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University of Southampton

Faculty of Environmental and Life Sciences

School of Biological Sciences

**Biogeographic processes determining the distributions of
European bats across spatial scales: The role of biotic
interactions and habitat preferences**

by

Roberto Novella Fernández

Thesis for the degree of Doctor of Philosophy

June 2020

University of Southampton

Abstract

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A better comprehension of how natural systems will respond to global environmental changes requires a deeper understanding of the processes that drive diversity. In this thesis I show how environmental filtering and biotic interactions operate across spatial scales contributing to shaping biogeographic patterns. Among the different environmental filtering factors that drive species' geographical ranges, habitat structure is thought to operate generally at more local scales than climatic factors. I show, however, that forest characteristics can be a primary factor driving the regional distribution of forest-specialist bats in a Mediterranean system, which has direct consequences for their vulnerability to climate change. The strength of this dependence on forests is driven by species' roosting ecology, being higher in species that roost in trees. Alongside environmental filtering, biotic interactions can impact species distributions by preventing functionally similar species from coexisting. I show how local-scale trophic shift can facilitate coexistence between the morphologically almost identical forest bats *Myotis escalerai* and *Myotis crypticus*. Increasing evidence supports the effect of biotic interactions on broader scale biogeographic patterns. I develop a measure that uses outputs of Species Distribution Models to detect the expected broad-scale patterns of geographic avoidance between pairs of species if competition contributes to shaping their ranges. When applying it to different sets of bats with high potential for competition, the measure showed higher values than random for two pairs of species that are ecologically very similar and have no known local-scale coexistence mechanisms. This suggests that local-scale coexistence mechanisms are a key process preventing biotic interactions from scaling up and having broader-scale consequences. Overall, this thesis highlights the importance of integrating new molecular techniques, functional analyses and a careful consideration of spatial scale for disentangling ecological and biogeographic processes.

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Abbreviations

AIC: Akaike Information Criterion.

AUC: Area Under the Curve.

ANML: metabarcoding primer for arthropods (Jusino *et al.* 2019).

BIN: Type of OTU used by BOLD.

B_A : Levin's Niche breadth measure.

BOLD: Barcode of Life Data System (<https://www.boldsystems.org>).

CCA: Canonical Correspondance Analysis.

DBH: Diametre at breast height.

EBD: Estación Biológica de Doñana.

GCM: Global Circulation Models.

GIS: Geographic Information Systems.

HMSC: Hierarchical modelling of communities.

JSDM: Joint Species Distribution Models.

NMDS: Non metrical multidimensional scaling.

OTU: Operational Taxonomic Unit.

O_{jk} : Pianka niche overlap measure.

PCR: Polymersase Chain Reaction.

POO: Percentage of occurrence.

RRA: Relative Read Abundance.

RCP: Representative Concentration Pathways. Scenarios of future carbon emissions from the Intergovernmental Panel on Climate Change (IPCC).

SDM: Species Distribution Models.

TSS: True Skill Statistic.

wPOO: weighted Percent of Occurrence.

ZBJ: metabarcoding primer for arthropods (Zeale *et al.* 2011).

Research Thesis: Declaration of Authorship

Roberto Novella Fernández

Biogeographic processes determining the distributions of European bats across spatial scales:
The role of biotic interactions and habitat preferences.

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

This work was done wholly or mainly while in candidature for a research degree at this University;

Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;

Where I have consulted the published work of others, this is always clearly attributed;

Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;

I have acknowledged all main sources of help;

Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;

None of this work has been published before submission.

Signature:

Date: 19th of June 2020

Author contributions

All three data chapters (Chapters 2-4) were prepared as manuscripts for publication and include co-authors beyond my PhD supervisors. I was the lead author of all chapters and carried out the majority of the fieldwork and lab work and all the data analysis, receiving guidance and support from my supervisors Dr. Orly Razgour and Prof. Patrick Doncaster and comments from all other collaborators.

Chapter 2: I conceptualised this chapter and the study design under the guidance of my supervisor Dr. Orly Razgour. I carried out all data processing and analysis. Dr Javier Juste, Prof Carlos Ibáñez and Jesus Nogueras provided the bat location records dataset for Andalusia. Prof Patrick Osborne advised on spatial analysis. I wrote the manuscript and co-authors listed above contributed to revisions.

Chapter 3: this chapter was part of the initial PhD proposal conceived by Dr. Orly Razgour. I developed the ideas and carried out all the fieldwork, lab work, bioinformatics and data analysis. Fieldwork was carried out with the support of Dr Javier Juste and Prof Carlos Ibanez. Metabarcoding sequencing was carried out at the genomic facility at Queen Mary University of London with the support and advice of Dr Beth Clare. Prof. C. Patrick Doncaster assisted with data analysis. I wrote the manuscript and co-authors listed above contributed to revisions.

Chapter 4: this chapter was jointly conceptualised by Dr. Orly Razgour and me. I carried out all the GIS and modelling work and developed the measure of Geographic Avoidance. Dr Laura Graham, Hynek Paul and Prof. C. Patrick Doncaster gave advice on methods. Dr Javier Juste, Prof Carlos Ibanez, Dr Hugo Rebelo, Dr Antton Alberdi, Prof Danilo Russo and Dr Andreas Kiefer provided location records data for the models. I wrote the manuscript and all co-authors listed above contributed to revisions.

During the execution of this PhD I have contributed to other projects besides this thesis, which has led to two publications:

Alberdi, A., Razgour, O., Aizpurua, O., Novella-Fernandez, R., Aihartza, J., Budinski, I., Garin, I., Ibáñez, C., Izagirre, E., Rebelo, H., Russo, D., Vlaschenko, A., Zhelyazkova, V., Zrnčić, V. & Gilbert, M.T.P. (2020) DNA metabarcoding and spatial modelling link diet diversification with distribution homogeneity in European bats. *Nature Communications*, 11, 1154.

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1. Chapter 1- General Introduction

1.1. Ecological framework: Processes shaping spatial diversity patterns from communities to species ranges

Understanding the processes that drive the patterns of diversity that we observe has been a fundamental theme of biogeography since the XIX century (Ebach 2015). Accumulated knowledge over decades have led to the development of some general principles and theories (Vuilleumier 1999; Wen *et al.* 2019) that constitute the foundation for predicting responses of diversity to changes in natural systems. However, we are still far from a complete understanding of the operation and interplay of the different biogeographical processes across spatial scales. As natural systems are predicted to be more and more threatened by human-induced changes such as habitat destruction (Haddad *et al.* 2015), invasive species (Molnar *et al.* 2008) and climate change (Parmesan 2006), increasing our understanding of how diversity patterns are shaped becomes more important than ever.

Two fields of ecology have focused on understanding processes shaping species diversity patterns. Biogeography has focused on broad-scale processes and patterns, typically on describing species distributions and understanding how different factors shape those, while community ecology has focused on the processes that contribute to the assembly of different sets of species, mostly at fine local scales (Chase & Myers 2011; Jenkins & Ricklefs 2011). Despite the distinction between both fields, the ecological processes involved are common to both disciplines. Evolutionary forces and dispersal constraints given by geographic barriers and species dispersal ability set the pool of species of a specific region. Then environmental factors filter the species that can thrive under specific local conditions. Species filtering occurs through specific species traits that link to their performance in that environment (Keddy 1992; LeRoy 1997). For instance, temperature restricts species geographic range based on their physiology, morphological or behavioural adaptations, e.g. species that inhabit high latitudes typically have low body size to surface ratios (Bergmann 1847) and long fur, use burrows (Hannon & Eleanor 1962), or can have physiological adaptations, for instance cold resistance proteins in insects subjected to freezing point temperatures (Doucet *et al.* 2009). Finally, interactions between species also influence diversity patterns. Mutualistic interactions can facilitate the presence of a species (Araújo & Luoto 2007), while predator-prey interactions may impact negatively prey populations as frequently seen with invasive species (Bellingham *et al.* 2010). Similarly, competitive interactions may prevent the presence of one competitor as predicted by the competitive exclusion principle (Gause 1932; Hardin 1960), which states that two

species that share the same ecological niche cannot coexist in sympatry. The resources that lead to competition can be trophic or space, such as roosting places and foraging territories, and competition can be through exploitation of the resource or through interference when one species negatively impacts the ability of another to access the resource (Miller 1967; Schoener 1983; Lang & Benbow 2013).

The different biogeographic processes are spatial-scale dependant. Environmental filtering mechanisms, such as climate, are thought to drive broad-scale diversity patterns, while other mechanisms, like specific habitat preferences, are thought to refine them at finer scales (Willis & Whittaker 2002). Yet, the interplay between factors is complex. Some act simultaneously across spatial levels (LeRoy 1997; Cushman & McGarigal 2004), and the relative contribution of fine-scale habitat factors vs broad-scale effects varies depending on specific ecological processes and study systems (Lawler & Torgersen 2019). For instance, the importance of different types of environmental factors across scales changes depending on bird and bat guilds (Zhang *et al.* 2013; Carrara *et al.* 2015; Ferreira *et al.* 2017), between taxonomic groups (rodents vs bats) (Presley *et al.* 2012), or latitudinally for bird communities (Barnagaud *et al.* 2013).

In contrast to environment filtering, the impact of biotic interactions on diversity patterns is a long-discussed question (Pianka 1981) that is still controversial (Wiens 2011). Their role is usually restricted to local scales (Willis & Whittaker 2002). According to the most widely accepted framework of animal community assembly (Niche theory: Chesson 2000; Chase & Leibold 2003; Letten *et al.* 2017), biotic interactions are thought to be a major force driving local species assemblages. Under niche theory, coexistence is promoted through differential use of resources driven by functional differences between species. Accordingly, co-occurring species are expected to be functionally dissimilar and use different resources (Schoener 1974), as has been shown in numerous studies of, for example, fish (Ross 1986), shorebirds (Bocher *et al.* 2014) or rodents (Codron *et al.* 2015). Niche differentiation in plants and other sessile organisms can be driven by trade-offs in energy allocation towards different life history traits (Kneitel & Chase 2004). Other alternative frameworks of community assembly mostly based on plants focus on neutral processes, such as dispersal limitation and stochasticity driving species assemblages (e.g. *Unified neutral theory of biodiversity and biogeography*: Hubbell 2001). The latter has been often used and as a null model to evaluate whether observed patterns deviate from neutral expectations (Alonso *et al.* 2006; McGill *et al.* 2006b).

Recent studies have suggested that biotic interactions can also contribute to driving patterns of species ranges at broad spatial scales. Out of 51 empirical studies reviewed by Sexton *et al.* (2009), 31 supported the role of biotic interactions in shaping species range limits, and additional eight studies provided partial support. Some examples reviewed by Wisz (2013) of species whose distribution areas are thought to be shaped by biotic interactions include competitive interactions between animals such as the two European hedgehog species *Erinaceus europaeus* and *Erinaceus roumanicus*, different equids in Africa, the replacement of puma by leopard in the Old World during early middle Pleistocene, or small birds on islands (Gotelli *et al.* 2010). There are also examples that include trophic interactions between plants and plant consumers, like butterflies (Araújo & Luoto 2007), or predatory interactions between animals, such as extinctions on islands after invasions of rats (Jones *et al.* 2008).

1.2. Methods for studying the biogeographic processes shaping diversity patterns

1.2.1. Understanding species-environment relationships

Approaches to understand how environmental factors drive species patterns include measuring species physiological responses to environmental factors (Dowd *et al.* 2015). Such empirically measured species responses to environment can be used in mechanistic models to predict limits to species distributions and changes in fitness and population growth rates under environmental change (Kearney *et al.* 2010; Leroux *et al.* 2013). Disadvantages are the high economic and time costs and ethical issues associated with animal experimentation. Moreover, animal behaviour modifies the direct relationship between species physiology and environment factors, for example, through changing the microhabitat to thermoregulate (Kearney *et al.* 2009). Species environmental responses can be, alternatively, inferred by analysing the environmental conditions where species are found. Species Distribution Models (SDMs), also known as ecological niche models or climate envelope models, compare environmental conditions in locations where species are known to be present to background conditions in order to build species responses to the environment (Guisan *et al.* 2017). Species-environment responses are then used to predict the geographic areas that are environmentally suitable for the species (Elith & Leathwick 2009). SDMs are therefore linked to both environmental filtering and niche theory. SDMs can have many applications beyond understanding species responses to the environment, such as identifying suitable areas for conservation management, directing survey efforts for unknown populations, assessing potential ranges of invasive species (Reviewed in: Araújo & Townsend Peterson 2012) and

predicting species range shifts under climate change (Guisan & Thuiller 2005). They do not require life history, demographic or physiological information about the species, and therefore are particularly suitable for use in conservation management and broad-scale multi-species analyses. However, they disregard other processes that shape diversity patterns, such as biotic interactions, dispersal and evolutionary adaptations (Pearson & Dawson 2003; Boulangeat *et al.* 2012; Kissling *et al.* 2012; Thuiller *et al.* 2013).

1.2.2. Understanding the role of interspecific competition

The controversy about the importance of competition in ecological processes arises in part due to challenges involved in unambiguously identifying its effects (Connell 1983; Schoener 1983). The best method to quantify the impact of competition is experimentally through removal or exclusion experiments, in which one species is excluded and the effect on the other species is assessed in terms of fitness, population growth or occupancy (Pianka 1981). Some classic examples of these experiments under laboratory conditions in animals involve beetles of the genus *Tribolium* (Park 1948) or crustacean microcosms (Neill 1974). The experimental approach can also be carried out under field conditions (reviewed in Schoener, 1983), although it is not feasible for many organisms, in particular those with environmental requirements that cannot be replicated under controlled conditions, like highly mobile animals, or species of conservation concern.

The ultimate consequence of competition in the absence of coexistence mechanisms is spatial exclusion (Gause principle: Gause 1932; Hardin 1960). If competitive exclusion influences species assemblages, the resulting observed pattern is a tendency of species to be absent in areas where the competitor is present. Identifying such a pattern of species avoidance sets the basis for inferring competitive effects from occurrence data. Accordingly, species co-occurrence is typically used in community ecology to study the role of biotic interactions in community assembly processes (Gotelli 2000; Götzenberger *et al.* 2012). The main difficulty when interpreting species occurrence patterns resulting from competition is distinguishing the effect of differential ecological preferences from a potential effect of geographic avoidance of competitors (Bar-Massada 2015). Recently developed analytical methods aim to disentangle the relative role of different factors using hierarchical models (Dormann 2018).

Species ecological niches or traits related to the acquisition of resources of coexisting species are frequently used to obtain inferences on the role of biotic interactions (e.g. Nicholls & Racey 2006; Jiang *et al.* 2008) instead of directly analysing patterns of species presence. However, the interpretation of patterns of ecological overlap as a result of competition is not

straightforward. High similarity in species ecological niches can result in competition, but it could also indicate coexistence due to non-limiting resources (Colwell & Futuyma 1971; Pianka 1974). Moreover, low niche similarity could indicate that species do not compete for resources, but it could equally indicate species partitioning their use of resources in response of competition (e.g. Andreas *et al.* 2012a; Emrich *et al.* 2014). In community ecology, ensembles (*sensu* Fauth *et al.* 1996) under strong biotic effects are expected, according to niche theory, to diverge in their use of ecological space. Accordingly, niche partitioning is often used to infer the relative role of different processes involved in community assembly (Luiselli 2008). An alternative approach to detect competition for pairs of potential competitors is comparing the ecological niche of species in allopatric versus sympatric populations (e.g. Salsamendi *et al.* 2012). Competition can be inferred if ecological niches are more separated in sympatric populations than in allopatric populations (Pianka 1981).

The portions of the ecological niche most commonly studied are habitat use and diet. Habitat use can be inferred using field-extracted data or Geographic Information Systems (GIS; Russo *et al.* 2014). Diet was traditionally obtained using morphological identification of stomach content or faeces. The more recent development of DNA metabarcoding and high throughput sequencing approaches enables affordable, high taxonomical resolution identification of prey items for large number of samples, which is providing new insights into species trophic ecology (Sousa *et al.* 2019).

At broader scales, parapatric ranges in morphologically similar or phylogenetically-related species were traditionally interpreted as a result of competitive interactions, especially in the absence of barriers to dispersal and when sharp edges do not match clear environmental gradients (Miller 1967; Bull 1991), but few studies have quantified the potential role of competition (Gutiérrez *et al.* 2014). Other approaches have attempted to model hierarchically the effect of interactions after accounting for environmental preferences, though their inferences have not been empirically validated yet (Godsoe *et al.* 2017; Dormann 2018; Zurell *et al.* 2018).

1.2.3. Using functional ecology to understand biogeographic patterns

Functional traits are morphological, physiological, ecological, life history or behavioural measurable characteristics of individuals. They can be useful for understanding biogeographic processes because they drive species performance (Ricklefs & Miles 1994), for instance thorax width affects the capacity of bees to fly in cold conditions (Osorio-Canadas *et al.* 2016), and therefore they are the units through which environmental filters operate (Keddy 1992; LeRoy

1997). Functional traits bring a mechanistic understanding of species-environment relationships that can be generalizable across systems (Wong *et al.* 2019). They can also be useful for understanding the relative role of environmental filtering and biotic effects in community assembly. According to niche theory, ensembles under strong biotic effects, are expected to be composed by species with differentiated traits, so that species use a different ecological space. In contrast, ensembles shaped by strong environmental filtering are expected to converge in the traits that allow them to be successful in that environment (Pausas & Verdú 2010). Functional traits such as body size, nesting preferences or plumage coloration have been shown to be useful in predicting habitat use of bird assemblages in the southern Kalahari (Seymour & Dean 2010). Ant body size, head width or antennae length have been shown to be related to vegetation structural complexity in urban green spaces in Australia (Nooten *et al.* 2019).

1.3. Bats as a model study system to understand biogeographic processes

The order Chiroptera, comprising all bats, is the second most species-rich and an extremely diversified order of mammals, including over 1421 species worldwide (Simmons & Cirranello 2020). The order, divided into the sub-orders Yangochiroptera and Yinpterochiroptera (Teeling *et al.* 2005), is unique among mammals due to the ability of their members to perform sustained flight. Bats are also remarkably long-lived and have slow reproductive rates for mammals of their body size (Barclay & Harder 2003). Bats are generally nocturnal, and most have evolved echolocation to orientate and capture prey. Bats show high diversity in size, from barely 3 g to 1 kg, and also functionally, including insectivorous, frugivorous, pollinivorous, carnivorous, piscivorous and even sanguinivorous species (Kunz & Brook 2003). Bats play important roles in ecosystems and provide ecosystem services such as suppression of arthropod pest populations, seed dispersal, pollination and forest regeneration (Kunz *et al.* 2011). In Europe there are 45 species included in the families Vespertilionidae (37), Rhinolophidae (5), Molossididae (1), Miniopteridae (1), Pteropodidae (1) (Petrov *et al.* 2018). All of them, except the pteropodid *Rousettus aegyptiacus*, which has very limited presence (Korine 2016), are small to medium size (4-40 g) primarily insectivorous bats.

Recent developments in molecular tools have led to the discovery of several new species of bats (Mayer & von Helversen 2001), primarily through the splitting of cryptic species that were classified as a single species because they are morphologically very similar (Pfenninger & Schwenk 2007). For instance, *Pipistrellus pipistrellus* and *P. pygmaeus* (Jones & Van Parijs 1993; Barratt *et al.* 1997) and more recently, the splitting of the *Myotis nattereri* species

complex in southern Europe into *Myotis escalerai* and *Myotis crypticus* (Juste *et al.* 2019). Cryptic species are more likely to have similar ecological requirements, and are therefore ideal systems for testing the role of biotic interactions (e.g. Arrizabalaga-Escudero *et al.* 2018).

1.3.1. Environmental determinants of bat biogeographic patterns

Global diversity patterns of bats show a negative latitudinal gradient from the tropics to high latitudes (Willig *et al.* 2003), though with replacement of family composition, such as the important temperate climate adapted family Vespertilionidae, which increases in richness at temperate latitudes both in North America and Europe (McCoy & Connor 1980; Ulrich *et al.* 2007; Ramos Pereira & Palmeirim 2013; Petrov *et al.* 2018). Bats have larger average range sizes than other mammals of similar sizes, but in contrast to other mammals, their range size does not correlate with body size (Willig *et al.* 2003). Other traits may better explain range characteristics, for example, wing morphology in vespertilionids, whereby high aspect ratio correlates positively to range size (Luo *et al.* 2019), or breadth of trophic niche explains homogeneity of continental ranges in Europe (Alberdi *et al.* 2020).

Temperature is one of the main drivers of broad-scale bat diversity patterns (McCain 2006; Ulrich *et al.* 2007), as well as at more regional-scale elevation gradients where warmer temperatures promote higher bat diversity (Wang *et al.* 2003; Presley *et al.* 2012). Water availability is also an important driver of bat diversity and activity (McCain 2006), especially in regions where its access can be limiting, such as Mediterranean areas during summer droughts (Amorim *et al.* 2018). Similarly, in desert environments, water availability structures bat communities (Razgour *et al.* 2011c), and in Africa it is one of the main factors driving bat species richness patterns (Szamocki *et al.* 2015; Cooper-Bohannon *et al.* 2016). The effects of temperature and water availability on bat diversity patterns are a synergy between the result of physiological constraints and trophic availability (McCain 2006). The high energetic demands of flight (Thomas & Suthers 1972) together with the high energetic cost associated with thermoregulation at low temperatures, combines with the direct dependence of insects on temperature. The aerial activity of insects is enabled only above a certain temperature threshold, for instance 8-17 °C in the Lepidoptera *Agrochola lychnidis* (Taylor 1963). Bats also have a particularly high rates of water loss (Studier *et al.* 1970) and require a source of drinking water within their home range (Rabe & Rosenstock 2005; Seibold *et al.* 2013). Hence water availability can impact their reproductive success (Amorim *et al.* 2015). Similarly, arthropod availability is also higher in humid environments and near aquatic habitats (Fukui *et al.* 2006).

Specific habitat requirements are also a major factor driving bat species diversity patterns (Fahr & Kalko 2011; Herkt *et al.* 2016). Many temperate species depend on forests (Walsh & Harris 1996), either as a foraging habitat and/or on trees as roosts. In North America, 25 out of the 45 species are linked to forest (Lacki *et al.* 2007b). Specifically, mature forest with heterogeneous structure and low tree densities provide a suitable habitat for more species (Lacki *et al.* 2007b). On the other hand, most bats species – though not all – generally tend to avoid arable land or improved grasslands (Walsh & Harris 1996). Bat-habitat preferences can be predicted based on bat traits. Bats interact with the spatial environment through echolocation. By emitting ultrasound and receiving echoes, bats are able to perceive obstacles, locate and target prey. Different acoustic call frequencies and wing morphologies enable bats to exploit different levels of spatially cluttered environments (e.g. Crome & Richards 1988; Patriquin & Barclay 2003). Species with high wing loading have high flight speeds and low manoeuvrability, defined as their ability to turn in a reduced space (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). These bats forage fast at high altitudes in open space and tend to use low frequency calls that are suitable for detecting prey across long distances. At the other extreme, bats with low wing loading and aspect ratio are highly manoeuvrable but fly at low speeds. They are able to detect prey in structurally very cluttered environments and forage within the forest canopy using either frequency modulated or high constant frequency echolocation calls (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). Apart from habitat spatial structure, another requirement that may drive habitat filtering is roost availability. European bat species roost in caves, mines, rock crevices, human structures, such as buildings and bridges, or trees (Dietz & Kiefer 2016). The presence of suitable caves and mines depends greatly on regional lithology and may limit ranges regionally (Parker *et al.* 1997). Suitable trees for roosting are found in mature forest structures (Lacki *et al.* 2007b) that are very limited in young European forests, and therefore have great potential to drive habitat filtering. On the other hand, bats that roost in human structures are expected to be less restricted by roost availability.

1.3.2. Contribution of biotic interactions to shaping bat assemblages

While environmental drivers of bat diversity are generally known, the contribution of biotic processes driving ensembles of bats is little known. Some studies show random patterns in the functional structure of ensembles (Willig & Moulton 1989), some show functional clustering, pointing to dominance of environmental filtering processes (Findley 1976; Findley & Black 1983), while others show higher functional divergence than expected by chance (Moreno *et al.* 2006; Schoeman & Jacobs 2008), pointing to some role of biotic interactions. More often,

however, studies that aim to understand the role of biotic interactions among bats focus on groups or pairs of morphologically similar species and measure the extent of niche partitioning. Partitioning has been often assessed but has only rarely been demonstrated to be the result of competition (e.g. Postawa *et al.* 2012). However comparisons between sympatric and allopatric populations are rare (Salinas-Ramos *et al.* 2020), only few studies thus far compared resource overlap in sympatric versus allopatric populations (e.g. Arlettaz *et al.* 1997; Postawa *et al.* 2012; Salsamendi *et al.* 2012). More commonly, studies show that bats respond to interspecific competition by partitioning their foraging habitat, which is regarded as the primary mechanism facilitating species coexistence in sympatric insectivorous bat species (Arlettaz 1999; Patterson *et al.* 2003; Nicholls & Racey 2006). Under competition, species may partition their habitat use, by changing from more open to more cluttered habitats (e.g. Salsamendi *et al.* 2012), their foraging strategy, for example by changing from hawking to gleaning, or the strata used, through consuming more prey from the ground as has been reported in *Myotis dasycneme* and *Myotis daubentonii* (Krüger *et al.* 2014). Other studies provide evidence for temporal partitioning of activity time in response to interspecific competition (Kunz 1973; Adams & Thibault 2006; Razgour *et al.* 2011c). Very few have addressed resource partitioning of roosts (Jacobs & Barclay 2009; Hillen 2011). Interspecific roost sharing occurs commonly in some species providing mutual benefits such as better thermoregulation or lower per-capita predation risk, it also may lead to negative interactions (Zeus *et al.* 2017).

1.4. *Myotis nattereri* species complex

Myotis nattereri is a complex of at least four small bat species with almost identical morphology, whose phylogenetic relationships have been disentangled only recently (Salicini *et al.* 2011, 2013; Juste *et al.* 2019). They speciated as a consequence of long-term isolation in the different Mediterranean glacial refugia during the second half of the early Pleistocene (Salicini *et al.* 2013). *M. nattereri* is thought to have become isolated in the Balkan glacial refugia, and subsequently rapidly colonised central and northern Europe (Salicini *et al.* 2013), where it is currently a common and widely distributed species (Fig. 1.1c). *Myotis escalerae* (Fig. 1.1a) was isolated in the Iberian Peninsula, where it is currently widely distributed up to the northern slopes of the eastern French Pyrenees near the Spanish border (Fig. 1.1c) (Evin *et al.* 2009; Puechmaille *et al.* 2012). *Myotis crypticus* (Fig. 1.1b) was isolated in the Italian Peninsula (Salicini *et al.* 2013) and currently is present in Italy, southern France, and the north of the Iberian Peninsula (Juste *et al.* 2019) where it overlaps with *M. escalerae* (Fig. 1.1c). In contrast to the other two lineages, the entire evolutionary history of *M. escalerae* has taken place inside

its glacial refugia (Razgour *et al.* 2015), and according to phylogeographical analysis, interspecific competition with *M. nattereri* and *M. crypticus* could have limited its post-glacial range expansion (Razgour *et al.* 2015). Finally, the little known species *Myotis zenatius* occurs in Morocco (Juste *et al.* 2019).

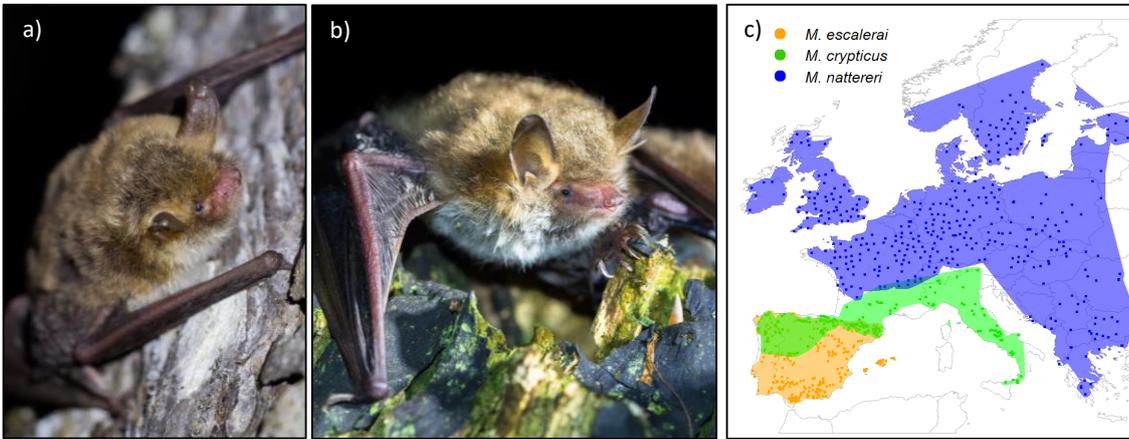


Fig. 1.1 – *Myotis escalerae* (a) from Sierra de Cazorla (Jaén, Spain) and *Myotis crypticus* (b) from Sierra de Cameros (La Rioja, Spain). Roberto Novella Fernández. c). Distribution of the three European species of the *M. nattereri* cryptic group. Overlapping range between *M. crypticus* and *M. nattereri* is not well known.

All four species are morphologically almost identical. The two phylogenetic clades have subtle diagnostic characters: *M. escalerae* and *M. zenatius* have a more pronounced bristled edge in the tail membrane, and the origin of the wing membrane is from the metatarsus instead of at the base of the foot as in *M. nattereri* and *M. crypticus*. Nevertheless, molecular confirmation is necessary for their identification. Species within the *M. nattereri*-*M. crypticus* and *M. escalerae*-*M. zenatius* groups are only distinguishable molecularly (Juste *et al.* 2019).

Most of the ecological knowledge of the group comes from the central-northern European species *M. nattereri*. This species is found in forests and open woodlands of any kind, broadleaved, coniferous, and mixed (Boye & Dietz 2005). It is a highly manoeuvrable species that flies low, very slowly and hovers close to the vegetation (de Jong 1995). It has been observed to feed mostly by gleaning, picking up prey from leaves with the tail membrane (Swift & Racey 2002). A gleaning foraging mode is also supported by the high amount of non-flying prey items in *M. nattereri*'s diet (Shiel *et al.* 1991). *M. nattereri* uses frequency-modulated search signals of very large bandwidth to perceive prey within a few centimetres of echo-cluttering vegetation, and select prey by size (Siemers & Schnitzler 2000). It has a broad diet containing mainly Araneae, Lepidoptera – including larval stages – and Diptera (Swift 1997; Vaughan 1997; Mortimer 2006; Hope *et al.* 2014; Galan *et al.* 2018). The home range is

small and maximum distance travelled per night is generally less than 4 km away from the roost (Boye & Dietz 2005; Zeale *et al.* 2016), which is usually located in trees or human structures (Smith & Racey 2005).

In contrast to their better-studied congener, *M. escalerae* and *M. crypticus* are poorly known. In general, they are assumed to be ecologically similar to *M. nattereri* due to their almost identical morphology. All species are thought to be associated with forests, although there is a scarcity of habitat use studies. In the Iberian Peninsula, observations and capture records (Juste, & Ibanez, personal communications) suggest that *M. crypticus* is associated with Atlantic forests while *M. escalerae* with Mediterranean forests. Morphological dietary studies of the *M. nattereri* group in Switzerland that are now attributed to *M. crypticus* show a similar diet to *M. nattereri* (Vaughan 1997). The trophic ecology of *M. escalerae* has not been studied yet. The clearest ecological difference between members of the group is their roost preferences. *M. escalerae* is a cave roosting species, while *M. crypticus* is primarily a tree-roosting species (Juste *et al.* 2019).

Thesis aim and objectives

Our understanding of how different biogeographic processes interact to drive diversity patterns has important knowledge gaps that hinder our capacity to predict and mitigate impacts that natural systems are experiencing as a consequence of human activity. In this thesis I aim to advance our knowledge on how the role of habitat filtering and biotic interactions operate across spatial scales to shape biogeographic patterns. The thesis contains three data chapters (Chapters 2-4) that address five objectives.

Chapter 2. Disentangling landscape-scale species-forest relationships: Tree roost availability limits the distribution of bats in Mediterranean systems.

Objective 1: To identify the contribution of landscape-level forest characteristics relative to climate to determining regional species distributions of forest-specialist Mediterranean bats.

Objective 2: To determine whether landscape-scale bat-forest relationships are driven by bat eco-morphological traits.

Chapter 3. Trophic resource partitioning drives fine-scale coexistence in cryptic bat species.

Objective 3: To identify whether trophic partitioning processes enable morphologically similar species to coexist. For that I use the recently described and morphologically almost identical cryptic species of bats *Myotis crypticus* and *Myotis escaleraei*, whose trophic ecology is not known, and whose ranges are parapatric.

Chapter 4. Geographic Avoidance: a new measure to detect the effect of biotic interactions on species ranges

Objective 4: To develop a measure that uses Species Distribution Models to detect the broad-scale patterns of geographic avoidance expected from competition if it exerts a role on limiting the range of species. I apply the measure to several groups of morphologically similar bats.

Objective 5: To assess the link between ecological similarity and fine-scale mechanisms of resource partitioning between species and their broad-scale patterns of geographic avoidance.

2. Chapter 2- Disentangling landscape-scale species-forest relationships: Tree roost availability limits the distribution of bats in Mediterranean systems

2.1. Abstract

Understanding the biogeographical processes that shape species diversity patterns is a principal aim of ecology that has important implications for predicting biodiversity responses to global environmental change. Forests are a key habitat for native wildlife in temperate latitudes. Their structure and composition determine their capacity to support biodiversity. While habitat structure and composition is important for shaping local assemblage patterns, its potential to drive broader-scale species distributions is little explored. I aim to disentangle the role of landscape-scale forest habitat characteristics in driving regional diversity patterns, following a trait-based approach that considers the operation of the different species-forest dependency mechanisms. I used detailed forest structure and composition inventory data from the Mediterranean, though climatically heterogeneous region of Andalusia (Spain), and distribution data of the nine resident forest bat species. I focus on forest bats due to their known close dependency on forests for both roosting and foraging through eco-morphological relationships. Forest structure and composition characteristics were more important in driving species assemblages and regional-scale ranges than climate. The regional distribution of tree-roosting bats was more strongly affected by forest characteristics than the distributions of bats that roost in buildings and caves, showing that roosting ecology plays a major role in driving regional-scale biogeographic patterns of forest bats in Mediterranean ecosystems. Tree-roosting bats were closely associated with mature heterogeneous forest structures and presence of trees with diameters > 425 mm. Conversely, and contrary to what previous local-scale studies show, wing morphology likely plays a more minor role explaining dependency towards forest at this spatial scale. This study identifies broad-scale implications of bat-forest relationships, highlights how different biogeographic mechanisms may operate at different spatial scales and the importance of considering the different habitat dependency mechanisms to disentangling these relationships.

2.2. Introduction

Understanding the biogeographical processes that shape species diversity patterns is a principal aim of ecology that has important implications for predicting biodiversity responses to global environmental changes (Barnagaud *et al.* 2013). Different abiotic factors filter from the regional pool the species for which local conditions are suitable (Keddy 1992; LeRoy 1997). The units through which environmental filters affect spatial patterns are species traits (Keddy 1992). For example, body colouration contributes to shaping dragonfly species ranges by affecting thermoregulation (Pinkert *et al.* 2017), or morphology predicts habitat use of bird assemblages across habitats in Africa (Seymour & Dean 2010), river forests in Brazil (Batisteli *et al.* 2018) or ant assemblages in forests in South East Australia (Nooten *et al.* 2019). The effect of environmental filters are dependent on spatial scale (Whittaker *et al.* 2001). Climate is thought to drive broad-scale species patterns while preferences to specific habitat characteristics are thought to act generally at finer scales (Willis & Whittaker 2002), though they may have broader scale consequences (Barnagaud *et al.* 2013). Forests are a key habitat for biodiversity (Brockhoff *et al.* 2017). The specific structure and composition of forests determines its suitability as habitat for different taxa (MacArthur & MacArthur 1961; Willson 1974; Sullivan *et al.* 2000; Díaz *et al.* 2005; Huang *et al.* 2014). Habitat structure is generally regarded to have impact mostly on local-scale patterns (Willis & Whittaker 2002). The potential for forest specific composition and structural characteristics to drive broader scale species ranges is little explored, yet understanding this has major consequences for assessing the responses of forest-specialist species to anthropogenically-driven global environmental changes.

Bats are the second most species rich order of mammals, with more than 1400 species (Simmons & Cirranello 2020), of which many are linked to forests (Lacki *et al.* 2007b; Peixoto *et al.* 2018). The dependency of bats on forests is driven at least in part by their traits, such as their roosting ecology and their wing morphology. Most bats that roost in trees rely on the presence of crevices or cavities formed through natural decay or excavated by woodpeckers that provide suitable thermal conditions and protection from predators (Barclay & Kurta 2007). Trees with large diameter and height in early-mid stages of decay are preferred (Lacki *et al.* 2007a; Silvis *et al.* 2015). Additionally, certain types of trees may provide more roosting opportunities, such as broadleaved species over coniferous ones (Alcalde *et al.* 2018), or tree species with low wood density that are prone to provide cavities at earlier ages, often due to action of woodpeckers. Second, forest structure filters the habitat use of bat species depending on eco-morphological traits (Crome & Richards 1988; Patriquin & Barclay 2003;

Froidevaux *et al.* 2016; Carr *et al.* 2020). Only bats with low wing loading and aspect ratio that use broad-band calls at high frequencies or constant frequency calls, are able to fly at very low speeds, echolocate, and locate prey in structurally cluttered environments (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). Finally, bats are also expected to respond to forest depending on trophic resources. However, trophic-habitat relationships have been addressed in only a few studies and are less direct (eg. Barclay 1991; Kusch *et al.* 2004; Lumsden & Bennett 2005; Fukui *et al.* 2006; Morris *et al.* 2010; Carr *et al.* 2020). The three mechanisms interact to drive the composition of local assemblages, for instance, prey abundance can drive bat activity after forest structure filters species based on their flight-related traits (Sleep & Brigham 2003).

Bat-forest relationships are usually studied at local spatial scales, typically comparing habitat use among a few differentiated forest sites (Patriquin & Barclay 2003; Lumsden & Bennett 2005; Dodd *et al.* 2012). However, and despite recent growing interest (Fuentes-Montemayor *et al.* 2013; Ferreira *et al.* 2017; Wood *et al.* 2017), there is an important knowledge gap regarding the operational scales of these dependency mechanisms, and specifically regarding medium-scale responses towards habitat (Lacki *et al.* 2007b; Fahr & Kalko 2011; Peixoto *et al.* 2018). Better comprehension of such responses is critical for understanding broad-scale diversity patterns for mobile organisms, such as bats, that have home ranges spanning across different habitats, and therefore are prone to be affected by landscape-level processes (Lacki *et al.* 2007b).

Mediterranean forests are expected to experience severe changes in forest structure and composition under climate change (Resco De Dios *et al.* 2007; Lindner *et al.* 2010) due to increases in summer drought severity and heat stress (Diffenbaugh *et al.* 2007; Allen *et al.* 2010; Carnicer *et al.* 2011) and increase in frequency of forest fires (Pausas 2004). A better understanding of the broad-scale habitat dependency of forest fauna is important for determining species vulnerability towards climate change and predicting impacts of habitat change on species ranges. I aim to disentangle the landscape-scale environmental filters that drive diversity patterns in forest-dependent bat species.

I use forest inventory data from the Mediterranean region of Andalusia in Spain (size 97,600 km²) and its forest-specialist bat fauna to (1) identify the importance of landscape-level forest characteristics in determining regional species distributions relative to climate, and (2) determine whether bat eco-morphological traits explain landscape-scale responses to forest characteristics and have an impact on species regional distributions. The use of traits enables a

more mechanistic understanding of the processes that shape diversity patterns than taxonomy-based studies, and better generalisations across study systems (McGill *et al.* 2006a). Roost availability is a crucial resource for bats (Sagot & Chaverri 2015) that is often in limited supply. Tree-roosting bats require the presence of trees with specific roosting characteristics, and require a high number of roosts due to frequent roost switching (Russo *et al.* 2005; Barclay & Kurta 2007). I hypothesise that tree roosting bats will show higher dependence towards forests and positive responses towards characteristics that promote roost availability. Given the ecomorphological link between bat wing morphology and local-scale habitat use (Aldridge and Rautenbach 1987), I also hypothesise that among the bats that exploit forests for foraging, those with morphological traits that enable them to fly in more structurally cluttered habitats (low wing loading and aspect ratio) will be more generalist forest users and less dependent on specific mature-forest characteristics and have greater tolerance towards forest structural clutter. I expect the latter relationship not to hold when including open-space foraging bats because forest spatial structure should not restrict their habitat use. Through following a trait-based approach I aim to disentangle the mechanisms behind species-forest relationships at the landscape scale.

2.3. Methods

2.3.1. Forest inventory data

I used the forest database *Tercer Inventario Nacional Forestal* (IFN3) (<https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3.aspx>). The database contains forest data based on plots regularly distributed over every 1 km of forested area in Spain sampled between 1997 and 2007. Plots are circular with variable radii (5-25 m) depending on tree diameter. Detailed forest variables describing forest structure and composition are available for each plot. Trees are defined as individuals of arborescent species with diameter at breast height (DBH) greater than 7.5 cm. I processed the database combining the different tables and summarised 52 structural and compositional variables that may be relevant for bat ecology at the forest plot level in R (R core team 2020)(Supplementary Table A1.1).

2.3.2. Study system

The study area covers the 97,600 km² of the Spanish region of Andalusia in the south of the Iberian Peninsula. The region is climatically Mediterranean, though heterogeneous, with an elevation range from sea level to more than 3000 masl, and composed by three differentiated

topographic units, Sierra Morena in the north, the valley of Guadalquivir river in centre-east, and the centre-east Mountain range of Sierras Béticas and Penibéticas (Supplementary Fig. A1.1). The dominant forests in the region are composed by the Mediterranean species *Quercus ilex*, *Pinus halepensis*, *Quercus suber*, and *Pinus pinea*, and in mountainous areas *P. pinaster*, *Pinus nigra*, and *P. sylvestris*. The Guadalquivir valley is largely deforested due to agriculture and livestock farming. A large proportion of the forests in the region are relative young due that they were exploited by rural population until the beginning of the second half of the XX century, and many of the current forest were planted during the decades 1940-1980 (Zambrana Pineda & Ríos Jiménez 2006). I considered all forest bat species present in the region (Table 2.1). *Myotis bechsteinii* and *Barbastella barbastellus* forage in forests and roost in trees, the first in tree holes and the second under loose bark (Boye & Dietz 2005). *Myotis escalerai*, *Myotis mystacinus*, *Myotis emarginatus*, *Plecotus austriacus*, *Rhinolophus euryale*, and *Rhinolophus hipposideros* forage in forests but roost in caves and mines or anthropogenic structures (Boye & Dietz 2005; Dietz & Kiefer 2016). Finally, *Nyctalus lasiopterus*, and *Nyctalus leisleri* roost in tree holes but constitute an ecologically different group because they forage in open habitats above the forest canopy (Boye & Dietz 2005; Estók *et al.* 2007). They are, accordingly, morphologically distinct, with higher wing loading (Supplementary Table A1.4), which enables them to fly fast at the expense of lower manoeuvrability. I included all these species in the study except *Myotis mystacinus* due to its low number of location records because of its extremely restricted presence in the region (Nogueras *et al.* 2013). I used the bat occurrence record database from EBD-CSIC (Spain). Most records were obtained through captures using mist-nets, harp traps or direct capture from roosts. Only a few (~1%) were based on acoustic identification. Types of locations sampled included forests, cave or mines entrances, buildings and bat boxes. The database initially contained 15,680 taxonomically validated and spatially precise (<50 m) records of the target bat species across the study area. It was filtered to only keep records between 1987 and 2018 to match the period of forest sampling (1997-2007, maximum temporal difference 20 years), resulting in 15,083 records.

I obtained from the literature bat traits that most directly relate to the environmental filters considered (Supplementary Table A1.4). I selected roosting ecology because it directly links with dependency on suitable trees for roosts. I selected wing loading and aspect ratio as the most important descriptors of bat flight performance (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). Wing loading describes the weight of the animal divided by the wing area, while aspect ratio is the square of the wingspan divided by area. They are both negatively linked with manoeuvrability and are shown to be negatively related to habitat use in highly cluttered areas

(Aldridge & Rautenbach 1987; Norberg & Rayner 1987), as it has been seen in several local-scale community studies (e.g. Crome & Richards 1988; Patriquin & Barclay 2003).

Table 2.1 – Bat species included in the study and their dependency on forests. *excluded due to low number of location records.

