

Raspodjela biomase simpatrijskih sisavaca u južnoj Europi

Pleskalt, Andro

Undergraduate thesis / Završni rad

2024

Degree Grantor / Ustanova koja je dodijelila akademski / stručni stupanj: **University of Zagreb, Faculty of Science / Sveučilište u Zagrebu, Prirodoslovno-matematički fakultet**

Permanent link / Trajna poveznica: <https://um.nsk.hr/um:nbn:hr:217:769711>

Rights / Prava: [In copyright](#)/[Zaštićeno autorskim pravom.](#)

Download date / Datum preuzimanja: **2024-12-14**



Repository / Repozitorij:

[Repository of the Faculty of Science - University of Zagreb](#)



Sveučilište u Zagrebu
Prirodoslovno-matematički fakultet
Biološki odsjek

Andro Pleskalt

**Raspodjela biomase simpatrijskih sisavaca
u južnoj Europi**

Završni rad

Zagreb, 2024.

University of Zagreb
Faculty of Science
Department of Biology

Andro Pleskalt

**Biomass distribution of sympatric mammals
in southern Europe**

Bachelor thesis

Zagreb, 2024.

Ovaj završni rad je izrađen u sklopu studijskog programa prijediplomski studij Znanosti o okolišu na Biodiversity Research Institute/Spanish National Research Council pod mentorstvom. dr. sc. Frederik Dalerum i komentorstvom prof. dr. sc. Perica Mustafić, Biološki odsjek PMF-a.

TEMELJNA DOKUMENTACIJSKA KARTICA

Sveučilište u Zagrebu
Prirodoslovno-matematički fakultet
Biološki odsjek

Završni rad

Raspodjela biomase simpatrijskih sisavaca u južnoj Europi

Andro Pleskalt

Rooseveltov trg 6, 10000 Zagreb, Hrvatska

Raspodjela biomase među trofičkim razinama i različitim vrstama organizama važna je karakteristika ekosustava i vjerojatno je doživjela velike promjene uzrokovane ljudskim aktivnostima. U ovom radu istražena je raspodjela biomase 10 vrsta sisavaca u Kantabrijskim planinama na sjeveru Španjolske koristeći podatke s fotozamki i model procjene brojnosti temeljen na zauzeću. Raspodjela nije slijedila pravilo prijenosa 10 % biomase po trofičkoj razini, niti je biomasa grabežljivaca rasla s eksponentom $\frac{3}{4}$ u odnosu na biomasu plijena. Umjesto toga, raspodjela je bila koncentrirana na niže trofičke razine s nerazmjerno malom biomasom grabežljivaca, osobito velikih mesoždera. Osim toga, omjer biomase potrošača i proizvođača bio je niži od teorijskih očekivanja. Rezultati ovog istraživanja vjerojatno predstavljaju gornji kraj raspona biomase sisavaca u umjerenim šumama južne Europe, budući da su podaci uglavnom prikupljeni iz kamera postavljenih unutar zaštićenih područja. Daljnja istraživanja s poboljšanim uzorkovanjem i metodologijom mogla bi povećati preciznost procjene biomase, ali smatram da uočena odstupanja između opaženih raspodjela biomase i teorijskih očekivanja predstavljaju jasan primjer radikalnih učinaka koje su ljudske aktivnosti imale na strukturu kopnenih ekosustava.

Ključne riječi: raspodjela biomase, sisavci, ekologija zajednica, umjerena šuma, fotozamke, model zauzeća

(18 stranica, 1 slika, 3 tablice, 71 literaturnih navoda, jezik izvornika: Engleski)

Rad je pohranjen u Središnjoj biološkoj knjižnici

Mentor: dr. sc. Frederik Dalerum

Komentor: prof. dr. sc. Perica Mustafić

BASIC DOCUMENTATION CARD

University of Zagreb
Faculty of Science
Department of Biology

Bachelor thesis

Biomass distribution of sympatric mammals in southern Europe

Andro Pleskalt

Rooseveltova trg 6, 10000 Zagreb, Croatia

The distribution of biomass among trophic levels and different types of organisms is an important characteristic of ecosystems and has likely seen large perturbations caused by human activities. The biomass distribution of 10 mammal species was investigated in the Cantabrian Mountains in northern Spain using camera trap data and an occupancy based abundance model. The distribution did not follow the rule of 10 % biomass transfer per trophic level nor did predator biomass scale with a $\frac{3}{4}$ power exponent in relation to the biomass of its prey. Instead, the distribution was bottom heavy with a disproportionately low predator biomass, in particular large carnivore biomass. In addition, the ratio of consumer to producer biomass was lower than theoretical expectations. Furthermore, the results in this study likely represent the upper end of the range of mammal biomass in southern European temperate forest, as the data were mostly derived from cameras placed inside protected areas. More research with improved sampling and methodology could increase the precision of biomass estimation, but I suggest that the observed deviations between the observed biomass distributions and theoretical expectations provide a strong example of the radical effects human activities has had on the structure of terrestrial ecosystems.

Keywords: biomass distribution, mammals, community ecology, temperate forest, camera trapping, occupancy models

(18 pages, 1 figure, 3 tables, 71 references, original in: English)

Thesis is deposited in Central Biological Library.

Mentor: assist. prof. Frederik Dalerum, PhD

Co-mentor: prof. Perica Mustafić, PhD

Contents

1. Introduction	1
2. Materials and methods.....	3
2.1. Study area.....	3
2.2. Camera trapping.....	4
2.3. Estimation of abundance, density, and total biomass	5
3. Results	7
4. Discussion.....	9
5. Conclusion.....	11
6. Acknowledgements.....	12
7. References	12
8. Curriculum Vitae	18

1. Introduction

Even though land covers only approximately 30% of Earth's surface, 85% the total biomass on Earth is located in terrestrial environments. The distribution of that mass is pyramid shaped, with primary producers having the largest share of it, followed by primary and secondary consumers. In terrestrial environments, the ratio of producers to consumers is approximately 12:1, whereas it is 1:5 in marine environments. Hence, in marine environments the relative distribution of producers and consumers is reversed with an inversed biomass pyramid (Bar-On et al 2018). As proposed by Lindeman (1942), it is expected that on average, approximately 10% of available energy is transferred from a lower to a higher trophic level. However, a study by Perkins et al. (2022) demonstrates that predator-prey biomass shows a sub-linear scaling pattern, where predator biomass scales with prey biomass with a $\frac{3}{4}$ power exponent, meaning that the more prey biomass there is, it supports proportionately less predator biomass. Primary production is primarily regulated by precipitation (Linger et al. 2020). Therefore, humid terrestrial environments have more producers and also more biomass. Forests, for instance, are highly productive. Although forests only cover approximately 30% of the land surface, they contain 80% of the total plant biomass on Earth (Kindermann et al. 2007).

