

Original Articles

How vulnerable are bryophytes to climate change? Developing new *species* and *community vulnerability indices*

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ABSTRACT

Species' vulnerability to climate change is often assessed by focusing on potential changes of species' ranges. This study aimed to develop community-level vulnerability indices which measure bryophyte community vulnerability to climate change, based on the best set of factors summarizing species' niche or geographic properties expected to respond to climate change.

We used a dataset on 39 saxicolous bryophytes from the Iberian Peninsula, highly sensitive to climate shifts. Niche metrics were calculated using a recently described hypervolume-based approach. Spatial metrics were derived from habitat suitability model (HSM) projections. We then compared regression models based on niche or spatial metrics to evaluate which ones improve species range shifts forecast. The final vulnerability score for each species, the Species Vulnerability Index (SVI), was calculated by applying a weighted sum of all the relevant parameters. We then generated a spatial representation of vulnerability values for the whole community through HSMs and obtained three Community Vulnerability Indices (CVIs), according to different statistical aggregation measures (average, maximum and standard deviation).

SVI assigns maximum vulnerability to species with smaller niche breadth and higher marginality in the community environmental niche space continuum, allowing to rank bryophyte species according to their vulnerability. Given the overall importance of niche-hypervolume metrics in SVI and CVIs, we rename it, respectively, as Niche Hypervolume Species Vulnerability Index (NHSVI) and Niche Hypervolume Community Vulnerability Indices (NHCVIs).

Overall, saxicolous bryophyte communities with the greatest average vulnerability to climate change are those at the high mountains of the northern, central and southern regions of the Iberian Peninsula. Results suggest that vulnerability patterns are structured locally not only due to species richness but also to community composition. The three NHCVIs provided complementary insights into the study area's community vulnerability distribution.

This study shows that NHSVI can prioritise vulnerable species to climate change, and NHCVIs can depict community-wise vulnerability hotspots, thereby informing policymakers in the definition of bryophyte species conservation measures.

1. Introduction

According to the 2030 Agenda for Sustainable Development (UN,

2019), it is urgent to take action to tackle climate change and its impacts. Climate change is affecting the composition and functioning of ecosystems across the globe and driving a universal redistribution of life

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on Earth (Pech et al., 2017). However, predicting the extent and directionality of future species range shifts is an ongoing challenge and crucial to conservation decision-making (Guisan et al., 2013).

Bryophytes comprise an important part of the Iberian biodiversity (Hodgetts et al., 2019), and species inhabiting mountains may be most at risk from the detrimental effects of climate change (Nogués-Bravo et al., 2007; Pauli et al., 2012). An elevational shift of bryophyte species was already detected in the last century, supporting the evidence that bryophyte species are extremely sensitive to climate change (Bergamini et al., 2009; Tuba et al., 2011). Nevertheless, it is generally not well known whether they can cope with future climate changes (He et al., 2016). A new study recently highlighted that even organisms like bryophytes with high dispersal capacities are expected to lag behind future climate change (Zanatta et al., 2020).

Species' vulnerability to global change can be affected by different types of species attributes, including habitat specialization, environmental tolerance, rarity or intrinsic traits (Foden et al., 2019; Pacifici et al., 2015). As such, the quantification of ecological niches, as an outcome of species-environment relationships, has regained interest in the context of climate change, raising the issue of the usefulness of niche quantification for predicting future species distributions (Broennimann et al., 2006; Cianfrani et al., 2018; Thuiller et al., 2005).

The ecological niche can be defined as an n -dimensional hypervolume in environmental space where species' populations can persist (Hutchinson, 1957). However, the quantification of species' niches remains challenging since there is no single best way to delineate hypervolumes (Blonder et al., 2018). Currently, several methods exist to estimate a hypervolume, each with different underlying assumptions and specific limitations, such as ordination procedures (e.g. principal component analysis; outlying means index) or bioclimatic envelope models (Blonder et al., 2014). Only recently, a new estimation method using a stochastic geometry approach was proposed, handling high-dimensional datasets and overcoming conceptual issues that have previously limited the development of a more direct approach to measuring hypervolumes (Blonder et al., 2014; Blonder et al., 2018). Geometrical concepts can be used to describe a hypervolume, which can be further defined as a subset of the space with an n -dimensional geometrical shape (Blonder, 2018). After being delineated in an n -dimensional space, a hypervolume can be summarized by several metrics related to different properties, including its breadth (also sometimes defined as width or size), position and overlap between other co-occurring species (Blonder et al., 2018). Niche breadth can provide a comparative or relative measure of the ecological specialization or climatic tolerance of a species, separating generalists, species with large and broad ecological niches that have wide environmental tolerances, from specialists, which have smaller niches and tolerate a limited range of environmental conditions (Devictor et al., 2010). Niche position measures species' marginality, i.e., how further its environmental requirements are from the mean conditions available in a given region (Devictor et al., 2010) or the mean conditions for a group of species or community. Niche overlap estimation is based on the assumption that species with a low rate of niche overlap co-occur with fewer species and, therefore, can be considered niche specialists, while species with a high rate of niche overlap co-occur with more species, being considered niche generalists (Broennimann et al., 2012). This metric, similarly to niche breadth and position, reflects species' response to the environment (*sensu* Grinnellian niche) and accounts for co-occurring species that are usually shaped by biotic interactions (*sensu* Eltonian niche).

Previous studies highlighted that niche properties might be powerful indicators of species sensitivity to climate change, including plants (Broennimann et al., 2006; Thuiller et al., 2005), bumblebees (Williams et al., 2007), frogs (Botts et al., 2013), reptiles (Nori et al., 2016), and otters (Cianfrani et al., 2018). Under projected climate changes, specialist species with narrower niche breadths are generally expected to be more sensitive and vulnerable to climate change than generalists and thus more threatened in the near-future (Broennimann et al., 2006;

Thuiller et al., 2005). Similarly, according to niche theory, marginal species, with requirements that do not correspond to average climate conditions in a given region, should also be more sensitive to climate change than species that have their optimum close to or coinciding with the centroid of the realized environmental space (Broennimann et al., 2006; Thuiller et al., 2005). Niche theory has also been applied in several bryophyte studies, using niche measures in structuring bryophyte communities (Birks et al., 1998; Glime & Vitt, 1987; Slack, 1997).

The most conspicuous application of the niche concept has been developing different methods to estimate the suitability of ecological conditions to evaluate species distributions (Cerdeira et al., 2018; Franklin & Miller, 2009; Guisan & Rahbek, 2011; Guisan & Zimmermann, 2000). Habitat suitability models combine species occurrence or abundance observations with the spatial representation of environmental factors to express species habitat suitability in a spatially explicit way across a study area (Guisan et al., 2017). Geographic range size is one of the fundamental ecological characteristics of a species and a strong predictor of extinction potential (Gaston & Fuller, 2009). Besides range size, other range characteristics, such as shape, boundaries, overlaps, and internal structure, are also important to understand the distribution of species and reflect the influences of environmental limiting factors and dispersal (Brown et al., 1996; Peterson et al., 2011).

The recent need to assess the potential consequences of future climate change on species has resulted in various approaches to assess climate change-driven risks that can contribute to adaptive management to elucidate current and future conservation decisions (Wheatley et al., 2017). Habitat suitability models (also called species distribution models or ecological niche models) have been the most widely used tool to assess the impact of projected climate change on future species distributions and biodiversity patterns (Guisan et al., 2017). Different modelling approaches have been proposed or applied at the community level (D'Amen et al., 2018; D'Amen et al., 2017; Ferrier & Guisan, 2006) and to different taxonomic groups, including bryophytes (Desamoredé et al., 2012; Patiño et al., 2016; Sérgio et al., 2014).

Another common approach to evaluate the effects of climate change on biodiversity is assessing species' sensitivity to climate change effects to derive coarse indices or categories of vulnerability (Pacifici et al., 2015). Several climate change vulnerability indices have already been developed and applied to different taxonomic groups, including plants (Rogers et al., 2017; Still et al., 2015). However, there is no single standardized way to measure vulnerability, and alternative approaches have been emerging, such as biological trait-based approaches, mechanistic analyses and combined approaches (Foden et al., 2019; Willis et al., 2015). Climate change vulnerability assessments commonly incorporate exposure, sensitivity and adaptability to determine the degree of threat that climate change poses at the species-level, but more studies are needed to understand global change responses at the community-level (Smith et al., 2020) and provide insight into the spatial variation in vulnerability across a study area (Davison et al., 2012; Rinnan & Lawler, 2019).

