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BIODIVERSITY RESEARCH

Scale-dependent effects of landscape variables on gene flow and population structure in bats

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ABSTRACT

Aim A common pattern in biogeography is the scale-dependent effect of environmental variables on the spatial distribution of species. We tested the role of climatic and land cover variables in structuring the distribution of genetic variation in the grey long-eared bat, *Plecotus austriacus*, across spatial scales. Although landscape genetics has been widely used to describe spatial patterns of gene flow in a variety of taxa, volant animals have generally been neglected because of their perceived high dispersal potential.

Location England and Europe.

Methods We used a multiscale integrated approach, combining population genetics with species distribution modelling and geographical information under a causal modelling framework, to identify landscape barriers to gene flow and their effect on population structure and conservation status. Genotyping involved 23 polymorphic microsatellites and 259 samples from across the species' range.

Results We identified distinct population structure shaped by geographical barriers and evidence of population fragmentation at the northern edge of the range. Habitat suitability (as captured by species distribution models, SDMs) was the most important landscape variable affecting genetic connectivity at the broad spatial scale, while at the fine scale, lowland unimproved grasslands, the main foraging habitat of *P. austriacus*, played a pivotal role in promoting genetic connectivity.

Main conclusions The importance of lowland unimproved grasslands in determining the biogeography and genetic connectivity in *P. austriacus* highlights the importance of their conservation as part of a wider landscape management for fragmented edge populations. This study illustrates the value of using SDMs in landscape genetics and highlights the need for multiscale approaches when studying genetic connectivity in volant animals or taxa with similar dispersal abilities.

Keywords

Biogeographical barriers, Chiroptera, edge populations, landscape genetics, spatial scale, species distribution modelling.

INTRODUCTION

Future climate change is predicted to result in major shifts in the distribution of species (Thomas, 2010), and therefore, identifying factors that facilitate movement and genetic connectivity among populations is a major challenge for conservation. Landscape genetics offers an interdisciplinary framework for relating spatial genetic patterns to the effects of landscape elements on the movement of organisms (Storfer *et al.*, 2007; Sork & Waits, 2010). The approach is

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based on the premise that geographical and environmental features of the landscape, such as barriers and habitat discontinuity, can structure genetic variation via their effects on dispersal and gene flow (Manel *et al.*, 2003). Landscape genetic approaches can benefit biogeographical studies by quantifying source-sink dynamics in metapopulations and by identifying biogeographical barriers that may limit species movements in response to climate change (Scoble & Lowe, 2010).

Despite their high taxonomic diversity, global distribution and great conservation need (Mickleburgh *et al.*, 2002) bats have been neglected in landscape genetic studies because flight allows bats to cross landscape or geographical barriers more easily than non-volant species. Yet, even with high potential for dispersal by flight, bat species show varying patterns of population structure due to differences in movement abilities, migration, mating behaviour (Burland & Worthington Wilmer, 2001), roosting behaviour and social organization (Rossiter *et al.*, 2012). Bats with low dispersal abilities due to high flight costs show pronounced population subdivision (Burland *et al.*, 1999) and may therefore be strongly affected by landscape elements that create barriers to gene flow.

A major challenge in landscape genetics, especially for volant animals, is determining the relationship between landscape elements and movement. The degree to which a particular feature impedes or facilitates movement translates into relative costs and is used to create a resistance surface. Because the true costs of different landscape elements are rarely known, objective parameterization of the resistance surface requires a combination of field data, expert opinion and model selection procedures in which a wide range of costs are correlated against measures of gene flow (Spear *et al.*, 2010; Koen *et al.*, 2012).

Habitat suitability measures based on species distribution models (SDMs) present an alternative objective way of parameterizing resistance surfaces in the absence of information on dispersal routes and specific habitat use during dispersal (Wang *et al.*, 2008; Koen *et al.*, 2012). SDMs model the environmental tolerance of species, representing an approximation of the realized niche, which is projected into geographical space to yield the potential spatial distribution of species (Guisan & Zimmermann, 2000). As such SDMs do not directly model landscape barriers to movement but rather estimate where suitable environmental conditions for the species occur. Nevertheless, species with limited long-distance movements may still avoid crossing large expanses of unsuitable areas in fragmented landscapes (Thomas, 2000; Van Dyck & Baguette, 2005). Despite their great potential to help explain the effect of landscape elements and habitat distribution on genetic population structure, SDMs remain under-utilized in landscape genetic studies (Row *et al.*, 2010). We argue that SDMs are valuable for describing the effects of landscape resistance on bats because of the complex nature of the effect of landscape elements on movement patterns and dispersal in volant animals. Rather than representing a single landscape feature that limits gene flow, SDMs provide a range of habitat suitability values based on combinations of a wide range of landscape and climatic variables.

A common pattern in biogeography is the scale-dependent effect of environmental variables, whereby climate may limit the distribution of species across their range, while local habitat variables become more important at finer spatial scales (Pearson & Dawson, 2003). Being volant, bats may be affected by broader-scale processes compared with other mammals of equivalent size (Willig *et al.*, 2003), yet they are also sensitive to fine-scale changes in habitat composition or prey densities (Grindal & Brigham, 1999). Therefore, it is important to consider scale when studying the conservation biogeography of bats, especially as scale can affect inferences made from landscape genetics regarding the contribution of variables to patterns of genetic differentiation among populations (Ortego *et al.*, 2012; Keller *et al.*, 2013).

We used a multiscale approach to identify landscape barriers to gene flow and their effect on the population structure, effective population size and conservation status of the grey long-eared bat, *Plecotus austriacus*. Although *P. austriacus* is relatively common and widespread in southern Europe, it is of conservation concern at the northern edge of its range (Harris *et al.*, 1995) and is predicted to experience severe range shifts under future climate change, with the majority of southern Europe becoming climatically unsuitable by the end of the century (Razgour *et al.*, 2013). The wing morphology of *P. austriacus* is energetically inefficient for long-distance flight (Norberg & Rayner, 1987), suggesting that long-distance dispersal ability may be limited and therefore there will be some level of genetic differentiation among colonies (Olival, 2012). Based on its relatively low vagility, sedentary nature and roosting behaviour (Swift, 1998), *P. austriacus* is also predicted to have medium levels of genetic population structure (inferred from Rossiter *et al.*, 2012) and to be particularly vulnerable to habitat fragmentation and population isolation (Entwistle *et al.*, 2000; Burland & Worthington Wilmer, 2001).

We combine genetic data with species distribution modelling and geographical information to test hypotheses regarding the role of landscape elements in impeding or facilitating gene flow in *P. austriacus* across spatial scales, including a fine-scale analysis of the northern edge-of-range population and a broad-scale analysis of the whole European range. In particular, we analysed the role of climatic and habitat variables in structuring the distribution of genetic variation at different spatial scales, and their effect on the conservation status of an edge-of-range population.

Using a causal modelling framework (Legendre & Trousselier, 1988; Legendre, 1993; Cushman *et al.*, 2006) carried out at both the colony and genetic population cluster level, we compared three possible causes of population structure: isolation by Euclidian (geographical) distance (IBD), isolation by geographical barriers and isolation by landscape resistance (IBR). We hypothesized that:

1. Landscape elements and geographical barriers play a more important role in structuring patterns of gene flow in *P. austriacus* across spatial scales than Euclidian distance alone.
2. Species distribution models can better capture the effect of landscape resistance on gene flow in bats than individual landscape elements.
3. The effect of land cover variables on gene flow becomes more pronounced at finer spatial scales corresponding to the scale-dependent effect of environmental variables on species distribution.

