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A model-based framework for assessing the vulnerability of low dispersal vertebrates to landscape fragmentation under environmental change



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ABSTRACT

Environmental changes are driving rapid geographic shifts of suitable environmental conditions for species. These might survive by tracking those shifts, however successful responses will depend on the spatial distribution of suitable habitats (current and future) and on their connectivity. Most herptiles (i.e., amphibians and reptiles) have low dispersal abilities, and therefore herptiles are among the most vulnerable groups to environmental changes. Here we assessed the vulnerability of herptile species to future climate and land use changes in fragmented landscapes. We developed and tested a methodological approach combining the strengths of Species Distribution Models (SDMs) and of functional connectivity analysis. First, using SDMs we forecasted current and future distributions of potential suitable areas as well as range dynamics for four herptile species in Portugal. SDM forecasts for 2050 were obtained under two contrasting emission scenarios, translated into moderate (low-emissions scenario) or large (high-emissions scenario) changes in climate and land use conditions. Then, we calculated and analysed functional connectivity from areas projected to lose environmental suitability towards areas keeping suitable conditions. Landscape matrix resistance and barrier effects of the national motorway network were incorporated as the main sources of fragmentation. Potential suitable area was projected to decrease under future conditions for most test species, with the high-emissions scenario amplifying the losses or gains. Spatiotemporal patterns of connectivity between potentially suitable areas signalled the most important locations for maintaining linkages and migration corridors, as well as potential conflicts due to overlaps with the current motorway network. By integrating SDM projections with functional connectivity analysis, we were able to assess and map the vulnerability of distinct herptile species to isolation or extinction under environmental change scenarios. Our framework provides valuable information, with fairly low data requirements, for optimizing biodiversity management and mitigation efforts, aiming to reduce the complex and often synergistic negative impacts of multiple environmental change drivers. Implications for conservation planning and management are discussed from a global change adaptation perspective.

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1. Introduction

Climate and land use changes are topics of scientific and political concern, especially when focusing on their potential

impacts on biodiversity as well as on ecosystem processes and services upon which human well-being is closely dependent (Thomas et al., 2004; Thuiller et al., 2011). Climate change and habitat loss due to land use change are thus among the most important threats to terrestrial biodiversity (Jetz et al., 2007; Sala et al., 2000), fostering modifications of key ecosystem functions, and often the depletion of essential ecosystem services (Bellard et al., 2012). Habitat loss, degradation and fragmentation, well-known threats to global biodiversity (IUCN, 2014), have been shown to be more important than climate change at regional and

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local scales (Dirnböck et al., 2003). Moreover, their effects are likely to be intensified under climate change (Bellard et al., 2012; Brook et al., 2008). These synergistic interactions between climate, land use and other habitat changes pose constant challenges for species to cope with, and they can produce unexpected responses that might go undetected using conventional monitoring schemes, therefore raising the issue of timely adaption (e.g., migration) (Pullin et al., 2013).

Climate and land use changes are resulting in the geographic shifting of species' suitable conditions (Chen et al., 2011), to which only some organisms can adapt, either via phenotypic or ecological plasticity and/or evolutionary changes (Williams et al., 2008). When suitable conditions change rapidly many species may not have enough time to adapt locally, hence their survival will depend on their capacity to track suitable environmental conditions and habitats at novel locations (Pearson, 2006). Thereby, extinctions may occur if populations cannot migrate or adapt fast enough (Williams et al., 2008).

In this context, landscape fragmentation is a determinant factor of species survival by potentially decreasing the connectivity between source areas and other patches with suitable conditions for the species (Taylor et al., 1993). In fact, habitat connectivity is recognized as one of the most important factors for maintaining biological diversity (Hodgson et al., 2009; Taylor et al., 1993), because gene flow is essential for genetic fitness and adaptation to environmental changes (Hanski, 1998). To minimise the threats associated with fragmentation, landscape connectivity should be enhanced, for example, by protecting linkages between suitable areas (Fahrig and Merriam, 1994), and by building efficient ecological networks to facilitate the movement of species under future environmental conditions (Devictor et al., 2007). This may be particularly important in the context of climate change where enhancing connectivity has been defined as an important strategy (among others) for adaptation (Heller and Zavaleta, 2009).

Functional connectivity, i.e., the degree to which the landscape promotes or hinders movements among resource patches for a given species (Taylor et al., 1993), is a major determinant of processes such as dispersion or gene flow, and includes species-specific aspects and their interaction with landscape structures (Taylor et al., 2006). Functional connectivity is therefore essential to support many conservation decisions and actions (Luque et al., 2012). In contrast, structural connectivity refers to the landscape elements that are physically or spatially connected through, for example, corridors (Taylor et al., 1993), regardless of specific interactions. Developing methods to effectively identify common landscape linkages for multiple species with conservation concern is a major challenge in conservation and landscape ecology (Beier et al., 2011). However, creating a standard approach is challenging due to the plethora of methods for quantifying connectivity and to the distinct ecological requirements of the different species (Luque et al., 2012). Thus, managers often focus on improving the structural connectivity of the landscape (which it is not species-specific), for example by establishing connections among forest patches, assuming an ad hoc equivalence with functional connectivity (Ribeiro et al., 2011). Furthermore, connectivity can be increased by conserving or restoring the habitat lying between current and future suitable areas for selected species (Akçakaya et al., 2007). Such an approach can reduce local extinctions by facilitating the 'rescue effect' of colonization, and also increase the rate of re-colonization after a local extinction (Rudnick et al., 2010).

This study aimed to incorporate the effects of functional landscape connectivity in predictions of species' responses to climate and land use changes in order to improve the design of ecological networks by identifying potential barriers to species movement; and, to prioritize areas for monitoring the responses of vulnerable species. For illustration purposes we selected reptiles

and amphibians as they are among those groups potentially more affected by ongoing and future environmental changes due to their low dispersal capacity (Blaustein et al., 2001; Gibbons et al., 2000). Using Species Distribution Models, we assessed whether the extent of potential suitable habitat is projected to increase or decrease under future environmental conditions. For each test species, we analysed functional connectivity from areas projected to lose environmental suitability to areas expected to maintain suitable environmental conditions by including species-specific landscape resistance effects. This approach also allowed the identification and evaluation of multiple least-cost paths (Pinto and Keitt, 2009) potentially establishing dispersal corridors under climate and land use changes in mainland Portugal. Finally, by forecasting how multiple environmental changes may affect the distribution of species under future conditions, our approach also allowed assessing species vulnerability to regional extinction and/or isolation. We concluded by discussing the value of our framework to inform authorities and managers about upcoming conservation priorities and mitigation actions, and to guide the set-up of efficient monitoring schemes to track biodiversity responses to multiple (and interacting) environmental change processes.

2. Methods

2.1. Analytical framework

The analytical approach (Fig. 1) encompassed three main steps. In the first step, we obtained spatial predictions on the distribution of current and future suitable areas using Species Distribution Models (SDM). In the second step, we combined current and future projections to obtain maps of species distribution dynamics informing about potential range shifts and changes in the distribution of suitable areas under future scenarios of climate and land use change. Finally, in the third step, we evaluated connectivity from areas projected to lose environmental suitability to areas projected to maintain suitable conditions. Connectivity analyses emphasized the assessment of potential barrier effects induced by the Portuguese motorway network.

2.2. Study area

The study area comprises mainland Portugal, southwest Europe, with an area of approximately 89100 km². Elevation ranges from 0 to 1993 meters a.s.l. with the mountain areas occurring mainly in the northern half of the territory. The climate ranges from temperate Atlantic in the northwest to dry Mediterranean in the southernmost areas (for more details see Supplementary material—Appendix S1).

2.3. Test species and distribution data

The test species were two amphibian and two reptile species occurring in the study area. Due to their biological characteristics, these two groups of vertebrates are very sensitive to environmental changes, particularly climate change (Araújo et al., 2006) and also, to fragmentation and degradation of habitats by action of human activities (Bennett and Saunders, 2010). In addition, with few exceptions, herptiles have poor dispersal ability (Blaustein et al., 2001), therefore their capacity to move to new suitable habitats is limited in comparison to endotherms. Moreover, during their migration events herptiles are very sensitive to unsuitable conditions being more exposed to predation, desiccation and human barriers. Specifically, large roads have been identified as major barriers for amphibians and reptiles with profound negative impacts on dispersal (Andrews et al., 2008).