		Foraging habitat dependency		
		Limited	Facultative	Exclusive
Roost in tree dependency	Facultative Limited		<i>R. euryale</i>	<i>R. hipposideros</i>
			<i>P. austriacus</i>	<i>M. escalerae</i>
	Exclusive			<i>M. emarginatus</i>
				<i>M. mystacinus*</i>
		<i>N. leisleri</i>	<i>B. barbastellus</i>	
		<i>N. lasiopterus</i>	<i>M. bechsteinii</i>	

2.3.3. Bat responses towards forest structure and composition

2.3.3.1. Generating the data for species distribution models

I un-clustered bat occurrence records at a distance of 500 m to reduce overrepresentation of forest conditions in highly sampled locations. This is because bat sampling is often heavily biased towards specific locations with previous successful captures. The final dataset included 1014 un-clustered records (Supplementary Table A1.5, Supplementary Fig. A1.2), representing the geographic distribution of each species in the region.

I interpolated the values of forest variables on bat occurrence locations by calculating the mean and mode (quantitative and categorical, respectively) of the nearest 2-5 forest plots up to 3 km distance. This approach takes into account that bats are usually caught in specific drinking, feeding, commuting or roosting locations within their broader home range. Then, I used random points to obtain an equivalently interpolated forest background data. I assumed no dispersal restrictions for flying animals like bats within the region, and therefore, used all Andalusia as background. Within the study extent, I generated a high number of random points (10,000) and thinned them at a distance of 5 km to avoid “duplication” of forest data in more than one random point. For each bat species I generated a different set of background random points. I removed from the available forest plots the ones that are near species occurrence records (<4 km, Supplementary Table A1.5) because they are likely to fall within the bat’s home range, and I interpolated the remaining background forest data to the random

points following the same process as with the occurrence records (Supplementary Fig. A1.2 for the location of occurrence and background data for each bat species). The interpolation parameters used (2-5 closest forest plots within 3 km of occurrence record/random point) were chosen based on forest bat ecology and to maximise the density of background random points given the relatively small working area available. The resulting average number of forest plots and distance used in the interpolation were 4.3- 4.9 forest plots at an average distance 1.13-1.7 km depending on the bat species (Supplementary Table A1.5), and therefore represent forest characteristics from a landscape-scale area of several km².

I selected a subset of 18 uncorrelated ($r < |0.70|$, Dormann *et al.* 2013) quantitative forest variables (Supplementary Fig. A1.4) and 6 categorical variables based on their contribution to single variable species distribution models and perceived importance for forest bats (Table 2.2). I classified forest variables into four mechanistic groups according to their link to bat ecology based on literature (Table 2.2):

1. Roost availability: known to be driven by the size and age of the trees, and the presence of dead ones (Barclay & Kurta 2007). We chose a DBH value of 425mm as a threshold indicating large tree size considering that only 6.5 % of all the forest plots in the inventory database had a higher average DBH.
2. Structural heterogeneity: forest horizontal and vertical structural variability, high values are characteristic of mature forests (Franklin & Pelt 2004) and may provide richness of resources (Ishii *et al.* 2004).
3. Forest clutter: the amount of spatial cluttering, driven by density of trees, canopy and understory cover. Higher cluttering restricts habitat use by bats depending on bat ecomorphology (Norberg & Rayner 1987).
4. Composition: the identity of tree and shrub species.

It is important to note that this classification is not exclusive because some variables are inherently difficult to categorise. For instance, forests with older and larger trees usually are also structurally more heterogeneous. Additionally, I selected, among a subset 15 climatic and topographic variables downloaded from Worldclim (www.worldclim.org; Supplementary Table A1.3), four uncorrelated variables ($r < |0.70|$) that summarise well the effects of climate on bat species ranges (elevation, annual precipitation, maximum temperature of warmest month and temperature seasonality). I named this set of variables “climatic” for convenience (Table 2.2; Supplementary Table A1.3). I also included in the final set, a variable describing the distance to forest as a measure of the importance of forest for the presence of bats

irrespective of its structural and compositional characteristics. For that, I used the land cover map ESACCI-LC16 (<https://cds.climate.copernicus.eu>), reclassified all forest categories to a unique forest category, and created a layer of distance to forest using ArcGIS after having projected it to an equal distance coordinate system. All raster variables were downloaded at a resolution of 30 arc-seconds (~1 km). After processing the climatic variables, I extracted the values from rasters (R package raster: Hijmans 2017) to forest plot locations and followed with those the same interpolation and subsequent downstream processing as with the forest data.

2.3.3.2. Assessing bat responses towards forest structure and composition

I generated species distribution models (SDMs) with the Maxent algorithm (Phillips et al. 2006), in the R package *dismo* (Hijmans et al. 2017) to assess the effect of forest versus climatic variables on the distributions of forest bats in Andalusia. I used occurrence records with interpolated data as presence points and background random points with interpolated data as pseudoabsences. I choose features and regularisation values for each species based on AICc using the R package ENMeval (Muscarella et al. 2018) (Supplementary Table A1.5). To avoid model oversimplification, I compared regularization values of 1-3. I assessed the contribution of the different individual and mechanistic groups of variables to each species' model based on the model training gain. I assessed model discrimination ability based on the Area under the receiver operator Curve (AUC) of eight cross-validations models using 25% occurrence records for model testing. To determine whether model discrimination ability was higher than random, for each bat species, model AUC test scores were compared to null models generated with 100 different sets of random presences with the same number of records and following the same downstream procedures of background data generation, interpolation and modelling as with the observed dataset. Observed models with AUC test scores that fell above the 95% confidence interval of the null models AUC test scores were regarding as performing better than random (Raes & Ter Steege 2007).

Table 2.2 – Selected uncorrelated forest (F) and climatic (C) variables. Forest variables are grouped based on their mechanistic link to bat ecology: roosting availability (Roost), spatial heterogeneity (Het), forest composition (Comp), spatial clutter (Clutt). Type of variable: quantitative (Q) or categorical (C), variable unit and variable description.

Var. name	Variable group	Forest group	Type	Unit	Description
Tree DBH	F	Roost	Q	mm	Average Diameter at Breast Height of the trees.
Tree H	F	Roost	Q	m	Average height of trees.
Dead den	F	Roost	Q	%	Density of dead trees.
> 425 DBH	F	Roost	Q	trees/ha	Density of trees with DBH > 425 mm.
SoftW >425	F	Roost	Q	trees/ha	Density of trees of soft wood trees > 425 mm DBH (Supplementary Table A1.2).
Dev stage	F	Roost	C	-	Development stage of main tree species.
Wood density	F	Roost	Q	g/cm ³	Weighted average wood density of trees.
Tree DBH ra	F	Het	Q	NA	DBH range. Thicker - thinner tree.
Tree H ra	F	Het	Q	m	Tree height range. Highest - shortest tree.
Forest type	F	Het	C		Morpho-structural type.
% plantations	F	Het	Q	NA	Proportion of plots with plantations (calculated when interpolating).
Sp1 DBH struct	F	Het	C	-	Structural heterogeneity category (regular to irregular) of the main tree species.
Sp comp	F	Comp	C	-	Type of tree specific composition.
Underst R	F	Comp	Q	n. sp	Richness of shrub species.
Broadleaved	F	Comp	Q	trees/ha	Density of broadleaved tree species.
Tree R	F	Comp	Q	n. sp	Tree species richness in plot of 25m.
Tree sp	F	Comp	C	-	Main tree species. Names shown in Supplementary Fig. A2.5
Sp1 D	F	Comp	Q	%	Dominance of tree Sp1 (rel. tree density).
Spatial distr	F	Het	C		Spatial distribution.
Tree C	F	Clutt	Q	%	Tree cover, estimated in percent.
Total C	F	Clutt	Q	%	Total vegetation cover, estimated in percent.
Underst C	F	Clutt	Q	% cover	Understory cover. Sum of cover of each shrub species.
Underst H	F	Clutt	Q	M	Average height of understory.
Trees/ha	F	Clutt	Q	trees/ha	Tree density (>75 DBH) in the plot.
Distance to forest	-	-	Q	m	
Elevation	C	-	Q	m	
Annual Precipitation	C	-	Q	mm	BIO12 Bioclim variable
Temp Seasonality	C	-	Q	°C	BIO4 Bioclim variable
Max Temp of Warm Month	C	-	Q	°C	BIO5 Bioclim variable

2.3.4. Trait-based functional responses to forest

I used ANOVA and Linear Models with the summed training gain of different sets of variables as response variable, functional traits as predictor variable and bat species as replicates (see for a similar approaches: Pöyry *et al.* 2008; Hanspach *et al.* 2010; Wittmann *et al.* 2016) to test our two hypothesis: H1-tree roosting species have higher dependence on forests and show positive responses towards characteristics that promote roost availability, and H2- among species that forage in forests, those with wing morphologies more adapted to flying in cluttered habitats (low wing loading and aspect ratio) are less dependent on forest-specific characteristics and show greater tolerance towards high structural cluttering. I included the number of occurrence records as covariate when testing if model training gain depends on each of the functional traits. This is because the presence of a species with fewer presence data points may be better explained by forest or climatic conditions, resulting in Maxent models with higher model gain.

2.3.5. Community-level analysis

I generated bat assemblages by pooling together occurrence records from the final bat location records database that were within 3 km of each other. I considered mist netting and harp trapping in the field, caves or anthropogenic structures as the least biased sampling methods for obtaining a representative picture of the bat assembly composition. Based on that, I built species accumulation curves using R package *vegan* (Oksanen *et al.* 2019) with assemblages sampled by either of those method for at least two nights (Supplementary Fig. A1.5). I used those curves to set a minimum of four sampling nights at which community composition was considered representative. The final set contained 38 bat assemblages (Supplementary Fig. A1.6).

I used a Canonical Correspondence Analysis (CCA) with community composition constrained by the quantitative forest variables (Table 2.2) including climatic variable as conditioning to assess what portion of the variability in species composition is explained by forest versus climatic variables. I used a Non-metric Multidimensional Scaling (NMDS) of community composition and a posterior fit of environmental factors (envfit, R package *vegan*: Oksanen *et al.* 2019) to test and visualise which environmental factors explain community dissimilarity. In addition, I used fourth corner analysis (Legendre *et al.* 1997, R package *Ade4*: Dray *et al.* 2020) with the bat assemblage data to further test whether species that roost in trees responded towards forest roost availability variables and whether wing loading or aspect ratio correlated with forest cluttering and heterogeneity variables.

2.4. Results

2.4.1. Contribution of forest and climatic variables to species models

AUCtest scores of Maxent models were >0.75 for all bat species except *M. escalerae* (0.70), *R. hipposideros* (0.66) and *R. euryale* (0.59) (Table 2.3). The AUCtest scores of the latter fell within the 95% CI of the null models (Supplementary Fig. A1.7), showing that the model discrimination ability was not better than random, and therefore *R. euryale* was excluded from further analyses. For all the eight species considered, forest variables accounted for a greater proportion of model training gain (54-82%, Fig. 2.1) than climatic variables (18-46%, Fig. 2.1). Climate played a relatively greater role (>25%, Fig. 2.1) for *R. hipposideros* (training gain = 0.13), *N. lasiopterus* (2.83), *P. austriacus* (1.13) and *N. leisleri* (1.46). Distance to forest was an important variable for all species (Fig. 2.1), which showed strong negative responses (Supplementary Fig. A2.1), but it had greatest relative training gain (>10%, Fig. 2.1) in *R. hipposideros* (0.05), *M. emarginatus* (0.20), *M. bechsteinii* (0.87), and *B. barbastellus* (0.91). The summed relative training gain of forest variables was highest (>76%, Fig. 2.1) for *M. bechsteinii* (6.08), *B. barbastellus* (6.28) and *M. emarginatus* (1.34). Among the different mechanistic groups of variables, contribution of forest composition variables was important and relatively constant across bats (19-33%, Fig. 2.1). The contribution of variables representing structural heterogeneity were more variable (11-32%, Fig. 2.1), being particularly important in *M. bechsteinii*. Cluttering variables contributed less (5-17%, Fig. 2.1). Finally, the contribution of roost availability variables varied greatly among species (2-19%, Fig. 2.1), being most important (>14%, Fig. 2.1) for *N. leisleri*, *M. bechsteinii*, and *N. lasiopterus*.

Table 2.3 – Evaluation of Maxent models for each bat species. Number of occurrence records used, overall training gain and test AUC values for each bat species. *denotes models that did not perform better than random. Species abbreviations shown.

Abbreviation	Species name	Occurrence records	Training gain	Test AUC
Bbar	<i>B. barbastellus</i>	18	2.28	0.95
Mbec	<i>M. bechsteinii</i>	49	1.69	0.92
Mema	<i>M. emarginatus</i>	98	0.57	0.78
Mes	<i>M. escalerae</i>	115	0.45	0.70
Nlas	<i>N. lasiopterus</i>	70	1.70	0.92
Nleis	<i>N. leisleri</i>	59	1.41	0.90
Paus	<i>P. austriacus</i>	123	0.96	0.85
Reur	<i>R. euryale</i>	173	0.11	0.59*
Rhip	<i>R. hipposideros</i>	322	0.18	0.66

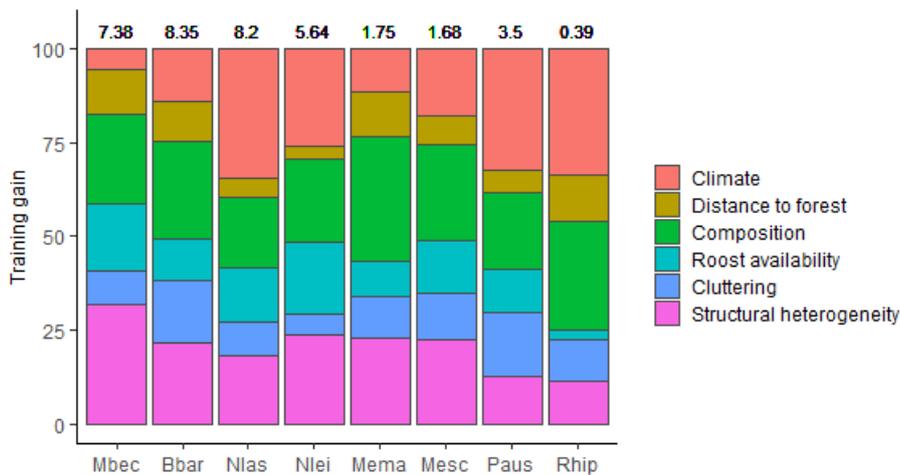


Fig. 2.1 – Relative training gain of the different mechanistic categories of variables in the Maxent models of the eight bat species included in the study. Values on top show the total training gain of variables in the model. Species abbreviations are shown in Table 2.3. The response of bats to individual forest variables

Identity of the dominant tree species was the most important variable in the models as well as the most important composition variable (Fig. 2.2). Most bat species showed a strong preference towards forest dominated by the tree species *Quercus pyrenaica* (*M. bechsteinii*, *M. escaleraei*, *P. austriacus*, *N. leisleri*) or *Pinus nigra* (*B. barbastellus*, *N. lasiopterus*), with the exception of *M. emarginatus* and *R. hipposideros* that showed more generalist preferences. The less suitable forest types for most bat species were the ones composed of the Mediterranean species *Pinus halepensis*, *Pinus pinea* and *Quercus ilex* (Supplementary Fig. A2.5). Tree richness was also an important composition variable (Fig. 2.2). The probability of occurrence of all bat species increased with tree species richness (Supplementary Fig. A2.8). Variables of forest structural heterogeneity that contributed to the models included the range of diameter at breast height (DBH) and tree height (Fig. 2.2). The former was important for the four tree roosting species (*M. bechsteinii*, *B. barbastellus*, *N. lasiopterus*, *N. leisleri*), and all but *N. lasiopterus* responded positively increasing their probability of occurrence with higher range of tree diameters (Supplementary Fig. A2.11). Tree height range was important for *M. bechsteinii* and *B. barbastellus* (Fig. 2.2), and strong positive responses were observed in *M. bechsteinii*, *N. lasiopterus*, *N. leisleri* and *M. escaleraei* (Supplementary Fig. A2.12). Responses towards percent of plantations differed among species. It was considerably important and negative for *N. lasiopterus*, *M. bechsteinii* and *N. leisleri*, and also negative for *M. escaleraei*, while positive for *M. emarginatus* and *P. austriacus* (Fig. 2.2, Supplementary Fig. A2.13). Tree cover was the most important forest cluttering variable (Fig. 2.2), for which all species except

B. barbastellus and *M. emarginatus* responded positively and increased their probability of occurrence with increasing values (Supplementary Fig. A2.15). The relationship with tree density was negative for *N. leisleri*, *M. emarginatus*, *M. escalerae* and *P. austriacus* (Supplementary Fig. A2.16). The most important roost availability variable was the density of trees larger than 425 mm, which was more important for the four tree roosting species (although less for the bark roosting *B. barbastellus*) (Fig. 2.2), and the density of soft wood trees larger than 425 mm, which was important for *M. bechsteinii* and *B. barbastellus* (Fig. 2.2). Density of dead trees had low gain in all species models (Fig. 2.2). See Appendix A2 for responses of each bat species towards each forest variable and Supplementary Fig. A1.8 for variable importance based on AUC.

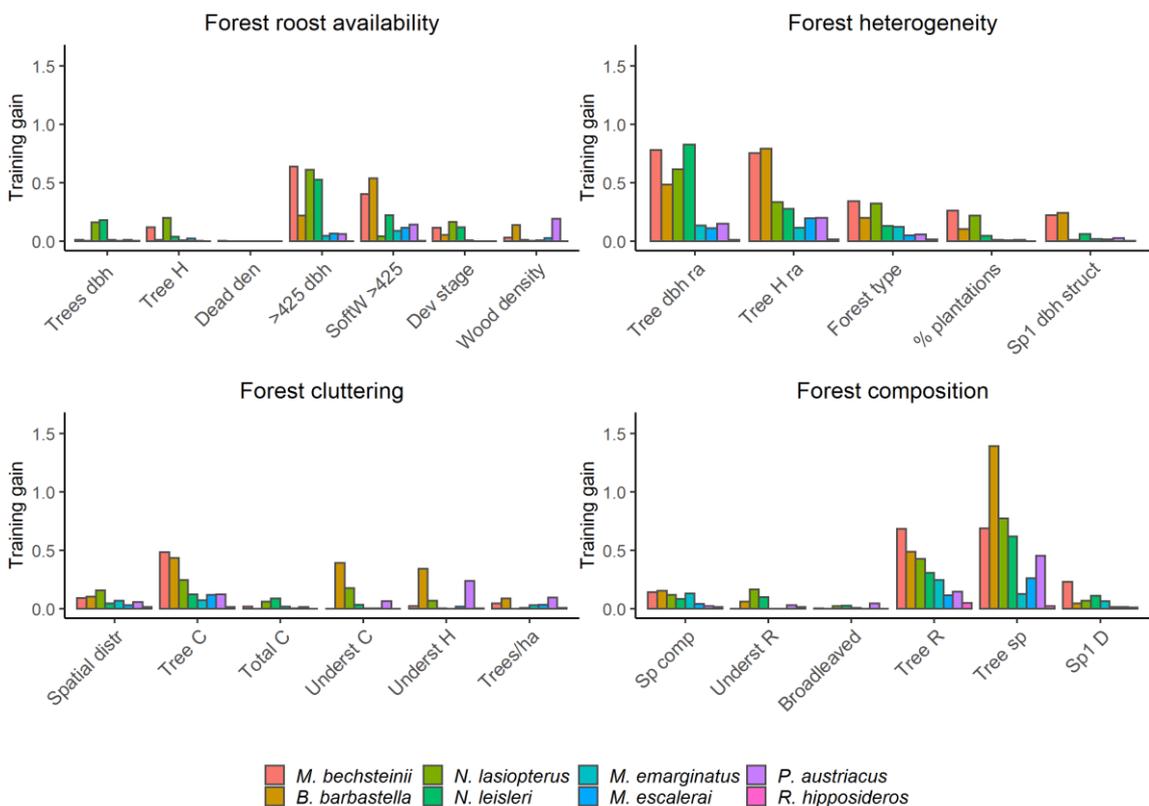


Fig. 2.2 – Contribution of forest variables to the models of the eight bat species based on training gain. Variables are separated into four mechanistic groups according to bat-forest dependence relationships: those linked to forest roost availability, forest structural heterogeneity, structural clutter and forest composition. Description of forest variables is shown in Table 2.2.

2.4.2. Trait-based functional responses to forest

2.4.2.1. Bat roosting ecology

Models of tree-roosting species had higher summed training gain than models of non-tree roosting species (Linear Model: $F_{2,5} = 24.16$, $p < 0.002$, $R^2 = 0.86$, Roosting ecology: $p = 0.009$; Fig. 2.3a), but were not affected by the number of occurrence records ($p = 0.204$). Models of tree-roosting species also had larger contribution of forest variables (ANOVA: $F_{1,6} = 29.8$, $p = 0.002$; Fig. 2.3b), and within them, of roost variables alone (ANOVA: $F_{1,6} = 68.4$, $p < 0.001$), composition (ANOVA: $F_{1,6} = 29.1$, $p = 0.002$), heterogeneity (ANOVA: $F_{1,6} = 35.27$, $p = 0.001$), and distance to forest (ANOVA: $F_{1,6} = 6.18$, $p = 0.042$), but not cluttering variables (ANOVA: $F_{1,6} = 3.99$, $p = 0.094$). Roosting ecology did not explained differences in training gain of climatic variables in models (ANOVA: $F_{1,6} = 3.40$, $p = 0.116$, Fig 3c). When looking at individual forest variables related to roost availability, the importance of density of trees larger than 425 mm DBH and structural stage of main tree species was higher for tree dwellers than for non-tree dwellers (ANOVA: $F_{1,6} = 21.74$, $p = 0.021$, $F_{1,6} = 23.28$, $p = 0.024$, Table 2.4, Fig. 2.4).

2.4.2.2. Eco-morphological relationships within forest foragers

Model training gain increased with wing loading but was not affected by the numbers of records (Linear Model: $F_{2,3} = 25.21$, $R^2 = 0.90$, Wing loading: $p = 0.023$, number occurrence records: $p = 0.088$; Fig. 2.3d). Wing loading was also correlated with training gain of forest variables ($F_{1,4} = 16.58$, $R^2 = 0.75$, $p = 0.015$; Fig. 2.3e), and when considering separately either roost ($F_{1,4} = 11.67$, $R^2 = 0.68$, $p = 0.027$), composition ($F_{1,4} = 15.01$, $R^2 = 0.75$, $p = 0.0179$), heterogeneity ($F_{1,4} = 10.7$, $R^2 = 0.66$, $p = 0.03$), cluttering ($F_{1,4} = 8.86$, $R^2 = 0.61$, $p = 0.040$) or distance to forest variables ($F_{1,4} = 15.7$, $R^2 = 0.75$, $p = 0.016$). However, wing loading was not independent from roosting ecology because bat species that roost in trees also had higher wing loading values (Supplementary Table A1.4). In contrast to wing loading, aspect ratio did not explain summed variable training gain ($F_{1,4} = 0.03$, $p = 0.863$; Fig. 2.3g), gain of forest variables ($F_{1,4} = 0.02$, $p = 0.905$; Fig. 2.3h) or any specific group of forest variables ($p > 0.05$). Neither wing loading nor aspect ratio explained differences in training gain of climatic variables ($F_{1,4} = 2.3$, $p = 0.212$; Fig. 2.3f, Linear model: $F_{1,4} = 0.19$, $p = 0.674$; Fig. 2.3i). In contrast to roosting ecology, neither wing loading nor aspect ratio were related to contribution of any specific cluttering or structural heterogeneity variables ($p > 0.05$).

The observed relationships between wing loading with training gain of models, forest variables and specific groups of forest variables with within-forest foragers was no longer apparent ($p > 0.05$) when including bats that forage in open space (Appendix A3).

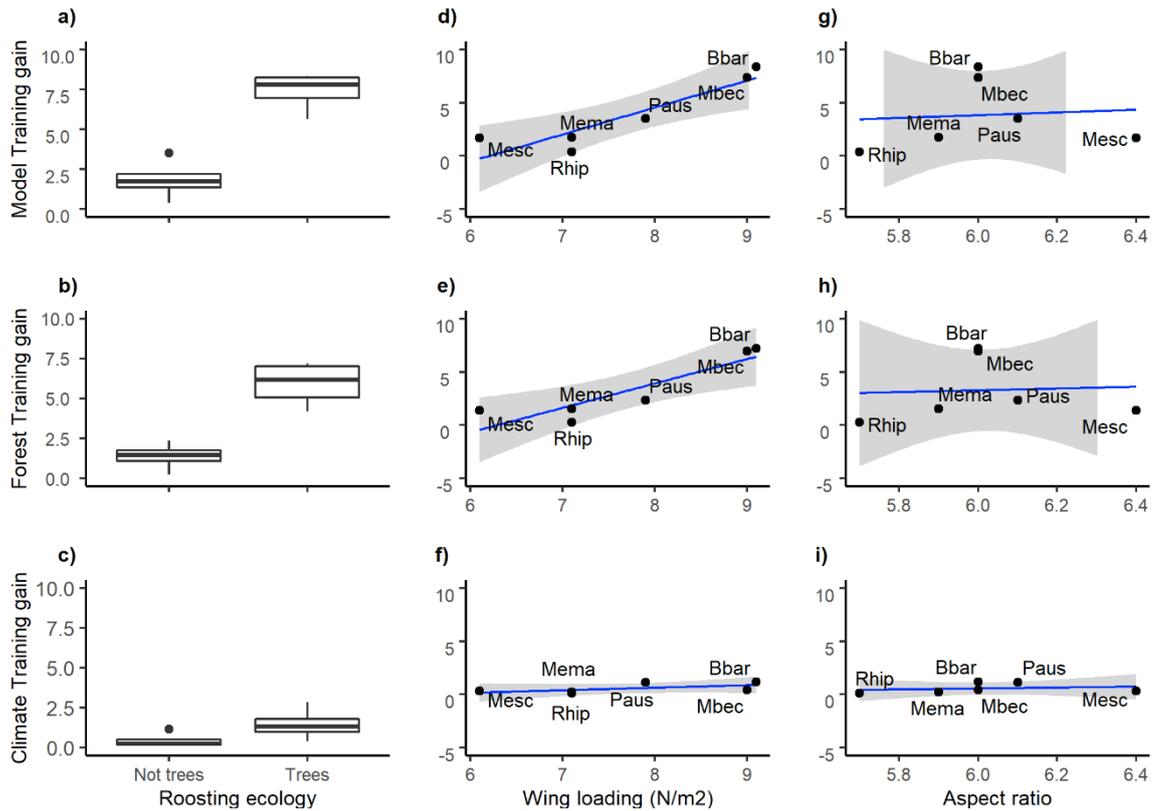


Fig. 2.3 – Correlation between functional traits (roosting ecology (a,b,c), wing loading (d,e,f) and aspect ratio(g,h,i)) with training gain of different sets of variables in Maxent models (overall gain of models (a,d, g), forest variables (b,e,h), and climate variables (c,f,i). See Supplementary Fig. A3.1 for results including open air foragers.

Table 2.4 – Variable importance of the roost availability variables depending on bat roosting ecology. Training gain in Maxent models as variable importance. ANOVA tests. *df* shows residual degrees of freedom. Test degrees of freedom is 1. *p adj*: *p* value after Holm correction for multiple comparisons. * denotes *p* values <0.05. Description of forest variables is shown in Table 2.2.

Forest variable	Non-tree roosting Mean \pm sd	Tree roosting Mean \pm sd	<i>F</i>	<i>df</i>	<i>p</i>	<i>p adj</i>
Tree DBH	0.007 \pm 0.004	0.088 \pm 0.094	2.97	6	0.14	0.521
Tree height	0.008 \pm 0.01	0.091 \pm 0.086	3.66	6	0.10	0.521
Dead den	0 \pm 0	0.001 \pm 0.001	0.9	6	0.38	0.756
>425 DBH den	0.043 \pm 0.029	0.497 \pm 0.193	21.74	6	0.00	0.021*
SoftW >425 den	0.088 \pm 0.06	0.302 \pm 0.216	3.65	6	0.10	0.521
Dev stage	0.002 \pm 0.003	0.112 \pm 0.046	23.28	6	0.00	0.02*
Wood density	0.056 \pm 0.091	0.045 \pm 0.062	0.04	6	0.85	0.846

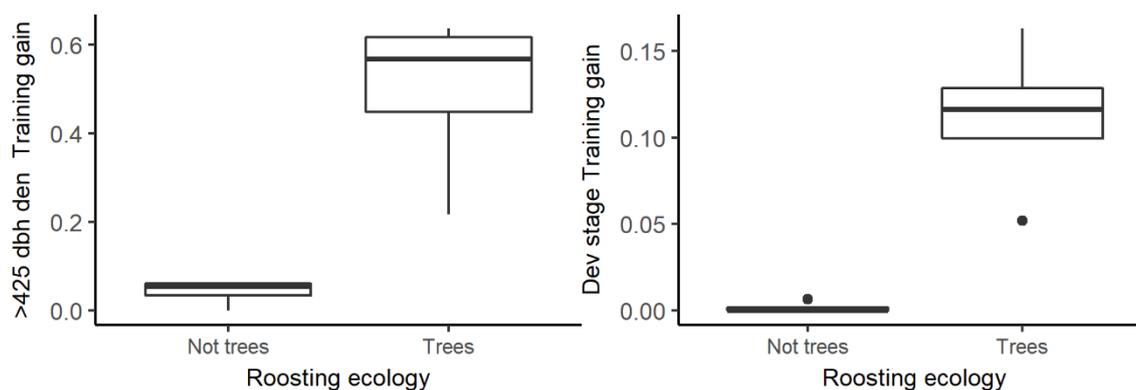


Fig. 2.4 – The contribution in Maxent models (training gain) of the forest variables density of trees larger than 425 mm DBH and development stage for tree roosting species versus non-tree roosting species.

2.4.3. Assemblage-level functional link between forest and traits

Based on the partial CCA analysis, community composition was primarily explained (43% of variance) by forest variables. Climatic factors accounted for 36% of variance, and 20% was not explained. NMDS ordination (Stress: 0.097) separated bat assemblages depending on their species composition. Tree roosting species were grouped on the left side of the axis, and the rest on the right side. *M. emarginatus*, the most facultative species, is in the middle. Some of the climatic variables (including elevation, temperature seasonality and temperature of warmest month) and forest variables explained community dissimilarity (environmental fit $p < 0.05$; Fig. 2.5). The following forest variables explained community dissimilarity: the roost availability variables tree height, wood density and density of softwood trees; the composition variable tree species richness; the heterogeneity variable tree height range; and the cluttering variables total cover, tree cover, understory cover and understory height. Assemblages characterised by *N. lasiopterus* and *N. leisleri* were most associated with tree height and understory richness, those characterised by *M. bechsteinii* with tree height range and tree richness, *B. barbastellus* with tree cover, and *P. austriacus* with elevation. The two rhinolophids were most associated with distance to forest and temperature of the warmest month, while *M. escaleraei* and *M. emarginatus* contributed little to community characterisation.

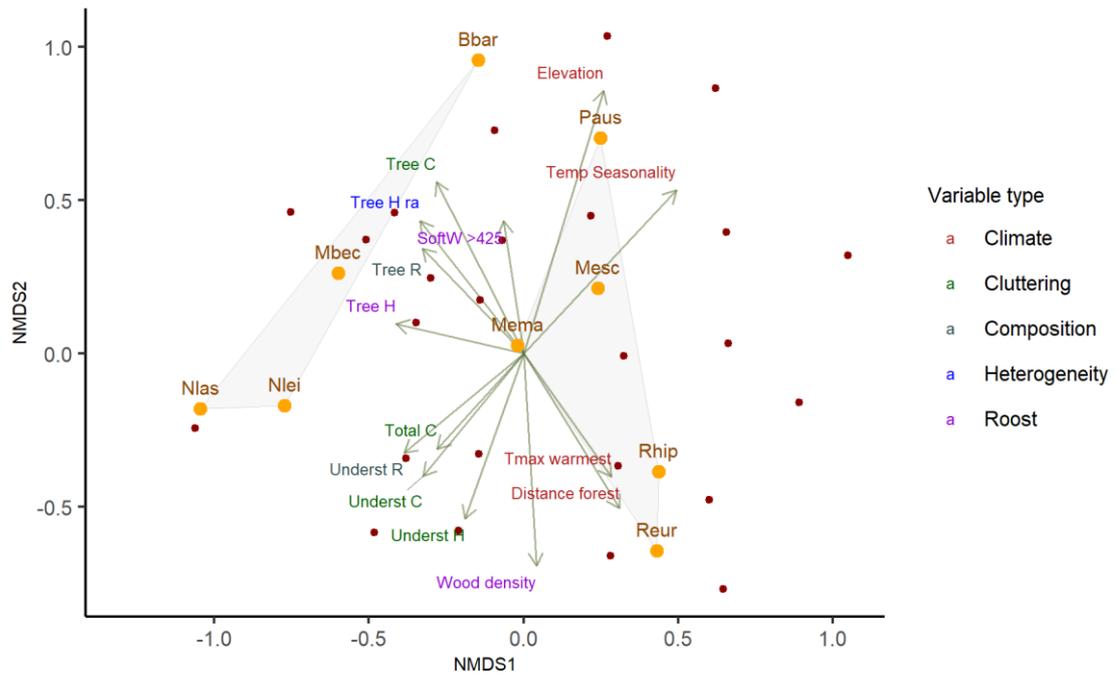


Fig. 2.5 – Non-metric multidimensional scaling (NMDS) of community composition. Brown dots represent bat assemblages. Yellow dots represent bat species. Position of bat species characterise the composition of nearby communities. Vectors show statistically detectable relations of variables with community dissimilarity. Length of the vector represents R^2 values. Shaded polygons separate tree roosting species (left polygon) from not tree roosting species (right polygon). Species abbreviations are shown in Table 2.3. Description of forest variables is shown in Table 2.2.

Table 2.5 – Results of the fourth corner analysis relating species roosting ecology with roosting availability forest variables. r Pearson correlation value. p value and adjusted p value after Holm correction for multiple comparisons. *Notes detectable effect at $p < 0.05$. Variable abbreviations are shown in Table 2.2.

Roost availability variable	r	p	p adj
Tree DBH	0.11	0.054	0.216
Tree height	0.23	0.001	0.007*
Dead den	0.05	0.417	0.417
>425 DBH den	0.24	0.001	0.007*
Sp1 dev stage	0.22	0.001	0.007*
SoftW >425 den	0.11	0.068	0.216
Wood density	-0.11	0.069	0.216

The fourth corner analysis confirms the results on functional analysis based on Maxent models. Tree roosting species responded positively to some of the variables that promote roost availability: densities of trees with DBH > 425 mm, development stage of the main tree species and average tree height (Table 2.5). Neither wing loading nor aspect ratio explained bat forest preferences towards heterogeneity or cluttering variables (p value adjusted >0.05).

2.5. Discussion

By integrating large extent detailed forest inventory data with species distribution models and a functional approach, I disentangle broader-scale implications of forest dependency relationships in forest-specialist taxa. I show that habitat characteristics can have broader-scale implications for the distribution of forest-specialist bats beyond local-scale effects (Willis & Whittaker 2002). The strength of bat-forest responses is driven by species roosting ecology, but there is no conclusive evidence for the role of flight eco-morphology in driving bat regional-scale distributions, as opposite to their known local scales effects (Froidevaux *et al.* 2016). These results have important implications for the conservation of forest-dependant taxa in Mediterranean systems.

2.5.1. Landscape-scale forest-species associations

Forest characteristics play important roles in driving community assemblage patterns of various taxonomic groups (McGarigal & McComb 1995; Edenius & Elmberg 1996; Drapeau *et al.* 2000). Yet, only few studies have addressed the role of these in shaping broader scale species distributions. An exception is range expansions in forest birds that were shown to be driven by changes in forest maturity (Gil-tena *et al.* 2009; Gil-Tena *et al.* 2010). The uniquely strong dependency relationship of forest bats on forests (Lacki *et al.* 2007b), makes them an ideal model system to test broader-scale implications of forest characteristics on species distributions. Our results from SDMs, community-level CCA and NMDS ordination analysis show that forest variables play a primary role in both assemblage composition and shaping the regional distribution of forest bats in Andalusia. The strong relative importance of forest characteristics seen in this study occurs despite the high climatic heterogeneity of the region, which has a broad elevation range (0-3000 m.a.s.l) and several differentiated topographic units. Responses towards forest characteristics were strong drivers of species distributions regardless other landscape-scale habitat features such as the wider landscape structure are known that can be relevant but were not considered in this study (Fahr & Kalko 2011; Ferreira *et al.* 2017). The importance of forest features on species ranges was, however, variable across bat specie. It was high for the tree-roosting species *M. bechsteinii*, *B. barbastellus*, *N.*

lasiopterus and *N. leisleri*, and lower for *P. austriacus*, *M. emarginatus*, *M. escalerae* and *R. hipposideros*. The regional distribution of *R. euryale* could not be explained by either forest or climatic variables, suggesting that it is a habitat generalist in the region. The species is known to be flexible using habitat, and can use edge hedgerows and forest edges for foraging (Goiti *et al.* 2008). In our study, identity of dominant tree species was the most important forest variable affecting the distribution of most forest bats. This variable had been identified as important in other studies, for example, driving richness and abundance of bird communities in boreal forests (Edenius & Elmberg 1996). The dependence of bats towards dominant tree species identity does not necessarily describe a mechanistic association because dominant tree species can relate to a wide set of forest characteristics, from certain forest structures (Castro 1997) to certain arthropod prey composition and abundances (Ozanne 1999; Vehviläinen *et al.* 2008). Furthermore, it may be difficult to tell apart the role of specific climatic conditions associated with each forest type (Elith & Leathwick 2009). The under-selection of forests dominated by the Mediterranean tree species *Q. ilex*, and *P. halepensis* that our results show has been reported previously (Alcalde *et al.* 2018), and may be due to the generally poorly developed structures of Mediterranean forest due to their slow development and high perturbation regime. Probability of occurrence of bat species increases with tree species richness. Tree richness is commonly reported as driving patterns of richness and abundance of other taxa, such as birds (Gillespie & Walter 2001) or herbivorous arthropod (O'Brien *et al.* 2017; Zhang *et al.* 2017). This relationship may be interpreted as the result of increased diversity of trophic resource availability across trophic levels (O'Brien *et al.* 2017; Zhang *et al.* 2017). In bats it may also represent increased roost availability through the presence of, usually less dominant, softwood tree species (Alcalde *et al.* 2018).

Mature forest structure is thought to promote biodiversity both in general (Edenius & Elmberg 1996; Begehold *et al.* 2015) and specifically of bats (Lacki *et al.* 2007b). Accordingly, in our study, variables describing structural heterogeneity that are characteristic of mature forests are most important for the majority of species. Structural heterogeneity could be linked, beyond species' ecomorphology, to higher diversity of microhabitats that provide more resources (Ishii *et al.* 2004). The presence of trees of high diameter and height and well developed forest structures is also important, as it has been shown in other studies (Begehold *et al.* 2015), though less than structural heterogeneity variables. The responses towards tree density are negative for almost all bat species, as expected based on ecomorphological constraints. Presence of dead trees is regarded as one of the key forest characteristics that provides suitable roosting habitats for tree roosting bats (Barclay & Kurta 2007), and therefore

the landscape-level density of standing dead trees can have a positive impact on bat abundance (Hayes 2007). However, in this study density of dead trees was not identified as an important variable. This might be because the forest database did not specify whether dead trees were standing up or lying down on the ground, the latter are not a valid roosting resource for bats. Tree plantations are tree monocultures characterised structurally by high tree densities of unimodal diametric class and very poor understory strata. They have an extensive presence in European landscapes, and their contribution for biodiversity has therefore important ecological repercussions. I find overall negative associations of bats with plantation forests, though not a complete avoidance, and even positive responses by some of the more generalist species, *M. emarginatus* and *P. austriacus*, that matches previous studies (Mortimer 2006; Kirkpatrick *et al.* 2017).

2.5.2. Trait-based functional responses of bats towards forest.

I found higher dependency of tree-roosting species on forest variables, in particular those relating to roost availability, thus confirming our first hypothesis. More specifically, tree-roosting bats were also closely associated with the density of trees > 425 mm DBH and forest development stage. The latter has been shown to be an important driver of habitat preferences for breeding birds in temperate forests in Germany (Begehold *et al.* 2015). Moreover, the probability of occurrence of tree roosting bats was also dependent on forest composition, structural heterogeneity variables and distance to forest, but not on forest cluttering variables. These inferences on the importance of forest characteristics for tree roosting species were further supported with the community based-fourth corner analysis, in which density of trees with DBH > 425 mm and development stage, as well as average tree height were positively related to tree roosting ecology. Among the tree roosting species, *B. barbastellus* is the only one that roosts under loose bark instead of tree holes, and consequently showed a weaker response towards roost availability variables. Hence, landscape-scale forest associations and their role in driving species distributions are closely linked to the roosting ecology of species.

The role of roost availability in limiting species ranges is not surprising when considering the high number of roosts that tree-roosting bats require due to frequent roost switching (Russo *et al.* 2005; Barclay & Kurta 2007) alongside the scarcity of mature forests in Mediterranean regions. Mediterranean forests may provide less of some of the key structural variables linked to roost availability compared to Atlantic forests, which may explain the scarcity of tree-

dwelling species in the South of the Iberian Peninsula (Alcalde *et al.* 2018), and may have wider implications for continental-level biogeographical patterns across Europe.

The dependency of forest foraging bats on forest variables increased with wing loading, which would, at first, suggest that in line with our predictions, more manoeuvrable bats would be less restricted by forest structure and clutter, allowing them to use a wider range of forest types and characteristics. *R. hipposideros*, the species with the lowest wing loading values, showed very low dependency on any forest specific characteristics, though it was still closely associated with forests, as seen by the importance of the distance to forest variable. However, the fact that in our study system the tree roosting bats are the ones that have the highest wing loading values makes it difficult to tease apart whether the causal factor is wing loading or roosting ecology. Both aspect ratio and wing loading are related negatively to manoeuvrability. High aspect ratio makes the animal slower to turn, while high wing loading increases its minimum flight speed which indirectly reduces its manoeuvrability (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). Our results only show a detectable relationship between morphology and forest dependency with wing loading, not with aspect ratio. Moreover, unlike roosting ecology, and contrary to ecomorphological predictions, neither wing loading nor aspect ratio explain the importance of any of the individual variables related to forest structural heterogeneity or cluttering. As expected, when including the open-air foragers in the analysis, the relationship between wing loading and dependence to forest variables or with any of the mechanistic groups of variables does not hold. Hence, while ecomorphological relationships are known to drive local-scale habitat use patterns (Crome & Richards 1988; Patriquin & Barclay 2003; Froidevaux *et al.* 2016), our results cannot support landscape-scale ecomorphological relationships driving species ranges. A similar pattern is suggested by another study of tropical forest bats in West Africa where the structure of bat functional groups based on habitat use and foraging guild was driven by vegetation structure only at the local-scale, but at the landscape-scale it was random (Fahr & Kalko 2011).

2.5.3. Conclusions

This study contributes to the understanding of how habitat filtering processes affect species biogeographic patterns. Through separating bat-forest filtering effects mechanistically, I identify roosting ecology as a major driver of bat-forest habitat dependency, playing a primary role in driving regional-scale ranges of forest bats in Andalusia. Observed relationships are likely generalisable to other Mediterranean systems since filtering mechanisms are common. This is an important step towards understanding the poorly explored (Lacki *et al.* 2007b)

broader-scale implications of the dependency of bats on forest habitats. Our results stress that managing forests to maintaining mature structures and presence of trees with diameters > 425 mm can have a larger benefit on the conservation of Mediterranean forest bats than previously thought, especially for those species that roost in trees. The strong relationship between wing morphology with roosting ecology in our dataset limits our ability to conclusively determine the contribution of landscape-scale bat-forest ecomorphological relationships to driving species regional distributions. However, it is likely that both forest dependency processes operate at different spatial scales, with wing morphology primarily limiting local-scale forest use. Using detailed and larger-scale forest datasets, such as available national forest inventory data, can contribute towards gaining a better understanding of the operation of the different environmental filtering processes across spatial scales and taxa. For example, the implementation of teledetection LiDAR technology in wildlife studies has recently been shown useful for understanding local scale habitat processes (Froidevaux *et al.* 2016) and promises great advances. This study highlights that considering the different species-environment dependency processes separately can enable a more detailed understanding of the biogeographic processes that drive diversity patterns. The results of this study are particularly relevant for assessing the vulnerability of tree roosting bats in regions as the Mediterranean, where forests characteristics that provide tree roosts can be limiting and forests are expected to experience substantial changes in structure and composition due to climate change (Allen *et al.* 2010; Carnicer *et al.* 2011).

