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DOCTORAL THESIS

A multifaceted approach to plant rarity: distribution, dynamics and interactions in a global change scenario

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Abstract

Background

In the current context of Global Change and the crisis of biodiversity, one of the biggests challenges that we face is to accurately estimate the vulnerability of species to changes in their environment. This is especially true for plants, which are strongly underrepresented in global assessments of species conservation despite being one of the major pillars of ecosystem function. In addition, plant species often show complex responses to global change that may differ significantly from those of animals. Thus, it is necessary that we deepen our knowledge on how plant species are distributed, their dynamics, vulnerability and threats as well as the potential consequences of their loss for the diversity and functioning of ecosystems. Although there are many ways to approach the vulnerability of a species, they are often difficult to assess, however, there are certain aspects of the ecology of a species that can serve as a proxy for their vulnerability. One such characteristic is rarity, as rare species are often regarded as more vulnerable or prone to extinction.

Objectives

In this thesis we explore the idea of rarity and how it applies to plant species at different ecological scales, from whole habitats to single populations, in order to better understand the relationship between rarity and species vulnerability. More specifically, we studied the patterns of distribution of rare plant species in the Pyrenees and their contribution to the taxonomic and phylogenetic diversity of the different habitats of the range, along with the phylogenetic patterns of rarity in the Pyrenean flora. In addition, we analyzed the population dynamics of the flora of Aragón and the diversity of interactions and visitors of six rare plant species of the Pyrenees.

Methods

In chapter 1 we characterized the different types of rarity in the flora of the Pyrenees and their distribution among different habitats using more than 18,000 plant inventories from the Information System of the Iberian and Macaronesican Vegetation. We also analyzed the contribution of rare species to the taxonomic and phylogenetic diversity of those habitats using a genus-level phylogeny from the flora of the whole region. In chapter 2 we used the same database and phylogeny to estimate the phylogenetic signal of each type of rarity in the Pyrenean flora at different phylogenetic scales, from phylogey-wide signal to patterns within clades. Furthermore, we explored the relationship between a species' rarity and its conservation status, along with the potential loss of phylogenetic diversity linked to the regional disappearance of each group of rare species. In chapter 3 we analyzed the population trends of 157 plant populations in all Aragón monitored through the "Adopt a Plant" citizen science program. To this end, we developed a Bayesian model that improves our estimates of population trends and their variance by including estimates of observation. Finally, in chapter 4 we characterized the diversity and composition of the communities of insects and bacteria that visit six rare plant species in the Pyrenees, with a special focus on the differences between patches of the same plant species but placed within populations of different size.

Results

Rarity is a widespread characteristic in the Pyrenean flora, with almost half of all species assessed in chapter 1 being rare under at least one of the criteria we used. In addition, these species, and in particular those with restricted geographic ranges and habitat specialists, tend to accumulate in rare and vulnerable habitats like rocky cliffs and aquatic habitats, where they make a disproportionate contribution to their taxonomic and phylogenetic diversity. The degree of phylogenetic association between rare species

varied between types, with habitat specialists and locally scarce species showing the strongest phylogenetic signal. In consequence, the disappearance of these species from the Pyrenees would lead to a loss of phylogenetic diversity significantly higher than expected by mere chance. Regarding the population trends of plants in Aragón, the vast majority of them (96.2%) had stable long-term growth rates, although 2.54% of the populations showed signs of significant decline and only 1.26% of them had significant population growth. Including estimates of observation error in our model improved its fit and led to an important reduction of the estimated interannual variability in growth rates and a reduction in extinction probabilities. Lastly, the six species of rare plants studied in chapter 4 are visited by a rich community of insects above ground and bacteria below ground. Although the number of visitor species and the relative abundance did not in a significant manner vary between patches of the same plant species, the composition of these communities did change between patches. As such, the patches located inside large populations were visited by communities that resembled one another more than those within the small population.

Conclusions

Overall, this thesis highlights the wide diversity of rare plant species in the flora of a rich heterogeneous landscape like the Pyrenees and Aragón, their distribution, dynamics and interactions; and the complex relation between rarity, vulnerability and conservation. On the one hand, rare species tend to accumulate in habitats vulnerable to Global Change, where they account for the majority of the biodiversity. This, coupled with their patterns of phylogenetic association entails that their loss would have a disproportionate impact on the taxonomic and phylogenetic diversity of the Pyrenean range as a whole, and certain habitats in particular. This loss could have potentially grave consequences for the functioning of ecosystems, not only due to the loss of plant diversity itself, but also

because rare plants help support a wide variety of organisms. On the other hand, most of the plant species in study, many of them rare, have stable population trends whether we take into account observation error or not. Thus, it is difficult to conclude that rare plant species in Aragón are in decline or more vulnerable to environmental changes. The work in this thesis shows that rarity can be used as a starting point to identify species potentially vulnerable to Global Change, but only an in-depth study of their dynamics and threats at different ecological scales will provide us with the essential information about their conservation status necessary to and help us plan successful strategies towards their preservation.

Resumen

Antecedentes

En el actual contexto de Cambio Global y crisis de la biodiversidad, uno de los mayores retos que afrontamos es el de estimar de forma precisa la vulnerabilidad de especies y ecosistemas a los cambios en su ambiente. Esto se hace especialmente patente cuando hablamos de especies vegetales, ya que estas se encuentran seriamente infrarrepresentadas en las diferentes valoraciones sobre el estado de conservación de la biodiversidad a nivel global a pesar de tratarse de uno de los pilares fundamentales del funcionamiento de los ecosistemas. Además, las plantas suelen mostrar respuestas complejas al cambio global que difieren de las de otros grupos de organismos más estudiados como puede ser la fauna. Por tanto, es necesario que ahondemos en los patrones de distribución de las especies vegetales, sus dinámicas, vulnerabilidad y amenazas, así como en las posibles consecuencias de su desaparición para la diversidad y el funcionamiento de los ecosistemas. Aunque existen multitud de aproximaciones para estimar la vulnerabilidad de las especies a los cambios en su medio, estas suelen ser de difícil evaluación y aplicación. Sin embargo, hay ciertos aspectos de la ecología y la biología de las especies que pueden servir como aproximaciones indirectas a dicha vulnerabilidad. Una de ellas es la rareza, ya que las especies raras suelen estar consideradas como más vulnerables o propensas a la extinción.

Objetivos

En esta tesis exploramos la idea de rareza aplicada a diversas especies vegetales en diferentes escalas ecológicas, desde hábitats completos hasta poblaciones individuales, con el objetivo de entender mejor la relación existente entre rareza y vulnerabilidad. Más específicamente, estudiamos los patrones de distribución de las especies raras en

el Pirineo y su contribución a la diversidad taxonómica y filogenética de los diferentes hábitats de la cordillera, así como los patrones filogenéticos de la rareza en la flora pirenaica. Además, analizamos las dinámicas poblacionales de la flora de Aragón y la diversidad de interacciones y visitantes en seis plantas raras del Pirineo.

Métodos

En el capítulo 1 caracterizamos los diferentes tipos de rareza en la flora del Pirineo y su distribución en los diferentes hábitats de la cordillera empleando más de 18,000 inventarios florísticos provenientes del Sistema de Información de la Vegetación Ibérica y Macaronésica. A su vez, se analizó la contribución de las especies raras a la diversidad taxonómica y filogenética de dichos hábitats, empleando para esto último una filogenia a nivel de género de toda la flora de la región. En el capítulo 2 se utilizaron esa misma base de datos y filogenia para estimar la señal filogenética de los diferentes tipos de rareza de la flora pirenaica a diferentes escalas filogenéticas, analizando patrones tanto a nivel de toda la filogenia como dentro de clados concretos. Además, exploramos la relación entre la rareza de cada especie y su estado de conservación, así como la potencial pérdida de diversidad filogenética asociada a la desaparición a nivel regional de los diferentes grupos de especies raras. En el tercer capítulo se analizaron las tendencias poblacionales de más de 157 poblaciones de plantas en todo Aragón monitorizadas gracias al programa de ciencia ciudadana “Adopta una Planta”. Para ello desarrollamos un modelo Bayesiano que permite incluir el error de observación durante el muestreo para mejorar nuestras estimaciones de tendencias de estas poblaciones. Finalmente, en el capítulo 4 caracterizamos las comunidades de insectos y bacterias que visitan seis especies de plantas raras en el Pirineo, haciendo especial hincapié en la diferencias entre parches de una misma especie de planta localizados en poblaciones de diferente tamaño.

Resultados

La rareza es una característica muy difundida entre la flora pirenaica, con casi la mitad de las especies evaluadas siendo raras según alguno de los criterios empleados. Además, estas especies, y en particular aquellas con distribución limitada dentro del Pirineo o especializadas en ambientes concretos, se concentran en hábitats raros y vulnerables como son las paredes rocosas y los hábitats acuáticos, a cuya diversidad taxonómica y filogenética contribuyen de forma desproporcionada. El grado de asociación filogenética entre las especies raras varía según el tipo de rareza, siendo las especialistas de hábitat y aquellas con baja abundancia local las que muestran una mayor señal filogenética. En consecuencia, la desaparición de estas especies en el Pirineo supondría una pérdida de diversidad filogenética considerablemente mayor de lo esperado por azar. En cuanto a las poblaciones de plantas en Aragón, la inmensa mayoría de ellas (96.2%) mostraron tasas de crecimiento estables y sin grandes variaciones, aunque el 2.54% de las poblaciones mostraron signos significativos de decrecimiento y el 1.26% de crecimiento. Incluir estimas del error de observación en nuestros modelos supuso una mejora en el ajuste de los modelos, así como una importante reducción en las estimas de variabilidad interanual de las tasas de crecimiento poblacional y un descenso de sus probabilidades de extinción. Por último, las seis especies de plantas raras examinadas en el capítulo 4 son visitadas por una rica comunidad de insectos en su parte aérea y de bacterias en sus raíces. Aunque el número de especies de visitantes y su abundancia relativa no varió de forma significativa entre parches de una misma especie de planta, la composición de estas comunidades sí que cambió entre parches. De esta forma, los parches localizados dentro de las poblaciones grandes son visitados por comunidades más parecidas entre sí en comparación con los parches en la población pequeña.

Conclusiones

Esta tesis destaca la gran diversidad de plantas raras en la flora de paisajes heterogéneos como son el Pirineo y Aragón, así como los patrones de distribución, dinámica poblacional e interacciones de estas especies. La relación entre rareza y vulnerabilidad en la flora de la región es compleja. Por un lado, las especies raras tienden a acumularse en algunos hábitats vulnerables al Cambio Global, donde suponen la mayoría de la diversidad taxonómica y filogenética. Esto, unido a sus patrones de asociación filogenética supone que su pérdida tenga un impacto desproporcionado en la diversidad taxonómica y filogenética de la cordillera pirenaica en general, y de ciertos hábitats en particular. Dicha desaparición supondría además un gran impacto en el funcionamiento de los ecosistemas de los que forman parte, no solo por la pérdida de diversidad vegetal en sí, si no también porque afectaría al gran número de organismos que soportan. Sin embargo, la mayoría de las poblaciones estudiadas, muchas de ellas de especies raras, tienen tendencias poblacionales estables, tanto si se tiene en cuenta el error de observación en estas estimas como si no. Por tanto, es difícil concluir que las plantas raras están en declive o son más vulnerables a los cambios en su ambiente. Sin embargo, el trabajo realizado en esta tesis demuestra que la rareza puede emplearse como guía y punto de partida para la identificación de especies potencialmente vulnerables al Cambio Global, pero solo un estudio pormenorizado de sus dinámicas y amenazas a diferentes escalas ecológicas puede proporcionarnos la información necesaria sobre su estado de conservación para ayudarnos a tomar la medidas adecuadas para su preservación.

1 Introduction

1.1 Global Change and its consequences for biodiversity

We are witnesses to an unprecedented crisis in biodiversity at the planetary scale (Cowie et al., 2022; Johnson et al., 2017; Pimm et al., 2014). Global Change, mainly through climate change, habitat transformation, overexploitation of natural resources or the introduction of invasive alien species, has led to an increase in species extinction risk several orders of magnitude above historical background rates (Ceballos et al., 2015; Cowie et al., 2022; Pimm et al., 2014), and current models of biodiversity change predict a continuation of this trend even in the most optimistic scenarios (IPBES, 2019; Pereira et al., 2010; Visconti et al., 2016). The consequences of this loss of diversity go beyond the sole disappearance of species and are felt across different ecological scales (Dirzo et al., 2014). All organisms contribute to the functioning of their natural ecosystems by participating in the flows of energy and matter via their own life histories as well as their interactions with other organisms (Bascompte & Jordano, 2017). If a species is extirpated from its local community all the functions and interactions that it performs are lost, dragging down with it any other species that may depend on it, which in turn can have a significant impact on the function and stability of that ecosystem (Dirzo et al., 2014; Tylianakis et al., 2008).

The likelihood of extinction of a species depends not only on the external threats, but also on many internal factors like its rarity or life history and ecological traits, which require a careful assessment before any conservation measures are taken (Cardillo & Meijaard, 2012; Lee & Jetz, 2011). However, we still lack this information for the majority of organisms on Earth (IUCN, 2024). Most estimates of trends in biodiversity are heavily biased towards vertebrates (Cowie et al., 2022; Loh et al., 2005; Pereira et al., 2012), particularly mammals, birds and amphibians, with some notable exceptions like pollinating insects (Potts et al., 2010; Wagner, 2020). Even the most inclusive assessments of the current state of biodiversity like the Red List published by the IUCN are heavily biased towards animals, with 81% of all known species of vertebrates assessed versus only 15% of all described plant species, and even lower levels of threat assessment for invertebrates (2%) or fungi and protists (7%) (IUCN, 2024). It is clear that plants are underrepresented in these global assessments of the status of biodiversity despite usually being the defining characteristic of most habitats as well as a key component of ecosystem functioning and dynamics (Turnbull et al., 2016). There are two reasons that may be key in explaining this pattern. First, there is a huge number of both known and unknown plant species on our planet, which hinders achieving a full assessment of their conservation status (Brummitt et al., 2015; Brummitt N et al., 2008; Corlett, 2016). Second, plants may not necessarily follow the same patterns and rules as animals regarding their responses to Global Change (T. J. Davies et al., 2011; Knapp, 2011). For example, several authors argue that plants tend to have slower responses to environmental change than animals, leading to delayed extinctions that might not be easily predicted in the present but will manifest in the future and giving a false impression of stability (Cronk, 2016; Nic Lughadha et al., 2020).

Most of the studies that explore the effects of Global Change on plant diversity are centered in local extinctions and changes in distribution and community composition (Kempel et al., 2020; Primack et al., 2018; Willis et al., 2017). The results from these studies paint a complex portrait of the effect of Global Change on plant diversity (Primack et al., 2018). On the one hand, some of these studies show a high number of local extinctions in plant communities during the last century (Kempel et al., 2020), with some of them predicting a global decrease in plant diversity in future decades (Harrison, 2020). On the other, some studies have not detected any significant changes in the local species richness of plant communities during the same time period, and argue for caution when estimating the effects of Global Change on plant diversity at different ecological scales (Vellend et al., 2013). This open debate makes clear that there is a need for more and better information regarding how plant populations and communities respond to Global Change at different scales and across space, in order to improve our understanding of the consequences of biodiversity changes for ecosystems and human societies (Paton et al., 2008; Pimm & Joppa, 2015; Primack et al., 2018). For these reasons, the research subject of this thesis will be the diversity, population trends and interaction of multiple plant species, with a special focus on rarity as a proxy for their vulnerability.

1.2 Vulnerability and rarity

Vulnerability is a seemingly intuitive idea that hides a complex conceptual framework when applied to nature, as it encompasses different ecological scales, from habitats to species and populations (Gauthier et al., 2013). As seen in Figure 1.1, we can distinguish between three major components of vulnerability: exposure, intensity and impact (K. Wilson et al., 2005). Exposure considers the probability of a threat affecting our focal study system. In the case of populations or species, it refers to their presence in places susceptible of being transformed (*e.g.* easily disturbed habitats like wetlands), as well as their probability of declining beyond certain thresholds that would lead to their extinction (Shaffer, 1981). Intensity includes measures of the magnitude and duration of a threat or perturbation like the degree of deforestation in a forest or the severity and duration of droughts. Impact, on the other hand, refers to the consequences of any perturbation for the focal species suffering that perturbation, as well as any other ecosystem functions or species that depend on it. For example, the extinction of a particular plant species implies not only a direct loss of species diversity, but also the loss of all its ecosystem functions, evolutionary history or species interactions (Aizen

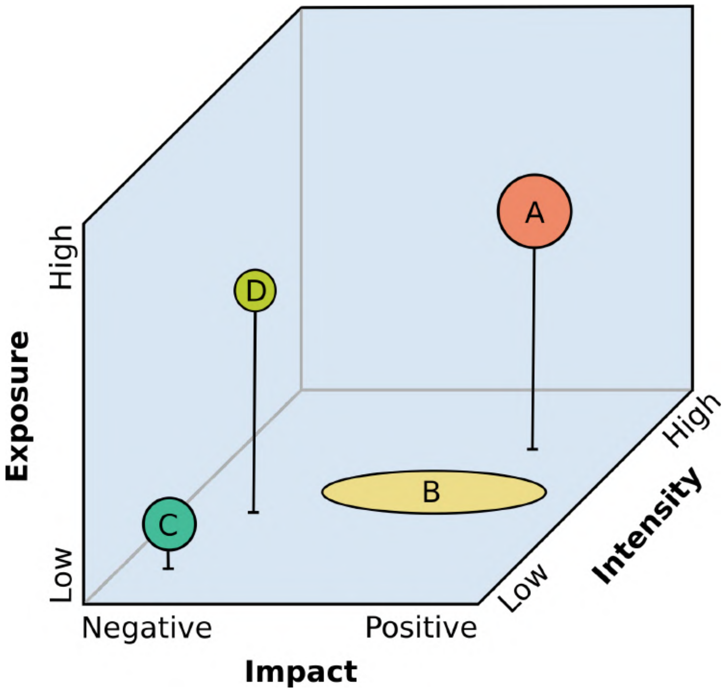

Figure 1.1: Example of four hypothetical species in the exposure-intensity-impact space. Adapted from K. Wilson et al. (2005).

et al., 2012; Bascompte & Jordano, 2007).

Of the three components of vulnerability only intensity is easily measurable, although usually only after the perturbation has already occurred. Exposure and impact, however, are difficult to assess because perturbations may never happen and their consequences are, more often than not, unpredictable. Thus, it is important to find traits and characteristics of species that may act as proxies for their vulnerability. In this thesis we will use rarity as a proxy for exposure based on the assumption that rare species are more susceptible to population decline and are often located in vulnerable habitats (K. F. Davies et al., 2004; Gaston, 1998).

Rarity usually refers to species that are restricted to small geographic areas or have low local abundances, although many more criteria can be applied depending on the biology of the species of interest (Gaston, 1994; Kondratyeva et al., 2019; Kunin & Gaston, 1997; Manne & Pimm, 2001). One of such criteria was introduced by Rabinowitz (1981) and considers the habitat specialization of a species in addition to its geographical range and local abundance. According to this classification, an organism can be rare in a geographical sense if it is limited to a specific area, such as endemic species or those with small and restricted geographic ranges, meaning that the decline of just a few populations could lead to the total disappearance of the species (Gaston, 1998; J. L. Payne & Finnegan, 2007). Organisms can also be rare if they are adapted to life in habitats that are scarce or with very specific environmental conditions, such as aquatic plants or those living in rocky cliffs, and thus they are susceptible to perturbations that may affect habitats as a whole (J. R. Prendergast et al., 1993; Schemske et al., 1994). Finally, species can be rare if their populations are small, meaning that they may not be able to cope with sudden environmental changes, demographic stochasticity or suffer from density dependent effects such as Allee effects (Mace & Kershaw, 1997; Matthies et al., 2004).

The importance of rarity for the management and conservation of species is highlighted by the use of such criteria in the IUCN Red Lists (IUCN, 2012), namely in its geographic distribution (criterion B) and local abundance aspects (criteria A, C and D). Therefore, it is fairly straightforward to think of rarity as a proxy for the vulnerability of species towards external threats that may lead to their decline or disappearance (Mace & Kershaw, 1997). However, we must carefully assess the different geographic and time scales at which this rarity manifests, paying special attention to the impact that the loss of rare species might have on different facets of biodiversity beyond taxonomic diversity such as its functional and phylogenetic or evolutionary aspects (Flynn et al., 2011).

1.3 Rarity in space and time

Rarity is intrinsically related with the distribution of species both by directly considering their geographic range or indirectly through their habitat specificity (Kunin & Gaston, 1997). Thus, it is interesting to explore how rare species distribute in space and in which areas or habitats they tend to accumulate in, especially since the aggregation of rare species in those habitats would increase their conservation priority (J. R. Prendergast et al., 1993). Previous studies on the distribution of rare plant species show that they tend to accumulate in particular regions and habitats such as climatically stable areas that allow their long-term persistence overtime (Enquist et al., 2019; Myers et al., 2000). However, we lack knowledge about how rare species distribute at regional levels, their contribution to the diversity of their local plant communities, both taxonomically and phylogenetically (Cadotte et al., 2010), and if certain types of rarity contribute more to that diversity (Heegaard et al., 2013; Lennon et al., 2003). Under the assumption that rare species tend to be more vulnerable to extinction, these species could be used as proxies for the susceptibility to species loss of the habitats they live in and thus the disappearance of potentially important ecological function (Gauthier et al., 2013; Lyons et al., 2005; Mouillot et al., 2013).

Although rarity itself is just a label that we put on a species based on some, more often than not, subjective criteria, there are many biological, ecological and historical factors behind the patterns of geographic distribution, specialization or local abundance that we find in nature and which ultimately determine the rarity of a species (Gaston, 1994; Lesica et al., 2006; Magurran & Henderson, 2003). For instance, endemicity may stem from recent speciation and a lack of dispersal abilities beyond the place where it evolved (neoendemics), or it can be caused by the reduction of its formerly bigger geographic range into its current, limited distribution (paleoendemics) (Laffan & Crisp, 2003). The size of the geographic range can also be determined by several factors: historical reasons similar to those of endemism, topographical like the presence of physical barriers such as mountains that impede dispersal or climatic like the inability of spreading to places with different environmental characteristics (Gaston, 1998; Sheth et al., 2020). The latter are related to the physiological constraints of that species, in other words, to how well adapted a species is to certain environments, and thus to its ecological niche (*sensu* Grinnell, 1917). This determines the habitat specificity of a species, which includes everything from climatic variables like temperature or humidity to the physicochemical properties of the soil it grows in, the amount of water contained in it, for example in aquatic or bog species, or in the case of species adapted to rocky habitats, the availability of features in the rock suitable for colonization and growth (Futuyma & Moreno, 1988). Finally, the local abundance of a species in a particular habitat is conditioned by all the preceding factors as well as biotic interactions that occur at a local scale like competition for resources, predation, facilitation or mutualism (Braz et al., 2020; Kolb et al., 2006).

All the criteria for rarity that we have described so far have a strong historical or evolutionary component, whether it is their speciation history, the past changes in regional environmental conditions, their dispersal capabilities or their degree of niche conservatism, all of which tend to be preserved during evolution (Holt, 1997; Orians, 1997). Thus, it is safe to assume that the rarity of species may show a certain degree of phylogenetic signal or, in other words, that species with similar rarities may be phylogenetically closer than expected by mere chance (Chalmandrier et al., 2015). Under the aforementioned assumption of association between rarity and vulnerability, this phylogenetic pattern would imply that the species most vulnerable to Global Change tend to be closely related (Cadotte et al., 2010), a pattern which has two important consequences. First, that certain branches of the tree of life are more susceptible to disappear than others, and the loss of closely related species could have disproportionate consequences in terms of loss of phylogenetic diversity, a proxy for evolutionary history, in comparison with other species (Faith, 2008; Purvis et al., 2000). Second, the phylogenetic relatedness between rare species means that we can estimate the vulnerability of other species by looking at their closest relatives and their rarity, helping in conservation efforts when we lack any other information regarding certain species of interest (Purvis, 2008). Nevertheless, it is important to note that although rarity implies vulnerability, it is the set of external perturbations they experience, their sensitivity to them, and the actual population dynamics of rare species what matters when assessing their vulnerability.

1.4 Improving estimates of population trends

Populations, understood as a group of individuals of the same species occurring together in a particular place (Berryman, 2002), are the basis of the long term persistence of species. If populations thrive, species can persist in those particular sites. Therefore, population dynamics shape the architecture of biodiversity at local scales. In the second half of the 20th century, scientists became aware of this and thus the importance of tracking the changes in population size and estimating their risk of extinction, prompting the development of population viability analysis (PVA) as a fundamental tool in conservation biology (Dennis et al., 1991; Reed et al., 2002; Shaffer, 1990). PVA allows us to assess the state of conservation of populations, make predictions about their future and guide management and action plans for their long term persistence (Chaudhary & Oli, 2020).

In its simplest form, PVA focuses on the changes in size of a population through time, which are a consequence of the balance between the vital rates of those populations like fecundity, survival or migration rates (Capdevila et al., 2022; Shaffer, 1990). One aspect of population dynamics with a particular importance for PVA is the variation of these vital rates through time, and thus a population's growth rate (Lande, Engen, & SÆther, 2003). This variation can be attributed to two main sources: demographic stochasticity, the random variability in vital rates inherent to that population; and environmental stochasticity, the effect of both abiotic and biotic variability on those vital rates (Engen et al., 1998). In either case, higher variability translates into lower long term growth rates and increased probability of going extinct, due to a higher chance of linking several "bad" years in a row, which is specially important for small populations unable to buffer those sudden changes (Lande, Engen, & SÆther, 2003; Tuljapurkar, 1990). Hence, correctly estimating the variation of growth rates in a population is a crucial step for population viability analysis (Doak et al., 2005). However, our estimates of variation due to demographic stochasticity and year-to-year changes in the environment can be biased by observation error (Herrick & Fox, 2013; See & Holmes, 2015). No matter how well designed a sampling or census protocol is, we are never capable of making perfect observations. On the one hand, we will probably only be able to observe part of a population at any given period of time, giving us an incomplete image of its dynamics (McLoughlin & Messier, 2004). On the other hand, we as humans are prone to observation errors such as missing individuals or counting them more than once, even when sampling sessile organisms like plants (Perret et al., 2023). These errors during the sampling process inadvertently bias our observations and add a new layer of variation in our estimates of population sizes and growth rates (See & Holmes, 2015). When not accounted for, we would assume that all the variation in those demographic parameters is caused solely by random changes in its population dynamics or the environment (Dennis et al., 2010). However, by adjusting our sampling designs to reduce observation error, and by including estimates of our own observation error in population viability analysis, we are able to improve our estimates of population growth and probabilities of long-term decline (Herrick & Fox, 2013). In this work we apply a novel approach to this problem on one of the largest citizen science initiatives in Spain, the "Adopt a Plant" program, which monitors the changes in population size and abundance of almost 350 plant populations in Aragón (García et al., 2021). Although observation error is a well-known issue in population monitoring, it is seldom addressed in practice (but see Pardo et al., 2015 for whole communities) and to our knowledge this is the first time that such approach for correcting observation error has been used in population viability analysis.

1.5 Beyond plant species: assessing the role of rare plants as hubs for diversity

All organisms live as part of a greater ecosystem, interacting with hundreds or sometimes thousands of different organisms, from the tiny bacteria that conform their microbiome to their predators which may be orders of magnitude bigger. Plants, independently of their rarity, are no different in this regard, and in most cases also act as important hubs linking other species that visit them both above and belowground (Dedeyn & Vanderputten, 2005; Wardle et al., 2004). In the simplest of instances, plants are a source of food for herbivores eating their leaves as well as for microbes that feed on their root exudates, but plants also offer a plethora of other resources, like refuge from predators to tiny critters, hunting grounds for their pursuers or places for mating and laying eggs. At the same time, the root system of plants creates a structure for bacteria and fungi to grow on, offers them a steady source of carbon in the form of root exudates (Bais et al., 2006) and controls the diversity and composition of those underground, microbial communities (Trivedi et al., 2020; van der Putten et al., 2013).

Considering the pivotal role of plants as maintainers of biodiversity and links between the above and belowground worlds of their ecosystems (Wardle et al., 2004), characterizing the diversity and composition of the communities associated with rare plants can give us precious insight on how these species help maintain their ecosystems beyond their usual functions (Tylianakis et al., 2008). If we assume the aforementioned idea that rare species are more prone to extinction, and that they are able to sustain a wide array of other organisms, the local extinction of those plant species would have important consequences for the functioning and diversity of the ecosystems they are part of

(Bascompte & Jordano, 2007; Tylianakis et al., 2010). As we have seen before, one important factor for the persistence of a population is its size, with smaller populations being more exposed to abrupt perturbations that might wipe off the whole population (Gabriel & Bürger, 1992). Thus, the communities of visitors associated with small populations of plants might also be at higher risk of losing a potentially vital resource if they are dependent on it (Aizen et al., 2012). In addition, if those communities are unique to small populations, rather than being a subset of a general meta-community of visitors associated with that plant species, the loss of those small populations would imply potential disappearance of unique interactions and ecosystem functions (Valiente-Banuet et al., 2015).

1.6 Study area

The work of this thesis focuses on the NE of the Iberian Peninsula, in particular on Aragón and the Pyrenees mountain range. Aragón is limited to the north by the Pyrenees and by the Iberian Mountains to the south, while being crossed west to east by the Ebro River Basin (Fig. 1.2A). This particular location, coupled with the strong contrast in altitude lead to a wide variety of habitats and climates, although we can distinguish between three major climatic areas (Cuadrat, 1999; Peña Monné et al., 2004): First, the continental climate of the lower regions surrounding the Ebro river, characterized by cold winters and hot summers and with low precipitation and strong winds year round. Second, the transition climate between the Ebro River Plain and the mountains to the north and south, with a similar continental character but higher precipitation and lower summer temperatures caused by the gradual change in elevation. And third, the mountain climate of the Pyrenees and Iberian Mountains, which is characterized by much lower temperatures and higher precipitation than the lowlands, although the Iberian Mountains are drier and less cold compared to the Pyrenees due to their continentality and the lower elevation (*Atlas climático de Aragón*, 2007; Cuadrat, 1999).

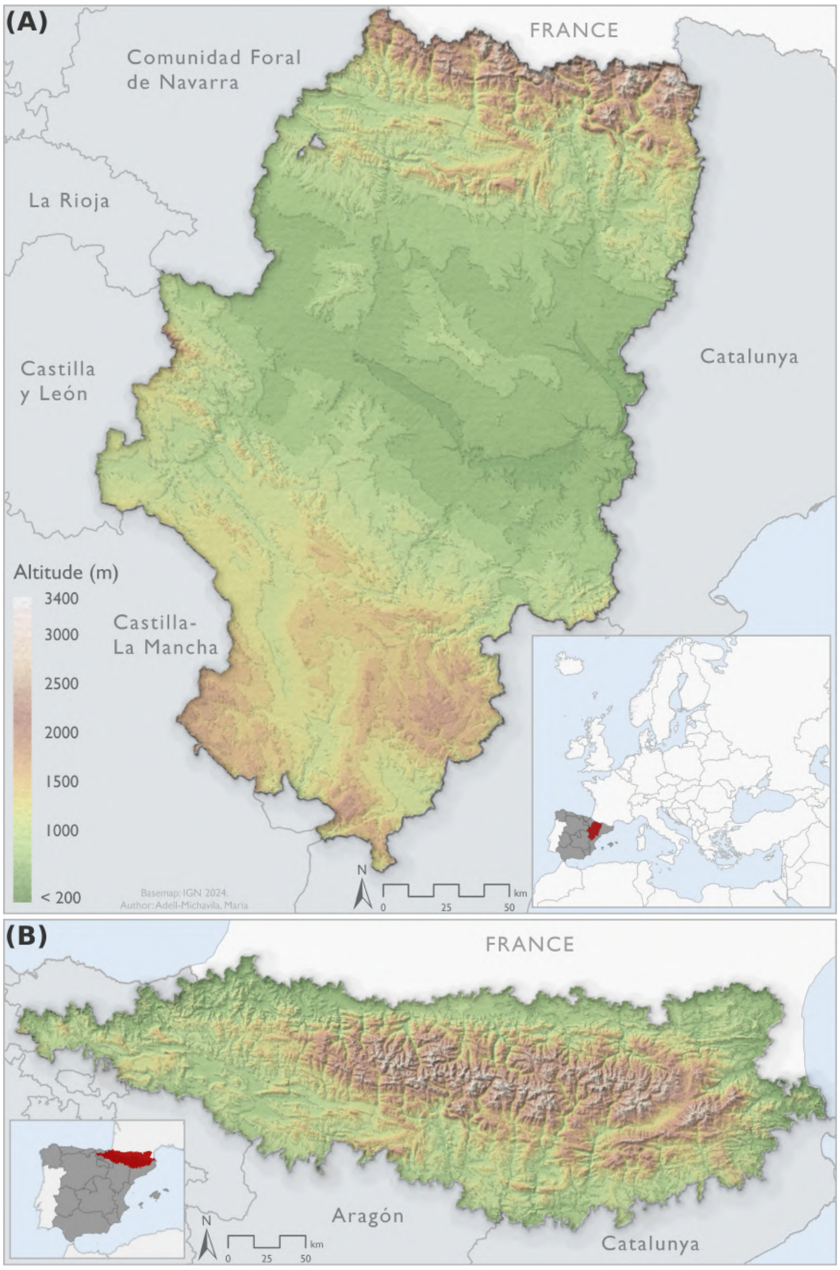

Figure 1.2: Map of the study region. Author: M. Adell-Michavila.

The particular location of the Pyrenees (Fig. 1.2B), at the intersection between Mediterranean, Atlantic and Alpine biogeographic regions, along with their wide altitudinal range and complex topography allow for a great variety of climates and habitats (Ninot et al., 2017). This diversity has resulted in a rich flora of over 3600 taxa (Gómez, García, et al., 2017), 5.5% of which are endemic to the region and around 10% are rare (Gómez, Lorda, et al., 2017). Thus, the Pyrenees are a unique place to study the diversity and distribution of rare plants, their contribution to the diversity of different habitats, and their population dynamics and interactions. This is of particular interest since the Pyrenean range, like the majority of mountain ranges on Earth, is undergoing complex changes in its diversity derived from Global Change (D. Payne et al., 2017; Perrigo et al., 2020). The major driver of these changes is land use change (Lasanta et al., 2017; Mottet et al., 2006). The abandonment of traditional uses such as extensive grazing by cattle or the extraction of natural resources at a local scale like firewood have allowed the colonization of pastures and deforested areas by trees and shrubs, changing the diversity and composition of plant species in those habitats (Améztegui et al., 2010; Gauthier et al., 2013; Lasanta & Vicente-Serrano, 2007). In addition, other drivers like climate change are also expected to have important consequences for mountain biodiversity, namely the reduction of altitudinal ranges for cold adapted species and uphill expansion of thermophilic species (Elsen & Tingley, 2015; Gottfried et al., 2012), a pattern that is also expected to occur in the Pyrenees (Pérez-García et al., 2013). The combination of all these processes may have important consequences for the biodiversity and ecosystems of the Pyrenees, especially for rare plant species, but the extent of those consequences may differ between species and habitats. Thus, it is crucial that we assess the vulnerability of habitats and species to external threats in order to act in accordance.

1.7 Main objectives

This thesis aims to shed some light on important gaps of knowledge around the concept of "rarity" such as the patterns of distribution of rare species among different habitats and the phylogenetic patterns behind rarity in the whole flora of a whole mountain range (the Pyrenees). Then, it explores the population dynamics of rare plant species and the effect of accounting for observation error during the sampling process, as well as the potential consequences of occurring in small populations for the overall diversity of their visitors. We focus on the rare plants of the NE of the Iberian Peninsula, the crossroad of the Eurosiberian and Mediterranean biogeographical regions, to answer the following specific questions:

- How are rare species distributed across different habitats of the Pyrenees, and how much do they contribute to the taxonomic and phylogenetic diversity of the plant communities in those habitats?
- Considering the abundance and typology of rare species that habitats harbor, what are the most vulnerable habitats to global change in the Pyrenees?
- Are there any phylogenetic patterns underlying rarity in the flora of the Pyrenees? If so, how could this pattern affect the overall loss of biodiversity by external factors?
- How much can we improve our estimates of population extinction risk by including simple estimates of observation error during the monitoring process?
- What are the population trends and extinction risks of plants species in Aragón?
- How much do rare plants contribute to maintaining the diversity of organisms visiting them above and below ground?
- How much influence does population size have on the structure and composition of communities of visitors in rare plants?

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2 Rare plant species as proxies for habitat vulnerability in the Pyrenees

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2.1 Introduction

Mountains around the globe are considered major plant diversity hotspots due to the large amount of habitats and species they harbor, along with a high level of endemism (Mittermeier et al., 2004). At the same time, these regions, and particularly those in or around the Mediterranean Basin, are among the most threatened areas by global change (Hock et al., 2019). Mountain biodiversity is widely acknowledged as highly vulnerable due to two main factors: temperatures increasing faster than the global average (Bravo et al., 2008; Cramer et al., 2018; Pachauri et al., 2014), and the dramatic habitat transformation caused by land use changes during the last century (García-Vega & Newbold, 2020; Mottet et al., 2006; Newbold et al., 2015).

The vulnerability of biodiversity within a region, however, is not defined solely by its exposure to external hazards like global change drivers. Some features relative to species distribution, specialization, or population abundance may result in rarity, prompting an intrinsic sensitivity to factors such as demographic stochasticity (K. F. Davies et al., 2004), or deterministic perturbations such as slow habitat succession (Weißhuhn et al., 2018). Rarity may arise from a variety of factors, which are biological, ecological and historical in nature (Stebbins, 1980), resulting in each type of rarity having different risks associated with them. For example, species with limited geographic range have been linked to higher extinction risk, likely due to a reduction in the buffering effect of range size against abiotic and biotic stressors (Harnik et al., 2012; J. L. Payne & Finnegan, 2007). Habitat specialists are constrained by certain environmental conditions and in turn are more vulnerable to habitat fragmentation and loss (B. Fontaine et al., 2007). Finally, species with smaller populations are more vulnerable to stochastic (Matthies et al., 2004) and denso-dependent phenomena like the Allee effect (Kuparinen et al., 2014). Since the type of rarity affects species vulnerability to particular factors or processes, a comprehensive analysis of the frequency of different kinds of rarity within a geographic region can give us a broader knowledge about the possible effects of global change drivers and other disturbances on biodiversity patterns of such areas (Caro & Girling, 2010).

The loss of rare species might, in turn, have strong implications for ecosystems beyond a reduction in taxonomic diversity. On the one hand, rare species can be considered important assets for ecosystem functioning as they sometimes perform unique or novel functions despite their relative low abundances (Jain et al., 2014; Lyons et al., 2005; Mouillot et al., 2013). On the other hand, biodiversity goes beyond the number and abundance of species present in a community and thus the consequences of their loss also extend to the evolutionary and functional aspects of diversity (Craven et al., 2018; Naeem et al., 2016). In consequence, exploring and comparing the frequency of various types of rare species across different communities, habitats or ecosystems, along with their contribution to taxonomic and phylogenetic diversity (PD), may help us assess not only their vulnerability to intrinsic factors, but also the consequences of their loss for those habitats.

The aim of this study is to explore how vulnerability of biodiversity varies across different habitats based on the frequency and type of rare species they shelter throughout a large and environmentally heterogeneous mountain area in Southern Europe: The Pyrenees. We used the largest available dataset of plant communities in the region (∼18,000 *relevés*) and classified each plant species according to four important features associated with rarity based on the proposal of Rabinowitz (1981): amplitude of their geographic distribution, regional abundance, ecological specificity, and local abundance. In particular, we strive to answer the following questions:

- Which kinds of rarity more prevalent in the Pyrenean range, and how is the frequency of rare plants distributed among habitats? We expect certain kinds of rare species, for instance habitat specialists, to accumulate in locations with highly distinct environmental conditions such as rocky habitats and alpine environments or wetlands (Boulangeat et al., 2012; Enquist et al., 2019; Harrison & Noss, 2017).

- What is the relationship between the frequency of rare plants, and taxonomic and phylogenetic diversity across habitats? We expect the proportion of rare species to increase in species-rich communities, as described by Heegaard et al. (2013), and in turn, with sesPD.
- Do rare species contribute more to the phylogenetic diversity than other species, and does this contribution differ across habitats and rarity types? Here, we hypothesize that the contribution of rare species to PD will be higher than their less rare counterparts as observed by Mi et al. (2012) across a global network of forest communities.

2.2 Methods

2.2.1 Study area

The Pyrenean range is located in the southwest of Europe, and separates the Iberian Peninsula from the rest of the continent (Fig. 2.1). Due to its location in the transition between the Alpine, Mediterranean, and Atlantic biogeographic regions, together with a broad altitudinal gradient (highest summit at 3,404 m a.s.l.), the Pyrenees show a wide variety of climatic conditions (Ninot et al., 2017). This, combined with intensive land use (García-Ruiz et al., 1996), and geological heterogeneity (García-Ruiz et al., 2015), results in a wide diversity of natural and semi-natural habitats. The Pyrenean flora is composed of more than 3,600 native vascular plants with a broad range of environmental requirements, from Mediterranean species adapted to dry, hot conditions; to boreo-alpine species inhabiting the cold environments of summits (Gómez, García, et al., 2017).

