

Beyond species distribution modeling: A landscape genetics approach to investigating range shifts under future climate change

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ABSTRACT

Understanding how biodiversity will respond to future climate change is a major conservation and societal challenge. Climate change is predicted to force many species to shift their ranges in pursuit of suitable conditions. This study aims to use landscape genetics, the study of the effects of environmental heterogeneity on the spatial distribution of genetic variation, as a predictive tool to assess how species will shift their ranges to track climatic changes and inform conservation measures that will facilitate movement. The approach is based on three steps: 1) using species distribution models (SDMs) to predict suitable ranges under future climate change, 2) using the landscape genetics framework to identify landscape variables that impede or facilitate movement, and 3) extrapolating the effect of landscape connectivity on range shifts in response to future climate change. I show how this approach can be implemented using the publicly available genetic dataset of the grey long-eared bat, *Plecotus austriacus*, in the Iberian Peninsula. Forest cover gradient was the main landscape variable affecting genetic connectivity between colonies. Forest availability is likely to limit future range shifts in response to climate change, primarily over the central plateau, but important range shift pathways have been identified along the eastern and western coasts. I provide outputs that can be directly used by conservation managers and review the viability of the approach. Using landscape genetics as a predictive tool in combination with SDMs enables the identification of potential pathways, whose loss can affect the ability of species to shift their range into future climatically suitable areas, and the appropriate conservation management measures to increase landscape connectivity and facilitate movement.

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1. Introduction

Understanding how biodiversity will respond to future climate change is a major conservation and societal challenge. Global climate change is predicted to force many species to shift their ranges in pursuit of suitable conditions (IPCC, 2014). There is ample evidence showing that species are already shifting their geographic distributions in line with changing climatic conditions (Chen et al., 2011; Parmesan and Yohe, 2003; Thomas, 2010). However, it is unclear whether species will be able to shift their ranges fast enough to track the velocity of climate change (Loarie et al., 2009), or if they are able to shift their ranges in face of anthropogenic habitat loss and fragmentation (Warren et al., 2001).

Conservation responses to climate change under constraints of urgency and uncertainty need to integrate a broad range of approaches and be guided by predictive forecasts and scientific evidence (Gillson et al., 2013). Species distribution modeling is an effective way of determining species conservation requirements and potential range changes under future climate change (Guisan and Thuiller, 2005). Predictive

modeling studies have warned that a high proportion of species will be committed to extinction, especially under the more severe climate change scenarios (Thomas et al., 2004), and identified reductions in species ranges, with some South-East Asian bats losing their entire current niche space (Hughes et al., 2012).

Despite their potential conservation applications, the practical use of species distribution models (SDMs) in conservation management and decision making has been limited by lack of communication and appropriate translation of scientific knowledge (Guisan et al., 2013). Moreover, instead of properly addressing species' dispersal abilities and range shift potential, studies thus far have commonly assumed one of two extreme, and mostly unrealistic, scenarios: no dispersal or unlimited dispersal to new climatically suitable areas (Bateman et al., 2013). The ability of species to reach new areas or shift their ranges away from areas that have become climatically unsuitable greatly depends on landscape connectivity (Krosby et al., 2010; Lawler, 2009), the extent to which individual movement is facilitated or impeded by the landscape (Taylor et al., 1993). Hence, understanding how the landscape affects species movement ecology is essential for developing strategies for conserving biodiversity under climate change (Sgrò et al., 2011).

The landscape genetics framework uses genetic data to understand the movement of individuals across the landscape and how global

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Table 1

List of landscape variables included in the landscape genetics analysis, their source maps, original scale, and scale after conversion to a resistance surface.