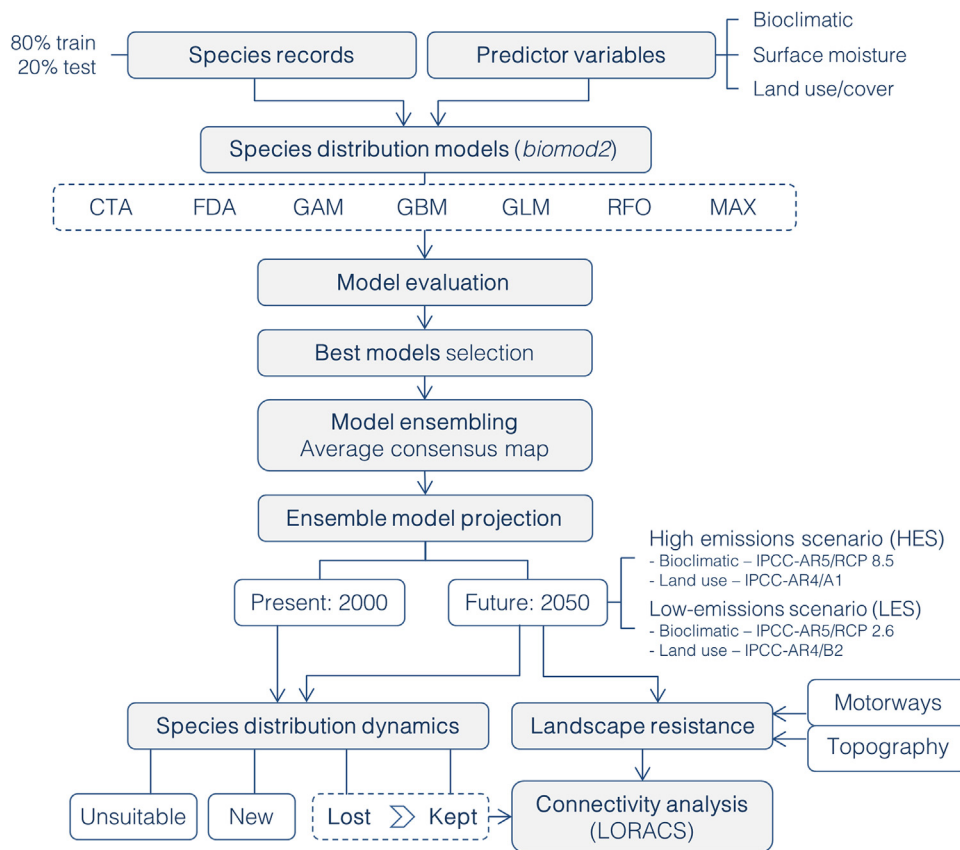


Fig. 1. Schematic representation of the methodological approach developed.

Species data included occurrence records for two amphibian and two reptile species distributed in Portugal: *Epidaleia calamita* (Laurenti, 1768), *Chioglossa lusitanica* (Bocage, 1864), *Lacerta schreiberi* (Bedriaga, 1878), and *Anguis fragilis* (Linnaeus, 1758). These species were selected due to their differences in terms of current distribution, range, IUCN conservation status and dispersal abilities (see Supplementary material—Appendix S1). We collected occurrence data from the Portuguese Atlas of Amphibians and Reptiles (Loureiro et al., 2008), based on a 1000 × 1000 m square grid (European Datum 1950—UTM 29N coordinate reference system). We verified and harmonized all available records. In order to remove duplicates and decrease spatial sampling bias and autocorrelation in presence records we used a spatial filtering routine (Boria et al., 2014). To achieve this goal, we filtered records by imposing a minimum pairwise distance between neighbouring points (optimized for each species) corresponding to a Clark-Evans aggregation index (CEAI; Clark and Evans, 1954) between [0.9, 1.0] (see Supplementary material—Appendix S2) allowing to decrease spatial clustering, while maintaining an appropriated number of records for model fitting. Afterwards, 191 presence-only records were available for *E. calamita*, 112 for *C. lusitanica*, 133 for *L. schreiberi*, and 178 for *A. fragilis* (see also Supplementary material—Appendix S2).

2.4. Climatic data and scenarios

The biology and ecology of amphibians and reptiles are tightly related to temperature and moisture (Angilletta et al., 2002; Duellman and Trueb, 1986), which thus constitute important limiting factors for the distribution of these species (Tingley and Herman, 2009). In order to relate these two factors with current

species records applying a SDM framework, we used the following five bioclimatic variables for model fitting (available in the WorldClim database; Hijmans et al., 2005): mean diurnal range (*BIO_02*), temperature seasonality (*BIO_04*), maximum temperature of warmest month (*BIO_05*), minimum temperature of the coldest month (*BIO_06*), and precipitation of the driest month (*BIO_14*). The climatic data for current conditions consists of an average for the period 1950–2000 with a spatial resolution of 30 arc-second (c.a. 900 m at the equator), resampled to 1000 × 1000 m (using bilinear interpolation) and registered in the same coordinate reference system as the species' presence records (see Supplementary material—Appendix S3 for a numeric description of these variables).

To forecast the distribution of suitable areas, we used climate projections for the reference year of 2050 (average for the period 2041–2060) for two contrasting emission scenarios (IPCC, 2014), namely: (i) IPCC AR-CMIP 5/RCP 8.5 (i.e., maximum energy requirements, emissions balanced between fossil and non-fossil sources) and, (ii) IPCC AR-CMIP 5/RCP 2.6 (lower energy requirements and thus lower emissions than RCP 8.5). Since uncertainty in forecasting future distributions is partly related to global circulation models (GCMs; see Buisson et al., 2010), we combined twelve different GCMs to produce an ensemble average of projections (see the full list of ensemble GCMs in Supplementary material—Appendix S4).

2.5. Topographic data

Topographic indices representing surface moisture gradients and water flow/drainage patterns have been used to explain the distribution of herptile species (Blank and Blaustein, 2012). To

introduce such effects in the SDMs, we used elevation data from the Shuttle Radar Topography Mission database (SRTM version-4; Jarvis et al. (2008); with a spatial resolution of 90×90 m) to calculate the Catchment Area (CAR), and the Topographic Wetness Index (TWI). While CAR provides a measure of catchment area and hydrological flow accumulation (Gruber and Peckham, 2008), TWI describes the tendency of a cell to accumulate water (Quinn et al., 1995). In order to match the spatial resolution of species and climatic data, we up-scaled TWI and CAR from the 90×90 m spatial resolution of SRTM data to 1000×1000 m, using the median (TWI_MD, CAR_MD) and standard-deviation (TWI_SD, CAR_SD) as aggregation functions (see also Supplementary material—Appendix S3 for a numeric description of these variables).

2.6. Land use data and scenarios

Land use has been previously related to herptile species richness and distribution (Martins et al., 2014; Trimble and van Aarde, 2014). In addition, land use change has also been linked to herptile community composition and diversity (Trimble and van Aarde, 2014; Wanger et al., 2010). Following this rationale, we considered land use data with a spatial resolution of 1 km as a categorical predictor in the models (hereafter termed *LULC_CL*). These data were available from the EURURALIS project (Eickhout and Prins, 2008), providing current land use information at European level as well as scenarios for future land use change. Scenario data for land use were obtained by the Dynamic Conversion of Land Use and its Effects Model (Dyna-CLUE) software, which integrates demand-driven changes in land area with locally determined conversion processes, thus allowing an exploration of the future dynamics of European land use and landscapes (Verburg and Overmars, 2009). We applied the model on pre-existing land use data for Europe based on a reclassified version of Corine Land Cover (EEA, 2007) which included a total of 16 land use types with eight types represented in the study-area (see complete list in Supplementary material—Appendix S5, and also the area coverage for each land use class, relative frequencies, and transition matrices between present and future scenarios). The most updated version of the land use projections dataset (for year 2050) was available for IPCC4 storylines A1 and B2, which was used for forecasting the test species distributions.

2.7. Model development: fitting, evaluation and projection

Before model fitting, we tested potential multicollinearity effects in the selected spatial covariates by calculating Pearson correlation (see Supplementary material—Appendix S6). Since all absolute pairwise correlations were below 0.75 we kept all ten initially selected variables for model fitting.

Model development used the *biomod2* platform (Thuiller et al., 2009). Seven modelling techniques were employed and combined with model parameters set to default: (1) generalized linear model (GLM); (2) generalized additive model (GAM); (3) generalized boosted models (GBM); (4) classification tree analysis (CTA); (5) flexible discriminant analysis (FDA); (6) random forests (RFO); and (7) maximum entropy (MAX). Since true absence data were unavailable, we generated 30 sets of randomly selected pseudo-absences, keeping an equal number of presences and pseudo-absences for each set. We calibrated the models with 80% of the data selected at random, and then evaluated the predictive performance of each model on the remaining 20% with two evaluation metrics: the area under the Receiver Operating Characteristic (ROC) curve (AUC; Fielding and Bell (1997); but see Lobo et al. (2008)) and the maximum true-skill statistic (TSS; Jolliffe and Stephenson (2003)). Although TSS is a threshold-dependent measure, *biomod2* tests multiple sequenced values, bounded within the prediction probability interval: [0,1000], to determine the threshold maximizing TSS. We performed holdout cross-validation for 10 rounds and then averaged the evaluation results across all rounds. We calculated variable importance by *biomod2* without accounting for interactions, and finally we averaged it for pseudo-absence sets, evaluation rounds, and modelling algorithms.

In order to produce robust forecasts for the test species distribution, we obtained an ensemble forecast combining the five best (out of seven) modelling techniques for each species. Then, for each technique we selected the upper 2.5% quantile of the best performing models as ranked by AUC. Model predictions from the selected models were then averaged to produce the final ensemble.

