The karstic rivers of the Dinaric Ecoregion supported greater diversity compared to those of the Pannonian Ecoregion, where bryophytes were mostly restricted to river margins, which was supported by differences in the life-form and life strategy spectra between the ecoregions. Most species preferred clear, neutral to basic karstic watercourses with low levels of nutrients and organic matter, i.e. pristine watercourses with a high proportion of natural land in the catchment area. Among them, species with very narrow ecological niches were singled out and recognised as good and reliable bioindicators. However, the most abundant and widespread species had very wide ecological niches, while only two, *Riccia fluitans* and *Leptodyctium riparium*, preferred hypereutrophic watercourses with a high proportion of intensive agriculture in the catchment area. In natural watercourses, mosses were the dominant component of the vegetation in only 14.42% of the investigated localities, with the Dinaric Ecoregion, i.e. its cold, fast karst watercourses with larger and more stable substrates, representing the distribution and diversity centre of these bryophyte dominated communities. Five communities were identified, with three most represented being characteristics for the karstic watercourses of the Dinaric Ecoregion, and two for the small streams of the Pannonian Ecoregion. They differed in species richness and composition, the share of bryophytes and their affinity for water as well as in life-form spectra. Furthermore, these communities were segregated along gradients of water chemistry (alkalinity and water quality), bioclimatic parameters related to water availability and its yearly distribution, as well as the size of the catchment area.

(75 pages, 154 references, original in Croatian)

Keywords: freshwater habitats, rheophytes, macrophytes, ecological responses, bioindicators, community, water quality, bioclimatic variables

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SADRŽAJ

1. PROŠIRENI SAŽETAK

Mahovine koje nastanjuju kopnene vode ne čine visok udio u ukupnoj raznolikosti mahovina (Vieira i sur. 2012b), no značajna su komponenta slatkovodnih ekosustava, posebice u izvorišnim područjima, gorskim i prigorskim vodotocima s izraženim padom te na slapištima (Shevock i sur. 2017). To im omogućuju brojne anatomske i fiziološke adaptacije zahvaljujući kojima uspješno odolijevaju mehaničkom stresu uslijed velikog protoka i brze struje vode, ali i dobro podnose razdoblja isušivanja, kada razina vode padne (Glime i Vitt 1984; Vitt i Glime 1984). Također, zahvaljujući ovim prilagodbama, one dominiraju u povremenim vodotocima i općenito tokovima s izraženom sezonalnosti u protoku (Gecheva i sur. 2017; Vieira i sur. 2018). Na takvim surovim staništima, koja su nepogodna za vaskularne makrofite, mahovine predstavljaju značajne primarne proizvođače te sudjeluju u ukupnoj trofičkoj dinamici. Njihove guste sastojine predstavljaju zaklon i stanište različitim skupinama beskralježnjaka, ali i pogodnu podlogu za rast perifitona (Steam Bryophyte Group 1999). Akvatičke i semiakvatičke mahovine nastanjuju i srednje i donje tokove tekućica, kao i stajaćice i njihove obale, ali su na tim staništima znatno rjeđe.

Dok prisutnost i pokrovnost mahovina prije svega ovise o stabilnosti korita i veličini supstrata (Suren 1996; Suren i Duncan 1999; Scarlet i O'Hare 2006; Tremp i sur. 2012), raznolikost i sastav vrsta uvjetovani su geološkim, klimatskim i fiziografskim čimbenicima, ali i fizikalno-kemijskim i kemijskim parametrima vode (Suren 1996; Ceschin i sur. 2012a; Tremp i sur. 2012; Vieira i sur. 2014; Ceschin i sur. 2015; Gecheva i sur. 2017; Vieira i sur. 2018). Također, hidromorfološke promjene, kao i antropogeno onečišćenje i eutrofikacija snažno utječu na mahovine kopnenih voda i njihove zajednice (Muotka i Virtanen 1995; Vanderpoorten i Durwael 1999; Vanderpoorten i Klein 1999b; Gecheva i sur. 2017). Zajednice vodenih biljaka, uključujući i mahovine, prepoznate su kao dobri bioindikatori kakvoće vode, ali i općenito biointegriteta slatkovodnih ekosustava te se stoga smatraju korisnima u biološkom monitoringu i procjeni ekološkog stanja tekućica i stajaćica (Birk i sur. 2007, 2012; Gecheva i Yurukova 2014), pri čemu kao sesilni organizmi preciznije ukazuju na lokalne promjene u okolišu, a zbog dugog životnog vijeka integriraju promjene tijekom duljih razdoblja, kao i uzastopne poremećaje.

S obzirom da su mahovine kopnenih voda na području Hrvatske nedovoljno istražene, uz iznimku pojedinih krških rijeka, te da su do sada prepoznate kao bitna komponenta slatkovodnih ekosustava sa značajnim bioindikatorskim potencijalom, glavni ciljevi ovog doktorskog rada bili su istražiti floru, vegetaciju i ekologiju mahovina u Hrvatskoj, odnosno: 1) utvrditi raznolikost i distribuciju vodenih mahovina u tekućicama i stajaćicama Hrvatske; 2) analizirati sastav mahovinske flore prema flornim elementima, životnim oblicima i životnim strategijama; 3) objasniti uvjetovanost pojavljivanja vodenih mahovina u tekućicama Hrvatske s obzirom na okolišne uvjete; 4) odrediti ekološke odgovore vrsta mahovina na ekološke čimbenike u tekućicama Hrvatske; 5) utvrditi rasprostranjenost, raznolikost, sastav i strukturu mahovinskih zajednica te njihovu fitocenološku pripadnost; 6) utvrditi na koji su način mahovinske zajednice u tekućicama Hrvatske uvjetovane okolišnim uvjetima te 7) definirati bioindikatorske vrste vodenih mahovina Hrvatske u ocjeni ekološkog stanja voda.

Provedena istraživanja su također jedna od rijetkih do sada provedenih na području jugoistočne Europe te jedina toga tipa za područje zapadnog Balkana, odnosno središnjeg i istočnog Mediterana. Rezultati istraživanja, objavljeni u pet znanstvenih radova, ispunili su sve istraživačke ciljeve i potvrdili hipoteze postavljene unutar ovog doktorskog rada.

U prve tri publikacije (**Rad 1–3**) objavljeni su rezultati florističkog istraživanja kojim je utvrđena raznolikost i distribucija mahovina u kopnenim vodama Hrvatske te su pronađene nove vrste za floru Hrvatske. Mahovine su zabilježene na 29 % istraživanih lokacija na prirodnim i umjetnim tekućicama i stajaćicama i to ukupno 83 vrste (68 pravih mahovina i 15 jetrenjarki), što čini 12 % do sad poznate raznolikosti mahovina u Hrvatskoj. Najučestalije vrste bile su *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Leptodyctium riparium* i *Cratoneuron filicinum.* Većina vrsta imala je vrlo malu učestalost s preko 70 % vrsta zabilježenih na manje od 10 lokaliteta. Također, većina zabilježenih vrsta bile su fakultativne akvatičke vrste karakteristične za lotička staništa. Veća raznolikost zabilježena je u krškim rijekama Dinaridske ekoregije i to njene Kontinentalne subekoregije, dok je najsiromašnija bila Panonska ekoregija. Ove dvije regije dijelile su 44 vrste, dok je njih 26 zabilježeno isključivo u Dinaridskoj, a 13 u Panonskoj ekoregiji. U flori mahovina kopnenih voda Hrvatske dominirali su cirkumpolarni i europski, odnosno tempratni elementi, što odgovara biogeografskim značajkama istraživanog područja. Usporedba ekoregija i subekoregija ustanovila je značajna preklapanja u flornim elementima, ali i neke osobitosti pojedinih ekoregija i subekoregija. Primjerice, nizak udio mediteransko-atlantskih elemenata, kao i suboceanskih te odsustvo oceanskih elemenata u Panonskoj ekoregiji u odnosu na Dinaridsku ekoregiju, posebice njenu Kontinentalnu subekoregiju, u velikoj mjeri odgovara klimatskim ograničenjima za razvoj ovih mahovina u Panonskoj ekoregiji. Naime, Kontinentalnu subekoregiju karakterizira veća godišnja količina oborina i niže temperature tijekom najvlažnijeg kvartala, što sugerira vlažniju klimu. Također, izostanak boreo-arktičkih i borealno-montanih te viši udio južno-tempratnih elementa u Mediteranskoj subekoregiji Dinaridske ekoregije odgovara klimatskim obilježjima ovoga područja za koje je uvelike karakteristična mediteranska klima, s višim temperaturama zraka i sušnim razdobljem ljeti. Među životnim oblicima najzastupljenije su bile vodene vrpčaste mahovine (engl. *aquatic trailings*), koje su najbolje prilagođene životu u kopnenim vodama te mahovine koje rastu u čupercima (engl. *turfs*), koje su karakteristične za sezonski plavljena staništa i povremene vodotoke. S obzirom na životne strategije, dominirale su perenijalne vrste karakteristične za stalne i brze tokove, a pratili su ih kolonisti, koji dolaze na emergentnim pozicijama i uz obalu. Razlike u spektru životnih oblika i životnih strategija između pojednih ekoregija ukazuju da su mahovine u Panonskoj ekoregiji većim dijelom ograničene na periodički plavljena obalna staništa, dok krške rijeke Dinaridske ekoregije predstavljaju povoljnija staništa s raznolikim mikrostaništima za akvatičke i semiakvatičke vrste te stoga podržavaju i višu raznolikost mahovina.

U četvrtoj publikaciji (**Rad 4**) istražena je ovisnost pojavljivanja vodenih mahovina u tekućicama Hrvatske o okolišnim čimbenicima te su na temelju ekoloških odgovora vrsta doneseni zaključci o njihovom bioindikacijskom potencijalu. Pojavljivanje pojedinih mahovina u tekućicama bilo je uvjetovano fizikalno-kemijskim parametrima vode koji su povezani s njenom kakvoćom, a među njima, najznačajniji su bili koncentracija otopljenog kisika, koncentracija hranjivih tvari (ukupnog dušika i ukupnog fosfora), kemijska potrošnja kisika i električna provodljivost. Također, mahovine su se razdvojile duž gradijenta alkaliteta, što je u vezi s geološkom podlogom, ali i duž gradijenata prirodnog i urbanog zemljišta u slivnom području. Ekološki odgovori vrsta pokazali su da većina vrsta preferira čiste, blago bazične, oligotrofne vode s niskom razinom organske tvari i niskom električnom provodljivosti te s visokim udjelom prirodnog, odnosno niskim udjelom urbanog zemljišta unutar slivnog područja. Međutim, manji broj vrsta imao je uske ekološke niše, dok je većina vrsta imala široku ekološku toleranciju spram spomenutih okolišnih čimbenika te su bile široko rasprostranjene. Vrste mahovina koje su imale uske ekološke niše s obzirom na kemijske parametre vode povezane s njenom kakvoćom, kao što su *Palustriella falcata, Eucladium vertcillatum, Dichodontium flavescens* i *Jungermannia atrovirens*, predstavljale su dobre i pouzdane bioindikatore. Također, više pokrovnosti vrsta *Cinclidotus aquaticus, Chiloscyphus polyanthos, Apopellia endiviifolia* i *Didymodon tophaceus* ukazivale su na oligotrofne uvjete, dok su visoke pokrovnosti vrsta *Leptodyctium riparium* i *Riccia fluitans* ukazivale na eutrofne uvjete.

U petoj publikaciji istražene su mahovinske zajednice u prirodnim tekućicama te njihova uvjetovanost okolišnim uvjetima (**Rad 5**). Ustanovljeno je ukupno pet zajednica u kojima mahovine predstavljaju dominantnu vegetacijsku komponentu. Ove zajednice razlikovale su se na temelju bogatstva i sastava vrsta, udjela mahovina u florističkom sastavu i njihovog afiniteta prema vodi, kao i udjela pojedinih kategorija u spektru životnih oblika, što je odražavalo njihove različite ekološke profile. Također, ove zajednice odvojile su se duž gradijenta kemije vode, bioklimatskih i fiziogeografskih varijabli. Naime, one su u najvećoj mjeri bile uvjetovane alkalitetom, koncentracijom hranjivih tvari, otopljenog kisika i količinom organske tvari, bioklimatskim varijablama povezanim s dostupnošću vode i njenom raspodjelom kroz godinu te veličinom slivnog područja.

Najzastupljenija i vrstama najbogatija zajednica bila je *Cinclidotus* zajednica s centrom rasprostranjenosti u stalnim i brzim krškim vodotocima Dinaridske ekoregije, tj. njene Kontinentalne subekoregije. Ova zajednica imala je najširi ekološki raspon s obzirom na kemiju vode te je bila vezana uglavnom za krške vodotoke pod utjecajem umjerene klime s visokom precipitacijom. Karakterizirao ju je visok udio mahovina u flornom sastavu, a među njima su dominirali reofiti, odnosno vodene vrpčaste vrste (engl. *aquatic trailings*) sugerirajući stalnost toka. Za krške rijeke Dinaridske ekoregije bile su karakteristične i vrstama nešto siromašnije zajednice *Didymodon tophaceus-Apopellia endiviifolia* i *Berula erecta-Cratoneuron filicinum*, koje su uglavnom bile vezane za vrlo čiste vodotoke s velikim slivnim područjem, pod utjecajem mediteranske klime s visokim srednjim temperaturama zraka u najsušem kvartalu, odnosno visokom količinom precipitacije u najhladnijem kvartalu. *Didymodon tophaceus-Apopellia endiviifolia* imala je visok udio hidrofita i vrsta koje rastu u čupercima (engl. *turfs*), koji sugeriraju određenu sezonalnost u dostupnosti vode i povremeno bujične tokove. Ova zajednica je doista i dolazila na povremenim vodotocima s malim slivnim područjem, dok je na većim vodotocima uglavnom bila vezana za slapišta. Također, srednja vrijednost pH vodotoka u kojima je dolazila bila je značajno viša u odnosu na druge zajednice te su za nju bile karakteristične sedrotvorne vrste *Didymodon tophaceus* i *Eucladium verticillatum*. *Berula erecta-Cratoneuron filicinum* bila je prijelazna zajednica stalnih tokova, u kojima mahovinska vegetacija postupno prelazi prema herbidnoj vegetaciji karakterističnoj za manje i pliće vodotoke u umjerenom pojasu Europe. Karakterizirao ju je visok udio vaskularnih biljaka u flornom sastavu, dok su među mahovinama dominirali reofiti, odnosno vodene vrpčaste vrste (engl. *aquatic trailings*), ali i značajna učestalost vrsta koje rastu u glatkim sagovima (engl. *smooth mats*) te je njihov odnos sugerirao da ona dolazi u mirnijim vodotocima u odnosu na

Cinclidotus i *Didymodon tophaceus-Apopellia endiviifolia*. U ovakvim vodotocima, koji odgovaraju nizvodnijim dijelovima rijeka te nizinskim krškim rijekama s blagim padom u kojima je struja vode mirnija, a supstrat sitniji, vaskularne biljke počinju zamjenjivati mahovine te je iz usporedbe ove tri zajednice uočljivo da se broj i abundancija vaskularnih vrsta makrofitske flore smanjuje s porastom raznolikosti i abundancije vodenih mahovina. Vrstama bogata *Oxyrrhynchium hians-Chiloscyphus pallescens* i vrstama siromašna *Fissidens pusillus-Veronica beccabunga* bile su karakteristične za eutrofne male vodotoke Panonske ekoregije s visokim vrijednostima srednje temperature u najvlažnijem kvartalu. U obje zajednice dominirali su higrofiti, tj. mahovine koje nastanjuju obalne zone kao glavno pogodno mikrostanište za mahovine na vodotocima Panonske ekoregije.

Uočeni geografski obrasci raznolikosti i rasprostranjenosti mahovinskih zajednica, ali i općenito akvatičkih i semiakvatičkih vrsta mahovina, pokazali su da relativno čiste, brze i hladne krške rijeke Dinaridske ekoregije predstavljaju staništa koja podržavaju veću raznolikost u odnosu na vodotoke Panonske ekoregije u kojoj dominiraju sporiji i topliji nizinski vodotoci od koji oni veći odgovaraju srednjim i donjim tokovima u kojima je stupanj trofije prirodno viši u odnosu na vodotoke Dinaridske ekoregije. U ovakvim vodotocima također prevladava sitniji i manje stabilan supstrat, koji je nepovoljan za naseljavanje i održanje većine vodenih mahovina. Dodatno su vodotoci Panonske ekoregije u većoj mjeri hidromorfološki degradirani te izloženi onečišćenju i eutrofikaciji u odnosu na vodotoke Dinaridske ekoregije (Plantak i sur. 2016; Vučković i sur. 2018, 2019, 2021; Medić i sur. 2020a, b, c; Musić i sur. 2020). Ovi antropogeni utjecaji smanjuju pogodnost staništa za akvatičke i semiakvatičke vrste te dovode do pada pokrovnosti i raznolikosti, odnosno do promjena u sastavu vrsta (Suren 1996; Gecheva i sur. 2010, 2017), što dodatno umanjuje pogodnost vodotoka u Panonskoj ekoregiji kao staništa za ovu grupu organizama.

U konačnici, potvrđene su sve istraživačke hipoteze postavljene unutar ovog doktorskog rada: 1) rasprostranjenost, taksonomska, funkcionalna i horološka raznolikost te učestalost pojedinih vrsta vodenih mahovina posljedica su geografskih trendova i ekoloških uvjeta na staništu (**Rad 1, 4, 5**); 2) rasprostranjenost, struktura i sastav mahovinskih zajednica u tekućicama posljedica su kombinacije ekoloških i geografskih čimbenika (**Rad 4, 5**); 3) sastav i struktura mahovinske flore i vegetacije ovisni su o kakvoći vode (**Rad 4, 5**); 4) broj i abundancija vaskularnih vrsta makrofitske flore smanjuje se s porastom raznolikosti i abundancije vodenih mahovina (**Rad 5**).

2. UVOD

2.1. Osnovne značajke mahovina slatkovodnih staništa

Mahovine koje nastanjuju kopnene vode i njihove obale ne čine visok udio u ukupnoj flori mahovina (Vieira i sur. 2012b), no značajna su komponenta slatkovodnih ekosustava. Vodene ekosustave naselile su sekundarno (Akiyama 1995; Cook 1999), zahvaljujući nizu morfoloških i fizioloških adaptacija (Glime i Vitt 1984; Vitt i Glime 1984) koje su se javile neovisno kod više linija kopnenih mahovina kao rezultat paralelne evolucije i prilagodbe visoko-specijaliziranim uvjetima prisutnim u pojedinim tipovima slatkovodnih staništa, kao i čitavom nizu mikrostaništa unutar njih (Slack i Glime 1985; Slack 1990; Glime 2020). Predstavnici svih triju evolucijskih linija koje nazivamo mahovinama nastanjuju različita slatkovodna staništa, od cretova, močvara, lokvi i jezera do potoka i rijeka, a najzastupljenije su prave mahovine (Bryophyta), zatim jetrenjarke (Marchantiophyta) te rožnjače (Anthoceratophyta) (Goffinet 2000). Mahovine nisu kolonizirale mora i oceane, dok ih samo nekolicina tolerira izraženiji osmotski stres u najvišim dijelovima zone plime i oseke.

Velika raznolikost slatkovodnih staništa, kao i pripadajućih mikrostaništa, odnosno ekoloških niša, otežava njihovu klasifikaciju, pa tako i podjelu mahovina koje ih nastanjuju. Umjesto toga, Vitt i Glime (1984) sugeriraju kako bi se one trebale promatrati kroz svoje prilagodbe na okolišne gradijente prisutne u vodenim ekosustavima, od kojih se u ovom slučaju najbitnijima smatraju intenzitet strujanja vode i fluktuacije u razini vode. Na krajevima gradijenta intenziteta strujanja vode mogu se u konačnici razlikovati limnofilne i reofilne vrste; limnofilne nastanjuju prvenstveno staništa u kojima nema strujanja vode ili je ono zanemarivo te reofilne, koje optimum imaju u brzim tokovima. Duž gradijenta fluktuacije razine vode mogu se razlikovati obligatne i fakultativne akvatičke vrste te semiakvatičke emergentne vrste. Akvatičke vrste žive uglavnom submerzno, međutim, dok obligatne akvatičke vrste ne toleriraju ili toleriraju samo minimalne fluktuacije u razini vode i s njima povezano isušivanje, fakultativne akvatičke mahovine jako dobro toleriraju i značajnije dnevne i sezonske fluktuacije u razini vode, kao i kraće ili dulja razdoblja isušivanja. Vrlo često su upravo limnofilne vrste, ujedno i obligatne akvatičke, dok su fakultativne akvatičke vrste uglavnom reofilne. One dolaze na staništima ili mikrostaništima na kojima prisutnost vode nije stalna te mogu preživjeti i potpuno potopljene i potpuno isušene, a u brzim i turbulentnim vodotocima dodatno su izložene mehaničkom stresu. Ovakve vrste stoga posjeduju niz strukturalnih i fizioloških adaptacija koje im omogućuju preživljavanje ovakvih uvjeta. Mnoge reofilne vrste imaju malene, izodijametrične stanice debljih i stoga čvršćih staničnih stijenki, listiće (filoidi) s dvoslojnim plojkama ili višeslojnim rubovima, dok su kod nekih vrsta listići preklopljeni uzdužno sredinom plojke pa nalikuju na lađice. Također, reofilne vrste često imaju izražena i duga središnja rebra, koja kod limnofilinih vrsta uglavnom izostaju. Nadalje, snažni i brojni korijenčići (rizoidi) reofilnim vrstama omogućuju prijanjanje za supstrat i uspješno odupiranje struji vode. S druge strane, razdoblja isušivanja dobro podnose zahvaljujući fiziološkim adaptacijama, a u manjom mjeri strukturalnima; primjerice brojnim papilama na stanicama plojke listića koje sprječavaju gubitak vode, omogućuju kapilarni prijenos i općenito povećavaju površinu za njenu apsorpciju.

Za razliku od limnofilnih i reofilnih akvatičkih vrsta, emergentne semiakvatičke vrste su one čije su vršne i aktivno rastuće regije terestričke, dok im je bazalni dio uronjen u vodu. Rastu uglavnom u plitkoj vodi uz rubove vodnih tijela, ali i na njihovim obalama na mjestima gdje je supstrat natopljen vodom. Njihove prilagodbe su stoga prvenstveno usmjerene na uspješno provođenje vode u vršne dijelove. To im omogućuje dobro razvijeni centralni dio stabalca (kauluoid) s dugim stanicama koje uspješnije provode vodu, kao i bogato razvijeni korijenčići, koji kod mnogih vrsta grade tomentum na površini stabalca, a zaslužni su za kapilarno provođene vode iz bazalnih dijelova prema vršnima. Druge vrste u istu svrhu imaju bogato razvijene nastavke na površini stabalca – parafilije, a česte su i papilozne stanice listićne plojke, kao i u slučaju nekih reofilnih vrsta. S druge strane, fiziološki mehanizmi tolerancije isušivanja slabije su izraženi kod ove grupe mahovina.

Ova podjela mahovina slatkovodnih staništa, nažalost nudi samo oskudnu listu vrsta za koje je predložena određena ekološka kategorija, te autori naglašavaju da pojedine vrste mogu pripadati u više kategorija, ovisno o interakciji ova dva okolišna čimbenika na staništu i samim adaptacijama pojedinih vrsta (Vitt i Glime 1984). S druge strane, Dierβenova (2001) klasifikacija na temelju afiniteta prema vodi, odnosno vlažnosti staništa, obuhvatila je znatno veći broj vrsta te je stoga češće primjenjivana u florističkim i ekološkim analizama mahovina slatkovodnih staništa. I ova klasifikacija razlikuje vrste koje dolaze submerzno u tekućim vodama (reofiti), kao i one koje dolaze submerzno u stajaćicama (limnofiti), a njima su pridruženi i amfifiti (vrste koje su periodički submerzne), hidrofiti (vrste koje toleriraju inundaciju) te higrofiti (vrste vrlo vlažnih staništa koje uglavnom nastanjuju periodički plavljene obale vodnih tijela). Dierβenova (2001) klasifikacija također za većinu vrsta predlaže nekoliko različitih kategorija te ju je preporučljivo upotrebljavati uzimajući u obzir specifične prilike zatečene prilikom terenskih istraživanja, kao i druge dostupne literaturne podatke

(Holmes i sur. 1998; Demars i Harper 2005; Hering i sur. 2006; Birk i sur. 2007; Vieira i sur. 2012a, 2014).

Broj obligatnih akvatičkih vrsta malen je u odnosu na one fakultativne i semiakvatičke, koje zahvaljujući svojim prilagodbama čine dominantnu biljnu komponentu prvenstveno u izvorišnim dijelovima rijeka i na slapištima. Također su bitna komponenta vegetacije vodotoka s izraženim sezonskim promjenama u protoku, odnosno povremenih vodotoka, kao jedini predstavnici makrofitske vegetacije koji se uspijevaju održati u periodički suhim koritima. U navedenim staništima mahovine grade bujne zajednice razreda *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956 (mahovinska vegetacija tekućih voda i slapišta koje rastu potopljene u vodi i u zoni prskanja) i *Montio-Cardaminetea* Br.-Bl. et Tx. ex Klika et Hadač 1944 (vegetacija izvorišta i sedrenih barijera) (Mucina i sur. 2016; Škvorc i sur. 2017), a također su značajne u sastavu vegetacije sredozemnih nakapnica i plitkih polušpilja razreda *Adiantetea* Br.-Bl. et al. 1952 (reliktna hazmofitska vegetacija zasjenjenih staništa izloženih prskanju vode na području Sredozemlja, atlantskih otoka, Sjeverne Afrike i Bliskog istoka). Na ovakvim staništima u kojima vladaju vrlo specifični ekološki uvjeti poput turbulentnog i vrlo brzog toka vode, niske temperature, niske koncentracije nutrijenata, često značajne zasjene, krupnog sedimenta i strmih obala, vegetacija vaskularnih biljka se ne uspijeva uspostaviti, niti održati (Suren 1996, Gecheva i sur. 2010, Ceschin i sur. 2015). Vodene mahovine, koje imaju značajke kolonizatora, uspijevaju nastaniti i održati se u ovakvim teškim uvjetima, prvenstveno na najstabilnijim supstratima, kao što su veće stijene ili pak baze drveća na obali. Mahovinama slatkovodnih staništa, odnosno, njihovih obala mogu se pridodati i malene efemerne vrste poput vrsta rodova *Riccia* i *Physcomitrium* koje se razvijaju na periodički plavljenim obalnim staništima za vrijeme niskog vodostaja unutar vegetacije razreda *Isoëto-Nanojuncetea* Br.-Bl. et Tx. in Br.-Bl. et al. 1952 (pionirska vegetacija niskih šaševa periodično plavljenih slatkovodnih staništa Eurazije) i *Bidentetea* Tx. et al. ex von Rochow 1951 (pionirska jednogodišnja vegetacija sezonski poplavljenih obala eutrofnih tekućica i stajaćica te antropogenih staništa bogatih hranjivim tvarima boreo-tempratnog pojasa Europe i Sjeverne Afrike) te močvarne vegetacije razreda *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941 (vegetacija tršćaka, rogozika i šiljeva Eurazije) (Mucina i sur. 2016; Škvorc i sur. 2017).

2.2. Floristička istraživanja mahovina kopnenih voda

Opsežniji floristički radovi koji obuhvaćaju šira geografska područja i daju pregled i analizu raznolikosti vrsta i viših taksonomskih grupa, njihovu rasprostranjenost i horološku analizu mahovina slatkovodnih staništa su rijetki. U Europi je na ovaj način istražena, primjerice, flora mahovina porječja rijeke Tiber u središnjoj Italiji (Ceschin i sur. 2012b), gdje je na 32 istraživana odsječka zabilježeno svega 20 vrsta iako je istraživanje uključilo i vrste koje dolaze na rubovima vodotoka, tj. supstratima koji su najvećim dijelom godine potopljeni. Najučestalije vrste bile su *Fontinalis antipytretica* Hedw. i *Rhynchostegium riparioides* (Hedw.) Cardot, široko rasprostranjene vrste koje su bilježene kao najčešće i u drugim dijelovima Europe unutar istraživanja fokusiranih na ekologiju mahovina (Scarlett i O'Hare 2006; Gecheva i sur. 2010; Ceschin i sur. 2015). U ovom istraživanju najzastupljenije porodice bile su Amblystegiaceae i Pottiaceae, koje općenito imaju značajan udio avatičkih i semiakvatičkih predstavnika (Glime 2020). U horološkom spektru mahovinske flore dominirali su cirkumpolarni tempratni i europski tempratni elementi, što je u skladu s bioklimatskim prilikama istraživanoga područja, dok je značajan udio mediteransko-atlantskog elementa objašnjen stabilnim i vlažnim uvjetima na mikrostaništima gornjih tokova istraživanih vodotoka.

Na području jugoistočne Europe i Balkana, floristička istraživanja mahovina kopnenih voda također su vrlo rijetka. U Grčkoj je istražena flora tri vodotoka u sjevernom i jednog vodotoka u središnjem dijelu zemlje. Zabilježeno je ukupno 36 vrsta pravih mahovina i pet jetrenjarki (Papp 1999). U horološkom spektru flore svih istraženih vodotoka dominirao je europski tempratni florni element, dok su submediteranski i suboceanski bili zastupljeniji na vodotocima u mediteranskom dijelu, a borealni i montani u centralnom dijelu Grčke. S obzirom na životne strategije, u flori svih istraživanih vodotoka dominirale su višegodišnje vrste (engl. *perennials*), a zatim kolonisti (engl. *colonists*). Veći udio kolonista na jednom od istraživanih vodotokova (Parga), objašnjen je promjenjivim protokom i razinom vode te negativnim antropogenim utjecajima koji promoviraju vrste koje bolje podnose stres. Floristička istraživanja tekućica provođena su i u Bugarskoj te su rezultirala znatno većim brojem zabilježenih vrsta. Papp i sur. (2006) zabilježili su 84 vrste (73 prave mahovine i 11 jetrenjarki) na 32 lokacije raspoređene na rijeci Iskr i njenim glavnim pritokama, dok je Gecheva (2004) zabilježila 73 vrste (66 prave mahovine i 4 jetrenjarke) na 23 lokacije duž toka rijeke Marice.

Istraživanje flore mahovina provedeno u sjeverozapadnom i centralnom dijelu Portugala obuhvatilo je čak 187 tekućica, ali je bilo ograničeno na njihove izvorišne dijelove (Vieira i sur.

2012a). Međutim, autori su zabilježili čak 140 vrsta mahovina, među kojima su također dominirale prave mahovine sa 102 vrste, dok su jetenjarke bile zastupljene s 37, a rožnjače s jednom vrstom. Vrste koje su dominirale u flori mahovina bitno su se razlikovale od seta vrsta koji je dominirao u istraženim vodotocima Italije i Bugarske. Naime, u Portugalu su to bile acidofilne i atlantske vrste *Racomitrium aciculare* (Hedw.) Brid., *Platyhypnidium lusitanicum* Ochyra & Sérgio, *Hylocomium armoricum* (Brid.) Wijk & Margad, *Scapania undulata* (L.) Dumort. i *Fissidens polyphyllus* Wilson ex Bruch & Schimp., dok su najzastupljenije porodice bile Brachytheciaceae, Grimmiaceae i Fissidentaceae.

Veća zastupljenost i učestalost pravih mahovina u odnosu na jetrenjarke i rožnjače, zabilježena u svim navedenim istraživanjima, očekivana je s obzirom da su jetrenjarke i rožnjače osjetljivije na mehanički stres kojem su prave mahovine izložene u turbulentnim vodotocima. Također, za razliku od pravih mahovina, jetrenjarke i rožnjače ne mogu živjeti submerzno duži period, a osjetljivije su i na isušivanje i smrzavanje. Zbog svega navedenog one uglavnom nastanjuju zaštićena i vlažna mikrostaništa uz zasjenjene vodotoke (Gimingham i Birse 1957; Kimmerer i Allen 1982; Vitt i Glime 1984; Suren 1996).

2.3. Ekološka uvjetovanost mahovina kopnenih voda i njihovih zajednica

Dosadašnja ekološka istraživanja vodenih mahovina uglavnom su se bavila izvorišnim dijelovima i gornjim tokovima rijeka budući da se radi o staništima koja podržavaju najveću raznolikost vodenih mahovina te je njihova pokrovnost na ovim staništima značajno veća nego u srednjim i donjim tokovima. Naime, izvorišnim dijelovima i gornjim tokovima tekućica dominiraju veće i stoga stabilnije veličinske frakcije supstrata koje su pogodne za naseljavanje mahovina. Osim stabilnosti, blokovi stijena i veliko kamenje čiji se vršni dijelovi nalaze izvan vode te su u različitoj mjeri izloženi prskanju i plavljenju, osiguravaju velik broj ekoloških niša i vertikalnu zonaciju vrsta različitog afiniteta prema vodi (Slack i Glime 1985; Vitt i sur. 1986; Glime i Vitt 1987; Muotka i Virtanen 1995). Ovakvi supstrati dodatno predstavljaju rezervoare iz kojih je moguća rekolonizacija mahovina nakon velikih bujica koje u ekstremnim slučajevima mogu osiromašiti vegetaciju u koritu. S druge strane, u srednjim i donjim tokovima, u kojima dominiraju sitnije veličinske frakcije supstrata poput mikrolitala (2–6 cm), akala (0,2–2 cm) i psamala (0,063–0,2 cm), mahovine su ograničene na rijetke veće strukture sedimenta te dodatno nastanjuju i periodički plavljene obale. U ovim dijelovima vodotoka vodene mahovine su također izložene intenzivnoj kompeticiji s vaskularnim biljkama, a sve navedeno rezultira njihovom niskom raznolikošću i pokrovnosti ili čak potpunim izostankom akvatičkih i semiakvatičkih mahovinama u najnizvodnijim dijelovima vodotoka.

Dok su prisutnost i pokrovnost mahovina u tekućicama određeni prije svega stabilnošću korita, odnosno stabilnošću i veličinom supstrata, raznolikost i sastav vrsta te struktura mahovinskih zajednica ovise o mnogim okolišnim čimbenicima, odnosno njihovoj heterogenosti (Slack i Glime 1985; Suren 1996; Suren i Ormerod 1998; Suren i Duncan 1999; Scarlett i O'Hare 2006; Tremp i sur. 2012). Hidrološki, fiziografski, geološki i klimatološki čimbenici, kao i fizikalno-kemijski parametri vode poput pH vrijednosti, temperature, električne provodljivosti i koncentracije hranjivih tvari (Suren 1996; Papp i Rajczy 1998b; Scarlett i O'Hare 2006; Ceschin i sur. 2012a, 2015; Gecheva i sur. 2017; Vieira i sur. 2018), prepoznati su kao glavni čimbenici koji oblikuju mahovinske zajednice u vodotocima. Rezultati istraživanja utjecaja okolišnih varijabli na sastav vrsta mahovina u vodenim staništima, kao i utvrđivanje najznačajnijih okolišnih čimbenika, u određenoj mjeri ovisit će o samom setu okolišnih varijabli koje se uzimaju u obzir, obuhvaćenom gradijentu razmatranih varijabli, odnosno o veličini i heterogenosti istraživanoga područja, zatim o metodama uzorkovanja i kartiranja te načinu obrade podataka. Mnoga istraživanja, pokrivaju ograničen broj i raspon vrijednosti okolišnih čimbenika, pokrivaju manja geografska područja ili se pak temelje na kvalitativnom pristupu ili odvojenim statističkim analizama okolišnih i vegetacijskih podataka.

Na području Europe do sada je provedeno nekoliko opsežnijih istraživanja koja su identificirala osnovne okolišne gradijente koji uvjetuju pojavljivanje i raznolikost mahovinskih zajednica u vodotocima (Muotka i Virtanen 1995; Scarlett i O'Hare 2006; Lang i Murphy 2012; Tremp i sur. 2012; Vieira i sur. 2018). Istraživanje provedeno na malim gorskim potocima u Njemačkoj, koje je uključilo čak šest regija i vrlo duge gradijente istraživanih okolišnih parametara, potvrdilo je da su sastav vrsta i tip zajednice određeni okolišnim varijablama koje djeluju na širem području, prvenstveno geološkom podlogom i o njoj ovisnim parametrima poput pH vrijednosti, alkalnosti i električne provodljivosti vode. S druge strane, čimbenici koji utječu na primarnu produkciju – količina dostupne svjetlosti i otopljenog ugljikovog dioksida, kao i veličina supstrata, značajno utječu na pokrovnost vodenih mahovina u gorskim potocima (Tremp i sur. 2012), a slično su zaključila i opsežna istraživanja provedene na Novom Zelandu (Suren 1996) i Nepalu (Suren i Ormerod 1998).

Nadalje, vrlo opsežno istraživanje vodenih mahovina i njihovih zajednica provedeno na engleskim i velškim rijekama, koje je uključilo čak 3 650 lokaliteta u različitim geografskim područjima i na različitim tipovima tekućica, utvrdilo je da je bogatstvo vrsta određeno i pozitivno uvjetovano veličinom supstrata i nadmorskom visinom izvora te da se smanjuje s udaljenošću od izvora, odnosno s padom nadmorske visine (Scarlett i O'Hare 2006). Iste varijable, uz geološku podlogu, nagib i dubinu vodotoka te koncentraciju fosfata, izdvojile su se kao one koje imaju najznačajniji utjecaj na sastav vrsta. Diskretne grupe, odnosno zajednice, u ovom istraživanju nisu identificirane, nego je ustanovljen kontinuum varijacije u sastavu vrsta od područja na višim nadmorskim visinama s geološkom podlogom s kiselom reakcijom prema nižim područjima na karbonatnoj podlozi s bazičnom reakcijom. Uvjetovanost sastava vrsta akvatičkih i semiakvatičkih mahovina o geološkoj podlozi, odnosno pH vode, ustanovila su i druga istraživanja provedena na manjem uzorku, odnosno užem geografskom području (Papp i Rajczy 1998a; Vanderpoorten i Klein 1999b; Lang i Murphy 2012; Vieira i sur. 2014), a ova dihotomija, odnosno razlikovanje kalcifilnih i kalcifugnih vrsta i njihovih zajednica jasno su izraženi i kod kopnenih mahovina (Bates 2000). Lang i Murphy (2012) istražili su mahovinske zajednice u škotskim potocima, doprinijevši poznavanju ekologije mahovine u tekućicama većih geografskih širina, no potvrdili su da su i ondje one prvenstveno uvjetovane stabilnošću korita (značajkama toka i protoka te veličinom i sastavom supstrata) i fizikalno-kemijskim čimbenicima vode (pH vrijednošću, električnom provodljivosti i koncentracijom kalcijevih iona). Duž ova dva složena okolišna gradijenta identificirali su četiri mahovinske zajednice, od kojih su vrstama i biomasom bile najbogatije one na stabilnim supstratima i to na staništima koja su bila izložena disturbacijama srednjeg intenziteta, u smislu bujica i ekstremnih vrijednosti protoka. U vrstama bogatim zajednicama, konstantne vrste bile su *Fontinalis antipyretica* i *Rhynchostegium ripariodes*, a duž gradijenta pH i alkaliteta, njima su se pridruživale acidofilne vrste poput vrsta *Scapania undulata* i *Hygrohypnella ochracea* (Turner ex Wilson) Ignatov & Ignatova, odnosno bazofilne vrste kao što su *Chiloscyphus polyanthos* (L.) Corda, *Hygrohypnum luridum* (Hedw.) Jenn. i *Palustriella falcata* (Brid.) Hedenäs. Na krajevima gradijenta stabilnosti supstrata, odnosno intenziteta i učestalosti disturbancija na staništu, nalazile su se vrstama siromašne zajednice koje su se razlikovale u opaženoj biomasi i dominantnim životnim oblicima, odnosno životnim strategijama. Vrlo niska ukupna biomasa mahovina i veća učestalost pionirskih vrsta koje rastu u čupercima (engl. *turf*) te dobro toleriraju stres bili su karakteristični za turbulentne tokove s izraženijim disturbacijama i dominantno nestabilnim supstratima. S druge strane, visoka biomasa malog broja vrsta, posebice vrste *Fontinalis antipyretica*, nitaste reofilne vrste (engl. *aquatic trailing*) s karakteristika dobrog kompetitora (Muotka i Virtanen 1995; Virtanen i sur. 2001; Lang i Murphy 2012) bila je značajka mirnijih tokova sa stabilnim supstratom.

Vrlo opsežno istraživanje zajednica vodenih mahovina provedeno je na mediteranskim vodotocima s izraženom sezonalnosti u protoku (Vieira i sur 2018). Uključivši čak šest mediteranskih zemalja i 474 lokacije ovo istraživanje obuhvatilo je do sada najšire geografsko područje prilikom istraživanja okolišne uvjetovanosti zajednica vodenih mahovina na razini Europe, a za razliku od do sada spomenutih istraživanja, uz fiziogeografske čimbenike te kemijske parametre vode, uključilo je i klimatske i bioklimatske varijable te ponudilo model rasprostranjenosti četiri mahovinske zajednice identificirane na području Mediterana. Ove zajednice su uvjetovane prije svega godišnjom razdiobom količine oborina, pH vrijednošću vode, koncentracijom kalcija i mangana u vodi te nadmorskom visinom. Predloženi model na području Hrvatske, tj. njenog mediteranskog dijela, predviđa pojavljivanje zajednice za koju su karakteristične vrste *Rhynchostegium riparioides, Fontinalis antipyretica, Leptodyctium riparium* (Hedw.) Warnst., *Fissidens crassipes* Wilson ex Bruch & Schimp., *Cinclidotus fontinaloides* (Hedw.) P. Beauv., *Cratoneuron filicinum* (Hedw.) Spruce i *Apopellia endiviifolia* (Dicks.) Nebel & D. Quandt. Ova zajednica je ujedno i najraširenija zajednica na Mediteranu, a prema Vieiri i sur. (2018), karakteristična je za neutralne i bazične vodotoke na područjima s višom količinom precipitacije tijekom godine te nižim temperaturama u najhladnijem mjesecu, odnosno, nižim temperaturnim maksimumima u najtoplijem mjesecu. Za razliku od ostalih mediteranskih zajednica u njenom sastavu dominiraju akvatičke vrste, što ukazuje na stabilnije uvjete kad je riječ o dostupnosti vode i promjenama u razini vode. Ovoj zajednici je vrlo slična zajednica u kojoj se javljaju sedrotvorni predstavnici poput vrsta *Palustriella commutata* (Hedw.) Ochyra, *Eucladium verticillatum* (With.) Bruch & Schimp. i *Didymodon tophaceus* (Brid.) Lisa. Ona je karakteristična za vodotoke s pH vrijednosti vode u bazičnom području te dolazi na područjima u kojima je viša precipitacija tijekom najsušeg kvartala. Njeno pojavljivanje prema Vieiri i sur. (2018) nije predviđeno u Hrvatskoj, iako su navedene sedrotvorne vrste, kao i druge koje se uz njih javljaju unutar ove zajednice poput vrsta *Marchantia polymorpha* L., *Apopellia endiviifolia*, *Cratoneuron filicinum*, *Rhynchostegium riparioides*, *Plagiomnium undulatum* (Hedw.) T.J. Kop., *Ptychostomum pseudotriquetrum* (Hedw.) J.R. Spence & H.P. Ramsay ex Holyoak & N. Pedersen, bilježene u krškim vodotocima i njihovim slapištima tijekom povijesnih istraživanja vodenih mahovina u Hrvatskoj (Pavletić 1955).

Važnost utjecaja klimatskih čimbenika u razdvajanju zajednica mahovina dolazi do izražaja i na manjim geografskih područjima te su se klimatski čimbenici povezani s dostupnošću vode, poput godišnje količine oborine i koeficijenta varijacije u količini oborina, uz kemijske parametre vode (alkalitet, električnu provodljivost i koncentraciju nitrata) te veličinu slivnog područja izdvojili kao najbitniji u oblikovanju čak osam mahovinskih zajednica prepoznatih u portugalskim vodotocima (Vieira i sur. 2014).

2.4. Bioindikacijski potencijal mahovina kopnenih voda

Ranije spomenuta istraživanja su se uglavnom koncentrirala na izvorišne dijelove vodotoka, gorske potoke, odnosno vodotoke u dobrom ekološkom stanju te pokušala razjasniti okolišnu uvjetovanost vodenih mahovina i njihovih zajednica u vodotocima u prirodnom stanju. Međutim, istraživanja mahovina provedena na antropogeno utjecajnim vodotocima pokazala su da su pojedine vrste vodenih mahovina te sastav, raznolikost i pokrovnost njihovih zajednica osjetljivi na eutrofikaciju, onečišćenje teškim metalima, kao i na hidromorfološke promjene vodotoka i stajaćica te da ih je moguće koristiti u svrhe biomonitoringa.

Ovaj pristup koji podrazumijeva procjenu kvalitete vode ili hidromorfološkog integriteta vodnog tijela, a temelji se na prisutnosti, odnosno odsutnosti pojedinih osjetljivih vrsta, zahtijeva temeljito poznavanje njihove ekologije (Vanderpoorten i Palm 1998; Ceschin i sur. 2012a). Značajan doprinos poznavanju ekologije vodenih mahovina i njihovog odgovora na stupanj trofije u europskim vodotocima pružila su primjerice istraživanja provedena u Francuskoj i Belgiji. Istraživanje na rijekama Meuse i Sambre u Belgiji pokazalo je da povećane koncentracije amonijaka, i ortofosfata, ali i teških metala, željeza, cinka, olova i bakra, imaju negativan učinak na bogatstvo vrsta i sastav zajednica vodenih mahovina (Vanderpoorten 1999). Sniženje koncentracije ovih zagađivača dovelo je do oporavka mahovinskih zajednica u smislu njihove raznolikosti od 1970-ih do 1990-ih godina, a zabilježene razlike u uzorcima ponovnog naseljavanja pojedinih vrsta dovedene su u vezu pak s porastom koncentracije nitrata u rijeci Sambre, u odnosu na rijeku Meuse u spomenutom razdoblju. Odgovor sastava vrsta mahovina na stupnj trofije istraživan je i na vodotocima porječja Rajne u pokrajini Alsace. Istraživanje je pokazalo da je na temelju sastava vrsta vodenih mahovina, unatoč generalno malenom broju vrsta, moguće procijeniti stupanj trofije vode te da on ima dugoročan utjecaj na mahovinske zajednice pa one daju točniju sliku ekološkog stanja vodotoka u odnosu na mjerene kemijske parametre vode (Vanderpoorten i Palm 1998). Istraživanje odgovora pojedinih vodenih vrsta i njihovih zajednica na stupanj trofije u istom geografskom području (Vanderpoorten i sur. 1999) pokazalo je da se vrste razdvajaju duž gradijenta koncentracije amonijaka, nitrata i ortofosfata te da je moguće identificirati vrste karakteristične za oligotrofne vode poput vrsta *Hygromblystegium tenax* (Hedw.) Jenn., *Apopellia endiviifolia* i *Chiloscyphus* *pallescens* (Ehrh.) Dumort, te one karakteristične za eutrofne vode. U vodotocima porječja Rajne, to su bile vrste *Hygroamblystegium fluviatile* (Hedw.) Loeske, *Cinclidotus danubicus* Schiffn. & Baumgartner, *C. riparius* (Host ex Brid.) Arn. i *Fissidens crassipes,* dok su vrste *Leptodyctium riparium, Fontinalis antipyretica* i *Rhynchostegium riparioides* imale široke ekološke niše, ali ipak veću učestalost u eutrofnim vodama (Vanderpoorten i sur. 1999). Međutim, istraživanje koje je obuhvatilo vodotoke dvije hidrografske mreže u Belgiji i Francuskoj ustanovilo je da vrste *Hygramblystegium tenax, H. fluviatile, Fissidens crassipes* i *Fontinalis antipyretica* imaju bitno različite ekološke odgovore na koncentraciju amonijaka i fosfata u različitim hidrografskim mrežama (Vanderpoorten i Durwael 1999). Primjerice, dok je optimum vrsta *Fontinalis antipyretica* i *Fissides crassipes* bio u oligotrofnim vodama jedne hidrografske mreže, u drugoj su tolerirale najzagađenije vode, a njihovi optimumi bili su u eutrofnim vodama kada su podaci iz obje hidrografske mreže razmatrani istovremeno. Autori su sugerirali da ove vrste uključuju nekoliko ekotipova s različitim zahtjevima s obzirom na trofičko stanje vodotoka, što je vjerojatno rezultat mikroevolucije kojoj pogoduje činjenica da su riječni slivovi rijetko međusobno povezani. Ove razlike između populacija iste vrste otežavaju njihovu upotrebu kao pouzdanih bioindikatora, stoga su daljnja istraživanja ekologije i bioindikacijskog potencijala vodenih mahovina koja pokrivaju nova geografska područja i široke ekološke gradijente i dalje potrebna.

Svega nekoliko istraživanja ekologije vodenih mahovina i njihovog bioindikacijskog potencijala provedeno je u susjednim zemljama, Mađarskoj i Italiji. U Mađarskoj je istraživan utjecaj kvalitete vode na zajednice vodenih mahovina u dijelu toka Dunava (Papp i Rajczy 1998b) te gorskim potocima (Papp i Rajczy 1998a). Oba istraživanja utvrdila su da je sastav mahovinskih zajednica osjetljiv na povećane koncentracije nutrijenata. U mađarskom dijelu toka Dunava, u kojem je vegetacija akvatičkih i semiakvatičkih mahovina uglavnom ograničena na umjetne supstrate poput obaloutvrda i starih brana, porast koncentracije amonijaka imao je najizraženiji učinak na zabilježene promjene u sastavu vegetacije mahovina. Vrste *Fissidens crassipes* i *Leptodyctium riparium* bile su obilno razvijene u uvjetima viših koncentracija amonijaka, dok su vrste *Cinclidotus fontinaloides* i *Leskea polycarpa* Hedw. u takvim uvjetima izostajale (Papp i Rajczy 1998b). U 12 gorskih potoka s različitom geološkom podlogom Papp i Rajczy (1998a) zabilježili su čak 91 vrstu te identificirali pet zajednica koje su uz koncentraciju amonijaka, nitrata i ortofosfata uvjetovane i pH vrijednošću te ukupnom tvrdoćom vode. Eutrofikacija je imala negativan utjecaj na raznolikost ovih zajednica te je razlika u sastavu vrsta u potocima na podlozi s kiselom i bazičnom reakcijom bila manja pod utjecajem onečišćenja. Vrste *Fontinalis antipyretica, Rhynchostegium riparioides, Brachythecium rutabulum* (Hedw.) Schimp i *Hygroamblystegium tenax* prepoznate su kao tolerantne s obzirom na onečišćenje, a prisutnost vrste *Leptodyctium riparium* ukazivala je na eutrofikaciju.

U Italiji je istraživana vegetacija mahovina u alpskim i apeninskim potocima (Ceschin i sur. 2015) te u vodotocima porječja rijeke Tiber (Ceschin i sur. 2012a). Oba istraživanja naglasila su nedovoljnu istraženost vodenih mahovina, ali i njihovu važnost u karakterizaciji makrofitske vegetacije gorskih i prigorskih tekućica, kao njene glavne ili jedine komponente, te potencijal vodenih mahovina u procijeni ekološkog stanja ovog tipa vodotoka. Naime, iako je većina od 36 zabilježenih vrsta imala vrlo nisku učestalost i pokrovnost, na preko 50 % od 46 istraživanih lokaliteta na gorskim i prigorskim potocima Apenina i Alpa, pokrovnost vodenih mahovina bila je iznad 10 %, odnosno iznad 5 % na 70 % lokaliteta (Ceschin i sur. 2015), prelazeći prag pokrovnosti nužan za uključivanje biološkog elementa makrofita u procjenu ekološkog stanja vodotoka prema Okvirnoj direktivi o vodama (Europska komisija 2000). Isto istraživanje utvrdilo je jasnu razliku u sastavu zajednica vodenih mahovina između alpskih i apeninskih potoka, koji se međusobno razlikuju na temelju temperature, pH vrijednosti i električne provodljivosti vode, režima kisika (kemijska potrošnja kisika) i količine nutrijenata, ali i zasjene, razine turbulentnosti toka i postotka megalitala u koritu. Nadalje, oba istraživanja utvrdila su preferencije pojedinih vrsta prema određenim ekološkim uvjetima te mogućnost njihova korištenja kao bioindikatora. Ceschin i sur. (2012a) su prilikom istraživanja 17 vodotoka porječja rijeke Tiber uključili i donje tokove ovih tekućica te su time obuhvatili duže gradijente kemijskih parametara vode u odnosu na istraživanja ograničena na gorske potoke i izvorišne dijelove vodotoka. Ovo se posebice odnosi na gradijente električne provodljivost i koncentracije nutrijenata budući da donji tokovi većih rijeka općenito imaju viši stupanj trofije te su dodatno izloženi antropogenom zagađenju. Većina od 14 vrsta zabilježenih u ovom istraživanju imala je optimum u bistrim, hladnim vodama s visokom koncentracijom otopljenog kisika te nižom električnom provodljivosti i nižim koncentracijama nutrijenata, posebice amonijaka i fosfata. One s uskim ekološkim nišama, *Cinclidotus aquaticus* (Hedw.) Bruch & Schimp., *Cratoneuron filicinum, Fissidens viridulus* (Sw.) Wahlenb. i *Palustriella commutata* prepoznate su kao pouzdani bioindikatori dobrog stanja vodotoka. Za razliku od njih, *Riccia fluitans* L. i *Leptodyctium riparius* su predloženi kao pokazatelji eutrofikacije.

Na području jugoistočne Europe i Balkana, najslabije istraženim europskim područjem s obzirom na mahovine općenito (Sabovljević i sur. 2001, 2011), istraživanja ekologije i bioindikacijskog potencijala akvatičkih i semiakvatičkih mahovina vrlo su rijetka. Sastav vrsta i njihova korelacija s okolišnim čimbenicima istraživani su na svega dvije grčke tekućice, Enipeas i Lycorrema (Papp i sur. 1998), dok su u Bugarskoj vodene mahovine nešto bolje istražene. Opsežnije ekološko istraživanje proveli su Gecheva i sur. (2010) u kojem su istražili ekološku uvjetovanost četiri najučestalije vrste vodenih mahovina (*Rhynchostegium riparioides, Brachythecium rivulare* Schimp., *Fontinalis antipyretica* i *Leptodyctium riparium*) na ukupno 51 lokalitetu na gorskim, prigorskim i nizinskim tekućicama. Električna provodljivost, režim kisika (biokemijska potrošnja kisika), koncentracija ukupnog dušika i fosfora te amonijaka i nitrata pokazali su se kao glavni čimbenici koji djeluju na ove vrste u gorskim i prigorskim tekućicama, dok je njihova distribucija u nizinskim tekućicama najbolje objašnjena koncentracijom ukupnog dušika i fosfora, nitrata i biološkom potrošnjom kisika. Istraživanje je ustanovilo da vrsta *Leptodyctium riparium* dolazi duž istraživanih gradijenata u svim uključenim tipovima tekućica te nije pouzdan indikator, dok su vrste *Rhynchostegium riparioides* i *Brachythecium rivulare* bile karakteristične za vodotoke dobre kvalitete vode.

Nadalje, u Bugarskoj su istraživane i vodene mahovine na 30 lokacija na mediteranskim rijekama s viskom sezonalnosti u protoku (Gecheva i sur. 2017). Istraživanje je pokazalo da bogatstvo vrsta i ukupna pokrovnost mahovina mogu poslužiti kao dobre metrike u praćenju, ne samo eutrofikacije, nego i hidromorfološke degradacije vodnih tijela. U ovom istraživanju, obje metrike reagirale su na koncentraciju ukupnog dušika u vodi, te hidromorfološku degradaciju vezanu uz promjene u riparijskoj vegetaciji i regulaciju vodotoka izgradnjom nasipa. Također zabilježene su i promjene u sastavu vrsta duž gradijenta koncentracije ukupnog dušika i udjela intenzivne poljoprivrede u slivnom području. Vrste *Rhynchostegium riparioides, Fontinalis antipyretica* i *Brachythecium rivulare* bile su karakteristične za lokacije na vodotocima s visokim udjelom prirodne vegetacije u slivnom području, dok je vrsta *Leptodyctium riparium* bila karakteristična za lokacije s visokom koncentracijom ukupnog dušika i visokim udjelom intenzivne poljoprivrede u slivu (Gecheva i sur. 2017).

Utjecaj hidromorfoloških promjena na vodene mahovine istraživan je i na rijeci Dunav na granici Mađarske i Slovačke (Papp i Rajczy 2009). Rezultati dugogodišnjeg monitoringa mahovinske vegetacije sporednih grana rijeke Dunav, koje su nakon preusmjeravanja vode iz glavnog toka u svrhu izgradnje hidroelektrane bile opskrbljivane značajno manjoj količinom vode, pokazali su da su ove promjene u hidrološkom režimu dovele do značajnih promjena u sastavu vrsta i njihovom spektru s obzirom na afinitet prema vodi. Naime, zabilježen je porast udjela mezofilnih efemernih i višegodišnjih vrsta u odnosu na akvatičke vrste. Utjecaj regulacije rijeka i povezanih hidroloških promjena na akvatičke i semiakvatičke mahovine istraživali su i Vanderpoorten i Klein (1996a,b) u Njemačkoj te Englund i sur. (1996) u Švedskoj potvrdivši da akvatičke i semiakvatičke mahovine specifično reagiraju na promjene u hidrologiji i morfologiji vodotoka te da se potencijalno mogu koristiti kao indikatori ovih poremećaja. Nadalje, Fritz i sur. (2009) dokazali su, istražujući mahovine šumskih vodotoka u Sjedinjenim Američkim državama, da određene vrste mahovina, njihove više taksonomske kategorije te životni oblici mogu poslužiti kao indikatori hidroloških režima, odnosno u razlikovanju stalnih, povremenih i efemernih tokova. Posljednje istraživanje ustanovilo je da je učestalost jetrenjarki viša u stalnim vodotocima, dok među pravim mahovinama prevladavaju pleurokarpne mahovine, a u spektru životnih oblika one koje rastu u sagovima (engl. *mats*) i rahlim prostirkama (engl. *wefts*). Za razliku od stalnih tokova, značajka efemernih tokova je veća učestalost akrokarpnih vrsta i to onih koje rastu u jastučićima (engl. *turfs*) i čupercima (engl. *tufts*) kada se u obzir uzima spektar životnih oblika (Fritz i sur. 2009).

Istraživanje provedeno na gorskim potocima u Portugalu prepoznalo je jasno razdvajanje različitih taksonomskih kategorija akvatičkih i semiakvatičkih mahovina, njihovih životnih oblika i životnih strategija duž hidroloških zona (koje se razlikuju po dubini vode, odnosno učestalosti i duljini poplavljivanja), duž gradijenta brzine vode te zasjene. Uočeno razdvajanje predstavlja temelj za praćenje antropogeno utjecajnih promjena u režimu toka, kao i promjena u osvijetljenosti njihovih mikrostaništa na temelju viših taksonomskih kategorija, odnosno životnih oblika i strategija mahovina slatkovodnih staništa (Vieira i sur. 2012b). U ovom istraživanju, ukupno bogatstvo vrsta mahovina te broj vrsta pravih mahovina bili su veći u hidrološkim zonama koje su rjeđe izložene plavljenju i većim brzinama toka, dok je u u brzim i stalnim tokovima broj vrsta i pravih mahovina i mahovina općenito bio manji. Za brze tokove sa stalnim protokom karakteristični životni oblici bile su nitaste vodene mahovine (engl. *aquatic trailings*), kao i one koje rastu u glatkim sagovima (engl. *smooth mats*), dakle čvrste i elastične vrste koje dobro podnose mehanički stres. Nadalje, na staništima izloženim sezonskim promjenama u razini vode, u spektru životnih oblika dominirale su vrste koje rastu u čupercima (engl. *turfs*), a mahovine koje rastu u kompaktnim jastučićima (engl. *tufts*) i rahlim prostirkama (engl. *wefts*) na staništima koja su potopljena rijetko, npr. u slučaju dužih kišnih razdoblja. Slične razlike također se mogu uočiti u spektru životnih strategija pa su tako višegodišnje vrste (engl. *perennials*) dominirale staništima koje su trajno poplavljena i u kojima vladaju ujednačeni ekološki uvjeti, dok su kolonisti (engl. *colonists*) bili zastupljeniji na staništima koja su plavljena sezonski te su u tom periodu izložena mehaničkom stresu uslijed jake struje vode.

Staništa koja su periodički plavljena nastanjivale su i kratkoživuće i dugoživuće sporadične vrste (engl. *short-lived* and *long-lived shuttle species*), koje se mogu smatrati indikativnima za obalne zone povremeno izložene eroziji. Ove strategije omogućuju im razvoj u mikrostaništima koja su stabilna do nekoliko godina, dok ne dođe do uništenja populacija uslijed poplave i erozije. Efemerne vrste s najkraćim životnim ciklusom (engl. *fugitives* and *annual shuttle species*) karakteriziraju pak mikrostaništa koja tijekom godine presušuju vrlo kratko tijekom sušeg dijela godine. Na ovakvim staništima, male efemerne vrste uspijevaju zatvoriti svoj životni ciklus unutar svega par mjeseci.

Kako su dosadašnja istraživanja pokazala da su vodene mahovine osjetljive na antropogene promjene u slatkovodnim ekosistemima, nekoliko sustava razvijenih za praćenje ekološkog stanja rijeka i jezera na temelju makrofita uključilo je i vodene mahovine. Kao indikatorske vrste one se koriste u više sustava razvijenih za ocjenu trofičkog stanja voda (Dawson i sur. 1999; Holmes i sur. 1999; Haury i sur. 2006; Szoszkiewicz i sur. 2006; Birk i sur. 2007; Birk i Willby 2010; Willby i sur. 2012; Szoszkiewicz i sur. 2020). Ovi sustavi procjene uglavnom se temelje na popisu indikatorskih svojti čije se indikatorske vrijednosti ponderiraju njihovom brojnošću, dok neki od indeksa u izračunu u obzir uzimaju i ekološke amplitude indikatorskih vrsta. Mahovine su također uključene kao indikatori u Referentni indeks makrofita (RI), koji je razvijen u svrhu praćenja opće degradacije vodenih staništa, a ne samo promjena povezanih s eutrofikacijom (Schaumburg i sur. 2004; Meilinger i sur. 2005). Većina vrsta mahovina koje su uključene u spomenute sustave procjene prepoznate su kao dobri indikatori s uskom ekološkom amplitudom te ih većina preferira oligotrofne i mezotrofne uvjete. Danas je većina ovih sustava kalibrirana i prilagođena upotrebi za procjenu ekološkog stanja vodnih tijela prema zahtjevima Okvirne direktive o vodama (Europska komisija 2000). Pri procjeni ekološkog stanja Okvirna direktiva o vodama zahtijeva holistički pristup koji je filozofski nešto drugačiji od tradicionalnih pristupa biomonitoringu te je bliži konceptima ekološkog integriteta i zdravlja ekosustava (Birk i Willby 2010; Birk i sur. 2012; Willby i sur. 2012). Naime, za svaki tip vodnog tijela koji prepoznaje nacionalna tipologija potrebno je identificirati referentne uvjete te degradaciju izraziti kvantitativno, kao odstupanje u sastavu vrsta i njihovoj brojnosti u odnosu na one koji bi bili očekivani u referentnim uvjetima. Prilikom toga, zasebno se procjenjuje stanje na temelju nekoliko bioloških elemenata (fitoplankton, fitobentos, makrofiti, makrozoobentos i ribe) te fizikalno-kemijskih i kemijskih parametara vode te hidromorfologije, koji se smatraju podržavajućim elementima. Makrofiti, uključujući i mahovine, u ovom slučaju se smatraju posebno prikladnima kao bioindikatori jer kao sesilni organizmi preciznije ukazuju na lokalne promjene u okolišu, a zbog dugog životnog vijeka integriraju promjene tijekom duljih razdoblja kao i uzastopne poremećaje (Tremp i Kohler 1995; Vanderpoorten i Palm 1998; Birk i sur. 2007, 2012; Gecheva i Yurukova 2014). Nadalje, vodene mahovine su posebice značajne za monitoring gorskih potoka i povremenih tokova u kojima zahvaljujući svojim adaptacijama predstavljaju dominantnu ili jedinu komponentu makrofitske vegetacije (Vieira i sur. 2014; Gecheva i sur. 2017). Implementacija Okvirne direktive o vodama (Europska komisija 2000) potaknula je niz istraživanja koja su unaprijedila poznavanje distribucije i ekologije spomenutih skupina pa tako i vodenih biljaka na europskoj razini, a monitoring koji se trenutno provodi u Hrvatskoj predstavlja prvo sveobuhvatno i sistematizirano istraživanje makrofitske vegetacije i vodenih mahovina u Hrvatskoj i jedno od rijetkih u jugoistočnoj Europi.

2.5. Pregled istraživanja mahovina u Hrvatskoj

Prva istraživanja mahovina u Hrvatskoj sežu u prva desetljeća 19. stoljeća, kada su podatke za Hrvatsko primorje i Dalmaciju sakupljali uglavnom austrijski i mađarski botaničari, dok najstariji podaci o mahovinskoj flori kontinentalnog dijela zemlje potječu iz šezdesetih godina istog stoljeća. Iako sporadična i nesistematizirana, ova prije svega floristička istraživanja, stvorila su temelj briologije u našoj zemlji (Alegro i sur. 2012). Sumarni pregled flore mahovina uklopljen u širi fitogeografski kontekst, kao i prvi pregled vegetacije mahovina dao je Horvat (1932) u djelu Građa za briogeografiju Hrvatske. U 20. stoljeću strani autori nastavljaju objavljivati pojedinačne nove nalaze mahovinskih vrsta u Hrvatskoj, a 1950-tih godina započinju i prva ekološka istraživanja, posebice mahovina krških rijeka i njihove uloge u formiranju sedre. Najopsežniji izvor dotadašnjih podataka o istraženosti flore Hrvatske je Prodromus flore briofita Jugoslavije (Pavletić 1955) koji je kompilacija ranijih istraživanja, uključujući nešto novih nalaza. U drugoj polovici 20. stoljeća vrlo je malo objavljenih radova o flori mahovina Hrvatske, a većina ih se bazira na već ranije objavljenim podacima (Alegro i sur. 2012). Nakon gotovo stotinu godina izostanka sustavnih istraživanja mahovina na području Hrvatske, prije desetak godina započela su nova floristička istraživanja koja su do sada detaljnije obuhvatila područja Medvednice (Rimac 2012), Gorskog Kotara, Velebita, Bjelolasice (Papp i sur. 2013b,c), Like (Alegro i sur. 2014) i Žumberka (Alegro i sur. 2015). Iako ova istraživanja predstavljaju značajan napredak, kontinuirano otkrivanje novih svojti u flori mahovina Hrvatske ukazuje na to da je ona još uvijek nedovoljno istražena (Papp i sur. 2013a; Sabovljević i sur. 2018; Alegro i sur. 2019; Rimac i sur. 2019; Šegota i sur. 2019; Ellis i sur. 2020, 2021a,b; Šegota i sur. 2021a,b,c). Tako su mnoge vrste koje se smatraju čestima na razini Europe, u Hrvatskoj do danas zabilježene na svega nekoliko lokaliteta (Alegro i Šegota 2022). Izuzev istraživanja ekologije cretnih (Modrić Surina 2011) i šumskih mahovina (Šegota 2021), recentna istraživanja ekologije mahovina i njihovih zajednica u potpunosti izostaju. Jedina dosadašnja istraživanja vodenih mahovina sežu u sredinu 20. stoljeća kada je Zlatko Pavletić istraživao sedrene slapove i barijere rijeke Krke (Pavletić 1954, 1957b), zatim Plitvičkih jezera (Pavletić 1957a) te rijeke Une (Pavletić 1959, 1960) i nekih drugih krških rijeka. Tijekom 1960-tih Pavletić je suradnji s kolegom zoologom Ivom Matoničkinom istraživao zajednice i odnose makrozoobentosa, algi i mahovina u krškim rijekama (Matoničkin i Pavletić 1959, 1960a,b, 1962a,b, 1963a,b, 1965; Pavletić i Matoničkin 1965), a završetak ovog plodnog i produktivnog razdoblja bio je ujedno i kraj istraživanja mahovina vodenih staništa u Hrvatskoj.

3. SVRHA I CILJEVI ISTRAŽIVANJA

Osnovna svrha provedenih istraživanja je pružiti uvid u ukupnu floru i vegetaciju vodenih mahovina na području Republike Hrvatske te ustanoviti geografsku rasprostranjenost i objasniti ekološku uvjetovanost pojedinih vrsta i čitavih mahovinskih zajednica u kopnenim vodama Hrvatske. U tu svrhu postavljeni su sljedeći istraživački ciljevi:

Ciljevi istraživanja

1. Utvrditi raznolikost i distribuciju vodenih mahovina u tekućicama i stajaćicama Hrvatske.
2. Analizirati sastav mahovinske flore prema flornim elementima, životnim oblicima i životnim strategijama.
3. Objasniti uvjetovanost pojavljivanja vodenih mahovina u tekućicama Hrvatske s obzirom na okolišne uvjete.
4. Odrediti ekološke odgovore vrsta mahovina na ekološke čimbenike u tekućicama Hrvatske.
5. Utvrditi rasprostranjenost, raznolikost, sastav i strukturu mahovinskih zajednica te njihovu fitocenološku pripadnost.
6. Utvrditi na koji su način mahovinske zajednice u tekućicama Hrvatske uvjetovane okolišnim uvjetima.
7. Definirati bioindikatorske vrste vodenih mahovina Hrvatske u ocjeni ekološkog stanja voda.

Ovo istraživanje razjasnit će geografske trendove u rasprostranjenosti, raznolikosti i učestalosti vodenih mahovina na području cijele Hrvatske. Nadalje, ekološka analiza razjasnit će ovisnost pojavljivanja vodenih mahovina o okolišnim faktorima i ekološkom stanju vodotoka, što će doprinijeti poznavanju ekologije pojedinih vrsta te mogućnosti njihove upotrebe kao bioindikatora. Time će se unaprijediti postojeće metode praćenja ekološkog stanja voda na temelju makrofita. Također, ovo istraživanje pružit će ekološku karakterizaciju mahovinskih zajednica te doprinijeti njihovom poznavanju na području središnjeg i istočnog Mediterana i Balkana, na kojima ovakva sveobuhvatna istraživanja nisu provođena.

Temeljem dosadašnjih istraživanja i postavljenih ciljeva ovoga istraživanja izvode se sljedeće hipoteze rada:

Hipoteze

1. Rasprostranjenost, taksonomska, funkcionalna i horološka raznolikost te učestalost pojedinih vrsta vodenih mahovina posljedica su geografskih trendova i ekoloških uvjeta na staništu.
2. Rasprostranjenost, struktura i sastav mahovinskih zajednica u tekućicama posljedica su kombinacije ekoloških i geografskih čimbenika.
3. Sastav i struktura mahovinske flore i vegetacije ovisni su o kakvoći vode.
4. Broj i abundancija vaskularnih vrsta makrofitske flore smanjuje se s porastom raznolikosti i abundancije vodenih mahovina.

4. ZNANSTVENI RADOVI

4.1. Popis radova

1. **Rimac, A.**; Šegota, V.; Alegro, A.; Vuković, N.; Koletić, N. (2022): Croatian freshwater bryoflora–diversity and distribution. *Biodiversity data journal*, 10(e83902): 1–33, doi: 10.3897/BDJ.10.e83902

2. **Rimac, A.**; Šegota, V.; Alegro, A.; Koletić, N.; Vuković, N.; Papp, B. (2019): New and noteworthy bryophyte records from drawdown zones in Croatia. *Herzogia*: 32(2): 315–325, doi: 10.13158/heia.32.2.2019.315

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4.2. Znanstveni rad 1

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Research Article

Croatian freshwater bryoflora-diversity and distribution

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Abstract

An extensive macrophyte field survey of running and standing waters was conducted from 2016 to 2021 at 786 sampling sites across Croatia as a part of the implementation of the Water Framework Directive. This survey is the first to present a comprehensive floristic catalogue of the freshwater bryoflora, along with an analysis of the distribution and diversity patterns on a national level. In all, 83 bryophyte species (68 mosses and 15 liverworts) were recorded in the 228 sites, with average species richness of 4.17 species per site. The most frequent species were *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Leptodictyum riparium* and *Cratoneuron filicinum*. The majority of the species encountered were rarely found, with over 70% of species recorded on less than 10 sampling sites and the majority of the species not being truly aquatic, rather being classified as facultative aquatics. The Dinaric Ecoregion, characterised by clean, cold, fast-flowing karstic rivers, especially in the Continental Subecoregion, supported higher freshwater bryophyte diversity than the lowland Pannonian Ecoregion, with mostly slow, eutrophic lowland watercourses with unstable sandy and gravelly alluvial sediments. Chorological comparison of Croatian eco- and subecoregions revealed the expected dominance of circumpolar and European elements, i.e. temperate chorotypes, as well as some biogeographical differences. The most frequent life forms were aquatic trailings and turfs. Amongst the recorded species, perennials and colonists were the most represented life strategies. The analysis of both the life-form and life-strategy spectra showed some differences amongst the Croatian regions, supporting the fact that the Dinaric Ecoregion

provides more truly aquatic habitats and microhabitats suitable for the freshwater bryophytes, while in the Pannonian Ecoregion freshwater bryophytes dominantly inhabit the periodically submerged riparian zones, for example shaded lowland forest streams and rivulets or gently sloping margins of rivers and lakes.

Keywords

aquatic bryophytes, liverworts, mosses, freshwater habitats, rivers, lakes, chorology, southeast Europe

Introduction

Bryophytes colonised aquatic and riparian environments through several independent phylogenetical lineages of terrestrial species, by a secondary process of colonisation and morphological and physiological adaptations to a highly specialised habitat (Vitt and Glime 1984, Akiyama 1995, Cook 1999). These bryophytes inhabit various aquatic and riparian habitats, from mires, ponds and lakes to streams and rivers, as well as an ample range of hydrological niches associated with these habitat types along two major environmental gradients – water flow and water level fluctuations (Vitt and Glime 1984). However, they failed to conquer saltwater environments, with only a few species tolerating intertidal cycles and none living submerged (Vitt and Glime 1984). On a larger scale, the diversity and community structure of bryophytes associated with freshwater habitats is governed not only by hydrological and hydromorphological, but also by geological and climatological factors, as well as by water chemistry and land use of the catchment area (Suren 1996, Suren and Ormerod 1998, Scarlett and O'Hare 2006, Tremp et al. 2012, Gecheva et al. 2017, Vieira et al. 2018). The presence and cover of bryophytes in freshwater habitats are primarily determined by riverbed stability and substrate size (Suren 1996, Scarlett and O'Hare 2006, Tremp et al. 2012) with bryophytes being the dominant component of the macrophyte vegetation within watercourses that provide large and stable substrates, such as source areas, headwater and mountain streams, as well as waterfalls (Vitt et al. 1986, Zechmeister and Mucina 1994, Suren 1996, Tremp et al. 2012, Ceschin et al. 2015, Mucina et al. 2016). Here, the other macrophyte groups, especially vascular plants, are almost completely absent, primarily because of the fast and turbulent flow, rocky substrates, steep slopes and low temperatures. Furthermore, bryophytes thrive in highly seasonal and intermittent rivers due to their wide variety of adaptations enabling desiccation tolerance and ability to withstand dry periods. Therefore, bryophytes play a vital and sometimes dominant role in freshwater ecosystems, constituting a significant part of macrophyte communities, acting as primary producers, having profound influences on nearly all aspects of nutrient and organic matter processing in streams, providing food and shelter for macroinvertebrates, as well as an epiphytic habitat of rich periphyton communities (Stream Bryophyte Group 1999).

The studies on bryophytes of aquatic and semi-aquatic habitats so far conducted in Europe (e.g. Muotka and Virtanen 1995, Papp 1999, Vanderpoorten and Klein 1999b, Papp et al.

2006, Scarlett and O'Hare 2006, Gecheva et al. 2010, Ceschin et al. 2012a, Ceschin et al. 2012b, Vieira et al. 2014, Ceschin et al. 2015, Gecheva et al. 2017, Vieira et al. 2018), as well in other continents (e.g. Craw 1976, Slack and Glime 1985, Suren and Ormerod 1998) revealed high diversity levels and the potential for these organisms to be used in the management of aquatic habitats. This group of plants and their communities are strongly influenced by anthropogenic alterations in natural freshwater ecosystems, with some representatives being recognised as good bioindicators of water quality or the hydromorphological degradation of aquatic habitats (Vanderpoorten and Durwael 1999, Vanderpoorten and Klein 1999a, Gecheva et al. 2010, Ceschin et al. 2012b). Therefore, they have been included, at least in some countries, in the assessment of the ecological status of water bodies for the Water Framework Directive (WFD) as a part of macrophyte vegetation (Gecheva and Yurukova 2014).

Comprehensive floristic studies on a national level, focusing on diversity, distribution, chorology or life-history traits of aquatic and semi-aquatic bryophytes are very scarce. In Europe, floristic studies were mostly focused on a single watercourse or particular river catchment (Papp 1999, Vanderpoorten and Klein 1999b, Papp et al. 2006, Yurukova and Gecheva 2014), while only several studies included larger regions, for example, central Italy (Ceschin et al. 2012a) and north-western Portugal (Vieira et al. 2012a). Moreover, both floristic and ecological studies were largely focused on headwater streams (Papp and Rajczy 1998b, Lang and Murphy 2012, Tremp et al. 2012, Vieira et al. 2014, Ceschin et al. 2015, Vieira et al. 2018) and only seldom included middle and lower river sections (e.g. Papp and Rajczy 1998a, Vanderpoorten and Klein 1999b, Scarlett and O'Hare 2006, Gecheva et al. 2010) or standing waters, in which bryophytes do occur, but are never the dominant part of the vegetation.

Regarding southeast Europe, freshwater bryoflora is significantly better investigated in Bulgaria than in the rest of this region. Several papers dealing with diversity, ecology, as well as the bioindication potential of these species and their communities are available (Papp et al. 2006, Gecheva et al. 2010, Yurukova and Gecheva 2014, Gecheva et al. 2017), while other parts of the region remain under-researched, with only a few studies dealing with aquatic and riparian assemblages from several watercourses in Greece (Papp et al. 1998, Papp 1999). Furthermore, only a few historical publications from the mid-20th century, focusing mainly on the karst river vegetation and the tufa-formation processes, have contributed to knowledge on this otherwise poorly known group in Croatia (e.g. Pavletić 1957, Matoničkin and Pavletić 1961, Pavletić and Matoničkin 1965). In general, the knowledge of the Croatian bryophyte flora is still insufficient and virtually all recent field studies have revealed new national records (e.g. Papp et al. 2013, Sabovljević et al. 2018, Alegro et al. 2019, Rimac et al. 2019a, Rimac et al. 2019b, Ellis et al. 2020, Šegota et al. 2021b, Šegota et al. 2021c, Ellis et al. 2021a, Ellis et al. 2021b). However, some species, regarded as common on a European level, have been recorded in only a few localities in Croatia (Alegro and Šegota 2022), indicating the necessity of further research into the bryophytes.

Given that systematic and comprehensive studies on bryophytes inhabiting freshwater habitats are absent from Croatia, we aimed to:

1. provide the first comprehensive inventory of this understudied group,
2. analyse the distribution and diversity patterns on a national level,
3. examine the chorological spectrum and life-history traits of bryophytes, as well as potential differences between Croatian hydrological and biogeographical regions.

Material and methods

Study Area

Data on the distribution of bryophytes of freshwater habitats were collected within the national surface water monitoring scheme, i.e. the monitoring of macrophyte vegetation, to assess the ecological status of the water bodies as required by the WFD (European Community 2000). The sampling sites were originally selected so as to encompass the heterogeneity of different water body types recognised by the recent typology developed as a basis for the monitoring of surface waters (Anonymous 2019). According to this typology, the territory of Croatia, of 56,594 km^2, is divided into two hydrological and biogeographical regions – the Pannonian and the Dinaric Ecoregion, the latter being subdivided into Continental and Mediterranean subecoregions (Fig. 1). A total of 382 watercourses (290 rivers and 92 artificial or heavily modified watercourses) and 45 standing water bodies (nine natural and 36 artificial or heavily modified) were surveyed during the vegetation seasons from 2016 to 2021. The survey included 786 sampling sites (648 on watercourses and 138 on standing waters) ultimately covering the whole of the Croatian territory (Fig. 1). The watercourses were represented by 528 sampling sites on streams and rivers and 120 on artificial and heavily-modified watercourses, while 40 sites were situated on natural lakes and 98 on artificial and heavily-modified standing water bodies (Fig. 2). Each sampling site was visited once during the survey. The altitude of sampling sites ranges from 1 to 711 m a.s.l., with 77.7% of the sampling sites located below 400 m a.s.l.

The Pannonian Ecoregion encompasses the continental part of the country, situated between three large rivers (Sava, Drava and Danube). This area consists of alluvial and diluvial plains with altitudes ranging between 80 and 135 m, along with rather low, solitary mountain massifs. According to lithological and geological composition, most of the Pannonian area belongs to silicate Quaternary deposits, while limestone is found only in the highest mountain areas. The climate is temperate, without a dry season, with warm summers in most of the territory (Cfb) and hot summers predominantly in the eastern part (Cfa) (Beck et al. 2018). The Dinaric Ecoregion is predominantly built of limestone and dolomite bedrock with characteristic karstic phenomena. This ecoregion is characterised by the Dinarides, the largest uninterrupted karst landscape in Europe occupying almost 50% of the territory of Croatia. As the area is, for the most part, built of calcareous and dolomite bedrock, many rivers have partly subterranean courses, flowing through impressive canyons or complex systems of barrage lakes and participating in the karst relief formation. The Continental Subecoregion is characterised by a continental climate (Cfb), while the climate of the Mediterranean Subecoregion is mostly Mediterranean, i.e. temperate with dry and hot summer months (Csa) (Beck et al. 2018). The Pannonian watercourses belong exclusively to the Black Sea Basin, as do the majority of the watercourses of the Dinaric-Continental Subecoregion. The watercourses of the Dinaric-Mediterranean Subecoregion, on the other hand, belong to the Adriatic Sea Basin. The estimated total length of natural and artificial watercourses in Croatia is 32,100 km (Biondić 2009), while there are only a dozen fairly large natural lakes in the country.

