

Títol del treball:

**ASSESSING THE HABITAT AND ANTHROPOGENIC DRIVERS
ON MESO- AND MACROMAMMALS DIVERSITY IN THE
WESTERN MEDITERRANEAN BASIN**

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INDEX

RESUM	i
RESUMEN	ii
ABSTRACT	iii
REFLECTIONS ON ETHICS, SUSTAINABILITY AND GENDER PERSPECTIVE	iv
INTRODUCTION	1
1.1. Diversity of mammals	1
1.2. Mammals in the Mediterranean Basin	2
1.3. Camera trapping as a tool to study mammal diversity	3
OBJECTIVES	3
MATERIAL AND METHODS	4
2.1. Study area	4
2.2. Data sources	4
2.3. Species diversity calculations	6
2.4. Spatial treatment of environmental parameters	8
2.5. Statistical treatments	12
RESULTS	13
DISCUSSION	20
CONCLUSIONS	23
BIBLIOGRAPHY	24

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RESUM

A la Conca del Mediterrani, considerada un punt calent de biodiversitat, s'hi troben 184 espècies de mamífers. La seva presència i abundància dins de la regió estan influenciades per diversos factors.

Aquest treball busca determinar si l'heterogeneïtat de paisatge, el grau d'antropització i la variació d'aquests en els darrers 30 anys afecten l'alfa i beta diversitat de macro i mesomamífers terrestres en aquesta regió. Per fer-ho, s'han utilitzat dades de càmeres de fototrampeig situades en 29 Parcel·les de Seguiment Permanent de Carnívors (PSPCs) repartides per Catalunya. Les espècies de mamífers terrestres amb un pes superior a 1 kg detectades s'han classificat en carnívors domèstics, herbívors domèstics, carnívors salvatges, ungulats salvatges, i lagomorfs i grans rosegadors, i s'ha calculat l'alfa i la beta diversitat de cada categoria, així com del global dels mamífers salvatges. S'han realitzat regressions lineals simples i anàlisis multimodels entre les diversitats i diferents variables relacionades amb el clima i les condicions ambientals, l'heterogeneïtat paisatgística o el grau d'antropització. Amb aquestes mateixes, s'han realitzat anàlisis de redundància (RDAs) per saber les variables i espècies que més determinen la composició de les comunitats de mamífers.

Els índexs que mesuren de forma directa l'heterogeneïtat del paisatge, el grau d'antropització i el seu canvi en els últims 30 anys no han mostrat correlació amb la diversitat. En canvi, la diferència d'altitud dins la PSPC i el RAI de carnívors domèstics sí mostren una major correlació. Malgrat això, les variables que mostren més correlació amb la diversitat són les ambientals, com la precipitació i l'altitud mitjana.

Els RDAs mostren unes poques espècies, tant generalistes (guineu i cabirol) com especialistes de camps oberts (conill), amb una influència molt alta en la configuració de les comunitats. Això indica la importància de conservar les zones obertes, així com els Pirineus, únic hàbitat d'algunes de les espècies detectades.

La disparitat de resultats en funció de la variable escollida per mesurar un factor impedeix treure conclusions fermes sobre les hipòtesis inicials. Malgrat això, el fet que les variables climàtiques hagin sigut generalment les més importants en determinar la diversitat de mamífers, indica que en el futur el canvi climàtic podria ser el principal factor d'amenaça per a les poblacions de mamífers en aquesta àrea.

RESUMEN

En la Cuenca del Mediterráneo, considerada un punto caliente de biodiversidad, se encuentran 184 especies de mamíferos. Su presencia y abundancia en la región están influenciadas por diversos factores.

Este trabajo busca determinar si la heterogeneidad de paisaje, el grado de antropización y la variación de estos en los últimos 30 años afectan la alfa y beta diversidad de macro y mesomamíferos terrestres en esta región. Para hacerlo, se han utilizado datos de cámaras de fototrampeo situadas en 29 Parcelas de Seguimiento Permanente de Carnívoros (PSPCs) repartidas por Cataluña. Las especies de mamíferos terrestres con un peso superior a 1 kg detectadas se han clasificado en carnívoros domésticos, herbívoros domésticos, carnívoros salvajes, ungulados salvajes, y lagomorfos y grandes roedores, y se ha calculado la alfa y la beta diversidad de cada categoría, así como del global de los mamíferos salvajes. Se han realizado regresiones lineales simples y análisis multimodelos entre las diversidades y diferentes variables relacionadas con el clima y las condiciones ambientales, la heterogeneidad paisajística o el grado de antropización. Con estas mismas, se han realizado análisis de redundancia (RDAs) para saber las variables y especies que más determinan la composición de las comunidades de mamíferos.

Los índices que miden de forma directa la heterogeneidad del paisaje, el grado de antropización y su cambio en los últimos 30 años no han mostrado correlación con la diversidad. En cambio, la diferencia de altitud dentro de la PSPC y el RAI de carnívoros domésticos sí muestran una mayor correlación. Pese a ello, las variables que muestran más correlación con la diversidad son las ambientales, como la precipitación y la altitud media.

Los RDAs muestran unas pocas especies, tanto generalistas (zorro y corzo) como especialistas de campos abiertos (conejo), con una influencia muy alta en la configuración de las comunidades. Eso indica la importancia de conservar las zonas abiertas, así como los Pirineos, único hábitat de algunas de las especies detectadas.

La disparidad de resultados en función de la variable escogida para medir un factor impide sacar conclusiones firmes sobre las hipótesis iniciales. Pese a ello, el hecho de que las variables climáticas hayan sido generalmente las más importantes en determinar la diversidad de mamíferos, indica que en el futuro el cambio climático podría ser el principal factor de amenaza para las poblaciones de mamíferos en esta área.

ABSTRACT

In the Mediterranean Basin, considered a biodiversity hotspot, 184 mammal species are found. Its presence and abundance inside the region are influenced by several factors.

This work aims to determine if landscape heterogeneity, anthropization degree and variation of both during the last 30 years affect the alpha and beta diversity of terrestrial macro and meso-mammals in this region. To do so, data from camera trapping in 29 Carnivores Permanent Tracking Plots (PSPCs) located along Catalonia was used. Detected species of terrestrial mammals with a weight higher than 1 kg were classified between domestic carnivores, domestic herbivores, wild carnivores, wild ungulates, and lagomorphs and big rodents. The alpha and beta diversity of each group, as well as the one for all wild mammals, have been calculated. Simple linear regressions and multimodal analysis have been conducted between diversities and different variables related with climate and environmental conditions, landscape heterogeneity and anthropization degree. With those, redundancy analyses (RDAs) have been conducted to know the variables and species that determine the composition of mammalian communities.

Indexes that measure in a direct way landscape heterogeneity, anthropization degree and its change in the last 30 years have shown no correlation with diversity. However, differences in elevation inside the PSPC and RAI of domestic carnivores have shown a greater correlation. Nonetheless, the variables that showed more correlation with diversity are the environmental ones, like rainfall and mean elevation.

RDAs show a few species, both generalists (red fox and roe deer) and open field specialists (rabbit), with a very high influence on the configuration of communities. That shows the importance of conserving open areas, as well as the Pyrenees, only habitat of some of the detected species.

The disparity among results depending on the chosen variable to measure a factor does not allow drawing firm conclusions about the initial hypothesis. However, the fact that climatic variables have been generally found as the most important determinants of mammal diversity, shows that in the future climate change might be the largest threat to mammal populations in this area.

REFLECTIONS ON ETHICS, SUSTAINABILITY AND GENDER PERSPECTIVE

Ethics

ICHN, the institution that includes FELIS Group, is a branch of the Institut d'Estudis Catalans, which receives most of its funding from public sources. Although that, the IEC is also financed by La Caixa Foundation and other private sponsors, as well as by its individual members. Ethics in animal ecology and conservation has a clearly utilitarianist vision, because it usually tries to protect the maximum number of species, even if this can imply concentrating less efforts or even harming other species with fewer risks. Despite that, and as happens in many other fields, ethical currents that defend animal rights are rising. The main technique used in this work, the camera trapping, is not intrusive and allows the study of animals with a minimum effect on them.

Sustainability

FELIS Group, as well as the ICHN, is very committed to sustainability. The research field of the group is very related with the Sustainable Development Goal (SDG) 15 (life on land), because it aims to study wildlife in forests and other terrestrial ecosystems. It is also related with other SDGs like the 13th (climate action, because its data can help to decide on measures to mitigate climate change) or the 17th (partnership for the goals, because it collaborates with other European research teams). Another field in which FELIS Group is committed is environmental sensibilization and education, as shown by its educative project "The wild cat, our forests feline", which includes itinerant expositions, talks in schools, field trips, etc.

