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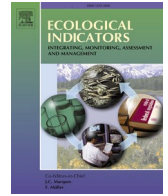
Co-occurrences and species distribution models show the structuring role of dominant species in the Vez watershed, in Portugal

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ABSTRACT

Knowing the structural role of species within communities is important for their conservation and management in the context of recent/ongoing biodiversity loss. In a community, dominant species can influence the distribution and composition of subordinate species. Despite existing research, an approach is lacking to help understand the important role of dominant species in the community, without requiring more detailed data. In this study, we describe an approach to rank the relative importance of plant species within a community based on their abundance and co-occurrence patterns. The Co-occurrence Community Importance Index (CoCII) – a newly proposed index translating the degree of influence that each dominant species has on all its co-occurring subordinate species – was calculated and analysed. We used both abiotic and biotic variables within a species distribution models framework, with data collected in the Vez watershed in the North of Portugal. Our analysis included 114 plants – 26 dominant and 88 subordinate species. Spearman correlations were used to analyse potential interspecific relationships between co-occurring dominant and subordinate species. Using the CoCII, we ranked the relative importance of each dominant species within the plant community. Our results support the role of plant-plant interaction patterns regarding our study area's most highly inter-correlated species. Our approach to ranking species' importance can be directly translated into conservation schemes for managing and maintaining the structure of plant communities. Moreover, it can provide insights into the relative importance of dominant species in a plant community from commonly available datasets including presence-absence, presence-only, or percentage cover data, which allows for the relatively cost-efficient in-field collection and monitoring infield. Furthermore, this approach could allow us to advance the field of community ecology by providing essential information on the species that assure the stability of natural or semi-natural habitats of conservation concern.

1. Introduction

Due to global environmental change, biodiversity has been under increasing pressure over the last decades (Tilman et al. 2017, Sun et al. 2020). Efforts to halt biodiversity loss have been manifold and include the development of conceptual and methodological approaches to advance existing knowledge to support management and conservation policies (Blüthgen and Kaiser-Bunbury 2015, Harvey et al. 2017, Triviño et al. 2018, Alves et al. 2019). In this regard, establishing the relative importance of species within a community is crucial to understanding how species interact with their environment (Agrawal et al. 2007), with applications to conservation such as prioritizing conservation targets

(Jordán et al. 2008). Despite existing research, an approach is lacking to help understand the important role of dominant species in the community in shaping interspecific relationships and biodiversity (spatial organization and abundance), without requiring complex data such as traits, and based only on the presence-absence or presence-only data.

Within a community, a few highly abundant species – i.e., "dominant species" – shape the biodiversity and ecosystem functions of the community, whereas many species that are uncommon or restricted in their range – i.e., "subordinate species" (Garbin et al. 2016) – often have weak to negligible structuring impact on their communities or ecosystem functions (Avolio et al. 2019). Dominant species can influence the distribution and composition of subordinate species through interactions of facilitation and competition. For example, species in abiotic stress conditions (stress-gradient hypothesis) tend to have more frequency of interactions of facilitation (Pellissier et al. 2010a). On the other hand, the competitive ability of the dominant plants can lead to losses of subordinate species by competitive exclusion (Wu et al. 2022). Species with pivotal roles within food webs are commonly called "keystone species" (Libralato et al. 2006, Delibes-Mateos et al. 2007, Avolio et al. 2019). Moreover, the spatial organization and abundance of subordinate species can be determined by biotic interactions such as competition and facilitation with dominant species (Boulangeat et al. 2012, Kunstler et al. 2015, Garbin et al. 2016, Lynn et al. 2019, von Oppen et al. 2021). Biotic interactions imposed by dominant species affect and shape subordinate plant species both positively (e.g., facilitation) and negatively (e.g., competition) throughout the lifecycle of most plants, besides other drivers such as environmental change and biological invasions (Kraft and Ackerly 2014, Franklin et al. 2016). In plant communities, the decline of growth and survival of a given species can be caused by negative interactions (e.g., Bullock et al. (2000); Wisz et al. (2013)), namely competition and parasitism (Kraft and Ackerly 2014). Conversely, Kraft and Ackerly (2014) reported that "nurse plants" allow other species with whom they have a positive association (facilitation) to resist harsh environments by modifying the microclimate nearby. As a result, the structural role of dominant species and their effect on other species from the regional species pool can be detected by statistical analyses (Pellissier et al. 2010a, Roux et al., 2014).

Complementing abiotic gradients, biotic interactions are key to understand community assembly (García-Girón et al., 2020). Biotic interactions have been analyzed using community data in a variety of approaches, from co-occurrence analyses (Kay et al., 2017) to species distribution models (Wisz et al. 2013). Patterns of species co-occurrences (i.e., heterospecific relationships) are limited by dispersal and biotic interactions (Pellissier et al. 2010a), which can be detected by co-occurrence analyses or Species distribution modelling (SDMs). Species distribution modelling (Elith and Leathwick 2009, Guisan et al. 2017) approaches have further been used to assess the impacts of biotic and abiotic conditions on biodiversity. Integrating biotic variables can increase our knowledge of individual species ranges and the spatial variation in species assemblages, as well as improve the predictive power of models and community richness and composition patterns (Pellissier et al. 2010a, Wisz et al. 2013, Araújo et al., 2014, Roux et al., 2014). Moreover, Giannini et al. (2013) compared different methods for including interspecific interactions in SDMs, concluding that ecological and biological knowledge should guide the choice of biotic information to be included in the models to improve their accuracy. On the other hand, Roux et al. (2014) used a surrogate for biotic interactions to improve community-level models and found that local richness was reduced by dominant species, especially where competition was strong. Finally, Klanderud et al. (2015) found different patterns in the importance of biotic variables to explain variation in species composition across sites with different environmental conditions, underlining the interactions between biotic and abiotic variables. This evidence is crucial to informing and predicting species distributions (Pellissier et al. 2010a, Roux et al., 2014). Moreover, other studies have used dominant species as proxies for biotic interactions based on subordinate species

and their distributions (Meier et al. 2010, Pellissier et al. 2010a, Roux et al. 2012, Roux et al., 2013, Roux et al., 2014). Enhanced predictions provided by such models are crucial to inform and support conservation, management, and monitoring efforts, as well as to project species trends and shifts under environmental change (Roux et al., 2014, Alves et al. 2019).

Information on species' characteristics and relative importance within a community are essential to disclose drivers of species distributions and relations with other species in community assemblages. However, information on species' biology, demography, and interactions is not frequently available since its collection is usually associated with high costs in terms of money, time, and expertise. As a result, such information is still underused as predictive variables in SDMs (Stephenson et al. 2022). On the other hand, species occurrence and abundance data are much more commonly available (e.g., BIOTIME (Dornelas et al. 2018)), but suitable methods to use them to achieve insights on the dynamics and interactions within a community are lacking. Thus, there is a pressing to develop robust methods taking advantage on existing data to deepen knowledge on the drivers shaping the communities and species, supporting the data-driven definition of conservation priorities and goals.

In this study, we describe an approach to rank the relative importance of plant species within a community based on their abundance and co-occurrence patterns – i.e. an aggregate measure of the average explanatory power of a given dominant species, within a community, as a predictor of the distribution of all of its co-occurring subordinate species. To that end, we use both abiotic (e.g., climate, land cover) and biotic variables (e.g., model predictions for subordinate species) within an SDM framework to address the following two research questions:

(i) Can different dominant species exhibit different levels of (positive and/or negative) interspecific correlations of their relative importance on subordinate species within a plant community?
(ii) Can we identify the species with the highest levels of overall relative importance within a plant community?

We illustrate our approach to ranking species' importance within plant communities by applying a newly-proposed Co-occurrence Community Importance Index with a pre-existing dataset that was collected in the Vez watershed, located in the North of Portugal.