Landscape variables	Source map	Original map scale	Resistance scale
Habitat suitability	Full SDM	0–100 (low–high suitability)	1–100 (decreases with habitat suitability)
Altitude	Digital elevation model	0–3370 m	1–102 (increases with altitude)
Slope	Digital elevation model	0–766	1–101 (increases with slope)
Percent tree canopy cover	Global forest change (Hansen et al. 2013)	0–100%	1–101 (decreases with tree cover)
Forest cover gradient	Reclassified GlobCover 2009	5 main forest cover categories	Categories: 1 = >40% forest 10 = 15–40% forest 25 = > 15% forest/shrub 50 = mosaic grassland with some forest 75 = mosaic arable with some forest 100 = arable, sparse, bare, water bodies
Distance to mosaic vegetation	Reclassified GlobCover 2009	Euclidian distances from variable	1–100 (increases with distance)
Distance to broadleaved woodland	Reclassified Corine Land Cover 2006	Euclidian distances from variable	1–100 (increases with distance)
Distance to all woodlands	Reclassified Corine Land Cover 2006	Euclidian distances from variable	1–100 (increases with distance)
Distance to unimproved grasslands	Reclassified Corine Land Cover 2006	Euclidian distances from variable	1–100 (increases with distance)

change affects evolutionary processes (Holderegger and Manel, 2013). Landscape genetics integrates population genetics, landscape ecology, and spatial statistics to study the effects of environmental heterogeneity on the spatial distribution of genetic variation. It can be used to quantify the effect of landscape composition, configuration, and quality on genetic connectivity and to identify barriers to gene flow and movement corridors (Manel et al., 2003; Storfer et al., 2007). However, to fulfill its potential to inform conservation management, landscape genetics needs to develop beyond describing patterns into a predictive discipline (Holderegger and Manel, 2013).

This study aims to use landscape genetics as a predictive tool to assess the ability of species to shift their range to climatically suitable areas and to identify range shift pathways to guide conservation management under future climate change. As a case study, I use the grey long-eared bat, *Plecotus austriacus*, in the Iberian Peninsula (hereafter Iberia). Bats have been suggested as good indicators of the effects of environmental changes on biodiversity because of their high diversity, wide habitat use, role as top predators, and sensitivity to disturbance (Jones et al., 2009). Future climate change is predicted to affect the distribution of many European bat species (Rebello et al., 2010), and *P. austriacus*, in particular, is predicted to experience severe range contractions in Iberia where populations have persisted across past climatic changes (Razgour et al., 2013). I focus on the Iberian Peninsula because of its evolutionary importance as a major Pleistocene glacial refuge for European biodiversity (Hewitt, 2004) and because it is where the effects of future climate change are predicted to be most severe (EEA, 2012).

The fine-scale approach is based on three steps. First, predictive SDMs are used to determine the future potential climatic range and identify populations at risk (located in areas that will become climatically unsuitable by the end of the century). Next, the landscape genetics framework is employed to identify landscape variables that impede or facilitate movement in the form of gene flow and genetic connectivity. In the final step, information from the two previous steps is combined to extrapolate the effect of landscape connectivity on range shifts in response to future climate change. Using this approach, I aim to provide

output maps and recommendations to inform conservation management under climate change.

2. Material and methods

This study is based on the *P. austriacus* microsatellite and location records datasets published in Razgour et al. (2013, 2014) and available to download from Dryad (<http://dx.doi.org/10.5061/dryad.pt0gh>). The microsatellite dataset includes samples from the five Iberian colonies with 6–18 samples each (N = 64), which were genotyped at 23 autosomal loci (Table A.1).

2.1. Species distribution modeling

Species distribution models (SDMs) were generated in Maxent v3.3.3 (Phillips et al., 2006) and included the same 142 genetically confirmed location records used in Razgour et al. (2013). The extent was set as the whole of Europe and model resolution as 30 arc seconds (approximately 1 km at the equator). I generated two types of SDMs: a climate model that was projected to 2070 to study how climate change will affect the distribution of suitable conditions for the species, and a full model, which included land cover variables and was used as a measure of habitat suitability in the landscape genetics analysis. The full SDM was cut to the extent of the Iberian Peninsula for use in the landscape genetics analysis.