Gender perspective

The ICHN Directive Council is formed by 17 men (70.8%) and 7 women (29.2%), so a bias towards a higher number of men is observed. Although that, the president of the Directive Council is a woman (Jordina Belmonte), so it seems there is not a glass ceiling in this institution. Inside the Council, the FELIS Group is represented by a woman (Joana Bastardas), although the other two members of the group that belong in the Council are men. Regarding the volunteers in charge of the PSPCs, there are 87 men (71.3%) and 35 women (28.7%). These proportions are practically identical to those found in the ICHN Directive Council, so in this case there is not a scissors graphic, but a bias in sex proportion in all research levels. This might be due to the more difficulties that women find in the current system to prosper in scientific careers, known as sticky floor.

INTRODUCTION

1.1. Diversity of mammals

Mammals form a class of vertebrates including more than 6,000 species from more than 1,000 genera and from 167 families (Burgin *et al.*, 2018), most of them placental. They are homeothermic, and this has allowed them to expand and reach almost every corner of the world. The heterogeneity of the group is shown by the great variety of habitats they occupy, from the polar regions to the deserts, and from the top of the mountains to the sea. They also present a huge range of size and weight. According to the International Union for the Conservation of Nature (IUCN), 27% of mammal species are threatened with extinction, being the second most threatened group of tetrapods, just after amphibians (IUCN, 2022).

Mammal diversity can be measured in different ways, and is affected by multiple factors. Its conservation, as it is the case in many other animal groups, is crucial because recovering it would take millions of years (Davis *et al.*, 2018). Mammal species richness is correlated, like most taxa, with the area studied, whereas other important factors were latitude, topographic and habitat heterogeneity, as well as historical biogeography, particularly on peninsulas (Ceballos & Brown 1995; Fløjgaard *et al.* 2010). Macroclimatic variables and human influence are also important predictors of mammal richness and are difficult to distinguish among them (Fløjgaard *et al.* 2010). Although mammals follow a latitudinal gradient of species richness, with more species found in the tropical zones, diversification rates in this group do not correlate with latitude (Soria-Carrasco & Castresana, 2012). In fact, the latitudinal gradient in mammals does not apply in most of Europe, as the highest mammal richness is found in Central Europe rather than in the South, where there is a higher degree of endemism due to the role of Southern Europe during the last glaciation (Baquero & Tellería, 2001). Species richness is an important parameter of alpha (α) diversity. Alpha diversity refers to the number of species present in a given area, while gamma (γ) diversity is the regional species diversity. Beta (β) diversity is the variation in species composition between areas of a region, that is to say, the relation between alpha and gamma diversities.

According to the resource-use hypothesis proposed by Vrba (1987), biome specialists have higher speciation and extinction rates because of their higher susceptibility to climate changes. This hypothesis has been tested several times at global and regional level, with most of studies showing other factors affecting diversity of mammals, such as climatic and geographical heterogeneity (Hernández Fernández & Vrba, 2005; Cantalapiedra *et al.*, 2011; Hernández Fernández *et al.*, 2022). Some studies have pointed out that species richness is mostly affected by environmental factors, such as climate (Oliveira *et al.*, 2016). However, a minority have pointed at the importance of habitat heterogeneity, measured as topographic heterogeneity and local variation in energy availability, in the richness of mammal species (Kerr & Packer, 1997). A study of small mammals in Utah showed that environmental variables (temperature, precipitation and habitat heterogeneity, among others) alone or in combination with others could not explain the species richness (Rowe, 2009).

Discrepancy between some of these studies might be explained by the anthropic effects on mammals. The relationship between mammals and anthropic disturbance has been extensively studied (Ohashi *et al.*, 2012; Oberosler *et al.*, 2017; Nix *et al.*, 2018; Cremonesi

et al., 2021; Rosalino *et al.*, 2022). Historically, humans have caused 96% of mammal extinctions during the last 126,000 years (Andermann *et al.*, 2020), mostly during the Quaternary extinction. Nowadays, it is debated whether mammal diversity is more affected by human activity or environmental conditions. Despite this, most studies give more importance to environmental conditions than to human factors in most mammalian groups (Real *et al.*, 2003). In this line, Santos *et al.*, (2020) found that a higher level of human disturbances correlated with greater species richness and trait diversity. Therefore, habitat loss and fragmentation is one of the most important threats to mammals, with terrestrial species of higher body mass and herbivores being the most affected when different indicators of genetic diversity are compared (Lino *et al.*, 2018).

These findings might be explained by another well-studied relationship between mammal diversity and habitat heterogeneity (August, 1993; Tews *et al.*, 2004). Pita *et al.* (2009) found that the highest carnivore richness in the Iberian Peninsula was found in mosaic landscapes with small agriculture fields, patches and corridors of woody vegetation and human presence. Swan *et al.* (2020) found a positive relationship between mammalian beta-diversity and habitat heterogeneity along the productivity gradient in environments with recurrent wildfires, while habitat heterogeneity had a weak negative effect on alpha-diversity. Furthermore, Regolin *et al.* (2020) found that spatial heterogeneity and habitat configuration were more in determining alpha and beta diversities of mammals than habitat composition in Brazil.

1.2. Mammals in the Mediterranean Basin

The Mediterranean Basin (MB) comprises all the territories surrounding the Mediterranean Sea, located among Southern Europe, Northern Africa and Eastern Asia, in the North hemisphere and in the Palearctic realm. Together with zones of California and Eastern North America, as well as certain areas in South Australia, South Africa and South America, it presents a Mediterranean climate, characterized by hot and dry summers and mild wet and warm winters (Lionello *et al.*, 2006). Although only 4.7% of the original extent remains as primary vegetation, it contains 13,000 plant species that are endemic, representing a 4.3% of the total number of plant species in the world and more than a half of the 25,000 plant species found in the zone (Myers *et al.*, 2000).

The Mediterranean Basin is considered as a biodiversity hotspot, containing 770 species of vertebrates, 235 of which are endemic, representing 0.9% of the global vertebrate species (Myers *et al.*, 2000). These numbers show a much higher degree of endemism among plants than among animals in the zone. Many of the vertebrate endemisms are found in islands and archipelagos.

In this region, 184 species of mammals are found, 46 of which are Mediterranean endemisms (Myers *et al.*, 2000). The Pyrenees and Pre-Pyrenees area (West corner of the MB) is considered a mammalian hotspot within the Iberian Peninsula (López-López *et al.*, 2011). On the other hand, after excluding humans and domestic animals, in Catalonia (NE of Iberian Peninsula) there are 103 extant mammal species of 25 families (Generalitat de Catalunya, 2021), representing more than 55% of the Mediterranean species, 1.5% of the world species and almost 15% of the families of mammals in the world. Among the main mammal groups, there are 16 species of terrestrial carnivores (two of them threatened, *Mustela lutreola* Linnaeus, 1761 and *Lynx pardinus* Temminck, 1827) and 7 of artiodactyls (none of them threatened), as well as 3 species of lagomorphs (one of them endangered,

Oryctolagus cuniculus Linnaeus, 1758). These regional numbers do not include exotic species that have not yet been established in the territory, such as the *Castor fiber* (Linnaeus, 1758) reintroduced about 20 years ago in the Ebro river (Halley *et al.*, 2021).

Different studies have been conducted in Catalonia relating the factors that affect the diversity of mammals. Hawkins & Pausas (2004) observed no influence of plant species richness on mammal species richness, while the last being more influenced by factors conditioning water availability, such as temperature, precipitation and humidity. These results were generally confirmed by Ferrer-Castán *et al.* (2016). Furthermore, Varga *et al.* (2019) found a higher mammal species richness in non-urban areas, specially in mixed forests ones. Nonetheless, studies focusing on the effects of both environmental and anthropic variables in mammal diversity are lacking, specifically in the Mediterranean Basin. A possible reason of this gap is that some of these mammal species are nocturnal or avoid direct contact with humans (Rogala *et al.*, 2011; Teixeira *et al.*, 2023), a fact that makes it more difficult to detect its presence and count its abundance.

1.3. Camera trapping as a tool to study mammal diversity

In recent years, camera trapping has become an essential tool to study large mammals. Camera trapping consists of automatic cameras that take photos when they detect movement, allowing to record hundreds of images with a low effort. The data obtained allows the study of the presence, relative abundance, density and behavior of species that typically avoid direct contact with humans, as well as nocturnal or low-density animals. Target taxons are usually terrestrial mammals (especially big carnivores) and some birds, although the method is applicable to a lot of species if adapted to their behavior and habitat.

Although the use of cameras to study wildlife is almost as old as the photography itself, its use skyrocketed in the last decade of the 20th century, with the advent of commercial camera traps (O'Connell *et al.*, 2011). Nowadays, many studies worldwide use camera trapping to study wildlife, and there are different protocols used to standardize their use (location, type and model of camera, etc.) depending on the objectives of the study and the target species (Meek *et al.*, 2014; Burton *et al.*, 2015). Only as examples, recently camera traps have been used to study the impacts of the COVID-19 lockdowns in mammals (Procko *et al.*, 2022), and to show the importance of protected areas in conserving mammal taxonomy diversity (Chen *et al.*, 2022). Several of the previously cited studies in this project also used camera trapping techniques (Ohashi *et al.*, 2012; Oberosler *et al.*, 2017; Azevedo *et al.*, 2018; Regolin *et al.*, 2020; Swan *et al.*, 2020; Cremonesi *et al.*, 2021; Rosalino *et al.*, 2022; Teixeira *et al.*, 2023). In this project, camera trapping data will be used to study diversity patterns of large mammals in Catalonia.