2. Material and methods

2.1. General approach

In this study, we present a model-based framework to rank the relative importance of dominant species within the community (Fig. 1). In this framework, both dominant and subordinate species occurrences are modelled as response variables, while both abiotic (e.g., physiography, land-use, climate) and biotic variables (e.g., percent cover of dominant species) are used as predictors. In the first step, three groups of Generalized Linear Models (GLMs) are fitted: (i) null models (i.e., with a single intercept term); (ii) abiotic models (i.e., with only abiotic predictors); and (iii) abiotic + biotic models (i.e., with both abiotic and biotic predictors). As a second step, performance is evaluated and compared between models using the difference between the Akaike Information Criterion (AIC) for the "best" model and each candidate model (with a correction for finite sample size, i.e., ΔAIC_c). Pairwise interspecific relationships are analysed using Spearman correlations. In step three, the Co-occurrence Community Importance Index – a newly proposed index translating the degree of influence that each dominant species has on all its co-occurring subordinate species – is calculated and analysed for each dominant species. This index allowed us to identify co-occurrence patterns and rank dominant species in terms of their relative importance within the community. The data used to apply this general framework was a pre-existing dataset located in the Vez watershed,
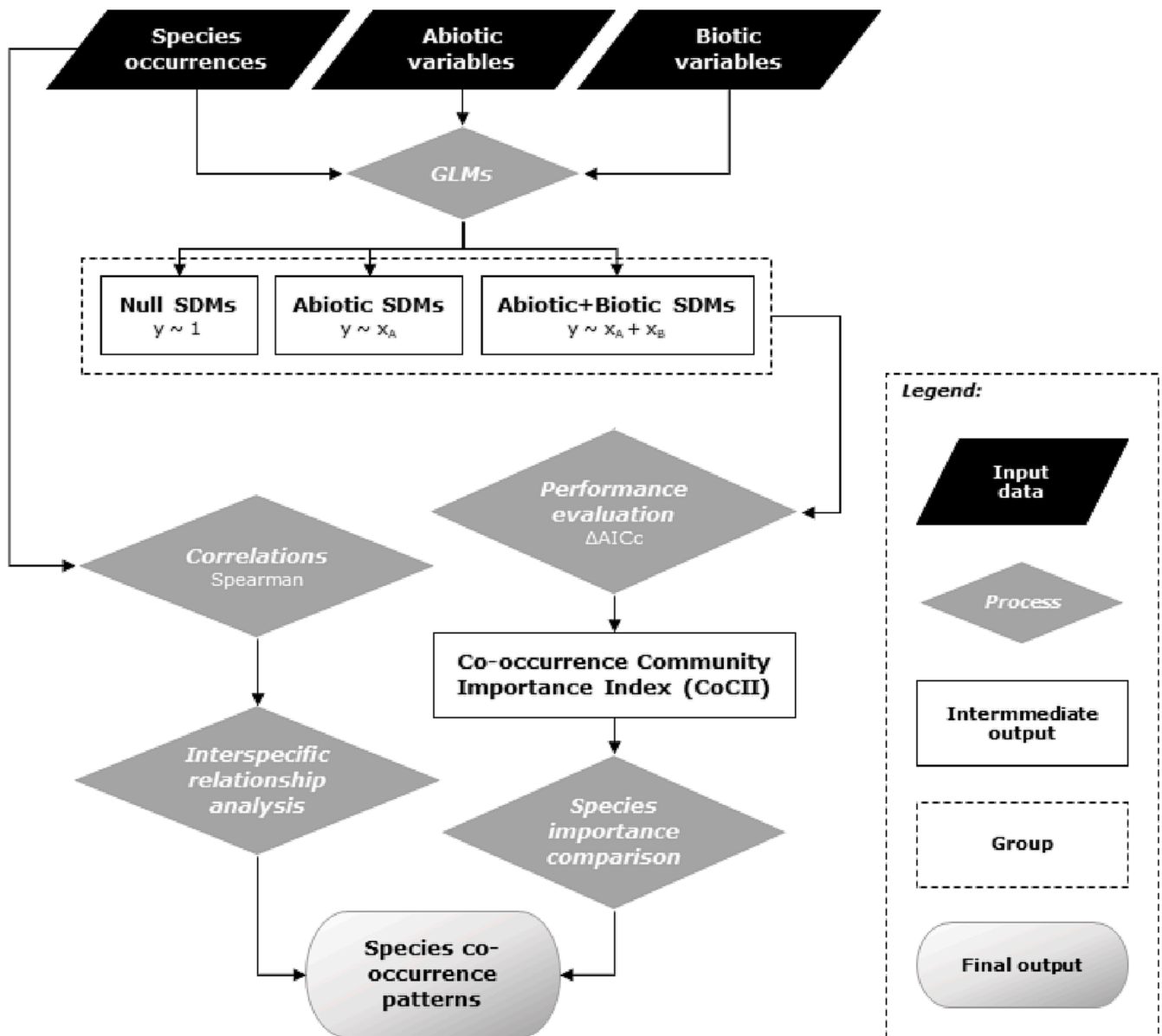
Fig. 1. Graphical representation of the workflow diagram – Input data of species occurrence, and abiotic and biotic variables are used to obtain: (i) Spearman correlations to analyze interspecific relationships; and (ii) species distribution models (SDMs), through Generalized Linear Models (GLMs), to evaluate and compare species importance. Together, those two outputs are used to analyze species co-occurrence patterns in the community.

located in the North of Portugal, as described hereinafter.

2.2. Study area

The Vez River is a tributary of the Lima River, and its watershed (252 km²) is located in the northwest portion of mainland Portugal (Fig. 2). This watershed includes important areas for biodiversity conservation, such as part of the Peneda-Gerês National Park and Natura 2000 network site (Civantos et al. 2018). Its topography is complex, with elevations ranging from 30 to 1400 m a.s.l., and slopes above 25% that shape 58% of the catchment (Carvalho-Santos et al. 2019). Precipitation is high all year round (1500 mm/year), except the summer (drier) months (July and August), and the average temperature is around 13 °C (Carvalho-Santos et al. 2019). This territory has been shaped by human activities contributing to a diverse landscape, mainly shaped by the agro-pastoral land management regime. In recent decades, this area has been impacted by rural abandonment, encroachment, and afforestation (Civantos et al. 2018). In addition, this area is also affected by frequent

fires during spring and summer.

3. Data

3.1. Biotic variables

Fieldwork was carried out between May and July 2014 to record plant species occurrence and habitat characterization (for a more detailed description, see Civantos et al. (2018)). A two-step nested spatial sampling scheme was employed to select the locations for the plant species surveys and habitat mapping (Civantos et al. 2018). This scheme allowed to distribute of the sampling units across the main environmental gradients throughout the study area (Civantos et al. 2018). Four main types of variables were included in the environmental stratification: climate, topography, soil types, and protection regime areas (for more detailed information regarding the sampling design supporting the collection of this data, see Supplementary Material 1, Table S1). Firstly, a stratified random sampling approach was used to
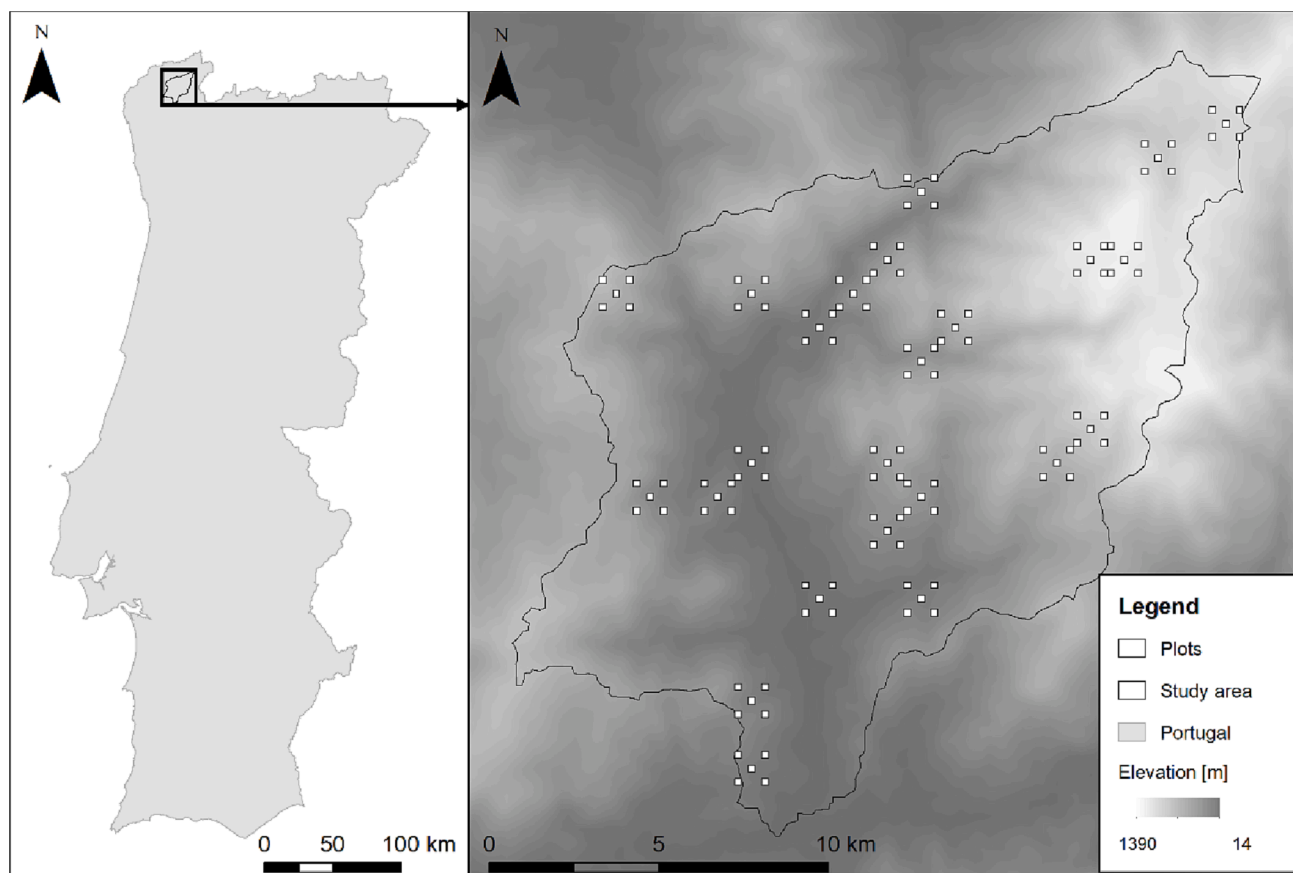
Fig. 2. Location of: the study area – the watershed of river Vez – in northwestern mainland Portugal (left); and the in-field sampling units (n = 120), within the study area (right).