After removing highly correlated variables (correlation coefficients ≥ 0.8 , tested with ENMTTools v1.3, Warren et al., 2010) and variables that did not contribute to the model, the following variables were included in the climate model: temperature annual range (BIO7), mean temperature of the warmest (BIO10) and coldest (BIO11) quarters, annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation during the warmest quarter (BIO18) (downloaded from WorldClim <http://www.worldclim.org>), altitude, and slope (generated from the Digital Elevation Model, CGIAR Consortium for Spatial Information <http://srtm.csi.cgiar.org/index.asp>). The full model also included the following variables: land cover type (GlobCover, 2009, ESA 2010 and UCLouvain, http://due.esrin.esa.int/page_globcover.php, reclassified into ten categories, Table A.2), distance to unimproved grasslands and distance to broadleaf woodlands (generated from Corine Land Cover map, 2006, <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3>), and human population density (LandScan, 2008 <http://www.ornl.gov/sci/landscan/>). The climate model was projected to the future using the HadGEM2_ES General Circulation Model and the IPCC5 'business as usual' climate scenario (8.5 W/m² Representative Concentration Pathway; IPCC, 2013).

Modeling methods followed the recommendations in Merow et al. (2013). I tested the effect of changing model parameters (regularization values, number of features included) on model fit in ENMTTools

Table 2Genetic (Fst) and geographic (Euclidian distances in kilometres) distances between the five Iberian *P. austriacus* colonies.

	La Rioja	Lisbon	Granada	Almeria	Jaen
La Rioja		614.34	575.76	547.67	473.60
Lisbon	0.046		472.86	533.44	481.04
Granada	0.022	0.047		79.58	107.85
Almeria	0.023	0.047	0.022		81.44
Jaen	0.020	0.045	0.024	0.018	

