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Hierarchical species distribution models in support of vegetation conservation at the landscape scale

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Abstract

Questions: Species distribution models (SDMs) based on habitat suitability and niche quantification are powerful tools in vegetation science. Recent findings suggest that they could be applied at the landscape scale as vegetation conservation tools, but that some environmental dimensions (e.g., climate) need to be considered at larger scales. What is the importance of applying hierarchical SDMs combining information from different scales to ensure consistent local vegetation management decisions?

Study Site: Mainland Spain and Biosphere Reserve of Sierra del Rincón (central Spain).

Methods: We generated SDMs for five tree species at the regional scale (mainland Spain) using climatic variables plus presence/absence data from the Spanish National Forest Inventory; and at the landscape scale (Sierra del Rincón Biosphere Reserve) using local environmental variables plus locally gathered vegetation presence/absence data. Predictions of both regional and landscape models were combined at the landscape scale following two different hierarchical approaches. The four resulting predictions were compared with correlation coefficients and independently evaluated with the AUC statistic and data collected in the study area.

Results: The regional SDMs depict suitable climatic conditions for the tree species, while the landscape SDMs capture important local ecological drivers that influence habitat suitability at finer scales. Expectedly, the regional SDMs predict larger suitable areas than the landscape SDMs. The predictions from the hierarchical approaches are reliable and provide on average better results than non-hierarchical ones.

Conclusions: SDMs can be valuable tools for local plant conservation programs. We present examples of the applicability of a hierarchical modeling approach and conceptual and methodological solutions related to the use of these tools in local vegetation conservation programs. For example, we show that landscape SDMs could be used to determine the current distribution of endangered plant species, while a hierarchical approach would be better suited to define areas to re-vegetate within a local restoration program.

KEYWORDS
conservation plan, ecological drivers, ensemble modeling, environmental niche, forest management, habitat suitability, hierarchical species distribution models, plants, spatial distribution, species distribution modeling, vegetation restoration

1 | INTRODUCTION

After an environmental disturbance, either natural (e.g., wind events, floods, or wildfires) or anthropogenic (e.g., open-cast mining, severe pollution events, or land-use conversion), conservation managers often have to evaluate how to alleviate potential undesirable environmental effects through a range of possible conservation actions (Acevedo, Sefair, Smith, Reichert, & Fletcher, 2015), such as restoring native vegetation in the area (van Andel & Aronson, 2012). Yet, such decisions often have to be made with incomplete knowledge (Perring et al., 2015), and spatial information about plant species distribution is most often lacking (Ferrier & Wintle, 2009; Tulloch et al., 2016). Species distribution modeling (SDM; Franklin, 2010; Guisan, Thuiller, & Zimmermann, 2017; Peterson et al., 2011) is an effective tool widely applied in numerous disciplines (Elith & Leathwick, 2009; Mateo, Felicísimo, & Muñoz, 2011). The resulting models can be used to support conservation planning decisions (Guisan et al., 2013; Tulloch et al., 2016), for instance by offering spatial knowledge on the potential suitability of plant species being considered for vegetation restoration programs (Gastón et al., 2014). There are numerous examples of SDMs applied to support management of endangered species (Guisan et al., 2006; Le Lay, Engler, Franc, & Guisan, 2010; Sousa-Silva, Alves, Honrado, & Lomba, 2014; Wang et al., 2015), assessment of climate change effects on biodiversity (Patiño et al., 2016), biodiversity conservation plans (Ramirez-Villegas et al., 2014), or reserve design (Mateo, de la Estrella, Felicísimo, Muñoz, & Guisan, 2013). However, despite the high potential applicability of SDMs for plant restoration (Gastón et al., 2014), they have rarely been applied for this purpose (but see; Burnside, Smith, & Waite, 2002; Gastón et al., 2014; van Loon et al., 2011). This lack of restoration use might be caused by limitations in conceptual and methodological issues arising when applying SDMs to conservation programs at the landscape scale, such as the need to integrate hierarchical levels (Gastón & García-Viñas, 2010), or the choice of an appropriate sampling strategy to sample the data at the landscape scale (Mateo, Gastón, Aroca-Fernández García-Viñas & Saura, 2018).