METHODS

Sample collection

We obtained 259 *P. austriacus* tissue samples from 82 locations spanning the entire known species' range (1–18 samples per location; Fig. 1; Table S1). Samples collected from juveniles were not included to avoid biasing the analyses due to the inclusion of closely related individuals. Individual samples were genotyped at 23 autosomal microsatellite loci as in Razgour *et al.* (2013). Laboratory procedures are outlined in Appendix S1 of Supporting Information.

Genetic data analysis

Analyses were carried out at either the colony or genetic cluster level (see analysis of population structure below). Colonies were defined based on individuals caught in the same roost or adjacent roosts within 10 km. All samples were included in the genetic cluster analysis (n = 259), while the colony analysis only included samples from locations with more than six individuals (n = 177). We combined six samples from Bulgaria from four locations within a radius of 120 km to represent a Balkan colony. The two Italian locations were also treated as a single colony due to their proximity (30 km apart), resulting in a total of 16 colonies (Table S2). The geographical location of the combined colonies was assigned as the sampling location with the highest number of samples (Fig. 1).

We estimated the effective population size (*Ne*) of the edge-of-range English population and the separate English

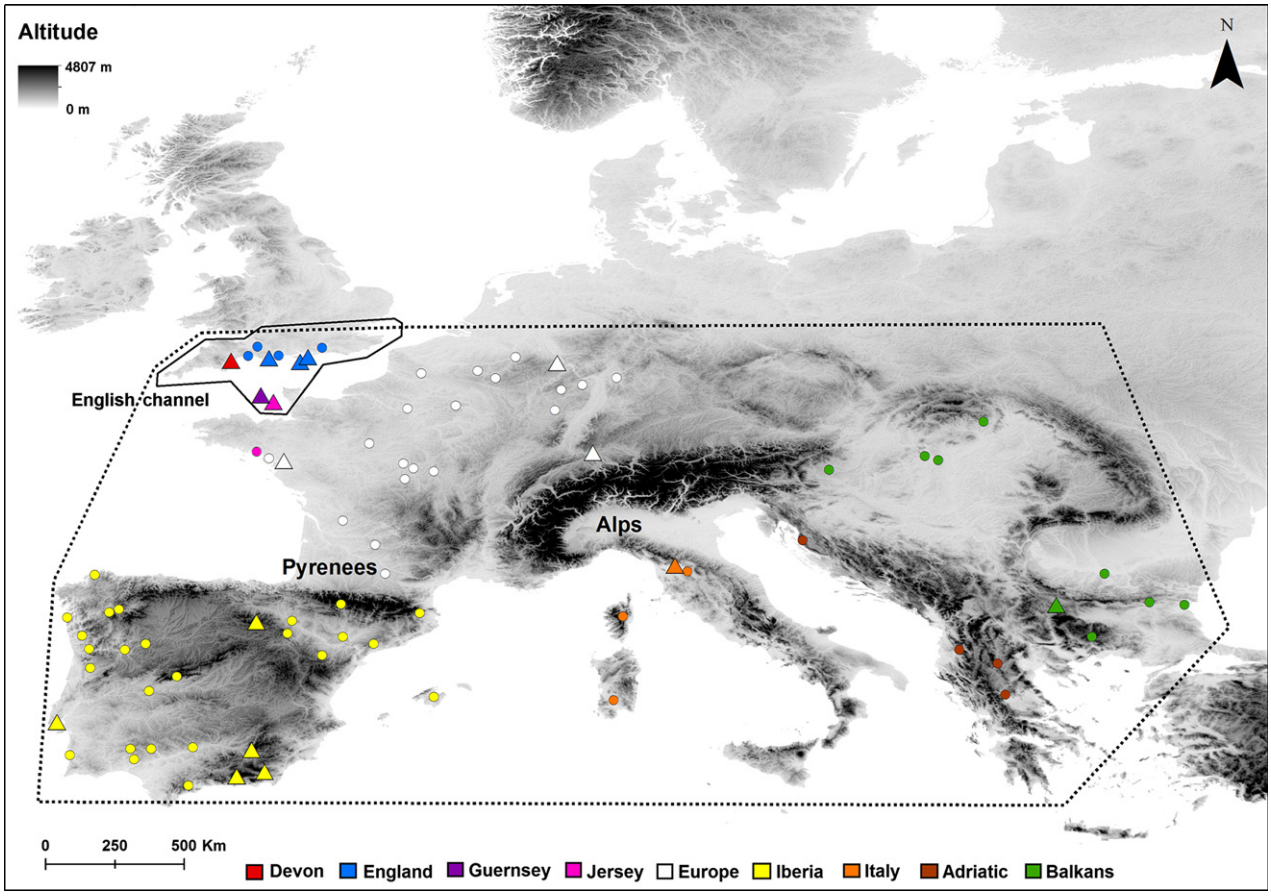

Figure 1 Spatial distribution of genetic population clusters relative to the geographical location of *Plecotus austriacus* samples based on the results of the Geneland analysis (Fig. S2). Sample locations are colour-coded according to their respective population clusters (Europe = mainland Western Europe) and presented over an altitude map. Triangles represent the location of the 16 colonies. Solid and broken black outlines represent the extents of the fine- and broad-scale analyses, respectively. The location of the three main geographical barriers (English Channel, Pyrenees and Alps) is indicated on the map.

colonies using the Linkage Disequilibrium approach in NeEstimator v2 (Do *et al.*, 2013). Estimated *Ne* was compared with that of the Iberian population and Iberian colonies because these represent the core of the species' range. We used the random mating model and the Jackknife method to estimate confidence intervals. We set the lowest allele frequency used to 0.01.

Analysis of population structure

Population structure and the number of genetic clusters were inferred using individual-based Bayesian assignment tests implemented in the R package Geneland v4.0.3 (Guillot *et al.*, 2005). Geneland combines genetic data with information on sample geographical location to account for spatial population structure. In a recent simulation study (Blair *et al.*, 2012), Geneland was shown to have the highest power and best performance among commonly used clustering and non-clustering methods for identifying linear barriers to gene flow. To test for convergence on similar parameter estimates, we ran 10 simultaneous independent runs of 10^6 MCMC iterations with a thinning value of 10^3 and repeated the analysis twice. Number of populations was set to 1–15. We selected the number of distinct spatial clusters based on the run giving the highest average posterior probability, as well as the frequency of the assigned number of populations across runs. Trace plots were checked for adequate mixing and convergence (Appendix S1).

Genetic differentiation among pairs of colonies or genetic clusters was estimated using Weir & Cockerham's (1984) F_{ST} estimation in SPAGeDi (Hardy & Vekemans, 2002) with 10^4 permutations (Appendix S1). F_{ST} was linearized as $F_{ST}/(1-F_{ST})$ when used as a genetic distance matrix (Rousset, 1997).