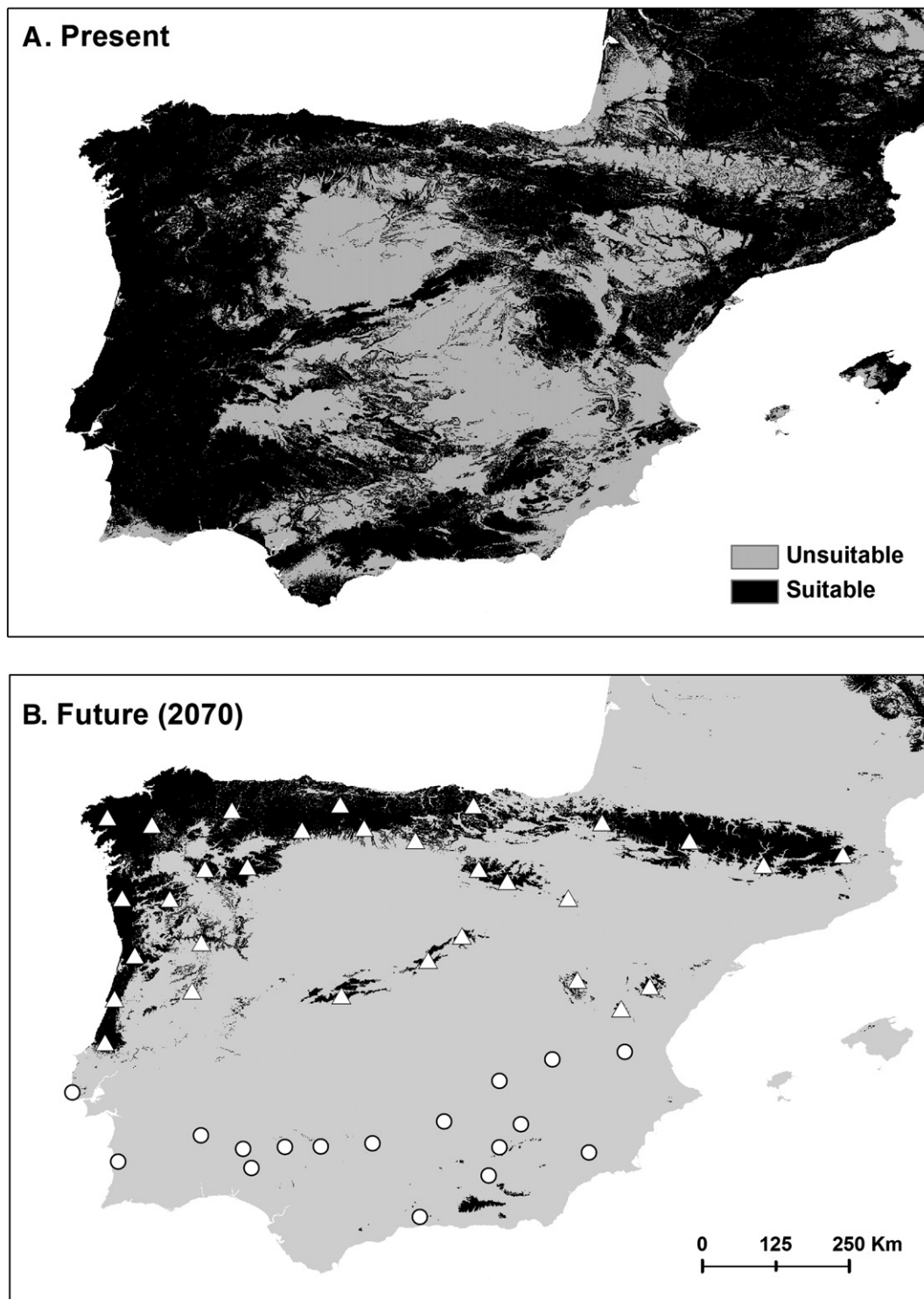
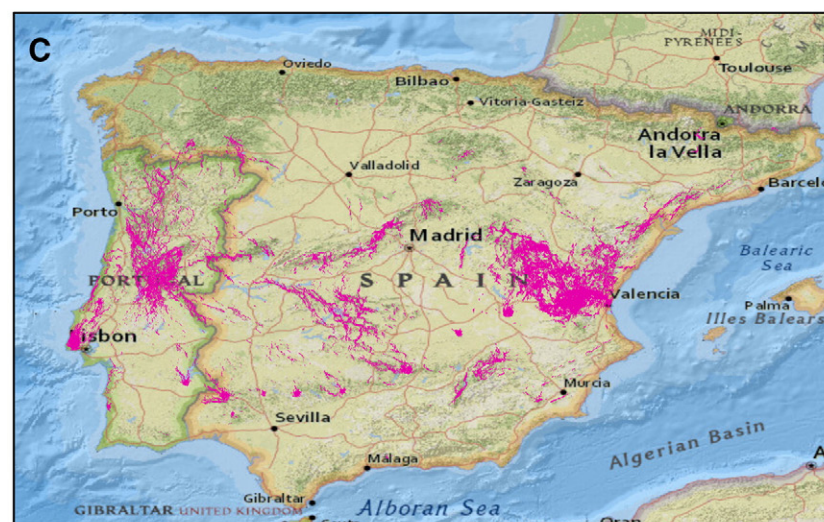
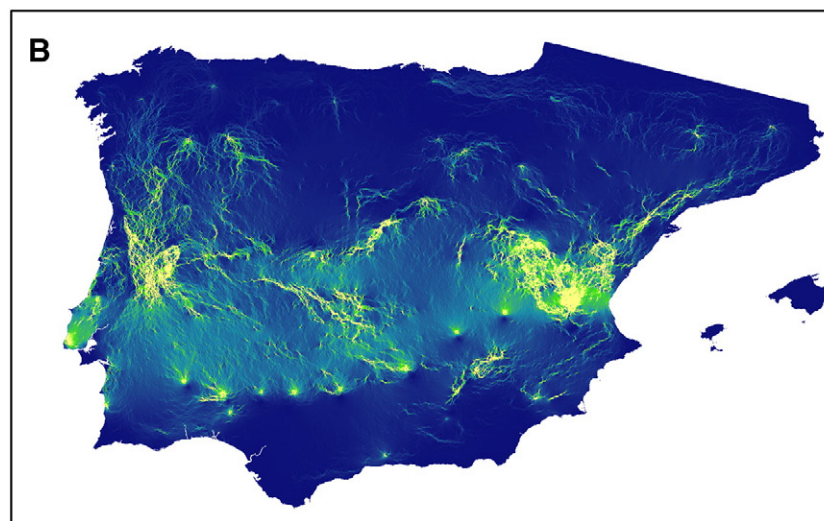
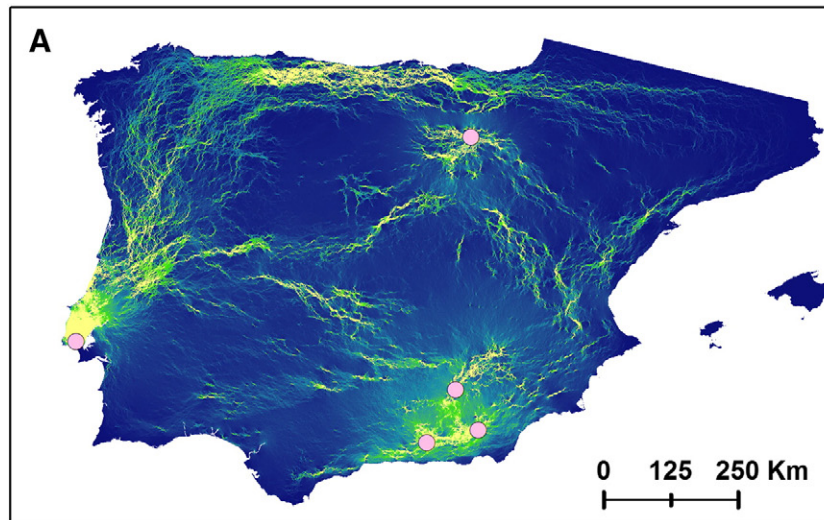