Using the ensemble model calibrated for current conditions, we projected the future distribution of the selected species using two sets of conditions for the reference year of 2050: (i) a low-emissions scenario (LES) combining climatic projections for IPCC-AR5/RCP 2.6 and land use projections for the IPCC-AR4/B2 scenario,

Table 1

Model performance statistics for *biomod2* partial models and the final ensemble model (“Ensemble” column). Results were averaged across the test sets, pseudo-absence sets and model runs. Two evaluation measures were calculated: AUC (area under the curve), and TSS (true-skill statistic). Seven modelling techniques were used: GLM (Generalized Linear Model), GBM (Generalized Boosting Model), GAM (Generalized Additive Model), CTA (Classification Tree Analysis), FDA (Flexible Discriminant Analysis), RFO (Random Forests), and MAX (Maximum Entropy Model). Modelling techniques highlighted with an asterisk (*; i.e., the best five techniques by species considering the AUC values) were included in the final ensemble. Column “Cutoff” displays the value used to partition ensemble probability maps (ranging from 0 to 1000) into suitable/unsuitable areas; values inside parenthesis represent respectively the Sensitivity (or true positive rate) and Specificity (or true negative rate). Species are *Anguis fragilis* (ANGFR), *Lacerta schreiberi* (LACSH), *Chioglossa lusitanica* (CHALU) and *Epidalea calamita* (EPCAL).

Species	Eval. measure	GLM	GBM	GAM	CTA	FDA	RFO	MAX	Ensemble	Cutoff (Sens./spec.)
ANGFR	AUC	0.82*	0.82*	0.87*	0.77	0.81	0.82*	0.82*	0.90	559.5
	TSS	0.56	0.58	0.65	0.52	0.56	0.58	0.57	0.68	(0.93; 0.75)
LACSH	AUC	0.73	0.75*	0.86*	0.67	0.74*	0.76*	0.76*	0.88	629.5
	TSS	0.45	0.48	0.62	0.35	0.44	0.48	0.48	0.61	(0.84; 0.77)
CHALU	AUC	0.88	0.90*	0.95*	0.82	0.89*	0.89*	0.89*	0.94	505.5
	TSS	0.71	0.74	0.83	0.63	0.74	0.74	0.73	0.80	(1.00; 0.80)
EPCAL	AUC	0.67*	0.68*	0.76*	0.60	0.66*	0.67*	0.66	0.83	502.5
	TSS	0.33	0.34	0.44	0.22	0.31	0.34	0.31	0.52	(0.87; 0.65)

and, (ii) a high-emissions scenario (HES) combining climatic projections for IPCC-AR5/RCP 8.5 and land use projections for the IPCC-AR4/A1 scenario. We partitioned ensemble probability maps for current and projected future conditions into binary maps of suitable/unsuitable areas by choosing the probability threshold (ranging from 0 to 1000) that minimized the distance between the ROC curve and the (0, 1) point (Liu et al., 2005; see also Table 1).

2.8. Species distribution dynamics

Model projections for current and future conditions allowed quantifying changes in suitable area distribution, therefore, allowing to define four distinct types of dynamics: (i) “unsuitable”, areas currently predicted as unsuitable that will remain unsuitable in future projections; (ii) “lost”, areas currently predicted as suitable that will lose suitability in the future; (iii) “kept”, areas

that are currently predicted as suitable that will remain with suitable conditions in the future, and (iv) “new”, areas that are currently predicted as unsuitable that may become suitable in the future.

In this analysis we assumed that populations affected by loss of environmental suitability (i.e., in areas identified as “lost”), due to combined effects of climate and land use changes, will be forced to migrate to stable areas that remain suitable under the future conditions (identified as “kept”). Thus, we analysed the likelihood of potential migrations from “lost” to “kept” areas by quantifying the functional connectivity between these two instances, measured as the degree to which the landscape facilitates or hinders the movement of each test species; the analysis was therefore both species and landscape-specific (Taylor et al., 1993; Watts et al., 2010). It would also be possible to study the potential colonization of projected new suitable areas by analysing connectivity between

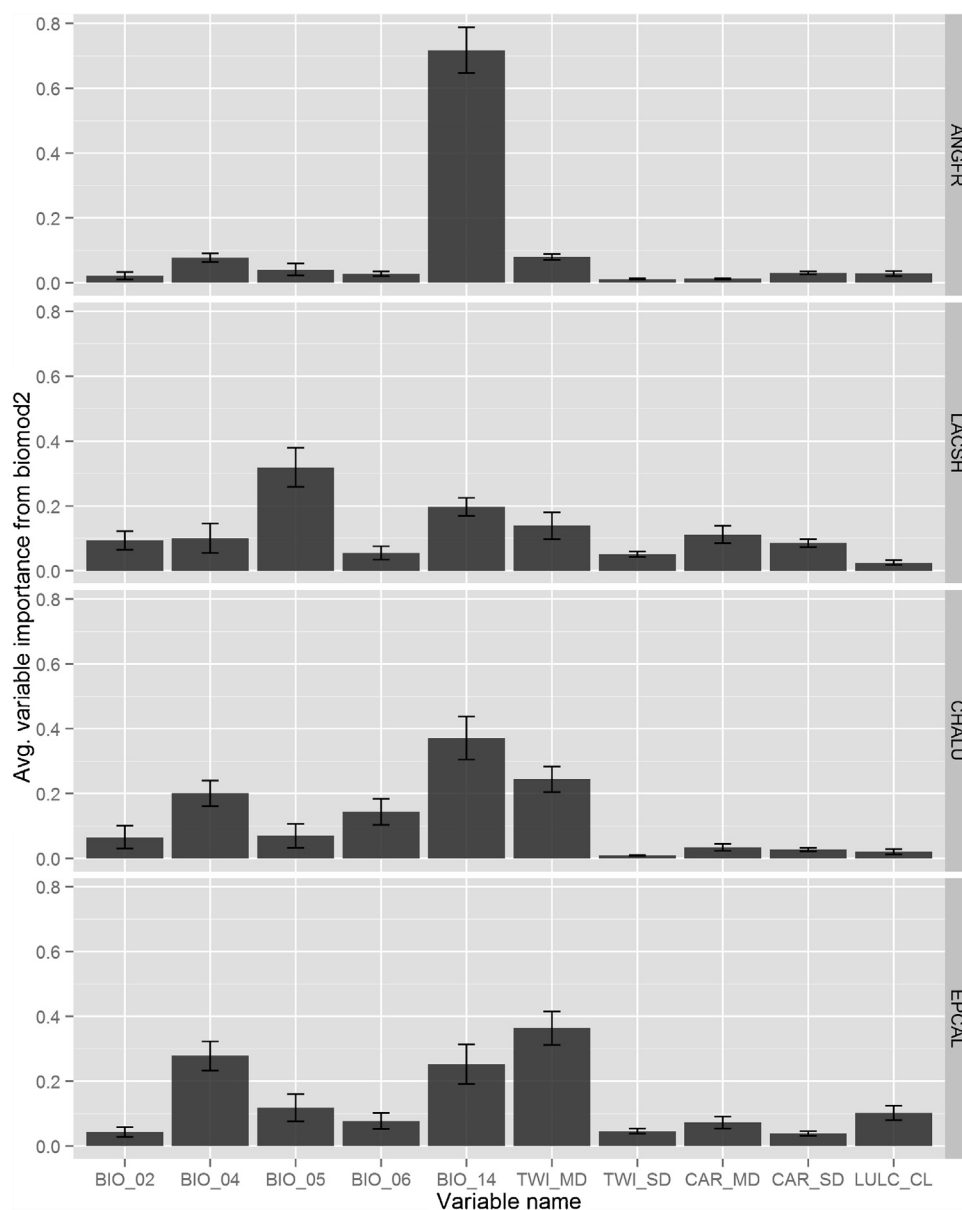


Fig. 2. Barplot displaying variable importance by species and averaged across all pseudo-absence sets, evaluation rounds and modelling algorithms. Error bars represent the standard-errors across modelling techniques. Species are *Anguis fragilis* (ANGFR), *Lacerta schreiberi* (LACSH), *Chioglossa lusitanica* (CHALU) and *Epidalea calamita* (EPCAL).

“kept” and/or “lost” areas to “new” areas. Nonetheless, in this test we focused our attention on how species will respond to loss of conditions by reaching stable areas, and thus on the likelihood of potential migrations from “lost” to “kept” areas.

2.9. Connectivity analyses

We performed connectivity analyses with LORACS software (Pinto and Keitt, 2009; Pinto et al., 2012) implementing a graph-theoretical approach to calculate corridor redundancy, while accounting for landscape matrix resistance. This procedure allowed evaluating multiple shortest-paths (SP) from “lost” to “kept” areas, assumed to represent potential dispersal corridors.

The parameterization of LORACS was set to a corridor width of 30% (which defines corridor breadth size) and 10 different SPs were calculated between each “lost” cell, hereafter denoted as a source area, $s_i, i \in \{1, \dots, m\}$, and the closest target “kept” area, denoted as $t_j, j \in \{1, \dots, n\}$ measured by the Euclidean distance between the two sites. We then aggregated the results for the 10 simulated SPs to the average cost distance, denoted as $c(s_i, t_j)$. In order to simulate variability in potential migration routes, we calculated the average cost distance between a source area and multiple k neighbouring target areas, residing in different and spatially disjoint “kept” habitat patches, $P_u, u \in \{1, \dots, p\}$ and $t \in P$ (see Supplementary material—Appendices S5 and S7). We computed connectivity to the five nearest-neighbours and averaged to calculate the Mean Functional Distance index (MFD; Eq. (1)), given by:

$$\text{MFD}_i = \frac{1}{k} \sum_{j=1}^k c(s_i, t_j) \quad (1)$$

This index represents a cost-based distance metric of functional connectivity which explicitly uses a cost-surface defining landscape matrix resistance (including, in this study: habitat

suitability, topographical complexity and road effects). MFD calculation is based on the assessment of multiple least-cost paths (within a predefined corridor breathe) thus allowing to analyse linkage redundancy and variability. The MFD index varies from >0 to an undefined upper bound and is measured on “resistance” units since it depends on the spatial configuration of source/target areas and the spatial patterning of landscape resistance values. Overall, higher values of MFD signal lower connectivity.