Estimating gene flow rates

We estimated contemporary gene flow rate and direction between individual samples across potential geographical barriers (the Pyrenees and Alps mountain ranges and the English Channel; Fig. S1) using BayesAss v3 (BA3; Wilson & Rannala, 2003). MCMC mixing parameter values of allele frequencies and inbreeding coefficients were adjusted to obtain the recommended acceptance rates. We performed 20 replicate runs with 10^7 MCMC iterations and a burn-in phase of 10^6 iterations, initializing each run with a different random number generator seed to verify convergence based on concordance between runs on mean parameter estimates. We determined MCMC chain mixing and convergence by visualizing the trace files in Tracer v1.5 (Rambaut & Drummond, 2009) and calculated ESS values. Results were compared with genetic barriers detected based on Monmonier's Maximum Difference algorithm in Alleles In Space v1.0 (Miller 2005) using raw genetic distances between the 16 colonies.

Landscape genetic analysis

We used Mantel and partial Mantel tests to determine the relative effect of Euclidian distance (IBD), geographical barriers (mountain ranges and seas) and landscape resistance (IBR) on genetic differentiation (linearized F_{ST}) between *P. austriacus* colonies and genetic clusters (obtained from the Geneland analysis). Adjacent genetic clusters with too few samples were pooled together. A flow diagram (Fig. 2) summarizes the landscape genetic methods used.

Euclidian distances between pairs of colonies were calculated using the Landscape Genetics tool (Etherington, 2011) in Arcgis v10 (ESRI). Euclidian distances between population clusters were calculated based on distances between the cluster centroids.

We characterized the effect of landscape resistance on genetic differentiation using resistance distance, an analysis based on circuit theory, implemented in Circuitscape v3.5 (McRae, 2006; McRae *et al.*, 2008). Circuitscape estimates potential movement routes across a heterogeneous landscape based on the cumulative cost of movement due to landscape resistance. This analysis incorporates all possible pathways

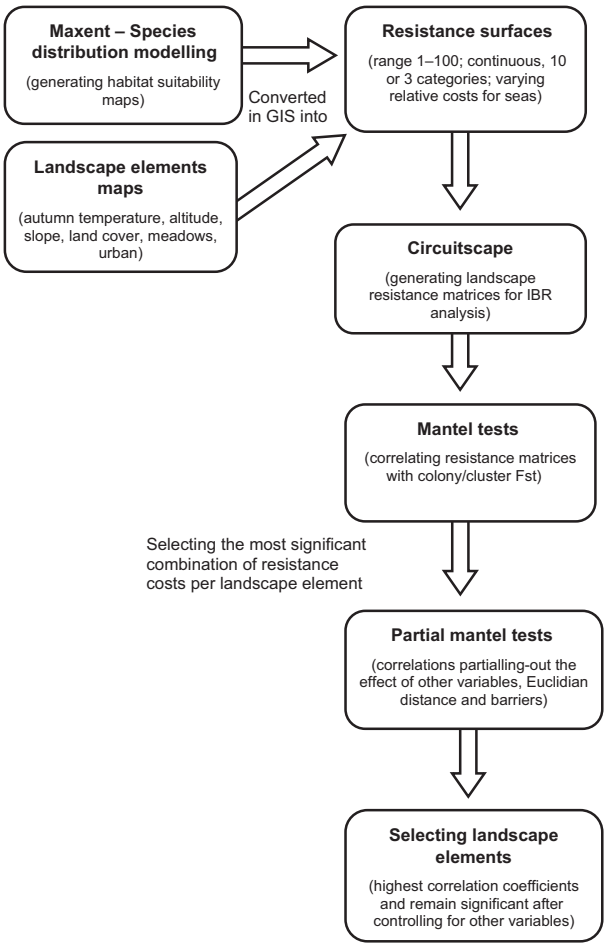

Figure 2 Flow diagram summarizing the landscape genetics analysis procedures.

connecting populations and therefore provides a better representation of the effect of landscape heterogeneity on gene flow than other commonly used measures, such as least cost path (McRae & Beiber, 2007). Resistance distances were calculated between colonies (using focal point analysis) or genetic clusters defined in Geneland (using focal region analysis).

The landscape genetics analysis was carried out at two spatial scales, across the European range (broad scale) and at the northern edge of the range, within England and the Channel Isles (fine scale) (Fig. 1). The resolution for the broad-scale models was 5 km (2.5 arc min), corresponding to the colony home range size of *P. austriacus* and the maximum distance travelled daily to foraging grounds (Razgour *et al.*, 2011). The resolution of the fine-scale models was 1 km (30 arc sec) to determine the effect of more fine-scale landscape elements. The broad-scale analysis was carried out both at the colony (16 colonies) and genetic cluster levels (eight clusters), while the fine-scale analysis was carried out only at the colony level (six colonies) due to insufficient clusters at this scale for Mantel test analysis.

Landscape variables were selected based on a combination of knowledge of the biology of the species (gained through radio-tracking studies; Razgour *et al.*, 2011) and information from SDMs on factors affecting distribution. We tested the use of SDMs and their output habitat suitability maps to parameterize the landscape resistance matrix vs. the use of individual landscape variables. Autumn temperature was included in the analysis at both spatial scales, while altitude, slope and distance to grasslands only in the broad-scale, and distance to meadows (lowland unimproved grasslands), distance to urban areas and land cover in the fine scale (Table 1; Appendix S1 for description of variables).

Table 1 Description of hypotheses tested in the landscape genetic analysis and the number of resistance categories (not including sea) used to parameterize the landscape resistance matrix in the broad- and fine-scale analyses. Landscape resistance costs range between 1 and 100 for hypotheses of landscape variable > or = sea (sea = 75 and 100, respectively), and between 1 and 75 for landscape variable < sea (sea = 100). Autumn temperature = mean Sep–Oct temperatures; Grasslands = includes improved and unimproved grasslands; Meadows = lowland un-semi-improved grasslands; Land cover = foraging habitats (broadleaf woodland, riparian, flooded, mosaic vegetation and shrub), occasionally used habitats (improved grassland and urban), limited use habitats (arable, conifer and barren)

Landscape variable	Resistance categories	Hypothesis tested	Description
Species Distribution Model (SDM) (both scales)	Continuous	SDM > sea	Highest resistance for SDM
		SDM < sea	Highest resistance for sea
		SDM = sea	Equal resistance
	10	SDM > sea	Highest resistance to SDM
		SDM < sea	Highest resistance for sea
		SDM = sea	Equal resistance
	3	SDM > sea	Highest resistance to SDM
		SDM < sea	Highest resistance for sea
		SDM = sea	Equal resistance
Altitude (broad scale)	10	Altitude > sea	Highest resistance for altitude
		Altitude < sea	Highest resistance for sea
		Altitude = sea	Equal resistance
	3	Altitude > sea	Highest resistance for altitude
		Altitude < sea	Highest resistance for sea
		Altitude = sea	Equal resistance
Slope (broad scale)	10	Slope > sea	Highest resistance for slope
		Slope < sea	Highest resistance for sea
		Slope = sea	Equal resistance
Autumn temperature (both scales)	10	Temperature > sea	Highest resistance for temp.
		Temperature < sea	Highest resistance for sea
		Temperature = sea	Equal resistance
Grassland (broad scale)	Continuous	Distance to grasslands	Resistance increases with distance
Meadows (fine scale)	Continuous	Distance to meadows	Resistance increases with distance
	2	(Meadows < land) < sea	Lowest resistance for meadows
		(Meadows > land) < sea	Lowest resistance for land
		Meadows > sea > land	Highest resistance for land
Urban (fine scale)	Continuous	Distance to urban areas	Resistance decreases with distance
Land cover (fine scale)	3	Land cover > sea	Highest resistance for land cover
		Land cover < sea	Highest resistance for sea

Generating landscape resistance maps

Species distribution models were generated in Maxent (Phillips *et al.*, 2006). The fine-scale SDM was taken from Razgour *et al.* (2011). The broad-scale model included the same 142 genetically confirmed location records used in Razgour *et al.* (2013). For variables included in the SDMs and Maxent modelling procedures see Appendix S1.