Through their wide-ranging influence on all environments on Earth, humans have changed how biomass is distributed among organism groups and trophic levels. For instance, present wild mammal biomass is lower, but total mammal biomass is higher, than pre-human values (Bar-On et al. 2018). Currently, the combined biomass of humans and livestock is far bigger than that of all the wild mammals combined (Bar-On et al. 2018). In addition, areas covered by forest, which is dense in biomass, is being replaced by cropland and pastures, which are lower in biomass density (Proulx et al. 2015, Hurtt et al. 2011). This deforestation has resulted in an overall decline in plant biomass on Earth (Ciais et al. 2013). However, human influences can also cause increased shares of plant biomass compared to higher trophic levels. These effects can be sufficiently strong to cause marine ecosystems, whose natural biomass distribution is top-heavy, to be transformed into a bottom-heavy biomass distribution (McCauley et al. 2018).

Earth's temperate zone is located between 23.5 and 66.5 degrees latitude on the north and the south hemisphere. Most of the climates inside it fall into C and D categories of Köppen's climate classification, characterizing them as having mild mean yearly temperatures and distinct seasonality, both in temperature and precipitation. A wide range of ecosystems can be found in temperate areas, including temperate forests, temperate grasslands, and even deserts.

Due to its climate, the temperate zone is home to a significant portion of the world's human population (Klinger and Ryan 2022) and is the most the most productive climate zone one in terms of agriculture (Gallup and Sachs 2000). The extended agriculture has caused a big destruction of temperate habitat (WWF 2020), which combined with the large human population has had negative effects on biodiversity in temperate areas (Wilson et al. 2016, Hunter 2007).

Mammalia, being one of the most known and investigated classes of the Animalia kingdom are made up of approximately 6000 extant species, which is low relatively low compared to other taxonomic groups, for instance the approximately 1 200 000 extant species within Arthropoda (Bánki et al. 2024). Total global biomass of mammals is also orders of magnitude smaller than that of terrestrial arthropods (Bar-On et al. 2018). However, given their relatively small biomass, mammals, especially larger bodied ones, have a disproportionally important role in the functioning of the biosphere (Enquist 2020). Through exertion of top-down and bottom-up processes mammals effect autotrophs, energy flow, and nutrient cycling (Lacher et al. 2019). For instance, small-bodied mammals are important pollinators and consumers of arthropods (Thomas et al. 2019), while larger ones are important in landscape modification (Frank et al. 1998). Mammals also influence community structures of autotrophs which in turn affect other vertebrates and invertebrates (Thomas et al. 2019). Some studies also claim that mammals influence disease dynamics, wildfires, carbon capturing, invasive species and biochemical exchanges (Estes et al. 2011).

In this study I aimed to investigate the distribution of mammal biomass in a temperate forest affected by human activity. I specifically aimed to evaluate if (i) it follows the rules of 10% transferring from a lower to a higher trophic level Lindeman (1942), (ii) it follows a $\frac{3}{4}$ power exponent scaling between prey and predators (Perkins et al. 2022), and (iii) it follows a 12:1 ratio of producers to consumers (Bar-on et al. 2018). To do so, I estimated the biomass of 10 mammal taxa, 6 from the order Carnivora (brown bear *Ursus arctos*, European badger *Meles meles*, European wildcat *Felis silvestris*, pine- and stone marten *Martes* sp., red fox *Vulpes vulpes* and wolf *Canis lupus*), 3 from the order Artiodactyla (wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, and red deer *Cervus elaphus*) and one from the order Rodentia (red squirrel *Sciurus vulgaris*). The biomass was further aggregated for each order as well as for three functional groups: herbivores (red deer, roe deer, red squirrel), omnivores (brown bear, wild boar, red fox, European badger) and predators (Iberian wolf, European wildcat and

martens). I estimated abundance of each species using camera trap data using the N-mixture model proposed by Royle (2004), which I then multiplied with body mass of each species to estimate biomass. In addition, I compared mammalian biomass to previous estimates of plant biomass from the same region.

2. Materials and methods

2.1. Study area

The study area is located on the northern coast of Spain, in the autonomous province of Cantabria (Fig. 1). Most of the study area lies inside the following protected areas; Parque Nacional de los Picos de Europa, Parque Natural Saja-Besaya, Parque Natural Montana Palentina, ZEPA Liebana and Parque Regional Montaña de Riaño y Mampodre. The study area covers 1125 km² and expands 130 km from east to west and 70 km from north to south. The human population of Cantabria is 600 000, most of it being in and around the area of two cities of Santander (180 000) and Torrelavega (60 000). The average population density is 109 individuals / km² and it declines from the coast towards the inland (Instituto Nacional de Estadística, 2024). Even though the study area largely lies inside protected areas, there are still human settlements, albeit not very populated, and farming of livestock such as cows and sheep. The topography of the region is characterized by rolling hills and valleys along the coast, with the terrain being more rugged moving inland, towards the study area. Elevation of the study area varies from 400 meters above sea levels (m.a.s.l.) to 2000 m.a.s.l. The climate is atlantic with mild winters (minimum average temperature of 9°C) and relatively cool summers (maximum average temperature 20°C) (Peel et al. 2007, Ancell Trueba and Célis Diaz 2012). Precipitation is around 1000 mm per year (Ancell Trueba and Célis Diaz 2012). Vegetation varies with elevation, ranging from pastures to deciduous forests, which are composed of hazel (*Corylus avellana*), beech (*Fagus sylvatica*), holly (*Ilex aquifolium*), birch (*Betula sp.*), chestnut (*Castanea sativa*) and oak (*Quercus sp.*) (Durán-Gómez 2014). Mammals present in the region range from large carnivores such as the grey wolf (*Canis lupus*) and the brown bear (*Ursus arctos*), a number of mesocarnivores, large herbivores like the red deer (*Cervus elaphus*), the roe deer (*Capreolus capreolus*) and the wild boar (*Sus scrofa*), and a number of smaller mammals (Palomo et al. 2007).