2.6. Chapter summary

In this chapter I quantified the importance of forest and climate filtering processes for explaining the regional distribution of forest-specialist bats, showing that the strength of forest filtering depends on bat species traits. The following two chapters cover another key process affecting species distributions, biotic interactions. In Chapter 3 I test the impact of biotic interactions on species coexistence at both the local and broad spatial scales, and whether trophic partitioning contributes to the local-scale coexistence of morphologically identical cryptic bat species.

3. Chapter 3 Trophic resource partitioning drives fine-scale coexistence in cryptic bat species.

Roberto Novella-Fernandez¹, Carlos Ibañez², Javier Juste^{2,3}, Elisabeth L. Clare⁴, C. Patrick Doncaster¹, Orly Razgour^{1,5}

[1] School of Biological Sciences, University of Southampton, Southampton, UK

[2] Estación Biológica de Doñana (CSIC), Sevilla, Spain.

[3] CIBER Epidemiology and Public Health (CIBERESP), Spain

[4] School of Biological and Chemical Sciences, Queen Mary University of London, UK

[5] Biosciences, University of Exeter, Exeter, UK

3.1. Abstract

Understanding the processes that enable species coexistence has important implications for assessing how ecological systems will respond to global change. Morphology and functional similarity increase the potential for competition, and therefore, co-occurring morphologically similar but genetically unique species are a good model system for testing alternative coexistence mechanisms. We used DNA metabarcoding and High Throughput Sequencing to characterise for first time the trophic ecology of two recently-described cryptic bat species with parapatric ranges, *Myotis escaleraei* and *Myotis crypticus*. We collected faecal samples from allopatric and sympatric regions and locations to describe the diet both taxonomically and functionally and compare prey consumption with prey availability. The two bat species had similar diets characterised by high arthropod diversity, particularly Lepidoptera, Diptera and Araneae, and a high proportion of prey that is not volant at night, which points to extensive use of gleaning. Diet overlap at the prey-item level was lower in locally sympatric than allopatric locations, supporting trophic shift under fine-scale sympatry. Furthermore, locally sympatric samples of *M. escaleraei* had a marginally lower proportion of not nocturnally volant prey, suggesting that the shift in diet may be driven by a change in foraging mode. Our findings suggest that fine-scale coexistence mechanisms can have implications for maintaining broad-scale diversity patterns. This study highlights the importance of including both allopatric and sympatric populations and choosing meaningful spatial scales for detecting ecological patterns. We conclude that a combination of high taxonomic resolution with a functional approach helps identify patterns of niche shift.

3.2. Introduction

Understanding the processes that enable species coexistence is a key theme of ecology with important implications for interpreting diversity patterns and predicting how systems respond to global change (Valladares *et al.* 2015). Interspecific competition is thought to have a major

influence on community structure for many taxonomic groups. Niche theory (Chesson 2000; Chase & Leibold 2003; Letten *et al.* 2017) asserts that species coexistence is promoted through differential use of resources driven by functional differences between species, which results in communities that tend to be assembled by functionally dissimilar species (Schoener 1974).

This has been shown in numerous cases, including fish (Ross 1986), shorebirds (Bocher *et al.* 2014) and rodent communities (Codron *et al.* 2015). Alternatively, community structure and coexistence, primarily in sessile organisms, has been often explained through neutral processes, such as dispersal or stochasticity (The neutral theory of biodiversity and biogeography; Hubbell 2001). This framework has been often used as a null model to evaluate whether observed patterns deviate from neutral expectations (Alonso *et al.* 2006; McGill *et al.* 2006b). Yet, some studies of mobile organisms have failed to identify evidence of resource partitioning (e.g. Luiselli 2008), suggesting that in some cases biotic interactions only play a minor role in governing community assembly, perhaps because resources are not limiting (Salinas-Ramos *et al.* 2020), and therefore neutral processes likely play a more important role.

Morphologically similar species pose a challenge for understanding mechanisms of coexistence from a niche theory perspective because they are more likely to be functionally similar, and therefore less likely to be able to use resources in a different way, a pre-requisite for resource partitioning (Weiher & Keddy 1999). Consequently, considerable attention has been given to understanding resource partitioning among morphologically identical (cryptic) or similar co-occurring species (e.g. Arlettaz *et al.* 1997; Razgour *et al.* 2011b; Gabaldón *et al.* 2013). Many studies have focused on the trophic dimension, an important aspect of species' ecological niche (Schoener 1974). DNA metabarcoding and High Throughput Sequencing (molecular diet analysis) approaches helped overcome many of the limitations of traditional morphological methods (Sousa *et al.* 2019), opening the door to new opportunities for studying mechanisms of species coexistence (Razgour *et al.* 2011a; Krüger *et al.* 2014; Arrizabalaga-Escudero *et al.* 2018). However, the majority of coexistence studies focus on only sympatric populations, preventing an evaluation of how the presence of a competitor may change resource use, thus limiting the power of inferences (Salinas-Ramos *et al.* 2020). Moreover, most studies also focus on diet only, disregarding prey selection relative to prey availability or resource limitation (Salinas-Ramos *et al.* 2019). Accounting for prey selection (e.g. Rytönen *et al.* 2019) can provide a more complete picture of consumer trophic preferences (Lawlor 1980).

The processes that govern community assembly, including coexistence mechanisms, vary with spatial scale (Snyder & Chesson 2004; Lewis *et al.* 2015; Viana & Chase 2019), yet spatial scale

is rarely considered in coexistence studies (Hart *et al.* 2017). A better understanding of the scale of coexistence mechanisms and how different processes interact is important for both basic and applied ecology (Peixoto *et al.* 2018).

This study aims to identify whether trophic ecology enables morphologically similar species to coexist across spatial scales. We focus on two recently described, morphologically nearly identical, insectivorous bat species, whose trophic ecology has not been studied to date, *Myotis crypticus* and *Myotis escalerai*. These bats are restricted to the Western Mediterranean Basin, where they overlap across the north of the Iberian Peninsula, but at the fine-scale are known to co-occur only in a few locations (Juste *et al.* 2019). Phylogeographic analysis and species distribution modelling suggest that their ranges have been shaped by competition (Razgour *et al.* 2015). These bats therefore provide an excellent case study for understanding mechanisms of coexistence among morphologically similar species. We use DNA metabarcoding and High Throughput Sequencing to characterise the trophic ecology of *M. crypticus* and *M. escalerai* by analysing their taxonomic and functional diets and their prey selection relative to prey availability in sympatric versus allopatric populations at both fine and broad spatial scales. Given their near identical morphology and echolocation calls, the overall trophic niches of the two bats are expected to be similar and niche overlap should be high. We hypothesise that if resource partitioning is the main process facilitating coexistence, competing species will diverge in their use of resources in sympatry compared to allopatry (e.g. Klawinski *et al.* 1994). We test the predictions that 1) trophic niche overlap and diet similarity are higher in allopatric than sympatric locations; and 2) differences in trophic niche overlap are most pronounced at the fine spatial scale where individuals of the two species share the same foraging areas.

3.3. Methods

3.3.1. Sampling design

Sampling took place in the Iberian Peninsula, focusing on two sympatric regions in the north where both *Myotis escalerai* and *Myotis crypticus* are found (La Rioja-Soria and southern Cantabria), and two allopatric regions: the south (Andalusia: Jaen and Granada), where only *M. escalerai* is found, and the north Atlantic coast (northern Cantabria), where only *M. crypticus* is found. Additionally, we sampled a single sympatric swarming site in Catalonia, where the two species use the same cave during the autumn mating season (Fig. 3.1). Within each region, 9-24 locations were sampled based on suitable habitat and accessibility, using monofilament mist nets and a harp trap placed over water sources, forest paths and cave entrances. The

sampling period extended from June to September 2017, for a total of 68 sampling nights (Supplementary Table B1.1 for list of sampling locations). Captured bats were kept in individual cotton bags for up to 1 hour. We collected faecal samples from the cotton bags for diet analysis, and biopsy punches (3 mm) from the wing membrane of the bats to confirm species identification. Dropping samples and wing biopsies were stored in absolute and 70% ethanol, respectively. Bat sampling was carried out under local permits and ethical approval from the University of Southampton (study ID: 26627).

We sampled the arthropod community in bat sampling locations using vegetation sweeping (Barclay 1991; Swift & Racey 2002) to assess bat prey selectivity relative to prey availability (Jones 1990; Kunz 2009). We chose vegetation sweeping because of the expected low flight and gleaning behaviour of the species based on their morphology and echolocation calls, and the foraging behaviour of the morphologically similar better studied member of the cryptic species complex, *Myotis nattereri* (de Jong 1995). During bat sampling nights, we set linear transects in each habitat type in the sampling location and swept the vegetation along each transect. After 10 sweeps, we collected the capture into a plastic bag and moved five steps further without sampling to increase spatial representativeness. Each sampling unit of 10 sweeps and five steps forward was repeated 5-10 times until the capture size was considered representative (> 100 individuals). Transect length ranged between 30 and 80 m. Arthropod specimens captured were separated from vegetation remains in the field and stored in 70% ethanol.

3.3.2. DNA extractions and species confirmation

Bat species identity was confirmed in the Estación Biológica de Doñana Laboratory of Molecular Ecology (LEM, EBD-CSIC, Spain). DNA was extracted from wing biopsy punches through precipitation with isopropanol. Part of the hypervariable region of the mtDNA control region was amplified using the primers CSBC-F 5'-CCTCTTAAATAAGACATCTCGATGG-3' (Wilkinson & Chapman 1991) and HV2-Mna-R 5'-ATGCGTGCGTGTGTAATGTC-3' (Garcia-Mudarra *et al.* 2020). Species specific differential amplification patterns for this primer set were used to confirm species identity through gel electrophoresis (Garcia-Mudarra *et al.* 2020).

DNA was extracted from all bat dropping samples using the Qiagen DNA stool mini kit, following the protocol in Zeale *et al.* (2011). A total of 43 sweeping samples from 23 locations with at least three bat dropping samples were selected (Supplementary Table B1.1). From those, all arthropod individuals ($N = 8366$) were first identified morphologically to taxonomic

order. Subsequently, whole specimens, if smaller than a drosophila, or a specimen part (leg or head) if larger, were separated out, dried and pooled together for DNA extraction. Arthropod DNA was extracted using the NucleoSpin DNA Insect kit with up to 35 mg of sample dry weight in each tube. Larger samples were split into several tubes. The following modifications were applied to the kit extraction protocol: In steep 2, vortex for 20 minutes in the MN Bead Tube Holder on a Vortex-Genie at maximum speed; after steep 3, pipette 550uL of clean supernatant in to a new 2mL Eppendorf, centrifuge again at 13,000RPM for 2 minutes and continue with steep 4; in steep 6, centrifuge for 3 minutes; in steep 7, add 50uL of ddH₂O and incubate for 3 minutes.

3.3.3. High Throughput Sequencing

Both dropping and sweeping samples were sequenced in the Bart's and the London Genome Centre, London, UK. DNA extracts were checked for quality and concentration on a TapeStation D1000. Two sets of primers were used together in order to reduce primer taxonomic bias (Alberdi *et al.* 2018), especially given the high diversity of prey types expected in the diet, ZBJ (Zeale *et al.* 2011) Forward: ZBJ-ArtF1c 5'-AGATATTGGAACWTTATATTTTATTTTGG-3' and Reverse: ZBJ-ArtR2c 5'-WACTAATCAATTWCCAAATCCTCC-3', and ANML (Jusino *et al.* 2019) Forward: LCO1490 5'-GGTCAACAAATCATAAAGATATTGG-3' and Reverse: CO1-CFMRa 5'-GGWACTAATCAATTTCCAAATCC-3'. For the ZBJ amplicon each 15µl PCR reaction used 7.5µl of Multiplex PCR mastermix (QIAGEN, Germany), 0.25 µL of each primer (10 µM), 5 µL H₂O and 2 µL template DNA. Negative and positive controls were included in PCR reactions and later sequencing. The thermal cycling protocol was as follows: 95°C for 15 min, 34 cycles of 94°C for 40s, 40°C for 1 min, 72°C for 30s, followed by a final extension of 72°C for 5 min. ANML regions were amplified in 15ul reactions following published protocols (Jusino *et al.* 2019). All products were visualised on a 1.5% agarose gel. Products were tagged using Fluidigm barcodes and checked on a TapeStation D1000 before pooling and sequencing on an Illumina MiSeq using paired end (2 x 250 bp) chemistry (Illumina, San Francisco, USA). We used two technical PCR replicates to reduce biases associated with PCR stochasticity. This led to each sample being sequenced four times (combination of two primer and two PCR replicates).

3.3.4. Bioinformatics

Sequencing runs were merged using USEARCH (Edgar 2010) and primers and adaptors removed using cutadapt (Martin 2011). Sequences were processed on the mBRAVE platform (<http://www.boldsystems.org/bin>) (Ratnasingham & Hebert 2007) setting the following

parameters: Min QV = 0 qv, Min Length = 100 bp, Max Bases with Low QV (<20) = 75%, Max Bases with Ultra Low QV (<10) = 75%, ID Distance Threshold = 1.5%, Exclude from OTU Threshold = 3%, Minimum OTU Size = 1, OTU Threshold = 2%. Sequences were compared with the BOLD reference libraries SYS-CRLINSECTA and SYS-CRLNONINSECTARTH to established Barcode Index Numbers (BINs). BINs are a type of Operational Taxonomic Unit (OTU) integrated in the BOLD system with advantages over traditional OTUs, such as being unique and stable (Ratnasingham & Hebert 2013). I used BINs as a proxy of taxonomic species. Some BINs identified may correspond taxonomically to relative species instead of the specific taxonomic species from the study area or include several species that have highly similar reference sequence at the amplified region. However, all BINs were retained given the purpose of the study of describing overall diet and similarities between bat species without focusing on the exact identity of prey species. Excluding those could furthermore bias the broader-taxonomic and functional diet composition.

After obtaining BIN (prey item) composition per sample and run, we removed singletons, i.e. BINs that only had a single read per run and sample, because they are likely to be PCR or sequencing errors (Alberdi *et al.* 2018). We established the threshold for the minimum number of reads per sample to retain an identification based on comparing composition similarity between molecular and morphological ID from sweeping samples and any prey present in blanks. Additionally, we controlled for potential contamination during extractions by removing the BINs present in extraction blanks from other samples in the same extraction run if present with a high number of reads (>100 in any blank sample) or with less than 10 times more reads in samples than in blank. We controlled for contamination from the sequencing process by removing BINs present in sequencing blanks from all the samples from the same primer following the same criteria as above.

We used two alternative approaches to combine data from PCR replicates. In the first, the additive criteria, BIN composition from both PCR replicates of each sample were added together. In the second, the conservative approach, only BINs that appeared in both PCR replicates were considered (Alberdi *et al.* 2018). Under this second criteria only samples in which the four runs contained a minimum number of reads (>100) were considered given that a failed sequencing run in a sample would lead to a null composition for both of the PCR replicates of a primer (52 samples, Supplementary Table B1.3). Finally, we combined taxa recovered from both primers to obtain the prey composition per dropping sample for downstream ecological analysis. Duplicated BINs in the same sample coming from different

PCR replicates or primers were removed. A flow chart describing the methods is shown in Supplementary Fig. B1.1. Ecological results from both approaches were very similar, thus we present results based on the additive approach (See Supplementary Fig. B1.10 for diet based on the conservative approach).

3.3.5. Characterising the diets of the two bat species

The contribution of different elements to the diet for a set of samples was quantified using weighted Percent of Occurrence (wPOO), which measures the relative occurrence of diet elements (prey items/OTUs/BINs) in a set of samples considering first their relative proportion per sample (Deagle *et al.* 2019). For example, a prey item found in a sample with 9 other prey items will be interpreted to contribute to the diet 1/10 of what it would if it was the only prey item present. Contributions to diet based on the two other commonly used metrics: Percent of Occurrence (POO) and Relative Read Abundance (RRA) (Deagle *et al.* 2019), are shown in Supplementary Fig. B1.2. We tested for differences in the number of BINs per sample between bat species for each of the orders that constitute at least 10% of the diet of either one of the bat species (Araneae, Diptera, Lepidoptera, and Hemiptera), using negative binomial generalised linear models (GLMs; in R) to fit data structure based on the distribution of model residuals. We measured order level and prey species level (BIN-level) diet composition overlap between bat species using Pianka's measure of niche overlap (O_{jk}) (R package: EcoSimR, Gotelli *et al.* 2015). We tested with an ANOSIM test (R package vegan, Oksanen *et al.* 2019) whether Jaccard distance in BIN composition was greater between than within bat species. The ANOSIM statistic R is based on the difference of mean ranks between and within groups, with a range between -1 and +1. A value of zero indicates that the group does not explain compositional differences. We visualised ordination of samples depending on their BIN composition with Non-Metric Multidimensional Scaling (NMDS, R package vegan: Oksanen *et al.* 2019). We calculated Levins', (1968) standardised measure of niche breadth (B_A) at the prey species (BIN) level for each bat species.

3.3.6. Functional diet assessment

Prey items were classified based on the literature (outlined in Supplementary Table B1.2) and an entomological taxonomist, Jorge Mederos, into three functional categories: non-volant, not actively-volant, nocturnally volant. Categorisation depended on their mobility and type of activity, reflecting their likelihood of being captured by gleaning or aerial hawking (Supplementary Table B1.2). The categorisation was done at family or finer taxonomic level by checking the literature for data on daily activity patterns of each family and presence in

nocturnal light traps (Supplementary Table B1.2 for criteria used). The non-volant category included wingless arthropod groups (Araneae, Isopoda and wingless insects such as some members of Blattodea, Orthoptera). The not actively-volant category included those able to fly but unlikely to have been captured by the bat through aerial hawking because they are not active fliers, either at night (diurnal Diptera), or not active fliers in general (e.g. Hemiptera, some Blattodea, Orthoptera and Coleoptera). The nocturnally volant category comprised arthropods with aerial and nocturnal activity, and therefore likely to be captured by aerial hawking (e.g. non-Ropalocera Lepidoptera, nocturnal Diptera, Neuroptera, Ephemeroptera, Trichoptera). This classification represents the likelihood of being captured by gleaning or aerial hawking rather than direct inference of the capture mode because nocturnally active aerial prey can also be captured by gleaning when resting on vegetation and not active nocturnal fliers could also be captured in the air (e.g. ballooning in spiders). Once all prey items were classified into functional groups, we obtained the functional diet of both bat species using weighted percent of occurrence (wPOO), and compared the percentage of not nocturnally volant (including both non-volant and not actively volant categories) per sample between bat species using a linear model.

3.3.7. Trophic niche overlap in allopatry vs sympatry across spatial scales

Locations from Andalucía (Mediterranean climate) and northern Cantabria (Atlantic climate) were classified as regionally allopatric. Locations from La Rioja and southern Cantabria (climatically Mediterranean to sub-Atlantic) as regionally sympatric (based on data from Razgour et al., (2019) and EBD records). At the fine-scale within the sympatric regions, we classified locations as locally sympatric or allopatric depending on whether they were within 3 km of records of the other species based on a conservative estimation of the home-range diameter of the better studied cryptic congener *M. nattereri* (Boye & Dietz 2005). The swarming location in Catalonia was removed from the fine-scale analysis because bats gather in swarming sites from distances of up to 60 km from their colonies for the purpose of breeding rather than foraging (Rivers *et al.* 2005), and therefore it is unclear whether those individuals forage in sympatric areas (Supplementary Table B1.1 for sampling locations and their broad and fine-scale sympatry category).

To identify differential use of certain prey orders and functional groups, we tested separately for allopatric and sympatric locations whether 1) the number of BINs per sample for each of the main arthropod orders, and 2) the percentage of not nocturnally volant functional groups differed between bat species. We used negative binomial zero inflated GLMs and a linear

model respectively. We run separate models for broad and fine spatial scales given that both fine scale sympatry and allopatry treatments are within regional sympatry. Cases where resource (prey order or functional group) use was different between bat species when sympatric but not when allopatric were regarded as evidence of resource partitioning. We measured prey species (BIN) level niche overlap (O_{jk}) between bat species in sympatry and in allopatry, and tested, using null models (R package ecosimR) whether overlap was lower or higher than random in sympatry versus allopatry. We tested whether O_{jk} differed between sympatric and allopatric locations by pooling the diet composition of each bat species per location and measuring O_{jk} between pairs of locations. At the regional scale we used a Gaussian Hurdle model due to the high density of zeroes in overlap values. At the local scale we used a linear model with log transformed values of O_{jk} to meet assumptions of normal distribution. All statistical analysis was carried out in R (R core team 2020).

3.3.8. Prey consumption relative to availability

For each location, we quantified the relative availability of each arthropod order and functional group using weighted percent of occurrence (wPOO) after pooling together sweeping samples from the different habitats. Similarly, we obtained bat diet composition (wPOO) per location of each arthropod order and functional group by pooling diet composition of all individual bats. Then, we subtracted from the bat diet wPOO the prey availability wPOO to obtain prey arthropod and functional group selection per location. A higher proportion of a given arthropod order in the diet than in sweeping samples indicates the bats may be preferentially consuming this resource, based on prey availability at the sampled strata. This analysis is based on assumptions of sampling representativeness (see discussion for detailed overview of methodological limitations).

3.3.9. Testing primer performance and representation of the DNA metabarcoding approach

For each arthropod order we described the number and proportion of BINs identified by each primer. Morphological identification of the arthropod communities allowed us to compare the performance of the primers and metabarcoding approaches. We compared the presence of orders in each sweeping sample based on molecular and morphological identification to determine whether metabarcoding offers a good estimation of arthropod community composition.

3.4. Results

We analysed a total of 138 dropping samples for *Myotis escalerai* and 90 for *Myotis crypticus* from 49 locations, 26 of which were in the broad-scale allopatric regions and 23 in sympatric regions. Within the sympatric regions (La Rioja and southern Cantabria), 91 samples were classified as locally allopatric and 28 as locally sympatric (Fig. 3.1, Table 3.1, Supplementary Table B1.1). We recovered a total of 2,859,300 reads (Supplementary Table B1.3 for details) from the 228 dropping samples for the four combinations of PCR replicates and primers (1,403,636 from ANML1 and 1,455,664 from ZBJ). These reads were associated into 1461 different BINs. Based on the BINs present in sequencing blanks, we removed for the ANML primer 6 BINs from the first run of 56 dropping samples, and 2 BINs for the second run of 10 samples. For the ZBJ primer, we removed 5 BINs from the first run of 10 samples and 23 BINs from the second run of 88 samples. Based on BINs present in extraction blanks, we removed a total of 39 BINs from 16 dropping samples.

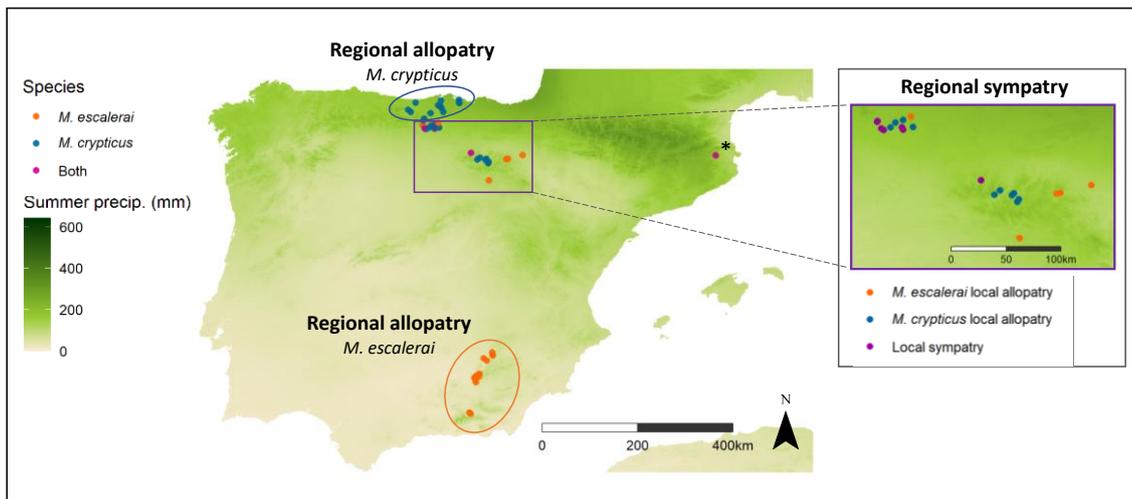


Fig. 3.1 – Sampling locations overlaying summer precipitation across Spain, with gradient from dry Mediterranean to wet Atlantic. Ovals encompass the two allopatric regions (Granada and Jaen for *M. escalerai* and northern Cantabria for *M. crypticus*). The rectangle encompasses the sympatric region (La Rioja and the Mediterranean climatic zone at the south of Cantabria). Insert shows the sympatric region with locally sympatric (purple) versus locally allopatric (blue and orange) locations. Black star on the sympatric location at the E side of the main map in Catalonia denotes a swarming site and was excluded from the analysis.

Table 3.1 – Number of bat dropping samples, sweeping samples, and locations for each bat species by allopatry/sympatry classification at broad (regional) and fine (local) spatial scales.

		Total	Broad-scale allopatric	Broad- scale sympatric	Fine-scale allopatric	Fine-scale sympatric
Dropping samples	<i>M. escalerai</i>	138	82	56	46	6
	<i>M. crypticus</i>	90	18	72	45	22
Sweeping samples	<i>M. escalerai</i>	13	5	8	3	5
	<i>M. crypticus</i>	15	2	13	6	7
Locations		49	26	23	14	8

3.4.1. Characterising the diet of *M. escalerai* and *M. crypticus*

A total 19 arthropod orders were obtained based on the 1461 BINs. The diets of *M. escalerai* and *M. crypticus* were characterised by high arthropod diversity, and were composed mostly of the orders Lepidoptera (*M. escalerai* = 26.6 %; *M. crypticus* = 23.7%), Diptera (24.8%; 33.2%), Araneae (20.7%; 17.2%), but also included Hemiptera (11.8%; 6.2%), Coleoptera (4.8%; 5.1%), and Orthoptera (4.3%; 4.8%), among others (<5%) (Fig. 3.2a-b; Supplementary Fig. B1.2 for diet composition based on POO and RRA measures). Diet composition at the prey order level was very similar between bat species ($O_{JK} = 0.98$, above 1000 null models). However there were differences in the number of BINs per sample of Diptera, which was lower in *M. escalerai* (5.27 versus 6.75) (Negative binomial GLM: $z_{1,226} = -2.03$, $p = 0.042$), and Hemiptera, which was higher in *M. escalerai* (2.09 versus 1.68) (Negative binomial GLM: $z_{1,226} = 2.85$, $p = 0.004$, Supplementary Fig. B1.3).

At the prey species (BIN) level, Levins' niche breadth was similar for both species, $B_A = 0.17$ for *M. escalerai* and $B_A = 0.19$ for *M. crypticus*. Niche overlap between species was higher than expected by chance ($O_{JK} = 0.71$, above 95% of 1000 null models). The samples from the two bat species showed some differences in prey item composition in NMDS ordination space (Fig. 3.3a, Stress: 0.25, $k=3$, non-metric fit $R^2=0.934$, Linear fit, $R^2= 0.532$). An analysis of similarity confirms that distance in prey item composition among samples is greater between species than within species (ANOSIM R statistic: 0.10, $p= 0.001$).

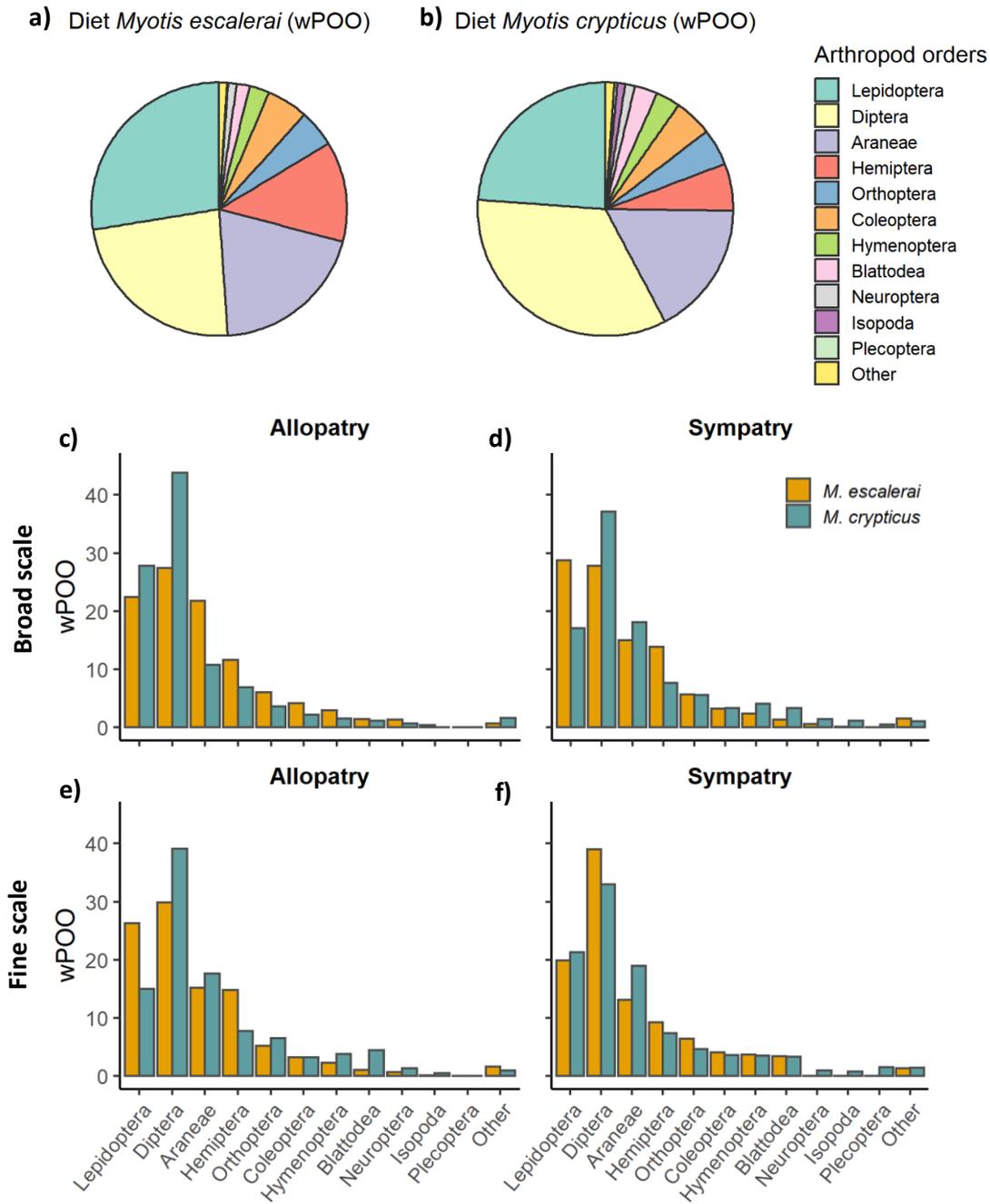


Fig. 3.2 – Overall diet composition of *M. escaleraei* and *M. crypticus* using weighted Percent of Occurrence (wPOO) (a, b). Dietary composition by scale of allopatry/sympatry (broad-scale: c, d, fine-scale: e, f).

3.4.2. Trophic partitioning in sympatric versus allopatric locations

At the arthropod order level, there is no clear pattern of shift from high similarity in order composition between species to differential use in sympatry at any of both spatial scales (O_{JK} regional allopatry = 0.88, O_{JK} regional sympatry = 0.96, >1000 null models, Fig 2c-d; O_{JK} local allopatry = 0.95, O_{JK} local sympatry = 0.98, >1000 null models, Fig 2e-f). When examining the number of BINs of the main arthropod orders per sample, there were differences between bat species between the allopatric regions for Araneae and Hemiptera, which were both higher in *M. escalerai* (*M. escalerai* = 4.00, 1.65, *M. crypticus* = 2.16, 0.55 respectively), and for Lepidoptera, which was higher in *M. crypticus* (4.6, 11.94) (Negative binomial GLM: $df=1,98$, $p<0.05$). In the sympatric region, the higher number of Hemiptera in *M. escalerai* holds (*M. escalerai* = 2.50, *M. crypticus* 1.50), and in Lepidoptera there is a shift whereby is *M. escalerai* the one that consumes a higher number (*M. escalerai* = 6.78, *M. crypticus* = 4.09, Negative binomial GLM: $p<0.05$). At the fine-scale, within the sympatric region, the only difference found between the bat species was the higher number of BINs per sample of Hemiptera (2.67, 1.49) (Negative binomial GLM: $z_{1,89} = -2.68$, $p=0.007$) and Lepidoptera (6.70, 3.64) in *M. escalerai* in allopatric locations (Negative binomial GLM: $z_{1,89} = -2.92$, $p=0.004$). There were no differences in arthropod orders consumed between the bat species in locally sympatric locations (Negative binomial GLM: $p>0.05$; Supplementary Fig. B1.4).

At the prey species (BIN) level, at the broad-scale, trophic niche similarity between species was lower in allopatric than in sympatric regions (O_{JK} allopatric = 0.35, O_{JK} sympatric = 0.62). Conversely, at the fine-scale, within the sympatric region, trophic niche overlap between species was higher in locally allopatric locations (O_{JK} = 0.56) than in locally sympatric locations (O_{JK} = 0.37). Despite the low values of overlap in regionally allopatric and locally sympatric locations, in all the four cases, observed niche overlap was higher than 1000 null models. When measuring trophic niche overlap between species using pairs of locations, we observed the same pattern. At the broad scale we found higher diet overlap in sympatric than allopatric locations (O_{JK} sympatric = 0.107 ± 0.056 , O_{JK} allopatric = 0.050 ± 0.04 ; Gaussian hurdle model: binomial GLM: $z_{1,316} = 4.76$, $p<0.05$; Gaussian GLM: $t_{1,265} = 8.26$, $p<0.05$). In contrast, at the fine-scale, niche overlap was lower among pairs of locally sympatric than among locally allopatric locations (O_{JK} sympatric = 0.099 ± 0.065 , O_{JK} allopatric = 0.126 ± 0.057 ; Linear model: $F_{1,73} = 6.34$, $p=0.014$; Fig. 3.3b).

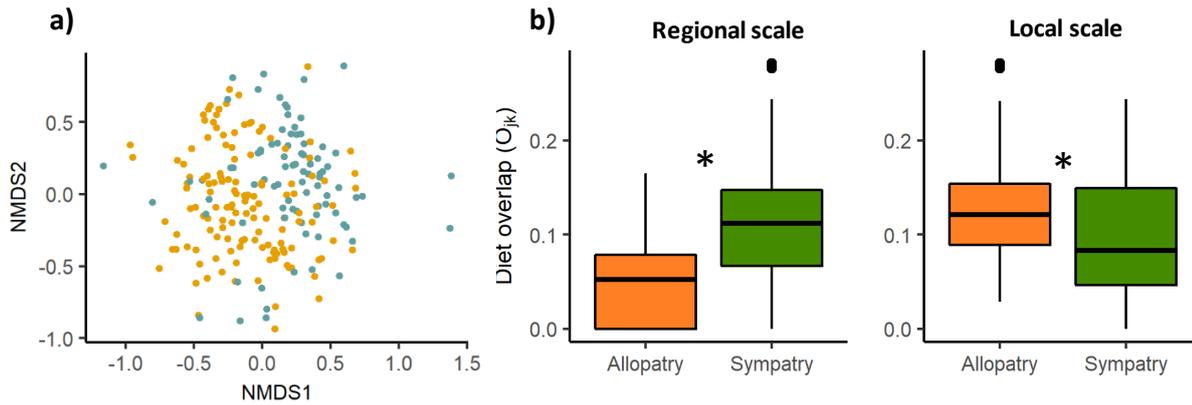


Fig. 3.3 – a) Non-Metric Multidimensional Scaling ordination of individual bat samples based on their BIN composition, with *M. escalerai* samples in yellow and *M. crypticus* in blue. b) Pianka's measure of niche overlap (O_{jk}) between the two bat species in allopatric versus sympatric locations at the regional (left) and local (right) scales. Replicates are values of overlap between pairs of locations of different bat species. Star denotes detectable differences between groups at $p < 0.05$.

3.4.3. Functional diet analysis

Both species had a similar high percentage of non-volant (*M. escalerai* = 21.4 %, *M. crypticus* = 19.5%) and not actively-volant (44.6%, 45.8%) prey items in the diet. Only 34.0% and 34.7% of weighted percent of occurrence (wPOO) was composed of arthropods classified as nocturnally volant (Fig. 3.4a). There were no differences in the overall percentage of not nocturnally volant prey taxa (BINs) per sample between bat species ($66\% \pm 20\%$, $66\% \pm 21\%$, Linear model: $F_{1,217} < 0.001$, $p = 0.990$; Fig. 3.4b). When analysing functional diet differences separately in allopatric versus sympatric regions, we found differences between species in allopatric regions, whereby *M. crypticus* consumed lower percentage of prey that were not nocturnally volant (allopatric regions: *M. escalerai* = $66\% \pm 19\%$, *M. crypticus* = $48\% \pm 25\%$; $F_{1,98} = 11.72$, $p < 0.05$; Fig. 3.4c; sympatric regions: $65\% \pm 22\%$, $71\% \pm 17\%$; $F_{1,117} = 2.3$, $p = 0.13$; Fig. 3.4d). At the fine-scale, there were no differences among bats in locally allopatric locations (*M. escalerai* = $67\% \pm 22\%$, *M. crypticus* = $72\% \pm 16\%$, $F_{1,89} = 1.325$, $p = 0.250$; Fig. 3.4e) while in locally sympatric locations the percent of prey that were not nocturnally volant was borderline lower in the diet of *M. escalerai* ($52\% \pm 17\%$) than *M. crypticus* ($68\% \pm 18\%$; $F_{1,26} = 4.03$, $p = 0.055$; Fig. 3.4f).

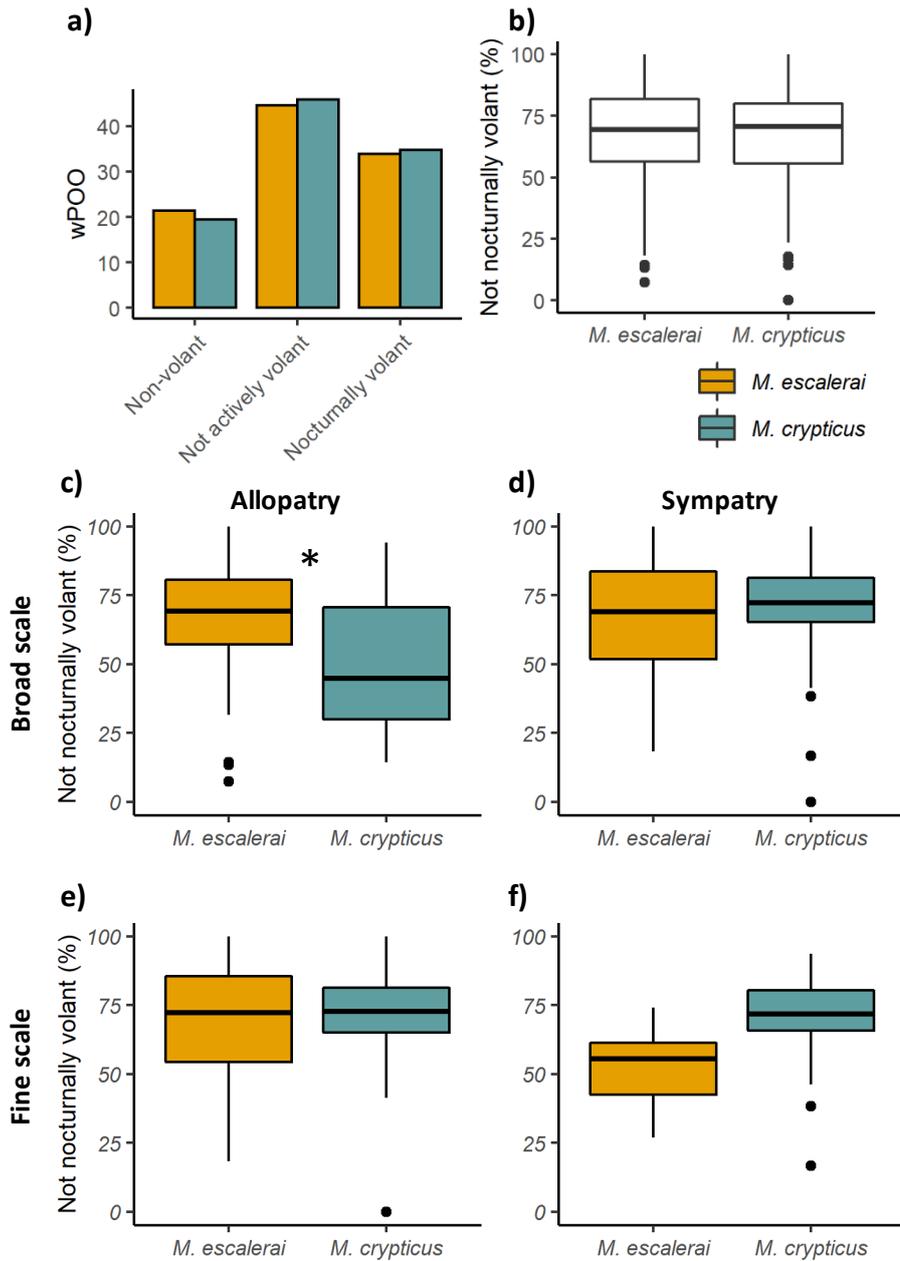


Fig. 3.4 – Functional diets of *M. escalerai* and *M. crypticus* depending on the nocturnal flight behaviour of the prey species, classified into non-volant (wingless arthropod groups), not actively-volant (able to fly but unlikely to have been captured through aerial hawking), nocturnally volant (likely to be captured by aerial hawking). Overall proportions of functional categories in the bat diets (a); proportion of not nocturnally volant prey items per dropping sample in *M. escalerai* and *M. crypticus* overall (b), in broad-scale allopatric versus sympatric regions (c) and in fine-scale locally allopatric versus locally sympatric locations (d). Star denotes detectable differences between groups at $p < 0.05$ (Linear Model).

3.4.4. Prey consumption relative to availability

In nearly all cases, we could not detect over- or under-selection of arthropod orders by the bats relative to their availability in sweeping samples. The distribution of prey order selection values between the 1st and 3rd quartiles overlapped with zero in all cases, except in the case of *M. escaleraei* and Lepidoptera, where positive selection values could indicate over-selection (1st-3rd quartile: +0.43 — +18.7; Supplementary Fig. B1.5).

3.4.5. Metabarcoding and primer performance

There were compositional differences in the prey orders that each primer recovered. A large proportion of the BINs identified in dropping samples were only recovered by one of the primers (Supplementary Fig. B1.6). Neuroptera, Orthoptera, Coleoptera were more frequently recovered by ZBJ, while Plecoptera and Thysanoptera, Dermaptera, Mantodea were more frequently recovered by ANML (Supplementary Fig. B1.6). Supplementary Fig. B1.7 shows composition for a subset of dropping samples comparing each primer.

In sweeping samples, 7065 insects were identified morphologically to order level, with an average of 174.3 individuals per sample (range 7-624). Using molecular tools, we recovered 899,853 reads (Supplementary Table B1.2), and identified 813 different BIN items. Some of the rarer orders were under-represented in the molecular analysis. Specifically, Opiliones, Dermaptera, and Archaeognatha, appeared in more than 10 sweeping samples each identified morphologically, but were rarely recovered in the molecular approach, despite being present in the reference databases (Supplementary Fig. B1.8).

3.5. Discussion

Morphologically almost identical species are likely to compete for resources, and therefore offer good case studies to understand processes that drive species coexistence. We find evidence of reduced trophic niche overlap in recently separated cryptic bat species in sympatric locations relative to allopatric ones based on DNA metabarcoding and high throughput sequencing. The functional analysis suggests that the subtle trophic shift seen may be driven by differential foraging mode. Our results support niche theory predictions of the role of biotic interactions in driving species assemblages (Schoener 1974). Trophic resource partitioning was only evident at the fine spatial scale, within areas of range overlap, suggesting that fine-scale mechanisms of coexistence could have implications for the maintenance of broad- scale diversity patterns (Godsoe *et al.* 2015).