Landscape variables were assigned resistance costs ranging from one (no resistance to movement) to 100 (strong barrier to movement). Because colonies and population clusters at both spatial scales were separated by large expanses of water (seas), all models included resistance costs for seas, set at either 50 (medium resistance), 75 (high resistance) or 100 (highest resistance). We varied the maximum resistance costs of each landscape variable relative to the costs assigned to seas and other variables, and selected the best parameter combination for each variable based on the magnitude of the Mantel correlations (Appendix S1 for resistance models and costs).

Based on 29 hypotheses (Table 1), we generated a total of 24 landscape resistance models at the broad-scale colony analysis (Table S6), 17 models at the broad-scale genetic cluster analysis (Table S7), and 19 fine-scale models (Table S8). 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.

Statistical analysis

We followed the causal modelling framework in Cushman *et al.* (2006) (Fig. 2) to determine the relative support for each driver of genetic differentiation (IBD, barriers and IBR) relative to other drivers. This approach is based on the premise that a particular hypothesis is supported if it is significantly correlated with genetic distance even after controlling for the effect of other competing hypotheses, while the remaining hypotheses cease to be significant after controlling for the *ith* hypothesis.

Mantel and partial Mantel tests were performed using the program ZT v1.1 (Bonnet & Van de Peer, 2002) with 10^4 randomized permutations to obtain probability values. First, we computed Mantel tests to select the strongest supported combination of resistance costs for each landscape element based on the magnitude of the Mantel correlations (correlation coefficient (r) and statistical significance). Only one combination of resistance costs was retained for each landscape element. Next, landscape elements that significantly explained genetic differentiation at their respective scale were correlated against the genetic distance matrix with competing Euclidian distance or barrier hypotheses partialled out in partial Mantel tests. Euclidian distances were log-transformed. Mountain and sea barriers were included in partial Mantel tests as binary matrices, whereby pairs of colonies separated by a barrier received a value of one, while those not separated by the barrier scored zero. We also included a combined barrier model, in which pairs of colonies separated by more than one barrier scored two.

RESULTS

Biogeographical population structure

Individual-based spatial assignment tests detected genetic population structure across the range of *P. austriacus*, dividing the dataset into nine spatial clusters: Devon, the rest of England, Guernsey, Jersey and north-western France, mainland Western Europe (France, Belgium, Germany and Switzerland), Iberia, Italy (including Sardinia and Corsica), Balkans (Bulgaria, Hungary, Slovakia and Austria) and the Adriatic Balkan coast (Croatia, Albania and Greece) (Fig. 1; Fig. S2 for posterior probability of cluster membership). In subsequent analyses, the two Balkan clusters (Balkans and Adriatic Balkan coast) were grouped together due to the small number of samples belonging to the Adriatic cluster, resulting in eight genetic clusters.

Genetic differentiation between the 16 colonies was moderate but significant ($P < 0.001$), with lower values between colonies within Iberia and higher levels of differentiation between colonies in different geographical regions (mean $F_{ST} = 0.062$, range: 0.001–0.128; Table S3). Similarly, genetic differentiation between the eight genetic clusters was also moderate, though minimum values were higher than in the colony analysis (mean $F_{ST} = 0.060$, 0.027–0.103; Table S4).

The effective size of the English population was estimated at a mean of 82 (95% confidence intervals: 63–112), while the Iberian population was estimated at a mean of 786 (423–4303). Estimations of the effective size of colonies within England varied between a mean of 20 for the Devon colony (15–28), and 27 for the two Isle of Wight colonies combined (21–38). Estimations for Iberian colonies were higher, with a mean of 47 (34–72) for Almeria and 61 (36–164) for Rioja.

Landscape genetics

Species distribution models had high predictive ability and did not overfit present data (broad-scale: $AUC_{train} = 0.951$, $AUC_{test} = 0.900$; fine-scale: $AUC_{train} = 0.994$, $AUC_{test} = 0.984$). The main ecogeographical variables contributing to SDMs at both scales were climatic variables, and in particular mean winter temperature, though land cover was also important at the fine scale (Fig. S3–S4).

Effect of geographical barriers

Of all potential geographical barriers, only the Pyrenees formed a major barrier to gene flow. Estimated gene flow rates across the Pyrenees were minimal (0.02–0.05). In contrast, both the Alps and the English Channel did not impede

recent gene flow from Italy into Western Europe (0.26), and from Western Europe (0.19) and the Channel Isles (0.28) into England (Table S5). Similarly, the first two genetic barriers identified in Monmonier's algorithm analysis separated the Spanish colonies from the rest of Europe, while the Italian colony was only separated on the 7th barrier (Fig. S5).

Effect of geographical distance

Although genetic differentiation between colonies increased with Euclidian distance at both spatial scales, the correlation coefficients were generally lower than in the IBR analysis (broad-scale [16 colonies]: $r = 0.55$, $P < 0.001$, Fig. 3a; fine scale [six colonies]: $r = 0.44$, $P < 0.05$, Fig. 4a). IBD was not significant in the genetic cluster analysis (Fig. 3c) and ceased to be significant after controlling for the effect of most landscape models in the colony analyses at both scales (Table 2–3). IBD remained significant after controlling for the effect of geographical barriers only at the broad-scale colony analysis.

Broad-scale landscape effects

Most landscape resistance models and most combinations of parameters had significant positive correlations with measures of genetic distance both between colonies and genetic clusters, with the exception of all altitude and slope models in the colony analysis (Table S6). The models with the highest correlation coefficients overall were the SDM model (colony analysis: $r = 0.73$, $P < 0.001$, Fig. 3b; genetic cluster analysis: $r = 0.90$, $P < 0.001$, Fig. 3d) and the autumn temperature model (colony analysis: $r = 0.62$, $P < 0.001$; genetic cluster analysis: $r = 0.88$, $P < 0.001$). The SDM model was the only model to fulfil all the causal modelling conditions, remaining significant after controlling for the effect of all other variables, while other variables were not significant after controlling for the effect of this model (Mantel tests: Table S6–7; partial Mantel tests: Table 2).

Fine-scale landscape effects

IBR models best explained genetic differentiation at the fine scale, with the IBR model of landscape resistance due to distance from meadows (Fig. 5a) attaining the highest correlation coefficient ($r = 0.77$, $P < 0.01$, Fig. 4b). This model also remained significant once controlling for the effect of Euclidian distance ($r = 0.81$, $P < 0.01$) and was the only model to fulfil all the causal modelling conditions. The IBR autumn temperature model ($r = 0.69$, $P < 0.01$, Fig. 5b) also remained significant after controlling for Euclidian distance. However, the model was highly correlated with Euclidian distance ($r \geq 0.9$), and IBD was borderline significant after partialling out the model ($P = 0.051$). In contrast, although IBD was not significant ($P = 0.2$) after controlling for the IBR SDM model (SDM model: $r = 0.67$, $P = 0.017$), the SDM model was marginally not significant ($P = 0.08$) after controlling for the effect of IBD (Table S8; Table 3).