Here, we evaluate more specifically the importance of hierarchical modeling approaches (see Cassini, 2011; Hattab et al., 2014; Hughes, Adams, & Stroh, 2012; Pearson, Dawson, & Liu, 2004; Petitpierre et al., 2016), starting from the premise that spatial distribution patterns of both species and biodiversity can be expected to be driven by different processes at different scales (Mateo, Mokany, & Guisan, 2017; McGill, 2010; Vicente et al., 2014; Wiens, 1989). Integrating models through a hierarchical approach has been proposed in previous studies (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012; Guisan et al., 2017; Mateo et al., 2017; Pearson et al., 2004; Petitpierre et al., 2016) to better account for different processes driving plant species distributions. Here, we test a hierarchical approach at two ecological and spatial scales (landscape and regional) to account for two crucial types of processes behind plant species distribution patterns. First, we consider SDMs fitted at the regional scale, which are expected to represent the ecological tolerances of plant species to predictors acting at large scales (e.g., climate), i.e., encompassing as much as possible of the whole distribution and the entire realized niche of the species (Pearson et al., 2004; Petitpierre et al., 2016). Second, we consider SDMs fitted at the landscape scale, which are expected to capture important local conditions for plant species (e.g., landscape features, microtopography). Importantly, we assume that the regional model will capture most of the climatic niche of the species, whereas this might be inadequately captured (Thuiller, Brotons, Araújo, & Lavorel, 2004) by models fitted across too small geographic extents, because the latter will not include the whole range of climatic conditions suitable for the species (Petitpierre et al., 2016). This can ultimately hamper proper climate change projections (Barbet-Massin, Thuiller, & Jiguet, 2010; Guisan et al., 2017; Pearson et al., 2004; Petitpierre et al., 2016; Thuiller et al., 2004; not performed here). Thus, fitting SDMs at the two scales offers complementary information that, we hypothesize, when properly integrated, could significantly improve the guidance of decision-making within local vegetation conservation programs (Young, Petersen, & Clary, 2005).

So far, many modeling studies, even when aimed at conservation applications, have been conducted over large extents (regional or continental) and coarse resolutions (km; Araújo, Thuiller, Williams, & Reginster, 2005; Mateo et al., 2016). However, modeling at the landscape scale with fine spatial resolution is, needed to accurately guide local vegetation conservation programs (Mateo et al., 2018). In this regard, a hierarchical modeling approach (Gallien et al., 2012; Pearson et al., 2004; Petitpierre et al., 2016) was shown to provide the appropriate tool to account for those environmental factors driving entire species range together with the resolution needed to account for processes operating over a smaller extent and at finer resolution, i.e., at the landscape scale, such as microtopography (Lenoir, Hattab, & Pierre, 2017; Vicente et al., 2014).

The principal objective of this study is to evaluate the possibility of obtaining more accurate hierarchical SDMs to be used in local vegetation conservation programs by the combination of SDMs developed at two different scales (landscape and regional). We assessed diverse conceptual and methodological concerns of hierarchical models in vegetation conservation programs, employing as study case a Biosphere Reserve (Sierra del Rincón) in central Spain, and focusing on five tree species that are native to this Reserve. The Sierra del Rincón is a relevant study area from the perspective of assessing the support to landscape vegetation conservation programs due to its medium size (15,231 ha), which is close to the scale at which forest management and restoration actions are planned and implemented, and it is ideal for modeling purposes due to its broad environmental variability (from 670 to 2,200 m in elevation). We focus on tree species because they are essential in conservation and restoration programs, through influencing local ecological conditions (shade, moisture, etc.) required for many other plant species that can establish under their canopy, and because they provide key habitat resources (foraging resources such as leaves and fruits, shelter, nesting spots, etc.) for many animal species. Our hypothesis is that hierarchical modeling improves fine-scale predictions of plant species distributions, and therefore should allow deriving better guidance of landscape conservation programs, such as vegetation restoration measures or the reintroduction of endangered species. We thus expect hierarchical models to outperform regional and landscape models and to allow more accurate spatial extrapolations since they will consider a larger proportion of the climatic conditions suitable for the species than landscape models alone (Guisan et al., 2017; Petitpierre et al., 2016). In addition, we hypothesize that regional models (considering only climatic variables) would predict larger suitable areas for plant species than landscape models (considering only local environmental variables).

2 | METHODS

2.1 | Regional and landscape-scale study areas

This work used two study areas at two different scales (extent and resolution), regional and landscape (local), the latter being nested within the former. The regional scale was the mainland Iberian Peninsula, covering 596.740 km^2 from 0 to 3,478 m in elevation. The landscape scale study area was the Sierra del Rincón Biosphere Reserve (41°03′ N, 3°29′ W, central Spain). Its flora is particularly rich with over 1,036 vascular plant species (Baonza Díaz, 2017) that make up a diverse vegetation cover consisting of forests such as Pyrenean oak (*Quercus pyrenaica*), holm oak (*Q. ilex* subsp. *ballota*), or reforested pinewoods (*Pinus sylvestris*, *P. nigra*, *P. pinaster*, and *P. uncinata*); a variety of shrublands (*Genista florida*, *Lavandula stoechas*¸ *Thymus* ssp., *Adenocarpus* spp., *Erica* spp., *Cistus* spp., etc.); and pastures. The area shows high ecological value, but it is nevertheless closely linked to traditional rural human activities, as befits its Biosphere Reserve designation. Its vegetation cover has been affected by land use change processes that have been going on within Spanish rural areas since the 1960s, including: decline of extensive livestock population; reduction of cropland extent; decrease of both timber extraction and other traditional forest management practices such as firewood collection or resin extraction; and intensification of recreational use. Within some areas of the Reserve, all these changes have induced degradation of the vegetation cover that ultimately has led to the loss of ecological value as well as land functionality for the rural population (a key point for conservation within Biosphere Reserves). The only restoration actions carried out to date were pine reforestations in the 1970s. Territorial diagnoses would be needed to develop a local conservation strategy that defines priority areas, allows guiding interventions to stop the degradation process, and ultimately recovers various ecosystem functions (biodiversity conservation, hydrological protection, recreational use, etc.). This could also help conserving the duality of ecological value and rural development often characterizing such Biosphere Reserves. Moreover, according to UNESCO, these Reserves are to be ‘Science for Sustainability support sites’. Thus the use of new tools such as hierarchical SDMs to manage changes and understand interactions between social and ecological systems is particularly relevant.