OBJECTIVES

The main objective of this work is to determine the main factors that affect alpha and beta diversity of carnivores and ungulates in Catalonia. Our hypothesis are the following:

1. The more heterogeneity of the habitat (land uses, climate, elevation, etc.), the more diversity we find.
2. The less anthropic disturbances in the area, the more diversity we find.
3. The less habitat heterogeneity loss in the last 30 years, the more diversity we find.

MATERIAL AND METHODS

2.1. Study area

Data used in this study was taken in different places along Catalonia, a region in the North-Eastern corner of the Iberian Peninsula, located in the South-West of Europe and thus in the Mediterranean Basin and the Palearctic realm. There is a gradient of humidity, temperature and elevation, finding the wettest and coldest zones in the North and the West, where the highest elevations are (especially in the Pyrenees), while the driest and hottest areas are found in the South and the East, generally zones with a lower elevation. Human presence since prehistoric times has resulted in significant changes in plant species composition and distribution of dominant species throughout history. Nowadays, land cover chiefly consists of forests (31%), evergreen shrublands (29%), and agricultural land (33%) (Vallecillo *et al.*, 2013). Most of the data of this study comes from natural protected areas (included in the Plan of Natural Interest Areas or PEIN), that occupy 1,026,501 ha (0.32% of the surface) (Generalitat de Catalunya, 2022). However, there is still a high heterogeneity of landscape among different locations, finding coniferous, broad-leaved and mixed forests, mountain areas, grasslands, pastures, urban areas, etc.

2.2. Data sources

Presence and abundance data: Data for the presence and relative abundance of macro- and meso-mammals was obtained by the FELIS Group, one of the research teams of the Catalan Natural History Institution (ICHN), created in 2018 to unify the research that was being conducted by different isolated groups about carnivores in Catalonia. The group is supported by the Barcelona Zoo Foundation, and it coordinates the Camera Trapping Project of Mammals in Catalonia, whose objective is to study the composition of the community of mammals across the Catalan territory and the presence and relative abundance of certain species. The project started in 2020-2021 with 18 Carnivores Permanent Tracking Plots (PSPCs), and in the season 2021-2022 it had 11 more PSPCs, raising the total number to 29 (Vilella *et al.*, 2022). In this project, data from 2022 from 29 PSPCs has been included, with each PSPC having at least 12 cameras spaced 1.5-2 km apart (Figure 1). A camera trap was deployed near the center of each square forming a continuous sampling area. The placements selected tried to enhance the probability of detecting each mammal species despite using no lures, nor baits. Therefore, structural elements such as fauna trails were taken into account in the selection of the sampling points. Cameras were set to operate during the whole day and to take three-photo bursts when the sensor was triggered and recorded data simultaneously during a minimum of 90 days. Although most of the cameras recorded for 90 days, data was only considered from cameras that were active at least 40 days, with any cameras recording less than this being excluded, mainly due to technical problems. To avoid double-counting, detections of the same species with the same camera were only counted as independent detections (contacts) if they were separated by a minimum time interval of one hour. This interval is commonly used in camera trapping studies and enables to maximize the number of theoretically independent contacts, allowing a more precise estimation of daily activity patterns (Azevedo *et al.*, 2018).

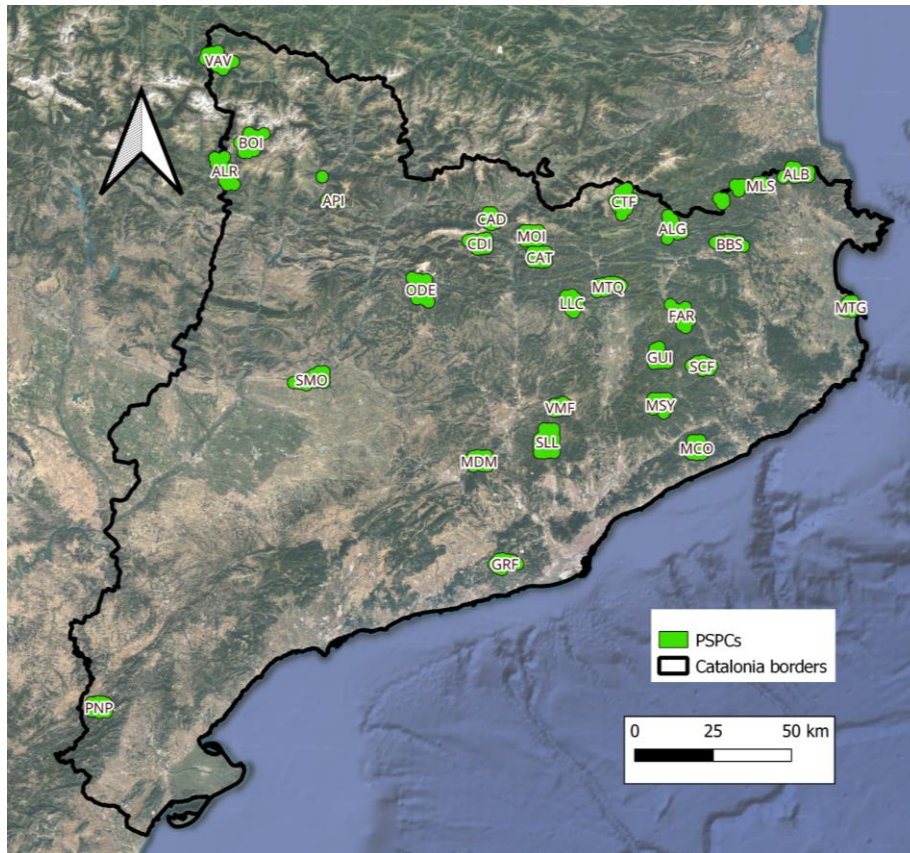


Figure 1: Map of the location of the PSPC in Catalonia with a buffer of 2 km around each camera. PSPC abbreviations mean the following: ALB: Paratge d'Interès Nacional de l'Albera; ALG: Espai d'Interès Natural de l'Alta Garrotxa; ALR: Alta Ribagorça; API: Parc Natural de l'Alt Pirineu; BBS: Beuda-Bassegoda; BOI: Vall de Boí-Parc Nacional d'Aigüestortes; CAD: Parc Natural del Cadí-Moixeró (Zona Cadí); CAT: Espai d'Interès Natural Serra del Catllaràs; CDI: Parc Natural del Cadí-Moixeró (Zona Cadí sud) CTF: Parc Natural de les Capçaleres del Ter i del Freser; FAR: El Far-Vall d'Hostoles; GRF: Parc del Garraf; GUI: Espai Natural de les Guillerries-Savassona; LLC: Lluçanès; MCO: Parc del Montnegre i el Corredor; MDM: Parc Natural de la Muntanya de Montserrat; MGR: Serra de Montgrony; MLS: Espai d'Interès Natural del massís de les Salines; MOI: Parc Natural del Cadí-Moixeró (Zona Moixeró); MSY: Parc Natural del Montseny; MTG: Parc Natural del Montgrí; MTQ: Parc del Castell de Montesquiú; ODE: Odèn-Solsonès; PNP: Parc Natural dels Ports; SCF: Santa Coloma de Farners; SLL: Parc Natural de Sant Llorenç del Munt i l'Obac; SMO: Serra de Montclar-La Noguera; VAV: Vall d'Aran; VMF: Vall de Marfà. Source: own making with Google Satellite as base map.

Environmental data: To compare the habitat, the anthropic and weather effects on mammal diversity, several environmental variables calculated for each PSPC were used. Firstly, the landscape data for each camera was obtained from CORINE Land Cover, both from maps of 2018 (European Union, Copernicus Land Monitoring Service, 2018) and of 1990 (European Union, Copernicus Land Monitoring Service, 1990). Secondly, to obtain data about weather variables (annual mean temperature and annual rainfall), the Hipermapa maps were used (Generalitat de Catalunya, 2023). Data from these maps comes from the Climatic Atlas of Catalonia (Martin-Vide *et al.*, 2008), and shows the averages of these variables between 1961 and 1990.

