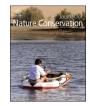


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### Making the most of scarce data: Mapping distribution range and variation in population abundance of a threatened narrow-range endemic plant

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#### ABSTRACT

The design of effective strategies for the conservation and management of threatened narrow-range species requires basic knowledge on their geographic distribution and abundance. When such knowledge is lacking, modelling techniques can provide an opportunity to acquire basic information and incorporate it immediately into conservation programs. This study used ecological niche modelling to map the potential distribution range and rangewide variation in population abundance of a threatened narrow-range endemic plant, Antirrhinum lopesianum Rothm. in the Iberian Peninsula. We simulated the potential geographic distribution of the species using the Ensemble Modelling approach based on 28 species occurrences and a set of readily available environmental data (Landsat 8 OLI/TIRS and LiDAR) and created a spatial model of the distance to the niche centroid. We tested the relationships between 35 records with abundance data for the species and their distance to the niche centroid using generalized regression models, and the resulting model was used to predict spatial estimations of A. lopesianum abundance across its entire potential distribution range. The ecological niche model of A. lopesianum covered the most suitable areas located along a narrow strip on the banks of the River Duero and River Sabor. We found a robust and negative relationship between observed abundance for the taxon and distance to the niche centroid. The spatially explicit model presented here provides a reliable tool for regional/ global management and conservation of A. lopesianum and an approach applicable for other narrow-range endemic plants. Finally, this approach maximization the exploitation of basic information through open resources (software and environmental variables), which makes it of high interest for institutions with limited resources.

#### 1. Introduction

Narrow-range endemic plant species are of conservation concern and are a challenge for conservation agencies due to their rarity and uniqueness. The difficulty increases when these species occupy remote areas or those difficult to explore. With ongoing environmental global change, these species are more susceptible to different environmental pressures (Breggin, George, & Pencak, 2003) and hence, reliable estimates of their potential distribution and abundance are necessary both to evaluate its risk of extinction and design conservation strategies (Guisan et al., 2013; Rodríguez, Brotons, Bustamante, & Seoane, 2007). However, data on the current and/or historical distribution, biology, and ecology of many of these species is sparse, due to the fact that their populations, are, in many cases, present in small patches of difficult access (Gogol-Prokurat, 2011). Incomplete knowledge of this basic information makes its prioritisation for conservation an enormous challenge.

Species distribution models (SDMs) offer a practical solution to improving our knowledge of narrow-range endemic plant species (Peterson et al., 2011), thus locating and prioritising areas for conservation actions. SDMs use known occurrence locations and spatially-explicit data on the environmental conditions believed to control the geographic distribution of the target species to predict habitat suitability across the landscape (Soberón & Nakamura, 2009).

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However, endemic plant species with narrow-range distributions and specialised habitat requirements represent a particular challenge for SDMs for several reasons: 1) such species have both small distributions and small sample sizes, creating issues that may compromise model robustness (Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2007); 2) sampling bias is inherent in occurrence data (Wisz et al., 2008); and 3) given that narrow-range species with specialised habitat requirements often have patchy distributions of occurrences, defining a general range becomes less useful from a management perspective compared to understanding habitat occupancy. This is a challenge for SDMs because they are meant to identify the overall extent of a species' range and may perform poorly if that range is heterogeneous or not well-sampled (McPherson & Jetz, 2007).

In recent years, a novel method to model geographic patterns of abundance based on the ecological niche theory, termed the Distance to the Niche Centroid (DNC) approach, was proposed by Martínez-Meyer, Díaz-Porras, Peterson, and Yáñez-Arenas (2013). This procedure is similar to those previously applied and based on orthogonal variables (Calenge, Darmon, Basille, Loison, & Jullien, 2008). This approach assumes that optimal conditions for a species are found towards the centroid of the ecological niche in a multidimensional space (Hutchinson, 1957; Maguire, 1973). Thus, a locality which environment is close to the centroid of the n-dimensional niche harbours better conditions for the species and, as a consequence, higher abundance would be expected at these localities (Yañez-Arenas, Guevara, Martínez-Meyer, Mandujano, & Lobo, 2014). The DNC approach fits a curve for the relationship between observed abundance across the species' geographic range and the distance to the ecological niche centroid that can be used to make range-wide estimates of the species' abundance. Based on this approach, different studies have successfully tested this hypothesis in different geographic contexts and at different scales (Manthey et al., 2015; Martínez-Gutiérrez, Martínez-Meyer, Palomares, & Fernández, 2018; Martínez-Meyer et al., 2013).

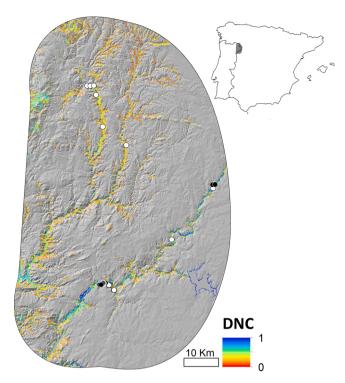
Expanding the use of the SDMs and DNC method to predict geographic patterns of distribution and abundances of narrowly endemic plants could be very helpful in designing management and conservation strategies. Here, we determined whether the distributional area of a narrow-range endemic plant, as well as variations in population abundance across its distribution range, can be accurately estimated at a fine scale using the SDMs and DNC method, based on very basic information of the species. We illustrate these approaches with the arribes snapdragon, *Antirrhinum lopesianum* Rothm., a threatened narrow-range endemic plant of the north-western Iberian Peninsula. Finally, the potential implications of the results for focussing future fieldwork and conservation efforts are discussed.