Our main aim is to develop community-level vulnerability indices capable of quantitatively and spatially assessing bryophyte community vulnerability to climate change. Particularly, our objectives were to (i) evaluate the evidence of niche or spatial metrics to forecast the vulnerability of species to climate change, (ii) assess spatial variation in the study area for the community vulnerability indices and, (iii) test spatially correlated patterns between species richness and community vulnerability indices.

We illustrate the applicability of the community vulnerability indices using saxicolous bryophyte communities from the Iberian Peninsula as an example of a conservation target to make effective decisions and prioritize bryophyte communities' conservation.

2. Methods

2.1. Study area and biological dataset

We used distribution data from three well-known saxicolous bryophyte genera, commonly found on open areas such as exposed rock outcrops in the Iberian Peninsula (Fig. 1). The study area climate ranges from dry Mediterranean in the Southeast to wet Temperate Atlantic in the North (Loidi, 2017). The main mountain ranges of the Iberian Peninsula are the Pyrenees, which reach 3404 m in height, the Cantabrian Mountains (2650 m) and the northwest mountain region in the northern region; the Iberian System (2316 m) and the Central System (2592 m) in the central region; and the Baetic System, with the highest point of Iberia located in the Sierra Nevada at 3478 m in the south region. Acidic rocks dominate in the western half of Iberia, while Carbonated materials such as limestone, marls, some dolomites and gypsum are frequently dominant in the east.

After proper revision of specimens from different herbaria, we compiled 4112 records of 39 species (8 belonging to *Andreaea* genus, 21 to *Grimmia* genus, and 10 to *Racomitrium* genus) (Appendix A). Only records with sampling locality at a spatial resolution of 1 Km and specimens revised for the Iberian Peninsula by the authors' HH, KC and JM, known from more than 10 Iberian localities, were used for this study.

2.2. Environmental variables

The nineteen Worldclim (version-1.4) bioclimatic variables at a spatial resolution of 1 Km were considered as independent variables (Hijmans et al., 2005). Different topographic indicators were also derived using elevation data from Shuttle Radar Topography Mission (SRTM, version 4) at 90 m of spatial resolution, namely, slope, aspect and topographic roughness index. We used the average value of all 90 m

pixels included in 1 Km to calculate such topographic indicators. Soil pH was derived from the quantitative map of estimated soil pH values across Europe (Map of Soil pH in Europe, 2010) and resampled from 5 Km to 1 Km (method bilinear) to match the spatial resolution of climate predictors. To avoid multicollinearity, we performed a preliminary correlation analysis between all the environmental variables and eliminated those variables in each pair that showed a Pearson correlation (r) value of $|r|$ greater than 0.8 (Guisan et al., 2017), and also taking into account the variables most relevant for explaining bryophyte species habitat. The final environmental dataset included the mean temperature of the coldest quarter (BIO11), precipitation of the driest quarter (BIO17), precipitation of the coldest quarter (BIO19), aspect (ASPR), topographic roughness index (TOPRI) and soil pH (SOIPH) (Table 1).

2.3. Habitat suitability modelling

We used the 'biomod2' R package, implementing a correlative multi-algorithm ensemble consensus approach (Thuiller, 2003; Thuiller et al., 2009) to investigate species-environment relations and to project the obtained Habitat Suitability Models (HSMs) for current climatic conditions (see Appendix C for more details). Based on HSM's, future projections (considering year 2050) were obtained for each species and independently for two different Global Climate Models (GCMs) recommended for Europe and Mediterranean climates (Brands et al., 2013). These were MPI-ESM-LR (Max-Planck-Institut für Meteorologie in Germany) and HadGEM2-ES (Hadley Centre for Climate Prediction and Research in the UK), under two Representative Concentration Pathways (RCP) 4.5 and 8.5 proposed by the Intergovernmental Panel on Climate Change. Species range contraction or the loss of environmentally suitable areas was calculated by comparing model projections between current and future climatic conditions.

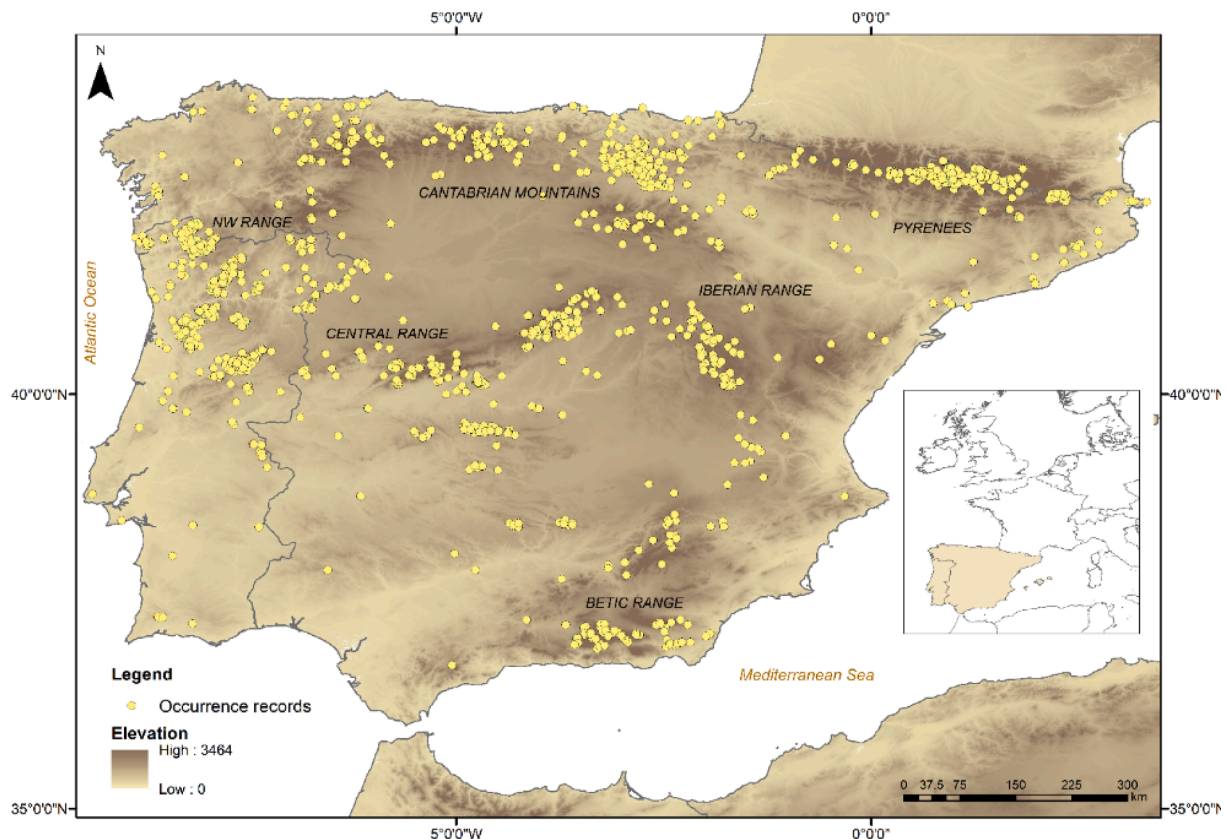


Fig. 1. Study area location and distribution of occurrence records for all species.