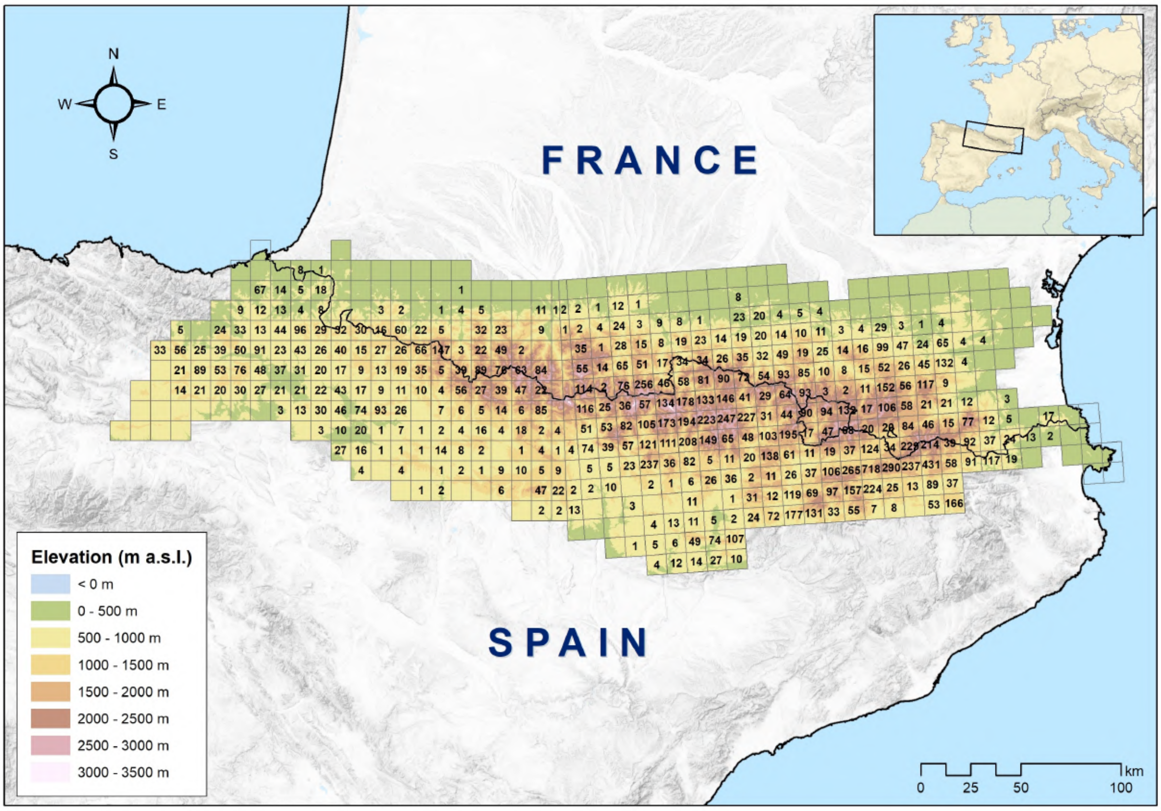

Figure 2.1: Map of the study region. The grid marks the UTM cells inside the limits established for the Pyrenees by the Working Community of the Pyrenees (CTP). Numbers within cells indicate the number of plant inventories located in it.

2.2.2 Plant data collection

We downloaded and validated 18,608 plant inventories or *relevés* from SIVIM, a database of Ibero-macaronesian vegetation (Font et al., 2017). They were located between 400 and 3,300 m a.s.l. and included over 400,000 records of a total of 2,550 species, which represent around 74.2% of the native mountain species in the Pyrenean flora (those occurring over 400 m a.s.l.; Gómez, García, et al., 2017).

Each inventory was categorized according to 14 European EUNIS habitats, a hierarchical classification system for the terrestrial and marine habitats of Europe and its surrounding waters (Moss, 2008). We used different EUNIS levels in order to better accommodate habitat frequency in the Pyrenees and obtain a more balanced sample of communities. Habitats with very high anthropic influence such as ruderal communities and irrigated meadows were excluded, and only inventories with more than five species were used. The final list of habitats was: surface waters (C), mires and fens (D), dry grasslands (E1), seasonally wet and wet grasslands (E3), alpine and subalpine grasslands (E4), woodland fringes and clearings and tall forb stands (E5), arctic, alpine and subalpine scrub (F2), temperate and Mediterranean-montane scrub and heathlands (F3-F4), garrigues (F6), broadleaved deciduous woodland (G1), broadleaved evergreen woodland (G2), coniferous woodland (G3), screes (H2), and inland cliffs, rock pavements and outcrops (H3). F3 and F4 habitats were joined together due to their low abundance in our dataset as well as ecological and floristic similarities. Some of these habitats are clearly associated to a specific altitudinal interval (the high altitude alpine grasslands, and the low and mid altitude broadleaved evergreen woodlands for example) while others extend over a wider altitudinal gradient (alpine and subalpine scrubs) or are relatively independent of altitude because they are intimately associated to specific abiotic elements (inland cliffs, rock pavements and outcrops, screes, inland surface waters and mires, bogs and fens).

All species names of this dataset were validated using the Atlas Flora Pyrenaea (http://www.atlasflorapyrenaea.eu/src/home/index.php?idma=0) with the exception of those genera for which species identification was not explicit in the inventory (*i.e.* the apomictic *Alchemilla* or *Hieracium*). Most inventories followed the classical Braun-Blanquet format, but the scale used to record plant cover-abundance varied between inventories. Consequently, we standardized all the values to the extended Braun-Blanquet scale, which ranges from 1 to 9 (van der Maarel, 1979).

2.2.3 Phylogenetic inference

We built a genus-level phylogeny of the Pyrenean flora (Fig. 2.2) using the workflow proposed by Roquet et al. (2013), and based on the species present in our data and in the atlas of the Pyrenean flora (FLORAPYR). We downloaded from Genbank three conserved chloroplastic regions (rbcL, matK, and ndhF) plus the ITS region for a subset of families, which we aligned separately by taxonomic clustering. We aligned all coding sequence clusters with *MACSE* (Ranwez et al., 2011) and noncoding ones with *MAFFT* (Katoh & Standley, 2013), and trimmed all alignments with *TrimAl* (Capella-Gutierrez et al., 2009). We concatenated all alignments to obtain a supermatrix. We then conducted maximum-likelihood (ML) phylogenetic inference analyses with *RAxML* (Stamatakis, 2014), applying the most appropriate partitioning scheme and substitution model obtained with *PartitionFinder* (Lanfear et al., 2014) and a supertree constraint at the family-level obtained with the online software *Phylomatic* v.3 (tree R20120829). Specifically, we performed 100 independent tree searches. The best ML tree (the one with the highest probability) was dated applying the penalized likelihood method in *treePL* (Smith & O'Meara, 2012) and the following node calibrations: we fixed the node corresponding to the ancestor of eudicots at 125 Ma based on the earliest eudicot fossil (Hughes & McDougall, 1990), and applied minimum age constraints to 15 nodes based on fossil information extracted from Smith et al. (2010) and Bell et al. (2010). To deal with unknown within-genera relationships, we simulated 10 scenarios of within-genera random branchings using a Yule process as implemented in the R package *apTreeshape* (Bortolussi et al., 2020). These 10 trees represent a distribution of possible hypotheses about evolutionary relationships in our dataset *sensu* Rangel et al. (2015). The only species lacking in our tree that were present in the inventories were those belonging to monotypic genera *Cytinus, Ptychotis* and *Xatardia* as the data available in GenBank was insufficient for proper phylogenetic inference. In order to explore and avoid potential biases derived from the limitations of our phylogenetic tree, we conducted our analysis with both our phylogeny and the ALLOTB tree published by Smith and Brown (2018), a publicly available and highly inclusive phylogeny of worldwide seed plants (Appendix 2.A).

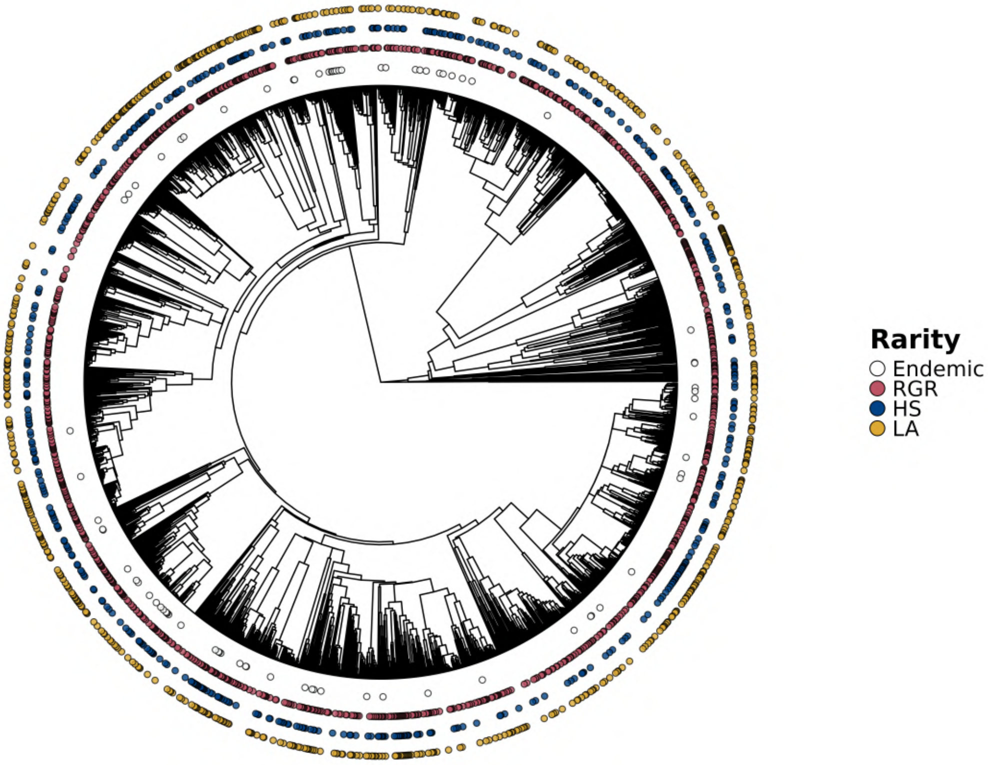

Figure 2.2: Example of the genus-level phylogeny used in our study after randomly resolving species-level branches. Dots indicate the location of rare species in the tree. Endemic: species exclusive to the Pyrenees; HS: habitat specialists; LA: species with low local abundance; RGR: species with limited regional geographic range.

As previous studies have shown, inferences based on phylogenies with deep initial bifurcations such as the one found between the major groups of terrestrial plants may be inconsistent depending on how species are distributed among the branches of the phylogeny (Molina-Venegas et al., 2015). In order to avoid this, all the analyses were conducted using only angiosperms, excluding gymnosperms and ferns from our communities and phylogeny.

2.2.4 Taxonomic and phylogenetic alpha diversity

Taxonomic diversity of the studied communities was measured as species richness. Phylogenetic diversity (PD) was estimated as the sum of the length of the branches from the phylogeny associated with the species in each inventory (Faith, 1992). As the latter measure is highly correlated with species richness and biases comparisons between communities (Tucker et al., 2017), we standardized the observed values by subtracting from them the expected mean phylogenetic diversity value for communities of a certain species richness and dividing the result by the standard deviation of said value (hereafter referred to as standardized phylogenetic diversity or sesPD). The calculation and standardization of phylogenetic diversity values was done using the *PhyloMeasures* R package (Tsirogiannis & Sandel, 2017). In order to consider all possible evolutionary hypotheses, we computed sesPD using all 10 phylogenetic trees and averaged the results.

2.2.5 Species rarity: Classification and contribution to habitat vulnerability

We classified each species present in our dataset based on the three criteria proposed by Rabinowitz (1981): geographic range, habitat specificity (HS) and local population size (LA). Given the difficulty of estimating total geographic range, we split it into endemic status (hereafter End, taxa restricted to the Pyrenean range), and regional geographic range (hereafter RGR, number of 10 km^2 UTM cells in which each species was found based on the location of the above mentioned *relevés*). Then, different thresholds were tentatively used to avoid overrepresentation of rare plants due to their regional geographic range. Finally, a species was considered to have a small regional geographic range (narrowly distributed) in the Pyrenees if its RGR was $<5\%$ of the maximum number of UTM cells occupied by any species in our study area. Habitat specificity was assessed from the number of habitats in which a species was found based on the habitat types associated with each *relevé*, with species having at least 90% of their occurrences in only one habitat being classified as habitat specific. In order to estimate each species' local abundance, we first calculated the specific average cover-abundance across all the inventories, along with its 95% confidence interval. We classified species as having low local abundance (locally scarce) if the upper limit of their cover-abundance confidence interval was lower than 2 in the extended Braun-Blanquet scale. Finally, we calculated the proportion of rare species per inventory from the number of species that fell within each of the rarity categories separately and any combination of them (hereafter referred to as rare species), and the total species richness of that inventory.

The contribution of rare species to the phylogenetic diversity of plant communities was calculated as the difference between the observed PD of an inventory and the PD resulting from removing any rare species from it, following a similar approach to Pool et al. (2014). We tested if this contribution differed from random expectation by comparing it with a null model. The null distribution of expected values for the difference in PD was obtained by randomly reassigning the rarity categories among the species in each inventory, removing any rare species from them and recomputing the difference in PD, and repeating this process 999 times. We then calculated the standard size effect by subtracting the expected difference in PD to the observed value and dividing the result by the expected standard deviation. A two-tailed test was applied, with values outside the range [-1.96, +1.96] considered as statistically higher or lower than expected by chance with a 95% confidence (Mazel et al., 2016). For this analysis we only used inventories containing at least one rare species in order to avoid the influence of communities without rare species, which comprise the majority of our inventories.

2.2.6 Statistical analysis

Differences between habitats regarding species richness, standardized phylogenetic diversity, proportion of each rarity type and overall rare species as well as their contribution to phylogenetic diversity were analyzed with generalized linear models using a Poisson distribution for species richness, a Gaussian distribution for community sesPD and the contribution of rare species to it, and a binomial distribution for the proportion of rare species. All analyses were conducted using R version 4.0.4 (R Core Team, 2021). The statistical significance of general differences between habitats were assessed using analysis of variance with the *car* package (Fox & Weisberg, 2019), and pairwise comparisons were done by estimating marginal means and their confidence intervals via the *emmeans* package (Lenth, 2021). In addition, we tested the relation between both species richness and sesPD and the proportion of each type of rare species using Pearson's correlation coefficient. For comparative purposes, we tested the correlation between the results obtained with our phylogeny and those from the ALLOTB phylogenetic tree.

2.3 Results

2.3.1 Patterns of taxonomic and phylogenetic diversity across habitats

Species richness varied greatly between habitats, ranging from 483 species in inland surface waters to 1230 in woodland fringes, clearings and tall forb stands (Table 2.1). Mean species richness per inventory was 19.7 (SD = 9.9), with the richest 1% of inventories found in alpine and subalpine grasslands, broadleaved deciduous forests and dry grasslands. Differences in species richness per inventory were statistically significant between habitats ($\chi^2 = 6843.1$, $df = 13$, $p < 0.0001$; Fig. 2.3A), with dry grasslands being the richest (26.34, $\mathrm{CI}_{95} = 25.86, 26.82$) and inland surface waters the poorest (9.27, $\mathrm{CI}_{95} =$

8.82, 9.75).

Mean sesPD of all inventories was -0.234 (SD = 1.26), with the 1% of inventories with the highest sesPD located in broadleaved deciduous forests, inland surface waters, mires, bogs and fens and seasonally wet grasslands. The lowest values were located in dry or alpine grasslands, woodland fringes and garrigues. Differences between habitats in standardized phylogenetic diversity per inventory were also statistically significant ($F = 425.93$, $df = 13$, $p < 0.0001$; Fig. 2.3B), with inland surface waters having the highest sesPD values (-0.595, CI_{95} = -0.660, -0.530) and dry grasslands the lowest (-1.915, CI_{95} = -1.943, -1.887).

2.3.2 Rare species: Differences in abundance across habitats, and relationship with diversity

Around 52% of the observed species showed some kind of rarity, and about one third of those were represented by nonendemic, nonspecialized and locally scarce species with small regional geographic ranges. Only seven species (0.3% of the species total) were included in the rarest category composed by endemic, specialized and locally scarce taxa with small regional geographic ranges.

Although rare species accounted, on average, for 22.64% (SD = 6) of species found in each habitat, the number and type of rare plants varied widely between them, with dry grasslands having the highest proportion of rare species and arctic and alpine scrubs the lowest. Endemic species were more prevalent in arctic, alpine and subalpine grasslands, screes and inland cliffs, rocky outcrops and pavements. Species with small regional geographic ranges were more abundant in garrigues, dry grasslands, and inland surface waters. Habitat specialists concentrated in inland surface waters; inland cliffs, rocky outcrops and pavements and woodland fringes and clearings and tall forb stands. Locally scarce species were most prominent in dry grasslands, garrigues and inland surface waters

Table 2.1: Number of inventories (*N*), total number of species (*Total*), rare species by rarity type and overall rare species richness pooled by all rarity types (*Total Rare*) per habitat; in parenthesis the percentage of rare species considering total richness.

EUNIS Habitat	***N***	**Total**	**Endemic**	**RGR**	**HS**	**LA**	**Total Rare**
Inland surface waters (C)	355	483	2 (0.4)	125 (25.9)	46 (9.5)	71 (14.7)	145 (30.0)
Mires, bogs and fens (D)	1203	658	6 (0.9)	149 (22.6)	46 (7.0)	79 (12.0)	174 (26.4)
Dry grasslands (E1)	1928	1156	21 (1.8)	334 (28.9)	59 (5.1)	249 (21.5)	380 (32.9)
Wet grasslands (E3)	431	672	3 (0.4)	119 (17.7)	21 (3.1)	72 (10.7)	141 (21.0)
Alpine and subalpine grasslands (E4)	3295	976	49 (5.0)	230 (23.6)	76 (7.8)	128 (13.1)	274 (28.1)
Woodland fringes and clearings and tall forb stands (E5)	1317	1227	19 (1.5)	308 (25.1)	98 (8.0)	215 (17.5)	366 (29.8)
Arctic and alpine scrubs (F2)	433	525	19 (3.6)	54 (10.3)	20 (3.8)	26 (5.0)	71 (13.5)
Temperate and Mediterranean-montane scrub and heathlands (F3-F4)	1149	1011	11 (1.1)	160 (15.8)	51 (5.0)	110 (10.9)	203 (20.1)
Garrigue (F6)	1080	838	18 (2.1)	243 (29.0)	42 (5.0)	175 (20.9)	271 (32.3)
Broadleaved deciduous forests (G1)	3401	1130	13 (1.2)	254 (22.5)	59 (5.2)	172 (15.2)	302 (26.7)
Broadleaved evergreen forests (G2)	450	563	6 (1.1)	114 (20.2)	20 (3.6)	82 (14.6)	130 (23.1)
Coniferous woodland (G3)	1322	795	24 (3.0)	81 (10.2)	31 (3.9)	55 (6.9)	115 (14.5)
Screes (H2)	1107	678	40 (5.9)	102 (15.0)	30 (4.4)	57 (8.4)	130 (19.2)
Inland cliffs, rocky outcrops and pavements (H3)	1137	906	43 (4.7)	224 (24.7)	83 (9.2)	136 (15.0)	270 (29.8)

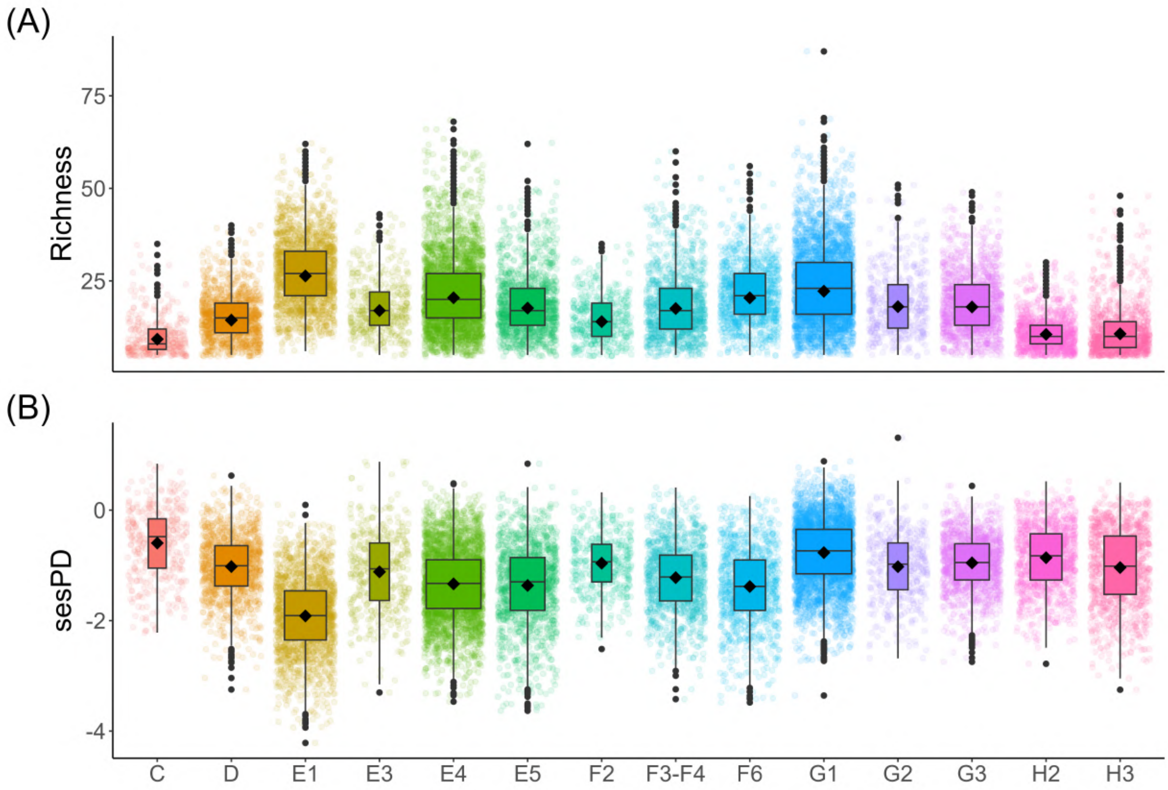

Figure 2.3: First, second, and third quartiles (boxplot) and mean values (black diamonds) of the distributions of species richness (A) and standardized phylogenetic diversity values (B) per habitat. Whiskers extend 1.5 times the interquantile range below and above the first and third quartiles respectively. C: Surface waters, D: Mires & fens, E1: Dry grasslands, E3: Wet grasslands, E4: Alp. & subalp. grasslands, E5: Tall forb stands, F2: Alp. & subalp. scrub, F3-F4: Temperate scrub, F6: Garrigue, G1: Broadleaved deciduous woodland, G2: Broadleaved evergreen woodland, G3: Coniferous woodland, H2: Screes, H3: Inland cliffs & rocks.

(Table 2.1).

The differences in overall proportion of rare species per *relevé* between habitats were statistically significant ($\chi^2 = 7187.3$, $df = 13$, $p < 0.0001$; Fig. 2.4A), with inland cliffs, rock pavements and outcrops showing higher proportions of rare species than the rest of habitats (0.15, $\mathrm{CI}_{95} = 0.14, 0.15$), followed by screes (0.13, $\mathrm{CI}_{95} = 0.13, 0.14$) and inland surface waters (0.13, $\mathrm{CI}_{95} = 0.12, 0.14$). Coniferous (0.02, $\mathrm{CI}_{95} = 0.01, 0.02$) forests and arctic, and alpine scrubs (0.03, $\mathrm{CI}_{95} = 0.02, 0.03$) showed the smallest proportion of rare species per inventory in any habitat.

The contribution of rare species to phylogenetic diversity significantly differed across habitats ($F = 4.3119$, $df = 13$, $p < 0.0001$): the highest contribution corresponded to evergreen forests (0.43, $\mathrm{CI}_{95} = 0.21, 0.65$) and surface waters (0.21, $\mathrm{CI}_{95} = -0.11, 0.52$), while the lowest were in mires, bogs and fens (-0.34, $\mathrm{CI}_{95} = -0.48, -0.20$) and wet grasslands (-0.19, $\mathrm{CI}_{95} = -0.47, 0.09$; Fig. 2.4B). Although the contribution of rare species to PD varied greatly between habitats and rarity types, it did not differ from random expectation, meaning that they do not contribute more than nonrare plants.

The relationship between diversity measures and the proportion of rare species was always significant, but coefficients were low and varied considerably between richness, sesPD and rarity types (Fig. 2.5). The proportion of rare species related negatively with species richness. The same applied for each type of rarity except for locally scarce species. The opposite trend was observed for sesPD and rare species proportion, with both variables relating positively except for locally scarce species.

The patterns of phylogenetic diversity we calculated with the ALLOTB phylogeny of Smith and Brown (2018) were highly correlated ($r = 0.72$) and consistent with our phylogeny (Appendix 2.A, Fig. 2.A.1). Although the distribution of sesPD in each habitat differed slightly between phylogenies (Appendix 2.A, Fig. 2.A.2A), the main pattern of species-poor habitats like inland surface waters, screes and inland cliffs, rock

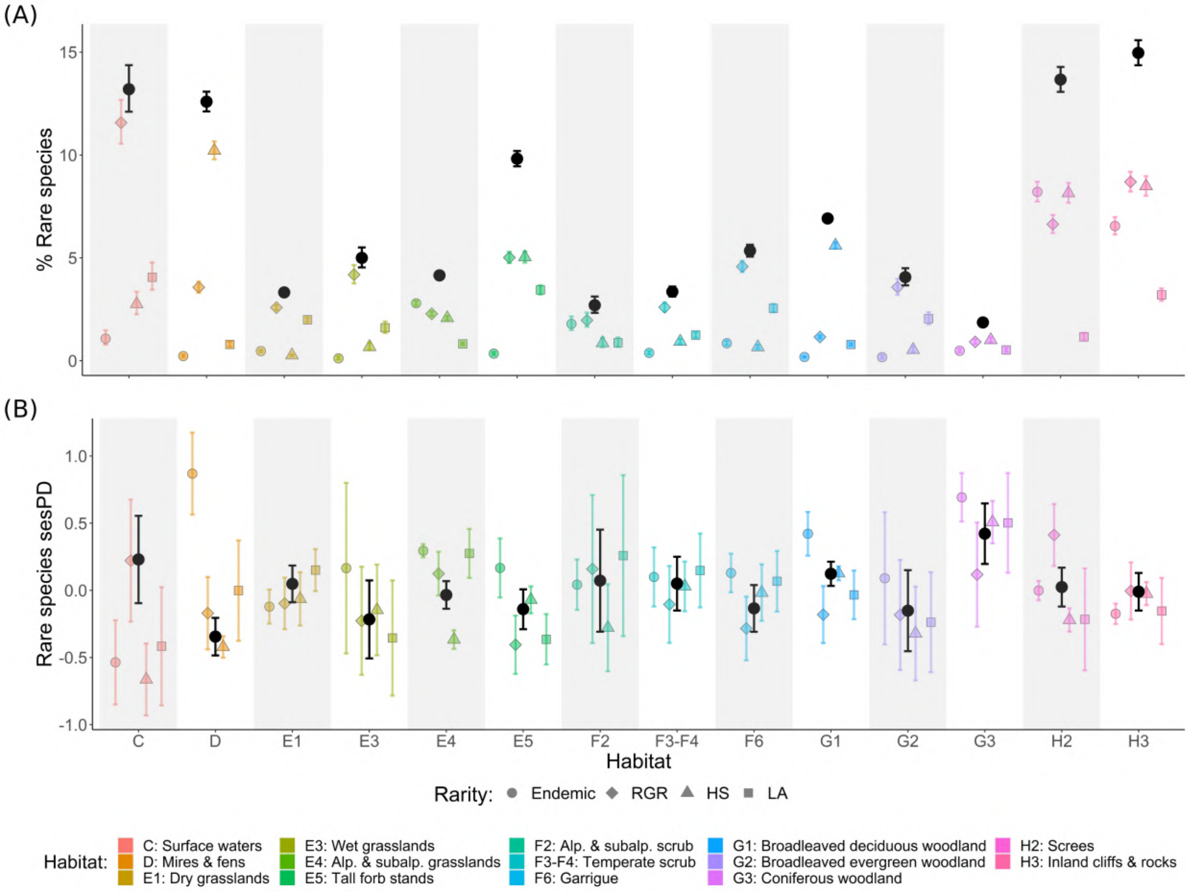

Figure 2.4: Estimated marginal mean and its 95% confidence interval per habitat of rare species proportion per inventory (A) and standardized contribution of rare species to PD in said inventories (B). In both plots black lines and symbols represent data coming from species with one or more rarity types and the ones in color represent data from each type individually. HS: habitat specialists; LA: low local abundance; RGR: small regional geographic range.

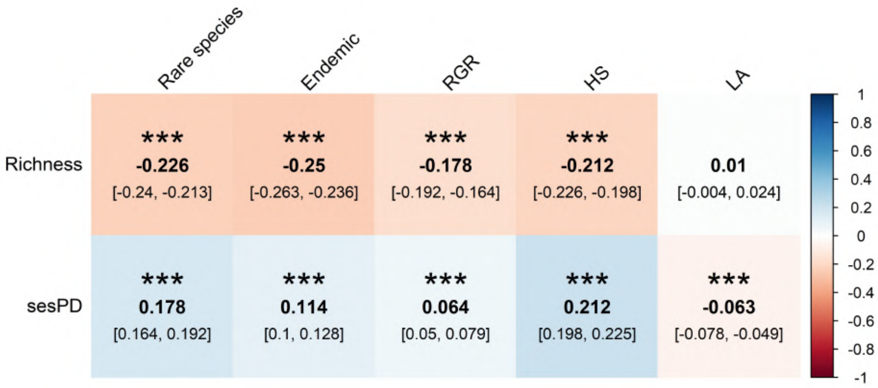

Figure 2.5: Relationship between proportion of rare species, richness and phylogenetic diversity based on Pearson's correlation coefficient. HS, habitat specialists; LA, Low local abundance; RGR, small regional geographic range. Brackets show 95% confidence intervals for each correlation index and asterisks indicate statistically significant values.

pavements and outcrops holding great phylogenetic diversity, and species-rich habitats like dry grasslands having low sesPD was still present. Regarding the contribution of rare species to the phylogenetic diversity of their communities, the results varied between phylogenies (Appendix 2.A, Table 2.A.1). However, this contribution did not differ significantly from randomness, supporting the results from our phylogeny (Appendix 2.A, Fig. 2.A.2B).

2.4 Discussion

Here, we presented the first comprehensive description and comparison of taxonomic and phylogenetic plant diversity patterns, as well as the abundance of rare species and their contribution to habitat species richness and PD in a temperate mountain range, the Pyrenees. Our analysis revealed that rocky and aquatic habitats shelter the highest proportion of rare species. We also found contrasting patterns in the relationship between diversity and rarity, with the richest habitats harboring the least amount of rare species but the most phylogenetically diverse habitats showing the highest proportion of rare species. Interestingly, the loss of rare species would not translate into a stronger reduction of phylogenetic diversity compared with the loss of more common plants. The phylogenetic analyses were consistent across the two different plant phylogenies, which support the robustness of the patterns we observed.

2.4.1 Diversity and rarity patterns across habitats

The observed patterns of species richness are partially consistent with the description of the Pyrenean flora made by Gómez, García, et al. (2017), who found grasslands to harbor the largest number of species, followed by wetlands. We, on the other hand, found the highest number of species in grasslands, broadleaved deciduous forests and shrublands. These differences between our study and theirs might arise from the use of regional herbarium dataset instead of a systematic sampling, as well as slight differences in habitat classification (Gómez, García, et al. (2017) used broader habitat categories, especially for grasslands). Concerning sesPD, the general patterns we found are in line with the phylogenetic patterns observed by Pardo et al. (2017) in a small but very diverse and representative area of the Pyrenees: the Ordesa and Monte Perdido National Park. Our results are also congruent with the sesPD patterns of European vegetation observed among a similar set of habitats by Lososová et al. (2021), in which nonforest habitats such as grasslands had reduced standardized phylogenetic diversity, whereas forests, rocky habitats and wetlands showed high values of sesPD.

Although more than half of the species present in our study were rare according to at least one criterion, these species were unevenly distributed among habitats. We observed a higher incidence of endemic species in rocky habitats and alpine grasslands, consistent with previous studies of the distribution of endemic plants in the Pyrenees (García et al., 2020; Tejero et al., 2017). Regarding the regional abundance of plant species in our study area, Gómez, Lorda, et al. (2017) observed that these species were located mostly in grasslands and wetlands, followed by rocky habitats. We found a similar pattern for wetlands and rocky habitats but not for grasslands, probably because the latter are much more abundant in the Pyrenees and thus species associated with them tend to have a broader distribution in the range. Another possibility is that we analyzed different types of grasslands separately while Gómez, Lorda, et al. (2017) pooled all of them together. Regardless of this, the abundance of species with narrow areas of distribution could be attributed to multiple factors (Schemske et al., 1994). Recent speciation promoted by isolation in particular habitats, for example, can lead to species accumulating in specific areas if their dispersal capabilities are limited (Lesica et al., 2006). Another opposite case scenario could be the reduction of a species' geographic range due to past environmental changes, which culminates in that species being secluded in refugial areas that are still suitable for them or have more stable conditions (Postigo Mijarra et al., 2009).

Habitat specialists in the Pyrenees tend to concentrate in distinct habitats with unique abiotic conditions compared with their surroundings like rocky cliffs, pavements and outcrops; screes; mires, fens and bogs, and tall forb stands. Gómez, Lorda, et al. (2017) showed that specialist plants in the Pyrenees were mostly restricted to grasslands and rocky or humid habitats, and Boulangeat et al. (2012) found that specialist taxa in the Alps were also prone to accumulate in distinctive environments such as wetlands. With the exception of forb stands, these rocky and aquatic habitats tend to be poor in species, which is usually a consequence of harsh environmental conditions such as cold temperatures in alpine areas, damp or poorly developed soils in mires and fens, and low nutrient availability in rocky cliffs and pavements (Adamidis et al., 2014; Kleidon et al., 2009; Niedrist et al., 2018). The filters that these environments impose promote the presence of species exclusively adapted to them, leading to high proportions of specialized taxa (Deák et al., 2018; Pandit et al., 2009). The phylogenetic patterns derived from these filters would depend on the distribution along the phylogenetic tree of the traits that allow plants to survive in such conditions. On the one hand, if these traits had evolved in just a few, phylogenetically close lineages, they would be located in specific areas of the phylogenetic tree, and thus the standardized phylogenetic diversity of habitats harboring these species would be low (Cavender-Bares et al., 2009). This seems to be the case for dry grasslands, which are the only habitat with significantly low sesPD, although they have high species richness. On the other hand, if these traits had evolved several times in separate lineages through a convergent evolution process, these communities would be phylogenetically overdispersed, as the species able to withstand those environmental filters would be scattered throughout the phylogenetic tree (Cavender-Bares et al., 2004). None of the habitats in the Pyrenees shows significant phylogenetic overdispersion, however, those with the highest values of sesPD, namely inland surface waters and rocky habitats, tend to have a limited number of species due to strong environmental filters, suggesting that the adaptations to these environments may have evolved several times across the phylogenetic tree, leading to higher sesPD.

2.4.2 Connecting species rarity and habitat vulnerability

Since species vary in their vulnerability to different factors depending on their rarity, the communities they inhabit will be more or less susceptible to diversity loss according to the type and abundance of rare species they harbor, although the consequences can differ between aspects of diversity. One of the most interesting results of our study is the contrasting contribution of rare species in habitats where they are frequent: their loss would translate into an important reduction of richness but would not translate into a significantly higher reduction of phylogenetic diversity than the loss of co-occurring and more common species. Nonetheless, their loss can lead to dramatic changes in ecosystem functioning and stability depending on its magnitude. Studies on the relation between community stability and biodiversity highlight the importance of the latter in ensuring the functioning of ecosystems: those with less species tend to show reduced asynchrony in species responses to abiotic factors and less functional redundancy, which lead to decreased stability (Schäfer et al., 2019; Xu et al., 2021). While more diverse and redundant communities can still function after the loss of part of its diversity thanks to the functional redundancy of the remaining species (Thibaut & Connolly, 2013; Yachi & Loreau, 1999), less diverse communities have more difficulties for compensating the possible loss of keystone species and in consequence are more vulnerable to disturbances. If, in addition, less diverse communities have a higher proportion of rare species, which are considered to be more vulnerable to extinction (Kempel et al., 2020), and tend to play important roles in ecosystem functioning (Jain et al., 2014; Mouillot et al., 2013), disturbances in those communities could have severe consequences for their stability and function.

2.4.3 Intrinsic vulnerability versus external hazards

It is noteworthy to mention that habitat vulnerability inferred from species rarity does not necessarily match habitat's exposure to global change drivers (K. Wilson et al., 2005). Our approach gives insight on a particular aspect of the intrinsic vulnerability of habitats due to the solely factor of species rarity. However, their vulnerability is still dependent on the combination of multiple internal and external factors like land use or climate change (Weißhuhn et al., 2018). According to the European Red List of Habitats (ERLH; Janssen et al., 2016), about half of the freshwater and grassland habitats in the European Union, along with more than 80% of mires and bogs are threatened by global change. Our rarity-based approach to vulnerability adds a new layer of concern to this assessment, given the high incidence of rare species in inland surface waters, mires, fens and bogs, and tall forb stands (which are included within the grassland category in the ERLH). Such coincidence translates into a double risk for these kinds of habitat, as they are highly vulnerable to both external and internal factors. Conversely, screes and inland cliffs, rocky pavements and outcrops, which our analyses pointed out as vulnerable, were deemed of least concern by the ERLH regardless of the sensitivity of the species in them. This highlights the importance of following a multifaceted course of action for conservation practices, integrating both intrinsic and extrinsic aspects of habitats and species (Dawson et al., 2011).

2.5 Conclusions

Our analyses provided insight on the patterns of taxonomic and phylogenetic plant diversity across habitats in a South European mountain range. They highlighted the role of distinct environments such as tall forb stands, aquatic, and rocky habitats as hotspots of both phylogenetic diversity and rare species. When taking into account the high proportion of rare species as an approximation to the intrinsic vulnerability of habitats, we found notable differences in habitat sensitivity. On the one hand, inland cliffs, rocky pavements and outcrops along with screes are particularly sensitive to demographic stochasticity due to small populations and low local abundances (Matthies et al., 2004). On the other hand, aquatic habitats and tall forb stands are sensitive to risks associated with low regional abundance and habitat specialization in addition to being among the most sensitive habitats to current global change drivers, as stated by the European Red List of Habitats. Through the study of both internal and external factors we can better identify the most vulnerable and priority habitats under the current climatic and land use change scenario. Our study highlights the importance of taking an integrative approach towards habitat vulnerability assessment, one that considers both internal and external drivers of vulnerability. It also shows how, in the absence of information about direct threats to species and habitats, accounting for rarity patterns could be a useful tool to guide conservation managers and policy makers.

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Appendix 2.A Comparison with the ALLOTB megaphylogeny

In order to assess possible biases in our analysis caused by our phylogeny, we repeated all our phylogenetic analysis using the ALLOTB phylogeny by Smith and Brown (2018). This is a megaphylogeny that includes over 350000 seed plant species and was constructed using the Open Tree of Life v9.1 as a backbone and data from the version 218 of GeneBank. In order to use this phylogeny, first we grafted all the missing species using the *V.PhyloMaker* R package (Jin & Qian, 2019) after matching plant species names between our dataset and the ALLOTB phylogeny. Then, we calculated the phylogenetic diversity of each plant inventory along with the contribution of rare species to that PD following the process described in the Methods section of the main text. In order to compare how each phylogeny behaved, we calculated Pearson's correlation coefficient between the results corresponding to each phylogenetic tree.

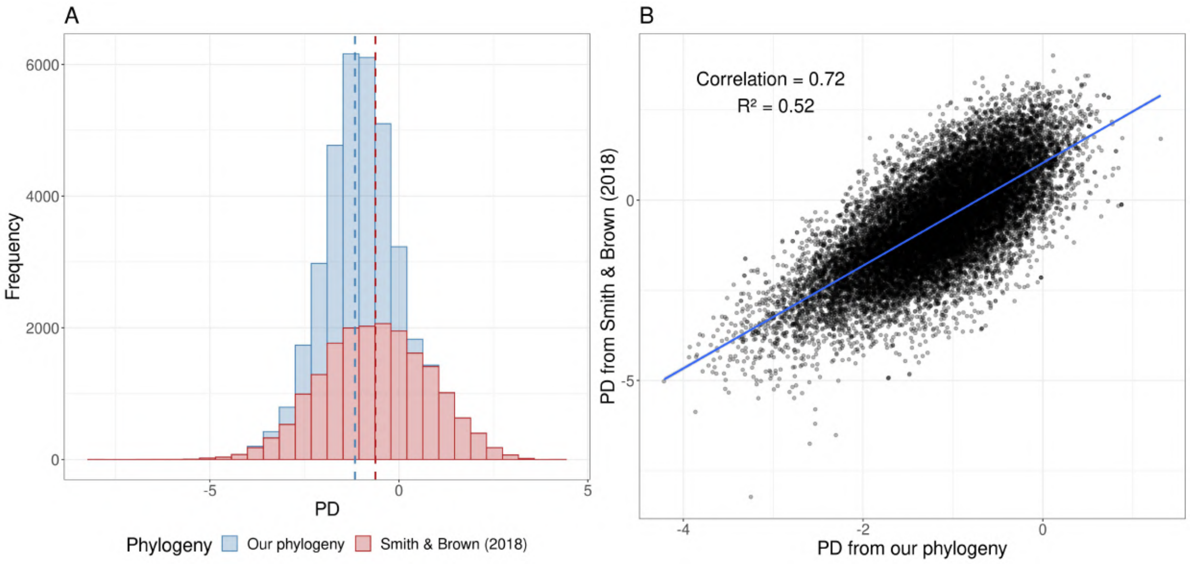

Figure 2.A.1: A: Frequency distribution of phylogenetic diversity values calculated using our phylogeny (blue bars) and Smith and Brown (2018) (red bars). Dashed lines show the mean of each distribution. B: Relationship between PD values calculated with our phylogeny and Smith & Brown's.

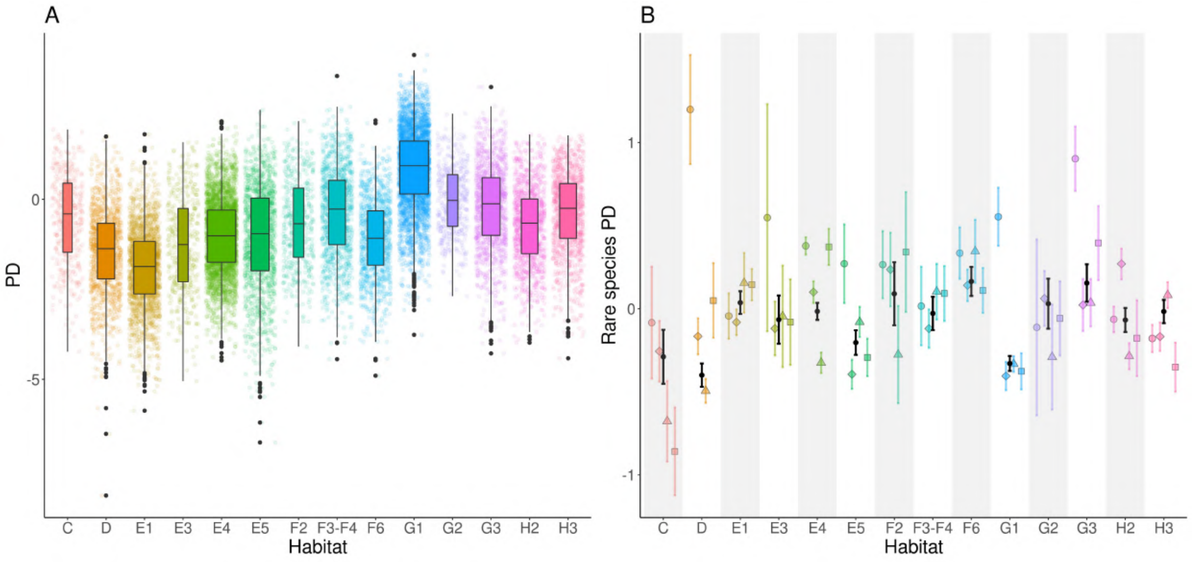

Figure 2.A.2: A: Boxplot of the distribution of standardized phylogenetic diversity values per habitat. B: Standardized contribution of rare species to phylogenetic diversity. Metric in both plots were calculated using the phylogeny of Smith and Brown (2018).