#### 2. Materials and methods

#### 2.1. Study area

We delimited the study area by generating a 15 km buffer around the current distribution range of *A. lopesianum* based on the IUCN distribution map (Amich-García, Bernardos-Hernández, González-Talaván, Caldas, & Alves, 2011). We assumed that this area reflects the geographic region that has been accessible to the species over relevant time periods (M in the BAM framework; Soberon & Peterson, 2005); Fig. 1).

This area is included in the Lusitan Duriensean biogeographical sector (Carpetan-Leonese subprovince) (Rivas-Martínez et al., 2002), with a Mediterranean pluviseasonal oceanic bioclimate, within the Mesomediterranean thermoclimatic belt, with two ombrotypes: dry and subhumid. The dominant rock is silicic, generally granite and quartz, which causes soils to be acidic (Bernardos, Crespi, Aguiar, Fernández, & Amich, 2004).



**Fig. 1.** Potential distribution range of *Antirrhinum lopesianum*: central western Iberian Peninsula. In colour, model of the ecological niche of *A. lopesianum* representing the distance to the niche centroid, with values from 0 (red) to 1 (blue). Absence prediction is represented in grey background. White dots indicate presence records (n = 28) and black dots abundance data (n = 35). The background image (digital elevation model) represents the complexity topographic of the study area (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



Fig. 2. The arribes snapdragon, *Antirrhinum lopesianum* Rothm. Photographed by R. Carbonell in Natural Park Arribes del Duero, Spain, June 2018.

#### 2.2. Study species

The arribes snapdragon, *A. lopesianum* (Fig. 2), is a perennial chamaephyte with woody stems, very lanuginose leaves and flowers that are white with violet stripes (Bernardos et al., 2006).

Flowering occurs in spring (April-May) and fructification in summer (July-September), it is insect-pollinated, and seeds are dispersed by barochory/semachory. *A. lopesianum* grows on shaded cracks in calcareous substrates and has a discontinuous and highly fragmented distribution due to possibly stochastic and historical effects of both colonization (dispersion) and extinction. This taxon is listed as Endangered due to its current severely fragmented distribution, with a low area of occupancy, below 500 km<sup>2</sup> (Amich-García et al., 2011).

#### 2.3. Presence data

Presence data across the current distribution range of the taxon were gathered from the literature (Gomes et al., 2013; Ramírez-Rodríguez & Amich, 2014) and the Arribes del Duero Natural Park. Presence records from the Global Biodiversity Information Facility (GBIF) were not used because the resolution at which they were uploaded into this database ( $\geq 1 \times 1$  km grids) is coarser than the resolution of the environmental variables used in this study. We obtained a total of 28 presence records for *A. lopesianum* (Fig. 1).

#### 2.4. Abundance data

Abundance data of the taxon were gathered across its potential distribution in the Duero Basin (Portugal and Spain) during the spring and autumn of 2018. Due to the geomorphological complexity of these "Arribes" territories (see Fig. A1), a motorboat was used to assist in our surveys. This allowed us to reach places that otherwise would have been impossible to explore. When the species was detected, we recorded geographical location (using a Garmin e-map GPS device) and abundance data (direct counting of all individuals as in Bernardos et al., 2006). A total of 35 records with abundance data for the taxon were gathered (Fig. 1).

#### 2.5. Environmental variables

As potential predictors to characterize the species' ecological niche, we used a set of variables related to topographic conditions, temperature, soil water availability and vegetation cover (Table 1). In areas with a rugged topography, the selection of variable resolution is a consequence of the availability and quality of data pertaining to the specific study area, which is typically the limiting factor in distribution studies (Zhang et al., 2016). Herein, predictor variables were derived by remote sensing data (Landsat 8 OLI/TIRS and LiDAR) and were chosen based on our knowledge of the species, and were assumed to be at least correlated with more proximal causal factors. Remote-sensing techniques have

#### Table 1

Variables used as predictors of the Antirrhinum lopesianum presence in the study area. See Table A1 for variable descriptions and estimation methods.