3.5.1. Trophic ecology of *Myotis escaleraei* and *Myotis crypticus*

Our results reveal that the two bat species have a broad generalist diet, tend to consume prey relative to their availability and use gleaning to a high extent. We found high similarity in their trophic ecology in terms of both order and prey species composition. Both bat species' diets are mostly composed of Lepidoptera, Diptera and Araneae, but also include several other prey orders. However, *M. escaleraei* consumes a higher percentage of Hemiptera, while *M. crypticus* Diptera. Functionally, the two bat species consume an equally high proportion of prey items that are not nocturnally volant, which suggests that both bats predominantly glean prey from vegetation.

The trophic ecology of these two recently described bat species is very similar to their cryptic sister-species *M. nattereri*, which also feeds mostly on Lepidoptera, Diptera and Araneae (Swift 1997; Vaughan 1997; Swift & Racey 2002; Hope *et al.* 2014) and is known to capture a high proportion of its prey through gleaning (Shiel *et al.* 1991; Arlettaz 1996; Swift 1997; Swift & Racey 2002; Hope *et al.* 2014). Similarly to our study, Shiel *et al.*, (1991) estimated that 68% of *M. nattereri*'s diet is made up of arthropod families that are not active at night. The row of hairs in the uropatagium border is a characteristic trait of members of the *M. nattereri* species complex that is thought to be functionally linked with gleaning (Czech *et al.* 2009). Although the presence of more developed hairs in *M. escaleraei* is one of the characters which separates these taxa (Juste *et al.* 2019), we found no difference in the extent of gleaning between the two bat species.

3.5.2. Trophic partitioning across spatial scales

Despite overall high trophic niche similarity between the two bat species at the prey order level, we detect a signature of trophic shift at the prey species (BIN) level, whereby diet overlap is lower in locally sympatric compared to locally allopatric locations at the fine-scale. This supports the contribution of trophic partitioning to species coexistence even when overall trophic niche overlap is high. A similar trend was seen at the functional level, whereby the proportion of prey items that are not nocturnally volant is borderline different between bat species only when locally sympatric. This suggests that the differentiation in diet composition seen at the prey species level when locally sympatric may be driven by a shift in foraging strategy (e.g. Krüger *et al.* 2014), through *M. escaleraei* decreasing its extent of gleaning. However, our inference is limited by small sample sizes, which reduced the power of the analysis. At the arthropod order level, we find differences in the use of some arthropod orders among allopatric regions, likely due to differences in arthropod availability between the

Mediterranean region, where only *M. escalerae* is found and the Atlantic region, where *M. crypticus* is present.

Several studies have identified trophic niche shifts from allopatry to sympatry, for instance between morphologically similar fish (Schmitt & Coyer 1983; Gkenas *et al.* 2019) and reptile species (Huey *et al.* 1974; Klawinski *et al.* 1994). However, in bats, previous coexistence studies looking at trophic ecology only focused on sympatric populations, and rarely found evidence of trophic resource partitioning. A few exceptions are the gleaning bats *M. nattereri*, *Plecotus auritus* and *Myotis bechsteini* in a sympatric population in central Europe (Andreas *et al.* 2012a), and evidence of low dietary overlap between sympatric *P. auritus* and *Plecotus macrobullaris* (Ashrafi *et al.* 2011).

The observed trophic shift, albeit subtle, suggests that the two bat species are likely competing for food resources. It has been previously hypothesised that arthropods are abundant and do not constitute a limiting resource for bats (Arlettaz 1999; Krüger *et al.* 2014). However, exclusion experiments in both tropical (Kalka *et al.* 2008) and temperate forests (Böhm *et al.* 2011) show that bats can control the abundance of arthropods, and therefore arthropods could be a limiting resource to competitors (Salinas-Ramos *et al.* 2020).

Our study does not refute the possibility that other coexistence mechanisms, such as habitat or temporal partitioning (Schoener 1974), occur among these two species, or the role of environmental variability in facilitating coexistence (Chesson & Warner 1981). Spatial partitioning is frequently cited as a key mechanism of coexistence in bat studies (e.g. Kunz 1973; Arlettaz 1999; Nicholls & Racey 2006; Emrich *et al.* 2014; Russo *et al.* 2014). Although in many cases, in contrast to our study, spatial partitioning may be driven by slight differences in bat morphology (e.g. Salsamendi *et al.* 2008, 2012), which would affect their performance in different habitats (Norberg 1994). However, in our study the two species were caught in the same sampling sites, some of which were forests, where they are known to forage, suggesting they may share the same foraging sites.

A better understanding of the spatial scales of species coexistence is an important advance in our understanding of the maintenance of diversity (Hart *et al.* 2017). Our finding that trophic partitioning only occurs at the fine spatial scale is consistent with other bat (Peixoto *et al.* 2018), ant (Albrecht & Gotelli 2001), parasitoid insects (Harvey *et al.* 2014) and bobcat (Lewis *et al.* 2015) studies, showing that interspecific interactions are more important for shaping community structure at fine rather than broad spatial scales. However, this pattern is not universal (e.g. Harmáčková *et al.* 2019). Fine-scale coexistence mechanisms could prevent

competitive effects from scaling-up (Godsoe *et al.* 2015), which in our study system could contribute to enabling broad-scale range overlap across the north of the Iberian Peninsula.

3.5.3. Prey consumption relative to availability

The diet of a species is a function of both consumer selection and trophic resource availability within the foraging habitat (Lawlor 1980). Therefore, considering resource availability allows for a better inference of species trophic preferences. Previous studies comparing bat prey consumption with prey availability pointed to selection of certain prey orders, such as Coleoptera by *Eptesicus fuscus* (Agosta *et al.* 2003), chironomid flies by *Myotis daubentoni* (Vesterinen *et al.* 2016) and certain prey traits like moth size by *Barbastella barbastellus* (Andreas *et al.* 2012b). Similarly, *M. nattereri* was found to over-select arachnids, Opiliones, Coleoptera, and several Diptera families, and under-select Hemiptera (Swift & Racey 2002). In this study we do not detect clear trends of over-selection for specific prey orders matching the generalist broad trophic niche of the studied bats. However, diet selection results should be interpreted with caution due to the difficulty of obtaining a representative estimation of arthropod availability. Any arthropod sampling technique is biased towards certain types of arthropods (Cooper & Whitmore 1990) and the habitats sampled and their respective sampling effort may not adequately represent where bats actually forage, especially given that they can use large areas and arthropod communities change depending on habitat type (Lamarre *et al.* 2016) and vertical stratification (Ulyshen 2011). Our molecular diet analysis results confirm that the two studied bat species indeed glean prey from the vegetation, and therefore the arthropod community sampled using sweep nets likely represents at least part of the prey resources available to the bats.

3.5.4. Methodological considerations and study limitations

Primer bias towards certain taxonomic groups is a major issue in metabarcoding studies (Elbrecht *et al.* 2019). In this study, prey items were frequently recovered by only one of the primers, and differences existed in the recovery of the different arthropod orders. This supports previous studies that suggest that more than one set of primers should be used when the expected diet covers a broader taxonomical spectrum (Alberdi *et al.* 2018). The inclusion in this study of a set of samples with known composition based on morphological analysis (albeit only at the order level) gives us some idea of potential biases in the molecular identification. Opiliones, in particular, were morphologically identified in several sweep net samples and are known to be present in the diet of *M. nattereri* (Swift 1997; Swift & Racey 2002; Galan *et al.*

2018), but were absent from the molecularly-characterised diets of the two bats. Thus, their absence in this study is likely the result of primer amplification bias.

Parameter choice during bioinformatic analysis can modify the diet composition recovered (Alberdi *et al.* 2018). The strong match between the inferences drawn using the additive and the conservative approach of dealing with PCR replicates (Supplementary Fig. B1.9), show that the results are robust to that choice, and mirror other studies showing that parameters choice does not change ecological conclusions (Clare *et al.* 2016). In the same manner, high similarity in diet composition based on weighted Percent of Occurrence (wPOO) and Relative Read abundance (RRA), indicates that the results are also robust to the measure used.

Because prey development stage cannot be identified using the metabarcoding approach, some of the prey species (BINs) classified as nocturnally volant may correspond to non-flying larval stages. This could be important in Lepidoptera, and could increase the inferred importance of the gleaned behaviour of both species because larval stages are known to be consumed by *M. nattereri* (Hope *et al.* 2014). More generally, nocturnal aerial activity is not directly quantifiable, and therefore our classification is subject to a certain degree of subjectivity. However, because arthropod orders most difficult to categorise due their diversity, like Coleoptera, are consumed in similarly low proportion by both bat species, potential classification biases are expected to be low and standardised across species. Nevertheless, due to potential classification biases and low sample sizes in sympatric locations, interpretations of functional prey shift should be considered with caution. The limited sample size of the study did not allow controlling for potential spatial autocorrelation in statistical models, which can affect model inference.

3.6. Conclusions

In line with niche theory predictions, we show that coexistence among morphologically identical (cryptic) species can be facilitated through fine-scale mechanisms of resource partitioning, despite high levels of trophic similarity at the broad-scale, even in sympatric regions. Hence, this study highlights the importance of using appropriated spatial scales when studying impacts of biotic interactions on community assembly (Viana & Chase 2019). Our findings that trophic resource partitioning is only evident at the fine spatial scale, within areas of range overlap, suggest that fine-scale mechanisms of coexistence could have implications for the maintenance of broad- scale diversity patterns. This is the first study to identify a trophic shift between allopatric and sympatric populations of insectivorous bats, supporting the role of trophic resource partitioning in enabling species co-occurrence in the same foraging

site. It thereby addresses some of the key limitations identified in a recent review of interspecific competition in bats (Salinas-Ramos *et al.* 2020). We highlight the importance of using high taxonomic resolution and allopatric populations at meaningful spatial scales for identifying patterns of niche shift, and the utility of using a functional approach that better links mechanistically with species trophic ecology. Understanding mechanisms of coexistence is essential for predicting species vulnerability under climate change because range shifts will result in new community assemblages and competitive interactions (HilleRisLambers *et al.* 2013). This is particularly relevant in our study system as both species are restricted to the Mediterranean region, where climate change is predicted to be particularly severe (Sala *et al.* 2000), and both are predicted to experience range shifts and changes in range overlap under climate change (Razgour *et al.* 2019).

3.7. Chapter summary

In this chapter I showed how biotic interactions can shape fine-scale spatial patterns and how trophic partitioning can allow local coexistence of morphologically almost identical species. In the next chapter I will move the emphasis of the role of biotic interactions and coexistence mechanisms to broader spatial scales and their implications for maintaining continental-scale diversity patterns.

4. Chapter 4 Geographic Avoidance: a new measure to detect the effect of biotic interactions on species ranges

4.1. Abstract

The need to forecast range shifts under future climate change has motivated an increasing interest in developing realistic predictive species distribution models (SDMs) that include processes that shape species ranges. However, a robust and feasible methodological framework for measuring the effect of biotic interactions on species ranges at broad spatial scales is yet to be developed. This study develops and evaluates a measure that uses SDM outputs to quantify geographic exclusion patterns expected if interspecific competition affects broad-scale distributions. I apply the measure to 10 Palearctic bat species belonging to four sets of morphologically similar cryptic groups (nine pairs in total) in which competition is likely to occur, and compare the outputs to null models based on virtual species. Values of geographic avoidance were above null expectations for two of the pairs of cryptic species, suggesting that interspecific competition could have played a role in shaping their geographic ranges. Inferences were in line with expectations based on ecological knowledge of the species, whereby high values correspond to cases of high ecological similarity between species and absence of trophic or habitat partitioning. Through applying the measure in a predictive manner, I show how considering the role of competition could modify predictions of range shift under future climate change. The results indicate that interspecific competition can play a role in limiting the geographic ranges of morphologically similar species in the absence of fine-scale mechanisms of coexistence. Although no method based on observational data can unequivocally measure competitive effects, I show that the measure is able to identify the expected broad-scale geographic patterns resulting from competition, and therefore can help identify cases where competition shapes species ranges. Unlike other recently developed methods, the measure has low data requirements, and hence is particularly suitable for broad-scale applications and for species that have not been sampled intensively.

4.2. Introduction

The need to forecast shifts in species distributions under global climate change is driving an emerging interest in the factors that shape species ranges (Pacifi *et al.* 2015). The presence of a species in a given location, and thus the species' range, depends on the abiotic environment (climate, topography and physical environment), biotic interactions and the spatial reachability of the location, which relates to species dispersal ability and evolutionary history (Soberón & Peterson 2005). However, the interplay between these factors is still not well understood. Climatic factors are commonly thought to shape the distribution of species at a broad spatial scale, whereas the impact of biotic factors is more pronounced at the local scale (Willis & Whittaker 2002), and their role in shaping macroecological patterns remains controversial (Wiens 2011). Local-scale biotic influence is supported by many studies (e.g. Soberón & Nakamura 2009; Fraterrigo *et al.* 2014), yet substantial evidence shows that competitive effects can also scale-up to the regional level. For instance, 31 and 8 studies out of 51 gave support and partial support to the role of competition in shaping species range limits (Sexton *et al.* 2009). These findings are echoed by modelling studies that identify broad-scale competitive effects (e.g. Gotelli *et al.* 2010) and several documented examples of macroecological effects of competition (reviewed in Wisz *et al.* 2013). However, our understanding of the conditions under which interspecific competition plays a role in shaping species ranges is still limited.

The ultimate consequence of interspecific competition in the absence of coexistence mechanisms is spatial exclusion (Gause principle: Gause 1932; Hardin 1960). Species can develop mechanisms, such as partitioning of the trophic, spatial or temporal ecological niche, that enable coexistence. Recent studies point that coexistence mechanisms can mediate whether the effect of competitive exclusion scales-up, suggesting that the effect appears at broader species-range scale only when coexistence mechanisms are not developed at finer spatial scales (Godsoe *et al.* 2015). If competitive exclusion scales-up and has an effect on species' ranges, the predicted observable pattern on species' occurrences would be a tendency of species to be absent from their environmentally suitable habitat in areas where the competitor is present. Identifying such a pattern of species avoidance sets the basis for inferring competitive effects from occurrence data. Indeed, analysis of species co-occurrence is typically used in community ecology to study the role of biotic interactions in community assembly processes (Gotelli 2000; Götzenberger *et al.* 2012). Similarly, at broader spatial scales, parapatric ranges in morphologically similar or phylogenetically-related species are traditionally interpreted as being the result of competitive interactions, especially in the

absence of geographical barriers to dispersal and when sharp edges do not match clear environmental gradients (Miller 1967; Bull 1991). The main difficulty when interpreting species occurrence patterns resulting from competition is separating environmental effects from species effects, i.e. distinguishing ecological preferences from geographic avoidance of competitors (Bar-Massada 2015).

Some methodological approaches aim to assess impacts of biotic interactions on species' ranges (Harris 2015; Warton *et al.* 2015), for example, through the inclusion of the geographic range of a potential competitor as an additional predictor layer in Species Distribution Models (SDMs) (Anderson 2017). More recent efforts focus on developing Joint Species Distribution Models (JSDMs), which model the presence of several species simultaneously based on their responses to environmental predictors and hierarchically incorporate the effects of other species in the model residuals (e.g. Pollock *et al.* 2014). Although these approaches are promising, there is still limited empirical evidence for the validity of their inferences, and recent studies warn about limitations in their ability to measure biotic interactions (Godsoe *et al.* 2017; Dormann 2018; Zurell *et al.* 2018). Therefore, currently there are no available methods that can be applied at broad spatial scales to measure expected geographic patterns when biotic interactions shape species ranges.

Cryptic species are morphologically very similar but genetically distinct species, and therefore an excellent model system for testing competitive interactions (e.g. Arrizabalaga-Escudero *et al.* 2018). Bats are a functionally diverse order that contains a high proportion of recently described cryptic species (e.g. Ibáñez *et al.* 2006), and thus offer excellent case studies for assessing the role of interspecific competition in shaping species ranges. Palearctic bat species are expected to be negatively impacted by climate change, with several species predicted to decline or lose their entire current suitable climatic range (Rebelo *et al.* 2010). There is increasing awareness that biotic interactions can play an important role in modifying responses towards climate change (HilleRisLambers *et al.* 2013) and that considering the role of biotic interaction is important for a better understanding of how climate change will impact diversity (Alexander *et al.* 2016).

I aim to test whether spatial exclusion between potentially competing species can be detected at species ranges scale. For that, I develop a measure of geographic avoidance between species that uses SDM outputs. I apply the measure to four sets of cryptic Palearctic bat species (10 bat species) that have different extent of ecological similarity and geographic overlap. I expect geographic avoidance to be detectable in pairs of species with higher

ecological similarity and in the absence of fine-scale coexistence mechanisms. I further show in which cases biotic interactions may modify future predictions of range shift under climate change.

4.3. Materials and Methods

4.3.1. Developing a measure of geographic avoidance

I developed a measure of geographic avoidance that uses the binary (thresholded) outputs of SDMs to calculate the following set of metrics for two potentially competing species (species i and j) with partially overlapping ranges:

Predicted Range (P_i): The geographic area that is environmentally suitable for species i .

Predicted Range overlap (PO_{ij}): The geographic overlap between the predicted ranges of species i and j . This is the expected geographic overlap between species according to their environmental requirements (Gutiérrez *et al.* 2014).

Realised Range (R_i): The area of the predicted range where species i is present. A high proportion of predicted range that is not realised suggests that processes not included in the abiotic model, such as the effects of biotic interactions, dispersal limitations and model inaccuracies (Soberón & Peterson 2005), are preventing the species from occupying its entire environmentally suitable range. The realised range is estimated by clipping the predicted range of the species by its known range limits based on detailed occurrence records or broad range maps available from the IUCN Red List (<https://www.iucnredlist.org>).

Realised Range overlap (RO_{ij}): The geographic overlap between the realised ranges of species i and j . It represents the overlap between the two species that occurs at the model resolution (cell size). High values denote species coexistence.

A species whose range is negatively affected by the presence of another is expected to leave relatively more range unrealised in areas where the competitor is present. Based on this assumption, I design a measure of GA_{ij} that establishes a relation between the unrealised proportion of the range of species i and j in overlapping (sympatric) (numerator in Equation 1) and non-overlapping (allopatric) areas (denominator in Equation 1). Values of $GA_{ij} = 1$ indicate an equivalent proportion of unrealised range of the species i and j in overlapping areas than in non-overlapping areas, while a value >1 indicates a larger unrealised range of species i and j in overlapping areas, as predicted if they occupy less of their suitable range in the presence of a

competitor. Because the measure is based on ratios, measures based on very small proportion of realised range overlap (<0.5%) are prone to high variability and are not reliable.

$$GA_{ij} = \frac{\left(\frac{PO_{ij}}{RO_{ij}}\right)}{\left(\frac{P_i+P_j-2(PO_{ij})}{R_i+R_j-2(RO_{ij})}\right)} \quad (1)$$

4.3.2. Testing geographic avoidance with an empirical dataset of cryptic bat species

4.3.2.1. Study system

The role of biotic interactions in shaping species ranges was assessed in four sets of cryptic bat species, 10 species in total. All species within each group share a very similar morphology but have different degrees of geographic and ecological overlap. I consequently expect different levels of competition to occur among them. The *Eptesicus* group contains two open-space flying bats with remarkably similar trophic, habitat and roosting ecology. They have a parapatric distribution, overlapping in a narrow contact zone in the Iberian Peninsula. *Eptesicus serotinus* has a broad Palearctic distribution, while *Eptesicus isabellinus* is restricted to the centre-south of the Iberian Peninsula and North Africa (Dietz & Kiefer 2016). The *Myotis* group contains two European forest bats thought to have similar ecological requirements, but different roosting and forest type preferences. *Myotis crypticus* is found in Italy, southern France, and the northern Iberian Peninsula, while *Myotis escaleraei* is restricted to the Iberian Peninsula and the south-eastern French Pyrenees (Juste *et al.* 2019). The *Plecotus* group contains four species that show slight differences in their habitat use and trophic ecology. *Plecotus auritus* and *Plecotus austriacus* are found across Europe and overlap widely over most of their ranges, while *Plecotus macbullaris* is restricted to mountain ranges across the Palearctic (Juste *et al.* 2004) and *Plecotus kolombatovici* is restricted to the Balkans (Spitzenberger *et al.* 2006). Finally, the *Rhinolophus* group includes *Rhinolophus euryale* and *Rhinolophus mehelyi*, which although have some small morphological differences (Dietz & Kiefer 2016), have similar ecological requirements and circa-Mediterranean distributions, though the latter is less abundant. Their distributions overlap substantially across all of their range, but when sympatric, *R. mehelyi* tends to use less structurally cluttered habitats (Salsamendi *et al.* 2012). See Appendix C1: Supplementary Table C1.1-C1.3 for overview of ecological similarity. I focus on the western Palearctic extending up to a longitude of 34.5°E, representing the full range of *E. isabellinus*, *M. escaleraei*, *M. crypticus*, *P. austriacus* and *P. kolombatovici*, and the majority of the range of the remaining species.

4.3.2.2. Occurrence and environmental data

In total, I gathered 13,408 species occurrence records. Of these, 6,976 came from five online databases: GBIF (www.gbif.org), BioGIS (www.biogis.huji.ac.il), NBN (nbn.org.uk), Eurobats (www.eurobats.org/) and Laji.fi (laji.fi), 1,892 from 64 publications (Appendix C2) and 4,540 were unpublished records provided by Javier Juste, Carlos Ibáñez, Hugo Rebelo, Danilo Russo, Antton Alberdi, Andreas Kiefer and Orly Razgour. Only records with validated species identification were used. In areas where the ranges of similar species overlap, I used records that were confirmed genetically or morphologically by bat experts, considering identification year relative to when the species were split taxonomically. When original published records consisted only of a locality descriptor, geographic coordinates were obtained manually whenever possible. Spatial quality of records was checked, removing low quality records in terms of spatial resolution and confirmed identification. I accounted for uneven sampling across the study area by removing clustered records in intensively sampled areas (Kramer-Schadt *et al.* 2013). I used the ArcGIS toolbox “SDMtools” (Brown 2014) to thin spatially clustered records. Most records used in the models (>95%) had a spatial precision <2 km. I included records with lower precision only in regions with very low sampling intensity (Eastern Europe and North Africa).

To model the predicted range of each species, I selected 36 environmental variables recognised as ecologically important for bats (16 climatic, six geographic, 13 habitat and three human disturbance variables; Supplementary Table C3.1). All raster layers were set at a resolution of 30 arc-seconds (~1 km). I tested for correlation among variables using ENMTools v1.3 (Warren *et al.* 2010) and selected the most ecologically relevant variable or the variable with the stronger effect on model performance on its own among highly correlated variables ($|r| > 0.75$). Additionally, I discarded variables that did not contribute to model gain. Whenever possible, I aimed to select the same variables for species in the same cryptic group (Supplementary Table C3.2– C3.5 for final variables included in each model).

4.3.2.3. Obtaining predicted and realised species ranges

I generated ensemble SDMs using the R package biomod2 (Thuiller *et al.* 2009), including five models (Maxent 3.4, Generalized Boosting Model, Classification Tree Analysis, Random Forests, Flexible Discriminant Analysis). For each model, I selected 10,000 random background points and 1000 maximum iterations. Maxent model parameters (number of features and regularization value) were selected based on Akaike information criterion (AIC) scores using ENMTools v1.3 (Supplementary Table C3.6 for final model features). To assess model

performance, I used tenfold cross-validations, with 75% of records used for training and 25% for model testing. The ability of the models to discriminate between presence locations and background pseudo-absences was evaluated with area under the curve (AUC) of the receiver operator characteristics (ROC) and True Skill Statistic (TSS). The 10 model replicates were combined to obtain a final predictive map for each of the five modelling methods. Ensemble models were obtained by using AUC values to proportionally weight each method according to its predictive power, excluding models with AUC <0.75. Binary presence-absence maps were generated based on the thresholding method that minimises the difference between sensitivity and specificity. Resulting SDM outputs were projected to the Gall-Peters equal-area projection to allow for accurate area calculations.

Realised range was calculated by clipping the binary predicted range by the extent of a hull around occurrence records and adding a buffer of 30 km (R package *concaveman*, Gombin et al. 2017). This distance considers a species home range (3-10 km depending on species (e.g. Catto et al. 1996; Zahn et al. 2010; Zeale et al. 2012, 2016) and seasonal or reproductive movements that typically occur outside species home range (e.g. Robinson & Stebbings 1997).

4.3.2.4. Assessing the performance of the measure using null models from virtual species

I tested whether the observed values of GA_{ij} were higher than the distributions of null values obtained for pairs of virtual species. For each bat species I created several sets of virtual ranges (R package *virtualspecies*, Leroy et al. 2015) that follow environmental gradients, using the method PCA. I selected from the resulting virtual species ranges the areas with highest suitability scores totalling the equivalent size of the realised range of the real species. I distributed within that area the same number of random occurrence records as used in the models of the real species. With this I obtained for each species different sets of occurrence records with the same number of records and covering the same area as the real species, but following different, though ecologically meaningful, environmental gradients and having different spatial distributions. I used these randomly generated sets of occurrence record to model predicted range and clip it to the realised range, following the same procedures outlined above for the empirical dataset. Finally, I calculated, for each pair of interacting species in the empirical dataset, values of GA_{ij} between all pair combinations of virtual ranges. These distributions constitute the null expectation of GA_{ij} values between virtual species with the same number of occurrence records and coverage extent, but arbitrary environmental preferences and different spatial distribution from the real species. I only used pairs of sets of virtual ranges whose realised range overlapped by more than 0.5% to reduce inaccuracies due

to the calculation of ratios with very small values. I compared a total of at least 100 null GA_{ij} values for each pair of empirical bat species.

4.3.2.5. Comparing measure outputs to patterns of ecological similarity

I compared values of geographic avoidance (GA_{ij}) of pairs of cryptic bat species to ranked ecological similarity and evidence of fine-scale resource partitioning between pairs of cryptic species based on expert opinion and the literature (Appendix C1). Bat pairs were ranked from 1 (minimum) to 5 (maximum) ecological similarity in terms of their foraging habitat, diet and roosting ecology by five experts (Carlos Ibañez, Javier Juste, Antton Alberdi, Danilo Russo and Orly Razgour).

4.3.2.6. Predicting future range losses considering current geographic avoidance

I modelled future range suitability for species in 2070 using projections based on the worst case emissions scenario (RCP 8.5) and three different European Global Circulation Models (GCMs: HadGEM2-ES, IPSL-CM5A-LR, and MPI-ESM-LR) obtained from www.worldclim.com. I included in the models the same climatic variables as in the main models (Supplementary Table C3.2– C3.5), excluding habitat variables because it is unknown how land cover will change, and altitude due to collinearity with climate. I combined the outputs from the three GCMs and considered future suitable areas if identified under two or more of them. I calculated predicted future geographic overlap between pairs of cryptic bat species. I modelled the present range of the bat species using the same variables as in future models but in present conditions (excluding habitat variables and altitude) to estimate range losses.

Accounting for species geographic avoidance could modify predictions of changes in species ranges under climate change. For instance, in pairs with high geographic avoidance, an increase in predicted future suitable overlap could produce an unexpectedly larger range that would not be realised due to strong biotic interactions, while a decrease in predicted future suitable overlap could lead to an unexpected larger suitable area due to competitive release. I identify the species pairs where high geographic avoidance could affect future range change predictions.

4.4. Results

4.4.1. Geographic avoidance between cryptic bat species

Ensemble SDMs performed well for all species and had good discrimination ability ($AUC_{\text{cross-validation}}$ range: 0.92–0.99, TSS: 0.65–0.93; Supplementary Table C3.7). Models predicted

different suitable ranges for members of the same cryptic group, but with some extent of suitable range overlap. *P. auritus* and *E. serotinus* were predicted to have a more northern European distribution, *P. austriacus*, *M. escaleraei* and *M. crypticus* a southern European distribution, while *Rhinolophus* spp. and *E. isabellinus* a circa-Mediterranean distribution. The percentage of unrealised range was particularly high (>40%) for *P. kolombatovici*, *M. escaleraei*, *M. crypticus* and *P. macrobullaris*, intermediate (15-30%) for *E. isabellinus*, *R. euryale*, *P. austriacus* and *R. mehelyi*, and low (<10%) for *P. auritus* and *E. serotinus* (Fig. 4.1, Supplementary Fig. C3.1).

The extent of geographic avoidance (GA_{ij}) was low (<1.6) for the pairs *P. auritus* – *P. austriacus*, *P. macrobullaris* – *P. kolombatovici*, *M. escaleraei* – *M. crypticus*, and *R. euryale* – *R. mehelyi*. Intermediate (<2.35) in *P. auritus* – *P. kolombatovici*, and *P. austriacus* – *P. macrobullaris*, and very high in *E. serotinus* – *E. isabellinus* (6.79), and *P. austriacus* – *P. kolombatovici* (5.98). Only in the latter two cases GA_{ij} values were higher than 95% of values of 100 null models (Table 4.1, Fig. 4.2). A comparison of measure outputs with ranked levels of ecological similarity and evidence of resource partitioning showed that the two highest values of GA_{ij} (*E. serotinus* – *E. isabellinus*, and *P. austriacus* – *P. kolombatovici*) belong to pairs of species that have highest levels of ecological similarity and no known mechanisms of resource partitioning (Table 4.1).

Table 4.1 – Results of the measure of geographic avoidance between pairs of cryptic bat species and their level of ecological similarity, including predicted (PO_{ij}) and realised range overlap (RO_{ij}), geographic avoidance (GA_{ij}), mean and 95% confidence intervals (CI) of null distribution of GA_{ij} values of virtual species, extent of ecological similarity among species pairs (range 1-5) according to foraging habitat, diet and roost selection and evidence of resource partitioning when sympatric based on expert opinion and the literature (details in Appendix C1: Supplementary Table C1.1 – C1.3). * denote values falling above the 95% CI of 100 null models. Realised range overlap between *P. auritus* and *P. kolombatovici* was too small to calculate the measure.

Species pair	PO_{ij} (%)	RO_{ij} (%)	GA_{ij} Obs	GA_{ij} virtual mean	GA_{ij} virtual CI	Ecological similarity			Resource part.
						Habitat	Diet	Roost	
<i>E. serotinus</i> – <i>E. isabellinus</i>	4.9	0.75	6.79*	1.73	1.16-2.72	4.5	4.7	4.5	No
<i>M. escaleraei</i> – <i>M. crypticus</i>	29.99	21.76	1.54	2.14	1.04-4.31	3.5	4.5	1.5	Some
<i>P. auritus</i> – <i>P. austriacus</i>	25.54	26.88	0.93	1.26	0.97-1.70	2.6	3.7	2.6	Yes
<i>P. auritus</i> – <i>P. kolombatovici</i>	2.29	0.23	NA	2.03	1.32-3.03	2.6	3.7	2.6	Yes
<i>P. auritus</i> – <i>P. macrobullaris</i>	15.19	7.73	2.14	1.92	1.30-3.23	2	3.5	2.7	Yes
<i>P. austriacus</i> – <i>P. kolombatovici</i>	12.43	2.32	5.98*	2.04	1.32-2.98	4.5	3.7	4	No
<i>P. austriacus</i> – <i>P. macrobullaris</i>	18.93	9.17	2.31	2.26	1.33-4.31	3.5	3.7	2.7	Some
<i>P. macrobullaris</i> – <i>P. kolombatovici</i>	11.28	11.32	1.0	2.47	1.03-5.14	3.5	4.7	2.7	Some
<i>R. euryale</i> – <i>R. mehelyi</i>	30.33	23.07	1.45	1.62	1.08-2.55	4	4.7	4.8	Yes

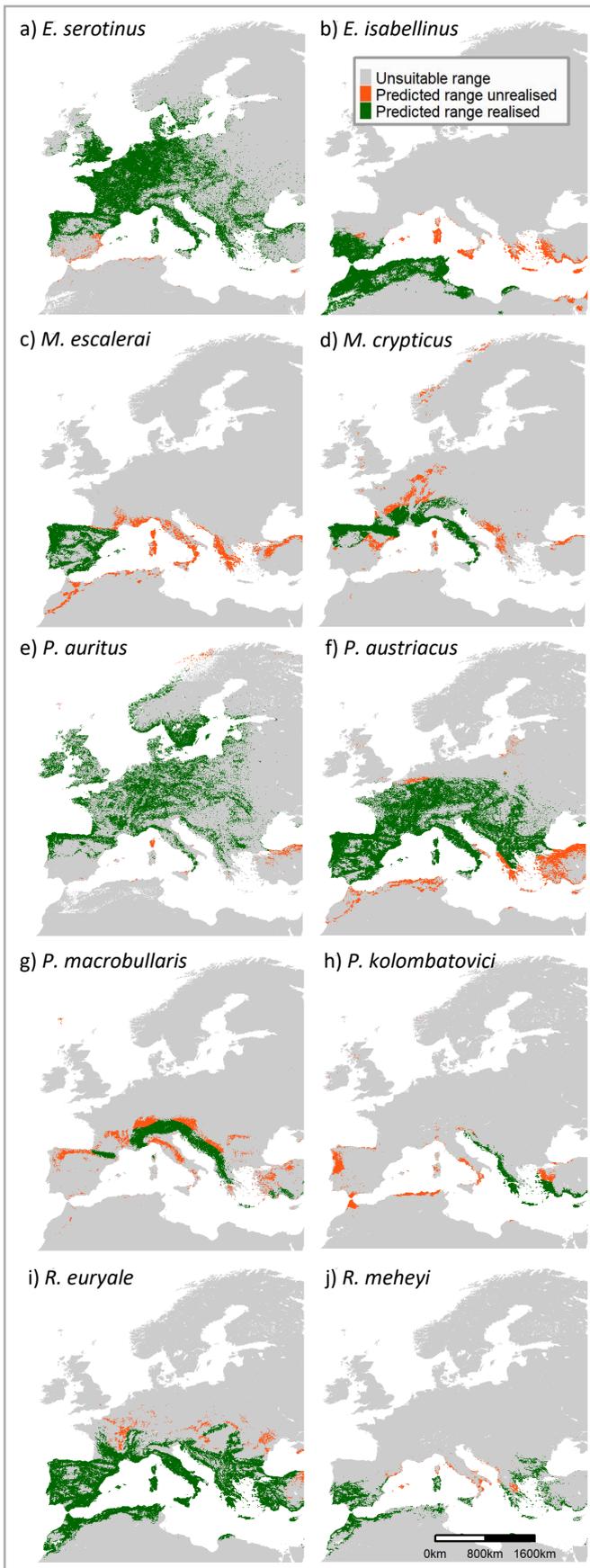


Fig. 4.1 – Predicted ranges of the four sets of cryptic bat species partitioned into portions that are realised (green) and unrealised (orange). *Eptesicus* group: (a, b), *Myotis* group (c, d), *Plecotus* group (e, f, g, h), *Rhinolophus* group (i, j).

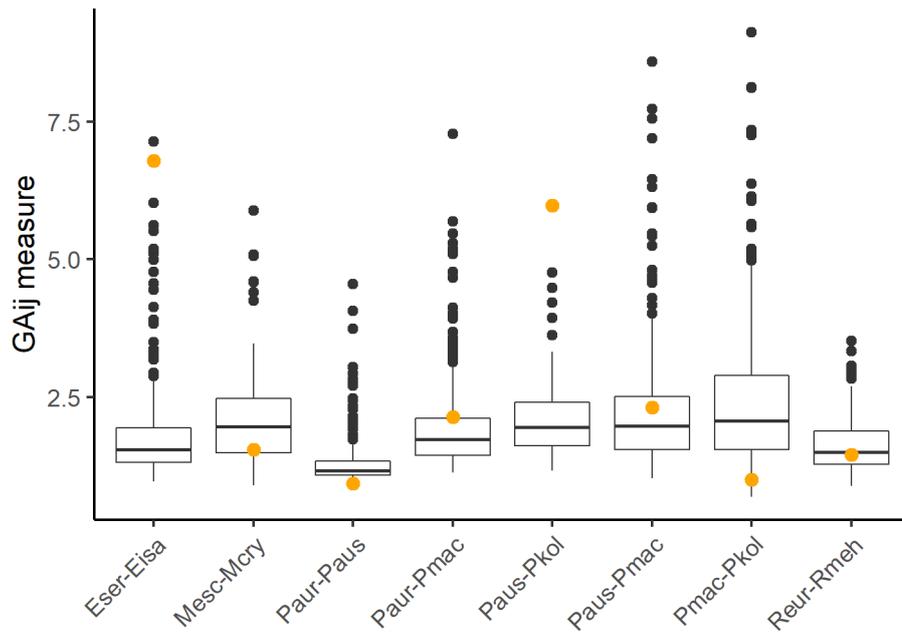


Fig. 4.2 – Geographic avoidance values for each pair of species (orange large dots) relative to null distributions of values (boxplots). Eser: *E. serotinus*, Eisa: *E. isabellinus*. Mesc: *M. escaleraei*. Mcry: *M. crypticus*. Paur: *P. auritus*. Paus: *P. austriacus*. Pkol: *P. kolombatovici*. Pmac: *P. macrobullaris*. Reur: *R. Euryale*. Rmeh: *R. mehelyi*. Box represents first and third data quartiles. Whiskers extend from the hinge to the largest value no further than 1.5 times the distance between the first and third quartiles. Data beyond the end of the whiskers are plotted individually.

4.4.2. Future range losses and overlap

Present projections with only climatic variables were very similar in extent to the ones including habitat variables and mostly differed in the fine-grained suitability values. When projected to the future, models predicted losses in climatic range suitability for *E. serotinus*, *M. escaleraei*, *M. crypticus*, *P. auritus* and *P. macrobullaris* under future climate change. In contrast, the suitable climatic ranges of *E. isabellinus*, *P. austriacus*, *P. kolombatovici*, *R. euryale* and *R. mehelyi* were predicted to increase by the end of the century (Supplementary Table C3.8). Under future climate change, range overlap was predicted to decrease in the pairs *E. serotinus* – *E. isabellinus*, *M. escaleraei* – *M. crypticus*, and *P. auritus* – *P. macrobullaris*. While range overlap in *P. auritus* – *P. kolombatovici*, *P. macrobullaris* – *P. kolombatovici*, and *R. euryale* – *R. mehelyi* was predicted to increase. For the pairs with high values of GA_{ij} , range overlap between *E. serotinus* and *E. isabellinus* was predicted to decrease (-37.9%), while overlap between *P. austriacus* and *P. kolombatovici* was predicted to increase substantially (71.4%) (Fig. 4.3, Table 4.2).

Table 4.2 – Comparison between present predicted overlap between pairs of cryptic bat species and future predicted overlap in 2070 under RCP 8.5. Differences in PO_{ij} compared to Table 4.1 are because these models did not include land cover variables.

Species pairs	Present PO_{ij} (%)	Future PO_{ij} (%)	Change in PO_{ij} (%)
<i>E. serotinus</i> – <i>E. isabellinus</i>	1.45	0.90	-37.93
<i>M. escalerai</i> – <i>M. crypticus</i>	24.59	15.67	-36.29
<i>P. auritus</i> – <i>P. austriacus</i>	25.07	20.46	-18.37
<i>P. auritus</i> – <i>P. macrobullaris</i>	13.84	12.47	-9.93
<i>P. austriacus</i> – <i>P. macrobullaris</i>	11.98	8.29	-30.83
<i>P. auritus</i> – <i>P. kolombatovici</i>	4.08	5.70	39.71
<i>P. austriacus</i> – <i>P. kolombatovici</i>	14.52	24.88	71.41
<i>P. macrobullaris</i> – <i>P. kolombatovici</i>	6.80	8.33	22.52
<i>R. euryale</i> – <i>R. mehelyi</i>	46.30	51.13	10.43

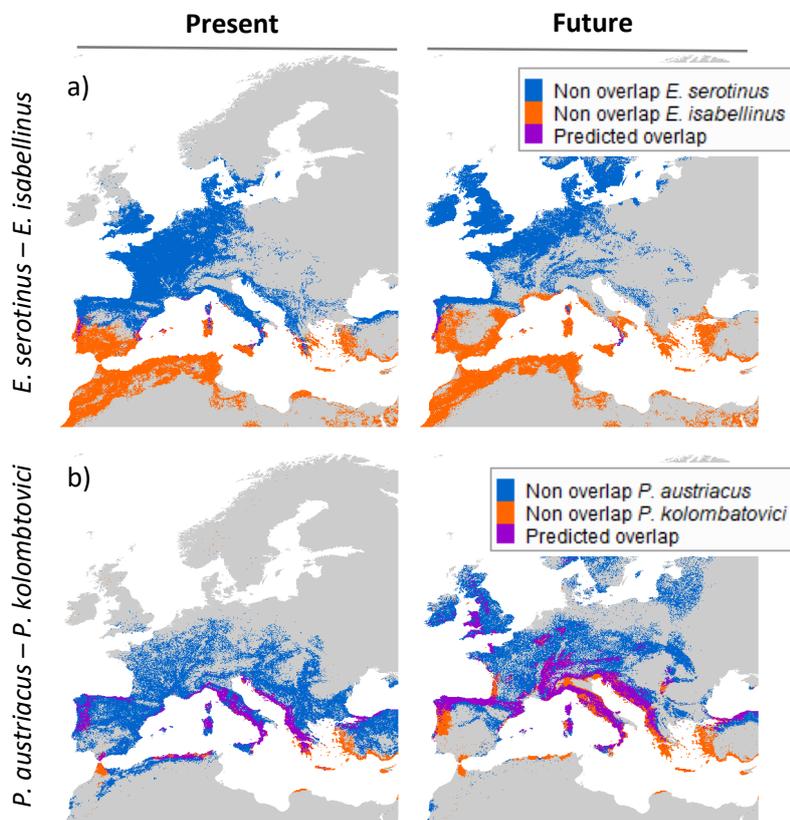


Fig. 4.3 – Present and future predicted range overlap for the two pairs of bat species where the measure the GA is higher than null models. Range overlap is predicted to decrease between *E. serotinus* and *E. isabellinus* (a), and increase between *P. austriacus* and *P. kolombatovici* (b).

4.5. Discussion

I propose a new and easy to implement approach that measures geographic avoidance between potential competitors based on SDM outputs. This approach is used to infer whether competition may affect species ranges over broad (regional-continental) spatial scales. I use an empirical dataset of four sets of cryptic Palearctic bat species and null models generated from virtual species to test the measure. I compare the results to expectations based on knowledge of the ecology of the species and evidence of fine-scale resource partitioning. Although methods based on observational data alone cannot unequivocally measure the effect of competition on species distributions, I show that the measure of geographic avoidance is able to identify the expected geographic patterns resulting from competition. When used together with ecological evidence, the measure presented can help identify cases where competitive effects have played a role in shaping species ranges. Biotic interactions, and in particular interspecific competition, can slow down climate tracking and prevent species from colonising new habitats (HilleRisLambers *et al.* 2013; Urban *et al.* 2013). Yet despite the urgent need to better understand the effect of biotic interactions on species vulnerability to future climate change, there is currently no adequate methodology to infer competitive effects at a regional or continental spatial scale.

4.5.1. Performance of the measure of geographic avoidance

Competitive exclusion is expected to scale-up and impact species ranges only when coexistence mechanisms such as diet or habitat partitioning are not developed at finer spatial scales (Godsoe *et al.* 2015). The measure of geographic avoidance that I introduce produces inferences on the effect of competition on species ranges that match evidence of similarity in ecological requirements and absence of fine-scale coexistence mechanisms. Hence, the measure provides a good representation of the effect of competition on species ranges. The two pairs of species with higher values of geographic avoidance than null models are the most ecologically similar pairs of species that lack fine-scale mechanisms of resource partitioning. *E. serotinus* and *E. isabelinus* are similar in their habitat use, being both open air foragers, have very similar diets composed mostly by Coleoptera and share similar roosting preferences (Supplementary Table C1.1– C1.3). Interspecific competition has been previously suggested to affect these species' ranges (Santos *et al.* 2014). *P. austriacus* and *P. kolombatovici* use similar semi-open habitats, feed mostly on Lepidoptera and roost in anthropogenic structures or caves (Supplementary Table C1.1 – C1.3). In contrast, pairs of species with lowest levels of geographic avoidance include *P. auritus* – *P. austriacus* and *R. euryale* – *R. mehelyi*, which are

known examples of pairs of bats of similar morphology and broad-scale range overlap that coexist through fine-scale habitat partitioning (Ashrafi *et al.* 2011; Razgour *et al.* 2011a) (Supplementary Table C1.1-C1.3).

4.5.2. Performance relative to other available approaches

Previous studies using SDM outputs to identify expected patterns of geographic exclusion resulting from competitive interactions focused on identifying in the predicted overlapping range an uneven proportion of occurrence records or a mismatch in the identity of the species present with the one with highest environmental suitability (Anderson *et al.* 2002; Gutiérrez *et al.* 2014). The applicability of these methods is limited by their assumptions of identical environmental preferences, sampling effort and detectability for both species in the potential predicted overlapping area. Similarly, the inclusion of a competitor's realised range in SDMs is thought primarily to suit simple systems (Anderson 2017). Indeed, it has been shown that correlations between environment and competitors make difficult to distinguish competitive from environmental effects using this approach (Godsoe *et al.* 2017).