LORACS software calculates multiple SPs enabling to compute the number of times that a given area is redundantly selected for the pathway of a given shortest-path, noted as $a(s_i, t_j) \in [0, 10]$ (with the maximum value equal to the number of simulated SPs). Calculating the total summation of $a(s_i, t_j)$ across all source areas (Eq. (2)), and k neighbors, we obtained a zonation of areas important for maintaining connectivity, as well as, potential migration corridors, defined as:

$$\text{SPsum} = \sum_{i=1}^m \sum_{j=1}^k a(s_i, t_j) \quad (2)$$

This index assumes integer-only values and varies from 0 to an undefined upper bound. In general, a higher amount of source areas increases the upper limit of SPsum , which means that particular areas are selected more frequently in least-cost pathways. For this index, higher values correlate to areas that are relatively more important for maintaining connectivity or potential corridors.

By mapping the SPsum index, we further analysed the intersection between important areas for connectivity (for which: $\text{SPsum} \geq 1$) and the national motorway network (considering a buffer of 500 m around each road) in order to evaluate conflicts for each species.

In order to determine shortest-paths, LORACS uses a cost-surface defining landscape matrix resistance to movement. In this

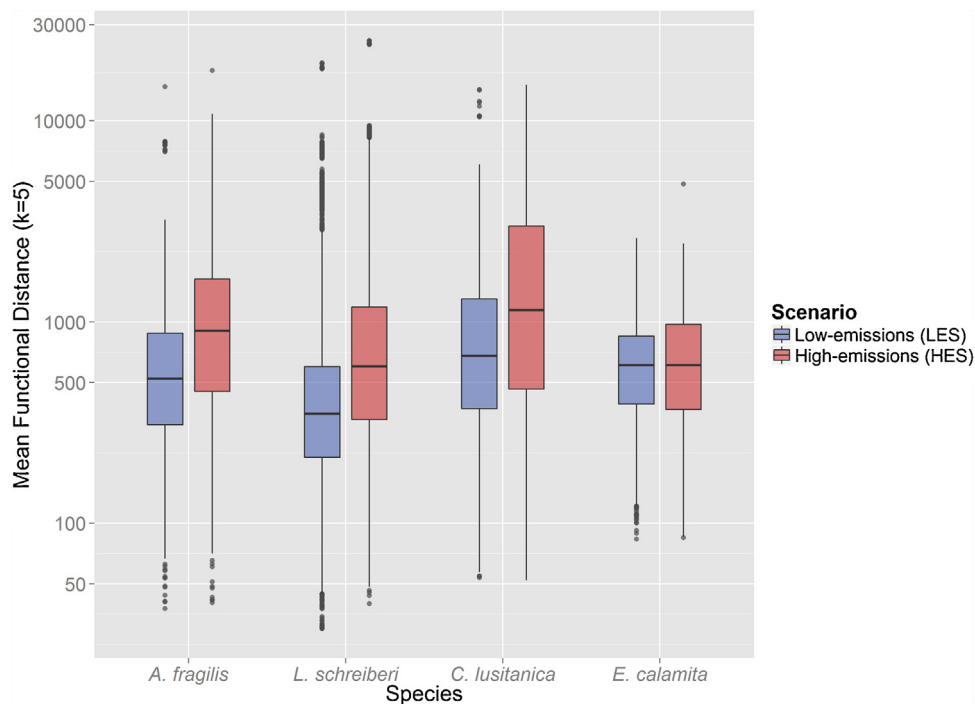


Fig. 3. Boxplot of the Mean Functional Distance index by species and scenario. The y-axis was log transformed and outliers, i.e., values 2 times the inter-quartile range outside the box, were represented as points. LES—low-emissions scenario (blue boxes); HES—high-emissions scenario (red boxes). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

study, the cost-surface included three main components hypothesized to affect movement or dispersal probabilities for each test species, thus affecting functional connectivity (Spear et al., 2010). These components were related to: (i) projected habitat suitability for each species, (ii) linear structures inducing barrier or high-resistance effects, and (iii) topographic roughness/heterogeneity. The total landscape resistance cost was obtained by a weighted sum of each rescaled partial component (see details in Supplementary material—Appendix S7). We implemented the connectivity analyses and spatial indices as a distributable R package (available by contacting the corresponding author).

3. Results

3.1. Model performance

Cross-validation tests indicated that overall model performance ranged from excellent to good considering AUC (0.94–0.83), while in general, TSS recorded more conservative performance ranging from good to moderate (0.80–0.52; Table 1). In a decreasing order, *C. lusitanica* recorded the best test results (0.94–AUC; 0.80–TSS) followed by *A. fragilis* (0.90–AUC; 0.68–TSS), *L. schreiberi* (0.88–AUC; 0.61–TSS), and *E. calamita* (0.83–AUC; 0.52–TSS). Overall, results also indicated that applying ensemble forecast techniques increased the model performance (see “Ensemble”

column, Table 1). When comparing different modelling algorithms, GAM was the best performing technique for all species, followed by GBM, Random Forests, and Maxent.

3.2. Species distribution dynamics under climate and land use changes

The distribution of potential suitable areas based on ensemble forecasting presented a diverse array of spatial responses to environmental changes across scenarios (Figs. 3–5; see also, Supplementary material—Appendices S8 and S9). The test species were overall more sensitive to climatic (especially BIO_14, BIO_04 and BIO_05) and topographic (mainly TWI_MD) than to land use variables (see Fig. 2 and Supplementary material—Appendix S10 for more details).

For three of the four species, a substantial decrease of their current distribution was projected for 2050 (–44.6% to –73.5%, Table 2) considering both scenarios, although range contraction was higher under the high-emissions scenario (HES). The net variation percentage (Table 2), balancing losses and gains of suitable area, was negative for the majority of species: *L. schreiberi* (LES: –61.2%, HES: –73.5%), *C. lusitanica* (LES: –54.1%, HES: –71.3%) and *A. fragilis* (LES: –44.6%, HES: –60.7%), but positive for *E. calamita*, the single species for which gains of suitable space were clearly higher than losses (LES: 51.9%, HES: 66.5%). Major losses were observed for areas exhibiting less pronounced or