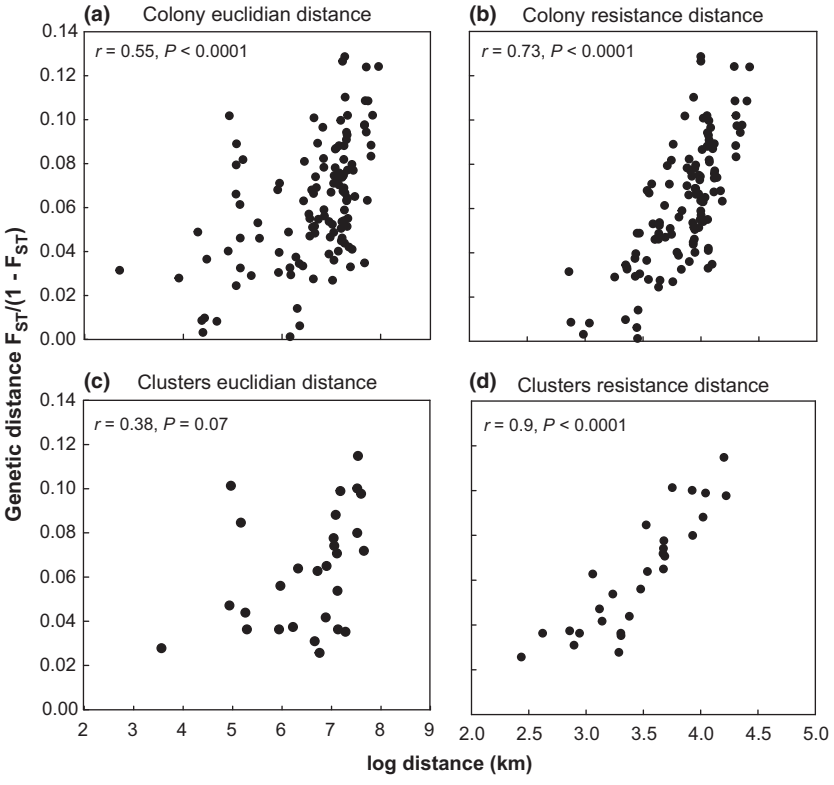

Figure 3 Broad-scale Mantel tests for the colony and genetic cluster analyses across Europe. Genetic distance is correlated against: (a) Euclidian distance between colonies, (b) resistance distance between colonies for the species distribution modelling (SDM) model, (c) Euclidian distance between genetic clusters, and (d) resistance distance between genetic clusters for the SDM model.

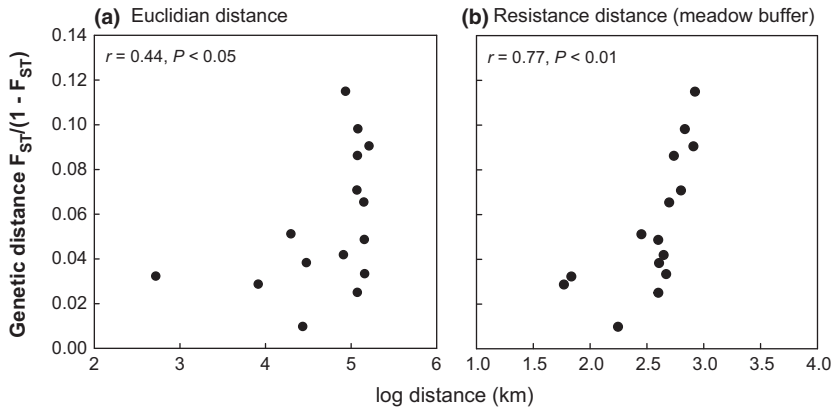

Figure 4 Fine-scale Mantel tests between colonies within England and the Channel Isles. Correlations of (a) genetic distance and Euclidian distance, and (b) genetic distance and resistance distance for the distance from meadows model.

Table 2 Broad-scale colony and genetic cluster causal modelling analysis, including Mantel and partial Mantel tests for isolation by Euclidian distance (IBD), and isolation by resistance distance (IBR). Models best explaining genetic differentiation are marked in bold (SDM = species distribution model, autumn = autumn temperature)

			Colony analysis		Cluster analysis	
Category	Independent variable	Partialled out variable	*r*	*P*	*r*	*P*
IBD	Euclidian distance		0.554	< 0.0001	0.380	0.07 (NS)
		Mountain barrier	0.520	< 0.001		
		Water barrier	0.615	< 0.0001		
		Combined barrier	0.450	< 0.05		
		Resist (SDM)		0.3 (NS)		
		Resist (grassland)	0.471	< 0.01		
		Resist (autumn)	0.430	< 0.01		
IBR	**Resist (SDM)**		**0.728**	**< 0.0001**	**0.898**	**< 0.0001**
		Euclidian distance	0.573	< 0.001	0.880	< 0.0001
		Mountain barrier	0.710	< 0.0001	0.891	< 0.0001
		Combined barrier	0.660	< 0.001	0.891	< 0.0001
	Resist (grassland)		0.348	< 0.05	0.500	< 0.05
		Euclidian distance		0.3 (NS)		0.08 (NS)
	Resist (altitude)			0.2 (NS)	0.521	< 0.05
		Euclidian distance			0.544	< 0.05
	Resist (slope)			0.3 (NS)	0.606	< 0.01
		Euclidian distance			0.585	< 0.05
	Resist (autumn)		0.618	< 0.0001	0.884	< 0.0001
		Euclidian distance	0.523	< 0.01	0.885	< 0.0001
		Mountain barrier	0.659	< 0.0001	0.887	< 0.0001
	Null model			0.1 (NS)		0.2 (NS)

DISCUSSION

We found that both climate and landscape elements play an important role in determining the biogeography of *P. austriacus* and patterns of genetic differentiation across its range, yet their contribution changes with spatial scale. Despite its flight ability, *P. austriacus* has a distinct population structure with varying levels of genetic differentiation among colonies determined by the extent of landscape resistance to movement and geographical distance.

At the core of the species' range, in Iberia, genetic differentiation among colonies is negligible and there is no evidence of further population substructuring, despite the large geographical area separating the northern, south-eastern and western Iberian colonies. In contrast, across a smaller geographical area at the northern edge of the range, in England, levels of genetic differentiation among colonies are higher and appear to exceed those estimated for the more common sympatric congener *Plecotus auritus* (mean F_{ST} = 0.019, Burland *et al.*, 1999). Moreover, the English population is split into two distinct genetic clusters (Devon and the rest of England), suggesting population fragmentation at the northern edge of the range.