Table 1
Predictive variables description.

| Environmental variables | |
|--|--|
| BIO11 | Mean Temperature of Coldest Quarter (derived from Worldclim 1 km) |
| BIO17 | Precipitation of Driest Quarter (derived from Worldclim 1 km) |
| BIO19 | Precipitation of Coldest Quarter (derived from Worldclim 1 km) |
| ASPBR | Aspect Beers Transformation (derived from DEM – SRTM 90 m) |
| TOPRI | Topographic Roughness Index (derived from DEM – SRTM 90 m) |
| SOIPH | Soil pH (derived from the European Soil Data Centre) |
| Predictors – Niche metrics | |
| Niche breadth | Log10 Niche hypervolume size using the SVM method |
| Niche position | Distance between species hypervolume centroid and the hypervolume centroid of all species records |
| Niche overlap | Average overlap between species hypervolumes (Jaccard Index) |
| Predictors – Spatial metrics | |
| Range size | Number of predicted suitable pixels (range size in km ² ; TSS metric as the threshold) |
| Spatial position | Distance between the centroid of each species suitable area and the centroid of all species suitable area (km) |
| Spatial overlap | Average overlap between species suitable area (Jaccard Index) |
| Response variables – Range contraction | |
| pLoss_he45 | % of loss in terms of suitable area for the HadGEM2-ES (RCP 4.5) 2050 scenario |
| pLoss_he85 | % of loss in terms of suitable area for the HadGEM2-ES (RCP 8.5) 2050 scenario |
| pLoss_mp45 | % of loss in terms of suitable area for the MPI-ESM-LR (RCP 4.5) 2050 scenario |
| pLoss_mp85 | % of loss in terms of suitable area for the MPI-ESM-LR (RCP 8.5) 2050 scenario |

2.4. Spatial and niche metrics

We derived a set of niche and spatial metrics that summarize each species’ niche and geographic properties, expected to respond to climate change shifts. For that, we jointly quantified species’ niches (in

environmental space) and their spatial distributions (in geographic space), using three main conceptually equivalent metrics but considering different spaces, i.e., the environmental and the geographic space: (i) niche breadth vs range size, (ii) niche position vs spatial position and, (iii) niche overlap vs spatial overlap (Fig. 2).

Spatial metrics (spatial predictors) were calculated for the geographic space based on HSM projections (Table 1; Appendix B). Using R, we calculated the range size as the total surface area (Km²) projected by the final models for current conditions, i.e. the surface of current suitable space for each species. The spatial position was calculated as the distance between the centroid of each species suitable area and the centroid of all species suitable areas. Spatial overlap was calculated as the average overlap between species suitable areas.

Niche metrics (niche predictors) were calculated using the ‘hypervolume’ R package (Blonder et al., 2014), combining the occurrence data and the six environmental variables selected. This method uses a stochastic geometry approach and is a new tool to quantify high-dimensional ecological hypervolumes. We applied the one-class Support Vector Machine estimation method since it is considered the most appropriate method in very-high dimensionality analyses and for most realized niche modelling applications where the limits of the observed data are of most interest (Blonder et al., 2018). We calculated the three following metrics: niche breadth, niche position and niche overlap (Table 1; Appendix B). Niche breadth was measured as the hypervolume size, niche position was estimated as the distance between the centroid of each species hypervolume, and the centroid of all species hypervolume (i.e. community-wise hypervolume, combining all species records) and niche overlap was calculated as the average overlap between one species hypervolume and the remaining ones.

2.5. Calculation of community vulnerability indices

The implementation of Community Vulnerability Indices includes the following three-step procedure: (i) Model selection; (ii) Species Vulnerability Index (SVI); and (iii) Community Vulnerability Indices (CVIs). All statistical analyses were developed in R statistical software (R Core Team, 2019).

i) Step I: Model selection

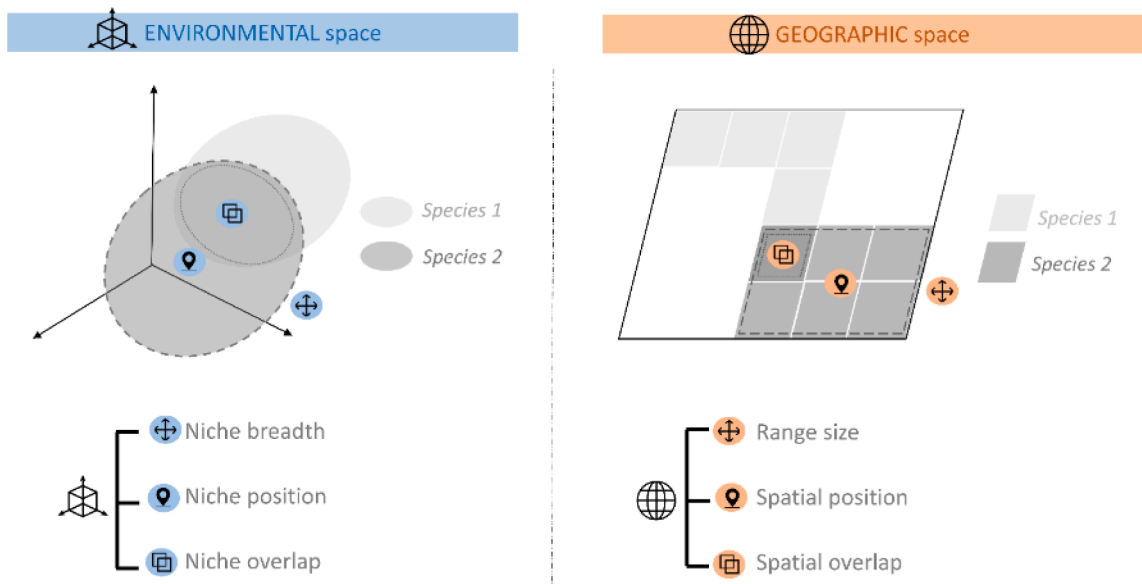


Fig. 2. Conceptual diagram of niche and spatial metrics in the environmental and geographic space, respectively. Icons representing niche and spatial metrics were downloaded from the noun project (<https://thenounproject.com/>): environmental space by Jamison Wieser; geographic space by Graphic Tigers; breadth/size by Tim Neumann; position by atlantamountain; overlap by Joe pictos.

Before model selection, exploratory univariate linear regression models were performed to relate niche or spatial metrics (predictors) with projected range contraction (response variable) (Fig. 3). In addition, to test for these relationships, the species occurrence dataset was randomly split into two independent subsets with equal size. Afterwards, we used each independent subset of species occurrences to train models (HSM and hypervolumes) and calculate both predictor and response variables. Linear regression was then used to show the association between response and predictors for set 1 against set 2 and vice-versa. The full dataset was also used for this purpose and compared with independent sets.

For performing a more in-depth analysis using multivariate models, we then devised a list of model hypotheses and candidate models based on niche or spatial metrics (Table 2) and evaluated which ones improve species vulnerability forecast (according to each climate change scenario).

We tested for additive or interactive effects using multiple linear regressions that test for the significance of the additive or nonadditive combination between niche or spatial metrics and range contraction. Prior to model fitting, all the niche and spatial metrics were standardized, subtracting the variable's mean and dividing the result by the standard deviation (i.e., z-scoring). We then used the Akaike's Information Criterion (AIC) multimodel selection approach to compare and rank the candidate models (Table 2). Complementarily, we also performed repeated k-fold cross-validation, in which a subset of the data are left out of the model and used instead for model testing, specifically 100 × 5-fold cross-validation. Based on this procedure, we calculated general measures of prediction performance (R^2 and Root-mean-square-error). Models selected by AIC-based multimodel were well-supported in cross-validation. Therefore, our model selection was based only on the AIC-based multimodel ranking approach (Appendix D), an appropriate and robust approach to compare the weight of evidence for any number of models and designed to approximate predictive performance (Tredennick et al., 2021). This framework enables comparing and

Table 2

Candidate model set.

| Model code | Candidate models | Type of models | Metrics |
|------------|--|----------------|---------|
| 1 | <i>Niche breadth</i> | Single | Niche |
| 2 | <i>Niche position</i> | Single | Niche |
| 3 | <i>Niche overlap</i> | Single | Niche |
| 4 | <i>Range size</i> | Single | Spatial |
| 5 | <i>Spatial position</i> | Single | Spatial |
| 6 | <i>Spatial overlap</i> | Single | Spatial |
| 7 | <i>Niche breadth + niche position + niche overlap</i> | Additive | Niche |
| 8 | <i>Range size + spatial position + spatial overlap</i> | Additive | Spatial |
| 9 | <i>Niche breadth + niche position</i> | Additive | Niche |
| 10 | <i>Niche breadth * niche position</i> | Interactive | Niche |
| 11 | <i>Null model</i> | | |

ranking multiple competing models through the Akaike Information Criterion adjusted for small sample size (AICc). Using the 'AICcmodavg' R package (Mazerolle, 2019), we selected only the models that were contained in the confidence set defined by a $\Delta AICc < 2$ (Burnham & Anderson, 2002). Finally, metrics selected more often in the AIC-based multimodel ranking approach were applied in the subsequent step.

ii) Step II: Species Vulnerability Index (SVI)