2.3. Species diversity calculations

For the purposes of this study, only terrestrial mammal species weighing more than 1 kg were included in the analyses. Consequently, birds, small mammals (such as hedgehogs, squirrels or weasels), as well as semi aquatic mammals (as otters or American minks) were not considered. The target species of terrestrial mammals were categorized into two groups and further divided into five subcategories. The first group pertains to wild mammals, which has been further classified into carnivores, ungulates, and lagomorphs and big rodents (Table 1). The second group comprises domestic mammals, which has been further subdivided into carnivores and ungulates. Notably, in the original data two of the categories were labeled as “Cattle” and “Domestics”. It is important to mention that, as diversity indices that consider species richness were not used for domestic animals (see below), individuals in this category were grouped in “Domestic herbivores” (“Cattle”) and “Domestic carnivores” (“Domestics”) subcategories without reclassification.

Table 1: Target species of terrestrial mammals included in two categories or subcategories in function of their origin and phylogeny. For each species the scientific, common name and the main habitat was provided. Data from main habitats was obtained from IUCN Red List and complemented with the *Enciclopedia Virtual de los Vertebrados Españoles* (IUCN, 2022; López & Martín, 2022)

Category	Subcategory	Scientific name	Common name	Main habitat
Wild mammals	Wild carnivores	<i>Felis silvestris</i> Schreber, 1777	European wildcat	Forest, shrubland and rocky areas, heterogeneous zones
		<i>Genetta genetta</i> Linnaeus, 1758	Common genet	Forest, shrubland and rocky areas, very generalist
		<i>Martes foina</i> Erxleben, 1777	Beech marten	Forest, shrubland, rocky areas, crops and urban areas, very generalist
		<i>Martes martes</i> Linnaeus, 1758	Pine marten	Forest
		<i>Meles meles</i> Linnaeus, 1758	European badger	Forest, shrubland, grassland, crops and urban areas, very generalist
		<i>Mustela putorius</i> Linnaeus, 1758	Western polecat	Forest, shrubland, grassland, wetlands and crops and urban areas, zones with water
		<i>Ursus arctos</i> Linnaeus, 1758	Brown bear	Forest, sometimes also shrubland
		<i>Vulpes vulpes</i> Linnaeus, 1758	Red fox	Forest, shrubland, grassland, crops and urban zones, very generalist

Table 1 (continuation)

Category	Subcategory	Scientific name	Common name	Main habitat
Wild mammals	Wild ungulates	<i>Capra pyrenaica</i> Schinz, 1838	Iberian wild goat	Forest, shrubland and rocky areas
		<i>Capreolus capreolus</i> Linnaeus, 1758	European roe deer	Forest, shrubland, grassland and crops
		<i>Cervus elaphus</i> Linnaeus, 1758	Red deer	Forest, shrubland, grassland and rocky areas, frequently ecotones
		<i>Dama dama</i> Linnaeus, 1758	Common fallow deer	Shrubland
		<i>Ovis orientalis</i> Gmelin, 1774	Mouflon	Forest, grassland, crops and rocky areas, frequently ecotones, more than 1,000 m
		<i>Rupicapra pyrenaica</i> Bonaparte, 1845	Southern chamois	Forest, shrubland, grassland and rocky areas, frequently ecotones
		<i>Sus scrofa</i> Linnaeus, 1758	Wild boar	Forest, shrubland, grassland, wetlands, crops and urban areas, very generalist
	Lagomorphs and big rodents	<i>Lepus europaeus</i> Pallas, 1778	European hare	Shrubland and grassland
		<i>Lepus granatensis</i> Rosenhauer, 1856	Granada hare	Forest, shrubland and grassland, very generalist
		<i>Oryctolagus cuniculus</i> Linnaeus, 1758	European rabbit	Shrubland, grassland and crops
		<i>Marmota marmota</i> Linnaeus, 1758	Alpine marmot	Grassland, crops and rocky areas, more than 1,300 m
	Domestic mammals	Domestic carnivores	<i>Canis familiaris</i> Linnaeus, 1758	Domestic dog
<i>Felis catus</i> Linnaeus, 1758			Domestic cat	-

Table 1 (continuation)

Category	Subcategory	Scientific name	Common name	Main habitat
Domestic mammals	Domestic herbivores	<i>Bos taurus</i> Linnaeus, 1758	Domestic cattle	-
		<i>Capra hircus</i> Linnaeus, 1758	Domestic goat	-
		<i>Equus asinus</i> Linnaeus, 1758	Domestic donkey	-
		<i>Equus caballus</i> Linnaeus, 1758	Domestic horse	-
		<i>Ovis aries</i> Linnaeus, 1758	Domestic sheep	-

Some cameras had detections of *Felis* sp. individuals, but without specifying whether they were a *F. silvestris* or a domestic cat *F. catus*. As there were only 6 individuals in this circumstance in all cameras, they have not been taken into account in the subsequent analyses.

In order to assess the relative abundance of each species, RAIs (Relative Abundance Indexes) were calculated at the camera level. RAIs are calculated as the number of independent contacts (detections) per 100 days of activity (as the number of detections multiplied by 100 and divided by the number of days each camera was active). At the PSPC level, RAIs were calculated as the sum of all camera RAIs within the PSPC.

To measure the species diversity within the study area, the Shannon index was used for alpha diversity, while beta diversity was measured using the modified Whittaker index ($1/((\alpha/\gamma)-1)$). These indices were calculated for wild animals as a whole, as well as for wild carnivores and wild ungulates separately.

2.4. Spatial treatment of environmental parameters

QGIS 3.28.2 software was used to analyze the landscape data. First, to determine the coverage of each landscape in the different PSPC, a buffer of 2 km from each camera was obtained and overlaid with a simplified CORINE Land Cover map from 2018 (European Union, Copernicus Monitoring Service, 2018), which was categorized into 16 landscape categories (Table 2) that have been considered to affect the most the presence and abundance of mammal species in Catalonia. Using this reclassified map, the landscape diversity index of Shannon (from now ahead as landscape index) was calculated for each PSPC with the LecoS Landscape Ecology Statistics 3.0.0 plugin (Jung, 2016).

Secondly, to assess the degree of anthropization of each location, the hemeroby index was used. This index is commonly used to estimate the degree of human perturbations in a location (Eurostat, 2017), and has been widely used in essays and reports that measures the extent of deviation from the potential natural vegetation caused by human activities

(Paracchini & Capitani, 2011; Walz & Stein, 2014; Szilassi *et al.*, 2017). It assumes that a change in natural vegetation is directly related with a more anthropized landscape. This index assigns a value between 1 (more natural vegetation) and 7 (more artificial vegetation) to each landscape category (Table 2). Thus, to determine the Hemeroby value for each CORINE landscape, the scoring was based on Paracchini & Capitani (2011) and Walz & Stein (2014). The Hemeroby final value is the result of adding all these values multiplied by the proportion of area they occupy within the 2 km buffer zone of the cameras within the PSPC (the same buffer that was used to calculate landscape indexes).

Thirdly, all the previously explained steps were then repeated for the CORINE Land Cover of 1990. With these data, absolute and relative differences between Shannon diversity index and Hemeroby index were calculated as the subtraction of the values between 1990 and 2018 (absolute difference) and as the decimal fraction of the subtraction with respect to the 1990 value (relative difference).

Table 2: Relation between CORINE codes and names, reclassified landscape categories used in this work to calculate landscape diversity indexes, and Hemeroby values assigned to each of them (with values going from 1, meaning more natural vegetation, to 7, meaning more artificial vegetation). Change of vegetation is used as an indicator of a higher anthropization degree. Reclassifications have been done considering the landscape categories that affect the most the presence and abundance of mammal species in Catalonia and Paracchini & Capitani (2011) and Walz & Stein (2014)

Code	Name	Landscape category	Hemeroby value
1.1.1	Continuous urban fabric	Urban areas	7
1.1.2	Discontinuous urban fabric	Urban areas	7
1.2.1	Industrial and commercial units	Urban areas	7
1.2.2	Roads and rail networks and associated land	Road infrastructures	7
1.2.3	Port areas	Urban areas	7
1.2.4	Airports	Urban areas	7
1.3.1	Mineral extraction sites	Urban areas	6
1.3.2	Dump sites	Urban areas	6
1.3.3	Construction sites	Urban areas	6
1.4.1	Green urban areas	Urban areas	6
1.4.2	Sport and leisure facilities	Urban areas	6
2.1.1	Non-irrigated arable land	Crops	5

Table 2 (continuation)

Code	Name	Landscape category	Hemeroby value
2.1.2	Permanently irrigated land	Crops	5
2.1.3	Rice fields	Crops	5
2.2.1	Vineyards	Crops	4
2.2.2	Fruit trees and berry plantations	Crops	4
2.2.3	Olive groves	Crops	4
2.3.1	Pastures	Pastures	4
2.4.1	Annual crops associated with permanent crops	Crops	4
2.4.2	Complex cultivation patterns	Crops	4
2.4.3	Land principally occupied by agriculture, with significant areas of natural vegetation	Crops	4
3.1.1	Broad-leaved forest	Broad-leaved forests	3
3.1.2	Coniferous forest	Coniferous forests	3
3.1.3	Mixed forest	Mixed forests	3
3.2.1	Natural grassland	Grasslands	3
3.2.2	Moors and heathland	Shrubs	2
3.2.3	Sclerophyllous vegetation	Shrubs	2
3.2.4	Transitional woodland/shrub	Shrubs	2
3.3.1	Beaches, dunes, sand	Sand and beaches	2
3.3.2	Bare rock	Areas with few or no vegetation	1
3.3.3	Sparsely vegetated areas	Areas with few or no vegetation	2
3.3.4	Burnt areas	Burnt areas	5

Table 2 (continuation)

Code	Name	Landscape category	Hemeroby value
3.3.5	Glaciers and perpetual snows	Snowdrifts	1
4.1.1	Inland marshes	Wet areas vegetation	2
4.2.1	Salt marshes	Wet areas vegetation	2
5.1.1	Water courses	Continental waters	4
5.1.2	Water bodies	Continental waters	4
5.2.1	Coastal lagoons	Sea waters	2
5.2.3	Sea and ocean	Sea waters	2

Figure 2 represents the map resulting from the landscape reclassification of the PSPCs.