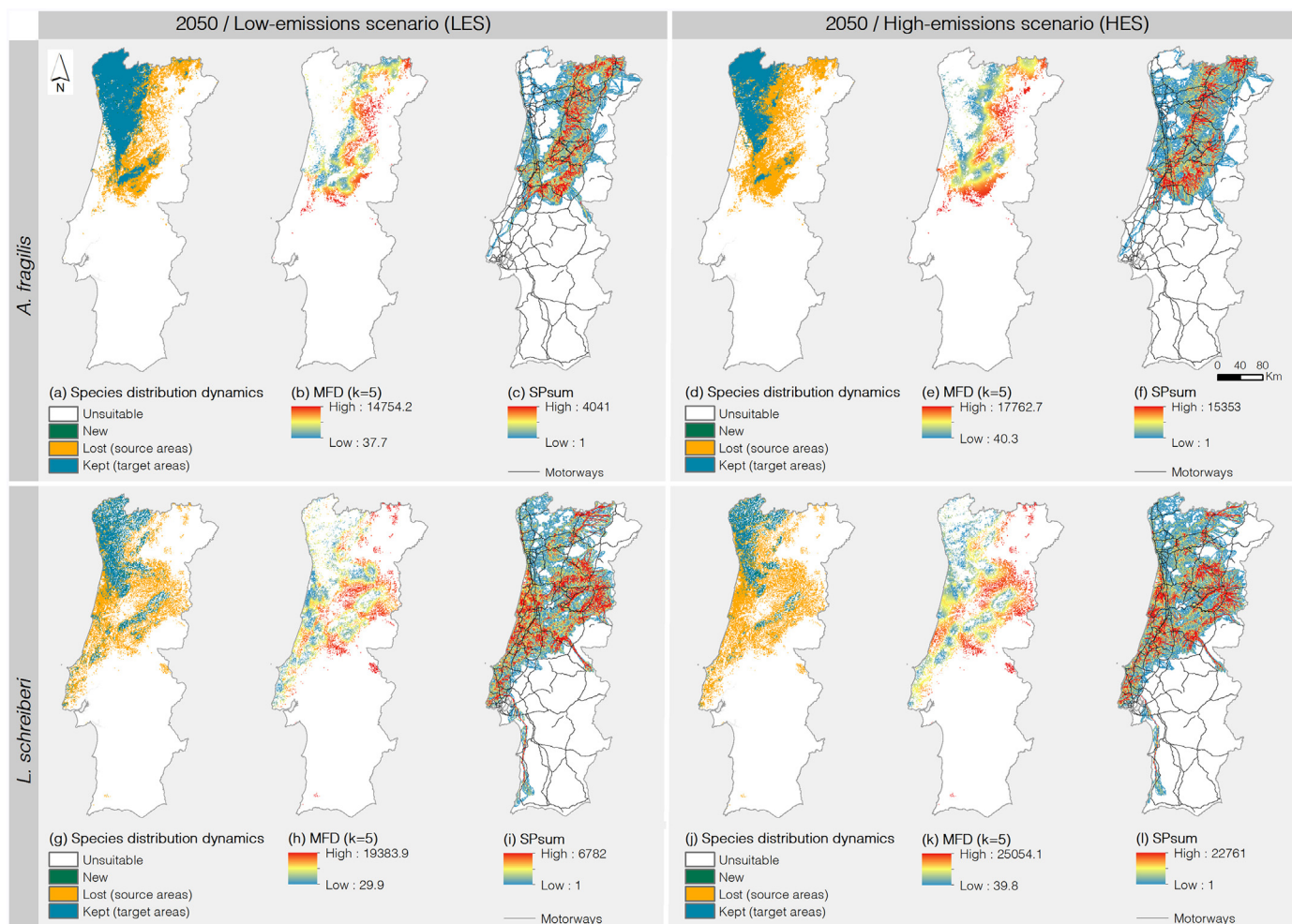


Fig. 4. Map representation of species distribution dynamics (a, d, g, and j), connectivity between “lost” (source areas) and “kept” (target areas) using the Mean Functional Distance index (MFD, $k=5$; b, e, h, and k), and the zonation of important areas for connectivity using the *SPsum* index (c, i, f, and l) for each reptile species (*A. fragilis*, *L. schreiberi*) and scenario (low-emissions scenario and high-emissions scenario).

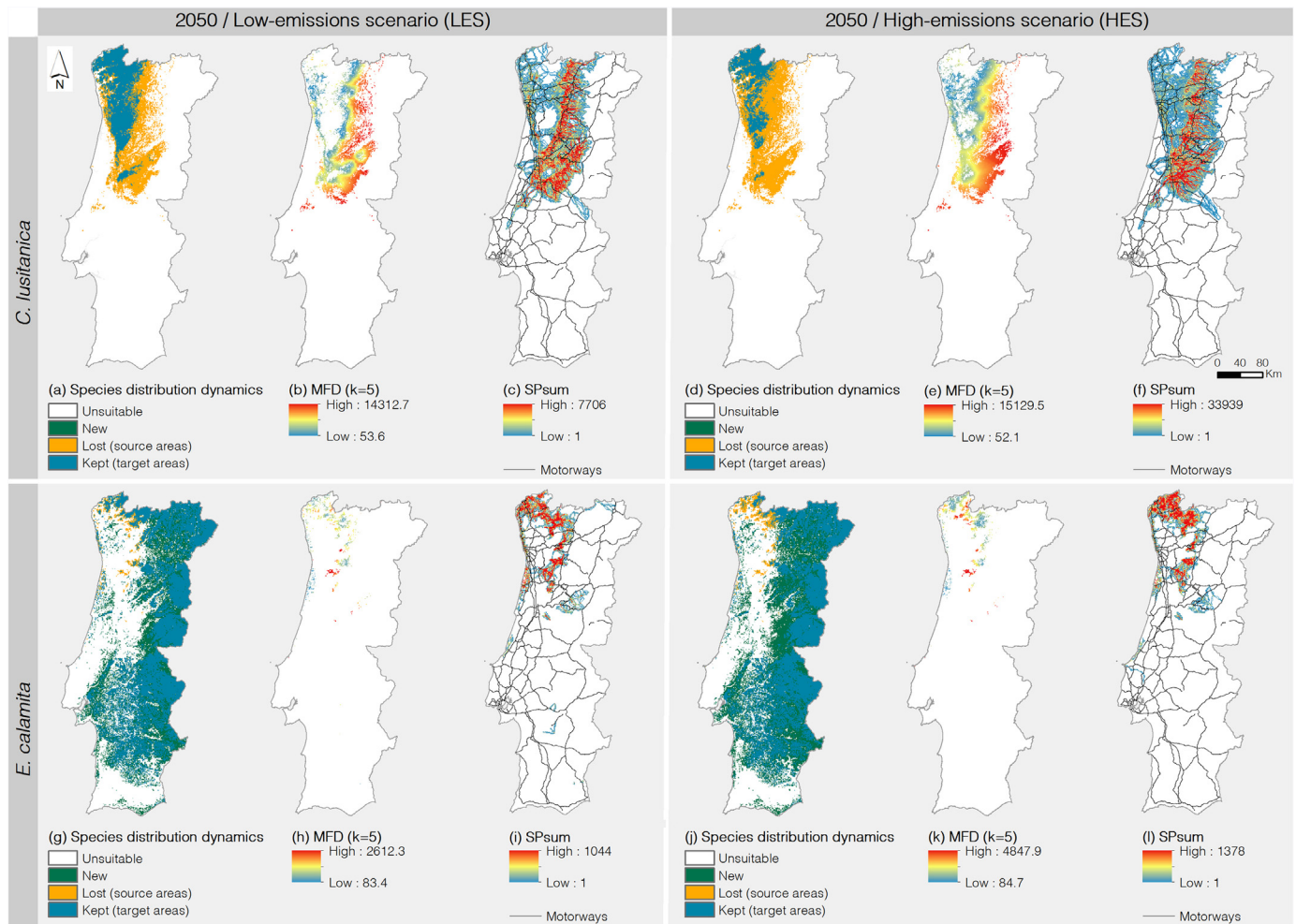


Fig. 5. Map representation of species distribution dynamics (a, d, g, and j), connectivity between “lost” (source areas) and “kept” (target areas) using the Mean Functional Distance index (MFD, $k=5$; b, e, h, and k), and the zonation of important areas for connectivity using the $SPsum$ index (c, i, f, and l) for each amphibian species (*C. lusitanica*, *E. calamita*) and scenario (low-emissions scenario and high-emissions scenario).

transitional Atlantic climatic characteristics. These areas are mostly distributed along the north and central-eastern inland regions of Portugal, the main mountain areas in the central region, and the north-east mountains (Figs. 4 a, d, g, and j and 5 a and d). Contrastingly, *E. calamita* major gains were projected for the eastern Mediterranean climatic regions and the centre south-western coast of Portugal (Fig. 5 g and j).

Table 2

Net variation in percentage ($\%nv = ((\text{New} + \text{Kept}) / (\text{Kept} + \text{Lost}) - 1) \times 100$) by species and scenario (2050 scenario: HES—high-emissions scenario; LES—low-emissions scenario) showing habitat area losses and gains, derived from the joint effects of climate and land use changes. Descriptive statistics (median) for the Mean Functional Distance index (MFD, $k=5$) by species and scenario.

Species	2050 scenario	%nv	Median MFD ($k=5$)
<i>A. fragilis</i>	LES	−44.6%	522.7
	HES	−60.7%	902.3
<i>L. schreiberi</i>	LES	−61.2%	350.2
	HES	−73.5%	602.6
<i>C. lusitanica</i>	LES	−54.1%	678.4
	HES	−71.3%	1143.2
<i>E. calamita</i>	LES	51.9%	611.0
	HES	66.5%	611.2

3.3. Effects of landscape fragmentation on regional connectivity

Connectivity results obtained for the Mean Functional Distance index (MFD, see Table 2, and Supplementary material—Appendix S11), considering the low-emissions scenario, revealed that *C. lusitanica* obtained the lowest connectivity, corresponding to the highest median value (678.4), followed by *E. calamita* (611.0), *A. fragilis* (522.7) and *L. schreiberi* (350.2). For the high-emissions scenario, *C. lusitanica* (1143.2) also presented the lowest connectivity, followed by *A. fragilis* (902.3), *E. calamita* (611.2) and *L. schreiberi* (602.6). Higher geographical distance between areas projected to lose environmental suitability and areas expected to maintain it in the future, combined with the conditions for higher

Table 3

Spatial intersection between important areas for connectivity (i.e., with $SPsum \geq 1$) and the motorway network (considering a buffer of 500 m around each road). HES—high-emissions scenario; LES—low-emissions scenario.