Fig. 1. Changes in the distribution of suitable conditions for *P. austriacus* under future climate change based on the predictions of the climate species distribution models for the present (A) and 2070 (B). Grey areas indicate areas predicted to be unsuitable, and black, suitable. White circles denote the location of colonies predicted to be located in climatically unsuitable areas, and white triangles, the locations chosen to represent future climatic range suitability in the future range shift analysis.


based on Akaike Information Criterion (AIC) values. The final models included all features with a regularization value of 1, 10,000 background points, and 2000 iterations. Model outputs were converted

into binary maps using the thresholding method that maximizes the sum of sensitivity and specificity (Liu et al., 2013). Model predictive ability was tested with ten-fold cross-validation and compared based


Fig. 2. Predicted movement (current) density maps for *P. austriacus* across the Iberian Peninsula as a factor of landscape resistance due to forest cover gradient: A) between the five study colonies (marked with pink circles), B) projected to represent range shift pathways to climatically suitable areas. Potential movement density ranges from low in dark blue to high in yellow. C) Range shift pathways based on the upper quantile of projected movement density shown over a National Geographic map of the Iberian Peninsula (ESRI; available as supplementary KMZ file).



 Range shift pathways

 Colonies genetic study

Movement density



High Low

on the area under the curve (AUC) of the receiver operator characteristics. Training and test AUC scores above 0.75 indicate reasonable to high model discrimination ability, and therefore good model performance (Elith et al., 2006).