The final vulnerability score for each species (i) in the community was calculated by applying a simple weighted sum of all the components of the index (i.e. based on the metrics selected more often in step I), according to the formula:

$$SVI_i = \sum_{j=1}^N w_j M_{ji} \quad (1)$$

In Eq. (1), w stands for the weight attributed to each selected spatial

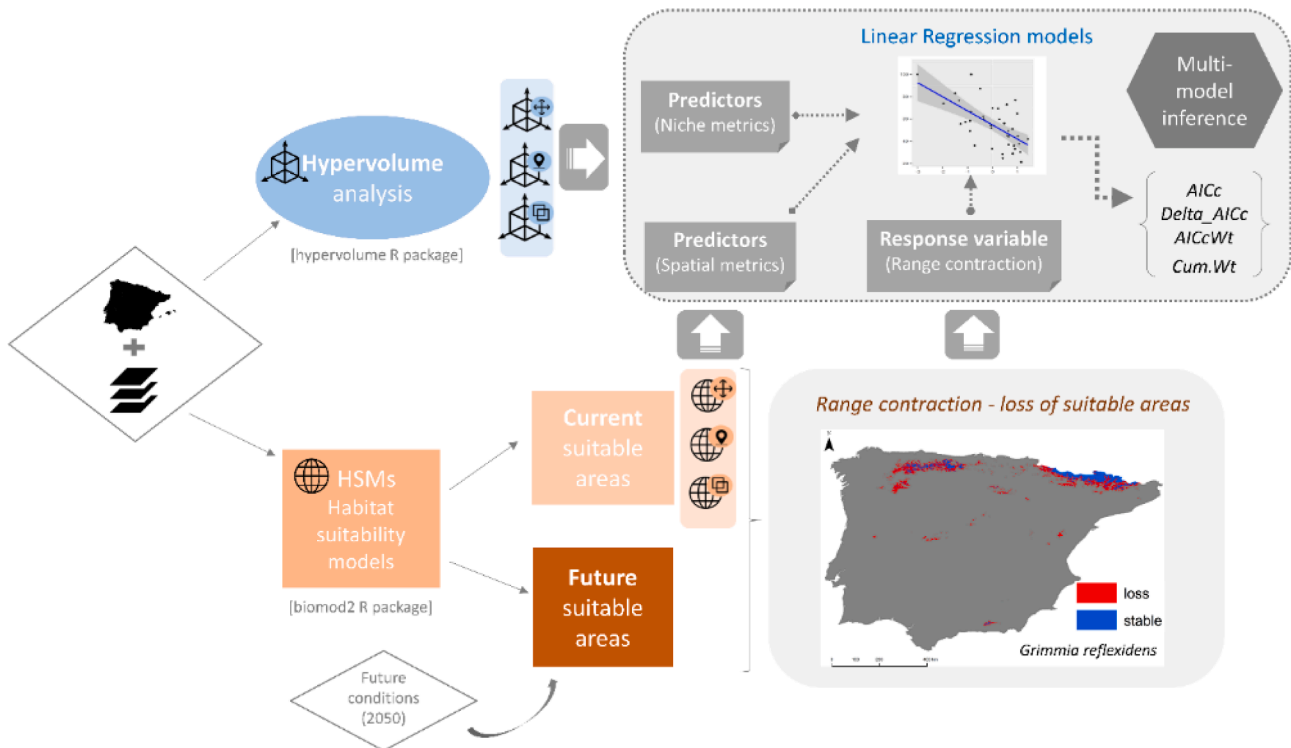


Fig. 3. Workflow detailing the process of selecting the metrics/predictors with 'good' predictive capacity of species vulnerability to climate change. See Fig. 2 for icons representing niche and spatial metrics. Additional icons were downloaded from the noun project (<https://thenounproject.com/>): the Iberian Peninsula by Zarthon; layer overlay by Stanislav Levin.

or niche-based metric, and M for the score of each selected metric j (with N equal to the total number of selected metrics). In our approach, weights were used to adjust each metric's scale and assign more or less importance to each selected one. In our case, selection frequency in AIC-based multimodel ranking (as a proxy of each metric importance) was also considered to assign weights. Also, the sign of each weight reflects if the overall effect of each metric on vulnerability is either positive or negative (e.g., greater range size is expected to have lower vulnerability hence the weight attributed to that metric would be negative).

After calculating the SVI_i for each i -th species in the community, values were normalized within the 0 – 1 range as follows:

$$SVIn = \frac{SVI_i - \min(SVI_{i=1 \dots S})}{\max(SVI_{i=1 \dots S}) - \min(SVI_{i=1 \dots S})} \quad (2)$$

where the $SVIn$ is the normalized vulnerability value for each species in the community, and S is the total number of species in the community ($S = 39$ in our particular case).

After calculating Eq. (2), we obtained the final vulnerability score for each species in the community. It should be noted that a $SVIn$ score of zero does not mean a species is not vulnerable. This simply derives from the normalization of the vulnerability score across species in the target community. A zero value is indicative of the species ranked less vulnerable in relative terms community-wise.

To generate a spatial representation of SVI , we first multiplied the final vulnerability score by the binary model of each species and then by the habitat suitability of each species obtained from habitat suitability models. By first multiplying the final vulnerability score by the binary model of each species, we eliminate from this spatial representation of community vulnerability locations with unsuitable environmental conditions. This multiplication also avoids diametrically opposing situations where vulnerability would be mapped in locations where a species is highly unlikely to occur. This way, we attribute higher vulnerability to those locations where the species is more likely to have suitable environmental conditions. Calculations were performed at pixel-level for each species $i = 1, \dots, S$ in the community (with S equal to the total number of species) by implementing the following straightforward formula:

$$SVIhs = B_i \times H_i \times SVIn \quad (3)$$

where B_i is the binary model of each species i , $B_i = \{0 - \text{non-suitable}, 1 - \text{suitable}\}$ and H_i is the habitat suitability value (rescaled by biomod2 package between 0 and 1000) for a given species i . Eq. (3) will assign higher spatial vulnerability to a species with larger SVI and suitability (but conditioned by the term B_i only to suitable locations).

iii) Step III: Community Vulnerability Indices (CVIs)

By applying Eq. (3), we obtained a stack of vulnerability maps for each species, with each pixel having a distribution of vulnerability values for the whole community. From this stack, we aggregated values pixel-wise and calculated specific quantities of interest, such as:

- the average, for understanding centrality of community vulnerability distribution ($CVIav$);
- the maximum, as a representation of the highest level of community vulnerability, found in a particular location ($CVImx$);
- the standard deviation, as a measure of the dispersion of community vulnerability rankings ($CVIstd$).

To analyse spatially correlated patterns between species richness and the different CVIs (average, maximum, standard deviation), we calculated the local Pearson correlation coefficients using the 'raster' R package (Hijmans, 2020), with a focal neighbourhood of 5 km.

3. Results

3.1. Niche and spatial metrics

To better infer the relationship between niche or spatial metrics (predictors) with projected range contraction (response variable), we followed a procedure based on cross-validation with two independent subsets of species occurrences (alternating) as both predictor and response variables. This procedure supports that the magnitude and direction of these associations are very similar across subsets (Fig. 4). Overall, range contraction is negatively correlated to niche breadth, niche overlap and range size across different scenarios (Fig. 4, example only shown for he – HadGEM2-ES and RCP's 4.5). Species with narrower niche breadth, lower niche overlap and restricted ranges are more likely to experience range contractions (Appendix D, Fig. D.2-5). On the other hand, range contraction is positively correlated with niche position (Fig. 4), indicating that species with a higher degree of marginality are more likely to experience range contractions (Appendix D, Fig. D.2-5).

The AIC-based multimodel ranking approach supported the evidence of niche breadth and niche position as reliable predictors to respond to climate change shifts since these metrics were selected more often (Fig. 5).

AIC-based model ranking showed that the best models explaining species range contractions, taking into account the HadGEM2-ES/RCP 4.5 scenario, are those including niche breadth as a single predictor and the additive combination of niche breadth and niche position (Appendix D – Table D.1). For the same GCM, but under the RCP 8.5 scenario, the best models included the niche breadth, range size and niche overlap as single predictors and the additive combination of niche breadth and niche position (Appendix D – Table D.2). Considering future projections obtained from the MPI-ESM-LR/RCP 4.5 scenario, the interactive combination of niche breadth and position is the best model explaining range contractions (Appendix D – Table D.3). For the same GCM, but under the RCP 8.5 scenario, the most important variables driving the predictions comprised niche position as a single predictor and the additive or interactive combination of niche breadth and niche position (Appendix D – Table D.4).