2.2 | Species distribution data

To assure a minimum sample size sufficient for accurate model fitting (Papeş & Gaubert, 2007), only tree species with a minimum of 15 occurrences in the vegetation plots locally sampled in the study area (see next section) were selected. Five tree species were hence analysed: holly tree (*Ilex aquifolium* L.), common juniper (*Juniperus communis* L.), Scots pine (*Pinus sylvestris* L.), Pyrenean oak (*Quercus pyrenaica* Wild.), and holm oak (*Q. ilex* L. subsp. *ballota* (Desf.) Samp). We followed Castroviejo (1986-2012) for nomenclature. For each species, three databases were separately compiled:

1. *Regional scale (Spain) training database:* Species presences and absences of the five tree species (Table 1) were gathered from the Spanish National Forest Inventory for mainland Spain (76,347 circular plots of 25 m radius). It follows a network with nodes separated by 1,000 m. This database was used to develop models at the regional scale.
2. *Landscape scale (Biosphere Reserve) training database:* Based on previous work in the study area (Mateo et al., 2018), an opportunistic sampling along roads and tracks was conducted. A total of 302 circular (10 m radius) plots were sampled at 1,000-m intervals, with presence and absence of tree species recorded in each plot (Table 1). This dataset was used to train the models. This database was used to develop models at the landscape scale.
3. *Independent landscape (Biosphere Reserve) database for evaluation:* An independent landscape sampling strategy was carried out to validate the generated SDMs. A regular sampling was designed a priori following a grid over the Biosphere Reserve with nodes separated by 1,000 m. Presence and absence of tree species were recorded in 132 circular plots of 10 m radius (Table 1).

2.3 | Environmental variables

We employed a set of data characterizing different environmental variables, and with different spatial resolutions at the two considered scales. At the regional scale, we used climatic variables available at a resolution of 30 arc-seconds (~1 km^2 at the equator) from WorldClim 2.0 (Fick & Hijmans, 2017) for the whole Spanish mainland for the adjustment of the regional SDMs. To avoid multicollinearity, we ran a pairwise correlation analysis on all the available variables (monthly precipitation, and monthly minimum, maximum, and mean temperatures), and in each pair with a correlation value greater than 0.7 (Dormann et al., 2013), we removed the variable expected to be the least causal for the species (based on literature knowledge). We obtained a final set of five ecologically (physiologically) meaningful variables for plants in Mediterranean climates, which we used to calibrate the models at the regional scale. These variables were: precipitation in April, precipitation in August, average temperature in October, minimum temperature in January, and maximum temperature in August. After calibration of the SDMs at the regional scale, we projected the models across the landscape study area (Sierra del Rincón Biosphere Reserve) by downscaling the five climatic variables to 25 m resolution (see Appendix S1).

At the landscape scale, plant species distributions are expected to be driven by different environmental factors (De Bello et al., 2013). In order to represent these factors, we generated different predictor variables at 25 m resolution: *northness* (orientation along the South–North axis), *eastness* (orientation along the West–East axis), monthly solar radiation, least surface distance to any stream, compound topographic index, heat load index, tree canopy cover fraction derived from a LIDAR image, elevation, curvature, and slope. To avoid multicollinearity, we used the same approach as for the regional predictors (above) based on pairwise correlations, to finally keep the five most uncorrelated and ecologically meaningful variables for explaining plant species distribution patterns (see; Mateo et al., 2018): (a) distance to streams: for each pixel, we calculated the least surface distance (m) to any stream (Fleming & Doan, 2013); (b) canopy cover above three meters derived from a LIDAR image (Centro Nacional de Información Geográfica): this is the fraction of ground area covered by the vertical projection of tree crown perimeters; (c) heat load index (HLI): this was calculated according to the method of McCune and Keon (2002), where a southwest-facing slope has warmer temperatures than a southeast-facing slope; (d) elevation: derived from a 25-m resolution digital elevation model (DEM, Centro Nacional de Información Geográfica); (e) slope: derived from the DEM. All the independent variables were generated at 25 m resolution and projected at ETRS89 UTM 30N using ArcGIS 10.3 (ESRI) and R 3.3.2 (R Core Team) software.