Available JSDM approaches, like HMSC (e.g. Warton *et al.* 2015; Ovaskainen *et al.* 2017), although directly incorporating biotic interactions into the models, are most suitable for community assemblage studies. They require presence-absence data for each cell, which is very rarely available at broad spatial extents and fine resolution. This limits their application in broad-scale studies. The use of JSDM with insufficient sampling intensity would result in a large amount of false absences that the model may interpret as negative residual correlations. Using larger cell size can help reduce false absences, but can also make it more difficult to capture the signal of competition (Araújo & Rozenfeld 2014; Zurell *et al.* 2018).

4.5.3. Including biotic interactions in climate change range shift predictions

Biotic interactions interact with range shift processes driven by climate change, and can for instance, modify the predicted species responses (HilleRisLambers *et al.* 2013; Ettinger & HilleRisLambers 2017) or modify the effects of biotic interactions by changing patterns of species co-occurrences, leading to increases of intensity of interactions or new interactions (Alexander *et al.* 2016). The importance of considering biotic interactions to assess climate change driven extinction risk have also been shown by theoretical models (Norberg *et al.* 2012). The outcome of the interaction between biotic and range shift processes are difficult to predict and currently lack of methodologies. In this study system, among the pairs of species whose current range I point to be most likely shaped by competition, future models predict a decrease in range overlap between *E. serotinus* and *E. isabellinus*, which would lead to a

smaller future competitive effect between the species that could lead to a competitive release effect and a larger realisation of their future suitable range than at present. Conversely, the ranges of *P. austriacus* and *P. kolombatovici* are predicted to overlap substantially more in the future, which may limit the ability, in particular of *P. kolombatovici*, which already has a very restricted range, to shift its range to track future suitable conditions. I show that disregarding biotic interactions can affect our ability to accurately predict species future distributions and their vulnerability to climate change.

4.5.4. Assumptions of the methodology

The proposed measure of geographic avoidance is based on expectations of the ultimate effect of competitive exclusion on species ranges. The approach is based on the assumption that SDMs are able to estimate representatively the predicted and realised ranges of the species, which equally to any other study based on SDM, is subjected to the quality of the occurrence data used and the inclusion of all the relevant environmental variables in the models (Guisan *et al.* 2017). When applying this methodology, data quality of species ranges should be similar for both members of the pair.

Additionally, the pattern of greater unrealised range in overlapping areas relative to non-overlapping areas that the measure quantifies could occur for other reasons than competitive effects, such as dispersal limitations in that area (Soberón & Peterson 2005; Guisan *et al.* 2017) or also by chance due to inaccuracies in model predictions in the specific area. Dispersal limitation is less likely to bias the conclusions with volant animals like bats, but more so with dispersal-limited taxa, such as other small mammals and reptiles or amphibians. In our empirical case study, at least one species of each cryptic group expanded from its glacial Mediterranean refugia to colonise higher latitudes across Europe, suggesting that dispersal limitations alone are not likely to account for the observed patterns. Additionally, the specific geometry of the species ranges (its size, shape, and location in geographic space) may cause greater decreases in overlapping areas than non-overlapping areas. However, the comparison between the observed patterns with null models based on virtual species allows to identify the cases where the observed pattern is greater than expected by chance, and therefore, cases where decreases in overlap are most likely to be the result of competition. Given that the measure is based on proportions, values can be highly variable when proportion of overlapping area is very small. Therefore, values of geographic avoidance extracted from very small values of range overlap should be considered with care. Finally, if estimating the measure with future

projected species ranges, the assumptions related to niche conservatism common to climate change range shift assessment also need to be accounted for (Parravicini *et al.* 2015).

Altogether, this approach is most suitable for pairs of species with well and equally known ranges and no or little dispersal restrictions. Inferences given by the measure should be taken as a geographic pattern consistent with a process of broad-scale competitive exclusion, and not as a direct inference of the effect of biotic interactions. A sensible interpretation of current biogeographical patterns also requires a careful interpretation of evolutionary history to tease-apart biotic and historical effects, in particular for species with limited dispersal and colonisation abilities (Warren *et al.* 2014; Dormann *et al.* 2018) and information on ecological similarity between species based on patterns of resource exploitation and morphological similarity.

4.6. Conclusions

No currently available methodology enables direct inference of competitive interactions from analysing co-occurrence patterns at broad spatial scales, especially with the commonly available density of occurrence data. The measure of geographic avoidance that I propose quantifies the expected geographic patterns resulting from broad-scale competitive exclusion and produces inferences consistent with predictions based on ecological information and evidence of coexistence mechanisms. Its simplicity and low data and computational requirements make this measure suitable for any pair of species with sufficient location data for SDMs and known range limits, and therefore it can be widely applied as a screening tool to forecast where biogeographical patterns may be shaped by competition. Using this measure, I show that in the absence of fine-scale mechanisms of resource partitioning the effects of interspecific competition can scale-up to impact species broad-scale geographic ranges. Moreover, I show that future range change predictions may be modified when considering the effect of biotic interactions. Further development and integration of community ecology models with species distribution models promises new insights into understanding the role of competition in ecology and biogeography. Yet, easy to implement measures like the ones I propose are particularly relevant for integrating biotic interactions into SDMs and improving projections of species responses to future climate change.

4.7. Chapter summary

In this chapter I explored broader-scale effects of biotic interactions on species ranges, showing that interspecific competition can play a role in limiting the geographic ranges of morphologically and ecologically similar species in the absence of fine-scale mechanisms of coexistence. In the next and last chapter I will integrate the insights obtained from the different data chapters and develop further the implications of the findings of thesis.

5. Chapter 5 General Discussion

5.1. Importance of different biogeographic processes across spatial scales

A better comprehension of how natural systems are predicted to respond under current global environmental changes requires a deeper understanding of how diversity is shaped by biogeographic processes. In this thesis I provide inferences on how environmental filtering and biotic interactions operate across spatial scales to contribute to shaping biogeographic patterns.

Among the environmental filtering factors, habitat structure is thought to operate generally at more local scales than climatic factors (Willis & Whittaker 2002). However, in Chapter 2, I show that forest characteristics can be a primary factor driving the regional distribution areas of forest-specialist bats. The strength of this dependence on forests is driven by the roosting ecology of species. The distribution area of bats that roost in trees in Andalusia, Spain, is greatly limited by tree composition and richness, structural heterogeneity and presence of large trees that provide good roosting opportunities. The landscape-level scale at which responses to forest are observed further supports how bat-forest roost dependency can operate at broader scales than the usually studied local scale (Lacki *et al.* 2007b; Peixoto *et al.* 2018). This strong contribution of forest characteristics to shaping species ranges of tree roosting bats can likely be generalised to other Mediterranean areas because the mechanisms involved are common to Mediterranean forests. The validity of these results for other specialised forest taxa with similar forest dependency mechanisms, such as tree dwelling animals like woodpeckers, some raptors and some forest mammals, is also substantial and deserves further studying.

Alongside environmental filtering, biotic interactions also play a role in driving local assemblages, which are, as a result, often composed by morphologically and functionally different species (Ross 1986; Bocher *et al.* 2014; Codron *et al.* 2015). In Chapter 3, I show how local-scale trophic shift can facilitate coexistence between two morphologically almost identical bat species, *Myotis escalerai* and *Myotis crypticus*. Niche shifts in the presence of a competitor have been reported previously in different taxa (Huey *et al.* 1974; Schmitt & Coyer 1983; Klawinski *et al.* 1994; Gkenas *et al.* 2019), although not commonly in insectivorous bats (Salinas-Ramos *et al.* 2020), where coexistence is usually thought to be driven by differences in habitat use (e.g. Salsamendi *et al.* 2012; Russo *et al.* 2014; Arrizabalaga-Escudero *et al.* 2018). This is one of the first studies showing trophic shifts in insectivorous bats in response to interspecific competition.

There is increasing evidence that biotic interactions can affect broader scale biogeographic patterns. In Chapter 4, I show how the measure of geographic avoidance between species that I developed can be applied to identify cases where biotic interactions impact species ranges. I conclude that species that are morphologically and ecologically similar and do not have known fine-scale mechanisms of coexistence, such as *Eptesicus serotinus* – *Eptesicus isabellinus* and *Plecotus austriacus* – *Plecotus kolombatovici*, are likely to avoid geographically each other across their broad-scale range. In contrast, species with differentiated niche or presence of coexistence mechanisms do not show a pattern of geographic avoidance. In line with expectations based on the local-scale coexistence mechanisms identified in Chapter 3 for *M. escalerai* and *M. crypticus*, in Chapter 4 I find that this pair of species do not avoid geographically each other across their range. My results add support that local scale coexistence mechanisms are key processes preventing biotic interactions from scaling-up and having broader scale consequences, as it has been previously suggested based on mathematical models (Godsoe *et al.* 2015). The integration of new high sensitivity molecular tools together with functional traits that link mechanistically with species-environment relationships and a careful consideration of the spatial scale at which processes occur was key for unravelling the consequences of ecological processes.

5.2. Competition among insectivorous bats

The ecological effects of competition are sometimes controversial. The results of both fine-scale trophic shift and broader scale geographic avoidance that I present in this thesis point to competition as an important process affecting cryptic species of insectivorous bats. These inferences add to other studies supporting the role of competition in bats. Some studies focusing on bat assemblages report overdispersion of niches or traits of the species that conform assemblages compared to null expectations, which points to biotic interactions limiting the similarity of the species that can coexist (Schoener 1974). For instance a guild of rhinolophids was found to be morphologically more distinct than expected by chance in a Malaysian rainforest (Kingston *et al.* 2000), and patterns of body size in bat assemblages in Southern Africa were found to be more regularly spaced than expected (Schoeman & Jacobs 2008). Recent evidence for the effects of competition in bats came from Southern Ontario, Canada, where *Eptesicus fuscus* increased its trophic niche breadth following an activity decline of *Myotis lucifugus* driven by white nose syndrome mass mortality (Morningstar *et al.* 2019). Other studies support the mechanisms through which competition occurs. Exploitative competition for trophic resources requires a limitation in prey availability, and traditionally it was assumed, though with limited evidence, that arthropods are unlikely to be a limiting

resource (Arlettaz 1999; Krüger *et al.* 2014). However, studies on bat resources that assess prey availability are uncommon (Salinas-Ramos *et al.* 2020). Several studies using exclusion experiments in both tropical (Kalka *et al.* 2008) and temperate forests (Böhm *et al.* 2011) show how bats can control the abundance of arthropods, setting the scene for exploitative competition for trophic resources.

Competition can also occur through interference when species are attaining the resources. Echolocation is a system particularly prone to interference given that calls of different individuals can disrupt others. Technical developments in ultrasonic acoustics are recently enabling inferences on bat communication and mechanisms whereby competition for space occurs. For instance, it is suggested that large aggregations of bats forage less effectively as consequence of echolocation interference (Amichai *et al.* 2015) and that competition mediated by interference can be actively promoted by bats, which can use specific “jamming” calls to disrupt competitors and make them miss targets (Corcoran & Conner 2014). Several bioacoustics studies have shown that bats can display territorial behaviour and use specific complex social calls to repel individuals of the same or other species from their foraging territories, especially in conditions when competition for food is high (Götze *et al.* 2020). Roeleke *et al.* (2018) interpret a shift in the use of space by *Nyctalus noctula* in response to simulated calls of *Pipistrellus nathusii*, but not in response to calls of the same species, as the result of interspecific competition for foraging territories driven through echolocation. My PhD thesis contributes to the body of literature using novel acoustic and molecular approaches to provide new insights into the effects of competitive interactions in bats.

5.3. Limitations and considerations

Using bats as biogeographical model organisms has several advantages such as a high species richness and the existence of groups of species with morphological similarity that are very valuable to understand species coexistence. The flight-related high mobility of bats means they use space at much broader spatial scales than terrestrial mammals of similar sizes, and often use complex landscapes formed by different habitats. While this offers interesting case studies to understand the operation of different biogeographic process across taxonomic groups with different levels of mobility, it hinders the study of some aspects of their ecology related to habitat use. Other limitations of using bats as model organisms are the lower data availability compared to other taxonomic groups due to their elusive aerial and nocturnal activity, although the development of acoustic ultrasonic sampling methods in the last decades has greatly contributed to reduce this bias.

More specific limitations of the thesis include in Chapter 2, the study system of Andalusia, which although it includes a considerable number of forest bat species (nine), it misses some tree-roosting bats that are only present in the north of the Iberian Peninsula (*Plecotus auritus*, *Myotis crypticus*, *Myotis alcathoe*, *Nyctalus noctula*, and *Myotis mystacinus*). Furthermore, the correlation between the roosting ecology of species with their wing loading values hinders the interpretation of the ecomorphological relationship between bats and forest structure. Mediterranean areas such as Andalusia are characterised by limited water availability, which translates into slower forest growth and results in generally less developed forest structures and very scarce presence of mature forests. Altogether, the expansion of the study design to include an additional working area in a different bioclimatic region and additional tree-roosting species would allow for a better interpretation of ecomorphological relationships of bats with forests. It would also reveal if the primary dependency of tree-roosting bats on forest characteristics holds in systems where mature forests are more common. However, comprehensive datasets of bat assemblies over broad (regional level) spatial scales are rare. Some other methodological considerations in Chapter 2 include the choice of the parameters for interpolation of the forest data on presence and background points. The maximum distance threshold chosen (3 km) represents the area upon which bats rely most strongly on forest. Results based on different distances and number of forest plots were consistent. When building species assemblages from different sampling locations, the radius used to consider individuals belonging to the same community may be subject to certain subjectivity, as well as the composition representativeness of different bat sampling methods. However, the overall similarity between these results with results based on species distribution models supports the validity of the analysis.

In Chapter 3, the number of locations considered as locally sympatric between *M. escalerae* and *M. crypticus* is low due to restrictions associated with limited parapatry between these bats. Another limitation is associated with the certain level of unavoidable subjectivity when classifying arthropod mobility into three groups based on their nocturnal volancy, which means that the results of the functional analysis should be interpreted with caution. Similarly, the analysis of diet selection should also be taken with precaution because of the difficulty of sampling the arthropod community in a representative manner. The molecular approach is not exempt from limitations either, some specific taxa may not appear in the diet, as pointed for example likely with Opiliones, or the exact arthropod species consumed by the bat may be absent from the molecular reference library. Despite these considerations, molecular diet analyses have been proven to allow to obtain valid ecological inferences (Sousa *et al.* 2019).

In Chapter 4, the assumptions on which the approach of measuring geographic avoidance between species relies include limitations related to Species Distribution Models. For instance, the assumption that they are able to estimate the predicted and realised ranges of the species. This is subjected to the environmental variables included in the models and the quality of the occurrence data used. Other types of models such as mechanistic or individual-based (Lurgi *et al.* 2015) could solve some of these limitations although the utility of those is very often limited by lack of the detailed physiological or demographic data. The more specific assumptions related to the measure of Geographic Avoidance are detailed in the chapter. The final consideration of this chapter is that inferences given by the measure should be taken as a geographic pattern consistent with a process of broad-scale competitive exclusion, and not as a direct inference of the effect of biotic interactions. Other sources of inferences that should be considered are the ecological and morphological similarity between species and their historical phylogeography.

5.4. Implications and future research

There are still many gaps in our understanding of the operation of different biogeographic processes across spatial scales and how they drive diversity patterns. Particularly urgent is understanding the responses of different taxonomic groups to the human-driven changes predicted to increasingly impact natural earth systems in the next decades, such as abiotic changes in temperature and precipitation patterns, salinization, contamination, habitat destruction and invasive species. Functional ecology is a key approach that can provide more mechanistic insights to understand ecological processes. Its use can also aid to disentangle the relative role of different biogeographic processes across spatial scales. For example, how body size or mobility could explain differential dependency on processes occurring at different spatial scales.

5.4.1. Importance of forest preferences for bat conservation under global change

The unprecedented importance of forest characteristics to driving regional distributions of forest bats that I show in Chapter 2 indicates that studies aiming to understand medium to broad scale processes driving the ranges of forest specialist will greatly benefit from using detailed forest structure and composition data. Forest inventory data are available for many European countries, yet surprisingly they are not often used in wildlife studies. Facilitating access to cross-country forest inventory data would allow for much finer inferences on the effect of habitat versus climate filtering processes on the distributions of forest-specialist fauna.

My results also suggest that future responses of forest specialists to climate change in Mediterranean regions will be mediated by changes in forest habitat. Forests of many regions across Europe, including Mediterranean areas, have experienced a transition from a negative tendency of decrease to an increase in extent and growth during the past decades due to a reduction in their exploitation and abandonment of rural activities (Mather 1992; Rudel *et al.* 2005; Cervera *et al.* 2019). While this forest transition is ongoing (Palmero-Iniesta *et al.* 2020), climate change is predicted to have uneven impacts on forests across climatic regions. In northern and western Europe, increasing levels of atmospheric CO₂ and warmer temperatures are predicted to result in positive effects on forest growth, while in Mediterranean areas, impacts on forest growth are expected to be negative. A decrease in precipitation is expected to cause a reduction in productivity, and together with the increase in temperature will lead to an increase in disturbance risk factors, such as fires, or mortality due to heat stress and increasing presence of pathogens (Lindner *et al.* 2010; Allen *et al.* 2015). Based on my findings, neglecting to account for future climate change effects on habitat structure may produce biases in the estimated climate change impacts on forest specialised fauna, especially considering that forests can respond abruptly to small gradual climatic changes (Huang *et al.* 2015; Reyer *et al.* 2015). This supports that land-use change projections should be increasingly incorporated into predictions of future climate change impacts on species ranges (Naeem *et al.* 2019). A future integration of forest dynamic models and climate change predictions with species distribution models (SDMs) could allow more realistic climate change predictions for forest-specialist species. Other implication of understanding the stronger dependency of tree roosting bats on forest is that it allows the development of informed conservation actions, such as monitoring specific at-risk bat populations or promoting adequate forest management that facilitates resilience towards climate change.

5.4.2. Role of biotic interactions across spatial scales

The role of biotic interactions is still a topic of great complexity and with many knowledge gaps that prevent our ability to predict and prevent impacts on natural systems. The findings presented in this thesis add to many other studies showing that biotic interactions play important ecological roles across spatial scales and support that future studies should continue developing our understanding of the impacts of these interactions. Coexistence mechanisms are key processes that modulate the broader-scale impact of biotic interactions. Their study across spatial scales and how their effect links to broader scale processes of competition should also be promoted. Studies aiming to infer biotic interactions through interpreting species niches should move from studying niche partitioning between small groups of

coexisting species towards comparing those niches in presence and absence of potential competitors and analysing niches across complete communities (Pausas & Verdú 2010). In these regards, technical improvements and decreasing cost of molecular techniques and their more widespread implementation promises many new and finer insights. Finally, the broad-scale impacts of biotic interactions identified in Chapter 4 support the need for further research to better understand these effects and implement them in future predictive methods that integrate more of the biogeographic processes.

5.4.3. Conclusions

Both environmental filtering and biotic interactions are main processes that operate across spatial scales contributing to shape biogeographic patterns. I show that forest-specialist bats respond strongly towards landscape-scale forest characteristics, and these responses are a primary factor driving the regional distribution of bats in Mediterranean ecosystems. The strength of this dependence is driven by species' roosting ecology. The regional range of bats that roost in trees are greatly limited by tree composition and richness, structural heterogeneity and presence of large trees that provide good roost opportunities. The broad-scale of bat-forest dependence relations is unprecedented and stresses the importance of considering land cover changes when predicting range changes under climate change. The results may have implications for other Mediterranean areas and other specialised forest taxa. This study adds support to the effect of biotic interactions on broader scale biogeographic patterns. Coexistence mechanisms such as the trophic shift among functionally similar species of bats that I report here can play a key role in preventing biotic interactions from scaling-up and having broader-scale consequences. The conditions and mechanisms whereby this process occurs should be further studied in order to better understand and predict the broad-scale role of biotic interactions. The integration of fine-scale niche measurement tools, such as molecular diet analysis or spatial analysis of habitat preferences, together with functional approaches and a careful consideration of the spatial scale at which processes occur are key for unravelling ecological processes.

6. References

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Appendix A Supplementary material for Chapter 2

A1 Supplementary tables and figures

Supplementary Table A1.1 – Forest variables thought to be relevant for bat ecology that have been generated from the Forest Inventory database. For each variable, the following information is presented: average, minimum, and maximum values, type of variable, mechanistic group and description.

Name	Units	Mean	Min	Max	Type	Calculated?	Mechanism	Description	
1	Forest type				Cat	As came	Heterogeneity	Morphostructural type.	
2	Spatial distr				Cat	As came	Cluttering	Spatial distribution.	
3	Sp comp				Cat	As came	Composition	Type of specific composition.	
4	Total C	(%)	88.9	2	100	Quant	As came	Cluttering	Total vegetation cover, estimated in percent.
5	Tree C	(%)	53.5	0	100	Quant	As came	Cluttering	Tree cover, estimated in.
6	Tree sp				Cat	Calculated	Composition	Identity of main species. Grouping rare species (dominant <1.5 % plots) in others.	
7	Dev stage				Cat	As came	Roost	Development phase of the main tree species.	
8	Sp1 DBH struct				Cat	As came	Heterogeneity	Structural heterogeneity category (regular to irregular) of the main tree species.	
9	Sp1 occupancy		7.6	1	10	Quant	As came	Composition	Percentage of occupation of the main tree species.
10	coniferous den	(trees/ha)	246.1	0	4877.21	Quant	Calculated	Cluttering	Density of trees of coniferous species.
11	Trees/ha	(trees/ha)	516.8	0	8994.02	Quant	Calculated	Cluttering	Tree density (>75 DBH) in the plot.
12	% coniferous	(prop)	0.5	0	1	Quant	Calculated	Composition	Proportion of coniferous trees
13	Sp1 density	(trees/ha)	449.7	5.09	8994.02	Quant	Calculated	Cluttering	Density of the species with more treedensity.
14	Sp1 D	(%)	0.9	0.2	1	Quant	Calculated	Composition	Dominance of tree Sp1 (rel. treedensity).
15	Broadleaved	(trees/ha)	261.6	0	8994.02	Quant	Calculated	Composition	Density of broadleaved tree species.
16	Tree DBH	(mm)	217.4	75	3072.8	Quant	Calculated	Roost	Average DBH of trees in the plot.
17	% broadleaved	(prop)	0.5	0	1	Quant	Calculated	Composition	Proportion of broadleaved trees.
18	Min tree DBH	(mm)	151.8	25	3071	Quant	Calculated	Roost	Diameter of the thinner tree.
19	Max tree DBH	(mm)	401.1	75	3071	Quant	Calculated	Roost	Diameter of the largest tree.
20	Tree DBH ra	(mm)	249.3	0	2524	Quant	Calculated	Heterogeneity	DBH range. Thicker - thinner tree.
21	DBH categories	1 to 7	3.1	0	7	Quant	Calculated	Heterogeneity	Number of diametrical classes.
23	% < 225	(%)	64.1	0	100	Quant	Calculated	Roost	Relative density of trees (%) with DBH less than 225 mm.
24	% < 325	(%)	82.4	0	100	Quant	Calculated	Roost	Relative density of trees (%) with DBH less than 325 mm.
25	% > 425	(%)	8.6	0	100.1	Quant	Calculated	Roost	Relative density of trees (%) with DBH larger than 425 mm.
26	% > 525	(%)	4.0	0	100.1	Quant	Calculated	Roost	Relative density of trees (%) with DBH larger than 525 mm.

Name	Units	Mean	Min	Max	Type	Calculated?	Mechanism	Description	
27	% > 625	(%)	1.9	0	100.1	Quant	Calculated	Roost	Relative density of trees (%) with DBH larger than 625 mm.
28	>425 DBH den	(trees/ha)	421.2	0	8753.5	Quant	Calculated	Roost	Density of trees with DBH less than 225 mm.
29	>425 DBH den	(trees/ha)	485.4	0	8994	Quant	Calculated	Roost	Density of trees with DBH less than 325 mm.
30	>425 DBH	(trees/ha)	9.7	0	285.2	Quant	Calculated	Roost	Density of trees with DBH larger than 425 mm.
31	>425 DBH den	(trees/ha)	3.5	0	178.3	Quant	Calculated	Roost	Density of trees with DBH larger than 525 mm.
32	>425 DBH den	(trees/ha)	1.4	0	122.2	Quant	Calculated	Roost	Density of trees with DBH larger than 625 mm.
33	Tree H	(m)	9.2	1.5	41.4	Quant	Calculated	Roost	Average height of trees.
34	Min tree height	(m)	6.6	1.4	39.5	Quant	Calculated	Roost	Height of the smallest tree.
35	Max tree height	(m)	13.4	1.5	59	Quant	Calculated	Roost	Height of the largest tree.
36	Tree H ra	(m)	6.8	0	51	Quant	Calculated	Heterogeneity	Tree height range. Highest - shortest tree.
37	Dead den	(trees/ha)	16.4	0	4138	Quant	Calculated	Roost	Density of dead trees (doesn't specify if they are in the ground or standing).
38	% dead trees	(trees/ha)	2.9	0	100.1	Quant	Calculated	Roost	Relative density of dead trees.
39	Tree R		4.4	1	24	Quant	Calculated	Composition	Tree species richness in the plot of 25m.
40	Underst C	(%)	54.8	0	347	Quant	Calculated	Cluttering	Understory cover, estimated as the sum of % cover of each scrub species.
41	Underst R		4.6	1	26	Quant	Calculated	Composition	Richness of shrub species.
42	Underst H	(m)	0.9	0	10.35	Quant	Calculated	Cluttering	Average height of shrub.
43	Underst max height	(m)	1.3	0	20	Quant	Calculated	Cluttering	Height of the highest shrub species.
45	Small tree density	(trees/ha)	732.4	0	17189	Quant	Calculated	Cluttering	Density of lesser trees on a 5 m plot.
46	Small tree sp1 den	(trees/ha)	951.5	127	15661	Quant	Calculated	Cluttering	Density of the main species of lesser trees.
47	Small tree height		34.7	2	170	Quant	Calculated	Cluttering	#N/D
48	Regeneration richness		2.6	0	16	Quant	Calculated	Composition	Species richness of regeneration.
49	Wood density	(g/cm3)	0.7	0.43	0.991	Quant	Calculated	Roost	Weighted average wood density of trees.
50	Wood density >425	(g/cm3)	0.7	0.43	0.99	Quant	Calculated	Roost	Weighted average wood density of trees larger than 425 mm (Supplementary Table A1.2).
51	SoftW tree den	(trees/ha)	288.7	0	4877.21	Quant	Calculated	Roost	Density of trees of soft wood (Supplementary Table A1.2).
52	HardW tree den	(trees/ha)	196.0	0	5124.79	Quant	Calculated	Roost	Density of trees of hard wood (Supplementary Table A1.2).
53	SoftW tree prop	(%)	0.6	0	1	Quant	Calculated	Roost	Relative density of trees of soft wood (Supplementary Table A1.2).
54	SoftW >425	(trees/ha)	5.6	0	285.21	Quant	Calculated	Roost	Density of trees of soft wood larger than 425 mm (Supplementary Table A1.2).

Supplementary Table A1.2 – Wood density data for the tree species. Used to calculate variables on wood density of trees (Softwood tree density, Hardwood tree density, Softwood tree prop, Softwood >425).

Species	Wood density (g/cm ³)	Category	Source
<i>Populus nigra</i>	0.43	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Tilia cordata</i>	0.44	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Populus x canadiensis</i>	0.457	Soft	(Vignote Peña 2014)
<i>Abies alba</i>	0.51	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Alnus glutinosa</i>	0.51	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Pinus radiata</i>	0.515	Soft	https://www.wood-database.com
<i>Pinus uncinata</i>	0.52	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Pinus pinaster</i>	0.52	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Populus alba</i>	0.53	Soft	(Vignote Peña 2014)
<i>Pinus sylvestris</i>	0.55	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Populus tremula</i>	0.56	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Eucalyptus globulus</i>	0.57	Soft	(Tejedor 2004)
<i>Pinus pinea</i>	0.59	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Castanea sativa</i>	0.59	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Betula pendula</i>	0.6	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Pinus halepensis</i>	0.61	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Pinus nigra</i>	0.62	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Juniperus thurifera</i>	0.648	Soft	infomadera.net
<i>Platanus hybrida</i>	0.66	Soft	(Vayreda Duran <i>et al.</i> 2005)
<i>Quercus robur</i>	0.675	Hard	https://www.wood-database.com
<i>Fraxinus excelsior</i>	0.68	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Fagus sylvatica</i>	0.69	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Fraxinus angustifolia</i>	0.69	Hard	(Vignote Peña 2014)
<i>Acer campestre</i>	0.69	Hard	https://www.wood-database.com
<i>Quercus petraea</i>	0.73	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Acer opalus</i>	0.73	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Pinus canariensis</i>	0.75	Hard	infomadera.net
<i>Quercus canariensis</i>	0.76	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Quercus pubescens (Q. humilis)</i>	0.77	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Robinia pseudoacacia</i>	0.77	Hard	https://www.wood-database.com
<i>Quercus cerrioides</i>	0.78	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Quercus faginea</i>	0.79	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Arbutus unedo</i>	0.82	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Quercus suber</i>	0.83	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Quercus ilex</i>	0.9	Hard	(Vayreda Duran <i>et al.</i> 2005)
<i>Quercus pyrenaica</i>	0.97	Hard	(Vignote Peña 2014)
<i>Olea europaea</i>	0.99	Hard	https://www.wood-database.com

Supplementary Table A1.3 – Climate variables considered prior to selection for its inclusion in models.

Variables	Source
Temperature Seasonality	www.worldclim.org
Temperature coolest month	www.worldclim.org
Temperature hottest month	www.worldclim.org
Temperature Annual Range	www.worldclim.org
Minimum April temperature	www.worldclim.org
Mean Temperature of Warmest Quarter	www.worldclim.org
Mean Temperature of Coldest Quarter	www.worldclim.org
Mean April temperature	www.worldclim.org
Mean precipitation	www.worldclim.org
Precipitation of Warmest Quarter	www.worldclim.org
Precipitation Seasonality	www.worldclim.org
Precipitation driest month	www.worldclim.org
Precipitation of Wettest month	www.worldclim.org
Precipitation of Wettest Quarter	www.worldclim.org
Elevation	www.worldclim.org
Slope	From “Elevation”
Abruptness	From “Elevation”
Distance to karst	http://arcweb.forest.usf.edu/flex/KarstRegions/
Lithology	http://ccgm.org/en/home/168-lithological-map-of-the-world-9782917310250.html
Distance to forest	From landcover variable (https://earthdata.nasa.gov/)
Human population year 2000	https://earthdata.nasa.gov/

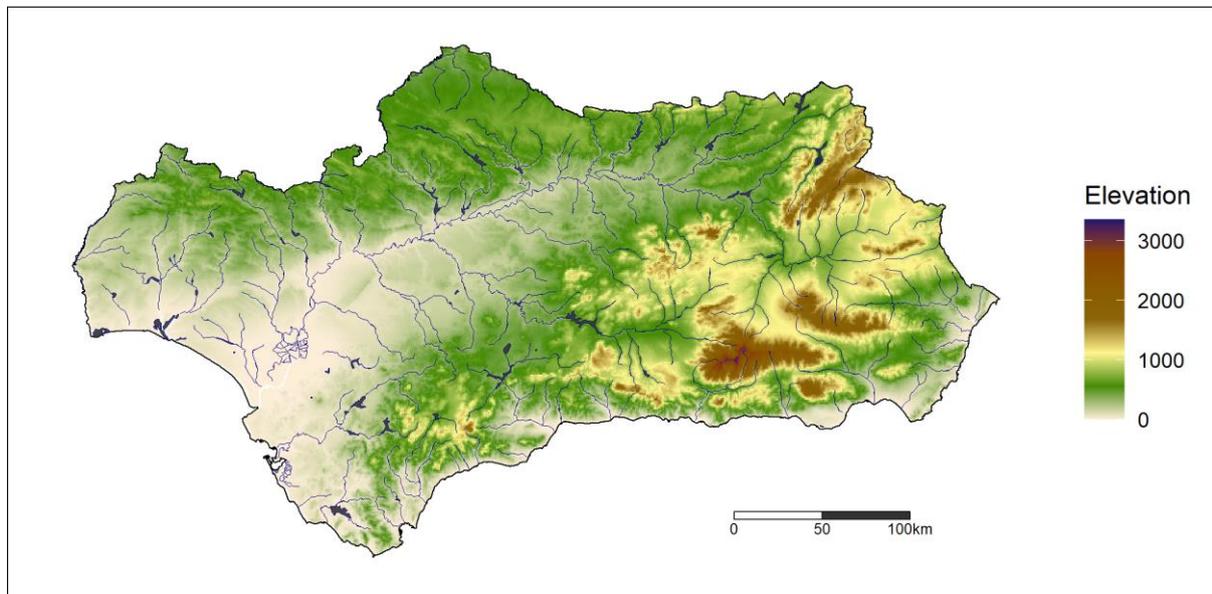
Supplementary Table A1.4 – Functional traits of the bat species included. Aspect ratio describes the square of the wingspan divided by the wing area. Wing loading describes the weight of the animal divided by the wing area.

Bat Species	Roost ecology	Aspect ratio	Wing loading (N/m ²)	Source
<i>M. bechsteinii</i>	Trees	6	9	(Norberg & Rayner 1987)
<i>B. barbastellus</i>	Trees	6	9.1	(Norberg & Rayner 1987)
<i>N. lasiopterus</i>	Trees	7.2	14.6	(Ibáñez et al. 2001)
<i>N. leisleri</i>	Trees	7.9	19.3	(Norberg & Rayner 1987)
<i>M. emarginatus</i>	Caves-buildings	5.9	7.1	(Norberg & Rayner 1987)
<i>M. escaleraei</i>	Caves-buildings	6.4	6.1	(Norberg & Rayner 1987)
<i>P. austriacus</i>	Caves-buildings	6.1	7.9	(Norberg & Rayner 1987)
<i>R. hipposideros</i>	Caves-buildings	5.7	7.1	(Norberg & Rayner 1987)

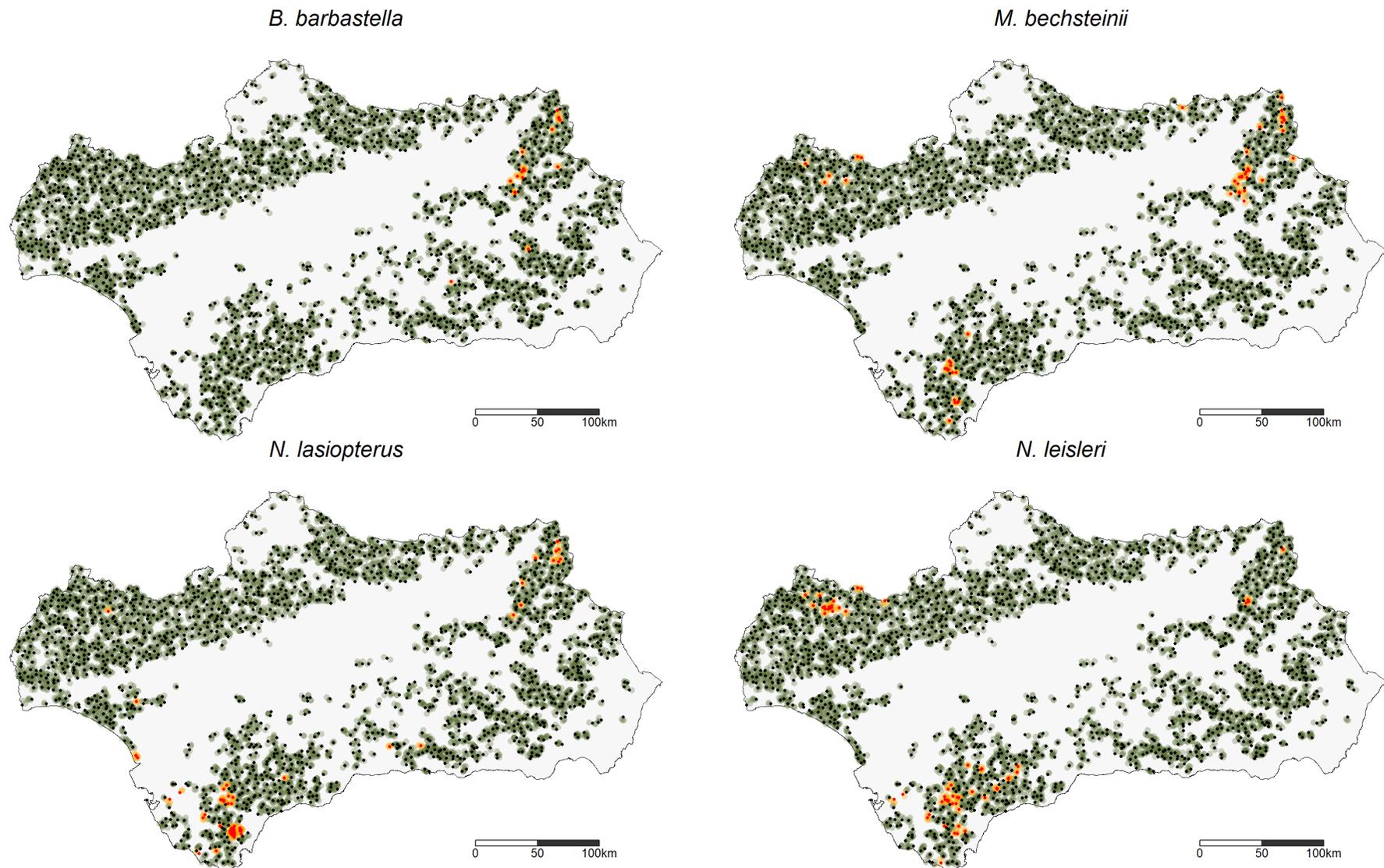
Supplementary Table A1.5 – Number of occurrence records for each bat species and results of their interpolation: average number of plots per occurrence record (OR) and random point (RP), and average distance from forest plots to OR and RP. Number of features in Maxent models F: (L: Linear, Q: quadratic, H: Hinge), regularisation parameter (r) and number of background points.

Supplementary Fig. A1.2 – Location of occurrence records Supplementary Fig. A1.2a-b.

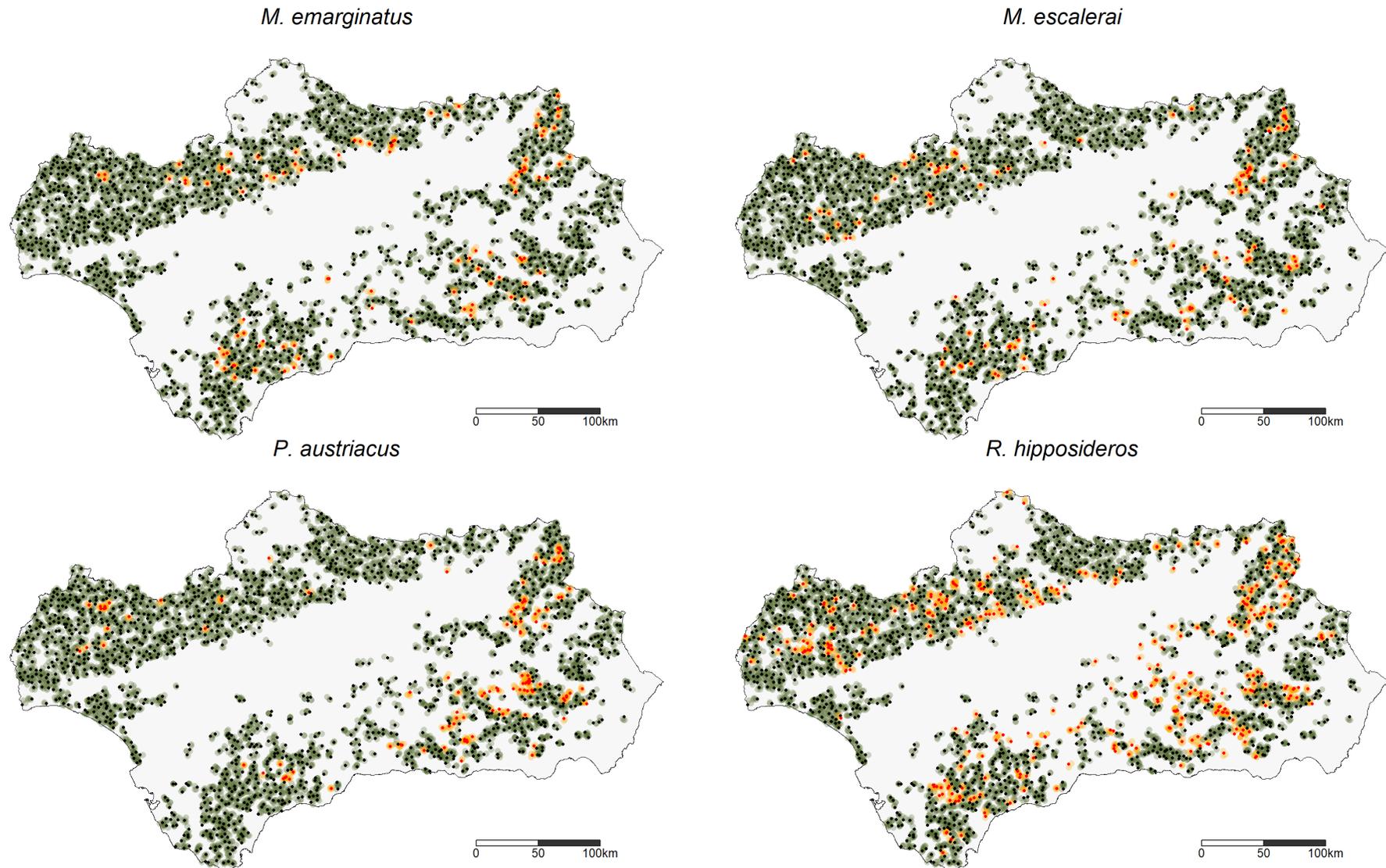
Bat species	Occurrence records	Mean plots/OR	Mean distance/OR	Mean plots/RP	Mean distance/RP	F	r	Background points
<i>B. barbastellus</i>	18	4.83	1.13	4.19	1.75	LQ	3	1617.75
<i>M. bechsteinii</i>	49	4.94	1.19	4.17	1.76	LQ	3	1625.875
<i>M. emarginatus</i>	98	4.64	1.5	4.12	1.77	L	3	1591.75
<i>M. escalerai</i>	115	4.59	1.44	4.1	1.78	L	3	1612.625
<i>N. lasiopterus</i>	70	4.89	1.17	4.16	1.76	L	3	1640.25
<i>N. leisleri</i>	59	4.86	1.19	4.15	1.76	L	3	1625.625
<i>P. austriacus</i>	123	4.62	1.42	4.12	1.77	L	3	1613.75
<i>R. hipposideros</i>	322	4.35	1.68	4.03	1.8	LH	3	1578.125



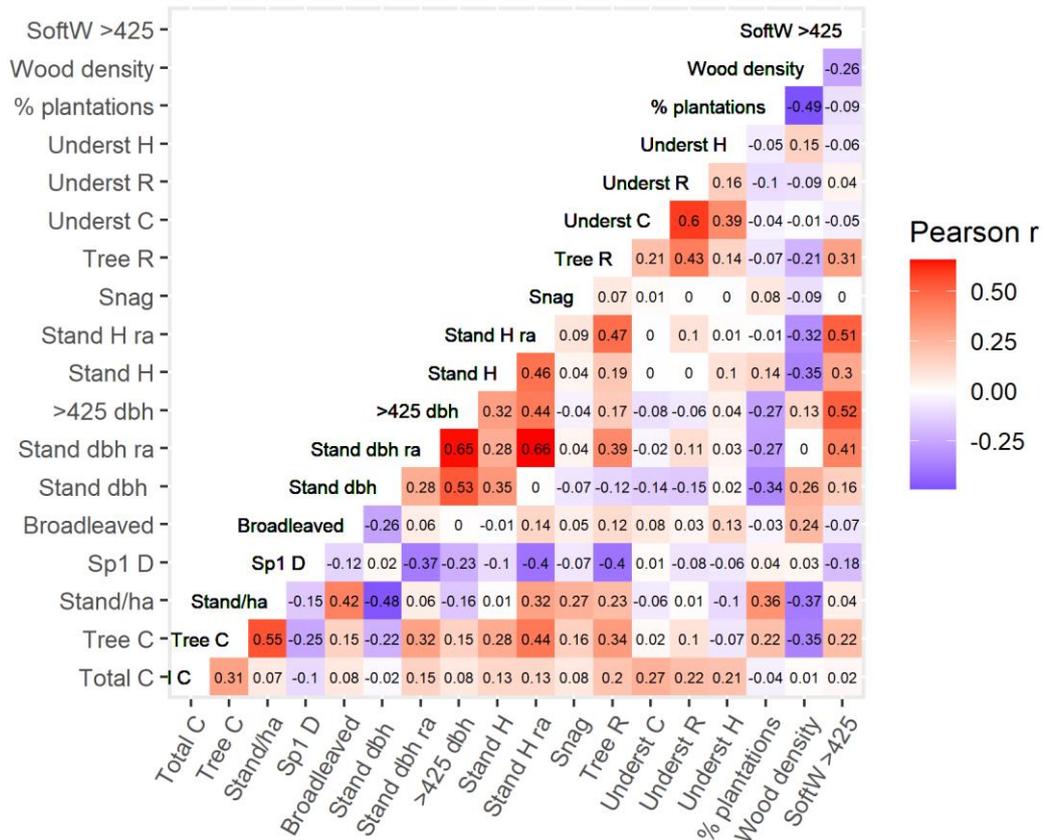
Supplementary Fig. A1.1 – Topography of the study working area of Andalusia.