identify the Primary Sample Units (PU) to select 24 PUs within a regular grid of 1000 × 1000 m square units. In a second step, to reduce the costs of the surveys, a systematic sampling approach was used to select five Secondary Sample Units (SU) with a size of 200 × 200 m located at the four corners plus the center of each 1000 × 1000 PU, resulting in a total of 120 SUs (for more detailed information see Supplementary Material 1).

In each plot (SU), habitats were mapped using the General Habitat Categories (GHC) methodology (Bunce et al. 2008). The concept of GHC is based on Raunkiaer's plant life form classification, which describes habitat structure connecting to climate, specific site conditions, and disturbance regimes. In each plot, all individual patches were characterised and mapped based on the dominant GHC and all the life forms with at least 10% cover. Within each patch, the dominant plant species of each stratum – i.e., the species with a higher percentage cover within the respective stratum, as long as that percentage was above 30% (Bunce et al. 2008) – was recorded, including its percentage cover. Moreover, all vascular plant species at the plot level were recorded.

The dataset of vascular plant species for the Vez watershed contains a total of 536 species recorded for all of the 120 SUs. From this initial number, only 114 species were analyzed, after excluding the ubiquitous i.e – with<10 absences – and the rare or uncommon ones i.e – with<30 presences (see Supplementary Material 1 for a complete list of the plant species analysed in this study). These thresholds were applied mainly due to two factors: (i) using very unbalanced data with insufficient records (i.e. the ratio between a number of presences vs. a number of absences) may decrease overall model performance, and (ii) low ratios between the number of observations vs. the number of predictor variables result in more saturated models. Furthermore, since ubiquitous species are present in (almost) all plots, they can grow in different

habitat types despite any environment or biotic filter. On the other hand, rare or uncommon species are almost absent. As such, both ubiquitous and rare/uncommon species present a challenge for modelling approaches because no particular rules or functions can explain their occurrence. This also relates to the scale of the analysis, since some species may have specific ecological requirements at a broad/coarse scale but may be somewhat generalists at a local/finer scale. Of these, species considered, 26 were considered dominant species (see Table 1), for which the respective percentages of cover within their vegetation stratum were retrieved from the habitat mapping dataset for the study area. These percentages of cover were obtained by multiplying the percentage of covers per patch by the total area of the patch, thus obtaining the average percentage of covers for each SU.

3.2. Abiotic variables

Six variables distributed by three main categories – Physiography, Land-use, and Climate – were selected for the analyses to represent the major environmental gradients in the study area (Table 2).

For Physiography, two variables were included: (i) Terrain Ruggedness Index (TRI), measuring the difference between a central cell and its surrounding ones; and (ii) log-distance to rivers Log-dist); both calculated from MERIT-DEM at 200 m (Yamazaki et al. 2017) using GDAL (GDAL 2020) and the R Statistical Environment (R Core Team 2021).

For Land-use, two other variables were included: the respective percentages of the cover of the 'Agricultural' (AGR) and 'Sparsely vegetated, shrubs and scrubs' (SN) categories, extracted from the habitat mapping dataset.

Finally, two additional variables representing bioclimatic indices

Table 1

List of dominant plant species in the study area, along with their respective acronyms and life form [(TPH/EVR (Tall Phanerophytes/Evergreen); CHE (Caespitose hemicryptophytes); THE (Therophytes); LPH/EVR (Low Phanerophytes/Evergreen); TPH/NLE (Tall Phanerophytes/Non-leafy evergreen); FPH/EVR (Forest Phanerophytes/Evergreen); LHE (Leafy hemicryptophytes); FPH/CON (Forest Phanerophytes /Coniferous); TPH/DEC (Tall Phanerophytes /Winter deciduous); MPH/EVR (Mid Phanerophytes/ Evergreen); HCH (Herbaceous Chamaephytes); MPH/NLE (Mid Phanerophytes/Non-leafy evergreen); LPH/NLE (Low Phanerophytes/ Non-leafy evergreen)].

Species name	Acronym	Life Form
Adenocarpus lainzii (Castrov.) Castrov	ADELAI	TPH/EVR
Agrostis truncatula subsp. *commista* Castrov. & Charpin	AGRCOM	CHE
Agrostis curtisii Kerguélen	AGRCUR	CHE
Arrhenatherum elatius subsp. *bulbosum* (Willd.) Schübl. & G.Martens	ARRBUL	CHE
Bromus hordeaceus L.	BROHOR	THE
Calluna vulgaris (L.) Hull	CALVUL	LPH/EVR
Coleostephus myconis (L.) Rchb. f.	COLMYC	THE
Cytisus striatus (Hill) Rothm.	CYTSTR	TPH/NLE
Dactylis glomerata L.	DACGLO	CHE
Erica arborea L.	ERIARB	TPH/EVR
Erica cinerea L.	ERICIN	LPH/EVR
Erica umbellata Loefl. ex L.	ERIUMB	LPH/EVR
Eucalyptus globulus Labill.	EUCGLO	FPH/EVR
Holcus lanatus L.	HOLLAN	CHE
Holcus mollis L.	HOLMOL	CHE
Mentha suaveolens Ehrh.	MENSUA	LHE
Pinus pinaster Aiton	PINPIN	FPH/CON
Plantago lanceolate L.	PLALAN	LHE
Pseudarrhenatherum longifolium (Thore) Rouy	PSELON	CHE
Pyrus cordata Desv.	PYRCOR	TPH/DEC
Quercus robur L.	QUEROB	FPH/DEC
Rubus ulmifolius Schott	RUBULM	MPH/EVR
Salix atrocinerea Brot.	SALATR	FPH/DEC
Sedum brevifolium DC.	SEDBRE	HCH
Ulex europaeus latebracteatus L.	ULELAT	MPH/NLE
Ulex minor Roth	ULEMIN	LPH/NLE

Table 2

Summary of the abiotic variables used in this study.

Name	Abbreviation	Source	Original Spatial resolution
Terrain Ruggedness Index	TRI	MERIT-DEM (Yamazaki et al. 2017)	3″ (~90 m)
Log-distance to rivers	Log-dist	MERIT-DEM (Yamazaki et al. 2017)	3″ (~90 m)
Agricultural	AGR	Vez habitat mapping dataset	200 m
Sparsely vegetated, shrubs and scrubs	SN	Vez habitat mapping dataset	200 m
Annual Mean Temperature	B01	CHELSA (Karger et al. 2017)	1 km
Precipitation of Wettest Quarter	B16	CHELSA(Karger et al. 2017)	1 km

were included: (i) 'Annual Mean Temperature (B01)', and (ii) 'Precipitation of Wettest Quarter (B16)'. Bioclimatic layers obtained from the CHELSA dataset (Karger et al. 2017) were downscaled from 1 km to 200 m, following a straightforward approach by fitting GLMs using a stepwise procedure with AIC as selection criteria. This type of downscaling of (bio)climatic variables using GLMs was successfully employed in previous studies (e.g. (Beuchat et al. 2012, Jaberalansar et al. 2018, Balmaceda-Huarte and Bettolli, 2022)).