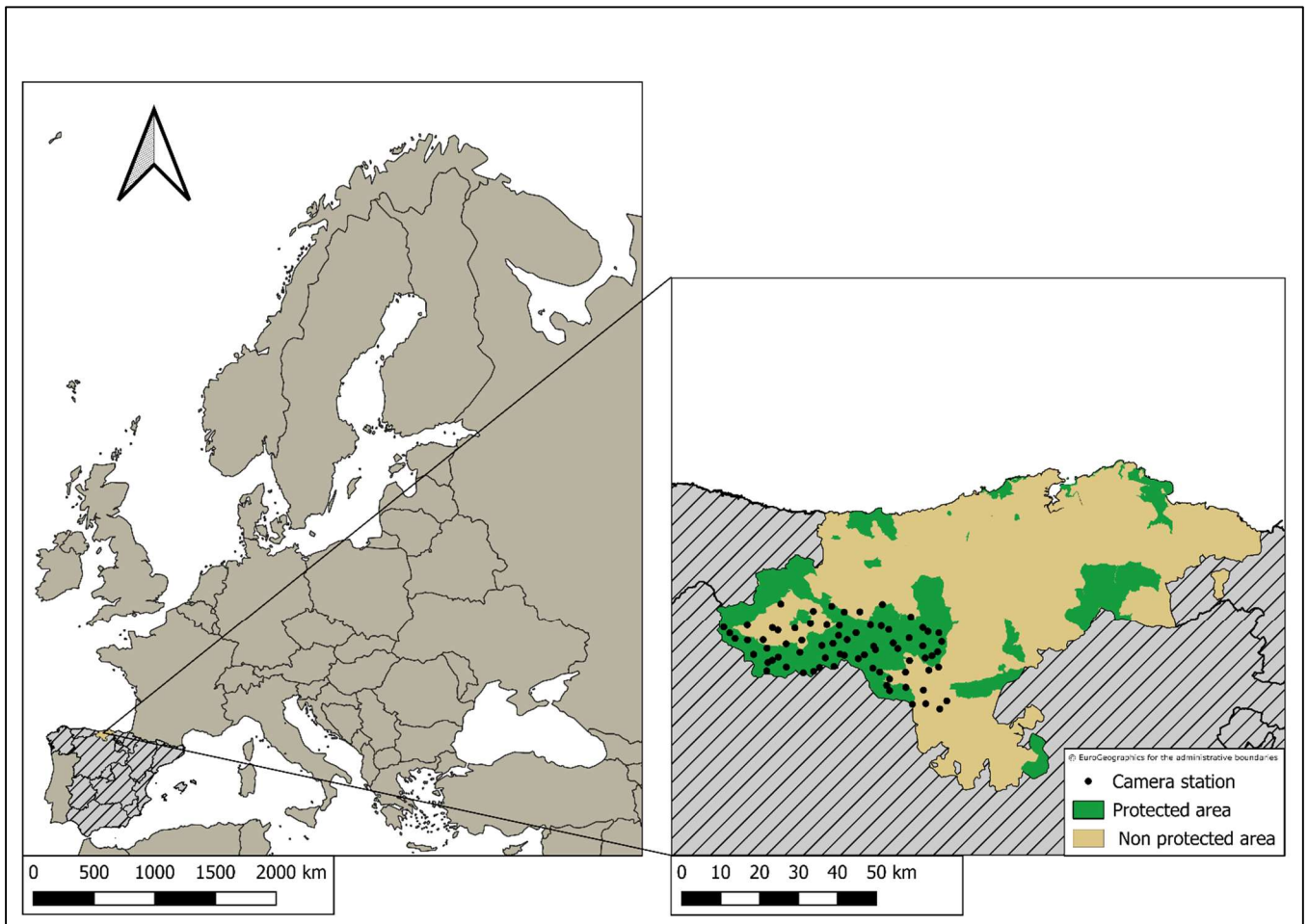


Figure 1. Location of the Autonomous Region of Cantabria in northern Spain and the locations of camera traps inside the province.

Source for administrative boundaries: <https://ec.europa.eu/eurostat/web/gisco/geodata/administrative-units/countries>

2.2. Camera trapping

I used data from a grid of camera traps owned by the Government of Cantabria and managed by the environmental consultancy IMATEC (Government of Cantabria 2021). Camera trapping was performed from 2016 until 2022 using a total of 85 cameras. The study area was divided into a grid consisting of 5*5 km cells. From 2016 until 2018 there were 36 cells, and in 2019, 14 cells were added, giving a total number of 45 cells. The Cantabrian mountains vary greatly in topography and land cover (Grilo et al. 2019; Álvarez García 2007). Each cell was therefore considered a spatially independent sample unit. One camera was placed randomly inside each cell, but constrained so that the minimum distance between two cameras always was above 3.5 km. These cameras were maintained in the same location throughout the study. Additionally,

from 2018 until 2022 there were 2-9 extra cameras added yearly, but these were moved between years and did also not follow the minimum distance of 3.5 km between cameras. Hence, the number of active cameras at any given year varied from 36 to 54. Each camera was active from 21 to 660 days (mean of 325 days \pm sd 171 days). Each camera was placed on a tree trunk approximately 1 m above the ground. To draw the animal into the optimal position for camera trapping, a bait made of fish scent was positioned approximately 7 m in front of each camera. Every camera was visited monthly to replace stolen or broken cameras, to replace batteries, to download images and to reapply the bait (Government of Cantabria 2021).

The survey used single motion triggered digital cameras (Bushnell Trophy Cam Aggressor No Glow, Bushnell, Corp., Overland Park, Kansas, USA). The angle of view of each camera was 35°, and the angle of detection was 43.9°. Maximum detection distance during the day was 25 m and during the night 20 m. The trigger speed of each camera was 0.6 s. With each trigger the camera took one photo and a brief video. During the day the video was 30 seconds long and during the night 15-seconds. After each photo and video, 6 s had to pass until the camera could be triggered again.