Species	% intersected by motorway network	
	LES	HES
<i>A. fragilis</i>	6.04%	6.27%
<i>L. schreiberi</i>	6.48%	6.67%
<i>C. lusitanica</i>	7.10%	6.89%
<i>E. calamita</i>	4.86%	4.71%

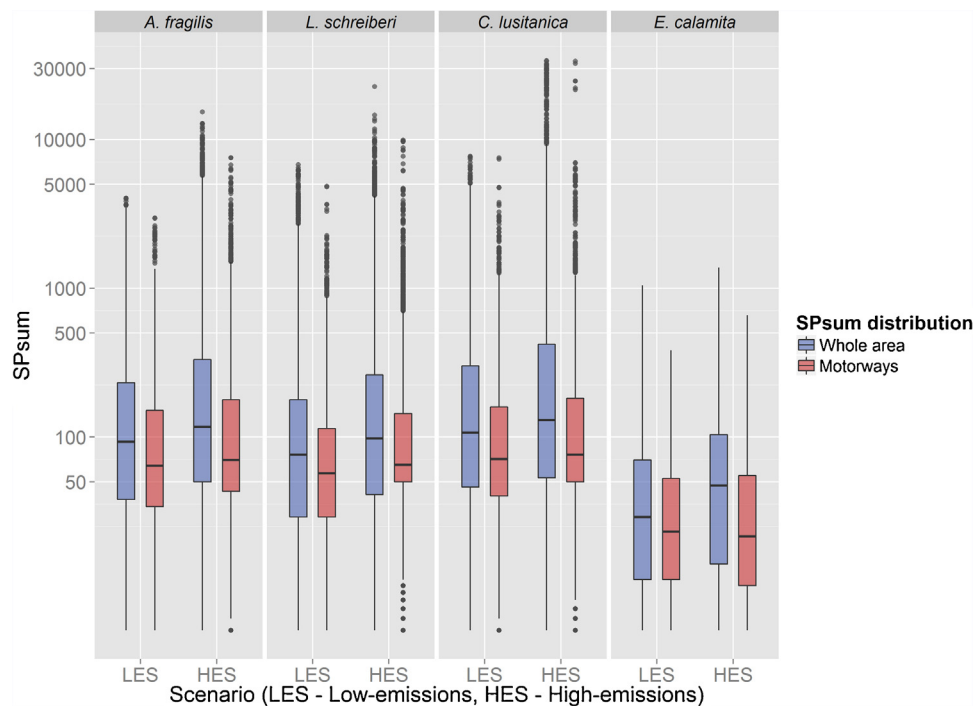


Fig. 6. Boxplot showing the distributions of *SPsum* values for all areas important for maintaining connectivity (i.e., with *SPsum* ≥ 1 ; blue boxes) and those areas intersected by motorways (red boxes) across species and scenarios (LES—low-emissions scenario and HES—high-emissions scenario). The y-axis was log-transformed, and, outliers, i.e., values lying outside the Box 2 times the inter-quartile range were represented as points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

landscape fragmentation and resistance to dispersal conducted invariably to the lowest connectivity values.

The *SPsum* index presented similar patterns for *A. fragilis* and *C. lusitanica* under both scenarios (Figs. 4 c and f and 5 c and f) with important areas for connectivity stretching from north to the center of the country in the interior region of Portugal. For *E. calamita* important connectivity areas were mainly located in the upper NW part of the country (Fig. 5 i and l). Finally, *L. schreiberi* presented a more complex spatial patterning, with the most important areas occurring in the central part of the country (Fig. 4 i and l).

The spatial intersection of motorways and important areas for connectivity presented similar values across all species and scenarios, varying from approximately 5–7% (Table 3), with *C. lusitanica* showing the highest values (LES: 7.10% and HES: 6.89%), followed by *L. schreiberi* (6.48% and 6.67%), *A. fragilis* (6.04% and 6.27%) and *E. calamita* (4.86% and 4.71%). Although spatial intersection presented relatively low values (Table 3), in many cases motorways have intersected areas with high values for the *SPsum* index, which represent an overlap with areas extremely important for maintaining connectivity in potential migration corridors (Fig. 6).

4. Discussion

4.1. Species distribution drivers, projections and uncertainty

Ecological and biogeographic theory establishes that species distributions are determined by processes acting at multiple spatial and temporal scales (Lomolino et al., 2006; Vicente et al., 2014). In this study at a regional scale, climatic and topographic variables were comparatively more important than land use

variables for predicting the test-species distributions, as previously observed in similar studies (Luoto et al., 2007; Martin et al., 2013; Sohl, 2014). Projected range shifts for our test-species were also more affected by changes in climate than in land use. These results may confirm that climate is known to determine species distributions at broader spatial scales (i.e., regional to global, e.g., Luoto et al., 2007; Pearson and Dawson, 2003). They may also reflect the relatively coarse resolution of the land use dataset used (1000 \times 1000 m), potentially generating a scale mismatch for estimating species–environment relations (Wiens et al., 2009).

Climate change scenarios have been extensively used to forecast potential changes of species distributions (Araújo et al., 2006; Thuiller et al., 2005). Land use and its dynamics are also used for modelling species distributions at local and regional scales (Dirnböck et al., 2003), but less often applied to forecast future distributions, probably due to the lack of publicly available post-processed products (Barbet-Massin et al., 2012). Although we found that in our study land use had relatively less predictive power, we incorporated future scenarios for this variable since it is well known that land use changes may cause habitat destruction, degradation and fragmentation, imposing severe pressures on species (Pimm and Raven, 2000; Sala et al., 2000) and further limiting their ability to cope with other environmental changes (Barbet-Massin et al., 2012). Interactions among different anthropogenic pressures may cause severe challenges for species and originate unforeseen responses (Brook et al., 2008; Jetz et al., 2007). Therefore, we stress that for adequately analysing these synergies improved and readily available land use/cover datasets are required for current conditions as well as for future scenarios (Martin et al., 2013; Tingley and Herman, 2009).

Our approach is not exempt of the uncertainties inherent to using SDMs (Guisan et al., 2013; Schwartz, 2012) resulting, among others,

from forecasting species' distributions into non-analogous climates (Fitzpatrick and Hargrove, 2009), from using different climatic projections, and/or from the modelling algorithms themselves (Buisson et al., 2010). To partially overcome some uncertainties associated with SDMs, we applied an ensemble forecasting approach combining several modelling algorithms (Thuiller et al., 2009). Still, further enhancements could be achieved by integrating correlative and mechanistic models (Buckley et al., 2010; Ceia-Hasse et al., 2014). Moreover, SDMs assume niche conservatism (broadly defined as the tendency of species to retain ancestral ecological characteristics; Wiens and Graham (2005)) affecting spatial and temporal model projections. Although caution should be taken assuming such assumption, recent studies have found evidence of niche conservatism for amphibians (Olalla-Tárraga et al., 2011), reptiles (Morales-Castilla et al., 2011) and other groups in a wider-breath review by Peterson (2011).

The usual lack of fine-scale resolution environmental data (e.g., on climate or land use) adds further limitations and uncertainty to model calibration (Wiens et al., 2009). Updated and fine-resolution occurrence data for herptiles is also still limited for Europe, which further imposes limitations to the development of SDMs and the robust assessment of species range shifts. Improving data quality is thus essential to produce better and more accurate assessments and model projections (Pôças et al., 2014; Vicente et al., 2014).

4.2. Assessing species vulnerability to climate and landscape changes

We proposed a three-step approach to assess the vulnerability of species to several environmental change processes, combining species distribution dynamics with functional connectivity. The approach relies on predictors related to climate, land use, and topography, delivering range shift projections based on future climate and land use dynamics. By integrating the statistical robustness and projections of SDMs (by applying ensemble forecasting) with functional connectivity analysis, we were able to obtain realistic projections for future dynamics of target species under contrasting scenarios. This integrative approach provides valuable insights considering the vulnerability of multiple species to isolation and ultimately to extinction under rapid environmental changes.

Determining the degree to which a given landscape facilitates or hinders the movement of species among suitable habitat or resource patches is essential for conservation and management of wildlife populations (Hamer and McDonnell, 2008; Taylor et al., 1993). We assessed broad scale habitat connectivity using a cost surface defining the resistance of the landscape matrix to species' movement, confirming the utility of raster-based models to investigate barriers or facilitators to connectivity, such as roads and/or topography (Cushman et al., 2006). Connectivity analyses allowed the identification and evaluation of migration corridors, based on a graph-theoretical approach explicitly accounting for species-specific landscape matrix resistance, an analytical approach holding wide breadth and acceptance (Decout et al., 2012; Minor and Urban, 2008; Pascual-Hortal and Saura, 2008). Our proposed approach allowed to quantify connectivity and assess potential migration corridors with a relatively small amount of input data compared to other widely used approaches, e.g., agent-based models (ABM) such as implemented in *MigClim* (Engler and Guisan, 2009) or coupled population dynamics-dispersal (CPDD) models such as *RangeShifter* (Bocedi et al., 2014). This data-related advantage makes our framework more generalizable and thus potentially more suited for assessing multiple species.

The proposed framework assumes some simplifications, e.g., by not including population or dispersal parameters, a clear advantage in the many cases where such information is simply not available (as in this study). In addition, species' movement

responses are strongly dependent on landscape structure and matrix resistance. As a consequence, dispersal may vary heterogeneously throughout the landscape and may be different across regions for the same species (Taylor et al., 2006) thus presenting many challenges for measurement and direct estimation (Jacobson and Peres-Neto, 2010). Although for example, dispersal parameters may be available for some species, frequently they are biased towards some specific landscapes or regions.

Complementarily, using the *MFD* or *SPsum* indices for comparing the full spectrum of connectivity values across a study area between different species will provide a preliminary regional-scale synoptic overview of connectivity patterns. This will allow comparing different regions, identifying critical situations and selecting a subset of relevant areas to develop detailed studies, e.g., by implementing ABM or CPDD models for assessing changes derived from climate and land use change (Bocedi et al., 2014; Engler and Guisan, 2009).