Geographical barriers and population structure

Geographical barriers contribute to population structure across the range of *P. austriacus*. Of the nine identified

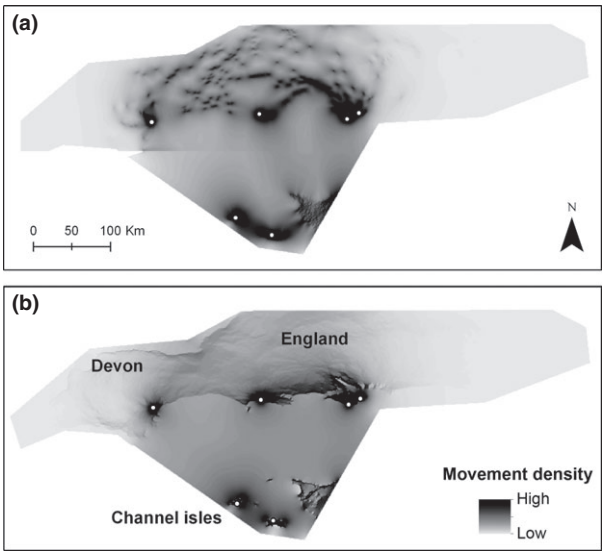

Figure 5 Potential movement pathways of *Plecotus austriacus* within England and the Channel Isles. Cumulative current maps generated by Circuitscape to indicate movement density between colonies as a factor of landscape resistance due to (a) distance to meadows and (b) autumn temperature. Connectivity between colonies ranges from high, in black, to low (limited movement), in light grey. White circles denote the location of colonies.

genetic clusters, only one (Devon) was not separated by either mountain ranges or large expanses of water. However, contemporary gene flow rates suggest that these barriers are not impermeable, and indeed there is some uncertainty on cluster membership in terms of the probability of individuals belonging to more than one cluster (Fig. S2). It is important to note that the incorporation of spatial information in Geneland means that genetic cluster assignment can mask the presence of migrants or admixture within clusters. Consequently, samples from mainland Western Europe appear to form a distinct genetic cluster despite the relatively high rates of recent gene flow into that area from Italy estimated with BA3. In contrast, non-spatial individual assignment tests identified high levels of admixture across mainland Western Europe and the presence of individuals of Italian ancestry (Razgour *et al.*, 2013).

Because BA3 restricts the proportion of migrants in a population to a maximum of 0.33, estimated gene flow rates among populations with low levels of genetic differentiation ($F_{ST} < 0.05$) should be treated with caution (Faubet *et al.*, 2007). However, in this analysis, we are not interested in exact estimations of gene flow rates but rather whether there is gene flow across the barriers. To overcome potential biases in gene flow estimations, we combined the BA3 analysis with Monmonier's algorithm analysis that directly identifies the location of genetic barriers between colonies.

Our finding that the Alps did not form a substantial barrier to gene flow in *P. austriacus* is surprising given their role in limiting gene flow in other bat species, including the migratory *Nyctalus noctula* (Petit & Mayer, 1999).

Table 3 Fine-scale causal modelling analysis of the effect of the landscape on genetic differentiation (F_{ST}), including Mantel and partial Mantel tests for isolation by Euclidian distance (IBD) and isolation by resistance distance (IBR). Models best explaining genetic differentiation are marked in bold (SDM = species distribution model, autumn = autumn temperature)

Category	Independent variable	Partialled out variable	F_{ST}	
			r	*P*
IBD	Euclidian distance		0.440	0.02
		Water barrier		0.1 (NS)
		Resist (SDM)		0.2 (NS)
		Resist (meadow)	NS†	
		Resist (land cover)		0.3 (NS)
		Resist (autumn)*		0.051
IBR	Resist (SDM)		0.673	0.017
		Euclidian distance	0.597	0.08 (NS)
	Resist (meadow)		**0.772**	**0.003**
		Euclidian distance	0.809	0.007
	Resist (land cover)		0.573	0.025
		Euclidian distance		0.2 (NS)
	Resist (autumn)		**0.691**	**0.003**
		Euclidian distance*	0.736	0.008
	Null model			0.3 (NS)

*High correlation between independent and partialled out variable ($r \geq 0.9$).

†Significant negative correlation ($P = 0.036$) – genetic distance decreases as Euclidian distance increases.

However, *Barbastella barbastellus* (mtDNA) and *Rhinolophus hipposideros* (mtDNA and microsatellites) show similar responses as *P. austriacus*, in that the Pyrenees, but not the Alps, restrict gene flow (Rebelo *et al.*, 2012; Dool *et al.*, 2013).

Large expanses of water do not necessarily form effective barriers to gene flow among bat populations. For example, some narrow strips of sea, such as the Straits of Gibraltar (14 km), have a stronger effect on female-mediated gene flow and on delimiting species distribution than much larger expanses of water, such as the Balearic Sea (> 85 km). However, the effect is not uniform across species (García Mudarra *et al.*, 2009) and may be an artefact of differential historical patterns of colonization by ecologically similar species and subsequent interspecific competition (Juste *et al.*, 2004). Despite its wing morphology and limited dispersal ability, *P. austriacus* has colonized most Mediterranean islands as well as the Atlantic island of Madeira (Juste *et al.*, 2004). Long-distance island colonization events probably result from unusual displacement movements rather than routine movements for foraging and mating

and therefore represent much greater dispersal distances than regularly travelled by sedentary species (Van Dyck & Baguette, 2005).

Landscape genetics of *P. austriacus*

Some level of IBD is commonly found in bats (Burland & Worthington Wilmer, 2001; Olival, 2012), with some species with very limited dispersal abilities, such as the bumblebee bat, showing such high levels of IBD ($r = 0.95$) that landscape resistance is unlikely to explain population differentiation any better than IBD alone (Puechmaille *et al.*, 2011). Yet in our study, IBD had limited explanatory power, in particular after controlling for the effect of landscape resistance. Instead, landscape resistance due to habitat suitability as captured by SDMs and distance to main foraging habitat best explains variation in genetic patterns at the broad and fine spatial scales, respectively.

While habitat suitability for *P. austriacus* across the range was primarily affected by climatic variables, at the fine scale, land cover, and in particular grasslands, also played an important role, though winter temperature was still the most important component of the fine-scale SDM. Similarly, land cover variables only affected population differentiation in the fine-scale analysis, and although the SDM model was significantly correlated with genetic differentiation between colonies, its explanatory power was limited after accounting for the effect of IBD. This scale-dependent effect of environmental variables, whereby climatic variables limit the genetic connectivity across the entire range while habitat and land cover type are only limiting at finer spatial scales (Pearson & Dawson, 2003), highlights the importance of a multiscale analysis in landscape genetics (Anderson *et al.*, 2010).

Although SDMs do not directly model movement or incorporate information on movement behaviour (Spear *et al.*, 2010), habitat preference of dispersers can be similar to that of residents (Zeller *et al.*, 2012) and therefore SDMs can be used as a proxy for habitat suitability during movement, especially for species with small home ranges or dispersal capacity. SDMs have been successfully used to parameterize landscape resistance surfaces for other species with limited long-distance dispersal such as the foxsnake, *Mintonius gloydi* (Row *et al.*, 2010) and the spiny rat, *Niviventer coninga* (Wang *et al.*, 2008). Moreover, they are particularly suitable for volant animals that are not likely to be solely affected by land cover elements because they encompass the combined effect of a range of environmental variables.

Autumn temperature was correlated with genetic differentiation across spatial scales, but its effect could not be teased apart from the general effect of IBD. During the autumn, even sedentary bat species move either to mating roosts or swarming sites that serve large catchment areas beyond regular foraging flight distances (Parsons *et al.*, 2003), and unsuitable temperatures may affect the distance individuals fly to mate.