2.3. Estimation of abundance, density, and total biomass

I used the N-mixture model proposed by Royle (2004) to estimate the relative abundance (average number of animals per camera station) of each species from the camera trapping data. This class of model is particularly useful to estimate abundance from unmarked individuals. I converted the abundance estimates to density estimates by multiplying the estimated abundance of each species with the average group size of that species and then divided the resulting number of individuals with the estimated capture area for each camera and species. This area was set to the same for all cameras. I estimated the value for each species as the median reported home range size for that species in similar environments (Table 1). To calculate total abundance of a species, I multiplied the estimated density with the total area of the camera trapping grid (1125 km²). Finally, I estimated the biomass of each species by multiplying the total abundance with the species' estimated body mass. I retrieved body mass data on our 10 selected species from Blanco (1998), which contains reports on animals with habitats in Spain (Table 1). Only adult body masses were taken. If there was a range of masses given, or exact masses of multiple individuals, an average was calculated and recorded. If there were masses of female and male individuals, again, the average of those was used.

Table 1. Body mass (kg) and home range sizes (km²) of 10 mammal species in the Cantabrian range, northern Spain. Body masses were taken from Blanco (1998) and are expressed in kilograms. Home ranges were estimated as the median of reported home range sizes from multiple sources and are expressed in square km.

Order	Scientific name	Common name	Body mass	Home range	Home range reference
Artiodactyla	<i>Capreolus capreolus</i>	Roe Deer	24.5	0.3	Blanco (1998), Cederlund et al. (2004)
	<i>Cervus elaphus</i>	Red Deer	72	4.7	Blanco (1998)
	<i>Sus scrofa</i>	Wild Boar	75	7.79	Garza et al. (2018), Cavazza et al. (2023)
Carnivora	<i>Canis lupus</i>	Iberian Wolf	30	182.75	Ciucci et al. (2009), Kusak et al. (2005), Cederlund G et al. (2004), Blanco (1998)
	<i>Felis silvestris</i>	European Wildcat	4.25	3.78	Blanco (1998)
	<i>Martes martes</i>	Pine Marten	1.3	6.3	Blanco (1998)
	<i>Meles meles</i>	European Badger	12	1.1	Acevedo et al. (2019)
	<i>Ursus arctos</i>	Brown Bear	99	128.8	Todorov et al. (2020), Huber and Roth (1993), De Angelis et al. (2021)
	<i>Vulpes vulpes</i>	Red Fox	6	1.49	Cavallini (1996), Meia and Weber (1995), Janko et al. (2012), Blanco (1998)
Rodentia	<i>Sciurus vulgaris</i>	Red Squirrel	0.3	0.48	Lurz (2010), Blanco (1998)

3. Results

Estimated total biomass of the 10 selected mammal species was 2 349 tonnes in the whole study area, which corresponds to an average of 2.09 tonnes / km². Herbivores contributed with most biomass with 1 733 tonnes (73.76%), followed by omnivores with 606 tonnes (25.80%). There was a very limited contribution by predators with 10 tonnes (0.42%) (Table 2). The mammalian order that contributed with most biomass was Artiodactyla with 2222 tonnes (94.57%), followed by Carnivora with 126 tonnes (5.38%). There was a very limited contribution of Rodentia with 1.20 tonnes (0.05%).

Table 2. Estimated total biomass in the study area (tonnes), density of biomass (tonnes / km²) as well as the percentage of total estimated biomass of three functional groups of mammals in the Cantabrian range, northern Spain. Biomass was estimated from abundances based on camera trap photographs of 10 mammal species.

Organism type	Total biomass	Biomass density	% of biomass
Herbivores	1174	1.54	73.76
Omnivores	606	0.54	25.80
Predators	10	0.01	0.42

The two species with the highest average densities were roe deer (26.10 individuals / km²) and red deer (12.50 individuals / km²), followed by the red fox (11.08 individuals / km²) (Table 3). Brown bear and wolf had the lowest average densities, with 0.02 and 0.17 individuals/km², respectively. Both roe deer (30.61% of mammal biomass) and red deer (43.11% of mammal biomass) also contributed with most biomass, followed by wild boar (20.84%). The lowest contribution to biomass had pine marten (0.06%) and red squirrel (0.05%).

Table 3. Total abundance (animals within the whole study area), density (individuals / km²), biomass (tonnes), biomass density (tonnes / km²) and contribution of biomass of each species to the total estimated biomass (%) of 10 mammal species in the Cantabrian range, northern Spain. Abundances were estimated from camera trap photographs.

Order	Scientific name	Common name	Total abundance	Density	Biomass	Biomass density	% of biomass
Arctiodactyla	<i>Capreolus capreolus</i>	Roe Deer	29357	26.1	719.26	6.39 x 10 ⁻¹	30.61
	<i>Cervus elaphus</i>	Red Deer	14068	12.5	1012.89	9.00 x 10 ⁻¹	43.11
	<i>Sus scrofa</i>	Wild Boar	6530	5.8	489.73	4.35 x 10 ⁻¹	20.84
Carnivora	<i>Canis lupus</i>	Iberian Wolf	190	0.17	5.7	5.07 x 10 ⁻³	0.24
	<i>Felis silvestris</i>	European Wildcat	635	0.56	2.7	2.40 x 10 ⁻³	0.11
	<i>Martes martes</i>	Pine Marten	1058	0.94	1.37	1.22 x 10 ⁻³	0.06
	<i>Meles meles</i>	European Badger	3316	2.95	39.8	3.54 x 10 ⁻²	1.69
	<i>Ursus arctos</i>	Brown Bear	20	0.02	1.98	1.76 x 10 ⁻³	0.08
	<i>Vulpes vulpes</i>	Red Fox	12466	11.08	74.79	6.65 x 10 ⁻²	3.18
Rodentia	<i>Sciurus vulgaris</i>	Red Squirrel	4013	3.57	1.2	1.07 x 10 ⁻³	0.05