2.2. Landscape genetics analysis

To identify the effect of the landscape on genetic differentiation, as a surrogate for gene flow between colonies, I used the landscape resistance approach implemented in Circuitscape v4.0.5 (McRae, 2006; McRae et al., 2008). Circuitscape estimates potential movement pathways across a heterogeneous landscape based on the cumulative cost of movement due to landscape resistance and calculates resistance distance matrices between populations. I compared the effect of nine landscape elements deemed to be potentially important for the species based on radio-tracking studies (in the UK: Razgour et al., 2011; in Iberia: Xavier Puig Montserrat, personal communications) and species distribution modeling (Table 1). Landscape variables were assigned resistance costs ranging from one (no resistance to movement) to 100 (strong barrier to movement). Maps were processed in ArcGIS v10.2 (ESRI). Euclidian distances between pairs of colonies were calculated using the landscape genetics tool (Etherington, 2011) in ArcGIS and were log-transformed. Although Euclidian distance was previously shown to have limited explanatory power (Razgour et al., 2014), it was included here in order to distinguish between the effect of geographic distance *per se* and landscape resistance to movement. All analyses also included a null model, representing a neutral landscape resistance surface (Spear et al., 2010) in which all land surfaces were assigned no resistance cost (1), while seas were assigned the highest resistance costs (100) to account for continent shape alone.

I used Mantel and partial Mantel tests (performed in Zt v1.1, Bonnet and Van de Peer, 2002) to identify the landscape variables that most significantly affect genetic differentiation, as a surrogate for gene flow between *P. austriacus* colonies, following the causal modeling framework in Cushman et al. (2006) and Razgour et al. (2014). Landscape variables that significantly explained genetic differentiation in the Mantel tests were correlated against the genetic distance matrix with competing Euclidian distance, null model, or landscape resistance matrices partialled out in partial Mantel tests. Genetic differentiation was determined based on linearized *Fst* values ($Fst/(1-Fst)$), calculated in GenAlEx v6.5 (Peakall and Smouse, 2012; Table 2).

2.3. Future analysis

Binary maps of predicted relative occurrence probabilities based on the future SDM were used to determine which areas will be climatically suitable for *P. austriacus* in 2070. To identify future range shift pathways, I used Circuitscape to generate movement density (current) maps between southern Iberian colonies that are predicted to be located in climatically unsuitable areas by 2070 ($N = 17$) and locations in the center, north, and northwest of the peninsula that are predicted to be climatically suitable in 2070 ($N = 30$). The latter locations were selected to represent the extent and shape of the predicted suitable areas (Fig. 1B). Because I was interested in movement from unsuitable to suitable areas rather than movement between colonies within each area, each area was treated as a single population with multiple location records. Landscape resistance to future movement was determined based on the landscape element identified in the causal modeling analysis as the variable that most significantly affected genetic differentiation between the five colonies after accounting for the effect of all other variables. I used the same resistance map as in the present landscape genetics analysis. The validity of using present landscape maps was assessed by comparing the extent and nature of land cover changes between the present and 2050 based on projections generated by the IMAGE 3.0 model (Stehfest et al., 2014; www.pbl.nl/image) based on predicted future climate change and human impacts (Global

Biodiversity Outlook, GBO4). To identify potential future movement pathways, the continuous output current (movement) density map was converted into a binary map based on the Jenk's optimization natural breaks method in ArcGIS and is also provided as a KMZ file to view in Google Earth.

3. Results

Both SDMs had high predictive ability and did not overfit presence data (full model: $AUC = 0.906$, $AUC_{crossvalidation} = 0.822 \pm 0.039$; climatic model: $AUC = 0.882$, $AUC_{crossvalidation} = 0.812 \pm 0.033$). The most important variables contributing to the climatic and full models were average temperature of the coldest quarter and land cover type (full model only; Fig. A.1–A.2). Future projections indicate considerable range losses in Iberia, with most of the center, south, and east of the peninsula predicted to become climatically unsuitable for the species by 2070 (Fig. 1).