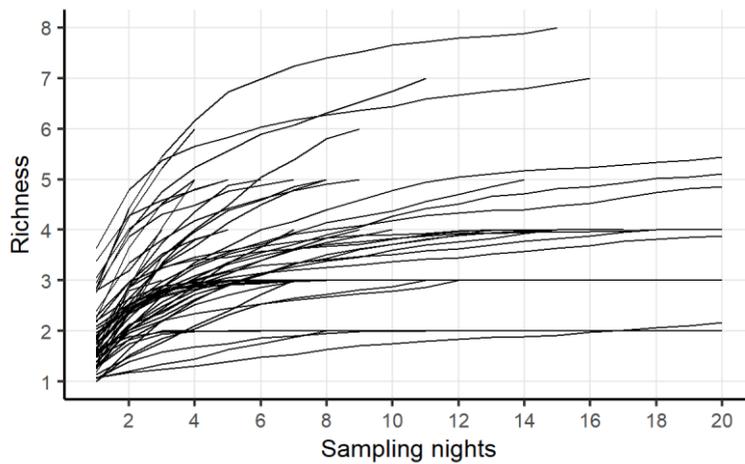
Supplementary Fig. A1.2 – Location of occurrence records (red dots) and generated background random points (black dots) for each species together with the location of forest plots used in the interpolation on both occurrence records (orange circles) and background random points (green circles).



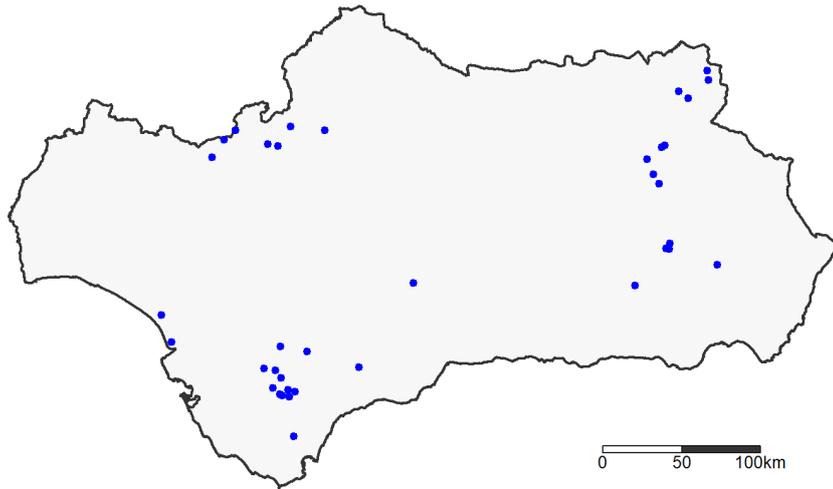
Supplementary Fig. A1.3 – Location of occurrence records (red dots) and generated background random points (black dots) for each species together with the location of forest plots used in the interpolation on both occurrence records (orange circles) and background random points (green circles).



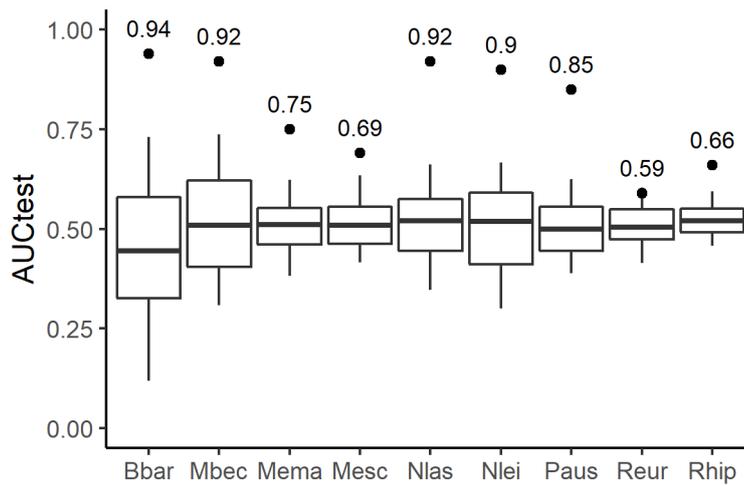
Supplementary Fig. A1.4 – Pearson correlation coefficient r between all pairs of forest variables included in the study. Variable names are shown in Table 2.2.



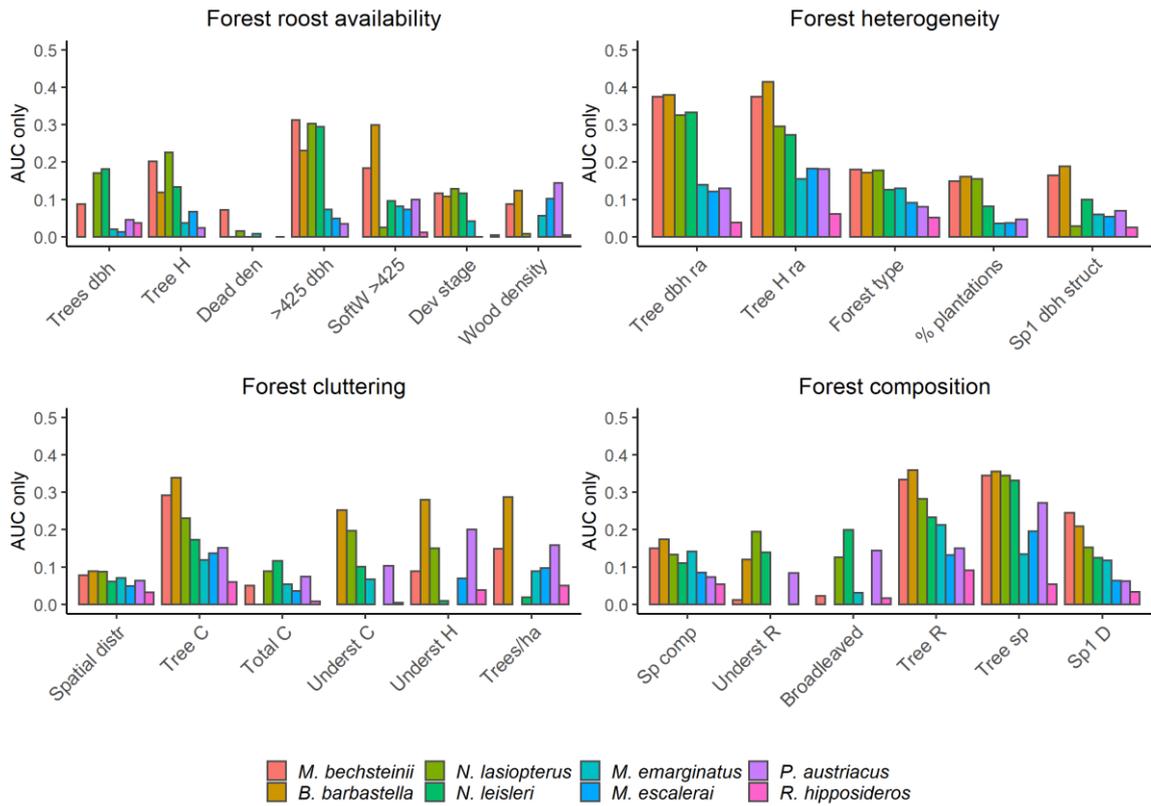
Supplementary Fig. A1.5 – Species accumulation curves of bat species assemblages. Each line represents a different location (<3 km) with bat compositional from at least two sampling nights based on mist nets or harp traps.



Supplementary Fig. A1.6 – Location of the bat assemblages considered to be sampled representatively that were included in the community-level analysis.



Supplementary Fig. A1.7 – AUCtest values of Maxent models for each bat species (dots) compared to null distributions of AUCtest values generated by running 100 Maxent models using random presence data. Boxes represent the first and third quartiles of AUCtest values. Whiskers show 0.95 CI of null distribution. All cases except in *R. euryale* have better fit than random (> CI 0.95). Bat species abbreviations are shown in Table 2.3.



Supplementary Fig. A1.8 – Individual AUC of variables in Maxent models (shown values have been subtracted 0.5 to show degree of departure from random). Forest variables are separated in the following mechanistic groups of variables: Forest roost availability, structural heterogeneity, cluttering and composition.

A2 Bat responses towards forest characteristics

All species responded strongly and negatively towards distance to forest (Supplementary Fig. A2.1). Strongest responses were found in *M. bechsteinii*, *B. barbastellus*, *M. emarginatus*, *R. hipposideros*, and *M. escaleraei*, while the weakest for *N. leisleri* and *P. austriacus*. In contrast, bats did not respond strongly towards type of forest, although *M. emarginatus* responded negatively towards forests other than natural (Supplementary Fig. A2.2). Similarly, responses towards spatial distribution of forest were not very strong, with only *M. escaleraei* and *R. hipposideros* showing preference towards forest fragments in small forests (Supplementary Fig. A2.3).

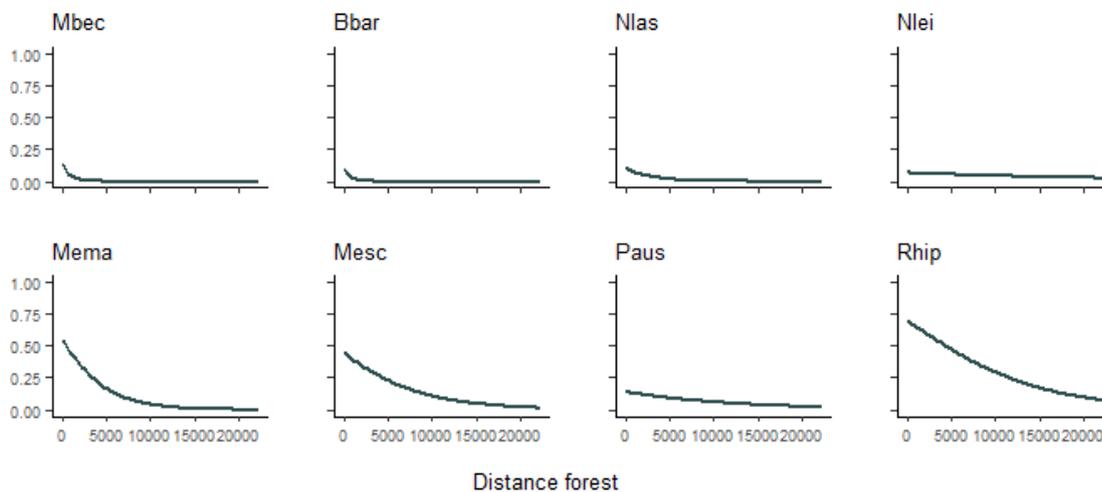
Responses towards specific composition of forest were not strong, although most species seemed to have some preference towards forest with more than one tree species (Supplementary Fig. A2.4). Bat species showed very strong responses towards the identity of the main tree species (Supplementary Fig. A2.5). *Quercus pyrenaica* and *Pinus nigra* were preferred by most bat species, while the tree species *Pinus pinea*, *Quercus ilex*, and *Pinus halepensis* were avoided by most. The most generalist species were *R. hipposideros*, *M. escaleraei* and *M. emarginatus*. Responses towards dominance were not strong (Supplementary Fig. A2.6), nor for density of broadleaved trees, although *P. austriacus* showed a clear positive preference (Supplementary Fig. A2.7). Most species showed strong positive responses towards tree richness except *B. barbastellus* and *M. escaleraei* (Supplementary Fig. A2.8). Responses towards understory species richness were weaker and mostly negative (Supplementary Fig. A2.9).

In terms of structural heterogeneity, the responses towards diametrical structure of the main tree species were not strong (Supplementary Fig. A2.10), while most bat species responded strongly positively towards range of DBH and tree height (Supplementary Fig. A2.11, Supplementary Fig. A2.12). Specifically, *P. austriacus*, *N. leisleri*, *M. bechsteinii*, and *M. emarginatus* for DBH range, and *M. escaleraei*, and *N. lasiopterus* for height range. Responses of bats towards the percentage of plantations were moderate and generally negative, although *M. emarginatus* and *P. austriacus* responded positively (Supplementary Fig. A2.13).

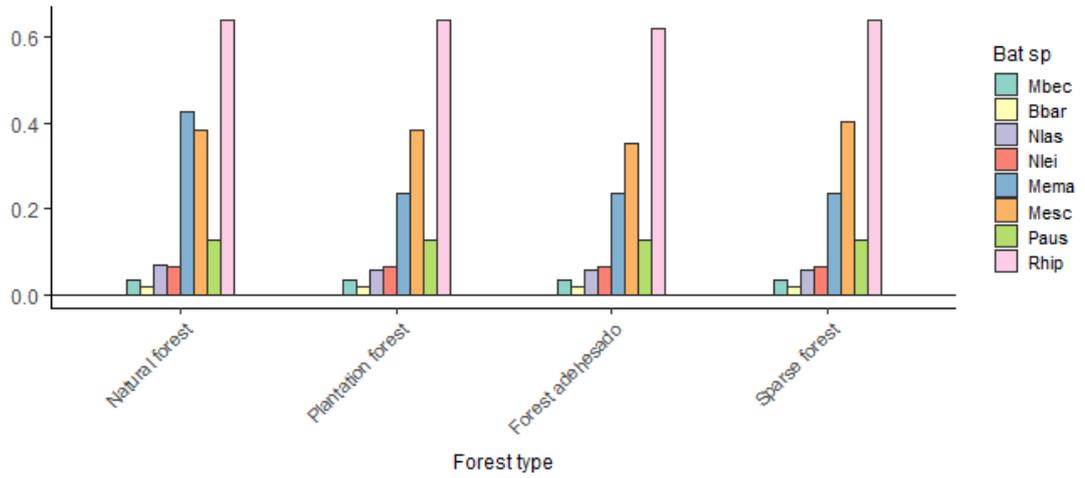
In terms of structural cluttering, bat responses towards total cover were weak. Some of the species, such as *N. leisleri*, *M. emarginatus* and *R. hipposideros*, responded positively, while others, such as *P. austriacus*, showed a negative response (Supplementary Fig. A2.14). Bats responded stronger and positively in all cases, except in *M. emarginatus*, towards tree cover (Supplementary Fig. A2.15). Responses towards density of trees per hectare were neutral or

negative, especially in *M. escalerae* (Supplementary Fig. A2.16). Responses towards understory cover were weakly positive for some species, such as *M. escalerae* and *N. lasiopterus*, and negative for others, such as *M. emarginatus* and *R. hipposideros* (Supplementary Fig. A2.17). Finally, responses towards understory height were not strong and slightly negative for most species (Supplementary Fig. A2.18).

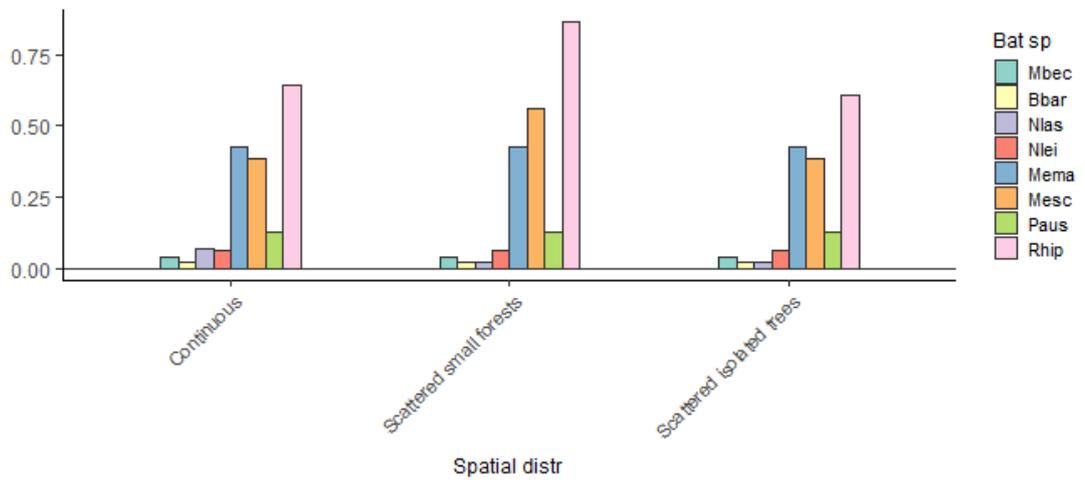
Regarding variables mechanistically related to roost availability, the responses towards forest development stage were weak for all species (Supplementary Fig. A2.19). Responses towards average tree DBH were positive for *M. bechsteini*, *N. lasiopterus* and *N. leisleri*, and negative for *M. emarginatus*, *M. escalerae* and *P. austriacus* (Supplementary Fig. A2.20). Responses towards tree height were positive for *N. lasiopterus*, *M. emarginatus*, *M. escalerae*, and slightly negative for *N. leisleri* and *R. hipposideros* (Supplementary Fig. A2.21). Bat responses towards density of trees larger than 425mm were neutral for most species and negative only for *R. hipposideros* (Supplementary Fig. A2.22), and similarly, responses towards density of dead trees were not strong (Supplementary Fig. A2.23). The responses towards wood density were positive for *R. hipposideros* and negative for *P. austriacus* (Supplementary Fig. A2.24), while the responses towards tree density of softwood trees larger than 425 were positive for *N. lasiopterus*, *N. leisleri*, and *M. emarginatus* (Supplementary Fig. A2.25).



Supplementary Fig. A2.1 – Probability of presence of each of the bat species depending on distance to forest. Abbreviations of species names are given in Table 2.3.

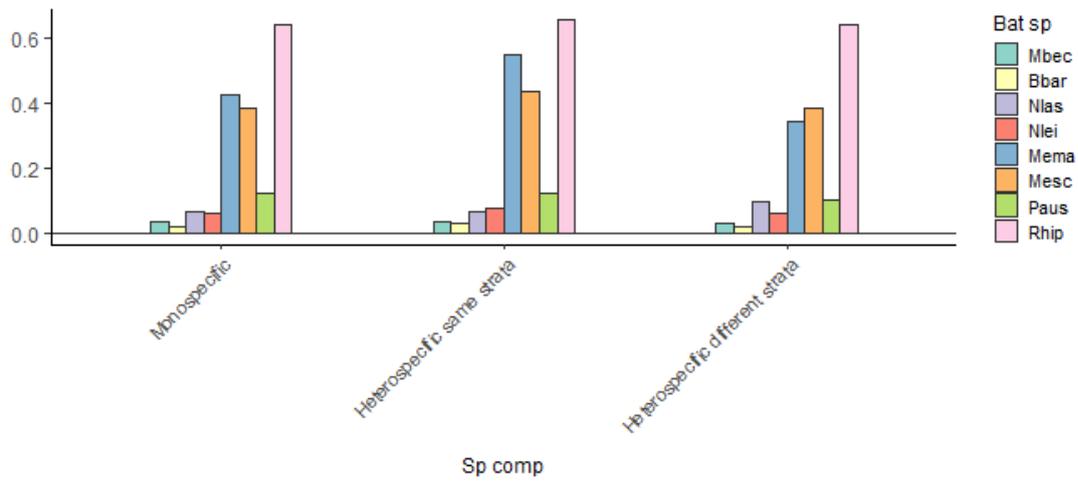


Supplementary Fig. A2.2 – Probability of presence of each of the bat species depending on the forest type. Abbreviations of species names are given in Table 2.3.

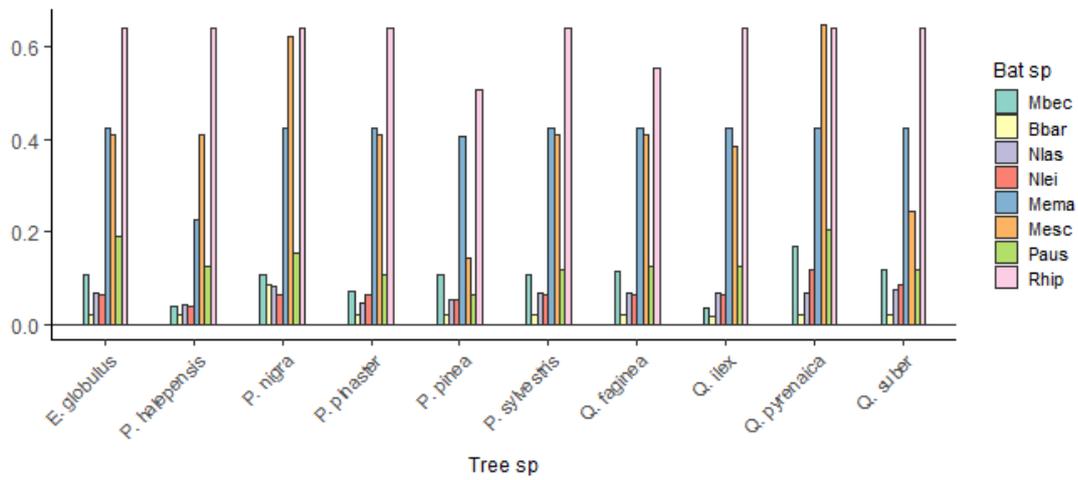


Supplementary Fig. A2.3 – Probability of presence of each of the bat species depending on forest spatial distribution. Abbreviations of species names are given in Table 2.3.

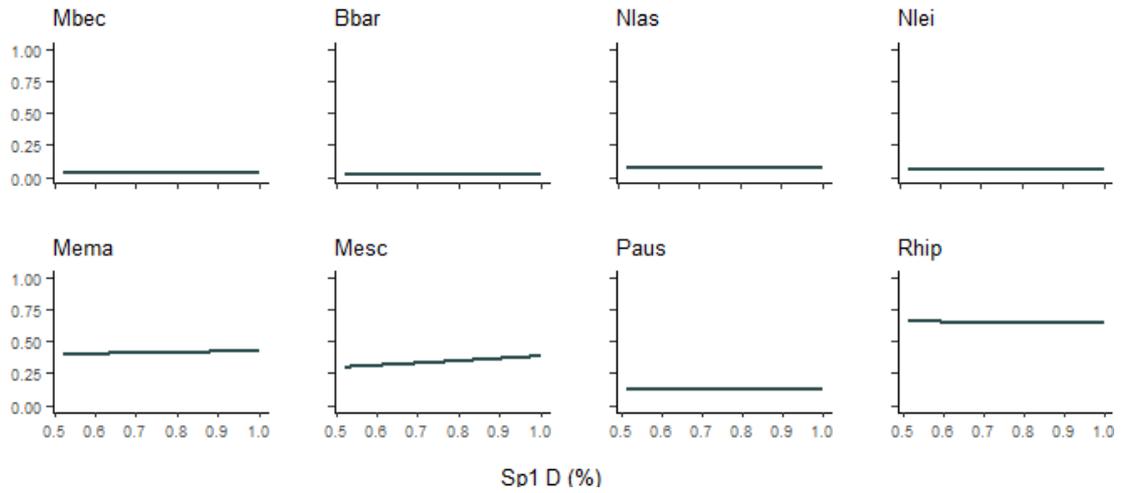
Responses towards forest composition variables



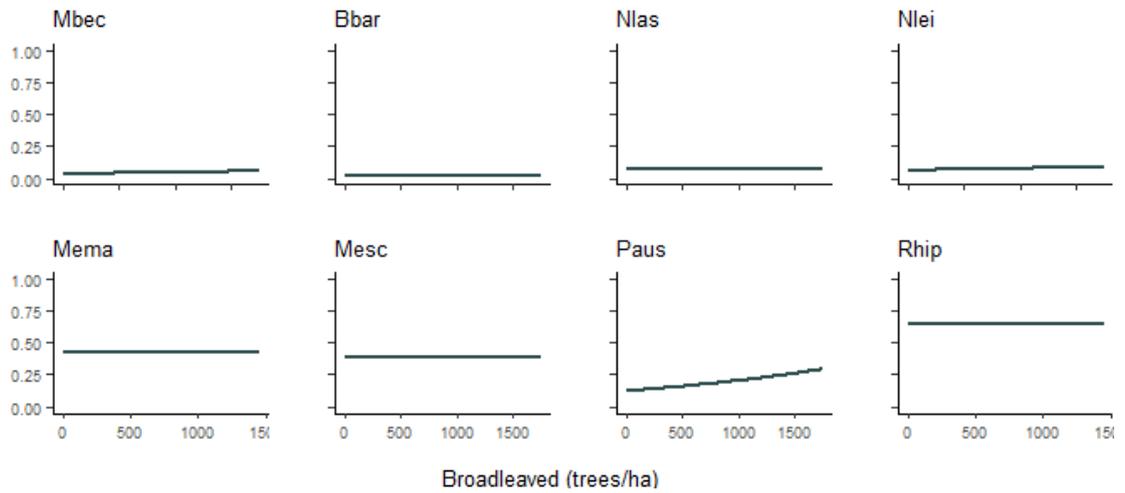
Supplementary Fig. A2.4 – Probability of presence of each of the bat species depending on specific composition. Abbreviations of species names are given in Table 2.3.



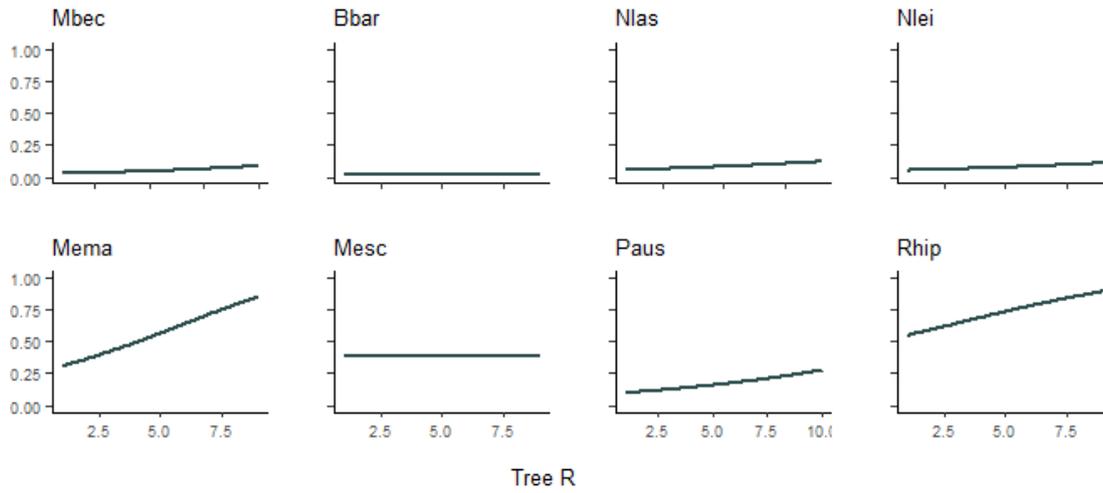
Supplementary Fig. A2.5 – Probability of presence of each of the bat species depending on tree species. Most ten common tree species are shown. Rare species in the region (dominant <1.5 % plots) are grouped as “others” and are not shown. Abbreviations of species names are given in Table 2.3.



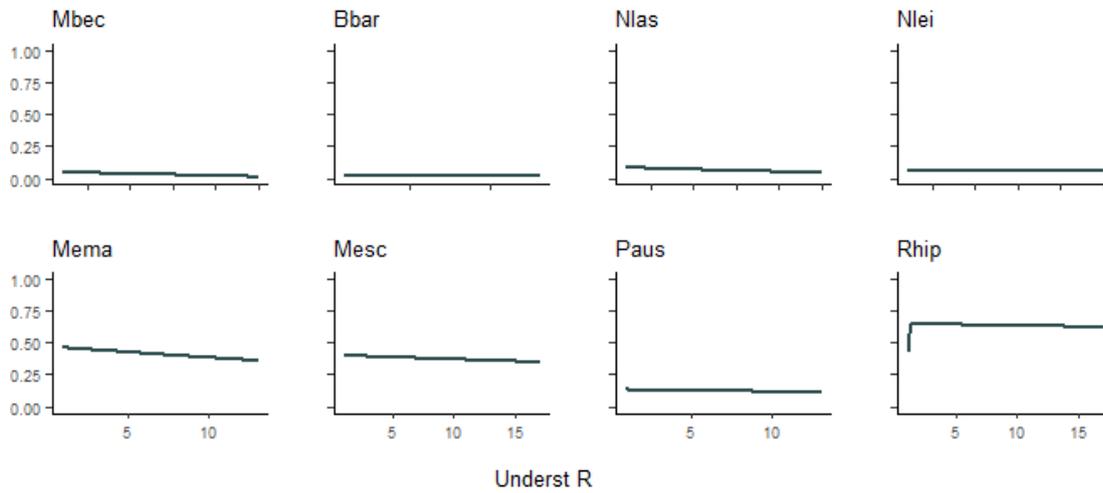
Supplementary Fig. A2.6 – Probability of presence of each of the bat species depending on tree species dominance. Abbreviations of species names are given in Table 2.3.



Supplementary Fig. A2.7 – Probability of presence of each of the bat species depending on the density of trees of broadleaved tree species. Abbreviations of species names are given in Table 2.3.

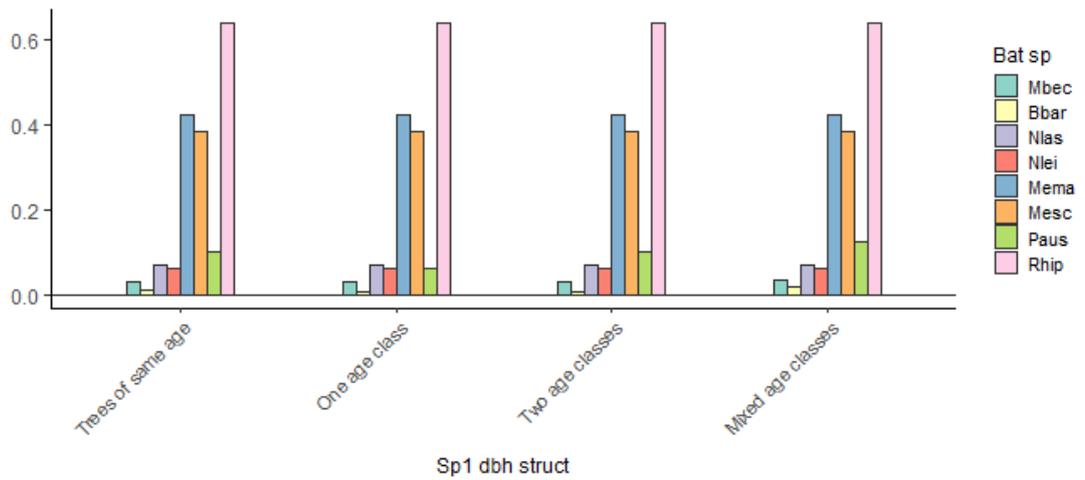


Supplementary Fig. A2.8 – Probability of presence of each of the bat species depending on the richness of tree species. Abbreviations of species names are given in Table 2.3.

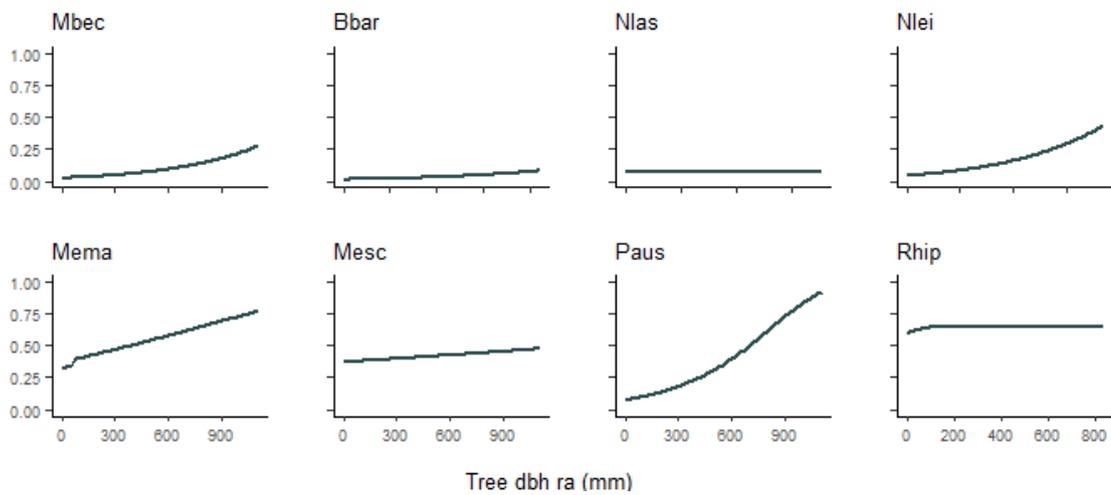


Supplementary Fig. A2.9 – Probability of presence of each of the bat species depending on the richness of understory species. Abbreviations of species names are given in Table 2.3.

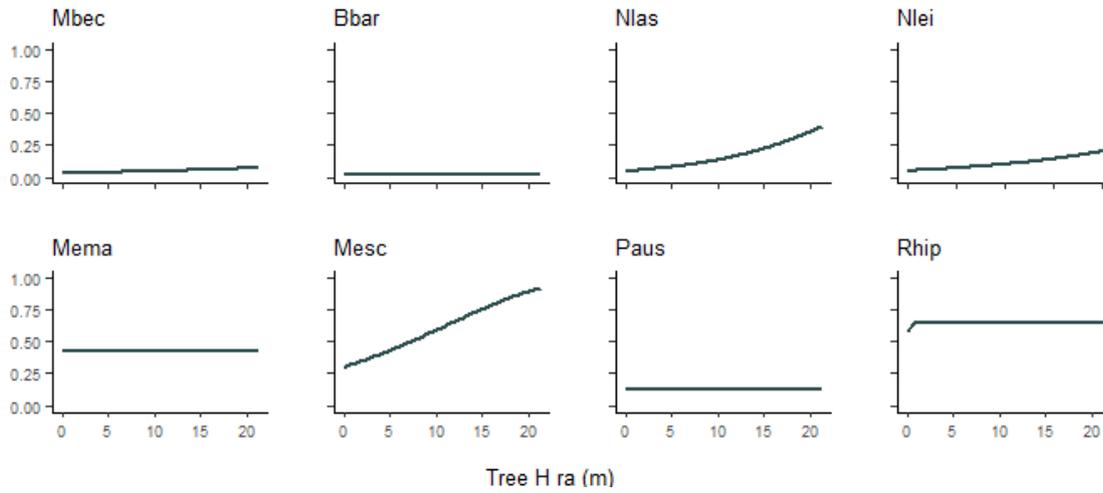
Responses towards forest structural heterogeneity



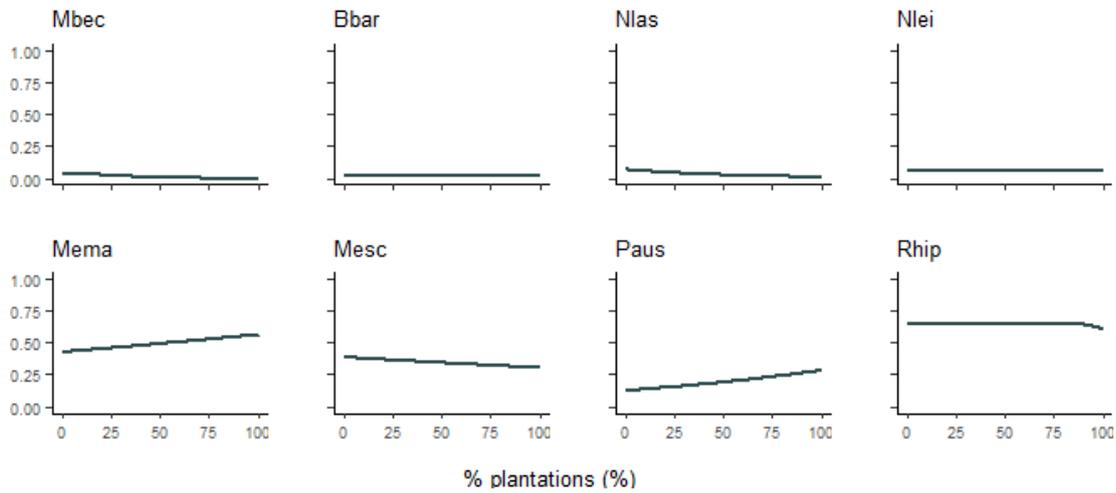
Supplementary Fig. A2.10 – Probability of presence of each of the bat species depending on the age structure of the dominant tree species. Abbreviations of species names are given in Table 2.3.



Supplementary Fig. A2.11 – Probability of presence of each of the bat species depending on range of tree DBH. Abbreviations of species names are given in Table 2.3.

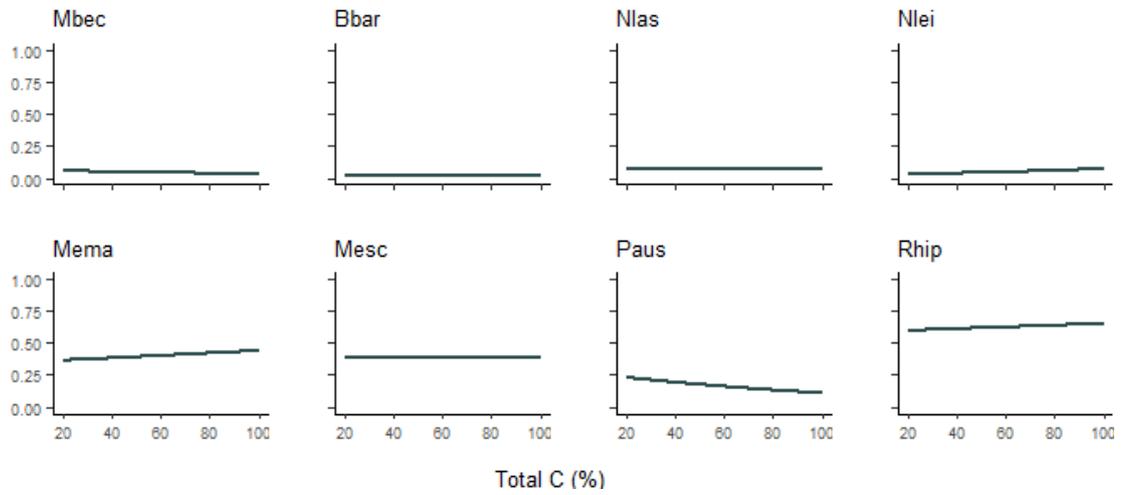


Supplementary Fig. A2.12 – Probability of presence of each of the bat species depending on average tree height. Abbreviations of species names are given in Table 2.3.

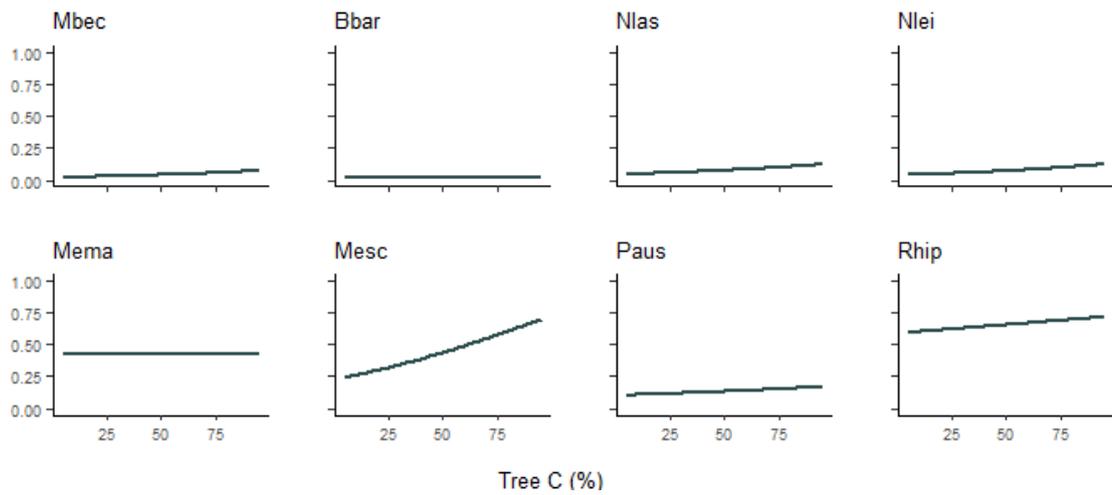


Supplementary Fig. A2.13 – Probability of presence of each of the bat species depending on % of plantations. Abbreviations of species names are given in Table 2.3.

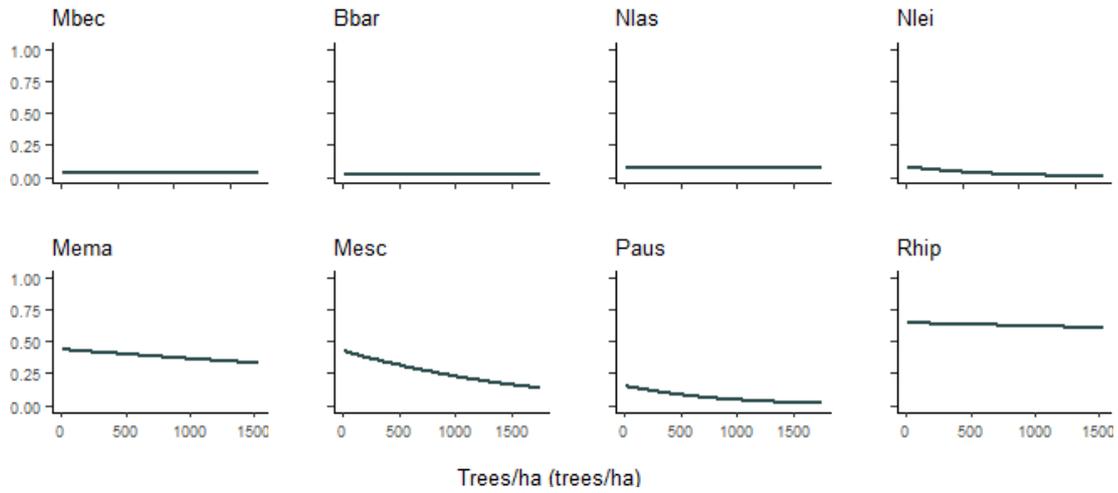
Responses towards forest clutter



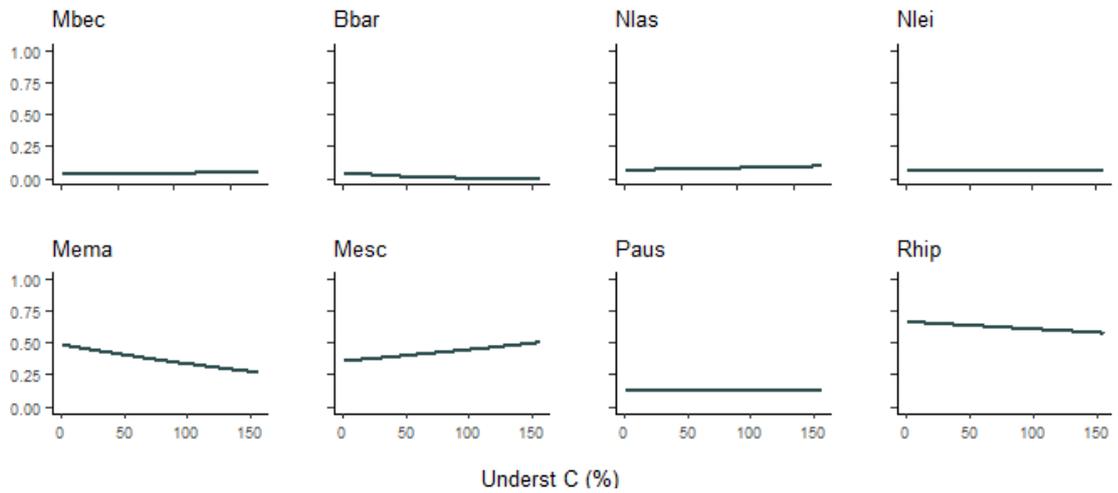
Supplementary Fig. A2.14 – Probability of presence of each of the bat species depending on total cover. Abbreviations of species names are given in Table 2.3.