Conservation implications

The edge-of-range English *P. austriacus* population appears to be of high conservation concern due to its small effective size and evidence of population fragmentation. Estimated *Ne* (63–112) is below the minimum viable effective population size necessary for retaining evolutionary potential and avoiding the accumulation of deleterious alleles ($Ne > 1000$), but a sufficient size to avoid inbreeding depression in the short term ($Ne > 50$) (Frankham *et al.*, 2010). In fact, the entire English population is estimated to be of equivalent size to a single Spanish colony. Yet, high rates of gene flow from mainland Europe may help augment the small English population size and therefore may be essential for its long-term survival. Colony effective size estimates suggest that English colonies may experience inbreeding depression unless sufficient levels of gene flow are maintained between colonies. Minimizing levels of inbreeding is important for the long-term survival of bat populations because inbreeding may reduce juvenile survival (Rossiter *et al.*, 2001). Small effective colony size estimates highlight the importance of maintaining connectivity and of managing the separate colonies as part of a larger interbreeding population.

Beyond the effect of climate and habitat suitability, we identified specific land cover elements that facilitate movement and therefore can be used in corridor design to promote population connectivity (Storfer *et al.*, 2007). We show that lowland unimproved grasslands (meadows), the main foraging habitat of *P. austriacus* (Razgour *et al.*, 2011), also play an important role in facilitating fine-scale gene flow, with the resistance model significantly explaining genetic differentiation even after controlling for the effect of Euclidian distance. Hence, the extensive decline of this habitat type in England in the past century due to agricultural intensification (Fuller, 1987) not only affects the persistence of *P. austriacus* colonies but also influences landscape connectivity and gene flow between colonies and therefore may be responsible for the observed fragmentation and decline (Razgour *et al.*, 2013) of the edge-of-range population.

CONCLUSIONS

The importance of landscape elements in restricting movement and gene flow in *P. austriacus* shows that despite their flight ability, volant animals with wing morphology that limits long-range dispersal can have a landscape-mediated genetic population structure. SDMs successfully explained patterns of genetic differentiation and gene flow after controlling for the effect of geographical distance and barriers, thus supporting their use in landscape genetic studies. Habitat suitability and genetic connectivity across the range of *P. austriacus* are primarily affected by climatic and topographic variables, while land cover variables become important at finer scales, at least at the northern edge of the range. These findings demonstrate that multiscale approaches are integral to landscape genetic and biogeography studies. The

strong effect of lowland unimproved grasslands on fine-scale genetic connectivity for the fragmented northern edge-of-range population suggests that wider landscape management should focus on the conservation of this endangered habitat type.

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REFERENCES

Anderson, C.D., Epperson, B.K., Fortin, M.-J., Holderegger, R., James, P.M.A., Rosenberg, M.S., Scribner, K.T. & Spear, S. (2010) Considering spatial and temporal scale in landscape–genetic studies of gene flow. *Molecular Ecology*, **19**, 3565–3575.

Blair, C., Weigel, D.E., Balazik, M., Keeley, A.T.H., Walker, F.M., Landguth, E., Cushman, S., Murphy, M., Waits, L. & Balkenhol, N. (2012) A simulation-based evaluation of methods for inferring linear barriers to gene flow. *Molecular Ecology Resources*, **12**, 822–833.

Bonnet, E. & Van de Peer, Y. (2002) ZT: a software tool for simple and partial Mantel tests. *Journal of Statistical Software*, **7**, 1–12.

Burland, T.M. & Worthington Wilmer, J. (2001) Seeing in the dark: molecular approaches to the study of bat populations. *Biological Reviews*, **76**, 389–409.

Burland, T.M., Barratt, E.M., Beaumont, M.A. & Racey, P.A. (1999) Population genetic structure and gene flow in a gleaning bat, *Plecotus auritus*. *Proceedings of the Royal Society of London B*, **266**, 975–980.

Cushman, S.A., McKelvey, K.S., Hayden, J. & Schwartz, M.K. (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist*, **168**, 486–499.

Do, C., Waples, R.S., Peel, D., Macbeth, G.M., Tillett, B.J. & Ovenden, J.R. (2013) NeEstimatorv2: re-implementation of software for the estimation of contemporary effective population size (*Ne*) from genetic data. *Molecular Ecology Resources*, **14**, 209–214.

Dool, S.E., Puechmaille, S.J., Dietz, C., Juste, J., Ibáñez, C., Hulva, P., Roué, S.G., Petit, E.J., Jones, G., Russo, D., Toffoli, R., Viglino, A., Martinoli, A., Rossiter, S.J. & Teeling, E.C. (2013) Phylogeography and postglacial recolonization of Europe by *Rhinolophus hipposideros*: evidence from multiple genetic markers. *Molecular Ecology*, **22**, 4055–4070.

Entwistle, A.C., Racey, P.A. & Speakman, J.R. (2000) Social and population structure of a gleaning bat, *Plecotus auritus*. *Journal of Zoology*, **252**, 11–17.

Etherington, T.R. (2011) Python based GIS tools for landscape genetics: visualising genetic relatedness and measuring landscape connectivity. *Methods in Ecology and Evolution*, **2**, 52–55.

Faubet, P., Waples, R.S. & Gaggiotti, O.E. (2007) Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Molecular Ecology*, **16**, 1149–1166.

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2010) *Introduction to conservation genetics*, 2nd edn. Cambridge University Press, Cambridge, UK.

Fuller, R.M. (1987) The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–84. *Biological Conservation*, **40**, 281–300.

García Mudarra, J.L., Ibáñez, C. & Juste, J. (2009) The straits of Gibraltar: barrier or bridge to Ibero-Moroccan bat diversity? *Biological Journal of the Linnean Society*, **96**, 434–450.

Grindal, S.D. & Brigham, R.M. (1999) Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience*, **6**, 25–34.

Guillot, G., Mortier, F. & Estoup, A. (2005) Geneland: a computer package for landscape genetics. *Molecular Ecology Notes*, **5**, 712–715.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Hardy, O.J. & Vekemans, X. (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes*, **2**, 618–620.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) *A review of british mammals: population estimates and conservation status of British mammals other than cetaceans*. JNCC, Peterborough, UK.

Juste, J., Ibáñez, C., Muñoz, J., Trujillo, D., Benda, P., Karatas, A. & Ruedi, M. (2004) Mitochondrial phylogeography of the long–eared bats (*Plecotus*) in the Mediterranean Palaearctic and Atlantic Islands. *Molecular Phylogenetics and Evolution*, **31**, 1114–1126.

Keller, D., Holderegger, R. & van Strien, M.J. (2013) Spatial scale affects landscape genetic analysis of a wetland grasshopper. *Molecular Ecology*, **22**, 2467–2482.

Koen, E.L., Bowman, J. & Walpole, A.A. (2012) The effect of cost surface parameterization on landscape resistance estimates. *Molecular Ecology Resources*, **12**, 686–696.

Legendre, P. (1993) Autocorrelation: trouble or paradigm. *Ecology*, **74**, 1659–1673.

Legendre, P. & Trousselier, M. (1988) Heterotrophic bacteria: modeling in the presence of spatial autocorrelation. *Limnology and Oceanography*, **33**, 1055–1067.

Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution*, **18**, 189–197.

McRae, B.H. (2006) Isolation by resistance. *Evolution*, **60**, 1551–1561.