Considering multiple climate change scenarios, the best models explaining species range contractions included the additive combination of both niche breadth and position, followed by the interactive combination of both niche breadth and position and the single effect of niche breadth, niche position, niche overlap and range size (Fig. 5; Appendix D).

3.2. Species vulnerability Index and species ranking

According to AIC-based multi-model ranking, the final implementation of the SVI , following Eqs. (1)–(3), gives maximum vulnerability to species with smaller niche breadth and higher marginality in the community environmental niche space continuum. Given the overall importance of niche-hypervolume metrics in SVI , we decided to rename it as Niche Hypervolume Species Vulnerability Index ($NHSVI$; Eq. (4)) based on the general formula expressed in Eq. (1):

$$NHSVI_i = -2Nb_i + Np_i \quad (4)$$

where Nb_i and Np_i respectively express the niche breadth (i.e., \log_{10} hypervolume size using the SVM method) and the niche position (i.e., the distance between species hypervolume centroid and the hypervolume centroid of all species records; Table 1) for the i -th species. Moreover, $NHSVI$ attributes twice more weight to niche breadth to simulate its higher selection frequency in the multi-model ranking (Fig. 4). In turn, the negative and positive sign attributed to each metric reflects their general effect on vulnerability, also based on linear model results (Appendix D).

Overall, 28 of the 39 species (72%) were highly susceptible to

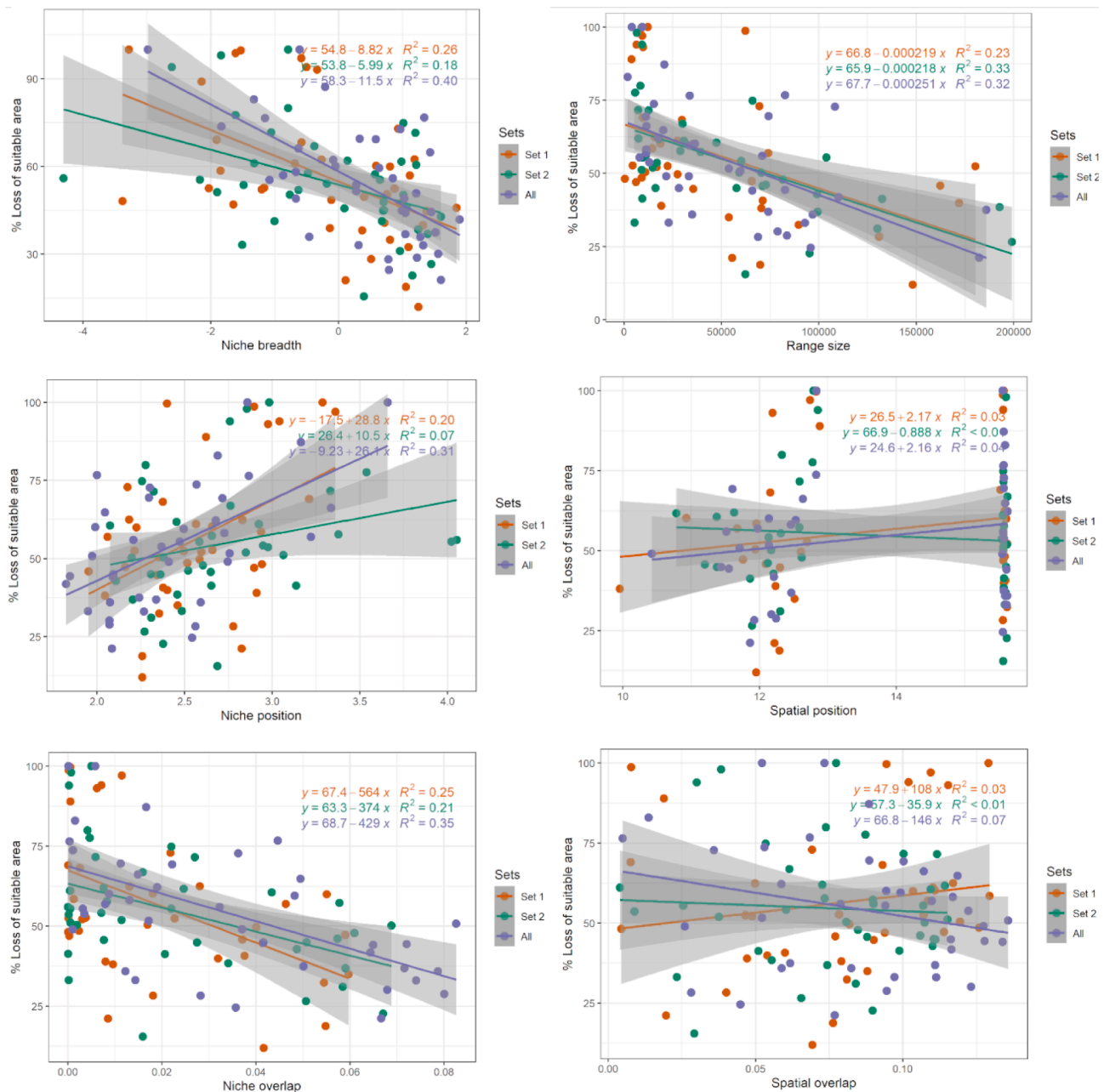


Fig. 4. Biplots displaying the association between niche or spatial metrics (x-axis) and estimated range contraction for the GCM HadGEM2-ES 2050 scenario (RCP 4.5; y-axis as Loss of suitable area). Points represent values for the 39 bryophyte species. For these regression analyses, the species occurrence dataset was used in full (all – blue points) or by cross-validating with two independent subsets of species occurrences as both predictor and response variables (set 1 – red points; set 2 – green points). “Set 1” means that independent set 1 was used to calculate response variables, and independent set 2 was used to calculate the predictors while “Set 2” the reverse. “All” uses the full species occurrence dataset to calculate variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

climate change, with SVI scores equal to or higher than 0.84 (Fig. 6). Bryophyte species with high SVI scores are primarily species that occur in high altitude sites with acidic rocks (e.g. RACFAC – *Racomitrium fasciculare*, ANDALP – *Andreaea alpestris*, GRIALP – *Grimmia alpestris*), calcareous rocks in the lowlands and montane areas (e.g. GRICRI – *Grimmia crinita*, GRITER – *Grimmia tergestina*) or are typical of oceanic areas (e.g. ANDHEI – *Andreaea heinemannii* subsp. *heinemannii*, ANDCRA – *Andreaea heinemannii* subsp. *crassifolia*). Bryophyte species with low SVI scores are usually indifferent to substrate and altitude and in very diverse situations such as *Racomitrium elongatum* (RACELO), the bryophyte species with the lowest SVI score.

3.3. Spatial pattern of the community vulnerability indices

Overall, HSMs had a predictive performance that can generally be considered good to very good across all species, considering the different evaluation metrics (AUC: 0.93–1.00; TSS: 0.72–1.00; Appendix C). Some of the present-day richest areas in saxicolous bryophytes (between 15 and 30 species) coincide with the main high mountain ranges located at northern and central Iberian mountain ranges (Fig. 7), which are predicted to contract by 2050, under the two GCMs and RCPs (Appendix C).