Table 2.A.1: Pearson's correlation coefficient (r) between the contribution of each type of rare species to the phylogenetic diversity of their communities calculated with our phylogenetic tree and the phylogeny from Smith and Brown (2018), along with its 95% confidence interval. Bold face indicates statistically significant values ($p < 0.05$). All: Any kind of rare species (according to 1, 2, 3 or the 4 criteria); Endemic: Species restricted to the Pyrenees; RGR: Species with small regional geographic range; HS: Habitat specialists and LA: Species with low local abundance.

Rarity type	**Pearson's r**	**Lower CI**	**Upper CI**
All	**0.412**	0.396	0.428
Endemic	**0.867**	0.859	0.875
RGR	**0.341**	0.320	0.362
HS	**0.761**	0.750	0.771
LA	**0.484**	0.459	0.509

3 Phylogenetic patterns of rarity in the Pyrenean flora

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3.1 Introduction

Rarity and the mechanisms behind it have interested ecologists for decades (Preston, 1948; Rabinowitz, 1981; Stebbins, 1980) as it is related to one of the central subjects of ecology: the abundance and distribution patterns of species across time and space. There is, however, a more pragmatic aspect of rarity that is of great importance for conservation biology and practice, especially in the current context of global change and biodiversity loss (Ceballos et al., 2015; Pimm et al., 2014): rare species are more likely to go extinct than common species (K. F. Davies et al., 2004; Mace & Kershaw, 1997). Rarity is a complex concept that can be approached from several angles, although the classification proposed by Rabinowitz (1981) has been widely adopted (Choe et al., 2019; Crisfield et al., 2020; Espeland & Emam, 2011; Loza et al., 2017). Her method classifies species into seven rarity categories based on their geographic range, habitat specificity (HS) and population size. Although Rabinowitz's ideas were not directly related to vulnerability or extinction risk, later studies have shown that rare species are more susceptible to different drivers of extinction, to the point that some aspects of what we can consider rarity, namely geographic range and population size, are part of the criteria for inclusion in IUCN's Red List (IUCN, 2012). First, species with restricted geographical ranges, such as narrow endemics or those with limited spatial distributions, have been shown to have higher extinction risk throughout history (Harnik et al., 2012; Mckinney, 1997; Saupe et al., 2015). Second, species limited to certain habitats or with very narrow environmental niches also show increased vulnerability to extinction as they are dependent on the preservation of particular abiotic conditions for their survival, and thus are very susceptible to environmental changes (Saupe et al., 2015; Staude et al., 2020). Finally, species with small populations are more vulnerable to stochastic processes that could lead to their disappearance (Lande, 1993; Matthies et al., 2004). Since different kinds of rarity may respond very differently to similar sets of stressors (*e.g.*

global warming, land use change or invasive species), identifying which species are rare and their type of rarity can help to optimize conservation efforts, regarding both the evaluation of vulnerability to different threats and the identification of potentially endangered species. Rarity is also a reflection of the evolutionary history of a species and its ability to establish itself and thrive in different regions and environments (Gaston & Kunin, 1997). Under the assumption that traits related to rarity are heritable to some extent (Mouquet et al., 2012), a phylogenetic approach can be helpful to identify potentially rare species (Webb & Gaston, 2003). In that case, we would expect rare plants to show some phylogenetic signal; that is, the tendency of phylogenetically close species to resemble one another more than other species (Münkemüller et al., 2012). These phylogenetic patterns vary depending on the spatial scale, the taxonomic group in study and the environmental conditions of the area (Zacaï et al., 2017). However, studying the phylogenetic patterns of rarity can contribute to the identification of potentially rare taxa for which there is no available field information assuming that related species would be similarly rare, which would help us find vulnerable taxa or clades in a phylogeny (Manne & Pimm, 2001; Robbirt et al., 2006; Toledo et al., 2014). The importance of finding such vulnerable and phylogenetically close taxa lies in that, if these rare species were particularly sensitive to one kind of global driver, the loss in phylogenetic diversity (PD) derived from it would be greater than expected by chance, given the non-random nature of these extinctions (Heard & Mooers, 2000; Thuiller et al., 2011). Here, we apply the rarity framework proposed by Rabinowitz (1981) to the flora of the Pyrenees, a mountain region in southwestern Europe, and investigate the existence of phylogenetic signal associated with geographic rarity (endemicity and regional geographic range (RGR) size), HS and local abundance (LA). In addition, we explore if these rarity types are taxonomically clustered. More specifically, we address the following questions and our expectations about them.

- Is there any phylogenetic signal for each kind of rarity among the rare plants of the Pyrenees? We expect different phylogenetic patterns for each rarity type because of different underlying mechanisms. For example, the phylogenetic signal of endemicity could depend on the fact that recently diverged species would be closely related (neoendemisms) and thus show phylogenetic signal, whereas species coming from ancient lineages would be phylogenetically isolated and thus would not show any signal (Mishler et al., 2014). We expect RGR to show some phylogenetic signal related to factors such as limited dispersal ability or niche breadth, which are assumed to be at least partially heritable (Saastamoinen et al., 2018; Sexton et al., 2017). Habitat specialization should also show phylogenetic signal under the assumption of niche conservatism, which has been already observed in plants (Prinzing et al., 2001). Locally scarce species, however, are not expected to show any phylogenetic signal given that many other current factors like resource availability, interspecific interactions, founder effects or environmental filtering have strong influences in the LA of species, dampening any possible phylogenetic patterns.

- Will the loss of PD be greater than expected by chance if rare plants become extinct? The loss of PD will depend on the degree of phylogenetic relatedness between rare species and the length of the branches in which they are located. If rare species are closely related and located in clades stemming from long branches, which capture more PD, their extinction will lead to a higher loss than expected by chance because that would affect larger and deeper sections of the phylogeny. In contrast, the loss of diversity will be less than randomly expected if rare species are overdispersed in the phylogeny. Finally, to test the relationship between patterns found in our study and practical conservation, we inquire in if threatened Pyrenean species included in the Pyrenean Red List of vascular plants are associated with phylogenetically close rare plant species. We expect a high degree of overlap between our assessment of rarity and the Red List, given that both share some classification criteria.

3.2 Methods

3.2.1 Data gathering

We downloaded 18,842 plant inventories carried out over the last 70 years in the Pyrenean area from the Iberian and Macaronesican Vegetation Information System (SIVIM) (Font et al., 2017). This dataset contained around 400,000 plant records of more than 2,300 taxa at species level. Each inventory included information on altitude, some habitat description (phytosociological association, alliance or other), species number and their abundance. The latter was recorded in different scales, depending on the inventories, although most of them follow the classic semi-quantitative scale of Braun-Blanquet that assigns an abundance value to each plant species based on its cover. To properly compare between all species, we transformed all data to the extended Braun-Blanquet scale following van der Maarel (1979), which ranges from 1 to 9. To focus on mountain habitats, we excluded coastal areas and discarded inventories located below 400 m a.s.l. In addition, we removed any inventories containing fewer than five species to ensure proper sampling size and plant representation. Plant names were validated using the Atlas of the Pyrenean Flora (FLORAPYR; www.atlasflorapyrenaea.eu/src/taxon/index.php?idma=0), an international project addressing the compilation of all the information available about vascular plants and bryophytes of the Pyrenees and its piedmont. To ensure that the species in our study were representative of the Pyrenean flora, we also excluded all non-native species according to the Atlas of the Pyrenean Flora. Finally, habitats were grouped into one of

14 European Nature Information System (EUNIS) habitats (Table 1; see García et al. (2022) for more information on their geographic distribution in the Pyrenees), a classification for the terrestrial and marine habitat types of the European continent (Moss, 2008).

3.2.2 Phylogenetic inference

We used the phylogeny published by Roquet and González (2022), a dated genus-level phylogeny built specifically for the Pyrenean flora, using sequences downloaded from GenBank of three chloroplastic regions (rbcL, matK and ndhF), plus the nuclear ribosomal ITS region for some families. It comprises all plant genera in the Pyrenees according to FLORAPYR, except *Cytinus*, *Ptychotis* and *Xatardia*, for which no useful phylogenetic markers were available in GenBank. To be able to work at the species level, we randomly resolved genus-level polytomies following a Yule process. This method randomly resolves polytomies assuming that all taxa have an equal probability of undergoing a speciation event at any moment in time and without following any particular speciation and extinction rates (Gernhard et al., 2008). We repeated this process ten times to produce a distribution of possible evolutionary hypotheses *sensu* Rangel et al. (2015).

3.2.3 Rarity assessment

We considered four rarity criteria: endemicity and RGR size as complementary components of geographic range; HS; and LA. A species was considered endemic when its global distribution was limited to the Pyrenees. RGR size was measured as the highest number of 10 x 10 km UTM cells occupied by the target species within the FLORAPYR grid or the SIVIM database. HS was estimated for each species by combining the frequency of each species and the frequency of the habitats where it occurs using Hurlbert's B' resource use index (Eq. 3.1) as described by Feinsinger et al. (1981):

$$B' = 1/\sum_i (p_i^2/q_i) \tag{3.1}$$

where p_i represents the proportion of occurrences of the target species in habitat i and q_i the relative abundance of such habitat in the study region. This index ranges from 0 for the rarest species to 1 for the most common species. Its main advantage is that it gives more weight to rare habitats, so that the rarest species are those found in just a few and scarce habitats. To obtain a more in-depth idea of the habitats with which each species is associated, we calculated the IndVal index of Dufrêne and Legendre (1997). This index gives a degree of association between a single species and each of the habitats in which it is found, considering the abundance of both the species and the habitats. Information on the abundance of habitats, measured as the number of inventories associated with each habitat, and the distribution of species in each of them, was extracted from the SIVIM database. LA for each species was estimated as its average abundance value among all the inventories in SIVIM. Prior to any further analysis, we standardized RGR, HS and LA values to z-scores (mean = 0 and SD = 1) to enable comparisons.

3.2.4 Phylogenetic patterns of rarity

We used two methods to study phylogenetic signal depending on the nature of each rarity type. For RGR, HS and LA we computed Pagel's λ (Pagel, 1999), which measures phylogenetic signal in continuous variables and compares it to a Brownian motion model. This index ranges between 0 and 1, with 0 indicating random distribution and 1 evolution under Brownian motion, implying phylogenetic signal. For endemism, which is a binary variable, we computed the D statistic of Fritz and Purvis (2010). This index employs a binomial distribution assuming a latent continuous variable and compares it to a Brownian motion model of evolution. For easier comparison with Pagel's λ we transformed D into $-D+1$, and thus values equal to 0 indicate random distribution and values close to 1 indicate phylogenetic signal (Goberna & Verdú, 2016). In addition, we computed pPCA as described in Revell (2009) based on the values of RGR, HS and LA. We applied this method for two reasons: first, it calculates a multivariate λ to test for phylogenetic signal in multiple traits at the same time (Ibanez et al., 2016), and second, it allows an easy visualization of the correlation between rarity components and the similarities between species taking into account phylogenetic information (Uyeda et al., 2015). Common phylogenetic signal metrics like Pagel's λ or Fritz and Purvis's D give a phylogeny-wide value without identifying the regions of the tree where species that closely resemble one another accumulate. To identify those regions, we computed the local index of phylogenetic association (LIPA) for each species and all rarity types (Keck et al., 2016). This measure is adapted from the local index of spatial association of Anselin (1995), which is a local case of Moran's autocorrelation index I. Positive LIPA values identify species that tend to share similar rarity values with their close relatives. We tested if LIPA values were statistically significant by comparing the observed values to a null model that randomly shuffles the tips of the phylogeny 999 times.

Finally, we tested if the loss of PD in the Pyrenees caused by the extinction of rare species with significant phylogenetic association (*i.e.* those with positive, significant LIPA values) would be greater than expected by chance. We considered as rare species those with values of RGR, HS and LA lower than average, and all endemics. Then, we followed a procedure similar to Von Euler (2001). First, we calculated the total PD of the phylogeny by summing the length of all branches in the tree and then, for each rarity type separately, we removed rare species from the phylogeny and recalculated PD for the resulting tree. To test if the loss of PD (*i.e.* the difference in PD before and after the removal of species) was greater than expected by chance, we repeated the process 999 times, removing a set of randomly chosen species of the same size as the number of rare species removed. To compare the loss of PD between rarity types we calculated the standard size effect of the loss ($\text{sesPD}_{\text{loss}}$) for each type, by subtracting the mean of the null values from the observed value and dividing by the standard deviation of the null distribution. Values were considered statistically different from random expectation with a 95% confidence if they were outside the [-1.96, 1.96] interval (Mazel et al., 2016).

Phylogenetic analyses are dependent on the phylogenetic scale used in them (Graham et al., 2018), especially if the phylogeny has deep bifurcations like the one between angiosperms and gymnosperms. Thus, we conducted all analyses using three sets of species: one with all vascular species; one with only angiosperms; and another containing only the oldest groups, gymnosperms and monilophytes. To consider all possible evolutionary hypotheses among plant species in the Pyrenees we repeated each analysis using our ten phylogenies and averaged the resulting indices.

3.2.5 Taxonomic patterns of rarity

To better understand how rarity is distributed among different taxonomic levels, we fitted a Bayesian random effect model for each rarity type (binomial for endemism and Gaussian for scaled and centered RGR, HS and LA) with rarity as dependent variable and a random effect consisting of genus nested within family and both nested within order. This method partitions the variation (variance for RGR, HS and LA, and deviance for endemism) of each rarity type among taxonomic levels and an unexplained residual component, while considering the nested nature of taxonomic classification (Asner & Martin, 2016; Martinelli et al., 2021; Oliveras et al., 2020). Models were fitted using uninformative priors and four Markov chains with 4,000 iterations each, a thinning interval of 10 and a burn-in period of 1,000 iterations. We calculated the proportion of variation explained by each taxonomic level by comparing it to the total variation explained by the random effects, including the random residual component.

3.2.6 Rarity and conservation status

The conservation status of the plants in our dataset was obtained from the Red List of the Pyrenean vascular flora published by the FLORAPYR project (www.opcc-ctp.org/en/florapyr). To explore how rarity relates to threatened species in the Red List (critically endangered: CR, endangered: EN and vulnerable: VU), each species of our dataset was plotted along the first two components of our phylogenetic principal component analysis (pPCA).

All analyses were conducted in R version 4.1.2 (R Core Team (2021), www.r-project.org). Pagel's λ and LIPA values were computed with the *phylosignal* package (Keck et al., 2016) while Purvis's D was calculated with the *caper* package (Orme et al., 2018). IndVals were calculated with the *labdsv* package (Roberts, 2019). Random models were fitted using the *rstanarm* package with the default uninformative priors and parameters provided by the *stan_glmer* function (Goodrich et al., 2020). The variance or deviance of the random effects of each random model was assessed with the *insight* package (Lüdecke et al., 2019). Package *phytools* was used for the phylogenetic PCA (Revell, 2012).

3.3 Results

According to the SIVIM database, plant species in the Pyrenees occupied, on average, 133.02 (SD = 114.87) 10 x 10 km UTM cells, had an average HS of 0.2 (SD = 0.12) and an average LA of 2.78 (SD = 0.87) in the Braun-Blanquet extended scale. Only 78 (3.31%) of the 2,351 species in our dataset were endemic to the region. Analysis found that 568 species (24.16% of the total) had below-average values of RGR, HS and LA at the same time. In addition, 28 of these species were also endemic to the region (Appendix 3.B, Table 3.B.3).

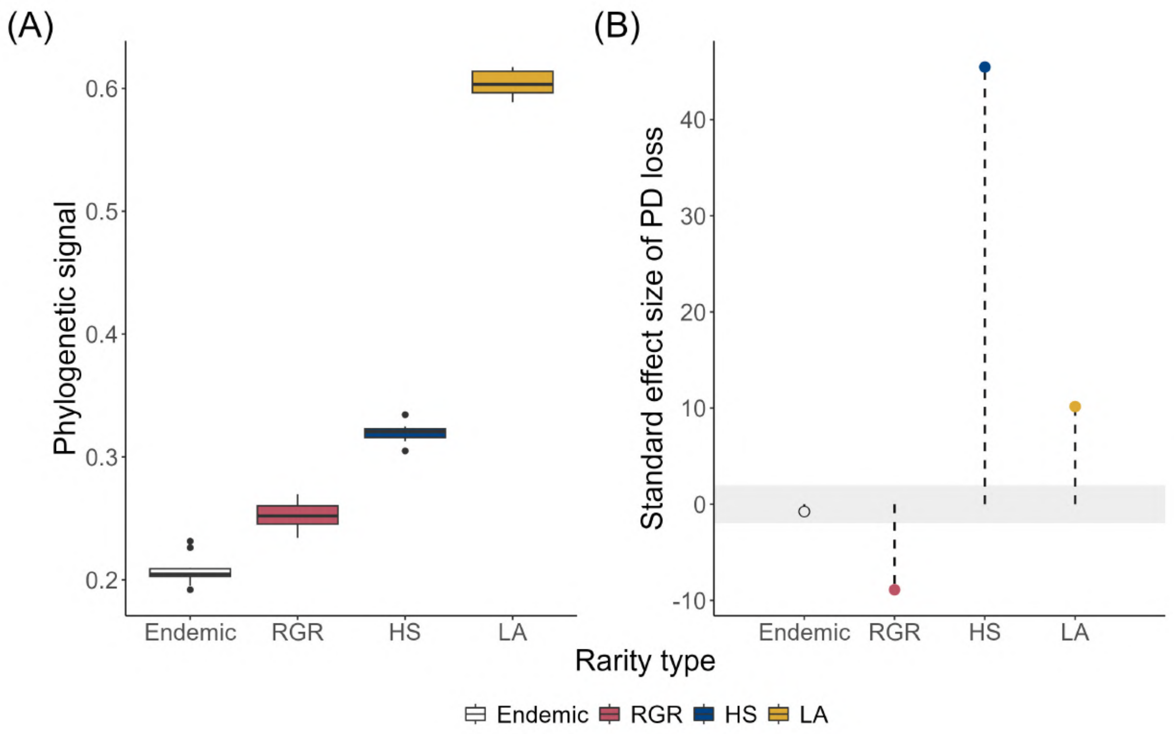

Figure 3.1: (A) Distribution of the estimated values of phylogenetic signal (Pagel's λ for regional geographic range (RGR), habitat specificity (HS) and local abundance (LA) and Purvis's $-D+1$ for endemism) using ten versions of the phylogeny for each rarity type. (B) sesPD$_{\text{loss}}$ after removing rare species with significant local index of phylogenetic association (LIPA) values. Shaded area indicates the 95% confidence interval [-1.96, 1.96].

3.3.1 Phylogenetic patterns of rarity and their consequences

We observed very similar and consistent patterns in phylogenetic signal between all three datasets of major plant groups (Fig. 3.1 and Appendix 3.A, Fig. 3.A.1) and thus only the results from the complete dataset are reported in the main text. Every rarity type showed statistically significant phylogenetic signal ($p < 0.05$), but the strength varied between types: LA exhibited the strongest signal, followed by HS, RGR and endemism (Fig. 3.1). The pPCA indicated a certain degree of signal for RGR, HS and LA together ($\hat{\lambda} = 0.43$, $SD = 0.01$).

595 out of 2,351 species (25.3%) had significant, positive LIPA values (Fig. 3.2,

Appendix 3.B, Table 3.B.1). Although we observed differences between each aspect of rarity type in how these species were distributed in the phylogeny, we detected that endemicity, RGR and HS presented clearly defined groups of species that contributed more to their phylogenetic signal, both for higher and lower values than the average (Fig. 3.2). LA, on the other hand, had significant LIPA values spread across the whole phylogeny, mostly caused by species with LA values lower than the average.

In contrast to the loss of other kinds of rare species with significant LIPA values greater than 0, the removal of endemics did not result in statistically significant changes in PD ($\text{sesPD}_{\text{loss}} = -0.76$). However, the decrease in PD differed between the other rarity types (Fig. 3.1B): the loss of habitat specialists ($\text{sesPD}_{\text{loss}} = 45.47$) and species with low LA ($\text{sesPD}_{\text{loss}} = 10.16$) resulted in a much higher PD loss than expected under the random loss, whereas the loss of species with limited RGR led to a lower PD loss than expected ($\text{sesPD}_{\text{loss}} = -8.89$).

3.3.2 Taxonomic patterns of rarity

The partitioning of variation (variance or deviance) of each rarity type among taxonomic levels using random models indicated that between 10 and 42% of variation was explained by taxonomy (Fig. 3.3A). Endemism and LA had the highest proportion of variation explained by all taxonomic levels together (42.5% and 36.4%, respectively). Between taxonomic levels, the highest variation was found at the genus level, except for LA, where family accounted for the highest proportion of variation. These results were congruent with the analysis of LIPA. The species with significant LIPA values for each rarity type belonged to families with a higher proportion of endemics and lower values of RGR, HS and LA, according to the random model (Appendix 3.B, Table 3.B.2).

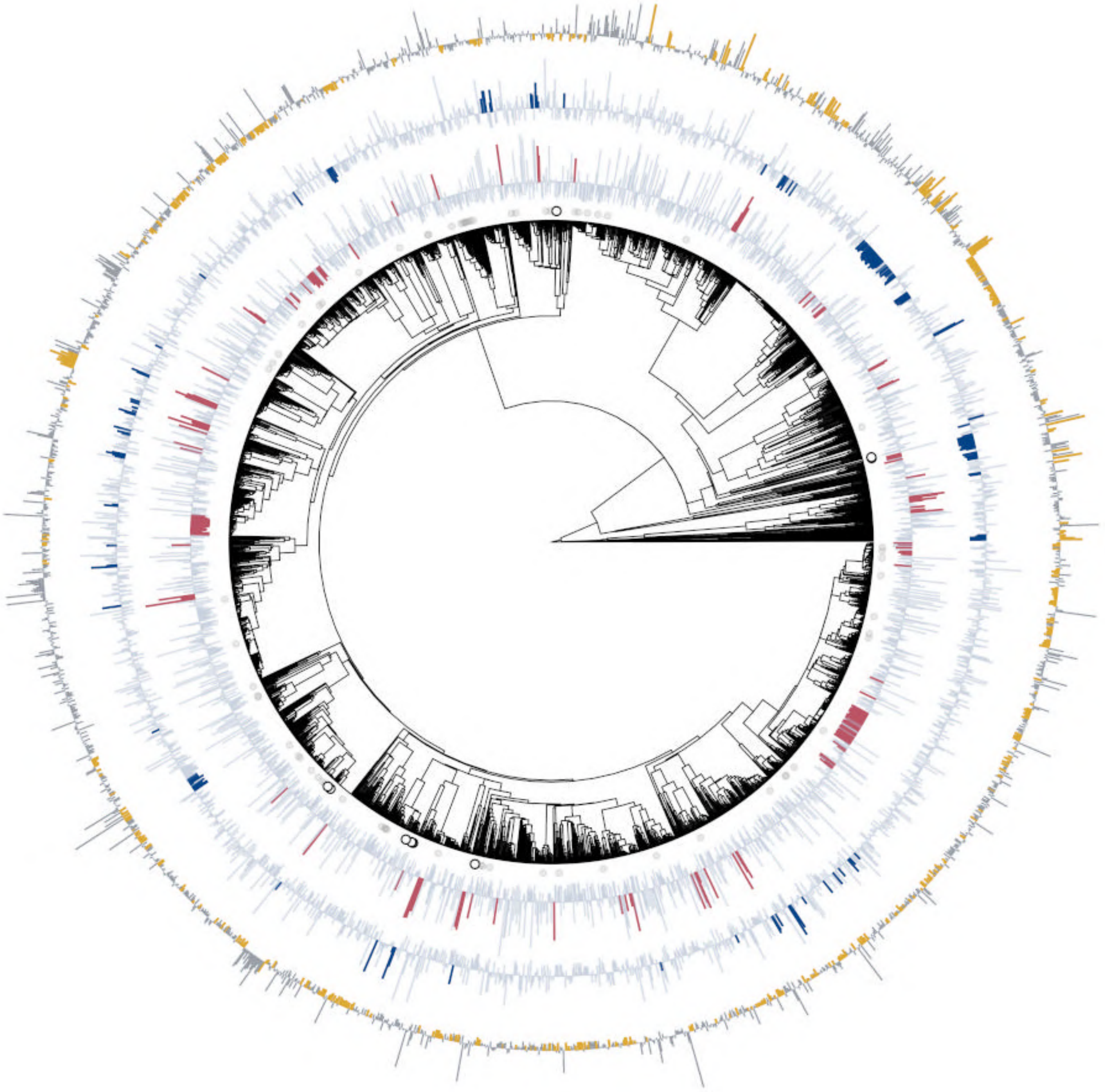

Figure 3.2: Phylogenetic tree of the Pyrenean species included in Iberian and Macaronesican Vegetation Information System (SIVIM) inventories (one of the ten versions produced), with dots and bars in color depicting those species with significant local index of phylogenetic association (LIPA) values ($p \leq 0.05$). Rings from the inside out: endemic species (white circles), scaled regional geographic range (RGR) values (red bars), scaled habitat specialization values (blue bars), scaled local abundance (yellow bars).

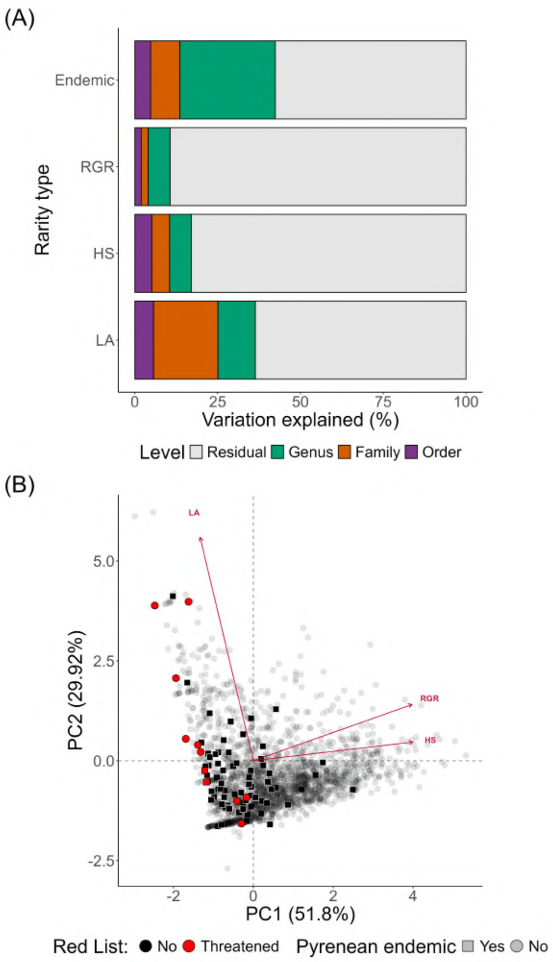

Figure 3.3: (A) Proportion of variation explained by each taxonomic level in the random models fitted for each rarity type. (B) First two components of the phylogenetic principal component analysis (pPCA) based on regional geographic range (RGR), habitat specificity (HS) and local abundance (LA). Squares indicate endemic species and colored points threatened species in the Red List of the Pyrenean vascular flora. Percentages in each axis indicate the amount of variance explained by each component.

3.3.3 Conservation status of rare plants in the Pyrenees

A total of 11 threatened species was present in our dataset, representing a small fraction of the 64 threatened taxa included in the Red List of the Pyrenean vascular flora (Appendix 3.B, Table 3.B.1). Half of these species (1 critically endangered and 5 vulnerable) had significant LIPA values and were endemic or had below-average values of RGR, HS or LA. In addition, all threatened species tended to have small RGR and be habitat specialists, but did not necessarily show low LA (Fig. 3.3B).

3.4 Discussion

We present the first study of the taxonomic and phylogenetic patterns of four kinds of rarity in the flora of a temperate and diverse mountain region, the Pyrenees. We detected significant phylogenetic signal of varying intensity for all aspects of rarity: endemism, RGR, HS and LA. In addition, our analysis of the local contribution of each species to phylogenetic signal revealed distinct groups of closely related species that were similar in different aspects of rarity, especially RGR and HS. The taxonomic analysis was congruent with the observed phylogenetic signal. These results support our hypothesis that rarity in plants is conserved to different degrees through phylogenies. Thus, rare species tend to be closely related, leading to phylogenetic clustering of species more vulnerable to extinction. Phylogenetic and taxonomic aspects of species rarity Rarity is a multifaceted and complex phenomenon whose phylogenetic patterns can vary depending on the spatial and phylogenetic scope of the analysis. These patterns can also vary depending on the group studied and type of rarity, due to the interplay between the environmental features of the study region and species traits, niche breadth or interspecific interactions (Wamelink et al., 2014; Zacaï et al., 2017). Despite this heterogeneity, the phylogenetic signal we observed in the flora of a temperate mountain system adds new evidence to the existence of this pattern, observed in other systems and organisms like tropical floras (Dexter & Chave, 2016; Loza et al., 2017) and North American continental fishes (Giam & Olden, 2018), and partly consistent with patterns observed in European birds (Cotgreave & Harvey, 1992; Pearman et al., 2014), amphibians (Bonetti & Wiens, 2014) and terrestrial vertebrates (Pie, Caron, & Divieso, 2021; Pie, Divieso, & Caron, 2021). Altogether, this suggests that processes ruling over the phylogenetic patterns of rarity might be consistent throughout regions despite differences in evolutionary history and climate, and that there is a certain degree of congruence in these processes between groups of plants and animals (Liu et al., 2020). Nevertheless, disentangling the evolutionary processes behind the phylogenetic patterns of different aspects of rarity can be a daunting task. An endemic species, for instance, can be limited to a particular area for different reasons such as recent speciation and not having had enough time to expand beyond its initial range, or because its formerly wider geographical range has been reduced and its congeneric species have gone extinct around the world (Kruckeberg & Rabinowitz, 1985; Stebbins & Major, 1965). The phylogenetic imprint left by either of these processes would be very different. Recently evolved species are expected to present significant phylogenetic clustering due to several closely related species coexisting in the region. Meanwhile, paleoendemics are presumed to show phylogenetic overdispersion, as these species would be evolutionarily isolated from the other extant species in the tree (Mishler et al., 2014). Our phylogenetic analysis, along with the high variation in endemism at the genus level, highlights the presence of clusters of endemic species throughout the phylogeny. Previous studies found an increase in diversification rates throughout the Pyrenees during the late Neogene due to the Alpine uplift (Boucher et al., 2016) and during the Quaternary period caused by climatic oscillations such as glaciation cycles (Kadereit et al., 2004; Roquet et al., 2021). This increase in diversification rates likely led to allopatric speciation and the high proportion of neoendemic species found in genera *Androsace* (Boucher et al., 2016), *Campanula* (Roquet et al. 2022) and *Saxifraga* (Vargas et al., 2018) within the Pyrenees (Ninot et al., 2017). Regional geographic range and habitat specialization follow a similar pattern of relatively weak phylogenetic signal accompanied by a few clusters of very closely related rare species. This pattern is further supported by the low importance of taxonomy regarding variation in rarity across the phylogenetic tree. Concerning geographic range, these sparse groups of phylogenetically close species with small geographic ranges could be the result of allopatric speciation coupled with limited abilities to disperse beyond their original distribution (Böhning-Gaese et al., 2006; Zacaï et al., 2017). These results are consistent with the geological history of the Pyrenees, where mountain uplifts and glacial cycles have expanded and contracted the geographic ranges of species, favoring allopatric speciation (Boucher et al., 2016; Kadereit et al., 2004; Ninot et al., 2017; Wallis et al., 2016). However, to fully understand the evolutionary mechanisms behind this pattern, it would be necessary to study not only the RGR of each species, but also the overlap between their spatial distributions. With respect to habitat specialization, the presence of separate clusters of species dispersed throughout the phylogeny highlighted by the analysis of local phylogenetic association suggests that the adaptations allowing species to inhabit very particular habitats have evolved several times and at different points in the evolutionary history of the region. The taxonomic analysis gives additional support to this hypothesis, as the limited variation explained by taxonomy is more or less evenly distributed among genera, families and orders, suggesting the diversification of habitat specialization at different evolutionary times. According to the IndVal measure of habitat specialization, around 75% of the specialist species with significant phylogenetic association (Appendix 3.B, Table 3.B.1) are present in aquatic habitats such as bogs, fens, mires and inland water bodies, indicating that the traits facilitating life in such particular environments have been conserved through evolutionary history after evolving at different times; this reflects the evolutionary pattern of adaptations to aquatic life observed in angiosperms by Cook (1996). It is noteworthy that habitat specialists living in other habitats often considered stressful, such as screes, rocky cliffs or high altitude grasslands, do not show a clear phylogenetic pattern. This is in contrast with the patterns of phylogenetic closeness observed in plants living in similar habitats of high altitude summits of other temperate mountain regions like the Alps observed by Marx et al. (2017), suggesting differences in the evolutionary processes in the flora of each region.

We observed a strong phylogenetic signal for LA, along with the highest proportion of variation explained by taxonomy of any rarity type. Although these results challenge our initial hypothesis, they follow the patterns of phylogenetic signal in LA found by other authors in birds (Cotgreave & Harvey, 1992), tropical plants (Dexter & Chave, 2016; Loza et al., 2017) and terrestrial vertebrates (Pie, Divieso, & Caron, 2021). Most species in our data show low LA, which could favor the strong phylogenetic signal we observed. However, disentangling the mechanisms behind this pattern is quite difficult. First, these abundance distribution patterns have been recently questioned in the literature because they can arise from non-biological mechanisms, as seen in other study systems (Keil et al., 2018; Warren et al., 2011). Second, the determinants of species LA are very diverse, ranging from intraspecific variation in life history traits (Kolb et al., 2006) to local environmental conditions (Bertness & Ellison, 1987), disturbance regimes (Guedo & Lamb, 2013) or interspecific interactions (Levine & Rees, 2002). However, the strong phylogenetic signal and the high proportion of variation explained by the family of each species suggests that certain traits determining the LA of species have been conserved at that taxonomic level. Several authors have highlighted the importance of traits such as plant growth form, plant height or specific leaf area as determinants of local plant abundance (Cornwell & Ackerly, 2010; Lauterbach et al., 2013; Murray et al., 2002). Studying the phylogenetic patterns of these traits, along with any other characteristics susceptible of influencing local abundance, would shed light on the evolutionary mechanisms that drive plant rarity.

3.4.1 Implications for conservation of the Pyrenean flora

The consequences derived from rare species being phylogenetically clustered in one way or another are straightforward from a conservation point of view: the higher extinction risk associated with these species implies a greater loss of phylogenetic diversity (PD) than expected under a random distribution of rarity (Heard & Mooers, 2000; Thuiller et al., 2011). However, the magnitude of the loss depends on the degree of phylogenetic relatedness of those rare species, as well as the amount of phylogenetic diversity they represent. For instance, the loss of phylogenetically related habitat specialist species in the Pyrenees would have an important effect on the PD of the region, with a much higher loss than the amount expected by chance. This suggests that these species are not only phylogenetically close, but that they are also located in branches representing large amounts of PD. The opposite can be found in species with small RGRs, whose disappearance would imply a smaller loss compared to other species, most likely due to these kinds of rare species being located in shorter branches of the phylogenetic tree. The loss of PD permeates into other aspects of diversity because it may potentially act as a proxy for multiple species traits and functions whose loss could have an impact on ecosystem function, particularly in the case of specialists that tend to concentrate in one habitat (Srivastava et al., 2012; Winter et al., 2013). The likelihood of extinction of a species depends on a combination of intrinsic factors like its rarity along with other external factors affecting these species and the scale at which they are assessed (Veron et al., 2017; K. Wilson et al., 2005). Regarding rarity, we found 28 species that we could consider very vulnerable to extinction, as they combine all four rarity types considered in this study. They belong to 17 different families, and approximately one third of them to the *Asteraceae* and *Saxifragaceae* families (Appendix 3.B, Table 3.B.2). This is congruent with our results from the phylogenetic PCA, which indicated a moderate phylogenetic signal for the combination of small RGR, habitat specialization and low LA. Most of our threatened plant species in the Pyrenees tend to be habitat specialists with small geographic ranges, which makes sense since one of the main criteria for threat assessment in the Red Lists is the geographic range of species. It is interesting to discover that threatened species do not necessarily have lower LA than other species. This indicates that, although these species might be threatened at a regional scale, they fare well within their local communities. Meanwhile, none of our rarest plant species were threatened, according to the Red List of the Pyrenean Flora. This may be caused by discrepancies between our criteria for rarity and those used for the Red List, because the rarest species are not necessarily the most threatened in the Pyrenees; or because our dataset only included a fraction of the listed species. Regarding external factors to the vulnerability of diversity, in Chapter 1 we explored the distribution patterns of plant rarity in the Pyrenees and observed that rare species tend to concentrate in distinct habitats like wetlands, mires and fens, or rocky outcrops. Here we find two very different situations. On the one hand, 16 (57%) of the rarest species were found in rocky habitats like cliffs and screes. These are very stable habitats which are considered contemporary refugia resistant to the impacts of global change, acting as safe havens of biodiversity (Brighenti et al., 2021; García et al., 2020). On the other hand, wetlands and mires are highly vulnerable to global change according to the European Red List of Habitats (Janssen et al., 2016), which puts any rare species inhabiting those areas in a double jeopardy of intrinsic and extrinsic factors contributing to their extinction risk and the subsequent potential loss of PD in the region. One positive aspect to the phylogenetic clustering of rarity is that it might be informative for conservation efforts: knowing that rare species tend to be phylogenetically close can help to identify potentially vulnerable groups of species for which we do not have enough information for proper vulnerability assessment (Winter et al., 2013). In this study, we used a huge number of plant inventories, information that might not be available in other regions, and found a good match between threatened species according to the regional Red List and our classification of rare species in terms of reduced RGR. If our results are confirmed for other areas, then conservation planning in vast territories could benefit from the premise that species related to rare taxa are likely to be rare too, and also vulnerable.

3.4.2 Caveats and limitations

There are two main limiting factors in our study. The first comprises possible biases caused by uneven sampling effort of our data through time and space. Using data gathered by different sources and at different time periods can lead to differences in how LA has been assessed, or to changes through time in the same location. However, the nature of the Braun-Blanquet scale used in the inventories buffers against large differences between observers: the smallest scores are very close together and mistakes in using them would still return small abundances, whereas the bigger scores are less prone to be wrongly applied as they encompass wider ranges of cover. The second factor is the resolution of our phylogeny. Any study involving phylogenetic analyses is conditioned by the scope of species included and the taxonomic resolution at which the phylogeny is resolved. Fully resolved phylogenies that include both living and extinct species from the area of interest would be more informative and lead to more precise results. However, the phylogeny that we used contains all plant genera in the Pyrenees, which ensures a good representation of evolutionary patterns up to that level. In addition, this phylogeny performed well when compared with other commonly used plant phylogenies (Appendix 2.A, Fig. 2.A.1), with the advantage of including more information specific to the

Pyrenean flora.

3.5 Conclusions

Our results support the pattern of phylogenetic relatedness between rare species found in other regions and groups of organisms. By exploring the strength and importance of such phylogenetic signal for biodiversity conservation, we found that the loss of habitat specialists and locally scarce species would lead to significant losses in phylogenetic diversity, with important consequences for other aspects of plant diversity such as functional diversity and, in turn, ecosystem function. This highlights the importance of a much-needed integrated insight into the evolutionary relationships of species, their function and role in the ecosystems they inhabit. Exploring the evolutionary patterns of rare species can help us to identify the most vulnerable branches of the Tree of Life and guide the management of vulnerable species before it is too late. This kind of knowledge can be very helpful for the conservation of the biodiversity of any territory, as it allows the preparation of plans to face the effects of global change.

3.6 References

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Appendix 3.A Phylogenetic signal of rarity in major plant groups

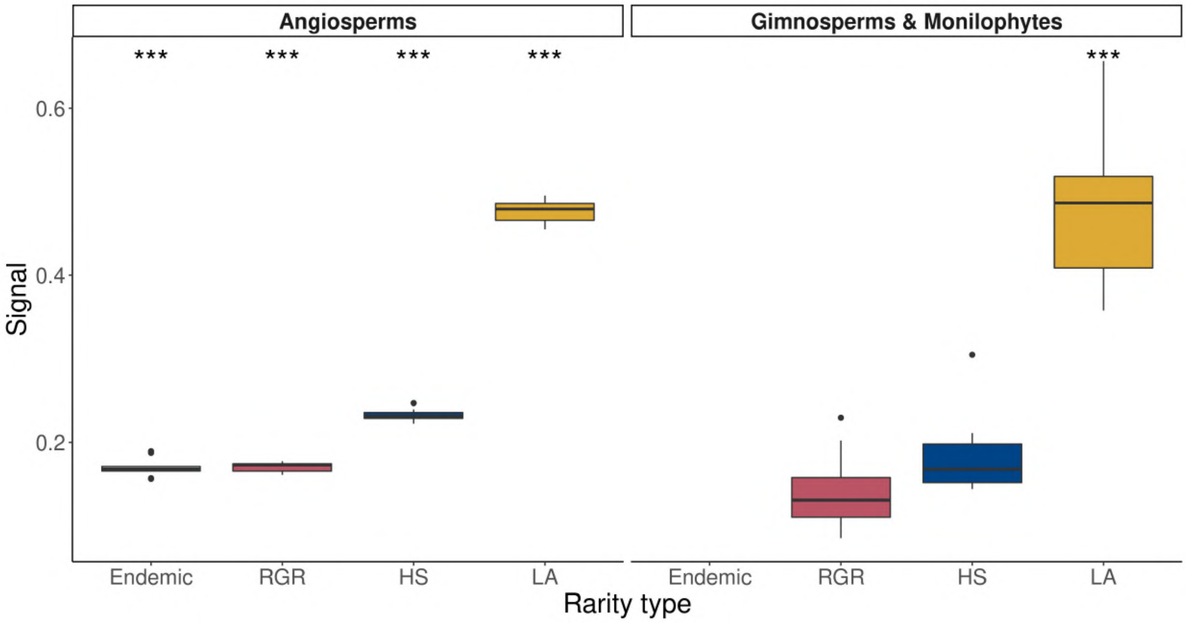

Figure 3.A.1: Boxplot of the estimated values of phylogenetic signal (Pagel's λ for regional geographic range (RGR), habitat specificity (HS) and local abundance (LA), and Purvis' $-D+1$ for endemism) using ten versions of the phylogeny for each rarity type. The panel on the left shows the result from using only Angiosperms and the one on the right those from only Gimnosperms and Monilophytes. There is no phylogenetic signal for endemics in the right panel because there are no endemic Gimnosperms or Monilophytes in our dataset.