Neither Euclidian distance ($r = 0.537$, $P = 0.208$) nor the null model ($r = 0.958$, $P = 0.058$) were significantly correlated with genetic differentiation. While Mantel tests of all forest variables were statistically significant, landscape resistance due to forest cover gradient best explained genetic differentiation between colonies, attaining the highest correlation coefficient ($r = 0.989$, $P < 0.01$, Fig. 2). This was the only model to remain significant after controlling for the effect of Euclidian distance ($r = 0.988$, $P < 0.01$), the null model, ($r = 0.864$, $P < 0.01$) and all other landscape variables, while other variables were not significant after controlling for the effect of this model. The remaining non-forest variables (altitude, slope, habitat suitability, and distance to unimproved grasslands and mosaic vegetation) were not significantly correlated with genetic differentiation (Table A.3).

Future projections based on landscape resistance due to forest cover gradient identified potential range shift pathways primarily along the east coast of Spain, the western coast (center and central coast of Portugal), and surrounding the southern central plateau (Meseta Central), but none across the plateau where forest cover is minimal (Fig. 2; Supplementary Google Earth file). Comparison of present and future (2050) land cover maps based on the IMAGE 3.0 model shows that 82% of the study area is predicted to experience no land cover changes. Conversion of forest habitats into non-forest habitats (agriculture and scrub) will occur in 3% of the peninsula, primarily along the north Atlantic coast, north-west, and the Pyrenees. Conversion of non-forest habitat (grassland) into forests is only predicted to occur in one grid cell (0.4% of the area) to the southwest of La Rioja colony.

4. Discussion

Whilst SDMs have been widely used to predict range losses and changes for biodiversity under future climate change (e.g. Araújo et al., 2006; Hughes et al., 2012; Thomas et al., 2004), a predictive landscape genetic approach can help identify how species will shift their ranges to track these changes and inform conservation measures that will facilitate movement.

SDMs predict that *P. austriacus* is vulnerable to the effects of future climate change in Iberia, as most of the peninsula will become climatically unsuitable for this species. Similar range contractions are predicted for Mediterranean bat species in general (Rebello et al., 2010), highlighting the importance of facilitating movement for bat populations' survival in Iberia, especially as this area contains high levels of genetic diversity due to its role as a major Pleistocene glacial refugia (Hewitt, 2004; Razgour et al., 2013).

Landscape resistance due to forest cover gradient best explains variation in genetic differentiation as a surrogate for gene flow. The strong correlations of all forest variables with genetic distance highlight the importance of this habitat type for *P. austriacus* in Iberia. A radio-tracking study has identified broadleaf woodlands as one of the main

foraging habitats of *P. austriacus* in the UK (Razgour et al., 2011). However, a landscape genetic analysis showed that distance to the most important foraging habitat, unimproved grassland, determined genetic connectivity in this fragmented edge-of-range population (Razgour et al., 2014), though the study did not include forest variables, thus precluding direct comparison. Distance to unimproved grasslands was not significantly correlated with genetic distance in this study, either due to differences in foraging behavior across the species' range or general land cover and habitat composition differences between the two geographical areas that result in differences in the importance of forest cover for movement behavior.

Circuitscape has so far been mainly used as a descriptive tool to identify landscape variables affecting genetic connectivity or movement corridors between populations (e.g. Castillo et al., 2014; McRae and Beier, 2007). Its use as a predictive tool has only been explored in a couple of recent studies, albeit not within the landscape genetics framework which allows testing whether the landscape variable actually affects movement in the form of gene flow. Cianfrani et al. (2013) used Circuitscape to assess the recolonization potential of otter populations into Switzerland based on the extent of predicted suitable habitat connectivity, but did not include genetic data and a comprehensive landscape resistance model selection approach. Lawler et al. (2013) used a similar approach to generate potential movement routes for 2903 vertebrate species in response to future climate change based on landscape resistance due to human influence index. However, modeling for many species over a large area required a very coarse resolution (50 km grid cells), which not only obscured fine-scale patterns but is also beyond the natal dispersal distances of many species. Moreover, no alternative landscape variables were tested in the multi-species analysis, and the effect of human influence index on movement was not confirmed with genetic data.