CVIs were renamed Niche Hypervolume Community Vulnerability Indices (NHCVIs) since their implementation was first based on NHSVIs and then combined through HSM spatial projections. The three NHCVIs

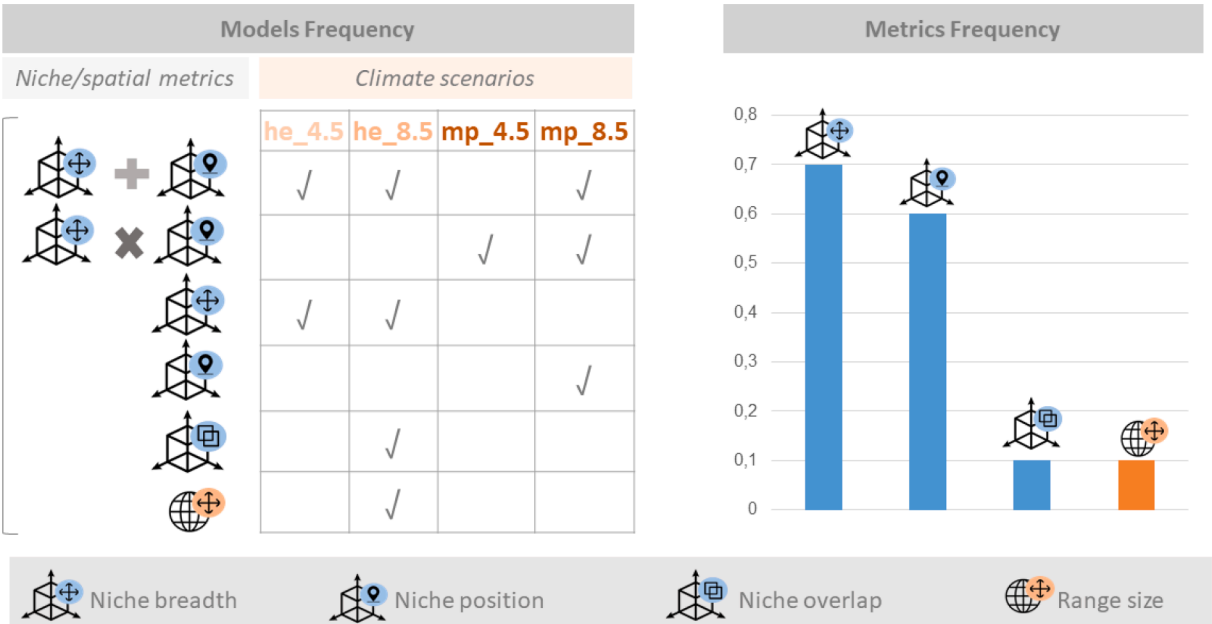


Fig. 5. Models and metrics relative selection frequency, calculated as N-selected/N-total models, across all climate scenarios: he – HadGEM2-ES, mp – MPI-ESM-LR and RCP’s 4.5/8.5 (CMIP-5); N-selected: number of times a model/metric is selected as the best model; N-total models: 10. The plus sign (+) indicates additive effects in models, while the cross sign (x) indicates interactive ones.

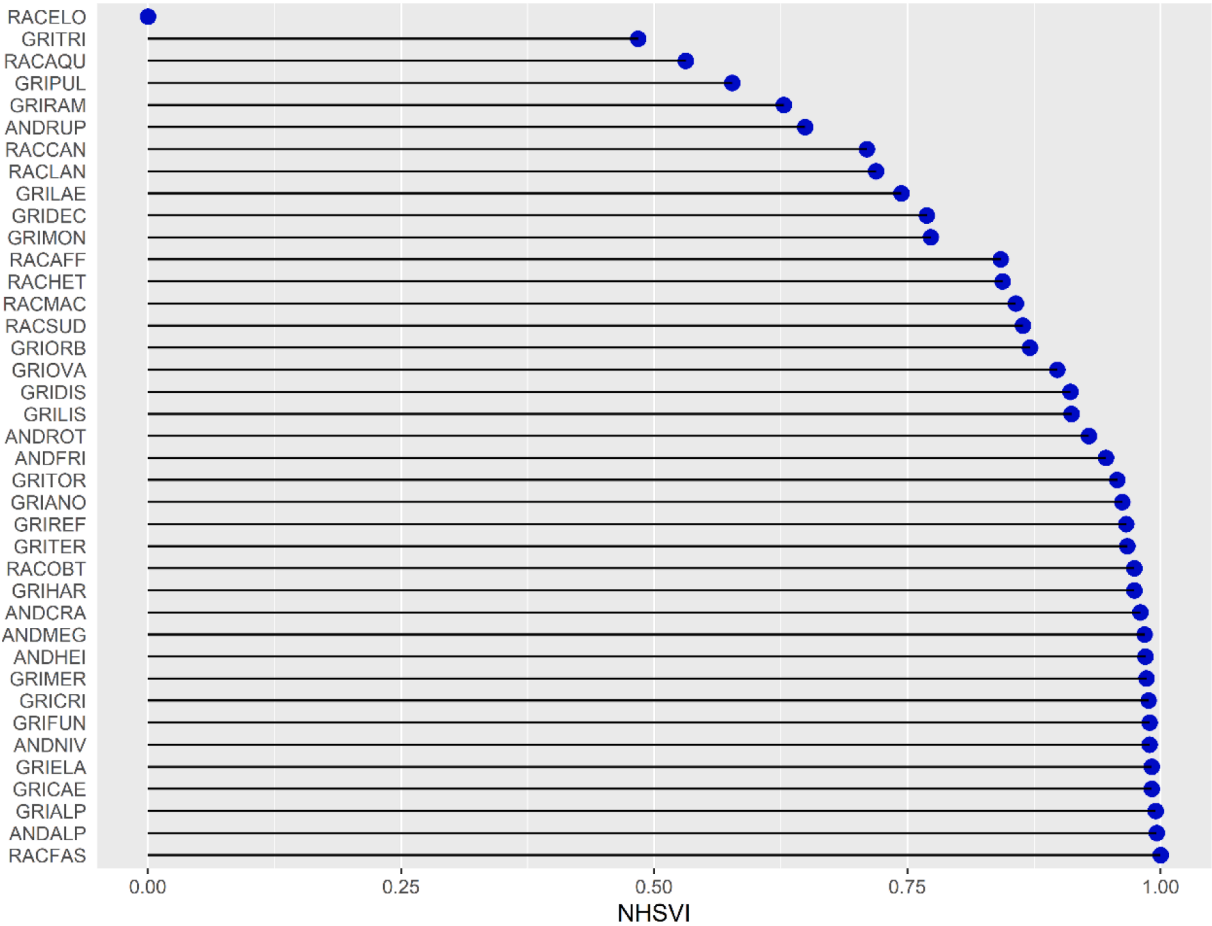


Fig. 6. Species ranking in terms of vulnerability using the Niche Hypervolume Species Vulnerability Index (NHSVI, x-axis). The y-axis shows each species code.

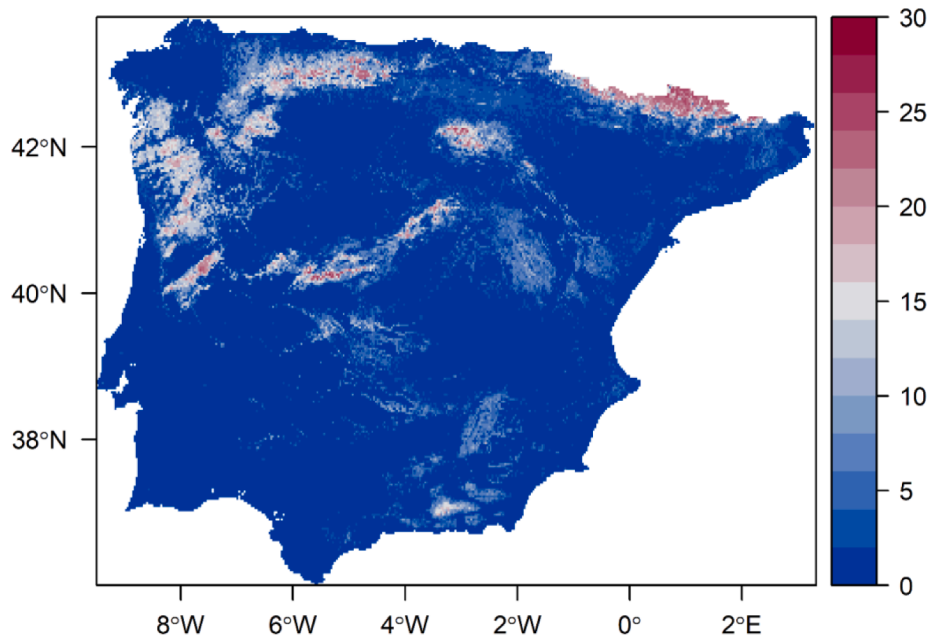


Fig. 7. Potential richness model of saxicolous bryophyte species in the Iberian Peninsula.

provided different insights into the study area's community vulnerability distribution (Fig. 8). *NHCVIav* values, as a representation of centrality in vulnerability distribution, were higher in the main high mountains of the northern and central region and the main mountain range in the southern region (Sierra Nevada). High average vulnerability in these regions indicates where community composition is most expected to change due to specific climate changes. On the other hand, clusters of high scores of *NHCVI_{mx}*, representing the greatest level of vulnerability found in a particular location, are distributed along a more considerable extent than average vulnerability values and outside the main high mountain ranges in the study area. Two main clusters of high *NHCVI_{std}* values are observed in the northwestern Iberian Peninsula and the Pyrenees, which means that high variation or dispersion of vulnerability values (i.e. both "low" and "high" vulnerability species in the community) occur in these regions.