4.3. Vulnerability of low dispersal vertebrates

Our results for two contrasting scenarios showed that, within a relatively short time-frame, environmental changes may cause severe impacts on the test species, with strong contractions in suitable area for most of them. Our findings are consistent with previous studies reporting substantial range contractions for herptile species in the Iberian Peninsula under future environmental changes (Araújo et al., 2006; Carvalho et al., 2010). The study species presenting current small ranges in Portugal (i.e., *C. lusitanica*, *A. fragilis* and *L. schreiberi*) will potentially suffer an important loss of suitable areas. Moreover, *C. lusitanica* and *L. schreiberi* are threatened by other pressures too (IUCN, 2014), exacerbating the synergistic effect of environmental changes. Conversely, *E. calamita*, with a widespread range and higher dispersal capacity, is projected to maintain or even expand its potential suitable area. However, projections of extensive geographic shifts in environmental conditions do not necessarily mean that species distributions will change likewise, as individuals will be able to move and survive in new areas as a function of their dispersal capacity and presence of adequate pathways connecting current and future suitable areas (Baguette et al., 2013). Yet, for less mobile species, such as amphibians and reptiles, projections of large range contractions may suggest higher risk of population isolation under future conditions (McLaughlin et al., 2002).

Connectivity analyses highlighted an overall pattern widely dependent on the complex interplay between the spatial configuration of source/target areas (i.e., respectively, areas with projected conservation or loss of environmental suitability in the future) and landscape elements increasing landscape resistance (such as motorways, future habitat suitability decrease, or higher topographic complexity). The complex local patterns of connectivity obtained were particularly evident in areas with similar Euclidean distance between source and target areas but contrasting functional connectivity distances. Additionally, species experiencing a higher contraction of suitable areas clearly showed lower connectivity due to an increase in landscape resistance and geographic distance between "lost" and "kept" areas. The stability and integrity of migration corridors for these species may be further impacted by the presence of motorways (Andrews et al., 2008), making these species even more vulnerable to extinction or isolation under future environmental changes.

4.4. Applications in conservation planning and management

The multispecies approach described here provides useful information for conservation and management, by anticipating the ecological effects of rapid environmental changes. On the one

hand, it allows the identification of priority areas for conservation together with a deeper understanding of how landscape resistance will promote or hinder species movements. On the other hand, connectivity analyses improve the identification of potential migration corridors, essential when designing appropriate conservation or protection measures for multi-objective environmental planning (Dennis et al., 2013; Nunez et al., 2013). More broadly, our approach can be used to define ecological networks for long-term metapopulation persistence, and to assess the impacts of infrastructures on species movements.

Likewise, our approach can be used to design management interventions and set priorities aiming to increase landscape connectivity, thereby contributing to climate change adaptation for multiple species (Heller and Zavaleta, 2009; Krosby et al., 2010) by facilitating dispersal and mitigating the impacts of land use dynamics. Previous studies have shown that habitat restoration along model-informed landscape corridors is a better promoter of metapopulation persistence, compared to expert-informed habitat restoration (Hodgson et al., 2011). In fact, the importance of considering landscape connectivity when selecting and designing habitat reserves has been widely acknowledged in the literature (e.g., Alagador et al., 2012; Minor and Urban, 2008).

The design of impact mitigation actions can also be improved using the approach described here. Mapping the intersections between key migration corridors and motorways can guide managers and planners in determining which motorway segments will most likely act as barriers, thus having the greatest impact on wildlife movement (McRae et al., 2012). This information can be used to plan and implement conservation measures intended to mitigate fragmentation effects, for example, specific road-crossing structures.

Finally, the application of our framework can improve the effectiveness of monitoring schemes, a main component of adaptive conservation management under global change (Lindenmayer and Likens, 2009), specifically by guiding the design of efficient observation networks. This corroborates the increasing application of SDMs for ecological monitoring and conservation, with successful examples for different taxa in different ecosystems (e.g., Carvalho et al., 2015; Vicente et al., 2016). Moreover, by integrating landscape corridors in the design of monitoring networks, valuable ecological information can be collected to explain and predict species movements under environmental change. This may be essential for species of high-conservation concern and with low dispersal capacity, such as amphibians and reptiles, for which patches playing an important connectivity role must be identified and highlighted as of conservation and/or monitoring priority (e.g., Minor and Urban, 2008; Pascual-Hortal and Saura, 2008). More broadly, the identification of potential dispersal corridors or areas of the landscape promoting dispersal is crucial for effectively long-term monitoring and adaptive management of the wildlife populations (Bennett and Saunders, 2010).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2016.05.003>.

References

- Akçakaya, H.R., Mills, G., Doncaster, C.P., 2007. The role of metapopulations in conservation. In: Macdonald, D.W., Service, K. (Eds.), *Key Topics in Conservation Biology*. Blackwell Publishing, pp. 64–84.
- Alagador, D., Triviño, M., Cerdeira, J.O., Brás, R., Cabeza, M., Araújo, M.B., 2012. Linking like with like: optimising connectivity between environmentally-similar habitats. *Landscape Ecol.* 27, 291–301.
- Andrews, K.M., Gibbons, J.W., Jochimsen, D.M., 2008. Ecological effects of roads on amphibians and reptiles: a literature review. In: Mitchell, J.C., Brown, R.E.J., Bartholomew, B. (Eds.), *Urban Herpetology. Society for the Study of Amphibians & Reptiles*. Salt Lake City, UT, pp. 121–143.
- Angilletta Jr., M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27, 249–268.
- Araújo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* 33, 1712–1728.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M., Turlure, C., 2013. Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.* 88, 310–326.
- Barbet-Massin, M., Thuiller, W., Jiguet, F., 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Glob. Change Biol.* 18, 881–890.
- Beier, P., Spencer, W., Baldwin, R.F., McRae, B.H., 2011. Toward best practices for developing regional connectivity maps. *Conserv. Biol.* 25, 879–892.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377.
- Bennett, A.F., Saunders, D.A., 2010. Habitat fragmentation and landscape change. In: Sodhi, N.S., Ehrlich, P.R. (Eds.), *Conservation Biology for All*. Oxford University Press, New York, US, pp. 88–106.
- Blank, L., Blaustein, L., 2012. Using ecological niche modeling to predict the distributions of two endangered amphibian species in aquatic breeding sites. *Hydrobiologia* 693, 157–167.
- Blaustein, A.R., Belden, L.K., Olson, D.H., Green, D.M., Root, T.L., Kiesecker, J.M., 2001. Amphibian breeding and climate change. *Conserv. Biol.* 15, 1804–1809.
- Bocedi, G., Palmer, S.C.F., Pe'er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K., Travis, J. M.J., Freckleton, R., 2014. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods Ecol. Evol.* 5, 388–396.
- Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Modell.* 275, 73–77.
- Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J., Sears, M.W., 2010. Can mechanism inform species' distribution models? *Ecol. Lett.* 13, 1041–1054.
- Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. *Glob. Change Biol.* 16, 1145–1157.
- Carvalho, S.B., Brito, J.C., Crespo, E.J., Possingham, H.P., 2010. From climate change predictions to actions—conserving vulnerable animal groups in hotspots at a regional scale. *Glob. Change Biol.* 16, 3257–3270.
- Carvalho, S.B., Gonçalves, J., Guisan, A., Honrado, J.P., 2015. Systematic site selection for multispecies monitoring networks. *J. Appl. Ecol.* n/a–n/a.
- Ceia-Hasse, A., Sinervo, B., Vicente, L., Pereira, H.M., 2014. Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. *Ecography* 37, 679–688.
- Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35, 445–453.
- Cushman, S.A., McKelvey, K.S., Hayden, J., Schwartz, M.K., 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *Am. Nat.* 168, 486–499.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026.
- Decout, S., Manel, S., Maud, C., Luque, S., 2012. Integrative approach for landscape-based graph connectivity analysis: a case study with the common frog (*Rana temporaria*) in human-dominated landscapes. *Landscape Ecol.* 27, 267–279.
- Dennis, R.L.H., Dapporto, L., Dover, J.W., Shreeve, T.G., 2013. Corridors and barriers in biodiversity conservation: a novel resource-based habitat perspective for butterflies. *Biodivers. Conserv.* 22, 2709–2734.
- Devictor, V., Godet, L., Julliard, R., Couvet, D., Jiguet, F., 2007. Can common species benefit from protected areas? *Biol. Conserv.* 139, 29–36.