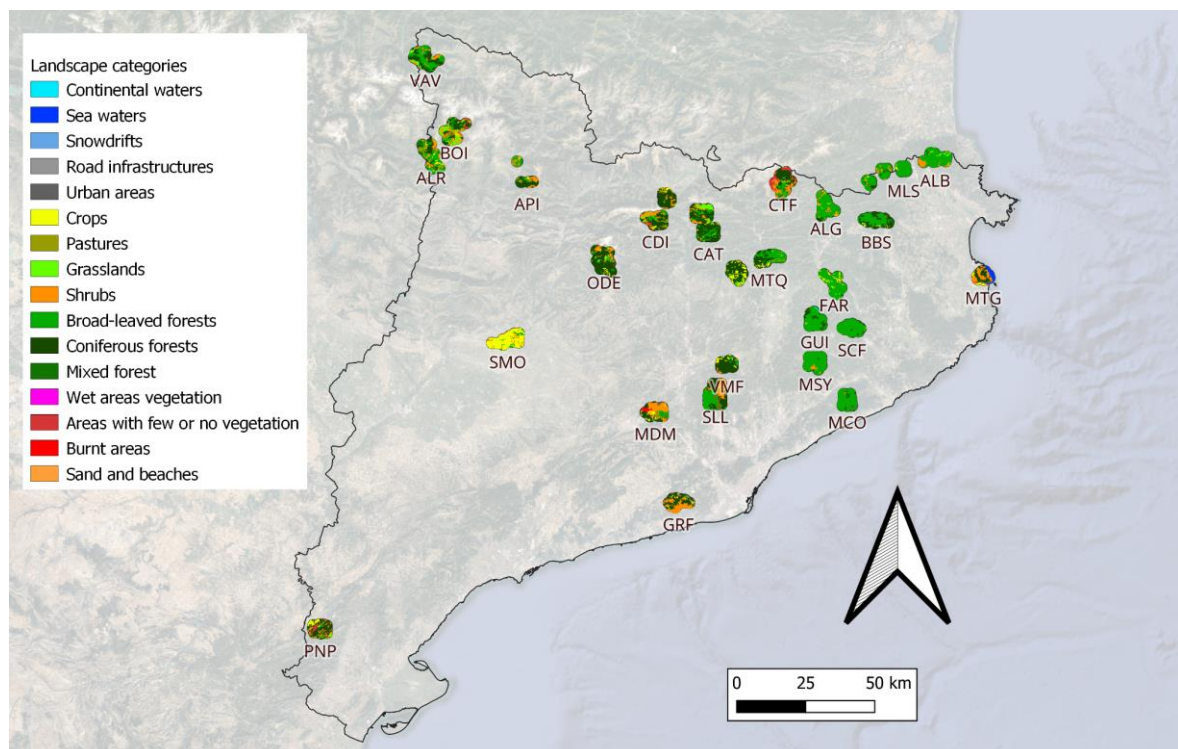


Figure 2: Map of PSPCs coloured to distinguish the different landscape categories used in this work and described in the legend. Source: own making with Google Satellite as base map.

Finally, several environmental variables (annual mean temperature and annual rainfall) were extracted from the Climatic Atlas of Catalonia (Martin-Vide *et al.*, 2008) and were used to characterize the climate in each location. For this purpose, polygon covers were used, in which temperature is shown within a margin of 1 °C and rainfall is shown with a 50 mm

span. The value given to each PSPC is the result of adding the mean value of each polygon within the buffer zone of 2 km from the cameras (for example, in the case of a polygon of 8-9 °C of mean temperature, the value used has been 8.5 °C, while for a polygon of 200-250 mm of annual rainfall, the value used has been 225 mm) multiplied by the proportion of the PSPC area occupied by the given polygon. As the extension of the Climatic Atlas limits to Catalonia, for this treatment those PSPCs whose buffer zone exceeded borders with France or Aragon, results have been adjusted to take into account only the surface situated within Catalonia and, therefore, shown in the Climatic Atlas, assuming similar climate in the adjacent areas.

2.5. Statistical treatments

To study the relationship between mammal diversity and the proposed predictors (climate, human disturbance, etc.) simple linear regressions, multimodal inference and redundancy analysis (RDA) were conducted with RStudio version 2022.7.1.554 (RStudio Team, 2022) and the packages `readx1` 1.4.1 (Wickham & Bryan, 2022), `car` 3.1-0 (Fox & Weisberg, 2019), `lmtest` 0.9-40 (Zeileis & Hothorn, 2002), `mblm` 0.12.1 (Komsta, 2019), `MuMIn` 1.47.1 (Bartón, 2022), and `vegan` 2.6-4 (Oksanen *et al.*, 2022).

The first treatments were simple linear regressions. Firstly, to avoid correlations between explanatory variables that might interfere in the results of the statistical tests, VIF (variance inflation factor) (Fox & Weisberg, 2019) was calculated. Criteria used was that no variable with a VIF higher than 10 will be used in further analysis. As a consequence, mean temperature was eliminated from the model given its high VIF (18.54), probably explained because of its strong correlation with elevation. Secondly, normality and homoscedasticity were tested with a Shapiro-Wilk test and a Breusch-Pagan, respectively. If the model did not fulfill one or both of the assumptions, the dependent variable (alpha or beta diversities) was transformed logarithmically. If after the transformation the model continued not to fulfill the assumptions, a median-based linear model was conducted instead of a simple linear regression. The Shannon index of alpha-diversity for carnivores, ungulates and wild mammals, as well as the Whittaker index of beta-diversity for the same groups were used as response variables. Landscape index, the Hemeroby Index, the change of both indexes between 1990 and 2018, annual rainfall, mean elevation, amplitude of elevation in the PSPC and RAIs of domestic carnivores and of domestic herbivores were used as independent variables using a simple linear regression.

After that, and in order to find what variables had more influence in determining the results of the species diversity indexes, a multimodal averaging was conducted using all the previously named independent variables. The importance of each variable was studied through the weight of each one in the models.

Finally, redundancy analysis was conducted to know how the different variables (the same used in the previous analysis as independent variables) influenced the abundance (measured as the RAIs) of the different wild species. This analysis was repeated for all the wild animals, only for the carnivores and only for the herbivores. To better test the significance of the analysis, as well as the significant axis and variables, 10 ANOVAs with 10,000 iterations have been conducted for each one.

RESULTS

The first analysis conducted were simple linear regressions, aiming to test which explanatory variables were capable of explaining the variability in each aspect of species diversity. Linear regressions showed that annual rainfall is the variable with the most explanatory power for differences in species diversity indexes. The correlation between annual rainfall and species diversity is positive in all cases, meaning that the more rainfall there is, the more diversity is found. This correlation was significant in every case except in beta-diversity with ungulates (Table 3).

Elevation was an important factor for mammal diversity in our region. Mean elevation was significantly correlated with all variables except alpha-diversity of carnivores, while the difference in elevation within the PSPC was positively correlated with alfa-diversities. These correlations were always positive between the variables. Hemeroby was found to have a significant negative correlation with alpha-diversity of wild animals and positive with beta-diversity of ungulates. RAI of domestic carnivores had a positive relation with beta-diversity of ungulates. No correlation was found between landscape indexes and species diversity ones (Table 3).

Table 3: Summarize of the simple linear regressions conducted using mammal species diversity indexes as dependent variables, and landscape index, hemeroby index, change in landscape diversity, increase of anthropization degree, annual rainfall, mean elevation, difference in elevation and RAI of domestic carnivores and herbivores as independent variables. The table shows the model coefficient, its standard deviation (\pm sd) or median absolute deviation (\pm MAD), and the associated p-value. The symbol + next to some independent variables means that the residuals of the model were not either normal or/nor homoscedastic, and thus the dependent variable has been transformed logarithmically. The symbol ^ next to the independent variables means that neither the residuals of the model with the original variable nor the ones with its logarithmical transformation were normal, and thus a median-based linear model has been conducted instead of a linear model.