4. Discussion

Herbivore biomass outweighed omnivore and predator biomass by almost 3 to 1, which gives the biomass distribution a bottom heavy shape and is in line with the expected characteristic of a terrestrial ecosystem. However, the bottom heaviness was higher than theoretical expectations since the ratio of herbivore to predator biomass was as high as 170 to 1, far higher than a 10% transfer per trophic level. It was also substantially higher than the transfer rate proposed by Perkins et al. (2022), who indicated that predator biomass would scale with a $3/4$ power exponent in relation to the biomass of its prey, the herbivores in this case. However, herbivore biomass was similarly very low in relation to plant biomass, with a ratio of 11 000 to 1 using a low estimate of above ground plant biomass in temperate forest of approximately 17 000 tonnes / km² (Szwagrzyk and Gazda 2007). This observation further highlights how bottom heavy the biomass distribution in this study area appears to have been. Furthermore, mammal abundance and biomass have been shown to be higher inside than outside protected areas (Magoulick 2024, Magioli 2021), so that the results in this study likely represent the upper end of the range of mammal biomass in southern European temperate forests.

I suggest that the reason for the deviations between the observed biomass distributions and theoretical expectations is most likely related to human activities. Humans have the potential to greatly alter community biomass (Bar-on et al. 2018), either by disproportionately targeting top level consumers in eradication campaigns (Estes et al. 2011) or hunting the largest herbivores for food (Dembitzer et al. 2022). Habitat loss and modification is regularly cited as a dominant driver of defaunation in terrestrial ecosystems (Collen et al. 2014), and these processes similarly had disproportionately large influences on large bodied species and species that feed on high trophic levels, such as large carnivores with wide-ranging home ranges (Woodroffe and Ginsberg 1998), like the ones in this study. Habitat fragmentation generally has negative effect on predator population size (Ryall and Fahrig 2006), which in turn disrupts top-down processes and reduces pressure on herbivores. Additionally, members of lower trophic levels, plants and herbivores, are less affected by habitat fragmentation than higher ones. (Nouhuys 2005).

The observed levels of mammal biomass (2.09 tonnes / km²) were substantially higher compared to a previous study by Turček (1971), who estimated biomass of a total of 44 mammal species in several types of European temperate forests. The median was 0.74 tonnes / km² and

the maximum value 1 tonne / km². European forests seem to have a lower level of mammal biomass compared to New Zealand, where Brockie and Moeed (1986) estimated the biomass of omnivores and predators such as possum (*Trichosurus vulpecula*), feral cats (*Felis catus*), Norwegian rats (*Rattus rattus*), house mice (*Mus musculus*) and stoats (*Mustela erminea*). Although ungulates such as red deer, wild boar and goat (*Capra hircus*) were present, their biomass was not estimated. In the tropical rain forest of Gabon, east Africa, Prins and Reitsma (1989) estimated biomass of mammals individually weighing more than app. 500 g at 1 tonne / km². Bulk of the biomass was made up of elephant (*Loxodonta Africana cyclotis*) and primates. Ratio of prey and predator biomass was 35:1, much lower compared to the ratio of 170:1 estimated in this study. On the other hand, the savanna ecosystem in the Serengeti in Kenya had a ratio of approximately 280:1, (Delany and Happold 1979). This high ratio may have been caused by the majority of prey is migratory, and subsequently could have resulted in the ecosystem probably harbouring relatively few predators (Houston 1979, Prins and Iason 1989).

My results indicated a disproportionately high depletion in predator biomass, and in particular large carnivore biomass. Predation is an important process for most ecosystem functions as it helps maintain ecosystem services and biodiversity (Miller et al. 2001, Ritchie and Johnson 2009, Terborgh et al. 1999). Subsequently, loss of large predators can have a disproportionately negative influence on ecosystem structure and function (Ripple et al. 2014) and lead to increased herbivory and degradation of vegetation (Ripple and Beschta 2004). Predators can have cascading effects on ecosystems through their combined direct and indirect effects on prey (Owen-Smith and Mills 2008, Ray et al. 2005, Schmitz and Suttle 2001). Directly, they can influence ecosystem properties through killing prey, and indirectly, by altering prey behaviour, physiology and morphology through responses to predation risk (Creel and Christianson 2008, Dalerum et al. 2016, Estes et al. 2011, Lima 1998, Taylor 1984). Loss of large predators can lead to cascading effects that disrupt the balance of species interactions and ecosystem services, known as “trophic downgrading” (Estes 2011). Large predators are most often defined as being above 15 kg of body weight (Prugh et al. 2009), and are self-regulated, meaning they are able to limit their own population density (Wallach et al. 2015). Their ecological role is that of the apex predators, denoting their high trophic status (Wallach et al. 2015). They influence their ecosystems through top down forces and trophic cascades, which effect other species and ecosystem services (Estes 2011). They control the population of prey and smaller predators,

limiting the total predation pressure and promote biodiversity (Estes 2011, Ripple et al. 2014).

There are several factors that might affect the results derived from the type of statistical model used in this study. First, both limited number of observations as well as a sub-optimal sampling design, with a very coarse grid of 5*5 km, could have caused low precision in the abundance estimate for some species. Second, it is necessary to specify an effective area around each camera to turn the abundance estimates into densities. I used home range values recorded from literature to specify these areas, which may further have added uncertainty to the biomass estimates. However, I used home range sizes recorded from the same study area when available, and when not, I used home range sizes from as similar environments as possible. More accurate home range values could potentially enhance the precision of the biomass estimates. Furthermore, I have assumed that the whole study area was saturated with animals. This may not have been accurate. For instance, a species such as the roe deer is primarily confined to the borders of forests and fields, and therefore have relatively small home ranges. This may result in inflated total abundance estimates if the densities are extrapolated across larger regions. This may have influenced the biomass estimates of some species. Finally, increasing the accuracy of both group sizes and body masses could also increase the precision of the estimated biomass. However, despite these methodological concerns, I assume that my results are at least qualitatively robust, and that they reflect the relative biomass ratio of predators to herbivores as well as the ratio of mammals to plants.

