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RESEARCH ARTICLE

Applying genomic approaches to identify historic population declines in European forest bats

Orly Razgour[1] | **Cecilia Montauban**[2] | **Francesca Festa**[1,3,4] | **Daniel Whitby**[5] | **Javier Juste**[6,7] | **Carlos Ibáñez**[6] | **Hugo Rebelo**[8,9] | **Sandra Afonso**[8] | **Michael Bekaert**[10] | **Gareth Jones**[11] | **Carol Williams**[12] | **Katherine Boughey**[12]

[1]University of Exeter, Exeter, UK; [2]Imperial College London, London, UK; [3]Istituto Zooprofilattico Sperimentale delle Venezie, Legnaro, Italy; [4]Università di Roma 'La Sapienza', Roma, Italy; [5]Bat Conservation & Research Unit, Fittleworth, UK; [6]Estacion Biologica de Doñana, Seville, Spain; [7]CIBER, CIBERESP, Madrid, Spain; [8]BIOPOLIS, CIBIO, Porto, Portugal; [9]Universidade de Lisboa, Lisbon, Portugal; [10]University of Stirling, Stirling, UK; [11]University of Bristol, Bristol, UK and [12]The Bat Conservation Trust, London, UK

Correspondence
Orly Razgour
Email: o.razgour@exeter.ac.uk

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Abstract

1. Anthropogenically driven environmental changes over recent centuries have led to severe declines of wildlife populations. Better tools are needed to assess the magnitude and consequences of these declines. Anecdotal evidence suggests European bat populations have suffered substantial declines in the past centuries. However, there is little empirical evidence of these declines that can be used to put more recent population trends into historic context.
2. This study is a collaboration between academics and conservation practitioners to develop molecular approaches capable of providing evidence of historic population changes that can inform conservation status assessments and management. We generated a genomic dataset of 46,872 SNPs for the Western barbastelle, *Barbastella barbastellus*, a regionally Vulnerable bat species, including colonies from across the species' British and Iberian ranges. We used a combination of landscape genetics and model-based inference of demographic history to identify both evidence of population size changes and possible drivers of these changes.
3. Levels of genetic diversity increased and inbreeding decreased with increasing broadleaf woodland cover around the colony. Genetic connectivity was impeded by artificial lights and facilitated by rivers and broadleaf woodland cover.
4. The demographic history analysis showed that both the northern and southern British barbastelle populations have declined by 99% over the past 330–548 years. These declines may be linked to the loss of large oak trees and native woodlands due to shipbuilding during the early colonial period.
5. *Synthesis and applications*. Genomic approaches can provide a better understanding of the conservation status of threatened species, within historic and contemporary contexts, and inform their conservation management. Our findings of will

directly influence the definition of the Favourable Conservation Status of the barbastelle, in turn influencing considerations of the conservation of the species in development plans. Knowledge gained will also help set species recovery targets. Policymakers are interested in using our approach for other species. This study shows how we can bridge the implementation gap between genomic research and direct conservation applications. There is an urgent need to carry out such collaborative studies for other priority species to enable informed species recovery interventions via policy mechanisms and project delivery.

KEYWORDS
biodiversity loss, Chiroptera, conservation genomics, demographic history, land-use change, landscape genetics

1 | INTRODUCTION

Anthropogenically driven environmental changes over the past two centuries have resulted in a period of mass global species extinction (IPCC, 2022). Wildlife population sizes are estimated to have declined on average by 69% since the 1970s (WWF, 2022). The ranges of nearly a third of terrestrial vertebrate species across the globe have decreased in the past century, indicating the disappearance of populations (Ceballos et al., 2017).

Assessment of vertebrate population declines is commonly based on either direct measure of changes in population sizes (WWF, 2022) or indirect indicators, such as proportion of range loss over time (Ceballos et al., 2017). While both approaches offer a good measure of change, they require baseline data, which are not available for all taxa, and in particular all populations. Changes in population size over time (the demographic history of a species) can instead be reconstructed using genomic data because information on ancestral genomes and the evolutionary forces that shaped them is found within an individual's genome (Beichman et al., 2018). Time series genomic data can improve estimations of genetic changes in populations over time, but these analyses can also be performed with contemporary samples (Habel et al., 2014) when combined with modelling approaches to infer effective population sizes across time points (Hoban et al., 2022). The advent of high-throughput sequencing technologies over the past 20 years means that genome sequence data are now widely available for nonmodel organisms, including species of conservation concern, and therefore can be used to inform their conservation management (Hohenlohe et al., 2021).