2.4 | Species distribution modeling

For each species, we generated four species distribution models (SDMs): one model at the regional scale (based on the regional database and climatic variables, Figure 1a), one model at the landscape scale (based on the landscape database and local environmental variables, Figure 1b), and two different hierarchical combinations of regional and landscape models (*hierarhical1* and *hierarhical2). Hierarchical1* was fitted using the local environmental variables, plus the suitability predicted by the regional model (originally trained for mainland Spain at 30 arc-seconds) when projected over the local study area (Sierra del Rincón Biosphere Reserve) at 25 m resolution using the five climatic variables (Figure 1c). *Hierarhical2* was

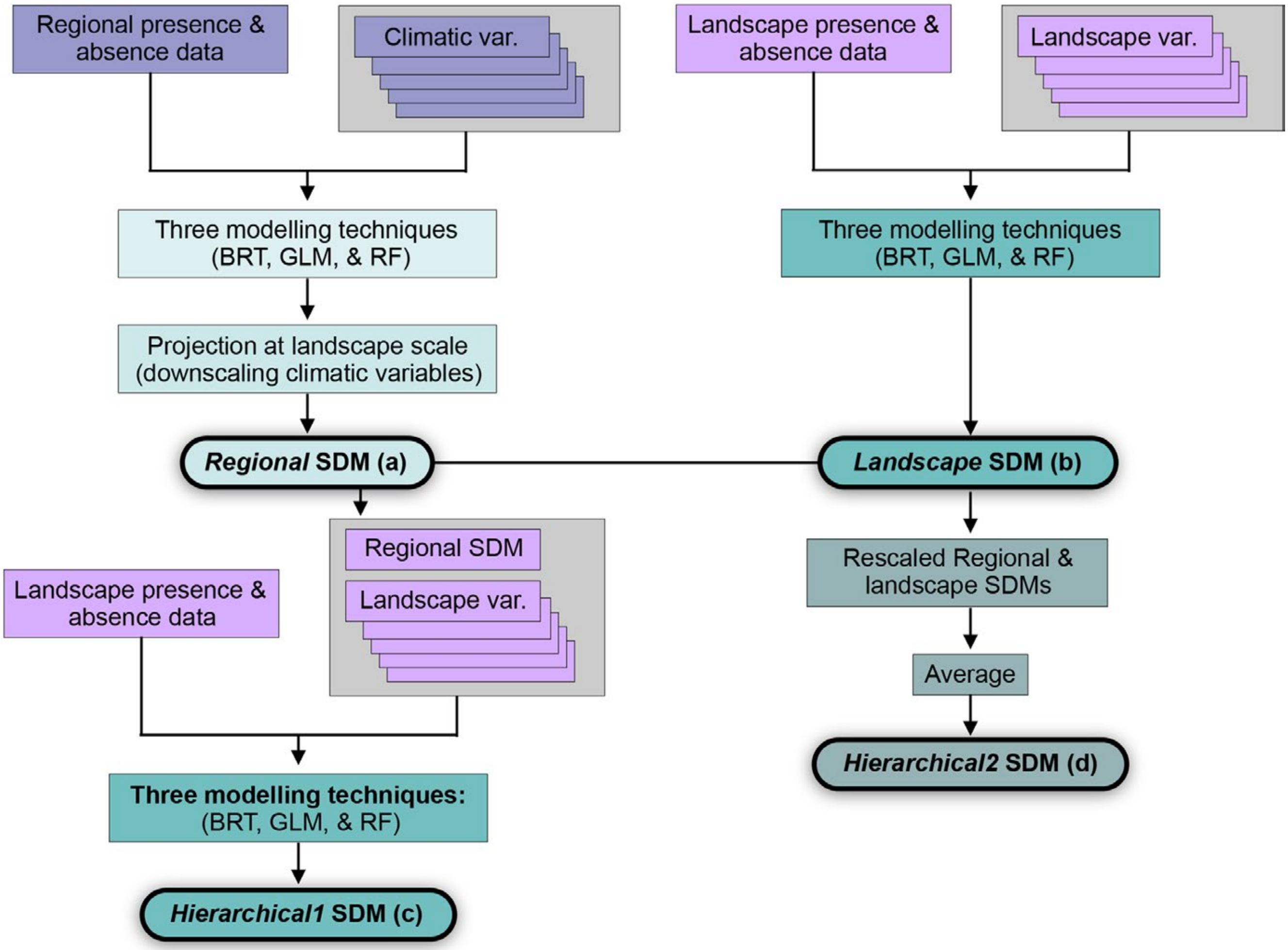

FIGURE 1 Workflow to generate regional (a), landscape (b), *hierarchical1* (c), and *hierarchical2* (d) species distribution models. BRT, boosted regression trees; GLM, generalized linear models; RF, random forests; SDM, species distribution model [Colour figure can be viewed at wileyonlinelibrary.com]

generated by averaging the landscape and the regional rescaled SDMs' suitability predictions (Figure 1d).