Appendix 3.B Rarity values per plant family and species

Table 3.B.1: Local Indicator of Phylogenetic Association (LIPA) values for one or more rarity types. RL indicates the status of species in the Red list of the Pyrenean vascular flora. The rest of the columns show their rarity values (End: Species exclusive to the Pyrenees, RGR: Regional Geographic Range, HS: Habitat Specialist, LA: Local Abundance) along with the EUNIS code of the habitat in which they are most frequently found according to the *IndVal* index. Rarity values in bold indicate statistically significant LIPA value for that species and rarity type.

Species	**Family**	**RL**	**End**	**RGR**	**HS**	**LA**	**Hab**
Alisma lanceolatum	Alismataceae			76	**0.03**	2.92	C
Alisma plantago-aquatica	Alismataceae			95	**0.05**	2.88	C
Aristolochia clematitis	Aristolochiaceae			8	**0.06**	2	F6
Aristolochia paucinervis	Aristolochiaceae			49	**0.08**	2.25	E3
Aristolochia pistolochia	Aristolochiaceae			195	**0.16**	2.32	G2
Aristolochia rotunda	Aristolochiaceae			31	**0.08**	2	G2
Avena sterilis	Poaceae			101	**0.07**	2	E5
Baldellia ranunculoides	Alismataceae			23	**0.02**	3.67	C
Chenopodium bonus-henricus	Amaranthaceae			153	**0.17**	3.57	E5
Chenopodium botrys	Amaranthaceae			42	**0.03**	2	C
Chenopodium chenopodioides	Amaranthaceae			10	**0.02**	2	C
Chenopodium glaucum	Amaranthaceae			15	**0.02**	6	C
Chenopodium murale	Amaranthaceae			60	**0.07**	2	E5
Chenopodium opulifolium	Amaranthaceae			43	**0.07**	2	E5

Chenopodium polyspermum	Amaranthaceae		173	**0.02**	2	C
Chenopodium vulvaria	Amaranthaceae		127	**0.07**	2	E5
Cistus albidus	Cistaceae		83	**0.02**	2.25	G2
Cistus clusii	Cistaceae		13	**0.06**	3.5	F6
Cistus laurifolius	Cistaceae		79	**0.15**	5	F6
Cistus populifolius	Cistaceae		14	**0.02**	5	G2
Cistus salviifolius	Cistaceae		173	**0.14**	2.85	G2
Cyperus fuscus	Cyperaceae		82	**0.05**	2.2	C
Cyperus longus	Cyperaceae		90	**0.03**	3.5	C
Cyperus rotundus	Cyperaceae		13	**0.04**	3.5	C
Digitaria sanguinalis	Poaceae		253	**0.03**	2	C
Echinochloa crus-galli	Poaceae		201	**0.05**	2.44	C
Eleocharis multicaulis	Cyperaceae		31	**0.07**	3.73	C
Eleocharis palustris	Cyperaceae		171	**0.06**	4.88	C
Eleocharis quinqueflora	Cyperaceae		126	**0.08**	3.74	D
Eleocharis uniglumis	Cyperaceae	NT	16	**0.02**	2	E3
Ephedra fragilis	Ephedraceae		8	**0.06**	2	H3
Ephedra major	Ephedraceae		41	**0.08**	4.43	F6
Eriophorum angustifolium	Cyperaceae		125	**0.07**	3.68	D
Eriophorum latifolium	Cyperaceae		141	**0.1**	4.33	D
Eriophorum scheuchzeri	Cyperaceae	NT	24	**0.11**	3.38	D
Eriophorum vaginatum	Cyperaceae		47	**0.06**	4.92	D
Glyceria declinata	Poaceae		92	**0.04**	4.78	C
Glyceria fluitans	Poaceae		202	**0.08**	2.89	C

Glyceria notata	Poaceae		100	**0.05**	4.7	C
Groenlandia densa	Potamogetonaceae		90	**0.02**	2	C
Halimium umbellatum	Cistaceae		15	**0.07**	5.09	F3-F4
Huperzia selago	Lycopodiaceae		112	**0.11**	2.46	F2
Isoetes echinospora	Isoetaceae	NT	26	**0.02**	5.14	C
Isoetes lacustris	Isoetaceae	NT	36	**0.02**	4.33	C
Isoetes setacea	Isoetaceae		15	**0.02**	3.33	C
Isolepis cernua	Cyperaceae		70	**0.1**	2.62	D
Isolepis setacea	Cyperaceae		132	**0.05**	2.5	E3
Juncus acutiflorus	Juncaceae		179	**0.06**	4.86	E3
Juncus alpinoarticulatus	Juncaceae		118	**0.07**	3.11	D
Juncus articulatus	Juncaceae		370	**0.11**	3.07	D
Juncus compressus	Juncaceae		43	**0.13**	4.22	E5
Juncus conglomeratus	Juncaceae		245	**0.09**	3.28	E3
Juncus effusus	Juncaceae		327	**0.11**	3.52	E3
Juncus hybridus	Juncaceae		9	**0.06**	2.25	C
Juncus maritimus	Juncaceae		29	**0.09**	5.14	E3
Juncus squarrosus	Juncaceae		43	**0.11**	2.83	D
Juncus subnodulosus	Juncaceae		98	**0.05**	2.61	E3
Juncus triglumis	Juncaceae		29	**0.06**	2.83	D
Laurus nobilis	Lauraceae		56	**0.08**	2	G2
Leersia oryzoides	Poaceae		25	**0.03**	3.5	C
Lemna minor	Araceae		153	**0.04**	2	C
Lycopodiella inundata	Lycopodiaceae	NT	29	**0.08**	3.38	D
Narthecium ossifragum	Nartheciaceae		116	**0.08**	4.83	D
Potamogeton nodosus	Potamogetonaceae		33	**0.02**	6.5	C

Pycreus flavescens	Cyperaceae	58	**0.02**	2	E3
Schoenoplectus lacustris	Cyperaceae	65	**0.03**	3.61	C
Schoenus nigricans	Cyperaceae	155	**0.05**	4.72	E3
Scirpoides holoschoenus	Cyperaceae	196	**0.07**	4.76	E3
Smilax aspera	Smilacaceae	142	**0.07**	3.27	G2
Sparganium angustifolium	Typhaceae	61	**0.02**	5.36	C
Sparganium emersum	Typhaceae	4	**0.02**	5	C
Sparganium erectum	Typhaceae	117	**0.04**	5.22	C
Tofieldia calyculata	Tofieldiaceae	147	**0.09**	3.37	D
Trichophorum cespitosum	Cyperaceae	88	**0.07**	5.82	D
Triglochin palustris	Juncaginaceae	83	**0.08**	2.91	D
Typha angustifolia	Typhaceae	70	**0.08**	5.67	C
Typha domingensis	Typhaceae	50	**0.03**	5	C
Typha latifolia	Typhaceae	217	**0.06**	3.31	C
Alchemilla alpigena	Rosaceae	**92**	0.36	2.95	E4
Alchemilla alpina	Rosaceae	**53**	0.46	2.4	G3
Alchemilla colorata	Rosaceae	**32**	0.3	2.59	E4
Alchemilla connivens	Rosaceae	**6**	0.44	2.25	D
Alchemilla coriacea	Rosaceae	**23**	0.09	2.34	C
Alchemilla demissa	Rosaceae	**1**	0.17	2	E4
Alchemilla fallax	Rosaceae	**3**	0.13	2	E3
Alchemilla filicaulis	Rosaceae	**1**	0.17	3	E4
Alchemilla fissa	Rosaceae	**22**	0.15	2.66	F2
Alchemilla flabellata	Rosaceae	**53**	0.32	2.84	E4

Alchemilla glabra	Rosaceae		**25**	0.2	2.56	E3
Alchemilla glaucescens	Rosaceae		**1**	0.17	3.5	E1
Alchemilla lapeyrousii	Rosaceae		**19**	0.31	2.47	E1
Alchemilla pentaphyllea	Rosaceae	VU	**1**	0.17	7	E4
Alchemilla saxatilis	Rosaceae		**60**	0.39	2.34	F2
Alchemilla straminea	Rosaceae		**1**	0.07	3	E5
Alchemilla transiens	Rosaceae		**5**	0.2	2.25	F2
Alchemilla vetteri	Rosaceae		**2**	0.26	2	E1
Alchemilla xanthochlora	Rosaceae		**47**	0.6	2.23	E5
Aphanes australis	Rosaceae		**38**	0.14	2.4	H3
Capparis spinosa	Capparaceae		**4**	0.06	7	H3
Chamaemelum nobile	Asteraceae		**61**	0.15	3.44	E1
Cochlearia aragonensis	Brassicaceae		**13**	0.06	5.75	H2
Cochlearia pyrenaica	Brassicaceae		**15**	0.06	5	C
Hieracium acuminatum	Asteraceae		**12**	0.07	2.38	G3
Hieracium amplexicaule	Asteraceae		**52**	0.1	2.49	H3
Hieracium bowlesianum	Asteraceae		**1**	0.06	3	H3
Hieracium candidum	Asteraceae		**9**	0.09	2.17	H3
Hieracium cantalicum	Asteraceae		**2**	0.18	2	G1
Hieracium cerinthoides	Asteraceae		**23**	0.38	3.07	H3
Hieracium eriopogon	Asteraceae		**2**	0.07	2	F2
Hieracium glanduliferum	Asteraceae		**5**	0.17	2.6	E4
Hieracium gouanii	Asteraceae		**2**	0.06	2.33	H3
Hieracium humile	Asteraceae		**1**	0.17	2	E4
Hieracium inuliflorum	Asteraceae		**1**	0.07	2	G3
Hieracium lachenalii	Asteraceae		**6**	0.25	2.78	G1

Hieracium laevigatum	Asteraceae			**3**	0.15	2.67	G2
Hieracium lamprophyllum	Asteraceae			**1**	0.06	3	H3
Hieracium lanceolatum	Asteraceae			**1**	0.02	5	F2
Hieracium lawsonii	Asteraceae			**37**	0.09	2.18	H3
Hieracium mixtum	Asteraceae			**14**	0.13	2.23	H3
Hieracium neopicris	Asteraceae			**2**	0.17	2.75	E4
Hieracium nobile	Asteraceae	NT		**2**	0.18	2	F3-F4
Hieracium phlomoides	Asteraceae			**15**	0.08	2.25	H3
Hieracium piliferum	Asteraceae			**12**	0.24	2.37	F2
Hieracium pseudo-cerinthe	Asteraceae			**1**	0.06	4.75	H3
Hieracium purpurascens	Asteraceae			**1**	0.07	2	E5
Hieracium ramondii	Asteraceae			**4**	0.31	2	E4
Hieracium rhomboidale	Asteraceae			**1**	0.07	2.33	G3
Hieracium solidagineum	Asteraceae			**7**	0.26	3	H3
Hieracium turritifolium	Asteraceae			**3**	0.18	2.33	G1
Hieracium umbellatum	Asteraceae			**15**	0.22	2.33	G1
Iberis ciliata	Brassicaceae			**24**	0.11	2	F3-F4
Leucanthemum graminifolium	Asteraceae		Yes	**21**	0.04	2.57	F2
Pilosella capillata	Asteraceae			**26**	0.22	2.71	F6
Santolina benthamiana	Asteraceae		Yes	**49**	0.15	2.62	F6
Santolina decumbens	Asteraceae			**60**	0.23	2.3	F6
Santolina villosa	Asteraceae			**37**	0.16	2.72	F6
Scirpus sylvaticus	Cyperaceae			**17**	0.23	3.7	D

Subularia aquatica	Brassicaceae	NT	**29**	0.02	4.45	C
Taraxacum aquilonare	Asteraceae		**4**	0.17	2	E4
Taraxacum marginellum	Asteraceae		**4**	0.16	2	E1
Taraxacum pyrenaicum	Asteraceae		**64**	0.33	2.41	E4
Teesdalia nudicaulis	Brassicaceae		**27**	0.18	3.5	F3-F4
Willemetia stipitata	Asteraceae		**25**	0.09	2.71	D
Aethionema marginatum	Brassicaceae		53	0.35	**2**	G2
Aethionema saxatile	Brassicaceae		116	0.41	**2.09**	F6
Ajuga chamaepitys	Lamiaceae		168	0.22	**2.12**	E1
Ajuga pyramidalis	Lamiaceae		143	0.26	**2.24**	E4
Ajuga reptans	Lamiaceae		326	0.3	**2.29**	G1
Amaranthus graecizans	Amaranthaceae		43	0.03	**2**	C
Ammi visnaga	Apiaceae		26	0.04	**2**	C
Anacamptis morio	Orchidaceae		147	0.09	**2**	F6
Anacamptis pyramidalis	Orchidaceae		286	0.19	**2.2**	E1
Anarrhinum bellidifolium	Plantaginaceae		44	0.42	**2**	E1
Anchusa azurea	Boraginaceae		71	0.17	**2**	E5
Andryala integrifolia	Asteraceae		172	0.39	**2.17**	E5
Antennaria carpatica	Asteraceae		82	0.21	**2.44**	E4
Antennaria dioica	Asteraceae		177	0.29	**2.44**	E4
Anthemis arvensis	Asteraceae		214	0.21	**2.48**	E5
Anthemis cotula	Asteraceae		94	0.23	**2**	D
Anthemis cretica	Asteraceae		35	0.21	**2.36**	E4
Anthriscus caucalis	Apiaceae		58	0.18	**2.33**	E5
Apium graveolens	Apiaceae		28	0.19	**2**	D
Aquilegia pyrenaica	Ranunculaceae		102	0.35	**2.45**	H3

Aquilegia viscosa	Ranunculaceae		Yes	50	0.18	**2.29**	H2
Aquilegia vulgaris	Ranunculaceae			387	0.39	**2.18**	G1
Arabidopsis thaliana	Brassicaceae			293	0.22	**2**	H3
Arabis alpina	Brassicaceae			260	0.24	**2.29**	H2
Arabis ciliata	Brassicaceae			138	0.35	**2.22**	E4
Arabis hirsuta	Brassicaceae			354	0.25	**2.19**	E1
Arabis nova	Brassicaceae			73	0.32	**2.36**	E5
Arabis planisiliqua	Brassicaceae			65	0.1	**2**	E1
Arabis soyeri	Brassicaceae	NT		17	0.02	**2**	C
Arceuthobium oxycedri	Santalaceae			52	0.12	**2**	G2
Armeria ruscinonensis	Plumbaginaceae			26	0.19	**2.41**	E4
Arnoseris minima	Asteraceae			19	0.06	**2.25**	F3-F4
Asarina procumbens	Plantaginaceae			87	0.07	**2.31**	H3
Asterolinon linum-stellatum	Primulaceae			132	0.17	**2**	F6
Astrantia major	Apiaceae			234	0.42	**2.56**	E5
Astrantia minor	Apiaceae			51	0.21	**2.53**	F2
Atractylis humilis	Asteraceae			73	0.09	**2.04**	F6
Atriplex patula	Amaranthaceae			195	0.14	**2.14**	E5
Barbarea intermedia	Brassicaceae			202	0.29	**2.17**	E5
Barbarea verna	Brassicaceae			43	0.2	**2.5**	E5
Barbarea vulgaris	Brassicaceae			31	0.22	**2.43**	E5
Bartsia trixago	Orobanchaceae			20	0.02	**2**	G2
Beta vulgaris	Amaranthaceae			30	0.07	**2**	E5
Biscutella brevifolia	Brassicaceae			27	0.23	**2.31**	E4
Biscutella coronopifolia	Brassicaceae			88	0.25	**2.12**	E1

Biscutella flexuosa	Brassicaceae		31	0.06	**2**	H2
Biscutella laevigata	Brassicaceae		144	0.53	**2.21**	G2
Biscutella valentina	Brassicaceae		8	0.46	**2**	F6
Blackstonia perfoliata	Gentianaceae		281	0.19	**2.21**	E3
Borago officinalis	Boraginaceae		83	0.07	**2**	E5
Brassica oleracea	Brassicaceae		18	0.07	**2**	E5
Bryonia dioica	Cucurbitaceae		331	0.3	**2.36**	E5
Bufonia paniculata	Caryophyllaceae		17	0.06	**2**	F6
Bufonia tenuifolia	Caryophyllaceae		59	0.15	**2**	E1
Buglossoides arvensis	Boraginaceae		165	0.14	**2.11**	E5
Bunium bulbocastanum	Apiaceae		29	0.17	**2**	E4
Bupleurum fruticescens	Apiaceae		74	0.09	**2.58**	G2
Bupleurum rigidum	Apiaceae		180	0.16	**2.54**	G2
Bupleurum tenuissimum	Apiaceae		15	0.06	**2**	D
Calendula arvensis	Asteraceae		88	0.07	**2.5**	E5
Campanula jaubertiana	Campanulaceae	Yes	26	0.18	**2.42**	H2
Campanula scheuchzeri	Campanulaceae		192	0.26	**2.5**	E4
Cardaria draba	Brassicaceae		122	0.09	**2**	E5
Carduncellus monspeliensium	Asteraceae		147	0.15	**2.3**	F6
Carlina acanthifolia	Asteraceae		254	0.31	**2.36**	E1
Carlina acaulis	Asteraceae		224	0.35	**2.3**	E4
Carlina hispanica	Asteraceae		110	0.22	**2.32**	F6
Carlina vulgaris	Asteraceae		359	0.32	**2.09**	E1
Carthamus lanatus	Asteraceae		132	0.14	**2.14**	E5
Catananche caerulea	Asteraceae		247	0.21	**2.46**	F6

Caucalis platycarpos	Apiaceae	155	0.21	**2.4**	E1
Centaurea jacea	Asteraceae	327	0.27	**2.56**	E3
Centaurium erythraea	Gentianaceae	286	0.22	**2.21**	E3
Centaurium pulchellum	Gentianaceae	193	0.11	**2.1**	E3
Centaurium tenuiflorum	Gentianaceae	45	0.11	**2.2**	D
Cephalaria leucantha	Caprifoliaceae	207	0.26	**2.43**	G2
Ceratocapnos claviculata	Papaveraceae	20	0.06	**2**	F3-F4
Chaenorhinum minus	Plantaginaceae	309	0.15	**2.31**	H2
Chaenorhinum origanifolium	Plantaginaceae	194	0.12	**2.49**	H3
Chondrilla juncea	Asteraceae	202	0.31	**2.14**	E1
Cichorium intybus	Asteraceae	262	0.24	**2.23**	E3
Clypeola jonthlaspi	Brassicaceae	69	0.07	**2**	G2
Coeloglossum viride	Orchidaceae	161	0.37	**2.1**	E4
Coincya monensis	Brassicaceae	171	0.32	**2.32**	E4
Comastoma tenellum	Gentianaceae	38	0.19	**2.25**	E4
Conopodium arvense	Apiaceae	126	0.51	**2.31**	F6
Coris monspeliensis	Primulaceae	211	0.1	**2.32**	F6
Cornus mas	Cornaceae	3	0.18	**2**	G1
Corrigiola telephiifolia	Caryophyllaceae	23	0.07	**2**	E5
Cotoneaster tomentosus	Rosaceae	80	0.32	**2.11**	F3-F4
Crucianella angustifolia	Rubiaceae	198	0.27	**2.11**	F6
Cuscuta approximata	Convolvulaceae	34	0.1	**2**	F6
Cynoglossum dioscoridis	Boraginaceae	89	0.14	**2**	E5
Dactylorhiza elata	Orchidaceae	150	0.03	**2.32**	E3
Dactylorhiza fuchsii	Orchidaceae	156	0.16	**2.4**	E3

Dactylorhiza incarnata	Orchidaceae			105	0.15	**2.23**	E3
Dactylorhiza maculata	Orchidaceae			298	0.25	**2.32**	D
Dactylorhiza majalis	Orchidaceae			168	0.12	**2.43**	D
Dactylorhiza sambucina	Orchidaceae			153	0.36	**2.24**	F3-F4
Daphne alpina	Thymelaeaceae	NT		11	0.22	**2.27**	E4
Daphne cneorum	Thymelaeaceae			109	0.28	**2.35**	E4
Daphne gnidium	Thymelaeaceae			49	0.14	**2**	F2
Daphne laureola	Thymelaeaceae			309	0.25	**2.38**	G1
Daphne mezereum	Thymelaeaceae			154	0.42	**2.33**	G3
Daucus carota	Apiaceae			435	0.29	**2.45**	E5
Delphinium halteratum	Ranunculaceae			113	0.14	**2.08**	E1
Dictamnus hispanicus	Rutaceae			2	0.18	**2**	G1
Digitalis lutea	Plantaginaceae			230	0.43	**2.2**	G1
Digitalis obscura	Plantaginaceae			1	0.06	**2**	F6
Digitalis purpurea	Plantaginaceae			164	0.43	**2.2**	F3-F4
Dittrichia viscosa	Asteraceae			107	0.12	**2.33**	F6
Ecballium elaterium	Cucurbitaceae			47	0.06	**2**	H3
Echinops ritro	Asteraceae			89	0.13	**2**	F6
Echinops sphaerocephalus	Asteraceae			89	0.26	**2.16**	E5
Echium vulgare	Boraginaceae			370	0.3	**2.18**	E1
Endressia castellana	Apiaceae			43	0.15	**2.4**	E1
Erigeron acris	Asteraceae			199	0.28	**2.07**	E1
Erigeron alpinus	Asteraceae			155	0.23	**2.25**	E4
Erigeron aragonensis	Asteraceae		Yes	59	0.22	**2.37**	E4
Erigeron glabratus	Asteraceae			23	0.17	**2.45**	E4
Erigeron uniflorus	Asteraceae			74	0.19	**2.23**	H2

Erinus alpinus	Plantaginaceae			316	0.14	**2.49**	H3
Erucastrum gallicum	Brassicaceae	NT		13	0.07	**2**	E5
Erucastrum nasturtiifolium	Brassicaceae			229	0.27	**2.19**	E5
Eryngium bourgatii	Apiaceae			207	0.36	**2.47**	E1
Eryngium campestre	Apiaceae			351	0.22	**2.4**	E1
Erysimum gorbeanum	Brassicaceae			41	0.26	**2.2**	H2
Erysimum incanum	Brassicaceae			56	0.06	**2**	H3
Erysimum mediohispanicum	Brassicaceae			63	0.13	**2**	G2
Erysimum ruscinonense	Brassicaceae			91	0.31	**2.11**	F3-F4
Erysimum seipkae	Brassicaceae		Yes	159	0.52	**2.26**	F6
Euphrasia minima	Orobanchaceae			145	0.28	**2.46**	E4
Euphrasia salisburgensis	Orobanchaceae			186	0.31	**2.32**	E4
Fallopia dumetorum	Polygonaceae			63	0.22	**2.14**	E5
Ficus carica	Moraceae			228	0.16	**1.95**	H3
Foeniculum vulgare	Apiaceae			268	0.26	**2.37**	E5
Fragaria viridis	Rosaceae			35	0.27	**2**	G1
Fumana ericoides	Cistaceae			178	0.14	**2.48**	F6
Fumaria officinalis	Papaveraceae			221	0.2	**2.4**	E5
Fumaria parviflora	Papaveraceae			70	0.11	**2.33**	H3
Gentianella campestris	Gentianaceae			151	0.23	**2**	E1
Gentianopsis ciliata	Gentianaceae			89	0.59	**2.22**	E1
Glaucium corniculatum	Papaveraceae			28	0.06	**2**	F6
Gratiola officinalis	Plantaginaceae			9	0.02	**2**	C
Gymnadenia austriaca	Orchidaceae			63	0.27	**2.2**	E4

Gymnadenia conopsea	Orchidaceae		317	0.45	**2.27**	E3
Gymnadenia gabasiana	Orchidaceae		94	0.07	**2.5**	C
Gymnadenia odoratissima	Orchidaceae		20	0.02	**2**	C
Haplophyllum linifolium	Rutaceae		7	0.07	**2**	E5
Helichrysum italicum	Asteraceae		42	0.06	**2**	F6
Helichrysum stoechas	Asteraceae		258	0.13	**2.29**	F6
Heliotropium europaeum	Boraginaceae		95	0.06	**2**	H2
Helleborus foetidus	Ranunculaceae		386	0.49	**2.16**	G1
Herniaria alpina	Caryophyllaceae	NT	8	0.18	**2.31**	H3
Herniaria glabra	Caryophyllaceae		132	0.16	**2.37**	H3
Herniaria latifolia	Caryophyllaceae		62	0.31	**2**	E1
Hieracium olivaceum	Asteraceae		5	0.18	**2.29**	G3
Himantoglossum hircinum	Orchidaceae		118	0.1	**2**	E1
Holosteum umbellatum	Caryophyllaceae		60	0.17	**2**	E1
Hornungia petraea	Brassicaceae		195	0.2	**2.12**	F6
Humulus lupulus	Cannabaceae		262	0.3	**2.55**	E5
Hydrocotyle vulgaris	Araliaceae		21	0.06	**2**	D
Hylotelephium maximum	Crassulaceae		91	0.45	**2.22**	G2
Hylotelephium telephium	Crassulaceae		138	0.45	**2.08**	F3-F4
Hyoseris radiata	Asteraceae	VU	5	0.17	**2.5**	E4
Hypochaeris glabra	Asteraceae		55	0.19	**2**	H3
Hypochaeris maculata	Asteraceae		142	0.34	**2.58**	E4
Hypochaeris radicata	Asteraceae		429	0.27	**2.33**	E1
Iberis amara	Brassicaceae		164	0.28	**2.46**	F6

Ilex aquifolium	Aquifoliaceae		396	0.24	**2.47**	G1
Illecebrum verticillatum	Caryophyllaceae		21	0.07	**2**	E3
Inula conyzae	Asteraceae		248	0.27	**2.03**	G2
Inula helenioides	Asteraceae		78	0.06	**2**	F3-F4
Inula helvetica	Asteraceae		26	0.36	**2.62**	E3
Inula montana	Asteraceae		206	0.13	**2.16**	F6
Inula salicina	Asteraceae		140	0.28	**2.53**	E1
Jacobaea vulgaris	Asteraceae		220	0.23	**2.26**	E3
Jurinea humilis	Asteraceae		66	0.32	**2.44**	E4
Kernera saxatilis	Brassicaceae		141	0.09	**2.15**	H3
Kickxia spuria	Plantaginaceae		139	0.06	**2**	C
Knautia arvensis	Caprifoliaceae		306	0.41	**2.3**	E1
Knautia collina	Caprifoliaceae		46	0.02	**2**	G2
Knautia lebrunii	Caprifoliaceae	Yes	24	0.07	**2**	E5
Knautia nevadensis	Caprifoliaceae		294	0.6	**2.37**	E5
Knautia subscaposa	Caprifoliaceae		35	0.39	**2.17**	E1
Lactuca perennis	Asteraceae		234	0.27	**2.28**	E1
Lactuca tenerrima	Asteraceae		129	0.23	**1.92**	H3
Laphangium luteoalbum	Asteraceae		40	0.02	**2**	C
Lappula squarrosa	Boraginaceae		75	0.13	**2**	F3-F4
Lapsana communis	Asteraceae		357	0.26	**2.35**	E5
Lathraea clandestina	Orobanchaceae		244	0.21	**2.33**	G1
Lathraea squamaria	Orobanchaceae		52	0.18	**2**	G1
Legousia scabra	Campanulaceae		84	0.06	**2**	F6
Leucanthemopsis alpina	Asteraceae		100	0.26	**2.44**	H2

Leucanthemum aligulatum	Asteraceae		1	0.02	**2**	E3
Leucanthemum gaudinii	Asteraceae		4	0.17	**2**	E4
Linaria arvensis	Plantaginaceae		79	0.16	**2.13**	E1
Linaria repens	Plantaginaceae		205	0.38	**2.44**	F3-F4
Linaria simplex	Plantaginaceae		103	0.1	**2**	E1
Linaria supina	Plantaginaceae		278	0.39	**2.09**	H2
Lithospermum officinale	Boraginaceae		298	0.28	**2.34**	E5
Lobelia urens	Campanulaceae		24	0.06	**2.5**	F3-F4
Lomelosia stellata	Caprifoliaceae		35	0.13	**2**	F6
Lonicera alpigena	Caprifoliaceae		89	0.34	**2.43**	G3
Lonicera caerulea	Caprifoliaceae	NT	7	0.07	**2.33**	G3
Lonicera etrusca	Caprifoliaceae		279	0.18	**2.48**	G2
Lonicera implexa	Caprifoliaceae		148	0.04	**2.27**	G2
Lonicera nigra	Caprifoliaceae		113	0.18	**2.45**	G3
Lonicera periclymenum	Caprifoliaceae		255	0.26	**2.61**	G1
Lonicera pyrenaica	Caprifoliaceae		208	0.12	**2.48**	H3
Lonicera xylosteum	Caprifoliaceae		391	0.29	**2.58**	G1
Lychnis alpina	Caryophyllaceae		72	0.2	**2.12**	E4
Lycopsis arvensis	Boraginaceae		87	0.07	**2**	E5
Lycopus europaeus	Lamiaceae		261	0.16	**2.36**	C
Lythrum borysthenicum	Lythraceae		6	0.02	**2**	C
Macrosyringion longiflorum	Orobanchaceae		46	0.1	**2.25**	F6
Malus sylvestris	Rosaceae		178	0.29	**2.1**	G1
Mantisalca salmantica	Asteraceae		153	0.18	**2.07**	E5

Melittis melissophyllum	Lamiaceae		137	0.22	**2.3**	G1
Mercurialis annua	Euphorbiaceae		188	0.28	**2.47**	H3
Moenchia erecta	Caryophyllaceae		35	0.2	**2.33**	E1
Moneses uniflora	Ericaceae		97	0.11	**2.21**	G3
Monotropa hypopitys	Ericaceae		221	0.19	**2.03**	G3
Murbeckiella pinnatifida	Brassicaceae		96	0.29	**2.22**	E4
Myosotis decumbens	Boraginaceae		151	0.37	**2.5**	E5
Myriophyllum spicatum	Haloragaceae		28	0.02	**2**	C
Neatostema apulum	Boraginaceae		44	0.06	**2**	F6
Neotinea maculata	Orchidaceae		74	0.18	**2**	G1
Neottia nidus-avis	Orchidaceae		242	0.24	**2.1**	G1
Nigella gallica	Ranunculaceae		126	0.07	**2**	E5
Nothobartsia spicata	Orobanchaceae		40	0.06	**2**	H3
Odontites cebennensis	Orobanchaceae		36	0.14	**2.5**	E1
Odontites luteus	Orobanchaceae		200	0.24	**2.42**	F6
Odontites pyrenaeus	Orobanchaceae	Yes	38	0.16	**2**	E1
Odontites viscosus	Orobanchaceae		110	0.19	**2.47**	G2
Ophrys apifera	Orchidaceae		223	0.27	**2**	E1
Ophrys bertolonii	Orchidaceae		29	0.15	**2**	F6
Ophrys castellana	Orchidaceae		116	0.28	**2**	E3
Ophrys ciliata	Orchidaceae		23	0.06	**2**	F6
Ophrys fusca	Orchidaceae		155	0.02	**2**	G2
Ophrys insectifera	Orchidaceae		187	0.18	**2.1**	E1
Ophrys picta	Orchidaceae		152	0.16	**2**	E1
Ophrys tenthredinifera	Orchidaceae		42	0.06	**2**	F6
Opopanax chironium	Apiaceae		34	0.1	**2**	E1

Orchis pallens	Orchidaceae		74	0.19	**2.5**	D
Orchis palustris	Orchidaceae		7	0.06	**2**	D
Orchis simia	Orchidaceae		54	0.25	**2**	E5
Orchis ustulata	Orchidaceae		262	0.15	**2.07**	E1
Orlaya grandiflora	Apiaceae	NT	52	0.09	**2.44**	E5
Orobanche amethystea	Orobanchaceae		86	0.15	**2**	F6
Orobanche artemisiae-campestris	Orobanchaceae		17	0.1	**2**	E1
Orobanche caryophyllacea	Orobanchaceae		66	0.16	**2**	E1
Orobanche gracilis	Orobanchaceae		283	0.19	**2.09**	E1
Orobanche haenseleri	Orobanchaceae		3	0.06	**2**	H2
Orobanche hederae	Orobanchaceae		159	0.18	**2.38**	G1
Orobanche reticulata	Orobanchaceae		16	0.06	**2**	F3-F4
Paeonia officinalis	Paeoniaceae		36	0.3	**2.24**	F3-F4
Pallenis spinosa	Asteraceae		173	0.25	**2.46**	E1
Papaver dubium	Papaveraceae		184	0.09	**2.33**	E5
Papaver lapeyrousianum	Papaveraceae		28	0.06	**2.5**	H2
Paronychia polygonifolia	Caryophyllaceae		113	0.22	**2.18**	E4
Pedicularis comosa	Orobanchaceae		55	0.25	**2.7**	E4
Pedicularis rosea	Orobanchaceae		10	0.25	**2.35**	E4
Pedicularis sylvatica	Orobanchaceae		180	0.14	**2.38**	D
Pedicularis tuberosa	Orobanchaceae		19	0.17	**2**	E4
Petrocallis pyrenaica	Brassicaceae		57	0.33	**2.48**	H3
Petrorhagia nanteuilii	Caryophyllaceae		58	0.1	**2.25**	E1
Phagnalon sordidum	Asteraceae		120	0.06	**2**	H3
Phillyrea angustifolia	Oleaceae		81	0.03	**2.23**	G2

Phlomis herba-venti	Lamiaceae	95	0.22	**2.36**	F6
Phyteuma globulariifolium	Campanulaceae	19	0.17	**2.38**	E4
Phyteuma hemisphaericum	Campanulaceae	140	0.29	**2.44**	E4
Phyteuma orbiculare	Campanulaceae	291	0.4	**2.4**	E1
Picnomon acarna	Asteraceae	56	0.06	**2**	F6
Picris hieracioides	Asteraceae	415	0.44	**2.37**	E5
Picris hispanica	Asteraceae	3	0.06	**2**	F6
Pistacia terebinthus	Anacardiaceae	200	0.06	**2.35**	G2
Platanthera bifolia	Orchidaceae	283	0.49	**2.06**	G1
Platanthera chlorantha	Orchidaceae	257	0.59	**1.99**	E1
Podospermum laciniatum	Asteraceae	116	0.17	**2.09**	E5
Polycarpon tetraphyllum	Caryophyllaceae	84	0.08	**2**	G2
Polycnemum arvense	Amaranthaceae	54	0.1	**2**	E1
Polygala alpestris	Polygalaceae	128	0.29	**2.31**	E4
Polygala alpina	Polygalaceae	114	0.29	**2.14**	G3
Polygala calcarea	Polygalaceae	279	0.51	**2.34**	G3
Polygala rupestris	Polygalaceae	36	0.17	**2.06**	G2
Polygala serpyllifolia	Polygalaceae	169	0.36	**2.3**	E1
Portulaca oleracea	Portulacaceae	184	0.03	**2.58**	C
Prenanthes purpurea	Asteraceae	195	0.25	**2.57**	G3
Pseudorchis albida	Orchidaceae	80	0.17	**1.9**	F2
Pulicaria vulgaris	Asteraceae	13	0.06	**2**	D
Pulmonaria affinis	Boraginaceae	267	0.29	**2.4**	G1
Pulmonaria longifolia	Boraginaceae	250	0.32	**2.4**	G1

Pyrola chlorantha	Ericaceae	96	0.13	**2.23**	G3
Pyrola minor	Ericaceae	149	0.16	**2.52**	G3
Pyrola rotundifolia	Ericaceae	8	0.25	**2**	G1
Raphanus raphanistrum	Brassicaceae	103	0.1	**2**	E1
Rapistrum rugosum	Brassicaceae	169	0.07	**2**	E5
Reichardia picroides	Asteraceae	63	0.26	**2.23**	E1
Reseda barrelieri	Resedaceae	20	0.2	**2**	E5
Rhaponticum coniferum	Asteraceae	230	0.16	**2.07**	F6
Ribes alpinum	Grossulariaceae	265	0.27	**2.32**	G1
Ribes petraeum	Grossulariaceae	114	0.35	**2.2**	G3
Ribes uva-crispa	Grossulariaceae	44	0.06	**2**	F3-F4
Rosa rubiginosa	Rosaceae	158	0.14	**2.35**	F3-F4
Rosa villosa	Rosaceae	98	0.21	**2.24**	F3-F4
Ruta angustifolia	Rutaceae	114	0.08	**2.08**	G2
Ruta montana	Rutaceae	45	0.15	**2**	F6
Samolus valerandi	Primulaceae	207	0.08	**2.47**	E3
Saponaria officinalis	Caryophyllaceae	335	0.23	**2.52**	E5
Scabiosa atropurpurea	Caprifoliaceae	132	0.26	**2.29**	E3
Scorzonera angustifolia	Asteraceae	129	0.17	**2**	F6
Scorzonera hispanica	Asteraceae	107	0.13	**2.36**	F6
Scrophularia crithmifolia	Scrophulariaceae	119	0.07	**2.42**	H2
Sempervivum arachnoideum	Crassulaceae	115	0.23	**2.39**	H3
Sempervivum montanum	Crassulaceae	132	0.34	**2.36**	E4
Sempervivum tectorum	Crassulaceae	210	0.36	**2.44**	H3
Senecio provincialis	Asteraceae	20	0.26	**2.06**	F6

Senecio vulgaris	Asteraceae		364	0.18	**2.04**	E5
Serapias lingua	Orchidaceae		191	0.2	**2.07**	E1
Serapias vomeracea	Orchidaceae		80	0.11	**2.33**	E3
Sesamoides interrupta	Resedaceae		38	0.22	**2.31**	E4
Sherardia arvensis	Rubiaceae		377	0.21	**2.37**	E1
Silaum silaus	Apiaceae		42	0.12	**2**	E3
Silene conica	Caryophyllaceae		32	0.07	**2**	E5
Silene nocturna	Caryophyllaceae		85	0.11	**2**	F6
Sisymbrella aspera	Brassicaceae		66	0.06	**2**	C
Solidago virgaurea	Asteraceae		392	0.42	**2.24**	G3
Sonchus asper	Asteraceae		320	0.17	**2.07**	E5
Sorbus torminalis	Rosaceae		212	0.22	**2.32**	G2
Spergula morisonii	Caryophyllaceae		11	0.06	**2**	H3
Spergula pentandra	Caryophyllaceae		22	0.06	**2**	H3
Stachys palustris	Lamiaceae		20	0.13	**2**	F3-F4
Staehelina dubia	Asteraceae		224	0.09	**2.56**	G2
Tamarix canariensis	Tamaricaceae		29	0.28	**2.33**	G1
Tanacetum corymbosum	Asteraceae		304	0.62	**2.24**	G2
Telephium imperati	Molluginaceae		107	0.42	**2.19**	G2
Thapsia villosa	Apiaceae		70	0.02	**2**	G2
Thesium alpinum	Santalaceae		113	0.39	**2.32**	E4
Thesium catalaunicum	Santalaceae	Yes	17	0.12	**2.33**	F6
Thesium humifusum	Santalaceae		240	0.16	**2.4**	F6
Thesium pyrenaicum	Santalaceae		156	0.36	**2.22**	E4
Thlaspi alliaceum	Brassicaceae		21	0.06	**2**	D
Thlaspi brachypetalum	Brassicaceae		46	0.17	**2.07**	E5

Thlaspi caerulescens	Brassicaceae		69	0.19	**2**	F3-F4
Thlaspi perfoliatum	Brassicaceae		188	0.47	**2.07**	E1
Tordylium maximum	Apiaceae		212	0.09	**2.31**	E5
Torilis arvensis	Apiaceae		262	0.2	**2.28**	E5
Torilis japonica	Apiaceae		246	0.16	**2.55**	E5
Torilis nodosa	Apiaceae		88	0.16	**2.31**	E5
Tozzia alpina	Orobanchaceae	NT	29	0.07	**2**	E5
Tragopogon crocifolius	Asteraceae		122	0.21	**1.71**	E5
Tragopogon dubius	Asteraceae		161	0.32	**2.11**	E4
Tragopogon lamottei	Asteraceae		39	0.1	**2**	E1
Tragopogon porrifolius	Asteraceae		105	0.25	**2.14**	E4
Tragopogon pratensis	Asteraceae		265	0.23	**2.03**	E1
Trinia glauca	Apiaceae		188	0.23	**2.27**	F6
Urospermum dalechampii	Asteraceae		60	0.16	**2.25**	E1
Urtica urens	Urticaceae		84	0.27	**2.52**	H3
Utricularia vulgaris	Lentibulariaceae		9	0.06	**2**	D
Verbascum blattaria	Scrophulariaceae		69	0.07	**2.67**	E5
Verbascum boerhavii	Scrophulariaceae		115	0.25	**2.18**	E5
Verbascum nigrum	Scrophulariaceae		65	0.13	**2**	H3
Verbascum pulverulentum	Scrophulariaceae		190	0.14	**2.11**	E5
Verbena officinalis	Verbenaceae		402	0.18	**2.36**	E5
Veronica aphylla	Plantaginaceae		111	0.26	**2.3**	E4
Veronica arvensis	Plantaginaceae		460	0.27	**2.35**	E1
Veronica chamaedrys	Plantaginaceae		387	0.44	**2.35**	G1
Veronica montana	Plantaginaceae		235	0.24	**2.36**	G1

Veronica nummularia	Plantaginaceae			64	0.12	**2.41**	H2
Viburnum lantana	Adoxaceae			397	0.3	**2.49**	G1
Vicia lutea	Fabaceae			105	0.26	**2.15**	F6
Vicia sepium	Fabaceae			428	0.33	**2.39**	G1
Vincetoxicum hirundinaria	Apocynaceae			340	0.54	**2.24**	G2
Vincetoxicum nigrum	Apocynaceae			86	0.03	**2.15**	G2
Viola cornuta	Violaceae			87	0.37	**2.58**	E4
Viola pyrenaica	Violaceae			91	0.33	**2.59**	E4
Viola rupestris	Violaceae			205	0.34	**2.12**	E4
Viscum album	Santalaceae			175	0.29	**2.09**	G3
Vitis vinifera	Vitaceae			156	0.26	**2.37**	G1
Wahlenbergia hederacea	Campanulaceae			94	0.2	**2.46**	E3
Xeranthemum inapertum	Asteraceae			150	0.25	**2.25**	E5
Borderea chouardii	Dioscoreaceae	CR	**Yes**	1	0.06	3	H3
Borderea pyrenaica	Dioscoreaceae		**Yes**	19	0.09	3.05	H2
Delphinium montanum	Ranunculaceae	NT	**Yes**	10	0.06	3	H2
Petrocoptis crassifolia	Caryophyllaceae		**Yes**	12	0.06	3.33	H3
Petrocoptis pseudoviscosa	Caryophyllaceae	VU	**Yes**	6	0.06	3.25	H3
Ramonda myconi	Gesneriaceae		**Yes**	170	0.08	2.93	H3
Atriplex prostrata	Amaranthaceae			53	**0.07**	**2**	E5
Chenopodium album	Amaranthaceae			396	**0.1**	**2.48**	E5
Coronopus squamatus	Brassicaceae			37	**0.02**	**2**	C
Aegonychon gastonii	Boraginaceae		**Yes**	1	0.17	**2**	E4
Glandora oleifolia	Boraginaceae	NT	**Yes**	5	0.06	**2**	H3
Onosma bubanii	Boraginaceae		**Yes**	16	0.29	**2.36**	E4

Bolboschoenus maritimus	Cyperaceae		**44**	**0.03**	4.12	C
Cladium mariscus	Cyperaceae		**29**	**0.06**	3.43	C
Kobresia simpliciuscula	Cyperaceae		**16**	**0.06**	2	D
Potamogeton alpinus	Potamogetonaceae		**28**	**0.02**	4.17	C
Potamogeton berchtoldii	Potamogetonaceae		**27**	**0.02**	3.17	C
Potamogeton natans	Potamogetonaceae		**28**	**0.02**	2	C
Potamogeton polygonifolius	Potamogetonaceae		**30**	**0.05**	4.62	C
Rhynchospora alba	Cyperaceae	NT	**28**	**0.06**	5.67	D
Stuckenia filiformis	Potamogetonaceae	VU	**4**	**0.02**	7	C
Andryala ragusina	Asteraceae		**69**	0.18	**2.5**	H2
Brassica montana	Brassicaceae		**18**	0.19	**2.35**	H2
Brassica repanda	Brassicaceae		**69**	0.26	**2.5**	F6
Bunias erucago	Brassicaceae		**43**	0.07	**2**	E5
Carpesium cernuum	Asteraceae		**9**	0.18	**2**	G1
Diplotaxis muralis	Brassicaceae		**38**	0.22	**2**	F6
Eruca vesicaria	Brassicaceae		**47**	0.07	**2**	E5
Hieracium gastonianum	Asteraceae		**1**	0.17	**2**	E4
Hieracium planchonianum	Asteraceae		**5**	0.29	**2**	G1
Hormathophylla lapeyrousiana	Brassicaceae		**55**	0.27	**2.34**	F6
Leucanthemum ageratifolium	Asteraceae		**35**	0.27	**2**	E1
Leucanthemum cantabricum	Asteraceae		**5**	0.24	**2.43**	E1

Lunaria rediviva	Brassicaceae	NT	**19**	0.18	**2**	G1
Matricaria chamomilla	Asteraceae		**14**	0.02	**2**	C
Matthiola fruticulosa	Brassicaceae		**38**	0.06	**2**	H2
Phagnalon saxatile	Asteraceae		**33**	0.06	**2**	H3
Teesdalia coronopifolia	Brassicaceae		**16**	0.06	**2**	F3-F4

Table 3.B.2: Plant families present in our data along with the number of species in each of them (N), the average and standard deviation of each rarity metric (RGR, HS, LA) and the number and proportion of rare species according to each rarity type (Endemic, N RGR, N HS, N LA). For regional geographic range (RGR), habitat specialization (HS) and local abundance (LA) rare species are those with scaled values lower than 0.