Anecdotal evidence based on range contractions suggests European bat populations have suffered substantial declines in the past few centuries following persecution and extensive land-use changes (Racey & Stebbings, 1972). However, there is little empirical evidence of these declines that can be used to put more recent population changes identified through monitoring efforts in the past 30 years (e.g. Barlow et al., 2015; van der Meij et al., 2015) into historic context and set appropriate targets for species recovery. This study is a collaboration between academics and conservation practitioners aiming to address the lack of empirical evidence of historical declines, which has been identified by conservation practitioners as a critical evidence need that impedes their work. Without historical context, it is difficult for practitioners and decision-makers to accurately assess the importance of recently measured population trends, particularly for species thought to be recovering from historical declines.

We focus on the Western barbastelle, *Barbastella barbastellus*, a globally Near Threatened bat species, distributed across Europe, The Canaries, the Caucuses and Morocco (Piraccini, 2016). This bat is classified as Vulnerable in Europe and is considered as a national conservation priority across most European countries (Hutson et al., 2007). The barbastelle has shown a slight increase in population size in hibernation sites across Europe in the past 20 years (van der Meij et al., 2015). However, globally, their population trend is decreasing, with several reports of local declines (Piraccini, 2016). The barbastelle is likely to be sensitive to anthropogenic land-use change due to its strong association with mature native woodlands both for roosting and foraging (Russo et al., 2004; Zeale et al., 2012). Because these bats roost in trees and tend to switch roosts every few days (Russo et al., 2020), surveying them is particularly challenging and their actual population sizes are unknown both locally and nationally, even in Britain (Mathews et al., 2018), where there is a national bat monitoring programme (Barlow et al., 2015).

This study used molecular tools to provide evidence of historic population changes, an estimation of the magnitude of these changes and an evaluation of possible drivers of these changes. As a collaborative study, the findings of this research will directly inform conservation action and key policy and strategy approaches and the national documentation that underpins these. Statutory bodies in Britain are currently developing definitions for the ‘Favourable Conservation Status’ of threatened species, which identify the conditions they need to thrive (Hanna, 2021). In England, this assessment has so far been limited to three bat species due to lack of knowledge on the population sizes of British bats relative to their historic sizes (Mathews et al., 2018) and on what healthy viable populations look like. A robust methodology to inform on the scale of historic decline and the drivers of changes is of paramount importance and has been a missing key element for a considerable time. We apply our approach to the barbastelle, focussing on the British population as a case study, to (1) inform the conservation status of the species, (2) identify landscape and environmental drivers of genetic diversity and connectivity, (3) identify long-term population trends and (4) show how genomic data can inform the development of conservation management recommendations. The approach developed in this study can be widely applied to other taxa and ecosystems.

2 | MATERIALS AND METHODS

2.1 | Field sampling

We sampled barbastelle bats (Figure 1b) during the summers of 2016–2019 in 15 forests across Britain and the Iberian Peninsula, representing parts of the western edge of the species' range. The study focusses on the British population because it is thought to have undergone a population decline in the past few centuries and its conservation status is unknown (Mathews et al., 2018). To provide a wider context to the results of the British population, we included four colonies from Spain and Portugal (Iberia), a region that represented one of the glacial refugia of the species, and therefore supported populations over extended periods of time (Rebelo et al., 2012). All forests sampled in Britain were old-growth deciduous woodlands, while forests in Spain and Portugal were a combination of deciduous and conifer forests. Bats were caught using mist nets and harp traps with the help of local expert groups. We collected wing biopsy punches from each bat for genomic analysis and stored the samples in RNAlater and −80°C freezers. We included 95 individual bats in the study (76% females), 57 from Britain (10 sites, 81% females) and 38 from Spain and Portugal (five sites, 66% females; Figure 1a; Table 1). Sites were grouped together into colonies, defined here as bats captured in the same woodland or adjacent woodlands that are likely part of the same breeding population. For population-level analyses (genetic diversity, inbreeding, genetic differentiation and landscape genetics), we only included individuals from colonies with five or more individuals. We grouped together two sites in Spain with low sample sizes that are within the foraging range of this bat (Zeale et al., 2012) (Table 1), to satisfy minimum sample sizes required to estimate within-population genetic diversity (Nazareno et al., 2017).