3.3. Co-occurrence community importance ranking

3.3.1. Species distribution models

For each of the 114 species, binomial ('logit') GLMs models were calibrated using presences and absences. As a generalization of ordinary linear regression models, GLMs are used here for their interpretability since, as parametric models, they allow for the analysis of linear relationships between response and predictors, even when their underlying relationship is not linear (Nelder and Wedderburn 1972, Austin 2007, Pellissier et al. 2010b). An abiotic-only model (i.e., using only abiotic predictors) was first calibrated for each species (either dominant or subordinate), resulting in 114 abiotic-only models. Then, models of the subordinate species were fit using both abiotic and biotic predictors, for each dominant-subordinate species pair with at least 20% co-occurrence, by including the percentage cover of the dominant species. The total number of models calibrated, including null and abiotic-only and abiotic + biotic models, was of 2999 GLMs.

Model performance was assessed using the ΔAIC_c metric to compare all models within each species, thus allowing us to evaluate which biotic models performed better than the abiotic and null models if any (Gonçalves et al. 2016). Moreover, Spearman rank correlations between the projected probabilities of the dominant vs. subordinate species were used to analyse the magnitude, sign, and statistical significance of the relationships between those species (Pellissier et al. 2013, Roux et al., 2014).

3.3.2. Co-occurrence community importance Index

The Co-occurrence Community Importance Index (CoCII) was obtained according to the following formula:

$$COCII = C \times (1 - A) = \left(\frac{n_c}{n}\right) \times \left(1 - \sqrt{\%c}\right)$$

where C is the co-occurrence factor, corresponding to the proportion of species that co-occur with the focal species from the total number of species; A is the abundance factor (the complementary value of a rarity factor), which can be calculated from the square-root of the total percentage cover of the focal species in the study area; n_c is the number of species that co-occur with the focal species, which can be considered to be equal to the number of biotic models for the focal species with ΔAIC_c lower than a certain predefined threshold (e.g., the ΔAIC_c for the abiotic or the null models); and n is the total number of species. This index provides an estimation of the relative importance of the targeted dominant species based on the number of subordinate species for which the models were improved by using the percentage cover of the target dominant species (i.e., $\%c$) as predictors.

3.3.3. Species importance ranking

To assess how the rank of the dominant species' relative importance within the community would change with different criteria when each species is considered to co-occur with a focal species, we established the following three criteria:

i) ($\Delta AIC_c < \Delta AIC_c$-abiotic) AND ($\Delta AIC_c < \Delta AIC_c$-null);
ii) $\Delta AIC_c < 4$; and
iii) $\Delta AIC_c < 2$.

We used these three nested criteria to simulate increasingly

demanding requirements for species to be considered as cooccurring, based on the obtained values of ΔAIC_c for their SDMs. For criterion (i), the ΔAIC_c of the biotic model was only required to be lower than those of both the abiotic and the null models. On the other hand, for criteria (ii) and (iii) we considered, as general rules of thumb, that biotic models with values of ΔAIC_c lower than four show reasonable support, while values of ΔAIC_c lower than two show considerable evidence to support the biotic model (Burnham 2002, Fabozzi et al. 2014, Gonçalves et al. 2016).

In addition to these three criteria, we also compared the results of the COCII when combining all of the three previous criteria (i.e., COCII-combined), by adding the values of the three criteria:

$$COCII_{combined} = COCII_{\Delta AIC_c < n \wedge a} + COCII_{\Delta AIC_c < 4} + COCII_{\Delta AIC_c < 2}$$

This method effectively attributes more weight to the most restrictive criteria (in this case $\Delta AIC_c < 2$), since each criterion is nested within the previous one(s). These criteria were then used to rank the importance of each dominant species within the community according to their respective values of the CoCII.

4. Results

4.1. Interspecific correlations

Our analysis was conducted on 114 species, of which 26 were considered 'dominant species' and 88 were considered 'subordinate species'. Fig. 3 shows the number of subordinate species correlated (positively or negatively; either significantly or non-significantly) with the dominant species.

The species with more positive significant correlations were QUEROB, DACGLO, PINPIN, SALATR, RUBULM, HOLLAN, PLALAN, and ADELAI. On the other hand, the species with more negative significant correlations were AGRCUR, CALVUL, PSELON, ERICIN, and AGRCOM. Regarding statistically significant interspecific correlations, we found both positive and negative relationships within the plant communities in the Vez watershed. More specifically, negative correlations were more frequently observed for species such as AGRCUR and CALVUL than positive relationships. On the other hand, species such as DACGLO, HOLLAN, and MENSUA were found to have more positive than negative correlations. These patterns point to a higher prevalence of competition processes associated with the first group of species, whereas facilitation seems to be more present for the second group.

4.2. Ranking of species importance

We found that the ranking of the dominant species' importance obtained from the different criteria used varied among species (Fig. 4). Using the combined criteria, the five top-ranked species were AGRCUR, DACGLO, HOLLAN, CALVUL, and MENSUA. Arboreal species such as EUCGLO, QUEROB, PINPIN, and SALATR were ranked in 11th, 12th, 15th, and 25th places, respectively.