Family	**N**	**Endemic**	**RGR**	**N RGR**	**HS**	**N HS**	**LA**	**N LA**
Adoxaceae	6	0	276.17	3	0.22	2	3.11	4
Alismataceae	3	0	64.67	1	0.03	1	3.15	2
Amaranthaceae	17	0	91.47	12	0.07	6	2.98	13
Amaryllidaceae	17	1	135.88	11	0.25	8	2.77	9
Anacardiaceae	2	0	138	1	0.05	1	2.73	1
Apiaceae	81	1	134.31	45	0.23	46	2.66	52
Apocynaceae	2	0	213	1	0.29	1	2.2	1
Aquifoliaceae	1	0	396		0.24		2.47	
Araceae	3	0	181	2	0.16	1	2.33	1
Araliaceae	2	0	221	1	0.16	1	2.99	1
Aristolochiaceae	4	0	70.75	3	0.1	3	2.14	2
Asparagaceae	21	0	170.52	10	0.28	12	2.48	14
Asphodelaceae	5	0	99.2	3	0.24	3	2.72	2
Aspleniaceae	21	0	198.67	11	0.19	11	2.5	12
Asteraceae	282	9	111.07	175	0.2	158	2.58	183
Balsaminaceae	1	0	49		0.24		2.69	
Berberidaceae	1	0	40		0.08		3.79	
Betulaceae	5	0	240.8	2	0.29	3	3.73	3
Boraginaceae	33	3	119.42	19	0.17	18	2.53	22
Brassicaceae	118	4	103.83	75	0.19	60	2.55	82

Buxaceae	1	0	420		0.45		5.07	
Campanulaceae	26	2	166	14	0.29	12	2.45	15
Cannabaceae	1	0	262		0.3		2.55	
Capparaceae	1	0	4		0.06		7	
Caprifoliaceae	40	1	150.7	24	0.21	24	2.66	27
Caryophyllaceae	108	12	123.01	70	0.21	58	2.5	64
Celastraceae	2	0	246.5	1	0.18	1	2.9	1
Cistaceae	23	0	115.91	15	0.14	12	3	15
Colchicaceae	2	0	168	1	0.29	1	2.24	1
Convolvulaceae	8	0	170	4	0.14	4	2.63	5
Coriariaceae	1	0	182		0.25		3.59	
Cornaceae	2	0	204.5	1	0.24	1	2.52	1
Crassulaceae	26	0	147.69	16	0.26	12	2.48	16
Cucurbitaceae	2	0	189	1	0.18	1	2.18	1
Cupressaceae	5	0	171.2	2	0.18	4	3.94	3
Cyperaceae	93	0	102.85	57	0.16	57	3.42	54
Dennstaedtiaceae	1	0	362		0.34		3.23	
Dioscoreaceae	3	2	140.33	2	0.14	2	2.84	1
Droseraceae	3	0	68.33	2	0.07	1	3.64	1
Ephedraceae	2	0	24.5	1	0.07	1	3.21	1
Equisetaceae	8	0	188.5	4	0.16	4	3.74	6
Ericaceae	25	0	126.76	14	0.17	15	3.73	11
Euphorbiaceae	24	0	152.75	13	0.21	13	2.47	13
Fabaceae	162	2	134.38	98	0.21	85	2.86	99
Fagaceae	12	0	188	7	0.22	3	4.45	7
Gentianaceae	18	0	131.94	11	0.24	11	2.44	10

Geraniaceae	22	2	182.64	13	0.23	12	2.83	14
Gesneriaceae	1	1	170		0.08		2.93	
Grossulariaceae	3	0	141	2	0.23	1	2.17	1
Haloragaceae	2	0	25.5	1	0.02		2.94	1
Hypericaceae	14	0	166.29	8	0.26	7	2.61	11
Iridaceae	11	0	89.45	6	0.19	6	2.47	8
Isoetaceae	3	0	25.67	1	0.02		4.27	1
Juncaceae	34	0	128.79	23	0.15	22	3.08	21
Juncaginaceae	1	0	83		0.08		2.91	
Lamiaceae	86	1	166.12	44	0.21	47	2.83	52
Lauraceae	1	0	56		0.08		2	
Lentibulariaceae	7	1	66.29	5	0.1	5	3	4
Liliaceae	9	0	119.11	5	0.28	6	2.41	7
Linaceae	13	0	165.23	6	0.2	6	2.57	6
Lycopodiaceae	4	0	62.5	3	0.16	2	3.09	1
Lythraceae	2	0	161	1	0.09	1	2.44	1
Malvaceae	10	0	160.4	5	0.13	6	2.57	5
Melanthiaceae	2	0	172	1	0.34	1	2.55	1
Menyanthaceae	1	0	64		0.08		4.95	
Molluginaceae	1	0	107		0.42		2.19	
Montiaceae	1	0	131		0.03		4.78	
Moraceae	1	0	228		0.16		1.95	
Nartheciaceae	1	0	116		0.08		4.83	
Oleaceae	6	0	224.83	4	0.16	3	3.09	4
Onagraceae	17	0	139.82	11	0.16	10	2.59	12
Ophioglossaceae	2	0	127	1	0.21	1	2.08	1

Orchidaceae	58	0	145.21	28	0.2	34	2.22	40
Orobanchaceae	52	1	92.33	32	0.18	26	2.38	27
Osmundaceae	1	0	81		0.18		3	
Oxalidaceae	1	0	320		0.29		3.18	
Paeoniaceae	1	0	36		0.3		2.24	
Papaveraceae	12	0	128.83	7	0.15	7	2.68	9
Pinaceae	6	0	169.17	3	0.2	3	3.97	2
Plantaginaceae	75	3	148.71	44	0.21	41	2.58	48
Plumbaginaceae	6	2	52.33	3	0.23	2	2.37	3
Poaceae	206	6	138.38	121	0.2	113	3.15	131
Polygalaceae	10	0	134.1	7	0.28	5	2.26	5
Polygonaceae	26	0	170.58	15	0.17	18	2.8	16
Polypodiaceae	14	0	202.21	7	0.24	6	2.51	7
Portulacaceae	1	0	184		0.03		2.58	
Potamogetonaceae	7	0	34.29	6	0.02	6	4.21	4
Primulaceae	30	4	109.87	17	0.17	17	2.89	17
Pteridaceae	3	0	115.67	2	0.11	2	2.7	1
Ranunculaceae	63	5	139.68	42	0.24	33	2.72	37
Resedaceae	8	0	104.88	5	0.21	5	2.2	5
Rhamnaceae	7	0	193.14	2	0.2	3	2.62	5
Rosaceae	109	0	133.58	67	0.24	57	2.75	75
Rubiaceae	32	1	178.47	17	0.27	20	2.57	19
Rutaceae	5	0	38.4	3	0.12	3	2.22	4
Salicaceae	22	2	145.41	15	0.22	10	3.83	10
Santalaceae	7	1	136.43	3	0.23	4	2.34	5
Sapindaceae	4	0	256.5	3	0.24	2	2.66	2

Saxifragaceae	33	8	88.61	22	0.17	19	3.08	22
Scrophulariaceae	14	1	161.21	7	0.22	6	2.35	7
Selaginellaceae	1	0	142		0.15		2.54	
Smilacaceae	1	0	142		0.07		3.27	
Solanaceae	7	0	150.43	4	0.14	4	3.52	4
Tamaricaceae	2	0	44	1	0.24	1	2.52	1
Taxaceae	1	0	193		0.29		2.75	
Thymelaeaceae	12	1	94.33	7	0.2	7	2.41	8
Tofieldiaceae	2	0	74	1	0.13	1	2.68	1
Typhaceae	6	0	86.5	4	0.04	3	4.93	1
Ulmaceae	2	0	302.5	1	0.25	1	3.31	1
Urticaceae	3	0	256	2	0.2	1	3.3	1
Verbenaceae	1	0	402		0.18		2.36	
Violaceae	20	1	141.35	13	0.26	8	2.51	13
Vitaceae	1	0	156		0.26		2.37	

Table 3.B.3: All plant species endemic to the Pyrenees that had below-average values of regional geographic range (RGR), habitat specialization (HS) and local abundance (LA). RL indicates if a species is present in the Red list of the Pyrenean flora and in which category. Habitat shows the EUNIS code of the preferred habitat by that species according to the *IndVal* index. Rarity values marked in bold print had positive and statistically significant LIPA values.

Species	**Family**	**RL**	**RGR**	**HS**	**LA**	**Habitat**
Achillea chamaemelifolia	Asteraceae		43	0.08	2.38	H3
Aegonychon gastonii	Boraginaceae		1	0.17	**2.00**	F2
Androsace cylindrica	Primulaceae		32	0.06	2.75	H3
Antirrhinum molle	Plantaginaceae		58	0.07	2.70	H3
Aquilegia viscosa	Ranunculaceae		50	0.18	2.29	H2
Armeria muelleri	Plumbaginaceae		2	0.17	2.25	E4
Campanula jaubertiana	Campanulaceae		26	0.18	2.42	H2
Centaurea costae	Asteraceae		68	0.14	2.10	E5
Centaurea emigrantis	Asteraceae		23	0.10	2.36	F6
Cerastium pyrenaicum	Caryophyllaceae		36	0.07	2.76	H2
Draba subnivalis	Brassicaceae		18	0.06	2.64	H3
Festuca pyrenaica	Poaceae		62	0.11	2.58	H2
Galium cespitosum	Rubiaceae		52	0.20	2.46	H2
Glandora oleifolia	Boraginaceae	NT	5	0.06	**2.00**	H3
Iberis spathulata	Brassicaceae		48	0.07	2.76	H2
Knautia lebrunii	Caprifoliaceae		24	0.07	2.00	E5
Leucanthemum graminifolium	Asteraceae		21	0.04	2.57	F2
Linaria bubanii	Plantaginaceae		37	0.07	2.43	H2
Odontites pyrenaeus	Orobanchaceae		38	0.16	2.00	E1

Petrocoptis montsicciana	Caryophyllaceae	13	0.06	2.77	H3
Salix ceretana	Salicaceae	21	0.06	2.00	D
Santolina benthamiana	Asteraceae	49	0.15	2.62	F6
Saxifraga geranioides	Saxifragaceae	55	0.19	2.52	H2
Saxifraga hariotii	Saxifragaceae	21	0.17	2.29	E4
Saxifraga intricata	Saxifragaceae	59	0.15	2.42	H3
Saxifraga pubescens	Saxifragaceae	75	0.12	2.59	H3
Thesium catalaunicum	Santalaceae	17	0.12	2.33	F6
Thymelaea calycina	Thymelaeaceae	18	0.11	2.60	F2

4 Population viability analysis of plant species in Aragón

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Manuscript in preparation

4.1 Introduction

All organisms show fluctuations in their population sizes and growth rates over time, caused by changes in abiotic conditions, biological interactions, and density effects. These drivers alter vital rates such as fecundity or survival, which in turn alter population growth. This stochastic variation in realized population growth rates is generally predicted to have a negative effect on long-term stochastic growth rate (Dennis et al., 1991; Gillespie, 1977; Lande, 1993; Tuljapurkar, 1990). Furthermore, this variability has a direct negative influence on the extinction risk of a population, as higher variance in growth rates increases the chance of a population having several "bad" years in a row and thus its probability of hitting quasi-extinction thresholds (Dennis et al., 1991; Lande & Orzack, 1988; Lande, 1993). This is particularly concerning for small populations because their size may not be sufficient to buffer the effects of prolonged negative growth (Shaffer, 1981). Hence, accurately estimating the variability of growth rates through time, in addition to mean growth, is a fundamental data requirement for an effective management of biodiversity in general, and for population viability analysis of threatened species in particular (Boyce et al., 2006).

The most common data sets available to estimate extinction risk or stochastic dynamics are based on time series of population counts (Global Population Dynamics Database, J. Prendergast et al., 2010). For either density independent or density dependent dynamics, the use of these types of population size estimates to estimate mean and variance in growth rates and to predict population behavior is well-established (Dennis et al., 1991; Morris & Doak, 2002). However, part of the observed variation in numbers over time results from the observation process itself, rather than underlying real changes in numbers themselves (H. B. Wilson et al., 2011). Neither the sampling process nor the observers can be perfect, and they are susceptible to biases that give us an imperfect picture of the actual population size by, for example, only sampling part of the population, missing individuals during the counting process, or counting the same individual more than once. Several frameworks for taking observation errors into account when estimating demographic parameters from count based data have been proposed (Buonaccorsi & Staudenmayer, 2009; Carpenter et al., 1994; Holmes, 2001) but in spite of these methods, observation errors are seldom measured during monitoring studies or taken into account in PVA studies (McLoughlin & Messier, 2004). When not accounted for, the observation error is folded into estimated environmental stochasticity in population growth (Holmes, 2001), leading to the possibility of biased and inaccurate estimates of population growth and extinction risk. Estimating the variation associated with observation error should allow us to decompose the observed variance in growth rates into true, or process, variance and variance due to observation errors, reducing the estimated stochastic variance of a population's size and improving our estimates of long-term growth rates and their variance (Dennis et al., 2010; Staples et al., 2004). This has direct implications for conservation practice. First, by reducing the estimated variance in population growth rates over time we will generally increase the estimated long-term growth rate of that population, and reduce the estimated probability of extinction or decline (See & Holmes, 2015). In turn, these improved assessments of population viability will allow us to develop better conservation plans and policies to help us manage the current biodiversity crisis (Cowie et al., 2022), especially in a context of limited resources for conservation actions that may require focusing our effort on some organisms over others (Ono et al., 2019). Here, we use the abundances of 157 plant populations obtained through the long-term “Adopt a Plant” collaborative citizen science program in Aragón Province, NE Spain (García et al., 2021) to explore how accounting for the observation error (OE) measured directly during the sampling process can affect our estimates of population growth and long-term quasi-extinction risk. This program is unique in the world in following dozens of species and populations using fieldwork sampling designs adapted to reduce observation error, and also including repeated censuses to account for observation error for most species. As we show, the combination of simple resampling done as part of field surveys and a straightforward Bayesian modeling approach can substantially improve the parameters resulting from population dynamics. To illustrate this approach, we first develop a Markov Chain Monte Carlo model which estimates the long-term growth rate of a population and its stochastic variance, while taking into account the variance associated with observation error (OE) to calculate the probabilities of quasi-extinction. Then, we use those estimates for each population and compare them with those from a model that does not consider OE. Finally, we compare the growth rates and quasi-extinction risk probabilities calculated for groups of species that are censused using different fieldwork sampling methods.

We focus our analyses on two main questions:

- Does accounting for observation errors estimated from repeating censuses substantially alter stochastic growth or quasi-extinction risk?
- Do different sampling methods tend to have more observation error and hence greater need to account for this error?

4.2 Methods

4.2.1 Plant population data

The "Adopt a plant" program is a collaborative citizen science initiative that aims to monitor the population trends and threats of hundreds of plant populations in NE Spain (García et al., 2021). Many of the species are listed as threatened and others are considered major structural elements for habitats of interest by the European Union. The sampling personnel involves almost 400 people, with the majority being volunteers and forest and park rangers, although a few ones are naturalists with high skills in botany. After a short training in the field, each participant team is in charge of visiting one or more populations of a plant species once a year to estimate abundance following a specific sampling design established by the managing scientists (see García et al. (2021) for more details). Some teams are in charge of several populations, but each population is always monitored by the same team to minimize observation biases. Each monitoring unit (MU) includes populations of one or more plant species that are monitored each year at a similar phenological stage to ensure consistency across years. The MUs cover significant environmental heterogeneity, from the high alpine in the Pyrenees to the arid lowlands of the Ebro river plains. The sampling design varies between plant species and sites, as it is adjusted in the field to be representative of the environmental variability of species occupancy and reduce sampling error (García et al., 2021), but can be categorized into four general sampling methods. The first two approaches involve counts of either all (hereafter referred to as counts), or only the reproductive (counts_R) individuals within one or more permanent sampling units (>70% of MUs). The third and fourth approaches score either the presence/absence (incidence) or the species coverture over multiple small quadrats (plant cover). Regardless of the method, plant abundance in each population is estimated using isolated plots or along transects, and in some cases using small quadrats and gridded plots along transects. The median number of sampling years is 9, with a minimum of 4 and a maximum of 14, while populations per species ranges from one to six.

4.2.2 Estimation of observation error

All participants were asked to do at least one double census during one of the monitoring years. This consisted of repeating the census on the same day or as soon as possible after that year's census, in all or part of the sampling units, and taking the same amount of time to complete the census both times. The mean across years and populations of a

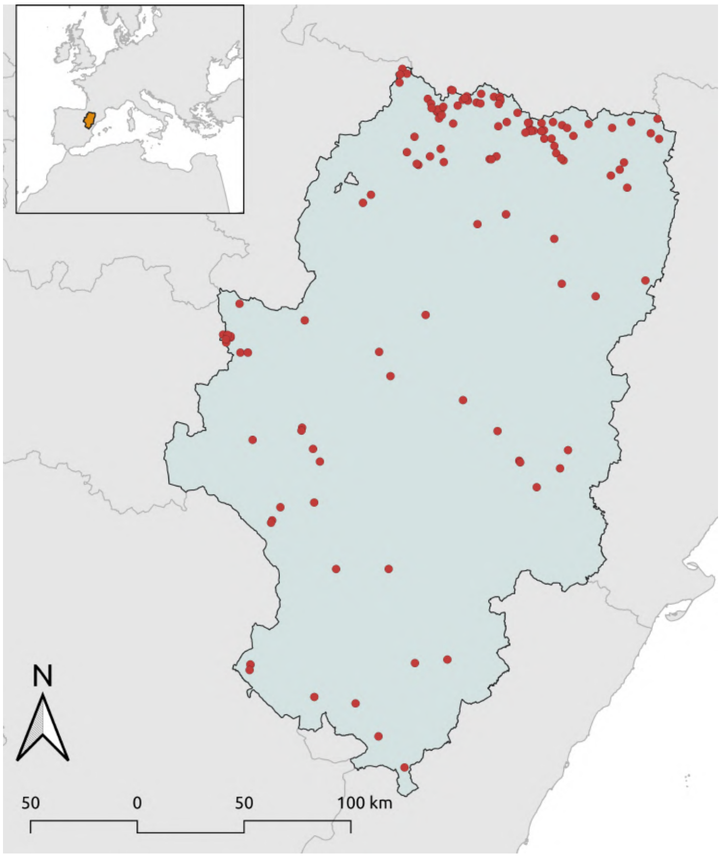

Figure 4.1: Location of the 157 populations included in this study.

species of the squared difference between the natural logarithms of the two abundance estimates taken in one census was used as an estimate of the observation error for that population. Use of the log of abundance to make an estimate of variance is based on an assumption of constant proportional errors in abundance, relative to the mean, such that variance on the log scale will be scale invariant, which was confirmed by examination of abundance *vs* squared differences of logged abundances (Appendix 4.A, Fig. 4.A.1). If a species lacked a double census in a particular population but had an estimate of observation error in others (19.6% of the cases), we used the double censuses from those populations as an approximation for the error. A total of 157 populations of 93 different plant species were double censused, and constitute the dataset for this analysis

4.2.3 Stochastic exponential model

To estimate the mean and variance of the annual stochastic population growth rate of each plant population while accounting for OE, we fit a density-independent stochastic exponential growth model using JAGS 4.3.0 (Plummer, 2003), *rjags* (Plummer, 2022) and *runjags* (Denwood, 2016). The model is built assuming that $\ln(\lambda_T)$ has a normal distribution with mean and variance equal to $\overline{ln(\lambda_T)}$ and $\sigma^2_{Process}$ respectively. We simultaneously fit this population growth process and the estimated variance from OE, ε^2_{OE}. Thus, the model uses both the data on observed numbers across time for a population as well as pairs of observations for the years and population sections with double count data. ε^2_{OE} and the population sizes from one year to the next advance according to a model defined by the following equations:

$$ln(M_T) = ln(\lambda_{T-1}) + ln(M_{T-1}) + \varepsilon_{T-1} - \varepsilon_T \tag{4.1}$$

$$ln(\lambda_T) \sim Normal(\overline{ln(\lambda_T)}, \sigma^2_{Process}) \tag{4.2}$$

$$\varepsilon_T \sim Normal(0, \varepsilon^2_{OE}) \tag{4.3}$$

$$\frac{1}{\varepsilon^2_{OE}} \sim Gamma(\frac{1}{2}, 2 * (ln(M_{T1}) - ln(M_{T2}))^2) \tag{4.4}$$

Where M_T is the observed count at time T, λ_T is the estimated growth rate from time $T-1$ to T, ε_T is the observation error for time T, $\sigma^2_{Process}$ is the process variance (the stochastic variance of $ln(\lambda_T)$ growth rates through time), ε^2_{OE} is the estimated observation error variance between and M_{T1} and M_{T2}. Equations 4.1 and 4.2 correspond to a simple exponential iteration, $N_T = \lambda_T * N_{T-1}$, but accounting for observation errors in observed population size (4.3). Each pair of double census values provide one estimate of ε^2_{OE} (4.4) and these estimates are assumed to follow a chi-square distribution (Cochran, 1934), fit in our models as a gamma distribution using the relationship between chi-square and gamma variants (Hogg et al., 1978). Note that in JAGS the normal distribution is parameterized with precision, the inverse of the variance, but to explain the model we express the normal with variance as is more common in the general literature. Finally, in the actual model we also include a random effect of *Plot* for the distribution of $\overline{ln(\lambda_T)}$ to account for variation between sampling units within a population. Table 4.1 gives prior distributions for each parameter and other information on the models. To assess model performance prior to applying it on real data we conducted a series of simulations (Appendix 4.B).

To fit the model with real data we ran 4 MCMC chains for 1,000,000 iterations with a burn-in period of 100,000 samples and a thinning interval of 10 samples. Convergence of the MCMC chains was assessed visually and with the Gelman-Rubin statistic, with values <1.05 being considered a good indicator of chain convergence. We fitted two separate models, one that distinguished between OE and process variance (OE model or model with observation error) and one that made no distinction between them (No OE model or model without observation error) to compare results between both methods. In addition, we fitted a model to estimate only the observation error of each population, using only the double count information, without the multi-year count data, as a baseline to compare the estimates of OE in the full model.

4.2.4 Probability of quasi-extinction

For each population we calculated the probability of quasi-extinction according to its estimated average growth rate and process variance. To take into account the uncertainty estimated by the Bayesian approach, we extracted the last 1,000 samples from each MCMC chain, for a total of 4,000 samples, to obtain samples of the average growth rate and process variance of each population. Then, we computed the probability of quasi-extinction of each population as the cumulative probability for that population's

Table 4.1: Prior distributions for the parameters used in each Bayesian model. Normal distributions are shown with their mean (μ) and precision, and gamma distributions with their shape (r) and rate (s) following the parameterization used in JAGS.

Model	**Parameter**	**Definition**
Population	Growth rate	$ln(\lambda_T) \sim N(\mu = 0, precision = 0.001)$
	Process variance	$\sigma^2_{Process} \sim Gamma(r = 0.001, s = 0.001)$
	OE variance	$Prec \sim Gamma(r = 0.001, s = 0.001)$
	Plot variance	$Plot \sim Gamma(r = 0.001, s = 0.001)$
Meta-analysis	Overall growth rate	$ln(\lambda) \sim N(\mu = 0.001, precision = 0.001)$
	Overall process variance	$\sigma^2_{Process} \sim Gamma(r = 0.001, s = 0.001)$
	Monitoring unit variance	$\sigma^2_{MU} \sim Gamma(r = 0.001, s = 0.001)$
	Species variance	$\sigma^2_{Taxon} \sim Gamma(r = 0.001, s = 0.001)$

size to fall below 10% of the initial population size in the next 50 years using the *extCDF* function in the *popbio* package (Stubben & Milligan, 2007), which applies the diffusion approximation method of Lande and Orzack (1988). We set an arbitrary initial size of 5,000 for all populations as the main goal was to showcase the effect of including OE in those estimates rather than calculating the extinction risk itself. Finally, we calculated the mean (p_{qe}) and variance (σ^2_{qe}) of the 4,000 samples to get an estimated overall probability of quasi-extinction. This process was repeated separately for each population and for the growth rates and variances estimated by the models with and without OE.

4.2.5 Analysis of growth rates

To characterize estimates of population dynamics across all populations, and to estimate the importance of considering OE and the magnitude of OE across the populations in our study, we followed the approach by Haase et al. (2023) and Pilotto et al. (2020) and conducted a set of Bayesian meta-analyses, using the output from our individual population model fits as input. In the first of these models, we used $\overline{ln(\lambda)}$ and $\sigma_{Process}$ estimated by models with observation error for each plant population. No populations were excluded from subsequent analyses because all of them had estimates for $\overline{ln(\lambda)}$ and $\sigma_{Process}$ with a Gelman-Rubin statistic between 0.95 and 1.05, indicating good MCMC chain convergence and model fit. Using this approach, we modeled the average trend across populations while taking into account the standard deviation of their posteriors as a measure of their uncertainty. The meta-analysis model assumed Gaussian distributions for $\overline{ln(\lambda)}$ and $\sigma_{Process}$, considered no fixed effects and included two random effects, one for MU and another for plant species nested within that MU to account for differences between monitoring units and species. We ran 4 MCMC chains for 1,000,000 iterations with a burn-in period of 100,000 samples and a thinning interval of 10. To summarize the quasi-extinction probabilities, we followed a similar approach but assuming that those probabilities followed a Beta distribution with a *logit* link function and whose shape parameters were estimated via moment matching using the following equations: $\alpha = \mu_{qe} ln(\frac{1}{\sigma^2_{qe}})$ and $\beta = \mu_{qe}(1 - \mu_{qe}) * ln(\frac{1}{\sigma^2_{qe}})$ were μ_{qe} and σ^2_{qe} are, respectively, the average quasi-extinction probability of a population in 50 years (p_{qe}) and its variance calculated over the 4,000 values of p_{qe} obtained from the posteriors of our initial model. To test if including an estimate of OE affected our estimates of growth rates and their variance as well as quasi-extinction probabilities, we followed the same meta-analysis approach just described, but with the posterior distributions estimated by the model without observation error and compared the resulting posteriors from both meta-analyses. Finally, we tested the differences between different sampling methods with a meta-regression model, which follows a similar approach as the previous meta-analysis models but also includes a fixed effect for the sampling method.

4.3 Results

The stochastic exponential model performed well on simulated data (Appendix 4.B, Figs. 4.B.1, 4.B.2 & 4.B.3) and correctly estimated the average growth rates and stochastic variances of real populations, showing good convergence. On real data, including the OE led to narrower credible intervals in both parameters (Appendix 4.C, Fig. 4.C.1A & B) and having longer data series improved the fit of the model and led to narrower credible intervals of the estimated parameters (Appendix 4.C, Fig. 4.C.1C & D). Including an estimate of observation error in the model did not have a significant effect on the estimated long term stochastic growth rates of most populations (Fig. 4.2A), however it substantially reduced the estimated process variance in all of them (Fig. 4.2B).

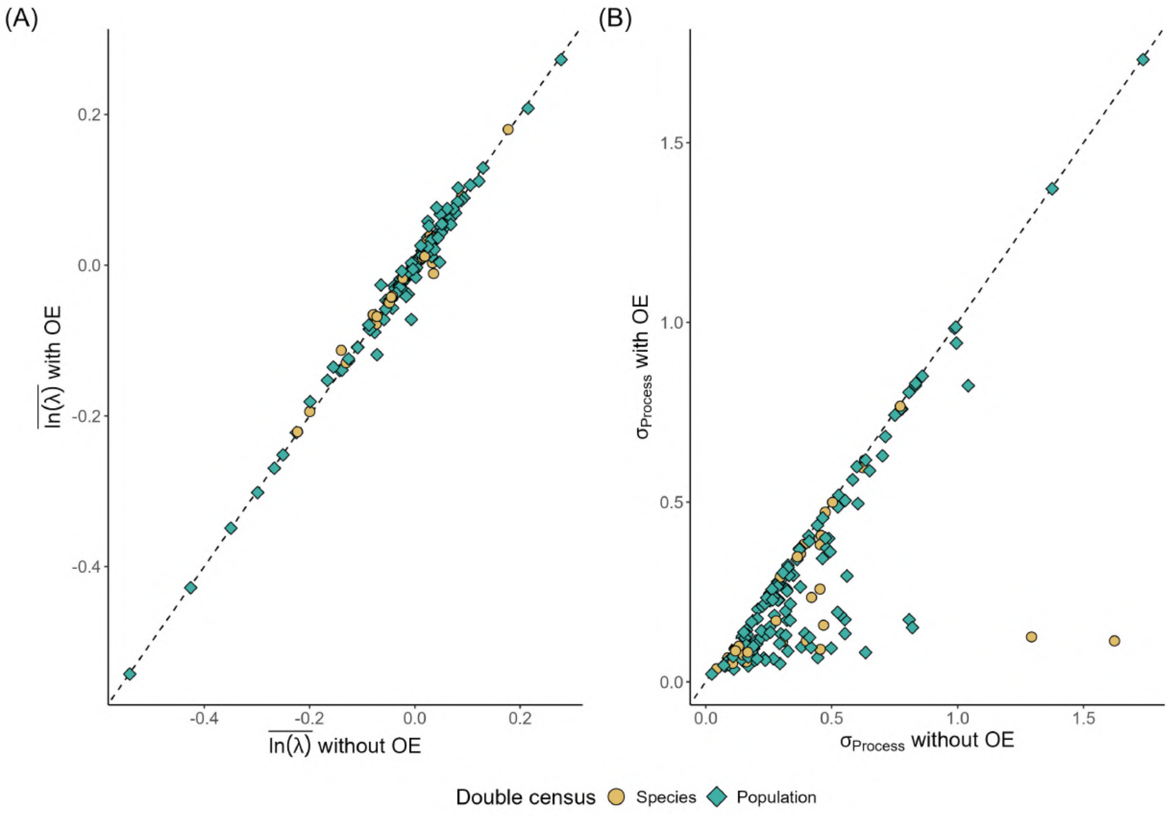

Figure 4.2: Relationship between estimates of $\overline{ln(\lambda)}$ (A) and $\sigma_{Process}$ (B) obtained from the models with and without observation error.

Although the proportion of variation associated with OE differed greatly between populations and sampling methods, on average it accounted for 31.8% (SD = 32.1) of the total variation in observed numbers, and ranged up to a maximum of 98.7% (Fig. 4.3A). In most cases, OE estimated directly within the exponential model was similar to that estimated on its own (Fig. 4.3B), although its 95% credible intervals tended to be narrower (Appendix 4.A, Fig. 4.A.2).

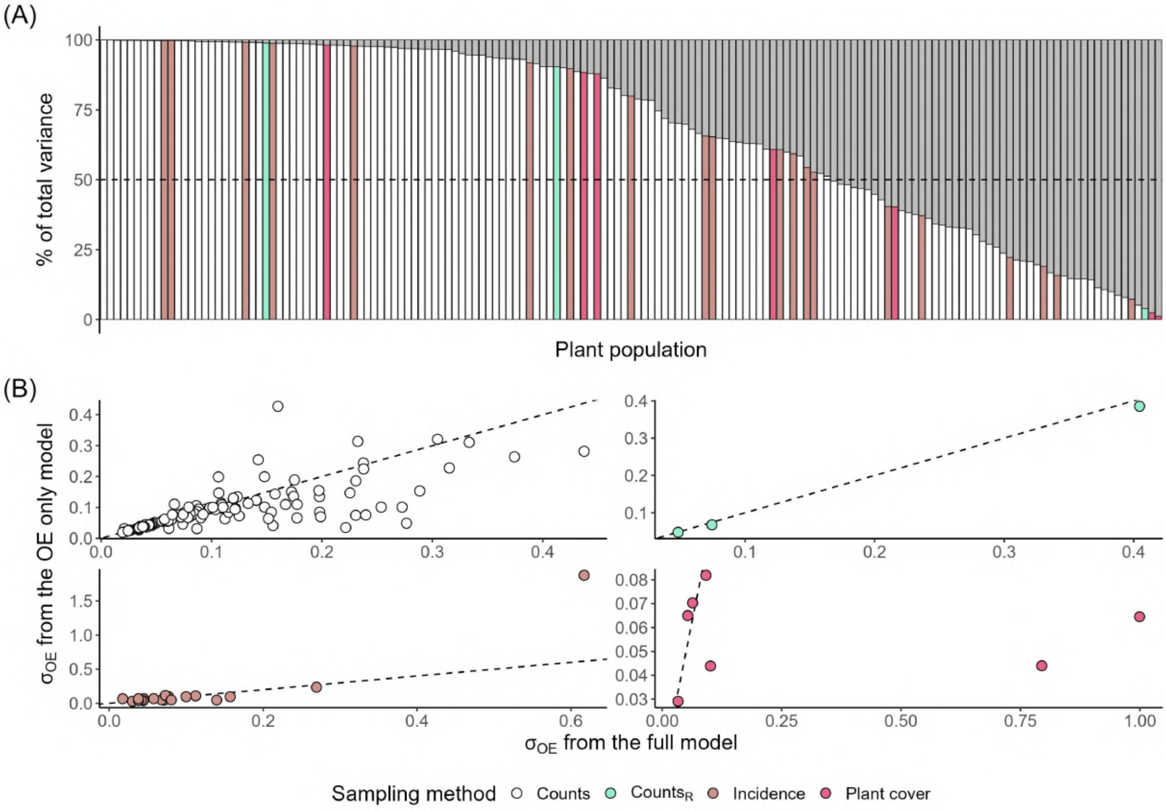

Figure 4.3: (A) Proportion of the total variance estimated for each population that corresponds to process variance (color) and observation error (gray). (B) Relationship between the OE variation estimated by the full model and the OE only model. Dashed lines in panel (B) indicate the one-to-one ratio.

At the individual population level, the model without OE estimated that only 3 of them (1.9%) had average growth rates that deviated from 0 (CI_{95} not overlapping with 0), with one showing an increase in population size over time whereas two showed signs of decline. On the other hand, the model with OE estimated that six populations (3.8%)

had growth rates that deviated from stability, of which four had negative growth rates and two positive ones.

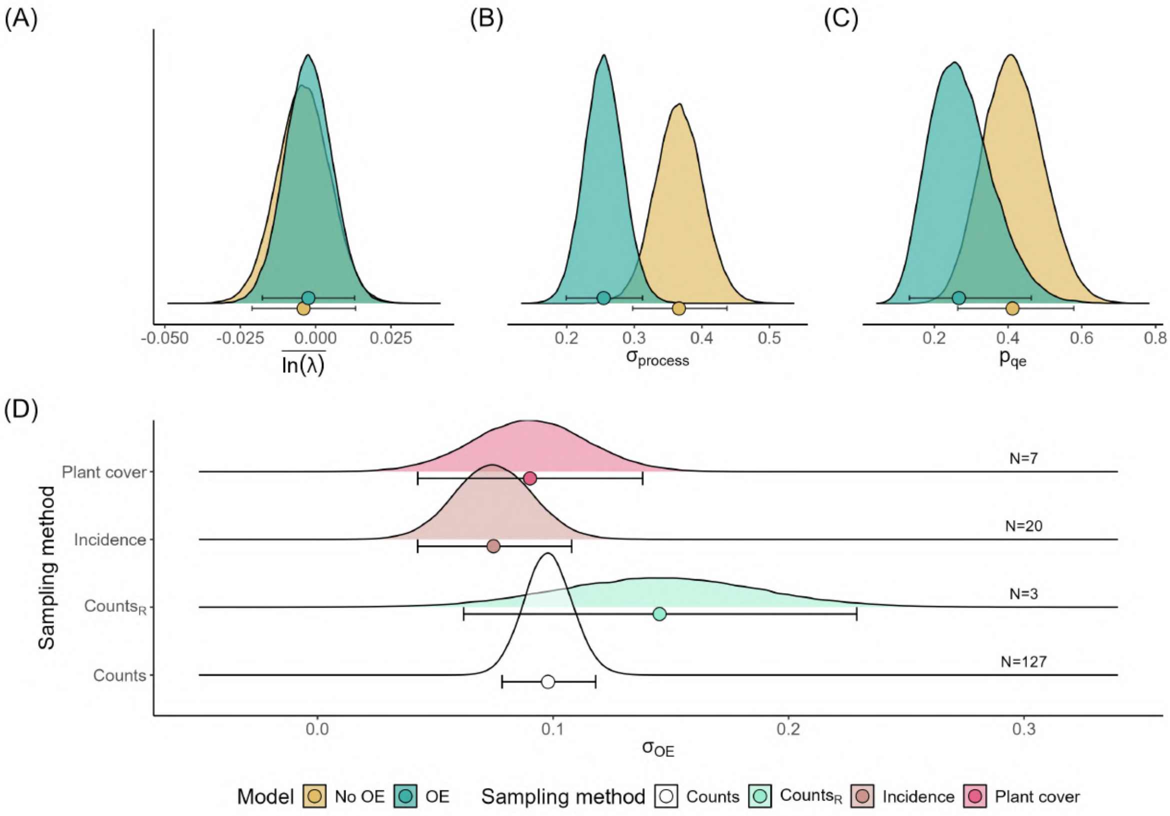

Figure 4.4: Posterior distributions of the average long term stochastic growth rate (A) of all populations, their variance (B) and the average quasi-extinction probability (C) estimated by the models with (blue) and without observation error (yellow). (D) Posterior distributions of the estimated effect of sampling method on observation error along with the number of populations where that method is used. In all panels points and whiskers indicate the median value of the corresponding distribution and its CI_{95}.

The Bayesian meta-analysis of the models with observation error estimated an overall population growth rate of -0.0024 with a 95% credible interval (CI_{95}) of -0.017 and 0.014 (Fig. 4.4A), and an average process variance of 0.25 (CI_{95} = 0.19, 0.31) (Fig. 4.4B). The average quasi-extinction probability in 50 years was 0.28 (SD = 0.086) (Fig. 4.4C). In contrast, the average growth rate estimated by models that did not account for OE was -0.0039 (CI_{95} = -0.021, 0.014) with an average $\sigma_{Process}$ of 0.37 (CI_{95} = 0.3, 0.44) and an average quasi-extinction probability of 0.42 (SD = 0.081). We also found that the magnitude of OEs were similar across all four survey methods (Fig. 4.4D), although incidence had the lowest OE variance (Median = 0.075, CI_{95} = 0.043, 0.11), followed by plant cover (Median = 0.09, CI_{95} = 0.043, 0.14), counts (Median = 0.098, CI_{95} = 0.078, 0.12) and counts_R (Median = 0.15, CI_{95} = 0.062, 0.23).

4.4 Discusion

In this study we applied a Bayesian approach to population viability analysis that takes into account the variance estimated with easily collected data on observation error. We applied it on 157 plant populations living across a wide range of environmental conditions and for which we had direct or indirect measures of observation error taken during the sampling process. We found that including such estimates directly into the population model improved the precision of parameter estimates. Whereas it had little to no impact on estimates of mean growth, it greatly reduced both the estimated stochastic variance of growth rates and the estimated quasi-extinction probabilities. The relative contribution of OE to the estimated variation in growth rates differed between populations, but on average it accounted for almost a third of the total variation. We also compared the observation error estimated by different sampling methods. Incidence-based methods were the most accurate, followed by plant cover and counts of individuals, with counts on only reproductive individuals being the least accurate. Most of the plant species that we studied show stable population growth rates over time, with only a very small fraction of them having significantly decreasing or increasing population sizes.