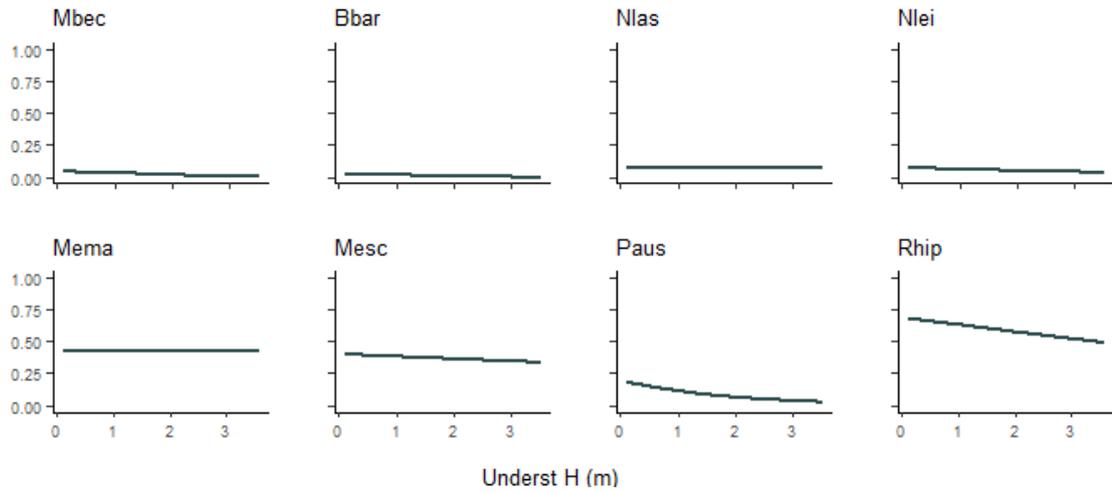
Supplementary Fig. A2.15 – Probability of presence of each of the bat species depending on tree cover. Abbreviations of species names are given in Table 2.3.



Supplementary Fig. A2.16 – Probability of presence of each of the bat species depending on density of trees/ha. Abbreviations of species names are given in Table 2.3.

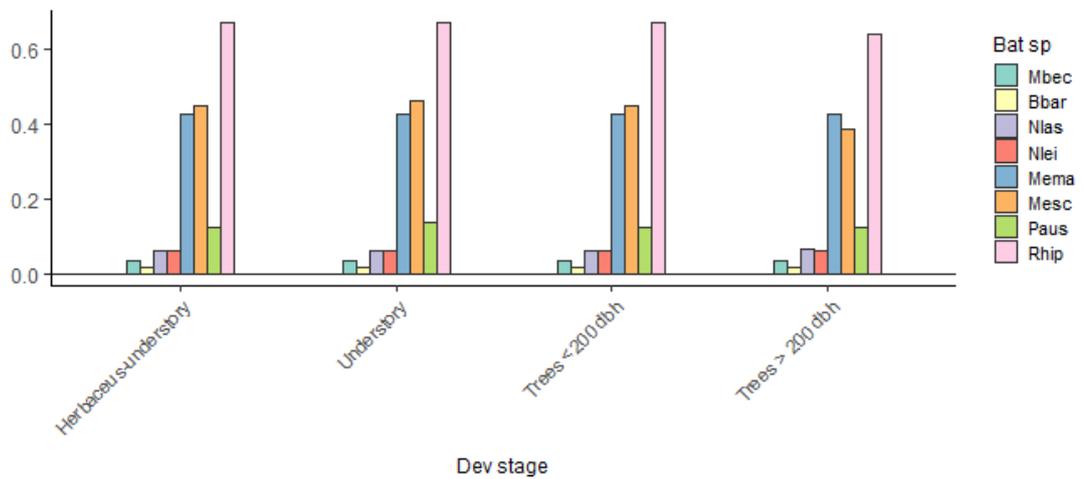


Supplementary Fig. A2.17 – Probability of presence of each of the bat species depending on understory cover. Abbreviations of species names are given in Table 2.3.

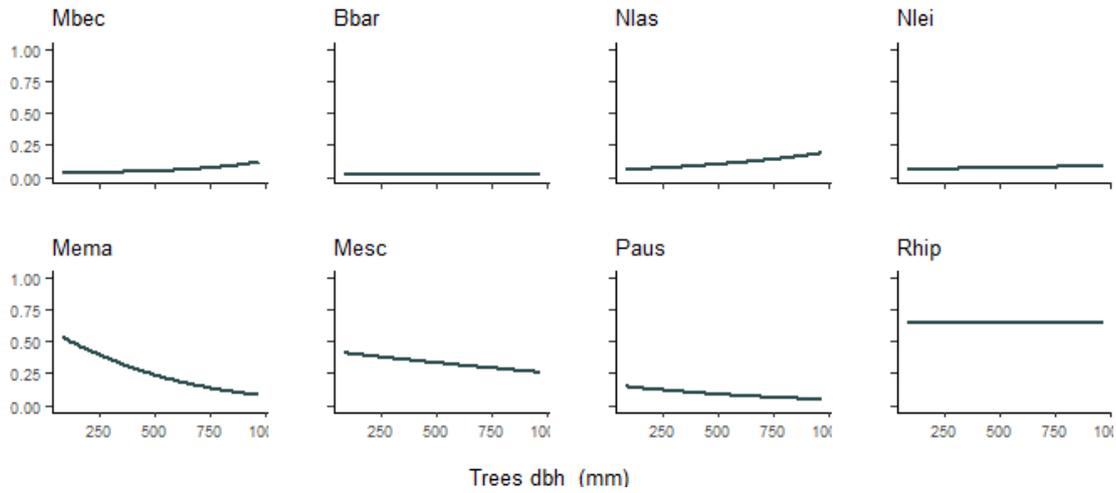


Supplementary Fig. A2.18 – Probability of presence of each of the bat species depending on understory height. Abbreviations of species names are given in Table 2.3.

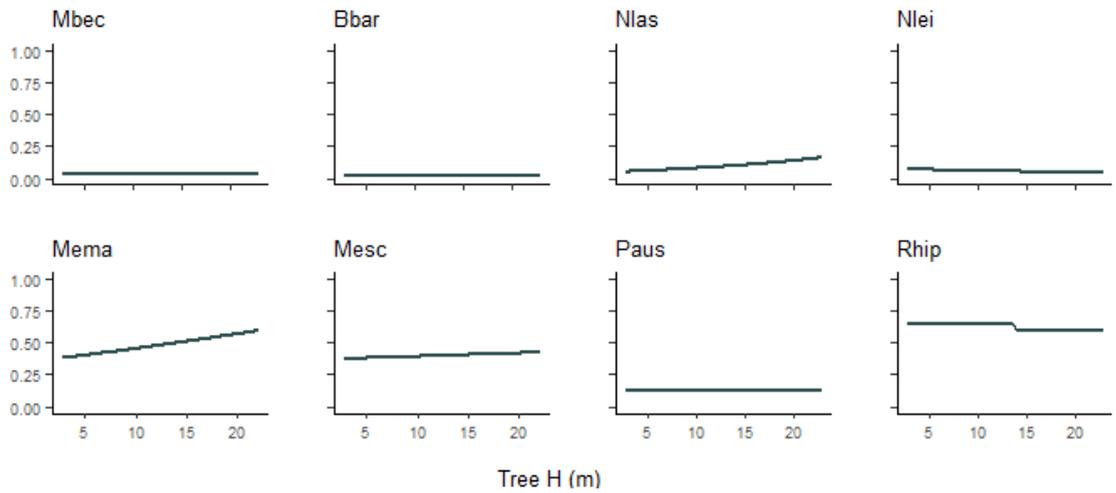
Responses towards roost availability variables



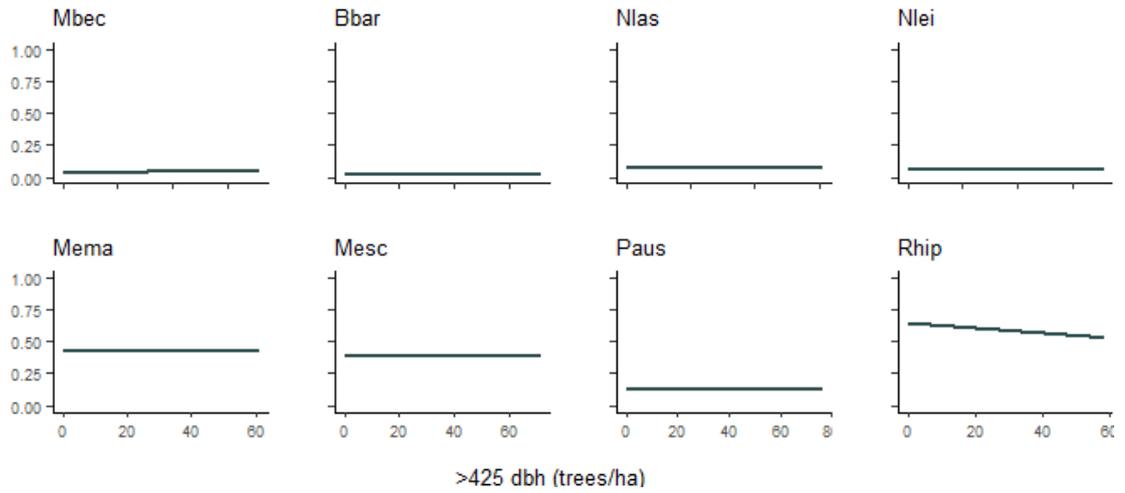
Supplementary Fig. A2.19 – Probability of presence of each of the bat species depending on forest development stage. Abbreviations of species names are given in Table 2.3.



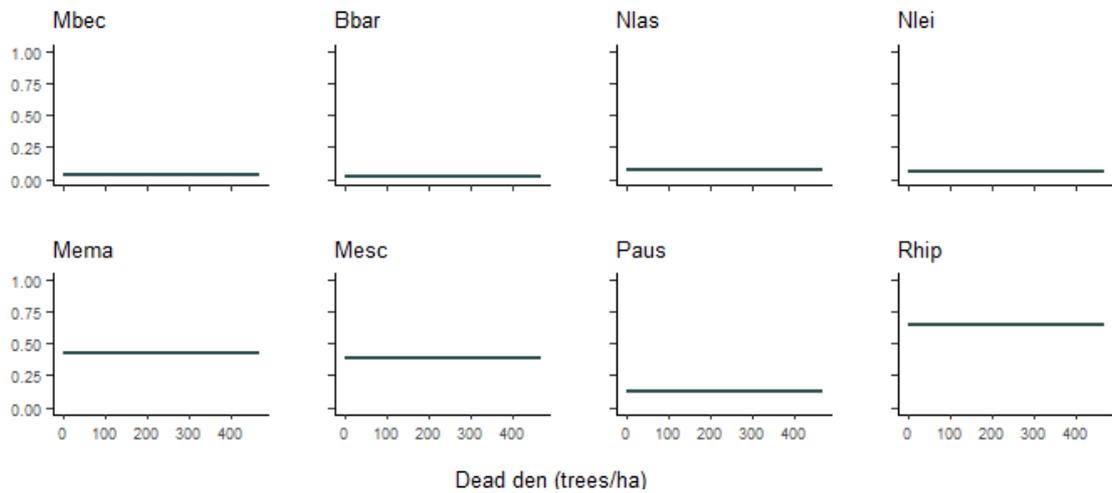
Supplementary Fig. A2.20 – Probability of presence of each of the bat species depending on average tree DBH. Abbreviations of species names are given in Table 2.3.



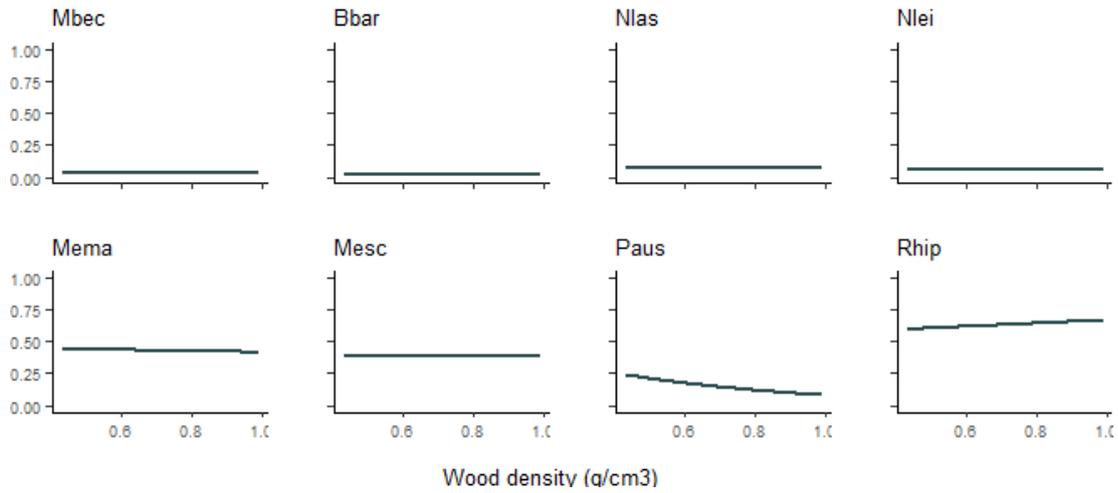
Supplementary Fig. A2.21 – Probability of presence of each of the bat species depending on average tree height. Abbreviations of species names are given in Table 2.3.



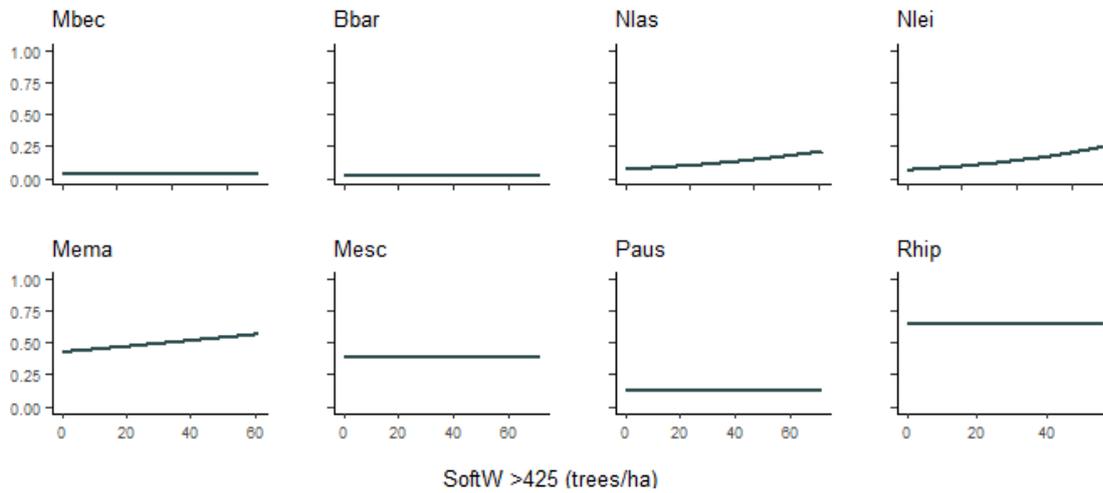
Supplementary Fig. A2.22 – Probability of presence of each of the bat species depending on density of trees larger than 425 mm. Abbreviations of species names are given in Table 2.3.



Supplementary Fig. A2.23 – Probability of presence of each of the bat species depending on proportion of dead trees. Abbreviations of species names are given in Table 2.3.



Supplementary Fig. A2.24 – Probability of presence of each of the bat species depending on weighted wood density of trees. Abbreviations of species names are given in Table 2.3.



Supplementary Fig. A2.25 – Probability of presence of each of the bat species depending of density of softwood tree species. Abbreviations of species names are given in Table 2.3.

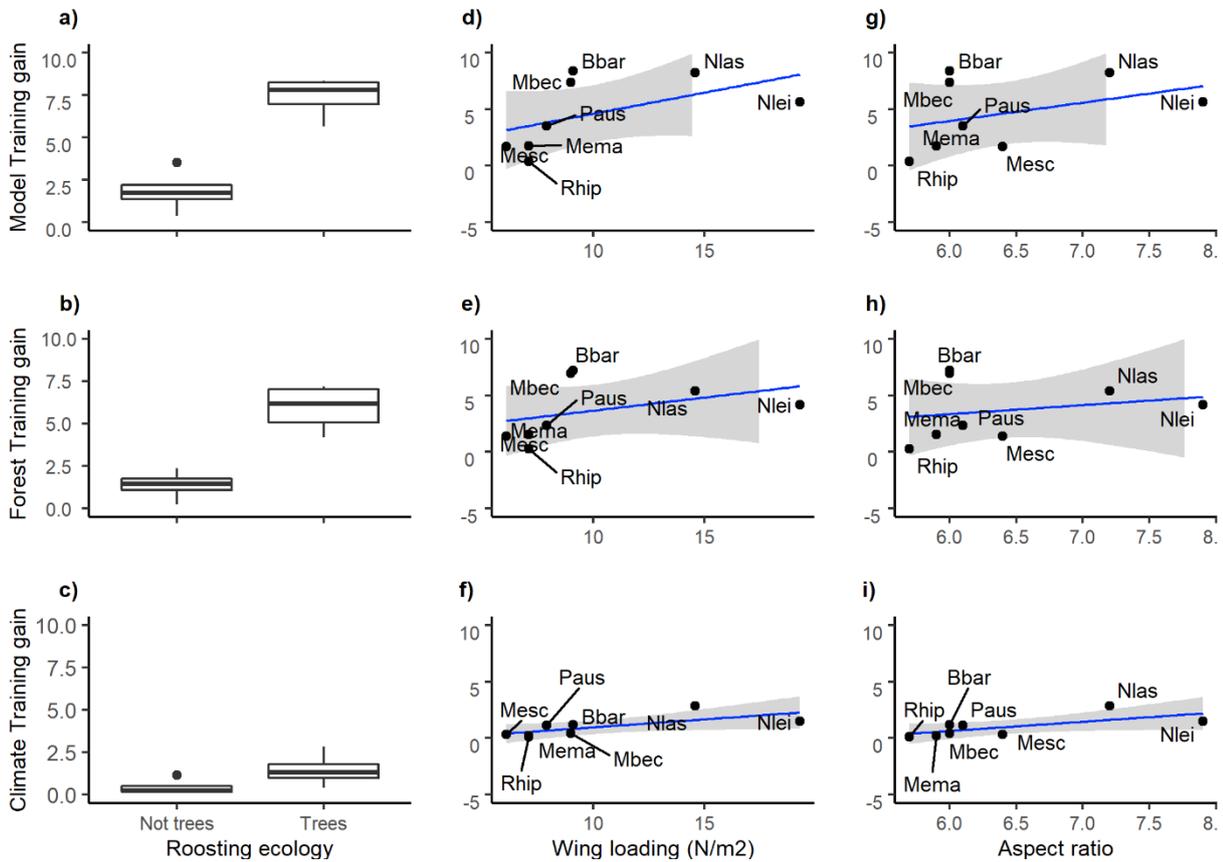
A3 Eco-morphological relationships including all bats

Wing loading and aspect ratio were correlated when including all bat species in the analysis (Linear model: $F_{1,6} = 36.52$, $p < 0.001$, $R^2 = 0.83$) and consequently behave similarly when I correlate them with contribution of different groups of variables.

Overall model training gain did not increase with wing loading, but was marginally affected by the number of records (Linear model: $F_{2,5} = 4.632$, $p = 0.072$, Wing loading: $p = 0.36$, number occurrence records: $p = 0.071$; Supplementary Fig. A3.1). Species wing loading did not correlate with training gain of forest variables (Linear model: $F_{1,6} = 1.127$, $p = 0.33$, Supplementary Fig. A3.1e), nor with any mechanistic group of variables (composition, heterogeneity, cluttering, roost ecology) nor distance to forest (Linear model: $F_{1,6}$ $p > 0.05$).

Similarly to wing loading, aspect ratio did not explain summed variable training gain of models (Linear model: $F_{2,5} = 3.606$, $p = 0.11$, Aspect ratio: $p = 0.75$, number occurrence records: $p = 0.07$; Supplementary Fig. A3.1g), gain of forest variables (Linear model: $F_{1,6} = 0.3311$, $p = 0.58$, Supplementary Fig. A3.1h) nor training gain for any specific group of forest variables composition, heterogeneity, cluttering nor distance to forest (Linear model: $F_{1,6}$ $p > 0.05$).

Both wing loading and aspect ratio had a borderline positive effect with training gain of climatic variables in the models (Linear model: $F_{1,6} = 5.89$, $p = 0.051$, $R^2 = 0.41$, Supplementary Fig. A3.1f)(Linear model: $F_{1,6} = 5.2$, $p = 0.06$, Supplementary Fig. A3.1i).



Supplementary Fig. A3.1 – Correlation between functional traits (Roosting ecology (a,b,c), wing loading (d,e,f) and aspect ratio(g,h,i)) with training gain of different sets of variables in Maxent models (Overall gain of models (a,d, g), forest variables (b,e,h), and climate variables (c,f,i). Bat species that roost in trees show higher overall model training gain and gain of forest variables, while not higher gain on climate variables. Wing loading does not explain training gain of total model nor forest, but explains higher contribution of climate variables. Aspect ratio does not correlate with any of the groups of variables. All plots contain the same set of bat species.

References for Appendix A

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Appendix B Supplementary material for Chapter 3

B1 Supplementary tables and figures

Supplementary Table B1.1 – Sampling locations and number of dropping samples processed in each location for each bat species (Mes: *Myotis escalerai*, Mcr: *Myotis crypticus*). Sampling region and category of the location as regionally sympatric or allopatric or locally sympatric and allopatric. SweepS: Number of sweeping samples analysed.

	Location name	Long.	Lat.	Sampling Region	Regional sympatry	Local sympatry	Mes	Mcr	SweepS
1	Alquife	-3.11	37.18	Andalucia	Allopatry	NA	2	0	NA
2	Arroyo Tejuelo	-2.57	38.32	Andalucia	Allopatry	NA	3	0	NA
3	Buenamar	-2.78	38.25	Andalucia	Allopatry	NA	1	0	NA
4	Cueva Murcielaguina Hormos	-2.71	38.22	Andalucia	Allopatry	NA	1	0	NA
5	El Chorro	-3.01	37.87	Andalucia	Allopatry	NA	29	0	NA
6	El Tobazo Villaescusa Ebro	-3.83	42.82	Cantabria	Sympatry	Allo	0	1	NA
7	Ermita de Somera	-4.02	42.87	Cantabria	Sympatry	Allo	0	1	NA
8	Fuente de la Garganta	-2.89	37.9	Andalucia	Allopatry	NA	3	0	NA
9	Lc1 Arroyo Frio o de Ubíos	-2.9	37.94	Andalucia	Allopatry	NA	11	0	2
10	Lc3 Siles	-2.57	38.32	Andalucia	Allopatry	NA	4	0	1
11	Lc4 Linarejos	-2.91	37.92	Andalucia	Allopatry	NA	1	0	NA
12	Lc6 Roblehondo	-2.88	37.95	Andalucia	Allopatry	NA	5	0	1
13	Lc7 Arroyo de la Canal	-2.96	37.79	Andalucia	Allopatry	NA	6	0	2
14	Lc8 Mina del gato	-3.09	37.16	Andalucia	Allopatry	NA	13	0	3
15	Lc9 Canada de los arroyos	-2.98	37.84	Andalucia	Allopatry	NA	1	0	NA
16	Lca1 Monte Hijedo corba	-3.93	42.89	Cantabria	Sympatry	Allo	0	2	1
17	Lca10 Buyezo Riega tornes	-4.5	43.13	Cantabria	Allopatry	NA	0	3	3
18	Lca11 Rubionzu	-3.81	43.25	Cantabria	Allopatry	NA	0	1	NA
19	Lca12 Liendo Manas Iseca	-3.36	43.37	Cantabria	Allopatry	NA	0	2	NA
20	Lca13A Pinar de nieves	-3.35	43.31	Cantabria	Allopatry	NA	0	1	NA
21	Lca13B Toberas	-3.37	43.32	Cantabria	Allopatry	NA	0	2	NA
22	Lca14 Pozos Valcava	-3.78	43.36	Cantabria	Allopatry	NA	0	1	NA
23	Lca15a Puente Mercadillo a	-4.22	42.88	Cantabria	Sympatry	Sym	0	7	2
24	Lca15b Puente Mercadillo p	-4.22	42.88	Cantabria	Sympatry	Sym	1	0	NA
25	Lca16 Hayedo X	-4.2	42.97	Cantabria	Allopatry	NA	0	1	NA
26	Lca17a San M. Valdelomar	-4.15	42.8	Cantabria	Sympatry	Sym	0	5	1
27	Lca17b Cuevaton	-4.17	42.81	Cantabria	Sympatry	Sym	1	2	3
28	Lca2 Coroneles	-4.07	42.82	Cantabria	Sympatry	Allo	0	8	1
29	Lca3 Velilla	-3.93	42.8	Cantabria	Sympatry	Sym	1	4	1
30	Lca4 Salcedo	-3.95	42.82	Cantabria	Sympatry	Sym	1	2	1
31	Lca5 Rio Torina	-4.04	43.11	Cantabria	Allopatry	NA	0	1	NA
32	Lca8 Liebana S. Pedro Bedoya	-4.56	43.18	Cantabria	Allopatry	NA	0	3	2
33	Lcat1 Ginebret	2.7	42.28	Catalunya	Sympatry	NA	4	5	1
34	Lr10 Rasillo	-2.72	42.2	La Rioja	Sympatry	Allo	0	3	2
35	Lr11 Ermita Lollano	-2.66	42.15	La Rioja	Sympatry	Allo	0	17	1
36	Lr12 Cueva Moro Valganon	-3.08	42.32	La Rioja	Sympatry	Sym	2	1	1
37	Lr14 Calamantio	-2.93	42.19	La Rioja	Sympatry	Allo	0	2	NA
38	Lr15 Valvanera	-2.87	42.23	La Rioja	Sympatry	Allo	0	1	NA
39	Lr16 Cueva 4 puertas	-2.25	42.2	La Rioja	Sympatry	Allo	3	0	1
40	Lr3 Cueva Cerraúco	-2.74	42.18	La Rioja	Sympatry	Allo	0	4	1
41	Lr5 Tunel Arnedillo	-2.2	42.2	La Rioja	Sympatry	Allo	8	0	2
42	Lr6 Dehesa de Villoslada	-2.68	42.12	La Rioja	Sympatry	Allo	0	6	1
43	Lr8 Cueva Azagra	-1.87	42.28	Navarra	Sympatry	Allo	15	0	NA
44	Ls1 Cueva Agua Villaciervos	-2.66	41.78	Castilla la	Sympatry	Allo	20	0	1

Location name	Long.	Lat.	Sampling Region	Regional sympatry	Local sympatry	Mes	Mcr	SweepS
			Mancha					
45 Parador Nacional	-2.96	37.9	Andalucia	Allopatry	NA	1	0	NA
46 Pena Olivar	-2.58	38.37	Andalucia	Allopatry	NA	1	0	NA
47 R Quejigal villacantiz	-4.19	43	Cantabria	Allopatry	NA	0	2	NA
48 R Regato troncos la Matilla	-3.94	42.82	Cantabria	Sympatry	Sym	0	1	NA
49 R Vega Villafufre	-3.85	43.26	Cantabria	Allopatry	NA	0	1	NA

Supplementary Table B1.2 – Summary of criteria followed in the functional classification of the BINs recovered according to the likelihood of the bat capturing the arthropod by gleaning or aerial hawking. 0: Non-volant. 1: not actively volant. 2: Nocturnally volant.

Order	Number of BINs	Functional groups	Criteria used	References
Araneae	140	0	Morphological	
Archaeognatha	1	0	Morphological	
Blattodea	7	0, 1	Morphological	
Coleoptera	87	1,2	Literature	(Haack et al. 2017) (Cerambycidae)(Nalepa 2013) (Coccinellidae)
Dermaptera	2	0	Morphological	
Diptera	423	1, 2	Taxonomist (Jorge Mederos) Literature	(Oosterbroek 2006)
Ephemeroptera	6	2	Literature	
Hemiptera	96	1	Literature	(Waloff & Bakker 1963)
Hymenoptera	68	1, 2	Literature	(Broad 2005; Short et al. 2006; Mazon et al. 2009; Lozan et al. 2010; Quicke 2014)(Ichneumonoidea, (Tilgner 2004) (Tenthredinidae)
Isopoda	2	0	Morphological	
Lepidoptera	560	2	Literature	
Mantodea	1	1	own observations	
Mecoptera	1	2	Literature	
Neuroptera	19	2	Literature	(Abraham & Vas 1999; Vas et al. 1999)
Odonata	5	1	Literature	(Corbet 1999)
Orthoptera	36	1	Literature	
Plecoptera	1	2	Literature	
Thysanoptera	2	0	Morphological	
Trichoptera	6	2	Literature	

Supplementary Table B1.3 – Number of reads obtained for each sample from each primer (ANML and ZBJ) and replicate (1 and 2). Sample type: D= Dropping sample, S= Sweeping sample. BlankD and BlankSweep: extraction blanks for dropping (D) and sweeping (Sweep) samples. Blankseq: sequencing blank. Failed: If TRUE, sample has been removed under the conservative criteria, due to insufficient number of reads in at least one of the runs.

Sample name	ANML_1	ANML_2	ZBJ_1	ZBJ_2	Sample type	Failed
RNF_1	3	30	839	2077	D	TRUE
RNF_2	4129	749	3271	7860	D	.
RNF_3	6015	8336	4615	8843	D	.
RNF_4	2779	2262	3967	3587	D	.
RNF_5	542	252	576	1310	D	.
RNF_6	5586	10536	5546	6788	D	.
RNF_7	441	610	1658	2735	D	.
RNF_8	3426	1385	3454	3254	D	.
RNF_9	761	310	2533	2198	D	.
RNF_10	2098	2015	3010	3960	D	.
RNF_11	571	614	484	447	D	.
RNF_12	265	159	546	376	D	.
RNF_13	2528	1075	2539	604	D	.
RNF_14	6233	7633	4613	4177	D	.
RNF_15	149	77	30	37	D	TRUE
RNF_16	7072	3610	2349	2680	D	.
RNF_17	1993	1934	216	251	D	.
RNF_18	2121	4254	526	419	D	.
RNF_19	2086	3701	4638	4492	D	.
RNF_20	6443	7418	3284	3187	D	.
RNF_21	3352	7350	1961	3072	D	.
RNF_22	2	772	39	81	D	TRUE
RNF_23	3700	1544	1546	320	D	.
RNF_24	1150	4350	2603	3363	D	.
RNF_25	649	2122	29	512	D	TRUE
RNF_26	669	247	2691	2537	D	.
RNF_27	3303	4512	4815	6308	D	.
RNF_28	6148	7204	1727	3799	D	.
RNF_29	144	668	3089	7763	D	.
RNF_30	45	25	147	1150	D	TRUE
RNF_31	372	330	1591	1802	D	.
RNF_32	338	136	1837	1287	D	.
RNF_33	6	7	967	888	D	TRUE
RNF_34	2929	3541	52	9	D	TRUE
RNF_35	3039	9730	4951	5396	D	.
RNF_36	6277	6511	4911	7008	D	.
RNF_37	6088	14238	4779	6216	D	.
RNF_38	5	9957	7127	6530	D	TRUE
RNF_39	6167	8827	2018	2368	D	.
RNF_40	6519	6599	7520	6833	D	.
RNF_41	3444	6308	4627	5045	D	.
RNF_42	3738	6604	1598	1822	D	.

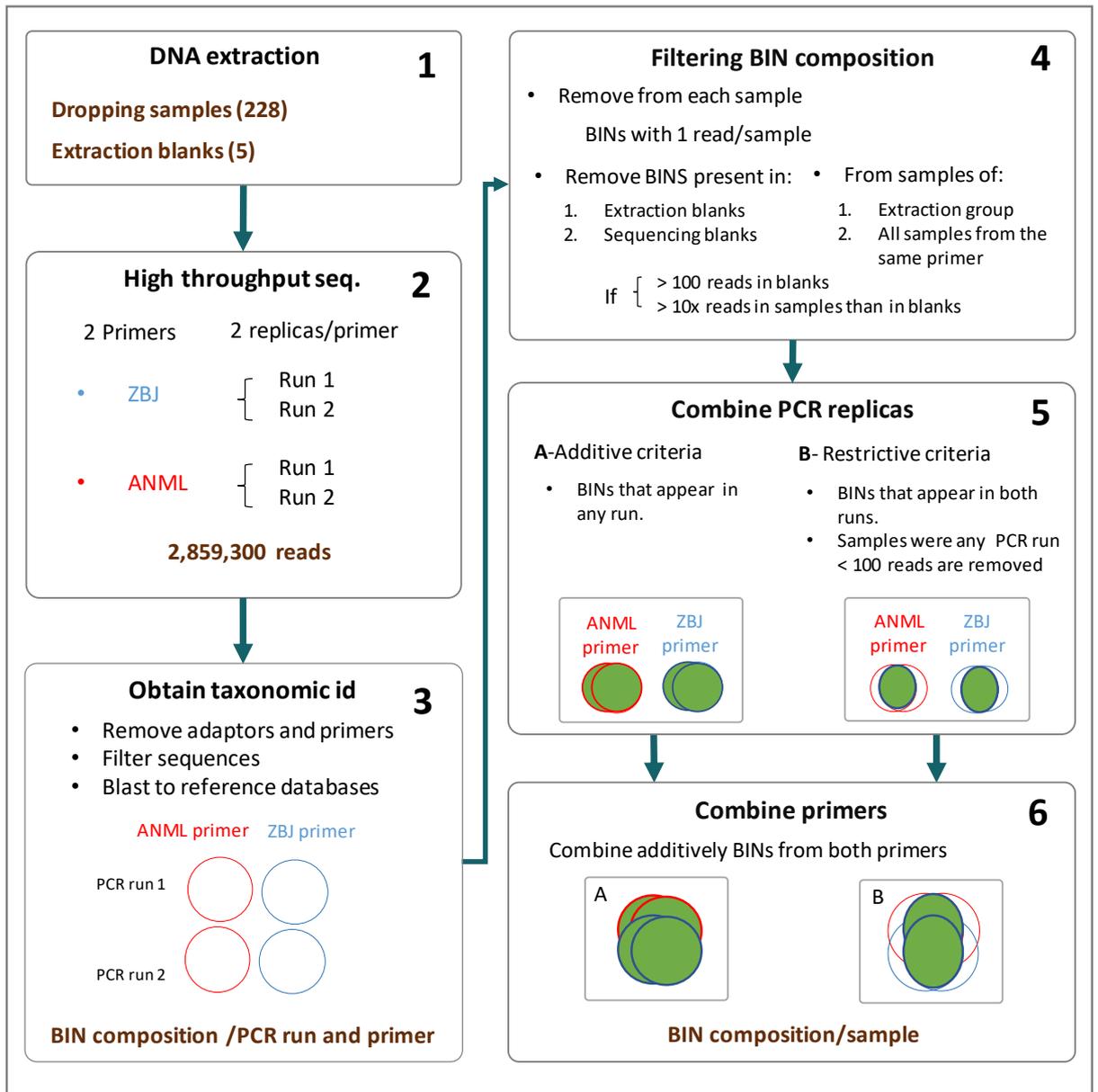
Sample name	ANML_1	ANML_2	ZBJ_1	ZBJ_2	Sample type	Failed
RNF_43	3436	13103	1163	181	D	.
RNF_44	4311	9291	541	5673	D	.
RNF_45	932	91	38	62	D	TRUE
RNF_46	3227	7602	3995	4363	D	.
RNF_47	6441	9061	6231	7498	D	.
RNF_48	1	3307	5372	6126	D	TRUE
RNF_49	2109	3973	4135	4434	D	.
RNF_50	3139	3421	7682	6700	D	.
RNF_52	46	1270	308	3337	D	TRUE
RNF_53	205	37	1054	3325	D	TRUE
RNF_54	1776	4670	1215	1306	D	.
RNF_55	110	75	66	72	D	TRUE
RNF_56	1360	1226	1336	1032	D	.
RNF_57	2260	1974	393	745	D	.
RNF_58	4156	5322	1124	1120	D	.
RNF_59	3	6320	975	1320	D	TRUE
RNF_60	5098	2525	366	578	D	.
RNF_61	1248	1579	1191	1391	D	.
RNF_62	5	2	1	8	D	TRUE
RNF_63	0	9	576	3	D	TRUE
RNF_64	2426	3131	5563	6426	D	.
RNF_65	1592	54	3583	5333	D	TRUE
RNF_66	1	467	62	14	D	TRUE
RNF_67	4008	3366	5413	5077	D	.
RNF_68	4480	8082	5730	6941	D	.
RNF_69	2330	3157	4818	5430	D	.
RNF_70	3477	6658	4769	4402	D	.
RNF_71	4111	7231	2528	922	D	.
RNF_72	1247	1629	2404	2133	D	.
RNF_73	7623	540	2515	3077	D	.
RNF_74	4321	5151	4381	6201	D	.
RNF_75	3140	5082	5570	6323	D	.
RNF_76	3150	4352	5146	6508	D	.
RNF_77	1256	1349	6153	5925	D	.
RNF_78	625	2246	2658	1740	D	.
RNF_79	3134	3759	2076	851	D	.
RNF_80	1911	3627	4292	3688	D	.
RNF_81	2447	3028	1306	1337	D	.
RNF_82	2820	2844	896	1001	D	.
RNF_83	3114	715	8495	7349	D	.
RNF_84	4330	3322	3637	6789	D	.
RNF_85	4789	5204	6422	7623	D	.
RNF_86	2954	9595	5067	6202	D	.
RNF_87	5940	11539	5340	6157	D	.
RNF_88	4735	10223	1815	3362	D	.
RNF_89	5501	9866	3752	4250	D	.
RNF_90	88	2448	81	297	D	TRUE
RNF_91	4266	8944	3216	3091	D	.

Sample name	ANML_1	ANML_2	ZBJ_1	ZBJ_2	Sample type	Failed
RNF_92	6646	4014	5294	6902	D	.
RNF_93	4813	8490	4773	4622	D	.
RNF_94	5237	4735	4001	5707	D	.
RNF_95	6347	8863	5118	6249	D	.
RNF_96	7575	7644	3536	5274	D	.
RNF_97	4823	7053	2823	2572	D	.
RNF_98	6786	7938	4842	2629	D	.
RNF_99	2985	1398	4005	4316	D	.
RNF_100	0	364	6	1	D	TRUE
RNF_101	7102	8656	6250	5290	D	.
RNF_102	111	21	1840	1607	D	TRUE
RNF_103	3844	3541	5300	5460	D	.
RNF_104	3150	6490	447	386	D	.
RNF_105	9	4	157	55	D	TRUE
RNF_106	1165	0	3323	3841	D	TRUE
RNF_107	5289	7522	8277	6929	D	.
RNF_108	3217	1652	4594	2726	D	.
RNF_109	80	6234	60	2099	D	TRUE
RNF_110	1716	2300	4433	5770	D	.
RNF_111	1886	2110	2617	3050	D	.
RNF_112	2537	2155	1457	1490	D	.
RNF_113	1508	939	3303	3006	D	.
RNF_114	6116	7359	5986	6927	D	.
RNF_115	5192	6602	4217	4112	D	.
RNF_116	694	597	2225	1768	D	.
RNF_117	4657	4713	4673	5374	D	.
RNF_118	5395	5967	2967	2711	D	.
RNF_119	3979	4633	4394	5807	D	.
RNF_120	4379	5066	6049	6878	D	.
RNF_121	7091	4851	4227	4442	D	.
RNF_122	98	66	2168	2321	D	TRUE
RNF_123	2242	3263	4219	5631	D	.
RNF_124	3157	3062	2815	5928	D	.
RNF_125	362	333	1324	1296	D	.
RNF_126	2527	2035	2281	1814	D	.
RNF_127	4780	6045	3036	3034	D	.
RNF_128	5264	7624	3298	3899	D	.
RNF_129	2984	3260	1875	1593	D	.
RNF_131	4252	3201	7604	7903	D	.
RNF_133	1427	1039	3688	3910	D	.
RNF_134	3824	990	7214	6999	D	.
RNF_135	604	800	3536	959	D	.
RNF_136	5365	858	1739	1494	D	.
RNF_138	3060	4052	4669	6847	D	.
RNF_139	3444	4457	6446	5079	D	.
RNF_140	3197	507	5524	5978	D	.
RNF_141	3683	4173	4753	1072	D	.
RNF_142	2798	1278	107	2610	D	.

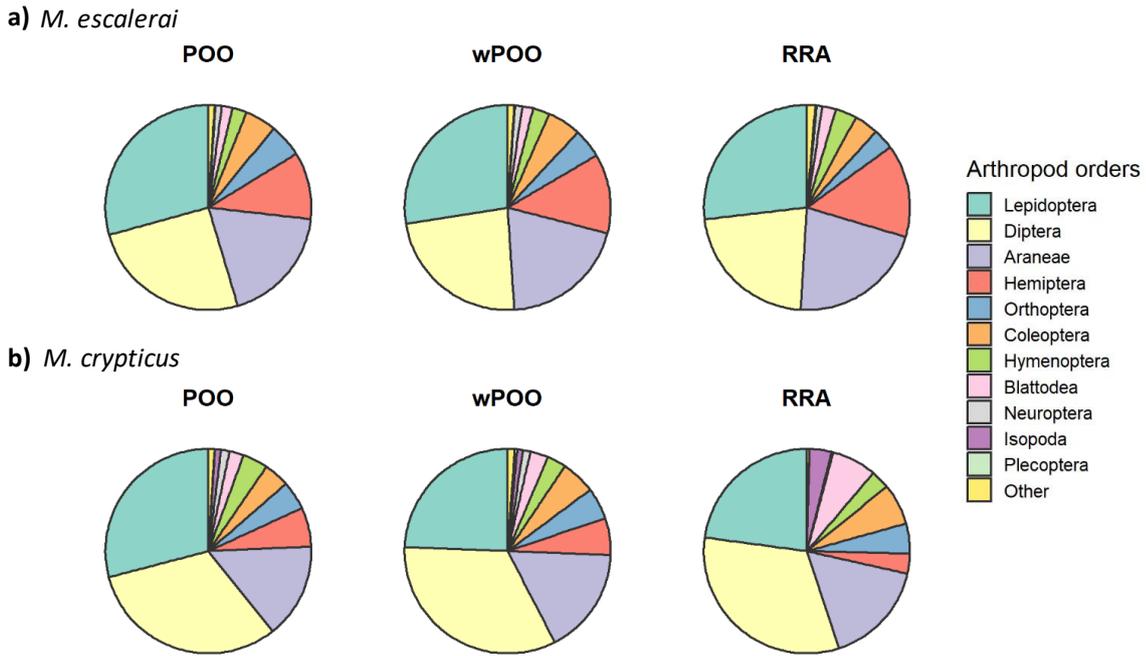
Sample name	ANML_1	ANML_2	ZBJ_1	ZBJ_2	Sample type	Failed
RNF_143	7502	8895	7143	9080	D	.
RNF_144	193	142	6769	4863	D	.
RNF_145	1	371	162	3884	D	TRUE
RNF_146	4123	6550	1961	8827	D	.
RNF_147	962	654	3436	3621	D	.
RNF_148	2806	3660	3483	3877	D	.
RNF_149	1173	927	1277	1269	D	.
RNF_150	2483	1417	6663	6024	D	.
RNF_151	1103	1253	18	17	D	TRUE
RNF_152	54	53	229	176	D	TRUE
RNF_153	5144	4410	5626	6397	D	.
RNF_154	3261	4193	4023	4331	D	.
RNF_155	1871	2347	1059	2661	D	.
RNF_156	718	397	567	599	D	.
RNF_157	4676	1109	4751	4233	D	.
RNF_158	580	625	2520	2480	D	.
RNF_159	4122	4938	5894	5099	D	.
RNF_160	843	4150	5843	7612	D	.
RNF_161	6199	6701	6677	7871	D	.
RNF_162	1458	1633	8001	7235	D	.
RNF_163	1480	836	4547	4094	D	.
RNF_164	5441	6215	7241	7267	D	.
RNF_165	4082	4721	975	1243	D	.
RNF_166	5439	5815	7199	7689	D	.
RNF_167	7025	7161	6153	7877	D	.
RNF_168	6703	7241	8372	8283	D	.
RNF_169	5960	8014	7334	8111	D	.
RNF_170	4916	3021	6141	7413	D	.
RNF_171	3935	4037	3470	5026	D	.
RNF_172	4617	4919	1375	6815	D	.
RNF_173	4845	5264	2605	3099	D	.
RNF_174	3541	2691	4243	2401	D	.
RNF_175	11	39	81	2	D	TRUE
RNF_176	982	152	8	3	D	TRUE
RNF_177	2743	1905	2015	3542	D	.
RNF_178	4644	1184	1919	3845	D	.
RNF_179	659	352	356	714	D	.
RNF_180	355	241	4	5	D	TRUE
RNF_181	719	219	513	32	D	TRUE
RNF_182	2906	684	25	36	D	TRUE
RNF_183	103	60	1287	1052	D	TRUE
RNF_184	1086	5	278	291	D	TRUE
RNF_185	350	554	101	277	D	.
RNF_186	120	128	8	5	D	TRUE
RNF_187	86	24	64	24	D	TRUE
RNF_189	1857	1441	1069	1159	D	.
RNF_191	1395	492	5304	5253	D	.
RNF_192	44	37	154	157	D	TRUE

Sample name	ANML_1	ANML_2	ZBJ_1	ZBJ_2	Sample type	Failed
RNF_193	1523	2329	810	3436	D	.
RNF_194	1917	1364	1371	1799	D	.
RNF_195	141	90	10	19	D	TRUE
RNF_197	4713	3298	651	1028	D	.
RNF_199	11	6	2	1	D	TRUE
RNF_201	3384	4436	2877	3498	D	.
RNF_202	5097	6577	43	6268	D	TRUE
RNF_203	2168	1852	2666	3115	D	.
RNF_204	2601	1099	5408	4882	D	.
RNF_206	20	9	90	564	D	TRUE
RNF_207	10	19	3	620	D	TRUE
RNF_208	3263	3977	1348	1644	D	.
RNF_209	189	6629	4384	6337	D	.
RNF_210	24	115	12	4	D	TRUE
RNF_211	6015	7813	1755	3155	D	.
RNF_212	31	4	2	105	D	TRUE
RNF_213	4380	5181	3236	2747	D	.
RNF_214	6248	7061	4687	5508	D	.
RNF_215	4209	5465	2486	2231	D	.
RNF_216	5070	5091	4007	4107	D	.
RNF_217	1091	2224	2362	4847	D	.
RNF_218	1902	1994	159	247	D	.
RNF_219	113	2	8	7168	D	TRUE
RNF_220	1881	1906	524	556	D	.
RNF_221	799	667	1212	2991	D	.
RNF_223	85	28	3640	3845	D	TRUE
RNF_224	6	9	84	433	D	TRUE
RNF_226	1422	1743	2376	2776	D	.
RNF_229	822	618	589	652	D	.
RNF_231	26	8	2750	2391	D	TRUE
RNF_234	38	8	33	5	D	TRUE
RNF_235	1003	972	3419	3627	D	.
RNF_236	21	7	4039	4344	D	TRUE
RNF_239	925	1302	369	1402	D	.
RNF_240	7792	8727	6179	7988	D	.
RNF_241	5326	6637	6102	7075	D	.
RNF_242	2850	2317	251	267	D	.
RNF_243	40	13	42	32	D	TRUE
RNF_244	851	1743	414	1961	D	.
RNF_248	5276	5072	5790	7816	D	.
RNF_249	4544	5122	3474	3411	D	.
RNF_251	7569	7149	7588	8956	D	.
RNF_B10	5	205	22	2	BlankD	.
RNF_B14	1	5	222	9	BlankD	.
RNF_B2	36	3	0	101	BlankD	.
RNF_B4	12	9	3	4	BlankD	.
RNF_BS1	28	1	0	59	BlankSweep	.
RNF_S1A	2721	3433	3616	4713	S	.