Dependent variable	Independent variable	Coefficient \pm sd (or mad)	p-value
Alpha-diversity of wild mammals	Landscape Index	0.193 \pm 0.166	0.256
	Hemeroby Index	-0.481 \pm 0.184	0.015*
	Change of landscape diversity [^]	-0.078 \pm 0.604	0.157
	Increase of anthropization degree	-1.839 \pm 0.508	0.001**
	Annual rainfall [^]	1.078·10 ⁻³ \pm 1.123·10 ⁻³	<0.001**
	Mean elevation	4.6·10 ⁻⁴ \pm 1.6·10 ⁻⁴	0.008**
	Difference in elevation [^]	7.0·10 ⁻⁴ \pm 8.5·10 ⁻⁴	<0.001**

Table 3 (continuation)

Dependent variable	Independent variable	Coefficient \pm sd (or mad)	p-value
Alpha-diversity of wild mammals	RAI Domestic Carnivores [^]	-0.028 \pm 0.089	0.056
	RAI Domestic Herbivores	9.1·10 ⁻⁴ \pm 8.0·10 ⁻³	0.910
Beta-diversity of wild mammals	Landscape Index+	0.196 \pm 0.168	0.252
	Hemeroby Index [^]	<10 ⁻⁴ \pm 0.660	0.695
	Change of landscape diversity+	0.259 \pm 0.268	0.341
	Increase of anthropization degree+	-1.066 \pm 0.592	0.083
	Annual rainfall [^]	8.127·10 ⁻⁴ \pm 7.807·10 ⁻⁴	<0.001**
	Mean elevation+	5.2·10 ⁻⁴ \pm 1.5·10 ⁻⁴	0.002**
	Difference in elevation [^]	<10 ⁻⁷ \pm 5.1·10 ⁻⁴	0.103
	RAI Domestic Carnivores [^]	<10 ⁻⁵ \pm 0.043	0.660
	RAI Domestic Herbivores [^]	<10 ⁻⁶ \pm 0.009	0.737
Alpha-diversity of carnivores	Landscape Index	-0.083 \pm 0.117	0.482
	Hemeroby Index	-0.170 \pm 0.139	0.233
	Change of landscape diversity	-0.211 \pm 0.182	0.257
	Increase of anthropization degree	-0.664 \pm 0.411	0.118
	Annual rainfall	5.968·10 ⁻⁴ \pm 2.525·10 ⁻⁴	0.026*

Table 3 (continuation)

Dependent variable	Independent variable	Coefficient \pm sd (or mad)	p-value
Alpha-diversity of carnivores	Mean elevation	$2.2 \cdot 10^{-4} \pm 1.2 \cdot 10^{-4}$	0.067
	Difference in elevation	$6.1 \cdot 10^{-4} \pm 1.9 \cdot 10^{-4}$	0.003**
	RAI Domestic Carnivores	-0.028 ± 0.020	0.170
	RAI Domestic Herbivores	$3.1 \cdot 10^{-4} \pm 5.5 \cdot 10^{-3}$	0.956
Beta-diversity of carnivores	Landscape Index [^]	$<10^{-3} \pm <10^{-3}$	0.944
	Hemeroby Index ⁺	0.219 ± 0.333	0.516
	Change of landscape diversity ⁺	0.169 ± 0.437	0.702
	Increase of anthropization degree ⁺	-1.229 ± 0.981	0.221
	Annual rainfall ⁺	$1.849 \cdot 10^{-3} \pm 5.422 \cdot 10^{-4}$	0.002**
	Mean elevation ⁺	$7.5 \cdot 10^{-4} \pm 2.5 \cdot 10^{-4}$	0.006**
	Difference in elevation ⁺	$7.0 \cdot 10^{-4} \pm 5.0 \cdot 10^{-4}$	0.176
	RAI Domestic Carnivores ⁺	0.053 ± 0.048	0.275
	RAI Domestic Herbivores [^]	0.028 ± 0.186	0.056
Alpha-diversity of ungulates	Landscape Index	0.236 ± 0.187	0.217
	Hemeroby Index	-0.081 ± 0.232	0.730
	Change of landscape diversity	0.267 ± 0.300	0.380

Table 3 (continuation)

Dependent variable	Independent variable	Coefficient \pm sd (or mad)	p-value
Alpha-diversity of ungulates	Increase of anthropization degree	-0.976 ± 0.675	0.160
	Annual rainfall	$8.678 \cdot 10^{-4} \pm 4.194 \cdot 10^{-4}$	0.049*
	Mean elevation+	$6.1 \cdot 10^{-4} \pm 1.6 \cdot 10^{-4}$	0.001**
	Difference in elevation	$8.1 \cdot 10^{-4} \pm 3.2 \cdot 10^{-4}$	0.018*
	RAI Domestic Carnivores	-0.032 ± 0.033	0.342
	RAI Domestic Herbivores	$3.0 \cdot 10^{-3} \pm 9.0 \cdot 10^{-3}$	0.743
Beta-diversity of ungulates	Landscape Index [^]	$<10^{-4} \pm 0.412$	0.244
	Hemeroby Index [^]	$<10^{-4} \pm <10^{-4}$	0.045*
	Change of landscape diversity [^]	$<10^{-4} \pm <10^{-4}$	0.689
	Increase of anthropization degree [^]	-0.364 ± 0.965	0.142
	Annual rainfall [^]	$1.210 \cdot 10^{-3} \pm 1.231 \cdot 10^{-3}$	0.335
	Mean elevation [^]	$3.3 \cdot 10^{-4} \pm 5.0 \cdot 10^{-4}$	0.009**
	Difference in elevation [^]	$<10^{-7} \pm 8.1 \cdot 10^{-4}$	0.182
	RAI Domestic Carnivores [^]	$<10^{-4} \pm <10^{-4}$	0.021*
	RAI Domestic Herbivores [^]	$<10^{-4} \pm <10^{-4}$	0.932

The multimodal analysis showed that all variables with a weight greater than 0.45 were positively correlated with the species diversity indexes in the models (Table 4), confirming the results of previous simple linear regressions. The exceptions were alpha-diversity of ungulates (which was mainly explained by mean elevation) and beta-diversity of wild animals (with annual rainfall, RAI of domestic carnivores and mean elevation with a similar weight). Landscape and hemeroby indexes, as well as their changes during the last 30 years, had a low weight in all cases (Table 4). All variables with a weight higher than 0.45 were positively correlated with species diversity indexes in the models.

Elevation differences seemed to explain the variability of alpha-diversities better, especially for carnivores, while annual rainfall appeared in almost every model of beta-diversity of carnivores, even though it had a low weight in models trying to explain alpha-diversity of this group. Among RAI of domestic species, carnivores and herbivores had low and similar weights among models of alpha-diversities, while carnivores had relatively high weights among models of beta-diversity of carnivores and wild animals.

Table 4: Summarize of the weights of each independent variable (landscape index, hemeroby index, changes of landscape diversity, increase in anthropization degree, annual rainfall, mean elevation, difference in elevation and RAI of domestic carnivores and herbivores) explaining species diversities in the multimodal analysis conducted. Variables with a weight higher than 0.75 are marked with bright green, while those with a weight between 0.50 and 0.75 are shown in light green.

	Alpha-Diversity			Beta-Diversity		
	Wild	Carnivores	Ungulates	Wild	Carnivores	Ungulates
Lands. Div.	0.31	0.25	0.32	0.29	0.24	0.21
Hemeroby	0.25	0.19	0.33	0.26	0.21	0.19
Δ Land.Div.	0.21	0.25	0.25	0.31	0.47	0.19
Δ Ant. Deg.	0.34	0.20	0.23	0.18	0.21	0.21
Rainfall	0.79	0.29	0.23	0.59	0.96	0.20
Elevation	0.20	0.22	0.70	0.52	0.22	0.27
Δ Elevation	0.67	0.82	0.49	0.38	0.17	0.54
RAI C Dom	0.19	0.21	0.18	0.54	0.75	0.19
RAI H Dom	0.18	0.20	0.19	0.35	0.19	0.25

According to the results from RDA (Table 5), studied variables were able to explain almost 70% of the variability in the abundance of all wild species. Wild animals RDAs were significant in 80% of the conducted tests in the case of wild animals (when they were not, the p-value was always lower than 0.055 in all the conducted tests). Nonetheless, when only carnivores or ungulates were considered, the explained variability fell below 50%, and RDAs for the two groups separately were never significant.

RDA1 was significant in 80% of the cases for wild animals, and never showed a p-value higher than 0.06. However, no RDA axis was found to be significant in either the analysis of carnivores or the one of ungulates.