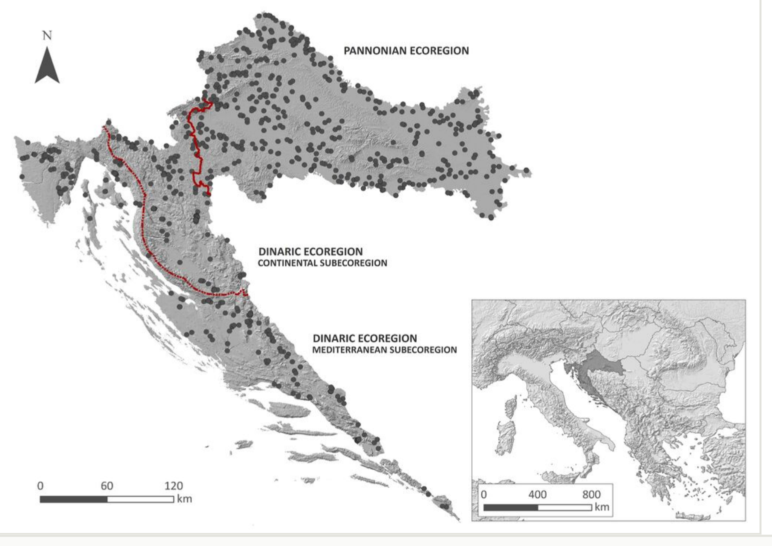

Figure 1. doi

Study area with 786 sampling sites distributed across Croatia (southeast Europe).

Sampling Method

A survey of macrophyte vegetation was performed according to the national methodology for macrophyte sampling (Anonymous 2019) from 2016 to 2021, from June to September when macrophyte vegetation is optimally developed and during the lowest water discharge levels. Watercourses were surveyed for macrophytes along 100 m-long transects, while 6×100 m transects were used when surveying macrophytes in lakes. The riverbeds were inspected for bryophytes from the banks and, if the water depth was low enough, by zigzagging across the channel. Standing waters were sampled by boat and additionally by walking along the banks. In less-accessible areas, the river/lake bottom was raked to reach the macrophytes, with the rake either on a long pole or at the end of a rope. Species coverage and abundance were assessed using the extended Braun-Blanquet scale (r = one individual, + = up to 5 individuals, 1 = up to 50 individuals, 2m = over 50 individuals, 2a = coverage 5–15%, 2b = coverage 15–25%, 3 = 25–50%; 4 = coverage 50–75%; 5 = coverage over 75%) (Barkmann et al. 1964, Braun-Blanquet 1964, Dierschke 1994). These classes were transformed into modified classes, representing the mean cover values of Braun-Blanquet classes (Tremp 2005), in order to calculate the species' average covers. Bryophytes were collected from various substrates (rocks, boulders, pebbles, woody debris, silt) within the riverbed, as well as from marginal submerged tree stumps and periodically flooded margin slopes (drawdown zone). The collected material was deposited in herbarium ZA (Thiers 2022). The nomenclature follows Hodgetts et al. (2020) and Erzberger and Schröder (2013) for *Bryum barnesii*.

Figure 2. doi

Examples of the sampling sites in Croatia: **Pannonian Ecoregion**: A–Petrinjčica River (Miočinovići), B–Trepča River (Trepča), C–Kravarščica River (Dabići); **Dinaric Ecoregion; Continental Subecoregion**: D–Curak River (at confluence with the Kupa), E–Kupa River (Kupari), F–Korana River (Veljun); **Dinaric Ecoregion; Mediterranean Subecoregion**: G–Krka River (Marasovine), H–Zrmanja River (Butiga), I–Kobilica River (Kusac).

Analysis

The chorological analysis of bryophyte flora was carried out according to Hill and Preston (1998), who divided floristic elements into categories with similar climatic requirements. The basis of this method is a two-dimensional grid, reflecting: 1) major biomes, which are combinations of zonobiomes (latitudinal zones) and the equivalent orobiomes (zones on mountains) and 2) the eastern limits in Eurasia. The analysis of life-form spectra was done using the classification given in Hill et al. (2007), while the life strategies were defined according to During (1992) given in Dierßen (2001). For a few species that were not listed in these classifications, we assigned one of the categories based on the known distribution of the particular species in case of the chorotypes and morphologically and ecologically similar species in case of life-forms and life strategies. The species' affinity to water, i.e.

different freshwater microhabitats in relation to humidity level, was analysed using the classifications given by Hill et al. (2007), Dierßen (2001) and Vitt and Glime (1984). The species' threat status follows Hodgetts et al. (2019). Margalef and Shannon-Wiener alpha diversity indices were calculated and presented through boxplots using Past 4.5 software (Hammer et al. 2001). The altitude was obtained from digital elevation model of 5×5 m resolution, while CHELSA climatological datasets (Karger et al. 2017) were used to describe the climatological conditions. Distribution maps were created using ArcGIS 10.5 software.

Results

Aquatic and semi-aquatic bryophytes were present at 228 (29%) of the sampling sites (Fig. 3). The sites with bryophytes were distributed on 160 (38%) of the surveyed water bodies, i.e. on 140 (37%) surveyed watercourses and 20 (45%) surveyed standing water bodies.

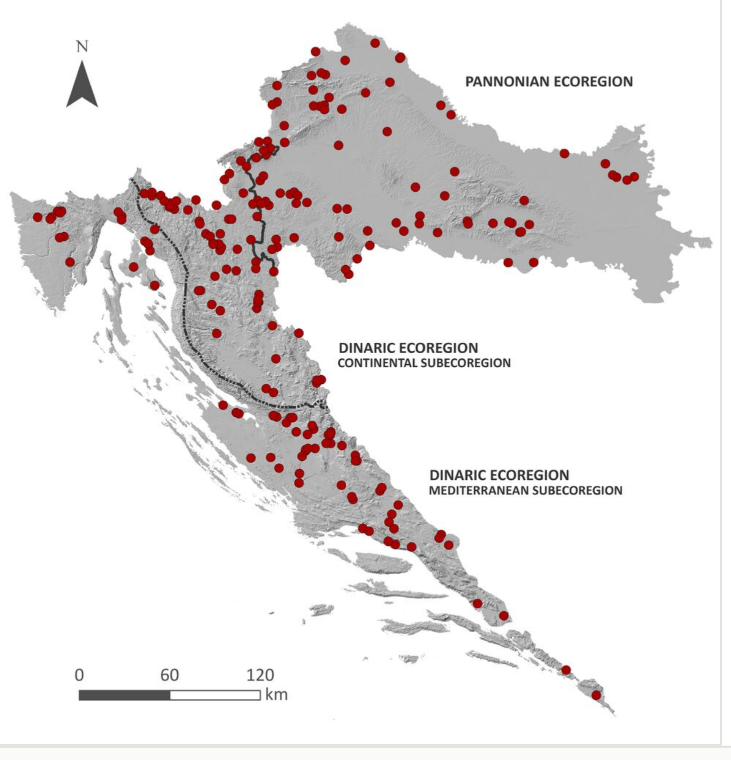

Figure 3. doi

Distribution of 228 sampling sites with freshwater bryophytes in Croatia.

Eighty-three bryophyte species, including 68 mosses (Bryophyta) and 15 liverworts (Marchantiophyta), were recorded (Table 1,Suppl. material 1). Mosses were represented by 43 acrocarpous and 25 pleurocarpous species, while liverworts included four leafy and

11 thalloid species. The most frequent species, found at as many as 53% of sampling sites, was *Fontinalis antipyretica*, followed by *Rhynchostegium riparioides* (45%), *Leptodictyum riparium* (33%) and *Cratoneuron filicinum* (32%) (Figs 4, 5). Amongst liverworts, the most common species were *Apopellia endiviifolia* (21%), *Marchantia polymorpha* (12%), *Chiloscyphus polyanthos* (11%) and *Conocephalum salebrosum* (7%). The majority of the 83 recorded species were rarely found. Over 40% of the species were registered at a maximum of three sampling sites, while over 70% of species were found on less than 10 sampling sites (Table 1).

Table 1.

List of bryophyte species, along with the number of occurrences in Croatia and sub- and ecoregions. P–Pannonian Ecoregion, D–Dinaric Ecoregion, C–Continental Subecoregion, M–Mediterranean Subecoregion.

Taxon	**Number of sampling sites per ecoregion/subecoregion**	**Total number of sampling sites**
Marchantiophyta		
Jungermanniopsida		
Jungermanniales		
Jungermanniaceae		
1. *Jungermannia atrovirens* Dumort	D: C (6), M (3)	9
Lophocoleaceae		
2. *Chiloscyphus pallescens* (Ehrh.) Dumort.	P (3); D: C (2), M (1)	6
3. *Chiloscyphus polyanthos* (L.) Corda	P (4); D: C (12), M (7)	23
4. *Lophocolea bidentata* (L.) Dumort.	D: C (2)	2
Pelliales		
Pelliaceae		
5. *Apopellia endiviifolia (Dicks.)* Nebel & D.Quandt	P (3); D: C (22), M (18)	43
6. *Pellia neesiana (Gottsche)* Limpr.	P (7)	7
Marchantiopsida		
Lunulariales		
Lunulariaceae		
7. *Lunularia cruciata* (L.) Dumort. ex Lindb.	P (1); D: C (1)	2
Marchantiales		
Conocephalaceae		
8. *Conocephalum salebrosum* Szweyk., Buczk. & Odrzyk.	P (8); D: C (6), M (1)	15
Marchantiaceae		
9. *Marchantia polymorpha* L.	P (6); D: C (16), M (2)	24
Ricciaceae		

Taxon	Number of sampling sites per ecoregion/subecoregion	Total number of sampling sites
10. *Riccia cavernosa* Hoffm.	P (4); D: C (1)	5
11. *Riccia fluitans* L.	P (6); D: C (3), M (1)	10
12. *Riccia frostii* Austin	P (1)	1
13. *Riccia glauca* L.	P (1)	1
14. *Riccia rhenana* Lorb. ex Müll.Frib.	P (3)	3
15. *Ricciocarpos natans* (L.) Corda	P (2)	2
Bryophyta		
Bryopsida		
Bartramiales		
Bartramiaceae		
16. *Philonotis marchica* (Hedw.) Brid.	D: C (1)	1
Bryales		
Bryaceae		
17. *Bryum argenteum* Hedw.	P (4); D: C (1)	5
18. *Bryum barnesii* J.B. Wood ex Schimp.	D: M (1)	1
19. *Bryum dichotomum* Hedw.	P (1); D: M (1)	2
20. *Bryum klinggraeffii* Schimp.	P (2)	2
21. *Bryum ruderale* Crundw. & Nyholm	D: C (1)	1
22. *Ptychostomum pseudotriquetrum* (Hedw.) J.R.Spence & H.P.Ramsay ex Holyoak & N.Pedersen	P (8); D: C (10), M (7)	25
Mniaceae		
23. *Mnium marginatum* (Dicks.) P.Beauv.	D: C (3)	3
24. *Plagiomnium affine* (Blandow ex Funck) T.J.Kop.	D: C (1)	1
25. *Plagiomnium elatum* (Bruch et Schimp.) T.J.Kop.	P (1)	1
26. *Plagiomnium ellipticum* (Brid.) T.J.Kop.	P (1); D: C (1)	2
27. *Plagiomnium undulatum* (Hedw.) T.J.Kop.	P (3); D: C (7)	10
28. *Pohlia melanodon* (Brid.) A.J.Shaw	P (12); D: C (2), M (2)	16
29. *Rhizomnium punctatum* (Hedw.) T.J.Kop.	P (1); D: C (1)	2
Dicranales		
Amphidiaceae		
30. *Dichodontium flavescens* (Dicks.) Lindb.	P (1); D: C (4)	5
31. *Dichodontium pellucidum* (Hedw.) Schimp.	P (2); D: C (3)	5
32. *Dicranella varia* (Hedw.) Schimp.	P (5); D: C (1), M (2)	8
Fissidentaceae		

Taxon	Number of sampling sites per ecoregion/subecoregion	Total number of sampling sites
33. *Fissidens adianthoides* Hedw.	P (4); D: C (1)	5
34. *Fissidens arnoldii* R.Ruthe	D: C (1)	1
35. *Fissidens crassipes* Wilson ex Bruch & Schimp.	P (6); D: C (19), M (14)	39
36. *Fissidens fontanus* (Bach.Pyl.) Steud.	P (3); D: M (1)	4
37. *Fissidens gracilifolius* Brugg.-Nann. & Nyholm	D: C (1), M (2)	3
38. *Fissidens pusillus* (Wilson) Milde	P (5)	5
39. *Fissidens taxifolius* Hedw.	P (2); D: C (1), M (2)	5
Pottiaceae		
40. *Barbula unguiculata* Hedw.	P (1); D: C (2)	3
41. *Bryoerythrophyllum recurvirostrum* (Hedw.) P.C.Chen	D: C (1)	1
42. *Cinclidotus aquaticus* (Hedw.) Bruch & Schimp.	D: C (20), M (16)	36
43. *Cinclidotus fontinaloides* (Hedw.) P.Beauv.	P (2); D: C (28), M (21)	51
44. *Cinclidotus riparius* (Host ex Brid.) Arn.	P (7); D: C (22), M (13)	42
45. *Didymodon fallax* (Hedw.) R.H.Zander	D: C (6), M (1)	7
46. *Didymodon insulanus* (De Not.) M.O.Hill	D: C (1)	1
47. *Didymodon luridus* Hornsch.	D: C (1), M (2)	3
48. *Didymodon spadiceus* (Mitt.) Limpr.	D: C (3)	3
49. *Didymodon tophaceus* (Brid.) Lisa	D: C (2), M (8)	10
50. *Eucladium verticillatum* (With.) Bruch & Schimp.	D: C (6), M (4)	10
51. *Gymnostomum aeruginosum* Sm.	D: C (1)	1
52. *Hymenostylium recurvirostrum* (Hedw.) Dixon	D: C (3)	3
53. *Trichostomum crispulum* Bruch	D: C (1)	1
Funariales		
Funariaceae		
54. *Funaria hygrometrica* Hedw.	P (1); D: C (3), M (2)	6
55. *Physcomitrium patens* (Hedw.) Mitt.	P (7); D: C (1)	8
56. *Physcomitrium eurystomum* Sendtn.	P (1)	1
57. *Physcomitrium sphaericum* (C.F.Ludw. ex Schkur.) Brid.	P (1)	1
Hypnales		
Amblystegiaceae		
58. *Cratoneuron filicinum* (Hedw.) Spruce	P (8); D: C (34), M (25)	67
59. *Drepanocladus aduncus* (Hedw.) Warnst.	P (2); D: C (2), M (4)	8

Taxon	**Number of sampling sites per ecoregion/subecoregion**	**Total number of sampling sites**
60. *Hygroamblystegium fluviatile* (Hedw.) Loeske	P (1)	1
61. *Hygroamblystegium humile* (P.Beauv.) Vanderp., Goffinet & Hedenäs	P (1)	1
62. *Hygroamblystegium tenax* (Hedw.) Jenn.	P (2); D: C (1), M (1)	4
63. *Hygroamblystegium varium* (Hedw.) Mönk.	P (2); D: C (3)	5
64. *Hygrohypnum luridum* (Hedw.) Jenn.	D: C (4)	4
65. *Leptodictyum riparium* (Hedw.) Warnst.	P (42); D: C (19), M (8)	69
66. *Palustriella commutata* (Hedw.) Ochyra	P (2); D: C (3), M (4)	9
67. *Palustriella falcata* (Brid.) Hedenäs	P (1); D: C (6), M (3)	10
Brachytheciaceae		
68. *Brachythecium mildeanum* (Schimp.) Schimp.	P (3); D: C (2)	5
69. *Brachythecium rivulare* Schimp.	P (2); D: C (10), M (3)	15
70. *Brachythecium rutabulum* (Hedw.) Schimp.	P (4); D: C (6), M (1)	11
71. *Brachythecium salebrosum* (Hoffm. ex F.Weber et D.Mohr) Schimp.	D: C (1), M (1)	1
72. *Oxyrrhynchium hians* (Hedw.) Loeske	P (8); D: C (4)	12
73. *Oxyrrhynchium schleicheri* (R.Hedw.) Röll	D: M (1)	1
74. *Oxyrrhynchium speciosum* (Brid.) Warnst.	P (6); D: C (4), M (1)	11
75. *Rhynchostegiella curviseta* (Brid.) Limpr.	D: C (1)	1
76. *Rhynchostegiella teneriffae* (Mont.) Dirkse & Bouman	D: C (3)	3
77. *Rhynchostegium riparioides* (Hedw.) Cardot	P (19); D: C (38), M (36)	93
Fontinalaceae		
78. *Fontinalis antipyretica* Hedw.	P (20); D: C (43), M (47)	110
79. *Fontinalis hypnoides* var. *duriaei* (Schimp.) Kindb.	P (1); D: C (2)	3
Leskeaceae		
80. *Leskea polycarpa* Hedw.	P (1); D: C (1), M (2)	4
Neckeraceae		
81. *Thamnobryum alopecurum* (Hedw.) Gangulee	D: C (3), M (2)	5
Pylaisiaceae		
82. *Calliergonella cuspidata* (Hedw.) Loeske	P (1); D: C (7), M (1)	9
Splachnales		
Meesiaceae		
83. *Leptobryum pyriforme* (Hedw.) Wilson	P (2)	2

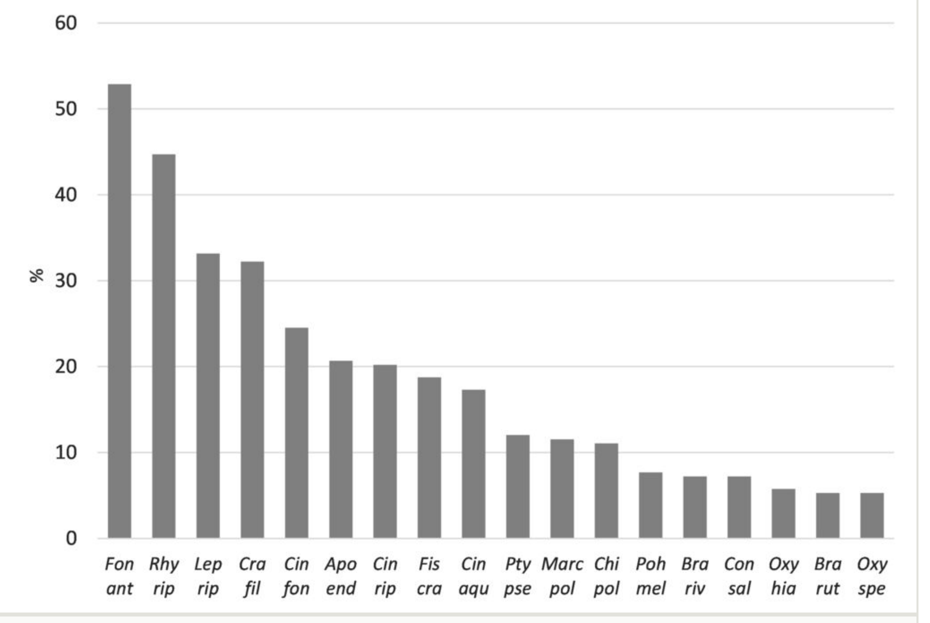

Figure 4. doi

The most frequent bryophyte species (only species present in over 10 sampling sites are shown) (Font ant–*Fontinalis antipyretica*, Rhy rip–*Rhynchostegium riparioides*, Lep rip–*Leptodictyum riparium*, Cra fil–*Cratoneuron filicinum*, Cin fon–*Cinclidotus fontinaloides*, Apo end–*Apopellia endiviifolia*, Cin rip–*Cinclidotus riparius*, Fis cra–*Fissidens crassipes*, Cin aqu–*Cinclidotus aquaticus*, Pty pse–*Ptychostomum pseudotriquetrum*, Marc pol–*Marchantia polymorpha*, Chi pol–*Chiloscyphus polyanthos*, Poh mel–*Pohlia melanodon*, Bra riv–*Brachythecium rivulare*, Con sal–*Conocephalum salebrosum*, Oxy hia–*Oxyrrhynchium hians*, Bra rut–*Brachythecium rutabulum*, Oxy spe–*Oxyrrhynchium speciosum*).

The overall average bryophyte species richness at the 228 sites was 4.17 ± 0.25 species per site, while 27% of the sites had only one species and other sites up to a maximum of 20 species (Fig. 6). Two-thirds of the sampling sites in the present study were species-poor (containing fewer than four species) and one third were species-rich (with more than four species).

The collected species belong to 10 orders, 21 families and 43 genera (Table 1). Regarding the number of recorded species, the families most represented were Pottiaceae (14), Amblystegiaceae and Brachytheciaceae (10 each), Fissidentaceae and Mniaceae (seven each), Bryaceae and *Ricciaceae* (six each) (Fig. 7). Genera with the highest number of recorded species were *Fissidens* (seven species) and *Bryum*, *Didymodon* and *Riccia* (five species each) (Table 1).

The vast majority of recorded species had quite low coverage in survey localities, with the mean coverage of all species being 3.3%. As many as 69 species had a mean cover in the investigated sites of less than 5%, whereas just three species displayed a mean coverage greater than 10% (*Hymenostylium recurvirostrum* – 22.5%, *Palustriella commutata* – 17.9% and *Cinclidotus aquaticus* – 17.1%).

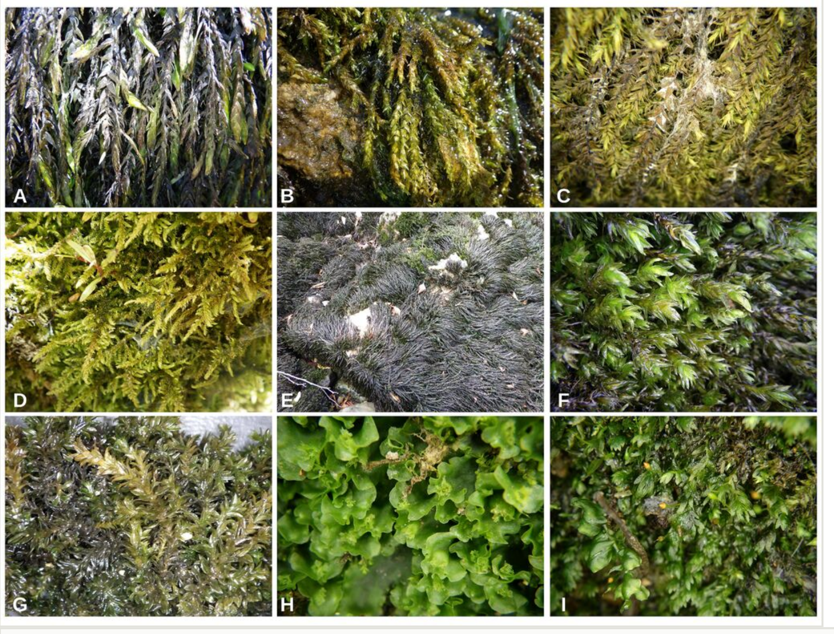

Figure 5. doi

The most common freshwater bryophyte species in Croatia: A–*Fontinalis antipyretica*, B–*Rhynchostegium riparioides*, C–*Leptodyctium riparium*, D–*Cratoneuron filicinum*, E–*Cinclidotus aquaticus*, F–*C. fontinaloides*, G–*C. riparius*, H–*Apopellia endiviifolia*, I–*Fissidens crassipes*.

The chorological analyses, based on major biomes, indicated the predominance of the temperate chorotype in Croatian freshwater bryoflora: temperate (30.1%), boreo-temperate (24.1%), southern-temperate (21.7%) and wide-temperate (8.4%). The biogeographical spectrum, based on the eastern limit, showed that the dominant chorotypes were circumpolar (54.2%) and European (31.3%). Analysis of life-forms, based on the species frequencies, revealed that the most dominant were aquatic trailings (28%), turfs (18%), rough mats (15%), smooth mats (11%) and wefts (11%). Regarding the life strategy, the most frequent were perennials (34%), colonists (30%) and competitive perennials (19%).

The recorded bryoflora displays rather wide niche heterogeneity concerning the humidity levels preferred. Only six recorded species could be classified as obligate aquatics, having little or no tolerance to drought conditions (*Fissidens arnoldii*, *F. fontanus*, *Fontinalis antipyretica*, *F. hypnoides* var. *duriaei*, *Hygroamblystegium fluviatile* and *Ricciocarpos natans*), while the majority (40 species) were facultative aquatics, having some degree of tolerance to desiccation and xerophytic conditions. Seven of the recorded species were semi-aquatic emergents, thriving on a periodically waterlogged substrate. Twenty-five recorded species were associated with moist or moderately moist substrates, whereas the least represented group with only five species was that characteristic of a well-drained terrestrial substrate.

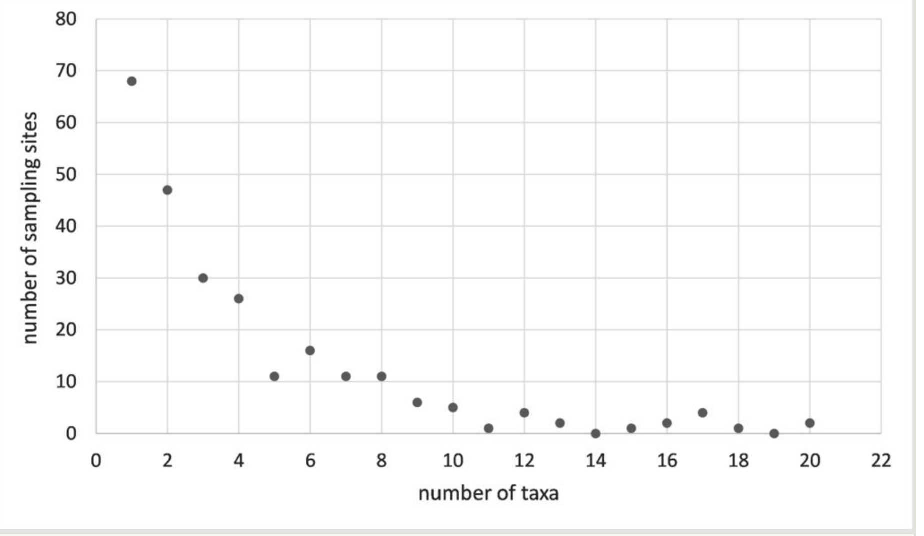

Figure 6. doi

The number of species per sampling site.

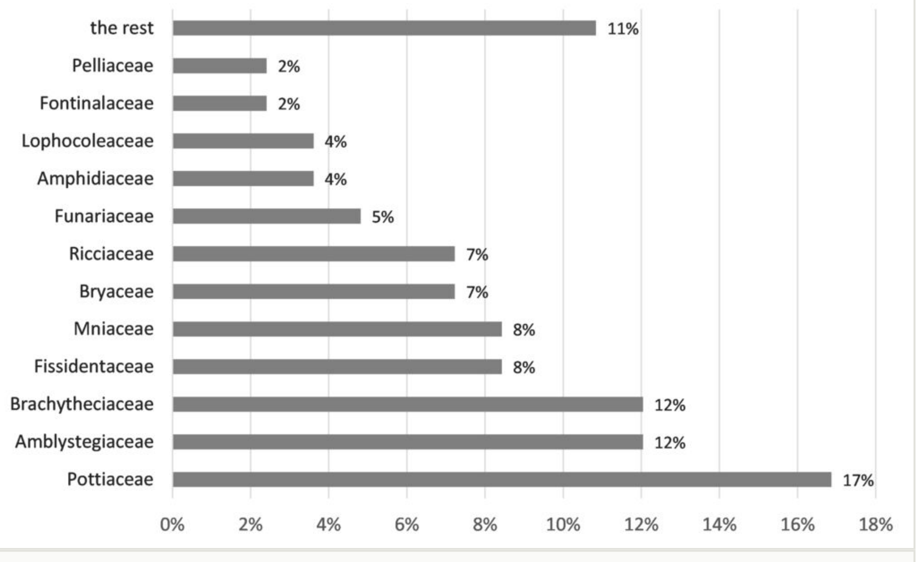

Figure 7. doi

The most represented families of freshwater bryophytes in Croatia.

Concerning the threat status, the majority of the recorded species are considered to be of least concern (LC). *Philonotis marchica* is evaluated as endangered (EN), while *Fissidens* *arnoldii*, *Physcomitrium eurystomum* and *Ph. sphaericum* are vulnerable (VU) species on a European level.

Dinaric vs. Pannonian Ecoregion

The study revealed that the Dinaric Ecoregion supports higher freshwater bryophyte diversity (70 bryophyte species, out of which 60 are mosses), than the Pannonian Ecoregion with 57 recorded bryophyte species (44 mosses) (Table 2). In contrast, both ecoregions were shown to harbour the same liverwort diversity in aquatic and semi-aquatic habitats, represented by four leafy and 11 thallose species. The two regions share as many as 44 species (53.0%), while 26 species (31.3%) were exclusively found in the Dinaric and 13 species (15.7%) in the Pannonian Ecoregion. In the Dinaric Ecoregion, the dominant species with occurrence frequencies higher than 30%, were *Fontinalis antipyretica*, *Rhynchostegium riparioides* and *Cinclidotus fontinaloides*, whereas in the Pannonian Ecoregion, the only truly dominant species was *Leptodictyum riparium*. The most common species occurring in both ecoregions were *Fontinalis antipyretica*, *Cratoneurum filicinum*, *Fissidens crassipes* and *Marchantia polymorpha*. The common species in the Dinaric Ecoregion were also *Cinclidotus fontinaloides*, *Apopellia endiviifolia*, *Cinclidotus aquaticus*, *Ptychostomum pseudotriquetrum*, *Didymodon tophaceus* and *Eucladium verticillatum*, while in the Pannonian Ecoregion *Pohlia melanodon*, *Conocephalum salebrosum*, *Oxyrrhynchium hians*, *Peelia neesiana*, *Physcomitrium patens*, *Oxyrrhynchium speciosum* and *Riccia fluitans* were frequent.

Table 2.

Comparison amongst Croatian ecoregions and subecoregions.

	(sub)ecoregion			
	Pannonian	**Dinaric**	**Dinaric–Continental**	**Dinaric–Mediterranean**
Total number of bryophyte species	**57**	**70**	**65**	**40**
Mosses (Bryophyta)	44	60	55	33
pleurocarpous	19	23	21	16
acrocarpous	25	37	34	17
Liverworts	15	15	10	7
leafy	4	4	4	3
thallose	11	11	6	4
dominant species more than 5 species	*Lept rip*	*Fon ant, Rhy rip, Cra fil, Cin fon*	*Fon ant, Rhy rip, Cra fil, Cin fon, Cin rip, Apo end*	*Fon ant, Rhy rip, Cra fil*
coverage % (mean)	2.40	3.60	4.04	4.15
species richness (total, mean ± SE)	3.40 ± 0.35	4.60 ± 0.33	5.90 ± 0.58	3.40 ± 0.29

	(sub)ecoregion			
	Pannonian	**Dinaric**	**Dinaric–Continental**	**Dinaric–Mediterranean**
range (min–max)	1–15	1–20	1–20	1–12
Families				
number of families	18	20	20	19
dominant families frequency over 30%	*Amb, Bra, Ricc, Fiss, Mni.*	*Pott, Brac, Ambl, Fiss, Mnia*	*Pott, Brac, Ambl, Mnia, Fiss*	*Pott, Ambl, Brac, Fiss, Brya*
Watercourses/sampling sites	**68/76**	**85/132**	**43/62**	**42/70**
rivers/sampling sites	50/56	69/107	39/57	30/50
artificial and heavily-modified watercourses / sampling sites	18/20	16/25	4/5	12/20
Standing waters/sampling sites	**3/3**	**14/17**	**6/8**	**8/9**
natural lakes/ sampling sites	-	5/5	3/3	2/2
artificial or heavily-modified standing waters / sampling sites	3/3	9/12	3/5	6/7
Altitude (m a.s.l.)				
mean ± SE	146 ± 8.23	231 ± 13.53	310 ± 18.32	162 ± 16.15
range (min-max)	81–547	1–711	111–703	1–711
Climate				
mean annual air temperature (°C) (± SE)	11.6 ± 0.1	12.4 ± 0.1	10.9 ± 0.1	13.7 ± 0.1
mean daily mean air temperatures of the wettest quarter (°C) (± SE)	17.4 ± 0.4	11.1 ± 0.2	11.6 ± 0.3	10.7 ± 0.3
mean daily mean air temperatures of the driest quarter (°C) (± SE)	3.3 ± 0.1	14.1 ± 0.8	6.5 ± 0.9	20.9 ± 0.6
annual precipitation amount (kg/m^2) (mean ± SE)	935.3 ± 14.6	1360.2 ± 20.5	1415.1 ± 24.7	1311.5 ± 31.0

The Dinaric Ecoregion had a higher species richness (4.6±0.33 species) and mean coverage (3.6%) per sampling site than the Pannonian Ecoregion (3.4±0.35 species; mean coverage 2.4%) per sampling site (Table 2). In the Dinaric Ecoregion, the dominant bryophyte families were Pottiaceae, Brachytheciace, Amblystegiaceae, Fissidentaceae and Mniaceae, while in the Pannonian Ecoregion, they were Amblystegiaceae, Brachytheciace, *Ricciaceae*, Fissidentaceae and Mniaceae.

Within the Dinaric Ecoregion, the Continental Subecoregion showed a higher species richness (65 bryophytes; 55 mosses and 10 liverworts) than the Mediterranean Subecoregion with 40 bryophyte species (33 mosses and seven liverworts) recorded within this study. Furthermore, the Continental Subecoregion features higher species richness (5.9 ± 0.58 species) per sampling site than the Mediterranean Subecoregion (3.4±0.29

species), while the mean coverage per sampling site was similar in both subecoregions (Table 2). The same trends are detectable from the Shannon-Wiener and Margalef alpha diversity indices (Fig. 8).

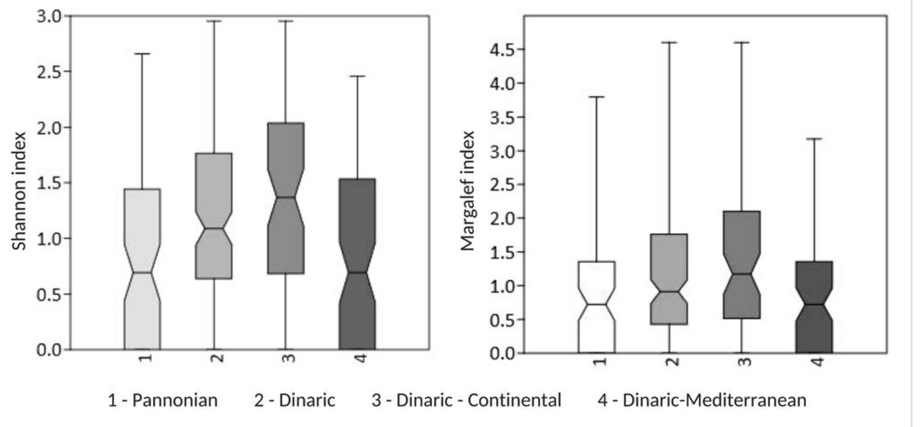

Figure 8. doi

Comparison of alpha diversity (Shannon-Wiener and Margalef alpha diversity indices) in the Pannonian Ecoregion, Dinaric Ecoregion, Dinaric–Continental Subecoregion and Dinaric–Mediterranean Subecoregion.

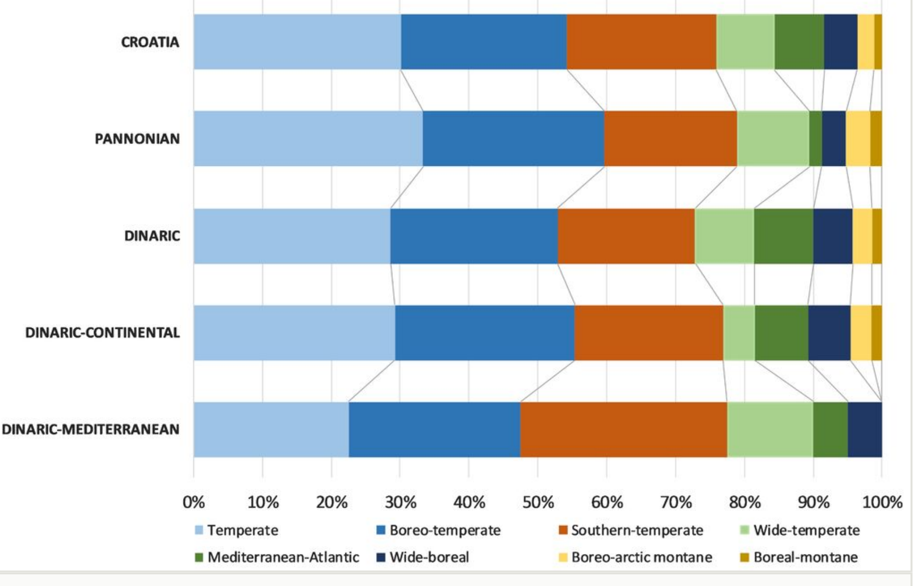

Figure 9. doi

Chorological spectra of freshwater bryophytes, based on major biomes for Croatia, Pannonian Ecoregion, Dinaric Ecoregion, Dinaric–Continental Subecoregion and Dinaric–Mediterranean Subecoregion.

The chorological comparison of Croatian eco- and subecoregions, based on major biomes, revealed large chorotype overlapping, with the dominance of temperate chorotypes; however, some biogeographical differences were highlighted. The Mediterranean-Atlantic chorotype was almost completely absent from the Pannonian Ecoregion, while within the Dinaric Ecoregion, this type was more frequent in the Continental Subecoregion. On the other hand, the boreo-arctic and boreal-montane chorotypes were absent in the Mediterranean Subecoregion (Fig. 9).

The chorological comparison of Croatian eco- and subecoregions, based on the eastern limit, showed the dominance of circumpolar and European chorotypes in all eco- and subecoregions (Fig. 10). The sub-oceanic and oceanic chorotypes are very rare in the Pannonian Ecoregion, while in the Dinaric Ecoregion they are more common in the Continental Subecoregion.

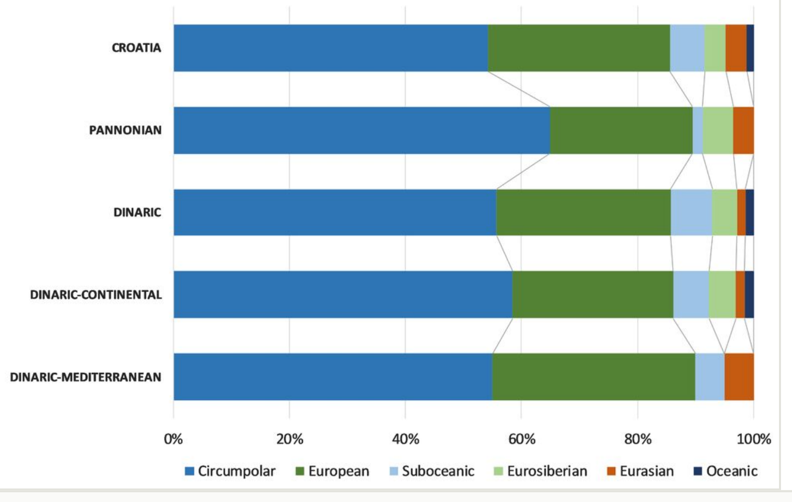

Figure 10. doi

Chorological spectra of freshwater bryophytes, based on the eastern limit for Croatia, Pannonian Ecoregion, Dinaric Ecoregion, Dinaric–Continental Subecoregion and Dinaric–Mediterranean Subecoregion.

Bryophyte life-forms were not evenly distributed within Croatian eco- and subecoregions (Fig. 11), with the most conspicuous difference in the share of the aquatic trailings. In the Dinaric Ecoregion, this life-form predominates (33%) and, in the Pannonian, it reaches only 14% considering the frequency of the species with that particular life-form. By contrast, rough mats are almost three times as frequent in the Pannonian (28%) as in the Dinaric Ecoregion (10%). Finally, wefts are twice as frequent in the Dinaric (13%) as in the Pannonian Ecoregion (6%).

Regarding the life strategies, all Croatian eco- and subecoregions feature the dominance of perennial and colonist bryophyte species. However, competitive perennial strategy is almost twice as frequent in the Dinaric Ecoregion (21%) as in the Pannonian (13%).

Contrarily, the annual shuttle strategy in the Dinaric Ecoregion is almost negligible (1%), while in the Pannonian Ecoregion, it is relatively more frequent (10%) (Fig. 12).

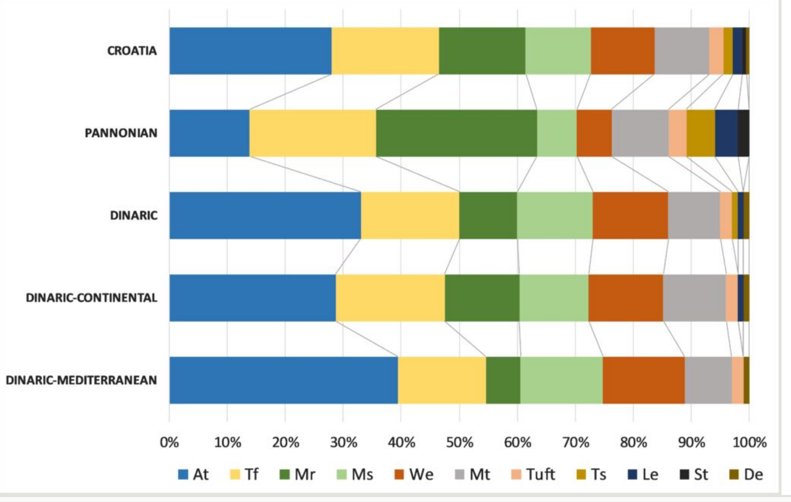

Figure 11. doi

Life-form spectra of freshwater bryophytes for Croatia, Pannonian Ecoregion, Dinaric Ecoregion, Dinaric–Continental Subecoregion and Dinaric–Mediterranean Subecoregion, based on species frequencies (At–Aquatic trailing, De–dendroid, Le– lemnoid, Mr–rough mat, Ms–smooth mat, Mt–thalloid mat, St–solitary thalloid, Tf–turf, Ts–scattered turf, Tuft–tuft and We–weft).

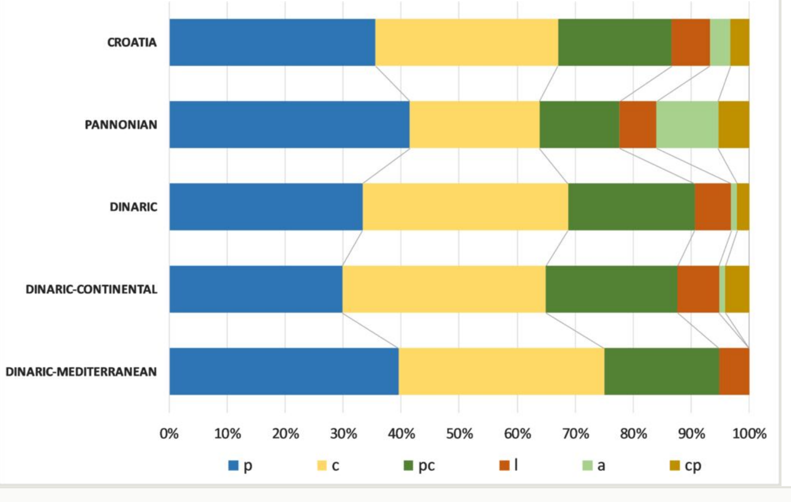

Figure 12. doi

Life strategy spectra of freshwater bryophytes for Croatia, Pannonian Ecoregion, Dinaric Ecoregion, Dinaric–Continental Subecoregion and Dinaric–Mediterranean Subecoregion, based on species frequencies (p–perennials, c–colonists, pc–competitive perennials, l–long-lived shuttle, a–annual shuttle, cp–pioneer colonists).

Discussion

The present study is the first to compile a comprehensive floristic catalogue on Croatian freshwater bryophyte species including 83 species representing 12% of Croatian bryoflora (Alegro and Šegota 2022). Mosses were represented with notably higher number of species than liverworts, as already reported in previous work focusing on the freshwater bryoflora (Muotka and Virtanen 1995, Scarlett and O'Hare 2006, Gecheva et al. 2010, Ceschin et al. 2012a, Vieira et al. 2012a), which was to be expected given their low resistance to mechanical water scouring and desiccation, as well as continuous submersion compared to mosses (Gimingham and Birse 1957, Kimmerer and Allen 1982, Vitt and Glime 1984). Furthermore, they also appear more sensitive to changes in catchment land use and to elevated stream nutrient levels (Suren 1996). While the foliose liverwort *Chiloscyphus polyanthos* was the only quite frequent liverwort in fast-flowing streams, thallose species were common in splash zones and margins of rivers (e.g. *Conocephalum salebrosum*, *Lunularia cruciata*, *Pellia neesiana*, *Apopellia endiviifolia*, *Marchantia polymorpha*) in our study.

The majority of species encountered are not considered to be truly aquatic, confirming other studies investigating the bryoflora of streams and rivers, for example, in the UK (Scarlett and O'Hare 2006), Portugal (Vieira et al. 2012a), Bulgaria (Gecheva et al. 2010) and Italy (Ceschin et al. 2012a). These studies, like our own, included both species growing permanently submerged in the riverbed, as well as those on riverbanks and other associated periodically submerged microhabitats. In our study, only six species (*Fissidens arnoldii*, *F. fontanus*, *Fontinalis antipyretica*, *F. hypnoides* var. *duriaei*, *Hygroamblystegium fluviatile* and *Ricciocarpos natans*) were considered obligate aquatics *sensu* Vitt and Glime (1984) or rheophilic or limnophylic *sensu* Dierßen (2001), living regularly submerged in running waters or on the surface of standing water (Hill et al. 2007) and having little or no tolerance to drought conditions and desiccation. About half the species were facultative or semi-aquatics *sensu* Vitt and Glime (1984) or hydrophytic to hygrophytic *sensu* Dierßen (2001). This was expected, since in general, only a few bryophyte species are considered truly aquatic and, additionally, obligate aquatics are more characteristic of limnophilous habitats (Vitt and Glime 1984), which were less represented in this study. By contrast, the more numerous facultative aquatics are better adapted to rheophilous environments (Vitt and Glime 1984), which were dominant in our study. The rest of the species can be described as mesophytic to hygrophytic, living on a moderately wet substrate, adapted to some degree of xerophytic conditions. They are mostly terricolous species that have found an alternative niche in riparian microhabitats.

As previously recorded in other studies (e.g. Ceschin et al. 2015), most of the freshwater bryophyte species show both low occurrences and low cover with respect to the sampled area. Species richness was lower in the Pannonian Ecoregion (3.4), while in the Dinaric, it was 4.6, which corresponds well with the species richness of highly seasonal Mediterranean rivers (4.8 species per site) (Vieira et al. 2018). The Continental part of the Dinaric Ecoregion harbours the highest species richness per site in Croatia (5.9) which is related to the very good ecological status of watercourses, with clear, cold, well-oxygenated and fast-flowing water, as well as rocky substrates (Mihaljević et al. 2020). This subecoregion largely corresponds to Mediterranean Mountains according to the European Environmental Stratification (Metzger et al. 2005), while the rest is in the Alpine Region. The average species richness of freshwater bryophytes for Mediterranean Mountains was estimated at 4.5 (Vieira et al. 2018), being somewhat lower than that of the Continental Subecoregion of Croatia.

The lowest diversity was observed in the Pannonian Ecoregion, which is presumably related to the dominant characteristics of the water bodies there. These are mostly slow, eutrophic lowland streams and rivers with unstable sandy and gravelly alluvial sediments and higher depth of the water column (Mihaljević et al. 2020). Moreover, the freshwater bryophytes here are subject to intense competition with vascular macrophytes, leading to an overall lower coverage and richness or the complete absence of bryophytes (Vitt and Glime 1984, Glime 1992). Furthermore, the majority of watercourses in the Pannonian Ecoregion are subjected to a significant level of hydromorphological alterations, such as flow regulation through canalisation, riverbed deepening and embankment, as well as considerable changes in land-use practice, with riparian vegetation being removed (Vučković et al. 2021), while nutrient input and water pollution are increasing substantially, thereby reducing the habitat quality for bryophytes. Bryophytes are generally absent from streams flowing through modified catchments of easily eroded geology or small substrate sizes and shallow gradients. These streams may also have relatively high nutrient levels affecting the bryophyte cover and communities (Suren 1996, Gecheva et al. 2010, Ceschin et al. 2012b, Gecheva et al. 2017).

The low mean coverages of all species (3.3%) can be explained by the fact that our study included evenly upper, middle and lower river sections. In our study, only three species with mean coverage greater than 10% were either tufa-forming mosses of waterfalls, such as *Hymenostylium recurvirostrum* and *Palustriella commutata* (Mucina et al. 2016, Lyons and Kelly 2017) or mosses characteristic of headwater streams as *Cinclidotus aquaticus* (Kochjarová et al. 2007, Ceschin et al. 2012b). In such habitats, the bryophytes form large colonies, having no competition from vascular plants which are not able to withstand such harsh environments, i.e. cold, fast-flowing water and rocky substrates (Suren 1996, Tremp et al. 2012). Additionally, bryophytes have lower demand for nutrients which allows them to thrive in headwater streams, characterised by low nutrient levels (Vanderpoorten and Goffinet 2009).

Fontinalis antipyretica and *Rhynchostegium riparioides*, the most abundant and common aquatic species in our study, were also amongst the most frequent aquatic species in other surveys (Scarlett and O'Hare 2006, Gecheva et al. 2010, Ceschin et al. 2012a, Ceschin et al. 2015). The occurrence of *F. antipyretica* was not previously related to specific physico-chemical and trophic conditions, suggesting a wide ecological behaviour (Muotka and Virtanen 1995, Vanderpoorten et al. 1999, Scarlett and O'Hare 2006, Ceschin et al. 2012b). On the other hand, different studies gave contradictory results regarding the ecological preferences of *R. riparioides*, most of them referring to this species as acid sensitive and characteristic of unpolluted running waters (Ceschin et al. 2012b, Tremp et al. 2012). While *F. antipyretica* was present in both Croatian ecoregions, both in watercourses and standing waters, *Rhynchostegium riparioides* was more frequently found in the Dinaric Ecoregion, while in the Pannonian Ecoregion, it was mostly restricted to smaller and faster streams. The only dominant species in the Pannonian Ecoregion was found to be *Leptodictyum riparium*, which has already been detected as the most abundant and characteristic species of middle and lower stream sections (Papp et al. 2006, Gecheva et al. 2010, Ceschin et al. 2012b) and is regarded as the most pollution-tolerant (Frahm 1974), with preferences for eutrophic waters (Vanderpoorten et al. 1999, Ceschin et al. 2012b).

Amongst dominant families, Amblystegiaceae, Brachytheciaceae, Fissidentaceae and Mniaceae were common in both ecoregions. However, the most represented family in the Dinaric Ecoregion was Pottiaceae, reflecting the presence of karstic watercourses in this region, a suitable habitat of aquatic species within the genus *Cinclidotus*, the tufa-forming *Didymodon tophaceus* and several other *Didymodon* species inhabiting the periodically submerged niches and splashing zones along karstic rivers. By contrast, in the Pannonian Ecoregion, the family *Ricciaceae* is the third most represented family, with free-floating *Riccia fluitans*, *R. rhenana* and *Ricciocarpos natans*, characteristic of stagnant and slow-flowing lowland streams or canals with eutrophic water and several other *Riccia* species recorded on fine gravelly and sandy drawdown zones of the watercourses and standing water bodies in the Croatian lowlands. The species exclusive to the Dinaric Ecoregion (*Didymodon insulanus*, *D. spadiceus*, *Hygrohypnum luridum*, *Hymenostylium recurvirostrum*, *Philonotis marchica*, *Rhynchostegiella curviseta*, *R. teneriffae* etc.) were associated with stable rocky substrates, cold, clear, well-oxygenated waters of karstic rivers and their springs, characteristic of this region (Mihaljević et al. 2020). The species restricted to the Pannonian Ecoregion (*Leptobryum pyriforme*, *Pellia neesiana*, *Physcomitrium eurystomum*, *Ph. sphaericum*, *Riccia frostii*, *R. glauca*, *R. rhenana*, *Ricciocarpos natans*, *Fissidens pusillus* etc.) were associated with moist and fine-textured substrata of the margins of lakes, reservoirs and rivers, with the exception of *F. pusillus*, a saxicolous species which was found in semi-mountain springs with a siliceous bedrock.

Considering the chorological spectrum of studied flora, the prevailing presence of temperate (circumpolar) species corresponds with the biogeographical characteristics of the studied area. This was also detected in the bryoflora of running waters of central Italy (Ceschin et al. 2012a) and the European Mediterranean Region (Vieira et al. 2018). The chorological comparison of Croatian sub- and ecoregions revealed some biogeographical peculiarities. The rarity of Mediterranean-Atlantic, as well as of suboceanic and oceanic chorotypes (e.g. *Rhynchostegiella curviseta*, *R. teneriffae*, *Lunularia cruciata*) in the Pannonian Ecoregion and the presence of those in the Dinaric–Continental Subecoregion largely corresponds with the climatic limitations. The mean air temperatures of the wettest quarter are significantly higher in the Pannonian (17.4±0.4°C) than in the Dinaric Ecoregion (11.1±0.2°C) and mean air temperatures of the driest quarter are significantly lower in the Pannonian (3.3±0.1°C) than in the Dinaric Ecoregion (14.1±0.8°C) (Karger et al. 2017). Moreover, the amount of precipitation is significantly lower in the Pannonian Ecoregion and highest in the Dinaric–Continental Subecoregion (Table 2). Similarly, the absence of boreo-arctic and boreal-montane chorotypes (e.g. *Dichodontium flavescens*, *D. pellucidum*, *Plagiomnium ellipticum*) in the Dinaric-Mediterranean Subecoregion is most likely conditioned by the higher mean annual air temperature and the annual precipitation amount in this region (Table 2).

Bryophyte life-forms can be interpreted as recurring arrangements of the photosynthetic tissues that minimise evaporative water loss and maximise primary production (Bates 1998). Life-forms of aquatic bryophytes present better adaptations to seasonal desiccation and dragging forces either during permanent submersion or flood events, with a firmer structure able to resist mechanical forces (Vitt and Glime 1984, Muotka and Virtanen 1995, Fritz et al. 2009). The dominant life-form in our study were aquatic trailings, described as aquatic bryophytes (mostly mosses) attached to the substrate and trailing in the water (Hill et al. 2007). They correspond with "streamers", a term defined by Glime (1968) and used in Vieira et al. (2012b), which includes long, dangling aquatics (e.g. *Chiloscyphus polyanthos*, *Cinclidotus aquaticus*, *C. fontinaloides*, *C. riparius*, *Fissidens fontanus*, *Fontinalis antipyretica*, *F. hypnoides* var. *duriaei*). They are associated with more deeply submerged sites (found up to 30 cm of depth), mostly in the slower currents of streambed in full sunlight (Vieira et al. 2012b). Turfs, the second most represented life-form, feature many loosely or closely packed vertical stems with limited branching (Bates 1998, Hill et al. 2007). They colonise microhabitats usually subjected to seasonal floods with a strong impact of water (e.g. *Ptychostomum pseudotriquetrum*, *Dichodontium flavescens*, *Didymodon tophaceus*, *Fissidens crassipes*, *Hymenostylium recurvirostrum*, *Philonotis marchica* etc.); however, they are not very hydrodynamic-resistant, both to desiccation and water abrasion (Vitt and Glime 1984, Vieira et al. 2012b). When the ecoregions are compared, the life-form spectra show considerable differences. While in the Dinaric Ecoregion, aquatic trailings associated with fast-flowing karst streams prevail (e.g. *Cinclidotus* spp.) (33%), in the Pannonian Ecoregion, a similar proportion is displayed by the rough mats category, represented by aquatic species (dominant *Leptodictyum riparium* and the quite rarely recorded *Hygroamblystegium fluviatile* and *H. tenax*) and species mostly found inhabiting riparian zones of the shaded lowland forest streams and rivulets (*Brachythecium mildeanum*, *B. rivulare*, *B. rutabulum*, *Oxyrrhynchium hians*, *O. speciosum*).

Amongst Croatian freshwater bryophytes, the most frequent are those with a potential lifespan longer than one year. This includes perennial life strategy (*Fontinalis*, *Palustriella*, *Brachytecium*, *Hygroamlystegium* etc.) and several-year life-span colonists (*Ptychostomum, Cinclidotus*, *Dichodontium*, *Didymodon*, *Fissidens*, *Apopeelia* etc.). This is concurrent with the fact that aquatic species are mostly perennial, pleurocarpous mosses (Glime 2020) and that submersed bryophyte communities are mostly characterised by perennials and ephemeral colonists (Vieira et al. 2012b). In general, perennials are more likely to be found in permanent fast-flowing currents, whereas colonists are more common in the lower currents or emergent positions (Glime 2020). In the Dinaric Ecoregion, the competitive perennial strategy is twice as frequent as in the Pannonian, mainly because of the high frequencies of species associated with karstic streams and tufa formations, (e.g. *Ptychostomum pseudotriquetrum*, *Calliergonella cuspidata*, *Chiloscyphus pallescens*, *Ch. polyanthos*, *Cratoneuron filicinum*, *Palustriella commutata*, *P. falcata*) which are absent from lowland Pannonian watercourses. On the contrary, the Pannonian Ecoregion shows a ten times higher frequency of annual shuttle life strategy than the Dinaric Ecoregion. Annual shuttle species (*Physcomitrium eurystomum*, *Ph. patens*, *Ph. sphaericum*, *Riccia cavernosa*, *R. fluitans*, *R. frostii*, *R. glauca*, *R. rhenana*, *Ricciocarpos natans*) are short-lived species with high reproductive effort, i.e. producing numerous spores (During 1979, Kürschner 2004). These ephemeral terricolous species are successful on the margins of lowland slow-flowing or stagnant waters, where they can germinate on deposited, fine-textured sediments and finish their whole life cycle within a brief period when water withdraws from gently sloping margins. This period is too short to enable perennial bryophytes to colonise and assume dominance, while ephemeral species thrive before the water level rises again in autumn (Furness and Hall 1981, Hugonnot 2005, Bijlsma et al. 2012). These species are considered relatively rare and threatened in Europe, for example, *Physcomitrium eurystomum* and *Ph. sphaericum* are vulnerable (VU) on the European level (Hodgetts et al. 2019), while their habitats are protected as NATURA 2000 habitats.

Besides the primary intention of the WFD to ensure water quality assessment on the national level, the implementation of monitoring in Croatia yielded a significant amount of new national bryophyte records. Through five years of intensive field surveys of Croatian freshwaters, as many as eight bryophyte species were found as new for national bryoflora: *Fissidens fontanus* (Alegro et al. 2019, Šegota et al. 2019), *Dichodontium flavescens*, *Ricciocarpos natans* (Alegro et al. 2019), *Physcomitrium eurystomum* (Rimac et al. 2019b), *Physcomitrium sphaericum* (*Ellis* et al. *2020*), *Riccia rhenana* (Ellis et al. 2021a) and *Bryum klinggraeffii* and *Philonotis marchica* (Rimac et al. 2021). In addition, several rare or doubtful species with only old historical data have been confirmed (*Fissidens arnoldii*, *Hygroamblystegium fluviatile*, *Leptobryum pyriforme*, *Physcomitrium patens*, *Riccia cavernosa*, *R. frostii*, *R. glauca*) within this study.

The added value of our study is that, along with watercourses, we examined standing water bodies for their bryoflora as well. Altogether, nine natural lakes and 36 artificial or heavily-modified standing water bodies were studied. Bryophytes were found at five lakes and 12 artificial or heavily-modified standing water bodies. Most of the 24 recorded bryophyte species occupied shallow waters, lacustrine drawdown zones and moist riparian habitats. However, in our study, scattered populations of the rare species in the Croatian flora, *Fissidens fontanus*, were found at a depth of 2.5 m in the riverine mesotrophic Lake Visovac (the Krka River, the Dinaric–Mediterranean Subecoregion) and large colonies of *Drepanocladus aduncus* at 4 to 6 m deep water in the mesotrophic Ponikve Reservoir (the Island of Krk, the Dinaric–Mediterranean Subecoregion). Although the majority of bryophyte species cannot inhabit deep waters and they maintain terrestrial reproduction features (Vitt et al. 1986), mosses can be found within the macrophyte vegetation of lakes, even at the lower depth limit, sometimes mixed with charophytes or vascular plants (Chambers and Kalff 1985, Riis and Sand-Jensen 2017). In temperate regions, mosses were found to be particularly abundant in oligotrophic lakes (Raven 1988, Arts 1990, Srivastava et al. 1995), primarily because of the sufficient amount of light penetrating to the deeper zones of clear lakes. Although we found several truly aquatic bryophytes in our lakes and although the majority of the surveyed lakes in the Dinaric Ecoregion were oligotrophic, bryophytes were not dominant in any of the lakes surveyed. On the contrary, oligotrophic lakes were often inhabited by charophytes, which flourished in karstic lakes with basic and alkaline water (Mihaljević et al. 2020).

Conclusions

Bryophytes are an important part of freshwater biodiversity in Croatia, inhabiting a wide variety of ecological niches associated with running and standing waters. The diversity of aquatic and semi-aquatic species is governed by the heterogeneity of different environmental factors, which determine their presence or absence, as well as the community structure. Our research revealed a quite high bryophyte diversity in aquatic and semi-aquatic habitats, with substantial differences between particular regions, especially in species richness and composition, as well as in life-form and life strategy spectra. The Water Framework Directive not only improved the assessment of the ecological status of water bodies in Croatia by including the bryophytes as a part of macrophyte vegetation, but it has proven to be a good tool for the detection of rare, neglected or overlooked bryophyte species. This is especially important in regions where the bryophytes are still generally little researched, as in the case of southeast Europe. This study is, therefore, a valuable contribution to the knowledge of freshwater bryophyte diversity of Croatia, as well as of southeast Europe.

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Author contributions

A. Rimac - field research, species identification, data preparation and analysis, manuscript writing

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A. Alegro - field research, species identification, manuscript editing

N. Vuković - field research, manuscript editing

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Supplementary material

Suppl. material 1: Complete list of the freshwater bryoflora of Croatia with distribution data, chorological and life-trait information on the species and altitude and climatological data of the sites. doi

Authors: Rimac, A; Šegota, V; Alegro, A; Vuković, N; Koletić, N.

Data type: Data table

Brief description: Coordinates are given in WGS84 system. Abbreviations: PAN–Pannonian Ecoregion, DIN CON–Dinaric Ecoregion, Continental Subecoregion, DIN MED–Dinaric Ecoregion, Mediterranean Subecoregion; life-forms: At–Aquatic trailing, De–dendroid, Le –lemnoid, Mr–rough mat, Ms–smooth mat, Mt–thalloid mat, St–solitary thalloid, Tf–turf, Ts–scattered turf, Tuft–tuft and We–weft); life strategy: p–perennials, c–colonists, pc–competitive perennials, l–long-lived shuttle, a–annual shuttle, cp–pioneer colonists, Braun-Blanquet cover and abundance classes: r = one individual, + = up to 5 individuals, 1 = up to 50 individuals, 2m = over 50 individuals, 2a = coverage 5–15%, 2b = coverage 15–25%, 3 = 25–50%; 4 = coverage 50–75%; 5 = coverage over 75%.

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Suppl. material 1: Complete list of the freshwater bryoflora of Croatia with distribution data, chorological and life-trait information on the species and altitude and climatological data of the sites.

Table S1(a): Species list with abbreviations, life-trait and chorological information. Abbreviations: life-forms: At–Aquatic trailing, De–dendroid, Le –lemnoid, Mr–rough mat, Ms–smooth mat, Mt–thalloid mat, St–solitary thalloid, Tf–turf, Ts–scattered turf, Tuft–tuft and We–weft); life strategy: p–perennials, c–colonists, pc–competitive perennials, l–long-lived shuttle, a–annual shuttle, cp–pioneer colonists.

Species	Abbreviation	Life strategy	Life-form	Chorotype (major biom)	Chorotype (eatern limit)	Family
Apopellia endiviifolia (Dicks.) Nebel & D.Quandt	Apo end	c	Mt	Southern-temperate	Circumpolar	Pelliaceae
Barbula unguiculata Hedw.	Bar ung	c	Tf	Wide-temperate	Circumpolar	Pottiaceae
Brachythecium mildeanum (Schimp.) Schimp.	Bra mil	p	Mr	Temperate	Circumpolar	Brachytheciaceae
Brachythecium rivulare Schimp.	Bra riv	pc	Mr	Boreo-temperate	Circumpolar	Brachytheciaceae
Brachythecium rutabulum (Hedw.) Schimp.	Bra rut	cp	Mr	Temperate	European	Brachytheciaceae
Brachythecium salebrosum (Hoffm. ex F.Weber et D.Mohr) Schimp.	Bra sal	cp	Mr	Wide-boreal	Circumpolar	Brachytheciaceae
Bryoerythrophyllum recurvirostrum (Hedw.) P.C.Chen	Bry rec	c	Tf	Boreo-temperate	Circumpolar	Pottiaceae
Bryum argenteum Hedw.	Bry arg	c	Tf	Wide-boreal	Circumpolar	Bryaceae
Bryum barnesii J.B. Wood ex Schimp.	Bry bar	c	Tf	Wide-temperate	European	Bryaceae
Bryum dichotomum Hedw.	Bry dic	c	Tf	Wide-temperate	European	Bryaceae
Bryum klinggraeffii Schimp.	Bry kli	ce	Tf	Temperate	European	Bryaceae
Ptychostomum pseudotriquetrum (Hedw.) J.R.Spence & H.P.Ramsay ex Holyoak & N.Pedersen	Pty pse	pc	Tf	Wide-boreal	Circumpolar	Bryaceae
Bryum ruderale Crundw. & Nyholm	Bry rud	ce	Tf	Temperate	European	Bryaceae
Calliergonella cuspidata (Hedw.) Loeske	Cal cus	pc	We	Temperate	Circumpolar	Pylaisiaceae
Chiloscyphus pallescens (Ehrh.) Dumort.	Chi pal	pc	Tf	Boreo-temperate	Circumpolar	Lophocoleaceae
Chiloscyphus polyanthos (L.) Corda	Chi pol	pc	At	Boreo-temperate	Circumpolar	Lophocoleaceae
Cinclidotus aquaticus (Hedw.) Bruch & Schimp.	Cin aqu	c	At	Southern-temperate	European	Pottiaceae
Cinclidotus fontinaloides (Hedw.) P.Beauv.	Cin fon	c	At	Southern-temperate	European	Pottiaceae
Cinclidotus riparius (Host ex Brid.) Arn.	Cin rip	c	At	Temperate	Eurosiberian	Pottiaceae
Conocephalum salebrosum Szweyk., Buczk. & Odrzyk.	Con sal	l	Mt	Boreo-temperate	Circumpolar	Conocephalaceae
Cratoneuron filicinum (Hedw.) Spruce	Cra fil	pc	We	Wide-temperate	Circumpolar	Amblystegiaceae

Species	Abbreviation	Life strategy	Life-form	Chorotype (major biom)	Chorotype (eatern limit)	Family
Dichodontium flavescens (Dicks.) Lindb.	Dic fla	c	Tf	Boreal-montane	European	Amphidiaceae
Dichodontium pellucidum (Hedw.) Schimp.	Dic pel	cp	Tf	Boreo-arctic montane	Circumpolar	Amphidiaceae
Dicranella varia (Hedw.) Schimp.	Dic var	ce	Tf	Boreo-temperate	Circumpolar	Amphidiaceae
Didymodon fallax (Hedw.) R.H.Zander	Did fal	c	Tf	Southern-temperate	Circumpolar	Pottiaceae
Didymodon insulanus (De Not.) M.O.Hill	Did ins	c	Tf	Southern-temperate	Eurasian	Pottiaceae
Didymodon luridus Hornsch.	Did lur	c	Tf	Mediterranean-Atlantic	Suboceanic	Pottiaceae
Didymodon spadiceus (Mitt.) Limpr.	Did spa	c	Tf	Temperate	European	Pottiaceae
Didymodon tophaceus (Brid.) Lisa	Did top	c	Tf	Southern-temperate	European	Pottiaceae
*Drepanocladus aduncu*s (Hedw.) Warnst.	Dre adu	p	We	Boreo-temperate	Circumpolar	Amblystegiaceae
Eucladium verticillatum (With.) Bruch & Schimp.	Euc ver	ps	Tuft	Southern-temperate	European	Pottiaceae
Fissidens adianthoides Hedw.	Fis adi	c	Tuft	Boreo-temperate	Circumpolar	Fissidentaceae
Fissidens arnoldii R.Ruthe	Fis arn	s	Tf	Temperate	Circumpolar	Fissidentaceae
Fissidens crassipes Wilson ex Bruch & Schimp.	Fis cra	l	Tf	Southern-temperate	European	Fissidentaceae
Fissidens fontanus (Bach.Pyl.) Steud.	Fis fon	c	At	Temperate	European	Fissidentaceae
Fissidens gracilifolius Brugg.-Nann. & Nyholm	Fis gra	c	Ts	Southern-temperate	European	Fissidentaceae
Fissidens pusillus (Wilson) Milde	Fis pus	ce	Ts	Southern-temperate	European	Fissidentaceae
Fissidens taxifolius Hedw.	Fis tax	c	Tf	Southern-temperate	European	Fissidentaceae
Fontinalis antipyretica Hedw.	Fon ant	p	At	Boreo-temperate	Circumpolar	Fontinalaceae
Fontinalis hypnoides Hartm. var. *duriaei* (Schimp.) Kindb.	Fon hyp	p	At	Wide-temperate	Circumpolar	Fontinalaceae
Funaria hygrometrica Hedw.	Fun hyg	f	Tuft	Wide-temperate	Circumpolar	Funariaceae
Gymnostomum aeruginosum Sm.	Gym aer	cp	Tf	Boreo-temperate	Circumpolar	Pottiaceae
Hygroamblystegium fluviatile (Hedw.) Loeske	Hyg flu	p	Mr	Boreo-temperate	European	Amblystegiaceae
Hygroamblystegium humile (P.Beauv.) Vanderp., Goffinet & Hedenäs	Hyg hum	p	Mr	Temperate	Circumpolar	Amblystegiaceae
Hygroamblystegium tenax (Hedw.) Jenn.	Hyg ten	P	Mr	Temperate	Circumpolar	Amblystegiaceae
Hygroamblystegium varium (Hedw.) Mönk.	Hyg var	p	Mr	Temperate	Circumpolar	Amblystegiaceae
Hygrohypnum luridum (Hedw.) Jenn.	Hyg lur	p	Mr	Boreo-temperate	Circumpolar	Amblystegiaceae

Species	Abbreviation	Life strategy	Life-form	Chorotype (major biom)	Chorotype (eatern limit)	Family
Hymenostylium recurvirostrum (Hedw.) Dixon	Hym rec	c	Tf	Boreo-temperate	Circumpolar	Pottiaceae
Jungermannia atrovirens Dumort.	Jun atr	c	Ms	Wide-boreal	European	Jungermanniaceae
Leptobryum pyriforme (Hedw.) Wilson	Lep pyr	f	Tuft	Wide-temperate	Circumpolar	Meesiaceae
Leptodictyum riparium (Hedw.) Warnst.	Lep rip	p	Mr	Temperate	Circumpolar	Amblystegiaceae
Leskea polycarpa Hedw.	Les pol	p	Mr	Temperate	Circumpolar	Leskeaceae Schimp.
Lophocolea bidentata (L.) Dumort.	Lop bid	pc	We	Temperate	European	Lophocoleaceae
Lunularia cruciata (L.) Dumort. ex Lindb.	Lun cru	p	Mt	Mediterranean-Atlantic	Suboceanic	Lunulariaceae
Marchantia polymorpha L.	Mar pol	c	Mt	Boreo-temperate	Circumpolar	Marchantiaceae
Mnium marginatum (Dicks.) P.Beauv.	Mni mar	l	Tf	Boreo-temperate	Circumpolar	Mniaceae
Oxyrrhynchium hians (Hedw.) Loeske	Oxy hia	cp	Mr	Temperate	Circumpolar	Brachytheciaceae
Oxyrrhynchium schleicheri (R.Hedw.) Röll	Oxy sch	p	Mr	Mediterranean-Atlantic	Suboceanic	Brachytheciaceae
Oxyrrhynchium speciosum (Brid.) Warnst.	Oxy spe	p	Mr	Temperate	European	Brachytheciaceae
Palustriella commutata (Hedw.) Ochyra	Pal com	pc	We	Boreo-temperate	Eurosiberian	Amblystegiaceae
Palustriella falcata (Brid.) Hedenäs	Pal fal	pc	We	Boreo-temperate	Circumpolar	Amblystegiaceae
Pellia neesiana (Gottsche) Limpr.	Pel nee	c	Mt	Boreo-temperate	Circumpolar	Pelliaceae
Philonotis marchica (Hedw.) Brid.	Phi mar	l	Tf	Southern-temperate	European	Bartramiaceae
Physcomitrium patens (Hedw.) Mitt.	Phy pat	a	Ts	Temperate	Eurosiberian	Funariaceae
Physcomitrium eurystomum Sendtn.	Phy eur	a	Tf	Temperate	Eurasian	Funariaceae
Physcomitrium sphaericum (C.F.Ludw. ex Schkur.) Brid.	Phy sph	a	Tf	Temperate	Eurasian	Funariaceae
Plagiomnium affine (Blandow ex Funck) T.J.Kop.	Pla aff	pc	Ms	Temperate	European	Mniaceae
Plagiomnium elatum (Bruch et Schimp.) T.J.Kop.	Pla ela	pc	Tf	Boreo-temperate	European	Mniaceae
Plagiomnium ellipticum (Brid.) T.J.Kop.	Pla ell	pc	Tf	Boreo-arctic montane	Circumpolar	Mniaceae
Plagiomnium undulatum (Hedw.) T.J.Kop.	Pla und	pc	Tf	Temperate	European	Mniaceae
Pohlia melanodon (Brid.) A.J.Shaw	Poh mel	c	Tf	Southern-temperate	Circumpolar	Mniaceae
Rhizomnium punctatum (Hedw.) T.J.Kop.	Rhi pun	l	Tf	Boreo-temperate	Circumpolar	Mniaceae
Rhynchostegiella curviseta (Brid.) Limpr.	Rhy cur	ps	Ms	Mediterranean-Atlantic	Oceanic	Brachytheciaceae

Species	Abbreviation	Life strategy	Life-form	Chorotype (major biom)	Chorotype (eatern limit)	Family
Rhynchostegiella teneriffae (Mont.) Dirkse & Bouman	Rhy ten	ps	Ms	Mediterranean-Atlantic	Suboceanic	Brachytheciaceae
Rhynchostegium riparioides (Hedw.) Cardot	Rhy rip	p	Ms	Southern-temperate	Circumpolar	Brachytheciaceae
Riccia cavernosa Hoffm.	Ric cav	a	St	Temperate	Circumpolar	Ricciaceae
Riccia fluitans L.	Ric flu	a	Le	Southern-temperate	Circumpolar	Ricciaceae
Riccia frostii Austin	Ric fro	a	St	Southern-temperate	Circumpolar	Ricciaceae
Riccia glauca L.	Ric gla	a	St	Southern-temperate	Circumpolar	Ricciaceae
Riccia rhenana Lorb. ex Müll.Frib.	Ric rhe	a	Le	Temperate	European	Ricciaceae
Ricciocarpos natans (L.) Corda	Ric nat	a	Le	Southern-temperate	Circumpolar	Ricciaceae
Thamnobryum alopecurum (Hedw.) Gangulee	Tha alo	p	De	Temperate	European	Neckeraceae
Trichostomum crispulum Bruch	Tri cri	p	Tf	Mediterranean-Atlantic	Suboceanic	Pottiaceae

Table S1(b): Cover and abundance of freshwater bryophytes at surveyed sites estimated using Braun-Blanquet classes.