The top-ranked species (AGRCUR) and the 4th ranked species (CALVUL) had more negative than significant positive correlations with other plant species. On the other hand, the second-best ranked species (DACGLO), the third-ranked species (HOLLAN), and the fifth-ranked species (MENSUA) had more positive than significant negative correlations. Overall, 17 out of the 26 dominant plant species analysed had predominantly positive correlations with other plant species in the study
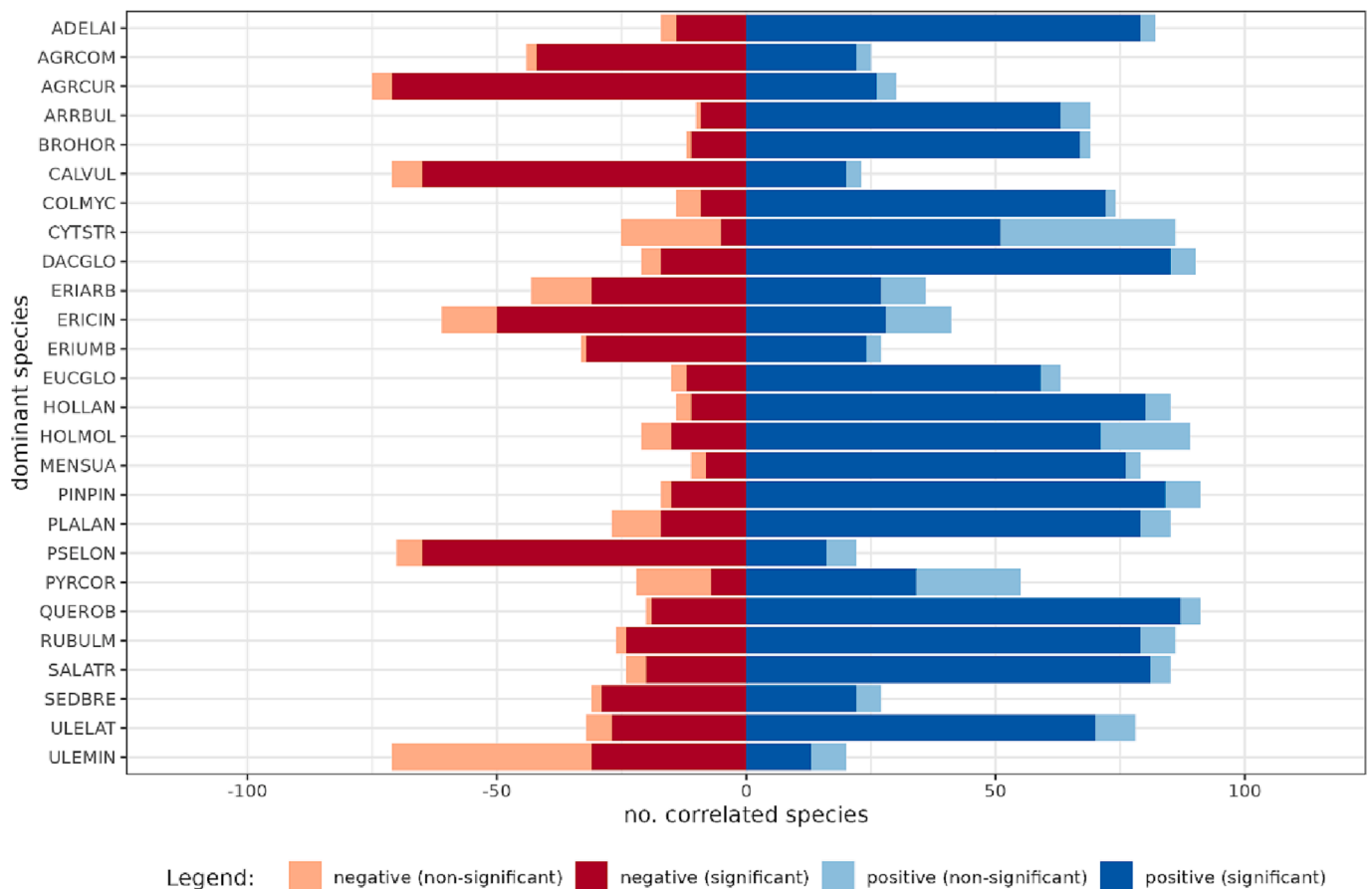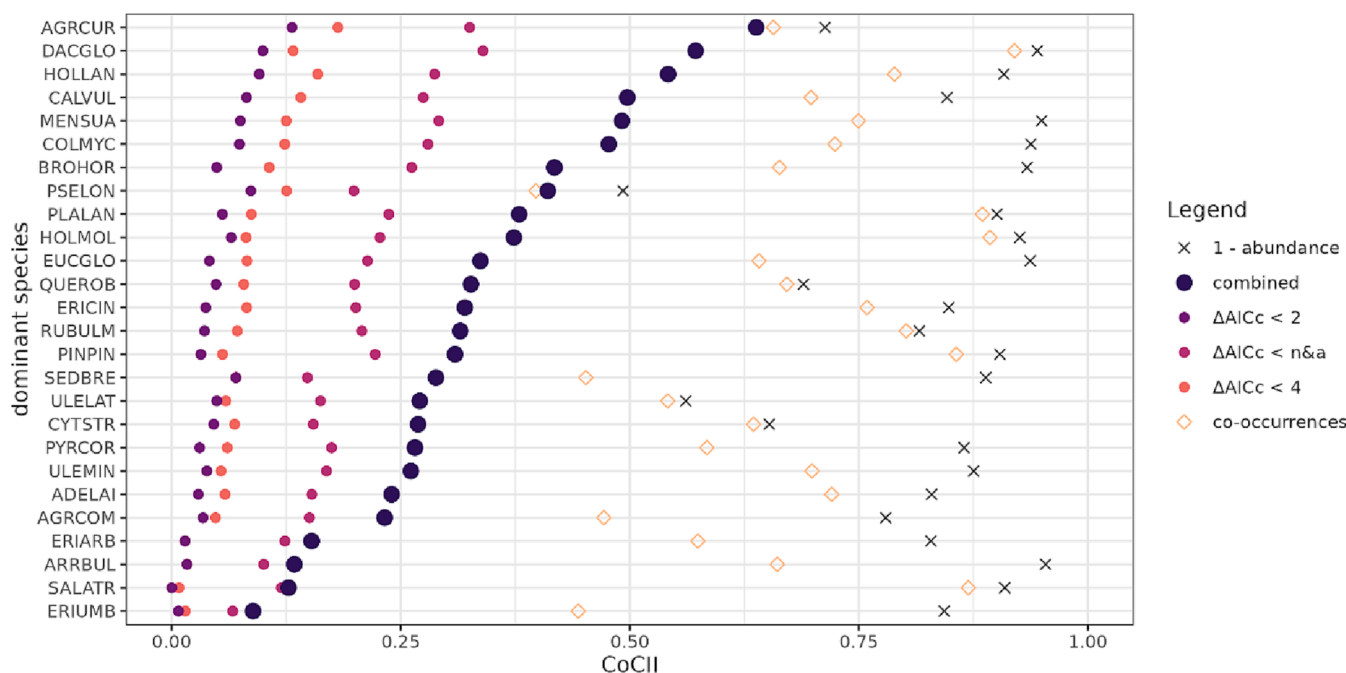

Fig. 3. Interspecific correlations obtained between each of the 26 dominant plant species and all co-occurring subordinate plant species (see Table 1 for detailed information on the dominant species, and Table S2 in Supplementary Material for detailed information on the complete list of plant species – dominant and subordinate – analysed).

Fig. 4. Values obtained for the Co-occurrence Community Importance Index (CoCII) for the dominant species analysed, using three different thresholds for ΔAIC_c – (i) lower than both the null and abiotic models ("$\Delta AICc < n\&a$"); (ii) lower than 4 ("$\Delta AICc < 4$"); and (iii) lower than 2 ("$\Delta AICc < 2$"), as well as combining all of those three criteria ("combined"). Additionally, the values of rarity ("1 - abundance") and percentage of co-occurrence ("co-occurrences") are also shown.

area, whereas the remaining nine had predominantly negative correlations.

5. Discussion

Overall, results support the role of plant-plant interaction (facilitation and competition) patterns regarding the most highly intercorrelated species in our study area. In turn, this validates the approach used in our study to infer potential species interactions from co-occurrence data. It must be noted, however, that the association detected in our study are correlative and that further analyses would be needed to investigate species interactions more conclusively and with more robust methods and data. Nevertheless, the results presented here, especially the ranking, can be directly translated into conservation schemes for managing and maintaining the structure of plant communities.

5.1. Potential interspecific relationships within a community

Ecologists have proposed methods to infer species interactions based on co-occurrences extracted from presence-absence data (Blanchet et al. 2020), and building on these methods, our approach allowed us to rank species. For example, Roux et al. (2013) found that the influence of plant-plant interactions (i.e. facilitation and competition) was stronger than herbivore impacts affecting the species occurrence and cover at fine scales. Also, Roux et al. (2012), found that the predominance of negative effects (i.e., competition) of the dominant species across an altitudinal gradient was relevant to explain species' distributions (lichen, bryophytes, and vascular plants) by using biotic variables (cover of the dominant species). Comparatively, patterns observed in our dataset (cf. Fig. 3) depicted a higher prevalence of competition processes associated with a group of species [*Agrostis curtisii* (AGRCUR), *Calluna vulgaris* (CALVUL), *Pseudarrhenatherum longifolium* (PSELON), *Erica cinerea* (ERICIN), and *Agrostis truncatula* subsp. *commista* (AGRCOM)], whereas for another group [*Quercus robur* (QUEROB), *Dactylis glomerata* (DACGLO), *Pinus pinaster* (PINPIN), *Salix atrocinerea* (SALATR), *Rubus ulmifolius* (RUBULM), *Holcus lanatus* (HOLLAN), *Plantago lanceolate*

(PLALAN), and *Adenocarpus lainzii* (ADELAI)] facilitation seems to be more present. In their research, Damgaard et al. (2009) reported that species such as *Calluna vulgaris* (CALVUL) exhibit competitive effects on *Deschampsia flexuosa* (L.) Trin. in heathland ecosystems. Also, Nemer et al. (2021) described competition effects of shrubland dominated by Ericaceae species (*Erica scoparia, Erica arborea, Erica cinerea, Calluna vulgaris*) and *Pseudarrhenatherum longifolium* (Thore.) Rouy on neighbouring plants in siliceous soils. On the other hand, Jensen et al. (2012) demonstrated that competition between shrubs and herbaceous vegetation indirectly facilitates the growth of young *Quercus robur* (QUEROB) trees. Also, Rodríguez-García et al. (2011) showed that shrubs might act as nurse plants facilitating *Pinus pinaster* (PINPIN) in Mediterranean forests, based on the overall positive and strong effect on seedling survival. Across a stress gradient (drought), signs of facilitation by neighbouring plants such as *Holcus lanatus* (HOLLAN) and *Pseudarrhenatherum longifolium* (PSELON), and the species *Arrhenatherum elatius* were found (Grant et al. 2014). Other studies have observed associations between abundance and interactions, with competition being associated with abundant species, and facilitation with rare species, across taxa and biogeographic regions (e.g., Hines and Keil (2020)). This pattern has been partially observed in our results, with some of the most abundant dominant species being associated with the prevalence of negative correlations with subordinate species (e.g., *Pseudarrhenatherum longifolium* (PSELON)), although this not was not always observed (e.g., *Ulex europaeus latebracteatus* (ULELAT)). Moreover, interaction patterns between species could be related to specific physiological traits. For instance, Garbin et al. (2016) found contrasting traits of dispersal and persistence between dominant and subordinate tropical plant species.