4.4.1 Accounting for observation error improves PVA estimates

The importance of observation error as a source of bias in population viability analysis is widely acknowledged in population viability literature, and different methods have been proposed to account for it (Dennis et al., 2006, 2010; Humbert et al., 2009; Staples et al., 2004). However, very few studies have measured that error directly during the sampling process or incorporated it into their models. Here, we estimated observation error by following a simple protocol: censusing twice all or part of the population of interest, and parameterizing the variance of those double censuses directly in our models. By considering the OE during the sampling process we were able to decompose the variance of growth rates into its process and observation components, improving our estimates of both of them. Including an error term slightly increased the estimated growth rates and greatly reduced the estimated variance in comparison with model fits that ignored OE. These results are consistent with expectations, since observed variance should be the sum of process variance and observation error, and higher process variance will negatively influence population viability (Gillespie, 1977; Lande & Orzack, 1988; Lande, 1993). Accordingly, this reduction in the estimated environmental stochasticity - process variance and the slight increase in average growth rates should have an important positive effect on the quasi-extinction probabilities of all populations, which were 14 percentage points lower when estimated using the growth rates and variances obtained from the model with observation error. While the direction of effects we find is entirely as predicted, another important finding was that OE accounted for a meaningful portion of the variation in population sizes and growth rates for most of our species and populations, suggesting that ignoring it when assessing the viability of populations might significantly bias our estimates of growth and extinction (McNamara & Harding, 2004; See & Holmes, 2015). We also found that longer time series resulted in better estimates for all population parameters, evidenced by narrower credible intervals in growth rates and their variance. Although the use of repeated measures through time is a well known method for improving the estimates of different PVA parameters (Dennis et al., 2010; Knape et al., 2013; See & Holmes, 2015), repeating censuses during the same sampling session or as close as possible to it is seldom considered in literature. To our knowledge this is the first study to make use of this simple method to estimate the error associated with the observation process, let alone doing so with such a large set of populations and years. A simple procedure like this can become a useful tool for improving extinction risk and thus contribute to population management (Lindenmayer & Likens, 2010).

While taking some double count data is clearly valuable, these can be used in different ways to estimate OE. In particular, an alternative approach to ours would be making a separate estimate of OE using only the double count data, then incorporating these estimates into a model to estimate the mean and variance in growth rates. However, we found that incorporating OE estimation directly into the model led not only to better estimates of the demographic parameters, but also to more accurate estimates of observation error itself. While this means using a more involved analysis method, it is still not difficult and could also be easily modified to, for example, include models in which annual growth rates depend upon environmental drivers such as climate variables.

4.4.2 The importance of sampling method

When it comes to sampling vegetation and its changes in abundance, many methods can be used, although the choice between them often boils down to the detectability of the focal plant (Elzinga & Salzer, 1998; Morrison, 2016). This, in turn, is determined by the size of the plant, its density in the study area, how easy it is to tell apart from other plants or the density of the surrounding vegetation (Morrison, 2016; Perret et al., 2023). Thus, the goal of choosing the appropriate sampling method is to reduce any biases during the observation process and produce the most accurate estimates of abundance possible (Bonham, 2013). Here, we used the workflow proposed by García et al. (2021) to choose between four different sampling methods based on the characteristics of the focal plant in order to minimize observation error. Thus, the abundance of plants that are difficult to count, such as those forming cushions or mats, was assessed using presence/absence or abundance-cover methods in quadrats. For larger species with clearer distinction between individuals we used counts of all individuals when possible or only reproductive individuals when distinction between those in vegetative states was difficult. Even with this a priori control of OE, the importance of using the appropriate sampling method is highlighted by the variability in sampling error between methods used in our study. Quadrat-based methods used to census as presence/absence or plant-cover had lower rates of observation error, most likely because they are less sensitive to abundance changes than counts of individuals (Vittoz et al., 2010). On the other hand, counting reproductive individuals had the highest error rates, which was unexpected since colorful flowers and fruit tend to be more conspicuous and thus easily detected than plants alone (Perret et al., 2023). However, counts based on flowering plants can vary considerably in a few days, and only three of the populations in our study followed that sampling method, so this pattern might be a consequence of a small sample of this method. With this exception, the patterns of observation error are fairly consistent with what could be intuitively expected, although a comparison between different sampling methods in the same population would be interesting to further explore these patterns. Nevertheless, our results highlight the importance of choosing the appropriate sampling method during the design process of any population under monitoring to reduce any potential biases, putting special attention on the particular characteristics of the plant detectability, as well as its surroundings (Morrison, 2016).

4.5 Conclusions

Population viability analysis is a fundamental tool in conservation biology, but estimates of extinction risk are heavily influenced by the data that are used to parameterize population models, including inaccuracies and biases in even the simplest metrics of population size or change. These inaccuracies can in turn bias our estimates of important population parameters like growth rates and their variability, namely by giving the impression that populations may fluctuate more than they actually do. Our study demonstrated that by using a simple method such as repeated censuses in all or part of the sampling area of a population during one or a few censuses of the temporal series, observation error can be taken easily into account, which considerably improves the estimates of viability models. In the current crisis of biodiversity loss, this is a crucial procedure for the correct assessment of the state of populations, which can help our decision making regarding species conservation.

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Appendix 4.A Visual examination of abundance *vs* squared difference of log abundances

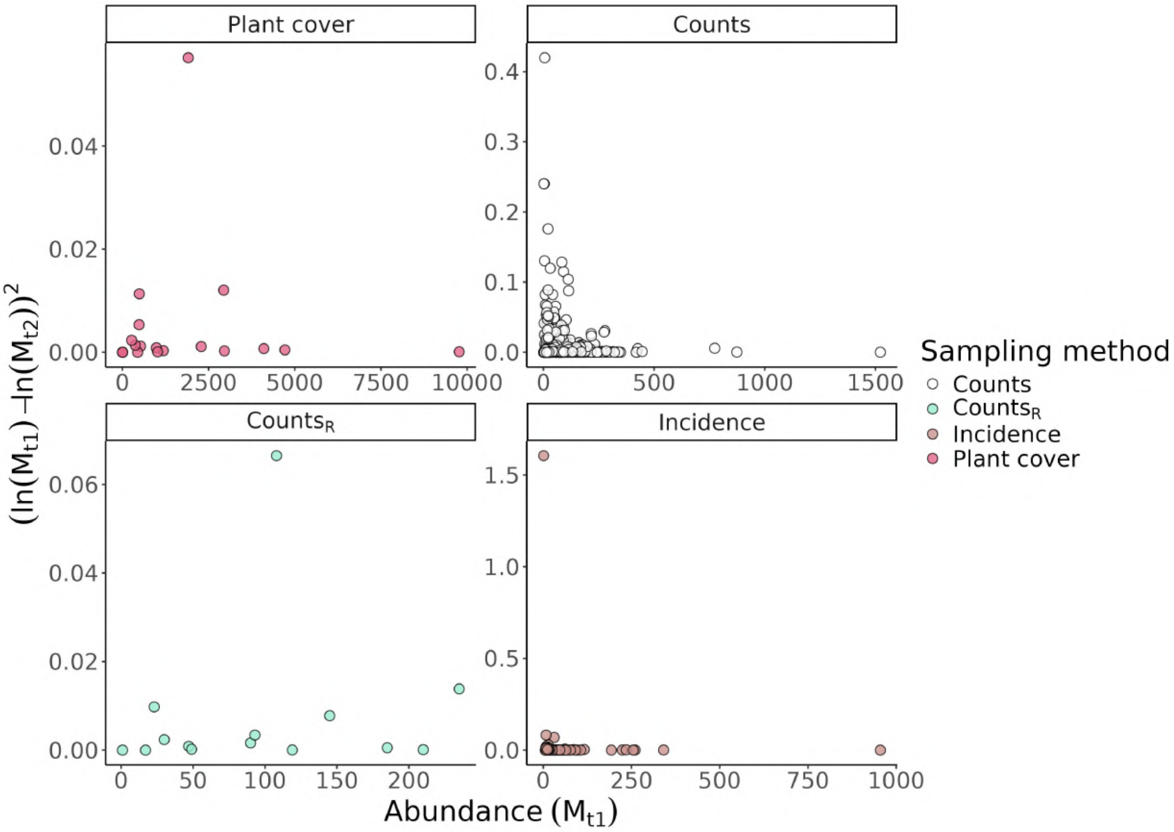

Figure 4.A.1: Abundance (M_{t1}) *vs* the squared differences of log abundances from the repeated censuses used to estimate observation error (M_{t1} and M_{t2}) using each sampling method in populations with double censuses. Each point represents one pair of abundance measures.

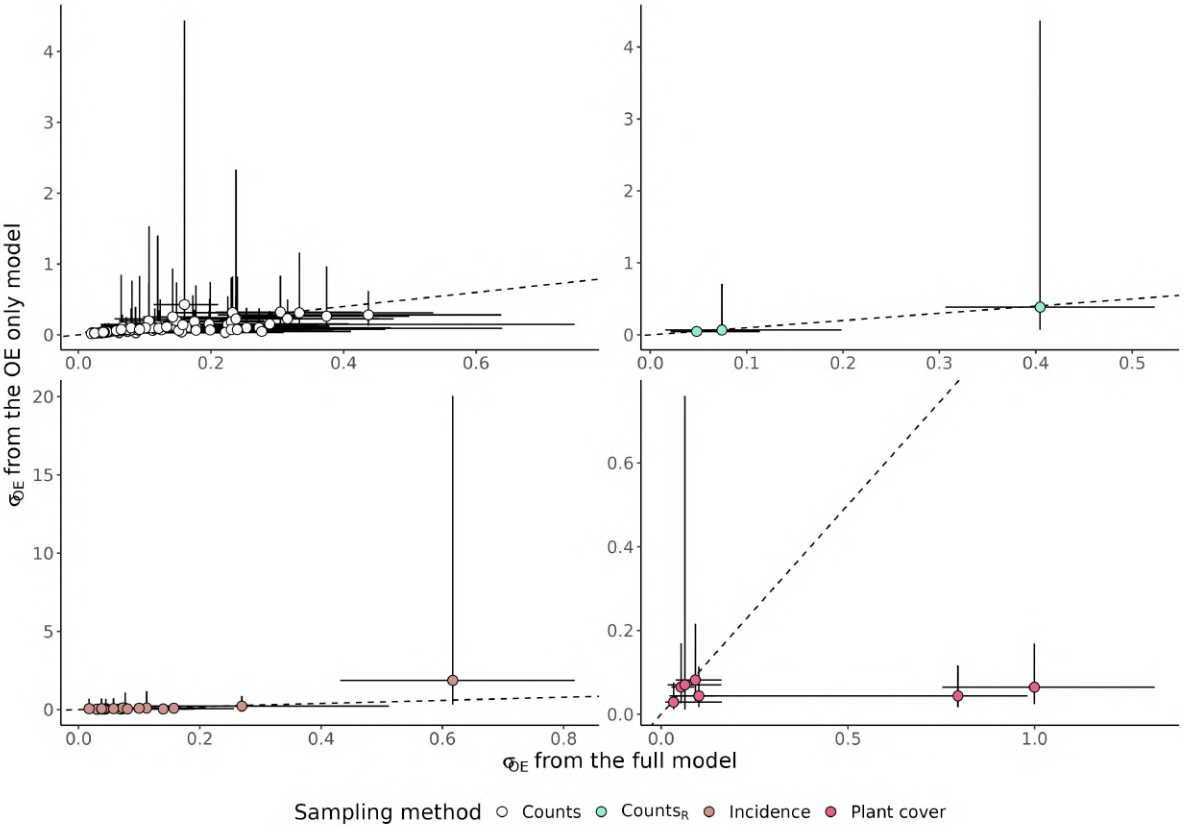

Figure 4.A.2: Relationship between the OE variation estimated by the full model and the OE only model with their respective 95% credible intervals. Dashed lines indicate the one-to-one ratio.

Appendix 4.B Model performance on simulated data

In order to assess the fit of our model, we simulated several population trends with varying average long-term growth rates ($\overline{\lambda}$, from 0.5 to 1.5 in increments of 0.25), process variances ($\sigma_{Process}$, from 1 to 3 in increments of 1) and observation error variance(ε^2_{OE}) as a proportion ranging from 0 to 0.9 in 0.1 increments with respect to the process variance, resulting in 150 different populations each one with a different combination of demographic parameters. We assigned a "true" long-term growth rate ($ln(\overline{\lambda_{True}})$) to each simulated population by sampling one random value from a normal distribution with mean equal to $ln(\overline{\lambda})$ and variance equal to $\sigma_{Process}$. Then, we simulated a 20 generations-long time series of population sizes using a log-transformed exponential growth model ($ln(N_T) = ln(\overline{\lambda_{True}}) + ln(N_{T-1})$) with a starting population size of $ln(100)$ individuals. We simulated the "observed" populations sizes by taking two random values from a normal distribution with mean equal to the true population size for that iteration and variance equal to the observation error variance (ε^2_{OE}). Each of these two values represented one repeated census in the same generation. Then, we fit our Bayesian model with observation error to each simulated population and its corresponding observation error using 4 MCMC chains, 10,000 burn-in samples, 100,000 effective samples, 10,000 adaptive samples and no thinning interval; and compared the true *vs* expected values. For the vast majority of populations model estimates of growth rate (Fig. 4.A.1), process variance (Fig. 4.B.1) and observation error variance (Fig. 4.B.2) were close to the true values, with 88% of those true values falling within the 95% credible interval of the estimated growth rate, 88.7% for the process variance and 83% for observation error variance. Note that in populations without any observation error the model still estimates a certain of variance, but values are very close to zero.

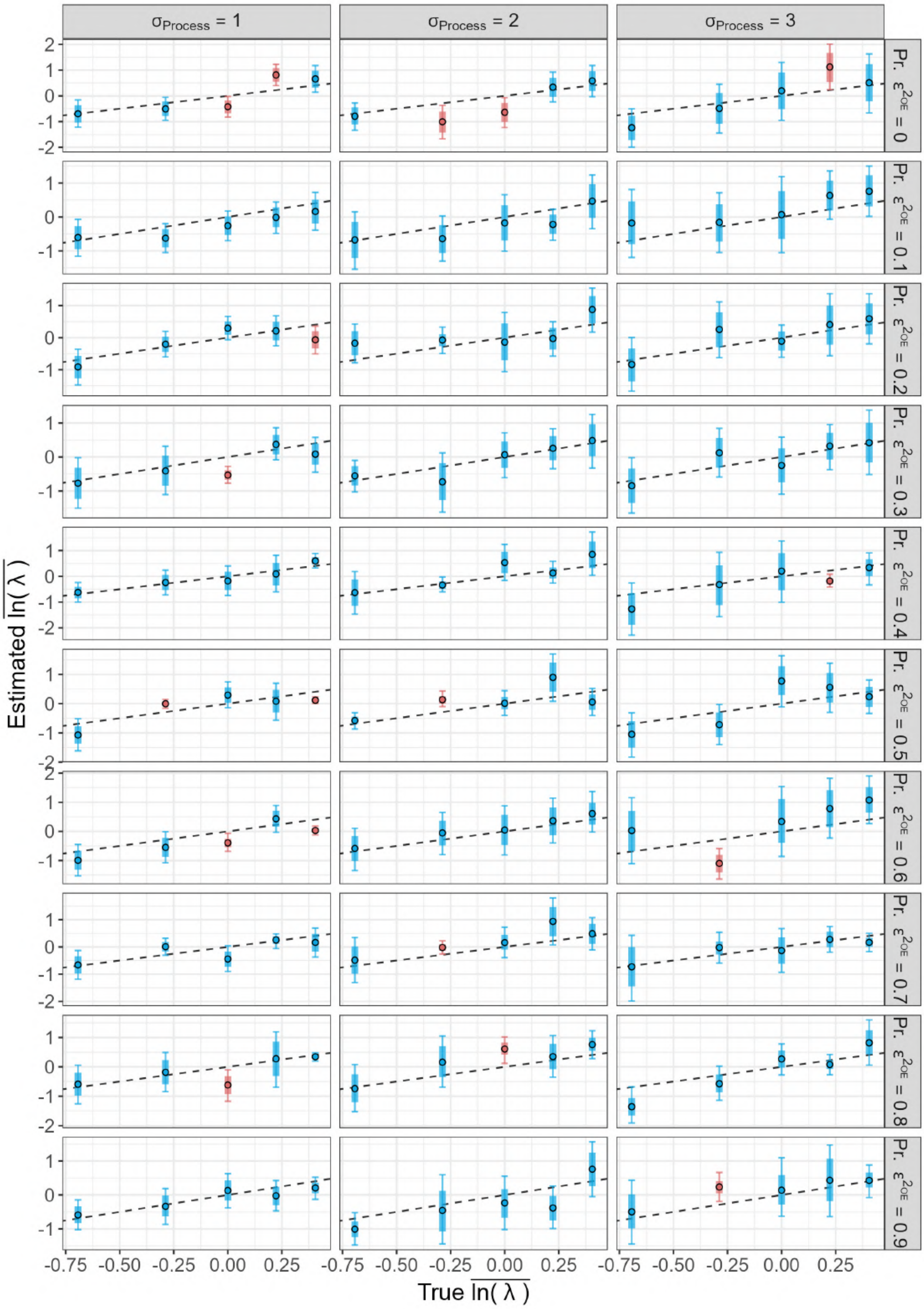

Figure 4.B.1: True *vs* estimated $\overline{ln(\lambda)}$ for each simulated population with different values of $\sigma_{Process}$ and proportion of ε^2_{OE}. Dots indicate the mean of the Bayesian posterior distribution for that parameter, error bars and thick lines indicate the 95% and 80% credible interval respectively.

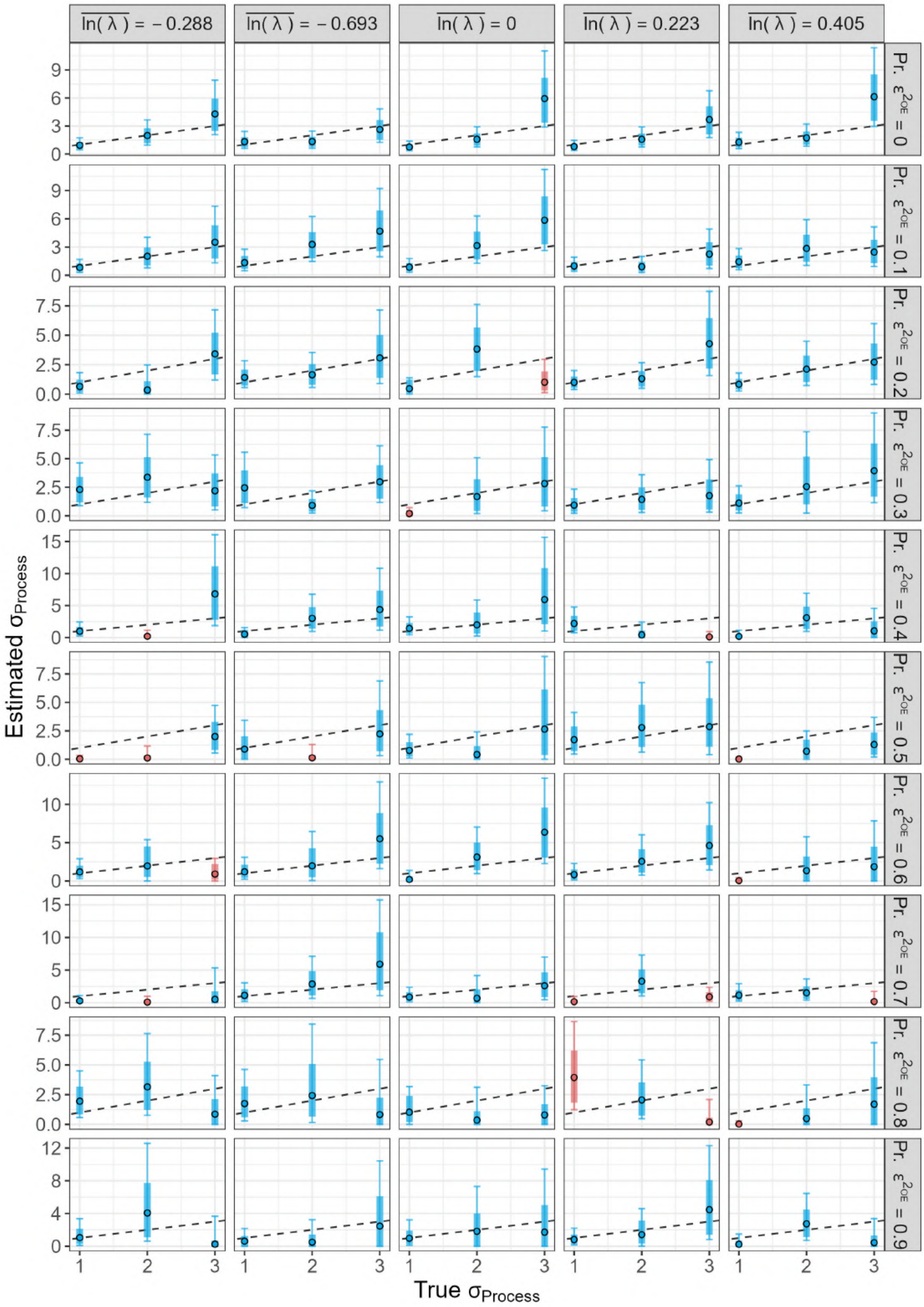

Figure 4.B.2: True *vs* estimated $\sigma_{Process}$ for each simulated population with different growth rates ($\overline{ln(\lambda)}$) and proportion of ε^2_{OE}. Dots indicate the mean of the Bayesian posterior distribution for that parameter, error bars and thick lines indicate the 95% and 80% credible interval respectively.

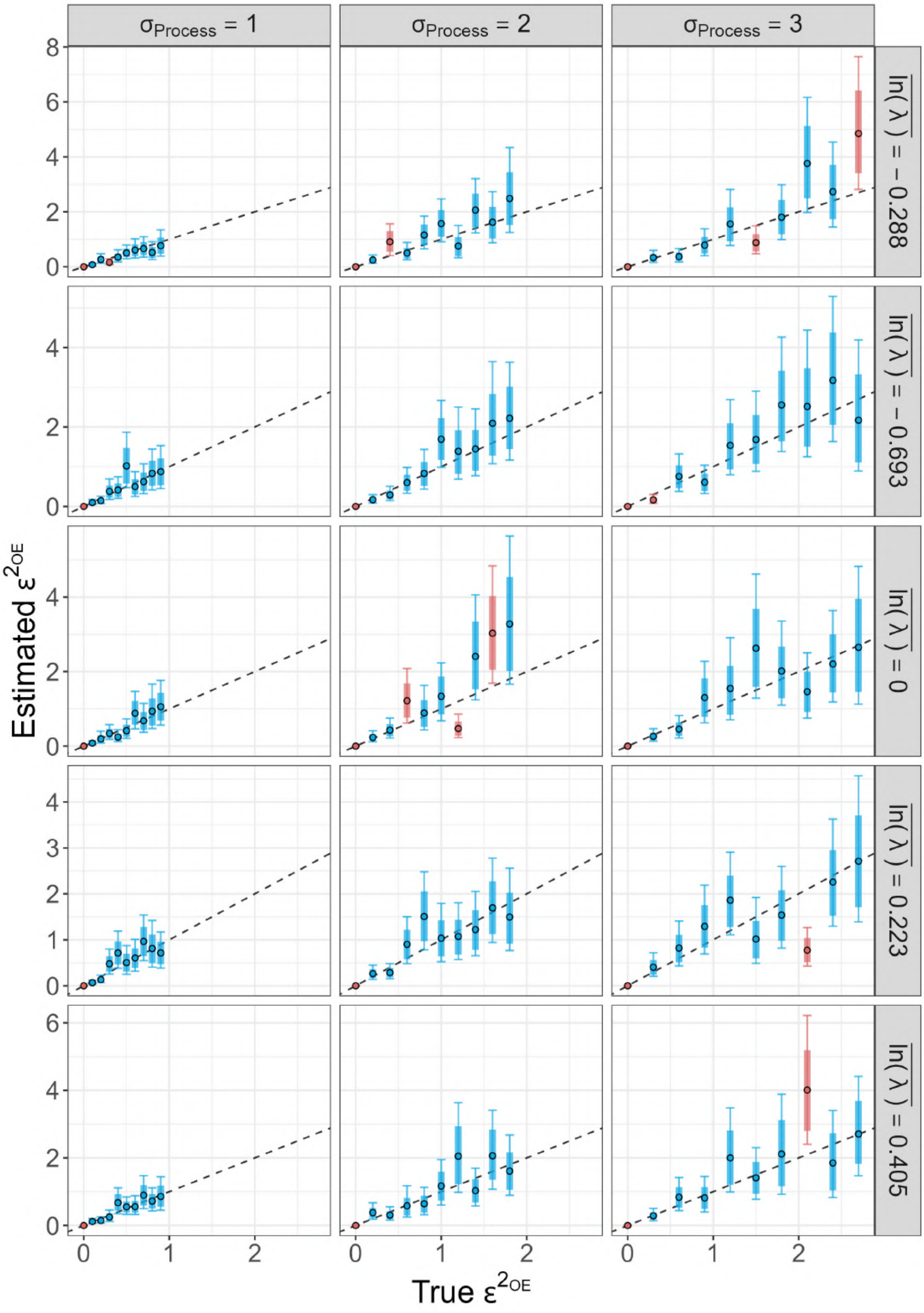

Figure 4.B.3: True *vs* estimated observation error variance (ε^2_{OE}) for each simulated population with different values of $\overline{ln(\lambda)}$ and $\sigma_{Process}$. Dots indicate the mean of the Bayesian posterior distribution for that parameter, error bars and thick lines indicate the 95% and 80% credible interval respectively.

Appendix 4.C $\overline{ln(\lambda)}$ vs $\sigma_{Process}$

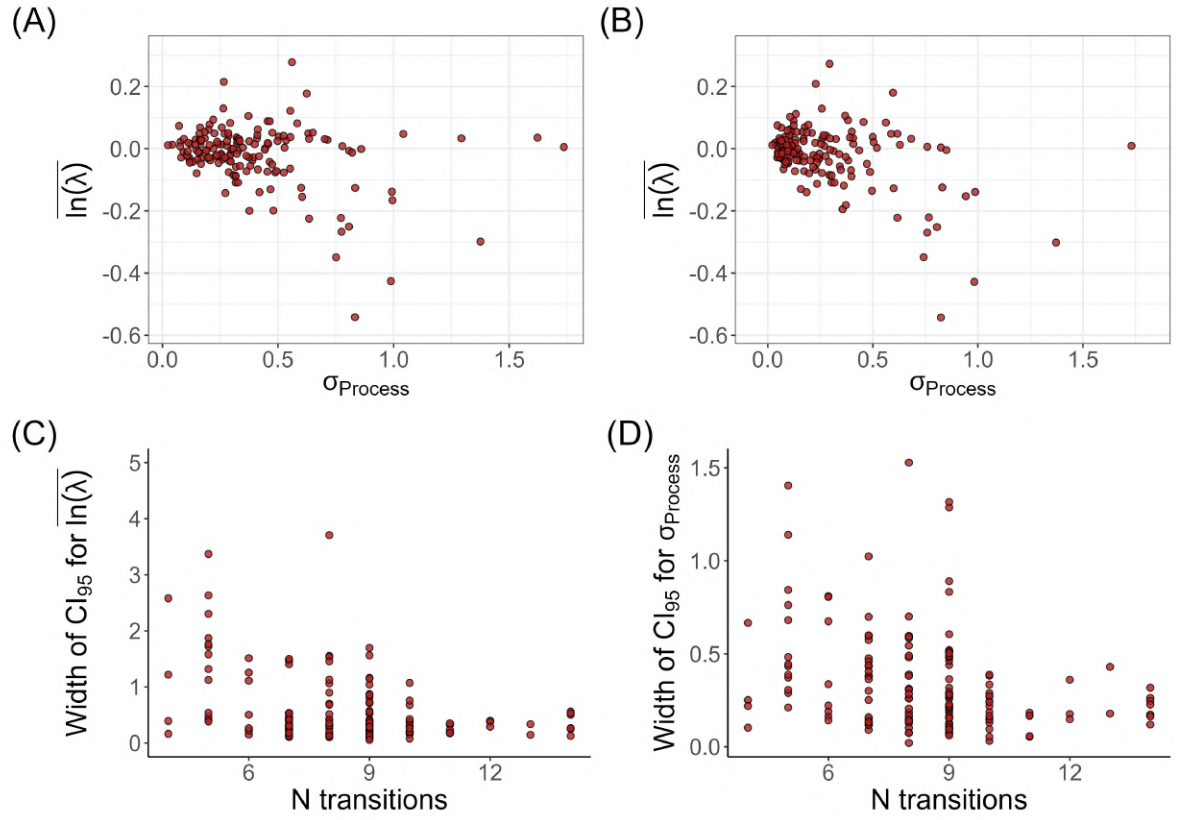

Figure 4.C.1: Relationship between the median estimated $\overline{ln(\lambda)}$ and $\sigma_{Process}$ for the models without (A) and with observation error (B). Panels (C) and (D) show the width of the CI_{95} of $\overline{ln(\lambda)}$ and $\sigma_{Process}$ in respect to the number of transitions used in the model with OE.

5 Rare plants as hubs for biodiversity

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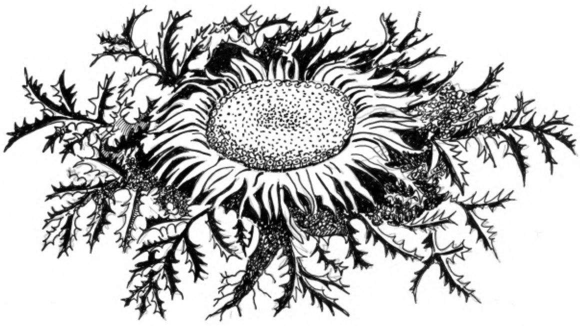

Manuscript in preparation

5.1 Introduction

Biotic interactions play a fundamental role in ecosystems. They participate in many of the mechanisms behind ecosystem functioning, from energy and nutrient flows due to predation, carnivory or herbivory to species abundances and distribution patterns via pollination, seed dispersal and facilitation (Hooper et al., 2005; Traill et al., 2010). Consequently, interactions contribute to the dynamics and long-term stability of populations, communities and ecosystems (Valiente-Banuet et al., 2015). In the universe of interaction networks plants often play a central position, acting as hubs by providing a large variety of resources like food and shelter for many species (Borges & Brown, 2001). The diversity and strength of plant-animal interactions are thus determined by the resources made available by the plants, as well as the local diversity and abundance of the species that may interact with them (Bascompte & Jordano, 2007; Burkle & Alarcon, 2011). More diverse networks of interactions are more robust to disturbances such as the extinction of their constituents, which leads to increased ecosystem stability by ensuring the persistence of ecosystem functions through time (Ollerton, 2017). For example, higher diversity of pollinators or seed dispersers has positive impacts on the reproductive success, diversity and productivity of plant communities, which ensures their long term persistence, and increases the resource availability for all the organisms in the ecosystem (C. Fontaine et al., 2005; Hale et al., 2020). Even interactions that are seemingly negative for plants, like herbivory, can contribute to maintaining plant diversity by limiting competition between plant species and promoting coexistence as long as the perturbation is kept under an optimal threshold (Borer et al., 2014). Although interactions are usually studied in relation to the aerial part of plants, belowground interactions also play an important role in plant performance (Berendsen et al., 2012). Microbial communities in the soil or rhizosphere are involved in many mutually beneficial interactions with their host plants. For instance, plants offer suitable microhabitats for bacteria and fungi, in addition to a supply of organic carbon in the form of root exudates (Bais et al., 2006). In turn, the activity of microbes may contribute to plant growth by different mechanisms like increasing availability of soil nutrients through organic matter degradation (Berendsen et al., 2012), nitrogen fixation Franche et al. (2009), improving to the uptake of soil nutrients through mycorrhizae (Vandenkoornhuyse et al., 2015), and preventing the proliferation of root pathogens (Trivedi et al., 2020).

Thus, plants and the organisms they interact with make up complex systems that should be considered in an integrative way, but we still lack knowledge about many aspects of them (Tylianakis et al., 2010). Most studies on plant-animal interactions focus on either trophic or mutualistic interactions (García-Callejas et al., 2018), whereas our understanding of how often plants interact with other organisms that approach them to rest, reproduce or forage, remains limited. Other unexplored aspects of plant interactions, particularly interesting in the case of rare or endangered species, are if populations of the same species interact with similar sets of organisms everywhere, or if the ensemble of interactions varies in space or according to population size.

Here we tackle both questions and explore the diversity of arthropod and bacterial communities found aboveground and belowground, respectively, in six rare plant species of conservation interest. First, we describe the community of visitors found in two populations of each plant species, each one with different size but close enough to share similar environmental characteristics. Then, we compare the diversity of visitors between similar sized patches within a large and a small population of the same plant species to test how similar they are. Plants in larger populations are expected to interact with a larger set of organisms just as a consequence of the larger spatial and environmental heterogeneity they cover. To make a more standardised and straightforward comparison with small populations, we delimited three patches spread over the large population with a similar size as a single patch of the small one (which covered most of the population), and then compared the diversity metrics between them. In principle, we do not expect differences in richness or abundance of species between patches because all plants in our study offer a general set of resources, which should not affect attraction capacity or impose any filter to potential visitors (Brosi, 2016; Waser et al., 1996). Similarly, we do not expect differences in root bacterial diversity nor composition between patches of the same plant species because host species and soil properties are the dominant drivers of root microbial communities and they are constant between patches (Berendsen et al., 2012; Goberna & Verdú, 2016). Finally, we test if the diversity patterns observed aboveground in each population across plant species are mimicked belowground, or if on the contrary, these patterns are independent from one another. We expect uncoupling between the diversity of arthropods and root bacteria because the factors that determine the diversity of visitors are different aboveground (*e.g.* structure and diversity of the surrounding vegetation and abiotic conditions Joern and Laws, 2013), and belowground (*e.g.* host species identity or soil properties, Trivedi et al., 2020).

5.2 Methods

5.2.1 Study area and plant species

Our study was carried out in the Spanish side of the Pyrenean range (Fig. 5.1). We chose six plant species of conservation interest (endemic to the area, isolated at continental scale, at limit of distribution, or "in Extinction risk"): *Borderea pyrenaica* (Dioscoreaceae), *Cypripedium calceolus* (Orchidaceae), *Galanthus nivalis* (Amaryllidaceae), *Gentiana lutea* (Gentianaceae), *Pinguicula longifolia* (Lentibulariaceae), *Ramonda myconi* (Gesneriaceae) (hereafter we refer to each focal species by its acronym: *borpyr*, *cypcal*, *galniv*, *genlut*, *pinlon* and *rammyc* respectively, Appendix 5.A Table 5.A.1). They were selected because due to their ecology, habitat specificity or morphological architecture,

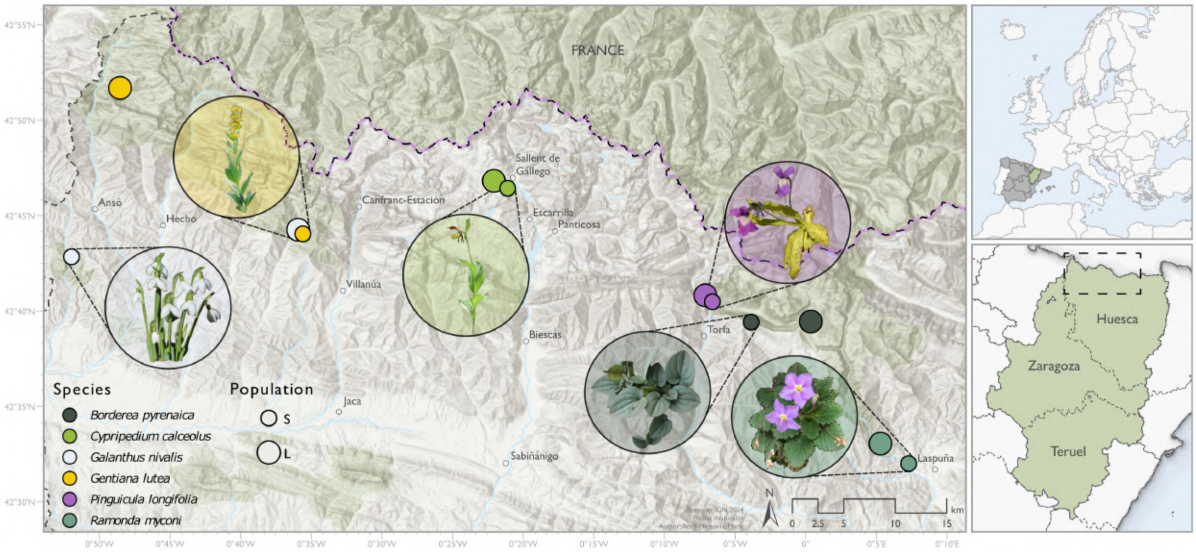

Figure 5.1: Study area and location of populations S and L of each plant species. Map courtesy of M. Adell-Michavila.

we knew they were involved in a wide variety of plant-animal interactions, such as pollination, seed dispersal, predation, carnivory or parasitism, and also offered a diverse number of microhabitats for visitors.

For each plant species, we located one large, continuous population (L) and one small (S) population, separated between 0.7 and 22 km depending on the species. To avoid any confounding factors between populations of each species, populations were chosen after an exhaustive search of the study area based on prior knowledge about the distribution of each species according to the records in the Herbarium JACA, one of the largest in Spain (http://www.ipe.csic.es/proyectos-de-investigacion) and specialized in the flora of the region. Populations shared similar climate and soil properties, and we recorded the density of the focal plant species as well as diversity and composition of accompanying plant species to test for any possible effects on visitor diversity (Appendix 5.A, Table 5.A.1). We also ensured that there were no other populations of the same plant species between our sampling areas to minimize any mixing between communities of interactors. In each small population we sampled a patch that covered most of the population area, and in the large populations we sampled three patches (L1, L2, L3) of similar size as the one sampled in S and separated between 40 and 300 m.

5.2.2 Aboveground interactions survey

The aboveground arthropod community was surveyed in 2016, 2017, and 2018 during the flowering season of the host plants. Sampling area and length of surveys varied among plant species, depending on size of plants and frequency of interactions, but at least 20 surveys were performed at each site, resulting in more than 9,000 minutes and 638 surveys overall (Appendix 5.A, Table 5.A.1). Sampling effort varied among plant species because they differed in the abundance or detectability of interactions (*e.g.* *galniv* was sampled for a shorter period because flowering occurs at the end of winter, when temperatures keep visitor activity low). However, sampling effort was kept similar among patches of the same plant species. All individuals visiting any part of flowering and non-flowering plants over an area covered visually by the observer were either visually identified or sampled to confirm identification later on. In addition, specific methods were used to unveil interactions that are not easily visible, like those by very small or hidden organisms (Appendix 5.A, Table 5.A.2). For example, acari sheltered in leaves of *rammyc* were sampled by Berlese funnel traps. Cafeteria experiments were used for *borpyr* and *galniv*, given that their seeds have an elaiosome attractive to ants. Fruits of *genlut* were also wrapped in mesh to capture arthropods emerging from eggs laid inside the fruit (Appendix 5.A, Table 5.A.2). In the particular case of the carnivorous *pinlon*, arthropods trapped by three sticky leaves of 15 plant individuals in each patch were also identified. Individuals not identified *in situ* were collected, photographed, and sent to expert taxonomists to be identified. When identification beyond a certain taxonomic level was not possible, morphospecies were used (*e.g.* diptera_1, diptera_2). The abundance of each visitor was measured as the number of times it was observed interacting with plants of the focal species.

5.2.3 Below ground interactions survey

Belowground prokaryotic communities were characterized for each plant population from samples of root material of a variable number of individuals within each patch (10-20, depending on species but using similar numbers among patches of each species). Roots were shaken vigorously, and their growing tips were cut and frozen until analysis (the soil particles adhered to the tips were considered as rhizosphere). Then, roots of each patch were mixed, and DNA extraction was carried out from three samples with 0.05-0.1 grams of root material using a Mobio PowerSoil DNA Isolation Kit (Mobio Laboratories). PCR and sequencing of the 16 rRNA gene was done with Illumina MiSeq (NGS) following the methods from the central genomic services of RTSF-MSU (Michigan State University, USA) (https://rtsf.natsci.msu.edu/). We analyzed the V4 variable region of the 16S rRNA gene (250 nucleotides) using primers F515 (5'-GTGCCAGCMGCCGCGGTAA-3') and R806 (5'-GGACTACHVGGGTWTCTAAT-3') (Caporaso et al., 2011). Raw rRNA gene sequences were processed using the UPARSE pipeline (Edgar, 2013) to identify zOTUS (zero-radius operational taxonomic units). Taxonomic assignment used the naive Bayes scikit-learn classifier implemented in *QIIME2* (Caporaso et al., 2010) and the SILVA 132 database (Quast et al., 2012). Chloroplast, mitochondrial, and unclassified sequences were excluded from further analyses. The original zOTU table was normalized by rarefying the sequences of all samples to a minimum threshold of 14,000 sequences/sample, to minimize biases from differences in sampling effort in diversity analyses.

5.2.4 Taxonomic diversity assessment

Alpha diversity of interacting species in each patch was estimated using Hill numbers (Hill, 1973), a measure of diversity that varies depending on the weight given to the relative abundance of species by changing the parameter q, as seen in Equation 5.1:

$$^{q}D = \sum_{i=1}^{S} (p_i^q)^{\frac{1}{(1-q)}} \tag{5.1}$$

Here, p_i is the relative abundance of species i and S is the number of species in the community. If $q = 0$, no weight is given to species abundance and the result is equivalent to species richness. As q increases, more weight is given to abundance and thus rare species have less importance in the community, giving us insight into its diversity and evenness (Chao et al., 2014). Here, we calculated alpha taxonomic diversity for each population using Hill numbers with q values 0, 1 and 2, which have the additional advantage that they can be easily transformed into other classic diversity indices like species richness ($q = 0$), the inverse Simpson diversity index ($q = 1$) and the exponential of Shannon entropy ($q = 2$).

5.2.5 Change in community composition

To assess differences in the community of interactors above and belowground among plant species and patches, we calculated the Bray-Curtis dissimilarity between them, which takes into account the abundance of each species, and then calculated the degree of turnover and nestedness between populations using the method of Baselga (2010) as implemented in the *betapart* package (Baselga & Orme, 2012).

5.2.6 Relationship between aboveground and belowground diversity

We used Pearson's correlation index to assess the relationship between each aboveground alpha diversity metric (${}^{0}D$, ${}^{1}D$, ${}^{2}D$) and its belowground counterparts across species. The relationship between aboveground and belowground beta diversity was tested using the Mantel test on the community dissimilarity matrices.

5.2.7 Statistical analysis

First, we assessed the completeness of our sampling using the *iNEXT* package (Hsieh et al., 2020). Then, we checked for any possible confounding effects on the diversity of interacting species caused by differences in host plant density, co-occurring plant diversity and soil conditions between host plant populations (Appendix 5.B). After that, we tested the differences in taxonomic alpha diversity of above and belowground interacting species between populations S, L1, L2 and L3 using two methods. First we calculated sample-size-based rarefaction curves for each patch individually as well as the aggregated L populations of each host using the *iNEXT* package. Then, we visually compared the overlap of the 95% confidence intervals of each plant species curve, both for S against the whole L populations and S against L1, L2 and L3. We tested the differences in diversity via mixed-design ANOVA using packages *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017). We included host plant species as a random variable to account for any differences in diversity between plant species caused by factors external to population size.