Site Id	Watercourse	Apo end	Bar ung	Bra mil	Bra riv	Bra rut	Bra sal	Bry rec	Bry arg	Bry bar	Bry dic	Bry kli	Pty pse	Bry rud	Cal cus	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Con sal	Cra fil
1.	Delnički potok																	2a	1	2m		1
2.	Kosteljina		+						+		+										1	1
3.	Kupa																	3	2m	2m		
4.	Kupa																	3	2m	2m		+
5.	Kupčina																		+	+		
6.	Sušica																					+
7.	Tomašnica																					
8.	Perna																					
9.	Rogstrug																					
10.	Mrežnica																		1			
11.	Batina																					
12.	Bednja																					
13.	Rakovnica																					
14.	Crna Rijeka																					2a
15.	Dobra																		1	1		
16.	Horvatska								+													
17.	Ivanec																					
18.	Jaruga																					
19.	Korana	+											1									
20.	Korana																					
21.	Korana																					
22.	Korana	1																1		2m		2m
23.	Krapina																					
24.	Krapina																					
25.	Krapina																					
26.	Moštanica																					
27.	Reka II																					
28.	Ribnik																			+		
29.	Utinja 1																					
30.	Žitomirka																					
31.	Boščak	2a																				
32.	Trebež																					
33.	Ilova																					
34.	Rajić																					
35.	Suvova					+																
36.	Šumetlica																					
37.	Korana																					
38.	Bistra III																					
39.	Voća																					
40.	Žarovnica																					
41.	Mirna																					
42.	Mirna																					
43.	Bračana																					
44.	Stara Mirna																					
45.	Raša																			1		
46.	Pazinčica																					
47.	Orljava																					
48.	Una																			1		
49.	Baščica																		1			
50.	Bregana																					2m
51.	Dretulja				+												+	2a				2a
52.	Dretulja																2a					
53.	Jaruga 3												1									
54.	Jaruga 2																					2a
55.	Kupčina	+																	+			+
56.	Velika Rijeka					1																1
57.	Rudarska Gradna					1																1
58.	Rudarska Gradna																					
59.	Gradna																					
60.	Lipovečka Gradna				1																	2m
61.	Svinica												2m									
62.	Bregana					1																2m
63.	Pazinčica																					
64.	Slapnica	+	+																			+

Site Id	Watercourse	Dic fla	Dic pel	Dic var	Did fal	Did ins	Did lur	Did spa	Did top	Dre adu	Euc ver	Fis adi	Fis arn	Fis cra	Fis fon	Fis gra	Fis pus	Fis tax	Fon ant	Fon hyp	Fun hyg	Gym aer
1.	Delnički potok																		1			
2.	Kosteljina													1							+	
3.	Kupa													1								
4.	Kupa													+					+			
5.	Kupčina																		2m			
6.	Sušica																					
7.	Tomašnica																					
8.	Perna											+							+			
9.	Rogstrug																					
10.	Mrežnica																		2m			
11.	Batina																					
12.	Bednja																		+			
13.	Rakovnica																					
14.	Crna Rijeka																					
15.	Dobra																		2b			
16.	Horvatska																					
17.	Ivanec																					
18.	Jaruga																		1			
19.	Korana								2a		1										1	1
20.	Korana																		1			
21.	Korana																		+			
22.	Korana								2b					1								
23.	Krapina																					
24.	Krapina													2a								
25.	Krapina																					
26.	Moštanica																					
27.	Reka II																		1			
28.	Ribnik																					
29.	Utinja 1																		2m			
30.	Žitomirka																					
31.	Boščak																					
32.	Trebež																					
33.	Ilova			+																		
34.	Rajić			+																		
35.	Suvova																					
36.	Šumetlica																1					
37.	Korana																		2a			
38.	Bistra III																					
39.	Voća																					
40.	Žarovnica																		+			
41.	Mirna																		2m			
42.	Mirna																		1			
43.	Bračana																		1			
44.	Stara Mirna																		1			
45.	Raša																		+			
46.	Pazinčica																		+			
47.	Orljava																					
48.	Una																		2m			
49.	Baščica																		2a			
50.	Bregana													2m					2m			
51.	Dretulja																					
52.	Dretulja																		2a			
53.	Jaruga 3								1													
54.	Jaruga 2																					
55.	Kupčina													1					+			
56.	Velika Rijeka																					
57.	Rudarska Gradna																					
58.	Rudarska Gradna																					
59.	Gradna																					
60.	Lipovečka Gradna																					
61.	Svinica																					
62.	Bregana						1							2m					1			
63.	Pazinčica																					
64.	Slapnica													1								

Site Id	Watercourse	Hyg flu	Hyg hum	Hyg ten	Hyg var	Hyg lur	Hym rec	Jun atr	Lep pyr	Lep rip	Les pol	Lop bid	Lun cru	Mar pol	Mni mar	Oxy hia	Oxy sch	Oxy spe	Pal com	Pal fal	Pel nee	Phi mar
1.	Delnički potok				1					1				+								
2.	Kosteljina									2m												
3.	Kupa					2m																
4.	Kupa																	+				
5.	Kupčina																					
6.	Sušica																					
7.	Tomašnica									1												
8.	Perna																					
9.	Rogstrug									1												
10.	Mrežnica																					
11.	Batina									+												
12.	Bednja																					
13.	Rakovnica																					
14.	Crna Rijeka																					
15.	Dobra									1												
16.	Horvatska																					
17.	Ivanec									+												
18.	Jaruga									1												
19.	Korana																			2m		
20.	Korana																					
21.	Korana																					
22.	Korana																					
23.	Krapina									1												
24.	Krapina									2b												
25.	Krapina									2a												
26.	Moštanica									1												
27.	Reka II									1												
28.	Ribnik																					
29.	Utinja 1									+												
30.	Žitomirka									2m									2m			
31.	Boščak																					
32.	Trebež																					
33.	Ilova												+									
34.	Rajić																				+	
35.	Suvova																					
36.	Šumetlica																					
37.	Korana																					
38.	Bistra III																					
39.	Voća									5												
40.	Žarovnica																					
41.	Mirna									2a												
42.	Mirna																					
43.	Bračana																					
44.	Stara Mirna																					
45.	Raša																					
46.	Pazinčica																					
47.	Orljava																					
48.	Una									2m												
49.	Baščica																					
50.	Bregana									1												
51.	Dretulja																					
52.	Dretulja																					
53.	Jaruga 3																					
54.	Jaruga 2																					
55.	Kupčina				+					2m				+								
56.	Velika Rijeka																	r				
57.	Rudarska Gradna													+								
58.	Rudarska Gradna									3				+								
59.	Gradna									2m				1								
60.	Lipovečka Gradna													1								
61.	Svinica																					
62.	Bregana													2m								
63.	Pazinčica									2b												
64.	Slapnica									+												

Site Id	Watercourse	Phy pat	Phy eur	Phy sph	Pla aff	Pla ela	Pla ell	Pla und	Poh mel	Rhi pun	Rhy cur	Rhy ten	Rhy rip	Ric cav	Ric flu	Ric fro	Ric gla	Ric rhe	Ric nat	Tha alo	Tri cri
1.	Delnički potok												1								
2.	Kosteljina												2m								
3.	Kupa												2a								
4.	Kupa												2a								
5.	Kupčina																				
6.	Sušica																				
7.	Tomašnica																				
8.	Perna																				
9.	Rogstrug																				
10.	Mrežnica												1								
11.	Batina																				
12.	Bednja																				
13.	Rakovnica																		1		
14.	Crna Rijeka												1								
15.	Dobra												1								
16.	Horvatska																				
17.	Ivanec																				
18.	Jaruga																				
19.	Korana												2a								
20.	Korana																				
21.	Korana																				
22.	Korana												2b								
23.	Krapina																				
24.	Krapina												2b								
25.	Krapina																				
26.	Moštanica																				
27.	Reka II																				
28.	Ribnik																				
29.	Utinja 1																				
30.	Žitomirka												2m								
31.	Boščak																				
32.	Trebež	2m												2m							
33.	Ilova	+							+				1								
34.	Rajić	+							+												
35.	Suvova																				
36.	Šumetlica												1								
37.	Korana																				
38.	Bistra III														1						
39.	Voća																				
40.	Žarovnica																				
41.	Mirna																				
42.	Mirna																				
43.	Bračana																				
44.	Stara Mirna																				
45.	Raša																				
46.	Pazinčica																				
47.	Orljava													1							
48.	Una												1								
49.	Baščica												1								
50.	Bregana												2m								
51.	Dretulja							+					4								
52.	Dretulja																				
53.	Jaruga 3																				
54.	Jaruga 2												2a								
55.	Kupčina												1								
56.	Velika Rijeka																				
57.	Rudarska Gradna												2m								
58.	Rudarska Gradna																				
59.	Gradna																				
60.	Lipovečka Gradna																				
61.	Svinica												2m								
62.	Bregana												2m								
63.	Pazinčica												2b								
64.	Slapnica												1								

Site Id	Watercourse	Apo end	Bar ung	Bra mil	Bra riv	Bra rut	Bra sal	Bry rec	Bry arg	Bry bar	Bry dic	Bry kli	Pty pse	Bry rud	Cal cus	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Con sal	Cra fil	Dic fla	Dic pel	Dic var	Did fal	Did ins	Did lur	Did spa	Did top	Dre adu	Euc ver	Fis adi	Fis arn	Fis cra	Fis fon	Fis gra	Fis pus	Fis tax	Fon ant	Fon hyp	Fun hyg	Gym aer	Hyg flu	Hyg hum	Hyg ten	Hyg var	Hyg lur	Hym rec	Jun atr	Lep pyr	Lep rip	Les pol	Lop bid	Lun cru	Mar pol	Mni mar	Oxy hia	Oxy sch	Oxy spe	Pal com	Pal fal	Pel nee	Phi mar	Phy pat	Phy eur	Phy sph	Pla aff	Pla ela	Pla ell	Pla und	Poh mel	Rhi pun	Rhy cur	Rhy ten	Rhy rip	Ric cav	Ric flu	Ric fro	Ric gla	Ric rhe	Ric nat	Tha alo	Tri cri
65.	Subocka	+		+	+	+																1									+																									1		+					1									+												
66.	Una	2b															2a	4	2m			2b																		2m														1																						2m								
67.	Una	+																							+														r	2b												1	r		+													r				+				+								
68.	Izvor Krke																		1																					2b												+																								3								
69.	Cetina																2m	2m				1																																								3														+								
70.	Cetina																	2m																						3																						2m																						
71.	Dubračana																																		1					1																																				1								
72.	Kamešnica																																																																													+								
73.	Krka																																							2a																																													
74.	Krupa	3			+												3					2m																		3																																				1								
75.	Krupa	3															4					2m																		4																																												
76.	Krupa																+																							3																																												
77.	Ombla																																																																													2m								
78.	Rumin																																							2a																																												
79.	Una																																		2m					3												1										2m														2b								
80.	Vojskova																2a	1																						2m																																				2m								
81.	Vrba	+																				+																																																																
82.	Zduški potok																	1																						1																																												
83.	Globornica																																							2m																																												
84.	Vitunjčica																	2b		2a																				2a												+																																
85.	Mačavarina Draga																		2a																																																									2a								
86.	Bistrica 1																		2m			2a																		2b																																				2a								
87.	Munjava																			+																				1												2m																								2a								
88.	Munjava																																							2m																																												
89.	Butižnica	1																3		1		2a			+					2m					1					2b																																				2a								
90.	Suha Ričina Baščanska																		+	+																																																																
91.	Zrmanja																														+									+																				+																+								
92.	Zrmanja																		+																					2m																																												
93.	Baščica																		1											1					2m					2m																																				2m								
94.	Potkoš																																							2m						1						2m	1																																	
95.	Cetina																																							2m										1																										2a								
96.	Bistra																																																																																			2a		
97.	Kanal Halašica																																																																															2a						
98.	Kanal Vl.																																																																															2a						
99.	Drava																																							+																																												
100.	Curak																	2b																																																										2a								
101.	Curak																		2a																							+																																						2a								
102.	Suvaja	+																																																																																				
103.	Cetina																				r																			2a																																				2m								
104.	Krka	1																																						2a																																												
105.	Kanal Gacka																																							2b																																												
106.	Odvodni kanal HE Orlovac																		+																																																																			
107.	Mirna																																																			1																																
108.	Butiznica																																							2m																																				+								
109.	Zvizda	2m																	1			2a													+																																											1								
110.	Zvizda	+																	+			+																																																																
111.	Ričica	2a											1						2m	2m												2a	2m		2m					2m										1																										2a								
112.	Dubračina																																																																													1								
113.	Dubračina																		2m	2a																																																										2a								
114.	Obuhvatni kanal Mufrin																																							2b																																												
115.	Gusić																	4	2b																																																																		
116.	Dubračina																		2a			2m																		1																																				2m								
117.	Butižnica																					1																		3										1											1															1								
118.	Šumetlica				2m																1																	+								+										+				+																+								
119.	Vrbova																																																			3																																
120.	Kutjevačka rijeka																																																			+																																
121.	Kanal Bistra			+					+			+																			+																				+														+														+				+			
122.	Skočinovac																																																																+							+												
123.	Vetovka																																		1											1						1																								1								
124.	Kaptolka																				1																															1								1												1												
125.	Peranački potok																																																			2a																																
126.	Peranački potok												+									1			+																											1				+				+			2m									1												
127.	Garešnica			+					+			+																																																							+										+		+				
128.	Jovača																																																			+																				+												

Site Id	Watercourse	Apo end	Bar ung	Bra mil	Bra riv	Bra rut	Bra sal	Bry rec	Bry arg	Bry bar	Bry dic	Bry kli	Pty pse	Bry rud	Cal cus	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Con sal	Cra fil	Dic fla	Dic pel	Dic var	Did fal	Did ins	Did lur	Did spa	Did top	Dre adu	Euc ver	Fis adi	Fis arn	Fis cra	Fis fon	Fis gra	Fis pus	Fis tax	Fon ant	Fon hyp	Fun hyg
129.	Velika																																										
130.	Brestača																																										
131.	Veliki Strug																																										
132.	Javošnica																																								1	
133.	Čatlan																																										
134.	Sutla																					2a																1					1		
135.	Posalitva																																								+		
136.	Matica 1																																								2m		
137.	Krbava																					1																					
138.	Pazinčica																				1	2b								1							2m							
139.	Cetina																																								2m		
140.	Jadro	+																	+	1	2a		1													2b					1		
141.	Žrnovnica																			3				2a																			2m		
142.	Cetina																																								+		
143.	Krčić																			2a				1																					
144.	Krka																																									1	
145.	Vrljika																																								2m		
146.	Kopačica																																								+		
147.	Petrinjčica																					+															+							
148.	Došnica	+																+					2m							2m					+						+
149.	Krka																																								2b		
150.	Zelina																																										
151.	Kupa																																								1		
152.	Kupa										+												2b		2a		+																		+		
153.	Kupa																				+	+																					+		
154.	Petrinjčica												+				1				+		2m	2m																2m	+			
155.	Golinja						2m							1			+					2m	2m																			2a		
156.	Kremešnica												1				1								1																1		2m		
157.	Rečica																																										
158.	Kravaršćica																	1					1	1																		1			
159.	Roženica												1			1																		+									
160.	Trepča																					1																2a				2m		
161.	Trepča												+						2b																		1				1		
162.	Glina																							+																		+		
163.	Kupčina																																										
164.	Reka 2																																										
165.	Korana					1												2b	1	2m		2a				+										2a					1		+
166.	Korana																																								2m		
167.	Brusovača																+																					1		2m		
168.	Slunjčica	1														1	3	1	2m		4																					
169.	Mrežnica																				+																						2m		
170.	Zagorska Mrežnica							2m									2b				4	2a												2m											
171.	Žumberačka reka	+				+																+													+									
172.	Dobra	1			+								1		+		1	1	1	1		1														+					2m		
173.	Gornja Dobra																			1		+																						1		
174.	Ribnjak	+												1				2a	1	1			1																				2m		
175.	Trebinja												+		+		+				+													+									
176.	Ruševica																																								1		
177.	Krapina																																				2a						
178.	Reka 1																					1																			1		
179.	Presečno																																										
180.	Kotoripski kanal																																										
181.	Gliboki potok																								+																	
182.	Kupa	+										+			+			2m	2m	+	+												+					2m		
183.	Kupa	+			2m	1									+		+	2a	2m	2a		2m	1	1		1			1					1					2m		
184.	Kupa	+				+							+				2m	2b	2m	2m	+	2a	1			+			+					1							
185.	Kupica	1															2m	3	1	2b		1					+								+					+		
186.	Curak	+			+			+							+			2m	1	+	+	2m	1			1			+						+							
187.	Čabranka	1		+	1													2m	+	1			2m		+		1									2m					+		
188.	Velika Belica	2m												2a		+				1		1	+				+						+			+					+		
189.	Gerovčica					1									+							2m																				
190.	Čedanj		+	+	1	+								+			2m			+	+	+	1	1												+							
191.	Gacka																	2m		1			1																			2a		
192.	Rječina				1														2b	2a	2m		1																					

Site Id	Watercourse	Gym aer	Hyg flu	Hyg hum	Hyg ten	Hyg var	Hyg lur	Hym rec	Jun atr	Lep pyr	Lep rip	Les pol	Lop bid	Lun cru	Mar pol	Mni mar	Oxy hia	Oxy sch	Oxy spe	Pal com	Pal fal	Pel nee	Phi mar	Phy pat	Phy eur	Phy sph	Pla aff	Pla ela	Pla ell	Pla und	Poh mel	Rhi pun	Rhy cur	Rhy ten	Rhy rip	Ric cav	Ric flu	Ric fro	Ric gla	Ric rhe	Ric nat	Tha alo	Tri cri
129.	Velika										+																																	
130.	Brestača										+																				+											
131.	Veliki Strug										+																													+			
132.	Javošnica										1																															
133.	Čatlan										+																								2m								
134.	Sutla																																											
135.	Posalitva										2b																															
136.	Matica 1										2b																															
137.	Krbava																																		1								
138.	Pazinčica										1																								3							2m	
139.	Cetina																																											
140.	Jadro																																		2a								
141.	Žrnovnica										2b																								2a								
142.	Cetina																																											
143.	Krčić																																		2a								
144.	Krka																																											
145.	Vrljika																																											
146.	Kopačica																																											
147.	Petrinjčica										+																															
148.	Došnica																					2m											1											
149.	Krka																																											
150.	Zelina										2m																															
151.	Kupa										+								+																							
152.	Kupa																																		3								
153.	Kupa																																											
154.	Petrinjčica			+							2m				+		+		+			+								+				1								
155.	Golinja										2m						+						2a							+	+		+			2m								
156.	Kremešnica					+					2m						+																			2m								
157.	Rečica										+																															
158.	Kravaršćica					+					1						1		+			1						+		+	+												
159.	Roženica																		1					1									+											
160.	Trepča										2m																															
161.	Trepča										2a																								1								
162.	Glina										3				+																				2b								
163.	Kupčina																																					1						
164.	Reka 2										+																															
165.	Korana															1		+																		2b							+	
166.	Korana										1																															
167.	Brusovača		+								+																															
168.	Slunjčica																																											
169.	Mrežnica																																											
170.	Zagorska Mrežnica					1																																					
171.	Žumberačka reka																	+			+														+								
172.	Dobra										1				+		+													+					2m								
173.	Gornja Dobra																																		1								
174.	Ribnjak																				1														2m								
175.	Trebinja																	+												+		+										
176.	Ruševica										+																															
177.	Krapina																																											
178.	Reka 1																																		1								
179.	Presečno										+																															
180.	Kotoripski kanal																																					+						
181.	Gliboki potok															+															+											
182.	Kupa										2a		r		+	+			+		+									+					2m								
183.	Kupa						2m		1						+						1														2a								
184.	Kupa								+						+						2a											+	+	+	2b								
185.	Kupica															+	+		+		2m									+			+	2b							1	
186.	Curak				+											+															+						2a							+	
187.	Čabranka						1									1	1														1				+	2m								
188.	Velika Belica						2a		2a						+								+								+				2m								+
189.	Gerovčica										1																			+					+								
190.	Čedanj								2m							+													+					2m								
191.	Gacka																																											
192.	Rječina																																		2m								

Site Id	Watercourse	Apo end	Bar ung	Bra mil	Bra riv	Bra rut	Bra sal	Bry rec	Bry arg	Bry bar	Bry dic	Bry kli	Pty pse	Bry rud	Cal cus	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Con sal	Cra fil	Dic fla	Dic pel	Dic var	Did fal	Did ins	Did lur	Did spa
193.	Rječina				1													2b	2a	1		2m							
194.	Rječina										2m							+	2m	2m									
195.	Joševica	2m														2m						2a							
196.	Rumin																												
197.	Mislina																												
198.	Kobilica	2m											1					+		+		2m							
199.	Zrmanja	1											+						1			2m				+			
200.	Zrmanja									+			1									1							
201.	Ričica	2m											+						2m	1		1							
202.	Zrmanja	1											1		+				1			1			+				
203.	Krupa	2m														2a		3	1			2m							
204.	Bribišnica																	1	1	+								+	
205.	Vrba	1																				1							
206.	Krka	1															+	1				1							
207.	Butižnica																												
208.	Krka	2m																2a				r							
209.	Kozjak	2m			r								2m									r							
210.	Galovac	r																											
211.	Milanovac	2m			r								2a								1	1							
212.	Sakadaš																								1				
213.	Biljsko jezero																												
214.	Jezero Sabljaci																												
215.	Jezero Sabljaci														2m														
216.	Akumulacija Golubić												1																
217.	Akumulacija Golubić												1							1									
218.	Akumulacija Prančević																		1	1									
219.	Brljansko jezero	1																				+							
220.	Akumulacija Gusić																												
221.	Akumulacija Gusić																		+										
222.	Akumulacija Razovac																		+										
223.	Prološko blato																												
224.	Akumulacija Ponikve																												
225.	Jezero Oćuša																												
226.	Visovačko jezero																												
227.	Akumulacija Kruščica																												
228.	Ribnjaci Donji Miholjac																												

Site Id	Watercourse	Did top	Dre adu	Euc ver	Fis adi	Fis arn	Fis cra	Fis fon	Fis gra	Fis pus	Fis tax	Fon ant	Fon hyp	Fun hyg	Gym aer	Hyg flu	Hyg hum	Hyg ten	Hyg var	Hyg lur	Hym rec	Jun atr	Lep pyr	Lep rip	Les pol	Lop bid	Lun cru	Mar pol	Mni mar
193.	Rječina																												
194.	Rječina																												
195.	Joševica											2a																1	
196.	Rumin											2a																	
197.	Mislina											+																	
198.	Kobilica	1					+					2m		1														+	
199.	Zrmanja	+		1			1															+							
200.	Zrmanja	2m		2a			+																						
201.	Ričica			+		2m	2m					1										+							
202.	Zrmanja										+	2a																	
203.	Krupa			+			1					3																2m	
204.	Bribišnica	1	1				2b																						
205.	Vrba																												
206.	Krka											2b												+					
207.	Butižnica											2m																	
208.	Krka								r			r																	
209.	Kozjak			2b					r												2a								
210.	Galovac			r																	3								
211.	Milanovac																				2b								
212.	Sakadaš																							1	+				
213.	Biljsko jezero																						2m						
214.	Jezero Sabljaci											2m																	
215.	Jezero Sabljaci		2m									1																	
216.	Akumulacija Golubić						1					1																	
217.	Akumulacija Golubić						1					2m																	
218.	Akumulacija Prančević																								+				
219.	Brljansko jezero			+					+			3												1					
220.	Akumulacija Gusić											+																	
221.	Akumulacija Gusić											1																	
222.	Akumulacija Razovac										+																		
223.	Prološko blato		1																										
224.	Akumulacija Ponikve		2a																										
225.	Jezero Oćuša											1																	
226.	Visovačko jezero							2m					2m																
227.	Akumulacija Kruščica																												
228.	Ribnjaci Donji Miholjac																												

Site Id	Watercourse	Oxy hia	Oxy sch	Oxy spe	Pal com	Pal fal	Pel nee	Phi mar	Phy pat	Phy eur	Phy sph	Pla aff	Pla ela	Pla ell	Pla und	Poh mel	Rhi pun	Rhy cur	Rhy ten	Rhy rip	Ric cav	Ric flu	Ric fro	Ric gla	Ric rhe	Ric nat	Tha alo	Tri cri
193.	Rječina																			2m								
194.	Rječina																											
195.	Joševica																											
196.	Rumin																											
197.	Mislina																					+						
198.	Kobilica																			1								
199.	Zrmanja				1															1							+	
200.	Zrmanja																			+								
201.	Ričica																			2m		+						
202.	Zrmanja		1			1										+				2a								
203.	Krupa															+				2a								
204.	Bribišnica																			1								
205.	Vrba																											
206.	Krka																			+								
207.	Butižnica																											
208.	Krka				r															3								
209.	Kozjak				4																							
210.	Galovac				2b																							
211.	Milanovac				4																							
212.	Sakadaš								1																			
213.	Biljsko jezero								2m	2m															+			
214.	Jezero Sabljaci																											
215.	Jezero Sabljaci																											
216.	Akumulacija Golubić																											
217.	Akumulacija Golubić																											
218.	Akumulacija Prančević																			1								
219.	Brljansko jezero																			1								
220.	Akumulacija Gusić																					1						
221.	Akumulacija Gusić																					+						
222.	Akumulacija Razovac																											
223.	Prološko blato																											
224.	Akumulacija Ponikve																											
225.	Jezero Oćuša																											
226.	Visovačko jezero																											
227.	Akumulacija Kruščica								+												+							
228.	Ribnjaci Donji Miholjac																				+		+					

Table S1(c): Coordinates in WGS84 coordinate system, altitude and climatological data of the sites. Abbreviations: PAN–Pannonian Ecoregion, DIN CON–Dinaric Ecoregion, Continental Subecoregion, DIN MED–Dinaric Ecoregion, Mediterranean Subecoregion.

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m^2)
1.	Delnički potok	watercourse	DIN CON	14.8504	45.4396	239.11	11.05	11.35	2.75	1536.8
2.	Kosteljina	watercourse	PAN	15.7539	46.174	206.77	10.95	20.35	2.85	1061.9
3.	Kupa	watercourse	DIN CON	15.2493	45.4557	161.63	11.45	11.75	3.35	1178.3
4.	Kupa	watercourse	DIN CON	15.3564	45.6453	130.96	11.65	16.75	3.45	1090.6
5.	Kupčina	watercourse	PAN	15.6182	45.6052	114.33	11.75	17.05	3.45	1009.7
6.	Sušica	watercourse	DIN CON	15.0078	45.4243	423.22	9.85	10.25	1.75	1584.7
7.	Tomašnica	watercourse	DIN CON	15.4758	45.5306	119.92	11.75	16.95	3.55	1160.2
8.	Perna	watercourse	PAN	15.9099	45.2668	131.80	11.75	11.95	3.75	1107
9.	Rogstrug	watercourse	PAN	17.2469	45.9993	108.87	11.55	21.25	3.15	780.2
10.	Mrežnica	watercourse	DIN CON	15.4311	45.1952	186.36	11.35	11.65	3.25	1368.8
11.	Batina	watercourse	PAN	16.1595	46.0588	166.06	11.45	19.95	3.25	893.7
12.	Bednja	watercourse	PAN	16.1691	46.241	200.72	11.15	20.55	2.95	950.1
13.	Rakovnica	watercourse	PAN	16.8089	46.3382	135.56	11.35	20.95	3.15	752.3
14.	Crna Rijeka	watercourse	DIN CON	15.6014	44.8434	646.18	9.15	9.65	18.25	1792.5
15.	Dobra	watercourse	DIN CON	15.3556	45.3728	142.04	11.65	11.85	3.55	1285.4
16.	Horvatska	watercourse	PAN	15.7552	46.0752	153.98	11.45	20.95	3.25	1018.7
17.	Ivanec	watercourse	PAN	16.1227	46.0515	161.27	11.45	19.95	3.25	889.3
18.	Jaruga	watercourse	DIN CON	15.2456	45.0312	489.91	10.05	10.45	1.85	1615.6
19.	Korana	watercourse	DIN CON	15.6186	44.9259	400.79	10.25	10.65	2.25	1697.6
20.	Korana	watercourse	DIN CON	15.5952	45.3917	115.36	11.65	11.85	3.55	1160.1
21.	Korana	watercourse	DIN CON	15.5952	45.3917	115.36	11.65	11.85	3.55	1160.1
22.	Korana	watercourse	DIN CON	15.5952	45.3917	115.36	11.65	11.85	3.55	1160.1
23.	Krapina	watercourse	PAN	15.818	45.9345	132.40	11.65	16.95	3.45	1007.1
24.	Krapina	watercourse	PAN	16.2012	46.1048	175.47	11.35	20.85	3.15	919.2
25.	Krapina	watercourse	PAN	15.8228	45.8348	121.52	11.75	16.95	3.35	916.6
26.	Moštanica	watercourse	PAN	16.3571	45.4396	98.67	12.05	12.15	3.85	923.5
27.	Reka II	watercourse	PAN	16.0692	46.0542	158.91	11.55	20.15	3.25	903.1
28.	Ribnik	watercourse	DIN CON	15.3143	45.6091	134.05	11.65	16.85	3.45	1069
29.	Utinja 1	watercourse	PAN	15.694	45.4583	113.42	11.85	11.95	3.55	1048.8
30.	Žitomirka	watercourse	PAN	16.1616	46.0322	165.72	11.35	19.95	3.25	915.9
31.	Boščak - kanal	watercourse	PAN	16.5972	46.429	146.81	11.35	20.85	3.05	778.4

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m^2)
32.	Trebež	watercourse	PAN	16.7737	45.3561	98.52	12.15	12.35	3.95	897.3
33.	Ilova	watercourse	PAN	17.2725	45.6599	136.49	11.65	19.65	3.45	930.9
34.	Rajić	watercourse	PAN	17.1228	45.2973	116.93	12.15	20.25	3.75	879
35.	Suvova	watercourse	DIN MED	16.4105	43.7052	428.27	12.55	8.85	21.45	1211.3
36.	Šumetlica	watercourse	PAN	17.3763	45.3645	397.73	9.95	17.55	2.05	1159.8
37.	Korana	watercourse	DIN CON	15.7409	45.0635	243.70	11.35	11.65	3.35	1269.7
38.	Bistra III	watercourse	PAN	18.648	45.6089	84.20	11.85	21.75	3.15	693.2
39.	Voća	watercourse	PAN	16.1329	46.2516	203.74	11.05	20.55	2.95	937.9
40.	Žarovnica	watercourse	PAN	16.0504	46.2348	216.82	10.95	20.35	2.85	1008.3
41.	Mirna	watercourse	DIN MED	13.7378	45.3575	0.74	14.55	15.15	6.95	1202.2
42.	Mirna	watercourse	DIN MED	13.9389	45.3983	34.25	13.55	13.95	5.85	1409.4
43.	Bračana	watercourse	DIN MED	13.9033	45.3955	25.82	13.95	14.35	6.25	1427
44.	Stara Mirna	watercourse	DIN MED	13.8563	45.3606	12.48	14.45	14.85	6.75	1225.9
45.	Raša	watercourse	DIN MED	14.0241	45.0954	1.03	14.65	15.45	7.45	1298.8
46.	Pazinčica	watercourse	DIN MED	13.9664	45.2472	248.76	13.15	13.75	5.75	1269.2
47.	Orljava	watercourse	PAN	17.7272	45.0955	89.81	12.15	20.35	3.75	886.1
48.	Una	watercourse	PAN	16.5498	45.2221	104.99	11.95	12.05	3.85	1019.5
49.	Baščica	watercourse	DIN MED	15.4619	44.2132	2.17	14.75	10.45	24.35	1282.5
50.	Bregana	watercourse	DIN CON	15.6755	45.8411	153.68	11.15	16.35	2.95	1138.2
51.	Dretulja	watercourse	DIN CON	15.3433	45.0744	379.97	9.85	10.25	1.75	1801.9
52.	Dretulja	watercourse	DIN CON	15.4239	45.0658	364.60	10.65	11.05	2.55	1620.3
53.	Jaruga 3	watercourse	DIN MED	15.7297	43.9541	109.67	14.65	10.75	23.85	1017.2
54.	Jaruga 2	watercourse	DIN MED	15.3302	44.2632	30.96	14.55	10.55	23.75	1325.4
55.	Kupčina	watercourse	DIN CON	15.4511	45.7216	218.66	11.05	16.15	2.95	1222.4
56.	Velika Rijeka	watercourse	PAN	17.8601	45.482	547.26	9.15	18.25	1.25	1103.2
57.	Rudarska Gradna	watercourse	DIN CON	15.667	45.7627	290.07	10.35	15.55	2.35	1323.4
58.	Rudarska Gradna	watercourse	DIN CON	15.6974	45.8	169.85	10.95	16.15	2.85	1171.9
59.	Gradna	watercourse	DIN CON	15.7023	45.7995	165.53	10.95	16.15	2.75	1175.9
60.	Lipovečka Gradna	watercourse	DIN CON	15.6454	45.7868	241.88	10.75	15.95	2.65	1287.1
61.	Svinica	watercourse	PAN	16.531	45.3089	120.39	11.85	11.95	3.65	957.1
62.	Bregana	watercourse	DIN CON	15.6028	45.8368	222.89	10.65	15.75	2.65	1225.7
63.	Pazinčica	watercourse	DIN MED	13.9292	45.2402	194.18	12.95	13.65	5.65	1242.7
64.	Slapnica	watercourse	DIN CON	15.5015	45.6882	167.05	11.35	16.55	3.15	1071

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m²)
65.	Subocka	watercourse	PAN	16.9745	45.3979	123.83	12.05	12.15	3.75	948.4
66.	Una	watercourse	DIN CON	16.1059	44.4019	387.00	11.15	6.85	20.35	1248.4
67.	Una	watercourse	DIN CON	15.9556	44.6968	235.89	11.25	11.55	20.45	1384.3
68.	Izvor Krke	watercourse	DIN CON	16.1451	44.4204	371.40	11.45	7.05	20.75	1055
69.	Cetina	watercourse	DIN MED	16.4281	43.9695	373.95	12.45	8.05	22.05	1184.9
70.	Cetina	watercourse	DIN MED	16.4425	43.9361	370.09	12.35	8.05	22.05	1188.4
71.	Dubračana	watercourse	DIN MED	14.6944	45.1769	3.34	13.45	13.75	22.85	1735.6
72.	Kamešnica	watercourse	PAN	16.5155	46.1331	211.91	10.95	20.35	2.75	1033.3
73.	Krka	watercourse	DIN MED	16.2252	44.0401	217.53	13.35	9.05	23.05	1245
74.	Krupa	watercourse	DIN MED	15.8869	44.1912	105.44	13.75	9.05	23.45	1174.8
75.	Krupa	watercourse	DIN MED	15.8869	44.1912	105.44	13.75	9.05	23.45	1174.8
76.	Krupa	watercourse	DIN MED	15.9094	44.1928	123.29	13.45	8.85	23.15	1210.9
77.	Ombla	watercourse	DIN MED	18.137	42.6761	15.66	14.65	11.75	22.45	1881.1
78.	Rumin	watercourse	DIN MED	16.6481	43.7762	299.26	12.95	8.65	22.45	1077.8
79.	Una	watercourse	PAN	16.3726	45.0498	117.89	11.95	12.05	3.85	1079.2
80.	Vojskova	watercourse	DIN MED	16.6319	43.7571	305.09	13.05	8.85	22.55	1111.9
81.	Vrba	watercourse	DIN MED	16.4	43.7224	413.95	12.85	8.95	21.85	1205.3
82.	Zduški potok	watercourse	DIN MED	16.4292	43.9367	373.03	12.45	8.05	22.05	1237.1
83.	Globornica	watercourse	DIN CON	15.38	45.3732	139.25	11.55	11.85	3.55	1260
84.	Vitunjčica	watercourse	DIN CON	15.1633	45.2836	334.91	10.65	10.95	2.55	1566.1
85.	Mačavarina Draga	watercourse	DIN MED	15.566	43.9493	44.53	15.45	11.55	24.65	1002.8
86.	Bistrica 1	watercourse	DIN CON	15.2863	45.2851	202.94	11.35	11.65	3.25	1432.4
87.	Munjava	watercourse	DIN CON	15.2857	45.1872	334.23	10.85	11.15	2.75	1576.2
88.	Munjava	watercourse	DIN CON	15.297	45.2037	323.38	10.85	11.15	2.85	1543.2
89.	Butižnica	watercourse	DIN MED	16.2201	44.0892	241.30	13.25	8.85	22.85	1239
90.	Suha Ričina Baščanska	watercourse	DIN MED	14.7417	44.9694	8.99	14.25	14.95	23.05	2062
91.	Zrmanja	watercourse	DIN MED	15.7759	44.1955	14.03	14.05	9.35	24.05	1204.3
92.	Zrmanja	watercourse	DIN MED	15.8577	44.162	50.03	14.15	9.45	24.05	1165.6
93.	Baščica	watercourse	DIN MED	15.4395	44.2197	34.36	14.45	10.25	23.95	1297.8
94.	Potkoš	watercourse	DIN MED	14.7309	45.3037	711.68	9.05	9.65	18.05	2219.2
95.	Cetina	watercourse	DIN MED	16.7583	43.4368	8.18	15.55	12.25	23.85	1038.4
96.	Bistra	watercourse	PAN	17.1593	46.0562	109.52	11.55	21.25	3.15	781.7

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m^2)
97.	Kanal Halašica	watercourse	PAN	18.6165	45.6229	84.15	11.75	21.65	3.15	693.7
98.	Kanal VI.	watercourse	PAN	18.5561	45.6915	84.35	11.75	21.55	3.15	676.4
99.	Drava	watercourse	PAN	16.3385	46.326	167.37	11.15	20.65	2.95	849.1
100.	Curak	watercourse	DIN CON	14.8929	45.4273	297.28	10.05	10.45	2.05	1543.1
101.	Curak	watercourse	DIN CON	14.8766	45.4456	250.86	10.95	11.35	2.75	1413.2
102.	Suvaja	watercourse	DIN MED	17.1347	43.4956	391.80	12.55	8.25	21.95	1268.8
103.	Cetina	watercourse	DIN MED	16.7009	43.4565	4.20	15.75	12.65	23.95	1025.8
104.	Krka	watercourse	DIN MED	16.0171	43.9952	79.36	14.15	9.85	23.65	1123.4
105.	Kanal Gacka	watercourse	DIN CON	15.2235	44.8624	445.80	10.75	11.15	20.25	1531.1
106.	Odvodni kanal HE Orlovac	watercourse	DIN MED	16.7822	43.6723	301.61	13.15	9.15	22.35	1206.9
107.	Mirna	watercourse	DIN MED	13.9252	45.387	28.35	13.95	14.35	6.15	1405.4
108.	Butiznica	watercourse	DIN MED	16.2262	44.1094	310.02	12.85	8.45	22.35	1262.4
109.	Zvizda	watercourse	DIN MED	16.891	43.4218	108.50	15.05	11.45	23.75	1248.5
110.	Zvizda	watercourse	DIN MED	16.891	43.4218	108.50	15.05	11.45	23.75	1248.5
111.	Ričica	watercourse	DIN CON	15.6871	44.3651	567.39	10.75	6.55	20.05	1384.2
112.	Dubračina	watercourse	DIN MED	14.6504	45.2315	72.77	13.05	13.45	22.45	1908.8
113.	Dubračina	watercourse	DIN MED	14.6801	45.2149	45.94	12.95	13.35	22.35	1862.8
114.	Obuhvatni kanal Mufrin	watercourse	DIN MED	13.8453	45.3485	10.62	14.55	15.05	6.85	1191.7
115.	Gusić	watercourse	DIN CON	15.1262	44.945	435.54	10.75	11.25	20.35	1542
116.	Dubračina	watercourse	DIN MED	14.6761	45.2197	50.89	13.15	13.55	22.65	1913.6
117.	Butižnica	watercourse	DIN MED	16.2205	44.0962	309.55	13.05	8.65	22.55	1240.8
118.	Šumetlica	watercourse	PAN	17.3832	45.3473	314.32	10.55	18.25	2.45	1090
119.	Vrbova	watercourse	PAN	17.8199	45.2933	119.82	11.95	20.05	3.45	838.8
120.	Kutjevačka rijeka	watercourse	PAN	17.9001	45.3388	130.74	11.75	19.95	3.25	831.5
121.	Kanal Bistra	watercourse	PAN	17.9319	45.112	88.42	12.05	20.25	3.55	772.6
122.	Skočinovac	watercourse	PAN	17.8304	45.2957	121.07	11.85	20.05	3.35	829.5
123.	Vetovka	watercourse	PAN	17.7523	45.3472	137.17	11.75	19.95	3.35	814.1
124.	Kaptolka	watercourse	PAN	17.728	45.3554	144.33	11.75	19.95	3.35	804.4
125.	Peranački potok	watercourse	PAN	17.5926	45.3492	166.08	11.65	19.75	3.25	847
126.	Peranački potok	watercourse	PAN	17.5926	45.3492	166.08	11.65	19.75	3.25	847
127.	Garešnica	watercourse	PAN	16.938	45.5687	110.55	11.95	17.25	3.75	890.9
128.	Jovača	watercourse	PAN	17.1865	45.5165	144.05	11.85	19.85	3.65	995.6

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m^2)
129.	Velika	watercourse	PAN	16.6993	45.901	108.13	11.75	16.95	3.55	812
130.	Brestača	watercourse	PAN	16.9689	45.3507	121.36	11.95	19.95	3.65	904.2
131.	Veliki Strug	watercourse	PAN	16.8376	45.3076	90.83	12.25	12.35	3.85	889.1
132.	Javošnica	watercourse	PAN	16.3455	45.0781	122.81	11.85	12.05	3.75	1059.8
133.	Čatlan	watercourse	PAN	16.4435	45.1419	117.23	11.95	12.05	3.85	1029.9
134.	Sutla	watercourse	PAN	15.7149	46.0593	165.39	11.15	16.25	3.05	1091.6
135.	Posalitva	watercourse	PAN	16.0831	46.378	200.36	11.05	20.55	2.95	924.5
136.	Matica 1	watercourse	DIN CON	15.7337	44.741	641.08	9.55	10.05	18.45	1552.8
137.	Krbava	watercourse	DIN CON	15.7658	44.544	703.36	9.45	5.45	18.45	1466.2
138.	Pazinčica	watercourse	DIN MED	13.9292	45.2402	194.18	12.95	13.65	5.65	1242.7
139.	Cetina	watercourse	DIN MED	16.7291	43.6176	294.39	13.75	9.95	22.65	1256.5
140.	Jadro	watercourse	DIN MED	16.4909	43.5339	1.56	15.85	12.75	23.85	1092.1
141.	Žrnovnica	watercourse	DIN MED	16.5421	43.5163	9.54	15.15	12.25	23.15	1165.4
142.	Cetina	watercourse	DIN MED	16.7473	43.5319	243.50	14.15	10.75	22.75	1285.7
143.	Krčić	watercourse	DIN MED	16.319	44.0274	354.49	12.45	8.15	21.95	1238.8
144.	Krka	watercourse	DIN MED	15.9892	43.9621	90.55	14.45	10.25	23.95	1100.8
145.	Vrljika	watercourse	DIN MED	17.1954	43.4313	264.51	13.55	9.15	23.15	1170.2
146.	Kopačica	watercourse	DIN MED	18.3766	42.5217	60.25	16.25	13.45	23.95	2313
147.	Petrinjčica	watercourse	PAN	16.2731	45.4413	97.13	12.05	12.25	3.85	995.7
148.	Došnica	watercourse	DIN MED	16.2056	44.0917	258.51	13.05	8.75	22.65	1259.8
149.	Krka	watercourse	DIN MED	16.0188	44.0026	79.22	14.05	9.75	23.55	1121.4
150.	Zelina	watercourse	PAN	16.2846	45.8186	106.55	11.95	17.25	3.55	898.4
151.	Kupa	watercourse	DIN CON	15.3564	45.6453	130.96	11.65	16.75	3.45	1090.6
152.	Kupa	watercourse	DIN CON	15.2493	45.4557	161.63	11.45	11.75	3.35	1178.3
153.	Kupa	watercourse	PAN	15.5977	45.4872	105.18	11.85	11.95	3.65	1050.7
154.	Petrinjčica	watercourse	PAN	16.2878	45.2728	222.10	11.35	11.55	3.35	1067.7
155.	Golinja	watercourse	PAN	16.0168	45.4775	105.86	11.95	12.15	3.75	978.7
156.	Kremešnica	watercourse	PAN	15.8734	45.5265	102.02	11.85	17.15	3.55	985.3
157.	Rečica	watercourse	PAN	15.6664	45.4811	105.20	11.85	11.95	3.65	1043.8
158.	Kravaršćica	watercourse	PAN	15.9074	45.5391	104.73	11.85	17.15	3.55	962.2
159.	Roženica	watercourse	PAN	15.9384	45.5188	109.32	11.85	17.15	3.65	960.8
160.	Trepča	watercourse	PAN	15.9262	45.4726	105.49	11.95	12.15	3.75	998.4
161.	Trepča	watercourse	PAN	15.9262	45.4726	105.49	11.95	12.15	3.75	998.4

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m^2)
162.	Glina	watercourse	PAN	15.7699	45.2101	140.27	11.85	11.95	3.75	1074.5
163.	Kupčina	watercourse	PAN	15.789	45.5322	103.31	11.85	17.15	3.55	981.7
164.	Reka 2	watercourse	PAN	15.6452	45.6333	114.91	11.75	17.05	3.45	955.8
165.	Korana	watercourse	DIN CON	15.5457	45.2525	141.15	11.55	11.85	3.55	1234.2
166.	Korana	watercourse	DIN CON	15.5903	45.121	215.08	11.25	11.55	3.25	1337
167.	Brusovača	watercourse	PAN	15.7592	45.2556	195.99	11.15	11.45	3.15	1180.4
168.	Slunjčica	watercourse	DIN CON	15.5896	45.0796	241.79	10.95	11.35	2.95	1491.7
169.	Mrežnica	watercourse	DIN CON	15.5598	45.4659	111.22	11.85	11.95	3.65	1128.3
170.	Zagorska Mrežnica	watercourse	DIN CON	15.2748	45.2243	314.67	10.95	11.25	2.85	1531.8
171.	Žumberačka reka	watercourse	PAN	15.5819	45.7417	353.41	9.75	14.85	1.85	1359.7
172.	Dobra	watercourse	DIN CON	15.106	45.3578	354.35	10.35	10.65	2.25	1547.1
173.	Gornja Dobra	watercourse	DIN CON	15.2003	45.2683	320.91	10.75	11.05	2.65	1547.9
174.	Ribnjak	watercourse	DIN CON	15.1119	45.3413	354.97	10.35	10.75	2.35	1553.1
175.	Trebinja	watercourse	PAN	15.6285	45.4682	109.20	11.75	11.95	3.55	1070.5
176.	Ruševica	watercourse	PAN	15.7247	45.1965	146.32	11.65	11.85	3.55	1126.9
177.	Krapina	watercourse	PAN	15.8228	45.8348	121.52	11.75	16.95	3.35	916.6
178.	Reka 1	watercourse	PAN	16.0651	46.1488	255.53	10.85	20.25	2.75	1018
179.	Presečno	watercourse	PAN	16.3115	46.0352	139.75	11.45	20.05	3.25	849.8
180.	Kotoripski kanal	watercourse	PAN	16.8156	46.3449	132.14	11.35	20.95	3.05	749.2
181.	Gliboki potok	watercourse	PAN	16.7238	46.1959	148.49	11.35	20.85	3.05	876.1
182.	Kupa	watercourse	DIN CON	15.0754	45.4845	181.79	11.05	11.35	2.85	1404.8
183.	Kupa	watercourse	DIN CON	14.7745	45.5074	252.58	10.95	11.25	2.75	1488.5
184.	Kupa	watercourse	DIN CON	14.7006	45.505	304.02	10.45	10.85	2.45	1532.8
185.	Kupica	watercourse	DIN CON	14.8568	45.4641	219.10	11.45	11.75	3.15	1420
186.	Curak	watercourse	DIN CON	14.8536	45.4501	229.92	11.25	11.65	3.05	1443.5
187.	Čabranka	watercourse	DIN CON	14.6996	45.5257	289.51	10.95	11.25	2.75	1386.8
188.	Velika Belica	watercourse	DIN CON	14.805	45.4755	233.16	11.35	11.65	3.15	1523.3
189.	Gerovčica	watercourse	DIN CON	14.6356	45.5162	571.37	9.65	10.05	1.75	1753.3
190.	Čedanj	watercourse	DIN CON	14.9087	45.4761	215.62	11.15	11.45	2.95	1304.4
191.	Gacka	watercourse	DIN CON	15.2956	44.8265	450.03	10.65	11.05	20.05	1547.6
192.	Rječina	watercourse	DIN MED	14.4497	45.3786	238.29	11.95	7.75	21.05	1783.2
193.	Rječina	watercourse	DIN MED	14.4178	45.4026	289.59	11.65	7.45	20.75	1760.1
194.	Rječina	watercourse	DIN MED	14.4482	45.3566	146.24	12.15	8.05	21.25	1719.9

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m²)
195.	Joševica	watercourse	DIN CON	16.1094	44.4171	375.46	11.15	6.85	20.45	1179.4
196.	Rumin	watercourse	DIN MED	16.6481	43.7762	299.26	12.95	8.65	22.45	1077.8
197.	Mislina	watercourse	DIN MED	17.6391	43.0061	4.16	15.35	11.25	24.65	1279
198.	Kobilica	watercourse	DIN MED	16.0836	44.1255	252.67	12.95	8.65	22.55	1320.3
199.	Zrmanja	watercourse	DIN MED	16.0334	44.0923	198.83	13.55	9.15	23.15	1178.5
200.	Zrmanja	watercourse	DIN MED	15.94	44.1076	123.38	14.15	9.65	23.75	1090
201.	Ričica	watercourse	DIN CON	15.7476	44.3419	554.31	10.65	6.45	19.85	1402.9
202.	Zrmanja	watercourse	DIN MED	16.0711	44.1469	266.25	13.05	8.65	22.55	1394.1
203.	Krupa	watercourse	DIN MED	15.9094	44.1928	123.29	13.45	8.85	23.15	1210.9
204.	Bribišnica	watercourse	DIN MED	15.7989	43.8905	96.10	14.65	11.05	23.35	972.2
205.	Vrba	watercourse	DIN MED	16.3146	43.7911	288.51	13.45	9.45	22.75	1249.1
206.	Krka	watercourse	DIN MED	16.0947	44.0106	206.98	13.65	9.35	23.15	1244.3
207.	Butižnica	watercourse	DIN MED	16.1869	44.0409	219.35	13.35	9.05	22.95	1276.2
208.	Krka	watercourse	DIN MED	15.9652	43.8025	43.14	15.15	11.45	24.15	1053.9
209.	Kozjak	stagnant	DIN CON	15.61602	44.87872	543.61	9.65	10.15	1.75	1759.7
210.	Galovac	stagnant	DIN CON	15.60872	44.87737	568.27	9.65	10.15	1.75	1759.7
211.	Milanovac	stagnant	DIN CON	15.6096	44.89465	531.35	9.65	10.15	1.65	1747.2
212.	Sakadaš	stagnant	PAN	18.800471	45.608242	80.92	11.85	20.15	3.15	684.3
213.	Biljsko jezero	stagnant	PAN	18.737324	45.589971	81.52	11.85	20.25	3.15	696.9
214.	Jezero Sabljaci	stagnant	DIN CON	15.226535	45.228559	319.21	10.85	11.25	2.85	1601.1
215.	Jezero Sabljaci	stagnant	DIN CON	15.226965	45.222151	319.22	10.85	11.25	2.85	1620.2
216.	Akumulacija Golubić	stagnant	DIN MED	16.22269	44.09892	308.49	13.05	8.65	22.55	1240.8
217.	Akumulacija Golubić	stagnant	DIN MED	16.22269	44.09892	308.49	13.05	8.65	22.55	1240.8
218.	Akumulacija Prančević	stagnant	DIN MED	16.70595	43.57055	271.15	13.85	10.35	22.45	1316.1
219.	Brljansko jezero	stagnant	DIN MED	16.037649	44.009559	187.07	13.75	9.55	23.25	1156.9
220.	Akumulacija Gusić	stagnant	DIN CON	15.111193	44.943584	426.49	10.75	11.25	20.45	1604.1
221.	Akumulacija Gusić	stagnant	DIN CON	15.111193	44.943584	426.49	10.75	11.25	20.45	1604.1
222.	Akumulacija Donji bazen, Razovac	stagnant	DIN MED	15.747564	44.204755	8.27	14.25	9.45	24.15	1231.8
223.	Prološko blato	stagnant	DIN MED	17.116991	43.473564	265.62	13.75	9.35	23.25	1286.6
224.	Akumulacija Ponikve	stagnant	DIN MED	14.560445	45.077241	17.19	14.25	14.95	22.85	1511.2
225.	Jezero Oćuša	stagnant	DIN MED	17.426206	43.081107	1.40	15.65	11.75	24.75	1226.8
226.	Visovačko jezero	stagnant	DIN MED	15.969	43.859472	48.65	15.25	11.25	24.45	1067.4

Site id	Name	water body type	(sub) ecoregion	x	y	Altitude (m a.s.l.)	Mean annual air temperature (°C)	Mean temperature of wettest quarter (°C)	Mean temperature of driest quarter (°C)	Annual precipitation (kg/m^2)
227.	Akumulacija Kruščica	stagnant	DIN CON	15.2662	44.6764	607.92	10.55	6.25	19.85	1665
228.	Ribnjaci Donji Miholjac	stagnant	PAN	18.210923	45.757475	99.24	11.55	21.35	3.15	726.1

4.3. Znanstveni rad 2

Rimac, A.; Šegota, V.; Alegro, A.; Koletić, N.; Vuković, N.; Papp, B. (2019): **New and noteworthy bryophyte records from drawdown zones in Croatia**. *Herzogia*: 32(2): 315–325.

New and noteworthy bryophyte records from lacustrine drawdown zones in Croatia

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Abstract: Rimac, A., Šegota, V., Alegro, A., Koletić, N., Vuković, N. & Papp, B. 2019. New and noteworthy bryophyte records from lacustrine drawdown zones in Croatia. – Herzogia **32**: 315–325.

Ephemeral bryophytes are short-lived species that can germinate and finish their whole life cycle within a brief period when favourable conditions occur. A significant number of these specialist species are associated with moist and fine-textured substrata of the margins of lakes, reservoirs and rivers, also known as drawdown zones. Our study of the vegetation of drawdown zones, the first focusing on these specific habitats in Croatia, resulted in significant records for Croatian bryoflora; a new species (*Physcomitrium eurystomum*), confirmation of two species, the occurrence of which was doubtful (*Riccia cavernosa* and *R. frostii*) and new localities of two extremely rare species (*Physcomitrella patens* and *Leptobryum pyriforme*). Although these species and their habitats are considered relatively rare and threatened in Europe, the low number of records in Croatia is to a considerable extent the result of there having been insufficient research into ephemeral habitats and the bryophyte flora in general.

Zusammenfassung: Rimac, A., Šegota, V., Alegro, A., Koletić, N., Vuković, N. & Papp, B. 2019. Neue und bemerkenswerte Moosfunde von lakustrinen Wasserstandsabsenkungszonen in Kroatien. – Herzogia **32**: 315–325.

Ephemere Moose sind kurzlebige Arten, welche die Keimung und den ganzen Lebenszyklus innerhalb einer kurzen Zeitspanne mit günstigen Lebensbedingungen schließen können. Eine beträchtliche Anzahl dieser spezialisierten Arten sind an den feuchten und fein texturierten Untergrund von See-, Stausee- und Flussuferwasserspiegelabsenkungszonen gebunden. Unsere Untersuchungen der Vegetation dieser Zonen, die erste dieser Art in Kroatien, hat zu bedeutenden Funden für die Moosflora Kroatiens geführt: eine neue Art (*Physcomitrium eurystomum*), Bestätigung von zwei bisher zweifelhaften Arten (*Riccia cavernosa* und *R. frostii*) und neue Fundorte für zwei sehr seltene Arten (*Physcomitrella patens* und *Leptobryum pyriforme*). Obwohl diese Standorte und ihre Arten in Europa relativ selten und gefährdet sind, ist die geringe Anzahl von Funden in Kroatien im beträchtlichen Ausmaß auch eine Folge des mangelnden Untersuchungsgrades solcher ephemerer Standorte als auch der kroatischen Moosflora allgemein.

Key words: Ephemerophytes, *Physcomitrium eurystomum*, *Physcomitrella patens*, *Riccia frostii*, *Riccia cavernosa*, Southeast Europe, river margins, lake margins, annual-shuttle strategy.

Introduction

Gently sloping margins of natural and artificial waterbodies provide important habitats for ephemeral mosses and liverworts (Atherton et al. 2010). These bryophytes can inhabit the drawdown zone of lakes, reservoirs, pools and ponds, as well as sloping margins of rivers. The water level regime and open, moist and fine-textured substrata are the essential characteristics of these habitats that enable the development of ephemeral bryophytes (Furness & Hall 1981, Hugonnot et al. 2005, Bijlsma et al. 2012, Rothero 2012).

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Habitats that favour the development of such species are subject to long periods of flooding until summer water-level fall. This part of the vegetation season is too brief to enable vascular plants and perennial bryophytes to colonise and assume dominance, while ephemeral bryophytes thrive and manage to finish their whole life-cycle before the water level rises again in autumn. In some suitable areas, favourable conditions may occur only during dry years, i.e., years when summer rainfall is low enough to cause a drought, which will expose the muddy or sandy substrata and in turn enable the regeneration of ephemeral bryophytes from long-lasting spores.

These specialised bryophytes mostly display an annual shuttle strategy and are to lesser extent colonists. In both cases, they possess adaptations that enable them to survive in drawdown zones of waterbodies; their key features are a short life span, rapid growth, high reproductive effort and persistent diaspores (During 1979, Kürschner 2004). Their propagules show remarkable longevity, which ensures survival in a habitat where favourable circumstances for growth arise very infrequently (Furness & Hall 1981).

Here we present new and noteworthy records of ephemeral bryophytes from water margins in Croatia. Along with the distribution of the studied species, we provide a habitat description for every locality. Having in mind that these species and their habitats are considered relatively rare and threatened in Europe (Hodgetts 2015), this contribution to the still underexplored bryophyte flora of Croatia (Sabovljević et al. 2001, 2011, Alegro et al. 2012) is of particular importance for conservation. Namely, one of the most important requirements that has to be met prior to conservation is systematic and comprehensive research. Although significant progress has been made during the past decade (Papp & Sabovljević 2009, Ellis et al. 2012a, 2012b, 2014, 2015, 2016, 2017, Papp et al. 2013a, 2013b, 2013c, Alegro et al. 2014, 2015, 2018, 2019, Sabovljević et al. 2018), continuous reporting of new species indicates that knowledge of bryophyte flora is still insufficient, highlighting the need for additional field surveys in Croatia. Even the species that are considered common throughout Europe or are associated with ubiquitous habitat types have been to this day documented in Croatia in only a few localities (Alegro & Šegota 2019). Apart from research into freshwater habitats (Pavletić 1956, 1957, 1959, 1960, Matoničkin & Pavletić 1961, 1963), peatlands (Alegro & Šegota 2010) and salt-rich grasslands (Papp et al. 2016), no other comprehensive research focusing on any specific habitat has been performed in Croatia.

Methods

The field research was undertaken in 2011, 2016 and 2017 as a part of the national monitoring of inland waters, carried out to meet the requirements of the Water Framework Directive (WFD). During the monitoring, more than 600 localities, ultimately covering most of the territory of Croatia, were inspected for aquatic and amphibious flora, including ephemeral bryophytes. A list of bryophytes and vascular plants at each locality investigated was made.

The nomenclature follows Ros et al. (2007, 2013) for bryophytes and Euro+Med (2019) for vascular plants. The syntaxonomical system proposed by Mucina et al. (2016) and Škvorc et al. (2017) was applied. Collected specimens are deposited in herbaria ZA and BP.

Particular waterbodies where ephemeral bryophytes have been recorded are described in more detail below:

Kruščica Reservoir (Fig. 1), located in the Lika Region in the southern part of central Croatia at 554 m a.s.l., is a hydroelectric reservoir created by damming a typical karstic river, the Lika, in its lower course. The total lake area is 3.9 km^2, its margins are relatively steep and subject to

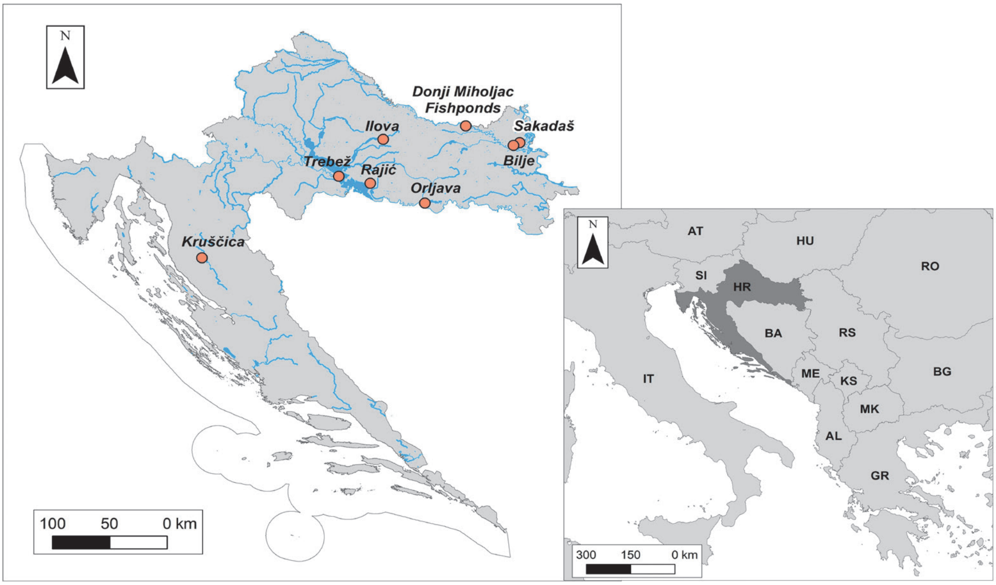

Fig. 1. Occurrence sites of ephemeral bryophytes in lacustrine drawdown zones in Croatia.

significant changes of water level due to the hydroelectric energy production. The water body is classified as heavily modified and oligotrophic.

Lakes Bilje and Sakadaš (Fig. 1) are located in the Baranja Region, a lowland area between the rivers Drava and Danube in the most eastern part of Croatia. Lake Bilje is an eutrophic oxbow lake, an old meander of the Drava River, with gently sloping muddy and sandy margins. The total area of the lake is 0.56 km^2 and it is situated at 84 m a.s.l. The waterbody is classified as heavily modified. Lake Sakadaš, as well eutrophic water body, is an abandoned gravel pit located in Kopački Rit, a part of the floodplain of the Drava River before its confluence into the Danube. The lake is an artificial waterbody with an area of 0.12 km^2, located at 86 m a.s.l., with relatively steep, muddy and sandy margins.

Donji Miholjac Fishponds (Fig. 1) are situated in the north-eastern part of Slavonia in the lowland area of eastern Croatia. They represent a completely natural system of classic carp fishponds, the Drava River ensuring an unlimited supply of water for fish production. The area covers 6.19 km^2 and the altitude is around 100 m a.s.l.

The lowland rivers the Ilova, Trebež (medium-sized) and Rajić (small-sized) are located in the Moslavina Region in Central Croatia and have been subjected to considerable hydromorphological alterations such as channelization, riverbed deepening and embankment. They are characterized by relatively steep drawdown zones with sandy or silty sediments. Similarly, the medium-sized Orljava River, situated in lowland Slavonia, has been subjected to river regulation resulting in considerable hydromorphological alterations.

Results and discussion

Ephemeral bryophytes have been found in the drawdown zones of four lowland rivers (the Rajić, Trebež, Orljava and Ilova) and of four standing waterbodies (Donji Miholjac Fishponds, Kruščica

Reservoir, Lake Bilje and Lake Sakadaš) (Fig. 1). We recorded one species new for Croatian bryoflora, *Physcomitrium eurystomum* Sendtn., and new localities of the rare and under-recorded species *Riccia frostii* Austin, *Riccia cavernosa* Hoffm., *Physcomitrella patens* (Hedw.) Bruch & Schimp. and *Leptobryum pyriforme* (Hedw.) Wilson (Fig. 2), described in detail below.

The species

Physcomitrium eurystomum Sendtn.

Specimen examined: Croatia, Baranja Region, Bilje oxbow lake, muddy margins of the lake, 18.736°E, 45.5901°N, altitude 84 m a.s.l., 23 September 2017, leg. A. Rimac, N. Koletić, N. Vuković, det. A. Rimac (ZA49325).

Physcomitrium eurystomum is a new species for Croatian flora (Alegro & Šegota 2019). On the margins of Lake Bilje, the species was associated with *Riccia fluitans* L., *Physcomitrella patens* (Hedw.) Bruch & Schimp. and *Leptobryum pyriforme* (Hedw.) Wilson. It was growing among vascular vegetation of the alliances Nanocyperion W. Koch ex Libbert 1932 and Phragmition australis W. Koch 1926. *Physcomitrium eurystomum* is an ephemeral moss that forms scattered or closely packed turfs on exposed drawdown zone of pools and reservoirs, and less often on muddy soil along streams (Smith 2004, Hill et al. 2007). It is a tropical temperate (Dierssen 2001) and sub-Mediterranean element (Düll 1984), widespread (Hill & Preston 1998, Smith 2004), but relatively rare in Western and Central Europe. In Southeast Europe, it has been reported so far from Bulgaria, Romania, Slovenia and Serbia (Hodgetts 2015, Papp et al. 2013d), while in the Mediterranean part of Europe it is known from Italy and France (Hodgetts 2015). The species is treated as endangered in Austria, Great Britain and Hungary and vulnerable in the Czech Republic, Estonia, Germany, Slovakia and Switzerland and it is a candidate for the new European Bryophyte Red List (Hodgetts 2015).

Riccia frostii Austin

Specimens examined: Croatia, Ribnjaci [Fish ponds] at Donji Miholjac, muddy soil in a lake, 15.2662°E, 44.6764°N, altitude 100 m a.s.l., 6 May 2011, leg. B. Papp, A. Alegro, V. Šegota, det. B. Papp (BP50857/H).

We have found no literature or herbarium evidence of the existence of *Riccia frostii* in Croatia, although it was listed in the checklist of Düll et al. (1999), but with no particular locality noted. Thus, our finding at Donji Miholjac Fishponds represents the definitive confirmation of the species. *Riccia frostii* is a thalloid liverwort, which forms rosettes on loamy banks that are waterlogged at least during the spring floods (Borovichev & Bakalin 2016) and on sandy-clayey alluvial deposits (Ştefureac & Mihai 1967). In favourable years when the water table of rivers is low after a warm and dry summer, this species can colonize the drying mud of riverbeds, as reported along the Danube in Hungary (Erzberger et al. 2015). *Riccia frostii* has a boreo-temperate circumpolar distribution (Bakalin 2009), considered a continental element in Europe (Düll 1983), however, according to Dierssen (2001) and Jovet-Ast (1986) the species has southern, subtropical and Mediterranean distribution. It is relatively rare in Europe, reported from only nine countries. In Southeast Europe, it has been listed for Serbia, Romania and Croatia (Hodgetts 2015). In Europe, it is considered regionally extinct in Austria and critically endangered in Italy and Romania (Hodgetts 2015). It is included in the Red Data Book of European Bryophytes (ECCB 1995) and a candidate for the new European Bryophyte Red List (Hodgetts 2015).

Riccia cavernosa Hoffm.

Specimens examined: Croatia, Donji Miholjac Fishponds, muddy soil in a lake, 15.2662°E, 44.6764°N, altitude 100 m a.s.l., 6 May 2011, leg. B. Papp, V. Šegota, A. Alegro, det. B. Papp (BP 50856/H); Lika Region, Kruščica Reservoir, sandy and silty drawdown zone of the lake, 15.2662°E, 44.6764°N, altitude 604 m a.s.l., 7 October 2017, leg. A. Alegro, N. Koletić, det. A. Alegro (ZA49316, ZA49317, ZA 49318, ZA 49319, ZA 49320, ZA 49321, ZA 49322); Slavonia Region, Orljava River at the confluence into the Sava River, sandy substrate on the river margins, 17.7272°E, 45.0955°N, altitude 105 m a.s.l., 23 August 2017, leg. A. Rimac, V. Šegota, det. A. Rimac, V. Šegota (ZA49327); Moslavina Region, Trebež River, sandy and silty drawdown zone, 16.7737°E, 45.3561°N, altitude 95 m a.s.l., 19 August 2017, leg. A. Rimac, det. A. Rimac (ZA49323).

Riccia cavernosa was mentioned for the first time for Croatia in the checklist of Düll et al. (1999), without any particular locality listed or herbarium specimen noted. Inspection of herbarium collection of Hungarian Natural History Museum revealed one specimen, collected along the banks of the Drava River in Osijek (Baranja Region), more than a hundred years ago (*Slavonia. Comit. Verőce* [Virovitica]. *In ripa fluvii Dráva ad Eszék* [Osijek], *30.08.1917.* leg. Zsák, Z. det. Boros, Á. sub. nom. *Riccia crystallina!*, BP31286/H). During our research, *R. cavernosa* was recorded in four new localities – on the margins of two rivers and two stagnant waterbodies. *Riccia cavernosa* is an annual thalloid liverwort, forming patches on moist and exposed muddy and sandy substrata by reservoirs, lakes and ponds. The species is a temperate circumpolar element (HILL et al. 2007) with documented occurrences in the majority of European countries (HODGETTS 2015). In Southeast Europe, the species has been reported from Montenegro and Romania, as well as from Croatia (HODGETTS 2015). The species is considered critically endangered in Switzerland, endangered in Austria and Italy and vulnerable in Germany and Norway, while in Finland it is treated as regionally extinct (HODGETTS 2015).

Physcomitrella patens (Hedw.) Bruch & Schimp.

Specimens examined: Croatia, Baranja Region, Bilje oxbow lake, muddy margins of the lake, 18.736°E, 45.5901°N, altitude 84 m a.s.l., 23 September 2017, leg. A. Rimac, N. Koletić, N. Vuković, det. A. Rimac, *s.n.*; Baranja Region, Kopački Rit, Lake Sakadaš, sandy margins of the lake, 18.8051°E, 45.6112°N, altitude 86 m a.s.l., 23 September 2017, leg. A. Rimac, det. A. Rimac (ZA49324); Lika Region, Kruščica Reservoir, sandy and silty drawdown zone of the lake, 15.2662°E, 44.6764°N, altitude 604 m a.s.l., 7 October 2017, leg. A. Alegro, N. Koletić, det. A. Alegro (ZA49313, ZA49314, ZA49315); Moslavina Region, Trebež River, sandy and silty drawdown zone, 16.7737°E, 45.3561°N, altitude 95 m a.s.l., 19 August 2017, leg. A. Rimac, det. A. Rimac (ZA49312); Moslavina Region, Ilova River, sandy substrate in drawdown zone, 17.2725°E, 45.6599°N, altitude 140 m a.s.l., 25 August 2017, leg. A. Rimac, det. A. Rimac, (ZA49326); Moslavina Region, Rajić River, sandy and silty substrate in drawdown zone 17.1228°E, 45.2973°N, altitude 114 m a.s.l., 25 August 2017, leg. A. Rimac, det. A. Rimac, s.n.

We found no historical herbarium specimens of *Physcomitrella patens* from Croatia, while the only literature reference is that one of HORVAT (1932), who recorded it in the central part of Croatia in the lowland Lonja River, a tributary of the Sava River, during the low water level. The present re-search confirms *P. patens* as a member of the bryophyte flora of Croatia after more than 85 years. During our research, it has been recorded in six localities, in the drawdown zones of both rivers and lakes. *Physcomitrella patens* is an ephemeral species growing in turf on muddy and sandy substrata by streams, ditches, ponds, lakes, reservoirs, on wet tracks and woodland ridges (SMITH 2004). It is Euro-Siberian temperate element (HILL & PRESTON 1998, SMITH 2004) reported from the majority of European countries, apart from Southern Europe, where it is known only from France and Italy. To this day it has been reported from nine Southeast European countries, including Croatia (HODGETTS 2015). It is considered critically endangered in Bulgaria and Estonia, endangered in Finland, and vulnerable in Germany, Slovakia, Slovenia and Switzerland (HODGETTS 2015).

Leptobryum pyriforme (Hedw.) Wilson

Specimens examined: Croatia, Baranja Region, Bilje oxbow lake, muddy margins of the lake, 18.736°E, 45.5901°N, altitude 84 m a.s.l., 23 September 2017, leg. A. Rimac, N. Koletić, N. Vuković, det. B. Papp (ZA49311).

There are only three previous records of this species in Croatia – from Mt Medvednica near Zagreb (HEINZ 1887), Mt Snježnik in the western part of the country (PAVLETIĆ 1955) and, relatively recently, from the karstic field Vrhovinsko Polje near the Plitvice Lakes National Park in the Lika Region (ALEGRO et al. 2014). *Leptobryum pyriforme* is a widely distributed species of the circumpolar wide-temperate element (HILL & PRESTON 1998, SMITH 2004). It is perennial more often than annual, forming loose tufts on different substrata such as rock, soil, sand and even decorticated wood (HILL et al. 2007). The species grows on disturbed ground in gardens, fields, by paths and roads and in inundation zones, i.e. on the margins of ponds and reservoirs (SMITH 2004). It is widespread throughout Europe, and considered vulnerable only in the Canary Islands (HODGETTS 2015).

Habitat characterization

The exploration of ephemeral vegetation of the drawdown zones tends to be rather challenging, given that the characteristic plants of these habitats are of extremely spasmodic temporal distribution (FURNESS & HALL 1981). In Croatia, those peculiar habitats have never been sur-

Fig. 2. Ephemeral bryophytes and their habitats in Croatia. **A.** The population explosion of *Riccia cavernosa* on the exposed mud of Kruščica Reservoir after the receding of the water. **B.** *Riccia cavernosa* from Kruščica Reservoir. **C.** Extensively fissured mud of Donji Miholjac Fishponds (a terrestrial form of *Hydrocharis morsus-ranae* visible). **D.** *R. cavernosa* and *R. frostii* colonising the mud surface and sides of the cracks at Donji Miholjac Fishponds. **E.** The margin of Lake Bilje with Nanocyperion and Phragmition vegetation. **F.** *Physcomitrium eurystomum* and *Leptobryum pyriforme* at Lake Bilje. **G.** Drawdown zone of the Trebež River. **H.** *Physcomitrella patens* at Trebež. Photos by A. Rimac and A. Alegro.

veyed and our field research of ephemeral bryophyte communities across the whole territory of Croatia revealed eight occurrence sites including the margins of a reservoir, lakes, and rivers.

The most astonishing scenario took place in early autumn 2017 at Kruščica Reservoir, when the water receded, exposing more than 100 m of both margins and the gently sloping lake bottom. The margins of the reservoir are subject to significant changes in water level due to the hydroelectric energy generation, and hence support intermittent occurrences of pioneer annual ephemerals. The open and moist, slowly drying and fine-textured substrate served as a favourable habitat for the unearthing of the bryophyte spores. In this locality, *Riccia cavernosa* was the most abundant ephemeral (Fig. 2), associated with less abundant *Physcomitrella patens*, growing in isolated patches. This plant community (Riccio cavernosae-Physcomytrelletum patentis Allorge ex Hübschmann 1957) belongs to the pioneer ephemeral vegetation of periodically flooded freshwater habitats (Isoëto-Nanojuncetea Br.-Bl. et Tx. in Br.-Bl. et al. 1952); however, it is characterised by the complete absence of vascular plants, in contrast to other communities of this order (Nebel & Philippi 2000, 2005). This bryophyte-dominated community develops during summer and early autumn, yet in the event of favourable climatic conditions, it can appear as early as in May (Nebel & Philippi 2005). This was the scenario at the beginning of May 2011 at Donji Miholjac Fishponds, which were subjected to complete water-drainage at that time. Subsequent drying and cracking of the surface enabled prolific growth of *R. cavernosa* and *R. frostii*, on both the surface of muddy margins and the fishpond bottom, as well as on the vertical faces of fissures (Fig. 2).

Drawdown zones of Lakes Sakadaš and Bilje and the Trebež, Orljava, Ilova and Rajić rivers were smaller than those of Kruščica Reservoir and Donji Miholjac Fishponds, ranging from several meters to less than a meter. In these localities *Physcomitrella patens* and *Riccia cavernosa* were the most common species, growing either unaccompanied or cohabiting. On the margins of Lake Bilje, *P. patens* was associated with *Physcomitrium eurystomum*, *Leptobryum pyriforme* (Fig. 2) and terrestrial form of *Riccia fluitans*, which formed small patches. On the Ilova River *P. patens* was associated with several more common species characteristic of moist, open and disturbed habitats (*Bryum argenteum* Hedw., *B. gemmiparum* De Not. and *Lunularia cruciata* (L.) Lindb.), on the Trebež River it was accompanied by *Riccia cavernosa*, while on the Orljava River, *R. cavernosa* was the only bryophyte species recorded in the drawdown zone (Fig. 2, Table 1). At the time of collection, annual shuttle species *Riccia cavernosa*, *Physcomitrella patens* and *Physcomitrium eurystomum* were abundantly fertile with many ripe capsules releasing spores. A colonist species, *Leptobryum pyriforme* was without capsules, but with plentiful rhizoidal tubers.

In contrast to the exclusive bryophyte dominance observed at Kruščica Reservoir and Donji Miholjac Fishponds (Fig. 2), the much restricted drawdown zones of the other six localities harboured vascular flora as well. This was vegetation of periodically flooded habitats on nutrient-poor soils (Isoëto-Nanojuncetea) or nutrient-rich soil (Bidentetea Tx. et al. ex von Rochow 1951). Isoëto-Nanojuncetea comprised annual vascular plants such as *Cyperus fuscus* L., *C. glomeratus* L., *C. michelianus* (L.) Link, *Eleocharis acicularis* (L.) Roem., *Gnaphalium uliginosum* L., *Juncus articulatus* L. and *Lindernia procumbens* (Krock.) Philcox (Table 1), most of which display striking ecological parallels with ephemeral bryophytes, while in Bidenteteta, *Bidens frondosa* L., *Persicaria lapathifolia* (L.) Delarbre and *Polygonum mite* Schrank occurred (Table 1). Both habitat types are considered threatened and are protected as NATURA 2000 habitats, thus all surveyed localities should be regularly monitored and considered for protection. As for coenological affiliation of the recorded drawdown zone ephemeral bryophytes, they are placed within either Isoëto-Nanojuncetea (Nebel & Philippi 2000, 2005, Mucina et al. 2016), where they can form extensive mats, or Bidentetea (Bijlsma et al. 2012), where they thrive in a more or less dense herb layer, while some authors place them in both

Table 1. Bryophyte and vascular plant species list of localities investigated.

Species	Reservoir Kruščica	Lake Sakadaš	Lake Bilje	Donji Miholjac Fishponds	Orljava River	Trebež River	Ilova River	Rajić River
Bryophytes								
Physcomitrium eurystomum Sendtn.			+					
Leptobryum pyriforme (Hedw.) Wilson			+					
Physcomitrella patens (Hedw.) Bruch & Schimp.	+	+	+			+	+	+
Riccia cavernosa Hoffm.	+		+	+	+	+		
Riccia frostii Austin				+				
Bryum argenteum Hedw.							+	
Bryum gemmiparum De Not.							+	
Dicranella sp.		+						
Lunularia cruciata (L.) Lindb.							+	
Riccia fluitans L.			+					
Pohlia sp.								+
Vascular plants								
Alisma plantago-aquatica L.			+					
Amaranthus blitum L.					+	+		
Bidens frondosus L.					+	+		
Butomus umbellatus L.			+					
Cyperus fuscus L.			+		+			+
Cyperus glomeratus L.			+		+	+		
Cyperus michelianus (L.) Link					+	+		
Eleocharis acicularis (L.) Roem. & Schult.		+						
Erigeron annuus (L.) Desf.								+
Gnaphalium uliginosum L.	+				+			
Hydrocharis morsus-ranae L.								
Juncus articulatus L.		+	+					
Lindernia procumbens (Krock.) Philcox					+	+		
Lysimachia nummularia L.		+						
Lythrum salicaria L.					+			
Myriophyllum spicatum L.								
Panicum capillare agg.	+							
Persicaria lapathifolia (L.) Delarbre	+				+			
Phragmites australis (Cav.) Trin. ex Steud.			+					
Poa annua L.	+							
Polygonum mite Schrank			+			+		
Portulaca oleracea L.					+	+		
Rorippa amphibia (L.) Besser						+		
Rorippa sylvestris (L.) Besser		+	+					
Sium latifolium L.			+					
Sparganium erectum L.			+					
Typha angustifolia L.			+					
Xanthium strumarium L.					+	+		

(Dierssen 2001). Along the eutrophic Trebež River, vascular species of Bidentetea vegetation was dominant, while only few *Riccia cavernosa* rosettes and *Physcomitrella patens* turfs were recorded underneath the herbs (Fig. 2). By contrast, at the Orljava River, Isoëto-Nanojuncetea vegetation was developed, but the abundance of *R. cavernosa* was not significantly different in comparison to that on the Trebež. In addition, at the eutrophic Lake Bilje, ephemeral bryophytes were present in reed vegetation of the Phragmito-Magnocaricetea Klika in Klika et Novák 1941 alliance (among *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha angustifolia* L. stands), experiencing competition from larger plants (Fig. 2). At the eutrophic Lake Sakadaš, ephemerals were confined to a narrow and steep drawdown zone, not inhabited by vascular plants, presumably because of the dynamics of water level fluctuations, which prevented their colonization.

Bearing it in mind that ephemeral bryophytes of drawdown zones show a spatio-temporal dynamics that is difficult to predict, we can assume that their distribution in Croatia is still not completely established and that these species are more frequent. However, their distribution is impacted by the management of natural water bodies in Croatia, which has profoundly altered their natural habitats through hydromorphological alterations such as channelization, riverbed deepening and embankment (Topić & Vukelić 2009). Population decline of *Physcomitrella patens* and *Riccia cavernosa* has been documented in some Rhine River segments in Germany precisely because of river regulation, where gravel pits became foster habitats for *R. cavernosa* (Nebel & Philippi 2000, 2005). Similarly, artificial reservoirs and fishponds (artificial water bodies as defined by Water Frame Directive), such as Kruščica Reservoir and Donji Miholjac Fishponds, where populations of ephemerals were highly abundant during the favourable conditions, serve as secondary habitats of great significance for these species and should be considered to be of crucial importance in their protection. Recordings of bryophytes in artificial habitats have increased dramatically in the last few decades, showing that there is a significant number of species that are most often found in these secondary habitats (Hugonnot 2005). In such habitats, alternating cycles of waterlogging and drying (drain-refill cycles) are of the utmost relevance for the survival of ephemeral species (Hugonnot 2005).

To conclude, the study of the ephemeral bryophyte vegetation of the drawdown zones resulted in very important findings for the bryoflora of Croatia - one new species (*Physcomitrium eurystomum*), confirmed localities of two dubious species (*Riccia cavernosa* and *R. frostii*) and new localities of two rare species (*Physcomitrella patens* and *Leptobryum pyriforme*). Interestingly, the rare species *Physcomitrium eurystomum* has been recently reported as a novelty for neighbouring Serbia as well, from the surroundings of artificial Lake Vlasina (Papp et al. 2013d).

Given that ephemeral bryophytes of drawdown zones are short lived and appear infrequently, being in the right place at the right time will be of essential importance in future field studies of these fascinating plants.

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4.4. Znanstveni rad 3

Rimac, A.; Alegro, A.; Šegota, V.; Koletić N.; Papp, B. (2021): ***Bryum klinggraeffii* and *Philonotis marchica*–new to the bryoflora of Croatia**. *Herzogia*, 34(2): 255–266.

Bryum klinggraeffii and *Philonotis marchica* – new to the bryoflora of Croatia

Anja Rimac, Antun Alegro*, Vedran Šegota, Nikola Koletić & Beata Papp

Abstract: Rimac, A., Alegro, A., Šegota, V., Koletić, N. & Papp, B. 2021. *Bryum klinggraeffii* and *Philonotis marchica* – new to the bryoflora of Croatia. – Herzogia **34**: 255 –266.

Two new records for the still quite underexplored Croatian bryophyte flora are presented. The ephemeral colonist *Bryum klinggraeffii* was recorded in pioneer dwarf-cyperaceous vegetation along sandy banks of two lowland watercourses of Central and Eastern Croatia (Continental Biogeographical Region), while turfs of *Philonotis marchica* were found on submerged and exposed carbonate rocks in a fast-flowing karstic river in the mountainous region of Gorski Kotar (Alpine Biogeographical Region). Here we provide a detailed description of ecological conditions and a vegetation account for all sites of occurrence of these species in Croatia. These findings of quite rare species, especially *P. marchica*, which is listed as endangered on European level, also represent a valuable contribution to the bryoflora of Southeast Europe, the European region with the greatest deficit in knowledge of bryophytes.

Zusammenfassung: Rimac, A., Alegro, A., Šegota, V., Koletić, N. & Papp, B. 2021. *Bryum klinggraeffii* und *Philonotis marchica* – Neufunde für die Moosflora Kroatiens. – Herzogia **34**: 255 –266.

Zwei Neufunde der noch recht unerforschten kroatischen Moosflora werden vorgestellt. *Bryum klinggraeffii*, ein ephemerer Kolonist, wurde in der Pionier-Zwergbinsenvegetation entlang sandiger Ufer von zwei Tieflandwasserläufen in Mittel- und Ostkroatien (Kontinentale biogeographische Region) nachgewiesen, während Räschen von *Philonotis marchica* auf untergetauchten und freigelegten Karbonatfelsen in einem schnell fließenden Karstfluss in der Bergregion Gorski Kotar (Alpine biogeographische Region) gefunden wurden. Hier geben wir eine detaillierte Beschreibung der ökologischen Bedingungen sowie Vegetationsaufnahmen für alle Fundorte dieser Arten in Kroatien an. Diese Neufunde seltener Arten, insbesondere der auf europäischem Niveau als gefährdet eingestuften *P. marchica*, stellen auch einen wertvollen Beitrag zur Moosflora Südosteuropas dar, einer der europäischen Regionen mit dem größten Wissensmangel über die Moose.

Key words: Southeast Europe, Water Framework Directive, river margin, karstic river, Nanocyperion, Platyhypnidio-Fontinalietea antipyreticae.

Introduction

Southeastern Europe is considered the least studied European region as far as bryology is concerned (Sabovljević et al. 2001, 2011). However, in the last few decades, considerable progress has been made in at least some of the countries, including Croatia. Still, knowledge of the Croatian bryophyte flora remains insufficient; this is particularly true for Central Croatia, while more bryological attention has been paid to the Mediterranean part, even though most of these studies date back to the 19th century (Alegro et al. 2012). Recent field studies conducted in Croatia continue to reveal new national records (e.g. Papp & Sabovljević 2009, Papp et al. 2013a, 2013b, Alegro et al. 2014, 2015, 2019, Sabovljević et al. 2018, Rimac

* corresponding author

et al. 2019a, Šegota et al. 2020a,b), and recently even a record of the very rare hornwort *Nothothylas orbicularis* (Schwein.) Sull., new for Southeastern Europe was made (Rimac et al. 2019b). In the last five years, as many as 27 new species have been reported as new for the Croatian bryoflora (Šegota et al. 2021). On the other hand, species common throughout Europe have been known from only a few localities in Croatia (Alegro & Šegota 2021). These facts indicate that further research is indeed needed, especially as a basis for the protection of bryophytes and their habitats, as well as for distinguishing truly rare species from those considered rare solely because of lack of information.