5.2. Patterns of relative dominant species importance

Our approach aimed to rank the relative importance of dominant species within plant communities based on an index that considers species co-occurrences and relative abundance. By applying the proposed approach to an existing dataset, our results showed how our index could be used with different criteria. It is important to note that, within the obtained ranking, the highest-ranked tree, *Eucalyptus globulus*

(EUCGLO), was ranked only in 11th place, with other trees such as *Q. robur* (QUEROB), *Pinus pinaster* (PINPIN), and *Salix atrocinerea* (SALATR) ranked further below. This could be partially explained by the unbalanced coverage of different vegetation types in the study area, which is mainly dominated by shrublands. However, this issue was partially addressed by including a weighting term in the proposed index benefiting species regionally less abundant. *E. globulus* – a non-native tree species – ranked above other native trees, predominantly showing positive correlations within the community, contrary to what was expected. While this would suggest that *E. globulus* promotes the presence of other species, this result is not in line with previous studies. For instance, low levels of plant species richness in *E. globulus* plantations were previously observed in the region that envelops our study area (e. g., Lomba et al. (2011)). Overall, such patterns have been related to higher levels of inhibition of understorey species richness by *E. globulus* in non-native regions such as Portugal (Becerra et al. 2018). Dominant species' responses to environmental change are crucial for the stability of the habitats in the future since these species are vulnerable (loss and extinction) under global environmental change. Furthermore, changes in the abundance of dominant species could indicate how communities will change over time and space (Avolio et al. 2019). Since dominant species have a key role within their communities, they can be used as an indicator for predicting biodiversity change, ecosystem function, and conservation (Avolio et al. 2019).

5.3. Inclusion of biotic variables in models

Recent methods derived from traditional SDMs have been incorporating biotic information in recent years. For instance, stacked species distribution models (SSDMs) can be used to obtain community-level ensemble predictions of species across a study area by "stacking" all the predictions from individual species-level models (Roux et al., 2014). On the other hand, joint species distribution models (JSDMs) estimate species co-occurrence beyond the environmental preferences of the species-level (Ford and Roberts, 2019). In recent years, several studies focusing on understanding and disentangling biotic interactions have been published, particularly regarding: food webs (Dunne et al. 2002, Jordán et al. 2008, Albouy et al. 2019), plant-pollinator networks (Burgos et al. 2007, Dormann and Strauss, 2014), functional traits (D'Amen et al. 2015, Estrada et al. 2016), plant-plant interactions (Delalandre and Montesinos-Navarro 2018), and species co-occurrence networks (Kay et al., 2017, Ford and Roberts, 2019). Approaches consisting in explicitly incorporating biotic variables, as proxies for interspecific interactions, into SDMs can help shed more light on species distribution patterns within communities beyond purely environmental (abiotic) constraints, such as climate and land use (Giannini et al. 2013, Wisz et al. 2013, Araújo et al., 2014, Roux et al., 2014). Other approaches attempted to quantify species' importance within communities by using structural network connectivity or dynamical simulations of functional importance indices (Jordán et al. 2008). However, such approaches require tailored datasets e.g., on plant traits, based on focused sampling design and infield collection. As so, compiling (infield collection and laboratory procedures) the required data is time-consuming, costly, and highly dependent on specialized human resources. Approaches such as the one proposed here provide insights into the relative importance of dominant species in a plant community from commonly available datasets including presence-absence, presence-only, or percentage cover data, which collection and monitoring infield are, in general, more cost-efficient. Therefore, they provide a way of overcoming limitations related to the availability of suitable data while contributing to (partly) fill the knowledge gaps on relevant aspects of the hierarchical structure of the communities.

6. Conclusions and future perspectives

Overall, our results, as well as their interpretation, were based on

observations of co-occurrences recorded at the plot level, rather than the patch level. This means that two species were assumed to co-occur when in the general vicinity of each other (i.e., within the same 200×200 m plot), which imposes limitations on the interpretation of results. Furthermore, it should be noted that correlations between species distributions do not necessarily translate into interspecific interactions (Giannini et al. 2013). Nevertheless, we argue that the proposed approach provides a methodological tool for the identification of potential "keystone" species. Using the proposed index, a keystone species would be expected to exhibit contrastingly higher values of the Co-occurrence Community Importance Index than all other co-occurring species, indicating strong dependency relationships within the community towards that particular species. Due to the importance of dominant species for the persistence of subordinate ones, it is vital to advance methods for identifying these species to support the definition of priorities and goals for conservation and management (Avolio et al. 2019, Sun et al. 2020). In this context, future research should focus on habitats (including priority communities) to obtain data-driven information on their respective key indicator species, – an essential aspect of habitat mapping and monitoring –, in space and time, while accounting for issues related to sampling, such as spatial autocorrelation. Overall, this approach could allow us to advance the field of community ecology by providing essential information on the species that assure the stability of natural or semi-natural habitats of conservation concern.

CRediT authorship contribution statement

Cristiana Alves: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Bruno Marcos:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **João Gonçalves:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Peter Verburg:** Writing – original draft, Writing – review & editing. **Loïc Pellissier:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Angela Lomba:** Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecolind.2023.110306.