To assess if community composition differed between patches, we carried out multivariate analysis of variance (PERMANOVA) using the *adonis2* function in the *vegan* package (Oksanen et al., 2019) including the host plant species as a grouping factor to control for any biases in community composition based on plant species.

5.3 Results

A total of 5,876 interactions were observed aboveground, which comprised 636 arthropod morphospecies. The average sampling completeness per population was 87.3% (SD = 5). Most visitors were identified to species (36.5%) or genus level (18.1%), while 28.5% were identified to family level and 16.4% to order level. The remaining taxa were identified to the class level. The most abundant orders were Diptera (27.3% of interactions recorded), Hymenoptera (16.9%), and Hemiptera (13.8%) (Appendix 5.C, Table 5.C.1). The belowground diversity consisted of a total of 3,691,306 million DNA sequences in roots, corresponding to 35,283 zOTUs. Average sampling completeness per population was 96.65% (SD = 1.7). Alphaproteobacteria were the most abundant bacteria group (21.29% of interactions), followed by Gammaproteobacteria (16.22%) and Bacteroidia (9.77%) (Appendix 5.C, Table 5.C.2).

5.3.1 Alpha diversity

The average aboveground arthropod richness (^0D) was 50.5 (SD = 37.27), with the highest and lowest values corresponding to *genlut* (mean = 118; SD = 9.5) and *galniv* (mean = 8.5; SD = 3.9) respectively (Fig. 5.2A).

The average zOTU richness was 5,780.71 (SD = 1,796.24) and the highest values per species were found in *rammyc* (7,701.25; SD = 550.16) while the lowest were observed in *cypcal* (2,822; SD = 1,794.74). The average ^1D, which considers the abundance of zOTUs and is better suited for comparisons between microbial communities, was 2,596.51 (SD = 1,117.16); with the highest values found in *rammyc* (3,898.11; SD = 490.19) and the lowest in *cypcal* (850.41; SD = 1,005.43).

We found no differences in aboveground species richness when comparing the rarefaction curves for S *vs* L nor S *vs* L1, L2 and L3 in most plant species, with the exception of *rammyc* where the combination of the L patches was richer (Fig. 5.2C). The comparison of zOTU rarefaction curves indicated that all patches differed in richness regardless of plant species. These results were confirmed by the mixed-effect ANOVA, which showed no statistically significant differences between patches in any of the alpha diversity metrics for q values 0, 1, and 2, except for zOTU richness (${}^{0}D$), in which small populations tended to be richer (Appendix 5.D, Table 5.D.1). Density of host plant individuals did not differ between patches of the same species ($F_{[1,17]} = 0.39$, $p = 0.54$) and it did not have a significant effect on visitor diversity (Appendix 5.B, Table 5.B.1). Although we detected statistically significant differences in co-occurring plant diversity between patches, with S patches having a higher number of species ($F_{[1,17]} = 6.51$, $p = 0.02$), it had no significant effect on any of the alpha diversity metrics of aboveground and belowground visitors (Appendix 5.B, Table 5.B.2).

5.3.2 Composition of visitor communities

Each host plant species tended to interact with a distinct community of visitors both above and belowground (Fig. 5.3). In addition, the S patches tended to have more distinct communities of visitors in comparison with the L patches irrespective of plant species with the exception of *G. lutea* for aboveground communities, and *R. myconi* in both communities (Fig. 5.3). PERMANOVA tests confirmed statistically significant differences in community composition between patches both aboveground and belowground (Appendix 5.D, Table 5.D.2). When we differentiated between the turnover and nestedness components of community composition between plant populations, we found that the species turnover accounted for the majority of the differences between S and L as a whole, with an average of 97.1% (SD = 3.8) for aboveground visitors and 93.1% (SD = 6.1) belowground. In addition, species turnover represented an average of 97.6% (SD = 3.5) of the dissimilarity between patches S, L1, L2 and L3 aboveground and 94.8% (SD = 6.3) belowground. The main differences between plant species as well as

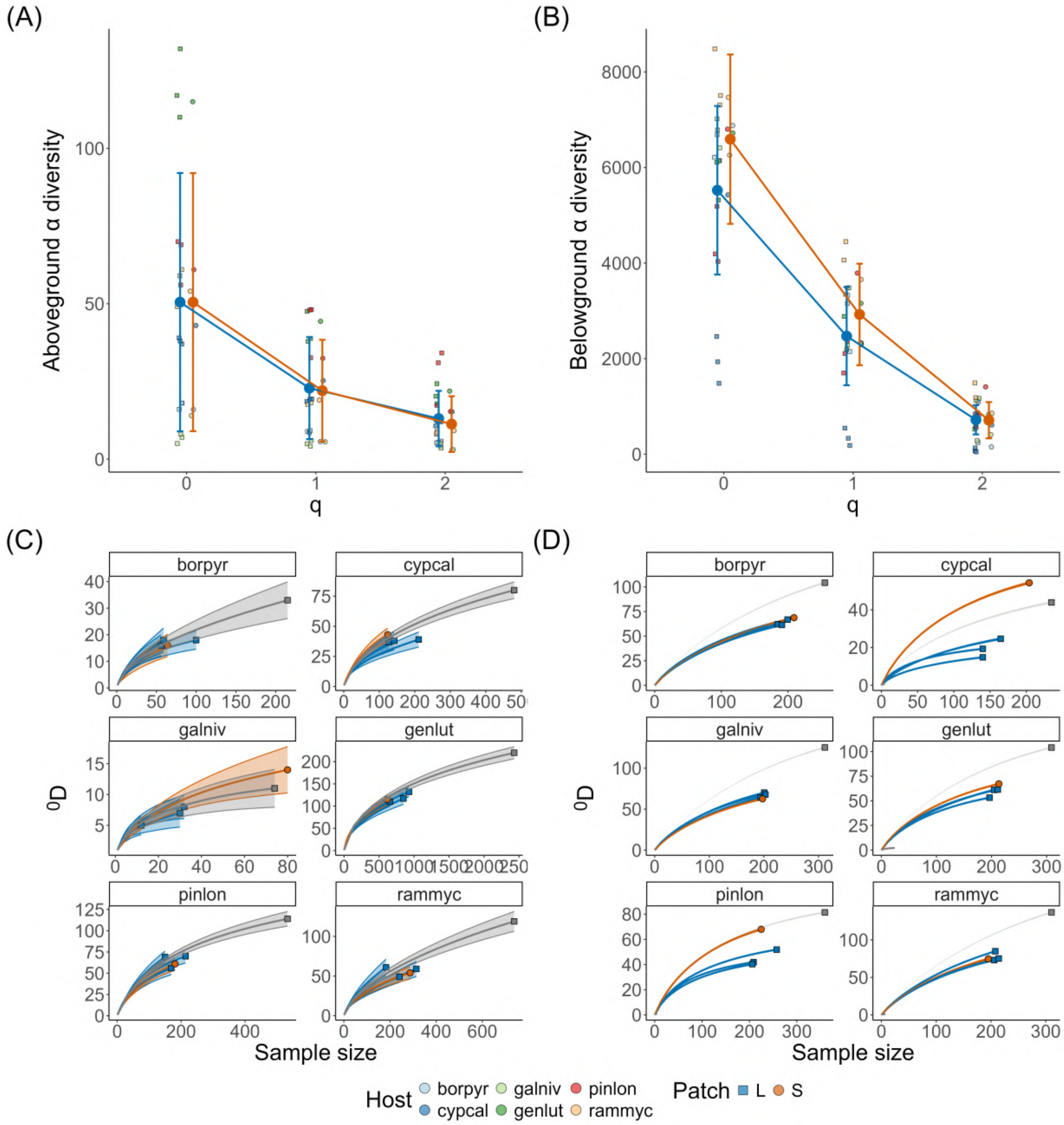

Figure 5.2: Alpha diversity of insects (A) and zOTUs (B) for Hill numbers of q = 0, 1 and 2, and host plant patch size. Individual-based rarefaction curves with their 95% CI for aboveground (C) species and belowground zOTU (D) richness (${}^0D$) in the S (orange) and L (blue for each patch and gray for the combination of them) populations of each plant species. In panels (A) and (B), orange and blue bold dots indicate the mean value and its 95% confidence interval from the GLMM for S and L plant populations, respectively. Smaller points indicate the diversity values for each population and species. Scales in panel (D) are multiplied by 0.01 for easier visualization.

between patches were related to the relative abundance of each taxa. For example, in the S populations of *B. pyrenaica* and *G. nivalis* the vast majority of the interactions corresponded to Hymenoptera and Diptera respectively (Appendix 5.C, Fig. 5.C.1), whereas the L populations tended to be more varied in composition. On the contrary, the S populations of other plant species like *P. longifolia* had a more even community of interactors in terms of the abundance of taxa they interacted with, at least at the order level. Regarding the root bacterial communities, some groups like Betaproteobacteriales, Sphingomonadales and Rhizobiales were common to all plant species, although the relative proportion of each bacterial group changed between hosts, with *C. calceolus* interacting with more diverse groups of bacteria (Appendix 5.C, Fig. 5.C.1). However, the relative abundance of major bacterial groups was similar between plant populations.

5.3.3 Correlation between aboveground and belowground diversity patterns

None of the aboveground diversity metrics showed statistically significant correlation with their belowground counterparts, and the correlation values were close to zero (Fig. 5.4). On the other hand, community composition metrics showed positive and statistically significant correlation (Fig. 5.4).

5.4 Discussion

Here, we made an in-depth characterization of the aboveground and belowground communities of organisms interacting with six plant species of conservation interest, and explored the differences in alpha and beta diversity of those communities between plant populations of different sizes. Our study plants hosted a wide community of visitors, ranging from pollinators and herbivores to many other organisms seeking shelter on

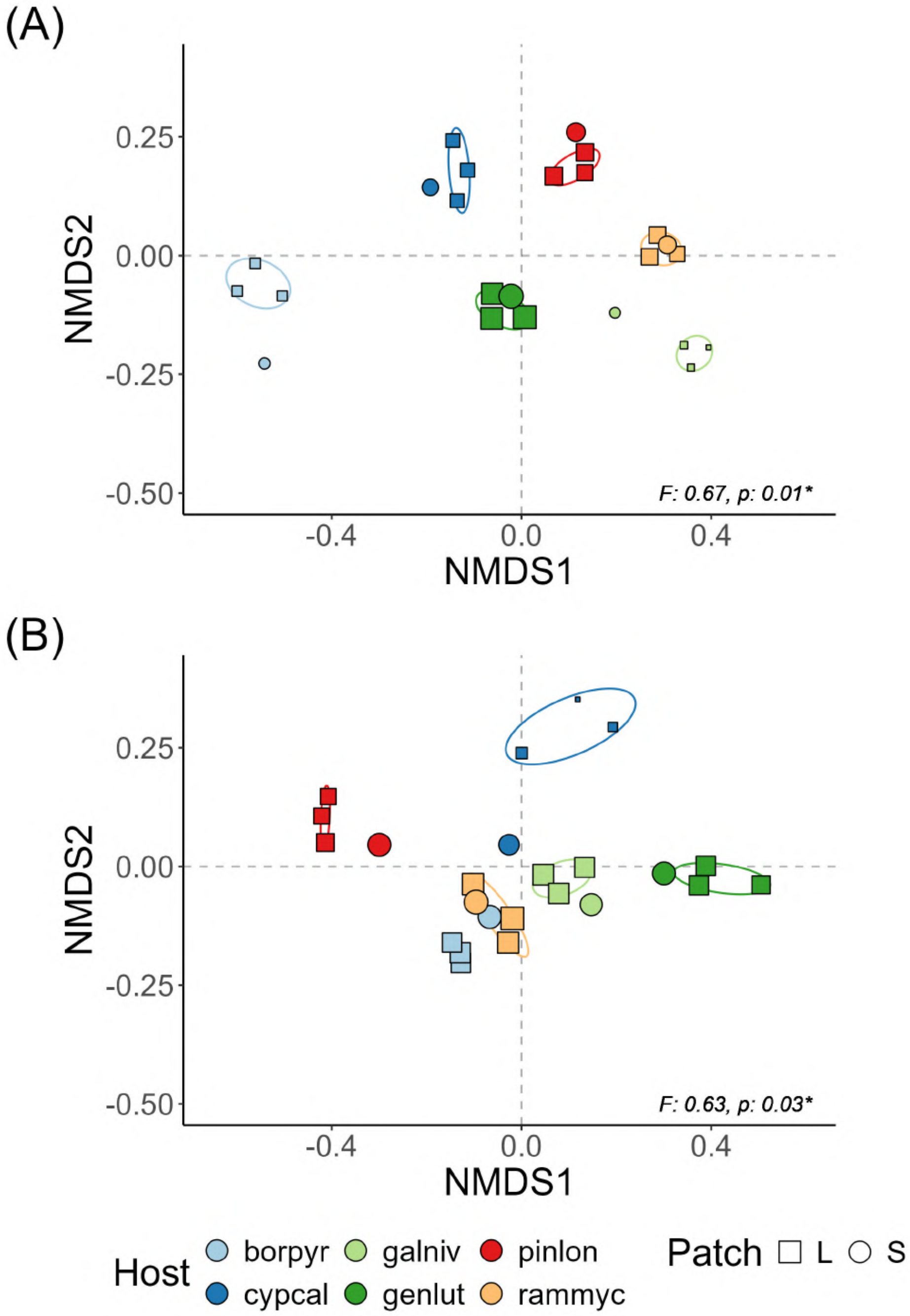

Figure 5.3: Nonmetric multidimensional scaling based on the taxonomic composition dissimilarities between each plant species' community of visitors above (A) and belowground (B). Symbol size indicates taxa richness. The F-statistic and p-value of the PERMANOVA analysis between plant patches are shown in the lower right corner of each plot. Numbers marked with an asterisk indicate statistically significant results with $\alpha = 0.05$.

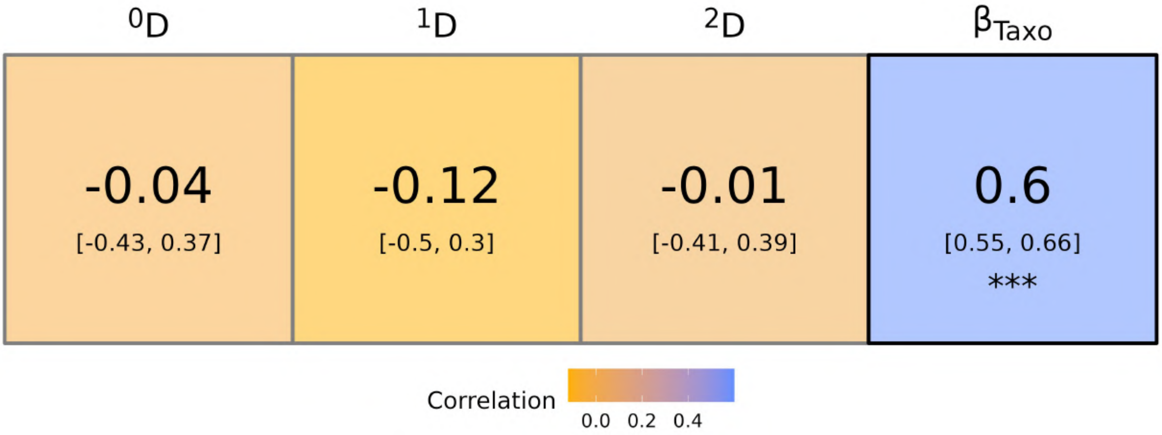

Figure 5.4: Correlation between aboveground diversity metrics and their belowground counterparts. Brackets indicate the 95% confidence interval and asterisks show statistically significant results with $\alpha = 0.05$.

the plant. Considering that similar sized patches within populations represent a kind or neighbour or "home range" of interactors, we found no major differences in species richness, Shannon and Simpson diversity between populations of different sizes, even after controlling for plant density and the diversity of co-occurring species. However, we did find differences in the composition of aboveground and belowground communities in most plant species, with small populations having more distinct communities of visitors in comparison with other patches within larger populations. We did not find any correlation between the patterns of alpha diversity above- and belowground, but we observed that community composition was positively correlated between both, with patches that resembled more one another in their aboveground visitor community also being more similar in their belowground composition.

5.4.1 Rare species as hubs for biodiversity

The diversity of visitors in most of the plant species in our study was high despite their differences in habitats of preference. The main exception was *G. nivalis*, most likely because it blooms in late winter and early spring, when visitor activity is still limited due to cold temperatures. Our results highlight the importance of rare plant species as maintainers of biodiversity in their ecosystems despite their relatively low abundance, and thus their role in preserving interactions that might be relevant to ecosystem functioning (Bracken & Low, 2012; Mouillot et al., 2013). This has potential consequences for conservation biology. Given that rare species may suffer from higher risk of extinction (K. F. Davies et al., 2004; Matthies et al., 2004), the visitor species that might benefit from those plants are susceptible to losing important resources, although the precise extent of that impact would be determined by the degree of specialization of the visitors towards the host (Aizen et al., 2012; Valiente-Banuet et al., 2015).

In this study we tried to characterize the whole universe of interactions of each plant as possible, instead of discriminating towards any specific group of organisms such as pollinators or herbivores. In doing so, we observed that rare plants do not only interact with many species that visit the plant seeking a direct benefit like the aforementioned herbivores and pollinators, but also with plenty of species displaying unknown or more subtle interactions such as using the plant as shelter, to keep their vital moisture, or lay eggs. Although these interactions might not directly benefit the host plant, they certainly play a role in supporting other species not seeking specialized resources (Valiente-Banuet et al., 2015). Thus, the loss of rare plant species may have a profound impact on many other organisms that use them and are not usually taken into consideration in studies dealing with plant-animal interactions because they are not easily observed interacting with their host plants (Jordano, 2016; Terry & Lewis, 2020).

5.4.2 Aboveground patterns of visitor diversity

We did not find any significant differences in the richness and abundance of aboveground visitors in similar sized patches between different populations for any of the host plant species. This is in line with our initial hypothesis that populations are visited by sets of species of similar diversity irrespective of total population size.

If visitors were specialized in using only certain aspects of the host, we would expect fewer and less diverse visitors in the small populations due to the lower availability of resources offered by the plant (Waser et al., 1996). The plant species in our study, although rare, offer a general set of resources (*e.g.* they do not have floral structures specialized towards specific pollinators or leaves palatable to only certain herbivores) which should not limit the diversity of interactions in small populations by attracting more generalist visitors that are not hindered by the low abundance of specific resources (Brosi, 2016).

Even though the richness and abundance of visitor species was similar between patches of different sized populations, the taxonomic composition of aboveground visitors differed. More precisely, the patches belonging to the L population resemble one another more than they did the S patch, a pattern consistent with the idea that plant patches closer in distance tend to interact with similar sets of species (Trøjelsgaard et al., 2015). These differences consisted mostly in species turnover, a pattern observed in other plant-pollinator interaction networks and habitats (Souza et al., 2021; Trøjelsgaard et al., 2015; White et al., 2022), and consistent with our previous idea that these plant species are visited by different generalist species in each patch instead of each patch being visited by a clear subset of a broader community of visitors. There are many factors that may affect the diversity and composition of aboveground visitors, like local climate, host plant density or the diversity and composition of the surrounding vegetation (Joern & Laws, 2013; Santamaría Bueno & Méndez Iglesias, 2021). Our sampling design controlled for the first factor, and neither the density of host plants nor the diversity of the plants that co-occurred with our focal plants had a significant effect on visitor richness (Appendix 5.B, Table 5.A.2). However we did find a significant positive relationship between the composition of visitors and plants accompanying them (Appendix 5.B), suggesting that species that co-occur with similar plant communities also tend to be visited by more similar sets of species (Burkle & Alarcon, 2011).

5.4.3 Belowground diversity patterns

The differences in alpha diversity of root microbial communities between patches contradict our initial expectations, based on the specificity between rhizosphere bacterial communities and the species of their plant host (Bulgarelli et al., 2013). However, we did find significant differences in the composition of said communities in each host species, with the S patches having more distinct communities than L patches between themselves. The diversity and composition of root bacterial communities depend on soil properties, root structure, composition of root exudates and health status of the host plant, and these factors impose filters that favour certain bacterial communities with specific traits and functionalities (Berendsen et al., 2012; Cordovez et al., 2019; Sasse et al., 2018). As such, plants of the same species tend to share communities with similar taxonomic diversity and composition (Goberna & Verdú, 2016). The intraspecific differences in bacterial diversity that we observed may respond to other factors such as within-species specialization of microbes towards specific genotypes in each plant patch (Eck et al., 2019; Pérez-Izquierdo et al., 2019) or differences in soil abiotic conditions that we may not have accounted for (Berg & Smalla, 2009).

5.4.4 Aboveground *vs* belowground patterns

We observed contrasting patterns between alpha diversity and community composition regardless of host plant and patch size. On the one hand, alpha diversity metrics correlated very weakly between the aerial and subterranean parts of the plants. On the other hand, community composition metrics above and belowground were positively and significantly correlated. As discussed earlier, the mechanisms shaping the diversity of communities interacting with plants differ between its aerial part (local climate and vegetation) and its roots (host plant and soil properties), although common factors may drive changes in the composition of both communities (Wardle et al., 2004). For instance, a healthy rhizosphere contributes to the good condition of its host plant, making it more attractive to potential visitors aboveground (Pineda et al., 2010). Furthermore, pathogens or herbivores can trigger defensive mechanisms in the plant that can affect the bacteria living in the roots as well as the visitors above through the release of different chemical compounds (Mithöfer & Boland, 2012; Pineda et al., 2010).Hence, any changes in the composition of aboveground arthropods could affect the microbiota in the roots and vice versa, leading to the positive correlation between dissimilarity measures that we observed (Berendsen et al., 2012; Dedeyn & Vanderputten, 2005; Heinen et al., 2018).

5.5 Conclusions

In this exhaustive study on rare plants and the diversity of arthropod and microbial visitors they interact with, we found clear and consistent patterns across all plant species analyzed. First, local species richness and abundance of visitors did not differ between plant patches aboveground, although small patches tended to have more diverse communities of root bacteria. Second, both aboveground and belowground community composition changed between patches, with most of that variation being associated with species turnover. Third, the composition of aboveground and belowground communities were positively correlated, suggesting the existence of some common underlying factors that shape them. These results add new evidence and insights on the assembly patterns of communities visiting rare and endangered plant species in populations of different sizes. In the current scenario of Global Change, in which habitats and plant populations are becoming smaller and more fragmented due to human pressures, our results shed light on the possible consequences of reduced plant populations for the community of visitors. Our study was carried out with rare plants, and it challenges the intuitive negative idea that small populations should maintain less diverse communities of visitors. emphasizing the role of small plant populations as valuable reservoirs able to sustain a large biological diversity both above and belowground.

5.6 References

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Appendix 5.A Host plant information

Table 5.A.1: Plant species in study and their abbreviation used throughout the text along with their rarity and additional information on the number of individuals, the sampling effort measured in surveys and minutes, and the number of records in each population (Taxa for aerial arthropods, and zOTU for bacteria in root tips). Rarity indicates species included in regional catalogues (RC), national catalogues (NC) and the European habitats directive (HD) as well as other criteria like being on its limit of distribution (LD), being endemic to the Pyrenees (PE), having a limited regional geographic range (RGR), being a habitat specialist (HS) and having low average local abundance (LA).

				Sampling effort		**# records (L1-L2-L3)**	
Species	**Rarity**	**Pop.**	**# ind.**	# surveys	Time	Taxa	zOTU
		S	1,000	24	480’	64	79,913
B. pyrenaica						101	59,646
borpyr	RC / PE	L	10,000	88	1,160’	56	69,825
	RGR / HS					60	68,925
		S	100	33	495’	124	32,997
C. calceolus						134	40,671
cypcal	NC / LD	L	500	110	1,650’	211	17,151
	RGR					144	23,075
		S	500	21	495’	80	65,382
G. nivalis						31	68,436
galniv	HD (V)	L	10,000	60	1,080’	33	53,131
	RGR / LA					13	28,350
		S	100	31	465’	622	67,124
G. lutea						856	68,303

genlut	HD (V)	L	1,000	91	1365’	928	74,302
						655	61,206
		S	200	23	345’	182	67,191
P. longifolia						151	42,884
pinlon	RC / PE	L	1,000	65	975’	169	80,435
	RGR / HS					214	56,202
		S	300	23	345’	289	75,217
R. myconi						189	64,282
rammyc	PE	L	5,000	69	1,035’	248	77,410
						322	74,896

Table 5.A.2: Plant species studied, the habitat of the population, the number of plant species found in inventories carried out within each patch and the approximate density of host plant individuals per square meter. Additional sampling methods include *in situ* cafeteria experiments in *B. pyrenaica* and *G. nivalis*. We also looked for dead insects on all flowers of *C. calceolus* and the sticky leaves of *P. longifolia* (1 leaf for every 45 plants). In patches of *G. lutea* we looked for fruit predators in 50 fruits per patch as well as any insects on senescent leaves (1 for every 45 plants). Finally, we sampled the underside of *R. myconi* leaves with *ex situ* Berlese funnels and *in situ* vacuuming of one leaf every 45 plants.

Name	**Pop.**	**Habitat**	**Plant Richness**	**Plant density**
B. pyrenaica	S	Alpine grassland	40	20
	L	Alpine grassland	13-15-19	19.3-18.5-12
C. calceolus	S	Mixed forest-grassland	20	0,4
	L	Mixed forest-grassland	27-21-8	1.5-0.5-0.4
G. nivalis	S	Bedrock in forest landscape	10	4,2
	L	Deciduous forest	9-10-5	154-22.4-166
G. lutea	S	Grassland	32	12
	L	Mixed forest-grassland	28-31-36	15-14-9
P. longifolia	S	Cliff	10	10
	L	Cliff	22-8-7	10-8.75-13.75
R. myconi	S	Shady vegetated rock	22	64
	L	Shady vegetated rock	19-11-22	25-10-27

Appendix 5.B Analysis of confounding factors

To rule out any possible confounding effects that may stem from local factors other than patch size we characterized the composition and diversity of plant communities co-occurring with each focal species, as well as the soil properties at each site, both of which have been observed to play a role in determining the community of species found both above and belowground. First, we tested for differences in host plant density between patches using mixed-effect ANOVA with patch as a fixed effect and host species as a random effect and found no significant differences (Fixed effect = -10.85, $F_{[1,17]} = 0.39$, $p = 0.54$). We also tested the effect of host plant density on each alpha diversity metric (^0D, ^1D, ^2D) using mixed-effect linear model with density as a fixed effect and host species as a random effect and found no statistically significant effects (Table 5.B.1). Then, we explored any possible differences in plant richness between patches using the same procedure as with host plant density. We observed that small patches had higher plant diversity than L patches (Fixed effect = 8.06, $F_{[1,17]} = 6.51$, $p = 0.02$). Thus, we tested the possible effect of plant diversity on each diversity metric of visitors both above and belowground using mixed-effect linear models with plant richness as a fixed effect and host plant species as a random effect. These models showed no statistically significant effects (Table 5.B.2). Then, we tested for differences in plant composition between host plant patches by using PERMANOVA analysis on the Bray-Curtis dissimilarity matrices of plant species composition while keeping host plant species as a grouping factor. This showed that S patches differed significantly from L patches (Fig. 5.B.1 and Table 5.B.3). We also tested the correlation between plant community and the composition of visitors above and belowground separately using a Mantel test on the dissimilarity matrices, revealing a weak but significant effect in both cases (Aboveground Mantel's $r = 0.21$, $p = 0.03$; belowground Mantel's $r = 0.11$, $p = 0.041$).

Table 5.B.1: Results of the mixed-effect models for the effect of host plant density on aboveground (AG) and belowground (BG) diversity measured with Hill numbers of q 0 to 2.

		^{0}D				**^{1}D**				**^{2}D**			
	Effect	$\boldsymbol{\beta}$	**SE**	$\boldsymbol{t}$	$\boldsymbol{p}$	$\boldsymbol{\beta}$	**SE**	$\boldsymbol{t}$	$\boldsymbol{p}$	$\boldsymbol{\beta}$	**SE**	$\boldsymbol{t}$	$\boldsymbol{p}$
AG	Density	-0.032	0.037	-0.87	0.39	-0.012	0.03	-0.39	0.70	-0.0057	0.027	-0.21	0.84
				SD				SD				SD	
	Random: Host			39.04				15.30				8.177	
BG	Density	4.31	6.26	0.69	0.49	7.36	4.28	1.72	0.10	4.19	1.96	2.13	0.044
				SD				SD				SD	
	Random: Host			1,552				844.0				228.6	

Table 5.B.2: Results of the mixed-effect models for the effect of co-occurring plant diversity on aboveground (AG) and belowground (BG) diversity measured with Hill numbers of q 0 to 2.

		^{0}D				**^{1}D**				**^{2}D**			
	Effect	β	**SE**	t	p	β	**SE**	t	p	β	**SE**	t	p
AG	Plant richness	0.16	0.17	0.95	0.35	0.099	0.14	0.71	0.48	0.055	0.13	0.44	0.66
				SD				SD				SD	
	Random: Host			38.70				15.25				8.21	
BG	Plant richness	23.08	28.74	0.80	0.43	-9.77	20.88	-0.47	0.64	-12.23	9.33	-1.31	0.20
			Varance	SD				SD				SD	
	Random: Host			1,644.7				920.5				225.6	

Table 5.B.3: PERMANOVA table for the differences in plant community composition between plant patches.

Variable	**DF**	**Sum Sq**	**R2**	***F***	**Pr (>*F*)**
Patch	1	0.33	0.04	0.81	0.0048
Residual	22	9.11	0.96		
Total	23	9.44	1		

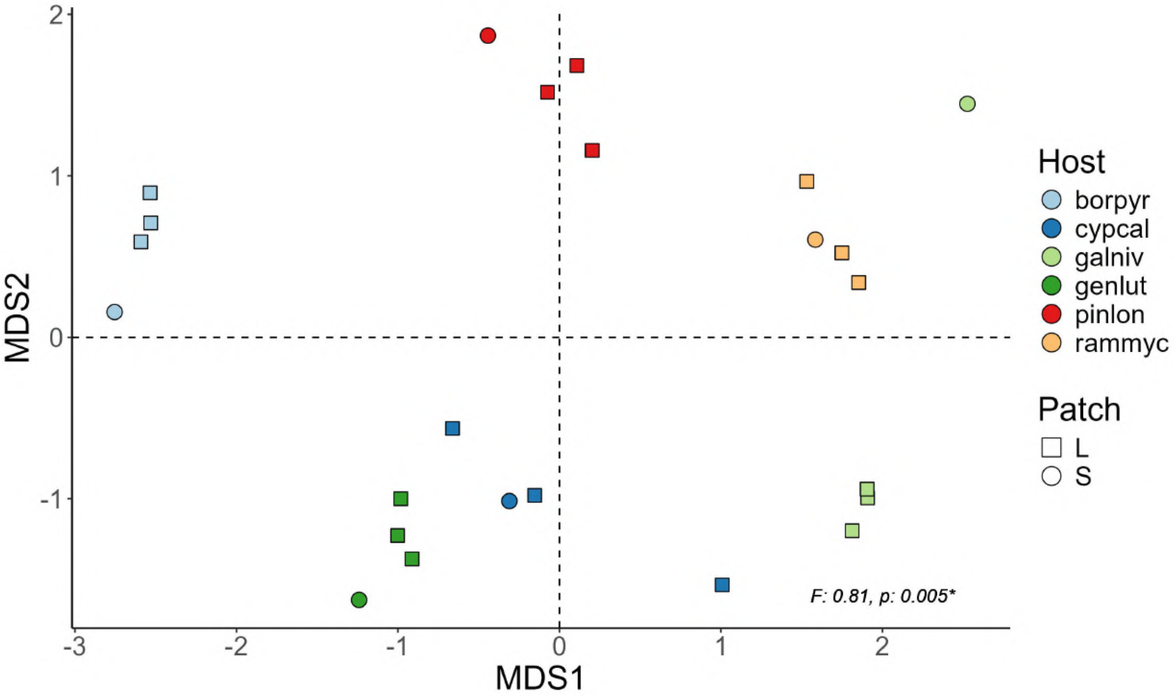


Figure 5.B.1: NMDS according to the Bray-Curtis dissimilarity between plant populations based on the community of plants they co-occur with. The F statistic and the $p - value$ of the PERMANOVA are shown at the lower right.

Regarding soil characteristics, first we tested if there were differences between each site by using PERMANOVA analysis on an Euclidean dissimilarity matrix based on 10 soil properties: pH, conductivity, % of nitrogen, % of carbon, % of phosphorus, % of organic matter content and proportion of sand (2,000-50 µm), coarse silt (50-20 µm), fine silt (20-2 µm) and clay (<2 µm) particles (Fig. 5.B.2 and Table 5.B.4). Following the same procedure as in previous analyses, we kept host plant species as a grouping factor in the permutations. Then we assessed the relationship between soil properties and rhizosphere community composition using the Mantel test on the Euclidean dissimilarity matrix for soil properties and the Bray-Curtis dissimilarity matrix for microbial community composition. The test showed very weak but statistically significant correlation (Mantel's $r = 0.10$, $p = 0.161$). All analyses listed above were done using the *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017) packages for the mixed effects models and the *vegan* (Oksanen et al., 2019) package for the PERMANOVA and Mantel tests.

Table 5.B.4: PERMANOVA table for the differences in soil conditions between plant patches.

Variable	**DF**	**Sum Sq**	**R2**	***F***	**Pr (>*F*)**
Patch	1	10.44	0.027	0.60	0.34
Residual	22	380.56	0.973		
Total	23	391.00	1		

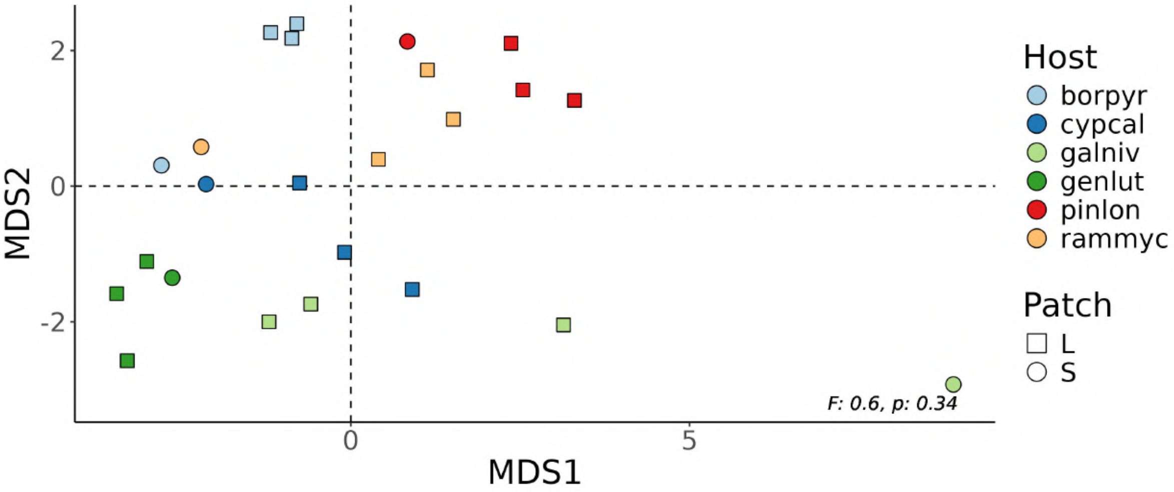


Figure 5.B.2: NMDS according to the Euclidean distances between host plant populations based on their soil conditions. The F statistic and the $p - value$ of the PERMANOVA are shown at the lower right.

Appendix 5.C Additional diversity information

Table 5.C.1: Total number and proportion (P) of aboveground interactions and morphospecies per order.

Order	**# int.**	***P* int.**	**# Morphosp.**	***P* Morphosp.**
Diptera	1,602	26.92	134	19.42
Hymenoptera	994	16.7	93	13.48
Hemiptera	826	13.88	79	11.45
Sarcoptiformes	638	10.72	47	6.81
Coleoptera	510	8.57	65	9.42
Araneae	283	4.75	63	9.13
Poduromorpha	188	3.16	11	1.59
Entomobryomorpha	187	3.14	25	3.62
Lepidoptera	169	2.84	54	7.83
Trombidiformes	155	2.6	23	3.33
Orthoptera	96	1.61	15	2.17
Symphypleona	75	1.26	9	1.3
Thysanoptera	68	1.14	20	2.9
Mesostigmata	45	0.76	10	1.45
Stylommatophora	27	0.45	7	1.01
Psocodea	15	0.25	8	1.16
Pulmonata	11	0.18	3	0.43
Architaenioglossa	9	0.15	2	0.29
Archaeognatha	9	0.15	1	0.14
Dermaptera	9	0.15	1	0.14
Neuroptera	8	0.13	2	0.29

Pseudoscorpiones	5	0.08	1	0.14
Opiliones	2	0.03	1	0.14
Ephemeroptera	1	0.02	1	0.14
Julida	1	0.02	1	0.14
Mecoptera	1	0.02	1	0.14
Polyxenida	1	0.02	1	0.14

Table 5.C.2: Number and proportion (P) of belowground interactions per microbial taxonomic group based on the average number of sequences detected.