Here we present two new additions to the bryophyte flora of Croatia, both from freshwater habitats, i.e. riverbeds and river margins, surveyed to assess the ecological status of water bodies as required by the Water Framework Directive (European Community 2000). Along with the distribution data on the species, we provide habitat descriptions and ecological notes for the localities, as well as detailed descriptions of the associated vegetation.

Furthermore, we aim to emphasize the benefits of monitoring of surface waters, not only as a tool for water quality assessment but also for its encouragement and enabling of research into freshwater habitats, as well as into freshwater vegetation (Koletić et al. 2018, 2019, 2021, Rimac et al. 2018, 2020), including bryophytes. With respect only to bryophytes, several new national records were made and published in the past few years as a result of this monitoring programme – e.g. *Fissidens fontanus* (Bach.Pyl.) Steud., *Dichodontium flavescens* (Dicks.) Lindb. (Alegro et al. 2019), *Riccia rhenana* Lorb. ex Müll.Frib. (Ellis et al. 2021), *Physcomitrium sphaericum* (C.F.Ludw. ex Schkuhr) Brid. (Ellis et al. 2020), *Physcomitrium eurystomum* Sendtn., and new localities of several rare ephemeral bryophytes of drawdown zones were identified (Rimac et al. 2019a).

Materials and methods

The field research was undertaken during the vegetation season 2019 and 2020 as a part of the national monitoring of surface waters. The objective of the monitoring was to assess the ecological status of the water bodies, which is one of the requirements of the Water Framework Directive (WFD) (European Community 2000). More than 400 localities including both watercourses and stagnant water bodies, ultimately representative of most of the territory of Croatia, were inspected for aquatic and amphibious flora. This included vascular plants, bryophytes and macroalgae growing in the riverbed and those growing on periodically flooded margins of the water bodies. A list of species at each locality was made. The nomenclature follows Hodgetts et al. (2020) for bryophytes, Euro+Med (2021) for vascular plants and AlgaeBase (Guiry & Guiry 2021) for macroalgae. The syntaxonomical system proposed by Mucina et al. (2016) was applied for vegetation. Collected specimens are deposited in herbarium collection ZA (Thiers 2021). Furthermore, all localities were also sampled for basic water physicochemical and chemical parameters including nutrients.

The water bodies where the new records were made (Fig. 1) are described in more detail below:

The Krka River is a large karstic river with tufa barrages forming a complex system of interchanging fast and slow water flow, waterfalls and barrage lakes. Seven waterfall systems harbouring tufa forming bryophyte communities are situated along the 73 km of the river course before the mouth into the Adriatic Sea. The area belongs to the Mediterranean Biogeographical Region (European Environmental Agency 2021), which largely corresponds to the

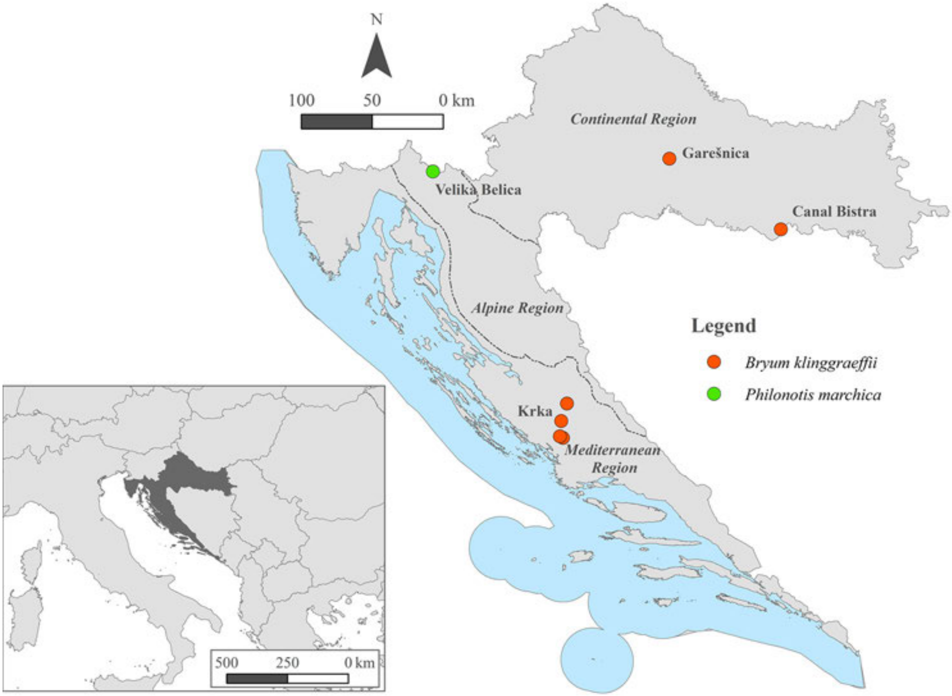

Fig. 1. Occurrence sites of *Bryum klinggraeffii* and *Philonotis marchica* in Croatia.

Mediterranean Subecoregion of the Dinaric Ecoregion according to the system used in the classification of the water bodies for the purposes of the WDF. It is protected as a national park and is a part of the Natura 2000 ecological network.

The Garešnica River is a small-sized river situated in the Moslavina Region in Central Croatia. The area belongs to the Continental Biogeographical Region (European Environmental Agency 2021), i.e. the Pannonian Ecoregion according to the WDF system. The Garešnica River is a tributary of the larger Ilova River, belonging to the Sava River catchment and the Black Sea Basin. At the site of the occurrence, the river has a lowland character and the riverbed has been recently heavily regulated, resulting in extremely steep banks. The substrate of the riverbed is sandy and clayey, while that of the drawdown zone is predominantly sandy.

The Bistra Canal is a medium-sized artificial water body situated in the Slavonia Region of Central Croatia, i.e. Continental Biogeographical Region and Pannonian Ecoregion. It serves as a drainage canal, connecting floodplain area Jelas Polje and the Sava River. The area of Jelas Polje, including the Bistra Canal is a part of the Natura 2000 ecological network and is protected as a significant landscape. Sandy and silty substrates are dominant in the riverbed of the canal and the drawdown zone, while the banks are extremely steep.

The Velika Belica River is a small-sized karstic river situated in the mountainous region of Gorski Kotar, belonging to the Alpine Biogeographical Region (European Environmental Agency 2021), i.e. Continental Subecoregion of the Dinaric Ecoregion according to the system developed for the WFD purposes. The river is a right tributary of the Kupa River in its upper course and as such belongs to the Black Sea Basin.

Results and discussion

Bryum klinggraeffii Schimp.

Specimens examined: Croatia, Mediterranean Region, Krka National Park, Roški Slap Waterfall on the Krka River, on limestone rock at a water mill, 15.97667°E, 43.90250°N, altitude 75 m a.s.l., 14 July 2018, leg. B. Papp, A. Alegro, V. Šegota, A. Rimac, det. B. Papp (BP195929); Croatia, Mediterranean Region, Krka National Park, Manojlovac Waterfall on the Krka River near Čitluk village, on a limestone rock at a waterfall, 16.02511°E, 44.01439°N, altitude 150 m a.s.l., 16 July 2018, leg. B. Papp, A. Alegro, V. Šegota, A. Rimac, det. B. Papp (BP196066); Croatia, Mediterranean Region, Krka National Park, Skradinski Buk Waterfall on the Krka River near Skradin, on limestone rock at a waterfall, 15.96542°E, 43.80247°N, altitude 48 m a.s.l., 17 July 2018, leg. B. Papp, A. Alegro, V. Šegota, A. Rimac, det. B. Papp (BP196093); Mediterranean Region, Krka National Park, Skradinski Buk Waterfall on the Krka River near Skradin, on limestone rock at a waterfall, 15.96511°E, 43.80578°N, altitude 23 m a.s.l., 17 July 2018, leg. B. Papp, A. Alegro, V. Šegota, A. Rimac, det. B. Papp (BP 196153); Croatia, Moslavina Region, Garešnica, the Garešnica River, sandy riverbank, 16.93796°E, 45.568712°N, altitude 112 m a.s.l., 22 August 2019, leg. A. Rimac, N. Koletić, det. A. Rimac, A. Alegro (ZA61988); Croatia, Slavonia Region, Migalovci, sandy banks of Canal Bistra, 17.93187°E, 45.111973°N, altitude 89 m a.s.l., 9 August 2019, leg. A. Rimac, V. Šegota, det. A. Rimac, A. Alegro (ZA61989)

Bryum klinggraeffii is a very small ruderal species growing scattered or more often in tufts only 2–5 mm high. The species belongs to the *B. erythrocarpum* complex, characterized by the presence of rhizoidal tubers, which are in *B. klinggraeffii* bright crimson, 70 – 100 µm in diameter, irregularly spherical, made of relatively few cells with distinctly protuberant walls (Fig. 2). The sporophytes are only occasionally developed and were absent from our sterile specimens but the presence of the rhizoidal tubers, which were abundantly developed on yellowish-brown and slightly papillose rhizoids (Fig. 2), enabled identification of this small species at six localities. Furthermore, the leaves of our specimens were lanceolate to elongate-ovate with a reddish base and acuminate apex, while the costa was shortly excurrent or ending in the leaf apex as expected for this species. The laminal cell size corresponded to the range known for *B. klinggraeffii*, cells being 50 – 70 µm long and 12–15 µm wide, while the leaf margin was hardly bordered, and faintly denticulate above (Smith 2004, Erzberger & Schröder 2013).

Bryum klinggraeffii was recorded in four localities on tufa waterfalls along the Krka River. Here, the species was found on limestone rocks and was mostly accompanied by basophilous species restricted to the splashing zone of the waterfalls and freshwater bryophytes characteristic of clean, cold and basic water. On Skradinski Buk Waterfall, *B. klinggraeffii* was accompanied by omnipresent aquatic mosses *Rhynchostegium riparioides* (Hedw.) Cardot, *Fontinalis antipyretica* Hedw., *Cinclidotus fontinaloides* (Hedw.) P.Beauv. and *Cratoneuron filicinum* (Hedw.) Spruce, as well as the species characteristic of carbonate and tufa substrates, such as *Palustriella commutata* (Hedw.) Ochyra, *Didymodon tophaceus* (Brid.) Lisa, *D. spadiceus* (Mitt.) Limpr., *Fissidens crassipes* subsp. *warnstorfii* (M.Fleisch.) Brugg.-Nann. and *Apopellia endiviifolia* (Dicks.) Nebel & D.Quandt. Furthermore, *Ptychostomum capillare* (Hedw.) Holyoak & N.Pedersen, *B. turbinatum* (Hedw.) J.R.Spence, *Didymodon sinuosus* (Mitt.) Delogne, and *Oxyrrhynchium hians* (Hedw.) Loeske were recorded at Skradinski Buk. A similar situation was found on the waterfalls Roški Slap and Manojlovac, where several more species of basic water were recorded, such as *Chiloscyphus polyanthus* (L.) Corda, *Hygrohypnum luridum* (Hedw.) Jenn. and tufa-forming *Eucladium verticillatum* Bruch & Schimp., as well as species of wet calcareous rocks, i.e. *Didymodon luridus* Hornsch., *Gymnostomum calcareum* Nees & Hornsch., *Gyroweisia tenuis* (Hedw.) Schimp., *Scorpiurium circinatum* (Bruch) M.Fleisch. & Loeske and *Trichostomum crispulum* Bruch. Furthermore, small ruderal species such as *Barbula unguiculata* Hedw., *Bryum ruderale* Crundw. & Nyholm, *Ptychostomum turbinatum* (Hedw.) J.R.Spence and *Funaria hygrometrica* Hedw. were recorded along *B. klinggraeffii.*

On the sandy banks of the Garešnica River (Fig. 2), the species was growing in pioneer ephemeral dwarf-cyperaceous vegetation characteristic of periodically flooded freshwater habitats. This vegetation belongs to the alliance Nanocyperion Koch 1926 of the class Isoëto-Nanojuncetea Br.-Bl. et Tx. in Br.-Bl. et al. 1952 (Mucina et al. 2016).

Here, the species was accompanied by vascular plants *Cyperus michelianus* (L.) Link, *C. fuscus* L., *C. glomeratus* L., *Gnaphalium uliginosum* L., *Gypsophila muralis* L., *Lindernia dubia* (L.) Pennell, *L. procumbens* (Krock.) Philcox and *Ludwigia palustris* (L.) Elliott. Furthermore, several other bryophyte species were recorded in the drawdown zone at this locality, such as *Brachythecium mildeanum* (Schimp.) Schimp., *Bryum argenteum* Hedw., *Physcomitrium sphaericum* (C.F.Ludw. ex Schkuhr) Brid., *Riccia glauca* L. and a terrestrial form of *Riccia fluitans* L. Aquatic vegetation was completely absent due to the recent riverbed regulation, which included riverbed deepening and canalization.

Regarding the vegetation, a similar situation was found on the banks of the Canal Bistra where *B. klinggraeffii* was growing on relatively steep banks accompanied by species characteristic of the Nanocyperion vegetation – *Cyperus fuscus, C. michelianus, Lindernia procumbens, Veronica peregrina* L. and helophyte *Gratiola officinalis* L. It was associated with several bryophyte species as well, such as *Brachythecium mildeanum, Bryum argenteum, Drepanocladus aduncus* (Hedw.) Warnst., *Leptobryum pyriforme* (Hedw.) Wilson, *Physcomitrium patens* (Hedw.) Mitt., *Riccia cavernosa* Hoffm. and *Riccia fluitans*. Aquatic vegetation was abundantly developed in the shallow canal and predominantly included species characteristic of slow-flowing and eutrophic freshwaters such as *Ceratophyllum demersum* L., *Lemna minor* L., *Potamogeton nodosus* Poir., *Potamogeton pusillus* L., *Salvinia natans* (L.) All. and *Spirodela polyrhiza* (L.) Schleid. and macroalgae *Rhizoclonium hieroglyphicum* (C.Agardh) Kützing and *Spirogyra* sp., along with helophyte species *Alisma plantago-aquatica* L., *Butomus umbellatus* L., *Lysimachia vulgaris* L., *Lythrum salicaria* L., *Polygonum mite* Schrank, *Sagittaria sagittifolia* L. and *Sparganium erectum* L.

An ephemeral colonist (Dierssen 2001), having a strategy in which seasonal fluctuations play an important part (During 1979), *B. klinggraeffii* was found on an open sandy substrate among amphibious vegetation typical for periodically flooded drawdown zones in Croatian localities situated in Continental Biogeographical Region and among bryophyte vegetation of wet limestone rocks on waterfalls in Mediterranean Biogeographical Region. This life strategy is shared with other members of the *B. erythrocarpum* complex, the main difference from the true colonists being the rarity of sporophyte occurrence and a strong reliance on asexual reproduction, through rhizoidal tubers in this case (During 1979). In our localities, *B. klinggraeffii* was associated with bryophytes mostly having annual shuttle strategy, such as *Physcomitrium sphaericum, P. patens, Riccia glauca* and *R. cavernosa* and other small ruderal species, one of them being *B. ruderale*, a member of the *B. erythrocarpum* complex as well. All these species are very well adapted to survival in ephemeral habitats such as drawdown zones of different water bodies (lakes, reservoirs, pools and ponds, as well as the sloping margins of rivers). They have a short life span, rapid growth, high reproductive effort and persistent diaspores, which ensures survival in a habitat where favourable circumstances for growth arise infrequently and last for only a brief period (Furness & Hall 1981, During 1979, Kürschner 2004). In the case of the water body's margins, the favourable period corresponds to the summer water-level fall followed by a long period of flooding. This favourable period is too brief to enable vascular plants and perennial bryophytes to colonise and assume dominance, while ephemeral bryophytes, as well as dwarf vascular species of *Nanocyperion* vegetation, thrive and manage to finish their whole life-cycle.

Apart from the margins of water bodies, as a pioneer species, *B. klinggraeffii* inhabits other frequently disturbed open habitats growing on highly calcareous to slightly acidic, sandy to clayey substrates on roadsides, along paths, in arable fields and river gravel bars (Dierssen 2001, Smith 2004, Natcheva & Ganeva 2007, Papp et al. 2015, Kalníková et al. 2017, 2018, Marka et al. 2018).

Bryum klinggraeffii has a wide distribution including North Africa, North and South America, and Asia (India, China, Japan, Turkey, Iran) and Europe (Smith 2004, Shirzadian et al. 2014, Kučera 2017). It is an European Temperate element (Hill & Preston 1998), widely distributed but with relatively scarce records probably being underrecorded due to its small size. It was so far reported from the majority of Southeastern European countries, with evidence of its occurrence still missing only from Bosnia and Herzegovina, Kosovo and the European part of Turkey (Hodgetts & Lockhart 2020). The species was recently recorded in Serbia (Kalníková et al. 2017), however, this was not listed in Hodgetts & Lockhart (2020). It is considered data deficient in Slovenia (Martinčič 2016) and is not evaluated in Bulgaria, with only one locality known from each country – a historical record

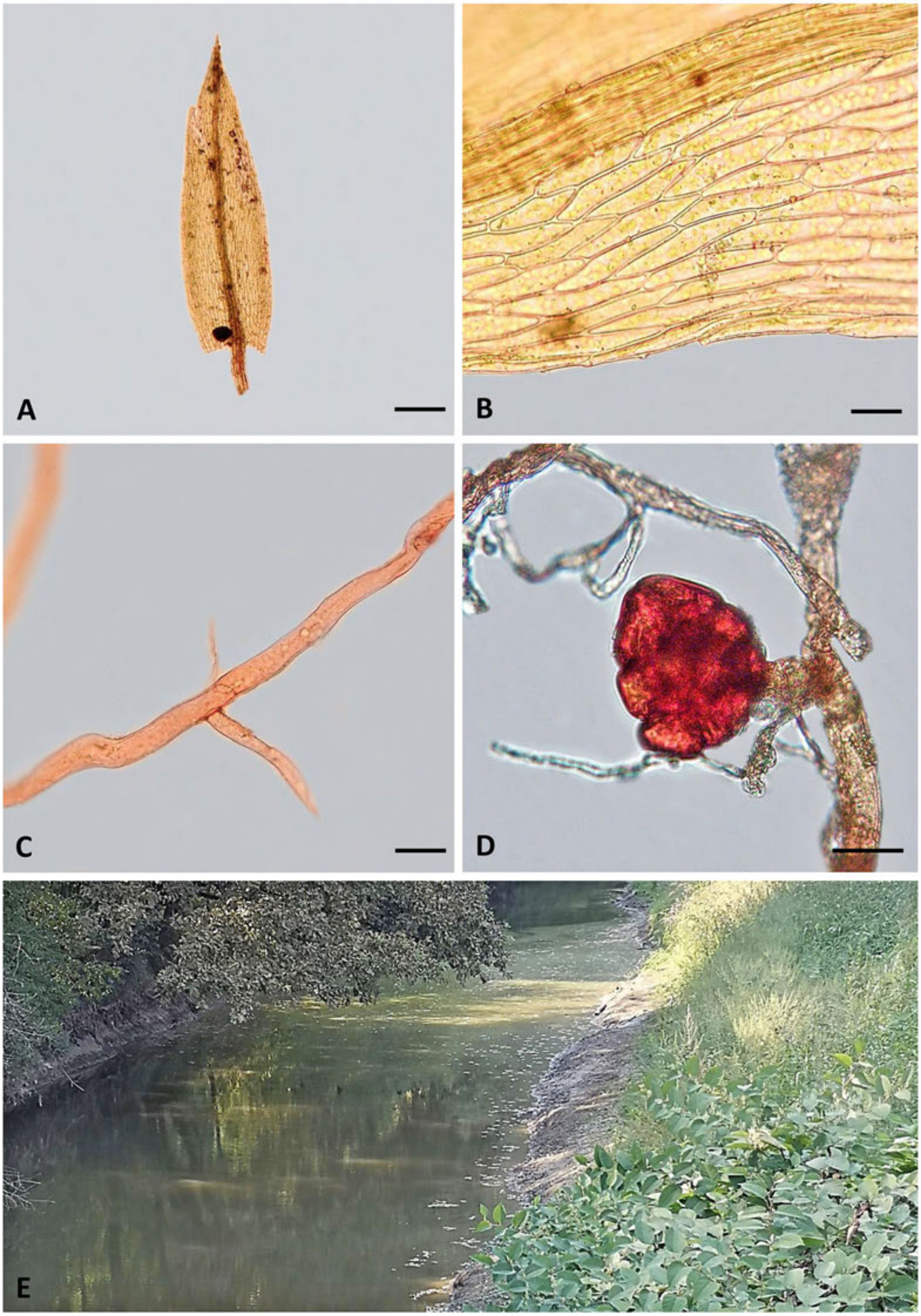

Fig. 2. *Bryum klinggraeffii*. **A** – Leaf. **B** – Laminal cells. **C** – Rhizoids. **D** – Rhizoidal tuber. **E** – Habitat at the Garešnica River. Scales A – 100 µm, B – 10 µm, C – 20 µm, D – 20 µm.

from the bank of the Drava River in Slovenia (BREIDLER 1891) and a relatively recent record from a ruderal habitat along the road in Western Bulgaria (NATCHEVA & GANEVA 2007). The species is assessed as endangered in Romania (ŞTEFĂNUŢ & GOIA 2012), however, such status is probably a consequence of *B. klinggraeffii* being overlooked and under-collected (PAPP et al. 2015). Interestingly, several first records of the species in Southeastern European countries have been made relatively recently – 2003 in Bulgaria (NATCHEVA & GANEVA 2007), 2010 in Albania (PAPP et al. 2018) and 2013 and 2014 in Serbia and Montenegro (KALNÍKOVÁ et al. 2017) pointing to satisfying recent progress in bryological research in this still quite underexplored region (SABOVLJEVIĆ et al. 2001, 2011).

Philonotis marchica (Hedw.) Brid.

Specimen examined: Croatia, Gorski Kotar Region, Kuželj, Velika Belica River, on large carbonate rocks, 14.805035°E, 45.475503°N, altitude 237 m a.s.l., 25 August 2020, leg. A. Rimac, A. Alegro, V. Šegota, det. A. Rimac, A. Alegro (ZA61987)

Philonothis marchica is a pale green, slender to medium-sized species, ca. 1–5 cm high. Our specimens were up to 1.5 cm high, with erect-patent to falcate second leaves. The leaves were 1.4 to 1.5 mm long and 0.4 – 0.5 mm wide, narrowly lanceolate and gradually tapering to an acuminate apex. As well as the leaf size and shape, the leaf margin appearance was characteristic of *P. marchica,* plane with basal marginal leaf cells smooth or weakly serrulate and distal margin uniserrate. The species is very well distinguishable by having distal leaf cells with mammillae/papillae at the distal cell end and no distinct mammilla/papilla at the proximal cell end (Fig. 3). These cells were of a shape and within a range reported for the species, i.e. rectangular, 22– 47 µm long and 7.5 –10 µm wide at the base and more elongated in the distal part of the lamina ca. 20 –50 µm long and 5 µm wide. Furthermore, the leaves had excurrent costa, 50 –75 µm wide at leaf base as expected in *P. marchica* (SMITH 2004, KOPONEN et al. 2012). In our specimens sporophytes were not developed, but this dioecious species is known for producing sporophytes only rarely and relying mainly on vegetative reproduction by bulbils produced in leaf axils (PETIT 1976).

Philonotis marchica was found in the lower course of the Velika Bjelica River near its confluence with the Kupa River. It was growing in the watercourse in turfs on submerged larger carbonate rocks as well as on those exposed during low water level and in the splash zone of the river bank. At the locality, the water was clean, up to 100 cm deep with a fast and moderately turbulent course. The dominant substrate in the riverbed was large rock (megalithal – > 40 cm) covering ca. 50 % of the investigated stretch, while smaller rocks (macrolithal – 20 – 40 cm) and pebbles (mesolithal 6.3 –20 cm) were represented with a smaller share of 20 % each, the rest being sandy and gravelly sediment. *Philonotis marchica* was here accompanied exclusively by bryophyte species forming a bryophyte community characteristic of fast-flowing, cold and clean karstic rivers belonging to the class Platyhypnidio-Fontinalietea antipyreticae Philippi 1956 (MUCINA et al. 2016). Total coverage of bryophytes was estimated to ca. 50 % of the investigated area and the species were in general confined to larger and thus the most stable rocks. Mean annual values of water physicochemical parameters show cold (T=10.9 °C), slightly basic (pH=8.2), alkaline ˙(TA= 179.1 mg$CaCO_3$/L), well-oxygenated (DO=11.6 mgO_2/L) water of low conductivity (EC=279.5 µS/cm) with low nutrient levels (mean concentration of ammonia was <0.003 mgN/L, of nitrates 0.695 mgN/L and of orthophosphates 0.019 mgP/L) and low total dissolved carbon ˙(TOC=1.346 mgC/L) and biochemical oxygen demand (BOD_5= 1.183 mgO_2/L). In these conditions, the most abundant associates of *P. marchica* were *Hygrohypnum luridum, Jungermannia atrovirens* Dumort., *Rhynchostegium riparioides, Ptychostomum pseudotriquetrum* (Hedw.) J.R.Spence & H.P.Ramsay ex Holyoak & N.Pedersen and *Apopellia endiviifolia*. Furthermore, *Cinclidotus fontinaloides, Cratoneuron filicinum, Eucladium verticillatum, Fissidens crassipes* Wilson ex Bruch & Schimp., *Fontinalis antipyretica* were recorded in the watercourse, while *Conocephalum salebrosum* Szweyk., Buczk. & Odrzyk., *Didymodon fallax* (Hedw.) R.H.Zander and *Pohlia melanodon* (Brid.) A.J.Shaw were restricted to the riverbank splash zone. Most of the recorded species are known to inhabit calcareous rivers showing an ecological preference for clean, neutral to basic waters (CESCHIN et al. 2012, 2015, VIEIRA et al. 2018).

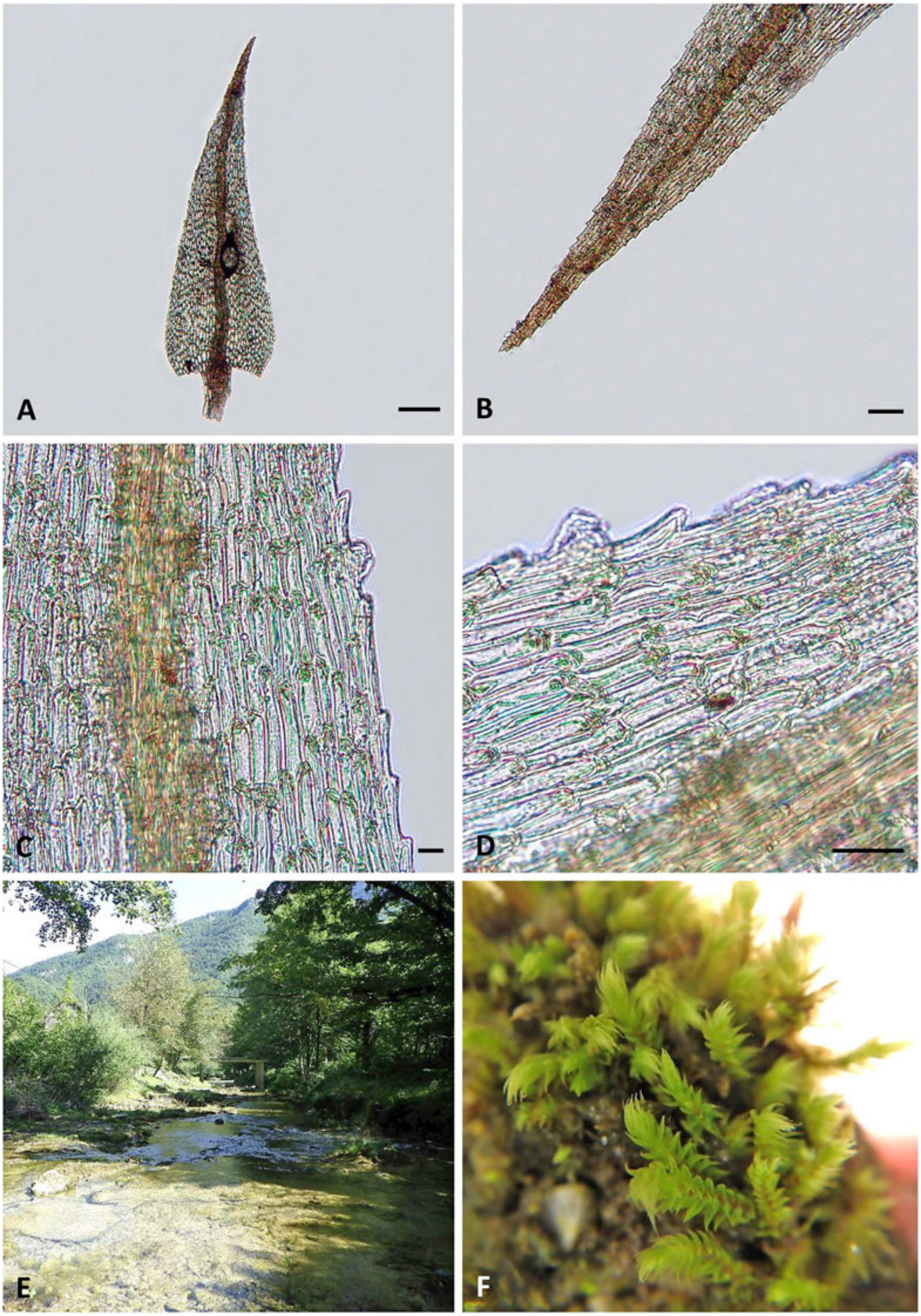

Fig. 3. *Philonotis marchica.* **A** – Leaf. **B** – Leaf apex. **C, D** – Leaf cells with papillae at distal cell end and uniserrate leaf margin. **E** – Habitat at the Velika Belica River. **F** – Habitus. Scales: A – 100 µm, B – 50 µm, C – 10 µm, D – 20 µm.

Philonotis marchica is in general known to grow mostly on limestone and sandstone substrate in the source areas of the watercourses, alongside and in streams and rivers as well as on waterfalls (PAVLETIĆ 1955, PAPP & ERZBERGER 2005, 2007, 2009, HÁJEK et al. 2007, HÁJKOVÁ et al. 2007, PAPP et al. 2015). Avoiding strong water current, as a semi-aquatic emergent species (VITT & GLIME 1984), it is more often confined to open rock surfaces with a permanent water film and the splash zone. Furthermore, it inhabits wet and moist sandy and clayey soils in marshes (GANEVA 2011), minerotrophic fens (ŠOLTÉS 2008) and wet meadows (PAPP et al. 2013c) and was recently found in a limestone quarry on wet lime gravel with spring water seeping from a nearby rock wall (BURYOVÁ & HRADÍLEK 2006), while in a cold area of the Russian Far East it grew on wet cliffs near a hot waterfall (KOPONEN et al. 2012).

The species has a very wide world distribution including North America (ZALES 1973), Northern Africa and Macaronesia (SMITH 2004, ROS et al. 1999), Southwest Asia (FREY & KÜRSCHNER 1991, AKHANI & KÜRSCHNER 2004, KÜRSCHNER & FREY 2011, UYAR & ÇETIN 2004) and Caucasus (IGNATOVA et al. 2008) and was recently also reported from the Russian Far East (KOPONEN et al. 2012). As a European Southern-temperate element, it is widely distributed but quite rare across Europe. It has been so far reported from all Southeastern European countries, with the evidence on its presence missing only from Croatia (HODGETTS & LOCKHART 2020). It is assessed as endangered in Bulgaria (NATCHEVA et al. 2006), near threatened in Romania (ŞTEFĂNUT & GOIA 2012) and Slovenia (MARTINČIČ 2016) and data deficient in Hungary (PAPP et al. 2010) and Albania (HODGETTS & LOCKHART 2020). According to the new Red List, the species is endangered on the European level (HODGETTS et al. 2020). The main threats to this species are habitat loss and fragmentation, mainly due to the drainage and cultivation of wetland habitats, as well as soil and water pollution in the case of localities near human settlements (GRIMS et al. 1999, GANEVA 2011). However, the Croatian locality in the Gorski Kotar Region is very well preserved and no threats to the species or its habitat could be identified. The river water is clean with low nutrient content and of very good ecological status, there are no significant hydromorphological alterations or other anthropogenic pressures. Although we surveyed localities with similar ecological conditions situated on small rivers, this isolated small population of *P. marchica* remains the only one in Croatia.

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4.5. Znanstveni rad 4

Rimac, A.; Alegro, A.; Šegota, V.; Vuković, N.; Koletić, N. (2022): **Ecological Preferences and Bioindication Potential of Freshwater Bryophytes – Insights from Croatian Watercourses**. *Plants* 11(24), 3451: 1–29.

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Article

Ecological Preferences and Indication Potential of Freshwater Bryophytes–Insights from Croatian Watercourses

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Abstract: A comprehensive survey of Croatian watercourses covering the whole of the national territory and investigating inherent watercourse heterogeneity was conducted to explore the ecological responses of the most frequent freshwater bryophytes with respect to water chemistry variables and land use within the catchment area. Direct multivariate ordination (CCA) of vegetation data paired with 18 environmental variables revealed that freshwater bryophytes and their assemblages were segregated along the gradients of water chemistry and the proportion of natural and urban area within the catchment. Generalized additive models (GAM) were employed to explore the ecological responses of individual species. The results showed that most of the investigated species preferred natural, clean, well-oxygenated watercourses, with low nutrient and organic matter content, as well as with low electrical conductivity. Species such as *Palustriella falcata*, *Eucladium vertcillatum*, *Dichodontium flavescens* and *Jungermannia atrovirens* had narrow ecological niches and were restricted to pristine watercourses, while the most frequent and widely distributed species, such as *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Cratoneuron filicinum*, *Fissidens crassipes*, *Cinclidotus fontinaloides* and *C. riparius*, had a wide ecological tolerance. *Riccia fluitans* and *Leptodyctium riparium* had wide ecological ranges, but with optima in hypereutrophic waters with high nutrient and organic content, as well as high electrical conductivity. Furthermore, these two species were frequently associated with a high share of intensive agriculture and a low share of natural land within the catchment.

Keywords: aquatic bryophytes; autecology; ecological responses; water quality; land use; bioindicators

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1. Introduction

Freshwater bryophytes are a common but unassuming and frequently overlooked component of freshwater ecosystems. They constitute an important part of macrophyte vegetation, especially in headwater streams, mountain and upland watercourses, and highly seasonal and intermittent rivers [1–5], and they are the most prominent part of the vegetation of waterfalls and cascades [6–9]. Bryophytes dominate the vegetation of such lotic habitats due to a wide variety of structural and physiological adaptations [6,10,11]. These make them resilient to seasonal desiccation, high water velocity and associated mechanical stress, which other macrophyte representatives cannot withstand. Freshwater bryophytes play a significant role in these harsh environments as dominant primary producers and influence the overall nutrient and trophic dynamics. Bryophyte beds make an excellent shelter and habitat for various invertebrate assemblages and provide a surface for the growth of epiphytic algae [12,13]. Freshwater bryophytes occur in middle and lower river reaches as well, but in much lower abundance, with the exception of some of the Mediterranean rivers. In middle and lower reaches, they are in general represented by a lower number of rheophyte taxa restricted to larger and thus more stable substrates, or by a somewhat more diverse set of semi-aquatic species inhabiting periodically flooded river margins [14,15].

While the presence and coverage of freshwater bryophytes are primarily determined by riverbed stability and substrate size [16–18], physiographic, geological, climatic and water chemistry factors have been identified as major environmental drivers influencing species diversity and composition [1–3,16–22]. Furthermore, changes in stream and river hydrology and morphology, as well as anthropogenically influenced changes in water chemistry, strongly impact individual bryophyte species and whole communities [20,23,24]. Aquatic plant communities, including bryophyte assemblages, have been recognized as valuable indicators of stream biointegrity and water quality [21,25–32] and thus useful in the bioassessment of rivers and lakes. Freshwater habitats have been subject to various anthropogenic pressures in the past decades, with eutrophication and hydromorphological degradation being the most prominent stressors, often acting simultaneously [33–35]. They are most often related to urbanization, industrialization, as well as intensive agriculture. Continued stress on the freshwater habitats and its detrimental impact on freshwater biota has resulted, however, in raised awareness of these issues, leading to encouraging progress in the understanding of the ecology of freshwater biota and their communities. This was followed by the development of corresponding biomonitoring methods and legislation frameworks such as the Water Framework Directive (WFD) [28,29,36].

The use of bryophytes as indicators of water quality and ecological status strongly depends on the knowledge of their distribution and ecological responses since the sensitivity of individual species (i.e., the presence or absence of species with narrow ecological niches) or their tolerance (widely distributed with broad niches) to stressors constitutes the basis of biomonitoring [3]. Several studies conducted in Europe have investigated how various physicochemical parameters influence freshwater bryophyte assemblages and how individual species behave along these gradients. Water temperature, pH, conductivity, dissolved oxygen, biochemical oxygen demand and nutrient concentration were identified as the most important among studied water physicochemical parameters [2,16,21,27,30,37–42]. Combined stressors, such as intensive agriculture, were recognized as important parameters in the segregation of bryophyte species as well [20]. Furthermore, species richness and total bryophyte abundance were proven to be good metrics indicative of eutrophication and trophic status in general [20,43].

Several systems developed for river monitoring based on aquatic plants include bryophytes as well; e.g., systems developed to monitor trophic status such as the Mean Trophic Rank (MTR) [44,45] and River Macrophyte Nutrient Index (RMNI) [46] developed in the UK, the L'Indice Biologique Macrophytique en Rivière (IMBR) developed in France [47], the Macrophyte Index for Rivers (MIR) originally developed in Poland [48,49], and the Index of Trophy for European Macrophytes (ITEM), which is a pan-European common metric for assessing nutrient enrichment, synthesizing various national macrophyte scoring systems [50]. These systems are based on a list of indicator taxa, while in the assessment of trophic status, average scores of indicative species are weighted by their abundance, with some of the indices taking into account the taxon's ecological amplitude as well [51]. The majority of included bryophytes are recognized as good bioindicators with narrow ecological tolerance, preferring oligo- and mesotrophic conditions. The above-mentioned indices were adjusted and calibrated to meet the requirements of assessing the ecological status of water bodies as required by the WFD. Bryophytes are also listed as indicator species in the German Reference Index (RI) [52,53], which was designed to meet the requirements of the WFD and to indicate non-specific anthropogenic disturbance, not solely trophic status. The basis of this index is the river type-specific definition of reference and non-specific disturbance-indicating taxa. The WFD adopts a more holistic approach to ecological assessment, being based on the structure and function of different biological quality elements in different types of waterbodies, which is philosophically different from traditional approaches to biomonitoring in Europe, and closer to concepts of biotic integrity or ecosystem health [46]. In this context, macrophytes, including bryophytes, have been considered particularly suitable because they are non-mobile and can thus more precisely indicate local changes in the environment, and additionally, they integrate changes over longer periods and successive disturbances, which is especially true for perennials [25,26].

Available research which has quantitatively investigated the relationship of freshwater bryophytes and water physicochemical variables mostly included limited geographic areas and river basins or was concentrated on a particular watercourse type, such as highly seasonal rivers [20]. Additionally, several studies have identified species which may have developed different ecotypes, displaying different ecological behaviour in different river basins and geographic areas [37,38]. For these reasons, further research into the ecology and bioindication potential of this group covering new geographic areas and wide ecological gradients is needed. Prior to our study, no similar work had been conducted in Croatia, and only a few papers on this topic exist from Southeastern Europe, all of them from Bulgaria [14,20,54].

Having this in mind, we conducted comprehensive field research covering the whole of Croatian territory and investigated the inherent watercourse heterogeneity including the karstic watercourses and their characteristic species. Our aims were to:

1. Determine how water physicochemical factors and land use influence species occurrences and segregation;
2. Explore ecological responses of freshwater bryophyte species and augment data on the autecology and ecological preferences of freshwater bryophytes;
3. Infer the bioindication potential of selected species from their optima and ecological tolerance.

2. Results

A total of 21 freshwater bryophyte species (8 rheophytes, 1 hydrophyte, 2 amphyphytes and 10 hygrophytes) were collected from at least five localities, out of 648 localities surveyed, and were thus included in further analysis. Finally, 182 localities were retained by this criterion, 124 within the Dinaric and 58 within the Pannonian Ecoregion of Croatia (Figure 1). This encompassed diverse watercourse types, from oligotrophic small streams to eutrophic large rivers and artificial canals (Table A1, Appendix A), therefore covering wide gradients suitable for the study of the autecology of selected species. In the Pannonian Ecoregion, the highest bryophyte richness was recorded in small lowland watercourses (16 species). In the Dinaric-Continental Subecoregion, this was true for montane and mid-altitude medium and large watercourses (20 species), followed by montane and mid-altitude small watercourses (18 species). In the Dinaric-Mediterranean Subecoregion, the highest bryophyte richness was recorded in lowland and mid-altitude small watercourses (16 species) (Table A2, Appendix A). As for lowland medium and large watercourses, they harboured a similar set of a total of 11 species and similar overall bryophyte frequency both in the Pannonian Ecoregion and the Dinaric-Mediterranean Subecoregion, while these were substantially higher in the Dinaric-Continental Subecoregion. Species number, as well as their overall frequencies and abundance, in both Dinaric subecoregions exceeded those in the Pannonian Ecoregion (Table A2, Appendix A, Table S1).

Among the most frequent species in our study were *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Cratoneuron filicnum* and *Leptodyctium riparium*, with the latter being more frequent in the Pannonian Ecoregion, i.e., its lowland watercourses. Species such as *Didymodon tophaceus*, *Eucladium verticillatum* and *Jungermannia atrovirens* were exclusive to the Dinaric Ecoregion, while *Cinclidotus aquaticus*, *Apopellia endiviifola*, *Brachythecium rivulare*, *Dichodontium flavescens* and *D. pellucidum* were more frequent in the Dinaric Ecoregion and within the Pannonian Ecoregion, restricted to only lowland small watercourses.

Species medians revealed the differences in species preferences across the gradients of selected variables, with *Riccia fluitans* and *Leptodyctium riparium* being most obviously separated from the rest of the species in terms of water chemistry and land use variables. These species showed preferences for hypereutrophic water with high nutrient loads, biochemical (BOD) and chemical (COD) oxygen demand and high electrical conductivity, and were more frequently associated with a higher share of intensive agriculture and a low share of natural land within the catchment area (Figure 2). Most other species had their median values in clean water, with lower nutrient content, low BOD, COD and electrical conductivity, indicative of good water quality status.

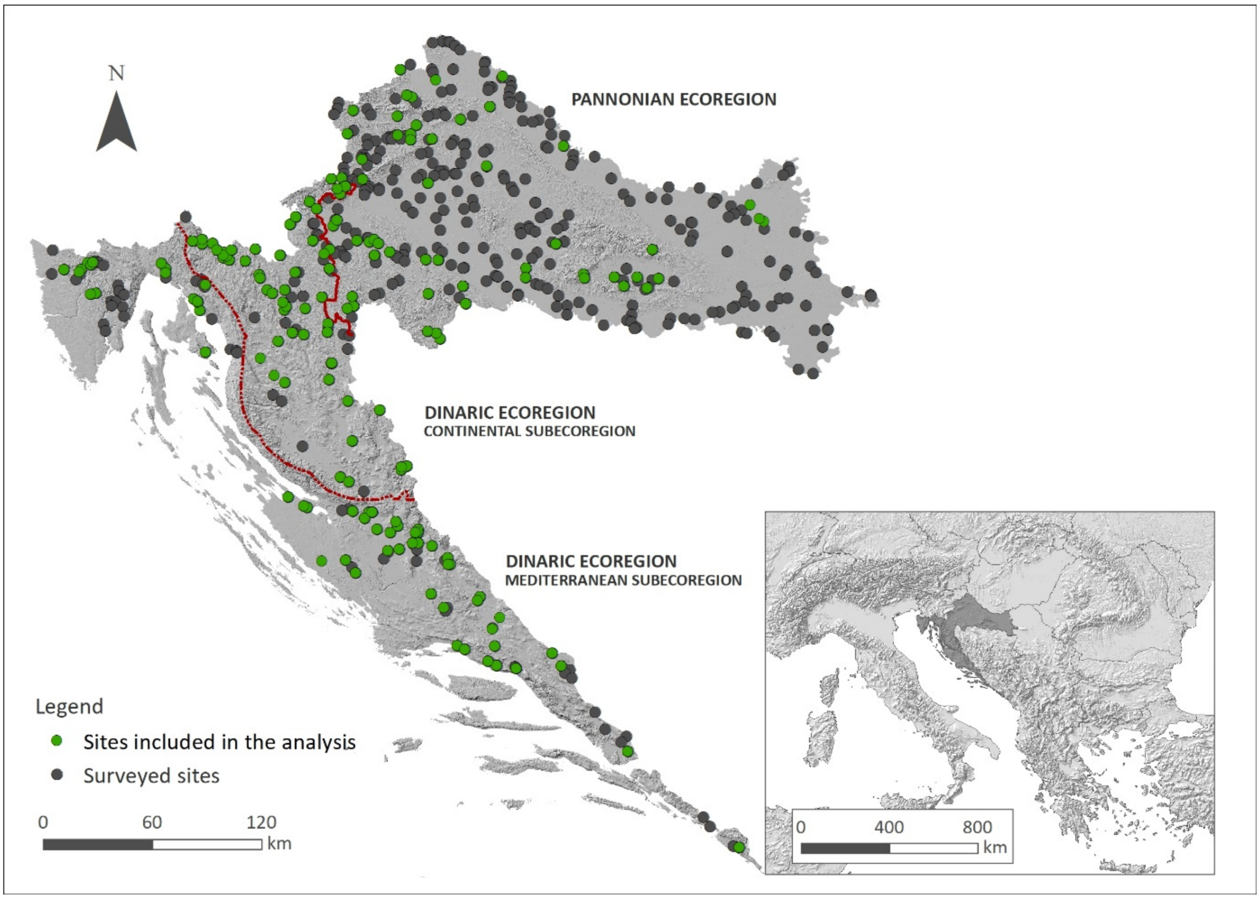
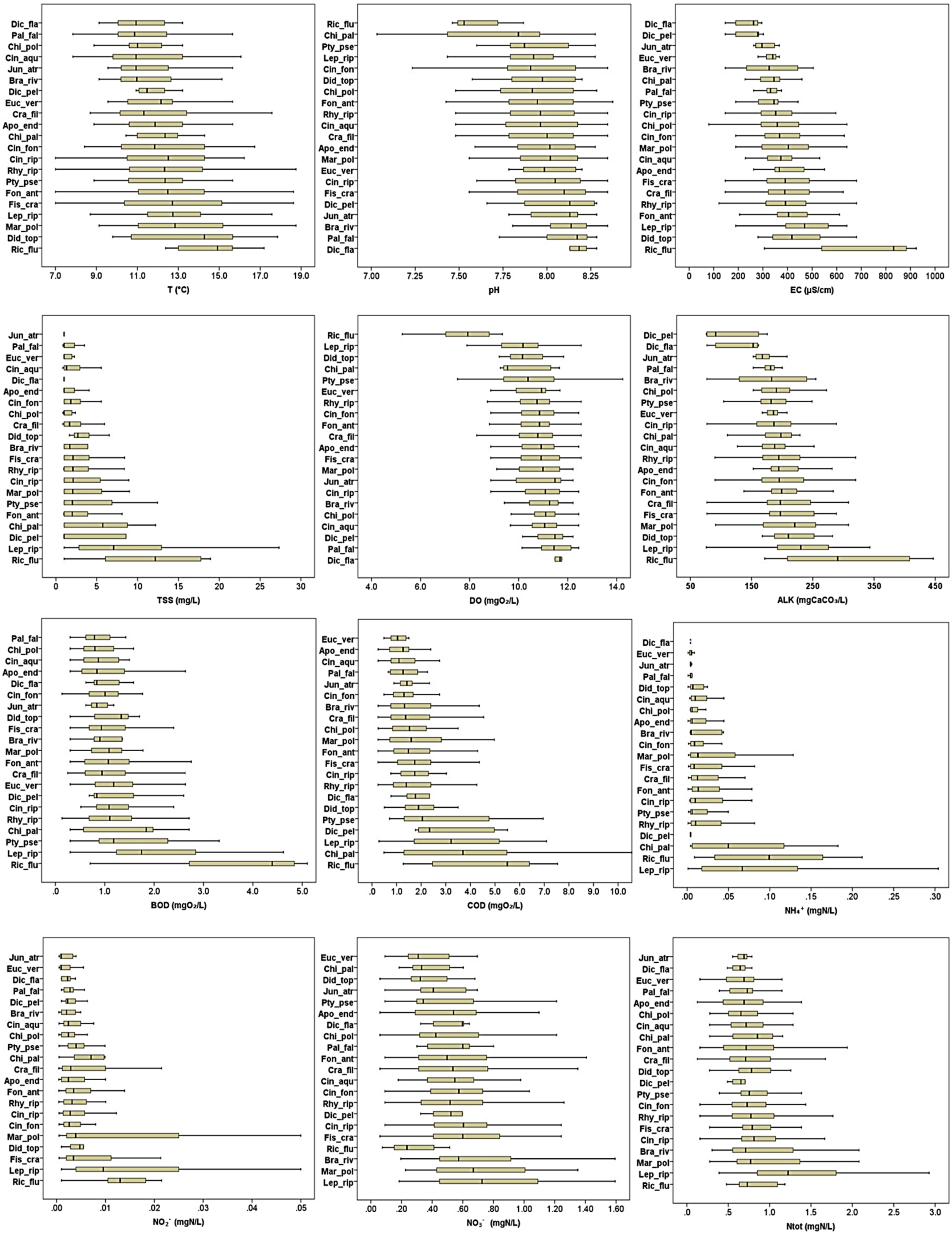


Figure 1. Study area with 648 sampling sites and the 182 sites included in the analysis covering the whole Croatian territory (Southeastern Europe).

Table 1. Environmental variables and abbreviations used.

	Environmental Variable	Abbreviation
Water physicochemical parameters	Water temperature	T (°C)
	Water pH	pH
	Electrical conductivity	EC (µS/cm)
	Total suspended solids	TSS (mg/L)
	Dissolved oxygen	DO (mgO_2/L)
	Total alkalinity	ALK ($mgCaCO_3$/L)
	Biochemical oxygen demand	BOD (mgO_2/L)
	Chemical oxygen demand	COD (mgO_2/L)
Water chemical parameters	Ammonium	NH_4^+ (mgN/L)
	Nitrites	NO_2^- (mgN/L)
	Nitrates	NO_3^- (mgN/L)
	Total nitrogen	N_{tot} (mgN/L)
	Orthophosphates	PO_4^{3-} (mgP/L)
	Total phosphorus	P_{tot} (mgP/L)
Land use within the catchment area	Natural area	NAT (%)
	Intensive agriculture	IAG (%)
	Extensive agriculture	EAG (%)
	Urban area	URB (%)



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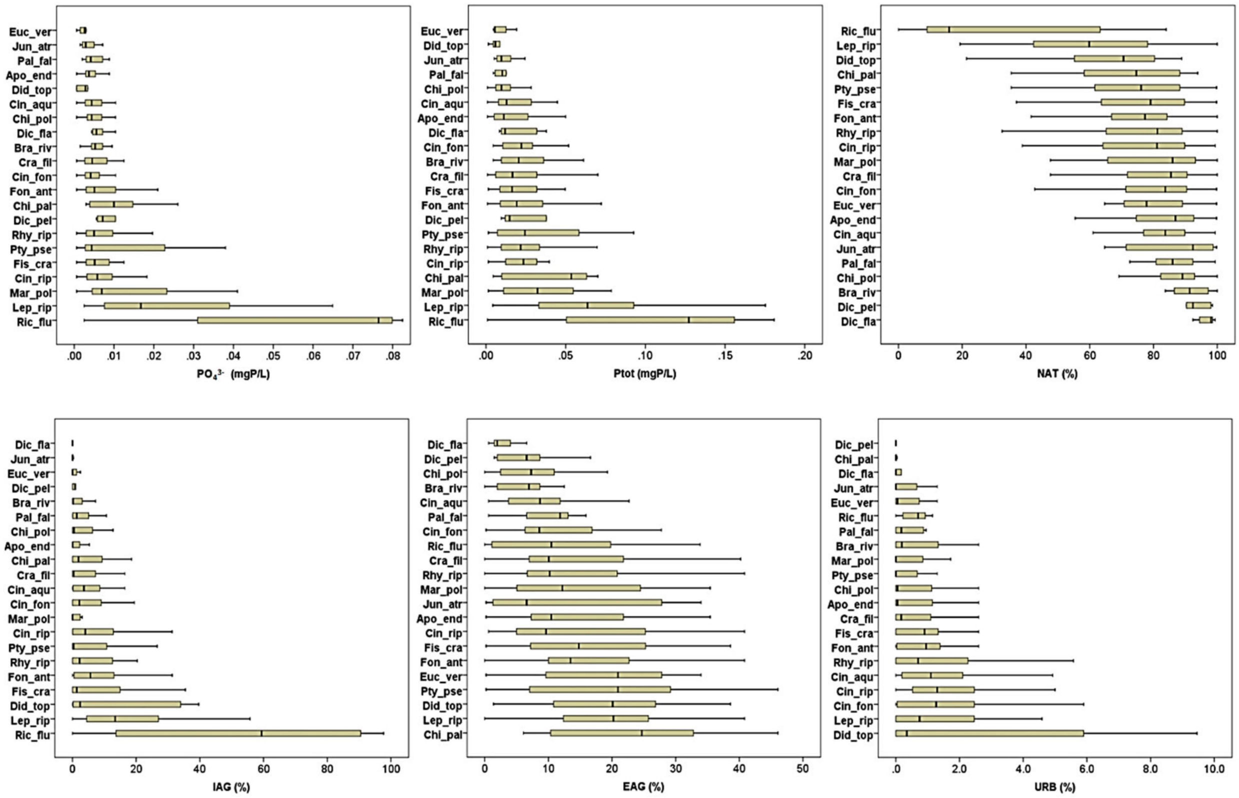


Figure 2. Box-plot graphs for ecological variables within the study for the freshwater bryophytes. For abbreviations of ecological variables see Table 1. Apo end–*Apopellia endiviifolia* (Dicks.) Nebel & D.Quandt, Bra riv–*Brachythecium rivulare* Schimp., Chi pal–*Chiloscyphus pallescens* (Ehrh. ex Hoffm.) Dumort., Chi pol–*Chiloscyphus polyanthos* (L.) Corda, Cin aqu–*Cinclidotus aquaticus* (Hedw.) Bruch et Schimp., Cin fon–*Cinclidotus fontinaloides* (Hedw.) P. Beauv., Cin rip–*Cinclidotus riparius* (Host ex Brid.) Arn., Cra fil–*Cratoneuron filicinum* (Hedw.) Spruce, Dic fla–*Dichodontium flavescens* (Dicks.) Lindb., Dic pel–*Dichodontium pellucidum* (Hedw.) Schimp., Did top–*Didymodon tophaceus* (Brid.) Lisa, Euc ver–*Eucladium verticillatum* (With.) Bruch et Schimp., Fis cra–*Fissidens crassipes* Wilson ex Bruch & Schimp., Fon ant–*Fontinalis antipyretica* Hedw., Jun atr–*Jungermannia atrovirens* Dumort., Lep rip–*Leptodictyum riparium* (Hedw.) Warnst., Mar pol–*Marchantia polymorpha* L., Pal fal–*Palustriella falcata* (Brid.) Hedenäs, Pty pse–*Ptychostomum pseudotriquetrum* (Hedw.) J.R.Spence & H.P.Ramsay ex Holyoak & N.Pedersen, Rhy rip–*Rhynchostegium riparioides* (Hedw.) Cardot, Ric flu–*Riccia fluitans* L.

2.1. Ordination Results

Results of the CCA revealed similar patterns in the ecological preferences of the studied species, except for *Riccia fluitans*, which, as an outlier, was excluded from this analysis. The first axis of the CCA explained 51.06% and the second 16.01% of the variation in the relationship between vegetation data and environmental factors, while eigenvalues of the first and the second axis equalled 0.4 and 0.1, respectively. Forward selection of environmental variables revealed a set of eight most-contributing and non-redundant variables in determining the freshwater bryophyte distribution (Appendix B). Total nitrogen concentration made the largest contribution to explaining the observed variation in bryophyte composition, followed by the share of the natural area within the catchment and chemical oxygen demand. Overall analysis was statistically significant ($p < 0.002$), which was confirmed by the Monte Carlo test (999 permutations).

The CCA analysis revealed the main compositional gradient representing the water quality along axis 1—from sites with well-oxygenated water, situated within unchanged catchment areas under little anthropogenic influence to sites with high nutrient loads, i.e., high concentration of total nitrogen and total phosphorous, as well as high chemical oxygen demand (Figures 3 and 4). Additionally, the share of the natural area within the catchment was strongly negatively correlated with agricultural land—extensive (AGE, $r_s = -0.72$, $p < 0.001$) and intensive agriculture (AGI, $r_s = -0.81$, $p < 0.001$). Regarding the nutrients, total phosphorus was highly positively correlated with orthophosphates (PO_4^{3-}, $r_s = 0.82$, $p < 0.001$), total suspended solids (TSS, $r_s = 0.73$, $p < 0.001$) and biochemical oxygen demand (BOD, $r_s = 0.73$, $p < 0.001$), and total nitrogen with nitrates (NO_3^-, $r_s = 0.85$, $p < 0.001$), while COD correlated with biochemical oxygen demand (BOD, $r_s = 0.76$, $p < 0.001$). Sites with higher nutrient loads, as well as COD and higher shares of agricultural land, were mostly those on the watercourses situated in the Pannonian Ecoregion and were quite well separated from the sites situated in the Dinaric Ecoregion on the CCA ordination biplot, especially those of its Mediterranean Subecoregion (Figure 3). The Dinaric Ecoregion included sites with intermediate values of the studied parameters, as well as sites within natural catchments, with oligotrophic, well-oxygenated water and somewhat higher pH.

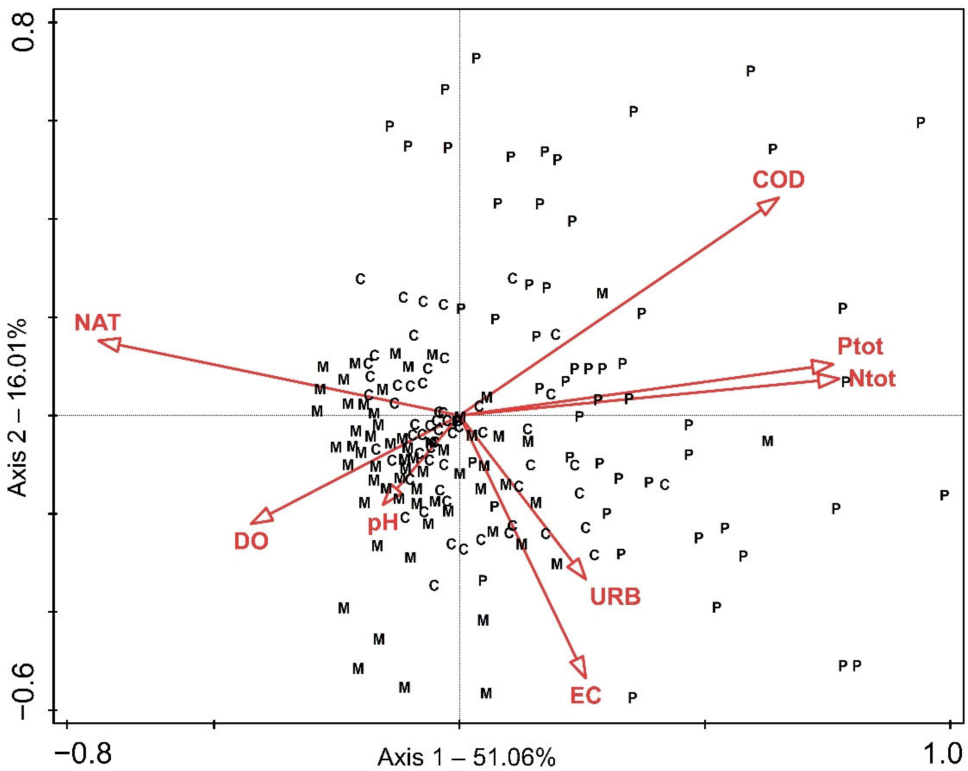


Figure 3. CCA biplot for samples and environmental variables. C—Dinaric-Continental Subecoregion, M—Dinaric-Mediterranean Subecoregion, P—Pannonian Ecoregion, COD—chemical oxygen demand, DO—dissolved oxygen, EC—electrical conductivity, NAT—natural area within the catchment, N_{tot}—concentration of total nitrogen, URB—urban area within the catchment.

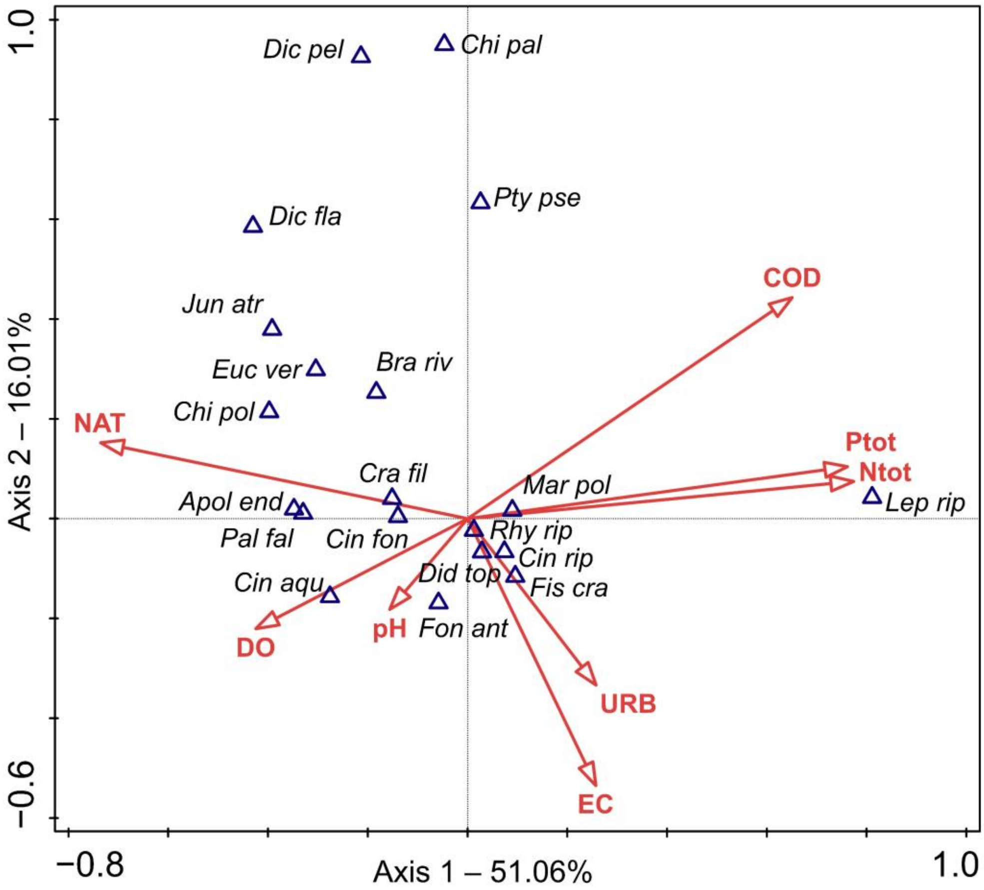


Figure 4. CCA biplot for species and environmental variables. COD—chemical oxygen demand, DO—dissolved oxygen, EC—electrical conductivity, NAT—natural area within the catchment, Ntot—concentration of total nitrogen, URB—urban area within the catchment. For abbreviations of species names, see Figure 2.

The CCA analysis demonstrated the affinity of particular freshwater bryophyte species to different water chemistry and land use (Figure 4). Mosses such as *Cinclidotus aquaticus*, *Eucladium verticllatum* and *Palustriella falcata*, as well as the liverworts *Apopellia endiviifolia*, *Chiloscyphus polyanthos* and *Jungermannia atrovirens*, preferred clean, well-oxygenated water and were more strongly correlated with a higher share of natural area within the catchment. On the other hand, *Leptodyctium riparium* was of all species investigated the most prominently associated with eutrophic water, while *Cratoneuron filicinum*, *Cinclidotus fontinaloides*, *C. riparius*, *Fontinalis antipyretica*, *Fissidens crassipes* and *Rhynchostegium riparioides* displayed intermediate behavior along the first axis. Among these, *Fissidens crassipes*, *Cinclidotus riparius* and *Rhynchostegium riparioides* were associated with a higher share of urban area within the catchment and higher electrical conductivity.

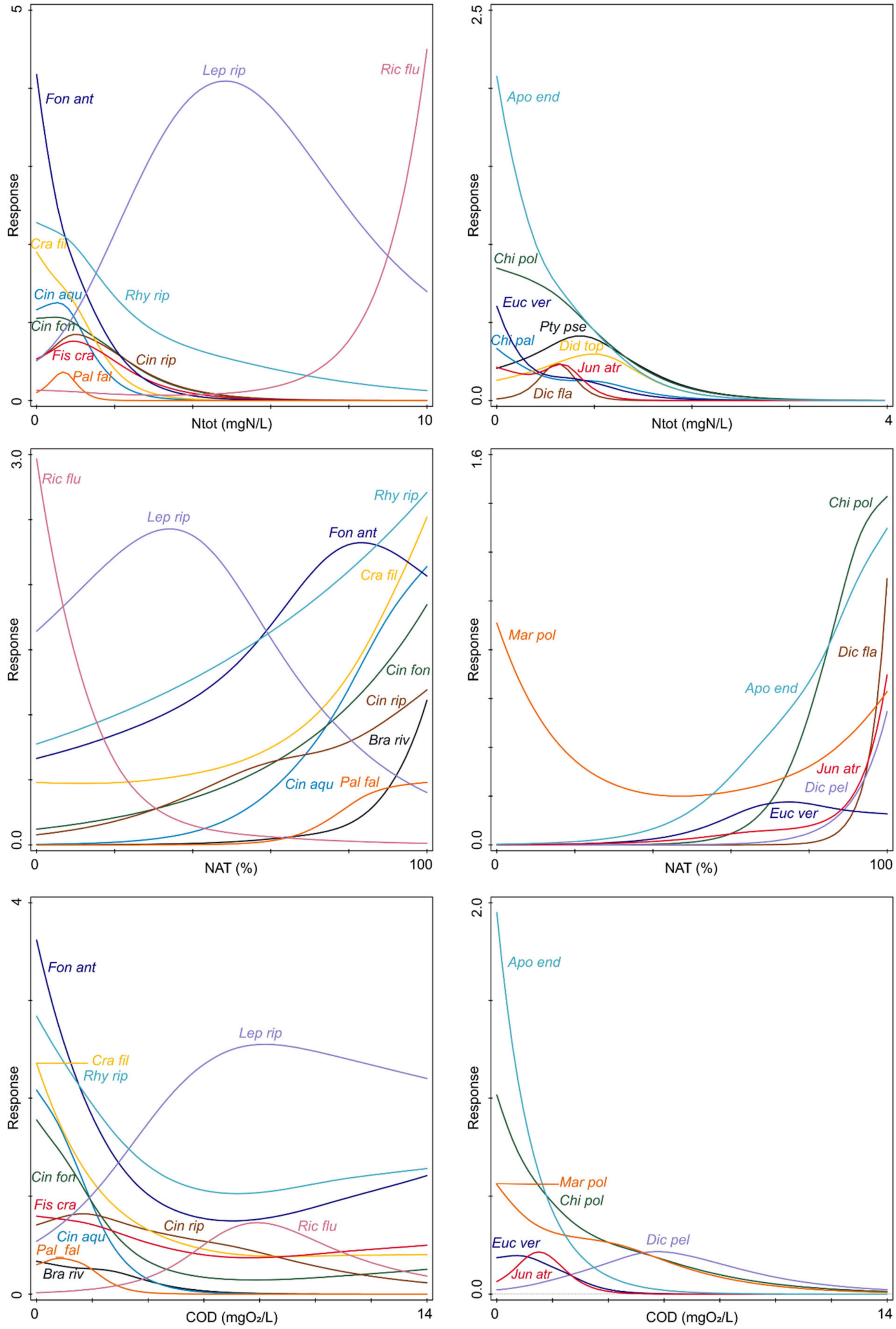
2.2. Species Responses to Environmental Variables

The GAM response curves of species abundances for the most influential environmental variables from the CCA additionally corroborated observed patterns (Figure 5). Response curves of GAMs fitted for *Riccia fluitans* and *Leptodyctium riparium* against total nitrogen and total phosphorus showed the preference of both species for hypereutrophic water with a high nutrient load. Regarding total nitrogen, the means of both species were quite high, 1.93 mgN/L for *Riccia fluitans* and 1.45 mgN/L for *Leptodyctium riparium* (Appendix C). *Leptodyctium riparium* displayed unimodal response with an optimum at 4.90 mgN/L, while *Riccia fluitans* had a monotonically increasing response curve and a maximum at 8.9 mgN/L. Other species had their optima at low levels of total nitrogen

(<0.5 mgN/L). A steep decline in abundance with increasing concentrations of total nitrogen was characteristic of most of these species (Figure 5). Species such as *Palustriella falcata*, *Jungermannia atrovirens*, *Dichodotium flavescens*, *Eucladium vericillatum*, *Didymodon tophaceus*, *Chilosyphus polyanthos* and *Apopellia endiviifolia* had quite low maxima and narrow niches, while the maxima of *Cratoneuron filicinum*, *Brachythecium rivulare*, *Cinclidotus fontinaloides*, *C. riparius*, *Fissidens crassipes*, *Fontinalis antipyretica* and *Marchantia polymorpha* were between 2 and 3 mgN/L, and the maximum of *Rhynchostegium riparioides* reached 5.18 mgN/L. These sets of species showed similar behavior with respect to nitrate and ammonium concentration, as well as other water chemistry parameters associated with water quality–orthophosphates, total phosphorus, the amount of organic compounds in water (COD, BOD) and electrical conductivity (Figures 1 and 5).

Regarding the total phosphorus concentration, most of the studied species displayed mean values below 0.04 mgP/L, while the mean values of *Riccia fluitans* and *Leptodyctium riparium* were 0.177 and 0.094 mgP/L, respectively, which corresponded to eutrophic water. The optima of both species were in hypereutrophic water; the optimum of *Leptodyctium riparium* amounted to 0.21 mgP/L, and of *Riccia fluitans* to 0.699 mgP/L (Figure 5). All other species had their optima in oligotrophic water with respect to phosphorus, with *Palustriella falcata*, *Eucladium verticillatum*, *Jungermannia atrovirens*, *Apopellia endiviifolia*, *Chiloscyphus polyanthos*, *Didymodon tophaceus* and *Dichodontium flavescens* having steep monotonically decreasing response curves and low maxima, and *Cinclidotus aquaticus* and *Brachythecum rivulare* tolerating somewhat higher concentrations and disappearing at 0.1 and 0.165 mgP/L, respectively. The abundance of rheophytes such as *Fontinalis antipyretica*, *Cinclidotus fontinaloides*, *C. riparius*, *Fissidens crassipes* and *Rhynchostegium riparioides*, as well as of the amphyphyte *Cratoneuron filicinum* and the hygrophytes *Chiloscyphus pallescens* and *Ptychostomum pseudotriquetrum*, decreased with increasing concentration of total phosphorus, but these species displayed tolerance to eutrophic water. Total phosphorus concentration was highly correlated with total suspended solids, and species preferring, or displaying a high degree of tolerance to, eutrophic water were tolerant of more turbid water as well. These were *Leptodyctium riparium, Fontinalis antipyretica, Rhynchostegium riparioides* and *Riccia fluitans*, persisting at TSS values over 40 mg/L. Nevertheless, the TSS means of all species were below 15 mg/L (Appendix C), i.e., in clear water.

Species response curves for chemical oxygen demand showed that the majority of the species had low optima (<1 mgO_2/L), while *Leptodyctium riparium* and *Riccia fluitans* peaked at high levels, 8.2 and 7.9 mgO_2/L, respectively, and *Dichodontium pellucidum* at 4.9 mgO_2/L (Figure 5). Again, the majority of rheophytes, as well as the amphiphyte *Cratoneuron filicinum*, showed tolerance to high levels of COD, although their abundance decreased with increasing COD. This was also the case with the hygrophyte *Chiloscyphus pallescens*, which was recorded at a maximum COD level of 10.67 mgO_2/L. GAMs were not successfully fitted for *Didymodon tophaceus* and *Ptychostomum pseudotriquetrum*, but these species tolerated very high COD levels as well, with maxima around 10.6 mgO_2/L. Species restricted to low levels were *Eucladium verticillatum*, *Jungermannia atrovirens*, *Apopellia endiviifolia*, *Cinclidotus aquaticus*, *Brachythecium rivulare* and *Chiloscyphus polyanthos*. Similar patterns in species preferences can be observed from the descriptive statistics regarding biochemical oxygen demand as well (Appendix C).



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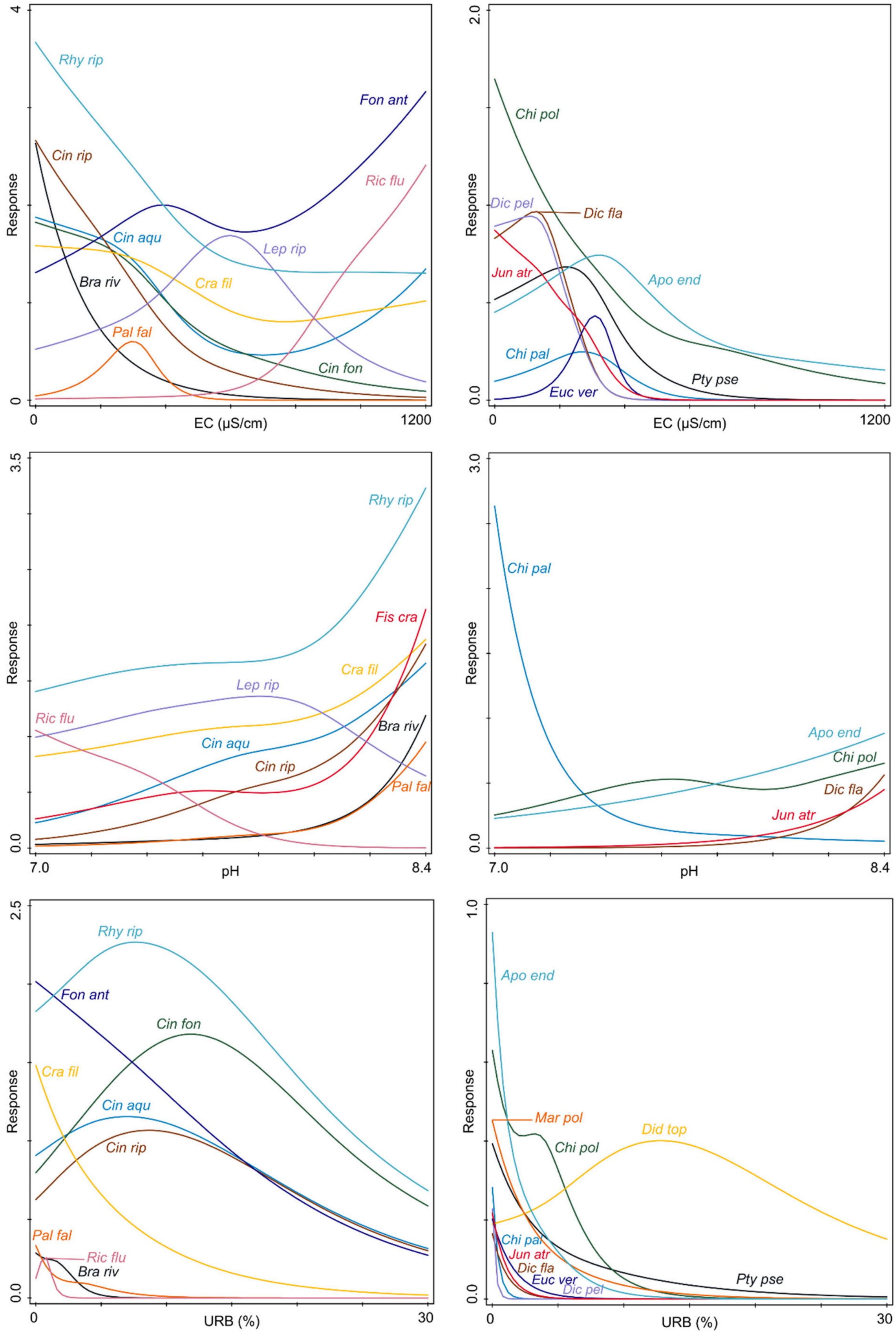

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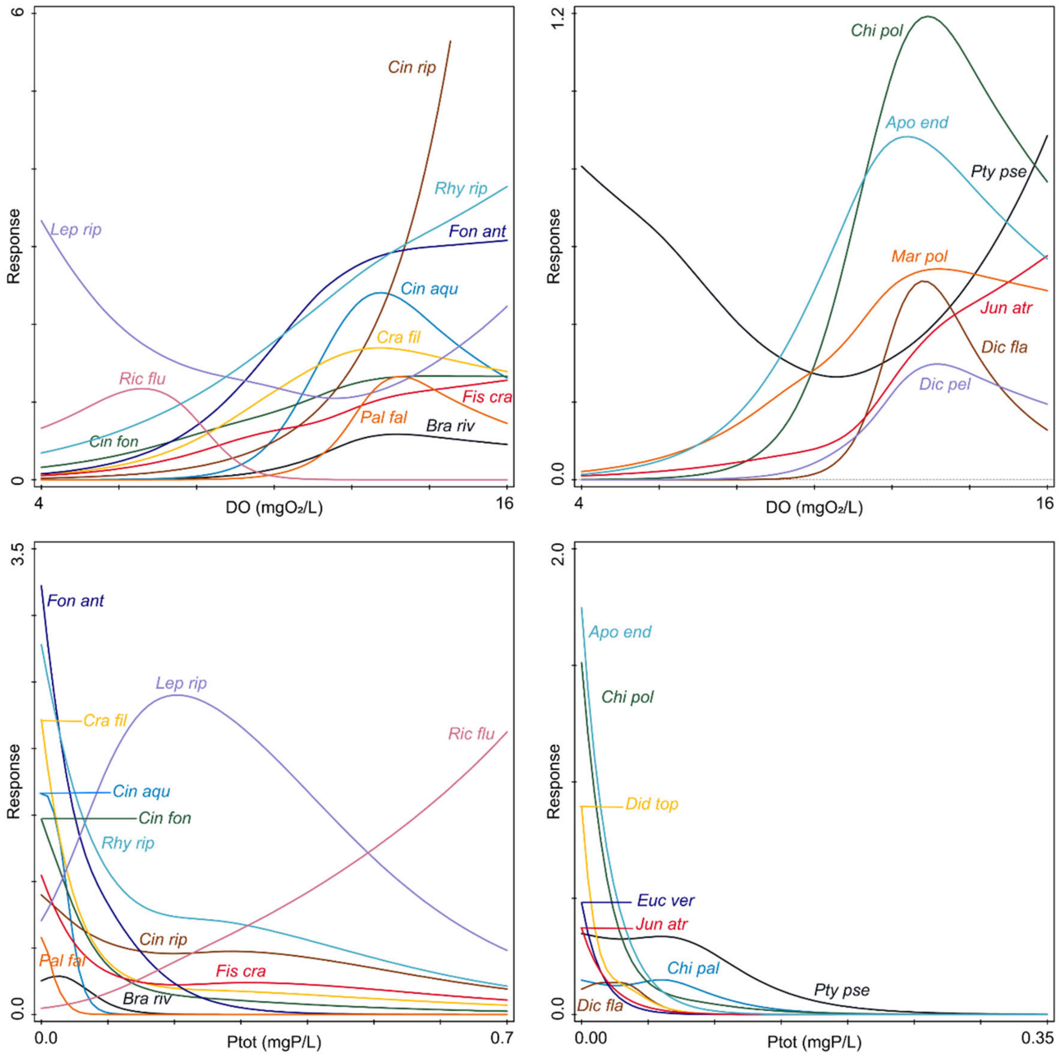

Figure 5. Species response curves for selected environmental gradients (most-contributing according to CCA forward selection) modelled by general additive model. For clarity, response curves of rheophytes, hydrophytes and amphyphytes are shown in graphs on the left and those of hygrophytes on the right side of the figure. Response—abundance estimated on van der Maarel ordinal scale. For species abbreviations, see Figure 2.

Response curves fitted against dissolved oxygen revealed that the majority of species investigated had their optima in well-oxygenated water (Figure 5). Mean values of this parameter ranged from 10.13 to 11.58 mgO_2/L, except for *Riccia fluitans.* This species peaked at 6.5 mgO_2/L, but was present within a quite wide range, from 5.25 to 9.34 mgO_2/L. The optimum of *Leptodyctium riparium* was at 4 mgO_2/L, with a prominent decrease in abundance with increasing oxygen concentration. This coincided with the rise in the abundance of other rheophyte species. Nevertheless, *Leptodyctium riparium* was still present in well-oxygenated watercourses, displaying wide tolerance. The set of species restricted to high dissolved oxygen concentration was similar to that characteristic of low nutrient and COD situations. These were *Brachytehcium rivulare*, *Palustriella falcata, Jungermannia atrovirens*, *Dichodontium flavescens*, *Chiloscyphus polyanthos*, *Apopellia endiviifolia* and *Cinclidotus aquaticus*, as well as *Dichodontium pellucidum* and *Chiloscyphus pallescens*. Other species, such as *Rhynchostegium riparioides*, *Fontinalis antipyretica*, *Fissidens crassipes*, *Cratoneuron filicinum*, *Cinclidotus fontinaloides*, *C. riparius* and *Ptychostomum pseudotriquetrum* had wider ranges and were present in less oxygenated watercourses, although in lower abundance.

The response curve was not successfully fitted for *Didymodon tophaceus*, but the mean value was at 10.13 mgO_2/L and the minimum as low as 7.51 mgO_2/L (Appendix C).