References

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M.G., Werner, E., 2007. Filling key gaps in population and community ecology. Front. Ecol. Environ. 5 (3), 145–152.
Albouy, C., Archambault, P., Appeltans, W., Araújo, M.B., Beauchesne, D., Cazelles, K., Cirtwill, A.R., Fortin, M.-J., Galiana, N., Leroux, S.J., Pellissier, L., Poisot, T., Stouffer, D.B., Wood, S.A., Gravel, D., 2019. The marine fish food web is globally connected. Nat. Ecol. Evol. 3, 1153–1161.
Alves, C., Sousa-Silva, R., Marcos, B., Georges, D., Lomba, A., 2019. Hoping the best, expecting the worst: forecasting the potential impacts of climate and land-use change on Iberian plants of conservation concern. Plant Ecology &. Diversity:1–12.
Avolio, M.L., Forrestel, E.J., Chang, C.C., La Pierre, K.J., Burghardt, K.T., Smith, M.D., 2019. Demystifying dominant species. New Phytol. 223 (3), 1106–1126.
Balmaceda-Huarte, R., Bettolli, M.L., 2022. Assessing statistical downscaling in Argentina: Daily maximum and minimum temperatures. Int. J. Climatol. 42 (16), 8423–8445.
Becerra, P.I., Catford, J.A., Inderjit, Luce McLeod, M., Andonian, K., Aschehoug, E.T., Montesinos, D., Callaway, R.M., Moles, A., 2018. Inhibitory effects of Eucalyptus globulus on understorey plant growth and species richness are greater in non-native regions. Glob. Ecol. Biogeogr. 27 (1), 68–76.
Beuchat, X., Schaefli, B., Soutter, M., Mermoud, A., 2012. A robust framework for probabilistic precipitations downscaling from an ensemble of climate predictions applied to Switzerland. J. Geophys. Res. Atmos. 117 (D3), n/a–n/a.
Blanchet, F.G., Cazelles, K., Gravel, D., Jeffers, E., 2020. Co-occurrence is not evidence of ecological interactions. Ecol. Lett. 23 (7), 1050–1063.
Boulangeat, I., Gravel, D., Thuiller, W., 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecol. Lett. 15, 584–593.
Bullock, J.M., Edwards, R.J., Carey, P.D., Rose, R.J., 2000. Geographical separation of two ulex species at three spatial scales: does competition limit species' ranges? Ecography 23, 257–271.
Bunce, R.G.H., Metzger, M.J., Jongman, R.H.G., Brandt, J., de Blust, G., Elena-Rossello, R., Groom, G.B., Halada, L., Hofer, G., Howard, D.C., Kovář, P., Mücher, C. A., Padoa-Schioppa, E., Paelinx, D., Palo, A., Perez-Soba, M., Ramos, I.L., Roche, P., Skånes, H., Wrbka, T., 2008. A standardized procedure for surveillance and monitoring European habitats and provision of spatial data. Landsc. Ecol. 23 (1), 11–25.
Burgos, E., Ceva, H., Perazzo, R.P.J., Devoto, M., Medan, D., Zimmermann, M., María Delbue, A., 2007. Why nestedness in mutualistic networks? J. Theor. Biol. 249 (2), 307–313.
Burnham, K.P., 2002. Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York.
Carvalho-Santos, C., Marcos, B., Nunes, J.P., Regos, A., Palazzi, E., Terzago, S., Monteiro, A.T., Honrado, J.P., 2019. Hydrological Impacts of Large Fires and Future Climate: Modeling Approach Supported by Satellite Data. Remote Sens. (Basel) 11, 2832.
Civantos, E., Monteiro, A.T., Gonçalves, J., Marcos, B., Alves, P., Honrado, J.P., 2018. Patterns of landscape seasonality influence passerine diversity: Implications for conservation management under global change. Ecol. Complex. 36, 117–125.
D'Amen, M., Dubuis, A., Fernandes, R.F., Pottier, J., Pellissier, L., Guisan, A., 2015. Using species richness and functional traits predictions to constrain assemblage predictions from stacked species distribution models. J. Biogeogr. 42 (7), 1255–1266.
Damgaard, C., Riis-Nielsen, T., Schmidt, I.K., 2009. Estimating plant competition coefficients and predicting community dynamics from non-destructive pin-point data: a case study with Calluna vulgaris and Deschampsia flexuosa. In: Van der Valk, A.G. (Ed.), Herbaceous Plant Ecology: Recent Advances in Plant Ecology. Springer, Netherlands, Dordrecht, pp. 323–333.
de Araújo, C.B., Marcondes-Machado, L.O., Costa, G.C., Silman, M., 2014. The importance of biotic interactions in species distribution models: a test of the Eltonian noise hypothesis using parrots. J. Biogeogr. 41 (3), 513–523.
Delalandre, L., Montesinos-Navarro, A., 2018. Can co-occurrence networks predict plant-plant interactions in a semi-arid gypsum community? Perspect. Plant Ecol. Evol. Syst. 31, 36–43.
Delibes-Mateos, M., Redpath, S.M., Angulo, E., Ferreras, P., Villafuerte, R., 2007. Rabbits as a keystone species in southern Europe. Biol. Conserv. 137 (1), 149–156.
Dormann, C.F., Strauss, R., Peres-Neto, P., 2014. A method for detecting modules in quantitative bipartite networks. Methods Ecol. Evol. 5 (1), 90–98.
Dornelas, M., Antão, L.H., Moyes, F., Bates, A.E., Magurran, A.E., Adam, D., Akhmetzhanova, A.A., Appeltans, W., Arcos, J.M., Arnold, H., Ayyappan, N., Badihi, G., Baird, A.H., Barbosa, M., Barreto, T.E., Bässler, C., Bellgrove, A., Belmaker, J., Benedetti-Cecchi, L., Bett, B.J., Bjorkman, A.D., Błażewicz, M., Blowes, S.A., Bloch, C.P., Bonebrake, T.C., Boyd, S., Bradford, M., Brooks, A.J., Brown, J.H., Bruelheide, H., Budy, P., Carvalho, F., Castañeda-Moya, E., Chen, C.A., Chamblee, J.F., Chase, T.J., Siegwart Collier, L., Collinge, S.K., Condit, R., Cooper, E. J., Cornelissen, J.H.C., Cotano, U., Kyle Crow, S., Damasceno, G., Davies, C.H., Davis, R.A., Day, F.P., Degraer, S., Doherty, T.S., Dunn, T.E., Durigan, G., Duffy, J.E., Edelist, D., Edgar, G.J., Elahi, R., Elmendorf, S.C., Enemar, A., Ernest, S.K.M.,
Escribano, R., Estiarte, M., Evans, B.S., Fan, T.-Y., Turini Farah, F., Loureiro Fernandes, L., Farneda, F.Z., Fidelis, A., Fitt, R., Fosaa, A.M., Daher Correa Franco, G.A., Frank, G.E., Fraser, W.R., García, H., Cazzolla Gatti, R., Givan, O.r., Gorgone-Barbosa, E., Gould, W.A., Gries, C., Grossman, G.D., Gutierréz, J.R., Hale, S., Harmon, M.E., Harte, J., Haskins, G., Henshaw, D.L., Hermanutz, L., Hidalgo, P., Higuchi, P., Hoey, A., Van Hoey, G., Hofgaard, A., Holeck, K., Hollister, R.D., Holmes, R., Hoogenboom, M., Hsieh, C.-H., Hubbell, S.P., Huettmann, F., Huffard, C.L., Hurlbert, A.H., Macedo Ivanauskas, N., Janík, D., Jandt, U., Jażdżewska, A., Johannessen, T., Johnstone, J., Jones, J., Jones, F.A.M., Kang, J., Kartawijaya, T., Keeley, E.C., Kelt, D.A., Kinnear, R., Klanderud, K., Knutsen, H., Koenig, C.C., Kortz, A.R., Král, K., Kuhnz, L.A., Kuo, C.-Y., Kushner, D. J., Laguionie-Marchais, C., Lancaster, L.T., Min Lee, C., Lefcheck, J.S., Lévesque, E., Lightfoot, D., Lloret, F., Lloyd, J.D., López-Baucells, A., Louzao, M., Madin, J.S., Magnússon, B., Malamud, S., Matthews, I., McFarland, K.P., McGill, B., McKnight, D., McLarney, W.O., Meador, J., Meserve, P.L., Metcalfe, D.J., Meyer, C.F. J., Michelsen, A., Milchakova, N., Moens, T., Moland, E., Moore, J., Mathias Moreira, C., Müller, J., Murphy, G., Myers-Smith, I.H., Myster, R.W., Naumov, A., Neat, F., Nelson, J.A., Paul Nelson, M., Newton, S.F., Norden, N., Oliver, J.C., Olsen, E.M., Onipchenko, V.G., Pabis, K., Pabst, R.J., Paquette, A., Pardede, S., Paterson, D.M., Pélissier, R., Peñuelas, J., Pérez-Matus, A., Pizarro, O., Pomati, F., Post, E., Prins, H.H.T., Priscu, J.C., Provoost, P., Prudic, K.L., Pulliainen, E., Ramesh, B.R., Mendivil Ramos, O., Rassweiler, A., Rebelo, J.E., Reed, D.C., Reich, P. B., Remillard, S.M., Richardson, A.J., Richardson, J.P., van Rijn, I., Rocha, R., Rivera-Monroy, V.H., Rixen, C., Robinson, K.P., Ribeiro Rodrigues, R., de Cerqueira Rossa-Feres, D., Rudstam, L., Ruhl, H., Ruz, C.S., Sampaio, E.M., Rybicki, N., Rypel, A., Sal, S., Salgado, B., Santos, F.A.M., Savassi-Coutinho, A.P., Scanga, S., Schmidt, J., Schooley, R., Setiawan, F., Shao, K.-T., Shaver, G.R., Sherman, S., Sherry, T.W., Siciński, J., Sievers, C., da Silva, A.C., Rodrigues da Silva, F., Silveira, F.L., Slingsby, J., Smart, T., Snell, S.J., Soudzilovskaia, N.A., Souza, G.B.G., Maluf Souza, F., Castro Souza, V., Stallings, C.D., Stanforth, R., Stanley, E.H., Mauro Sterza, J., Stevens, M., Stuart-Smith, R., Rondon Suarez, Y., Supp, S., Yoshio Tamashiro, J., Tarigan, S., Thiede, G.P., Thorn, S., Tolvanen, A., Teresa Zugliani Toniato, M., Totland, Ø., Twilley, R.R., Vaitkus, G., Valdivia, N., Vallejo, M.I., Valone, T.J., Van Colen, C., Vanaverbeke, J., Venturoli, F., Verheye, H.M., Vianna, M., Vieira, R.P., Vrška, T., Quang Vu, C., Van Vu, L., Waide, R.B., Waldock, C., Watts, D., Webb, S., Wesolowski, T., White, E.P., Widdicombe, C.E., Wilgers, D., Williams, R., Williams, S.B., Williamson, M., Willig, M.R., Willis, T.J., Wipf, S., Woods, K.D., Woehler, E.J., Zawada, K., Zettler, M.L., Hickler, T., 2018. BioTIME: A database of biodiversity time series for the Anthropocene. Glob. Ecol. Biogeogr. 27 (7), 760–786.
Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol. Lett. 5 (4), 558–567.
Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu. Rev. Ecol. Evol. Syst. 40 (1), 677–697.
Estrada, A., Morales-Castilla, I., Caplat, P., Early, R., 2016. Usefulness of Species Traits in Predicting Range Shifts. Trends Ecol. Evol. 31 (3), 190–203.
Fabozzi, F.J., Focardi, S.M., Rachev, S.T., Arshanapalli, B.G., 2014. The Basics Of Financial Econometrics: Tools, Concepts, And Asset Management Applications. John Wiley & Sons.
Ford, B.M., Roberts, J.D., Tittensor, D., 2019. Evolutionary histories impart structure into marine fish heterospecific co-occurrence networks. Glob. Ecol. Biogeogr. 28 (9), 1310–1324.
Franklin, J., Serra-Diaz, J.M., Syphard, A.D., Regan, H.M., 2016. Global change and terrestrial plant community dynamics. PNAS 113 (14), 3725–3734.
Garbin, M.L., Guidoni-Martins, K.G., Hollunder, R.K., Mariotte, P., Scarano, F.R., Carrijo, T.T., 2016. Spatial segregation of subordinate species is not controlled by the dominant species in a tropical coastal plant community. Perspect. Plant Ecol. Evol. Syst. 18, 23–32.
García-Girón, J., Heino, J., García-Criado, F., Fernández-Aláez, C., Alahuhta, J., 2020. Biotic interactions hold the key to understanding metacommunity organisation. Ecography 43 (8), 1180–1190.
GDAL. 2020. Geospatial Data Abstraction Library.
Giannini, T.C., Chapman, D.S., Saraiva, A.M., Alves-dos-Santos, I., Biesmeijer, J.C., 2013. Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants. Ecography 36 (6), 649–656.
Gonçalves, J., Alves, P., Pôças, I., Marcos, B., Sousa-Silva, R., Lomba, Â., Honrado, J.P., 2016. Exploring the spatiotemporal dynamics of habitat suitability to improve conservation management of a vulnerable plant species. Biodivers. Conserv. 25 (14), 2867–2888.
Grant, K., Kreyling, J., Heilmeier, H., Beierkuhnlein, C., Jentsch, A., 2014. Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. Ecol. Res. 29 (5), 991–1001.
Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models: With Applications in R. Cambridge University Press, Cambridge.
Harvey, E., Gounand, I., Ward, C.L., Altermatt, F., Cadotte, M., 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. J. Appl. Ecol. 54 (2), 371–379.
Hines, J., Keil, P., 2020. Common competitors and rare friends. Nat. Ecol. Evol. 4, 8–9.
Jaberalansar, Z., Tarkesh, M., Bassiri, M., 2018. Spatial downscaling of climate variables using three statistical methods in Central Iran. J. Mt. Sci. 15 (3), 606–617.
Jensen, A.M., Löf, M., Witzell, J., 2012. Effects of competition and indirect facilitation by shrubs on Quercus robur saplings. Plant Ecol. 213 (4), 535–543.
Jordán, F., Okey, T.A., Bauer, B., Libralato, S., 2008. Identifying important species: linking structure and function in ecological networks. Ecol. Model. 216 (1), 75–80.