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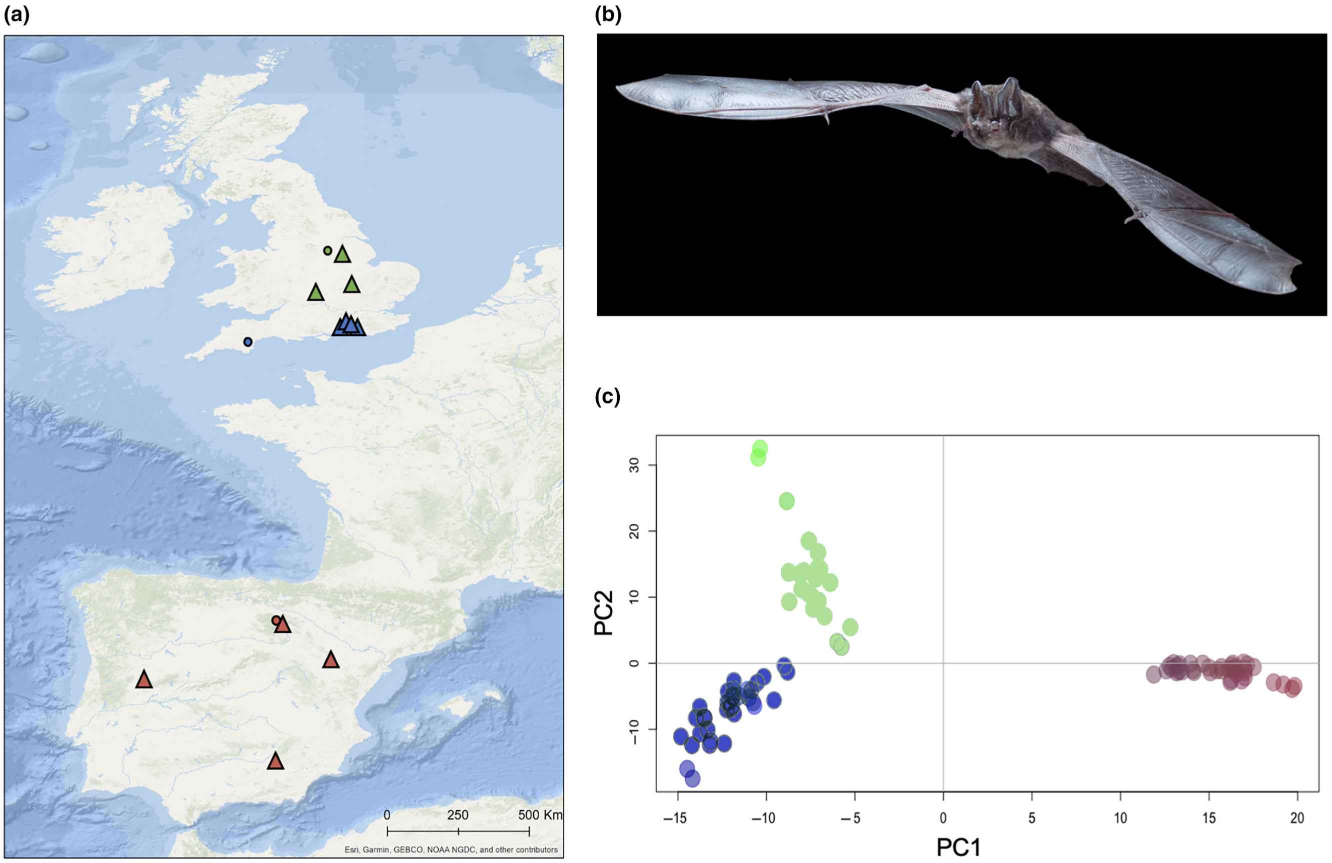

FIGURE 1 (a) Sampling locations of barbastelle colonies marked with triangles and individual locations with circles and colour-coded according to their population cluster assignment based on the PCA. (b) Photograph of a barbastelle in flight (credit: Antton Alberdi). (c) Results of the PCA based on genetic distances between individual barbastelle bats (PCA Axis 1: 5%; Axis 2: 2.4%). Pink—bats from Iberia (Spain and Portugal), blue—Britain south and green—Britain north.

TABLE 1 Location, attributed colony, sample sizes (*N*) and sampling years (Year) for the barbastelle bat sampling sites included in the study.

Site	County	Country	Colony	Latitude	Longitude	*N*	Year
Parham	Sussex	Britain	Par	50.91	−0.49	11	2018
Ebernoe	Sussex	Britain	Eb	51.04	−0.61	11	2019
Drove	Sussex	Britain	NA	50.93	−0.76	1	2016
Goodwood	Sussex	Britain	Good	50.87	−0.75	7	2016
Slindon	Sussex	Britain	Slin	50.86	−0.65	5	2016
Dartmoor	Devon	Britain	NA	50.61	−3.73	1	2016
Whichford	Warwickshire	Britain	War	52.01	−1.57	6	2016
Norton	Nottinghamshire	Britain	Nott	53.13	−0.69	6	2016
Creswell	Nottinghamshire	Britain	Nott	53.26	−1.19	1	2016
Swineshead	Bedfordshire	Britain	Bed	52.29	−0.44	8	2016
Cazorla	Jaén	Spain	Caz	37.95	−2.88	10	2016, 2018
Cameros	La Rioja	Spain	Rio	42.18	−2.74	3	2016, 2018
Arguijo	Soria	Spain	Rio	41.99	−2.52	4	2018
Olalla	Teruel	Spain	Ter	40.98	−1.14	11	2015–2016
Sabugal	Sabugal	Portugal	Port	40.44	−7.02	10	2018

Note: Some sites were grouped together into colonies for the population-level analysis. These sites have the same colony code under the Colony column (NA represents samples excluded from the population-level analysis).