5. Conclusion

To conclude, the biomass distribution of 10 mammal species residing mostly inside protected areas in a human-modified landscape did not follow the 10% transfer per trophic level, nor did predator biomass scale with a $\frac{3}{4}$ power exponent in relation to the biomass of its prey. Instead, the biomass distribution was exceptionally bottom heavy with a disproportionately low predator biomass. This was particularly pronounced for large carnivores. Results in this study likely represent the upper end of the range of mammal biomass in southern European temperate forest, as they were mostly derived from inside protected areas. Therefore, I suggest that the deviations between the observed biomass distributions and theoretical expectations represent a strong example of ecological changes caused by human activities.

6. Acknowledgements

The Government of Cantabria and IMATEC provided the camera trap data.

© EuroGeographics for the administrative boundaries.

7. References

- Acevedo P., Prieto M., Quirós P., Merediz I., de Juan L., Infantes-Lorenzo J. A., Triguero-Ocaña R., Balseiro A. (2019): Tuberculosis Epidemiology and Badger (*Meles meles*) Spatial Ecology in a Hot-Spot Area in Atlantic Spain. *Pathogens* 8: 292.
<https://doi.org/10.3390/pathogens8040292>
- Álvarez García M. A. (2007): La cartografía temática ambiental del Principado de Asturias. *Conservación Vegetal* 11: 25–26.
- Ancell Trueba R., Célis Díaz R. (2012): Termoplumiometría de Cantabria durante el periodo 1981–2010 [Thermoplumiometry of Cantabria during the period 1981–2010]. State Meteorological Agency, Madrid
- Bar-On Y. M., Phillips R., Milo R. (2018): The biomass distribution on Earth. *PNAS* 115(25): 6506-6511. <https://doi.org/10.1073/pnas.171184211>
- Bánki O., Roskov Y., Döring M., Ower G., Hernández Robles, D. R., Plata Corredor C. A., Stjernegaard Jeppesen T., Örn A., Vandepitte L., Hobern D., Schalk P., DeWalt R. E., Ma K., Miller J., Orrell T., Aalbu R., Abbott J., Adlard R., Aedo C., et al. (2024): Catalogue of Life (Annual Checklist 2024). Catalogue of Life, Amsterdam, Netherlands.
<https://doi.org/10.48580/dg9ld>
- Brockie R.E. and Moeed A. (1986): Animal biomass in a New Zealand forest compared with other parts of the world. *Oecologia* 70(1): 24-34. doi: 10.1007/BF00377108
- Cavallini, P. (1996): Variation in the social system of the red fox. *Ethology Ecology & Evolution* 8(4): 323–342. <https://doi.org/10.1080/08927014.1996.9522906>
- Cavazza S., Brogi R., Apollonio M. (2023): Sex-specific seasonal variations of wild boar distance traveled and home range size. *Current Zoology* zoad021.
<https://doi.org/10.1093/cz/zoad021>
- Carlos Blanco J. (1998): Mamíferos de España, Editorial Planeta, Barcelona ISBN 84-08-02749-2
- Ciais P., Sabine C., Bala G., Bopp L., Brovkin V., Canadell J., Chhabra A., DeFries R., Galloway J., Heimann M., Jones C., Le Quéré C., Myneni R. B., Piao S. and Thornton (2013): Carbon and Other Biogeochemical Cycles. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Cederlund G., Liberg O., Kjellander P. (2004): Bockjakt ändrar inte reviren. In Jansson G, Seiler C, Andrén H (Eds.) Skogsvilt III: Vilt och landskap i förändring, pp.107-110. Grimsö forskningsstation, Ridrarhyttan.

Ciucci P., Boitani L., Francisci F., Andreoli G. (2009): Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology* 243: 803-819
<https://doi-org.sire.ub.edu/10.1111/j.1469-7998.1997.tb01977.x>

Collen B., Whittton F., Dyer E. E., Baillie J. E., Cumberlidge N. et al. (2014): Global patterns of freshwater species diversity, threat and endemism. *Glob. Ecol. Biogeogr.* 23: 40–51
doi: [10.1111/geb.12096](https://doi.org/10.1111/geb.12096)

Creel S., and Christianson D. (2008): Relationships between direct predation and risk effects. *Trends in Ecology & Evolution* 23: 194–201. doi: [10.1016/j.tree.2007.12.004](https://doi.org/10.1016/j.tree.2007.12.004)

Dalerum F., Hellström P., Miranda M., Nyström J., Ekenstedt J., Angerbjörn A. (2016): Network topology of stable isotope interactions in a sub-arctic raptor guild. *Oecologia* 182: 511–518. doi: [10.1007/s00442-016-3658-6](https://doi.org/10.1007/s00442-016-3658-6)

Dembitzer J., Barkai R., Ben-Dor M., Meiri S. (2022): Levantine overkill: 1.5 million years of hunting down the body size distribution. *Quaternary Science Reviews* 276.
<https://doi.org/10.1016/j.quascirev.2021.107316>

Delany M. J. and Happold D. C. P. (1979): *Ecology of African Mammals*. Longman, London

De Angelis D., Huber D., Reljic S., Ciucci P., Kusak J. (2021): Factors affecting the home range of Dinaric-Pindos brown bears. *Journal of Mammalogy* 102: 481-493.
<https://doi.org/10.1093/jmammal/gyab018>

Durán-Gómez J. A. (2014): *Catálogo de la Flora Vasculare de Cantabria [Catalogue of the Vascular Flora of Cantabria]*. Monografías e Botánicas Iberica No 13. Jolube Consultor Botánico y Editor, Jaca

Enquist, B.J., Abraham, A.J., Harfoot, M.B.J. et al. (2020): The megabiota are disproportionately important for biosphere functioning. *Nat. Commun.* 11(699).
<https://doi.org/10.1038/s41467-020-14369-y>

Estes J.A. et al. (2011): Trophic Downgrading of Planet Earth. *Science* 333: 301-306. doi: [10.1126/science.1205106](https://doi.org/10.1126/science.1205106)

European Commission, Eurostat (ESTAT), GISCO (2020):
<https://ec.europa.eu/eurostat/web/gisco/geodata/administrative-units/countries>
(accessed: 5. 05. 2024.)