Annual rainfall and hemeroby index were consistently found to be significant across all conducted analyses for wild animals. Additionally, the difference in elevation was significant in over 90% of the cases for wild animals. For carnivores, the hemeroby index was consistently significant, while the RAI of domestic carnivores was significant in 30% of the cases. Finally, the only variable that was found significant in all the ungulates analysis was the difference in elevation.

Table 5: Results of RDAs conducted with landscape index, hemeroby index, change in landscape diversity, increase of anthropization degree, annual rainfall, mean elevation, difference in elevation and RAI of domestic carnivores and herbivores as explanatory variables of the RAIs of the different species.

	Wild	Carnivores	Ungulates
Constrained proportion	0.698	0.487	0.426
Constrained proportion (RDA1)	0.592	0.401	0.266
Constrained proportion (RDA2)	0.056	0.043	0.133
R² adjusted	0.547	0.231	0.140

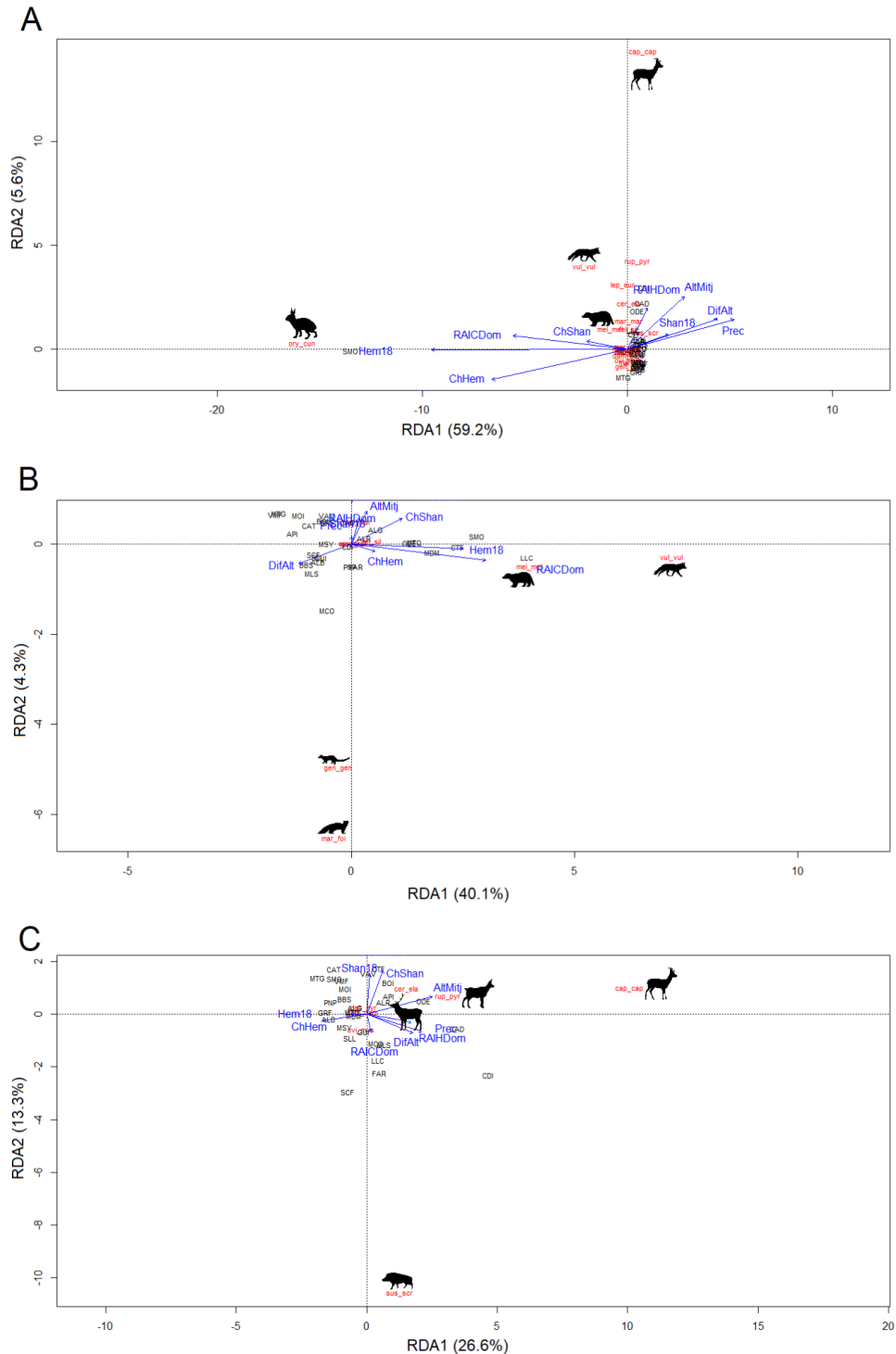


Figure 3: Plots of the conducted RDAs. A) RDA of wild animals; B) RDA of carnivores; C) RDA of ungulates. Explanatory variables are shown in blue and abbreviations mean the following: AltMitj: Mean elevation; ChHem: Change in hemeroby index between 1990 and 2018; ChShan: Change in landscape index between 1990 and 2018; DifAlt: Difference of elevation; Hem18: Hemeroby index in 2018; Prec: Annual rainfall; RAICDom: RAI of domestic carnivores; RAIHDom: RAI of domestic herbivores; Shan18: Landscape index in 2018. Species are shown in black and abbreviations mean the following: cap_cap: *C. capreolus*; cap_pyr: *C. pyrenaica*; cer_ela: *C. elaphus*; dam_dam: *D. dama*; fel_sil: *F. silvestris*; gen_gen: *G. genetta*; lep_eur: *L. europaeus*; Lep_gra: *L. granatensis*; mar_foi: *M. foinea*; mar_mar: *M. martes*; mar_mot: *M. marmota*; mel_mel: *M. meles*; mus_put: *M. putorius*; ory_cun: *O. cuniculatus*; ovi_mus: *O. orientalis*; rup_pyr: *R. pyrenaica*; sus_scr: *S. scrofa*; urs_arc: *U. arctos*; vul_vul: *V. vulpes*. PSC are shown in red and abbreviations are the same as in Figure 1. Silhouettes of selected mammals are included to highlight the main results.

The X-axis of the RDA for wild animals (Figure 3A) (59.2% of the variability) showed a clear relation with the hemeroby index, with the highest values observed in the PSPC Serra de Montclar-La Noguera (abbreviated as SMO) area. Most species were clustered near the X-axis, except for the European rabbit, which was mainly located in the SMO area. Additionally, the red fox and the European badger were also shifted from the point where most species appeared in the X-axis. On the other hand, the Y-axis (5.6% of the variability) appeared to be more closely related to the RAI of domestic herbivores and mean elevation, and placed the roe deer further apart from every other species, which were more evenly distributed along the Y-axis.

The RDA of carnivores (Figure 3B) showed that the X-axis (40.1% of the variability) was mainly influenced by hemeroby index, RAI of domestic carnivores (which had a relatively good direct relation), and difference in elevation (which was opposite to the two previous variables). In places with a high hemeroby index, more domestic carnivores were found, which particularly reflect higher abundance of red foxes and European badgers. The Y-axis (4.3% of the variability) did not have a clearly dominant explanatory variable. This axis explained the abundance of the beech marten and the common genet.

The RDA of ungulates (Figure 3C) showed an X-axis (26.6% of the variability) influenced by several variables, mainly mean elevation, difference of elevation, mean rainfall, RAI of herbivore domestics (all these variables with a positive relationship among them) and change in hemeroby index (with a negative relationship with the previous ones). This axis mainly explained the abundance of the European roe deer, as well as the Southern chamois and the red deer. The Y-axis (13.3% of the variability) was mostly influenced by the change of landscape diversity and the RAI of domestic carnivores. Moreover, this axis was strongly related with the abundance of the wild boar. Wild boars tend to be found in places with a high RAI of domestic carnivores and loss of landscape diversity during the last 30 years.

DISCUSSION

Landscape diversity, measured as landscape index, does not appear to have a significant effect on any metric of species diversity. Nonetheless, the difference in elevation is indeed correlated with some measures of the species diversity, particularly with alpha-diversity. This variable is commonly seen as another way to measure landscape diversity (Kerr & Packer, 1997). The fact that difference of elevation explains species diversity better than landscape diversity might be due to the presence of some species that are only found in the Pyrenees (López-López *et al.*, 2011; IUCN, 2022; López & Martín, 2022), where the differences of elevation in a relatively small area are much higher than in plain zones nearer the coast. This implies that landscape diversity might be related to mammal species diversity, especially with that of carnivores, although not in the way of a simple index like the one that has been used in this work (the Shannon index, commonly used to measure species diversity), but in more complex ways, at least in areas where most mammal species are generalists and species richness is located in a specific zone, like the Pyrenees in the case of Catalonia.