Variables	Description	Range (min to max)
slope	Slope of the terrain (degrees)	0.119 to 55.92
LST_avg	Average of the land surface temperature in growing season (°C)	20.46 to 38.09
northness	South-north aspect	-1 to 1
SAVI_avg	Average of the Soil-Adjusted Vegetation Index in growing season	-0.063 to 0.608
eastness	West-East aspect	1 to -1
NDII_avg	Average of the soil water availability in growing season	-0.370 to 0.772
TPI	Topographic position index (m)	-13.19 to 9.984

transformed ecological research by providing both spatial and temporal perspectives on ecological phenomena that would otherwise be difficult to study (He et al., 2015; Hernández-Lambraño, Rodríguez de la Cruz, & Sánchez-Agudo, 2019). A key advantage of these techniques is the capability to perform synoptic, spatially continuous and frequent observations of ecological indicators without interpolation or geographical biases at varying spatial and temporal resolutions (He et al., 2015), advantages that have huge potential when it improves the ability to predict the distribution at fine scale of a threatened narrow-range endemic plant. Other potentially important environmental variables such as edaphic, geological, phytocenotic and human influence variables, are not used due to the lack of a thematic cartography compatible with the resolution used in this study. To reduce multicollinearity between variables, we calculated the Variance Inflation Factor (VIF) using the VIF function of the "HH" package in R (Heiberger, Richard, & Holland, 2004). Variables with values of VIF > 5 were excluded (Table A1). All environmental data were standardised to Universal Transverse Mercator coordinates (Datum ETRS-89) at a spatial resolution of  $30 \times 30$  m using ArcGIS ver. 10.3.1 (ESRI, 2015). See Appendix A1 for a more detailed description of the variables and estimation methods.

#### 2.6. Ecological niche-based distribution modelling

We modelled the ecological niche of *A. lopesianum* using Ensemble Modeling approach (EM). EM was built to reduce the biases and limitations inherent to the use of single SDM techniques (Araújo & New, 2007). We used BIOMOD2 version 3.3–7 (Thuiller, Georges, Engler, & Breiner, 2016) in R version 3.4.2 (R Core Team, 2017), to fit four modelling methods: Generalised Linear Models (GLM), Generalised Boosting Models (GBM), Maximum Entropy (MaxEnt) and Random Forest (RF). These models have shown good performance in other modelling exercises (Breiner, Guisan, Bergamini, & Nobis, 2015; Elith et al., 2006; Williams et al., 2009).

Models were calibrated with 28 presences of the specie and 10 000 random pseudo-absence points. Pseudo-absence data were limited to within 5 km from the known presence records (Williams et al., 2009). The Continuous Boyce Index (CBI) (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006), a metric specifically designed for presence only models and insensitive to pseudo-absences was used to evaluate the model performance. We considered models to be "wrong" when CBI values were below -0.5, "average to random" for values ranging from -0.5 to 0.5, and "good" for values above 0.5. For each model, we computed CBI by performing ten-fold split sampling (80 % training data and 20 % test data). We assembled all individual models into a single EM by weighting projections based on the individual CBI scores (CBI > 0.5). EM evaluation consisted of calculation of CIB using independent data. In this case, the abundance data gathered from field surveys were used as presence records for the EM validation. EM output was converted into a discrete binary map of presence/absence, using the minimum training presence (MTP) value. Finally, variable importance was calculated to assess the relevance of each predictor through all considered models and response curves were calculated to interrogate the relationship between the response (i.e., presence) and each explanatory variable (See Appendix A2 for a more detailed description of model implementation).

Here, we assume that the niche model is a good estimator/approximation of the fundamental niche of a plant with scarce knowledge about its biology, but we acknowledge that it is difficult to capture the true fundamental niche without an ecophysiological approach for the species (Peterson et al., 2011).

#### 2.7. Distance to the niche centroid

Following Martínez-Gutiérrez et al. (2018), the niche centroid was calculated in the environmental space from potential distribution range. The niche centroid is located at the centre of the multidimensional

envelope of the presence records in the environmental space. To obtain the DNC, we first extracted values of environmental variables for all grid cells where the species were predicted to be present according to the EM binary map, which represents a list of all unique environmental combinations along the potential geographic distribution of the species (Martínez-Gutiérrez et al., 2018). To avoid biases introduced by differences in scales among the 7 dimensions of the ecological niche, we converted them to a common scale (i.e., standardisation procedure, mean = 0 and standard deviation = 1). We calculated multidimensional Euclidean distance from each grid cell with a presence prediction to the niche centroid as follows:

$$DNC = \sqrt{\sum_{j} \left(P_{ij} - N_{j}\right)^{2}}$$

where DNC is distance to the niche centroid, N*j* is mean of variable *j* and P*ij* is value of the variable *j* in grid cell *i*.

Finally, we represented the DNC in a raster map (Fig. 1) using raster calculator in ArcGIS and rescaled the values between 0 and 1, with 0 representing the shortest DNC and 1 the largest distance to this centroid.

## 2.8. Relationship between the abundance and the Distance to the Niche Centroid, and abundance map

We analysed relationships between abundance data of *A. lopesianum* (i.e., response variable) to DNC measures (i.e., predictor variable) using a Generalized Linear Model (GLM). We modelled the error terms of the GLM using a negative binomial distribution (Abundance  $\sim$  DNC, family = negbin(link="log")), which is typically used for count data when overdispersion occurs (Gelman & Hill, 2007).