Frank D. A., McNaughton S. J., Tracy B. F. (1998): The ecology of the Earth's grazing ecosystems. *BioScience* 48: 513–521. <http://links.jstor.org/sici?sici=0006-3568%28199807%2948%3A7%3C513%3ATEOTEG%3E2.0.CO%3B2-E>

Garza S. J., Tabak M. A., Miller R. S., Farnsworth M. L., Burdett C. L. (2018): Abiotic and biotic influences on home-range size of wild pigs (*Sus scrofa*). *Journal of Mammalogy* 99: 97-107.

<https://doi.org/10.1093/jmammal/gyx154>

Grilo C., Lucas P. M., Fernández-Gil A., Seara M., Costa G., Roque S., Rio-Maior H., Nakamura M., Álvares F., Petrucci-Fonseca F., Revilla E. (2019): Refuge as major habitat driver for wolf presence in human modified landscapes. *Anim. Conserv.* 22: 59–71.

<https://doi.org/10.1111/acv.12435>

Government of Cantabria (2021): Red de seguimiento de fauna silvestre de Cantabria [Wildlife monitoring network of Cantabria]. Government of Cantabria, Santander.

Gallup J. L., Sachs J. D. (2000): Agriculture, Climate, and Technology: Why Are the Tropics Falling Behind? *Amer. J. Agr. Econ.* 82(3): 731-737. doi: [10.1111/0002-9092.00071](https://doi.org/10.1111/0002-9092.00071)

Houston D. C. (1979): The adaptations of scavengers. In Sinclair ARE & Norton-Griffiths M (Eds.) *Serengeti: Dynamics of an Ecosystem*, pp. 263-286. Chicago University Press, Chicago.

Huber D., Roth H.U. (1993): Movements of European brown bears in Croatia. *Acta Theriologica* 38: 151-159.

Hurt G., Chini L., Frolking S., Betts R., Feddema J., Fischer G., Fisk J., Hibbard K., Houghton R., Janetos A., Jones C., Kindermann G., Kinoshita T., Klein Goldewijk K., Riahi K., Shevliakova E., Smith S., Stehfest E. Thomson A. Wang Y. (2011): Harmonization of Land-Use Scenarios for the Period 1500-2100: 600 Years of Global Gridded Annual Land-Use Transitions, Wood Harvest, and Resulting Secondary Lands. *Climatic Change*. 109(1): 117-161.

doi: [10.1007/s10584-011-0153-2](https://doi.org/10.1007/s10584-011-0153-2)

Hunter P. (2007): The human impact on biological diversity. How species adapt to urban challenges sheds light on evolution and provides clues about conservation. *EMBO Rep* 8(4): 316-318. doi: [10.1038/sj.embor.7400951](https://doi.org/10.1038/sj.embor.7400951)

Instituto Nacional de Estadística (2024): <https://www.ine.es> (accessed 18. 04. 2024.)

Janko C., Schröder W., Linke S., König A. (2012): Space use and resting site selection of red foxes (*Vulpes vulpes*) living near villages and small towns in Southern Germany. *Acta Theriol.* 57: 245–250. <https://doi-org.sire.ub.edu/10.1007/s13364-012-0074-0>

Kindermann G., McCallum I., Fritz S., Obersteiner M. (2007): A Global Forest Growing Stock, Biomass and Carbon Map Based on FAO Statistics. *Silva Fennica*. 42(3). doi: [10.14214/sf.244](https://doi.org/10.14214/sf.244)

Klinger B. A., Ryan S. J. (2022): Population distribution within the human climate niche. *PLOS Clim* 1(11): e0000086. <https://doi.org/10.1371/journal.pclm.0000086>

- Kusak J., Skrbinišek A. M., Huber D. (2005): Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *Eur. J. Wildl. Res.* 51: 254–262. <https://doi-org.sire.ub.edu/10.1007/s10344-005-0111-2>
- Lacher T., Davidson A., Fleming T., Gomez-Ruiz E., McCracken G., Owen-Smith N., Peres C., Wall S. (2019): The functional roles of mammals in ecosystems. *Journal of Mammalogy*. 100: 942-964. doi: 10.1093/jmammal/gyy183
- Lima S. L. (1998): Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48: 25–34. <https://doi.org/10.2307/1313225>
- Lindeman R. L. (1942): The trophic-dynamic aspect of ecology. *Ecology* 23: 399–417. <https://doi.org/10.2307/1930126>
- Linger E., Aaron Hogan J., Cao M., Zhang W., Yang X., Hu Y. (2020): Precipitation influences on the net primary productivity of a tropical seasonal rainforest in Southwest China: A 9-year case study. *Forest Ecology and Management* 467(2): 118153. <https://doi.org/10.1016/j.foreco.2020.118153>
- Lurz P. (2010): *Red Squirrels: Naturally Scottish*, Scottish Natural Heritage, Redgorton.
- Magioli M., Rios E., Benchimol M., Cavenague Casanova D., et al. (2021): The role of protected and unprotected forest remnants for mammal conservation in a megadiverse Neotropical hotspot, *Biological Conservation* 259. <https://doi.org/10.1016/j.biocon.2021.109173>
- Magoulick, K.M., Hull, V. Liu, J. (2024): Mammal recovery inside and outside terrestrial protected areas. *Ambio* 53: 1296–1306. <https://doi.org/10.1007/s13280-024-02014-7>
- McCauley D. J., Gellner G., Martinez N. D., Williams R. J., Sandin S. A., Micheli F., Mumby P. J., McCann K. S. (2018): On the prevalence and dynamics of inverted trophic pyramids and otherwise top-heavy communities. *Ecol. Lett.* 21(3): 439-454. doi: 10.1111/ele.12900
- Meia J. S., Weber J. M. (1995): Home ranges and movements of red foxes in central Europe: stability despite environmental changes. *Canadian Journal of Zoology* 73: 1960-1966. <https://doi-org.sire.ub.edu/10.1139/z95-230>
- Miller B., Dugelby B., Foreman D., Martinez del Rio C., Noss R., Phillips M., Soulé M. E., Terborgh J., Wollcox L. (2001): The importance of large carnivores to healthy ecosystems. *Endangered Species Update* 18: 202–210.
- Nouhuys S. (2005): Effects of Habitat Fragmentation at Different Trophic Levels in Insect Communities. *Annales Zoologici Fennici* 42(4): 433–447. <http://www.jstor.org/stable/23735888>
- Owen-Smith N, Mills M. G. (2008): Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology* 89(4): 1120-1233. doi: 10.1890/07-0970.1
- Palomo J., Gisbert J., Blanco J. C. (2007): *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid

- Peel M. C., Finlayson B. L., McMahon T. A. (2007): Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth. Syst. Sci.* 11: 1633–1644.
<https://doi.org/10.5194/hess-11-1633-2007>
- Perkins D. M., Hatton I. A., Gauzens B., Barnes A. D., Ott D., Rosenbaum B., Vinagre C., Brose U. (2022): Consistent predator-prey biomass scaling in complex food webs. *Nat. Commun.* 13(4990). <https://doi.org/10.1038/s41467-022-32578-5>
- Prins H. H. T., Reitsma J. M. (1989): Mammalian Biomass in an African Equatorial Rain Forest. *The Journal of Animal Ecology* 58(3): 851-861. doi:10.2307/5128
- Prins H. H. T., Iason G. R. (1989): Dangerous Lions and Nonchalant Buffalo. *Behaviour* 108(3/4): 262–296. <http://www.jstor.org/stable/4534754>
- Proulx R., Rheault G., Bonin L., Roca I. T., Martin C. A., Desrochers L., Seiferling I. (2015): How much biomass do plant communities pack per unit volume? *PeerJ*. 3(3): e849
<https://doi.org/10.7717/peerj.849>
- Prugh, L., Stoner, C., Epps, C., Bean, W., Ripple, W., Laliberte, A., Brashares, J. (2009): The Rise of the Mesopredator. *Aspen Bibliography* 59. doi: 10.1525/bio.2009.59.9.9
- Ray J. C., Redford K. H., Steneck R. S., Berger J. (Eds.). (2005): Large carnivores and the conservation of biodiversity. Washington DC, Island Press.
- Ripple W. J., and Beschta R. L. (2004): Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience* 54(8): 755-766.
 doi: [10.1641/0006-3568\(2004\)054\[0755:WATEOF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2)
- Ripple, W. J., Estes J., Beschta, R., Wilmers C., Ritchie E., Hebblewhite M., Berger J., Elmhagen B., Letnic M., Nelson M., Schmitz O., Smith D., Wallach A., Wirsing A. (2014): Status and Ecological Effects of the World's Largest Carnivores. *Science* 343.
 doi: 10.1126/science.1241484
- Ritchie, E. G., and Johnson, C. N. (2009): Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12: 982–998. doi: [10.1111/j.1461-0248.2009.01347.x](https://doi.org/10.1111/j.1461-0248.2009.01347.x)
- Royle, J.A. (2004), N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* 60: 108-115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x>
- Ryall K. L., and Fahrig L. (2006): Response of Predators to Loss and Fragmentation of Prey Habitat: A Review of Theory. *Ecology* 87(5): 1086–1093.
<http://www.jstor.org/stable/20069047>
- Schmitz O. J., and Suttle K. B. (2001): Effects of top predator species on direct and indirect interactions in food webs. *Ecology* 82(8): 2072-2081. doi: [10.2307/2680070](https://doi.org/10.2307/2680070)

Szwagrzyk J., Gazda A. (2007): Above-ground standing biomass and tree species diversity in natural stands of Central Europe. *Journal of Vegetation Science* 18: 555-562.
doi: [10.1111/j.1654-1103.2007.tb02569.x](https://doi.org/10.1111/j.1654-1103.2007.tb02569.x)

Taylor R. J. (1984): *Predation*. Springer Verlag.

Terborgh J., Estes J. A., Paquet P., Ralls K., Boyd-Heger D., Miller B. J., Noss R. F. (1999): The role of top carnivores in regulating terrestrial ecosystems. In M. E. Soulé and J. Terborgh (Eds.), *Continental conservation: Scientific foundations of regional reserve networks*, pp. 39–64. Island Press.

Todorov V., Zlatanova D., Valchinkova K. (2020): Home range, mobility and hibernation of brown bears (*Ursus arctos*, Ursidae) in areas with supplementary feeding. *Nature Conservation Research* 5: 1-15. <https://dx.doi.org/10.24189/ncr.2020.050>

Thomas L., Davidson A., Fleming T., Gomez-Ruiz E., McCracken G., Owen-Smith N., Peres C., Wall S. (2019): The functional roles of mammals in ecosystems. *Journal of Mammalogy* 100: 942-964. doi: [10.1093/jmammal/gyy183](https://doi.org/10.1093/jmammal/gyy183)

Turček F.J. (1971): On vertebrate secondary production in forests. In Duvigneaud P (Ed.), *Productivity of forest ecosystems: proceedings of the Brussels Symposium*, pp. 348–354. UNESCO, Paris

Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J. and Shanas, U. (2015): What is an apex predator? *Oikos* 124: 1453-1461. <https://doi.org/10.1111/oik.01977>

Wilson M. C., Chen X. Y., Corlett R. T. et al. (2016): Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecol.* 31: 219–227.
<https://doi.org/10.1007/s10980-015-0312-3>

Woodroffe R., and Ginsberg J. R. (1998): *Edge Effects and the Extinction of Populations Inside Protected Areas*. *Science* 280: 2126-2128. doi: [10.1126/science.280.5372.2126](https://doi.org/10.1126/science.280.5372.2126)

WWF (2020): *Living Planet Report 2020 - Bending the curve of biodiversity loss*. Almond R. E. A., Grooten M. and Petersen T. (Eds). WWF, Gland, Switzerland.

8. Curriculum Vitae

My name is Andro Pleskalt. I was born on October 31, 2001, in Zagreb. After completing Gustav Krklec Primary School in 2016, I enrolled in the 1st Gymnasium in Zagreb, which I completed in 2020. That same year, I enrolled in the undergraduate program in Environmental Science at the Faculty of Science, University of Zagreb, which I am set to complete in 2024 with a thesis titled 'Biomass distribution of sympatric mammals in southern Europe,' under the mentorship of Frederik Dalerum PhD and co-mentorship of prof. Perica Mustafić PhD.