Hemeroby index does not show clear patterns with mammal diversity. This might mean either that most of the studied species are not clearly affected by human presence, or that its response to anthropization varies highly among species (Suraci *et al.*, 2021). For instance, Santos *et al.* (2020) found that human disturbances correlated with a higher species richness and trait diversity assemblages, as some species can take benefit of

human disturbances. In our study area, many species are generalists in terms of habitat and diet requirements, allowing them to take advantage of anthropogenic resources that humans provide, and to adapt its habits and activity patterns to take the maximum possible advantage. This is especially clear in the case of the most generalist species, like the red fox (Alexandre *et al.*, 2019), the wild boar (Stillfried *et al.*, 2017) and the roe deer (Bonnot *et al.*, 2012).

Another explanation of the lack of association between anthropization and mammal diversity might simply be that the hemeroby index is not a good way to measure anthropization degree in this case. The hemeroby index is only based on the deviation of the natural potential vegetation and only presents 7 degrees of human disturbance, from 1 to 7. Furthermore, all forests (broad-leaved, coniferous and mixed) present the same degree of hemeroby, irrespective of the degree of human disturbance (population, number of tourists, traffic, etc.). This, added to the fact that most of our sites are found in clearly forestial areas, like Natural Parks, probably tends to homogenize the value of the hemeroby index among the different areas.

RAI of domestic carnivores is generally found to be more explanatory than the hemeroby index. This measure can also be assumed as an anthropization indicator, as urban zones tend to present more domestic carnivores, like cats and dogs (Riem *et al.*, 2012). However, results show that the RAI of domestic carnivores is positively correlated with species diversity measures, especially with beta-diversity, contradicting one of the hypotheses proposed by this work. This contradicts previous studies about this effect (Lessa *et al.*, 2016; Trouwborst *et al.*, 2020), although other issues have found that, even if domestic carnivores like cats might have an impact on the abundance of certain vertebrate species (Loss & Marra, 2017), its presence does not always affect mammal diversity (Lilith, 2007). To clarify these results and obtain more solid conclusions about the anthropic effect on mammal diversity, other variables could be used in future analysis to measure anthropization degree, like distance to the nearest urban center, human population density or kilometers of roads inside the PSPC.

Results regarding the anthropization degree may also be linked with the evolution of the demographic variables in Catalonia, similar to the ones of most of Europe and the Western countries. The concentration of population in the cities (Wolff *et al.*, 2018), the abandonment of lands previously used as crops or pasture lands due to the decline of the agriculture and livestock (Rey Benayas *et al.*, 2007) and the consequent forestial expansion (Keenan *et al.*, 2015) might be causing a homogenization of most of the territory, especially in zones included in mountain protected areas (Ametzegui *et al.*, 2021), like most of the PSPCs studied here. This can also be a limitation of the anthropic effects to mammal diversity, as they might be relatively small in most of the territory and only affect transition zones, like the ones near crops or urban areas, not present in most of the PSPCs.

No significant correlation has been found between species diversity indexes and the changes of both landscape diversity and hemeroby index in the last 30 years. This result suggests either that the loss of landscape diversity, with the consequent landscape homogenization, already had its main effects more than 30 years ago, or that mammals respond very quickly to landscape changes, diluting the effect of changes over the 30 year period.

According to the RDAs, wild boars tend to be found in places with a higher loss of landscape diversity. As previously stated, in Western countries, this loss of landscape diversity is

commonly related to a forestial expansion (Keenan *et al.*, 2015; Ametzegui *et al.*, 2021), and this might be one of the main reasons for the recent expansion of wild boars (Tack, 2018).

The European rabbit, one of the few species among those studied in this work that mainly inhabits open fields, is the one that influences the relative abundance of wild mammals the most. These areas, like crops, have a higher hemeroby index than forests, and that explains why this index appears to be one of the most important variables explaining the distribution of wild animals.

The results of this work emphasize the importance of conserving areas with open fields and grassland, as it is the main habitat of the only threatened species found in the analysis: the European rabbit. Although it might appear so clearly distanced of the other species because SMO is the only PSPC with a clear majority of crops in its area, the fact is that this type of areas are regressing in Europe (Donald *et al.*, 2001; Stoate *et al.*, 2009; Reif & Hanzelka, 2020) and, concretely, in Catalonia, having decreased an 11.9% between 2001 and 2021 (Institut d'Estadística de Catalunya, 2022). To confirm these results, however, more PSPCs should be located in open fields zones, in order to have more replicas of this type of areas and to assure SMO is not a simple outlier whose results are explained by other factors. During the next campaigns, the FELIS Group should prioritize locating new PSPCs in non-forestry zones, like crops, and transition zones, like small forests near urban areas or the coast.

Studied variables only explained significantly well the relative abundance of wild mammals. In the case of carnivores and ungulates alone, studied variables are not capable of explaining most of the variation in RAIs. That means that there should be other variables not included here that could influence them, like, for example, humidity or water presence. Most of RDAs are clearly dominated by a few species, like the European rabbit, the European roe deer or the red fox. Some of these species are less generalist than others, like the European rabbit. On the other hand, the European roe deer and the red fox are more generalist species that tend to better tolerate human presence (Tixier *et al.*, 1997; Dell'Arte *et al.*, 2007; Suárez-Tangil & Rodríguez, 2023). For example, the red fox is located in zones with a higher RAI of domestic carnivores and hemeroby index, both indicators of a higher anthropization degree. This suggests that this species can take profit from a higher amount of resources provided to humans (Alexandre *et al.*, 2019), as probably also do other generalist species as well.

The results from the different analysis indicate that climatic variables, such as annual rainfall and mean elevation, are generally the most significant predictors of terrestrial mammal diversity. Consistent with these results, other authors found that environmental factors were the most important affecting the diversity of mammals (Real *et al.* 2003; Oliveira *et al.* 2016). However, it must be taken into account that climatic data was used as the mean between 1961 and 1990, and from that point these variables might have changed. Therefore, further analysis with current data of these variables might be appropriate.

The fact that environmental variables have an overall stronger effect on mammal diversity than landscape variables highlights the importance that climate change might have on mammals. To monitor it, similar analyses could be repeated using precipitation and temperature of the year of study, instead of past averages. Habitat specialists will probably be more affected than generalists, with higher dispersal ability and adaptability, as it has happened before in previous climate changes (Teacher *et al.*, 2011).

As the Iberian Peninsula will be, according to most climate predictions, one of the European regions most ravaged by climate change, especially by severe droughts (Pörtner *et al.*, 2022), this is probably going to also affect wildlife. In the case of mammals, the Iberian Peninsula is usually considered a “hotspot inside the Mediterranean Basin hotspot” and could become the European region with a higher loss of species (Maiorano *et al.*, 2011).

Inside the Iberian Peninsula, the Pyrenees are a key area for biodiversity (Maiorano *et al.*, 2013). This, added to the previously stated fact that some of the mammal species present in Catalonia, especially ungulates, only inhabit zones with a high elevation, makes the Pyrenees a key area for conservation of mammals in Catalonia. Considering that anthropization degree seems to have much lower relationship with mammal diversity than environmental factors, climate change might become increasingly important for mammal conservation in the coming decades. If further research confirms the results of this work, conservation actions should then be focused to mitigate the impacts of climate change in the Pyrenean ecosystems, in order to prevent the loss of an iconic group such as large and mid-sized mammals.

CONCLUSIONS

The fact that amplitude of elevation is highly correlated with species diversity measures, especially with alpha-diversity, supports the first hypothesis of this work, that the more heterogeneity of the habitat will host more mammal diversity. In contrast, other measures of habitat heterogeneity, such as landscape diversity, were not found to have a significant effect on species diversity. This suggests that the relation between species diversity and habitat heterogeneity is a complex one, difficult to measure with simple indexes.

The second hypothesis of this work, which stated that less anthropic disturbances in the area would be related to more species diversity, is not fully supported, as no clear correlation has been found between the hemeroby index and the species diversity variables. However, domestic carnivores, which can also be considered as a measure of anthropization degree, are positively correlated with mammal diversity, especially regarding beta-diversity, contradicting the second hypothesis.

Changes in hemeroby index and in landscape diversity do not correlate well with any of the species diversity variables studied, consequently, the third hypothesis of this work, that stated that the less heterogeneity loss in the habitat in the last 30 years, the more diversity we find, was not supported.

The European rabbit, the only species found in this work classified as Endangered by the IUCN Red List, seems to be highly dependent on open fields. As these types of areas are in regression in Europe, its conservation should be prioritized to protect biodiversity. However, further analysis is required to confirm these results, as only one out of the 29 total PSPCs was mainly composed of crops. In order to get more robust results, during the next campaigns the FELIS Group should prioritize locating more PSPCs in non-forestry areas and transition zones.

As environmental variables seem to be more important affecting mammal diversity, climate change might be in the future its biggest threat, at least in the Mediterranean Basin. Thus, it would be better to center measures on mitigation and adaptation to protect mammals from the effects climate change will have. Within Catalonia, the Pyrenees are a key area for biodiversity which should be prioritized in conservation actions.

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