Models in the regional, local and *hierarchical1* approaches were all generated following an ensemble procedure (Araújo & New, 2007; Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009) including three statistical techniques: generalized linear models (GLM; McCullagh & Nelder, 1989), boosted regression trees (BRT; Friedman, 2001), and random forests (RF; Breiman, 2001). All the ensemble models were generated using the biomod2 (Thuiller, Lafourcade, Engler, & Araújo, 2009) R package with default parameters for each of the five species at the three scales (regional, local and *hierarchical1*). For each of the three modeling techniques (GLM, BRT, and RF), the corresponding dataset was randomly split ten times into an 80% dataset to generate ten resampling run models and a 20% dataset to estimate their predictive accuracy (i.e., repeated split-sample cross-validation); therefore, we generated 30 models per species (10 resampling runs models × three techniques). After elimination of all models with an AUC < 0.5 (not different from or worse than random), we generated for each species an ensemble prediction consisting of the weighted mean of the different resampling run predictions, where the weight of each model in the ensemble was proportional to its predictive accuracy (AUC value). We used a ratio of 1.3 between a weight and the following or prior one (prob.mean.weight.decay = 1.3) in the Ensemble Modeling function of the biomod2 package (Thuiller et al., 2009). Finally, we rescaled the predictions of the landscape and the regional SDMs to have the same minimum and maximum values, and the *hierarhical2* model was generated by averaging these rescaled predictions.

The four final SDMs (regional, landscape, *hierarchical1*, and *hierarchical2*) were independently evaluated with the independent landscape database, i.e., none of the plots in the evaluation dataset were used to train the models. We used a threshold-independent statistic that estimates the ability of the model to discriminate between presences and absences: the area under the curve (AUC) of an ROC plot (evaluation AUC; Fielding & Bell, 1997; Swets, 1988). This evaluation AUC value should rather be understood as an assessment of the local predictive power of the models, because this independent database was gathered at the landscape scale. Additionally, the four final maps of predicted suitability were compared, for each species, by applying the Spearman correlation coefficient by pairs.

We hypothesized that regional models (only climatic variables) would predict a larger suitable range for the species than landscape models (environmental variables). To assess this hypothesis, we converted original (continuous suitability index) regional and landscape model predictions into binary predictions (presence/absence) applying two different threshold criteria: a threshold derived from the ROC plot (i.e., selecting the threshold point closest to the top-left corner of the ROC plot), and the threshold maximizing the Kappa statistics (Liu, White, & Newell, 2013). The thresholds were calculated using the landscape-scale training database. For all species, models and threshold criteria, we counted the number of pixels predicted to be suitable. Finally, we calculated the percentage of the total local study area predicted as suitable for the different species.

TABLE 1 Number of observed presences for each species and sampling strategy (regional, landscape, and evaluation) employed in this study

Sampling	*I. aqui*	*J. comm*	*P. sylv*	*Q. ilex*	*Q. pyre*
Landscape	16	53	92	46	141
Regional	6,949	15,861	13,380	7,458	42,671
Evaluation	6	24	43	14	57

Species abbreviations: *I. aque*: *Ilex aquifolium* (holly tree); *J. comm*: *Juniperus communis* (common juniper); *P. sylv*: *Pinus sylvestris* (Scots pine); *Q. ilex*: *Quercus ilex* subsp. *ballota* (holm oak); *Q. pyre*: *Quercus pyrenaica* (Pyrenean oak).

TABLE 2 AUC values (independent evaluation at the landscape scale) achieved for the regional, landscape, *hierarchical1*, and *hierarchical2* SDMs and the five tree species considered in this study (species abbreviations as in Table 1)

	I. aqui	*J. comm*	*P. sylv*	*Q. ilex*	*Q. pyre*
Regional	0.883	0.535	0.831	0.729	0.746
Landscape	0.734	0.724	0.859	0.802	0.848
Hierarchical1	0.763	0.753	0.878	0.799	0.863
Hierarchical2	0.878	0.637	0.874	0.750	0.876

3 | RESULTS

The final models at the landscape scale showed evaluation-AUC values (on the independent landscape database) >0.75 for the five species (Table 2). Values were, however, superior than 0.75 only for two species when regional models were projected at the landscape scale (Table 2).

The hierarchical combinations of landscape and regional models presented evaluation AUC values greater than 0.75 for the five species for the *hierarchical1* models and for four species for the *hierarchical2* models (Table 2). For one species (*Juniperus communis*), the AUC value was low (0.637 for *hierarchical2* model), indicating an unreliable model. This species is rather ubiquitous and opportunistic, and as such exhibits a broad ecological range (Pearman et al., 2008), which could explain the low AUC value obtained (Mateo, Felicísimo, & Muñoz, 2010).