- Dirnböck, T., Dullinger, S., Grabherr, G., 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *J. Biogeogr.* 30, 401–417.
- Duellman, W.E., Trueb, L., 1986. *Biology of Amphibians*. McGraw Hill, New York.
- EEA, 2007. CLC2006 Technical Guidelines. Office for Official Publications of the European Communities, Luxembourg, pp. 70.
- Eickhout, B., Prins, A.G., 2008. Eururalis 2.0—Technical Background and Indicator Documentation. Wageningen UR and Netherlands Environmental Assessment Agency (MNP) Bilthoven, The Netherlands.
- Engler, R., Guisan, A., 2009. MigClim: predicting plant distribution and dispersal in a changing climate. *Divers. Distrib.* 15, 590–601.
- Fahrig, L., Merriam, G., 1994. Conservation of fragmented populations. *Conserv. Biol.* 8, 50–59.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Fitzpatrick, M.C., Hargrove, W.W., 2009. The projection of species distribution models and the problem of non-analog climate. *Biodivers. Conserv.* 18, 2255–2261.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, Déjà Vu Amphibians. *BioScience* 50, 653.
- Gruber, S., Peckham, S., 2008. Land-surface parameters and objects in hydrology. In: Hengl, T., Reuter, H.I. (Eds.), *Geomorphometry: Concepts, Software, Applications—Developments in Soil Science*. Elsevier.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–1435.
- Hamer, A.J., McDonnell, M.J., 2008. Amphibian ecology and conservation in the urbanising world: a review. *Biol. Conserv.* 141, 2432–2449.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* 142, 14–32.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very High Resolution Interpolated Climate Surfaces for Global Land areas. John Wiley & Sons, Ltd., pp. 1965–1978.
- Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *J. Appl. Ecol.* 48, 148–152.
- Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. *J. Appl. Ecol.* 46, 964–969.
- IPCC, 2014. *Climate Change 2014—Synthesis Report (Longer Report)*, Fifth Assessment Synthesis Report, p. 116.
- IUCN, 2014. *The IUCN Red List of Threatened Species*. Version 2014.3., Version 2014.3. ed.
- Jacobson, B., Peres-Neto, P.R., 2010. Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go? *Landsc. Ecol.* 25, 495–507.
- Jarvis, A., Reuter, H.I., Nelson, A., Guevara, E., 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90 m Database. <http://srtm.csi.cgiar.org>.
- Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* 5, e157.
- Jolliffe, I.T., Stephenson, D.B., 2003. *Forecast Verification—A Practitioner's Guide in Atmospheric Science*, 1st ed. John Wiley & Sons, Chichester, West Sussex, England.
- Krosby, M., Tewksbury, J., Haddad, N.M., Hoekstra, J., 2010. Ecological connectivity for a changing climate. *Conserv. Biol.* 24, 1686–1689.
- Lindenmayer, D.B., Likens, G.E., 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends Ecol. Evol.* 24, 482–486.
- Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–393.
- Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* 17, 145–151.
- Lomolino, M.V., Riddle, B.R., Brown, J.H., 2006. *Biogeography*, 3rd ed. Sinauer Associates, Sunderland, MA.
- Loureiro, A., Ferrand de Almeida, N., Carretero, M.A., Paulo, O.S., 2008. *Atlas dos Anfíbios e Répteis de Portugal*, 1st ed. Instituto da Conservação da Natureza, Lisboa.
- Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. *Glob. Ecol. Biogeogr.* 16, 34–42.
- Luque, S., Saura, S., Fortin, M.-J., 2012. Landscape connectivity analysis for conservation: insights from combining new methods with ecological and genetic data. *Landsc. Ecol.* 27, 153–157.
- Martin, Y., Van Dyck, H., Dendoncker, N., Titeux, N., 2013. Testing instead of assuming the importance of land use change scenarios to model species distributions under climate change. *Glob. Ecol. Biogeogr.* 22, 1204–1216.
- Martins, I.S., Proença, V., Pereira, H.M., 2014. The unusual suspect: land use is a key predictor of biodiversity patterns in the Iberian Peninsula. *Acta Oecol.* 61, 41–50.
- McLaughlin, J.F., Hellmann, J.J., Boggs, C.L., Ehrlich, P.R., 2002. Climate change hastens population extinctions. *Proc. Natl. Acad. Sci.* 99, 6070–6074.
- McRae, B.H., Hall, S.A., Beier, P., Theobald, D.M., 2012. Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. *PLoS One* 7, e2604.
- Minor, E.S., Urban, D.L., 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conserv. Biol.* 22, 297–307.
- Morales-Castilla, I., Olalla-Tárraga, M.A., Bini, L.M., De Marco Jr., P., Hawkins, B.A., Rodríguez, M.A., 2011. Niche conservatism and species richness patterns of squamate reptiles in eastern and southern Africa. *Austral Ecol.* 36, 550–558.
- Nunez, T.A., Lawler, J.J., McRae, B.H., Pierce, D.J., Krosby, M.B., Kavanagh, D.M., Singleton, P.H., Tewksbury, J.J., 2013. Connectivity planning to address climate change. *Conserv. Biol.* 27, 407–416.
- Olalla-Tárraga, M.A., McInnes, L., Bini, L.M., Diniz-Filho, J.A.F., Fritz, S.A., Hawkins, B.A., Hortal, J., Orme, C.D.L., Rahbek, C., Rodríguez, M.A., Purvis, A., 2011. Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. *J. Biogeogr.* 38, 2237–2247.
- Pascual-Hortal, L., Saura, S., 2008. Integrating landscape connectivity in broad-scale forest planning through a new graph-based habitat availability methodology: application to capercaillie (*Tetrao urogallus*) in Catalonia (NE Spain). *Eur. J. For. Res.* 127, 23–31.
- Pearson, R.G., 2006. Climate change and the migration capacity of species. *Trends Ecol. Evol.* 21, 111–113.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.
- Peterson, A.T., 2011. Ecological niche conservatism: a time-structured review of evidence. *J. Biogeogr.* 38, 817–827.
- Pimm, S.L., Raven, P., 2000. Biodiversity: extinction by numbers. *Nature* 403, 843–845.
- Pinto, N., Keitt, T., 2009. Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. *Landsc. Ecol.* 24, 253–266.
- Pinto, N., Keitt, T.H., Wainright, M., 2012. LORACS: JAVA software for modeling landscape connectivity and matrix permeability. *Ecography* 35, 388–392.
- Pôças, I., Gonçalves, J., Marcos, B., Alonso, J., Castro, P., Honrado, J.P., 2014. Evaluating the fitness for use of spatial data sets to promote quality in ecological assessment and monitoring. *Int. J. Geogr. Inf. Sci.* 28, 2356–2371.
- Pullin, A.S., Sutherland, W., Gardner, T., Kapos, V., Fa, J.E., 2013. Conservation priorities: identifying need, taking action and evaluating success. In: Macdonald, D.W., Willis, K.J. (Eds.), *Key Topics in Conservation Biology*. 1st ed. John Wiley & Sons, pp. 3–22.
- Quinn, P.F., Beven, K.J., Lamb, R., 1995. The $\ln(a/\tan \beta)$ index: how to calculate it and how to use it within the TOPMODEL framework. *Hydrol. Processes* 9, 161182.
- Ribeiro, R., Carretero, M., Sillero, N., Alarcos, G., Ortiz-Santaliestra, M., Lizana, M., Llorente, G., 2011. The pond network: can structural connectivity reflect on (amphibian) biodiversity patterns? *Landsc. Ecol.* 26, 673–682.
- Rudnick, D.A., Ryan, S.J., Beier, P., Cushman, S.A., Dieffenbach, F., Epps, C.W., Gerber, L.R., Hartter, J., Jenness, J.S., Kintsch, J., Merenlender, A.M., Perki, R.M., Preziosi, D.V., Trombulak, S.C., 2010. The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Issues Ecol.* 16.
- Sala, O.E., Stuart Chapin, F., Armesto III, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Hueneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M.N., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Schwartz, M.W., 2012. Using niche models with climate projections to inform conservation management decisions. *Biol. Conserv.* 155, 149–156.
- Sohl, T.L., 2014. The relative impacts of climate and land-use change on conterminous united states bird species from 2001 to 2075. *PLoS One* 9, e112251.
- Spear, S.F., Balkenhol, N., Fortin, M.-J., McRae, B.H., Scribner, K.I.M., 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Mol. Ecol.* 19, 3576–3591.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573.
- Taylor, P.D., Fahrig, L., With, K.A., 2006. Landscape connectivity: a return to the basics. In: Crooks, K.R., Sanjayan, M. (Eds.), *Connectivity Conservation*. Cambridge University Press, New York, USA.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373.
- Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., Araújo, M.B., 2011. Consequences of climate change on the tree of life in Europe. *Nature* 470, 531–534.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 8245–8250.
- Tingley, R., Herman, T.B., 2009. Land-cover data improve bioclimatic models for anurans and turtles at a regional scale. *J. Biogeogr.* 36, 1656–1672.
- Trimble, M.J., van Aarde, R.J., 2014. Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemicity. *Anim. Conserv.* 17, 441–453.
- Verburg, P., Overmars, K., 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landsc. Ecol.* 24, 1167–1181.

- Vicente, J.R., Alagador, D., Guerra, C., Alonso, J.M., Kueffer, C., Vaz, A.S., Fernandes, R. F., Cabral, J.A., Araújo, M.B., Honrado, J.P., 2016. Cost-effective monitoring of biological invasions under global change: a model-based framework. *J. Appl. Ecol.* n/a–n/a.
- Vicente, J.R., Gonçalves, J., Honrado, J.P., Randin, C.F., Pottier, J., Broennimann, O., Lomba, A., Guisan, A., 2014. A framework for assessing the scale of influence of environmental factors on ecological patterns. *Ecol. Complex.* 20, 151–156.
- Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tschardtke, T., 2010. Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi Indonesia Efectos del Cambio de Uso de Suelo sobre la Composición de la Comunidad de Anfibios y Reptiles en Sulawesi, Indonesia. *Conserv. Biol.* 24, 795–802.
- Watts, K., Eycott, A., Handley, P., Ray, D., Humphrey, J., Quine, C., 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. *Landsc. Ecol.* 25, 1305–1318.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. U. S. A.* 106 (Suppl. 2), 19729–19736.
- Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36, 519–539.
- Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* 6, e325.