The fit model was evaluated using a randomly split 80/20 data for training/validation. We re-estimated the GLM model using the 80 % section of the data, and the resulting section was used to predict the abundance of the remaining 20 % data. The process of splitting the data was repeated ten times and the mean of  $R^2$  (i.e., the squared correlation between the observed outcome values and the predicted values by the model) and its standard deviation were calculated as a performance metric for the fitted models. We used the R packages "tidyverse" ver. 1.2.1 (Wickham, 2017) and "caret" ver. 6.0–77 (Kuhn, Wing, & Weston, 2017) for the procedure of model evaluation. Since the specie's presence can be given by historical and stochastic processes, we only validate DNC with those points where we have detected its presence.

The fitted GLM describing the relationship between abundance and DNC was used to generate an estimated abundance map of *A. lopesianum* across its entire potential distribution using the "predict" function of the R package "raster" ver. 3.0–7 (Hijmans, 2019) (see Table A2). We only showed spatial predictions for the observed range of abundances. Finally, we constructed correlograms and calculated global Moran's I in ArcGIS using residuals from the GLM and evaluated it for evidence of autocorrelation. We did not detect strong spatial autocorrelation in the residuals of the GLM (see Fig. A2).

#### 3. Results

#### 3.1. Ecological niche-based distribution modelling

The CBI average values, ranging between 0.618 and 0.801, indicated that the single-algorithm model predictions exhibited a good discrimination capacity compared to the expected value (0.5) from a random prediction. Despite the initial good performance of the models, the EM outclassed the accuracy of their predictions with an CIB value of 0.818. The threshold value of consensus to produce the binary map of presence/absence was = 0.291. According to the resolution used, the potential habitat distribution covered an area of 273 km<sup>2</sup>. Most suitable areas were located along a narrow strip on the banks of the rivers

(Fig. 1). The binary map includes areas with suitable environments where the species has not yet been recorded. These predicted areas were located in the south and middle parts of the Sabor Basin (Portugal), and another in the south and middle parts of the Duero River (Portugal-Spain).

From the seven predictors considered for running the models, terrain slope (slope), land surface temperature (LST\_*avg*), north-south aspect (northness) and soil-adjusted vegetation index (SAVI\_*avg*) were the variables with the consistent highest contributions (Fig. 3).

These results identify variables related to landscape topographic features and land-cover as the most important to explain the potential distribution of the taxon. The model response curves in respect to these variables (Fig. 4), reveal that the most suitable areas for *A. lopesianum* are those that have steep slopes facing north with an average temperature for the growth season of approximately 21 °C. Moreover, they are areas with low vegetation cover and high humidity that are in relatively deeper valleys.

### 3.2. Relationship between observed abundance and distance to ecological centroid

The GLM showed that the observed abundance of *A. lopesianum* was significantly negatively associated with the DNC (regression coefficient of -26.09  $\pm$  4.276 SE; p < 0.001) and the model for this species explained 0.598 of variation in abundance as a function solely of nichecentroid distance (Fig. 5). As expected, the observed abundance drops when the environmental conditions depart from those found near the species' ecological niche centroid.

According to the validation procedure, GLM averaged an R<sup>2</sup> of  $0.712 \pm 0.274$  (p < 0.001). Abundance estimates are within reasonable ranges (4–73 individuals) and coincide with our observed field data (1–65 individuals). Finally, spatial predictions of *A. lopesianum* abundance across its entire potential habitat distribution were estimated with the coefficients of the GLM (Fig. 6; Table A2). Areas with high estimated abundances are predicted along the Sabor Basin, mainly in the south and middle parts, north part of the Maças River, and another in the south and middle zones of the Duero Basin (Portugal-Spain).

#### 4. Discussion

#### 4.1. Potential distribution range of Antirrhinum lopesianum

Herein, we developed a spatially-explicit model to represent the potential habitat distribution of the threatened narrow-range endemic A. lopesianum across its entire distributional range. The value of performance (CIB) of our SDM indicates a high dependence on the occurrence data and the set of variables included in the analysis. This result, however, may be an artefact of the small sample size used for the model calibration (Yañez-Arenas et al., 2014). This effect has often been reported for species with restricted distributions, or when study area is extremely large compared to narrow species distribution (Lobo, Jiménez-Valverde, & Real, 2008). Our SDM indicates that the potential habitat distribution covered the most suitable areas located along a narrow strip on the banks of the River Duero (north-eastern Portugal and central western Spain) and River Sabor (north-eastern Portugal). These findings are congruent with known range limits described by Bernardos et al. (2006) but expand them considerably. Results from the analysis of predictor importance revealed that the distribution patterns of A. lopesianum appear to be mostly influenced by topographic features (i. e., slope, aspect) and land surface temperature. In fact, the taxon presents a special preference for spatially heterogeneous areas. In these environments, the species likely finds refuge on humid and shady slopes, which reduce insolation and maintain water balance in the dry season. In addition, the presence probability of the taxon responds positively to zones with high soil moisture. These environments facilitate vegetative propagation via the production of new shoots with many adventitious