The *Hierarchical1* model showed evaluation-AUC values greater than the values obtained for the landscape model for the five species. The *Hierarchical2* model showed evaluation-AUC values greater than the values obtained for the landscape model for three of the five species.

The landscape and regional models differed significantly (Figure 2). The mean value of the correlation coefficient (Table 3) when comparing landscape and regional models was 0.59 (0.15 standard

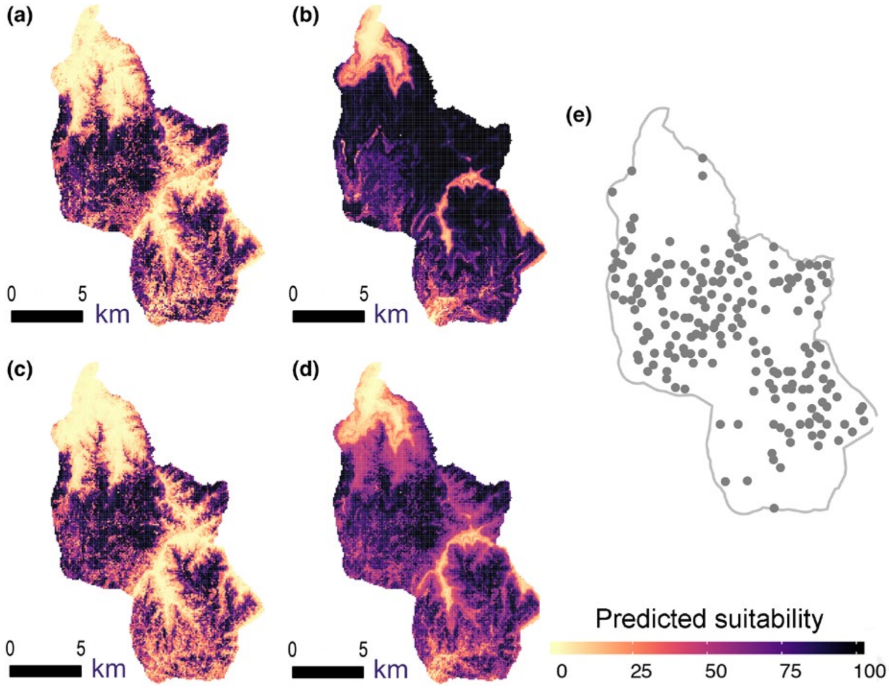

FIGURE 2 Landscape (a), regional (b), *hierarchical1* (c), and *hierarchical2* (d) SDMs derived for the Pyrenean oak (*Quercus pyrenaica*) and projected in the Biosphere Reserve of Sierra del Rincón (central Spain). All the models were rescaled from 0 to 100 predicted suitability values (as shown in the graphical legend). The regional model was created using data from mainland Spain and projected at the landscape resolution and scale. Grey dots (e) represent the presence data available for the Pyrenean oak in the three (regional, local, and evaluation) databases [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Mean Spearman correlation coefficient and standard deviation (in brackets) for the pairwise comparison of the generated SDMs (regional, landscape, *hierarchical1* and *hierarchical2)* for the five tree species considered in this study

	Regional	Landscape	*Hierarchical1*	*Hierarchical2*
Regional	1(0)	0.59(0.15)	0.67(0.11)	0.85(0.10)
Landscape		1(0)	0.90(0.09)	0.87(0.06)
Hierarchical1			1(0)	0.88(0.05)

deviation). On the other hand, landscape, *hierarchical1* and *hierarchical2* models were more similar, with correlation coefficients of 0.87 or higher (Table 3).

The suitable area predicted by the regional models for each of the five species was greater than that of the landscape models, irrespective of the applied threshold criteria (Table 4).

4 | DISCUSSION

Here, we simultaneously compared the predictive power at fine spatial scales of different species distribution models build with information at the regional scale only, with information at the landscape scale only, and by combining information from the two spatial scales. Following our initial hypothesis, the predictions of SDMs at the two scales were different and combining them in a hierarchical way led to higher predictive performance, indicating that integrating information from regional and local scales can be useful to obtain better local predictions potentially useful for local vegetation conservation managers (Lomba et al., 2010; Vicente et al., 2011).

4.1 | Comparison of species distribution models at different scales

The SDMs developed at local and regional scales differed significantly (Table 3). This was expected since SDMs trained at different scales characterized various drivers of plant spatial distribution and niche conditions (Lortie et al., 2004; Mateo et al., 2017). These results reflect the varying strengths and limitations of ecological models trained at various scales (Anderson & Raza, 2010).