Kaiser-Bunbury, C.N., Blüthgen, N., 2015. Integrating network ecology with applied conservation: a synthesis and guide to implementation. AoB PLANTS 7, plv076.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4, 170122.

Kay, G.M., Tulloch, A., Barton, P.S., Cunningham, S.A., Driscoll, D.A., Lindenmayer, D.B., 2017. Species co-occurrence networks show reptile community reorganization under agricultural transformation. Ecography 41 (1), 113–125.

Klanderud, K., Vandvik, V., Goldberg, D., Armas, C., 2015. The Importance of Biotic vs. Abiotic Drivers of Local Plant Community Composition Along Regional Bioclimatic Gradients. PLoS One 10 (6), e0130205.

Kraft, N.J.B., Ackerly, D.D., 2014. Assembly of Plant Communities. In: Monson, R.K. (Ed.), Ecology and the Environment. Springer New York, New York, NY, pp. 67–88.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.-F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2015. Plant functional traits have globally consistent effects on competition. Nature 529 (7585), 204–207.

le Roux, P.C., Lenoir, J., Pellissier, L., Wisz, M.S., Luoto, M., 2013. Horizontal, but not vertical, biotic interactions affect fine-scale plant distribution patterns in a low-energy system. Ecology 94 (3), 671–682.

le Roux, P.C., Pellissier, L., Wisz, M.S., Luoto, M., Heard, M., 2014. Incorporating dominant species as proxies for biotic interactions strengthens plant community models. J. Ecol. 102 (3), 767–775.

Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecol. Model. 195 (3-4), 153–171.

Lomba, A., Vicente, J., Moreira, F., Honrado, J., 2011. Effects of multiple factors on plant diversity of forest fragments in intensive farmland of Northern Portugal. For. Ecol. Manage. 262 (12), 2219–2228.

Lynn, J.S., Kazenel, M.R., Kivlin, S.N., Rudgers, J.A., 2019. Context-dependent biotic interactions control plant abundance across altitudinal environmental gradients. Ecography 42 (9), 1600–1612.

Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.-C., Thuiller, W., Araújo, M.B., Guisan, A., Zimmermann, N.E., 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. Ecography 33 (6), 1038–1048.

Nelder, J.A., Wedderburn, R.W.M., 1972. Generalized Linear Models. Journal of the Royal Statistical Society: Series A (General) 135, 370–384.

Nemer, D., Liancourt, P., Delerue, F., Randé, H., Michalet, R., 2021. Species stress tolerance and community competitive effects drive differences in species composition between calcareous and siliceous plant communities. J. Ecol. 109 (12), 4132–4142.

Oppen, J., Normand, S., Bjorkman, A.D., Blach-Overgaard, A., Assmann, J.J., Forchhammer, M., Guéguen, M., Nabe-Nielsen, J., Sabatini, F.M., 2021. Annual air temperature variability and biotic interactions explain tundra shrub species abundance. J. Veg. Sci. 32 (2), e13009.

Pellissier, L., Anne Bråthen, K., Pottier, J., Randin, C.F., Vittoz, P., Dubuis, A., Yoccoz, N. G., Alm, T., Zimmermann, N.E., Guisan, A., 2010a. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. Ecography 33 (6), 1004–1014.

Pellissier, L., Anzini, M., Maiorano, L., Dubuis, A., Pottier, J., Vittoz, P., Guisan, A., Cousins, S., 2013. Spatial predictions of land-use transitions and associated threats to biodiversity: the case of forest regrowth in mountain grasslands. Appl. Veg. Sci. 16 (2), 227–236.

R Core Team. 2021. R: A Language and Environment for Statistical Computing,.

Pellissier, L., Fournier, B., Guisan, A., Vittoz, P., 2010b. Plant traits co-vary with altitude in grasslands and forests in the European Alps. Plant Ecol. 211, 351–365.

Rodríguez-García, E., Bravo, F., Spies, T.A., 2011. Effects of overstorey canopy, plant–plant interactions and soil properties on Mediterranean maritime pine seedling dynamics. For. Ecol. Manage. 262 (2), 244–251.

Roux, P.C.l., Virtanen, R., Heikkinen, R.K., Luoto, M., 2012. Biotic interactions affect the elevational ranges of high-latitude plant species. Ecography 35 (11), 1048–1056.

Stephenson, F., Gladstone-Gallagher, R.V., Bulmer, R.H., Thrush, S.F., Hewitt, J.E., Iacona, G., 2022. Inclusion of biotic variables improves predictions of environmental niche models. Divers. Distrib. 28 (7), 1373–1390.

Sun, X., Zhao, L., Zhao, D., Huo, Y., Tan, W., 2020. Keystone species can be identified based on motif centrality. Ecol. Ind. 110, 105877.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. Nature 546 (7656), 73–81.

Triviño, M., Kujala, H., Araújo, M.B., Cabeza, M., 2018. Planning for the future: identifying conservation priority areas for Iberian birds under climate change. Landsc. Ecol. 33 (4), 659–673.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol. Rev. 88 (1), 15–30.

Wu, W., Wang, X., Ren, Z., Zhou, X., Du, G., 2022. N-induced species loss dampened by clipping mainly through suppressing dominant species in an alpine meadow. Front. Plant Sci. 13.

Yamazaki, D., Ikeshima, D., Tawatari, R., Yamaguchi, T., O'Loughlin, F., Neal, J.C., Sampson, C.C., Kanae, S., Bates, P.D., 2017. A high-accuracy map of global terrain elevations. Geophys. Res. Lett. 44 (11), 5844–5853.