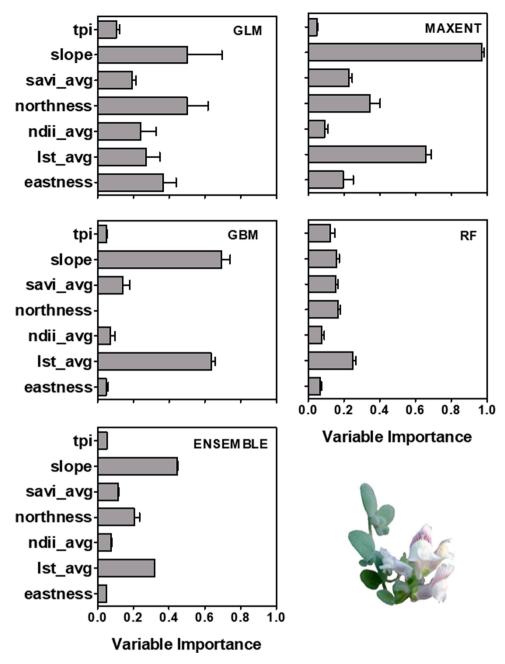


Fig. 3. Relative environmental variable importance derived from the single-algorithm models and ensemble model, with the error bars corresponding to standard deviation computed for each variable. See Table 1 for variable descriptions.

roots that are introduced in the fissures of the rock walls that colonises (Bernardos et al., 2006).

As we noted in the environmental variables section, our SDM has several limitations regarding other potentially important environmental variables that may influence the presence of *A. lopesianum*. Despite these limitations, the SDM-based distribution model represented the potential habitat patterns of the taxon fairly well and could serve as a first approximation for the species. Finally, any characterisation of the species' ecological niche will always be partial, inherent to the multidimensional niche (Martínez-Gutiérrez et al., 2018).

# 4.2. Relationship between observed abundance and distance to ecological centroids

We implemented the DNC approach to estimate the potential abundance of *A. lopesianum* across its entire potential distribution range. We

found a significant, negative relationship between observed abundance for the taxon and DNC. Ecological theory has proposed that optimal conditions for species are found towards the centroid of their multidimensional ecological niche, thus abundance under such conditions should be maximal (Maguire, 1973). Our results provide empirical support for these ideas, as a strong inverse relationship was found between the distance to the centroid and observed values of abundance, indicating that the internal structure of the species' ecological niche contributes to population abundance Brown, Mehlman, and Stevens (1995)).

Our results were similar to those reported by Yañez-Arenas, Martínez-Meyer, Mandujano, and Rojas-Soto (2012); Ureña-Aranda et al. (2015) and Martínez-Gutiérrez et al. (2018), regarding the DNC– abundance relationship. These authors found that the abundance distribution followed a centralized pattern in the ecological space, where abundance tends to be highest toward the centre of these spaces and

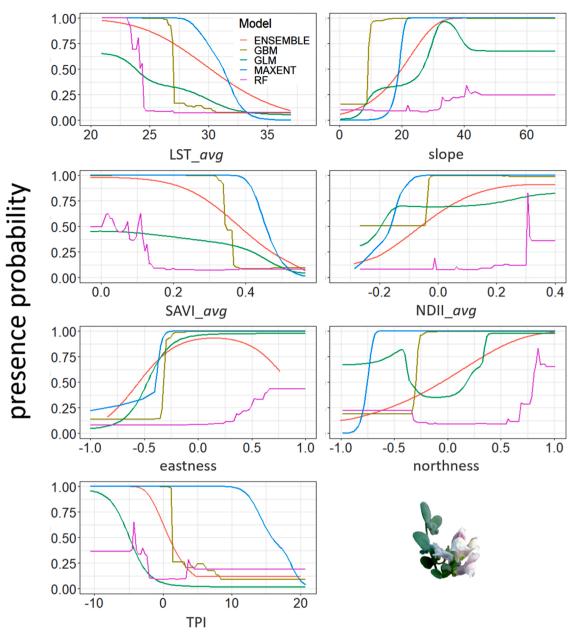


Fig. 4. Response curves: the panel represents the response curves of the environmental variables explaining the presence of *Antirrhinum lopesianum* derived from the single-algorithm models and ensemble model. Response curves were calculated for the models calibrated with all presence records (n = 28). See Table 1 for variable descriptions.

decrease toward the boundaries. On the other hand, the relationship that we found was not as strong as that reported for Odocoileus virginianus  $(R^2 = 0.902; Yañez-Arenas et al., 2012)$ . If the hypothesis that the centroid of the ecological niche encompasses the optimal conditions for the species is correct, differences in the explanatory power of the model could be due to other factors that were not taken into account in characterising the species' niche (Brown et al., 1995; Osorio-Olvera, Soberón, & Falconi, 2019). For instance, A. lopesianum grows in vertical habitats, rocky cliffs, and on fissures in granitic walls with carbonate crusts (Bernardos et al., 2006). In addition, due to the habitat of A. lopesianum, rocky cliffs along riverbanks (Fig. A4), the majority of produced seeds may fall into the river, which could cause difficulties for new colonization and low population numbers in suitable habitats. Therefore, besides the abiotic variables considered in this study (i.e., climatic, topographic, and land cover), variables such as edaphic features, historic events, disturbances and biotic interactions are important factors that also drive species' distributions (Hernández-Lambraño,

González-Moreno, & Sánchez-Agudo, 2018; Osorio-Olvera et al., 2019; Santini, Pironon, Maiorano, & Thuiller, 2019), and ultimately influence the presence and abundance of the species.