Phylum	**Class**	**# int.**	***P* int.**	**# zOTU**	***P* zOTU**
Proteobacteria	Alphaproteobacteria	772,458	21.29	3,989	11.31
Proteobacteria	Gammaproteobacteria	588,608	16.22	2,483	7.04
Bacteroidetes	Bacteroidia	354,305	9.77	3,418	9.69
Actinobacteria	Actinobacteria	288,464	7.95	1,315	3.73
Verrucomicrobia	Verrucomicrobiae	235,011	6.48	2,198	6.23
Planctomycetes	Planctomycetacia	179,380	4.94	3,917	11.1
Proteobacteria	Deltaproteobacteria	157,479	4.34	2,417	6.85
Acidobacteria	Subgr. 6	150,428	4.15	1,088	3.08
		145,754	4.02	3,506	9.94
Actinobacteria	Thermoleophilia	126,028	3.47	1346	3.81
Acidobacteria	Blastocatellia (Subgr. 4)	97,076	2.68	771	2.19
Acidobacteria	Acidobacteriia	58,208	1.6	997	2.83
Chloroflexi	Anaerolineae	53,818	1.48	412	1.17
Firmicutes	Bacilli	42,445	1.17	173	0.49
Chloroflexi	Chloroflexia	35,672	0.98	451	1.28
Planctomycetes	Phycisphaerae	33,857	0.93	1078	3.06
Actinobacteria	Acidimicrobiia	31,408	0.87	534	1.51
Chloroflexi	KD4-96	28,364	0.78	166	0.47
Gemmatimonadetes	Gemmatimonadetes	27,290	0.75	563	1.6
Acidobacteria	Thermoanaerobaculia	19,305	0.53	192	0.54
Cyanobacteria	Oxyphotobacteria	16,788	0.46	289	0.82

Acidobacteria	Subgr. 17	15,158	0.42	169	0.48
Thaumarchaeota	Nitrososphaeria	13,302	0.37	48	0.14
Proteobacteria		11,444	0.32	341	0.97
Acidobacteria	Holophagae	11,390	0.31	184	0.52
Chloroflexi	TK10	7,918	0.22	140	0.4
Rokubacteria	NC10	7,403	0.2	83	0.24
Actinobacteria	MB-A2-108	6,524	0.18	105	0.3
Chloroflexi	Ktedonobacteria	6,610	0.18	171	0.48
Chloroflexi	Dehalococcoidia	6,093	0.17	107	0.3
Latescibacteria		6,012	0.17	203	0.58
Actinobacteria		5,788	0.16	105	0.3
Armatimonadetes	Fimbriimonadia	5,680	0.16	109	0.31
Actinobacteria	Rubrobacteria	5,371	0.15	55	0.16
Nitrospirae	Nitrospira	5,479	0.15	51	0.14
Planctomycetes	OM190	5,429	0.15	160	0.45
Bacteroidetes	Ignavibacteria	5,192	0.14	131	0.37
Armatimonadetes	Armatimonadia	4,621	0.13	52	0.15
Entotheonellaeota	Entotheonellia	4,724	0.13	90	0.26
Chloroflexi	Gitt-GS-136	3,721	0.1	40	0.11
Cyanobacteria	Melainabacteria	3,604	0.1	81	0.23
Acidobacteria	Subgr. 25	2,946	0.08	61	0.17
Acidobacteria	Subgr. 22	2,631	0.07	114	0.32
Firmicutes	Clostridia	2,555	0.07	45	0.13
Acidobacteria	Subgr. 5	2,289	0.06	98	0.28
Gemmatimonadetes	Longimicrobia	2,023	0.06	55	0.16
Chloroflexi	JG30-KF-CM66	1,654	0.05	49	0.14

Chloroflexi	OLB14	1,751	0.05	32	0.09
Dependentiae	Babeliae	1,969	0.05	95	0.27
Elusimicrobia	Lineage IIa	1,873	0.05	108	0.31
Armatimonadetes	Chthonomonadetes	1,457	0.04	50	0.14
Chloroflexi		1,569	0.04	17	0.05
Deinococcus-Thermus	Deinococci	1,313	0.04	4	0.01
Elusimicrobia	Lineage IIb	1,507	0.04	73	0.21
Fibrobacteres	Fibrobacteria	1,339	0.04	45	0.13
Patescibacteria	Saccharimonadia	1,528	0.04	40	0.11
Gemmatimonadetes	S0134 terrestrial gr.	976	0.03	40	0.11
Acidobacteria	AT-s3-28	761	0.02	23	0.07
Acidobacteria	Subgr. 11	885	0.02	16	0.05
Actinobacteria	0319-7L14	816	0.02	30	0.09
Armatimonadetes	uncultured	846	0.02	41	0.12
Chlamydiae	Chlamydiae	549	0.02	23	0.07
FBP	uncultured bacterium	769	0.02	24	0.07
Planctomycetes	Pla4 lineage	884	0.02	55	0.16
Planctomycetes	vadinHA49	807	0.02	26	0.07
Planctomycetes		573	0.02	27	0.08
Acidobacteria	Subgr. 18	261	0.01	9	0.03
Acidobacteria	Subgr. 9	333	0.01	4	0.01
Acidobacteria		200	0.01	10	0.03
Bacteroidetes	Rhodothermia	384	0.01	13	0.04
Chloroflexi	AD3	285	0.01	15	0.04
Cyanobacteria	Sericytochromatia	207	0.01	9	0.03
Elusimicrobia	Elusimicrobia	444	0.01	16	0.05

FBP		517	0.01	24	0.07
Firmicutes	Erysipelotrichia	191	0.01	2	0.01
Gemmatimonadetes	AKAU4049	506	0.01	11	0.03
Gemmatimonadetes	BD2-11 terrestrial gr.	240	0.01	22	0.06
Planctomycetes	BD7-11	471	0.01	23	0.07
Planctomycetes	Pla3 lineage	210	0.01	10	0.03
Spirochaetes	Leptospirae	349	0.01	6	0.02
Spirochaetes	Spirochaetia	300	0.01	12	0.03
WS2	uncultured soil bacterium	185	0.01	7	0.02
Zixibacteria		231	0.01	8	0.02
Euryarchaeota	Thermoplasmata	59	0	3	0.01
Euryarchaeota		14	0	2	0.01
Nanoarchaeaeota	Woesearchaeia	20	0	1	0
Acidobacteria	Subgr. 15	59	0	8	0.02
Acidobacteria	Subgr. 19	4	0	1	0
Acidobacteria	Subgr. 20	59	0	5	0.01
Actinobacteria	Coriobacteriia	21	0	2	0.01
Actinobacteria	Nitriliruptoria	177	0	6	0.02
BRC1	metagenome	55	0	2	0.01
BRC1	uncultured Acidobacteria	44	0	2	0.01
BRC1	uncultured BRC1 bacterium	28	0	1	0
BRC1		72	0	7	0.02
Bacteroidetes		144	0	6	0.02

Chloroflexi	P2-11E	76	0	5	0.01
Chloroflexi	SHA-26	16	0	1	0
Cyanobacteria		27	0	3	0.01
Dadabacteria	Dadabacteriia	26	0	1	0
Elusimicrobia	Lineage IIc	90	0	6	0.02
Elusimicrobia		14	0	1	0
FBP	metagenome	15	0	2	0.01
FBP	uncultured soil bacterium	107	0	6	0.02
FCPU426	metagenome	92	0	2	0.01
Fibrobacteres	Chitinivibrionia	142	0	3	0.01
Firmicutes	Negativicutes	65	0	4	0.01
GAL15	uncultured bacterium	150	0	5	0.01
Hydrogenedentes	Hydrogenedentia	88	0	3	0.01
Kiritimatiellaeota	Kiritimatiellae	47	0	3	0.01
Latescibacteria	Latescibacteria	163	0	3	0.01
Latescibacteria	metagenome	10	0	1	0
Latescibacteria	uncultured Fibrobacteres	30	0	1	0
Latescibacteria	uncultured Pelobacter sp.	134	0	8	0.02
Latescibacteria	uncultured soil bacterium	26	0	2	0.01
Nitrospirae	4-29-1	5	0	1	0
Omnitrophicaeota	Omnitrophia	63	0	3	0.01
Patescibacteria	Gracilibacteria	126	0	3	0.01

Patescibacteria	Microgenomatia	47	0	3	0.01
Patescibacteria	Parcubacteria	119	0	11	0.03
WPS-2	metagenome	29	0	2	0.01
WPS-2	uncultured bacterium	176	0	24	0.07
WPS-2		39	0	2	0.01
WS2		73	0	5	0.01
Zixibacteria	uncultured bacterium	94	0	3	0.01

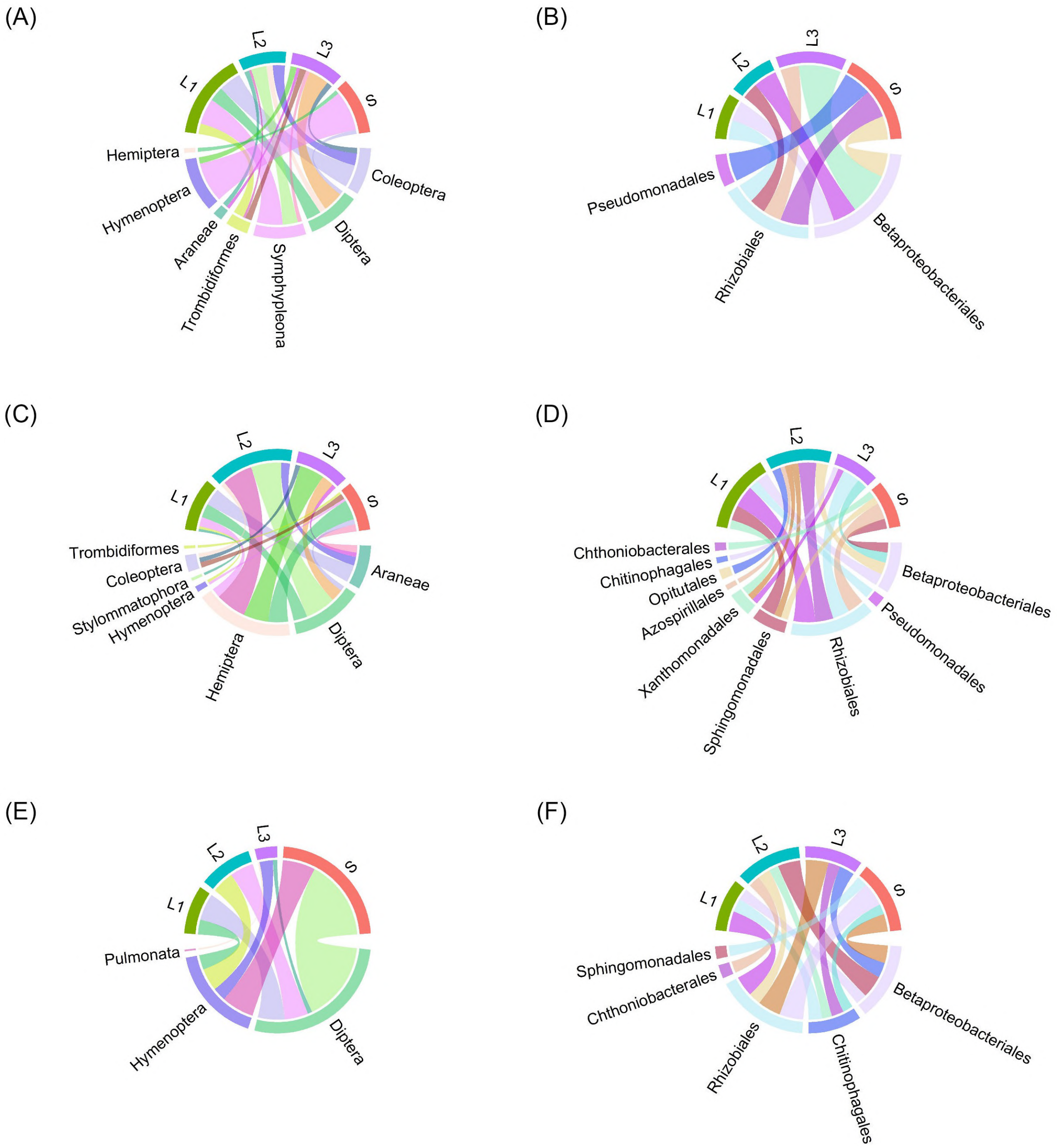


Figure 5.C.1: Chord diagrams depipcting the abundance of interactions for the top 10% most common orders of arthropods (left column) and zOTUs (right column) found in each patch aboveground and belowground respectively for *borpyr* (A, B), *cypcal* (C, D), *galniv* (E, F), *genlut* (G, H), *pinlon* (I, J) and *rammyc* (K, L).

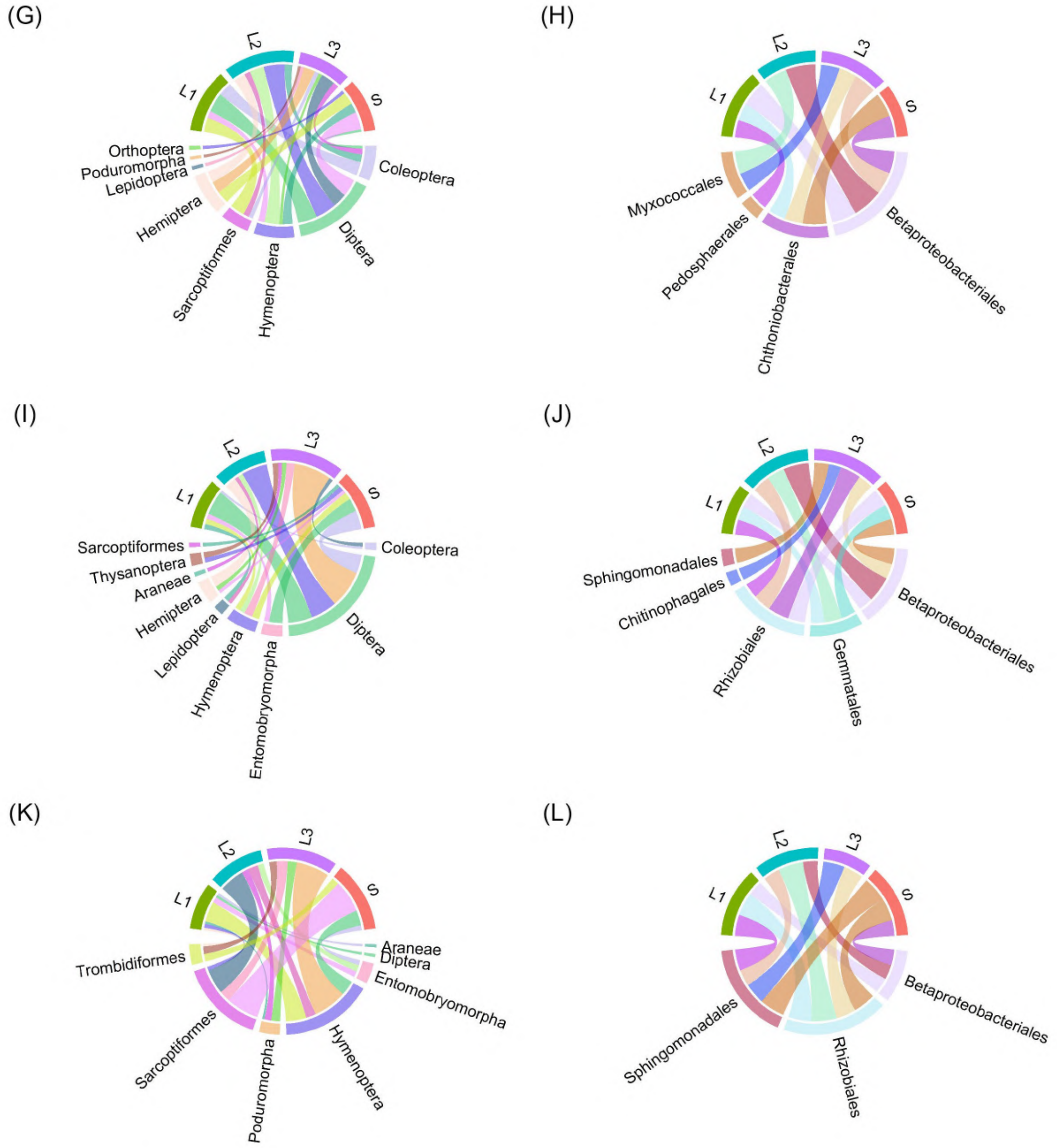


Figure 5.C.1 (cont.): Chord diagrams depipcting the abundance of interactions for the top 10% most common orders of arthropods (left column) and zOTUs (right column) found in each patch aboveground and belowground respectively for *borpyr* (A, B), *cypcal* (C, D), *galniv* (E, F), *genlut* (G, H), *pinlon* (I, J) and *rammyc* (K, L).

Appendix 5.D Statistical analyses results

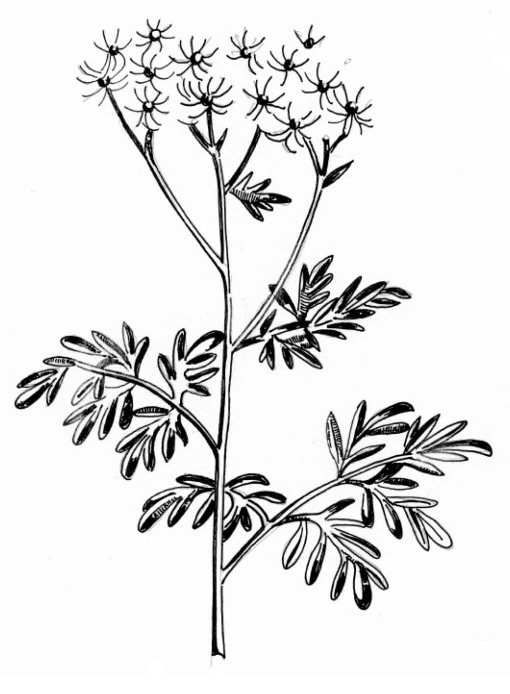
Table 5.D.1: Results of the mixed-effect ANOVA on different alpha diversity metrics of aboveground (AG) and belowground (BG) visitor communities. Bold face indicates statistically significant differences with $\alpha = 0.05$.

Location	***q***	**Sum Sq**	**DFinter**	**DFintra**	***F***	**Pr (>*F*)**
AG	0	0	1	17	0	1
	1	3	1	17	0.14	0.71
	2	14.2	1	17	0.81	0.38
BG	**0**	**5,146,167**	**1**	**17**	**7.40**	**0.014***
	1	929,558	1	17	1.91	0.18
	2	304.4	1	17	0.0021	0.96

Table 5.D.2: Results of the PERMANOVA analysis on dissimilarity metrics for community composition above (AG) and belowground (BG). Bold face indicates statistically significant effects with $\alpha = 0.05$

Location	**Variable**	**DF**	**Sum Sq**	**R2**	***F***	**Pr (>*F*)**
AG	**Patch**	**1**	**0.28**	**0.03**	**0.67**	**0.01***
	Residual	**22**	**9.33**	**0.97**		
	Total	**23**	**9.61**	**1.00**		
BG	**Patch**	**1**	**0.18**	**0.03**	**0.63**	**0.03***
	Residual	**22**	**6.43**	**0.97**		
	Total	**23**	**6.62**	**1.00**		

6 General discussion



In this study we have explored the patterns of distribution and phylogenetic relatedness of rare plant species in heterogeneous landscapes, as well as their population trends and interactions with other organisms. Our integrative approach of rarity covered components of community ecology, population biology and biological interactions, in order to provide a sound conclusion on the conservation biology of rare plants, their role for biodiversity structure around them, and their overall population stability.

We found that rare plant species in the Pyrenees tend to accumulate in certain habitats, namely rocky cliffs, screes and aquatic areas; and that these species had a disproportionate contribution to those habitats' taxonomic and phylogenetic diversity (Chapter 1). These results are in line with previous work on the distribution of rare plants in the Pyrenees by Gómez, Lorda, et al. (2017) and are also congruent with our own analysis on the phylogenetic patterns of rarity in the Pyrenean flora (Chapter 2), which showed that two types of rare plants, locally rare and habitat specialists, tended to be phylogenetically close. Both results indicate that the loss of rare species would have a disproportionate impact on the taxonomic and phylogenetic diversity of the habitats in which they appear and for the phylogenetic diversity of the Pyrenees as a whole. This is particularly noticeable for mountain wetlands, mires and bogs and wet grasslands, which are already considered as vulnerable by the European Union. In Chapter 3 we explored the population trends of more than one hundred populations of different plant species in Aragón, which spanned a wide environmental gradient and included both rare, vulnerable and common species. We found that most plant populations under surveillance had very stable population sizes and trends, and that this pattern was even reinforced when we included estimates of observation error into our analyses. Finally, we explored the role of six rare pyrenean plant species as supporters of other organisms visiting their aerial and underground parts, with a particular interest on the population size of the host (Chapter 4). We found that these plants are visited by a wide variety of organisms, and that the diversity of the community of visitors is similar between patches of the same plant despite their different sizes, although the composition of the visitors changes between them.

Overall, this work highlights the importance of rare plant species as a fundamental part of the diversity and functioning of their ecosystems, a pattern that has been shaped by historical and evolutionary processes in the region. Although the population trends of these species are mostly stable, some of them have small population sizes, which makes them far more vulnerable to sudden perturbations and changes in their environment. Since small populations of rare plants are able to sustain a big amount of diversity, their hypothetical disappearance would have an important impact on the diversity and function of the ecosystems they inhabit.

6.1 Vulnerable species accumulate in vulnerable habitats

The consequences of Global Change may differ between organisms and habitats based on their particular characteristics. Thus, although all organisms may be susceptible to decline and extinction due to sudden changes or perturbations in their environment, some species are more prone to disappearing than others (Pacifici et al., 2015). However, assessing this vulnerability can be a daunting task, as there are a plethora of factors involved in how a species might respond to any perturbation. These include intrinsic factors like population size, demographic rates, competitive ability with other species (González-Suárez et al., 2013; Pacifici et al., 2015); and external factors like the nature of the perturbation itself (*e.g.* climate change or habitat degradation) as well as its strength, frequency or spatial extent (K. Wilson et al., 2005). Although rarity has puzzled ecologists for a long time, it is difficult to deny that it suggests an a prior

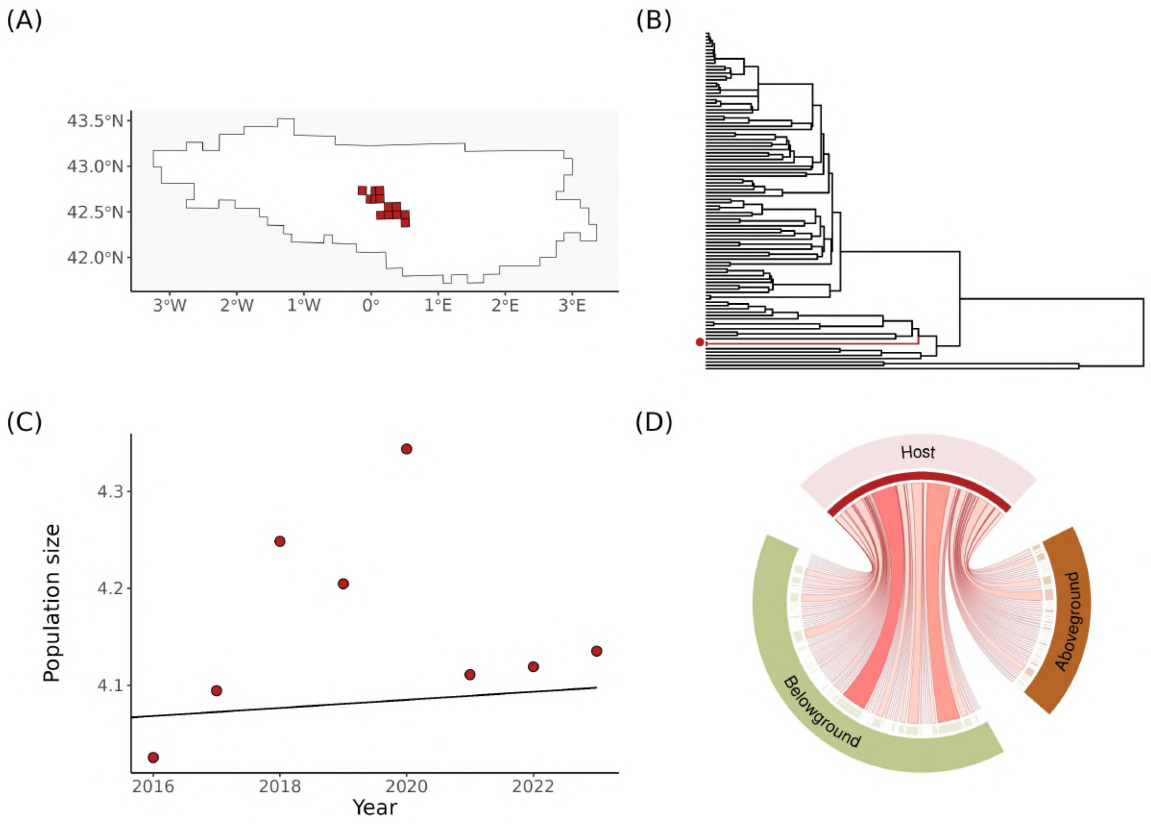


Figure 6.1: A paradigmatic example of the complex idiosyncrasies of rarity. *Borderea pyrenaica* is endemic to the Pyrenees, lives in rocky soils at high altitudes, has a restricted distribution (A), belongs to a relict genus (B) but has stable populations (C) and supports a wide range of interactions above and below-ground (D).

disposition for disappearance (Gaston, 1998). Thus, species with limited geographical ranges or habitat specialists are more prone to extinction should any strong perturbation occur within their distribution limits or affect those habitats (Hartley & Kunin, 2003; Schemske et al., 1994). In turn, species with smaller populations could be less capable of buffering the negative effects of changes in their environment or in the variability of their vital rates, opening the possibility of chaining several “bad” years in a row that might take that population to extinction (Gabriel & Bürger, 1992).

Considering this increased risk of decline of rare species, we can extend this framework beyond individual species to address the vulnerability of habitats, as those with a higher proportion of rare species would be in increased danger of losing important parts of their diversity (Gauthier et al., 2013). This is of particular interest if we take into consideration that rare species often have disproportionate contributions to ecosystem functioning (Jain et al., 2014; Lyons et al., 2005; Mouillot et al., 2013) and phylogenetic diversity (Mi et al., 2012). Our study in the Pyrenean range demonstrated that rare plant species are more prevalent in rare habitats like rocky cliffs and screes, aquatic habitats like lakes and mires, and tall forb stands. This was no surprise, as some of the factors that determine the rarity of those species, namely their geographic distribution, are intrinsically linked with the distribution of their habitats and thus rare species would be more prevalent in rare habitats (Slatyer et al., 2013). In addition, the relative contribution of each type of rarity to the diversity of their communities differed between habitats, with regionally scarce species and habitat specialists being the major type of rare taxa in lakes and mires respectively, while rocky habitats and forbs had a more balanced proportion between all types of rare species. It is noteworthy that in all habitat types species with low local abundances contributed the least to the diversity of their communities, suggesting that rare species tend to be abundant within their communities (see also Boulangeat et al., 2012 and Lesica et al., 2006). Our overall results partially reflect other assessments of the distribution of rare plant species in the Pyrenees by Gómez, García, et al. (2017), who found the largest accumulation of rare species in grasslands, wetlands and rocky habitats, although they used different criteria for rarity. These patterns are not unique to the Pyrenees and mimic the findings of other authors in different temperate mountain ranges such as the European Alps (Boulangeat et al., 2012) and the Rocky Mountains (Lesica et al., 2006). There, habitat specialists and species with restricted geographical ranges were more present in harsh alpine environments and wetlands, and, similarly to our results, those rare species were abundant in their communities.

As previously stated, the vulnerability of a species depends not only on intrinsic factors but is also heavily influenced by the characteristics of the external perturbations that might occur. Habitats, just as organisms, may be affected differently by changes in their environmental conditions (Eigenbrod et al., 2015; Gauthier et al., 2013). Since habitat degradation often precedes diversity loss (Brooks et al., 2002; Chase et al., 2020), rare species located in habitats more vulnerable to external threats would also be in increased danger. To assess the vulnerability of the habitats of the Pyrenees we used the Red List of European Habitats, a readily available description of the threats and vulnerabilities of Europe's natural habitats (Janssen et al., 2016). According to this classification, freshwater ecosystems in alpine and mountain regions along with mires and bogs are vulnerable to external threats like climate change or the modification of their hydric regime (Janssen et al., 2016; Salimi et al., 2021). Recent studies in the Pyrenees have already observed changes in the amount of precipitation, primarily snowfall, during the last fifty years (López-Moreno & García-Ruiz, 2004; López-Moreno et al., 2008), along with an increase in evapotranspiration in the region (Clavera-Gispert et al., 2023; Vicente-Serrano et al., 2021). These changes might affect the water regimen of mountain wetlands, putting at risk not only those delicate habitats but also the rich community of rare species that inhabit them and which contribute greatly to the taxonomic and phylogenetic diversity of those areas. Other habitats like rocky cliffs and screes in the Pyrenees also harbor a high proportion of rare and phylogenetically diverse species (Chapter 1). However, they are also very stable through time and have a low risk of disappearing, sometimes even acting as climatic refugia that allow the persistence of relict species (Buschke et al., 2020; García et al., 2020). Thus, although they may contain species that are highly vulnerable to environmental changes or the destruction of their habitat, the likelihood of any perturbation reaching these communities is relatively low (Buschke et al., 2020; Fitzsimons & Michael, 2017). Pyrenean forests also host many rare species but face a more complex situation (Ninot et al., 2017). On the one hand, the decrease in human pressures such as logging for firewood and land clearing for pastures have favored the expansion of forests, which have reclaimed some of their past areas of distribution (Améztegui et al., 2010; García-Ruiz et al., 2015). But on the other hand, increased temperatures and more severe drought periods caused by climate change are forcing changes in the distribution, demography and composition of forest plant communities (Améztegui et al., 2010; Batllori & Gutiérrez, 2008; Camarero et al., 2011). The consequences of those changes in treeline dynamics also affect other habitats, particularly the semi-natural grasslands of the Pyrenees (Pardo et al., 2013). According to our assessment, they contain a relatively low proportion of rare species (but see Gómez, García, et al., 2017) and thus we would consider them as being at low risk of diversity loss. However, some of those man-made grasslands, especially those located below the treeline that were historically kept free of woody vegetation by human activities, are susceptible to the colonization and expansion of shrubs and trees, which are reducing the extension of grassland communities (Barrio et al., 2013; Mottet et al., 2006; Ninot et al., 2017). Therefore, these habitats may suffer from deep changes in the diversity and composition of their communities even if the species affected are not considered vulnerable themselves.

6.2 Phylogenetic patterns of rarity in the Pyrenean flora

In order to explain the patterns of phylogenetic diversity observed in Chapter 1 it is necessary to assess the phylogenetic relationships between rare plant species of the Pyrenees. Rarity depends heavily on the context in which it is assessed, but some of the traits that determine it tend to be preserved during the evolutionary process, or at least reflect the past histories of taxa (Gaston, 1994; Holt, 1997). The dispersal abilities of a species, their specificity to certain environmental conditions or life history traits tend to be similar between closely related species and are also determinants of the rarity of a species (Murray et al., 2002). Thus, closely related species should share some kind of rareness, being similarly rare in either the size of their geographic range, their habitat specificity or their local abundance (Losos, 2008).In chapter 2 we found that at a phylogeny-wide scale all rarity types had relatively low phylogenetic signal in the flora of the Pyrenees. However, an analysis at the tips of the phylogeny revealed clusters of highly related rare species in the tips of the phylogeny, especially for endemics, species with limited regional distribution and habitat specialists. Locally scarce species, on the other hand, were more evenly distributed throughout the phylogeny. The removal of rare species from the phylogeny indicated that habitat specialists, followed by species with low local abundance, made a disproportionate contribution to the phylogenetic diversity of the Pyrenean flora. As expected, threatened species according to the Red List of the Pyrenean vascular flora tend to be rare, with a narrow regional distribution, high specialization and low local abundances, although this might be a reflection of the typical criteria used in the Red List: reduced spatial distribution.

Disentangling the evolutionary mechanisms behind rarity is, however, a complex and difficult task because these mechanisms may differ between rarity types. For instance, the diversification history of the Pyrenean flora plays an important role in explaining the lack of any significant phylogenetic patterns in endemicity. On the one hand, many of the endemic plants included in our studies are relatively young in evolutionary terms, having diverged from their main lineages during the Late Miocene and Early Pliocene (Ninot et al., 2017). This includes species in genera *Petrocoptis* (Cires & Prieto, 2015), *Androsace* (Boucher et al., 2016), *Saxifraga* (Vargas et al., 2018), *Borderea* (Viruel et al., 2016) and *Campanula* (Roquet et al., 2021). Due to their recent diversification, species in these genera represent short branches of the phylogeny and hence a small proportion of the total phylogenetic diversity in the region. On the other hand, other endemic species with significant phylogenetic association (Table 3.B.1) like *Ramonda myconi* (Petrova et al., 2015), *Aegonychon gastonii* (Chacón et al., 2019), *Glandora oleifolia* (Del Hoyo et al., 2012) and *Onosma bubanii* (Weigend et al., 2009) evolved during the Mid Miocene around 13M aand thus represent a higher amount of phylogenetic diversity than other endemics, but because they conform a small fraction of all the species in the tree, they exert a weak influence on the overall phylogenetic patterns of endemicity. The influence of those longer branches is, however, noticed at finer scales, where those species show significant association in their rarity near the tips of the phylogeny, whereas younger genera with high endemicity do not show any statistically significant phylogenetic patterns (Chapter 2). Thus, the lack of phylogenetic signal in endemicity and small contribution to phylogenetic diversity made by endemic species observed in chapter 2 is likely a consequence of the mixed opposing influences of shorter branches in the phylogeny represented by younger species and also longer branches of relict taxa.

Likewise, the patterns of phylogenetic association between species with restricted distribution in the Pyrenees are likely determined by past evolutionary and ecological processes (Jones et al., 2005). On the one hand, recently diverged species, such as the aforementioned endemic species, tend to have narrow distribution ranges because they have not had enough time to disperse beyond their original distributions (Pigot et al., 2012). Thus, genera with many young species would show significant phylogenetic signal given their closeness and limited range, which can be easily appreciated in the presence of clusters in the phylogeny of species with small ranges along with the lower than expected contribution of these species to the phylogenetic diversity of the Pyrenees (Chapter 2, Fig. 3.1). On the other hand, older species that were once widespread in the region may have been relegated to their present-day distribution by past changes in environmental conditions, like the cycles of glaciation and deglaciation, occupying the last remnants of suitable habitat for them (Kadereit et al., 2004; Ninot et al., 2017). However, very few Pyrenean plant species located in longer branches of the phylogeny had small geographic ranges and significant phylogenetic association, indicating low support for this hypothesis (Chapter 2, Fig. 3.2).

Another important factor influencing the width of the distribution range of species is their degree of specialization to certain habitats, as the distribution of the adequate environmental conditions for that species will determine the disposition in the region (Slatyer et al., 2013). In our case, the vast majority of habitat specialists with significant phylogenetic association were species with a strong preference for aquatic habitats, and formed several but clear clusters within the phylogeny. This pattern mirrors the apparition of water related adaptations in angiosperms as a whole, which emerged several times in their evolutionary history (Cook, 1996). It was surprising, however, that other highly specialized plants like those adapted to living in rocky cliffs, outcrops and screes did not show any significant phylogenetic pattern. We expected that species adapted to life in such limiting environments would be clustered within clades, as seen in orders with many rock-dwelling species such as Saxifragales (De Casas et al., 2016; Folk et al., 2021), and thus would have significant phylogenetic aggregation. However our results indicate that plant species in the Pyrenees specialized in rocky habitats are not exclusively concentrated in particular clades and instead are dispersed throughout the phylogeny. This suggests that the adaptations that permit life in such environments have appeared multiple times within clades that are not exclusively adapted to those habitats, with only a few species being able to occupy rocky habitats.

The phylogenetic patterns in local abundance are not easily explained either. Other studies regarding the phylogenetic signal of local abundance in plants have found similar patterns of similarity between related species, but did not explore the possible mechanisms behind them (Dexter & Chave, 2016; Loza et al., 2017). The widespread low abundance of plant species in the Pyrenees may arise not from an evolutionary process, but instead it may merely be a reflection of a well known pattern in species abundance distributions where a few very abundant species coexist with many rare species (Enquist et al., 2019; Matthews & Whittaker, 2015) (but see Warren et al., 2011 and Keil et al., 2018). If most plant species in the Pyrenees show low local abundance the likelihood of closely related species having similar abundances is high, which would appear as a strong phylogenetic signal regardless of the mechanisms that have led to that pattern. However, it is important to note that some traits related to low local abundance like growth form and life history traits do show a certain degree of phylogenetic conservatism and thus could be playing a role in determining the patterns that we observed (Burns et al., 2010; Dexter & Chave, 2016; Qian et al., 2017).

Regardless of the mechanisms that have led to these phylogenetic patterns, our results indicate that some of the most vulnerable plant species in the Pyrenees tend to be phylogenetically close. This translates into increased extinction risk for some branches of the tree of life and disproportionate losses of phylogenetic diversity if they were to disappear, a pattern already predicted by Thuiller et al. (2011) for the flora of Southern Europe using a smaller set of species and lower phylogenetic resolution. Although these results might be alarming at first, there are two important appreciations to make about them. On the one hand, vegetation survey databases (our source for this analysis) only represent part of the actual distribution and abundance of plant species, and thus some species may seem rarer than they actually are (Kaye et al., 2019). On the other hand, only a proper assessment of the threats and population trends of those species will determine their vulnerability and actual risk of extinction.

6.3 Population viability analysis of plants in Aragón

To better understand the conservation status of rare and common plants in our study area, in chapter 3 we explored the trends of 157 plant populations in the Aragón monitored through a collaborative science program, putting a special focus on the effects of observation error when estimating trends in population abundance. The results indicate that roughly 96% of populations in study have very stable trends and that including the observation error in population viability analysis has a big impact on the estimates of growth rates and their variability. Although we did not distinguish between rare and common species, our results follow those from a previous assessment by García et al. (2021) using an earlier version of the same dataset, who observed that rare and threatened plant species had similar growth rates than common species, along with less temporal fluctuations over time. This stability is quite important for the long-term persistence of these populations.

Although all populations have a certain degree of variation in their growth rates that stems from changes in their environment or their vital rates (Lande, Engen, & Saether, 2003), this interannual variability in population growth rates has a negative effect on the average long-term growth rate of a population, increasing its probabilities of decline (Gillespie, 1977; Lewontin & Cohen, 1969; Tuljapurkar, 1990). In addition, this variability is also directly related with the probability of extinction of a population, as higher variability of growth rates between years implies a higher chance of falling below viable population size (Morris & Doak, 2002). Part of this variation, however, does not always stem from the dynamics of the population itself, but is rather caused by observation error during the sampling process (Dennis et al., 2006; McNamara & Harding, 2004). We are rarely able to observe all the individuals in a population, which means that our estimates of its size tend to be biased, adding an extra layer of variation to the growth rates (Staples et al., 2004). Although this problem has had significant attention in the population viability literature, it has rarely been addressed in practice (Buonaccorsi & Staudenmayer, 2009; Dennis et al., 2006; See & Holmes, 2015; Staples et al., 2004).

Here we applied a very simple procedure to estimate observation error, repeated censuses in all or part of the population of interest during the same sampling session. These estimates were incorporated directly into our population models using a novel Bayesian method that decomposed the estimated population variability into its process and error components. To our knowledge this is the first time that such a procedure has been implemented in practice for monitoring plant populations (but see Pardo et al. (2015) for monitoring plant communities). Accounting for observation error in our models results in improved estimates of growth rates and their variance, both if which had narrower credible intervals, indicating more precise estimates. In concordance with theory, the growth rates estimated by the model that accounted for observation error were 39% higher than in the base model, and their variance was greatly reduced (31%). Owing to the increase in growth rates and strong reduction in variability, the estimates of quasi-extinction probability in 50 years derived from the model considering the observation error were 35% lower than the simple model. Observation error was responsible for around one third of the total variation estimated by the model, although it varied a lot between populations and sampling methods. The appropriate choice of the latter has a critical role in determining the observation error of the estimates (Morrison, 2016), and should be selected based on the characteristics of the focal plant as well as its surroundings in order to minimize any potential biases (Perret et al., 2023). The "Adopt a Plant" citizen science program uses the framework proposed by García et al. (2021) to establish the sampling design of each population to reduce observation error as much as possible. Despite this adjustment, we found differences in the observation error estimated for each method. Presence/absence and plant cover estimates were the most precise, likely because these methods are less sensitive to small changes in abundance and thus the estimates are more constant throughout each repeated census. Counting individuals, which was used in the majority of populations, had slightly higher observation error than plant cover estimates. Counts of only reproductive individuals had the highest observation error, which was surprising given that conspicuous flowers tend to be easily detectable and thus should lead to lower error (Perret et al., 2023).

These results showcase that despite our efforts to reduce observation error during the sampling process it is inevitable to have a certain amount of noise introduced by our own perceptual limitations. This error can have a strong influence on estimates of temporal variability of population growth and thus any population viability analysis should take great consideration to control for it in order to yield the best estimates possible. This is particularly important for rare and endangered species which require careful monitoring of their populations to inform actions towards their conservation.

6.4 Rare plant species as hubs of visitor diversity

Throughout this thesis we have used the concept of rarity as an indirect approximation to the vulnerability of plant species to extinction. So far, the focus has been placed on plant communities, single species and populations as entities separate from their surroundings, without acknowledging their position as important assets for maintaining the diversity of their ecosystems. However, plants, like any other organisms, are part of a complex network of interactions with their surroundings and many other species, interactions that contribute to the long-term persistence of both the plants and their visitors (Tylianakis et al., 2010). Rare plants are no different in this regard, although the increased vulnerability to extinction associated with rarity puts their visitors at a higher risk of losing valuable resources, especially if those species have a high degree of specialization (Valiente-Banuet et al., 2015).

In chapter 4 we characterized the whole community of visitors of six rare species of plants, five of them also included in our assessment of rarity in Chapter 1, and showed how those rare plant species not only interact with a wide variety of species, but also how the diversity of those visitors is kept similar between host plant populations of different size when accounting for sampling effort and plant density. We did, however, find differences in the composition of visitor communities between host plants. Previous studies have shown a negative correlation between plant population size and the abundance of pollinators (Brown & Gilbert, 2020; Dauber et al., 2010; Mustajärvi et al., 2001; Sõber et al., 2009). Initially, we challenged that assumption arguing that our focal plants, although rare, were generalist species offering a wide array of resources, and thus they would attract generalist visitors that would not be affected by plant population size (Brosi, 2016). Our results supported this hypothesis, and indicate that smaller populations are not visited by less diverse communities, even when accounting for sampling effort and plant density. Studies by Wei et al. (2021), Benadi and Gegear (2018) and Klank et al. (2010) show that rare plants can benefit from co-occurring with more abundant species, as these would attract visitors which also interact with rare plants. In chapter 4 we observed that the diversity of visitors was not influenced by the richness of co-occurring plant species at each patch, However, we did find significant differences in the composition of visitors between populations, with small patches being visited by a different community than patches in the large population. Trøjelsgaard et al. (2015) showed a positive correlation between the composition of visitors and the distance between plant populations, which would explain the higher degree of similarity between the three patches located within the large population. The differences in visitor composition described in chapter 4 consisted mostly in species replacement between patches, a pattern that has already been observed by Souza et al. (2021), Trøjelsgaard et al. (2015) and White et al. (2022) in other communities of plant visitors.

Root bacteria followed slightly different patterns than aboveground visitors, showing differences in both alpha diversity and community composition between plant populations. Initially, we expected that populations of the same plant species would share a similar number and composition of OTUs given the specificity of root bacteria to their hosts (Bulgarelli et al., 2013). However, we found that patches within small populations were more diverse and distinct than those in the larger population. Previous studies have shown that intra-specific variation in traits like plant productivity (Pérez-Izquierdo et al., 2019) and host health (Berendsen et al., 2012) or external factors like abiotic stress (Hartman & Tringe, 2019) and soil conditions (Berg & Smalla, 2009) may affect the root microbiome. Thus, we cannot rule out the effects of any possible unknown variables that may be causing those differences between patches in chapter 4. Despite the differences in diversity and composition between patches and communities of visitors, we observed a positive correlation between the composition of aboveground and belowground interactors, suggesting the existence of shared factors shaping the differences in community composition between patches of the same host plant (Wardle et al., 2004).

6.5 Further prospects

Rarity is a complex and multifaceted concept. The study of rare organisms requires careful assessment of a variety of possible variables involved in it (causes) and how they can increase their vulnerability (consequences). Although rarity has historically been linked to higher extinction risk, only a proper study of the extrinsic factors that might affect rare species, such as any potential threats, along with their intrinsic factors like population size in nature or demographic dynamics, might shed light on the actual vulnerability towards extinction of rare plant species.

The results in this thesis set a path forward in improving our understanding of the relationship between rarity and conservation risk. The next logical step in that direction would be to deepen our knowledge on the distribution and abundance of plant species, as well as obtaining fully-resolved phylogenies that better reflect the evolutionary relationships between taxa. Integrating that knowledge with high quality time series of the changes in species abundance and in-depth evaluations of any potential threats to those populations constitutes the best tool to assess the conservation status and future vulnerability of rare plant species. Thus, expanding and promoting initiatives that gather high quality, long-term demographic data such as the “Adopt a Plant” program, is a pivotal requirement for improving conservation science and practice. Finally, although we have seen that rare species are visited by a wide range of organisms, studying such patterns at a more general scale, with a thorough analysis of all the factors involved in these patterns would advance our understanding of how rare plant species help support the diversity and function of their ecosystems. The work in this thesis opens up several interesting paths towards a better understanding of the relationship between rarity, ecology and conservation science.

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7 General conclusions

1. In this doctoral thesis we have explored the concept of rarity as a proxy of vulnerability in plant species at different biological and ecological scales. On the one hand, by analyzing the distribution of rarity among the Pyrenean flora across different habitats, their phylogenetic patterns and their tendency to accumulate in vulnerable habitats. On the other hand, by assessing the performance of populations of a variety of rare and common plants in the NE of the Iberian Peninsula, and comparing the relative contribution of small and large populations to maintaining the community of visitors they host.

2. From the analysis of more than 18,000 plant inventories, we found that many of the plant species in the Pyrenees can be considered rare due to their endemicity (3%), limited distribution within the region (48%), habitat specialization (21%) or low local abundances (70%).

3. Rare plant species in the Pyrenees are unevenly distributed between habitats. Vulnerable or infrequent habitats like mountain lakes and streams, mires and bogs, rocky cliffs, screes and tall forb stands harbor the highest proportion of rare species. In addition, rare species contribute more than expected to the phylogenetic diversity of communities where they occur.

4. Rarity types show different phylogenetic patterns in the phylogenetic tree of the Pyrenean flora. Endemics and species with limited distribution do not show any clear phylogenetic signal. Habitat specialists, and those adapted to water related habitats in particular, show a strong phylogenetic signal and are grouped in the tips of the phylogeny. Species with low local abundance also show significant signal, although this pattern may respond to still unknown ecological factors rather than evolutionary process.

5. Phylogenetic patterns behind rarity of the Pyrenean flora could lead to a higher

than expected loss of phylogenetic diversity if rare species were to go extinct, particularly for habitat specialists and locally scarce species.

6. The vast majority of 157 plant populations monitored through a citizen science program in Aragón, many of them rare or threatened, show very stable trends (96.2%), with only a tiny fraction of them declining (2.54%) or increasing (1.26%).
7. Observation error is inevitable when censusing plant populations in the field, and it can account for an important part of the estimated variation in population trends. Overlooking such an effect often leads to overestimating extinction probabilities. Our study demonstrated that both adjusting the sampling method in the field and repeating censuses just one year over the time series to estimate the observation error considerably reduce this bias.
8. Rare plants can host or provide resources to a wide diversity of arthropods aboveground and bacteria belowground and thus they should be considered within the greater context of their ecosystem. Although the diversity of visitors was similar between patches of the same plant species located in different sized populations, their composition differed, suggesting different mechanisms determining each aspect of biodiversity.
9. Considering the increased extinction risk of rare plants, other organisms that depend on them to complete their life cycles are also at risk of losing important resources for their survival. Thus, ensuring the long-term persistence of rare species populations, both small and large, can contribute to safeguarding the stability and function of ecosystems.