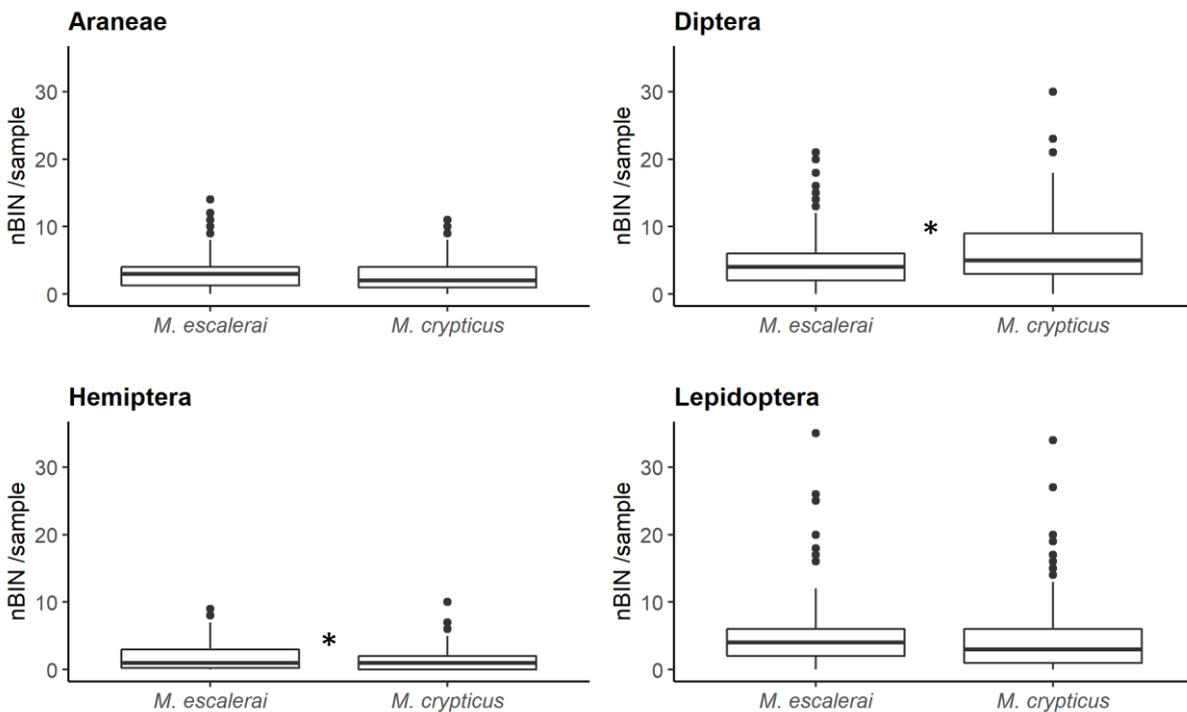
Sample name	ANML_1	ANML_2	ZBJ_1	ZBJ_2	Sample type	Failed
RNF_S1B	3892	5309	4309	5364	S	.
RNF_S2	3683	3624	3234	3333	S	.
RNF_S5	2182	3408	2575	3053	S	.
RNF_S6A	4661	6410	4070	5612	S	.
RNF_S6B	5825	10345	5076	6571	S	.
RNF_S7A	427	303	782	1369	S	.
RNF_S7B	5410	6218	5150	5301	S	.
RNF_S7C	1605	1957	1033	1536	S	.
RNF_S9A	6007	7438	4362	5368	S	.
RNF_S9B	4957	7397	3659	5258	S	.
RNF_S10A	4903	7393	1687	3377	S	.
RNF_S10B	3008	5563	3720	5096	S	.
RNF_S11	3160	4694	3595	4348	S	.
RNF_S12A	7278	9584	6244	7521	S	.
RNF_S12B	4373	4934	3280	3804	S	.
RNF_S13A	5244	7284	5526	5081	S	.
RNF_S13A(2)	2998	3454	5259	6543	S	.
RNF_S13B	3591	6380	5316	5434	S	.
RNF_S13B(2)	7771	7322	6704	7391	S	.
RNF_S14	2422	2350	3481	4608	S	.
RNF_S17	3510	3084	2626	3666	S	.
RNF_S18A	6063	4411	4986	6718	S	.
RNF_S18B	6169	7288	5871	6400	S	.
RNF_S19A	7090	9155	7223	8311	S	.
RNF_S19B	2419	4835	6949	8085	S	.
RNF_S20A	2577	2162	3005	3604	S	.
RNF_S20B	7805	5498	5901	6610	S	.
RNF_S21	3829	3563	3740	3473	S	.
RNF_S25A	6585	4753	4692	6217	S	.
RNF_S25B	10220	6346	6604	6839	S	.
RNF_S25C	6625	6353	6693	6334	S	.
RNF_S26A	6577	5389	8583	7922	S	.
RNF_S26B	5974	4564	7523	8999	S	.
RNF_S26C	8655	7406	7441	8409	S	.
RNF_S31A	4310	5690	4514	4762	S	.
RNF_S31B	5959	4798	6715	5267	S	.
RNF_S33	6876	7165	4873	6014	S	.
RNF_S34A	6414	4449	6819	7131	S	.
RNF_S34B	6350	6948	6825	7253	S	.
RNF_S34C	7882	3835	7449	10340	S	.
RNF_S35	4734	4591	1695	3005	S	.
RNF_S36	5852	5626	4809	4297	S	.
RNF_Seq Blank1	3	1	3	19	Blankseq	.
RNF_Seq Blank2	2	1	4	8	Blankseq	.
RNF_Seq Blank3	24	4	22	8	Blankseq	.
RNF_Seq Blank4	10	8	3	162	Blankseq	.
RNF_Seq Blank5	6	1	4	125	Blankseq	.



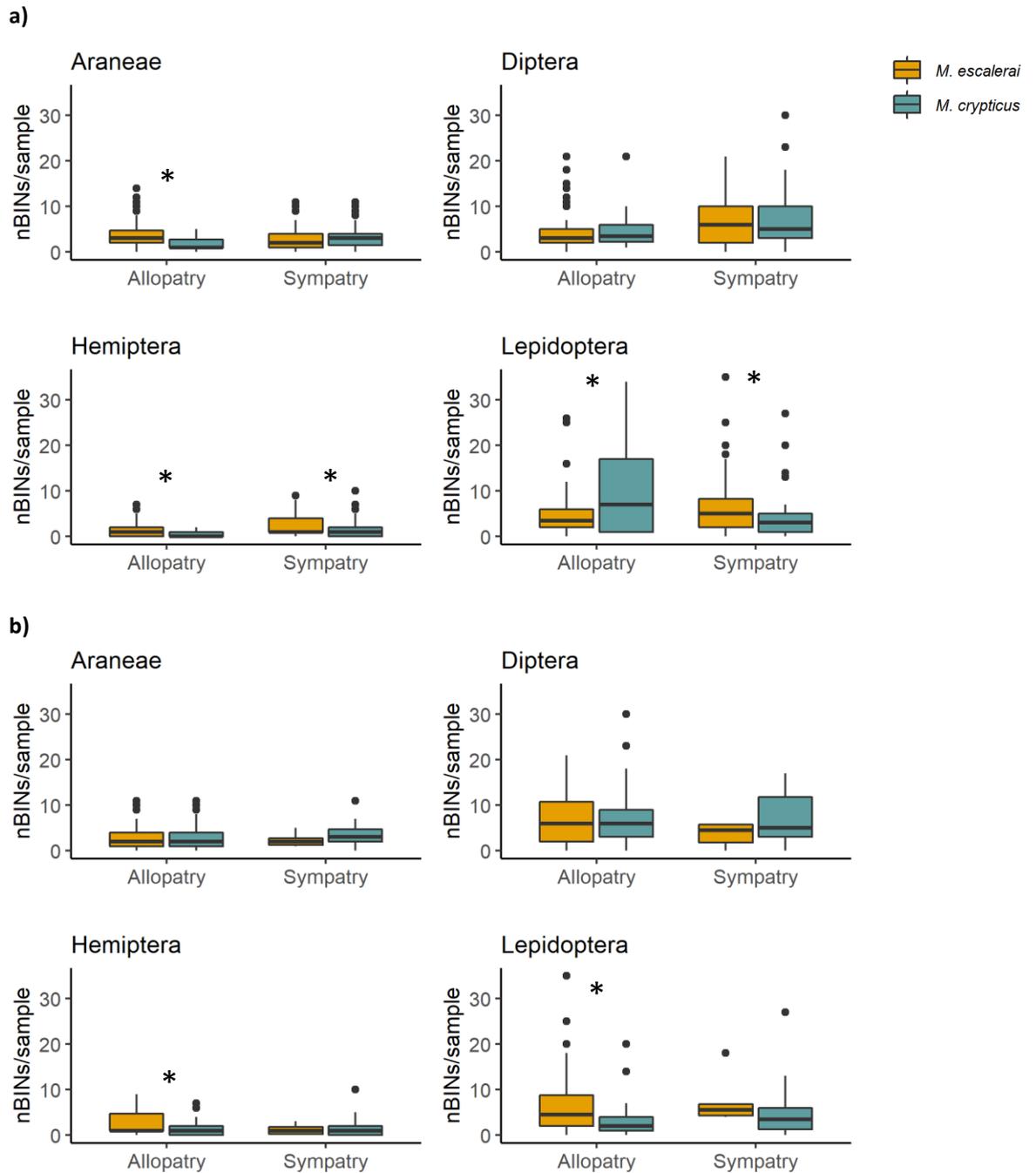
Supplementary Fig. B1.1 – Flow chart summarising the process followed to obtain taxonomic prey composition from dropping samples of *M. escaleraei* and *M. crypticus*.



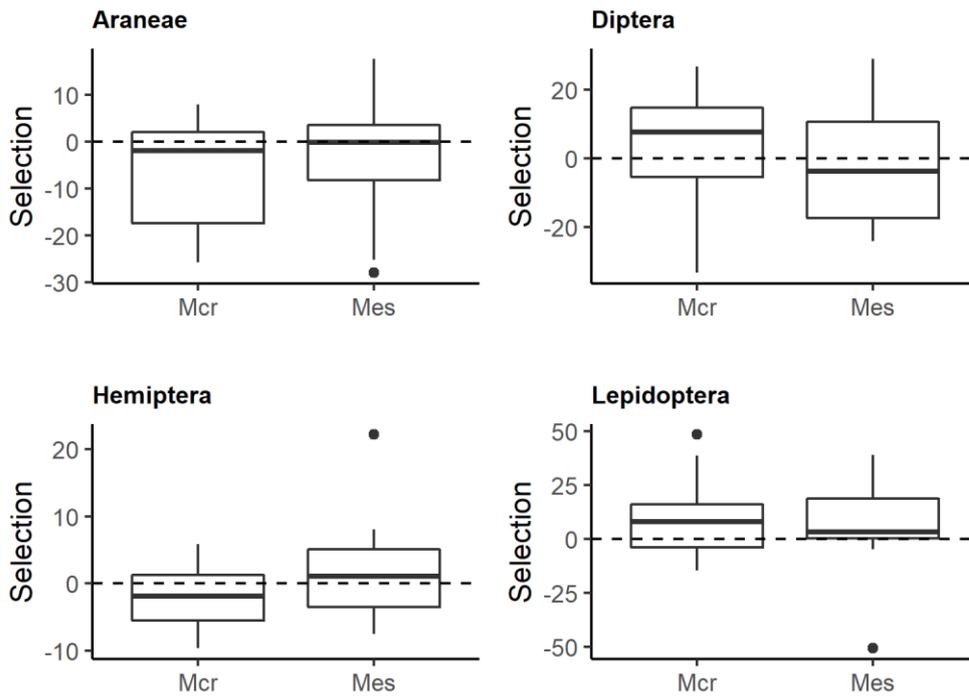
Supplementary Fig. B1.2 – Diet of *Myotis escalerai* (a) and *Myotis crypticus* (b) according to percent frequency of occurrence (POO), weighted percent of occurrence (wPOO) and relative read abundance (RRA).



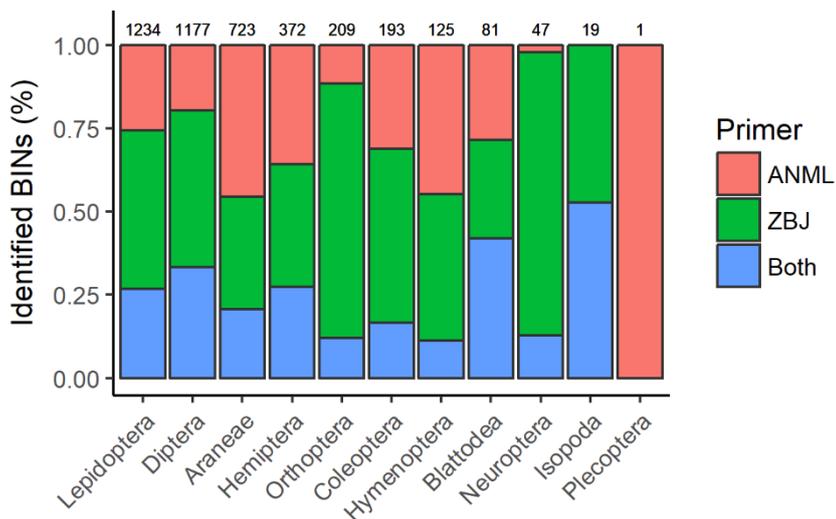
Supplementary Fig. B1.3 – Number of BINs/sample of each of the four main Arthropod orders in the diet of *Myotis escalerai* and *Myotis crypticus*. Box represents first and third data quartiles. Whiskers extend from the hinge to the largest value no further than 1.5 * distance between the first and third quartiles. Data beyond the end of the whiskers are plotted individually. Statistically detectable differences at $p < 0.05$ are noted with a star.



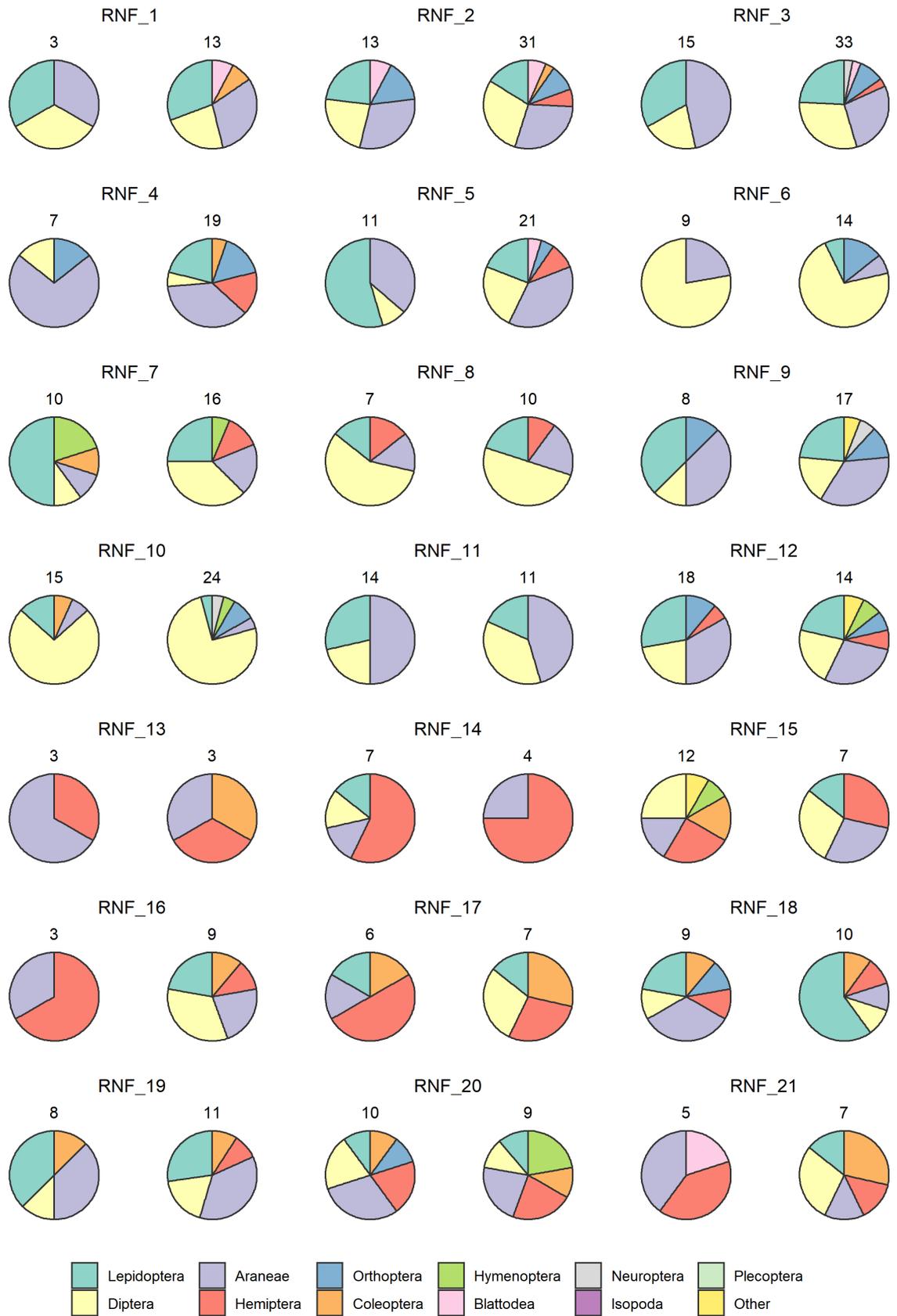
Supplementary Fig. B1.4 – Number of BINs of each of the four main Arthropod orders in bat samples from sympatric and allopatric locations at the regional scale (a) and at fine scale (b). Statistically detectable differences at $p < 0.05$ are noted with a star. Boxplot interpretation is detailed in Supplementary Fig. B1.3.



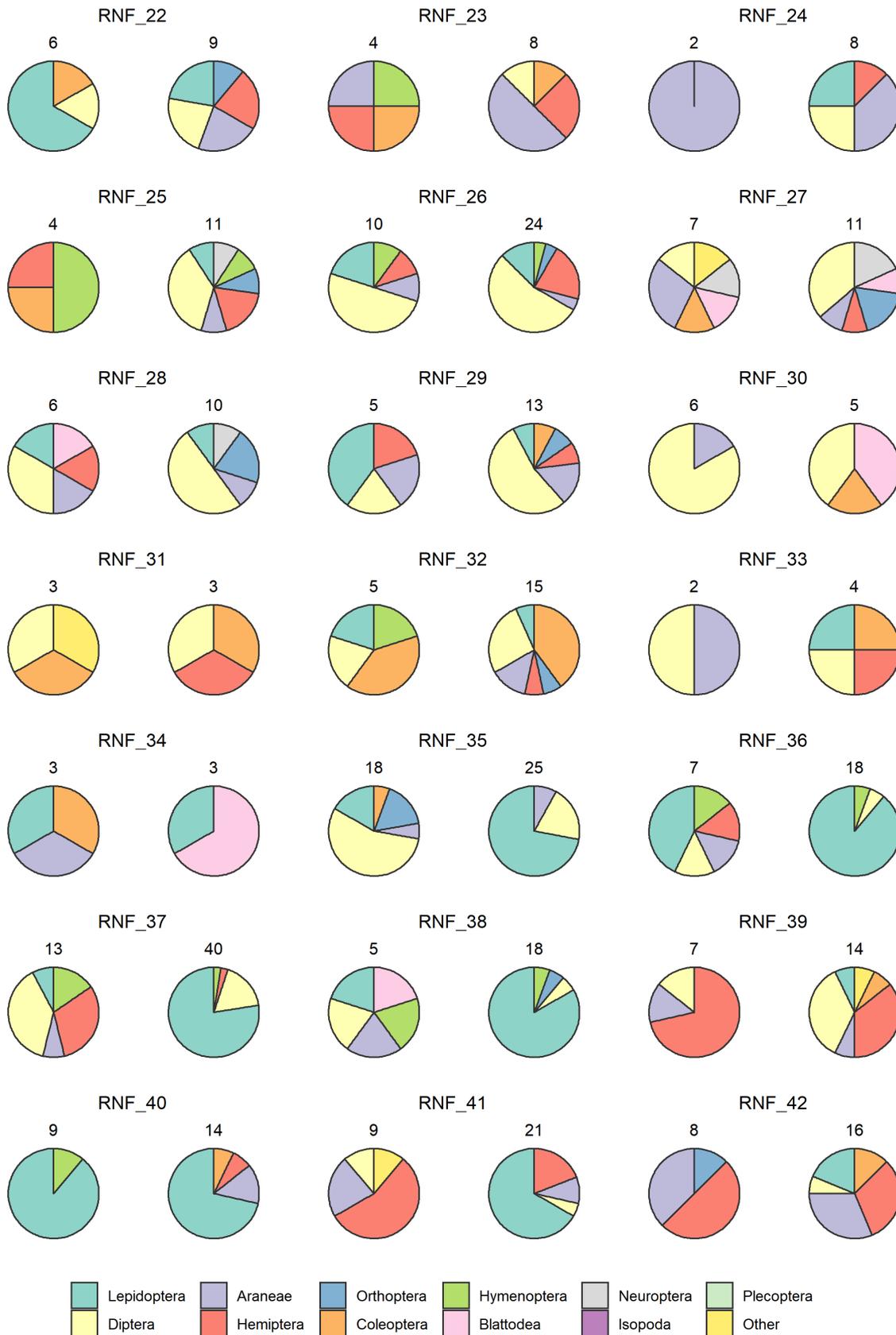
Supplementary Fig. B1.5 – Selection values (bat diet wPOO – Arthropod availability) of *M. escalerai* and *M. crypticus* towards each of the main arthropod orders. Boxplot interpretation is detailed in Supplementary Fig. B1.3.



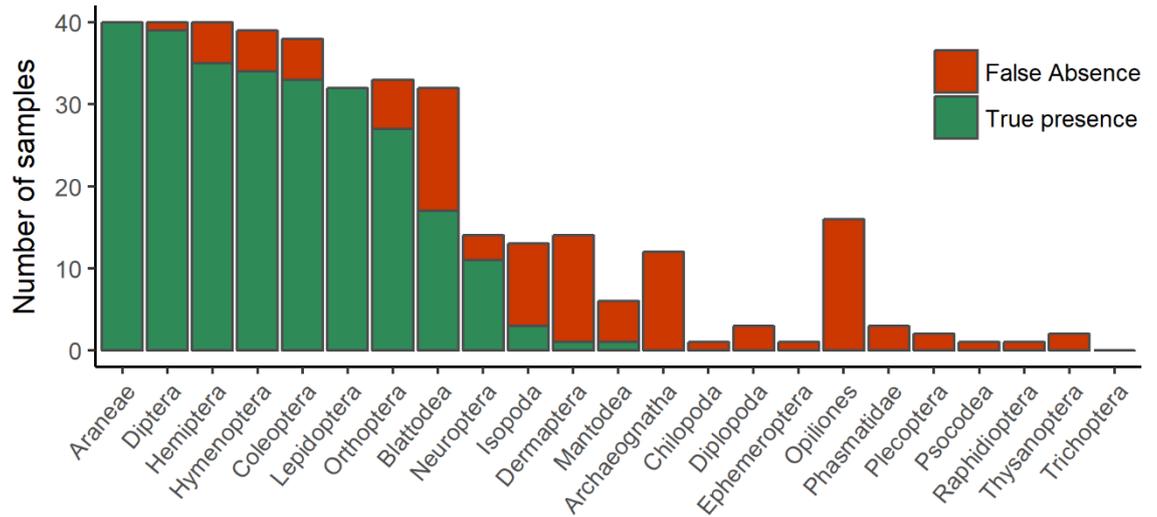
Supplementary Fig. B1.6 – Proportion of BINS of each arthropod order, depending on the primer from which it was recovered. Red recovered uniquely by ANML, green uniquely by ZBJ, and blue recovered by both. Numbers above columns show number of BINS.



Supplementary Fig. B1.7 – Prey order composition of a subset of individual dropping samples (RNF 1-21) comparing ANML (left) and ZBJ (right) primers. Number on top of each pie chart shows total BINs recovered.



Supplementary Fig. B1.8 – Prey order composition of a subset of individual dropping samples (RNF 22-42) comparing ANML (left) and ZBJ (right) primers. Number on top of each pie chart shows total BINs recovered.

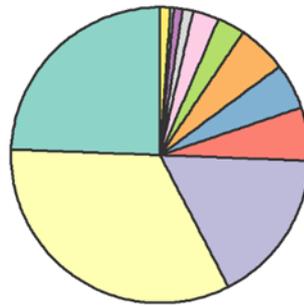
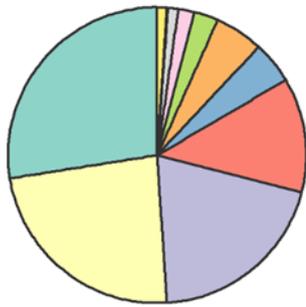


Supplementary Fig. B1.9 – Number of samples in which each arthropod order appears in the molecular identification (green) relative to the morphological identification of sweeping samples (total bar height).

a) Inclusive criteria

Diet *Myotis escaleraei* (wPOO)

Diet *Myotis crypticus* (wPOO)



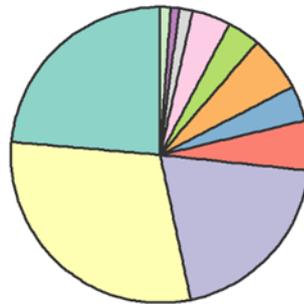
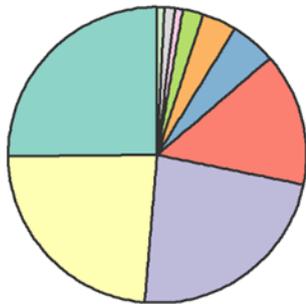
Arthropod orders

- Lepidoptera
- Diptera
- Araneae
- Hemiptera
- Orthoptera
- Coleoptera
- Hymenoptera
- Blattodea
- Neuroptera
- Isopoda
- Plecoptera
- Other

b) Conservative criteria

Diet *Myotis escaleraei* (wPOO)

Diet *Myotis crypticus* (wPOO)



Supplementary Fig. B1.10 – Overall diet composition of *M. escaleraei* and *M. crypticus* using weighted Percent of Occurrence (wPOO). Using the inclusive criteria (a) and the conservative union criteria (b) to pool prey composition from PCR replicates.

References for Appendix B

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Appendix C Supplementary material for chapter 4

C1 Ecological information on species

Supplementary Table C1.1 – Habitat use of species (full references are presented at the end of Appendix C).

Species	Main habitat type used	References
<i>E. serotinus</i>	Generalist open air forager, over woodlands, arable land	(Robinson & Stebbings 1997)
<i>E. isabellinus</i>	Generalist open air forager, scrublands, water courses	(Lisón <i>et al.</i> 2014; Lisón 2017)
<i>M. escalerae</i>	Linked to forest, Mediterranean	Personal observation, 2018
<i>M. crypticus</i>	Linked to forest, Atlantic and “middle-mountain”	Personal observation, 2018 (Alcalde <i>et al.</i> 2018)
<i>P. auritus</i>	Linked to forest. Prefers broadleaved but can exploit any type, including dense coniferous	(Entwistle <i>et al.</i> 1996; Boye & Dietz 2005; Murphy <i>et al.</i> 2012; Ashrafi <i>et al.</i> 2013)
<i>P. austriacus</i>	More semi open habitats, can use deciduous forests but also agricultural mosaics and unimproved grasslands, and suburban areas in the north of its range.	(Boye & Dietz 2005; Razgour <i>et al.</i> 2011b; Ashrafi <i>et al.</i> 2013)
<i>P. macrobullaris</i>	High mountain meadows and grasslands in the Pyrenees, but reported in forests in the Alps.	(Alberdi <i>et al.</i> 2012, 2013; Preatoni <i>et al.</i> 2012; Ashrafi <i>et al.</i> 2013)
<i>P. kolombatovici</i>	Open and semi open habitats, including steppe, deciduous forests, open woodlands, olive groves, shrubland, clearings, and meadows.	(Tvrtković 2006; Davy <i>et al.</i> 2007; Hutson <i>et al.</i> 2008; Ivanisin-Kardum <i>et al.</i> 2019)
<i>R. euryale</i>	Linked to forest, especially broadleaved although also could exploit edge habitats.	(Russo <i>et al.</i> 2002, 2005; Aihartza <i>et al.</i> 2003; Goiti <i>et al.</i> 2003, 2008; Salsamendi <i>et al.</i> 2012)
<i>R. mehelyi</i>	Semi open habitats and mosaics.	(Russo <i>et al.</i> 2005; Salsamendi <i>et al.</i> 2012)

Supplementary Table C1.2 – Diet of species (full references at the end of Appendix C).

Species	Main prey order	References
<i>E. serotinus</i>	Mainly Coleoptera	(Robinson & Stebbings 1993, 1997; Vaughan 1997; Zukal & Gajdosik 2012)
<i>E. isabellinus</i>	Mainly Coleoptera	(Benda et al. 2014; Lisón et al. 2015)
<i>M. escaleraei</i>	Great variety but mostly Diptera, Lepidoptera, Araneae	This thesis, Chapter 3.
<i>M. crypticus</i>	Great variety but mostly Diptera, Lepidoptera, Araneae	This thesis, Chapter 3.
<i>P. auritus</i>	Mainly Lepidoptera and Diptera, but other groups as well	(Swift & Racey 1983; Rydell 1989; Beck 1995; Vaughan 1997; Ashrafi et al. 2011; Razgour et al. 2011a)
<i>P. austriacus</i>	Mainly Lepidoptera and Diptera, but other groups as well	(Beck 1995; Ashrafi et al. 2011; Razgour et al. 2011a)
<i>P. macrobullaris</i>	Lepidoptera specialist	(Ashrafi et al. 2011; Alberdi et al. 2012)
<i>P. kolombatovici</i>	Mainly Lepidoptera, lower proportions of Hemiptera and Diptera	(Pavlinić 2008; Whitaker & Karatas 2009)
<i>R. euryale</i>	Lepidoptera specialist	(Goiti et al. 2004; Salsamendi et al. 2012; Arrizabalaga-Escudero et al. 2018)
<i>R. mehelyi</i>	Lepidoptera specialist	(Goiti et al. 2008; Salsamendi et al. 2012; Arrizabalaga-Escudero et al. 2018)

Supplementary Table C1.3 – Roost use of species (full references at the end of Appendix C).

Species	Main roost type used	References
<i>E. serotinus</i>	Crevice, mainly in anthropogenic structures, but also in natural rock	(Catto et al. 1996; Dietz & Kiefer 2016)
<i>E. isabellinus</i>	Crevice, mainly in natural rock, but also in anthropogenic structures	(Dietz & Kiefer 2016)
<i>M. escaleraei</i>	Crevice, in caves and mines and in anthropogenic structures	(Dietz & Kiefer 2016; Juste et al. 2019)
<i>M. crypticus</i>	Tree cavities, but also crevice in anthropogenic structures	(Dietz & Kiefer 2016; Alcalde et al. 2018; Juste et al. 2019)
<i>P. auritus</i>	Tree cavities and anthropogenic structures	(Swift 1998; Boye & Dietz 2005; Alcalde et al. 2018)
<i>P. austriacus</i>	Anthropogenic structures, caves and crevice in natural rock	(Swift 1998; Boye & Dietz 2005)
<i>P. macrobullaris</i>	Rock crevice in Pyrenees, anthropogenic structures in the Alps and Basque Country	(Mattei-Roesli 2010; Alberdi et al. 2015)
<i>P. kolombatovici</i>	Anthropogenic structures, caves, rock crevice, trees	(Hutson et al. 2007; Marnell & Presetnik 2010; Dietz & Kiefer 2016)
<i>R. euryale</i>	Caves and mines	(Alcalde et al. 2018)
<i>R. mehelyi</i>	Caves and mines	(Alcalde et al. 2018)

C2 List of publications from which occurrence records for SDMs were extracted

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C3 Supplementary Tables and Figures

Supplementary Table C3.1 – Variables used in the Species Distribution Models. Code used in

Supplementary Table C3.2-C3.5.

Type	Variable code	Variables	Source
Clim	bio_4	Temperature Seasonality	www.worldclim.org
	bio_6	Temperature coolest month	www.worldclim.org
	bio_5	Temperature hottest month	www.worldclim.org
	bio_7	Temperature Annual Range	www.worldclim.org
	tmin4	min April temperature	www.worldclim.org
	bio_10	Mean Temperature of Warmest Quarter	www.worldclim.org
	bio_11	Mean Temperature of Coldest Quarter	www.worldclim.org
	tmean9_10	Mean Autumn temperature (Sept-Oct)	www.worldclim.org
	tmin9_10	Min Autumn temperature (Sept-Oct)	www.worldclim.org
	tmean4	Mean April temperature	www.worldclim.org
	bio_12	Mean precipitation	www.worldclim.org
	bio_18	Precipitation of Warmest Quarter	www.worldclim.org
	bio_15	Precipitation Seasonality	www.worldclim.org
	bio_14	Precipitation driest month	www.worldclim.org
	bio_13	Precipitation of Wettest month	www.worldclim.org
bio_16	Precipitation of Wettest Quarter	www.worldclim.org	
Geog	elevation	Elevation	www.worldclim.org
	slope	Slope	From "Elevation"
	abruptness	Abruptness	From "Elevation"
	karst	distance to karst	http://arcweb.forest.usf.edu/
	litho	Lithology	http://ccgm.org/
Hab	dstc_rivers	Distance to permanent rivers	www.diva-gis.org
	landcover	Land cover type	ESACCI-LC 16 (https://cds.climate.copernicus.eu)
	dstc_forest	Distance to forest	From "landcover"
	dstc_broadl	Distance to broadleaved forest	From "landcover"
	dstc_coni	Distance to conifer forest	From "landcover"
	dstc_mixed	Distance to mixed forest	From "landcover"
	dstc_shrub	Distance to shrubland	From "landcover"
	dstc_crop	Distance to cropland	From "landcover"
	dstc_grass	Distance to grasslands	From "landcover"
	dstc_urban	Distance to cities	From "landcover"
	dstc_mosaic	Distance to mosaic	From "landcover"
	tree_cover	% tree canopy cover (2000)	http://earthenginepartners.appspot.com/
	habrichness	Habitat heterogeneity	From "landcover"
Hum	pop_2000	Human population year 2000	https://earthdata.nasa.gov/
	INDI	Light developing index	http://ngdc.noaa.gov/eog/download.html

Supplementary Table C3.2 – Variables used for the *Eptesicus* group SDMs and their importance in the model.

<i>E. serotinus</i>		<i>E. isabellinus</i>	
Variable	Imp	Variable	Imp
bio_11	0.27	bio_14	0.50
bio_10	0.22	dstc_shrub	0.35
dstc_urban	0.21	bio_11	0.33
bio_4	0.19	bio_10	0.20
lc	0.08	bio_4	0.18
bio_14	0.07	tree_cover	0.08
tree_cover	0.06	elevation	0.08
dstc_grass	0.05	dstc_mosaic	0.08
dstc_shrub	0.03	lc	0.08
dstc_crop	0.02	Habr richness	0.07
Habr richness	0.02	slope	0.06
elevation	0.02	dstc_urban	0.05
slope	0.02	dstc_crop	0.02
litho	0.01	karst	0.02
karst	0.01	litho	0.01

Supplementary Table C3.3 – Variables used for the *Myotis* group SDMs and their importance in the model.

<i>M. escalerae</i>		<i>M. crypticus</i>	
Variable	Imp	Variable	Imp
bio_4	0.31	elevation	0.46
bio_11	0.23	bio_11	0.34
elevation	0.17	bio_4	0.30
dstc_conifer	0.16	bio_18	0.25
bio_5	0.14	dstc_broadlv	0.12
bio_18	0.13	bio_15	0.07
slope	0.10	ldni	0.07
tree_cover	0.06	tree_cover	0.07
bio_15	0.06	karst	0.07
dstc_mosaic	0.04	bio_5	0.06
lc	0.03	bio_13	0.03
karst	0.01	lc	0.02
		litho	0.01

Supplementary Table C3.4 – Variables used for the *Plecotus* group SDMs and their importance in the model.

<i>P. auritus</i>		<i>P. austriacus</i>		<i>P. macrobullaris</i>	
Variable	Imp	Variable	Imp	Variable	Imp
bio_6	0.18	bio_6	0.18	bio_13	0.36
lc	0.14	dstc_forest	0.15	dstc_shrub	0.33
bio_18	0.14	bio_4	0.12	slope	0.17
tree_cover	0.13	dstc_shrub	0.10	bio_6	0.16
bio_5	0.11	lc	0.10	Habr richness	0.12
bio_4	0.10	bio_5	0.10	bio_15	0.08
dstc_forest	0.04	Habr richness	0.07	ldni	0.05
litho	0.03	tree_cover	0.04	litho	0.04
elevation	0.03	bio_15	0.04	lc	0.04
Habr richness	0.02	slope	0.04	dstc_forest	0.03
pop_2000	0.02	dstc_rivers	0.02	dstc_rivers	0.02
bio_15	0.02	pop_2000	0.02	tree_cover	0.02
ldni	0.02	litho	0.02		
dstc_rivers	0.01	elevation	0.02		
slope	0.01	ldni	0.01		
		karst	0.01		

Supplementary Table C3.5 – Variables used for the *Rhinolophus* group SDMs and their importance in the model.

<i>R. euryale</i>		<i>R. mehelyi</i>	
Variable	Imp	Variable	Imp
bio_10	0.41	bio_10	0.56
abrupness	0.34	dstc_shrub	0.20
bio_4	0.12	lc	0.13
bio_6	0.10	dstc_broadlv	0.13
dstc_broadlv	0.09	abrupness	0.13
karst	0.08	bio_13	0.07
tree_cover	0.06	bio_15	0.07
bio_13	0.05	bio_6	0.05
lc	0.03	bio_4	0.04
Habr richness	0.02	elevation	0.03
ldni	0.02	pop_2000	0.03
elevation	0.01	tree_cover	0.02
pop_2000	0.01	ldni	0.02
litho	0.01	karst	0.01

Supplementary Table C3.6 – Parameters used in Maxent final models for each species based on best AIC performance.

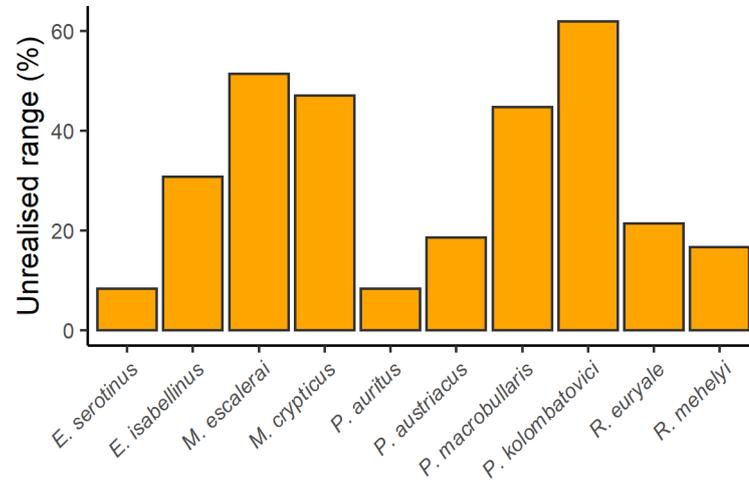
Species	Features	Regularization
<i>E. serotinus</i>	4	1.5
<i>E. isabellinus</i>	4	1.5
<i>M. escalerae</i>	4	1
<i>M. nattereri</i>	4	1
<i>M. crypticus</i>	4	1.5
<i>P. auritus</i>	4	1.5
<i>P. austriacus</i>	4	1.5
<i>P. macrobullaris</i>	4	1
<i>R. euryale</i>	4	1.5
<i>R. mehelyi</i>	4	1

Supplementary Table C3.7 – Area Under the Curve (AUC) and True Skill Statistic (TSS) scores for test data of the ensemble Species Distribution Models.

Species	TSS	AUC
<i>E. serotinus</i>	0.686	0.924
<i>E. isabellinus</i>	0.893	0.984
<i>M. escalerae</i>	0.931	0.991
<i>M. crypticus</i>	0.91	0.99
<i>P. auritus</i>	0.647	0.911
<i>P. austriacus</i>	0.729	0.942
<i>P. macrobullaris</i>	0.915	0.987
<i>R. euryale</i>	0.804	0.962
<i>R. mehelyi</i>	0.865	0.982

Supplementary Table C3.8 – Changes in predicted range size from present to future climate change scenario RCP 8.5 in 2070 for each bat species.

Bat species	Change in predicted range area (%)
<i>E. serotinus</i>	-16.82
<i>E. isabellinus</i>	6.08
<i>M. escalerae</i>	-48.59
<i>M. crypticus</i>	-15.74
<i>P. auritus</i>	-49.81
<i>P. austriacus</i>	0.60
<i>P. macrobullaris</i>	-46.04
<i>P. kolombatovici</i>	113.92
<i>R. euryale</i>	33.26
<i>R. mehelyi</i>	65.98



Supplementary Fig. C3.1 – Percent of predicted suitable range of each species based on SDM models that is unrealised, i.e. unoccupied based on the real known range limits of the species.

References for Appendix C

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