Regarding electrical conductivity, most of the species had optima below 400 μS/cm but displayed different tolerances to higher values. Hygrophyte species had quite narrow niches, with *Apopellia endiviifolia* and *Chiloscyphus polyanthos* and *Ptychostomum pseudotriquetrum* being more tolerant to elevated electrical conductivity than other hygrophytes. Response curves were not fitted for *Dydimodon tophaceus* and *Marchantia polymorpha* but descriptive statistics indicated wide tolerance with respect to electrical conductivity (Appendix C). Similar behavior can be seen in the case of the majority of rheophyte species, except for *Brachythecium rivulare* and *Palustriella falcata*, which were restricted to waters with lower conductivity, while *Rhynchostegium riparioides*, *Cratoneuron filicinum*, *Cinclidotus aqauticus*, *C. riparius* and *C. fontinaloides* showed tolerance to high values of electrical conductivity. The optimum of *Leptodyctium riparium* was around 600 μS/cm, while the abundance of *Fontinalis antipyretica* and *Riccia fluitans* displayed a continuous rise until the maxima above 900 μS/cm (Figure 5). Concerning water pH values, most of the species preferred basic water and showed an increase in abundance above pH 7.9. *Leptodyctium riparium* peaked at 7.87, which was followed by a relatively steep decrease in abundance, which coincided with the increase in the abundance of basophilous species (Figure 5). Furthermore, the abundance of *Riccia fluitans* decreased along the pH gradient and the species disappeared when pH exceeded 7.87. Similarly, *Chiloscyphus pallescens* showed a sharp decrease along this gradient, being most abundant around pH 7, but still present at 8.2.

GAM response curves fitted against the share of the natural land within the catchment area revealed that the majority of the freshwater bryophytes studied had their optima at values over 80%. Exceptions were again *Riccia fluitans* and *Leptodyctium riparium*. *Riccia fluitans* displayed a steep monotonically decreasing curve with an optimum in the least natural catchments (Figure 5). The optimum of *Leptodyctium riparium* was at 33.57% of the natural area within the catchment but it was present in more natural catchments as well, although in lower abundance. Mean values of this parameter were over 80% for the set of species that were restricted to waters with low nutrient content, low COD, BOD and electrical conductivity, and high dissolved oxygen (*Eucladium verticillatum*, *Apopellia endiviifolia*, *Cinclidotus aquaticus*, *Jungermannia atrovirens*, *Palustriella falcata*, *Chiloscyphus polyanthos*, *Dichodontium flavescens* and *D. pellucidum*), and ranged between 60 and 80% for all other species with wider niches, except for *Riccia fluitans* with a mean value equal to 34.91% (Appendix C). This species was highly associated with intensive agriculture, with the mean value of this parameter being 52.20% and a maximum of 97.69% (Figure 1, Appendix C). On the other hand, species such as *Eucladium verticillatum*, *Brachythecium rivulare*, *Palustriella falcata*, *Dichodontium flavescens*, *D. pellucidum*, *Chiloscyphus polyanthos*, *Apopellia endiviifolia* and *Jungermannia atrovirens* had mean values of intensive agriculture within the catchment area lower than 5% and maxima lower than 15%. Considering the urban area within the catchment, most species preferred low levels, with rheophytes such as *Rhynchostegium riparioides, Cinclidotus fontinaloides, C. aquaticus, C. riparioides, Fontinalis antipyretica* and *Cratoneuron filicinum* peaking below 12% and then decreasing in abundance and finally disappearing at around 30% of urban area within the catchment.

3. Discussion

Our results are in line with previous studies, confirming that different water chemistry factors associated with water quality influence the distribution and segregation of freshwater bryophytes [37,38]. Similarly, changes in land use within the catchment area, such as an increase in the share of intensive agriculture or urban area, which are most often associated with water pollution and eutrophication, also influence freshwater bryophytes [20].

The results of our study reveal that most of the studied freshwater bryophytes prefer natural catchments with clear, well-oxygenated water that has low nutrient levels, both nitrogen and phosphorus, as well as a low amount of organic matter. Similar results were obtained from the study of the freshwater bryophytes in the Tiber River Basin (Italy), where the majority of the species showed a general preference for fast-flowing, clear, cold and oxygenated water with a low nutrient load, especially low ammonia and orthophosphates [21].

Although most species in our study had their optima in water of good quality, differences in their responses to investigated ecological gradients revealed a set of species with very narrow ecological niches concerning this group of parameters. Species such as *Palustriella falcata*, *Eucladium verticillatum*, *Jungermannia atrovirens* and *Dichodontium flavescens* were mostly characteristic of the Dinaric Ecoregion and were recorded in pristine karstic watercourses with low nutrient content and low organic matter. Similar results were reported earlier for these species. In a study dealing with Natura 2000 petrifying sources in Belgium, the occurrence of *Eucladium verticillatum*, a tufa-forming species, was negatively correlated with ammonium and phosphate concentration, and the species preferred open habitats with lots of light [41]. *Palustriella falcata*, known as calcicole, is mostly linked to base-rich, neutro-alkaline, cold and turbulent oligotrophic streams with low conductivity [3,18,39], while *Jungermannia atrovirens* was reported in both oligotrophic and meso-oligotrophic waters [55]. *Dichodontium flavescens* was in our study almost exclusive to the Dinaric-Continental Subecoregion and restricted to clean, cold and turbulent karstic watercourses with almost completely natural catchment areas. Similarly, according to Dierßen [56], *Dichodontium flavescens* inhabits areas under no or only weak human impact.

Additionally, species such as *Cinclidotus aquaticus*, *Chiloscyphus polyanthos*, *Apopellia endiviifolia* and *Didymodon tophaceus* had somewhat wider niches, with optima in oligotrophic waters but tolerating elevated nutrient levels to some extent. However, their presence in higher abundance may be indicative of good water quality. *Cinclidotus aquaticus*, was previously reported as a species of clear, cold and turbulent oligotrophic waters and highlighted as a valid indicator of water quality [21], unlike *Apopellia endiviifolia* which was found across a broader spectrum of water quality, from oligotrophic [38,57] to eutrophic [21,41,58], tolerating high nitrate, ammonium and orthophosphate concentration.

All the above-mentioned species are basophilous and are either exclusive to or dominantly occur in karstic rivers of the Dinaric Ecoregion. These rivers flow over carbonate bedrock which influences water pH and alkalinity, as well as species assemblages where basophilous, i.e., acid-sensitive, taxa dominate. An important influence of geology, water pH and alkalinity on aquatic bryophytes has been already demonstrated on the European level [1,2,4,5,30,39,57] and beyond [6,17,40,59], and clear segregation of aquatic bryophytes along the alkalinity and pH gradient was recently demonstrated for Croatian bryophyte-dominated watercourses as well [22]. The latter study identified three communities characterized by different basophilous species which were mostly associated with karstic rivers of the Dinaric Ecoregion, and two communities in small rivers situated in the Pannonian Ecoregion, which were dominated by a high share of hygrophyte taxa inhabiting periodically flooded river margins. The influence of the water pH on aquatic bryophytes was evident in our study as well, although the investigated pH gradient was quite short. The majority of the species included in our study preferred near-neutral to basic water, with the mosses *Eucladium verticillatum*, *Didymodon tophaceues*, *Palustriella falcata, Brachythecium rivulare, Fissidens crassipes* and *Cinclidotus aquaticus*, as well as the liverworts *Apopellia endiviifolia* and *Chiloscyphus polyanthos*, being most strongly associated with higher water pH and having high frequencies and abundance in the watercourses of the Dinaric Ecoregion. This ecoregion is known to harbor greater diversity regarding freshwater bryophytes [15] and their communities [22] since its fast, cold montane and semi-montane karstic rivers with larger and more stable substrates provide more suitable habitats than the lowland rivers of the Pannonian Ecoregion, which are usually slow and warmer, with dominantly sandy and gravelly substrates. This was demonstrated in our study as well, with the highest number of species recorded in montane and mid-altitude small watercourses, followed by montane and mid-altitude medium and large watercourses of the Continental Subecoregion, which are both characterized by the dominance of large and medium substrates.

Widely distributed and frequent species such as *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Cratoneuron filicinum*, *Fissdens crassipes*, *Brachythecium rivulare*, *Cinclidotus riparius* and *C. fontinaloides* displayed in our research broad ecological tolerance regarding the investigated environmental gradients, with their maxima of ammonium, nitrate and total nitrogen concentrations exceeding the thresholds for good water chemistry status set for all water body types included in this analysis according to the Croatian Regulation on Water Quality Standard [60]. Furthermore, the same was observed in the case of their maxima for total phosphorus, except for *Brachythecium rivulare* and *Fontinalis antipyretica*. The maxima of the latter two species did exceed the values set for good status considering total phosphorous for all water body types of the Dinaric Ecoregion, which are naturally more oligotrophic. However, for all investigated Pannonian water body types, they exceeded the values set for very good status. Regarding the organic matter content, the COD maxima of *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Cratoneuron filicinum*, *Fissdens crassipes*, *Cinclidotus riparius* and *C. fontinaloides* again exceeded thresholds set for good status for all types in the study, while that of *Brachythecium rivulare* exceeded thresholds set for all investigated Dinaric types, as well as thresholds for very good status regarding this parameter for investigated Panonnian types. Nevertheless, all of these species had their optima in clean, oligotrophic, oxygenated and slightly basic water of low electrical conductivity, except for *Fontinalis antipyretica*, which preferred high values of the latter parameter. *Fontinalis antipyretica* and *Rhynchostegoium riparioides*, which are both widespread and the most common species in Croatia [15], are often found together occupying a wide range of freshwater habitats [18,39,61,62]. Their broad trophic range, and in general wide ecological behavior, have been emphasized by several authors [3,18,24,25,38], with *Fontinalis antipyretica* being more tolerant of eutrophication and elevated electrical conductivity [21,38]. However, its frequency was reported to increase with decreasing concentrations of nitrates and phosphates [21], as was the case with its abundance in our study. Interestingly, *Fontinalis antipyretica*, as well as *Fissides crassipes*, displayed distinctly different response curves in two hydrographic networks in France and Belgium [37], having a maximal frequency in oligotrophic water in one and tolerating the most polluted waters in the other, while their overall optima within the study were in eutrophic waters when data from both hydrographic networks were considered simultaneously. The authors suggested that such species may include several ecotypes with different trophic requirements within different hydrographic networks, which is possibly a result of microevolution, favoured by the fact that river basins are rarely interconnected. The observed differences in autecology between populations of the same species complicate the use of certain aquatic bryophytes as bioindicators of water quality on a large scale, and thus further research on their distribution and ecological responses, as well as their taxonomy, microevolution processes and ecophysiology, is still welcomed to elucidate the influence of environmental factors on the species that have so far shown contradictory behavior.

Furthermore, studies encompassing larger geographic areas and gradients of water quality parameters could improve the knowledge of the autecology and ecological tolerance of species that have shown contradictory behavior in different studies. An example of contradictory findings being reported for the same species can be seen in the case of the common basophilous species, *Cratoneuron filicinum*. It was reported as a valid bioindicator of water quality with narrow ecological tolerance, preferring clear, turbulent waters, with temperature below 12 °C, low conductivity (below 300 μS/cm), and low concentration of nutrients (phosphates about 0.01 mg/L, a maximum concentration of ammonium 0.10 mg/L and nitrates 0.90 mg/L), in a study covering the Tiber River Basin [21], while tolerance to light to moderate eutrophication has been reported in several other studies as well [20,41,58]. In our study, which encompassed a larger and more diverse geographic area with many different hydrographic networks, a broader ecological behavior of this species was observed. It was more frequent in colder watercourses, but occurred in much warmer waters as well, with a maximum of 18.75 °C. Similarly, it preferred medium conductivity of about 420 μS/cm, while tolerating levels as high as 941 μS/cm. Regarding the nutrients, its optimum was in clean water of low trophy level, but the species persisted in waters with a great nutrient load as well (e.g., maximum concentration of total phosphorous 0.28 mgP/L, orthophosphates 0.09 mgP/L, total nitrogen 2.00 mgN/L and ammonium 0.86 mgN/L).

Riccia fluitans and *Leptodyctium riparium* showed markedly different behavior from all the other species in our study, preferring neutral, warmer, hypereutrophic water with high electrical conductivity and organic matter content, which is in line with previous findings [18,21,23,26,37,63]. In our study, although these species displayed quite wide water quality niches, their abundance was the highest in eutrophic situations, with a prominent fall in abundance with an increase in water quality. Similarly, the frequency of these species was positively correlated with the concentration of phosphates and ammonia, as well as electrical conductivity, in a study conducted by Ceschin et al. [21] in Italy. While these authors referred to both species as indicators of eutrophication, others found that *Leptodyctium riparium* exhibited a broad ecological range [37], from oligotrophic streams to hypertrophic rivers, and did not appear as a reliable indicator, although its frequency increased under eutrophic conditions [38]. Noteworthy is that in our study, the optima of *Riccia fluitans* for total nitrogen and total phosphorous (8.9 mgN/L and 0.7 mgP/L, respectively) were considerably higher than those of *L. riparium* (4.9 mgN/L and 0.21 mgP/L, respectively), and the species favoured the sites with the least natural catchment areas with a large proportion of intensive agriculture. *Leptodyctium riparium* was also associated with a low proportion of natural area within the catchment, with an optimum of 33.57%. The case was similar in highly seasonal rivers in Bulgaria, where the species was characteristic for sites located in regions with increased intensive agriculture and watercourses with reduced flow and pronounced silting, as well as elevated total nitrogen concentration [20]. Both species had a higher frequency in the Pannonian than in the Dinaric Ecoregion of Croatia, which is clearly related to the characteristics of its water bodies; these are more frequently slow and eutrophic lowland streams, rivers and canals with unstable sediment [64], which are known as less suitable habitats for bryophytes and support only modest diversity [10,15,65]. Here, the aquatic form of *Riccia fluitans* was recorded floating mostly in stagnant waters of hypereutrophic artificial canals, while *Leptodyctium riparium* was growing on rarely present large stable rocks, dead wood, periodically submerged tree bases and margins of the watercourses, having the highest frequency in lowland small watercourses, followed by lowland medium and large watercourses. These watercourses naturally have higher trophic status and the vast majority of them are additionally subjected to substantial changes in land use associated with high nutrient input, as well as hydromorphological degradation [66], which are known to reduce habitat quality for bryophytes, resulting in reduced cover, diversity and changes in community structure [14,17,20,22]. Thus, as expected, freshwater bryophytes which occur in higher frequency within this region are those which can tolerate poorer water-quality and inhabit less-natural catchment areas, such as *Leptodictyum riparium*, *Cratoneuron filicinum*, *Cinclidotus riparius*, *Rhynchostegium riparioides*, *Fontinalis antipyretica* and *Fissidens crassipes*.

As the data used in this study were gathered in the course of the national macrophyte monitoring conducted for the purpose of assessing the ecological status of waterbodies as required by the WFD, we want to emphasize the importance of its implementation, as it encouraged research into freshwater bryophytes and their ecology on a national [15,22,67–72] and European level [1,2,4,5,14,28,29,50,51,53] by including this group as a part of macrophyte vegetation. Our research is the first into the ecology of the aquatic bryophytes in Croatia, exploring the ecological responses of the most frequent species and determining the influence of different environmental variables on their occurrence. These results make a solid base from which the bioindication potential of these particular species can be inferred, based on their optima and niche width, and a starting point crucial for the improvement and adjustment of the national methodology regarding the bryophytes as an integrative part of macrophyte vegetation. It should be noted that WFD takes a more holistic approach than traditional monitoring practices and requires the assessment of the ecological status, which must be determined type-specifically. Namely, for each type of water body recognized by the national typology, reference conditions should be identified, and degradation has to be quantified as the deviation in species composition and abundance from those that would be present at reference conditions [73]. Having this in mind, our results are a good starting point, because they add information on species currently not included and additional information on ecological responses for a few species already included in the Croatian methodology. However, particular species scores and the inclusion of new species into this methodology should be derived considering the type-specific reference conditions to meet the requirements of the WFD.

4. Materials and Methods

4.1. Study Area

A total of 648 sampling sites on 382 different watercourses were surveyed during vegetation seasons from 2016 to 2021. Surveys were carried out within the national surface water monitoring scheme, which is conducted to assess the ecological status of water bodies as required by the Water Framework Directive (WFD). The sampling sites were preselected to encompass the heterogeneity of different water body types recognized by the typology developed as a basis for the monitoring of surface waters [60], with all water body types represented proportionally and fulfilling the requirements of the stratified sampling. This typology recognizes two hydrological and biogeographical regions in Croatia—the Pannonian and the Dinaric Ecoregion, the latter being subdivided into Continental and Mediterranean subecoregions (Figure 1).

The Pannonian Ecoregion refers to the continental, lowland part of the country, largely converted into agricultural areas. The geological bedrock is dominantly siliceous, while the climate is temperate, without a dry season, with warm summers (Cfb), becoming hotter towards the east (Cfa) [74]. The Dinaric Ecoregion refers to the central and western part of the country, with a dominant karstic landscape, developed on limestone and dolomite bedrock. It is divided into the Continental Subecoregion, characterized by a temperate climate (Cfb), and the Mediterranean Subecoregion with mostly Mediterranean climate, with dry and hot summer months (Csa) [74]. The Pannonian watercourses and the majority of the watercourses of the Dinaric-Continental Subecoregion belong to the Black Sea Basin, while the watercourses of the Dinaric-Mediterranean Subecoregion belong to the Adriatic Sea Basin.

4.2. Vegetation Data Sampling

Macrophyte vegetation was surveyed from June to September, during the main vegetation period and the lowest water discharge levels. Following the national methodology for macrophyte sampling [60], watercourses were surveyed along 100 m-long transects from the banks and by zigzagging across the channel if the water depth was low enough. The vegetation survey included all macrophyte representatives (bryophytes, vascular plants and macroalgae), and the cover and abundance of each species was assessed using the standard Central European phytocoenological methodology, i.e., extended Braun–Blanquet scale (r = one individual, + = up to 5 individuals, 1 = up to 50 individuals, 2m = over 50 individuals but coverage < 5%, 2a = coverage 5–15%, 2b = coverage 15–25%, 3 = 25–50%; 4 = coverage 50–75%; 5 = coverage over 75%) [75–77], which was further transformed to the van der Maarel scale from 1 to 9 [78] (Appendix D). To investigate the ecological preferences and autecology of freshwater bryophytes, further analysis included only bryophytes with $\geq$5 occurrences that fall into categories of greater water affinity according to Dierßen [56]. These were collected from various substrates (e.g., rocks, boulders, pebbles, xylal) within the riverbed, as well as from the periodically flooded river margins. Voucher specimens were deposited at the Herbarium collection ZA [79]. The nomenclature follows Hodgetts et al. [80].

4.3. Environmental Data Sampling and Acquisition

All localities were also sampled for basic water physicochemical and chemical analysis once a month throughout the year. Water temperature, electrical conductivity, pH and dissolved oxygen were measured in situ with a Hach HQ40D Portable Multi Meter under standard conditions. Furthermore, water samples were collected and analyzed in an accredited laboratory (Central Water Management Laboratory, Zagreb) for total alkalinity, total suspended solids, biochemical oxygen demand and chemical oxygen demand, as well as for nitrogen and phosphorus compounds (ammonium, nitrites, nitrates, total nitrogen, orthophosphates and total phosphorus) (Table 1). The land use in the catchment area of each sampling site was obtained from the database of Hrvatske vode—the legal entity for water management. Here, four distinct categories are recognized and calculated from the CORINE land cover dataset [81]—natural area, urban area, and intensive and extensive agricultural land (Table 1).

4.4. Data Analysis

Data analysis included rheophyte, hydrophyte, amphyphyte and hygrophyte species [56] occurring in at least five of the surveyed localities (a total of 21 species from 182 localities) (Table S1) matched with 18 environmental variables (Table S2). This data set included thirteen different types of watercourses according to the current national typology (Appendix A, Table A1) and was used to compile a frequency table from the species occurrence within each type (Appendix A, Table A2). Basic descriptive statistics (min, max, mean, SE, SD and median) of all environmental variables were calculated for the species (Appendix C) in Past 4.9 software [82] and their distribution along the gradient of each environmental variable was shown with box-plot graphs created in SPSS software (Figure 1). Furthermore, the descriptive statistic was calculated for all environmental variables for the Pannonian and Dinaric Ecoregion (Table A6, Appendix E), as well as for the Dinaric-Continental and Dinaric-Mediterranean subecoregion (Table A7, Appendix E).

To assess the relationship between the environmental variables and patterns in freshwater bryophyte species composition, a direct ordination method, canonical correspondence analysis (CCA), was used. After removing the outliers, vegetation and environmental data from 176 localities were included in the analysis. CCA was selected because the response data were compositional with a gradient longer than 4.2 SD units, meaning that analysis based on a unimodal, rather than the linear model, is preferred [83]. A step-forward selection procedure in CANOCO 5 [83,84] was used to identify the most-contributing subset of environmental predictors influencing the freshwater bryophytes. Eight variables with the highest conditional effect and with a 5% significance cut level ($p < 0.05$; Monte Carlo test, 499 permutations) were included. Prior to the analysis, species abundance values were square-rooted and rare species downweighted.

Generalized additive models (GAM) were employed to model the probability of occurrence of individual bryophyte species as a function of eight environmental variables highlighted in the CCA analysis. GAMs were selected as an efficient tool in ecology since they do not require an assumption about the shape of species response along the environmental gradient [83–86]. We used Poisson distribution with log link function and df = 2 in fitting the species response curves and Akaike Information Criterion (AIC) available in CANOCO 5 [83,84] to select the best model. AIC considers not only the goodness of fit but also selects the most parsimonious model. Species for which no candidate model had an AIC value lower than the null model were automatically detected and removed by this procedure. Furthermore, only statistically significant models ($p < 0.05$) were retained and shown in graphs (Table S3).

5. Conclusions

The present study revealed that freshwater bryophytes and their assemblages were segregated along the gradients of the water chemistry and the proportion of natural and urban area within the catchment. The two latter variables represent the degree of combined stress, because they are often related to the extent of eutrophication, and pollution in general as well as hydromorphological degradation, of the watercourses. Furthermore, the ecological responses of individual species were examined to determine their optima, degree of tolerance and bioindication potential regarding the studied variables. The results showed that most of the investigated species preferred natural, clean, well-oxygenated, oligotrophic watercourses, with low organic matter content and electrical conductivity. However, the widely distributed and most frequent species, such as *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Cratoneuron filicinum*, *Fissidens crassipes*, *Cinclidotus fontinaloides* and *C. riprarius*, showed wide ecological tolerance to studied water chemistry variables and are thus not reliable bioindicators concerning these variables. On the other hand, species such as *Palustriella falcata*, *Eucladium verticillatum*, *Dichodontium flavescens* and *Jungermannia atrovirens* had narrow ecological niches and were restricted to pristine watercourses. *Riccia fluitans* and *Leptodyctium riparium* were the most obviously separated from the rest of the species, being the most tolerant to poor water quality. These species had wide ecological ranges, but preferred neutral, hypereutrophic waters with high nutrient and organic content, as well as electrical conductivity. Furthermore, they were frequently associated with a higher share of intensive agriculture and a low share of natural land within the catchment.

The ecological responses of several species obtained from our study do not perfectly correlate with previous findings. This might be a result of different methodological approaches concerning data collection and analysis, differences in the gradient length encompassed within each study, or the existence of different ecotypes of particular freshwater bryophytes, which display different ecological behavior in different geographical areas. Nevertheless, our study covered a considerable geographic area, included many different types of watercourses, from ground-fed streams to eutrophic large rivers, and thus encompassed substantially long gradients of the environmental parameters investigated. This has provided new data on the ecology and bioindication potential of freshwater bryophytes, contributing to the existing body of knowledge on both subjects.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/plants11243451/s1, Table S1: Cover and abundance of the species at each surveyed locality with coordinates of localities in WGS84; Table S2: Yearly mean values of 18 environmental parameters for all surveyed localities, Table S3: Results of the generalized additive models (GAMs).

Author Contributions: Conceptualization, methodology, A.R. and A.A.; validation, A.A.; data collection and sampling, A.R., A.A., V.Š., N.V. and N.K.; data analysis, A.R. and A.A.; resources, A.A.; writing—original draft preparation, A.R.; writing—review and editing, A.A., V.Š. and N.V.; visualization, A.R.; supervision, A.A.; project administration, N.V.; funding acquisition, A.A. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Types of surveyed watercourses according to the national methodology with main characteristics. ALT–altitude, CA–catchment area.

	Watercourse Type	No. of Sites	ALT (m a.s.l.)	CA (km^2)	Substrate Size
Pannonian Ecoregion					
1.	Montane and mid-altitude small watercourses	7	200–>500	10–100	large, medium
2.	Lowland small watercourses	33	<200	10–100	small
3.	Lowland medium and large watercourses	15	<200	100–10,000	small, medium
Dinaric-Continental Ecoregion					
4.	Montane and mid-altitude small watercourses	24	200–>500	10–100	large, medium
5.	Montane and mid-altitude medium and large watercourses	17	200–>500	100–10,000	large, medium, small
6.	Lowland medium and large watercourses	10	<200	100–10,000	small, medium
7.	Montane and mid-altitude intermittent watercourses	8	200–>500	10–100	large, medium
Dinaric-Mediterranean Ecoregion					
8.	Lowland and mid-altitude small watercourses	17	0–500	10–100	medium, large
9.	Mid-altitude medium and large watercourses	12	200–500	100–10,000	medium, large
10.	Lowland medium and large watercourses	11	<200	100–10,000	medium, large
11.	Lowland and mid-altitude watercourses running through karst field	4	<200–500	10–1000	small
12.	Intermittent rivers of Mediterranean Subecoregion	14	<200–500	10–1000	large, small
Artificial canals					
13.	Artifical waterbodies	10	<200–500	10–10,000	small, medium, large

Table A2. Species frequencies across different types of watercourses. For abbreviations of species' names see Figure 2, and for types see Table A1 of Appendix A.

Watercourse Type	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
No. of sites	7	33	15	24	17	10	8	17	12	11	4	14	10
Fon ant	29	18	40	42	59	70	75	65	92	55	75	43	30
Rhy rip	57	33	27	58	71	70	38	59	50	45	.	64	10
Lep rip	14	76	73	42	18	10	50	18	17	18	.	.	.
Cra fil	29	24	7	58	53	50	38	53	33	18	.	36	.
Cin fon	.	3	13	33	76	40	25	29	8	18	.	50	30
Fis cra	.	6	27	33	35	50	13	35	8	18	.	21	.
Cin rip	.	.	40	25	59	60	25	24	.	.	.	14	.
Cin aqu	.	3	.	21	47	60	13	41	33	.	.	14	10
Apo end	.	6	.	25	41	20	13	41	25	9	25	14	.
Mar pol	.	15	7	38	24	20	13	12	.	.	.	.	.
Chi pol	.	12	.	8	47	10	.	35	17	.	.	.	.
Pty pse	.	21	7	4	18	10	13	6	8	18	.	7	.
Bra riv	.	6	.	17	29	20	.	6	.	.	.	.	.
Pal fal	.	3	7	.	24	10	.	.	25	.	.	.	.
Did top	.	.	.	.	6	10	.	18	8	18	.	14	.
Chi pal	14	9	.	4	.	10	.	6	.	.	.	.	.
Ric flu	.	.	7	.	6	.	.	.	.	.	25	.	40
Jun atr	.	.	.	8	18	.	13	.	.	9	.	.	.
Euc ver	.	.	.	4	12	.	13	6	.	18	.	.	.
Dic fla	.	3	.	8	12	.	.	.	.	.	.	.	.
Dic pel	.	6	.	4	12	.	.	.	.	.	.	.	.

Appendix B

Table A3. Results of the forward selection procedure of environmental variables for the canonical correspondence analysis, CCA. For abbreviations of environmental variables see Table 1.

Variable	Explains % (Simple Effect)	Explains % (Conditional Effect)	Contribution %	Pseudo-F	*p*
N_{tot}	4.8	4.8	23.3	8.9	0.002
NAT	4.6	2.9	13.8	5.4	0.002
COD	3.9	1.5	7.1	2.8	0.004
EC	2.0	1.2	5.8	2.3	0.008
pH	1.1	1.1	5.5	2.2	0.008
P_{tot}	4.5	1.0	5.2	2.1	0.012
URB	1.5	1.0	4.9	2.0	0.022
DO	2.3	1.1	4.8	2.0	0.030

Appendix C

Table A4. Descriptive statistics of all environmental variables for 21 freshwater bryophytes. For abbreviations of species' names see Figure 2, and for environmental variables see Table 1.

		Apo end	Bra riv	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Did top	Euc ver	Fis cra	Fon ant	Jun atr	Lep rip	Mar pol	Pal fal	Pty pse	Rhy rip	Ric flu
T (°C)	**Min**	8.88	9.13	10.45	8.88	7.85	8.42	7.00	8.70	9.13	10.94	9.80	9.57	7.00	7.00	9.57	7.00	9.13	7.85	8.88	7.00	12.38
	Max	17.58	17.15	14.29	15.30	16.06	16.73	16.22	18.75	13.21	13.21	17.85	15.66	18.63	19.30	15.66	20.17	18.75	15.65	17.85	18.75	17.19
	Mean	12.14	11.73	12.15	11.33	11.59	12.22	12.37	12.13	11.13	11.81	13.64	11.98	12.74	12.73	11.66	12.86	13.35	11.21	12.43	12.38	14.54
	SE	0.38	0.62	0.53	0.28	0.36	0.34	0.37	0.32	0.74	0.43	0.90	0.77	0.44	0.24	0.80	0.29	0.60	0.71	0.57	0.26	0.68
	SD	2.18	2.34	1.41	1.37	2.15	2.35	2.22	2.50	1.65	0.95	2.84	2.03	2.70	2.27	2.11	2.31	2.94	2.25	2.49	2.43	1.80
	Med	11.87	10.98	12.36	11.01	10.94	11.85	12.51	11.32	10.94	11.48	14.28	12.16	12.71	12.49	10.94	12.73	12.84	10.87	12.36	12.33	14.92
pH	**Min**	7.59	7.48	7.03	7.48	7.48	7.13	7.60	7.03	7.87	7.66	7.58	7.78	7.56	7.13	7.78	7.03	7.56	7.73	7.13	7.13	7.06
	Max	8.28	8.35	8.28	8.28	8.35	8.35	8.35	8.35	8.28	8.28	8.20	8.20	8.35	8.38	8.28	8.28	8.35	8.28	8.28	8.35	7.87
	Mean	7.97	8.07	7.70	7.94	7.96	7.93	8.01	7.96	8.14	8.04	7.94	8.00	8.02	7.95	8.05	7.89	8.00	8.09	7.89	7.95	7.55
	SE	0.04	0.06	0.17	0.05	0.04	0.04	0.03	0.03	0.07	0.12	0.07	0.07	0.04	0.03	0.07	0.03	0.04	0.06	0.06	0.03	0.10
	SD	0.22	0.23	0.46	0.24	0.22	0.26	0.20	0.25	0.16	0.27	0.23	0.17	0.24	0.24	0.19	0.22	0.22	0.20	0.27	0.25	0.26
	Med	8.02	8.14	7.84	7.92	7.96	7.91	8.05	8.00	8.18	8.13	7.97	7.99	8.10	7.95	8.13	7.92	8.02	8.17	7.87	7.96	7.53
EC (µS/cm)	**Min**	262.08	147.04	227.33	80.34	228.58	189.33	147.04	147.04	147.04	147.04	280.10	280.10	147.04	80.34	147.04	80.34	189.36	262.08	189.36	121.05	306.33
	Max	941.71	504.75	458.82	719.00	1073.0	802.91	802.91	941.71	295.42	302.20	941.71	366.75	941.71	1073.0	366.75	641.75	641.75	435.57	583.91	948.33	923.50
	Mean	412.45	335.01	335.57	374.50	410.76	400.31	365.58	419.20	234.66	240.17	483.75	331.49	418.57	449.88	292.20	460.15	401.99	335.74	343.62	420.05	700.75
	SE	21.55	29.32	28.97	30.85	30.39	19.51	21.33	19.91	28.44	30.38	62.98	12.07	23.55	17.98	28.37	15.51	25.72	15.41	22.43	18.33	97.80
	SD	123.82	109.71	76.65	147.94	179.77	135.18	127.96	156.74	63.59	67.94	199.17	31.95	145.16	169.59	75.07	124.08	126.02	48.74	97.76	171.00	258.76
	Med	366.75	325.55	345.00	358.50	373.00	367.83	351.97	389.04	262.08	279.42	417.89	340.14	390.84	404.50	296.17	469.18	403.47	330.75	345.00	391.90	831.75
TSS (mg/L)	**Min**	1.00	1.00	1.00	0.85	0.85	1.00	1.00	0.85	1.00	1.00	1.64	1.00	1.00	0.95	1.00	1.00	1.00	0.85	1.00	0.95	1.00
	Max	17.12	16.00	12.20	20.92	8.92	23.00	27.33	18.90	8.59	20.92	6.53	6.53	27.33	49.50	1.64	49.80	21.54	3.50	20.92	47.94	40.17
	Mean	2.67	3.75	5.50	2.94	2.25	2.83	4.29	3.23	2.52	6.50	3.33	2.06	3.91	4.79	1.09	10.22	4.66	1.61	4.78	4.05	14.42
	SE	0.66	1.20	1.77	0.98	0.31	0.50	0.93	0.50	1.52	3.89	0.50	0.77	0.85	0.86	0.09	1.34	1.17	0.34	1.20	0.67	5.03
	SD	3.81	4.48	4.69	4.68	1.85	3.49	5.60	3.92	3.39	8.70	1.59	2.03	5.22	8.09	0.24	10.70	5.74	1.07	5.23	6.26	13.32
	Med	1.00	1.70	5.75	1.00	1.30	1.82	2.11	1.67	1.00	1.00	2.68	1.00	2.09	2.00	1.00	7.07	2.06	1.00	2.02	2.08	12.17
DO (mgO_2/L)	**Min**	8.86	9.42	9.25	9.69	9.66	7.95	8.86	8.29	10.78	10.16	7.51	8.86	8.86	5.57	8.86	4.84	9.11	10.13	6.15	6.15	5.25
	Max	12.45	12.22	11.66	12.45	12.45	12.45	14.25	12.55	12.22	12.22	11.84	11.68	12.55	14.25	12.22	14.25	12.22	12.45	14.25	14.25	9.34
	Mean	10.76	11.06	10.26	11.07	11.07	10.63	11.04	10.65	11.58	11.29	10.13	10.50	10.78	10.64	10.83	9.99	10.80	11.40	10.32	10.60	7.74
	SE	0.15	0.21	0.42	0.15	0.11	0.15	0.21	0.12	0.23	0.37	0.38	0.38	0.16	0.12	0.49	0.22	0.19	0.25	0.41	0.12	0.57
	SD	0.84	0.77	1.10	0.74	0.66	1.06	1.23	0.93	0.52	0.82	1.21	1.02	1.02	1.12	1.29	1.74	0.95	0.78	1.78	1.13	1.50
	Med	10.92	11.26	9.54	11.10	11.06	10.85	11.09	10.78	11.68	11.48	10.16	10.93	10.92	10.85	11.48	10.17	10.99	11.44	10.38	10.75	7.93
ALK (mg-$CaCO_3$/L)	**Min**	98.67	77.03	110.67	48.00	126.92	90.33	77.03	77.03	77.03	76.19	167.64	167.64	77.03	48.00	77.03	48.00	91.45	152.75	76.19	59.82	171.58
	Max	281.67	255.00	229.17	272.55	252.10	344.62	288.60	308.41	161.50	175.70	282.40	208.04	288.60	344.62	208.04	343.33	308.41	200.14	308.41	344.62	446.67
	Mean	202.95	180.30	187.63	180.76	188.77	203.13	185.85	207.25	128.55	116.38	218.63	185.50	207.53	205.16	160.72	228.16	209.49	179.42	184.85	196.81	306.08
	SE	6.93	15.26	15.54	12.12	5.31	7.86	8.38	6.48	18.29	21.61	12.54	5.35	8.10	5.16	15.52	8.19	11.22	4.54	13.11	6.17	43.45
	SD	39.80	57.11	41.12	58.10	31.39	54.47	50.29	51.05	40.90	48.32	39.65	14.15	49.94	48.68	41.07	65.48	54.98	14.37	57.16	57.55	114.95
	Med	194.57	182.80	198.00	190.50	187.78	195.26	186.55	197.04	152.75	91.45	210.23	185.83	197.15	199.20	167.64	230.38	220.50	181.21	181.92	194.57	290.58

Table A4. *Cont.*

		Apo end	Bra riv	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Did top	Euc ver	Fis cra	Fon ant	Jun atr	Lep rip	Mar pol	Pal fal	Pty pse	Rhy rip	Ric flu
BOD (mgO_2/L)	Min	0.30	0.30	0.30	0.30	0.30	0.14	0.52	0.25	0.62	0.69	0.30	0.30	0.30	0.30	0.62	0.30	0.30	0.30	0.30	0.14	0.70
	Max	2.70	2.90	2.71	2.64	2.64	2.80	3.32	7.33	1.58	2.60	1.71	2.63	3.44	3.60	2.63	6.90	2.90	1.43	3.32	9.78	5.10
	Mean	1.00	1.18	1.42	0.96	0.97	1.05	1.32	1.24	1.02	1.30	1.16	1.27	1.17	1.20	1.09	2.08	1.19	0.83	1.53	1.37	3.62
	SE	0.11	0.20	0.36	0.13	0.09	0.07	0.12	0.14	0.18	0.36	0.14	0.29	0.11	0.09	0.27	0.15	0.15	0.12	0.20	0.13	0.62
	SD	0.62	0.75	0.94	0.64	0.55	0.51	0.73	1.10	0.40	0.81	0.45	0.76	0.71	0.83	0.70	1.19	0.71	0.39	0.88	1.22	1.63
	Med	0.84	0.90	1.84	0.80	0.87	1.01	1.09	0.94	0.84	0.84	1.33	1.18	0.93	1.07	0.84	1.75	1.09	0.79	1.18	1.10	4.39
COD (mgO_2/L)	Min	0.25	0.25	0.49	0.25	0.25	0.49	0.77	0.25	0.78	1.77	0.50	0.49	0.25	0.25	0.89	0.29	0.25	0.66	0.72	0.25	1.27
	Max	4.36	4.36	10.67	5.51	4.30	10.68	6.95	10.67	4.97	5.51	10.68	2.52	10.68	10.68	2.34	13.11	4.97	2.26	10.67	10.83	7.55
	Mean	1.30	1.65	4.06	1.89	1.32	1.59	2.13	1.82	2.26	3.30	2.66	1.19	2.12	2.03	1.46	3.78	1.98	1.32	3.19	2.19	4.58
	SE	0.15	0.32	1.35	0.32	0.13	0.22	0.26	0.22	0.72	0.80	0.93	0.26	0.31	0.20	0.18	0.35	0.31	0.19	0.61	0.25	0.95
	SD	0.87	1.18	3.58	1.54	0.79	1.53	1.56	1.75	1.62	1.80	2.95	0.68	1.89	1.92	0.48	2.76	1.52	0.60	2.64	2.30	2.51
	Med	1.27	1.33	3.70	1.53	1.10	1.30	1.74	1.37	1.77	2.34	1.89	1.04	1.74	1.48	1.42	3.21	1.60	1.26	2.05	1.40	5.50
NH_4+ (mgN/L)	Min	0.001	0.004	0.004	0.004	0.003	0.002	0.003	0.002	0.004	0.004	0.001	0.001	0.002	0.001	0.002	0.001	0.002	0.001	0.002	0.001	0.009
	Max	0.221	0.221	0.361	0.313	0.149	0.665	0.665	0.862	0.004	0.313	0.044	0.009	0.665	0.498	0.009	1.697	0.221	0.017	0.361	0.862	0.212
	Mean	0.025	0.034	0.094	0.023	0.019	0.041	0.056	0.047	0.004	0.066	0.013	0.005	0.047	0.049	0.005	0.169	0.042	0.006	0.057	0.057	0.103
	SE	0.008	0.017	0.050	0.013	0.005	0.016	0.021	0.015	0.000	0.062	0.004	0.001	0.019	0.009	0.001	0.041	0.012	0.002	0.025	0.014	0.032
	SD	0.046	0.064	0.133	0.064	0.028	0.109	0.126	0.121	0.000	0.138	0.013	0.003	0.120	0.089	0.002	0.327	0.058	0.005	0.110	0.131	0.079
	Med	0.006	0.005	0.050	0.006	0.010	0.009	0.010	0.013	0.004	0.004	0.007	0.005	0.008	0.013	0.004	0.067	0.013	0.004	0.006	0.010	0.099
NO_2^- (mgN/L)	Min	0.000	0.000	0.001	0.000	0.001	0.001	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.000	0.001
	Max	0.050	0.025	0.021	0.043	0.019	0.215	0.215	0.061	0.004	0.006	0.062	0.006	0.215	0.106	0.004	0.215	0.061	0.006	0.062	0.215	0.296
	Mean	0.008	0.004	0.008	0.005	0.004	0.011	0.011	0.008	0.002	0.003	0.013	0.002	0.014	0.009	0.002	0.023	0.012	0.003	0.008	0.010	0.052
	SE	0.002	0.002	0.003	0.002	0.001	0.005	0.006	0.002	0.001	0.001	0.007	0.001	0.006	0.002	0.001	0.005	0.003	0.000	0.003	0.003	0.041
	SD	0.013	0.006	0.007	0.009	0.005	0.034	0.036	0.012	0.001	0.002	0.021	0.002	0.036	0.017	0.002	0.036	0.016	0.001	0.014	0.027	0.107
	Med	0.002	0.002	0.007	0.002	0.002	0.003	0.003	0.003	0.002	0.002	0.005	0.001	0.003	0.004	0.001	0.010	0.004	0.003	0.004	0.003	0.013
NO_3^- (mgN/L)	Min	0.060	0.196	0.184	0.060	0.179	0.092	0.092	0.060	0.325	0.325	0.060	0.092	0.060	0.092	0.092	0.184	0.225	0.301	0.092	0.092	0.075
	Max	1.098	1.594	0.603	1.212	1.594	1.594	1.594	1.594	0.643	1.212	0.909	0.695	1.594	1.472	0.695	4.442	1.350	0.802	1.212	4.442	3.142
	Mean	0.512	0.683	0.385	0.518	0.571	0.611	0.632	0.556	0.516	0.613	0.399	0.372	0.634	0.554	0.441	0.920	0.731	0.549	0.477	0.612	0.655
	SE	0.051	0.098	0.062	0.061	0.047	0.045	0.051	0.041	0.063	0.157	0.079	0.087	0.056	0.033	0.082	0.100	0.070	0.051	0.066	0.055	0.418
	SD	0.289	0.365	0.163	0.294	0.277	0.313	0.309	0.326	0.141	0.351	0.251	0.229	0.344	0.313	0.216	0.798	0.342	0.163	0.286	0.517	1.106
	Med	0.540	0.573	0.331	0.424	0.548	0.574	0.605	0.536	0.598	0.523	0.323	0.309	0.600	0.497	0.408	0.725	0.669	0.600	0.342	0.517	0.236
Ntot (mgN/L)	Min	0.125	0.305	0.275	0.278	0.275	0.158	0.158	0.125	0.489	0.489	0.275	0.158	0.158	0.158	0.158	0.389	0.275	0.393	0.158	0.158	0.478
	Max	1.385	2.081	1.159	1.606	1.765	2.243	2.243	2.000	0.786	1.606	1.257	1.150	2.243	2.458	0.786	5.176	2.638	1.150	1.606	5.176	8.900
	Mean	0.713	0.937	0.782	0.717	0.765	0.820	0.895	0.791	0.636	0.801	0.793	0.653	0.891	0.789	0.617	1.499	1.040	0.711	0.807	0.886	1.938
	SE	0.060	0.137	0.131	0.071	0.055	0.060	0.068	0.052	0.053	0.205	0.096	0.128	0.070	0.047	0.081	0.128	0.126	0.070	0.078	0.067	1.164
	SD	0.338	0.512	0.346	0.339	0.327	0.415	0.408	0.408	0.118	0.458	0.302	0.340	0.431	0.442	0.215	1.015	0.615	0.221	0.339	0.625	3.080
	Med	0.692	0.711	0.853	0.653	0.716	0.728	0.812	0.711	0.645	0.653	0.782	0.691	0.790	0.716	0.691	1.223	0.771	0.730	0.755	0.774	0.730
PO_4^{3-} (mgP/L)	Min	0.001	0.002	0.003	0.001	0.001	0.001	0.001	0.001	0.004	0.006	0.001	0.001	0.001	0.001	0.002	0.003	0.001	0.002	0.001	0.001	0.003
	Max	0.020	0.040	0.026	0.026	0.027	0.179	0.179	0.089	0.010	0.026	0.029	0.003	0.179	0.095	0.007	0.188	0.070	0.009	0.038	0.179	0.473
	Mean	0.005	0.008	0.011	0.006	0.006	0.009	0.014	0.009	0.006	0.011	0.005	0.002	0.012	0.011	0.004	0.035	0.015	0.005	0.012	0.011	0.110
	SE	0.001	0.003	0.003	0.001	0.001	0.004	0.005	0.002	0.001	0.004	0.003	0.000	0.005	0.002	0.001	0.005	0.004	0.001	0.003	0.002	0.062
	SD	0.005	0.010	0.009	0.005	0.005	0.026	0.030	0.015	0.002	0.009	0.009	0.001	0.030	0.015	0.002	0.043	0.017	0.002	0.013	0.022	0.163
	Med	0.004	0.005	0.010	0.004	0.004	0.004	0.006	0.005	0.006	0.007	0.003	0.003	0.005	0.005	0.003	0.017	0.007	0.004	0.004	0.005	0.077

Table A4. *Cont.*

		Apo end	Bra riv	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Did top	Euc ver	Fis cra	Fon ant	Jun atr	Lep rip	Mar pol	Pal fal	Pty pse	Rhy rip	Ric flu
Ptot (mgP/L)	Min	0.001	0.005	0.005	0.001	0.001	0.005	0.002	0.001	0.008	0.010	0.002	0.005	0.002	0.001	0.005	0.004	0.002	0.005	0.002	0.001	0.001
	Max	0.064	0.079	0.070	0.091	0.045	0.271	0.271	0.280	0.038	0.091	0.042	0.025	0.271	0.175	0.025	1.067	0.223	0.034	0.093	0.271	0.699
	Mean	0.018	0.027	0.039	0.016	0.018	0.027	0.036	0.028	0.020	0.033	0.011	0.010	0.030	0.030	0.012	0.094	0.043	0.013	0.034	0.035	0.177
	SE	0.003	0.006	0.011	0.004	0.002	0.006	0.008	0.006	0.006	0.015	0.004	0.003	0.008	0.004	0.003	0.018	0.010	0.003	0.007	0.005	0.090
	SD	0.017	0.022	0.030	0.019	0.012	0.038	0.050	0.045	0.014	0.034	0.014	0.008	0.048	0.034	0.007	0.141	0.050	0.010	0.031	0.045	0.239
	Med	0.011	0.021	0.054	0.010	0.013	0.022	0.023	0.017	0.012	0.015	0.006	0.006	0.016	0.019	0.010	0.064	0.032	0.010	0.025	0.022	0.127
NAT (%)	Min	4.22	61.05	35.37	69.16	52.06	21.34	38.85	0.00	92.36	78.02	21.34	64.71	0.00	0.00	64.71	19.32	0.00	72.60	35.37	0.00	0.00
	Max	99.78	100.00	93.88	100.00	99.39	99.78	99.39	100.00	99.39	98.51	88.82	99.78	99.78	100.00	99.78	100.00	100.00	99.39	99.78	100.00	83.99
	Mean	80.60	88.47	70.98	88.04	82.32	78.92	76.22	78.76	96.55	91.45	65.64	80.30	72.89	73.10	85.30	59.87	77.75	85.90	72.82	75.65	34.91
	SE	3.09	3.09	8.28	1.68	2.04	2.51	2.88	2.40	1.35	3.71	6.44	5.06	3.72	1.91	6.00	2.62	4.57	2.57	4.21	2.16	12.87
	SD	17.76	11.57	21.90	8.07	12.06	17.39	17.25	18.88	3.01	8.31	20.36	13.39	22.94	18.03	15.87	20.93	22.40	8.13	18.33	20.15	34.05
	Med	86.90	91.33	74.62	89.08	83.69	83.69	81.08	85.47	98.05	92.36	70.57	77.82	79.09	77.32	92.36	59.81	86.00	85.99	76.14	81.24	15.88
IAG (%)	Min	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Max	79.09	14.94	18.57	12.72	39.63	44.02	39.63	82.45	0.87	5.37	39.63	2.51	82.45	82.45	0.87	70.01	82.45	10.64	35.46	82.45	97.69
	Mean	4.23	2.53	5.58	3.48	6.40	6.79	7.44	6.29	0.17	1.45	12.96	0.74	9.90	8.95	0.18	17.59	7.30	2.74	7.72	8.60	52.20
	SE	2.43	1.19	2.70	0.99	1.40	1.53	1.54	1.71	0.17	1.00	5.27	0.43	2.78	1.22	0.13	2.07	3.70	1.14	2.77	1.55	16.12
	SD	13.97	4.45	7.13	4.77	8.28	10.60	9.25	13.43	0.39	2.24	16.66	1.14	17.14	11.52	0.34	16.56	18.14	3.59	12.05	14.48	42.65
	Med	0.07	0.27	1.85	0.47	3.61	2.14	4.03	0.43	0.00	0.87	2.39	0.00	1.39	5.63	0.00	13.43	0.00	1.36	0.38	2.24	59.37
EAG (%)	Min	0.22	0.00	6.07	0.00	0.61	0.22	0.61	0.00	0.61	1.49	1.36	0.22	0.22	0.00	0.22	0.00	0.00	0.61	0.22	0.00	0.00
	Max	35.42	30.24	46.06	19.27	35.42	38.61	40.83	46.06	6.59	16.61	38.61	33.99	38.61	46.10	33.99	46.10	35.42	23.75	46.06	46.06	33.83
	Mean	14.27	8.31	23.30	7.60	9.44	12.26	14.40	14.05	2.93	7.06	18.97	18.56	15.92	16.51	14.14	20.28	14.13	10.72	18.62	14.13	12.30
	SE	1.77	2.30	5.88	1.17	1.31	1.44	2.02	1.40	1.07	2.75	4.01	4.90	1.77	1.09	5.82	1.43	2.19	2.09	3.20	1.22	4.96
	SD	10.17	8.60	15.56	5.63	7.76	9.97	12.13	11.00	2.40	6.15	12.68	12.97	10.92	10.27	15.40	11.45	10.71	6.62	13.96	11.36	13.12
	Med	10.45	6.94	24.68	7.28	8.68	8.57	9.63	10.07	1.95	6.59	20.10	20.93	14.78	13.48	6.59	20.22	12.19	11.85	20.93	10.20	10.47
URB (%)	Min	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Max	8.14	2.60	0.95	3.97	9.87	11.23	9.87	9.87	1.54	0.17	9.46	1.30	6.80	9.87	1.30	25.55	9.87	3.82	9.46	11.23	1.15
	Mean	0.89	0.69	0.14	0.88	1.84	2.03	1.93	0.90	0.34	0.03	2.43	0.40	1.29	1.44	0.37	2.26	0.82	0.64	0.83	1.63	0.59
	SE	0.30	0.22	0.13	0.28	0.38	0.38	0.36	0.22	0.30	0.03	1.12	0.22	0.29	0.21	0.22	0.59	0.42	0.37	0.50	0.25	0.17
	SD	1.74	0.84	0.36	1.36	2.24	2.62	2.14	1.76	0.67	0.08	3.55	0.57	1.78	2.01	0.59	4.76	2.05	1.17	2.20	2.35	0.46
	Med	0.05	0.19	0.00	0.05	1.10	1.27	1.30	0.17	0.00	0.00	0.35	0.05	0.91	0.95	0.00	0.75	0.00	0.18	0.00	0.70	0.70

Appendix D

Table A5. Braun–Blanquet and van der Maarel cover and abundance scales.

Braun–Blanquet Code	Cover/Abundance	van der Maarel Code
r	one individual, coverage < 5%	1
+	up to 5 individuals, coverage < 5%	2
1	up to 50 individuals, coverage < 5%	3
2m	over 50 individuals, coverage < 5%	4
2a	coverage 5–15%	5
2b	coverage 15–25%	6
3	coverage 25–50%	7
4	coverage 50–75%	8
5	coverage over 75%	9

Appendix E

Table A6. Descriptive statistics for all environmental variables calculated for the Pannonian and Dinaric Ecoregion. For abbreviations of environmental variables, see Table 1.

	Pannonian Ecoregion						Dinaric Ecoregion					
	Min	Max	Mean	SE	SD	Med	Min	Max	Mean	SE	SD	Med
T (°C)	7.00	25.02	13.35	0.34	2.58	12.93	7.85	18.75	12.58	0.22	2.50	12.33
pH	7.03	8.29	7.88	0.04	0.28	7.93	7.13	8.38	7.94	0.02	0.23	7.95
EC (µS/cm)	80.34	923.50	468.27	23.64	180.03	472.50	147.04	1073.00	444.81	14.82	164.39	405.20
TSS (mg/L)	1.00	49.80	13.30	1.38	10.49	10.83	0.85	45.50	3.74	0.56	6.22	1.94
DO (mgO_2/L)	4.84	14.25	9.50	0.25	1.91	9.56	7.51	12.55	10.64	0.08	0.94	10.80
ALK ($mgCaCO_3$/L)	48.00	446.67	235.13	11.55	87.94	246.11	77.03	344.62	206.29	4.15	46.25	200.41
BOD (mgO_2/L)	0.85	9.78	2.81	0.20	1.52	2.66	0.14	2.98	1.04	0.05	0.58	1.05
COD (mgO_2/L)	1.75	13.11	4.89	0.30	2.26	4.53	0.25	10.68	1.48	0.11	1.17	1.26
NH_4^+ (mgN/L)	0.004	6.056	0.286	0.110	0.839	0.081	0.001	0.862	0.042	0.009	0.105	0.013
NO_2^- (mgN/L)	0.001	0.296	0.025	0.005	0.042	0.011	0.000	0.215	0.010	0.002	0.023	0.003
NO_3^- (mgN/L)	0.075	4.442	0.907	0.119	0.904	0.667	0.060	1.594	0.558	0.029	0.320	0.505
N_{tot} (mgN/L)	0.389	8.900	1.650	0.186	1.417	1.324	0.125	2.638	0.784	0.040	0.448	0.692
PO_4^{3-} (mgP/L)	0.005	0.473	0.052	0.009	0.069	0.034	0.001	0.179	0.009	0.002	0.018	0.004
P_{tot} (mgP/L)	0.014	0.699	0.115	0.013	0.103	0.085	0.001	0.271	0.027	0.003	0.035	0.018
NAT (%)	0.00	100.00	53.81	3.29	25.04	53.31	0.00	99.78	76.80	1.46	16.27	80.59
IAG (%)	0.00	97.69	25.86	3.03	23.05	20.61	0.00	82.45	7.51	1.03	11.51	4.54
EAG (%)	0.00	46.06	18.54	1.63	12.38	20.01	0.00	46.10	14.03	0.86	9.58	12.22
URA (%)	0.00	25.55	1.79	0.63	4.78	0.26	0.00	11.23	1.66	0.21	2.29	0.96

Table A7. Descriptive statistics for all environmental variables calculated for the Continental and Mediterranean Subecoregion of the Dinaric Ecoregion. For environmental variables' abbreviations, see Table 1.

	Continental Subecoregion						Mediterranean Ecoregion					
	Min	Max	Mean	SE	SD	Med	Min	Max	Mean	SE	SD	Med
T (°C)	7.85	17.85	12.75	0.29	2.30	12.66	8.42	18.75	12.39	0.35	2.70	12.12
pH	7.13	8.26	7.89	0.03	0.23	7.91	7.48	8.38	7.99	0.03	0.22	8.03
EC (μS/cm)	189.33	1073.00	491.21	25.52	202.58	415.80	147.04	641.75	396.08	11.57	89.65	391.57
TSS (mg/L)	0.85	45.50	4.25	0.97	7.73	2.03	1.00	23.00	3.21	0.52	4.05	1.70
DO (mgO_2/L)	7.51	12.14	10.52	0.12	1.00	10.65	8.86	12.55	10.77	0.11	0.86	10.87
ALK ($mgCaCO_3$/L)	90.33	344.62	205.77	6.36	50.90	197.25	77.03	281.67	206.86	5.31	41.13	205.08
BOD (mgO_2/L)	0.14	2.64	0.93	0.07	0.59	0.80	0.25	2.98	1.15	0.07	0.55	1.09
COD (mgO_2/L)	0.25	10.68	1.49	0.18	1.47	1.17	0.25	3.03	1.46	0.10	0.75	1.40
NH_4^+ (mgN/L)	0.002	0.862	0.043	0.017	0.134	0.013	0.001	0.359	0.042	0.008	0.063	0.010
NO_2^- (mgN/L)	0.000	0.215	0.012	0.004	0.030	0.003	0.001	0.061	0.007	0.002	0.012	0.003
NO_3^- (mgN/L)	0.060	1.327	0.407	0.033	0.264	0.348	0.092	1.594	0.719	0.038	0.296	0.685
N_{tot} (mgN/L)	0.125	2.243	0.602	0.046	0.370	0.503	0.158	2.638	0.978	0.057	0.445	0.868
PO_4^{3-} (mgP/L)	0.001	0.179	0.010	0.003	0.024	0.003	0.002	0.070	0.009	0.001	0.010	0.006
P_{tot} (mgP/L)	0.001	0.271	0.026	0.005	0.039	0.014	0.005	0.223	0.028	0.004	0.030	0.022
NAT (%)	21.34	99.19	76.73	2.02	16.14	80.19	0.00	99.78	76.88	2.13	16.54	81.08
IAG (%)	0.00	48.97	8.26	1.43	11.41	4.88	0.00	82.45	6.71	1.50	11.66	3.22
EAG (%)	0.61	46.10	13.04	1.18	9.45	10.92	0.00	40.83	15.09	1.25	9.68	13.58
URA (%)	0.00	11.23	1.97	0.33	2.65	0.92	0.00	9.87	1.32	0.23	1.80	0.97

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Table S1: Cover and abundance of the species at each surveyed locality with coordinates of localities in WGS84. DIN-CON–Dinaric Ecoregion, Continental Subecoregion, DIN-MED –Dinaric Ecoregion, Continental Subecoregion, PAN–Pannonian Ecoregion, Am–amphyphyte, Hyd–hydrophyte, Hyg–hygrophyte, Rh–rheophyte, Apo end–*Apopellia endiviifolia*, Bra riv–*Brachythecium rivulare*, Chi pal–*Chiloscyphus pallescens*, Chi pol–*Chiloscyphus polyanthos*, Cin aqu– *Cinclidotus aquaticus*, Cin fon–*Cinclidotus fontinaloides*, Cin rip–*Cinclidotus riparius*, Cra fil–*Cratoneuron filicinum*, Dic fla–*Dichodontium flavescens*, Dic pel–*Dichodontium pellucidum*, Did top–*Didymodon tophaceus*, Euc ver–*Eucladium verticillatum*, Fis cra–*Fissidens crassipes*, Fon ant–*Fontinalis antipyretica*, Jun atr–*Jungermannia atrovirens*, Lep rip–*Leptodictyum riparium*, Mar pol–*Marchantia polymorpha*, Pal fal–*Palustriella falcata*, Pty pse–*Ptychostomum pseudotriquetrum*, Rhy rip–*Rhynchostegium riparioides*, Ric flu–*Riccia fluitans*. For watercourse types see Table A1 in Appendix A.

						Affinity to water	Hyg	Rh	Hyg	Hyg	Rh	Rh	Rh	Am	Hyg	Hyg	Hyg	Hyg	Rh	Rh	Hyg	Rr	Hyg	Am	Hy	Rh	Hyd
Site id	**Watercourse**	**water body type**	**(sub) ecoregion**	**watercourse type**	**X_WGS_84**	**Y_WGS_84**	**Apo end**	**Bra riv**	**Chi pal**	**Chi pol**	**Cin aqu**	**Cin fon**	**Cin rip**	**Cra fil**	**Dic fla**	**Dic pel**	**Did top**	**Euc ver**	**Fis cra**	**Fon ant**	**Jun atr**	**Lep rip**	**Mar pol**	**Pal fal**	**Pty pse**	**Rhy rip**	**Ric flu**
1.	Delnički potok	river	DIN-CON	7	14.850377	45.439597					2a	1	2m	1						1		1	+			1	
2.	Kosteljina	river	PAN	2	15.753680	46.174112								1					1			2m					
3.	Kupa	river	DIN-CON	6	15.249287	45.455731					3	2m	2m						1							2a	
4.	Kupa	river	DIN-CON	6	15.357011	45.645606					3	2m	2m	+						+						2a	
5.	Sušica	river	DIN-CON	7	15.007823	45.424297								+													
6.	Tomašnica	river	DIN-CON	4	15.475788	45.530604																1					
7.	Rogstrug	river	PAN	3	17.245095	45.998644																1					
8.	Mrežnica	river	DIN-CON	5	15.431130	45.195165						1								2m						1	
9.	Batina	river	PAN	2	16.159547	46.058829																+					
10.	Bednja	river	PAN	1	16.168649	46.241186														+							
11.	Crna rijeka 1	river	DIN-CON	2	15.601431	44.843360								2a												1	
12.	Dobra	river	DIN-CON	5	15.355603	45.372808						1	1							2b		1				1	
13.	Jaruga 1	river	DIN-CON	7	15.245560	45.031223														1		1					
14.	Korana	river	DIN-CON	5	15.618615	44.925884	+										2a	1						2m		2a	
15.	Korana	river	DIN-CON	5	15.590271	45.120980														+		+					
16.	Korana	river	DIN-CON	6	15.595546	45.391984	1				1		2m	2m			2b		1							2b	
17.	Krapina	river	PAN	3	15.817678	45.934250																1					
18.	Krapina	river	PAN	2	16.201168	46.104956													2a			2b				2b	
19.	Krapina	river	PAN	3	15.823185	45.835165																2a					
20.	Moštanica	river	PAN	2	16.357067	45.439367																+					
21.	Moštanica	river	PAN	2	16.357095	45.439527																1					
22.	Ribnik	river	DIN-CON	4	15.314320	45.609055							+														
23.	Žitomirka	river	PAN	2	16.161737	46.032383																2m				2m	
24.	Šumetlica	river	PAN	1	17.376298	45.364489																				1	
25.	Bistra 3	canal	PAN	13	18.647960	45.608399																					1
26.	Voća	river	PAN	1	16.132401	46.251948																5					
27.	Bračana	river	DIN-MED	12	13.903323	45.395547														1							
28.	Stara Mirna	river	DIN-MED	10	13.856276	45.360623														1							
29.	Pazinčica	river	DIN-MED	8	13.966364	45.247188														+							
30.	Una	river	PAN	3	16.549762	45.222087							1						1	2m		2m				1	
31.	Baščica	river	DIN-MED	12	15.461889	44.213225						1								2a						1	
32.	Bregana	river	DIN-CON	4	15.675482	45.841100								2m					2m	2m		1				2m	
33.	Dretulja	river	DIN-CON	6	15.343299	45.074416		+		+	2a			2a												4	
34.	Dretulja	river	DIN-CON	5	15.423854	45.065826				2a										2a							
35.	Jaruga 3	river	DIN-MED	12	15.729667	43.954073											1								1		
36.	Jaruga 2	river	DIN-MED	12	15.330190	44.263227								2a												2a	
37.	Kupčina	river	DIN-CON	4	15.451081	45.721602	+					+		+					*1*	+		2m	+			1	
38.	Velika rijeka	river	PAN	1	17.860220	45.482312								1													
39.	Rudarska Gradna	river	DIN-CON	4	15.666957	45.762693								1									+			2m	
40.	Rudarska Gradna	river	DIN-CON	4	15.697405	45.799964																3	+				
41.	Gradna	river	DIN-CON	4	15.702300	45.799549																2m	1				
42.	Lipovečka Gradna	river	DIN-CON	4	15.645352	45.786765		1						2m									1				
43.	Svinica	river	PAN	2	16.530964	45.308869																			2m	2m	
44.	Bregana	river	DIN-CON	4	15.602827	45.836773								2m					2m	1			2m			2m	
45.	Slapnica	river	DIN-CON	4	15.501519	45.688221	+							+					1			+				1	

		Affinity to water					Hyg	Rh	Hyg	Hyg	Rh	Rh	Rh	Am	Hyg	Hyg	Hyg	Hyg	Rh	Rh	Hyg	Rr	Hyg	Am	Hy	Rh	Hyd
Site id	Watercourse	water body type	(sub) ecoregion	watercourse type	X_WGS_84	Y_WGS_84	Apo end	Bra riv	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Did top	Euc ver	Fis cra	Fon ant	Jun atr	Lep rip	Mar pol	Pal fal	Pty pse	Rhy rip	Ric flu
46.	Subocka	river	PAN	2	16.974057	45.397398	+	+						1									1				
47.	Una	river	DIN-CON	4	16.105937	44.401939	2b			2a	4	2m		2b						2m						2m	
48.	Una	river	DIN-CON	9	15.955647	44.696754	+													2b		1				+	
49.	Krka 2	river	DIN-CON	8	16.145145	44.420356						1								2b		+				3	
50.	Cetina	river	DIN-MED	9	16.428127	43.969528				2m	2m			1										3			
51.	Cetina	river	DIN-MED	9	16.442504	43.936107					2m									3				2m			
52.	Dubračina	river	DIN-MED	12	14.694398	45.176866													1	1						1	
53.	Kamešnica	river	PAN	1	16.515771	46.133465																				+	
54.	Krupa	river	DIN-MED	8	15.887189	44.190639	3	+		3				2m						3						1	
55.	Krupa	river	DIN-MED	8	15.886790	44.190956	3			4				2m						4							
56.	Krupa	river	DIN-MED	8	15.908922	44.192500				+										3							
57.	Zrmanja	river	DIN-MED	10	16.033380	44.092277	2m					2a		2m			+	1	1		+				1	2a	
58.	Una	river	PAN	3	16.372592	45.049785													2m	3		1		2m		2b	
59.	Vojskova	river	DIN-MED	8	16.630715	43.756800				2a	1									2m						2m	
60.	Zduški potok	river	DIN-MED	12	16.429238	43.936657					1									1							
61.	Vitunjčica	river	DIN-CON	4	15.163285	45.283566					2b		2a							2a		+					
62.	Mačavarina Draga	canal	DIN-MED	13	15.566025	43.949253						2a														2a	
63.	Bistrica 1	river	DIN-CON	4	15.286329	45.285330						2m		2a						2b						2a	
64.	Munjava	river	DIN-CON	4	15.285698	45.187223							+							1		2m				2a	
65.	Munjava	river	DIN-CON	4	15.296957	45.203676														2m							
66.	Butižnica	river	DIN-MED	9	16.220097	44.089242	1				3			2a			2m		1	2b						2a	
67.	Suha Ričina Baščanska	river	DIN-MED	12	14.741692	44.969401						+	+														
68.	Zrmanja	river	DIN-MED	10	15.775856	44.195503														+						+	
69.	Zrmanja	river	DIN-MED	10	15.857687	44.161971														2m							
70.	Baščica	river	DIN-MED	12	15.439523	44.219688						1					1		2m	2m						2m	
71.	Potkoš	river	DIN-MED	7	14.730900	45.303710														2m		2m					
72.	Cetina	river	DIN-MED	10	16.758348	43.436788														2m						2a	
73.	Kanal Halašica	canal	PAN	13	18.616795	45.622935																					2a
74.	Kanal VI.	canal	PAN	13	18.556142	45.691388																					2a
75.	Drava	canal	PAN	13	16.337635	46.326198														+							
76.	Curak	river	DIN-CON	4	14.892896	45.427254					2b															2a	
77.	Curak	river	DIN-CON	4	14.876561	45.445632						2a														2a	
78.	Suvaja 2	river	DIN-MED	11	17.134724	43.495638	+																				
79.	Cetina	river	DIN-MED	10	16.700886	43.456527														2a						2m	
80.	Kanal Gacka	canal	DIN-CON	13	15.223481	44.862430														2b							
81.	Odvodni kanal HE Orlovac	canal	DIN-MED	13	16.782248	43.672256						+															
82.	Mirna	river	DIN-MED	10	13.925169	45.386998																1					
83.	Butižnica	river	DIN-MED	9	16.226223	44.109445														2m						+	
84.	Zvizda	river	DIN-MED	12	16.891139	43.421032	2m					1		2a					+							1	
85.	Zvizda	river	DIN-MED	12	16.890772	43.421651	+					+		+													
86.	Ričica	river	DIN-CON	7	15.687101	44.365058	2a					2m	2m					2a	2m	2m	1				1	2a	
87.	Dubračina	river	DIN-MED	12	14.650437	45.231533																				1	
88.	Dubračina	river	DIN-MED	12	14.680145	45.214877						2m	2a													2a	
89.	Obuhvatni kanal Mufrin	canal	DIN-MED	13	13.845253	45.348507														2b							
90.	Gusić	canal	DIN-CON	13	15.126233	44.944960					4	2b															
91.	Dubračina	river	DIN-MED	12	14.676096	45.219689						2a		2m						1						2m	
92.	Butižnica	river	DIN-MED	9	16.220514	44.096236								1						3						1	
93.	Šumetlica	river	PAN	2	17.383364	45.346493		2m															+			+	
94.	Vrbova	river	PAN	2	17.819508	45.293597																3					

		Affinity to water					Hyg	Rh	Hyg	Hyg	Rh	Rh	Rh	Am	Hyg	Hyg	Hyg	Hyg	Rh	Rh	Hyg	Rr	Hyg	Am	Hy	Rh	Hyd
Site id	Watercourse	water body type	(sub) ecoregion	watercourse type	X_WGS_84	Y_WGS_84	Apo end	Bra riv	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Did top	Euc ver	Fis cra	Fon ant	Jun atr	Lep rip	Mar pol	Pal fal	Pty pse	Rhy rip	Ric flu
95.	Kutjevačka rijeka	river	PAN	2	17.900266	45.338907																+					
96.	Vetovka	river	PAN	2	17.752276	45.347172																1				1	
97.	Peranački potok	river	PAN	2	17.593012	45.350016																1					
98.	Peranački potok	river	PAN	2	17.592751	45.349389																2a					
99.	Peranački potok	river	PAN	2	17.592772	45.349039								1								1	+		+		
100.	Jovača	river	PAN	2	17.185848	45.516071																+					
101.	Velika	river	PAN	3	16.699387	45.901534																+					
102.	Brestača	river	PAN	2	16.969488	45.350857																+					
103.	Javošnica	river	PAN	2	16.345513	45.078081																1					
104.	Sutla	river	PAN	3	15.714876	46.059238							2a						1	1							
105.	Posalitva	river	PAN	2	16.083312	46.377626														+		2b					
106.	Matica 1	river	DIN-CON	7	15.733698	44.741036														2m		2b					
107.	Krbava	river	DIN-CON	7	15.765785	44.544026								1												1	
108.	Pazinčica	river	DIN-MED	8	13.929240	45.240175						1	2b						2m			1				3	
109.	Cetina	river	DIN-MED	9	16.729088	43.617646														2m							
110.	Jadro	river	DIN-MED	8	16.490931	43.533856	+				+	1	2a	1					2b	1						2a	
111.	Žrnovnica	river	DIN-MED	8	16.542129	43.516277					3			2a						2m		2b				2a	
112.	Cetina	river	DIN-MED	9	16.747346	43.531851														+							
113.	Krčić	river	DIN-MED	12	16.319002	44.027372					2a			1												2a	
114.	Vrljika	river	DIN-MED	11	17.195427	43.431283														2m							
115.	Kopačica	river	DIN-MED	11	18.376559	42.521688														+							
116.	Petrinjčica	river	PAN	3	16.273084	45.441261							+						+			+					
117.	Došnica	river	DIN-MED	8	16.205649	44.091707	+			+				2m			2m		+								
118.	Krka	river	DIN-MED	7	16.018833	44.002614														2b							
119.	Zelina	river	PAN	3	16.285091	45.818407																2m					
120.	Kupa	river	DIN-CON	6	15.359170	45.645155														1		+					
121.	Kupa	river	DIN-CON	6	15.354981	45.646101					2m		2m						+	1						2m	
122.	Kupa	river	PAN	3	15.597712	45.487189						+	+							+							
123.	Petrinjčica	river	PAN	2	16.287826	45.272807				1					2m	2m						2m	+		+	1	
124.	Golinja	river	PAN	2	16.016777	45.477538			+					2m						2a		2m			1	2m	
125.	Kremešnica	river	PAN	2	15.873438	45.526513				1						1				2m		2m			1	2m	
126.	Kravaršćica	river	PAN	2	15.907384	45.539067			1					1								1					
127.	Roženica	river	PAN	2	15.938369	45.518797			1																1		
128.	Trepča	river	PAN	3	15.910003	45.461375							1									2m					
129.	Trepča	river	PAN	3	15.911045	45.461395							2b							1		2a			+	1	
130.	Glina	river	PAN	3	15.769945	45.210090								+						+		3	+			2b	
131.	Kupčina	river	PAN	3	15.618217	45.605219						+															
132.	Kupčina	river	PAN	3	15.788989	45.532173																					1
133.	Reka 2	river	PAN	2	15.645161	45.633291																+					
134.	Korana	river	DIN-CON	6	15.595513	45.392189														1							
135.	Korana	river	DIN-CON	6	15.545735	45.252514		1			2b	1	2m	2a					2a	1			1			2b	
136.	Brusovača	river	PAN	2	15.759246	45.255601				+										2m		+					
137.	Slunjčica	river	DIN-CON	5	15.589645	45.079570	1			1	3	1	2m	4													
138.	Mrežnica	river	DIN-CON	6	15.559840	45.465917						+								2m							
139.	Zagorska Mrežnica	river	DIN-CON	4	15.274771	45.224335						4															
140.	Dobra	river	DIN-CON	5	15.105964	45.357840	1	+		1		1	1	1					+	2m		1	+		1	2m	
141.	Gornja Dobra	river	DIN-CON	5	15.200320	45.268317					1									1						1	
142.	Ribnjak	river	DIN-CON	2	15.111945	45.341319	+			2a	1	1		1						2m				1	1	2m	
143.	Ruševica	river	PAN	2	15.724668	45.196528																+					

		Affinity to water					Hyg	Rh	Hyg	Hyg	Rh	Rh	Rh	Am	Hyg	Hyg	Hyg	Hyg	Rh	Rh	Hyg	Rr	Hyg	Am	Hy	Rh	Hyd
Site id	Watercourse	water body type	(sub) ecoregion	watercourse type	X_WGS_84	Y_WGS_84	Apo end	Bra riv	Chi pal	Chi pol	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Did top	Euc ver	Fis cra	Fon ant	Jun atr	Lep rip	Mar pol	Pal fal	Pty pse	Rhy rip	Ric flu
144.	Reka 1	river	PAN	1	16.065072	46.148917								1						1						1	
145.	Reka 1	river	PAN	2	16.069043	46.054274														+		+					
146.	Presečno	river	PAN	2	16.311593	46.035296																+					
147.	Kotoripski kanal	canal	PAN	13	16.815486	46.344863																					+
148.	Gliboki potok	river	PAN	2	16.723784	46.195923																	+				
149.	Kupa	river	DIN-CON	6	15.075441	45.484505	+		+				2m	+					+	2m			+	+	+	2m	
150.	Kupa	river	DIN-CON	5	14.774464	45.507431		2m		+	2a	2m	2a	2m	1	1			1	2m	1		+	1		2a	
151.	Kupa	river	DIN-CON	5	14.700611	45.504959	+			2m	2b	2m	2m	2a	1				1		+		+	2a	+	2b	
152.	Kupica	river	DIN-CON	5	14.856837	45.464067	+			2m	3	1	2b						+	+				2m		2b	
153.	Curak	river	DIN-CON	4	14.853625	45.450091	+	+			2m	1	+	2m	1				+				+			2a	
154.	Čabranka	river	DIN-CON	5	14.699631	45.525658	1	1		2m		1		2m		+			2m				1			2m	
155.	Velika Belica	river	DIN-CON	4	14.805035	45.475503	2m					1		+				+	+	+	2a		+		2a		
156.	Gerovčica	river	DIN-CON	4	14.635590	45.516163								2m								1				+	
157.	Čedanj	river	DIN-CON	4	14.908660	45.476094		1		1			+	+	1	1			+		2m					2m	
158.	Gacka	river	DIN-CON	5	15.295610	44.826532				2m		1		1						2a							
159.	Rječina	river	DIN-MED	5	14.449662	45.378609		1			2b	2a	2m	1												2m	
160.	Rječina	river	DIN-MED	5	14.417830	45.402581		1			2b	2a	1	2m												2m	
161.	Rječina	river	DIN-MED	5	14.448235	45.356626					+	2m	2m														
162.	Joševica	river	DIN-CON	4	16.109352	44.417062	2m		2m					2a						2a			1				
163.	Mirna	river	DIN-MED	10	13.737779	45.357547																2a					
164.	Mirna	river	DIN-MED	10	13.938908	45.398349														1							
165.	Rumin	river	DIN-MED	8	16.648138	43.776176														2a							
166.	Vojskova	river	DIN-MED	8	16.631274	43.756905				2a	2m															1	
167.	Mislina	river	DIN-MED	11	17.639145	43.006055														+							+
168.	Kobilica	river	DIN-MED	8	16.083563	44.125494	2m				+		+	2m			1		+	2m			+		1	1	
169.	Zrmanja	river	DIN-MED	10	15.940022	44.107609								1			2m	2a	+						1	+	
170.	Ričica	river	DIN-CON	5	15.747645	44.341856	2m					2m	1	1				+	2m	1	+				+	2m	+
171.	Zrmanja	river	DIN-MED	9	16.071088	44.146896	1					1		+						2a				1	+	2a	
172.	Zrmanja	river	DIN-MED	10	15.857687	44.161971						+															
173.	Krupa	river	DIN-MED	8	15.909732	44.193332	2m		2a		3	1		2m				+	1	3			2m			2a	
174.	Bribišnica	river	DIN-MED	8	15.798854	43.890522					1	1	+				1		2b							1	
175.	Vrba	river	DIN-MED	8	16.399989	43.722419	1							2m													
176.	Vrba	river	DIN-MED	8	16.314560	43.791072								1													
177.	Krka	river	DIN-MED	9	16.094719	44.010631				+	1									2b		+				+	
178.	Krka	river	DIN-MED	9	16.225207	44.040146														2a							
179.	Butižnica	river	DIN-MED	9	16.186935	44.040930														2m							
180.	Ljubina	river	PAN	1	16.285494	45.086497			+																	+	
181.	Vučjak	river	PAN	2	17.657635	45.303222								+												2a	
182.	Bistrica 1	river	DIN-CON	4	15.286380	45.284347		2m			4	3	2a	+					1			1				1	

Table S2: Yearly mean values of 18 environmental parameters for all surveyed localities. For abbreviatoions of environmental variables see Table 1.