In contrast, the fine-scale approach developed in this study is designed to first identify the most important landscape elements affecting connectivity and only then use this information to predict future range shift patterns at a fine enough scale to direct and inform conservation management action. Species-specific analysis is necessary given that the effect of landscape variables cannot be generalized across species (Storfer et al., 2010). Increasing availability of genetic datasets through data archiving repositories (e.g. Dryad) and journal requirements for data accessibility means that such fine-scale analysis can be carried out on multiple species without the need for extensive field and molecular laboratory work or high costs.

Predictive future forest cover maps may be more suitable for identifying future range shift pathways, but these maps are only available at a very coarse resolution (50 km grid cells). Yet future land cover projections (IMAGE 3.0 model) suggest that at least at the broad scale, there will be little changes in forest cover in the south, center, and eastern, and western coasts of Iberia, where the majority of range shift movement is predicted to take place (Figure A.3). Therefore, at least in this study area, current forest cover gradient can offer a good approximation of future forest cover. Moreover, forests may show a lag in their response to future climate change in the trailing edge of their range because adult trees can persist in areas where conditions have become progressively less suitable due to their longevity and phenotypic plasticity (Jump et al., 2009), and therefore climate change may have limited effect on forest cover in the short term.

Although projected forest losses at the north and northwest of Iberia are unlikely to affect the ability of *P. austriacus* to reach climatically suitable areas, they are likely to affect population establishment and its ability to survive in these areas in the long term. Indeed, land use changes can exacerbate range contractions and species declines under future climate change (Jetz et al., 2007) and are predicted to be a major driver of terrestrial biodiversity changes this century, especially in Mediterranean ecosystems (Sala et al., 2000).

Species distribution modeling offers an effective tool for forecasting how climate change will alter global species diversity and

distribution (Guisan and Thuiller, 2005). However, projecting species future distributions based on global circulation models (GCMs) of predicted climatic changes may be problematic not only because of uncertainties associated with GCM projections but also because species geographic distributions are not determined by climate alone. Most predictive modeling approaches used to date have been criticized for being over-simplistic and failing to integrate key eco-evolutionary processes that shape species ranges, such as biotic interactions and evolutionary adaptations (Thuiller et al., 2013). While interspecific competition may limit the ability of species to shift their range into climatically suitable areas, adaptations may enable populations to survive in areas with climatic conditions outside the species' current environmental niche. Taking these factors into account can alter the predicted future suitable ranges of species, but not how landscape barriers to movement will affect species' ability to expand their range into climatically suitable areas.

Like other landscape genetics studies, the novel approach described in this study may be sensitive to the parameterization of the landscape resistance or cost surfaces that are used as a measure of functional connectivity (Koen et al., 2012). To avoid biases, this study primarily used continuous variables that can be transformed into linear cumulative resistance values bound between 1 and 100, and retained a similar cumulative linear approach with the categorical variable. Cumulative values are particularly suitable for identifying landscape or environmental features that facilitate or constrain genetic connectivity, but predicting how future landscapes may affect genetic connectivity and movement is particularly challenging due to uncertainty about future environments (Spear et al., 2010).

5. Conclusions

Using landscape genetics as a predictive tool in combination with SDMs has allowed the identification of potential pathways whose loss can affect the ability of species to shift their range into climatically suitable areas in response to future changes. These areas should be the focus of conservation efforts aimed to increase landscape connectivity to facilitate species movement, an important management strategy for climate change adaptation (Heller and Zavaleta, 2009) and for increasing evolutionary resilience (Sgrò et al., 2011). Through identifying the exact landscape variable that enhances connectivity, this fine-scale approach can also directly inform conservation management. In the case of *P. austriacus*, connectivity can be achieved by maintaining and enhancing forest availability along range shift pathways. More specifically, unlike the remaining forest variables, forest cover gradient also included low resistance costs for more open forest habitats, suggesting that even low forest cover can aid future range shifts for this species. Such informative analysis can be achieved using publicly available ecological and genetic datasets and can be extrapolated to other areas across species ranges where conditions are similar.

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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.ecoinf.2015.05.007>. These data include Google map of the most important areas described in this article.

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