For instance, the landscape SDMs should reflect properly the local ecological conditions available for the plant species, but they may fail to represent the complete climatic niche of species (Petitpierre et al., 2016; Thuiller et al., 2004). Consequently, models fitted with data from a partial section of a species' niche can produce truncated response curves (Sánchez-Fernández, Lobo, & Hernández-Manrique, 2011), which can result in biased predictions of distribution (Petitpierre et al., 2016; Thuiller et al., 2004). On the contrary, the regional SDMs were expected to capture a larger part of the climatic niche of the species than the landscape SDMs, but were expected to overpredict suitable areas for the species at the

TABLE 4 Percentage of the potential suitable range for each species in the local study area as predicted by the landscape and regional binary SDMs generated with two different threshold criteria (Liu et al., 2013): a threshold derived from the ROC plot (upper value), and the threshold maximizing the Kappa statistics (lower value). Species abbreviations are as in Table 1

	I. aqui (%)	*J. comm* (%)	*P. sylv* (%)	*Q. ilex* (%)	*Q. pyre* (%)
Landscape	2.81	17.77	33.95	14.09	47.40
	3.22	21.02	33.95	19.29	47.40
Regional	16.31	38.32	36.19	17.74	79.56
	31.30	38.32	48.53	45.79	66.84

landscape scale. Accordingly, for the five tree species considered, the suitable area predicted for the species by the regional SDMs was greater than that of the landscape SDMs (Table 4). Expectedly, when projected at the landscape scale, the regional SDMs showed a poorer fit than the landscape SDMs (Table 2) because the former were adjusted only with large-scale climatic variables, but then evaluated through occurrence data gathered at the landscape scale. This effect was likely strengthened because the evaluation dataset was sampled at the same spatial and temporal scale as the one used to fit the landscape SDMs.

4.2 | The contribution of hierarchical species distribution models

Examples of studies using hierarchical approaches to integrate multiple geographical scales in SDMs are still scarce (but see; Gastón & García-Viñas, 2010; Gallien et al., 2012; Hattab et al., 2014; Keil, Belmaker, Wilson, Unitt, & Jetz, 2013; Menke, Holway, Fisher, & Jetz, 2009; Pearson et al., 2004), despite the importance of this issue (Mateo et al., 2017). Here, the hierarchical combination of landscape and regional SDMs (*hierarchical1* and *hierarchical2* models) provided, on average across species, better results (higher AUC values, Table 2) than non-hierarchical ones. This increased performance is likely due to the fact that the hierarchical SDMs jointly consider regional and landscape drivers of species distributions, thus overcoming the limitations that landscape and regional SDMs have separately. They consider a larger part of the realized climatic niche of species (as they integrate a regional SDM component), reducing the risk of biased prediction, but they are still able to reflect local ecological processes responsible for the fine-scale spatial patterning of species distributions. This further reduces the risk of extrapolation if model would be used to derive projections in space and time, which is essential in studies involving climate change projections or biological invasions (Gallien et al., 2012; Petitpierre et al., 2016).

The superiority observed here of hierarchical models over classical (single scale) models is, however, conditioned by appropriate modeling practices. We can highlight five of them: (a) an appropriate selection of ecologically meaningful variables inside a conceptual framework that considers different sets of independent variables at the different scales (climatic at the regional scale and environmental at the landscape scale), in accordance with ecological theory (Austin, 2002; McGill, 2010); (b) the correct downscaling of climatic variables from the regional to the landscape scale and fine spatial resolution (meters, Appendix S1); (c) a proper hierarchical methodological combination of regional and landscape SDMs (Figure 1); (d) the consideration of detailed environmental variables (slope, HLI, etc.) at the landscape resolution (meters), including variables derived from LIDAR images; (e) the availability of accurate presence/absence data at the regional and the landscape scales. All these points should be considered cautiously for a successful application of hierarchical SDMs in vegetation conservation programs.

4.3 | Conceptual framework and applicability of hierarchical species distribution models

Both hierarchical models offered different results (Table 3, Figure 2, Appendix S2). The *hierarchical1* model considered the regional model as an independent variable together with landscape environmental variables. By doing so, the final significance of the regional model in the final hierarchal model could be different for each species, and essential for some species, but trivial for others. On the other hand, the *hierarchical2* model was calculated as the mean of both regional and landscape rescaled models. Therefore, here, the relative significance of the regional model (regional climatic niche) in the final model was always equivalent and noticeable for all the species. Both hierarchical models were evaluated with current landscape data; therefore, it was expected that *hierarchical1* models would yield better results than *hierarchical2* models. This is because the latter will be theoretically more prone to commission errors in areas that are climatically suitable but where the species is absent due to other environmental or human-related factors. However, this over-prediction pattern may be useful in some cases. If the objective of a local program is the restoration of natural vegetation, *hierarchical2* models could provide useful information to assist spatial decision-making. Model predictions could guide the identification of candidate areas for natural regeneration, plantations, or seeding strategies (Guisan et al., 2013) by identifying areas with suitable climatic conditions for the species but where it is currently absent. For example, Figure 2 shows all the plots where the Pyrenean oak was reported (grey dots). Certain zones are shown in the four maps in dark or purple, which indicates high suitability for this species. However, the species was not actually found in these zones, even after intense fieldwork, or it was only occasionally found there as small seedlings or just a few individuals. The Sierra del Rincón has suffered remarkable human impacts on the vegetation. In the past, these suitable areas for the Pyrenean oak (dark areas without grey dots or with only an occasional representation of the species) may have been forests dominated by this species, or at least mixed forests with a significant component of Pyrenean oak. These areas, mainly highlighted in the regional and *hierarchical2* model predictions, could thus be potential targets for being re-vegetated with this broadleaved tree.