site id	watercourse	water body type	(sub) ecoregion	watercourse type	T (°C)	pH	EC (µS/cm)	TSS (mg/L)	DO (mgO_2/L)	ALK ($mgCaCO_3/L$)	BOD (mgO_2/L)	COD (mgO_2/L)	NH_4^+ (mgN/L)	NO_2^- (mgN/L)	NO_3^- (mgN/L)	N_{tot} (mgN/L)	PO_4^{3-} (mgP/L)	P_{tot} (mgP/L)	NAT (%)	IAG (%)	EAG (%)	URB (%)
1.	Delnički potok	river	DIN-CON	7	9.82	8.04	290.00	<2.00	10.80	166.08	1.08	0.85	0.010	0.001	0.978	1.101	0.027	0.040	86.69	0.00	3.43	9.87
2.	Kosteljina	river	PAN	2	9.72	8.04	548.83	8.71	11.38	280.75	3.44	5.31	0.061	0.011	1.230	1.674	<0.025	0.041	37.01	37.61	25.37	0.00
3.	Kupa	river	DIN-CON	6	14.14	8.20	307.29	5.55	11.67	155.92	0.64	1.50	0.009	0.002	0.652	0.879	0.006	0.023	88.29	2.24	8.47	0.99
4.	Kupa	river	DIN-CON	6	14.27	8.18	332.08	3.04	10.97	169.00	0.65	1.58	0.011	0.002	0.690	0.908	<0.005	0.024	81.08	7.83	10.00	1.10
5.	Sušica	river	DIN-CON	7	8.96	8.11	296.29	<2.00	11.12	153.67	1.53	1.37	0.063	0.002	0.612	0.800	0.008	0.024	89.06	4.86	5.23	0.86
6.	Tomašnica	river	DIN-CON	4	12.33	8.03	458.31	6.33	10.65	257.75	1.24	2.23	0.091	0.004	0.866	1.223	0.014	0.046	60.31	14.60	25.09	0.00
7.	Rogstrug	river	PAN	3	12.94	7.96	557.67	5.08	8.07	277.17	1.24	2.32	0.115	0.033	0.654	1.375	0.040	0.088	46.75	37.26	13.53	2.47
8.	Mrežnica	river	DIN-CON	5	12.29	7.86	400.57	1.54	10.90	211.00	1.00	0.93	0.028	0.003	0.698	0.984	<0.007	0.024	81.79	9.97	7.54	0.70
9.	Batina	river	PAN	2	12.25	7.99	570.58	10.83	11.50	296.25	2.41	4.11	0.103	0.024	0.716	1.155	<0.025	0.077	41.89	33.55	24.56	0.00
10.	Bednja	river	PAN	1	25.02	7.90	526.67	17.00	8.81	243.42	2.31	3.94	0.373	0.052	1.090	1.940	0.062	0.150	53.39	19.20	25.49	1.92
11.	Crna rijeka 1	river	DIN-CON	2	8.85	8.08	434.00	<2.00	11.31	225.00	<0.5	<0.70	<0.008	<0.002	0.655	0.806	<0.005	0.015	78.86	0.00	21.14	0.00
12.	Dobra	river	DIN-CON	5	12.86	7.76	495.36	1.25	11.12	182.67	1.15	1.36	0.076	0.004	0.753	1.050	<0.007	0.016	84.25	4.49	9.26	2.00
13.	Jaruga 1	river	DIN-CON	7	11.05	7.91	428.92	2.00	9.20	207.04	2.25	0.84	0.010	0.002	0.706	1.178	0.004	0.009	70.27	15.43	14.31	0.00
14.	Korana	river	DIN-CON	5	12.16	8.16	331.50	2.27	10.93	187.43	1.43	0.66	<0.002	<0.002	0.679	1.150	0.003	0.006	84.30	2.27	13.10	0.32
15.	Korana	river	DIN-CON	5	13.56	8.06	391.23	2.79	10.05	204.25	1.42	2.59	0.095	0.002	0.833	1.162	0.015	0.050	59.93	15.94	22.74	1.39
16.	Korana	river	DIN-CON	6	15.14	7.96	379.93	2.92	9.93	196.08	1.42	1.73	0.044	<0.002	0.909	1.257	0.010	0.032	55.40	16.47	26.84	1.29
17.	Krapina	river	PAN	3	12.74	8.09	628.17	15.15	9.39	279.00	2.15	3.93	0.316	0.094	1.227	2.073	0.065	0.167	39.77	33.66	24.73	1.85
18.	Krapina	river	PAN	2	11.15	8.13	561.08	7.13	9.97	272.50	0.93	2.43	0.082	0.021	0.841	1.251	0.044	0.084	38.34	35.46	26.20	0.00
19.	Krapina	river	PAN	3	13.23	8.13	612.92	13.80	10.48	267.00	1.77	3.73	0.178	0.041	1.284	1.928	0.050	0.138	39.91	33.39	24.25	2.45
20.	Moštanica	river	PAN	2	13.62	7.71	570.22	6.10	5.13	290.88	2.84	5.22	1.697	0.062	0.438	2.448	0.136	0.202	21.09	19.49	33.86	25.55
21.	Moštanica	river	PAN	2	13.62	7.71	570.22	6.10	5.13	290.88	2.84	5.22	1.697	0.062	0.438	2.448	0.136	0.202	21.09	19.49	33.86	25.55
22.	Ribnik	river	DIN-CON	4	12.08	7.95	400.08	13.58	9.93	208.58	1.40	3.03	0.120	0.007	1.107	1.487	0.013	0.080	66.97	17.11	15.92	0.00
23.	Žitomirka	river	PAN	2	11.74	7.88	601.50	10.25	10.75	328.33	3.68	6.52	0.048	0.022	0.588	1.349	<0.025	0.085	42.40	20.32	37.29	0.00
24.	Šumetlica	river	PAN	1	12.67	8.23	121.05	4.83	9.18	59.82	9.78	1.91	0.080	<0.0094	0.342	0.568	0.055	0.205	100.00	0.00	0.00	0.00
25.	Bistra 3	canal	PAN	13	15.99	7.52	857.00	11.11	5.25	381.67	5.10	6.37	0.164	<0.026	<0.15	0.588	0.059	0.096	0.00	97.69	2.21	0.10
26.	Voća	river	PAN	1	20.17	7.43	443.33	16.33	4.84	263.33	1.92	3.21	0.083	<0.010	0.187	<1.000	<0.025	0.142	47.49	25.62	26.89	0.00
27.	Bračana	river	DIN-MED	12	13.78	8.18	420.56	1.69	11.20	198.00	1.24	2.02	0.046	<0.010	0.531	0.764	0.040	0.072	84.12	4.94	10.93	0.00
28.	Stara Mirna	river	DIN-MED	10	13.70	7.65	571.40	16.61	9.55	252.00	1.62	2.60	0.039	<0.010	0.755	1.089	0.038	0.092	80.02	5.55	13.46	0.97
29.	Pazinčica	river	DIN-MED	8	13.07	8.08	487.00	2.69	9.97	222.44	1.67	2.32	0.016	<0.010	0.355	0.573	0.041	0.059	68.21	4.73	26.38	0.68
30.	Una	river	PAN	3	7.00	8.25	446.50	8.40	12.30	214.00	0.85	1.75	<0.008	0.004	0.680	0.870	0.007	0.019	63.67	16.07	19.32	0.94
31.	Baščica	river	DIN-MED	12	16.73	7.13	781.33	4.05	8.04	344.62	0.96	1.33	0.099	0.106	0.905	1.393	0.005	0.025	22.98	32.07	37.71	7.24
32.	Bregana	river	DIN-CON	4	11.33	8.28	488.75	2.55	12.55	261.25	0.59	0.81	0.010	0.003	0.770	0.908	0.005	0.022	83.18	1.75	14.87	0.20
33.	Dretulja	river	DIN-CON	6	9.77	7.48	450.20	1.70	10.79	243.00	0.87	0.76	0.008	<0.002	0.959	1.284	<0.007	0.009	86.55	7.78	4.73	0.94
34.	Dretulja	river	DIN-CON	5	10.28	7.86	425.89	2.22	10.94	238.78	1.26	1.59	0.031	<0.002	0.919	1.248	<0.007	0.021	77.32	11.23	10.15	1.30
35.	Jaruga 3	river	DIN-MED	12	17.85	7.80	515.00	2.45	7.51	268.55	0.80	2.05	0.020	0.062	0.304	0.628	0.029	0.042	55.18	34.00	1.36	9.46
36.	Jaruga 2	river	DIN-MED	12	16.13	7.68	929.25	2.50	9.58	304.43	0.81	2.35	0.862	0.021	0.153	0.413	0.002	0.006	37.60	48.97	7.57	5.87
37.	Kupčina	river	DIN-CON	4	15.23	7.68	479.75	2.10	10.10	255.33	0.81	0.79	0.038	0.050	1.035	1.348	0.020	0.050	85.31	0.00	14.69	0.00
38.	Velika rijeka	river	PAN	1	11.85	8.29	189.89	5.94	8.73	96.14	7.33	3.11	0.026	<0.0094	0.631	0.969	0.089	0.280	100.00	0.00	0.00	0.00
39.	Rudarska Gradna	river	DIN-CON	4	18.75	7.77	626.50	16.65	9.39	278.25	1.10	2.46	0.140	0.061	1.350	2.000	0.070	0.223	74.47	0.00	25.53	0.00
40.	Rudarska Gradna	river	DIN-CON	4	16.88	7.83	641.75	5.45	10.61	274.00	1.38	0.68	0.126	<0.05	1.300	1.560	0.034	0.070	76.01	0.00	23.57	0.42
41.	Gradna	river	DIN-CON	4	18.65	7.98	529.25	2.85	11.27	250.25	1.24	0.53	0.072	<0.05	1.082	2.638	0.015	0.036	77.16	0.00	21.12	1.72
42.	Lipovečka Gradna	river	DIN-CON	4	17.15	7.81	504.75	9.00	10.41	254.25	0.66	0.43	0.128	<0.05	0.913	1.302	<0.01	0.041	87.50	0.00	12.50	0.00
43.	Svinica	river	PAN	2	17.83	7.87	443.00	12.44	6.15	248.80	1.50	3.92	0.214	0.005	0.296	0.932	0.030	0.074	58.60	35.46	5.94	0.00
44.	Bregana	river	DIN-CON	4	18.63	7.56	474.00	<2	9.11	263.00	0.33	0.25	0.042	<0.05	0.966	<1.000	<0.01	0.019	0.00	82.45	17.55	0.00
45.	Slapnica	river	DIN-CON	4	17.58	7.59	522.00	<2.00	10.15	281.67	0.60	0.29	0.070	<0.05	1.098	1.385	<0.01	0.016	71.79	0.02	28.19	0.00
46.	Subocka	river	PAN	2	15.13	8.02	491.00	16.00	9.42	255.00	2.70	4.36	0.221	0.010	0.335	0.935	0.010	0.061	66.70	3.06	30.24	0.00
47.	Una	river	DIN-CON	4	11.26	7.91	393.86	1.30	11.49	206.71	0.54	0.49	0.006	0.014	0.312	0.545	0.004	0.007	89.08	0.47	10.45	0.00
48.	Una	river	DIN-CON	9	12.38	8.23	501.80	2.08	10.67	204.65	1.70	1.25	<0.002	<0.002	0.513	0.774	0.008	0.011	78.42	4.92	16.36	0.31
49.	Krka 2	river	DIN-CON	8	10.52	7.78	418.17	1.17	11.86	220.63	0.66	0.97	0.013	0.008	0.399	0.744	0.003	0.006	78.60	4.59	16.78	0.03

site id	watercourse	water body type	(sub) ecoregion	watercourse type	T (°C)	pH	EC (µS/cm)	TSS (mg/L)	DO (mgO_2/L)	ALK ($mgCaCO_3/L$)	BOD (mgO_2/L)	COD (mgO_2/L)	NH_4^+ (mgN/L)	NO_2^- (mgN/L)	NO_3^- (mgN/L)	N_{tot} (mgN/L)	PO_4^{3-} (mgP/L)	P_{tot} (mgP/L)	NAT (%)	IAG (%)	EAG (%)	URB (%)
50.	Cetina	river	DIN-MED	9	10.16	7.73	321.86	0.85	12.14	171.96	0.75	0.77	0.013	0.003	0.370	0.519	0.002	0.005	83.51	5.08	11.37	0.04
51.	Cetina	river	DIN-MED	9	7.85	8.00	375.50	3.50	11.04	180.50	<0.6	0.75	0.017	0.002	0.301	0.445	<0.006	0.011	80.82	6.55	12.45	0.18
52.	Dubračina	river	DIN-MED	12	14.31	8.26	262.42	2.78	11.03	98.92	1.65	1.16	0.017	0.004	0.427	0.548	0.003	0.022	89.77	0.00	6.73	3.51
53.	Kamešnica	river	PAN	1	13.05	8.10	374.00	2.60	10.10	178.50	3.45	9.70	<0.008	0.004	0.225	0.465	0.009	0.077	99.98	0.00	0.02	0.00
54.	Krupa	river	DIN-MED	8	10.60	8.15	358.50	<2.00	11.10	190.50	<0.6	<0.50	<0.012	<0.0009	0.196	0.305	<0.006	<0.009	92.68	0.00	7.28	0.03
55.	Krupa	river	DIN-MED	8	10.60	8.15	358.50	<2.00	11.10	190.50	<0.6	<0.50	<0.012	<0.0009	0.196	0.305	<0.006	<0.009	92.68	0.00	7.28	0.03
56.	Krupa	river	DIN-MED	8	10.63	7.92	374.00	<2.00	11.07	195.17	<0.6	<0.50	<0.012	<0.0009	0.203	0.278	<0.006	<0.009	93.88	0.00	6.07	0.05
57.	Zrmanja	river	DIN-MED	10	15.66	7.99	340.14	1.64	10.38	167.64	0.68	1.50	0.006	0.004	0.342	0.691	0.003	0.005	77.82	0.38	21.80	0.00
58.	Una	river	PAN	3	15.65	8.23	435.57	3.50	10.44	200.14	1.39	2.26	<0.008	0.003	0.524	0.701	0.007	0.034	72.60	10.64	15.89	0.87
59.	Vojskova	river	DIN-MED	8	12.49	7.62	719.00	0.95	11.45	209.50	2.64	2.08	0.034	0.002	0.360	0.851	0.007	0.016	82.26	12.72	1.05	3.97
60.	Zduški potok	river	DIN-MED	12	16.06	7.81	1073.00	6.51	10.59	179.50	2.50	4.30	0.028	0.019	0.426	1.074	0.021	0.038	65.24	23.84	9.55	1.37
61.	Vitunjčica	river	DIN-CON	4	12.33	7.98	373.00	2.00	11.63	172.13	1.50	1.78	0.078	0.007	0.784	1.209	0.008	0.027	82.33	3.61	14.06	0.00
62.	Mačavarina Draga	canal	DIN-MED	13	15.80	7.23	623.67	1.93	7.95	319.97	<0.27	0.85	<0.003	0.002	1.260	1.437	0.018	0.021	42.79	44.02	1.96	11.23
63.	Bistrica 1	river	DIN-CON	4	12.30	7.75	391.90	1.70	9.72	185.20	1.14	1.48	0.133	0.008	0.852	1.219	<0.007	0.029	83.69	7.23	7.78	1.30
64.	Munjava	river	DIN-CON	4	14.79	8.04	441.44	6.22	10.04	262.89	1.49	2.20	0.216	0.006	0.609	1.110	0.008	0.027	42.36	12.45	40.83	4.36
65.	Munjava	river	DIN-CON	4	15.13	8.11	431.44	7.44	10.23	268.56	1.58	2.56	0.138	0.005	0.552	0.932	0.013	0.036	38.41	24.60	31.54	5.45
66.	Butižnica	river	DIN-MED	9	10.06	8.07	941.71	2.25	10.98	194.57	<0.60	0.50	0.013	0.003	0.179	0.275	<0.006	<0.009	88.82	0.16	10.82	0.20
67.	Suha Ričina Baščanska	river	DIN-MED	12	14.92	7.87	802.91	2.13	8.98	276.64	0.83	0.79	0.006	0.001	0.380	0.445	<0.003	0.014	77.52	12.60	7.58	2.30
68.	Zrmanja	river	DIN-MED	10	11.47	8.13	378.00	<2.00	11.12	196.50	<0.60	<0.50	<0.012	0.001	0.228	0.353	<0.006	<0.009	81.24	2.17	16.58	0.01
69.	Zrmanja	river	DIN-MED	10	12.31	7.80	395.57	<2.00	11.10	208.14	<0.60	<0.50	<0.012	0.001	0.223	0.327	<0.006	<0.009	81.12	2.04	16.83	0.01
70.	Baščica	river	DIN-MED	12	16.33	7.58		3.90	9.21	282.40	1.25	10.68	0.008	0.003	0.497	0.885	0.003	0.009	21.34	34.15	38.61	5.90
71.	Potkoš	river	DIN-MED	7	9.03	7.67	394.25	3.62	9.46	137.50	1.24	1.53	0.012	0.003	0.689	0.808	0.005	0.034	44.52	0.00	46.10	9.38
72.	Cetina	river	DIN-MED	10	13.88	8.26	404.50	<2.00	10.71	180.25	<0.6	1.13	<0.012	0.001	0.314	0.415	0.007	0.014	72.80	12.81	13.27	1.12
73.	Kanal Halašica	canal	PAN	13	14.92	7.66	923.50	18.92	7.93	434.58	5.05	6.43	0.131	<0.021	0.165	0.730	0.077	0.131	15.88	59.37	24.75	0.00
74.	Kanal VI.	canal	PAN	13	15.30	7.87	908.92	16.58	8.73	446.67	4.39	5.50	0.068	<0.021	0.140	1.003	0.083	0.181	7.44	91.86	0.00	0.70
75.	Drava	canal	PAN	13	14.95	7.93	268.45	49.50	9.55	160.83	1.68	3.13	<0.04	<0.01	0.893	1.483	<0.03	0.062	72.70	12.36	11.46	3.48
76.	Curak	river	DIN-CON	4	9.18	8.15	301.00	<2.00	11.17	146.17	1.09	0.70	0.008	<0.001	0.653	0.688	0.007	0.022	69.78	6.03	19.26	4.93
77.	Curak	river	DIN-CON	4	8.42	8.15	308.67	<2.00	11.37	153.33	1.24	0.68	0.005	<0.001	0.707	0.740	0.005	0.024	72.92	5.29	16.89	4.90
78.	Suvaja 2	river	DIN-MED	11	11.98	8.02	361.17	17.12	10.57	171.67	1.87	1.66	0.018	0.004	0.958	1.137	0.005	0.050	72.14	12.06	14.46	1.34
79.	Cetina	river	DIN-MED	10	12.52	7.95	454.00	<2.00	10.83	161.00	1.35	0.94	0.020	0.002	0.268	0.568	0.004	0.096	72.27	13.38	13.32	1.03
80.	Kanal Gacka	canal	DIN-CON	13	9.73	7.65	460.83	<2.00	10.17	244.67	0.90	0.68	0.015	0.002	0.433	0.505	<0.003	0.035	66.84	15.06	16.76	1.34
81.	Odvodni kanal HE Orlovac	canal	DIN-MED	13	11.50	8.03	299.33	4.10	10.27	145.50	1.25	1.57	0.016	0.003	0.201	0.370	0.006	0.052	63.93	19.43	15.85	0.78
82.	Mirna	river	DIN-MED	10	13.25	7.92	437.83	12.78	10.08	230.67	1.08	1.13	0.030	0.009	0.387	0.527	0.017	0.068	82.21	5.55	11.13	1.11
83.	Butižnica	river	DIN-MED	9	10.80	7.83	948.33	2.80	10.20	190.00	1.10	0.82	0.005	<0.001	0.172	0.210	<0.003	0.034	89.63	0.17	10.20	0.00
84.	Zvizda	river	DIN-MED	12	9.98	7.84	550.80	2.94	10.50	281.00	1.40	1.40	0.017	0.002	0.592	0.692	<0.003	0.026	92.81	0.00	7.19	0.00
85.	Zvizda	river	DIN-MED	12	9.98	7.84	550.80	2.94	10.50	281.00	1.40	1.40	0.017	0.002	0.592	0.692	<0.003	0.026	92.81	0.00	7.19	0.00
86.	Ričica	river	DIN-CON	7	10.37	7.83	353.83	<2.00	9.42	185.83	0.93	1.04	0.004	<0.001	0.092	0.158	<0.003	0.025	64.71	0.00	33.99	1.30
87.	Dubračina	river	DIN-MED	12	9.10	7.82	449.67	<2.00	10.50	218.83	1.47	1.37	0.040	0.006	0.517	0.677	0.010	0.033	90.84	0.00	3.58	5.58
88.	Dubračina	river	DIN-MED	12	10.63	8.05	189.33	2.92	11.40	90.33	1.77	1.18	0.018	0.003	0.353	0.487	<0.003	0.025	87.99	0.00	7.05	4.96
89.	Obuhvatni kanal Mufrin	canal	DIN-MED	13	14.82	7.72	591.33	45.50	9.65	283.50	1.21	1.59	0.023	0.004	1.327	1.500	0.028	0.101	74.95	1.35	23.69	0.00
90.	Gusić	canal	DIN-CON	13	9.77	7.77	379.17	3.67	10.28	197.50	1.16	0.86	0.014	0.003	0.267	0.362	<0.003	0.045	69.70	11.12	17.75	1.44
91.	Dubračina	river	DIN-MED	12	10.55	7.93	214.17	2.08	10.77	101.67	1.50	1.11	0.022	0.003	0.320	0.442	0.003	0.030	88.55	0.00	6.97	4.48
92.	Butižnica	river	DIN-MED	9	11.07	7.93	935.33	<2.00	10.58	182.50	1.33	0.73	0.006	<0.001	0.129	0.195	<0.003	0.029	88.89	0.16	10.75	0.20
93.	Šumetlica	river	PAN	2	12.65	8.03	223.00	3.91	9.95	105.36	2.90	2.89	0.044	0.005	1.068	2.081	0.040	0.079	100.00	0.00	0.00	0.00
94.	Vrbova	river	PAN	2	13.67	8.14	616.45	11.39	10.70	270.23	2.51	4.25	0.030	0.026	3.948	5.174	0.046	0.082	19.32	70.01	9.35	1.33
95.	Kutjevačka rijeka	river	PAN	2	12.81	7.92	469.45	10.83	9.38	192.09	3.92	4.52	0.124	0.049	3.496	4.701	0.088	0.123	55.97	38.04	2.32	3.66
96.	Vetovka	river	PAN	2	12.78	7.80	475.55	13.05	9.66	215.77	2.45	3.18	0.035	0.045	4.442	5.176	0.050	0.074	32.50	55.77	9.12	2.61
97.	Peranački potok	river	PAN	2	12.32	7.98	583.91	5.75	9.24	308.41	2.66	4.54	0.018	0.004	0.725	1.385	0.034	0.060	47.67	26.62	25.71	0.00
98.	Peranački potok	river	PAN	2	12.32	7.98	583.91	5.75	9.24	308.41	2.66	4.54	0.018	0.004	0.725	1.385	0.034	0.060	47.67	26.62	25.71	0.00
99.	Peranački potok	river	PAN	2	12.32	7.98	583.91	5.75	9.24	308.41	2.66	4.54	0.018	0.004	0.725	1.385	0.034	0.060	47.67	26.62	25.71	0.00

site id	watercourse	water body type	(sub) ecoregion	watercourse type	T (°C)	pH	EC (μS/cm)	TSS (mg/L)	DO (mgO_2/L)	ALK ($mgCaCO_3/L$)	BOD (mgO_2/L)	COD (mgO_2/L)	NH_4^+ (mgN/L)	NO_2^- (mgN/L)	NO_3^- (mgN/L)	N_{tot} (mgN/L)	PO_4^{3-} (mgP/L)	P_{tot} (mgP/L)	NAT (%)	IAG (%)	EAG (%)	URB (%)
100.	Jovača	river	PAN	2	13.93	7.57	275.00	10.38	8.58	121.21	3.23	7.06	0.029	0.010	2.357	2.927	0.045	0.110	24.96	61.68	11.73	1.64
101.	Velika	river	PAN	3	14.09	7.91	445.80	49.80	6.99	237.80	3.96	13.11	0.494	0.062	0.770	1.931	0.188	0.342	35.01	47.26	17.23	0.50
102.	Brestača	river	PAN	2	14.00	7.94	538.56	41.50	7.89	260.22	4.62	10.96	0.971	0.061	0.728	2.821	0.112	0.259	96.92	1.41	0.00	1.67
103.	Javošnica	river	PAN	2	14.38	7.81	361.40	17.58	8.92	192.60	2.74	6.10	0.304	0.017	0.228	0.813	0.018	0.102	53.31	7.13	39.56	0.00
104.	Sutla	river	PAN	3	14.90	8.06	596.80	18.48	10.26	288.60	2.40	4.64	0.044	0.039	1.181	1.666	0.049	0.136	38.85	31.27	28.90	0.97
105.	Posalitva	river	PAN	2	8.88	7.81	611.60	8.10	11.25	335.70	3.22	5.45	0.102	0.007	1.407	1.691	0.032	0.093	41.62	20.89	37.48	0.00
106.	Matica 1	river	DIN-CON	7	11.05	8.13	480.33	1.95	9.60	210.18	2.98	2.36	0.067	0.014	1.082	1.895	0.022	0.036	67.09	2.66	25.67	4.57
107.	Krbava	river	DIN-CON	7	10.80	8.03	438.42	<2.00	10.43	189.67	2.10	2.40	0.016	<0.002	0.373	0.830	0.010	0.017	62.17	0.00	37.54	0.29
108.	Pazinčica	river	DIN-MED	8	14.53	7.70	630.42	2.08	8.90	228.00	1.73	4.77	0.665	0.215	1.243	2.243	0.179	0.271	67.74	4.44	25.29	2.53
109.	Cetina	river	DIN-MED	9	12.87	8.05	389.83	<2.00	11.51	179.92	<0.60	1.11	0.012	0.002	0.300	0.388	0.006	0.009	72.20	13.67	13.12	1.01
110.	Jadro	river	DIN-MED	8	15.13	7.66	403.49	<2.00	10.29	187.27	0.52	1.17	0.149	<0.03	0.556	0.928	0.010	0.017	75.52	9.34	10.14	5.00
111.	Žrnovnica	river	DIN-MED	8	14.79	7.76	379.25	<2.00	10.33	181.09	0.49	1.05	0.029	<0.03	0.453	0.591	<0.005	0.004	74.55	13.04	7.95	4.47
112.	Cetina	river	DIN-MED	9	13.35	8.19	397.25	<2.00	11.51	168.83	<0.60	1.18	0.011	0.002	0.302	0.390	<0.006	<0.009	72.22	13.50	13.23	1.05
113.	Krčić	river	DIN-MED	12	9.72	7.92	350.00	1.14	11.39	187.78	<0.60	<0.50	<0.012	<0.001	0.278	0.320	<0.006	<0.009	87.84	2.44	8.68	1.03
114.	Vrljika	river	DIN-MED	11	12.48	7.76	386.33	2.04	11.19	199.08	<0.60	0.60	<0.012	0.001	0.315	0.358	<0.006	0.015	70.05	12.44	15.50	2.00
115.	Kopačica	river	DIN-MED	11	13.80	7.81	415.80	<2.00	10.77	223.80	0.60	1.19	0.051	<0.03	<0.23	0.239	<0.005	<0.002	72.36	6.51	17.47	3.66
116.	Petrinjčica	river	PAN	3	15.89	8.01	395.50	27.33	10.32	196.30	2.89	4.37	0.352	0.012	0.301	0.956	0.018	0.070	53.31	17.30	25.19	4.20
117.	Došnica	river	DIN-MED	8	15.30	8.20	532.29	4.07	9.81	224.39	1.57	3.50	0.004	0.043	0.060	0.674	<0.0012	0.002	80.36	0.00	19.27	0.37
118.	Krka	river	DIN-MED	7	13.82	7.62	543.00	1.28	10.37	214.17	<0.60	0.76	0.011	0.002	0.358	0.399	<0.006	<0.009	76.29	7.19	15.65	0.88
119.	Zelina	river	PAN	3	14.65	7.93	637.20	13.83	9.87	282.30	3.31	7.09	0.136	0.023	1.130	2.655	0.129	0.199	38.83	34.06	22.52	4.59
120.	Kupa	river	DIN-CON	6	14.23	8.21	333.75	<2.00	10.85	190.42	1.07	2.04	0.009	0.008	0.643	0.830	0.006	0.013	81.08	7.83	10.00	1.10
121.	Kupa	river	DIN-CON	6	14.23	8.21	333.75	<2.00	10.85	190.42	1.07	2.04	0.009	0.008	0.643	0.830	0.006	0.013	81.08	7.83	10.00	1.10
122.	Kupa	river	PAN	3	16.22	8.23	350.10	<2.00	10.40	195.10	0.98	2.25	0.013	0.006	0.535	0.708	0.005	0.014	73.74	10.36	14.47	1.43
123.	Petrinjčica	river	PAN	2	13.21	7.87	189.36	8.59	10.78	91.45	1.58	4.97	0.004	0.002	0.325	0.489	0.010	0.038	98.51	0.00	1.49	0.00
124.	Golinja	river	PAN	2	12.36	7.84	345.00	5.75	9.36	204.42	2.71	10.67	0.361	0.021	0.184	1.009	0.010	0.070	35.37	18.57	46.06	0.00
125.	Kremešnica	river	PAN	2	11.48	7.66	282.83	20.92	10.16	76.19	2.60	5.51	0.313	0.006	1.212	1.606	0.026	0.091	78.02	5.37	16.61	0.00
126.	Kravaršćica	river	PAN	2	10.68	7.03	385.67	10.33	9.54	229.17	1.84	5.14	0.052	0.010	0.567	1.159	0.026	0.054	49.62	10.17	40.21	0.00
127.	Roženica	river	PAN	2	10.45	7.13	264.18	7.18	9.42	163.18	1.95	5.82	0.050	0.010	0.462	1.066	0.019	0.057	66.85	8.46	24.68	0.00
128.	Trepča	river	PAN	3	12.73	7.81	205.45	8.80	14.25	104.64	3.32	6.95	0.024	0.005	0.304	0.698	0.038	0.093	53.85	13.07	32.69	0.40
129.	Trepča	river	PAN	3	12.73	7.81	205.45	8.80	14.25	104.64	3.32	6.95	0.024	0.005	0.304	0.698	0.038	0.093	53.85	13.07	32.69	0.40
130.	Glina	river	PAN	3	12.94	7.97	420.75	3.31	9.56	230.08	1.31	3.76	0.016	0.003	0.335	0.567	0.012	0.033	60.57	13.78	25.47	0.17
131.	Kupčina	river	PAN	3	13.95	8.16	520.90	4.60	10.50	293.80	1.08	2.15	0.017	0.006	0.653	0.863	0.014	0.027	63.15	8.28	27.74	0.82
132.	Kupčina	river	PAN	3	12.38	7.06	306.33	40.17	7.88	171.58	2.79	7.55	0.212	0.022	0.515	1.185	0.077	0.127	61.56	22.48	14.83	1.12
133.	Reka 2	river	PAN	2	14.08	7.51	532.42	7.00	11.79	324.25	1.47	2.37	0.091	0.030	0.818	1.415	0.109	0.141	43.60	40.81	7.07	8.51
134.	Korana	river	DIN-CON	6	15.16	8.38	378.75	2.26	11.43	205.50	1.21	2.85	<0.008	0.002	0.465	0.611	0.008	0.017	55.40	16.47	26.84	1.29
135.	Korana	river	DIN-CON	6	14.29	8.35	386.18	2.96	11.29	214.91	1.10	2.75	0.004	0.002	0.548	0.716	0.007	0.013	61.05	14.94	22.68	1.33
136.	Brusovača	river	PAN	2	12.15	8.03	80.34	11.08	11.15	48.00	1.26	5.20	0.004	0.001	0.255	0.389	0.007	0.028	100.00	0.00	0.00	0.00
137.	Slunjčica	river	DIN-CON	5	10.77	7.70	441.25	2.37	10.92	246.33	0.62	1.37	0.023	0.001	0.763	0.916	0.005	0.011	90.57	2.83	5.94	0.65
138.	Mrežnica	river	DIN-CON	6	15.73	8.17	368.92	7.98	11.42	211.50	1.02	2.18	0.040	0.005	0.421	0.604	0.008	0.022	77.86	8.77	12.11	1.26
139.	Zagorska Mrežnica	river	DIN-CON	4	15.37	7.80	458.33	23.00	9.17	230.17	2.80	2.37	0.359	0.028	1.370	1.882	0.018	0.067	84.54	6.73	7.81	0.92
140.	Dobra	river	DIN-CON	5	11.01	8.15	348.91	1.69	11.23	189.91	0.93	2.39	0.004	0.003	0.885	1.095	0.004	0.009	88.88	0.33	8.19	2.60
141.	Gornja Dobra	river	DIN-CON	5	11.83	8.18	349.75	3.08	11.07	202.83	1.27	2.45	0.010	0.004	0.808	1.057	0.004	0.009	86.82	1.29	10.08	1.81
142.	Ribnjak	river	DIN-CON	2	8.88	7.76	348.75	1.00	10.13	195.42	1.11	1.10	0.004	0.002	0.802	0.858	0.004	0.030	87.67	0.00	12.33	0.00
143.	Ruševica	river	PAN	2	11.53	7.83	409.33	17.33	10.19	210.25	1.58	2.68	0.183	0.007	1.588	1.842	0.016	0.076	60.42	22.10	16.56	0.92
144.	Reka 1	river	PAN	1	11.67	8.28	463.90	18.90	11.04	266.70	3.35	5.55	0.018	0.010	0.826	1.032	0.011	0.043	92.24	1.45	6.14	0.17
145.	Reka 1	river	PAN	2	12.03	8.04	603.80	13.51	10.28	321.50	3.60	4.18	0.286	0.068	1.472	2.458	0.095	0.175	54.06	31.30	13.16	1.49
146.	Presečno	river	PAN	2	10.88	7.67	599.08	23.50	8.85	343.33	2.34	4.39	0.131	0.012	0.824	1.298	<0.025	0.084	35.94	40.40	23.66	0.00
147.	Kotoripski kanal	canal	PAN	13	13.32	7.53	711.00	12.17	6.17	290.58	4.63	3.34	6.056	0.296	3.142	8.900	0.473	0.699	10.47	89.18	0.02	0.34
148.	Gliboki potok	river	PAN	2	12.40	8.05	466.00	21.54	10.70	229.50	1.78	4.80	0.073	0.028	1.217	1.842	0.041	0.146	57.18	30.19	11.87	0.75
149.	Kupa	river	DIN-CON	6	13.21	8.28	316.08	1.00	11.66	181.92	0.84	1.93	0.004	0.006	0.603	0.755	0.005	0.010	89.06	1.85	8.14	0.95

site id	watercourse	water body type	(sub) ecoregion	watercourse type	T (°C)	pH	EC (μS/cm)	TSS (mg/L)	DO (mgO_2/L)	ALK ($mgCaCO_3/L$)	BOD (mgO_2/L)	COD (mgO_2/L)	NH_4^+ (mgN/L)	NO_2^- (mgN/L)	NO_3^- (mgN/L)	N_{tot} (mgN/L)	PO_4^{3-} (mgP/L)	P_{tot} (mgP/L)	NAT (%)	IAG (%)	EAG (%)	URB (%)
150.	Kupa	river	DIN-CON	5	10.94	8.28	279.42	1.00	12.22	161.50	0.78	1.77	0.004	0.004	0.598	0.705	0.007	0.012	92.36	0.87	6.59	0.17
151.	Kupa	river	DIN-CON	5	10.06	8.18	262.08	1.00	11.76	152.75	0.62	1.42	0.004	0.003	0.643	0.786	0.004	0.008	99.39	0.00	0.61	0.00
152.	Kupica	river	DIN-CON	5	10.79	8.22	330.00	1.00	12.45	183.00	0.80	1.86	0.004	0.003	0.628	0.794	0.009	0.013	93.12	0.07	2.99	3.82
153.	Curak	river	DIN-CON	4	9.13	8.23	295.42	1.00	11.68	160.00	1.29	0.78	0.004	0.001	0.606	0.645	0.005	0.032	94.43	0.00	4.03	1.54
154.	Čabranka	river	DIN-CON	5	11.08	8.27	302.20	1.00	11.80	175.70	0.69	1.89	0.005	0.002	0.523	0.653	0.006	0.015	90.30	1.03	8.67	0.00
155.	Velika Belica	river	DIN-CON	4	9.57	8.17	296.17	1.00	11.68	172.25	1.18	0.89	0.002	0.001	0.695	0.748	0.002	0.019	99.78	0.00	0.22	0.00
156.	Gerovčica	river	DIN-CON	4	8.70	8.02	264.33	5.03	10.72	150.67	1.68	1.69	0.005	0.002	0.267	0.447	0.007	0.034	96.18	0.00	0.00	3.82
157.	Čedanj	river	DIN-CON	4	12.33	8.13	147.04	1.00	11.48	77.03	0.84	2.34	0.004	0.001	0.408	0.553	0.006	0.010	98.05	0.00	1.95	0.00
158.	Gacka	river	DIN-CON	5	12.22	7.74	494.36	<2.00	9.69	272.55	0.96	1.53	0.013	0.005	0.424	0.553	0.006	0.010	69.16	12.27	17.31	1.27
159.	Rječina	river	DIN-MED	5	10.20	8.18	228.58	2.28	11.61	126.92	1.36	0.88	0.005	0.002	0.449	0.537	0.005	0.030	97.20	0.20	1.10	1.51
160.	Rječina	river	DIN-MED	5	9.68	8.06	233.17	1.00	11.46	130.00	1.35	0.77	0.004	0.001	0.477	0.544	0.002	0.026	99.19	0.00	0.61	0.20
161.	Rječina	river	DIN-MED	5	12.19	8.11	315.75	2.51	11.06	157.08	1.37	0.82	0.004	0.002	0.419	0.531	0.002	0.030	96.18	0.38	1.05	2.40
162.	Joševica	river	DIN-CON	4	11.31	8.02	458.82	1.00	11.45	226.09	0.30	0.66	0.006	0.001	0.323	0.355	0.003	0.010	74.62	0.00	25.38	0.00
163.	Mirna	river	DIN-MED	10	16.25	7.98	488.92	37.29	10.48	253.42	0.77	2.81	0.009	0.013	0.621	0.885	0.007	0.029	75.39	5.05	18.93	0.62
164.	Mirna	river	DIN-MED	10	15.33	8.05	466.83	18.37	11.98	256.17	1.08	2.37	0.066	0.018	0.528	0.772	0.031	0.054	82.33	5.63	10.91	1.14
165.	Rumin	river	DIN-MED	8	12.58	7.84	405.67	<2.00	11.41	183.83	0.61	1.28	0.011	<0.030	0.338	0.478	<0.005	<0.002	68.63	8.85	22.46	0.06
166.	Vojskova	river	DIN-MED	8	13.01	7.74	641.75	1.00	10.44	215.50	0.54	1.19	0.010	0.015	0.517	0.633	0.003	0.001	82.26	12.72	1.05	3.97
167.	Mislina	river	DIN-MED	11	17.19	7.46	831.75	<2.00	9.34	209.42	0.70	1.59	0.033	<0.030	0.236	0.478	<0.005	<0.002	83.99	4.81	10.47	0.73
168.	Kobilica	river	DIN-MED	8	13.41	7.60	430.58	2.02	11.84	233.79	0.95	1.35	0.025	0.006	0.270	0.484	0.001	0.002	64.58	0.00	35.42	0.00
169.	Zrmanja	river	DIN-MED	10	10.70	8.20	280.10	6.53	11.03	179.33	1.71	2.52	0.005	0.006	0.263	0.872	0.001	0.006	76.56	2.51	20.93	0.00
170.	Ričica	river	DIN-CON	5	12.69	7.78	366.75	1.00	8.86	208.04	2.63	1.27	0.009	0.001	0.309	0.679	0.003	0.005	65.02	0.00	33.83	1.15
171.	Zrmanja	river	DIN-MED	9	12.44	8.10	356.64	1.00	11.23	179.64	0.30	0.72	0.006	0.001	0.343	0.393	0.003	0.005	76.14	0.11	23.75	0.00
172.	Zrmanja	river	DIN-MED	10	13.45	7.79	414.09	5.13	11.55	208.36	<0.6	1.16	<0.012	0.001	0.275	0.335	<0.006	<0.009	81.12	2.04	16.83	0.01
173.	Krupa	river	DIN-MED	8	12.74	7.90	351.91	1.00	11.17	198.00	0.30	0.49	0.006	0.002	0.225	0.275	0.003	0.005	93.88	0.00	6.07	0.05
174.	Bribišnica	river	DIN-MED	8	9.80	7.86	405.20	5.31	9.66	252.10	1.48	2.14	0.003	0.006	0.488	1.013	0.001	0.007	52.06	39.63	1.50	6.80
175.	Vrba	river	DIN-MED	8	13.00	7.85	467.25	<2.00	10.02	234.58	0.54	1.27	0.026	<0.030	<0.230	<0.250	<0.005	<0.002	86.90	5.27	7.49	0.35
176.	Vrba	river	DIN-MED	8	14.10	8.21	552.83	<2.00	8.29	257.83	0.53	1.37	0.016	<0.030	<0.230	<0.250	<0.005	<0.002	85.62	6.10	7.57	0.72
177.	Krka	river	DIN-MED	9	11.65	7.95	531.00	1.00	10.52	201.73	0.30	0.91	0.030	0.004	0.368	0.444	0.007	0.012	78.27	7.26	13.48	0.99
178.	Krka	river	DIN-MED	9	10.66	7.80	406.09	<2.00	11.51	194.09	<0.60	0.47	0.014	<0.001	0.385	0.424	<0.006	<0.009	87.32	4.22	7.78	0.69
179.	Butižnica	river	DIN-MED	9	12.36	8.03	900.45	4.44	11.36	195.09	0.61	1.09	0.013	0.002	0.225	0.320	0.014	0.028	79.99	2.44	16.87	0.70
180.	Ljubina	river	PAN	1	14.29	7.73	227.33	12.20	9.25	110.67	2.00	3.70	0.183	0.007	0.331	0.853	<0.02	0.070	87.45	0.00	12.55	0.00
181.	Vučjak	river	PAN	2	12.91	8.14	542.56	5.19	10.52	239.28	2.59	4.27	0.043	0.006	0.517	1.503	0.008	0.043	64.50	14.81	20.69	0.00
182.	Bistrica 1	river	DIN-CON	4	10.23	7.81	441.75	8.92	10.44	240.08	0.81	0.88	0.042	<0.002	1.594	1.765	0.009	0.036	83.69	7.23	7.78	1.30

Table S3: Results of the generalized additive models (GAMs). R2 (%)–response strength, p–statistical significance, DF–degrees of freedom, statistically nonsignificant (>0.05) are in italic. For abbreviatoions of species names see Table S1 and for environmental variables see Table 1.

	R^2[%]	p	DF
N_{tot}			
Apo_end	14	<0.00001	3
Chi_pal	7.2	0.00762	3
Chi_pol	8	<0.00001	3
Cin_aqu	7	<0.00001	3
Cin_fon	3.2	0.00055	3
Cin_rip	3.6	0.00048	3
Cra_fil	8.7	<0.00001	3
Dic_fla	21.7	0.0001	3
Did_top	6.2	0.00139	3
Euc_ver	10	0.00091	3
Fis_cra	3.4	0.00139	3
Fon_ant	13.7	<0.00001	3
Jun_atr	17.6	0.00001	3
Lep_rip	13.9	<0.00001	3
Pal_fal	11.7	<0.00001	3
Pty_pse	6.8	0.00038	3
Rhy_rip	3.7	0.00006	3
Ric_flu	6.2	0.01099	3
NAT			
Apo_end	14.8	<0.00001	3
Bra_riv	24.8	<0.00001	3
Chi_pol	26.8	<0.00001	3
Cin_aqu	17.1	<0.00001	3
Cin_fon	8.9	<0.00001	2
Cin_rip	5.2	0.00002	3
Cra_fil	10.9	<0.00001	3
Dic_fla	47.2	<0.00001	2
Dic_pel	24.8	<0.00001	2
Did_top	2.3	*0.08687*	3
Euc_ver	6.6	0.00876	3
Fon_ant	7.1	<0.00001	3
Jun_atr	21.7	<0.00001	3
Lep_rip	15.9	<0.00001	3
Mar_pol	7.5	0.0002	3
Pal_fal	16.7	<0.00001	3
Pty_pse	2.3	*0.06457*	3
Rhy_rip	4	<0.00001	2
Ric_flu	42.1	<0.00001	3
COD			
Apo_end	19.3	<0.00001	2
Bra_riv	6.1	0.00184	3
Chi_pal	4	*0.0663*	3
Chi_pol	5.6	0.00005	3

	R^2[%]	p	DF
COD			
Cin_aqu	19	<0.00001	3
Cin_fon	15.2	<0.00001	3
Cin_rip	2.3	0.00667	3
Cra_fil	9.3	<0.00001	3
Dic_pel	9.4	0.00713	3
Euc_ver	8.4	0.00252	3
Fis_cra	2.1	0.01744	3
Fon_ant	12.9	<0.00001	3
Jun_atr	12.4	0.00026	3
Lep_rip	11.6	<0.00001	3
Mar_pol	4	0.00967	3
Pal_fal	13.2	<0.00001	3
Pty_pse	1.7	*0.06426*	2
Rhy_rip	6	<0.00001	3
Ric_flu	25.8	<0.00001	3
EC			
Apo_end	5.1	0.0001	3
Bra_riv	14.1	<0.00001	2
Chi_pal	11.6	0.00045	3
Chi_pol	4.2	0.00056	3
Cin_aqu	8.7	<0.00001	3
Cin_fon	7.2	<0.00001	3
Cin_rip	11.5	<0.00001	3
Cra_fil	2.6	0.00199	3
Dic_fla	44.6	<0.00001	3
Dic_pel	43.2	<0.00001	3
Euc_ver	30.9	<0.00001	3
Fis_cra	1.3	*0.07788*	3
Fon_ant	2.9	0.00038	3
Jun_atr	27.8	<0.00001	3
Lep_rip	8.4	<0.00001	3
Mar_pol	2.3	*0.06494*	3
Pal_fal	24.5	<0.00001	3
Pty_pse	14.2	<0.00001	3
Rhy_rip	4	0.00002	3
Ric_flu	36.8	<0.00001	3
pH			
Apo_end	1.3	0.03433	2
Bra_riv	10	0.00006	3
Chi_pal	16.1	0.00003	3
Chi_pol	1.6	*0.0591*	3
Cin_aqu	2.1	0.00221	3
Cin_rip	5.4	0.00001	3
Cra_fil	1.2	*0.0498*	3
Dic_fla	11.5	0.00037	2
Dic_pel	4.4	*0.09611*	3
Euc_ver	3.6	*0.07431*	3

	R^2[%]	p	DF
pH			
Fis_cra	7.5	<0.00001	3
Fon_ant	1	*0.05916*	3
Jun_atr	6.7	0.0028	2
Lep_rip	2.1	0.00597	3
Mar_pol	1.3	*0.08073*	2
Pal_fal	8.4	0.0001	3
Rhy_rip	2.8	0.00046	3
Ric_flu	25.8	<0.00001	3
URB			
Apo_end	10.1	<0.00001	3
Bra_riv	6.4	0.00154	3
Chi_pal	19	0.00002	2
Chi_pol	4.4	0.00039	3
Cin_aqu	2	0.00552	2
Cin_fon	4.2	0.00021	2
Cin_rip	5.8	0.00001	2
Cra_fil	5.7	<0.00001	2
Dic_fla	8.7	0.00223	2
Dic_pel	23.3	0.00253	2
Did_top	4.7	0.01562	2
Euc_ver	6.7	0.0029	2
Fis_cra	1.7	*0.05044*	2
Fon_ant	1.5	0.02158	2
Jun_atr	9.4	0.00047	2
Mar_pol	8.2	0.00016	2
Pal_fal	6	0.0013	3
Pty_pse	9.1	0.00007	2
Rhy_rip	2.8	0.00118	2
Ric_flu	12.5	0.0014	3
DO			
Bra_riv	10.1	0.00004	3
Pty_pse	2.7	0.04069	3
Chi_pol	12.1	<0.00001	3
Cin_aqu	19.3	<0.00001	3
Cin_fon	2.8	0.0016	3
Cin_rip	13	<0.00001	2
Cra_fil	6.1	<0.00001	3
Dic_fla	22.6	<0.00001	3
Dic_pel	9.7	0.00591	3
Fis_cra	3.6	0.00115	3
Fon_ant	10.2	<0.00001	3
Jun_atr	6.8	0.0108	3
Lep_rip	3.3	0.00031	3
Mar_pol	3.6	0.01515	3
Pal_fal	21.5	<0.00001	3
Apo_end	5.5	0.00006	3
Rhy_rip	4.7	<0.00001	3
Ric_flu	46	<0.00001	3

	R^2[%]	p	DF
P_{tot}			
Apo_end	25.1	<0.00001	2
Bra_riv	6.4	0.00155	3
Chi_pal	5.3	0.02591	3
Chi_pol	21	<0.00001	3
Cin_aqu	22.1	<0.00001	3
Cin_fon	10.6	<0.00001	3
Cin_rip	2	0.01442	3
Cra_fil	16.7	<0.00001	3
Dic_fla	10.1	0.00345	3
Did_top	20.8	<0.00001	3
Euc_ver	18.3	<0.00001	2
Fis_cra	7	<0.00001	3
Fon_ant	17	<0.00001	3
Jun_atr	14.3	0.00002	2
Lep_rip	11.6	<0.00001	3
Pal_fal	19.6	<0.00001	3
Pty_pse	3.9	0.00992	3
Rhy_rip	9.6	<0.00001	3
Ric_flu	19.1	<0.00001	2

4.6. Znanstveni rad 5

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Article

Environmental Gradients Shaping the Freshwater Bryophyte Communities of Croatia (Western Balkans)

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Abstract: A comprehensive field survey of 527 sites on 293 watercourses across Croatia revealed 76 sites (14.42%) in which bryophytes were the dominant part of the macrophyte vegetation. Using classification and ordination analyses, we obtained five community types segregated across the gradients of several climatic, physiographic and water chemistry parameters. The *Didymodon tophaceus–Apopellia endiviifolia* and the *Berula erecta-Cratoneuron filicinum* communities were mostly confined to the clean and basic karstic rivers of the Dinaric Ecoregion under the influence of the Mediterranean climate, with the *Didymodon tophaceus–Apopellia endiviifolia* community being a tufa-forming community associated with the seasonally dry watercourses of small catchment areas and cascades along the larger karstic rivers, while the *Berula erecta–Cratoneuton filicinum* community was mostly associated with rivers with larger catchment areas and permanent flow. On the other hand, the *Oxyrrhynchium hians–Chiloscyphus pallescens* community and the *Fissidens pusillus–Veronica beccabunga* community were associated with eutrophic water restricted to small rivers of the Pannonian Ecoregion under the influence of the temperate climate and flowing over silicate bedrock. The most represented and widespread in Croatia was the *Cinclidotus* community, displaying the widest ecological range in the study. It was mostly associated with the relatively clean karstic rivers of large catchment areas belonging to the Dinaric Ecoregion, with the majority of the sites under the influence of a temperate climate with higher precipitation during the warm period of the year. The geographical patterns of the freshwater bryophyte communities showed that the relatively clean, fast and cold karstic rivers belonging to the Dinaric Ecoregion provide habitats that harbour a greater diversity of bryophyte communities than the watercourses of the Pannonian Ecoregion, where bryophyte-dominated communities are restricted to a small number of small lowland and semi-montane rivers and predominantly occupy periodically flooded microhabitats such as river margins.

Keywords: bryophytes; macrophytes; rheophytes; Mediterranean; karstic rivers; water chemistry; bioclimatic variables

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1. Introduction

Bryophytes are an important part of freshwater biodiversity, inhabiting a wide variety of aquatic and riparian habitats and ecological and hydrological niches associated with running and standing waters [1,2]. They are a dominant part of macrophyte vegetation in headwater and mountain streams, where they thrive in oligotrophic, clear, cold water with fast and usually torrential flow over very stable rocky substrates in a harsh environment unsuitable for the majority of other macrophytes [3,4]. Here, a wide variety of adaptations enables them to withstand mechanical stress from high water velocity and associated drag forces and shear stress [5]. The same features enable their complete dominance in waterfalls, where they develop the most luxuriant communities [6]. Namely, in such turbulent habitats, the thin boundary layer positively affects the amount of CO_2 available for photosynthesis, as well as nutrients. On the other hand, in middle and lower river sections dominated by unstable substrates of smaller fractions, bryophytes are confined to larger rocks or periodically flooded river margins and are subject to intensive competition with vascular plants, leading to lower cover or complete absence of bryophytes [5,7]. Furthermore, bryophytes make a particularly significant component of vegetation in highly seasonal and intermittent Mediterranean rivers [8], primarily due to a set of diverse adaptations enabling desiccation tolerance during dry periods, as well as endurance for mechanical stress from strong flash flows. In such conditions of impermanent flows, freshwater bryophyte assemblages are characterized by a higher share of hygrophyte and drought-tolerant species [8,9], whereas rheophytes dominate the vegetation of streams and rivers with permanent flows [10]. However, truly aquatic bryophytes are rather rare [5], with some authors completely disputing this category, suggesting that all rheophylous species should be regarded as facultative aquatics since they have at least some degree of desiccation tolerance [4].

The diversity of these species is governed by the heterogeneity of different environmental factors, which determine their presence or absence, as well as the community structure. While the presence and cover of bryophytes in freshwater habitats are primarily determined by riverbed stability and substrate size [4,6,11], diverse environmental factors influence diversity and community structure. Hydrological, physiographic, geological and climatological factors, as well as water chemistry, have been recognized as the main groups of parameters influencing freshwater bryophyte communities [4,6,8,11–13]. Furthermore, these communities, as well as particular species, have been recognized as sensitive to changes in the land use of the catchment area and to related habitat degradation and water pollution [6,13]. Accordingly, representatives of the group, as well as community parameters such as total bryophyte cover, species richness and composition, have been recognized as good bioindicators of water quality and the hydromorphological degradation of aquatic habitats [13–18]. Therefore, freshwater bryophytes have been included as a part of the aquatic vegetation in the assessment of the ecological status of waterbodies conducted according to the Water Framework Directive (WFD) [19]. This has been especially important in headwater streams, where bryophytes are by far the dominant part of vegetation [3], or in highly seasonal rivers, where they are the only macrophyte representatives during the summer months when these rivers dry out [8].

Several models regarding the environmental gradients influencing freshwater bryophyte communities exist for different European regions, covering, for example, small mountain streams in Germany [4], lower mountain streams in the boreal zone [20] and the bryophyte communities of upland and lowland sites in English and Welsh rivers [11]. A comprehensive study of bryophyte communities in highly seasonal Mediterranean rivers from six countries provided an insight into their diversity and composition as well as a predictive model of their distribution in the Mediterranean area [8]. Furthermore, bryophyte assemblages were investigated in the Alpine and Apennine mountain streams of Italy [3], while in Southeast Europe, research into freshwater bryophyte communities is mostly limited to Bulgaria, where several studies investigating the ecology and bioindication potential of these communities were conducted [13,16,21,22]. However, further research is needed on this subject in this bryologically understudied European region [23,24] as a basis for future monitoring and protection.

The only research on bryophyte communities in Croatian watercourses so far conducted dates back to the middle of the 20th century, when the tufa waterfalls of the Krka River [25,26] were studied, followed by the waterfalls of the Plitvice Lakes system [27] and by the Una River [28,29]. During the 1960s, work was focused on the relationship between macrozoobenthos, bryophytes and algae in freshwater communities [30–38] and the end of this short but very fruitful period also marked the end of the research into the freshwater bryophytes in Croatia up to the present day. Croatian territory, a part of Southeast Europe, is divided into the Pannonian and the Dinaric Ecoregion, with the latter subdivided into the Continental and the Mediterranean Subecoregion. Since these regions reflect the climatological, geological and hydrological heterogeneity of Croatia, it can be expected that the geographical segregation of the bryophyte communities follows this division and that those communities would show some degree of affinity towards a particular region.

Given that systematic and comprehensive studies on freshwater bryophyte communities have never been conducted in Croatia and do not exist with respect to the Western Balkans, including the corresponding part of the Mediterranean, we aimed to (1) explore the distribution, diversity and species composition of freshwater bryophyte communities; (2) explore the inherent variability of particular ecoregions in terms of bryophyte communities; and (3) identify the environmental gradients that influence bryophyte communities. This will improve the knowledge on this subject on the European level and provide a basis for further monitoring and protection, including the mitigation of the negative impacts of climate change and associated changes in hydrological regimes, as well as of human-induced eutrophication and changes in both hydrological regimes and morphology of streams and rivers.

2. Results

Bryophytes were the dominant component of macrophyte vegetation in 76 sites out of the 527 (14.42%) surveyed sites on streams and rivers situated across the whole Croatian territory and encompassing the heterogeneity of Croatian watercourses in terms of the recent typology of the waterbodies developed for WFD implementation. The majority of the sites (61, to be precise) were situated in the Dinaric Ecoregion, accounting for 31.12% of a total 196 sites surveyed within the particular region. The Dinaric–Continental Subecoregion was the richest, with as many as 40.23% of sites with bryophyte communities out of a total 87 sites surveyed, while 23.85% out of 109 sites in the Dinaric–Mediterranean Subecoregion harboured macrophyte vegetation with bryophyte predominance. On the other hand, this proportion was comparatively low in the Pannonian Ecoregion, amounting to only 4.53%.

A total of 130 macrophyte taxa were recorded in bryophyte dominated sites, i.e., 68 bryophyte and 43 vascular plant species, along with 19 macroalgae taxa. Among 68 bryophyte species, 59 were mosses (Bryophyta) and only 9 were liverworts (Marchantiophyta) (Table S1). Overall mean bryophyte species richness was 7.57 $\pm$ 0.50 species per site. The most frequent bryophyte species, with a frequency of over 30%, were *Rhyncgostegium riparioides* (79.5%) and *Cratoneurn filicinum* (60.3%), followed by *Fontinalis antipyretica* (50.0%), *Cinclidotus fontinaloides* (44.9%), *Apopellia endiviifolia* (37.2%), *Cinclidotus aquaticus* (35.9%), *Fissidens crassipes* (35.9%) and, finally, *Cinclidotus riparius*, present in 34.6% of the 76 bryophyte-dominated sites. According to the classification proposed by Dierßen [10], the majority of the abovementioned species were rheophytes except for the amphyphyte *C. filicinum* and the hygrophyte *A. endiviifolia*. Regarding the vascular representatives, only 5 hydrophyte species were recorded, while the helophytes prevailed with as many as 38 species.

2.1. Community Groups

TWINSPAN classification of bryophyte-dominated sampling sites at maximal distance established five groups after three levels of division (Soerensen dissimilarity, max distance = 0.77). An ANOSIM test confirmed the overall significant difference among the TWINSPAN groups (coded hereafter as 1–5), i.e., the existence of discrete communities among the sampling sites (overall R = 0.50, p(same) < 0.0001) based on the species composition. Furthermore, ANOSIM pairwise comparisons showed that all community groups were significantly different (Table 1).

With respect to the distribution of 76 bryophyte-dominated sites within the different sub- and ecoregions, 80.26% were located in the Dinaric Ecoregion (61 sites), with 46.05% (35 sites) situated in the Continental Subecoregion and 34.21% (26 sites) in the Mediterranean Subecoregion. The Pannonian Ecoregion was comparatively poor, with only 19.74% (15 sites) out of 76 sites (Figure 1, Table 2).

Table 1. R statistics of the pairwise ANOSIMs of bryophyte-dominated communities obtained from TWINSPAN classification (groups 1–5) (overall R = 0.50, p(same) = 0.0001), * $p < 0.001$, ** $p < 0.005$.

	1	2	3	4	5
1					
2	0.68 *				
3	0.58 **	0.70 *			
4	0.66 *	0.36 *	0.56 **		
5	0.67 *	0.33 *	0.75 *	0.42 *	

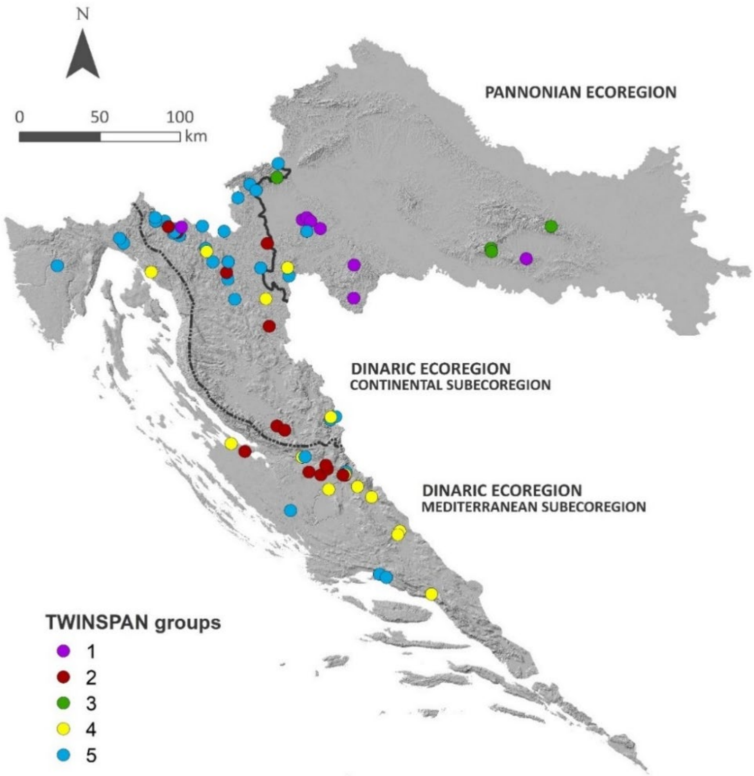

Figure 1. Distribution map of TWINSPAN groups in Croatia and its hydrological and biogeographical sub- and ecoregions.

Table 2. Distribution of the TWINSPAN groups over the hydrological and biogeographical sub- and ecoregions.

	Pannonian Ecoregion	Dinaric Ecoregion		Total
		Dinaric–Mediterranean Subecoregion	Dinaric–Continental Subecoregion	
Surveyed localities	331	109	87	527
Bryophyte-dominated localities	15	26	35	76
TWINSPAN group				
1	7	-	1	8
2	-	8	8	16
3	3	-	1	4
4	1	10	4	15
5	4	8	21	33

Some main patterns are recognisable when taking into account the distribution of particular TWINSPAN communities between the sub- and ecoregions; however, a certain overlap is present. Groups 1 and 3 are mainly confined to the Pannonian Ecoregion, while all others are more frequent in the Dinaric Ecoregion, with Group 2 being exclusive for this region and equally distributed in both the Continental and the Mediterranean subecoregions. On the other hand, Group 4 was more frequent in the Mediterranean Subecoregion, while Group 5 was more characteristic of the Continental Subecoregion (Figures 1 and 2; Table 2).

Figure 2. Examples of the sampling sites belonging to different TWINSPAN communities. Group 1: (**A**) Petrinjčica River (Miočinovići), (**B**) Vučjak River (Požega), (**C**) Kravarščica River (Dabići); Group 2: (**D**) Kobilica River (Kusac), (**E**) Korana River (settlement Korana); Group 3: (**F**) Šumetlica River (upper course); Group 4: (**G**) Krka River (Marasovine); (**H**) Joševica River (Donja Suvaja), (**I**) Cetina River (Barišići); Group 5: (**J**) Kupa (Kupari), (**K**) Rječina (Kukuljani), (**L**) Krupa (Mandići).

The characteristic species of Group 1 (*Oxyrrhynchium hians–Chiloscyphus pallescens* community) (Appendix A) were mostly hygrophytic species confined to periodically submerged river margins, such as the mosses *Oxyrrhynchium hians*, *Plagiomnium undulatum*, *Pohlia melanodon*, and the liverworts *Chiloscyphus pallescens*, *Pellia neesiana*, *Conocephalum salebrosum*, along with the moss *Dichodontium pellucidum*, collected from periodically submerged rocks within the riverbeds. However, the constant species included rheophytes such as *Rhynchostegium riparioides* and *Leptodictyum riparium*, as well as an ampyphyte, *Cratoneuron filicinum*. The hygrophytes *Didymodon tophaceus*, *Apopellia endiviifolia* and *Funaria hygromet-*

rica, as well as the amphiphyte *Eucladium verticillatum* and the rheophyte *Fissidens crassipes*, were the characteristic species of Group 2 (*Didymodon tophaceus–Apopellia endiviifolia* community). Group 3 (*Fissidens pusillus–Veronica beccabunga* community) was characterized by bryophytes such as *Brachythecium rutabulum*, *Fissidens pusillus* and *Oxyrrhynchium speciosum*, as well as by the vascular helophytes *Veronica beccabunga* and *Persicaria dubia* (Appendix A). In general, Groups 1, 2 and 3 were characterized by a higher frequency of hygrophyte bryophyte species (1–65.9%, 2–44.1%, 3–56.3%), followed by rheophytes (1–18.7%, 2–37.0%, 3–31.3%) (Figure 3).

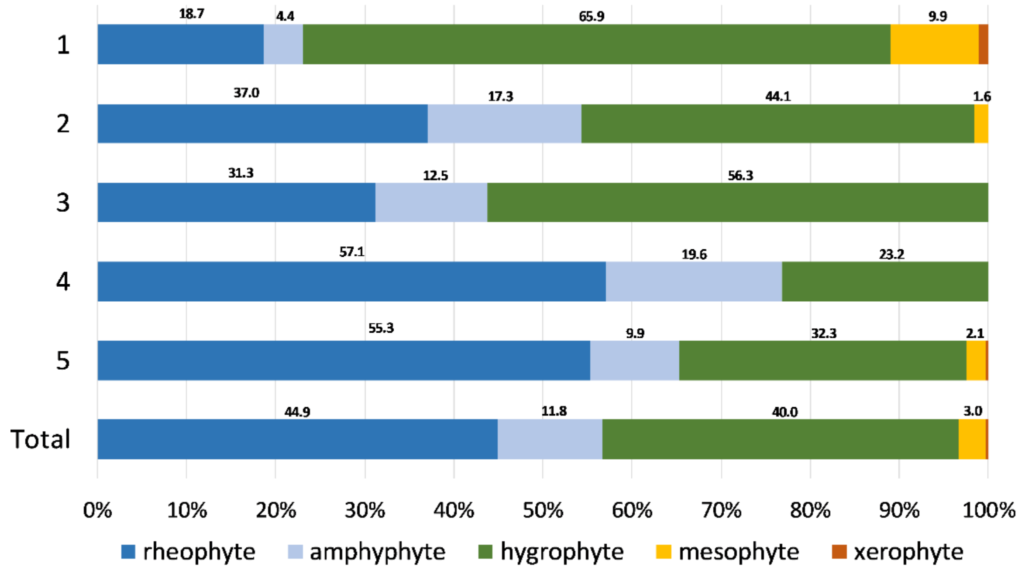

Figure 3. Bryophyte affinity to water for TWINSPAN groups and a total sample of 76 bryophyte-dominated sites.

The characteristic species of Group 4 (*Berula erecta–Cratoneuron filicinum* community) were the vascular helophytes *Berula erecta*, *Menta aquatica* and *Sparganium erectum*, while the rheophyte mosses *Rhynchostegium riparioides* and *Fontinalis antipyretica* and the amphyphyte *Cratoneuron filicinum*, along with *Mentha aquatica*, were constant species with high frequencies within the group (Appendix A). This group was characterized by the highest frequency of rheophytes in all the groups (57.1%), followed by hygrophytes (23.2%) and amphyphytes (19.6%), while mesophyte and xerophyte bryophytes were completely absent (Figure 3). The characteristic species of Group 5 (*Cinclidotus* community) were *Cinclidotus riparius* and *Cinclidotus aquaticus*, both being constant species as well, along with *Cinclidotus fontinaloides*, *Fontinalis antipyretica*, *Rhynchostegium riparioides* and *Cratoneuron filicinum*. The rheophyte bryophytes were predominant in this group as well, accounting for 55.3% of all bryophyte occurrences within the group, followed by hygrophytes (32.3%) and amipyphytes (9.9%) (Figure 3).

Analysis of the TWINSPAN groups regarding macrophyte taxa richness revealed that sites belonging to the Group 1 had the highest mean value (12.25 ± 1.33), followed by Group 2 (10.56 ± 1.21) and Group 5 (10.24 ± 1.02). The same pattern was observed when considering the bryophyte species alone. Namely, the mean bryophyte species richness of sites belonging to Group 1 was highest (11.38 ± 1.18), again followed by Groups 2 (8.94 ± 0.91) and 5 (8.21 ± 0.83) (Table 3). The share of the bryophyte species in total number of taxa was the highest in Group 1 (86%) and over 50% within Groups 5 (56.3%) and 2 (59.3%), while in Group 4, it amounted to 33.33%. On the other hand, this group harboured the overall highest number of vascular plant species (28 species) and had a lower mean taxa richness and mean bryophyte species richness (4.4 ± 0.46) than Groups 1, 4, and 5. Finally, Group 3 was the most taxa-poor group, with the lowest mean taxa richness and mean bryophyte species richness (Table 3).

Table 3. Comparison of the number of taxa belonging to different macrophyte components and mean taxa and bryophyte species richness among TWINSPAN groups.

	TWINSPAN Groups					Total
	1	**2**	**3**	**4**	**5**	
Number of relevés	8	16	4	15	33	76
Number of taxa *	43	59	18	51	80	130
Bryophyte species	37	35	9	17	45	68
Mosses (Bryophyta)	31	29	7	12	38	59
pleurocarpous	14	11	6	7	18	25
acrocarpous	17	18	1	5	20	34
Liverworts	6	6	2	5	7	9
leafy	3	2	0	3	4	4
thallose	3	4	2	2	3	5
Vascular plant species	3	16	7	28	17	43
hydrophytes	0	0	0	1	5	5
helophytes	3	16	7	27	12	38
Macroalgae taxa *	3	8	2	6	18	19
Taxa richness						
mean ± SE	12.25 ± 1.33	10.56 ± 1.21	6.75 ± 1.49	9.27 ± 1.02	10.24 ± 1.02	10.14 ± 0.58
range (min–max)	7–18	4–24	3–10	4–20	4–25	3–25
Bryophyte species richness						
mean ± SE	11.38 ± 1.18	8.94 ± 0.91	4.00 ± 1.08	4.4 ± 0.46	8.21 ± 0.83	7.57 ± 0.50
range (min–max)	7–16	3–17	2–7	1–9	2–20	1–20

* Representatives of the genera *Batrachospermum* sp., *Mougeotia* sp., *Nostoc* sp., *Spirogyra* sp., *Vaucheria* sp. and *Zygnema* sp. were not identified at the species level.

When present, vascular plants were mostly represented by helophyte species. A comparison of species richness and Shannon–Wiener alpha diversity index of bryophytes and vascular plants between the groups revealed that the vascular plant alpha diversity was the highest in Group 4, followed by Group 3, reaching that of bryophytes in some localities within Group 4 (Figure 4). By contrast, Groups 1 and 5 had a very low vascular plant alpha diversity; it was somewhat higher in Group 2, but still considerably lower than the bryophyte alpha diversity (Figure 4).

Mosses were the dominant representatives of bryophytes in all groups, representing over 80% of the total number of the bryophyte species in Groups 1 (83.8%), 2 (82.9%) and 5 (84.4%), and over 70% in Groups 3 (77.8%) and 4 (70.6%). Among the moss species, the plurocarpous prevailed in all groups.

The chorological comparison of TWINSPAN groups based on major biomes revealed large chorotype overlapping, with a dominance of temperate chorotypes; however, some biogeographical differences were highlighted (Figure 5). The southern-temperate chorotype had the highest frequency in Group 2 (54.2%), while its lowest frequency was in Group 1 (18.7%). Furthermore, Group 4 was characterized by a higher frequency of boreo-temperate (36.5%) and wide-boreal elements (19.0%) than other groups. The Mediterranean–Atlantic chorotype was completely absent from Groups 3 and 4, with the highest, still quite low in proportion (2.2%) in Group 5. Boreal-montane and boreo-arctic montane chorotypes were most represented in Group 1, with 2.2% and 5.5% respectively.

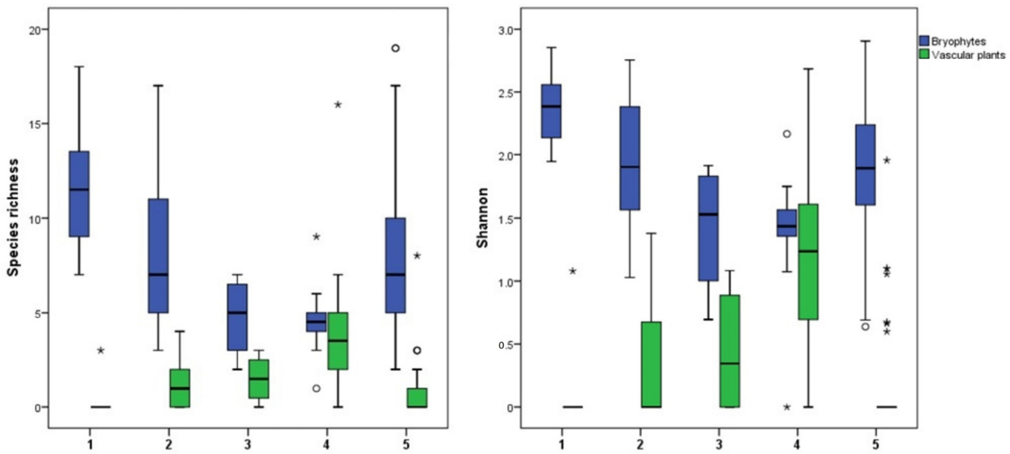

Figure 4. Comparison of bryophyte and vascular plant alpha diversity (species richness and Shannon-Wiener alpha diversity index) between the TWINSPAN groups (outliers: o—"out" values, *—"far out" or extreme values).

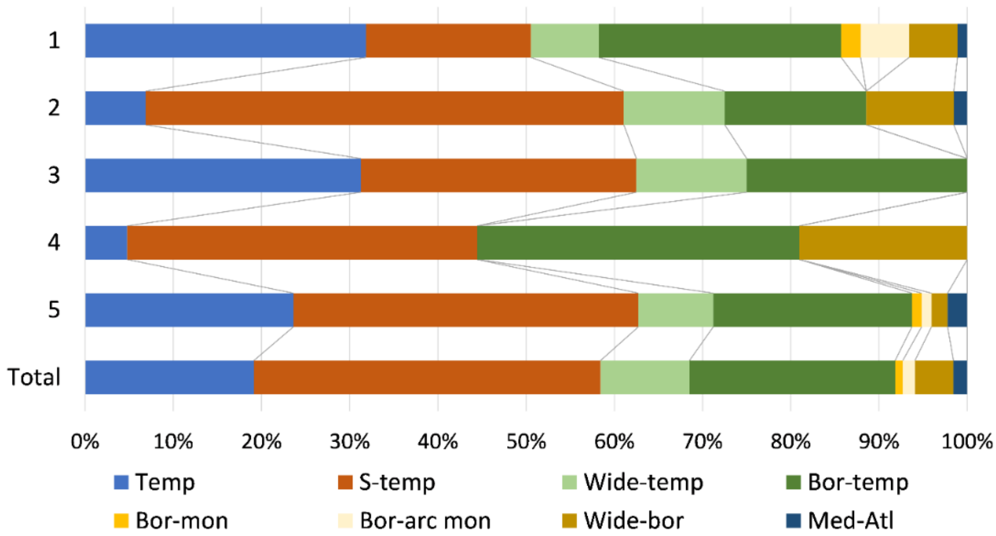

Figure 5. Chorological spectrum of freshwater bryophytes based on major biomes for TWINSPAN groups and a total sample of 76 bryophyte-dominated sites.

The chorological comparison based on the eastern limit showed the dominance of circumpolar and European chorotypes in all communities, while other chorotypes were absent or present with frequencies lower than 5%, except for the Eurosiberian chorotype, which accounted for 7.7% of Group 5.

Bryophyte lifeforms were not evenly distributed among the TWINSPAN groups, with the most conspicuous difference in the share of aquatic trailings, rough mats and turfs (Figure 6). Namely, Groups 4 and 5 had the highest proportion of aquatic trailings, 46.0% and 33.9%, respectively, while this category was absent from Group 3 and represented with low frequency in Group 1 (6.6%). On the other hand, these latter two groups had a higher frequency of rough mats than the other groups, 37.5% for Group 3 and 24.2% for Group 1. Furthermore, Group 1 was characterized by a high frequency of turfs (39.56%), similar to Group 2, where turfs accounted for 30.5%.

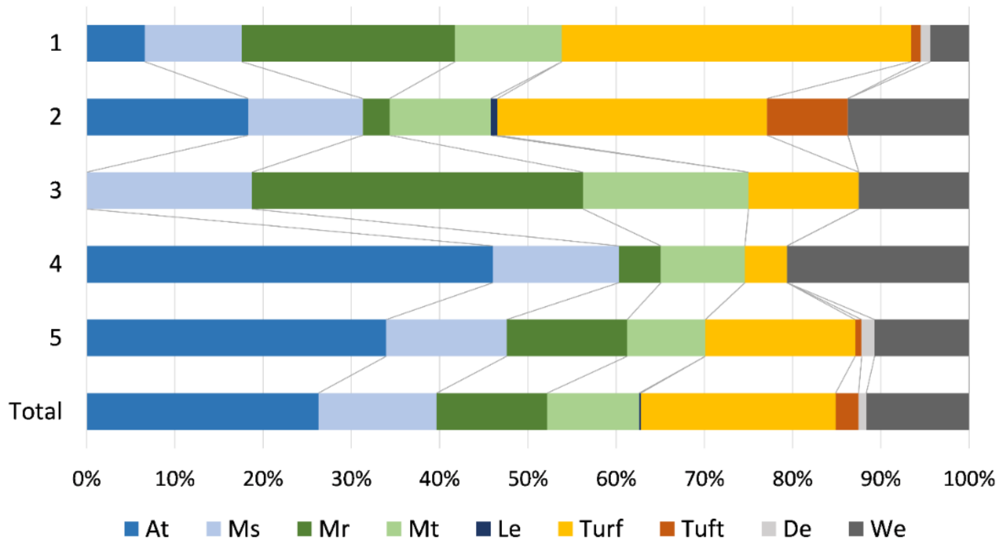

Figure 6. Lifeform spectrum of freshwater bryophytes for TWINSPAN groups and a total sample of 76 bryophyte-dominated sites (At—aquatic trailing, Ms—smooth mat, Mr—rough mat, Mt—thalloid mat, Le—lemnoid, De—dendroid, We—weft).

Regarding the life strategies, all TWINSPAN groups feature the overall dominance of perennials, followed by colonist bryophyte species (Figure 7). The share of perennials was lowest in Group 2 (19.1%) and highest in Group 3 (37.5%), followed by Group 4 (33.3%). A similar pattern was revealed when observing all perennial categories together; they were most represented in Group 4 (68.3%), followed by Group 3 (56.3%) and Group 5 (50.9%). The share of colonists within Groups 2, 4 and 5 was over 35% and was lowest within Group 3 (12.5%). Taking into account all three colonist categories, the highest proportion was recorded in Group 2 (41.2%), followed by Groups 5 (40.9%) and 1 (40.7%).

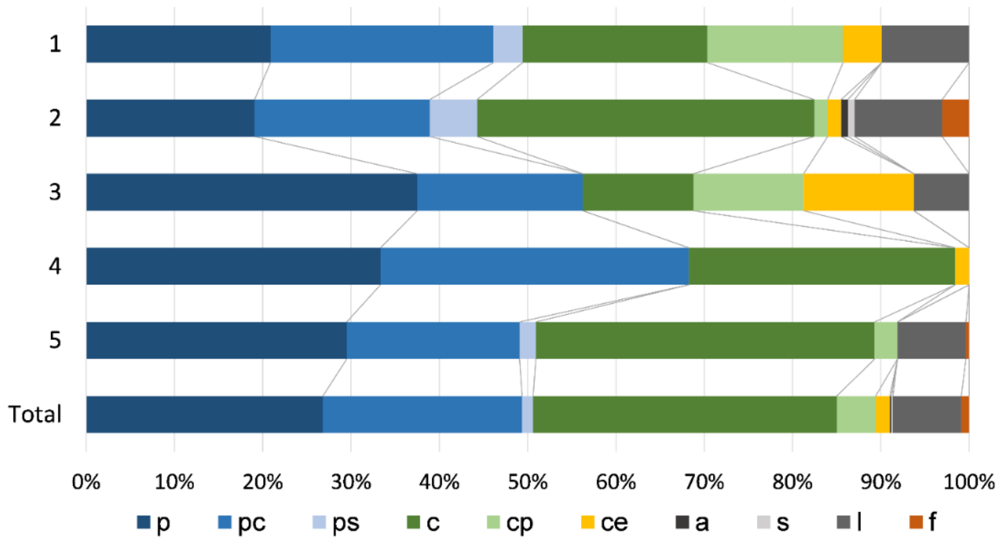

Figure 7. Life strategy spectrum of freshwater bryophytes for TWINSPAN groups and a total sample of 76 bryophyte dominated sites (p—perennials, pc—competitive perennials, ps—stress-tolerant perennials, c—colonist, cp—pioneer colonist, ce—ephemeral colonist, a—annual shuttle, s—short-lived shuttle, l—long-lived shuttle, f—fugitives).

2.2. Environmental Gradients

DCA analysis showed the separation of discrete groups with some overlapping. The axis 1 eigenvalue was 0.34, and for axis 2, it was 0.29. The lengths of axes 1 and 2 were 3.8 and 2.9, respectively. The nature of the established gradients in the DCA analysis was further assessed with weighted Ellenberg indicator values, passively projected over the ordination as vectors. This revealed a gradient from the sites with higher mean indicator values for temperature, light and moisture and low values for continentality (Group 4) compared to those with higher values for continentality but lower temperature and light values (Group 1), with the sites belonging to Group 5 being intermediate across this gradient (Figure 8). Group 2 included the sites with higher Ellenberg indicator values for reaction. DCA axis 2 was the most strongly correlated with nutrient content, indicating the higher values in Group 3, as well as in some sites of Group 5.

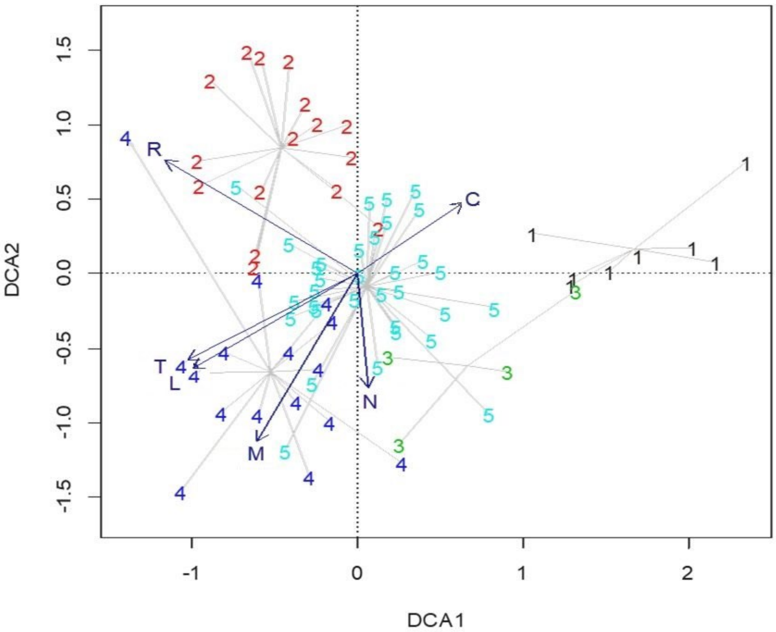

Figure 8. Ordination plot of DCA analysis with weighted Ellenberg indicator values passively projected as vectors over the ordination of TWINSPAN groups (C—continentality, L—light, M—moisture, N—nutrients, R—reaction, T—temperature).

The first axis of the CCA explained 23.65% and the second axis explained 42.39% of the variation in the relationship between vegetation data and environmental factors. Eigenvalues of the first and second axes equalled 0.35 and 0.27, respectively. Ordination was statistically significant (F = 1.41, $p = 0.001$) according to the Monte Carlo permutation test (999 permutations). As expected, variables that explain the majority of the variance in the data were also highly correlated with axis 1. An ordination plot of the CCA analysis revealed a strong gradient along axis 1 from sites with high values of orthophosphates and biochemical oxygen demand, and elevated total nitrogen values (groups 1 and 3) to the sites with low values of these water chemistry parameters and high values of total alkalinity, as well as dissolved oxygen (Groups 2 and 4) (Table 4, Figures 9 and 10). However, the Mann–Whitney pairwise test showed that the latter two groups differed significantly in pH values, with Group 2 being associated with more basic water (Appendices B and C). Sites belonging to Group 5 were distributed along the longest part of the CCA gradient, suggesting, in general, intermediate values for the abovementioned parameters compared to other groups. Total suspended solids (TSS) showed a similar pattern among the groups (Figure 10, Appendix B), and the Mann–Whitney pairwise test indicated a significant difference between Groups 1 and 3 with high values and the other three groups with low TSS (Appendix C).