The overall correlation between predicted species richness (Fig. 7) and community-level vulnerability was found to be significantly high and positive (*NHCVI_{av}*, $r = 0.97$; *NHCVI_{mx}*, $r = 0.66$; *NHCVI_{std}*, $r = 0.91$).

However, Fig. 8 shows that the local correlation varies over the study area, from high and negative correlation values to high and positive correlation values, and are differently distributed according to each community-level vulnerability measure. *NHCVI_{av}* scores are mostly higher in areas of high species richness (Fig. 8). The spatial distribution of *NHCVI_{std}* values also shows a similar spatial pattern with species richness across several regions of the study area. On the contrary, high scores of *NHCVI_{mx}* do not always spatially match areas of high species richness (Fig. 8). In such cases, areas with low values of species richness can be identified, where the degree of vulnerability is high (pixels highlighted in yellow and orange that indicate low and negative correlation values), which should be determined by species whose *NHSVI* (at the species level) is clearly higher.

4. Discussion

We applied a straightforward approach to estimate community-level vulnerability indices capable of quantitatively and spatially assessing bryophyte community vulnerability to climate change.

We first addressed how different metrics (breadth, position and overlap) calculated either from the environmental or the geographic

space could be used to predict and infer projected range contractions according to distinct climate change scenarios. We then compared models based on niche or spatial metrics to evaluate which ones improve our ability to forecast species range shifts. The final vulnerability score for each species in the community was calculated by applying a simple weighted sum of all the relevant parameters of the Species Vulnerability Index. To generate a spatial representation of the community's vulnerability values, we obtained a stack of vulnerability maps for each species by multiplying the final vulnerability score by each species' habitat suitability (calculated from HSMs).

Our results confirm that a given species' vulnerability to climate change depends mainly on its niche properties related to breadth and position. Consequently, the proposed *NHSVI* gives maximum vulnerability to species with smaller niche breadth and higher marginality in the community environmental niche space continuum. Moreover, *NHCVI_s*, based on *NHSVI* and combined with habitat suitability models, can depict the location of high levels of vulnerability for the whole community. The proposed methodology is a step forward in community modelling considering climate change.

4.1. Niche and spatial metrics as predictors of species' vulnerability to climate change

According to niche theory, under predicted climate changes, species with narrower niche breadths and higher marginality are expected to come under threat in the near future and be more sensitive to climate change than generalist species (Broennimann et al., 2006; Thuiller et al., 2005). Previous studies support the positive correlation between range size and niche breadth within bryophytes (Callaghan & Ashton, 2008; Cleavitt, 2005). Our main finding supports the hypothesis that both niche breadth and position in the environmental space, reflecting not only species climatic tolerance but also its degree of marginality, alone or combined, are good indicators of a species' vulnerability to global climate change, which is in agreement with previous studies (Broennimann et al., 2006; Nori et al., 2016; Thuiller et al., 2005; Williams et al., 2007). Within our framework, the ability of niche overlap to predict species' vulnerability to climate change was tested for the first time in the present study. Even though we found a significant correlation between niche overlap and range contraction, this metric was only selected once in models explaining range shifts compared to other metrics

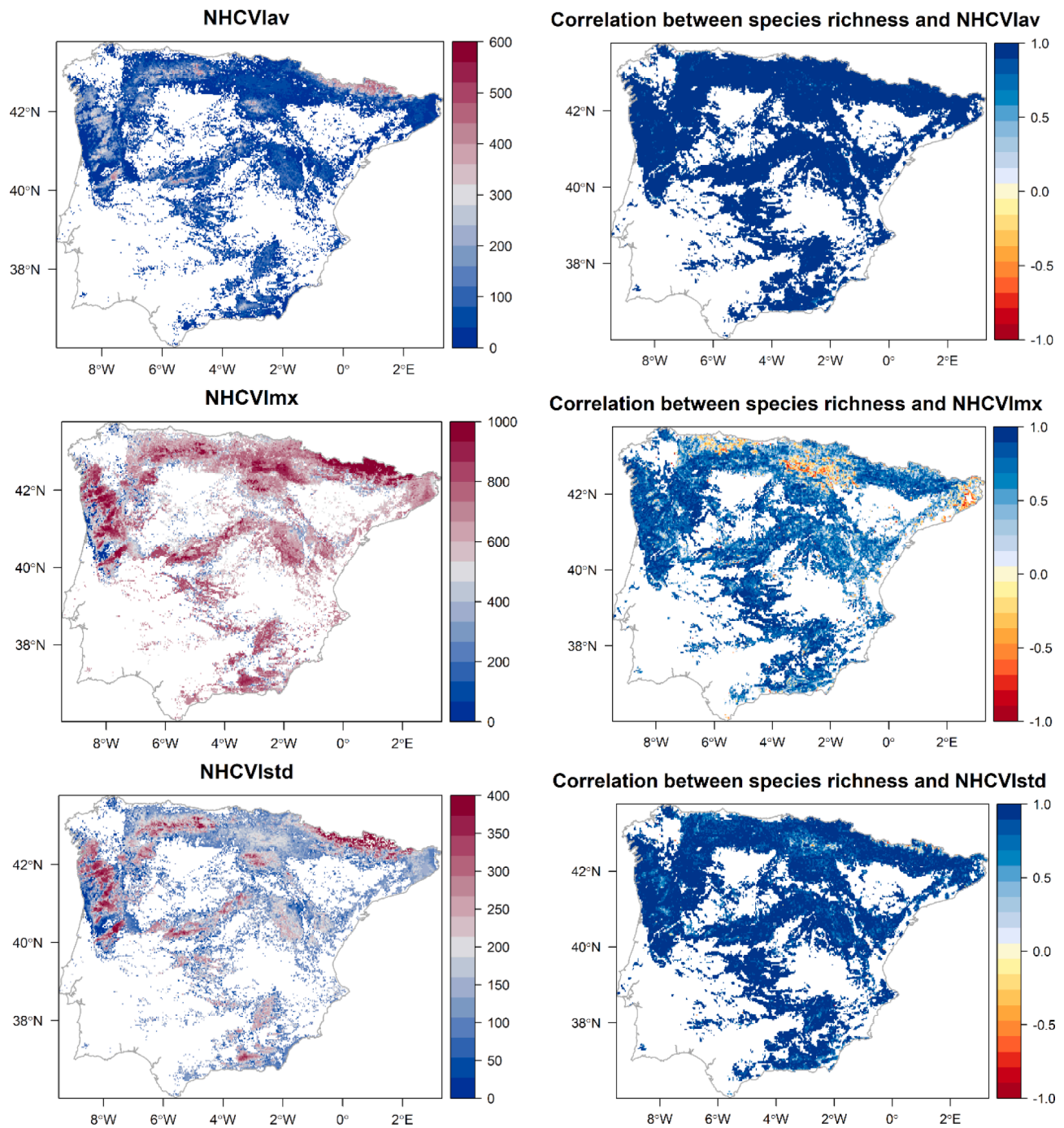


Fig. 8. Spatial patterns of Niche Hypervolume Community Vulnerability Indices (NHCVI; in the left side) and their local correlation with species richness (right side). *NHCVIav* - average of community vulnerability; *NHCVI mx* - maximum of community vulnerability; *NHCVIstd* - standard deviation of community vulnerability.

selected a greater number of times, such as niche breadth or niche position. In the end, niche overlap was not included in the final selection of the best metrics potentially explaining species vulnerability to climate change.

Previous studies pointed out different geographic variables as good indicators of species' vulnerability to global climate change (Broennimann et al., 2006; Gaston & Fuller, 2009; Pearson et al., 2014; Thuiller et al., 2005). According to our results, the most relevant spatial metric explaining species' vulnerability to climate change was range size. However, geographical range size alone is a weak predictor of species vulnerability to climate change. This has important implications in the way that we assess species' vulnerability to climate change since most

studies are focused on potential changes of species' ranges. Although tested for the first time in the present study, spatial position and spatial overlap did not explain species vulnerability to climate change.

Overall, models with niche metrics as predictors had greater support over models with spatial metrics, suggesting that spatial metrics have less predictive capacity than niche-based metrics and cannot fully explain species' vulnerability to climate change.