Recently Dallas, Decker, and Hastings (2017), performed a meta-analysis in which they suggest that distance-abundance relationships may be rare, difficult to detect, or are an oversimplification of the complex biogeographical forces that determine species spatial abundance patterns. However, the fact that the authors failed to detect significant relationships may result from methodological artefacts or ecological factors (Osorio-Olvera et al., 2019; Soberón, Peterson, & Osorio-Olvera, 2018), rather than to non-existence of such relationships. In fact, Dallas et al. (2017), limited their analyses to a given geographic area, irrespective of the range-wide distribution of the species considered, which can result in important biases in the estimate of distance from centre to edge, and in large under-estimation of species niches (Santini et al., 2019; Soberón et al., 2018).

The application of our abundance model must incorporate an

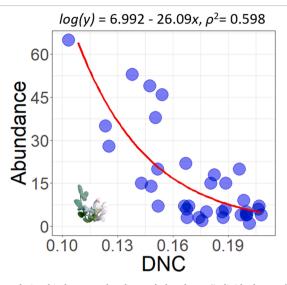


Fig. 5. Relationship between the observed abundance (individuals' number of *Antirrhinum lopesianum*) and the distance to the niche centroid.

understanding of potential biases. Performance of the DNC model is affected by sampling bias in the occurrence data and sample size (Yañez-Arenas et al., 2014); therefore, the accuracy of the estimates will depend on the quantity and quality of the data used. The DNC approach is a static method that does not capture the dynamic nature of population fluctuations over time (Yañez-Arenas et al., 2012). Also, the approach assumes that optimal conditions are always close to the mean values for all variables, and this may not necessarily hold true, due to the fact that for some variables optimal conditions may be closer to the extreme values (Yañez-Arenas et al., 2012). Despite these shortcomings, our results indicate that DNC is a good proxy for estimating *A. lopesianum* abundance across its potential distribution range (Fig. 6); therefore, mapping the distance to the centroid may be a useful approach for obtaining a spatial approximation of the potential abundance for other narrow-range endemic plants, in cases that such data are not available.

#### 4.3. Management implications and future research

While we may be able to define rough range limits for these species at a landscape scale, conservation management actions require planning at the scale of habitat occupancy within the defined range (Margules & Pressey, 2000; Williams et al., 2009). At a conceptual level, range and habitat occupancy are fundamentally different concepts (Gaston, 2003) and SDMs have mostly been applied to predict species ranges. However, the better an SDM, the more it can distinguish between the characteristics of places where species occur and the surrounding background matrix where they are absent, i.e. a species' habitat occupancy (Williams et al., 2009). The modelling approach presented in this study is based on a solid ecological foundation (ecological niche theory; Hutchinson, 1957; Maguire, 1973), therefore facilitating the interpretation of results. The method is relatively simple, requiring only: 1) an occurrence dataset (presence-only or presence-absence) with or without associated abundance information, 2) a proper set of environment variables to characterise species' niche, 3) a reliable SDM and 4) a DNC calculation.

The fact that new occurrences of the taxon were discovered at locations where the binary map indicated favourable habitat suggests that our modelling approach can discriminate between the background matrix and potential habitat at fine scales. In this sense, the information provided by the binary map can support the identification of priority areas for population management such as, reinforcement, introductions

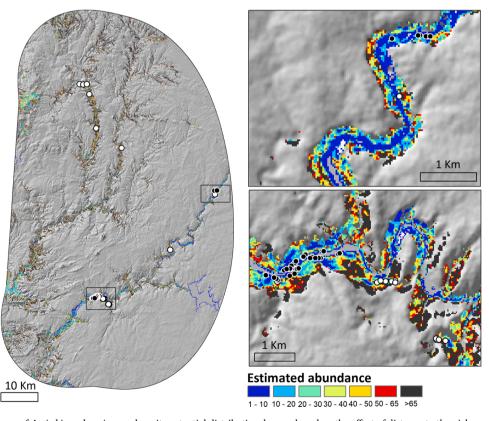


Fig. 6. Estimated abundance of *Antirrhinum lopesianum* along its potential distributional range based on the effect of distance to the niche centroid. We only showed spatial predictions for the observed rank of abundances; therefore, in black, we represent areas with an abundance prediction above the maximum observed. Absence prediction is represented in grey background. White dots indicate presence records and black dots abundance data.

## and translocations (Borthakur et al., 2018; Guisan et al., 2006; IUCN/SSC, 2013).

The validation of our DNC model ( $R^2$  of 0.712) also suggests that the differential values of abundance estimated by the model might also be used to guide other types of conservation management decisions. These could include identifying potential restoration sites or scoring aggregate conservation values based on high densities of cells with high values of expected abundance for the taxon (Williams et al., 2009). On the other hand, our SDM can also support accurate forecasts of range dynamics under scenarios of climate change. Specifically, for our test species the model highlighted a high dependence on features of the temperature regime, which would support more accurate forecasts if climate change scenarios are applied (Sala et al., 2000).