Table 4. Summary of TWINSPAN groups' main features.

Group 1—*Oxyrrhynchium hians–Chiloscyphus pallescens* Community
Characteristic species: *Oxyrrhynchium hians, Pellia neesiana, Conocephalum salebrosum, Fissidens taxifolius, Chiloscyphus pallescens, Plagiomnium undulatum, Dichodontium pellucidum, Pohlia melanodon, Hypnum cupressiforme, Plagiomnium ellipticum*   **Constant species:** *Oxyrrhynchium hians, Pellia neesiana, Conocephalum salebrosum, Fissidens taxifolius, Chiloscyphus pallescens, Plagiomnium undulatum, Rhynchostegium riparioides, Cratoneuron filicinum, Ptychostomum pseudotriquetrum, Leptodyctium riparium*   **Distribution:** Mainly Pannonian Ecoregion   **Ecology:** Mostly restricted to the small lowland rivers with small catchment areas and under the influence of a temperate climate; in water with high values of orthophosphates, BOD and TSS, as well as low alkalinity due to silicate substrate; occurring on shaded habitats along river stretches flowing through forests. Characterized by high bryophyte richness, a high share of hygrophyte bryophytes growing on river margins and rough mats and turfs in lifeform spectrum.
Group 2—*Didymodon tophaceus–Apopellia endiviifolia* Community
Characteristic species: *Didymodon tophaceus, Eucladium verticillatum, Apopellia endiviifolia, Fissidens crassipes, Funaria hygrometrica*   **Constant species:** *Didymodon tophaceus, Apopellia endiviifolia, Fissidens crassipes, Funaria hygrometrica, Rhynchostegium riparioides, Cratoneuron filicinum, Ptychostomum pseudotriquetrum, Cinclidotus fontinaloides*   **Distribution:** Dinaric Ecoregion   **Ecology:** Mainly tufa-forming community, occurring in karstic rivers with high alkalinity and pH values reflecting the dominant carbonate bedrock; in clean water with low nutrient content and BOD values and high dissolved oxygen levels. Characteristic for watercourses with considerable seasonality in water flow (intermittent rivers with small catchment areas, under the influence of the Mediterranean climate with dry and hot summers) and cascades in the lower courses of karstic rivers with larger catchment areas. Characterized by a high share of hygrophyte species and turfs in lifeform spectrum.
Group 3—*Fissidens pusillus–Veronica beccabunga* Community
Characteristic species: *Brachythecium rutabulum, Fissidens pusillus, Veronica beccabunga, Persicaria dubia, Oxyrrhynchium speciosum*   **Constant species:** *Brachythecium rutabulum, Fissidens pusillus, Veronica beccabunga, Persicaria dubia, Oxyrrhynchium speciosum, Rhynchostegium riparioides, Cratoneuron filicinum, Marchantia polymorpha*   **Distribution:** Mainly Pannonian Ecoregion   **Ecology:** Occurring mainly in small, semi-montane watercourses with small catchment areas and under the influence of a temperate climate; in waters with high nutrient levels, BOD and TSS, and lower dissolved oxygen concentrations. Species-poor community, characterized by a higher share of hygrophytes and rough mats in lifeform spectrum, which grow on periodically submerged substrates.
Group 4—*Berula erecta–Cratoneuron filicinum* Community
Characteristic species: *Mentha aquatica, Berula erecta, Sparganium erectum*   **Constant species:** *Cratoneuron filicinum, Rhynchostegium riparioides, Fontinalis antipyretica, Mentha aquatica*   **Distribution:** Mainly Dinaric Ecoregion, Mediterranean Subecoregion   **Ecology:** Transitional community of karstic rivers with large catchment areas and permanent flow, where vascular species start to outcompete bryophytes. Occurring in clean water with low nutrient content and BOD values, where helophytes occupy the river margins and shallower water, while bryophytes are confined to the riverbed. Characterized by a high share of rheophytes and aquatic trailings in lifeform spectrum, but low overall bryophyte species richness.
Group 5—*Cinclidotus* Community
Characteristic species: *Cinclidotus riparius, C. aquaticus*   **Constant species:** *Cinclidotus riparius, C. aquaticus, C. fontinaloides, Rhynchostegium riparioides, Cratoneuron filicinum, Fontinalis antipyretica*   **Distribution:** Mainly Dinaric Ecoregion, i.e., its Continental Subecoregion   **Ecology:** The most widespread community, with a wide ecological range; in general, in waters with intermediate values of the water quality parameters (orthophosphates, total nitrogen and biochemical oxygen demand) and climatic variables associated with precipitation and water availability. Mostly in permanent karstic rivers with large catchment areas flowing over carbonate bedrock in neutral to basic water. Species-rich community characterized by a high share of rheophyte species and aquatic trailing in lifeform spectrum.

Additionally, CCA indicated the importance of climatic variables in the segregation of the investigated sites along axis 1 as well. This was especially prominent for precipitation in the coldest quarter (bio19) with the highest values associated with sites belonging to Group 2, followed by Group 4. This variable was highly positively correlated with the precipitation of the wettest month (bio13, $r_s = 0.97$, $p < 0.001$) and the precipitation of the wettest quarter (bio16, $r_s = 0.94$, $p < 0.001$), the values of which had the same pattern among the groups. Similarly, Groups 2 and 4 were associated with higher values of the mean temperature of the driest quarter (bio9) than the other groups. This variable was highly and significantly ($p < 0.001$) correlated with other climatic variables (bio5, $r_s = 0.89$; bio6, $r_s = 0.96$; bio10, $r_s = 0.91$; bio11, $r_s = 0.98$; bio14, $r_s = -0.73$; bio 18 $r_s = -0{,}86$) describing the hot and dry summer conditions characteristic of the Mediterranean climate associated with the sites aggregated on the right side of the CCA plot, in contrast to the sites on the left end of the CCA axis 1, influenced by more temperate climatic conditions (Table 4). On the other hand, higher values of the mean temperature of the wettest quarter (bio8) were associated with the sites on the left part of the CCA ordination plot.

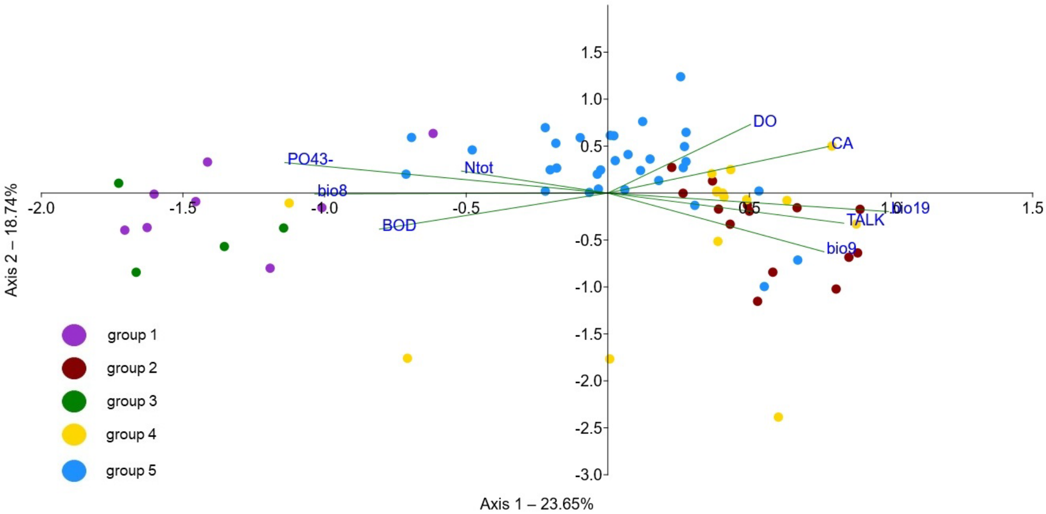

Figure 9. CCA ordination biplot with sampling sites belonging to different TWINSPAN groups and environmental variables (CA—catchment area, BOD—biochemical oxygen demand, DO—dissolved oxygen, N_{tot}—total nitrogen, PO_4^{3-}—orthophosphates, TALK—total alkalinity, bio8—mean temperature of the wettest quarter, bio9—mean temperature of the driest quarter, bio19—precipitation of coldest quarter).

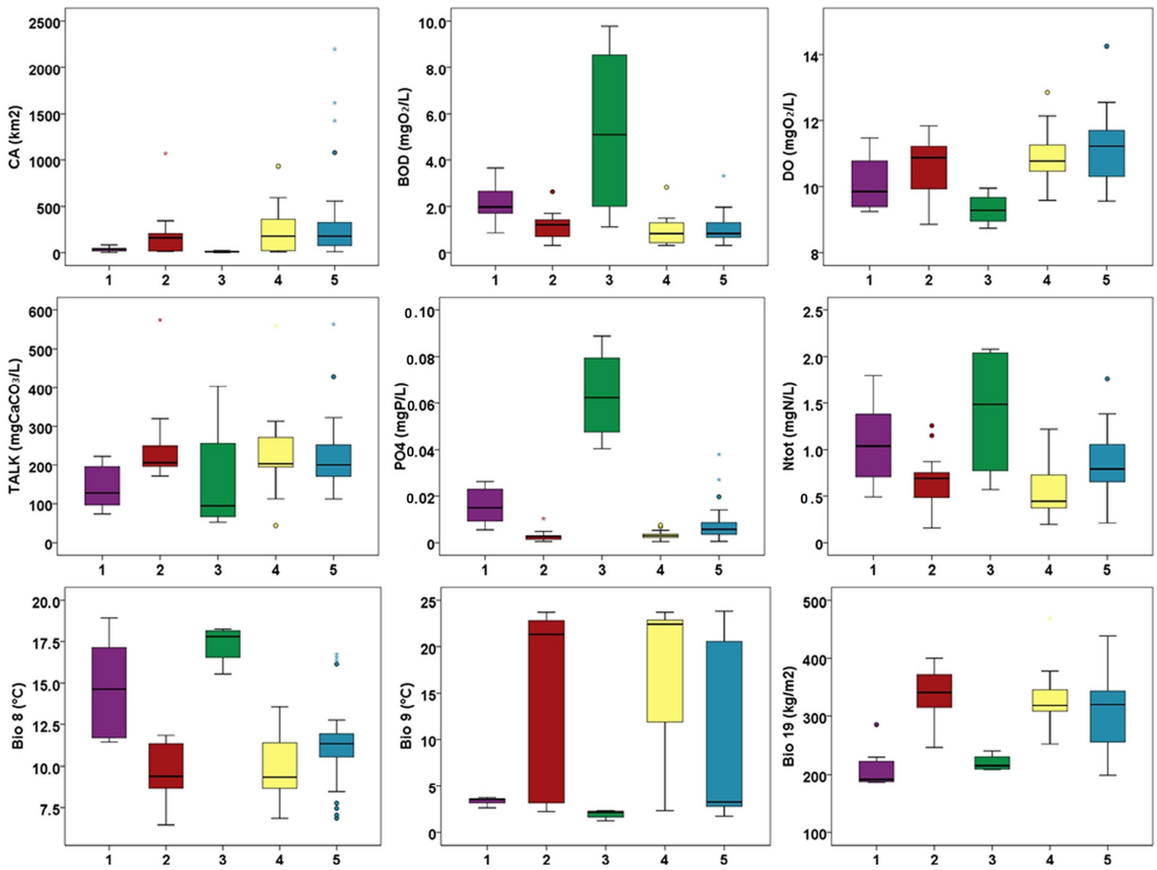

Figure 10. Cont.

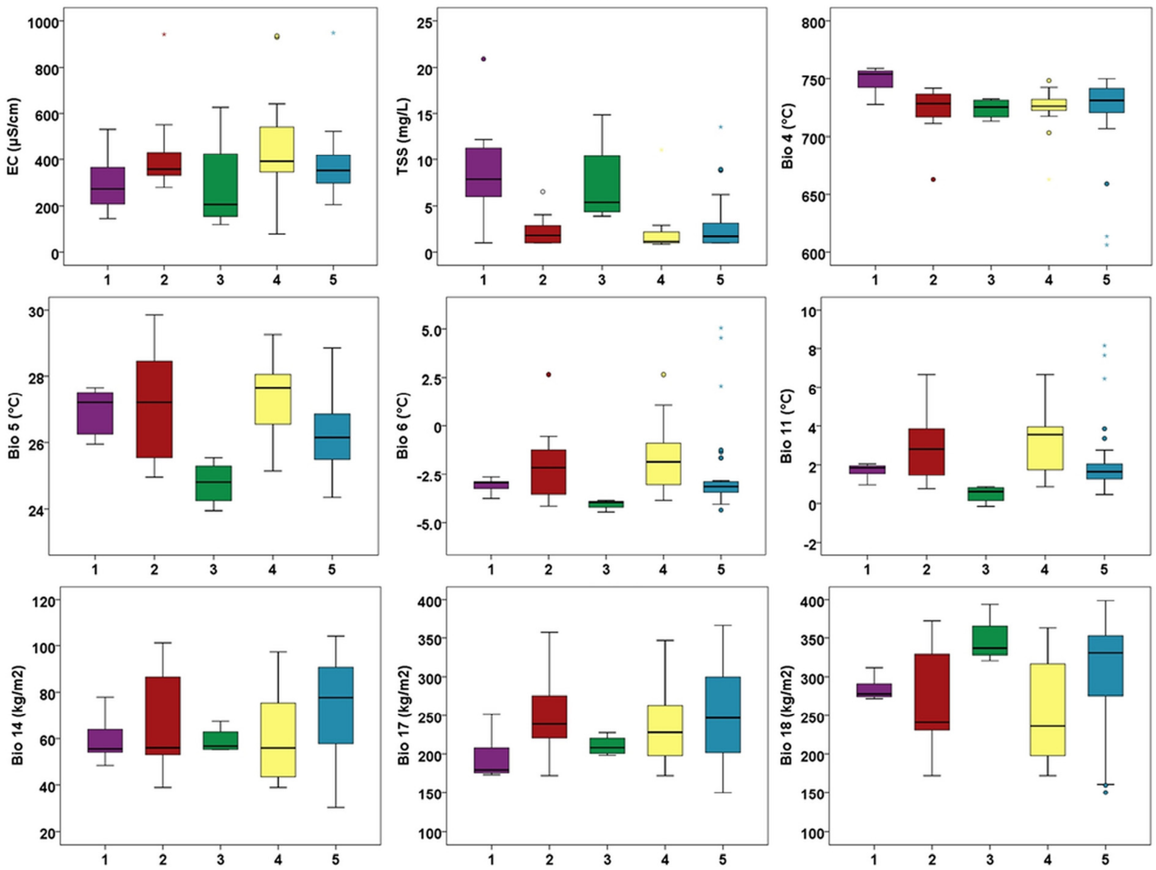

Figure 10. Boxplot diagrams of environmental variables included in CCA analysis and variables highly correlated (Spearman correlation coefficient ≥ |7|, $p < 0.001$) to CCA variables (for abbreviations, see Table 5; outliers: o—"out" values, *—"far out" or "extreme values").

Regarding the physiographic variables, the catchment area was the most important in explaining the patterns in vegetation and environmental data, with groups 1 and 3 having generally smaller catchment areas (Table 4). This was corroborated by Mann–Whitney pairwise test; i.e., Group 3 was significantly different from Groups 2, 4 and 5, while Group 1 differed significantly from Groups 2 and 5 in the Mann–Whitney pairwise test (Appendix C).

3. Discussion

The present study is the first comprehensive study dealing with the freshwater bryophyte communities and the environmental gradients underpinning their diversity, composition and distribution in Croatia and the Western Balkans, filling the gap in the existing knowledge on this subject at the European level.

While the presence and cover of bryophytes in freshwater habitats are primarily determined by riverbed stability, substrate size, stream slope and localized flow type [4,6,11], the diversity and community structure are governed by environmental variables operating on a larger scale. Geological, physiographic, and climatic factors, as well as water chemistry parameters, have been identified as essential drivers shaping freshwater bryophyte communities [4,6,8,11–13,39].

Our findings confirm the importance of climatic, physiographic and water chemistry factors as major drivers influencing the diversity and composition of freshwater bryophyte communities, as well as their geographical segregation. Regarding water chemistry parameters, such as pH and alkalinity, which reflect the underlying geology, the distinction between hard- and soft-water bryoflora has been demonstrated by several authors on the European level and beyond [4,8,12,39–42]. Water trophy level, i.e., water nutrient content, has also been recognized as an important factor influencing bryophyte cover and diversity, as well as community structure, with anthropogenically influenced eutrophication having a detrimental impact on freshwater communities [13–16,18,41,43,44]. Finally, climatic factors, especially those related to precipitation and water availability, as well as their distribution over a year, have been proven to regulate freshwater bryophyte communities, especially in highly seasonal Mediterranean rivers [8,39].

In our study, communities confined to karstic rivers with high alkalinity and pH values, reflecting the dominant carbonate bedrock, and clean and oxygenated water (Groups 2 and 4), were characterized by basophilous species. The *Didymodon tophaceus–Apopellia endiviifolia* community (Group 2) showed a stronger bryophyte dominance in macrophyte species composition, with tufa-forming species such as *Didymodon tophaceus* and *Eucladium verticillatum* being among the characteristic species of the community, along with basophilous *Apopellia endiviifolia* and *Fissides crassipes*. The cooccurrence of other basophilus species of oligotrophic water, such as *Palustriella commutata* and *P. falcata* and the liverwort *Jungermannia atrovirens* [45], was recorded within the community as well. Similar species assemblages have already been described for calcareous rivers in Europe, especially from the Mediterranean area, and were regarded as typical of neutral to basic clean water with low nutrient content in undisturbed flush flow fed streams with regular or low current conditions, as well as from cascades [46–48]. This community showed a prevalence of hygrophyte taxa in our study, and this was corroborated by a high frequency of turfs, species with vertical stems with little or no branching [49], within the lifeform spectrum. These are known to thrive in seasonally flooded habitats, with the strong impact of water [50] suggesting an interplay between flash flows and low water table periods in the *Didymodon tophaceus–Apopellia endiviifolia* community. Additionally, this community had the highest proportion of colonists in the life-strategy spectrum, indicative of a higher share of microhabitats flooded seasonally with strong discharge [50]. Regarding bryophyte composition, the *Didymodon tophaceus–Apopellia endiviifolia* community corresponds well with the community described by Vieira et al. [8] as a freshwater bryophyte community that, in Mediterranean Europe, has an extensive predicted presence, according to environmental niche modelling, in highly seasonal rivers in Spain, southern France, Italy and Greece [8]. The same research concluded that this particular community was characteristic of highly seasonal streams at low to moderate altitudes and high values of precipitation in the driest quarter that sustain permanent flows. However, our study revealed that the most important bioclimatic variable influencing both this community and the *Berula erecta-Cratoneuron filicinum* community (Group 4) within Croatia was the precipitation of the coldest quarter, a good surrogate for the hydrological patterns of Mediterranean rivers, as well as the mean temperature of the driest quarter. These communities were associated with higher values for these bioclimatic parameters, characteristic of a Mediterranean climate with dry and hot summers where higher precipitation occurs during warm winters [51], and were subsequently characterized by the high proportion of southern-temperate chorotypes. On the other hand, they were characterized by overall large catchment areas, i.e., hydrological watersheds. Namely, Groups 2 and 4 were recorded on karstic rivers of the Dinaric Ecoregion, which are most often a part of large and complex hydrographic networks, and receive water from numerous springs, with overground and subterranean courses supplying water from the Dinaric mountains of both Croatia and neighbouring Bosnia and Herzegovina [52]. However, the *Didymodon tophaceus–Apopellia endiviifolia* community (Group 2) included several sites on intermittent rivers with small catchment areas, while on the sites with large catchment areas, it was mostly confined to cascades. The *Berula erecta-Cratoneuron filicinum* community (Group 4) had higher mean catchment area values and significantly lower water pH than the *Didymodon tophaceus–Apopellia endiviifolia* community. Being the transitional community in which vascular species start to outcompete bryophytes, it harboured the highest vascular species number and alpha diversity in comparison to all other groups. Vascular helophytes such as *Mentha aquatica*, *Berula erecta* and *Sparganium erectum* which thrive in the shallow and slower water along the river margins, indicated the gradual transition of completely bryophyte dominated vegetation towards the herbland vegetation of small freshwater streams and the shallow waterbodies of temperate Europe belonging to the alliance of *Glycerio–Sparganion* Br.-Bl. et Sissingh in Boer 1942 [53]. However, with the greatest proportion of rheophyte bryophytes confined to the riverbed, this was the most truly aquatic bryophyte community within the study. This was supported by the analysis of the lifeform spectrum, which revealed the highest proportion of aquatic trailings and a moderate proportion of smooth mats, lifeforms best adapted to permanent submergence [50]. Aquatic trailings are mostly associated with slower currents, whereas smooth mats prefer the more torrential water zones [2,50], so their ratio in the *Berula erecta–Cratoneuron filicinum* community reflects a permanent, slower and more streamlined flow. Regarding the life-strategy spectrum, perennial species were the most represented, indicating constant ecological and hydrological conditions in these watercourses.

The *Oxyrrhynchium hians–Chiloscyphus pallescens* community (Group 1) was mostly restricted to small lowland rivers located in the Pannonian Ecoregion [54], with a quite low mean value for the catchment area. The sites belonging to this community were characterized by eutrophic and turbid water with low alkalinity. The latter is a result of the underlying geology, since the silicate bedrock is dominant within the Pannonian Ecoregion, while the predominant substrates in these localities are sandy and gravelly alluvial deposits of silicate origin. Furthermore, the higher values of the mean temperature of the wettest quarter were associated with this group, indicating more temperate or even continental climatic conditions present in the Pannonian Ecoregion. The overall high proportion of hygrophytes within this community corresponds with the prevalence of turfs and rough mats (creeping pleorocarpous species with lateral branches erect) [49] in the lifeform spectrum, which inhabit periodically submerged margins of river stretches flowing through forests of the Pannonian lowland. Regarding the rheophytes, the most frequent were *Rhynchostegium riparioides* and *Leptodyctium riparium*. While *L. riparium* is unambiguously recognized as a pollution-tolerant aquatic moss [55], with a preference for eutrophic waters [16,17,41,44], *R. riparioides* was omnipresent in our study, reaching the threshold set for constant species in all communities and being present along the entire gradient of nutrient concentration covered by this study, which suggests that the species is weakly linked to trophic conditions, highlighting its wide ecology range as previously reported by several authors [41,44].

The species-poorest community, *Fissidens pusillus–Veronica beccabunga* (Group 3), was the least represented in our study and mostly restricted to eutrophic and turbid small semi-montane watercourses within the Pannonian Ecoregion, with a single locality in the Dinaric–Continental Subecoregion on a small, lowland watercourse with a pebbly–gravelly substrate [54]. The vascular helophytes *Veronica beccabunga* and *Persicaria dubia* were among the constant and characteristic species of this community, which harboured the second highest vascular plant species richness following that of the *Berula erecta–Cratoneuron filicinum* community. The high share of hygrophytes, such as the characteristic species *Brachythecium rutabulum*, *Oxyrrhynchium speciosum* and *Marchantia polymorpha*, as well as a complete absence of aquatic trailings and a high share of rough mats (a lifeform with an adaptive advantage in microhabitats occurring above the normal level of maximum floods) [50] in the lifeform spectrum, confirmed that the periodically submerged rocks and alluvial sediments of river margins make the dominant microhabitat available to freshwater bryophytes in the watercourses of the Pannonian Ecoregion.

The *Cinclidotus* community (Group 5) was dominant in our study and displayed the widest ecological range regarding water quality and climatic variables associated with precipitation. While the majority of the sites were situated in the Dinaric–Continental Subecoregion, with a temperate climate with high values of precipitation in the warmest quarter, some of the sites were recorded in the source areas, as well as in the lower courses of Mediterranean rivers with permanent flow. Temperate chorotypes were dominant within the community, which was the case for all communities in the study, but here, they were represented by a high proportion of both southern-temperate and boreo-temperate elements. Additionally, the presence of the boreal, wide-boreal and Mediterranean–Atlantic chorotypes distinguished this community from the *Didymodon tophaceus–Apopellia endiviifolia* community and the *Berula erecta–Cratoneuron filicinum* community, which were dominantly under Mediterranean influence. Furthermore, the *Cinclidotus* community was characterized by neutral to basic water, related to the dominant carbonate bedrock in the area of its distribution and the slightly lower mean values of alkalinity in the *Didymodon tophaceus–Apopellia endiviifolia* and *Berula erecta–Cratoneuron filicinum* communities. The characteristic species of this group, *Cinclidotus aquaticus* and *C. riparius*, have already been reported in situations of high alkalinity and are associated with carbonate bedrock [39,56,57]. *Cinclidots aquaticus* is characteristic of clean, cold, well-oxygenated waters with low nutrient content [17,39] and is a typical species in the fast water of source areas, permanent torrential watercourses, rapids and waterfalls [39,58]. On the other hand, *C. riparius* was usually found in more sheltered microhabitats, not directly exposed to water dragging forces, while *C. fontinaloides*, a constant species of the *Cinclidotus* community, was most often found on periodically submerged rocks or tree stumps. Among constant species, *Fontinalis antypyretica* was the most truly aquatic species, with the least desiccation tolerance, growing completely submerged and attached either to rocks or to logs in moving water. The occurrence of *F. antipyretica* has not been closely related to specific physicochemical or trophic conditions in the majority of the available studies [11,14,20,44], although an increase in its frequency was observed with the decreasing concentrations of nitrates and phosphates [17]. Additionally, the constant species *Rhynchostegium riparioides* and *Cratoneuron filicinum*, as well as frequent cooccurrence of *Fissidens crassipess*, *Leptodyctium riparium* and *Apopellia endiviifolia*, make this community quite close to the bryophyte community most commonly found in the Mediterranean and predicted to occur in the freshwater streams of its eastern part, as well as in northern Spain and France [8]. This community was regarded as having a high proportion of exclusively aquatic species characteristic of riverbeds and many boreal elements as compared to other communities identified for the Mediterranean in the particular study. Similarly, the *Cinclidotus* community in our study was a prominently aquatic community with a high proportion of rheophyte species, which was corroborated by the high proportion of aquatic trailing, as well as smooth mats.

The geographical patterns of the freshwater bryophyte communities in Croatia show that the Dinaric Ecoregion provides substantially more suitable habitats than the Pannonian Ecoregion, harbouring all five communities identified in this study, with different bryophyte communities recorded at as many as 31.12% of all surveyed sites. This was expected, since fast, relatively clean and cold karstic rivers are a prominent feature of this ecoregion, and freshwater bryophytes are known to thrive and are the dominant component of the macrophyte vegetation in conditions of fast and turbulent flow, rocky substrates and low temperatures, which vascular plants cannot withstand [3,4,6,46,53,59]. They are a prominent part of the vegetation in highly seasonal Mediterranean rivers as well, where they successfully cope with the interchange of dry periods and periods with flash flows of strong water currents due to their diverse morphological and physiological adaptations. In contrast, the Pannonian Ecoregion harbours a very small number of sites with bryophyte vegetation, with only 4.53% of all surveyed sites having this vegetation type. Watercourses in the Pannonian Ecoregion are mostly slow, eutrophic lowland streams and rivers with unstable sandy and gravelly alluvial sediments unsuitable for bryophytes, which are here additionally subjected to competition with vascular plants [5,7]. Furthermore, the majority of these watercourses are subjected to flow regulation through canalization, riverbed deepening and embankment, as well as considerable changes in land-use practices, including the removal of the riparian vegetation [60], all of which have a negative impact on aquatic vegetation in general.

Our study was limited by the predefined survey sites that were included in the assessment of ecological status, which, according to the WFD, includes waterbodies with catchment areas greater than 10 km^2, while omitting the majority of the source areas and smaller headwater streams in which bryophyte communities are expected to occur.

With this in mind, future research should focus on these habitats, especially in parts of the Pannonian Ecoregion with mountain areas of high geological and geomorphological heterogeneity. However, we want to emphasise the importance of the WFD, which encouraged our research into freshwater bryophyte communities by including this group in its assessment of the ecological status of waterbodies. So far, substantial progress has been made [3,8,17,39], which is especially important in regions where bryophytes are still generally poorly researched [24], as in the case of Southeast Europe [13,16], with our findings contributing to knowledge with respect to the ecology and vegetation of bryophyte communities of the Mediterranean and providing the first insights into this subject for the Western Balkans.

4. Materials and Methods

4.1. Study Area

Data on the distribution of bryophyte-dominated freshwater communities was collected within the national surface water monitoring scheme conducted to assess the ecological status of waterbodies as required by the Water Framework Directive (WFD) [61]. The sampling sites were originally selected so as to encompass the heterogeneity of different waterbody types recognized by the recent typology developed as a basis for the monitoring of surface waters [54]. According to this typology, the land area of Croatia, 56,594 km^2, is divided into two hydrological and biogeographical regions—the Pannonian and the Dinaric Ecoregion, the latter being subdivided into the Continental and Mediterranean Subecoregion (Figure 11). In all, 293 watercourses were surveyed during the vegetation seasons from 2016 to 2021. The survey included as many as 527 sampling sites, ultimately covering the whole of Croatian territory (Figure 11).

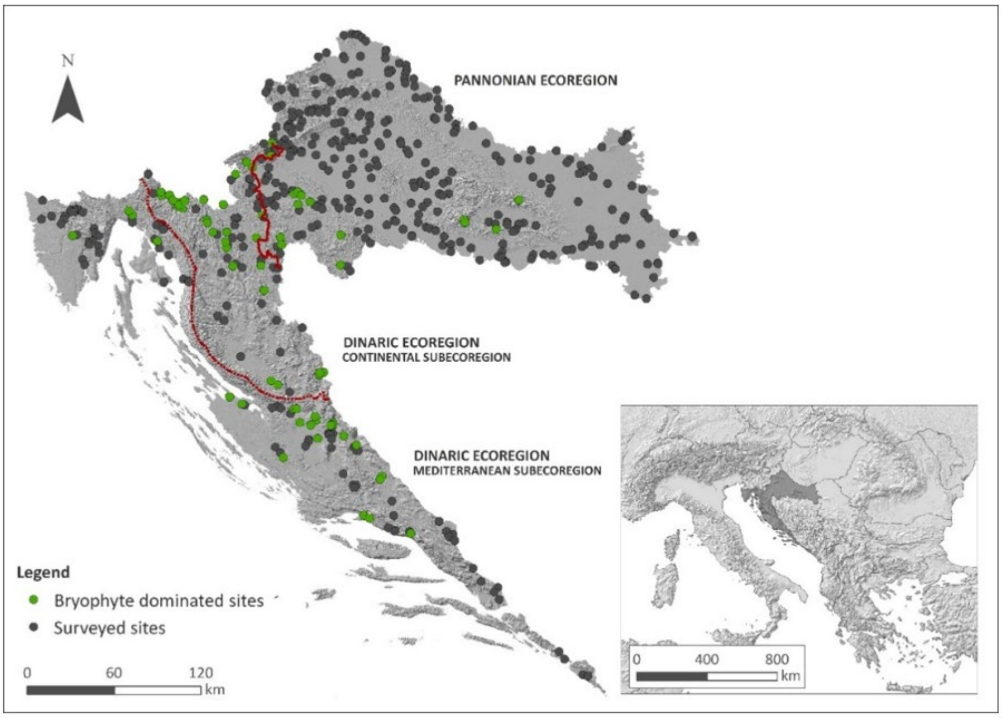

Figure 11. Study area with 527 sampling sites distributed across Croatia (Southeast Europe).

The Pannonian Ecoregion refers to the alluvial and diluvial plains in the inland part of the country bounded by three large rivers (Sava, Drava and Danube). This area ranges between 80 and 135 m a.s.l., with a small number of rather low, solitary mountain massifs reaching 1000 m a.s.l. The lithological and geological composition is mostly silicate quaternary deposits, while limestone is present only locally, in higher mountain areas. The climate is temperate, with warm summers throughout most of the area (Cfb), hot summers predominately in the eastern part (Cfa) and no dry season [62]. On the contrary, the Dinaric Ecoregion is predominately built from Mesozoic limestone and dolomite bedrock and is characterized by karstic phenomena. This ecoregion includes the Dinarides, the largest uninterrupted karst landscape in Europe, occupying almost 50% of the territory of Croatia. Because of the predominantly calcareous and dolomite bedrock, many rivers in the area have partly subterranean courses, or flow through impressive canyons or complex systems of barrage lakes, participating in the karst relief formation. The Continental Subecoregion is characterized by a temperate climate (Cfb), while the climate of the Mediterranean Subecoregion is mostly Mediterranean, i.e., temperate with dry and hot summer months (Csa) [62]. The Pannonian watercourses and the majority of the watercourses of the Dinaric–Continental Subecoregion belong to the Black Sea Basin, while the watercourses of the Dinaric–Mediterranean Subecoregion belong to the Adriatic Sea Basin.

4.2. Macrophyte Vegetation Sampling

A survey of macrophyte vegetation was performed according to the national methodology for macrophyte sampling [54] from June to September, when macrophyte vegetation is optimally developed, and during the lowest water discharge levels. Watercourses were surveyed for macrophytes along 100 m-long transects from the banks and, if the water depth was low enough, by zigzagging across the channel. In less accessible areas, the river bottom was raked to reach the macrophytes, with the rake either on a long pole or at the end of a rope.

Macrophyte survey included all representatives, i.e., bryophytes and vascular plants, as well as macroalgae. The survey included both vascular hydrophytes (truly aquatic macrophytes living submerged or floating on the water surface, rooted in the substrate or not) and helophytes (mostly marshland vascular species growing emergent along the water margins). Species coverage and abundance were assessed using the standard Central European methodology, i.e., extended nine-degree Braun–Blanquet scale (r = one individual; + = up to 5 individuals; 1 = up to 50 individuals; 2m = over 50 individuals, coverage < 5%; 2a = coverage 5–15%; 2b = coverage 15–25%; 3 = 25–50%; 4 = coverage 50–75%; 5 = coverage over 75%) [63–65].

Bryophytes were collected from various substrates (e.g., rocks, boulders, pebbles, xylal) within the riverbed, as well as from the periodically flooded river margins. Other macrophytes were collected for identification in the laboratory only if it was not possible to make accurate identification in the field. The collected material was deposited in herbarium ZA [66]. The nomenclature follows Hodgetts et. al. [67] for bryophytes, Euro + Med [68] for vascular plants and AlgaeBase [69] for algae.

4.3. Environmental Data Sampling and Collection

All localities were also sampled for basic water physicochemical and chemical parameters once a month throughout the year. Conductivity, pH, water temperature and dissolved oxygen were measured in situ with a Hach HQ40D Portable Multi Meter under standard conditions. Water samples were collected and analysed in an accredited laboratory (Central Water Management Laboratory, Zagreb, Croatia) for nine additional water chemistry parameters (Table 5).

Furthermore, physiographic and climatic environmental variables were obtained from several data sets using ArcGIS 10.5 software. Altitude was obtained from the digital elevation model EU-DEM v1.0 [70], distance from the source from topographic maps 1:25,000 [71], catchment area from the database of Hrvatske vode—the legal entity for water management and bioclimatic variables from CHELSA climatological datasets [72] (Table 5).

Table 5. Environmental variables and abbreviations used.

	Environmental Variable	Abbreviation
Water physicochemical parameters	Water temperature	T (°C)
	Water pH	pH
	Electrical conductivity	EC (µS/cm)
	Total suspended solids	TSS (mg/L)
	Dissolved oxygen	DO (mgO_2/L)
	Total alkalinity	TALK ($mgCaCO_3$/L)
	Biochemical oxygen demand	BOD (mgO_2/L)
Water chemical parameters	Ammonium	NH_4^+ (mgN/L)
	Nitrites	NO_2^- (mgN/L)
	Nitrates	NO_3^- (mgN/L)
	Total nitrogen	N_{tot} (mgN/L)
	Orthophosphates	PO_4^{3-} (mgP/L)
	Total phosphorus	P_{tot} (mgP/L)
Physiographical variables	Altitude	Alt (m a.s.l.)
	Catchment area	CA (km^2)
	Distance from the source	DFS (m)
Climatic variables	Mean annual air temperature	Bio1 (°C)
	Mean diurnal air temperature range	Bio2 (°C)
	Isothermality	Bio3 (°C)
	Temperature seasonality	Bio4 (°C)
	Max temperature of the warmest month	Bio5 (°C)
	Min temperature of the coldest month	Bio6 (°C)
	Temperature annual range	Bio7 (°C)
	Mean temperature of wettest quarter	Bio8 (°C)
	Mean temperature of driest quarter	Bio9 (°C)
	Mean temperature of warmest quarter	Bio10 (°C)
	Mean temperature of coldest quarter	Bio11 (°C)
	Annual precipitation	Bio12 (kg/m^2)
	Precipitation of wettest month	Bio13 (kg/m^2)
	Precipitation of driest month	Bio14 (kg/m^2)
	Precipitation seasonality	Bio15 (kg/m^2)
	Precipitation of wettest quarter	Bio16 (kg/m^2)
	Precipitation of driest quarter	Bio17 (kg/m^2)
	Precipitation of warmest quarter	Bio18 (kg/m^2)
	Precipitation of coldest quarter	Bio19 (kg/m^2)

4.4. Data Analysis

Seventy-six sites in which bryophytes were the dominant component of macrophyte vegetation were selected for further analysis out of 527 surveyed sites. TWINSPAN analysis, a polythetic divisive classification method [73] modified by Roleček et al. [74], was conducted on vegetation relevés using Soerensen dissimilarity to assess whether discrete bryophyte communities occurred in any of the watercourses surveyed. TWINSPAN analysis was performed in Juice 7.1 [75]. The groups established by TWINSPAN were then tested for a significant difference based on species composition with the nonparametric test ANOSIM (using Bray–Curtis distance and 9999 permutations) [76] run in Past 4.9 software [77].

The groups resulting from these analyses were further analysed with respect to species composition. The synoptic table (Appendix A) was compiled in Juice 7.1. software. For all species within a particular group, e.g., community, φ-coefficients were calculated and tested for significance with the Fischer test. This statistical fidelity measure of particular species belonging to the previously defined groups was used to define characteristic species ($\varphi \geq 0.40$, $p < 0.05$) [78]. Constant species were defined as those having the frequency within a particular group equal to or higher than 50%.

Bryophyte communities were analysed based on their affinity to water [10], chorotype composition [79], lifeform [49] and life strategies spectra [10] of bryophyte species. Furthermore, the alpha diversity (species richness and Simpson index) of the communities was analysed and visualized through boxplot graphs in SPSS 22.0 software.

Community structure was assessed using the indirect ordination method, Detrended correspondence analysis (DCA), run in R software (Vegan package) through Juice 7.1.-R connection. In DCA, weighted Ellenberg indicator values (EIV) for continentality, light, moisture, nutrients, temperature and pH reaction [49] were passively projected as vectors over the ordination to assess the possible environmental gradients. DCA revealed that the data were compositional with gradient longer than 3.0 SD units, indicating that a constrained analysis based on a unimodal model was most suitable for describing the data [80]. Subsequently, canonical correspondence analysis (CCA) was used as a direct ordination method to assess the relationship between environmental variables and patterns in species composition [81], while the statistical significance of the relationship between vegetation and environmental variables was tested by Monte Carlo permutation test using 999 permutations. Environmental data were log-transformed using the base-10 logarithm. Preselection of environmental variables was based on a correlation matrix between the variables and explorative DCA. Among highly positively correlated variables, those represented with the longest vectors in DCA were retained. This was performed in Past 4.9 software [77].

Additionally, a basic descriptive statistic (mean ± SE and min–max) of all environmental variables for groups derived from TWINSPAN analysis was calculated (Appendix B). A significant difference between groups was tested for each environmental variable with the nonparametric Kruskal–Wallace test, followed by Mann–Whitney pairwise *post hoc* tests (Appendix C). Nonparametric tests were selected since the majority of variables (32 out of 35) did not have a normal distribution, which was determined with the Shapiro–Wilk normality test in Past 4.9 [77].

5. Conclusions

The present study confirmed the importance of the climatic, physiographic and water chemistry gradients as major drivers shaping the diversity, composition and distribution of freshwater bryophyte communities. Comprehensive research revealed five community types and the patterns in their distribution across Croatia. Relatively clean and cold karstic rivers in the Dinaric Ecoregion that flow over carbonate bedrock and stable substrates represent far more suitable habitats, harbouring greater diversity of freshwater bryophyte communities in comparison to the rivers of the Pannonian Ecoregion. The *Didymodon tophaceus–Apopellia endiviifolia* and the *Berula erecta–Cratoneuton filicinum* are mostly confined to the karstic rivers of the Dinaric Ecoregion under the influence of the Mediterranean climate. The *Didymodon tophaceus–Apopellia endiviifolia* community is a tufa-forming community associated with the seasonally dry watercourses of small catchment areas and cascades along the larger karstic rivers, while the *Berula erecta–Cratoneuton filicinum* community is associated with rivers with a permanent and more streamlined flow. The *Cinclidotus* community is the most widespread in Croatia, having a wide ecological range and with the centre of its distribution being in the Dinaric–Continental Subecoregin, i.e., in fast and cold karstic rivers with permanent flow due to large catchment areas and high precipitation that are characteristic of this subecoregion. The species-rich *Oxyrrhynchium hians–Chiloscyphus pallescens* community and the species-poor *Fissidens pusillus–Veronica beccabunga* community are quite rare and are restricted to small eutrophic and turbid rivers of low alkalinity situated mainly in the Pannonian Ecoregion. These communities are characterized by a low share of rheophytes and a high share of species inhabiting the periodically flooded river margins, which is mainly related to low riverbed stability limiting the development of truly aquatic bryophyte communities in Pannonian rivers.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/plants11121542/s1, Table S1: Cover and abundance of the species at each surveyed locality with coordinates of localities in WGS84 (DIN-CON—Dinaric Ecoregion, Continental Subecoregion, DIN-MED—Dinaric Ecoregion, Continental Subecoregion, PAN—Pannonian Ecoregion).

Author Contributions: Conceptualization, methodology, A.R. and A.A.; validation, A.A.; data collection and sampling A.R., A.A., V.Š., N.V. and N.K.; data analysis A.R. and A.A.; resources, A.A.; writing—original draft preparation, A.R.; writing—review and editing, A.A., V.Š. and N.V.; visualization, A.R.; supervision, A.A.; project administration, N.V.; funding acquisition, A.A. All authors have read and agreed to the published version of the manuscript.

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Appendix A. Synoptic Table with Percentage Frequency and Modified Fidelity Index φ-Coefficients

Table A1. Characteristic species (φ ≥ 40.00) are marked in bold, and constant species (frequency ≥ 50.00) are provided in grey cells.

TWINSPAN Group	1		2		3		4		5	
Number of Relevés	**8**		**16**		**4**		**15**		**33**	
Oxyrrhynchium hians (Hedw.) Loeske	**100**	**94.6**	.	—	.	—	.	—	9	—
Pellia neesiana (Gottsche) Limpr.	**50**	**66.7**	.	—	.	—	.	—	.	—
Conocephalum salebrosum Szweyk., Buczk. & Odrzyk.	**62**	**63**	.	—	.	—	.	—	18	2.8
Fissidens taxifolius Hedw.	**50**	**61.3**	6	—	.	—	.	—	.	—
Chiloscyphus pallescens (Ehrh.) Dumort.	**50**	**58.7**	.	—	.	—	7	—	3	—
Plagiomnium undulatum (Hedw.) T. J. Kop.	**50**	**57**	.	—	.	—	.	—	12	—
Dichodontium pellucidum (Hedw.) Schimp.	**38**	**51**	.	—	.	—	.	—	6	—
Pohlia melanodon (Brid.) A. J. Shaw	**38**	**41.5**	19	—	.	—	.	—	.	—
Hypnum cupressiforme Hedw.	**25**	**45.9**	.	—	.	—	.	—	.	—
Plagiomnium ellipticum (Brid.) T. J. Kop.	**25**	**42.2**		—	.	—	.	—	3	—
Dichodontium flavescens (Dicks.) Lindb.	25	36.1	.	—	.	—	.	—	9	—
Didymodon tophaceus (Brid.) Lisa	.	—	**50**	**64**	.	—	.	—	3	—
Eucladium verticillatum (With.) Bruch & Schimp.	.	—	**44**	**59.1**	.	—	.	—	3	—
Apopellia endiviifolia (Dicks.) Nebel & D. Quandt	.	—	**75**	**49.6**	.	—	40	—	33	—
Fissidens crassipes Wilson ex Bruch & Schimp.	12	—	**69**	**48.8**	.	—	.	—	48	25.7
Funaria hygrometrica Hedw.	.	—	**25**	**42.2**	.	—	.	—	3	—
Rhynchostegium riparioides (Hedw.) Cardot	75	—	81	—	75	—	60	—	94	20.1
Cratoneuron filicinum (Hedw.) Spruce	50	—	62	—	50	—	73	—	61	—
Ptychostomum pseudotriquetrum (Hedw.) J. R. Spence & H. P. Ramsay ex Holyoak & N. Pedersen	50	—	50	31.8	.	—	7	—	9	—
Leptodictyum riparium (Hedw.) Warnst.	50	33.2	.	—	.	—	13	—	48	31.3
Cinclidotus fontinaloides (Hedw.) P. Beauv.	.	—	56	—	.	—	33	—	64	35.8
Fontinalis antipyretica Hedw.	25	—	44	—	.	—	67	—	61	—
Brachythecium rutabulum (Hedw.) Schimp.	38	24.1	.	—	**50**	**40.1**	.	—	6	—
Fissidens pusillus (Wilson) Milde	38	23.9	.	—	**50**	**40.0**	7	—	.	—
Veronica beccabunga L.	.	—	.	—	**50**	**66.7**	.	—	.	—
Persicaria dubia (Stein) Fourr.	.	—	.	—	**50**	**66.7**	.	—	.	—
Oxyrrhynchium speciosum (Brid.) Warnst.	25	—	.	—	**50**	**47.4**	.	—	3	—
Marchantia polymorpha L.	12	—	12	—	50	—	7	—	33	12.3
Hygroamblystegium tenax (Hedw.) Jenn.	.	—	.	—	25		.	—	3	—
Brachythecium rivulare Schimp.	12	—	.	—	25	—	.	—	27	21.3
Juncus buffonius L.	.	—	.	—	25	—	.	—	.	—

Table A1. *Cont.*

TWINSPAN Group **Number of Relevés**	**1** **8**		**2** **16**		**3** **4**		**4** **15**		**5** **33**	
Mentha aquatica L.	.	—	6	—	25	—	**60**	**52.6**	3	—
Chiloscyphus polyanthos (L.) Corda	38	—	6	—	.	—	47	29.2	21	—
Berula erecta (Huds.) Coville	.	—	6	—	.	—	**47**	**52**	9	—
Sparganium erectum L.	.	—	.	—	.	—	**27**	**47.5**	.	—
Agrostis stolonifera L.	.	—	25	—	25	—	33	—	15	—
Vaucheria A.P.de Candolle sp.	.	—	.	—	25	—	13	—	9	—
Lythrum salicaria L.	12	—	.	—	25	—	20	—	6	—
Rorippa sylvestris (L.) Besser	.	—	.	—	25	—	13	—	3	—
Cinclidotus riparius (Host ex Brid.) Arn.	12	—	25	—	.	—	7	—	**64**	**51.2**
Cinclidotus aquaticus (Hedw.) Bruch & Schimp.	.	—	19	—	.	—	40	—	**58**	**40.6**
Cladophora glomerata (Linnaeus) Kützing	.	—	19	—	25	—	13	—	33	19.8
Hygroamblystegium varium (Hedw.) Mönk.	25	—	6	—	.	—	.	—	6	—
Heribaudiella fluviatilis (Areschoug) Svedelius	25	—	.	—	.	—	7	—	6	—
Mnium spinulosum Bruch & Schimp.	12	—	.	—	.	—	.	—	.	—
Fissidens bryoides Hedw.	12	—	.	—	.	—	.	—	.	—
Plagiomnium elatum (Bruch et Schimp.) T. J. Kop.	12	—	.	—	.	—	.	—	.	—
Brachythecium mildeanum (Schimp.) Schimp	12	—	.	—	.	—	.	—	.	—
Hygroamblystegium humile (P.Beauv.) Vanderp., Goffinet & Hedenäs	12	—	.	—	.	—	.	—	.	—
Bryum ruderale Crundw. & Nyholm	12	—	.	—	.	—	.	—	.	—
Leersia oryzoides (L.) Sw.	12	—	.	—	.	—	.	—	.	—
Scirpoides holoschoenus (L.) Soják L.	.	—	19	31.1	.	—	7	—	.	—
Batrachospermum Roth sp.	.	—	19	31.1	.	—	7	—	.	—
Calliergonella cuspidata (Hedw.) Loeske	.	—	19	—	.	—	.	—	9	—
Spirogyra Link. Sp.	.	—	19	—	.	—	.	—	9	—
Jungermannia atrovirens Dumort.	12	—	25	—	.	—	7	—	6	—
Chara vulgaris L.	.	—	19	35.3	.	—	.	—	3	—
Dicranella varia (Hedw.) Schimp.	.	—	12	32	.	—	.	—	.	—
Palustriella commutata (Hedw.) Ochyra	.	—	12	22.6	.	—	7	—	.	—
Palustriella falcata (Brid.) Hedenäs	.	—	12	9.3	.	—	13	10.8	12	8.6
Oenanthe fistulosa L.	.	—	12	—	.	—	13	—	.	—
Didymodon fallax (Hedw.) R. H. Zander	.	—	12	—	.	—	.	—	15	—
Deschampsia cespitosa (L.) P. Beauv.	.	—	6	—	.	—	7	—	9	—
Hygrohypnum luridum (Hedw.) Jenn.	.	—	6	—	.	—	.	—	9	—
Oxyrrhynchium schleicheri (R. Hedw.) Röll	.	—	6	—	.	—	.	—	.	—
Riccia fluitans L.	.	—	6	—	.	—	.	—	.	—
Veronica longifolia L.	.	—	6	—	.	—	.	—	.	—
Fissidens adianthoides Hedw.	12	—	6	—	.	—	.	—	.	—
Gymnostomum aeruginosum Sm.	.	—	6	—	.	—	.	—	.	—
Philonotis marchica (Hedw.) Brid.	.	—	6	—	.	—	.	—	.	—
Bryum dichotomum Hedw.	.	—	6	—	.	—	.	—	.	—
Alisma lanceolatum With.	.	—	6	—	.	—	7	—	.	—
Mentha longifolia (L.) L.	.	—	6	—	.	—	7	—	.	—
Iris pseudacorus L.	.	—	6	—	.	—	7	—	.	—
Bolboschoenus maritimus (L.) Palla	.	—	6	—	.	—	.	—	.	—
Juncus compressus Jacq.	.	—	6	—	.	—	.	—	.	—
Brachythecium salebrosum (Hoffm. Ex F.Weber & D.Mohr) Schimp.	.	—	6	—	.	—	.	—	.	—
Poa palustris L.	.	—	6	—	.	—	.	—	.	—
Fissidens arnoldii R. Ruthe	.	—	6	—	.	—	.	—	.	—
Trichostomum crispulum Bruch	.	—	6	—	.	—	.	—	.	—
Lemanea fluviatilis (Linnaeus) C.Agardh	.	—	6	—	.	—	.	—	6	—
Bangia atropurpurea (Mertens ex Roth) C.Agardh	.	—	6	—	.	—	.	—	6	—
Drepanocladus aduncus (Hedw.) Warnst.	.	—	6	—	.	—	.	—	3	—
Audouinella hermannii (Roth) Duby	.	—	6	—	.	—	.	—	3	—
Ranunculus trichophyllus Chaix	.	—	.	—	.	—	20		6	—
Lysimachia vulgaris L.	.	—	.	—	.	—	13	33.1	.	—
Lysimachia nummularia L.	.	—	.	—	.	—	13	33.1	.	—
Caltha palustris L.	.	—	.	—	.	—	13	33.1	.	—
Scirpus sylvaticus L.	.	—	.	—	.	—	13	33.1	.	—
Schoenoplectus lacustris (L.) Palla	.	—	6	—	.	—	13	—	.	—
Juncus articulatus L.	.	—	6	—	.	—	13	—	6	—
Nostoc Vaucher ex Bornet & Flahault sp.	.	—	6	—	.	—	13	—	3	—
Veronica anagallis-aquatica L.	.	—	6	—	.	—	13	—	3	—
Zygnema C.Agardh sp.	12	—	.	—	.	—	13	—	3	—
Lycopus europaeus L.	.	—	.	—	.	—	13	—	3	—
Hygroamblystegium fluviatile (Hedw.) Loeske	.	—	.	—	.	—	7	—	.	—
Alisma plantago-aquatica L.	12	—	.	—	.	—	7	—	.	—
Myosotis scorpioides L.	.	—	.	—	.	—	7	—	.	—

Table A1. *Cont.*

TWINSPAN Group	**1**		**2**		**3**		**4**		**5**	
Number of Relevés	**8**		**16**		**4**		**15**		**33**	
Samolus valerandi L.	.	—	.	—	.	—	7	—	.	—
Juncus inflexus L.	.	—	.	—	.	—	7	—	.	—
Ranunculus repens L.	.	—	.	—	.	—	7	—	.	—
Rorippa amphibia (L.) Besser	.	—	.	—	.	—	7	—	.	—
Helosciadium repens (Jacq.) W. D. J. Koch	.	—	.	—	.	—	7	—	.	—
Thamnobryum alopecurum (Hedw.) Gangulee	12	—	.	—	.	—	.	—	12	—
Fissidens fontanus (Bach.Pyl.) Steud.	.	—	.	—	.	—	.	—	9	—
Didymodon spadiceus (Mitt.) Limpr.	.	—	.	—	.	—	.	—	9	—
Rhynchostegiella teneriffae (Mont.) Dirkse et Bouman	12	—	.	—	.	—	.	—	9	—
Potamogeton nodosus Poir.	.	—	.	—	.	—	.	—	9	—
Didymodon luridus Hornsch.	.	—	.	—	.	—	.	—	6	—
Hildenbrandia rivularis (Liebmann) J.Agardh	.	—	.	—	.	—	.	—	6	—
Rhizoclonium hieroglyphicum (C.Agardh) Kützing	12	—	.	—	.	—	.	—	6	—
Mnium marginatum (Dicks.) P.Beauv.	.	—	.	—	.	—	.	—	6	—
Rhynchostegiella curviseta (Brid.) Limpr.	.	—	.	—	.	—	.	—	3	15.6
Lemanea rigida (Sirodot) De Toni	.	—	.	—	.	—	.	—	3	15.6
Potamogeton perfoliatus L.	.	—	.	—	.	—	.	—	3	—
Chaetophora lobata Schrank	.	—	.	—	.	—	.	—	3	—
Barbula unguiculata Hedw.	12	—	.	—	.	—	.	—	3	—
Stuckenia pectinata (L.) Börner	.	—	.	—	.	—	.	—	3	—
Carex acuta L.	.	—	.	—	.	—	.	—	3	—
Rhizomnium punctatum (Hedw.) T.J.Kop.	12	—	.	—	.	—	.	—	3	—
Tribonema viridae Pascher	.	—	.	—	.	—	.	—	3	—
Didymodon insulanus (De Not.) M.O.Hill	.	—	.	—	.	—	.	—	3	—
Myosoton aquaticum (L.) Moench	.	—	.	—	.	—	.	—	3	—
Fontinalis hypnoides Hartm. Var. *duriaei* (Schimp.) Kindb.	.	—	.	—	.	—	.	—	3	—
Mougeotia C.Agardh sp.	.	—	.	—	.	—	.	—	3	—
Galium palustre L.	.	—	.	—	.	—	.	—	3	—
Myriophyllum spicatum L.	.	—	.	—	.	—	.	—	3	—
Chara contraria A.Braun ex Kützing	.	—	.	—	.	—	.	—	3	—
Lophocolea bidentata (L.) Dumort.	.	—	.	—	.	—	.	—	3	—
Lemanea fucina Bory	.	—	.	—	.	—	.	—	3	—

Appendix B

Table A2. Basic descriptive statistic (mean ± SE and range (min–max)) of 35 environmental variables (for abbreviations, see Table 5).

	TWINSPAN Group				
	1	**2**	**3**	**4**	**5**
ALT (m a.s.l.)					
mean ± SE	153.8 ± 20.6	282.3 ± 39.5	385.2 ± 56.2	231.1 ± 30.5	218 ± 18.7
min–max	102.3–227.9	93.0–564.0	290.1–538.8	31.4–376.6	0.3–384.2
DFS (km)					
mean ± SE	13.1 ± 2.5	19.9 ± 7.9	4.4 ± 0.8	6.6 ± 2.5	21.1 ± 5.1
min–max	1.4–21.5	3.6–116.0	3.2–6.5	0.2–33.8	0.04–118.2
CA (km^2)					
mean ± SE	36.2 ± 8.5	198.5 ± 72.1	9.8 ± 4.2	230.7 ± 71.8	361.8 ± 93.2
min–max	2.7–79.8	13.3–1070.7	0.7–20.8	8.8–933.1	10.5–2199.4
T (°C)					
mean ± SE	12.3 ± 0.5	12.1 ± 0.6	14 ± 1.6	11.39 ± 0.45	12.01 ± 0.39
min–max	0.1–28.4	2.8–25.6	2.9–24.2	4.4–20.3	1.2–25.3
pH					
mean ± SE	7.70 ± 0.15	8.03 ± 0.05	8.08 ± 0.12	7.87 ± 0.04	7.99 ± 0.04

Table A2. *Cont.*

	TWINSPAN Group				
	1	**2**	**3**	**4**	**5**
min–max	6.50–9.30	7.10–8.80	7.62–8.60	6.90–8.40	7.16–9.00
EC (μS/cm)					
mean ± SE	296.56 ± 43.34	416.29 ± 45.69	290.11 ± 114.12	459.71 ± 60.55	372.31 ± 24.36
min–max	69.00–722.00	129.00–1041.00	71.00–654.00	61.00–1049.00	8.00–1057.00
TSS (mg/L)					
mean ± SE	9.03 ± 2.07	2.19 ± 0.42	7.38 ± 2.52	2.12 ± 0.66	2.97 ± 0.53
min–max	<1.60–50.00	<0.53–17.2.	<1.60–33.00	<0.53–74.00	<0.53–69.00
TALK (mgCaCO$_3$/L)					
mean ± SE	141.91 ± 20.2	247.13 ± 27.69	161.19 ± 81.57	236.96 ± 29.35	213.24 ± 15.39
min–max	36.70–327.00	130.10–631.00	14.00–479.00	32.00–624.00	44.20–636.00
DO (mgO$_2$/L)					
mean ± SE	10.09 ± 0.29	10.63 ± 0.23	9.31 ± 0.25	10.88 ± 0.22	11.07 ± 0.15
min–max	5.46–14.55	6.95–14.00	2.72–13.16	7.50–14.01	4.90–16.90
BOD (mgO$_2$/L)					
mean ± SE	2.15 ± 0.30	1.17 ± 0.16	5.28 ± 1.99	0.97 ± 0.17	1.02 ± 0.10
min–max	<0.50–7.83	<0.09–4.60	0.81–16.47	<0.10–5.64	<0.10–14.3
NH_4^+ (mgN/L)					
mean ± SE	0.126 ± 0.050	0.010 ± 0.003	0.0730 ± 0.0250	0.077 ± 0.057	0.026 ± 0.008
min–max	<0.003–<0.880	<0.0008–0.1480	<0.005–0.300	<0.003–3.420	<0.0008–1.277
NO_2^- (mgN/L)					
mean ± SE	0.0215 ± 0.0135	0.0050 ± 0.0029	0.0189 ± 0.01411	0.0041 ± 0.0016	0.0063 ± 0.0018
min–max	0.0010–1.3030	0.0005–0.2210	0.0015–0.1100	0.0005–0.0790	0.0005–0.0900
NO_3^- (mgN/L)					
mean ± SE	0.527 ± 0.114	0.427 ± 0.069	0.848 ± 0.224	0.424 ± 0.060	0.626 ± 0.053
min–max	0.001–2.615	0.017–1.871	0.070–2.180	0.010–1.400	0.010–2.391
N_{tot} (mgN/L)					
mean ± SE	1.067 ± 0.163	0.676 ± 0.080	1.405 ± 0.376	0.563 ± 0.072	0.847 ± 0.060
min–max	0.100–2.632	0.110–1.944	0.215–2.440	0.100–3.565	0.190–2.452
PO_4^{3-} (mgP/L)					
mean ± SE	0.0157 ± 0.0029	0.0029 ± 0.0007	0.0635 ± 0.0104	0.0033 ± 0.0005	0.0079 ± 0.0014
min–max	<0.0040–<0.0900	<0.0012–0.0460	<0.0050–0.7600	<0.0010–0.0316	<0.0012–0.2020
P_{tot} (mgP/L)					
mean ± SE	0.0544 ± 0.0087	0.0122 ± 0.0028	0.1861 ± 0.043	0.0154 ± 0,0030	0.0232 ± 0.0200
min–max	<0.0030–<0.3200	<0.0015–0.1150	0.0200–0.7600	<0.002–0.1840	<0.002–0.3220
bio1 (°C)					
mean ± SE	11.58 ± 0.13	12.21 ± 0.42	9.95 ± 0.28	12.60 ± 0.36	11.67 ± 0.25
min–max	10.95–11.95	10.25–15.05	9.15–10.35	10.35–15.05	9.85–15.85
bio2 (°C)					
mean ± SE	9.18 ± 0.16	8.81 ± 0.25	8.93 ± 0.17	8.77 ± 0.29	8.38 ± 0.21
min–max	8.20–9.60	5.90–9.60	8.70–9.40	5.90–9.90	4.70–9.80

Table A2. *Cont.*

	TWINSPAN Group 1	2	3	4	5
bio3 (°C)					
mean ± SE	30.53 ± 0.44	30.1 ± 0.56	31.03 ± 0.38	30.08 ± 0.63	29.06 ± 0.43
min–max	27.9–31.7	24.2–31.8	30.2–31.9	24.2–32.9	21.6–32.2
bio4 (°C)					
mean ± SE	749.30 ± 3.99	723.76 ± 5.48	724.23 ± 4.48	723.81 ± 5.11	722.45 ± 6.28
min–max	727.80–759.30	662.90–741.70	713.30–732.60	662.90–748.30	606.20–749.90
bio5 (°C)					
mean ± SE	26.94 ± 0.25	27.11 ± 0.45	24.78 ± 0.34	27.39 ± 0.31	26.22 ± 0.20
min–max	25.95–27.65	24.95–29.85	23.95–25.55	25.15–29.25	24.35–28.85
bio6 (°C)					
mean ± SE	−3.07 ± 0.13	-2.06 ± 0.5	−4.05 ± 0.14	−1.68 ± 0.46	−2.41 ± 0.41
min–max	−3.75–−2.65	−4.15–2.65	−4.45–−3.85	−3.85–2.65	−4.35–5.05
bio7 (°C)					
mean ± SE	30.01 ± 0.17	29.17 ± 0.38	28.83 ± 0.25	29.07 ± 0.40	28.63 ± 0.38
min–max	29.40–30.70	24.50–30.40	28.40–29.50	24.50–30.40	21.50–30.50
bio8 (°C)					
mean ± SE	14.68 ± 1.13	9.59 ± 0.47	17.35 ± 0.62	9.89 ± 0.47	11.36 ± 0.46
min–max	11.45–18.95	6.45–11.85	15.55–18.25	6.85–13.55	6.85–16.75
bio9 (°C)					
mean ± SE	3.38 ± 0.13	15.36 ± 2.62	1.98 ± 0.25	17.36 ± 2.34	8.50 ± 1.59
min–max	2.65–3.75	2.25–23.75	1.25–2.35	2.35–23.75	1.75–23.85
bio10 (°C)					
mean ± SE	21.13 ± 0.16	21.59 ± 0.43	19.23 ± 0.36	21.99 ± 0.35	20.93 ± 0.21
min–max	20.55–21.55	19.35–23.75	18.25–19.85	19.65–23.75	18.95–23.85
bio11 (°C)					
mean ± SE	1.71 ± 0.13	2.82 ± 0.47	0.48 ± 0.22	3.24 ± 0.42	2.21 ± 0.34
min–max	0.95–2.05	0.75–6.65	−0.15–0.85	0.85–6.65	0.45–8.15
bio12 (kg/m^2)					
mean ± SE	1041.98 ± 41.05	1357.79 ± 49.47	1171.93 ± 52.28	1306.52 ± 55.65	1334.00 ± 43.27
min–max	960.80–1304.40	1090.00–1697.60	1101.30–1323.40	1077.80–1913.60	972.20–1801.90
bio13 (kg/m^2)					
mean ± SE	110.90 ± 4.40	160.38 ± 5.07	133.43 ± 4.03	157.63 ± 6.79	151.32 ± 5.27
min–max	101.30–139.20	122.50–183.10	125.60–144.70	124.90–236.30	107.70–221.80
bio14 (kg/m^2)					
mean ± SE	59.14 ± 3.29	65.30 ± 5.71	59.03 ± 2.87	61.23 ± 5.32	72.50 ± 3.73
min–max	48.30–78.00	38.90–101.20	55.30–67.40	38.90–97.30	30.20–104.10
bio15 (kg/m^2)					
mean ± SE	18.54 ± 0.44	23.71 ± 1.41	21.05 ± 0.51	24.67 ± 1.61	21.87 ± 0.94
min–max	15.90–19.80	16.60–36.10	20.20–22.40	16.60–36.10	16.40–37.60

Table A2. *Cont.*

	TWINSPAN Group				
	1	**2**	**3**	**4**	**5**
bio16 (kg/m^2)					
mean ± SE	305.74 ± 14.9	441.85 ± 15.42	351.6 ± 18.67	430.73 ± 20.77	424.94 ± 15.27
min–max	279–405.7	339.9–524.4	323.8–406.6	343–675.3	299.1–619.7
bio17 (kg/m^2)					
mean ± SE	193.66 ± 9.79	251.63 ± 14.65	210.55 ± 6.47	237.29 ± 13.50	251.38 ± 10.77
min–max	173.10–251.50	171.90–357.90	198.30–227.50	171.9–346.70	149.80–367.00
bio18 (kg/m^2)					
mean ± SE	283.76 ± 4.78	267.39 ± 17.79	347.05 ± 16.07	251.72 ± 17.43	304.32 ± 12.03
min–max	272.00–311.80	171.90–372.80	320.80–393.90	171.90–363.70	149.80–398.80
bio19 (kg/m^2)					
mean ± SE	209.61 ± 12.13	340.66 ± 11.69	219.98 ± 7.28	331.24 ± 12.60	304.98 ± 11.97
min–max	186.70–285.30	246.40–400.10	208.80–240.4	252.40–469.50	199.00–438.20

Appendix C

Table A3. Results of Mann–Whitney pairwise post hoc tests; significant differences between TWINSPAN group pairs are marked with an asterisk (* $p < 0.05$, ** $p < 0.001$) (for abbreviations, see Table 5).

Environmental Variable	TWINSPAN Group Pairs Compared									
	1–2	**1–3**	**1–4**	**1–5**	**2–3**	**2–4**	**2–5**	**3–4**	**3–5**	**4–5**
T								*		
pH						*				
TSS	*		*	*	*			*	*	
TALK	*		*	*						
DO				*	*			*	*	
BOD	*		*	**	*			*	*	
NH_4^+	*			*	*			*	*	
NO_2^-	*		*		*			*		
NO_3^-										*
N_{tot}			*					*		*
PO_4^{3-}	**	*	**	*	*		**	*	*	*
P_{tot}	**	*	**	*	*		*	*	*	
ALT	*	*							*	
DFS			*		*	*				*
CA	*			*	*			*	*	
bio1		*			*			*	*	*
bio2				*						
bio3							*		*	
bio4	*	*	*	*						
bio5		*			*			*	*	*

Table A3. *Cont.*

Environmental Variable	TWINSPAN Group Pairs Compared									
	1–2	1–3	1–4	1–5	2–3	2–4	2–5	3–4	3–5	4–5
bio6		*			*			*	*	*
bio7	*	*		*						
bio8	**		**	*	*			*	*	*
bio9		*	*		*			*	*	*
bio10		*			*			*	*	*
bio11		*			*			*	*	*
bio12	**	*	*	**						
bio13	**	*	**	**	*			*		
bio14				*						
bio15	*	*	*	*						
bio16	**	*	*	**	*			*		
bio17	*		*	*						
bio18		*								*
bio19	**		**	**	*			*	*	

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Table S1(a): Cover and abundance of the species at each surveyed locality. DIN-CON—Dinaric Ecoregion, Continental Subecoregion, DIN-MED—Dinaric Ecoregion, Continental Subecoregion, PAN—Pannonian Ecoregion.

				Marchantiophyta									Bryophyta																																																										
site id	watercourse	(sub) ecoregion	TWINSPAN group	Apo end	Chi pal	Chi pol	Con sal	Jun atr	Lop bid	Mar pol	Pel nes	Ric flu	Bar ung	Bra mil	Bra riv	Bra rut	Bra sal	Bry dic	Bry rud	Cal cus	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Dic var	Did fal	Did ins	Did lur	Did spa	Did top	Dre adu	Euc ver	Fis adi	Fis arn	Fis bry	Fis cra	Fis fon	Fis pus	Fis tax	Fon ant	Fon hyp	Fun hyg	Gym aer	Hyg flu	Hyg hum	Hyg ten	Hyg var	Hyg lur	Hyp cup	Lep rip	Mni mar	Mni spi	Oxy hia	Oxy sch	Oxy spe	Pal com	Pal fal	Phi mar	Pla ela	Pla ell	Pla und	Poh mel	Pty pse	Rhi pun	Rhy cur	Rhy ten	Rhy rip	Tha alo	Tri cri
1.	Delnički potok	DIN-CON	5							+											2a	1	2m	1																		1							1			1																	1		
2.	Kupa	DIN-CON	5																		3	2m	2m															1												2m																			2a		
3.	Kupa	DIN-CON	5																		3	2m	2m	+																		+																											2a		
4.	Kupa	DIN-CON	5	+						+												2m	1																			2m										2a							2m										1		
5.	Korana	DIN-CON	2	+																												2a		1										1	1														2m										2a		
6.	Korana	DIN-CON	2	1																	1		2m	2m								2b						1																															2b		
7.	Trepča	PAN	5																				2b																2b			2b										2a																			2a		
8.	Šumetlica	PAN	3																																					1																													1		
9.	Bregana	DIN-CON	5																					2m														2m				2m										1																	2m		
10.	Dretulja	DIN-CON	5			+									+						2a			2a																																							+						4		
11.	Jaruga 2	DIN-MED	4	3																				2a																																													2a		
12.	Kupčina	DIN-CON	5	+						+												+		+														1				+							+			2m																	1		
13.	Velika rijeka	PAN	3													1								1																																	r														
14.	Rudarska Gradna	DIN-CON	3							+						1								1																																													2m		
15.	Slapnica	DIN-CON	5	+									+											+														1														+																	1		
16.	Una	DIN-CON	5	2b		2a			1												4	2m		2b																		2m																											2m		
17.	Krka 2	DIN-CON	5																			1																				2b										+																	3		
18.	Cetina	DIN-MED	4			2m															2m			1																																			3										+		
19.	Krupa	DIN-MED	4	3		4																		2m																		4																													
20.	Rumin	DIN-MED	4																																							2a																													
21.	Zrmanja	DIN-MED	2	2m				+														2a		2m				+				+		1				1																											1				2a		
22.	Vitunjčica	DIN-CON	5																		2b		2a																			2a										+																			
23.	Bistrica	DIN-CON	4																			2m		2a																		2b																											2a		
24.	Munjava	DIN-CON	5																				+																			1										2m																	2a		
25.	Butižnica	DIN-MED	2	1																	3			2a			+					2m						1				2b																											2a		
26.	Baščica	DIN-MED	2																			1										1						2m				2m																											2m		
27.	Curak	DIN-CON	5																		2b																																																2a		
28.	Curak	DIN-CON	2																			2a																						+																									2a		
29.	Butižnica	DIN-MED	5																																							2m																											+		
30.	Zvizda	DIN-MED	2	2m																		1		2a														+																															1		
31.	Zvizda	DIN-MED	4	+																		+		+																																															
32.	Ričica	DIN-CON	2	2a				1														2m	2m											2a	2m			2m				2m																								1				2a		
33.	Dubračina	DIN-MED	4																			2a		2m																		1																											2m		
34.	Butižnica	DIN-MED	4					1																1																		3																	1										1		
35.	Šumetlica	PAN	3				1			+					2m																									+								+										+											+		
36.	Pazinčica	DIN-MED	5																			1	2b							1								2m														1																	3	2m	
37.	Jadro	DIN-MED	5	+																	+	1	2a	1														2b				1																											2a		
38.	Žrnovnica	DIN-MED	5																		3			2a																		2m										2b																	2a		
39.	Krčić	DIN-MED	4																		2a			1																																													2a		
40.	Došnica	DIN-MED	2	+		+																		2m								2m						+						+															2m						1								
41.	Petrinjčica	PAN	1			1	+			+	+														2m	2m														2m	+						+					2m			+		+							+	+				1		
42.	Golinja	PAN	1		+		2m				2a					2m								2m																		2a										2m			+								+	+		1	+			2m		
43.	Kremešnica	PAN	1			1																				1														1		2m							+			2m			+											1				2m		
44.	Kravarščica	PAN	1		1		1				1													1																	1								+		r	1			1		+				+		+	+							
45.	Roženica	PAN	1		1						1																								+																r				1									+	1						
46.	Trepča	PAN	5																				1																2a				2m									2m																			
47.	Trepča	PAN	5																				2b																1			1										2a														+				1		
48.	Glina	PAN	5							+														+																		+										3																	2b		
49.	Korana	DIN-CON	5							1					1						2b	1	2m	2a				+										2a				1		+											+														2b	+	
50.	Korana	DIN-CON	2	1																														3																								2a							2m						
51.	Brusovača	PAN	4			+																																		1		2m				+						+																			
52.	Slunjčica	DIN-CON	4	1		1															3	1	2m	4																																															
53.	Zagorska Mrežnica	DIN-CON	2														2m			2b		4											2m																1																						
54.	Dobra	DIN-CON	5	1		1				+					+					+		1	1	1														+				2m										1			+								+		1				2m		
55.	Ribnjak	DIN-CON	4	+		2a															1	1		1																		2m																	1						1				2m		
56.	Kupa	DIN-CON	5			+		1		+					2m	1				+	2a	2m	2a	2m	1	1		1			1							1				2m								2m									1										2a		
57.	Kupa	DIN-CON	5	+		2m	+	+		+						+					2b	2m	2m	2a	1			+			+							1																					2a						+	+	+	+	2b		

Table S1(a). *Cont.*

site id	watercourse	(sub) ecoregion	TWINSPAN group	Vascular helophytes																																						Vascular hydrophytes					Macroalgae																		
				Agr sto	Ali lan	Ali pla	Ber ere	Bul mar	Cal pal	Car acu	Dec ces	Gal pal	Hel rep	Iri pse	Jun art	Jun buf	Jun com	Jun inf	Lee ory	Lyc eur	Lys num	Lys vul	Lyt sal	Men aqu	Men lon	Myo sco	Myo aqu	Oen fis	Per dub	Poa pal	Ran rep	Rop amp	Ror syl	Sam val	Sch lac	Sci hol	Sci syl	Spa ere	Ver ana	Ver bec	Ver lon	Myr spi	Pot nod	Pot per	Ran tri	Stu pec	Aud her	Ban atr	Bat sp.	Cha lob	Cha con	Cha vul	Clad glo	Her flu	Hil riv	Lem flu	Lem fuc	Lem rig	Mou sp.	Nos sp.	Rhy hie	Spi sp.	Tri vir	Vau sp.	Zyg sp.
1.	Delnički potok	DIN-CON	5																																																														
2.	Kupa	DIN-CON	5																																							1	2a								2m					1					1				
3.	Kupa	DIN-CON	5																																								+	+		+																			
4.	Kupa	DIN-CON	5	+																																																													
5.	Korana	DIN-CON	2																																																	+													
6.	Korana	DIN-CON	2	+																																																													
7.	Trepča	PAN	5																																																														
8.	Šumetlica	PAN	3																																																												2m	
9.	Bregana	DIN-CON	5																																																		4												
10.	Dretulja	DIN-CON	5																																																														
11.	Jaruga 2	DIN-MED	4		1		+														+	+	1											r	1																														
12.	Kupčina	DIN-CON	5																																																														
13.	Velika rijeka	PAN	3																				+	+					+																																				
14.	Rudarska Gradna	DIN-CON	3	1												+													1				+							1													3												
15.	Slapnica	DIN-CON	5																																																														
16.	Una	DIN-CON	5																																																									2b				2a	
17.	Krka 2	DIN-CON	5																																																														
18.	Cetina	DIN-MED	4				1																	1	2m	1																																	1					
19.	Krupa	DIN-MED	4																																																														
20.	Rumin	DIN-MED	4	1			2m																					2m																																					
21.	Zrmanja	DIN-MED	2																																																														
22.	Vitunjčica	DIN-CON	5																																		+						1																					
23.	Bistrica	DIN-CON	4																					+														+	+						+																				
24.	Munjava	DIN-CON	5	+																																																													
25.	Butižnica	DIN-MED	2																																												+	1	+							2m										
26.	Baščica	DIN-MED	2					2m																											+	4			r																										
27.	Curak	DIN-CON	5																																													+						1	1			1				2a			
28.	Curak	DIN-CON	2																																																											+			
29.	Butižnica	DIN-MED	5				1																																									+					1				1								
30.	Zvizda	DIN-MED	2	+											2m													r								1													1			2a													
31.	Zvizda	DIN-MED	4																																	2b													2a																	
32.	Ričica	DIN-CON	2																																																														
33.	Dubračina	DIN-MED	4	+		+			+		2m			1	+					+	1	+	+	+							1	3	+		+		+																												
34.	Butižnica	DIN-MED	4				1																	1																																								2m	
35.	Šumetlica	PAN	3																																			+																											
36.	Pazinčica	DIN-MED	5																																																														
37.	Jadro	DIN-MED	5																																																		5												
38.	Žrnovnica	DIN-MED	5																																																		3												
39.	Krčić	DIN-MED	4	4																								4					2m						2m						2m																				
40.	Došnica	DIN-MED	2											r																																																			
41.	Petrinjčica	PAN	1																																																			1											
42.	Golinja	PAN	1																																																														
43.	Kremešnica	PAN	1			+													1				+																																					2a				
44.	Kravaršćica	PAN	1																																																														
45.	Roženica	PAN	1																																																														
46.	Trepča	PAN	5																																								1																					2a	2a	
47.	Trepča	PAN	5																																																		4												
48.	Glina	PAN	5																																																											2b				
49.	Korana	DIN-CON	5	3						1	+	+								+			+	1			+																									1							1			1			1
50.	Korana	DIN-CON	2	1																																																													
51.	Brusovača	PAN	4	+																+			+	+																																									
52.	Slunjčica	DIN-CON	4				2b		1				2a		+									2b													1	+																											
53.	Zagorska Mrežnica	DIN-CON	2																											2b											2m																										
54.	Dobra	DIN-CON	5																																										1								2b												
55.	Ribnjak	DIN-CON	4																					+																					+																				
56.	Kupa	DIN-CON	5	+							+				+																																+						+			+									
57.	Kupa	DIN-CON	5																																																		2m	2m								2m			

Table S1(a). *Cont.*

site id	watercourse	(sub) ecoregion	TWINSPAN group	Marchantiophyta									Bryophyta																								
				Apo end	Chi pal	Chi pol	Con sal	Jun atr	Lop bid	Mar pol	Pel nes	Ric flu	Bar ung	Bra mil	Bra riv	Bra rut	Bra sal	Bry dic	Bry rud	Cal cus	Cin aqu	Cin fon	Cin rip	Cra fil	Dic fla	Dic pel	Dic var	Did fal	Did ins	Did lur	Did spa	Did top	Dre adu	Euc ver	Fis adi	Fis arn	Fis bry
58.	Kupica	DIN-CON	5	+		2m															3	1	2b						+								
59.	Curak	DIN-CON	5	+			+			+					+					+	2m	1	+	2m	1			1			+						
60.	Čabranka	DIN-CON	5	1		2m				1					1							1		2m		+		1									
61.	Velika Belica	DIN-CON	2	2m			1	2a		+										+		1		+				+						+			
62.	Čedanj	DIN-CON	1			1	+	2m					+	+	1	+			+				+	+	1	1											
63.	Rječina	DIN-MED	5												1						2b	2a	2m	1													
64.	Rječina	DIN-MED	5												1						2b	2a	1	2m													
65.	Joševica	DIN-CON	4	2m	2m					1														2a													
66.	Vojskova	DIN-MED	4			2a															2m																
67.	Kobilica	DIN-MED	2	2m						+											+		+	2m								1					
68.	Zrmanja	DIN-MED	2															+						1								2m		2a			
69.	Ričica	DIN-CON	2	2m				+				+										2m	1	1										+		2m	
70.	Zrmanja	DIN-MED	2	1																+		1		+			+										
71.	Krupa	DIN-MED	5	2m	2a					2m											3	1		2m										+			
72.	Bribišnica	DIN-MED	5																		1	1	+							+		1	1				
73.	Krka	DIN-MED	4			+															1																
74.	Ljubina	PAN	1		+		1																														+
75.	Vučjak	PAN	1				1									2m								+													
76.	Bistrica	DIN-CON	5												2m						4	3	2a	+													

site id	watercourse	Bryophyta (cont.)																																	
		Fis cra	Fis fon	Fis pus	Fis tax	Fon ant	Fon hyp	Fun hyg	Gym aer	Hyg flu	Hyg hum	Hyg ten	Hyg var	Hyg lur	Hyp cup	Lep rip	Mni mar	Mni spi	Oxy hia	Oxy sch	Oxy spe	Pal com	Pal fal	Phi mar	Pla ela	Pla ell	Pla und	Poh mel	Pty pse	Rhi pun	Rhy cur	Rhy ten	Rhy rip	Tha alo	Tri cri
58.	Kupica	+				+											+		+		+		2m				+					+	2b	1	
59.	Curak	+										+															+						2a	+	
60.	Čabranka	2m												1			1									1						+	2m		
61.	Velika Belica	+				+								2a										+				+	2a				1		+
62.	Čedanj	+																	+								+						2m		
63.	Rječina																																2m		
64.	Rječina																																2m		
65.	Joševica					2a																													
66.	Vojskova					1																											1		
67.	Kobilica	+				2m		1																					1				1		
68.	Zrmanja	+																											1				+		
69.	Ričica	2m				1																							+				2m		
70.	Zrmanja				+	2a														1			1					+	+				2a		
71.	Krupa	1				3																											2a		
72.	Bribišnica	2b																															1		
73.	Krka					2b										+																	+		
74.	Ljubina				+													+	+								+						+		
75.	Vučjak			1	+														+							+						+	2a	+	
76.	Bistrica	1														1																	1		

Table S1(a). *Cont.*

Site id	watercourse	(sub) ecoregion	TWINSPAN group	Vascular helophytes																																						Vascular hydrophytes					Macroalgae																		
				Agr sto	Ali lan	Ali pla	Ber ere	Bul mar	Cal pal	Car acu	Dec ces	Gal pal	Hel rep	Iri pse	Jun art	Jun buf	Jun com	Jun inf	Lee ory	Lyc eur	Lys num	Lys vul	Lyt sal	Men aqu	Men lon	Myo sco	Myo aqu	Oen fis	Per dub	Poa pal	Ran rep	Rop amp	Ror syl	Sam val	Sch lac	Sci hol	Sci syl	Spa ere	Ver ana	Ver bec	Ver lon	Myr spi	Pot nod	Pot per	Ran tri	Stu pec	Aud her	Ban atr	Bat sp.	Cha lob	Cha con	Cha vul	Clad glo	Her flu	Hil riv	Lem flu	Lem fuc	Lem rig	Mou sp.	Nos sp.	Rhy hie	Spi sp.	Tri vir	Vau sp.	Zyg sp.
58.	Kupica	DIN-CON	5								1																																							+			+		1										
59.	Curak	DIN-CON	5																																																														
60.	Čabranka	DIN-CON	5																																																														
61.	Velika Belica	DIN-CON	2	1							+						+								+																												1							2m		2b			
62.	Čedanj	DIN-CON	1																																																			1											2m
63.	Rječina	DIN-MED	5																																																		4												
64.	Rječina	DIN-MED	5																																																														
65.	Joševica	DIN-CON	4	1														+						1														2a																											+
66.	Vojskova	DIN-MED	4				2m																																														2a	+						2m					
67.	Kobilica	DIN-MED	2																																	r																	+									+			
68.	Zrmanja	DIN-MED	2																																																	+													
69.	Ričica	DIN-CON	2		1		1																	2m				2m																					2m																
70.	Zrmanja	DIN-MED	2																																																		1												
71.	Krupa	DIN-MED	5				2m																																																									+	
72.	Bribišnica	DIN-MED	5												2m								+										2m																																
73.	Krka	DIN-MED	4				2a																	1														2m															1											+	+
74.	Ljubina	PAN	1																																																														
75.	Vučjak	PAN	1																																																														
76.	Bistrica	DIN-CON	5	+			2a																																														2a												

Species and genera abbreviations:

Apo end	*Apopellia endiviifolia* (Dicks.) Nebel & D.Quandt
Chi pal	*Chiloscyphus pallescens* (Ehrh. ex Hoffm.) Dumort.
Chi pol	*Chiloscyphus polyanthos* (L.) Corda
Con sal	*Conocephalum salebrosum* Szweyk., Buczk. & Odrzyk.
Jun atr	*Jungermannia atrovirens* Dumort.
Lop bid	*Lophocolea bidentata* (L.) Dumort.
Mar pol	*Marchantia polymorpha* L.
Pel nes	*Pellia neesiana* (Gottsche) Limpr.
Ric flu	*Riccia fluitans* L.
Bar ung	*Barbula unguiculata* Hedw.
Bra mil	*Brachythecium mildeanum* (Schimp.) Schimp.
Bra riv	*Brachythecium rivulare* Schimp.
Bra rut	*Brachythecium rutabulum* (Hedw.) Schimp.
Bra sal	*Brachythecium salebrosum* (Hoffm. ex F. Weber et D. Mohr) Schimp.
Bry dic	*Bryum dichotomum* Hedw.
Bry rud	*Bryum ruderale* Crundw. & Nyholm
Cal cus	*Calliergonella cuspidata* (Hedw.) Loeske
Cin aqu	*Cinclidotus aquaticus* (Hedw.) Bruch et Schimp.
Cin fon	*Cinclidotus fontinaloides* (Hedw.) P. Beauv.
Cin rip	*Cinclidotus riparius* (Host ex Brid.) Arn.
Cra fil	*Cratoneuron filicinum* (Hedw.) Spruce
Dic fla	*Dichodontium flavescens* (Dicks.) Lindb.
Dic pel	*Dichodontium pellucidum* (Hedw.) Schimp.
Dic var	*Dicranella varia* (Hedw.) Schimp.
Did fal	*Didymodon fallax* (Hedw.) R. H. Zander
Did ins	*Didymodon insulanus* (De Not.) M. O. Hill
Did lur	*Didymodon luridus* Hornsch.
Did spa	*Didymodon spadiceus* (Mitt.) Limpr.
Did top	*Didymodon tophaceus* (Brid.) Lisa
Dre adu	*Drepanocladus aduncus* (Hedw.) Warnst.
Euc ver	*Eucladium verticillatum* (With.) Bruch & Schimp.
Fis adi	*Fissidens adianthoides* Hedw.
Fis arn	*Fissidens arnoldii* R. Ruthe
Fis bry	*Fissidens bryoides* Hedw.
Fis cra	*Fissidens crassipes* Wilson ex Bruch & Schimp.
Fis fon	*Fissidens fontanus* (Bach.Pyl.) Steud.
Fis pus	*Fissidens pusillus* (Wilson) Milde
Fis tax	*Fissidens taxifolius* Hedw.
Fon ant	*Fontinalis antipyretica* Hedw.
Fon hyp	*Fontinalis hypnoides* Hartm. var. *duriaei* (Schimp.) Kindb.
Fun hyg	*Funaria hygrometrica* Hedw.
Gym aer	*Gymnostomum aeruginosum* Sm.
Hyg flu	*Hygroamblystegium fluviatile* (Hedw.) Loeske
Hyg hum	*Hygroamblystegium humile* (P.Beauv.) Vanderp., Goffinet & Hedenäs
Hyg ten	*Hygroamblystegium tenax* (Hedw.) Jenn.
Hyg var	*Hygroamblystegium varium* (Hedw.) Mönk.
Hyg lur	*Hygrohypnum luridum* (Hedw.) Jenn.
Hyp cup	*Hypnum cupressiforme* Hedw.
Lep rip	*Leptodictyum riparium* (Hedw.) Warnst.
Mni mar	*Mnium marginatum* (Dicks.) P.Beauv.
Mni spi	*Mnium spinulosum* Bruch & Schimp.
Oxy hia	*Oxyrrhynchium hians* (Hedw.) Loeske
Oxy sch	*Oxyrrhynchium schleicheri* (R. Hedw.) Röll
Oxy spe	*Oxyrrhynchium speciosum* (Brid.) Warnst.
Pal com	*Palustriella commutata* (Hedw.) Ochyra
Pal fal	*Palustriella falcata* (Brid.) Hedenäs
Phi mar	*Philonotis marchica* (Hedw.) Brid.
Pla ela	*Plagiomnium elatum* (Bruch et Schimp.) T. J. Kop.
Pla ell	*Plagiomnium ellipticum* (Brid.) T. J. Kop.
Pla und	*Plagiomnium undulatum* (Hedw.) T. J. Kop.
Poh mel	*Pohlia melanodon* (Brid.) A. J. Shaw
Pty pse	*Ptychostomum pseudotriquetrum* (Hedw.) J.R.Spence & H.P.Ramsay ex Holyoak & N.Pedersen
Rhi pun	*Rhizomnium punctatum* (Hedw.) T. J. Kop.
Rhy cur	*Rhynchostegiella curviseta* (Brid.) Limpr.
Rhy ten	*Rhynchostegiella teneriffae* (Mont.) Dirkse et Bouman
Rhy rip	*Rhynchostegium riparioides* (Hedw.) Cardot
Tha alo	*Thamnobryum alopecurum* (Hedw.) Gangulee
Tri cri	*Trichostomum crispulum* Bruch
Agr sto	*Agrostis stolonifera* L.
Ali lan	*Alisma lanceolatum* With.
Ali pla	*Alisma plantago-aquatica* L.
Ber ere	*Berula erecta* (Huds.) Coville
Bul mar	*Bolboschoenus maritimus* (L.) Palla
Cal pal	*Caltha palustris* L.
Car acu	*Carex acuta* L.
Dec ces	*Deschampsia cespitosa* (L.) P. Beauv.
Gal pal	*Galium palustre* L.
Hel rep	*Helosciadium repens* (Jacq.) W. D. J. Koch
Iri pse	*Iris pseudacorus* L.
Jun art	*Juncus articulatus* L.
Jun buf	*Juncus buffonius* L.
Jun com	*Juncus compressus* Jacq.
Jun inf	*Juncus inflexus* L.
Lee ory	*Leersia oryzoides* (L.) Sw.
Lyc eur	*Lycopus europaeus* L.
Lys num	*Lysimachia nummularia* L.
Lys vul	*Lysimachia vulgaris* L.
Lyt sal	*Lythrum salicaria* L.
Men aqu	*Mentha aquatica* L.
Men lon	*Mentha longifolia* (L.) L.
Myo sco	*Myosotis scorpioides* L.
Myo aqu	*Myosoton aquaticum* (L.) Moench
Oen fis	*Oenanthe fistulosa* L.
Per dub	*Persicaria dubia* (Stein) Fourr.
Poa pal	*Poa palustris* L.
Ran rep	*Ranunculus repens* L.
Rop amp	*Rorippa amphibia* (L.) Besser
Ror syl	*Rorippa sylvestris* (L.) Besser
Sam val	*Samolus valerandi* L.
Sch lac	*Schoenoplectus lacustris* (L.) Palla
Sci hol	*Scirpoides holoschoenus* (L.) Soják
Sci syl	*Scirpus sylvaticus* L.
Spa ere	*Sparganium erectum* L.
Ver ana	*Veronica anagallis-aquatica* L.
Ver bec	*Veronica beccabunga* L.
Ver lon	*Veronica longifolia* L.
Myr spi	*Myriophyllum spicatum* L.
Pot nod	*Potamogeton nodosus* Poir.
Pot per	*Potamogeton perfoliatus* L.
Ran tri	*Ranunculus trichophyllus* Chaix
Stu pec	*Stuckenia pectinata* (L.) Börner
Aud her	*Audouinella hermannii* (Roth) Duby
Ban atr	*Bangia atropurpurea* (Mertens ex Roth) C. Agardh
Bat sp.	*Batrachospermum* Roth sp.
Cha lob	*Chaetophora lobata* Schrank
Cha con	*Chara contraria* A.Braun ex Kützing
Cha vul	*Chara vulgaris* L.
Clad glo	*Cladophora glomerata* (Linnaeus) Kützing
Her flu	*Heribaudiella fluviatilis* (Areschoug) Sve delius
Hil riv	*Hildenbrandia rivularis* (Liebmann) J.Agardh
Lem flu	*Lemanea fluviatilis* (Linnaeus) C.Agardh
Lem fuc	*Lemanea fucina* Bory
Lem rig	*Lemanea rigida* (Sirodot) De Toni
Mou sp.	*Mougeotia* C.Agardh sp.
Nos sp.	*Nostoc* Vaucher ex Bornet & Flahault sp.
Rhy hie	*Rhizoclonium hieroglyphicum* (C.Agardh) Kützing
Spi sp.	*Spirogyra* Link. sp.
Tri vir	*Tribonema viridae* Pascher
Vau sp.	*Vaucheria* A.P.de Candolle sp.
Zyg sp.	*Zygnema* C.Agardh sp.