Within this framework, we combined state-of-the-art methods for assessing species niches and their spatial distributions. Particularly, we used a novel method that has proven to help estimate high-dimensional ecological hypervolumes, although it has been the subject of much discussion in the literature (Blonder et al., 2018). We are aware that the

accuracy of niche estimations depends on the research question and data limitations. However, since there is not a single best algorithm or method that fits with all data configurations for estimating species niches, we consider that the estimation method we applied, with its underlying assumptions, is the most appropriate for our specific data and is a robust approach for delineating the volume of n -dimensional hypervolumes.

4.2. Species and community vulnerability indices

By emphasizing on two niche hypervolume metrics, *NHSVI* holds simplicity and conceptual coherence. It can be argued that an index using few variables is less reliable than a more complex one; however, since one of the aims of this study was exploring an index that could be spatially applicable, choosing few relevant variables can reduce redundancy and help to obtain a feasible and straightforward index (Moreno-Amat et al., 2015).

The final implementation of the *NHSVI* gives maximum vulnerability to species with smaller niche breadth and higher marginality in the community environmental niche space continuum and attributes twice more weight to niche breadth to mimic its higher selection frequency in the multi-model ranking. The selection and weighting process of different factors based on modelling is advantageous since it makes the approach more adaptable to different species and communities. This also results in a more objective way to select potential indicators linked with vulnerability, overcoming common sources of uncertainty in climate change vulnerability assessments that rely on the subjectivity involved in expert judgment scoring (Pacifi et al., 2015).

The best combination of metrics that may explain species' vulnerability to climate change was estimated in reference to the whole community (i.e. relative estimation outcome), by combining results comprehensively at the community level. This way, it can substantially increase our capacity to forecast climate change impacts on biodiversity as a whole and improve conservation and management strategies that best retain biodiversity into the future.

Overall, our findings suggest that *NHCVis*, based on *NHSVI* and then combined with *HSMs*, are useful for scoring a whole community and provides spatially explicit insight into geographic patterns of community vulnerability. Similarly to other combined approaches that have been emerging as a way to measure vulnerability (Willis et al., 2015), our proposed methodology is an integrative framework that uses both the traditional "predict first, assemble later" community-level modelling strategy and a Species Vulnerability Index. The standard approach of stacking individual species predictions derived from habitat suitability models (Mateo et al., 2012) was already applied for bryophytes and allowed the identification of detailed richness patterns in the Iberian Peninsula (Helena Hespanhol et al., 2015). The implementation of a Species Vulnerability Index based on niche metrics is the first time applied to bryophytes, and is here considered as a niche-based approach, alternative to 'standard' spatial and model-based approach to predict changes in bryophyte species' ranges (Désamors et al., 2012; Patiño et al., 2016; Sérgio et al., 2014).

Saxicolous bryophyte communities with the greatest average vulnerability of species to climate change are those at the high mountains of the northern, central and southern region of the Iberian Peninsula, which generally coincides with the spatial pattern of bryophyte species richness for the Iberian Peninsula (Hespanhol et al., 2015). Our results strongly indicate that more diverse communities are more vulnerable to climate change. There is already some evidence that significant losses in bryophyte diversity can be expected due to the sensitivity to temperature and water availability, particularly in areas with a high number of species and higher altitudes (He et al., 2016). On the other hand, high scores of maximum community vulnerability do not always spatially match areas of high species richness, suggesting that vulnerability patterns are structured locally not only due to species richness but also to community composition. Particularly for saxicolous

communities, environmental heterogeneity and habitat structure have an important influence on the distribution patterns of bryophyte species (Hespanhol et al., 2011). Additionally, the high standard deviation in community vulnerability highlight locations in the study area where more differentiated communities occur (i.e., with high amount of variation of vulnerability values). This situation also strengthens that other *NHCVis*, based on different aggregation measures, such as the 75% or 95% percentiles, could also be meaningful and judicious community vulnerability measures. Therefore, the three proposed *NHCVis*, based on different statistical aggregation measures, provide complementary insights into the study area's community vulnerability distribution.

4.3. Limitations, applicability and implications for conservation

We acknowledge that our models, like any model, have some limitations. Our approach is based on sufficient knowledge of species' realized climate niches and does not consider species' responses modified by their interactions with other species, nor the possible influence of dispersal and adaptation processes on species' local persistence. Our vulnerability indices should be interpreted as conservative measures, accounting only for species losses and not gains through immigration processes, and cannot be used as estimates for determining the ability of species to persist under future climates. This can be a limitation, since if a species is on the trailing edge (i.e., the contracting or retreating edge), then species are vulnerable, but if on the leading edge (i.e., the expanding or colonizing edge), then species may benefit from climate shifts and vulnerability is overestimated. The factors we used to estimate bryophyte community vulnerability, although relevant, only allow an approximation of total vulnerability. Hence, other potentially important species attributes that may affect species' vulnerability to global change should be tested in future studies, such as dispersal ability (Zanatta et al., 2020), functional traits (D'Amen et al., 2018), eco-evolutionary (Thuiller et al., 2013) or biotic factors (Wisze et al., 2013). Some studies argue that including interactions between species attributes may improve trait-based predictions (Pearson et al., 2014) and, consequently, the predictive power of species' vulnerability to climate change. Regarding biotic factors, there are still some research gaps on the influence of biotic interactions under the context of climate change, although some studies have already shown that including biotic factors can lead to better predictions of species' distributions (Araújo & Luoto, 2007). The proposed *NHSVI*, when used with other complementary approaches such as trait-based or mechanistic, could help provide a more complete, spatially-explicit picture of species vulnerability.

Furthermore, although there are multiple model assessment approaches, which vary in their objectives to select a set of models, we consider that the model assessment approach applied, based on the Akaike's Information Criterion (AIC), is appropriate and a robust approach to compare the weight of evidence for any number of models. We are aware that our vulnerability outcomes may depend on variation in the spatial or environmental inputs. We also acknowledge that our conclusions obtained via statistical inference require further replication and validation across a broader range of conditions. However, we managed to decrease the uncertainty of these analyses by using appropriate variables and running different combinations of climate models and modelling algorithms.

Nonetheless, our proposed index based on niche metrics can be useful to complement changes in range size for Red List assessments (Breiner et al., 2017) and, when incorporated into IUCN conservation assessments (Hodgetts et al., 2019), may enhance our understanding of species climate risks.

Our recommended *NHCVis* can be a valuable tool for decision-makers to prioritize bryophyte communities' conservation under climate change, usually not included. Recommended conservation actions could involve monitoring species' habitat and should be directed toward the geographic locations of greatest vulnerability, which may better detect early signs of climate-related impacts. If all species are

managed similarly, conservation actions should be towards the geographic locations where average community vulnerability is highest. If only the most vulnerable species are prioritized, conservation actions should be towards the geographic locations in which maximum community vulnerability is greatest.

To our best knowledge, this is one of the first studies focusing on the development and application of Community Vulnerability Indices for bryophytes, which are ideal indicators of the impact of climate change on biodiversity patterns and whose response to climate change is still poorly explored (Di Nuzzo et al., 2021). The indices developed here can be calculated for other taxonomic groups within different assessment areas, although some modifications may be required. Our approach could be used to comparatively rank vulnerability to climate change among different taxonomic groups with contrasting life-strategies that may respond at different rates.

5. Conclusions

Based on the best set of factors summarizing species' niche or geographic properties expected to respond to climate change, we present three community-level indices that measure bryophyte community vulnerability to climate change. Our results suggest that bryophyte species' vulnerability depends upon its niche properties related to breadth and position by applying a novel method to estimate high-dimensional ecological hypervolumes.

Our proposed Niche Hypervolume Species Vulnerability Index (NHSVI) is fully quantitative and allows to rank bryophyte species according to their vulnerability. Moreover, Niche Hypervolume Community Vulnerability Indices (NHCVis), based on NHSVI and combined with habitat suitability models, provide a spatial representation of vulnerability values. NHCVis can highlight geographic regions of high bryophyte community vulnerability, inform resource management decisions, and direct conservation efforts. We consider that it offers great potential for other taxonomic groups.

CRediT authorship contribution statement

H. Hespanhol: Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **K. Cezón:** Conceptualization, Data curation, Writing – original draft. **J. Muñoz:** Conceptualization, Methodology, Writing – review & editing. **R.G. Mateo:** Conceptualization, Methodology, Writing – review & editing. **J. Gonçalves:** Conceptualization, Methodology, Formal analysis, 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.

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Appendices. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.108643>.

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