Since there are still a lot of unanswered questions about the ecological processes involved in the persistence of the taxon, it is crucial to develop several research lines to provide an effective conservation plan in the long term. The DNC model can help to design new studies to address knowledge gaps, for example flowering phenology, plant size, and genetic and breeding systems of the species to assess the main factors affecting female reproductive success (Bernardos et al., 2006).

#### Authors' contributions

R.E.H-L and J.A.S-A. jointly conceived the ideas; R.E.H-L. developed the methodology, R.C, R.E.H-L and J.A.S-A collected and analysed the data and R.E.H-L led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### **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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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2020.125889.

#### References

- Amich-García, F., Bernardos-Hernández, S., González-Talaván, A., Caldas, F. B., & Alves, P. (2011). Antirrhinum lopesianum. In *The IUCN Red list of threatened species* 2011 (Vol. 2018). e.T161986A5523922.
- Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. Trends in Ecology & Evolution, 22, 42–47.
- Bernardos, S., Amado, A., Aguiar, C., Santos, C., Fernández-Diez, J., González-Talaván, A., ... Amich, F. (2006). Conservation status of the threatened Iberian Peninsula narrow endemic Antirrhinum lopesianum Rothm. (Scrophulariaceae). Plant Biosystems - an International Journal Dealing With All Aspects of Plant Biology, 140, 2–9.

- Bernardos, S., Crespi, A., Aguiar, C., Fernández, J., & Amich, F. (2004). The plant communities of the Rumici indurati-Dianthion lusitani alliance in the Lusitan Duriensean biogeographical sector (NE Portugal and CW Spain). Acta Botanica Gallica, 151, 147–164.
- Borthakur, S. K., Sharma Baruah, P., Deka, K., Das, P., Sarma, B., Adhikari, D., ... Tanti, B. (2018). Habitat distribution modelling for improving conservation status of Brucea mollis Wall. ex Kurz.–An endangered potential medicinal plant of Northeast India. *Journal for Nature Conservation*, 43, 104–110.
- Breggin, L., George, S. M., & Pencak, E. H. (2003). Planning for biodiversity: Authorities in state land use laws. Washington, DC: Environmental Law Institute.
- Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in Ecology and Evolution*, 6, 1210–1218.
- Brown, J. H., Mehlman, D. W., & Stevens, G. C. (1995). Spatial variation in abundance. Ecology, 76, 2028–2043.
- Calenge, C., Darmon, G., Basille, M., Loison, A., & Jullien, J.-M. (2008). The factorial decomposition of the mahalanobis distances in habitat selection studies. *Ecology*, 89, 555–566.
- Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, 20, 1526–1533.
- Elith, J. H., Graham, C. P., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., ... E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions
- from occurrence data. *Ecography*, 29(2), 129–151. ESRI. (2015). *ARCMAP version 10.3.1* (10.3.1. ed.) California, USA.
- Gaston, K. J. (2003). The structure and dynamics of geographic ranges. Oxford University Press on Demand.
- Gelman, A., & Hill, J. (2007). Data analysis using regression and multilevel/hierarchical models (1st edn.). New York, USA: Cambridge University Press.
- Gogol-Prokurat, M. (2011). Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. *Ecological Applications*, 21, 33–47.
- Gomes, A., Fortalezas, S., Pimpão, R., Figueira, I., Maroco, J., Aguiar, C., ... Santos, C. N. (2013). Valuing the endangered species Antirrhinum lopesianum: Neuroprotective activities and strategies for in vitro plant propagation. Antioxidants (Basel, Switzerland), 2, 273–292.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N. G., Lehmann, A., ...
  Zimmermann, N. E. (2006). Using niche-based models to improve the sampling of rare species. *Conservation Biology*, *20*, 501–511.
  Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R.,
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., ... Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, 16, 1424–1435.
- He, K. S., Bradley, B. A., Cord, A. F., Rocchini, D., Tuanmu, M.-N., Schmidtlein, S., ... Pettorelli, N. (2015). Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, 1, 4–18.
- Heiberger, Richard, M., & Holland, B. (2004). Statistical analysis and data display: An intermediate course with examples in S-Plus, r, and SAS. Springer Texts in Statistics.
- Hernández-Lambraño, R. E., González-Moreno, P., & Sánchez-Agudo, J.Á. (2018). Environmental factors associated with the spatial distribution of invasive plant pathogens in the Iberian Peninsula: The case of Phytophthora cinnamomi Rands. *Forest Ecology and Management*, 419-420, 101–109.
- Hernández-Lambraño, R. E., Rodríguez de la Cruz, D., & Sánchez-Agudo, J.Á. (2019). Spatial oak decline models to inform conservation planning in the Central-Western Iberian Peninsula. Forest Ecology and Management, 441, 115–126.
- Hijmans, R. J. (2019). Raster: Geographic Data Analysis and modeling. R package version 3.0-7. https://CRAN.R-project.org/package=raster.
- Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, 199, 142–152.
- Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22, 415–427.
- IUCN/SSC. (2013). Guidelines for reintroductions and other conservation translocations. Version 1.0. Switzerland: IUCN Species Survival Commission Gland.
- Kuhn, M., Wing, J., & Weston, S. (2017). Caret: Classification and regression training. R packag version 60-77. https//CRANR-project.org/package=caret.
- Lobo, J. M., Jiménez-Valverde, A., & Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145–151.
- Maguire, B. (1973). Niche response structure and the analytical potentials of its relationship to the habitat. *The American Naturalist, 107*, 213–246.
- Manthey, J. D., Campbell, L. P., Saupe, E. E., Soberón, J., Hensz, C. M., Myers, C. E., ... Barve, N. (2015). A test of niche centrality as a determinant of population trends and conservation status in threatened and endangered North American birds. *Endangered Species Research*, 26, 201–208.
- Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. Nature, 405, 243–253.
- Martínez-Gutiérrez, P. G., Martínez-Meyer, E., Palomares, F., & Fernández, N. (2018). Niche centrality and human influence predict rangewide variation in population abundance of a widespread mammal: The collared peccary (Pecari tajacu). *Diversity* & *Distributions*, 24, 103–115.
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, 9, Article 20120637.
- McPherson, M. J., & Jetz, W. (2007). Effects of species' ecology on the accuracy of distribution models. *Ecography*, 30, 135–151.
- Osorio-Olvera, L., Soberón, J., & Falconi, M. (2019). On population abundance and niche structure. *Ecography*, 42, 1415–1425.