McRae, B.H. & Beiber, P. (2007) Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences USA*, **104**, 19885–19890.

McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008) Using circuit theory to model connectivity in ecology, evolution and conservation. *Ecology*, **89**, 2712–2724.

Mickleburgh, S.P., Hutson, A.M. & Racey, P.A. (2002) A review of the global conservation status of bats. *Oryx*, **36**, 18–34.

Miller, M.P. (2005) Alleles In Space (AIS): computer software for the joint analysis of interindividual spatial and genetic information. *Journal of Heredity*, **96**, 722–774.

Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B*, **316**, 335–427.

Olival, K.J. (2012) Evolutionary and ecological correlates of population genetic structure in bats. *Evolutionary history of bats: fossils, molecules and morphology*. (ed. by G.F. Gunnell and N.B. Simmons), pp. 267–316. Cambridge University Press, Cambridge, UK.

Ortego, J., Aguirre, M.P. & Cordero, P.J. (2012) Landscape genetics of a specialized grasshopper inhabiting highly fragmented habitats: a role for spatial scale. *Diversity and Distributions*, **18**, 481–492.

Parsons, K.N., Jones, G., Davidson-Watts, I. & Greenaway, F. (2003) Swarming of bats at underground sites in Britain – implications for conservation. *Biological Conservation*, **111**, 63–70.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Petit, E. & Mayer, F. (1999) Male dispersal in the noctule bat (*Nyctalus noctula*) where are the limits? *Proceedings of the Royal Society of London B*, **266**, 1717–1722.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Puechmaille, S.J., Ar Gouilh, M., Piyapan, P., Yokubol, M., Mie, K.M., Bates, P.J., Satasook, C., New, T., Bu, S.S.H., Mackie, I.J., Petit, E.J. & Teeling, E.C. (2011) The evolution of sensory divergence in the context of limited gene flow in the bumblebee bat. *Nature Communications*, **2**, 537.

Rambaut, A. & Drummond, A. (2009) *Tracer, a program for analyzing results from Bayesian MCMC programs such as BEAST & MrBayes, version 1.5*. Available at http://tree.bio.ed.ac.uk/software/tracer/ (accessed 11 November 2013).

Razgour, O., Hanmer, J. & Jones, G. (2011) Using multi–scale modelling to predict habitat suitability for species of conservation concern: the grey long–eared bat as a case study. *Biological Conservation*, **144**, 2922–2930.

Razgour, O., Juste, J., Ibáñez, C., Kiefer, A., Rebelo, H., Puechmaille, S.J., Arlettaz, R., Burke, T., Dawson, D.A., Beaumont, M. & Jones, G. (2013) The shaping of genetic variation in edge-of-range populations under past and future climate change. *Ecology Letters*, **16**, 1258–1266.

Rebelo, H., Froufe, E., Brito, J.C., Russo, D., Cistrone, L., Ferrand, N. & Jones, G. (2012) Postglacial colonization of Europe by the barbastelle bat: agreement between molecular data and past predictive modelling. *Molecular Ecology*, **21**, 2761–2774.

Rossiter, S.J., Jones, G., Ransome, R.D. & Barratt, E.M. (2001) Outbreeding increases offspring survival in wild greater horseshoe bats (*Rhinolophus ferrumequinum*). *Proceedings of the Royal Society of London B*, **268**, 1055–1061.

Rossiter, S.J., Zubaid, A., Mohd-Adnan, A., Struebig, M.J., Kunz, T.H., Gopal, S., Petit, E.J. & Kingston, T. (2012) Social organization and genetic structure: insights from co-distributed bat populations. *Molecular Ecology*, **21**, 647–661.

Rousset, F. (1997) Genetic differentiation and estimation of gene flow from F statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

Row, J.R., Blouin-Demers, G. & Lougheed, S.C. (2010) Habitat distribution influences dispersal and fine–scale genetic population structure of eastern foxsnakes (*Mintonius gloydi*) across a fragmented landscape. *Molecular Ecology*, **19**, 5157–5171.

Scoble, J. & Lowe, A.J. (2010) A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning. *Diversity and Distributions*, **16**, 343–353.

Sork, V.L. & Waits, L. (2010) Contributions of landscape genetics – approaches, insights, and future potential. *Molecular Ecology*, **19**, 3489–3495.

Spear, S.F., Balkenhol, N., Fortin, M.-J., McRae, B.H. & Scribner, K. (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology*, **19**, 3576–3591.

Storfer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L. & Waits, L.P. (2007) Putting the 'landscape' in landscape genetics. *Heredity*, **98**, 128–142.

Swift, S.M. (1998) *Long–eared bats*. Poyser Ltd., London, UK.

Thomas, C.D. (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London B*, **267**, 139–145.

Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.

Van Dyck, H. & Baguette, M. (2005) Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*, **6**, 535–545.

Wang, Y.H., Yang, K.C., Bridgman, C.L. & Lin, L.K. (2008) Habitat suitability modelling to correlate gene flow with landscape connectivity. *Landscape Ecology*, **23**, 989–1000.

Weir, B.S. & Cockerham, C.C. (1984) Estimating F–statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.

Wilson, G.A. & Rannala, B. (2003) Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, **163**, 1177–1191.

Zeller, K.A., McGarigal, K. & Whiteley, A.R. (2012) Estimating landscape resistance to movement: a review. *Landscape Ecology*, **27**, 777–797.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary methods

Figure S1 The location of samples included in the analysis of gene flow rates across the three geographical barriers.

Figure S2 Geneland maps of probability of assignment to the nine genetic clusters.

Figure S3 Variables included in the fine-scale SDM (UK) and their relative contribution to the model.

Figure S4 Variables included in the broad-scale SDM (Europe) and their relative contribution to the model.

Figure S5 The location of genetic barriers identified in the Monmonier's algorithm analysis.

Table S1 The geographical location of the 259 *Plecotus austriacus* genetic samples included in the study.

Table S2 Population genetic analysis of *Plecotus austriacus* colonies.

Table S3 Genetic differentiations between pairs of *Plecotus austriacus* colonies.

Table S4 Genetic differentiations between pairs of *Plecotus austriacus* population clusters.

Table S5 Contemporary gene flow rates across geographical barriers.

Table S6 Mantel test results for the broad, European scale colony analysis.

Table S7 Mantel test results for the broad, European scale genetic cluster analysis.

Table S8 Mantel test results for fine, England-Channel Isles scale colony analysis.

DATA ACCESSIBILITY

Microsatellite loci have been submitted to EMBL (Accession Numbers: HE983997–HE984016). Microsatellite data and sample location records are deposited in DRYAD.

BIOSKETCH

Orly Razgour is currently a research fellow at the University of Stirling. Orly carries out multidisciplinary research, combining genetic and genomic tools with ecological modelling and applied conservation approaches to study the ecological and evolutionary consequences of climate change and anthropogenic habitat modification. This paper is part of her PhD research at the University of Bristol.

Author contributions: O.R. and G.J. conceived the ideas and led the writing; O.R., J.J., C.I., H.R., S.J.P. and A.K. collected/provided the genetic samples; O.R. performed the molecular laboratory work and analysis; T.B. provided the laboratory space. D.A.D., H.R. and S.J.P. advised on analysis. All authors contributed to revisions.

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