Table S1(b): Surveyed sites with coordinates in WGS84 (DIN-CON—Dinaric Ecoregion, Continental Subecoregion, DIN-MED—Dinaric Ecoregion, Continental Subecoregion, PAN—Pannonian Ecoregion).

Site id	Watercourse	(sub) ecoregion	X_WGS_84	Y_WGS_84
1.	Delnički potok	DIN-CON	14.850197	45.439065
2.	Kupa	DIN-CON	15.249773	45.456294
3.	Kupa	DIN-CON	15.356800	45.645632
4.	Kupa	DIN-CON	15.075857	45.483644
5.	Korana	DIN-CON	15.617522	44.925282
6.	Korana	DIN-CON	15.595184	45.391685
7.	Trepča	PAN	15.910178	45.461265
8.	Šumetlica	PAN	17.376298	45.364489
9.	Bregana	DIN-CON	15.675482	45.841072
10.	Dretulja	DIN-CON	15.343407	45.074827
11.	Jaruga 2	DIN-MED	15.330390	44.263055
12.	Kupčina	DIN-CON	15.451233	45.721521
13.	Velika rijeka	PAN	17.860565	45.482297
14.	Rudarska Gradna	DIN-CON	15.666957	45.762693
15.	Slapnica	DIN-CON	15.501507	45.688227
16.	Una	DIN-CON	16.105968	44.402052
17.	Krka 2	DIN-CON	16.145108	44.420621
18.	Cetina	DIN-MED	16.428127	43.969528
19.	Krupa	DIN-MED	15.886942	44.191167
20.	Rumin	DIN-MED	16.648155	43.776172
21.	Zrmanja	DIN-MED	16.033380	44.092277
22.	Vitunjčica	DIN-CON	15.163285	45.283566
23.	Bistrica	DIN-CON	15.286383	45.285326
24.	Munjava	DIN-CON	15.285822	45.187190
25.	Butižnica	DIN-MED	16.220142	44.089207
26.	Baščica	DIN-MED	15.438921	44.219624
27.	Curak	DIN-CON	14.892896	45.427254
28.	Curak	DIN-CON	14.876561	45.445632
29.	Butižnica	DIN-MED	16.226322	44.109590
30.	Zvizda	DIN-MED	16.890764	43.421739
31.	Zvizda	DIN-MED	16.891177	43.421104
32.	Ričica	DIN-CON	15.687133	44.365191
33.	Dubračina	DIN-MED	14.675960	45.219671
34.	Butižnica	DIN-MED	16.220820	44.096091
35.	Šumetlica	PAN	17.383172	45.346589
36.	Pazinčica	DIN-MED - ISTRA	13.929240	45.240175
37.	Jadro	DIN-MED	16.490370	43.534161
38.	Žrnovnica	DIN-MED	16.542296	43.516203
39.	Krčić	DIN-MED	16.319235	44.027128
40.	Došnica	DIN-MED	16.205566	44.091775
41.	Petrinjčica	PAN	16.287826	45.272807
42.	Golinja	PAN	16.016777	45.477538

Site id	Watercourse	(sub) ecoregion	X_WGS_84	Y_WGS_84
43.	Kremešnica	PAN	15.873438	45.526513
44.	Kravaršćica	PAN	15.907058	45.538579
45.	Roženica	PAN	15.939146	45.518345
46.	Trepča	PAN	15.910606	45.461270
47.	Trepča	PAN	15.909916	45.461313
48.	Glina	PAN	15.769945	45.210090
49.	Korana	DIN-CON	15.545735	45.252514
50.	Korana	DIN-CON	15.618415	44.925865
51.	Brusovača	PAN	15.758529	45.256124
52.	Slunjčica	DIN-CON	15.589664	45.079564
53.	Zagorska Mrežnica	DIN-CON	15.274797	45.224672
54.	Dobra	DIN-CON	15.105964	45.357840
55.	Ribnjak	DIN-CON	15.113185	45.341161
56.	Kupa	DIN-CON	14.774885	45.507333
57.	Kupa	DIN-CON	14.700611	45.504959
58.	Kupica	DIN-CON	14.856837	45.464067
59.	Curak	DIN-CON	14.857948	45.449164
60.	Čabranka	DIN-CON	14.697270	45.526015
61.	Velika Belica	DIN-CON	14.805064	45.476384
62.	Čedanj	DIN-CON	14.90866	45.476094
63.	Rječina	DIN-MED	14.449641	45.378638
64.	Rječina	DIN-MED	14.418386	45.404192
65.	Joševica	DIN-CON	16.108708	44.417565
66.	Vojskova	DIN-MED	16.631926	43.757003
67.	Kobilica	DIN-MED	16.084189	44.125411
68.	Zrmanja	DIN-MED	15.940022	44.107609
69.	Ričica	DIN-CON	15.747437	44.341835
70.	Zrmanja	DIN-MED	16.071088	44.146896
71.	Krupa	DIN-MED	15.909381	44.192752
72.	Bribišnica	DIN-MED	15.799097	43.890532
73.	Krka	DIN-MED	16.094719	44.010631
74.	Ljubina	PAN	16.285494	45.086497
75.	Vučjak	PAN	17.657635	45.303222
76.	Bistrica	DIN-CON	15.286428	45.284303

5. RASPRAVA

Istraživanja provedena u svrhu izrade ovog doktorskog rada predstavljaju prva opsežna i sistematizirana istraživanja flore, vegetacije i ekologije mahovina kopnenih voda u Hrvatskoj te su jedna od rijetkih do sada provedenih na području jugoistočne Europe. Rezultati istraživanja, objavljeni u pet znanstvenih radova, ispunili su sve istraživačke ciljeve i potvrdili hipoteze postavljene unutar ovog doktorskog rada.

Istraživanje flore mahovina tekućica i stajaćica i njihovih obalnih zona pružilo je uvid u raznolikost i distribuciju akvatičkih i semiakvatičkih mahovina u Hrvatskoj (**Rad 1–3**) te je omogućilo analizu sastava mahovinske flore prema flornim elementima, životnim oblicima i životnim strategijama (**Rad 1**). Mahovine su zabilježene na 228 (29 %) od ukupno 786 istraživanih lokacija, dok je prosječan broj vrsta po lokaciji iznosio 4,17. Zabilježene su 83 vrste, što čini 12 % ukupnog broja do sada poznatih vrsta mahovina u flori Hrvatske (Alegro i Šegota 2022). Prave mahovine (Bryophyta) bile su zastupljenije (68 vrsta) u odnosu na jetrenjarke (Marchantiophyta) (15 vrsta), što su pokazala i ranija istraživanja mahovina kopnenih voda provedena u Europi (Muotka i Virtanen 1995; Scarlett i O'Hare 2006; Gecheva i sur. 2010; Ceschin i sur. 2012b; Vieira i sur. 2012a). Naime, za razliku od pravih mahovina, jetrenjarke slabije podnose mehanički stres uslijed jakog strujanja vode, osjetljivije su na isušivanje, a loše podnose i duže periode poplavljivanja pa samo rijetke vrste nastanjuju same tokove dok većina dolazi u zoni prskanja, odnosno na obalama (Gimingham i Birse 1957; Kimmerer i Allen. 1982; Vitt i Glime 1984). Listatsta jetrenjarka *Chiloscyphus polyanthos* bila je tako jedina česta vrsta u vodenim tokovima u ovom istraživanju (**Rad 1**), dok su talozne vrste poput vrsta *Conocephalum salebrosum*, *Lunularia cruciata*, *Pellia neesiana*, *Apopellia endiviifolia* i *Marchantia polymorpha* često bilježene na obalama istraživanih kopnenih voda.

Ovo istraživanje također je utvrdilo da je u flori mahovina kopnenih voda Hrvatske zastupljeno 10 redova, 21 porodica, odnosno 43 roda mahovina. Najzastupljenije porodice na razini Hrvatske, s obzirom na broj vrsta, bile su Pottiaceae, Amblystegiaceae, Brachytheciaceae, Fissidentaceae, Ricciaceae i Bryaceae, što je očekivano s obzirom da se radi o porodicama koje uključuju veći broj akvatičkih i semiakvatičkih vrsta (Glime 2020), a slične rezultate dala su i istraživanja mahovina vodenih tokova u Italiji (Ceschin i sur. 2012b) i Portugalu (Vieira i sur. 2012a). Nadalje, rodovi s najvećim brojem zabilježenih vrsta u ovom istraživanju (**Rad 1**) bili su *Fissidens*, *Bryum*, *Didymodon* i *Riccia*, dok su najučestalije vrste bile *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Leptodyctium riparium* i *Cratoneuron filicinum*, što je u skladu s rezultatima istraživanja mahovina vodenih tokova, primjerice, u Mađarskoj (Papp i Rajczy 1998a), Italiji (Ceschin i sur. 2012b), Bugarskoj (Gecheva i sur. 2012), Njemačkoj (Tremp i sur. 2012), Poljskoj (Jusik i sur. 2015) i Engleskoj (Scarlett i O'Hare 2006). Većina zabilježenih vrsta imala je nisku učestalost, kao i nisku srednju pokrovnost na istraživanim lokacijama, što je također zabilježeno u drugim istraživanjima (Ceschin i sur. 2015). Naime, preko 40 % vrsta zabilježeno je na do tri, odnosno 70 % na do 10 istraživanih lokaliteta. Nadalje, srednja pokrovnost čak 83 % (69) vrsta bila je manja od 5 %, dok je prelazila 10 % za svega tri vrste – *Hymenostylium recurvirostrum* i *Palustriella commutata*, sedrotvorne vrste koje uglavnom dolaze na slapištima (Zechmeister i Mucina 1994; Tomaselli i sur. 2011; Mucina i sur. 2016) te *Cinclidotus aquaticus*, vrstu karakterističnu za izvorišne dijelove i male brze tekućice (Kochjarová i sur. 2007; Sérgio i sur. 2007; Ceschin i sur. 2012a). Navedena staništa su posebice povoljna za akvatičke mahovine te ovdje one tvore bogate zajednice s visokom ukupnom pokrovnosti zahvaljujući brojim anatomskim i fiziološkim prilagodbama koje im omogućuju nastanjivanje i održavanje u surovim uvjetima, u hladnim, brzim vodama, na krupnim, stjenovitim sedimentima, koji uglavnom isključuju pojavljivanje vaskularnih predstavnika makrofita (Suren 1996; Tremp i sur. 2012). Također, mahovine imaju skromnije zahtjeve spram količine dostupnih hranjivih tvari, što im dodatno osigurava uspjeh u oligotrofnim izvorišnim dijelovima vodotoka (Vanderpoorten i Goffinet 2009).

Analiza distribucije akvatičkih i semiakvatičkih mahovina utvrdila je razlike u sastavu vrsta i raznolikosti mahovina između pojedinih ekoregija koje se razlikuju na temelju hidroloških, geoloških i klimatskih značajki. Dinaridska ekoregija je podržavala veću raznolikost mahovina u svojim kopnenim vodama (70 vrsta) u odnosu na Panonsku ekoregiju (57 vrsta). Ove ekoregije dijelile su 53 % (44 vrste) od ukupno 83 zabilježene vrste, dok je njih 26 bilo prisutno isključivo u Dinaridskoj, a 13 isključivo u Panonskoj ekoregiji. Vrste zabilježene samo u Dinaridskoj ekoregiji, kao što su *Didymodon tophaceus*, *D. spadiceus*, *Hygrohypnum luridum*, *Hymenostylium recurviristrum*, *Philonotis marchica*, *Rhynchostegiella cruviseta* i *R. teneriffae* bilježene su na većem i stabilnijem supstratu, u bistrim, hladnim i dobro oksigeniranim vodama krških rijeka, koje su karakteristične za ovu regiju. Nadalje, visok udio vrsta iz porodice Pottiaceae također odražava prisutnost pogodnih slatkovodnih staništa unutar ove ekoregije. Među njima su najučestaliji bili reofiti iz roda *Cinclidotus*, već spomenuta sedrotvorna vrsta *Dydimodon tophaceus* te druge vrste roda *Didymodon*, koje su nastanjivale periodički plavljene niše i zone prskanja vode duž krških rijeka. S druge strane, vrste zabilježene samo u Panonskoj ekoregiji, poput *Leptobryum pyriforme*, *Pellia neesiana*, *Physcomitrium eurystomum*, *Ph.*

sphaericum, *Riccia frostii*, *R. glauca* i *R. rhenana*, bilježene su uglavnom na vlažnom i sitnom supstratu na rubovima stajaćica i tekućica, uz iznimke poput saksikolne (vezan za stijene) vrste *Fissidens pusillus* ili plutajućih jetrenjarki – vrste *Ricciocarpos natans* i akvatičkih formi vrsta *Riccia fluitans* i *R. rhenana*, karakterističnih za eutrofne, gotovo stajaće, nizinske tekućice i kanale.

Bogatstvo Dinaridske ekoregije s obzirom na povoljna staništa za akvatičke i semiakvatičke vrste očitovalo se i u većem bogatstvu vrsta po istraživanom lokalitetu. Ono je u Dinaridskoj ekoregiji iznosilo 4,6 vrste po lokalitetu, dok je u Panonskoj bilo 3,4 vrste po lokalitetu. Nadalje, unutar Dinaridske ekoregije, bogatija je bila Kontinentalna subekoregija s ukupno 65 zabilježenih vrsta i prosječnim bogatstvom od 5,9 vrsta po lokalitetu, dok je u Mediteranskoj zabilježeno 40 vrsta, odnosno prosječno 3,4 vrste po lokalitetu. Za usporedbu, Kontinentalna subekoregija najvećim dijelom odgovara regiji Mediteranskih planina prema okviru Europske okolišne stratifikacije (Metzger i sur. 2005), u kojoj je prosječno bogatstvo akvatičkih i semiakvatičkih vrsta mahovina iznosilo 4,5 vrste po lokalitetu (Vieira i sur. 2018), što je nešto niže u odnosu na rezultate za Kontinentalnu subekoregiju u Hrvatskoj.

Analiza flornih elemenata pokazala je da u mahovinskoj flori kopnenih voda Hrvatske dominiraju cirkumpolarni i europski elementi s obzirom na istočnu granicu pojavljivanja, odnosno tempratni elementi prema podjeli na glavne biome (Hill i Preston 1998). Isto je ustanovljeno primjerice za briofloru tekućica u centralnoj Italiji (Ceschin i sur. 2012b) te u mediteranskom dijelu Europe (Vieira i sur. 2018) te dobro odgovara biogeografskim značajkama istraživanog područja. Usporedba hrvatskih ekoregija i subekoregija ustanovila je značajna preklapanja u flornim elementima, ali i neke osobitosti pojedinih regija. Nizak udio mediteransko-atlantskih elemenata, kao i suboceanskih te odsustvo oceanskih elemenata u Panonskoj ekoregiji u odnosu na Dinaridsku ekoregiju, posebice njenu Kontinentalnu subekoregiju, u velikoj mjeri odgovara klimatskim ograničenjima za razvoj ovih mahovina u Panonskoj ekoregiji. Naime, Kontinentalnu subekoregiju karakterizira veća godišnja količina oborina i niže temperature tijekom najvlažnijeg kvartala (Karger i sur. 2017) što podrazumijeva vlažniju klimu koja pogoduje ovim elementima. Također, izostanak boreo-arktičkih i borealno-montanih te viši udio južno-tempratnih elementa u Mediteranskoj subekoregiji Dinaridske ekoregije odgovara klimatskim obilježjima ovoga područja za koje je uvelike karakteristična mediteranska klima, s višim temperaturama zraka i sušnim razdobljem ljeti.

Rezultati analize životnih oblika pokazali su da u flori mahovina kopnenih voda dominiraju vodene vrpčaste vrste (engl. *aquatic trailings*), koje su svojom građom najbolje prilagođene životu u tekućicama te najvećim dijelom odgovaraju kategoriji reofita (Dierßen 2001), odnosno fakultativnih akvatičkih vrsta (Vitt i Glime 1984). To su vrste poput *Chiloscyphus polyanthos, Cinclidotus aquaticus, C. fontinaloides, C. riparius, Fissidens fontanus, Fontinalis antipyretica* i *F. hypnoides* var. *duriaei*. Drugi najzastupljeniji životni oblik predstavljale su vrste koje rastu u čupercima (engl. *tufts*), koje nastanjuju mikrostaništa izložena sezonskim plavljenjima kao vrste *Ptychostomum pseudotriquetrum, Dichodontium flavescens, Didymodon tophaceues, Hymenostilium recurvirostrum* i *Philonotis marchica*. Kada se usporede ekoregije, može se uočiti prilična razlika u spektru životnih oblika. Dok u obje subekoregije Dinaridske ekoregije dominiraju vrpčaste vodene mahovine (npr. *Cinclidotus* spp.), u Panonskoj ekoregiji dominantni životni oblik čine mahovine koje rastu u grubim sagovima (engl. *rough mats*). Ova kategorija u Panonskoj ekoregiji uključuje vodene vrste kao što je *Leptodyctium riparium*, koja je ujedno i najučestalija vrsta u vodotocima Panonske ekoregije, zatim rjeđe bilježene vrste *Hygroamblystegium fluviatile* i *H. tenax*, ali i vrste koje nastanjuju obalna staništa zasjenjenih nizinskih vodotoka, kao što su *Brachythecium mildeanum, B. rivulare, B. rutabulum, Oxyrrhinchium hians* i *O. speciosum*. S druge strane, udio vrsta koje su bolje prilagođene životu u samim tokovima i jezerima, kao što su vodene vrpčaste mahovine i one koje rastu u glatkim prostirkama (engl. *smooth mats*) bio je niži, što dobro odražava značajke vodotoka Panonske ekoregije u kojima su mahovine ograničene na obalna staništa, rijetke veće supstrate u nizinskim tekućicama, a jedina istinski učestala vrsta s frekvencijom iznad 30 % je *Leptodyctium riparium*, koja je općenito jedna od rijetkih vrsta koje dolaze u donjim tokovima rijeka (Gecheva i sur. 2010). Ovome u prilog ide i veći udio solitarnih taloznih (engl. *solitary thalloid*) oblika jetrenjarki koje isto tako nastanjuju obale jezera i rijeka. Također, u Panonskoj ekoregiji dolazi nekoliko plutajućih lemnoidnih vrsta (engl. *lemnoids*) (*Ricciocarpos natans, Riccia fluitans* i *R. rhenana*), koje ovdje uglavnom nastanjuju stajaće vode eutrofnih kanala. Nadalje, udio vrsta koje žive u glatkim prostirkama (engl. *smooth mats*) bio je veći u obje Dinaridske subekoregije u odnosu na Panonsku, što također odražava veću pogodnost vodnih tijela Dinaridske ekoregije za nastanjivanje akvatičkih vrsta.

S obzirom na životne strategije, u flori mahovina kopnenih voda Hrvatske dominirale su perenijalne vrste (engl. *perennials*) i kolonisti (engl. *colonists*) sa životnim ciklusom od nekoliko godina, što je u skladu s činjenicom da su akvatičke mahovine uglavnom višegodišnje pleurokarpne vrste (Glime 2020) te da su vodene mahovinske zajednice karakterizirane uglavnom perenijalnim vrstama koje preferiraju stalne i brze tokove, dok su kolonisti karakteristični za dijelove uz obalu i emergentne pozicije (Vieira i sur. 2012b; Glime 2020).

Spektri životnih strategija akvatičkih i semiakvatičkih mahovina u hrvatskim ekoregijama i subekoregijama pokazuju značajna preklapanja, s najizraženijom razlikom u zastupljenosti kategorije jednogodišnjih sporadičnih vrsta (engl. *annual shuttle species*), koja je bila zastupljenija u Panonskoj ekoregiji. Ovoj kategoriji pripadaju male efemerne vrste čiji životni ciklus traje do godinu dana, a karakterizira ih i visok reproduktivni napor (engl. *reproductive effort*), prilikom čega se isključivo oslanjaju na seksualnu reprodukciju proizvodeći manji broj velikih, dugoživućih i otpornih spora (During 1979; Kürschner 2004). Ove vrste dolaze na blago položenim obalama tekućica i stajaćica, na sitnom, vlažnom supstratu u zoni koja ostaje neko vrijeme vlažna nakon povlačenja vode ljeti i u ranu jesen. Na nekim pogodnim staništima povoljni uvjeti za razvoj efemernih vrsta ne javljaju se svake godine, već samo tijekom suših godina, kada dolazi do značajnijeg povlačenja vode ili presušivanja vodnog tijela. U vrlo kratkom razdoblju, ponekad unutar svega nekoliko tjedana ili mjeseci, one uspijevaju završiti čitav životni ciklus, a to kratko razdoblje nije dovoljno dugo da bi došlo do kolonizacije drugih mahovina i vaskularnih biljaka s duljim životnim ciklusima (Furness i Hall 1981; Hugonnot 2005; Bijlsma i sur. 2012; Rothero 2012). Tijekom ovog istraživanja jednogodišnje sporadične mahovine (engl. *annual shuttle species*), poput vrsta *Physcomitrium patens*, *Ph. eurystomum, Ph. sphaericum*, *Riccia cavernosa*, *R. frostii*, *R. glauca* i *R. rhenana* bilježene vrlo rijetko (ukupno 12 lokaliteta) i to uglavnom na obalama i stajaćica i tekućica Panonske ekoregije, uz iznimku akumulacije Kruščica u Kontinentalnoj subekoregiji Dinaridske ekoregije (**Rad 1, 2**). U Panonskoj ekoregiji bilježene su na obalama kanala te malih i srednje velikih rijeka, koje su dobrim dijelom hidromorfološki značajno izmijenjene (kanaliziranje i produbljivanje korita, izgradnja nasipa) te su neke od njih klasificirane kao jako promijenjena vodna tijela (Europska komisija 2000; Vučković i sur. 2021). Također, pogodna staništa ove mahovine pronašle su i na obalama umjetnih ili jako promijenjenih stajaćica (ribnjaci, šljunčara, stari meandar velike rijeke) (**Rad 2**). Zanimljivo je da su upravo umjetna vodna tijela, kao što su šljunčare poslužila kao sekundarno stanište koje su efemerne vrste *Physcomitrium patens* i *Riccia cavernosa* nastanile nakon što je zabilježen pad u njihovim populacijama u dijelovima rijeke Rajne u Njemačkoj uslijed regulacije korita (Nebel i Philippi 2000, 2005). Imajući u vidu da je pojavljivanje efemernih mahovina relativno nepredvidivo, odnosno prostorno i vremenski izrazito dinamično, može se pretpostaviti da njihova distribucija ustanovljena ovim istraživanjem u Hrvatskoj nije konačna te da su navedene vrste češće, pogotovo s obzirom da su do sada uglavnom bilježene na antropogeno utjecanim vodnim tijelima.

Ovo istraživanje pružilo je značajan doprinos poznavanju raznolikosti mahovinske flore kopnenih voda Hrvatske (**Rad 1–3**), a tijekom višegodišnjih terenskih istraživanja, koja su razmjerno uključila sve tipove vodnih tijela prema tipologiji razvijenoj u svrhu praćenja ekološkog stanja površinskih voda (NN 96/19) prema Okvirnoj direktivi o vodama (Europska komisija 2000), zabilježeno je čak osam vrsta koje ranije nisu bile poznate u flori Hrvatske – *Fissidens fontanus*, *Dichodontium flavescens*, *Ricciocarpos natans* (Alegro i sur. 2019), *Physcomitrium sphaericum* (Ellis i sur. 2020), *Riccia rhenana* (Ellis i sur. 2021a), *Physcomitrium eurystomum* (**Rad 1**), *Philonotis marchica* i *Byum klinggraeffii* (**Rad 3**). Također, zabilježeno je i nekoliko rijetkih vrsta, do ovog istraživanja poznatih sa samo jednog (*Fissidens arnoldii*, *Hygroamblystegium fluviatile*, *Phycomitrium patens*, *Riccia cavernosa*), odnosno tri lokaliteta (*Leptobryum pyriforme*) te za floru Hrvatske do sada dvojbena vrsta *Riccia frostii* (**Rad 1, 2**).

Ekološka analiza uključila je vegetacijske podatke prikupljene na tekućicama, odnosno vrste koje su bile prisutne na barem pet lokaliteta i to one koje imaju veći afinitet prema vodi, budući da je njihovo pojavljivanje u većoj mjeri određeno uvjetima u samim vodotocima za razliku od obalnih vrsta, koje su pod složenijim utjecajem mnogih čimbenika na prijelazu vodenih u kopnena staništa. U konačnici, analiza je uključila 182 lokaliteta, od malih oligotrofnih vodotokova do velikih eutrofnih rijeka i umjetnih kanala, obuhvaćajući vrlo široke ekološke gradijente 18 istraživanih okolišnih varijabli (**Rad 4**). Kanoničkom analizom korespondencije (engl. *Cannonical Correspondance Analysis, CCA*) (Kent 2011) utvrđena je raspodjela istraživanih vrsta duž gradijenata kemije vode i udjela prirodnog, odnosno urbanog zemljišta unutar slivne površine. Skup najznačajnijih fizikalno-kemijskih parametara vode koji objašnjavaju pojavljivanje istraživanih vrsta mahovina uključio je one povezane s kakvoćom vode (koncentracija ukupnog dušika, ukupnog fosfora i otopljenog kisika, kemijska potrošnja kisika, električna provodljivost) te pH vrijednost vode, koja uglavnom odražava geološke prilike na istraživanim lokalitetima i njihovim slivnim područjima. Ovi rezultati potvrdili su zaključke ranijih istraživanja da na distribuciju i sastav vrsta vodenih mahovina utječe kakvoća vode (Vanderpoorten i Durwael 1999; Vanderpoorten i sur. 1999; Gecheva i sur. 2010; Ceschin i sur. 2012a), odnosno promjene u načinu korištenja zemljišta unutar slivnog područja, primjerice povećanje udjela intenzivne poljoprivrede ili urbanih područja, što je uglavnom povezano s onečišćenjem vode i eutrofikacijom (Gecheva i sur. 2017). Rezultati kanoničke korespondencijske analize, kao i ekološki odgovori vrsta modelirani pomoću generalnih aditivnih modela (engl. *General Additive Model, GAM*) (Yee i Mitchell 1991) pokazali su da većina vrsta preferira, odnosno ima optimum u čistim vodotocima s neizmijenjenim slivovima, odnosno vodama s visokom koncentracijom otopljenog kisika, niskom razinom hranjivih tvari i organske tvari te niskom električnom provodljivosti. Slično je ustanovljeno i za vodene mahovine u slivu rijeke Tiber (Italija), gdje je većina vrsta preferirala brze, hladne, oksigenirane vode s niskim koncentracijama hranjivih tvari, posebice amonijaka i ortofosfata (Ceschin i sur. 2012a).

Na temelju ekoloških odgovora, tj. optimuma i tolerancije vrsta spram istraživanih parametara, bilo je moguće izdvojiti set vrsta čije je pojavljivanje ograničeno na prirodne i čiste oligotrofne tekućice. Među njima su bile bazofilne vrste karakteristične za krške rijeke Dinaridske ekoregije, kao su *Palustriella falcata*, *Eucladium verticillatum*, *Jungermannia atrovirens* i *Dichodontium flavescens* (**Rad 1, 4**). *Eucladium verticillatum* i *Palustriella falcata*, poznate kao vrste izvorišta i plitkih potoka u kojima se stvara sedra (Zechmeister i Mucina 1994; Mucina i sur. 2016) te je njihovo pojavljivanje bilo negativno korelirano s koncentracijom hranjivih tvari. Za vrstu *Eucladium verticillatum* dokazano je da je osjetljiva na povišene koncentracije amonijaka i fosfata (Couvreur i sur. 2016), dok je za vrstu *Palustriella falcata* dokumentirano da dolazi u čistim oligotrofnim vodama (Peñuelas i Catalan 1983; Vanderpoorten i Klein 1999a; Scarlett i O'Hare 2006; Tremp i sur. 2012) pod niskim antropogenim utjecajem te da je vrlo osjetljiva na eutrofikaciju, što je čini dobrim indikatorom kakvoće vode (Empain 1978; Haury i sur. 1996; Ceschin i sur. 2012a). *Jungermannia atrovirens* bilježena je u oligotrofnim, i mezo-oligotrofnim vodama (Klein i sur. 1995), dok je za vrstu *Dichodontium flavescens* poznato da je ograničena na potpuno prirodne vodotoke, odnosno one pod slabim ili vrlo slabim utjecajem čovjeka (Dierßen 2001).

Vrste *Cinclidotus aquaticus*, *Chiloscyphus polyanthos*, *Apopellia endiviifolia i Didymodon tophaceus* su imale nešto šire ekološke niše s obzirom na koncentraciju nutrijenata, razinu organske tvari te električnu provodljivost vode, no više abundancije ovih vrsta ukazivale su na čiste vode, odnosno vode visoke kakvoće (**Rad 4**). Vrsta *Cinclidotus aquaticus* je i ranije opisivana kao vrsta čistih, hladnih i turbulentnih voda te je istaknuta kao pouzdan bioindikator (Ceschin i sur. 2012a, 2015), za razliku od vrste *Apopellia endiviifolia* koja je utvrđena u širem rasponu, od oligotrofnih (Papp i Rajczy 1998b; Vanderpoorten i Klein 1999b) do eutrofnih voda (Ceschin i sur. 2012a; Sossey-Alaoui i Rosillo 2013; Couvreur i sur. 2016). Vrsta *Chiloscyphus polyanthos* bilježena je do sada uglavnom u vodama s niskom razinom hranjivih tvari, međutim, u nekoj mjeri također tolerira i povišene koncentracije dušika (Sossey-Alaoui i Rosillo 2013).

Sve gore navedene vrste su bazofilne i u Hrvatskoj dolaze isključivo ili dominantno u krškim rijekama Dinarske ekoregije koje teku preko karbonata, što utječe na pH i alkalitet vode te posredno na sastav vrsta. Važan utjecaj geologije, pH vrijednosti i alkaliteta vode na mahovine kopnenih voda pokazao je velik broj istraživanja (Glime 1968; Suren 1996; Papp i Rajczy 1998a; Vanderpoorten i Klein 1999b; Lang i Murphy 2012; Vieira i sur. 2014; Tessler i sur. 2014; Vieira i sur. 2018; Jusik i sur. 2015; Szoszkiewicz i sur. 2018; Glime 2020), prilikom čega se na krajevima gradijenta pH vrijednosti, koje podržavaju vodenu biotu, nalaze bazofilne vrste karakteristične za karbonatne podloge, visoke vrijednosti pH i alkaliteta vode, odnosno acidofilne vrste koje dolaze u vodotocima koji teku preko pologa s kiselom reakcijom, poput silikata. Značajan utjecaj alkaliteta i pH vode na vodene mahovine dokazan je i u ovom istraživanju (**Rad 4, 5**), iako je obuhvaćeni gradijent bio relativno kratak. Većina vrsta je preferirala neutralnu od baziènu vodu, dok su mahovine *Eucladium verticillatum*, *Didymodon tophaceus*, *Palustriella falcata*, *Brachythecium rivulare*, *Fissidens crassipes* i *Cinclidotus aquaticus*, kao i jetrenjarke *Apopellia endiviifolia* i *Chiloscyphus polyanthos* pokazivale najveći afinitet prema bazičnim vodama (**Rad 4**).

Široko rasprostranjene vrste, koje su ujedno bile i među najučestalijima, kao *Fontinalis antipyretica*, *Rhynchostegium riparioides*, *Cratoneuron filicinum*, *Fissidens crassipes*, *Brachythecium rivulare*, *Cinclidotus riparius* i *C. fontinaloides* su u ovom istraživanju imale široke ekološke niše s obzirom na istražene okolišne gradijente zbog čega se ne mogu smatrati pouzdanim bioindikatorima (**Rad 4**). Primjerice, iako su one imale optimume u oligotrofnim vodama, njihovi maksimumi koncentracije amonijaka, nitrata i ukupnog dušika prelazili su granice postavljene za dobro stanje za sve tipove vodnih tijela koji su navedeni u Uredbi o standardu kakvoće voda (NN 96/2019), a koji su ujedno uključeni u ovo istraživanje. Isto je vrijedilo i za maksimume koncentracije ukupnog fosfora za sve navedene vrste izuzev vrsta *Brachythecium rivulare* i *Fontinalis antipyretica.* Naime, maksimumi koncentracije ukupnog fosfora ove dvije vrste prelazili su prag postavljen za dobro stanje za sve tipove u Dinaridskoj ekoregiji, koji prirodno imaju niže koncentracije fosfora u odnosu na vodotoke Panonske ekoregije pa su i granice strože, dok su za sve tipove Panonske ekoregije maksimumi koncentracije fosfora ove dvije vrste prelazili prag postavljen za vrlo dobro stanje kemije vode. Slično je uočeno i za isti set vrsta s obzirom na kemijsku potrošnju kisika, dok je iznimka u ovom slučaju bila samo vrsta *Brachythecium rivulare* čije su maksimalne COD vrijednosti ponovno prelazile prag za dobro stanje za sve tipove u Dinaridskoj ekoregiji, odnosno za vrlo dobro stanje u Panonskoj ekoregiji. *Fontinalis antipyretica* i *Rhynchostegium riparioides,* najučestalije mahovine u vodotocima Hrvatske (**Rad 1, 5**), koje naseljavaju raznolika staništa unutar prirodnih tekućica, kanala, kao i prirodnih i umjetnih stajaćica (Murphy i Eaton 1983; Kelly i Witton 1987; Karttunen i Toivonen 1995; Whitton 1999; Scarlett i O'Hare 2006; Lang i Murphy 2012) su i u ranijim istraživanjima bilježene u vodama širokog trofičkog raspona. Vrsta *Fontinalis antipyretica* je u nekim od istraživanja imala optimum u eutrofnim vodama (Vanderpoorten i Durwael 1999; Vanderpoorten i sur. 1999), dok je u našem istraživanju optimum ove vrste bio u oligotrofnim vodnim tijelima, što su zaključili i Ceschin i sur. (2012a) u vodotocima porječja rijeke Tiber. Slično tome, u literaturi postoje oprečne informcije i o ekologiji vrste *Rhynchostegium riparioides*. Dok neki autori opisuju ovu vrstu kao tipičnu vrstu nezagađenih oligotrofnih i čistih voda (Privitera 1990; Vanderpoorten 1999b), drugi ističu njenu toleranciju prema visokim razinama hranjivih tvari poput nitrata i fosfata, povezujući njenu prisutnost s lošom kakvoćom vode (Empain 1978; Peñuelas i Catalan 1983; Allegrini 2000). Međutim, značajan je broj istraživanja koja su se složila da obje vrste imaju široke ekološke niše, da se javljaju duž širokog raspona trofičkog stanja (Glime 1968; Muotka i Virtanen 1995; Vanderpoorten i sur. 1999; Scarlett i O'Hare 2006; Ceschin i sur. 2012a; Tremp i sur. 2012) te kao takve nisu dobri bioindikatori (Ceschin i sur. 2012a). Različita istraživanja dala su kontradiktorne rezultate i za ekološke odgovore drugih široko rasprostranjenih vrsta, primjerice vrste *Cratoneuron filicinum* (Empain 1978; Vanderpoorten 1999a; Vanderpoorten i sur. 2000; Tremp i sur. 2012; Ceschin i sur. 2012a; Sossey-Alaoui i Rosillo 2013; Ceschin i sur. 2015; Couvreur i sur. 2016) i *Cinclidotus fontinaloides* (Vanderpoorten i Durwael 1999; Vanderpoorten i sur. 1999). Oprečni rezultati su vjerojatno posljedica uporabe različitih metoda kartiranja i analize podataka, različitih raspona obuhvaćenih okolišnih varijabli te općenito broja i tipa istraživanih varijabli u pojedinim istraživanjima. Stoga su daljnja istraživanja ekologije vodenih mahovina, koja bi obuhvatila šira geografska područja i duže gradijente okolišnih parametara i dalje potrebna kako bi se poboljšalo znanje o ekološkim preferencijama i toleranciji vrsta za koje su do sada objavljivani kontradiktorni podatci. Također, za vrste *Fontinalis antipyretica* i *Fissides crassipes* ustanovljeno je da imaju različite ekološke odgovore u dvije hidrografske mreže u Francuskoj i Belgiji (Vanderpoorten i Durwael 1999). Dok su u jednoj hidrografskoj mreži obje vrste imale optimum u oligotrofnoj vodi, u drugoj su preferirale eutrofne vode. Autori su predložili da se radi o ekotipovima s različitim trofičkim zahtjevima. Uočene razlike u autekologiji populacija iste vrste dodatno otežavaju geografski širu uporabu vodenih mahovina kao bioindikatora te su daljnja istraživanja njihove distribucije i ekoloških odgovora, kao i njihove taksonomije, mikroevolucijskih procesa i ekofiziologije također potrebna.

Među istraživanim vrstama, *Leptodyctium riparium* i *Riccia fluitans* izdvojile su se kao jedine koje preferiraju neutralnu, topliju, hipereutrofnu (koncentracija ukupnog fosfora > 0,096 mgP/L) vodu s visokom električnom provodljivosti (> 500 μS/cm), kao i visokim sadržajem organske tvari tvari (COD > 7,5 mgO_2/L) (**Rad 4**), što je u skladu s ranijim istraživanjima (Vanderpoorten i Palm 1998; Vanderpoorten i Durwael 1999; Vanderpoorten i Klein 1999a; Scarlett i O'Hare 2006; Ceschin i sur. 2012a).

Dok neki autori obje vrste smatraju dobrim indikatorima eutrofnih voda (Ceschin i sur. 2012a), drugi su zaključili da *Leptodyctium riparium* nije pouzdan bioindikator s obzirom na to da se javlja duž širokog raspona trofičkog stanja, od oligotrofnih potoka do hipereutrofnih rijeka (Vanderpoorten i Durwael 1999; Vanderpoorten i Klein 1999a). U ovom istraživanju, obje vrste su imale široke niše s obzirom na većinu istraživanih ekoloških parametara, no brojnost i pokrovnost im je bila najveća u hipereutrofnim vodama s naglim padom s poboljšanjem kakvoće vode tako da veća abundancija i pokrovnost ovih vrsta upućuju na eutrofne, tj, hipereutrofne uvjete (**Rad 4**). Također, obje vrste su pokazale veći afinitet prema izmijenjenim vodotocima s manjim udjelom prirodnog zemljišta u slivnom području u odnosu na sve ostale istraživane vrste, prilikom čega je vrsta *Riccia fluitans* preferirala više koncentracije ukupnog fosfora i dušika u odnosu na *Leptodyctium riparium* te je bila vezana za vodna tijela s višim udjelom intenzivne poljoprivrede u slivnom području. Obje vrste imale su veću učestalost u Panonskoj ekoregiji u odnosu na Dinaridsku (**Rad 1, 4**), što je povezano s dominantnim značajkama vodotoka na području Panonske ekoregije. Naime, unutar ove regije prevladavaju sporiji i topliji nizinski vodotoci, od koji oni veći odgovaraju srednjim i donjim tokovima u kojima je stupanj trofije prirodno viši u odnosu na vodotoke Dinaridske ekoregije. U ovakvim vodotocima također prevladava sitniji i manje stabilan supstrat, koji je nepovoljan za naseljavanje i održanje većine vodenih mahovina. Dodatno su vodotoci Panonske ekoregije u većoj mjeri hidromorfološki degradirani, uglavnom zbog regulacija tokova u svrhu obrana od poplava te su u većoj mjeri izloženi onečišćenju i eutrofikaciji jer i u većoj mjeri prolaze kroz naseljena i industrijska područja te obradive površine (Plantak i sur. 2016; Vučković i sur. 2018, 2019, 2021; Medić i sur. 2020a,b,c; Music i sur. 2020). Ovi antropogeni utjecaji smanjuju pogodnost staništa za akvatičke i semiakvatičke vrste te dovode do pada pokrovnosti i raznolikosti, odnosno do promjena u sastavu vrsta (Suren 1996; Gecheva i sur. 2010, 2017) te dodatno umanjuju pogodnost staništa u Panonskoj ekoregiji. Stoga Panonska ekoregija podržava manju raznolikost akvatičkih i semiakvatičkih mahovina, kao i njihovih zajednica (**Rad 1, 5**), a vrste koje u ovoj ekoregiji imaju veću učestalost su upravo one koje dobro podnose i vode višeg stupnja trofije, odnosno vodotoke s izmijenjenim slivnim područjima kao što su *Leptodyctium riparium, Cratoneuron filicinum, Rhynchostegium riparioides, Fontinalis antipyretica, Cinclidotus riparius, Ptychostomum pseudotriquetrum i Fissidens crassipes*, dok su vrste oligotrofnih voda znatno rjeđe ili izostaju (**Rad 1, 5**).

Iako akvatičke i semiakvatičke vrste mahovina nastanjuju raznolika slatkovodna staništa i njihove obalne zone (**Rad 1–3**), odnosno brojne ekološke i hidrološke niše povezane s lotičkim i lentičkim staništima (Slack i Glime 1985; Glime 2020), one su posebno značajna komponenta makrofitske vegetacije u brzim i hladnim gorskim potocima, na slapištima, zatim u rijekama s izraženom sezonalnosti u protoku, odnosno u povremenim vodotocima (Tremp i sur. 2012; Ceschin i sur. 2015; Jusik i sur. 2015; Szoszkiewicz i sur. 2018; Vieira i sur. 2018). Na ovakvim staništima se razvijaju čiste mahovinske zajednice ili zajednice u kojima mahovine čine dominantnu komponentu makrofitske vegetacije. Zajednice u kojima su mahovine bile dominantna komponenta vegetacije zabilježene su u ovom istraživanju na svega 76 (14,42 %) od ukupno 527 lokacija na prirodnim vodotocima (**Rad 5**). Analiza njihove geografske rasprostranjenosti utvrdila je da je Dinaridska ekoregija znatno bogatija u odnosu na Panonsku ekoregiju. Naime, od ukupnog broja istraživanih lokacija u ovoj regiji, 31,12 % podržavalo je razvoj ovakvih zajednica, dok je u Panonskoj ekoregiji taj udio bio svega 4,53 %. Također, s obzirom na distribuciju 76 lokacija na kojima su mahovine prevladavale, njih čak 80,26 % (61 lokalitet) bilo je u Dinardskoj ekoregiji, odnosno 46,05 % (35 lokaliteta) u njenoj Kontinentalnoj subekoregiji te 34,21 % (26 lokaliteta) u Mediteranskoj subekoregiji, dok je svega 19,74 % (15 lokaliteta) zabilježeno u Panonskoj ekoregiji (**Rad 5**). Budući da ove regije odražavaju klimatsku, geološku i hidrološku raznolikost prisutnu na području Hrvatske te da su upravo ove grupe okolišnih čimbenika, uz kemijske parametre vode, ranija istraživanja ustanovila kao najbitnija u oblikovanju mahovinskih zajednica u tekućicama (Suren 1996; Suren i Ormerod 1998; Vanderpoorten i Durwael 1999; Scarlett i O'Hare 2006; Tremp i sur. 2012; Vieira i sur. 2014, 2018; Gecheva i sur. 2017), bilo je za očekivati da tekućice Hrvatske podržavaju razvoj većeg broja različitih zajednica te da njihova geografska segregacija prati ovu podjelu, odnosno da pojedine zajednica pokazuju određeni afinitet spram pojedinih ekoregija i subekoregija. Pomoću multivarijatne klasifikacijske analize TWINSPAN (engl. *Two-way Indicator Species Analysis*) (Hill 1979) modificirane prema Rolečeku i sur. (2009) i multivarijatnih ordinacijskih metoda (detrendirana korespondencijska analiza, engl. *Detrended Correspondence Analysis, DCA* i kanonička korespondencijska analiza, *CCA*) (Kent 2011), ovo istraživanje ustanovilo je pet ekološki jasno određenih zajednica koje su se razlikovale po sastavu i raznolikosti vrsta, njihovom afinitetu prema količini vode te su bile karakterizirane različitim udjelom pojedinih kategorija u spektru životnih oblika i životnih strategija, što odražava ekološke prilike na njihovim staništima (**Rad 5**). Glavni okolišni čimbenici koji su uvjetovali njihovo razdvajanje bili su fizikalno-kemijski i kemijski parametri vode – alkalitet, režim kisika (biokemijska potrošnja kisika), koncentracija otopljenog kisika, ortofosfata i ukupnog dušika, zatim klimatski parametri koji su u vezi s dostupnošću vode i njenom distribucijom kroz godinu te veličina slivnog područja.

Najzastupljenija zajednica u tekućicama Hrvatske, *Cinclidotus* zajednica, imala je najširi ekološki raspon u pogledu kemijskih parametara vode i klimatskih varijabli povezanih s precipitacijom. Centar rasprostranjenosti ove zajednice bila je Kontinentalna subekoregija Dinaridske ekoregije s umjerenom klimom i visokim vrijednostima precipitacije u najtoplijem kvartalu, gdje je ova zajednica bilježena u njenim neutralnim do blago bazičnim vodama. Također je bilježena i u izvorišnim područjima i donjim tokovima stalnih vodotoka Mediteranske subekoregije, dok se najrjeđe pojavljivala u Panonskoj ekoregiji, u kojoj je bila ograničena na slapiće srednje velikih vodotoka. Ova zajednica podržavala je najveći ukupni broj vrsta mahovina (45 vrsta) te visoku prosječnu vrijednost bogatstva vrsta mahovina po istraživanom lokalitetu (8,21), a karakteristične vrste (*fidelity index*, $\phi \geq 0{,}40$, $p < 0{,}05$) ove zajednice bili su reofiti *Cinclidotus aquaticus* i *C. riparius.* Vrsta *Cinclidotus aquaticus* je tipična vrsta oligotrofnih voda (**Rad 4**), odnosno izvorišnih dijelova vodotoka i slapišta, te općenito brzih, bujičnih ili turbulentnih dijelova vodenih tokova (Kochjarová i sur. 2007; Sérgio i sur. 2007; Price i Vivien 2010). Za razliku od vrste *Cinclidotus aquaticus,* vrsta *C. riparius* je u ovom istraživanju dolazila na zaštićenijim mikrostaništima, koja nisu bila izravno izložena snažnom djelovanju vode, dok je *C. fontinaloides,* konstantna vrsta (učestalost unutar zajednice ≥ 50 %) *Cinclidotus* zajednice, dolazila na stijenama te bazama drveća povremeno uronjenim u vodu. Konstantne vrste ove zajednice, *Cinclidotus riparius*, *C. fontinaloides*, *Rhynchostegium riparioides*, *Cratoneuron filicinum* i *Fontinalis antipyretica*, kao i relativno učestale vrste *Fissidens crassipes* i *Marchantia polymorpha* imale su vrlo široke ekološke niše s obzirom na parametre povezane s kvalitetom vode (**Rad 4**), što je u skladu s opaženim širokim ekološkim rasponom ove zajednice. Sastavom vrsta ova zajednica vrlo dobro odgovara mahovinskoj zajednici koja je prepoznata kao najčešća u vodotocima na području Mediterana (Vieira i sur. 2018), dok je modeliranjem predviđeno njeno pojavljivanje u njegovom istočnom i središnjem dijelu, uključujući i dio Hrvatske, te na sjeveru Španjolske i Francuske. Ova zajednica imala je visok udio akvatičkih vrsta karakterističnih za riječna korita, kao i viši udio borealnih elemenata u odnosu na druge zajednica ustanovljene na Mediteranu (Vieira i sur. 2018). Slično tome, *Cinclidotus* zajednica je u ovom istraživanju imala visok udio reofita, ali i vodenih vrpčastih mahovina (engl. *aquatic trailings*) te onih koje rastu u glatkim sagovima (engl. *smooth mats*) u spektru životnih oblika, što upućuje da je vezana uz stalne tokove. Također, i u *Cinclidotus* zajednici zabilježena je prisutnost borealnih, ali i mediteransko-atlantskih elemenata koji sugeriraju klimu s više vlage i precipitacije, što odgovara njenoj velikoj učestalosti upravo u Kontinentalnoj subekoregiji Dinaridske ekoregije.

Za krške rijeke Dinaridske ekoregije bile su karakteristične i zajednice *Didymodon tophaceus*-*Apopellia endiviifolia* i *Berula erecta*-*Cratoneuron filicinum*. Ove zajednice bile su podjednako zastupljene u istraživanju, no znatno rjeđe u odnosu na *Cinclidotus* zajednicu (**Rad 5**). Obje su dolazile u čistim, bistrim vodama s visokom koncentracijom otopljenog kisika te niskim vrijednostima biokemijske potrošnje kisika, kao i niskim koncentracijama hranjivih tvari. Značajan udio bazofilnih vrsta u ovim zajednicama u skladu je s njihovim pojavljivanjem upravo na krškim rijekama, čije vode imaju više vrijednost pH i alkaliteta. Iako su imale sličan ukupan broj makrofitskih vrsta te slično prosječno bogatstvo makrofitskih vrsta po lokalitetu, *Didymodon tophaceus*-*Apopellia endiviifolia* zajednica se odlikovala višim udjelom mahovina u florističkom sastavu (59,32 %) te je njihova srednja vrijednost broja po lokalitetu iznosila 8,94, dok je unutar zajednice zabilježeno ukupno 35 vrsta mahovina. Među karakterističnim vrstama bile su sedrotvorne vrste *Didymodon tophaceus* i *Eucladium verticillatum* te bazofilne *Apopellia endiviifolia* i *Fissidens crassipes* (**Rad 5**), a u zajednici su se pojavljivale i druge bazofilne vrste oligotrofnih voda kao što su prave mahovine *Palustriella commutata* (Ceschin i sur. 2012a, 2015) i *P. falcata* te jetrenjarka *Jungermannia atrovirens*.

Unutar zajednice *Didymodon tophaceus*-*Apopellia endiviifolia* zabilježen je viši udio higrofita u odnosu na ostale zajednice karakteristične za Dinaridsku ekoregiju, a to je podržano i višim udjelom vrsta koje rastu u čupercima (engl. *turfs*) u spektru životnih oblika, odnosno kolonistima u spektru životnih strategija, koji su karakteristični za sezonski plavljena staništa, odnosno mikrostaništa, te sugeriraju da se radi o staništima koja su izložena isušivanju tijekom sušeg dijela godine, ali i mogućim bujičnim tokovima tijekom vlažnog dijela godine (Vieira 2012b). Prema sastavu vrsta, zajednica *Didymodon tophaceus*-*Apopellia endiviifolia* dobro odgovara zajednici koju su Vieira i sur. (2018) na razini Mediterana zabilježili u vodotocima s viskom sezonalnosti u količini protoka koji dolaze na niskim i srednjim nadmorskim visinama. Pojavljivanje ove zajednica je modeliranjem predviđeno za rijeke s visokom razinom sezonalnosti u količini protoka na području Španjolske, južne Francuske, Italije i Grčke, međutim ne i Hrvatske (Vieira i sur. 2018). U Hrvatskoj je pojavljivanje zajednice *Didymodon tophaceus-Apopellia endiviifolia,* kao i zajednice *Berula erecta-Cratoneuron filicinum,* bilo povezano s višim vrijednostima precipitacije u najhladnijem kvartalu karakterističnim za mediteransku klimu sa suhim i vrućim ljetima i vlažnom sezonom s maksimumom precipitacije tijekom toplih zima. Također, za pojavljivanje obje zajednice bila je značajna i slivna površina. Naime, obje su bilježene uglavnom na krškim rijekama Dinaridske ekoregije, koje su najčešće dio velikih i složenih hidrografskih mreža, a vodu dobivaju iz brojnih izvora te nadzemnih i podzemnih tokova koji dovode vodu iz dinarskih planina. Međutim, zajednica *Didymodon tophaceus-Apopellia endiviifolia* dolazila je i na povremenim vodotocima s malim slivnim područjima, dok je na onima s velikim slivnim područjima uglavnom bila ograničena na slapišta.

Zajednica *Berula erecta-Cratoneuron filicinum* imala je više srednje vrijednosti veličine slivnog područja i značajno niži pH u odnosu na zajednicu *Didymodon tophaceus-Apopellia endiviifolia.* Prema sastavu vrsta jasno je da se radi o prijelaznoj vegetaciji u kojoj vaskularni makrofiti počinju zamjenjivati mahovine. Udio mahovina u njenom florističkom sastavu je iznosio 27,45 % (17 od ukupno 51 vrste makrofita), dok je srednja vrijednost broja vrsta mahovina po lokalitetu bila 4,4. S druge strane, ova zajednica je imala najviši udio vaskularnih vrsta u florističkom sastavu te su u njoj zabilježene više vrijednosti *alfa* raznolikosti (bogatstvo vrsta i Snannon-Wiener indeks) vaskularnih makrofita, od kojih su svega 3,57 % bili pravi makrofiti, tj. hidrofiti (1 vrsta od ukupno 28 vrsta vaskularnih makrofita), a veliku većinu u florističkom sastavu činili su helofiti. Upravo su helofitske vrste *Menta aquatica*, *Berula erecta* i *Sparganium erectum* bile karakteristične vrste ove zajednice. One su uglavnom nastanjivale pliće dijelove uz obale vodotoka, a njihovo pojavljivanje ukazivalo je na postupni prijelaz iz vodene vegetacije u kojoj su mahovine dominantna komponenta prema herbidnoj vegetaciji karakterističnoj za manje i pliće vodotoke u umjerenom pojasu Europe, koja pripada svezi *Glycerio-Sparganion* Br.-Bl. et Sissingh in Boer 1942 (Mucina i sur. 2016). Međutim, u ovoj zajednici su se mahovine pojavljivale uglavnom u samom vodotoku pa je ona imala najviši udio reofita, ali i vodenih vrpčastih mahovina (engl. *aquatic trailings*) (46,0 %) u spektru životnih oblika. Među njima je bila, primjerice, konstantna vrsta *Fontinalis antipyretica* te drugi reofiti kao *Cinclidotus riparius*, *C. fontinaloides* te *Chiloscyphus polyanthos*. Također je zabilježena i značajna učestalost (14,3 %) vrsta koje rastu u glatkim sagovima (engl. *smooth mats*), kao što su *Rhynchostegium riparioides,* još jedna konstantna vrsta ove zajednice, te *Jungermannia atrovirens*. Vodene vrpčaste mahovine, posebice *Fontinalis antipyretica*, uglavnom preferiraju nešto sporije i mirnije tokove u odnosu na one koje rastu u glatkim sagovima te je iz udjela i odnosa zastupljenosti ova dva životna oblika, koji su najbolje prilagođeni životu u vodotoku (Vieira i sur. 2012b), vidljivo da zajednica *Berula erecta-Cratoneuron filicinum* preferira mirnije vodotoke u odnosu na *Cinclidotus* zajednicu. Također, niži udio mahovine koje rastu u čupercima (engl. *turfs*) sugerira stalne vodotoke bez sezonskih bujica. U ovakvim vodotocima, koji odgovaraju nizvodnijim dijelovima rijeka te nizinskim krškim rijekama s blagim padom u kojima je struja vode mirnija, a supstrat sitniji, vaskularne biljke počinju zamjenjivati mahovine te je iz usporedbe tri zajednice karakteristične za krške rijeke uočljivo da se broj i abundancija vaskularnih vrsta makrofita smanjuje s porastom raznolikosti i abundancije vodenih mahovina (**Rad 5**).

Zajednice čiji je centar distribucije bio u Panonskoj ekoregiji, *Oxyrrhynchium hians-Chiloscyphus pallescens* i *Fissidens pusillus-Veronica beccabunga*, odvojile su se od ranije spomenutih zajednica duž gradijenta alkaliteta, parametara povezanih s kakvoćom vode, veličine slivnog područja, ali i bioklimatskih varijabli. Obje zajednice dolazile su u vodama s visokim vrijednostima koncentracije hranjivih tvari i biokemijske potrošnje kisika te niskom koncentracijom otopljenog kisika. Nadalje, za razliku od zajednica Dinaridske ekoregije, ove zajednice dolazile su u vodama s nižim alkalitetom i pH, što je u vezi s geološkom podlogom koja je u Panonskoj ekoregiji uglavnom silikatna. Nadalje, pojavljivanje obje zajednice bilo je povezano s višim vrijednostima srednje temperature zraka u najsušem kvartalu te precipitacije u najhladnijem kvartalu. Također, obje zajednice zabilježene su na vodotocima s malim slivnim područjem koji ne obiluju vodom.

Zajednica *Oxyrrhynchium hians-Chiloscyphus pallescens* podržavala je visoku raznolikost mahovina, imala je visoku srednju vrijednost broja vrsta mahovina po lokalitetu (11,38) te je njihov udio u ukupnom broju vrsta bio također visok (86,05 %), dok su unutar nje zabilježene samo tri vaskularne vrste. Međutim, među mahovinama, najzastupljeniji u ovoj zajednici bili su higrofiti (65,9 %), dok je učestalost reofita bila svega 18,7 %. U usporedbi s ostalim zajednicama u ovom istraživanju, ona je imala najveću učestalost higrofita i mezofita te najmanji udio reofita. Karakteristične vrste ove zajednice bili su upravo higrofiti (*Oxyrrhynchium hians, Plagiomnium undulatum, P. ellipticum, Pohlia melanodon, Chiloscyphus pallescens, Pellia neesiana, Conocephalum salebrosum, Dichodontium pellucidum*) te mezofiti (*Fissidens taxifolius* i *Hypnum cupressiforme*), koji su nastanjivali periodički plavljene obale zasjenjenih malih panonskih tekućica sa sitnim pjeskovitim supstratom, dok su među konstantnim vrstama bili i reofiti *Rhynchostegium riparioides* i

Leptodyctium riparium. Za vrstu *Leptodyctium riparium* je poznato da preferira eutrofne vode te da je jedna od rijetkih akvatičkih vrsta koje dolaze u nizinskim tekućicama (Frahm 1974; Papp i Rajczy 1998a,b; Vanderpoorten i sur. 1999; Gecheva i sur. 2010; Ceschin i sur. 2012a), što je potkrijepljeno i ovim istraživanjem u kojem je vrsta *Leptodyctium riparium* bila jedina dominantna u vodotocima Panonske ekoregije (**Rad 1**) te je imala optimum u čak hipereutrofnim vodama (**Rad 4**). Za razliku od nje, mahovina *Rhynchostegium riparioides* je bila sveprisutna, s nešto većom učestalošću u vodotocima Dinaridske ekoregije (**Rad 1**) te je njegova učestalost u svim zajednicama prelazila prag postavljen za konstantne vrste (≥ 50 %), što upućuje na to da se radi o vrsti sa širokom ekološkom tolerancijom što je potvrđeno i u **Radu 4** koji je obuhvatio veći broj lokaliteta i šire gradijente kemijskih parametara vode. Široke ekološke niše s obzirom na koncentraciju ukopnog fosfora i dušika te količinu organske tvari uočene su i kod vrsta *Chiloscyphus pallescens* i *Dichodontium pellucidum* te vrste *Ptychostomum pseudotriquetrum*, koja je bila konstantna vrsta ove zajednice.

Fissidens pusillus-Veronica beccabunga zajednica bila je najrjeđa i vrstama najsiromašnija zajednica u našem istraživanju sa svega četiri lokaliteta od kojih je većina bila na mutnim i eutrofnim malim prigorskim vodotocima Panonske ekoregije. Imala je najnižu srednju vrijednost broja vrsta (6,75) i broja mahovina (4,00) po lokalitetu. Karakterizirao ju je viši udio vaskularnih biljaka u florističkom sastavu (50 %), drugi najviši nakon zajednice *Berula erecta-Cratoneuron filicinum* u ovom istraživanju. Kao i u *Oxyrrhynchium hians-Chiloscyphus pallescens* zajednici i u _ovoj zajednici dominirali su higrofiti (učestalost 56,3 %), Među njima su bile, primjerice, karakteristične i konstantne vrste *Brachythecium rutabulum*, *Oxyrrhynchium speciosum* i *Marchantia polymorpha*. Dominacija higrofita, visok udio mahovina koje rastu u grubim prostirkama (engl. *rough mats*), kao i visok udio vrsta koje rastu u čupercima (engl. *turfs*), odnosno nizak udio ili potpuni izostanak vodenih vrpčastih mahovina (engl. *aquatic trailings*) u zajednicama karakterističnim za Panonsku ekoregiju potvrđuju da su obale malih vodenih tokova dominantna staništa koje mahovine naseljavaju u Panonskoj ekoregiji. S druge strane, čiste, brze i hladne krške vode Danaidske ekoregije s krupnim i stabilnim sedimentom pružaju bogatiji skup ekoloških i hidroloških niša te podržavaju znatno veću raznolikost akvatičkih i semiakvatičkih vrsta mahovina, kao i njihovih zajednica (**Rad 1, 4, 5**).

6. ZAKLJUČAK

1. Akvatičke i semiakvatičke mahovine zabilježene su na 29 % istraživanih lokacija na prirodnim i umjetnim tekućicama i stajaćicama. Flora mahovina ovih površinskih kopnenih voda obuhvaća ukupno 83 vrste (68 pravih mahovina i 15 jetrenjarki), što čini 12 % do sad poznate raznolikosti mahovina u Hrvatskoj. Veća raznolikost zabilježena je u krškim rijekama Dinaridske ekoregije (70 vrsta, prosječno 4,6 vrste po lokalitetu) i to njene Kontinentalne subekoregije (65 vrsta, prosječno 5,9 vrsta po lokalitetu), dok je najsiromašnija vrstama bila Panonska ekoregija (57 vrsta, prosječno 3,4 vrste po lokalitetu). Ove dvije regije dijelile su 44 vrste, dok je njih 26 zabilježeno isključivo u Dinaridskoj, a 13 u Panonskoj ekoregiji.
2. U flori mahovina kopnenih voda Hrvatske dominiraju cirkumpolarni i europski, odnosno tempratni elementi, što odgovara biogeografskim značajkama istraživanog područja. Među životnim oblicima najzastupljenije su vodene vrpčaste mahovine (engl. *aquatic trailings*), koje su najbolje prilagođene životu u kopnenim vodama, a zatim mahovine koje rastu u čupercima (engl. *turfs*), karakteristične za sezonski plavljena staništa i povremene tokove. S obzirom na životne strategije, dominiraju perenijalne vrste karakteristične za stalne i brze tokove te kolonisti koji dolaze na emergentnim pozicijama i uz obalu.
3. Pojavljivanje pojedinih vrsta i sastav vrsta mahovina u tekućicama uvjetovani su fizikalno-kemijskim parametrima vode koji su povezani s njenom kakvoćom, među kojima su najznačajniji koncentracija otopljenog kisika, koncentracija hranjivih tvari, kemijska potrošnja kisika i električna provodljivost. Također, mahovine su se razdvojile duž gradijenta alkaliteta što je u vezi s geološkom podlogom, ali i duž gradijenata prirodnog i urbanog zemljišta u slivnom području.
4. Ekološki odgovori vrsta pokazali su da većina vrsta preferira čiste, blago bazične, oligotrofne vode s niskom razinom organske tvari i niskom električnom provodljivosti te s visokim udjelom prirodnog, odnosno niskim udjelom urbanog zemljišta unutar slivnog područja. Međutim, manji broj vrsta ima uske ekološke niše, dok većina vrsta ima široku ekološku toleranciju spram spomenutih okolišnih čimbenika.
5. U prirodnim tekućicama Hrvatske ustanovljeno je pet zajednica u kojima mahovine predstavljaju dominantnu vegetacijsku komponentu. Ove zajednice razlikuju se na temelju bogatstva i sastava vrsta, udjela mahovina u florističkom sastavu i njihovog afiniteta prema vodi, kao i udjela pojedinih kategorija u spektru životnih oblika, što odražava njihove

različite ekološke profile. Najzastupljenija i vrstama najbogatija zajednica je *Cinclidotus* zajednica s centrom rasprostranjenosti u stalnim i brzim krškim vodotocima Dinaridske ekoregije, odnosno njene Kontinentalne subekoregije. Za krške rijeke ove ekoregije karakteristične su i vrstama siromašnije zajednice *Didymodon tophaceus-Apopellia endiviifolia* i *Berula erecta-Cratoneuron filicinum*. *Didymodon tophaceus-Apopellia endiviifolia* ima visok udio hidrofita i vrsta koje rastu u čupercima (engl. *turfs*) te je dolazi na povremenim vodotocima i slapištima većih rijeka, dok je *Berula erecta-Cratoneuron filicinum* prijelazna zajednica stalnih tokova u kojoj vaskularne biljke počinju zamjenjivati mahovine, među kojima dominiraju reofiti i vodene vrpčaste vrste (engl. *aquatic trailings*). Raznolikost i zastupljenost mahovinskih zajednica znatno je niža u Panonskoj ekoregiji za koju su karakteristične vrstama bogata *Oxyrrhynchium hians-Chiloscyphus pallescens* zajednica i vrstama siromašna *Fissidens pusillus-Veronica beccabunga* zajednica u kojima dominiraju higrofiti, tj. mahovine koje nastanjuju obalne zone kao glavno pogodno mikrostanište za mahovine na vodotocima Panonske ekoregije.

6. Mahovinske zajednice u tekućicama Hrvatske uvjetovane su bioklimatskim varijablama povezanim s dostupnošću vode i njenom raspodjelom kroz godinu, zatim fizikalno-kemijskim karakteristikama vode (alkalitet, koncentracija hranjivih tvari, otopljenog kisika i količina organske tvari) te veličinom slivnog područja. Zajednice *Oxyrrhynchium hians-Chiloscyphus pallescens* i *Fissidens pusillus-Veronica beccabunga* karakteristične su za eutrofne male vodotoke s visokim vrijednostima srednje temperature u najvlažnijem kvartalu, dok su *Didymodon tophaceus-Apopellia endiviifolia* i *Berula erecta-Cratoneuron filicinum* uglavnom vezane za čiste, krške rijeke s velikim slivnim područjem pod utjecajem mediteranske klime s visokim srednjim temperaturama zraka u najsušem kvartalu, odnosno visokom količinom precipitacije u najhladnijem kvartalu. *Cinclidotus* zajednica imala najširi ekološki raspon s obzirom na kemiju vode te je vezana uglavnom za krške vodotoke pod utjecajem vlažnije varijante umjerene klime s visokom precipitacijom.

7. Vrste uskih ekoloških niša s obzirom na kemijske parametre vode povezane s njenom kakvoćom, kao što su *Palustriella falcata, Eucladium vertcillatum, Dichodontium flavescens* i *Jungermannia atrovirens*, čine dobre i pouzdane bioindikatore. Također, više pokrovnosti vrsta *Cinclidotus aquaticus*, *Chiloscyphus polyanthos*, *Apopellia endiviifolia* i *Didymodon tophaceus* ukazuje na oligotrofne uvjete, dok visoka pokrovnost vrsta *Leptodyctium riparium* i *Riccia fluitans* ukazuje na eutrofne uvjete.

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8. ŽIVOTOPIS

Anja Rimac rođena je 16.8.1986. godine u Sisku. Osnovnu školu i opću gimnaziju završila je u Petrinji te potom upisala preddiplomski studij Biologije na Prirodoslovno-matematičkom fakultet Sveučilišta u Zagrebu. Na istom fakultetu diplomirala je 2012. na studiju Eksperimentalne biologije s temom „Flora mahovina u šumskim zajednicama Medvednice“. Tijekom studija bila je članica Udruge studenata biologije BIUS te voditeljica njene Sekcije za botaniku. Tijekom 2013.volontirala je na Botaničkom odjelu Prirodoslovnog muzeja u Zagrebu na digitaliziranju i georeferenciranju herbarske zbirke te se potom zaposlila kao pripravnik u Centralnom vodnogospodarskom laboratoriju Hrvatskih voda, gdje se bavila monitoringom ekološkog stanja površinskih voda na temelju makrofita, fitoplanktona i fitobentosa. Od 2015. do 2017. zaposlena je u Odjelu za zaštitu voda, okoliša i prirode u tvrtki Elektroprojekt. d.o.o, gdje izrađuje elaborate zaštite okoliša, studije utjecaja zahvata na okoliš te studije prihvatljivosti zahvata za ekološku mrežu Natura 2000. Nakon toga, u rujnu 2017. zapošljava se kao asistentica na Botaničkom zavodu Biološkog odsjeka PMF-a, gdje vodi vježbe iz kolegija Botanika, Vegetacijska ekologija i Nomenklatura i determinacija bilja. Njezina znanstvena aktivnost posvećena je istraživanju raznolikosti, rasprostranjenosti i ekološke uvjetovanosti vodene vegetacije te mogućnosti njene upotrebe kao indikatora ekološkog stanja voda. Također se bavi istraživanjem raznolikosti i biogeografije kopnenih mahovina u Hrvatskoj. Kao istraživač sudjelovala je također na brojnim stručnim projektima koji su se bavili travnjacima i njihovom sukcesijom, monitoringom cretne vegetacije, istraživanjem i monitoringom mahovina šumskih staništa, kao i monitoringom alga parožina. Do sada je objavila 29 znanstvenih članaka, sedam kratkih znanstvenih priopćenja i tri stručna rada, dok je na znanstvenim skupovima sudjelovala sa 44 priopćenja. Dugogodišnja je članica Hrvatskog botaničkog društva te je kao članica znanstvenih odbora 2022. godine sudjelovala na dva znanstvena skupa u organizaciji Društva – „7. hrvatski botanički kongres s međunarodnim sudjelovanjem i „10th Conference of European Committee for Conservation of Bryophytes“.

Pregled po CROSBI profilu: Anja Rimac (CROSBI Profil: 34356, MBZ: 364166)

RADOVI U ČASOPISIMA

Izvorni znanstveni članci

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Kratka znanstvena priopćenja

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Stručni radovi

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SAŽECI SA SKUPOVA

Sažeci u zbornicima i časopisima

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RADIONICE

IUCN SSC Bryophyte Specialist Group and IAB Council Training: IUCN red-listing workshop, bryophytes; Madrid, Španjolska, od 7. do 8.7.2019.

Joint EPPO and Institute for Plant Protection and Environment (Belgrade) Training Workshop: Introduction to methodologies for conducting Pest Risk Analysis for Invasive Alien Plants; Beograd, Srbija, od 30.11. do 1.12.2018.