On the other hand, the landscape SDMs reflect the local ecological conditions available for the plant species, and they will be good candidates for use in conservation management if the objective is, for instance, to determine the current distribution of an endangered species.

4.4 | Future lines of research

The findings presented here are promising and suggest avenues for future research. In particular, hierarchical SDMs could be further evaluated and tested for their use in a variety of local conservation efforts (see Guisan et al., 2013), such as reintroduction programs (Araújo & Peterson, 2012), management of endangered plant species (Wang et al., 2015), species selection in vegetation restoration programs (Gastón et al., 2014), comparing various scale preferences in partnership with stakeholders (Hughes et al., 2012), forest management (Mateo et al., 2018), and, especially, in the development of local restoration programs in the context of climate change (Eitzel et al., 2012; Jiang & Zhang, 2016). The consequences of climate change for the application of vegetation restoration, in particular, need further investigation (Harris, Hobbs, Higgs, & Aronson, 2006). In this regard, SDMs were already shown to have a considerable potential to support the integration of future climatic conditions into conservation and management programs (Schwartz, 2012; Guisan et al., 2013). However, the accurate estimation of climate change effects relies on the correct evaluation of plant distribution drivers at the local level (Randin et al., 2009), and on the proper capture of the full species climatic niche (Guisan et al., 2017; Petitpierre et al., 2016), provided it remains constant in the future (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014; Petitpierre et al., 2012; Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). Consequently, for an optimal local restoration program able to adequately forecast and account for climate change scenarios, a hierarchical approach considering information at different scales and incorporating uncertainty would seem preferable (Mateo et al., 2017).

One dimension that could be developed in future studies is the assessment of error propagation and uncertainty assessment (Barry & Elith, 2006) throughout the hierarchical model building process, as here two models are combined which can increase the uncertainty in the final predictions (i.e., ensembles of models are prone to uncertainty; Marmion et al., 2009). It would also be an added value to provide managers with an uncertainty map associated with each species prediction (Guisan et al., 2013).

5 | CONCLUSIONS

To our knowledge, this work is the first to exemplify the use of hierarchical modeling approaches in support of conservation planning for vegetation at the landscape scale. Hierarchical SDMs could allow supporting more objective decisions thanks to the generation of more informative and accurate predictions of plant species and community distributions. However, as landscape, regional, and hierarchical models showed different results but also have different conceptual bases, managers should select the most appropriate model for their conservation objectives. For example, regional or hierarchical models that capture an entire species' climatic niche should be employed if the objective is to study the effects of climate change on the distribution of plant species or to determine suitable areas to restore the natural vegetation. On the other hand, landscape models could be enough if the objective is to estimate the current local distribution of endangered plant species.

A model is, however, a simplified picture of reality and considers only some specific properties of real ecological systems (Guisan & Zimmermann 2000; Levins, 1966; Mateo et al., 2011). Spatial predictions from plant distribution models based on habitat suitability and ecological niches are, of course, only cartographic representations of the suitability for the presence of a plant species given the considered environmental variables, but they should not be interpreted as the actual distribution of species (Mateo et al., 2011). Consequently, the SDMs should always be used as a complement to other sources of information in conservation programs (e.g., field observations, expert criteria, other modeling approaches, or remote-sensing information). SDMs also represent a useful tool to foster science–society (e.g., modellers–stakeholders) interactions (Guisan et al., 2013). Knowledge of the requirements of these stakeholders may be of high significance to modellers, and vice-versa, the knowledge of modellers (if incorporated sufficiently early in the decision process) can help managers to design more effective conservation strategies (Guisan et al., 2013). Such bilateral interactions could be implemented within an adaptive framework and its outcomes used to update the practical decisions continuously (Guisan et al., 2006). This would allow proposing management solutions that are increasingly fit to current ecosystems and applicable to current and future situations (Schwartz, 2012).

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DATA ACCESSIBILITY

Data used come from two different sources. Regional data were downloaded from the Spanish Forest Inventory (https://www.mapa.gob.es/es/desarrollo-rural/temas/politica-forestal/inventario-cartografia/inventario-forestal-nacional/). Landscape data were locally sampled at the Sierra del Rincón Reserve (central Spain). Landscape data will be available in Dryad at the end of the research project (2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Downscaling of climatic variables.

Appendix S2 Landscape, regional, *hierarchical1* and *hierarchical2* SDMs derived for the five species considered in this study.

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