#### R.E. Hernández-Lambraño et al.

- Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., ... Araújo, M. B. (2011). *Ecological niches and geographic distributions* (MPB-49) (Vol. 56). Princeton, New Jersey: Princeton University Press.
- R Core Team. (2017). R: A language and environment for statistical computing version 3.4.2. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project. org/.
- Ramírez-Rodríguez, R., & Amich, F. (2014). Notes on rare and threatened flora in western-central Iberia. *Lazaroa, 35*, 221–226.
- Rivas-Martínez, S., Díaz-González, T. E., Fernández-González, F., Izco-Sevillano, J., Loidi-Arregui, J. J., Fernandes-Lousā, M., ... Penas Merino, Á. (2002). Vascular plant communities of Spain and Portugal: Addenda to the syntaxonomical checklist of 2001. *Itinera geobotanica*, 15, 433–922.
- Rodríguez, J. P., Brotons, L., Bustamante, J., & Seoane, J. (2007). The application of predictive modelling of species distribution to biodiversity conservation. *Diversity & Distributions*, 13, 243–251.
- Sala, O. E., Stuart Chapin, F., Iii, Armesto, J. J., Berlow, E., Bloomfield, J., ... Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. Science, 287, 1770.
- Santini, L., Pironon, S., Maiorano, L., & Thuiller, W. (2019). Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. *Ecography*, 42, 696–705.
- Soberón, J., & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. Proceedings of the National Academy of Sciences, 106, 19644.
- Soberon, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, 2, 1–10.

- Journal for Nature Conservation 57 (2020) 125889
- Soberón, J., Peterson, A. T., & Osorio-Olvera, L. (2018). A comment on "Species are not most abundant in the centre of their geographic range or climatic niche". *Rethinking Ecology*, 3, 13–18.
- Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2016). biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7. In https://CRAN.R-project. org/package=biomod2.
- Ureña-Aranda, C. A., Rojas-Soto, O., Martínez-Meyer, E., Yáñez-Arenas, C., Landgrave Ramírez, R., & Espinosa de los Monteros, A. (2015). Using range-wide abundance modeling to identify key conservation areas for the micro-endemic Bolson Tortoise (Gopherus flavomarginatus). *PloS One, 10*, Article e0131452.
- Wickham, H. (2017). Tidyverse: Easily install and load "tidyverse" packages. R Packag version 121. https://CRANR-project.org/package=tidyverse. In.
- Williams, J. N., Seo, C., Thorne, J., Nelson, J. K., Erwin, S., O'Brien, J. M., ... Schwartz, M. W. (2009). Using species distribution models to predict new occurrences for rare plants. *Diversity & Distributions*, 15, 565–576.
- Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., ... Group, N. P. S. D. W. (2008). Effects of sample size on the performance of species distribution models. *Diversity & Distributions*, 14, 763–773.
- Yañez-Arenas, C., Guevara, R., Martínez-Meyer, E., Mandujano, S., & Lobo, J. M. (2014). Predicting species' abundances from occurrence data: Effects of sample size and bias. *Ecological Modelling*, 294, 36–41.
- Yañez-Arenas, C., Martínez-Meyer, E., Mandujano, S., & Rojas-Soto, O. (2012). Modelling geographic patterns of population density of the white-tailed deer in central Mexico by implementing ecological niche theory. *Oikos, 121*, 2081–2089.
- Zhang, L., Liu, S., Sun, P., Wang, T., Wang, G., Wang, L., ... Zhang, X. (2016). Using DEM to predict Ables faxoniana and Quercus aquifolioides distributions in the upstream catchment basin of the Min River in southwest China. *Ecological Indicators*, 69, 91–99.