Portuguese Environment Agency (452 I 2016/CAPT), and ethics committee approval of the University of Southampton (41912).

2.2 | Generating the genomic datasets

We used double digest restriction-site-associated DNA sequencing, ddRADseq (Peterson et al., 2012), to generate a genomic dataset containing thousands of anonymous single nucleotide polymorphisms (SNPs) from across the species' genomes. From the raw sequencing dataset, we generated a high-quality neutral SNP dataset with <5% missing data, including 46,872 SNPs and 95 individual bats. We generated a smaller genomic dataset for the demographic history analysis, including 85 bats and 25,844 SNPs, a sufficient number of SNPs to accurately detect population trends using coalescent-based approaches (Nunziata & Weisrock, 2018) (see Appendix S1 for laboratory and bioinformatics procedures; Razgour, 2023, for SNP datasets).

2.3 | Characterising genetic composition

We calculated genetic diversity in Plink v1.9 (Purcell et al., 2007) based on coefficient estimation of observed versus expected individual-level heterozygosity (het function, which is calculated as follows: 1 − (observed homozygous − expected homozygous)/(total observations − expected homozygous)) and individual levels of inbreeding based on estimates of nonrandom mating resulting in excess of similar genotypes (ibc function, Fhat1, which is the variance-standardised relationship minus 1). Heterozygosity and inbreeding are commonly used measures of genetic diversity between and within individuals, with low level of genetic diversity and high levels of inbreeding being associated with small population sizes (Hoban et al., 2022). We averaged individual values to generate colony means.

We determined population genetic structure using a PCA of Euclidian genetic distances based on allele frequencies, generated with the R package Adegenet (Jombart, 2008). We then ran a discriminant analysis of the principal components (DAPC) to identify the optimal discriminant axes that maximise the between-group variation while minimising the within-group variation. In addition, we used admixture analysis to generate ancestry coefficient plots with the snmf function in the R package LEA (Frichot & François, 2015). We identified the number of population clusters existing in our dataset based on cross-entropy values and plot visualisation. We tested a range of 1–10 population clusters and ran five replicates for each.

We calculated the extent of genetic differentiation between colony pairs using the F_{ST} and Jost's Dest measures in the R package DiveRsity (Keenan et al., 2013). We tested whether differentiation between pairs of colonies is significantly different from zero based on 95% confidence intervals, using 100 bootstraps. As values of genetic differentiation based on these measures were highly correlated ($R^2 = 0.822$, $p = 0.0001$; Table S3), we only included the results of the F_{ST} analysis.

2.4 | Identifying landscape drivers of genetic diversity

We ran linear models and Spearman correlations in R (CRAN) to relate levels of genetic diversity and inbreeding in the bat colonies to landscape variables likely to be important for the species, including per cent broadleaf forest, arable and urban land covers, differences in their per cent cover between 1990 and 2019, habitat diversity, artificial lighting, mean patch area and aggregation index (Appendix S1). This analysis was carried out for the full colony dataset as well as separately for the British colonies. We selected the best supported models based on Akaike's Information Criterion adjusted for small sample sizes (AICc) and adjusted R^2 values.

2.5 | Landscape genetics analysis

We used the landscape genetics approach (Manel et al., 2003) to identify barriers to genetic connectivity in the British populations based on resistance surfaces representing hypothesised relationships between landscape features and gene flow (Spear et al., 2010). We compared eight candidate models containing resistance surfaces generated from landscape variables thought to affect genetic connectivity in the barbastelle (Russo et al., 2020) (Tables S1 and S2; Appendix S1). Landscape resistance, calculated with Circuitscape v4.0.5 (McRae, 2006), was compared with levels of genetic differentiation (F_{ST}) between colonies. To account for the tendency of geographically close individuals to be more similar genetically than distant individuals due to dispersal limitations (isolation by distance), we divided log F_{ST} (adding 1 to avoid negative values) by log Euclidean distance between colonies. We used the maximum likelihood population effect approach (van Strien et al., 2012) and the R packages lme4 (Bates et al., 2015) and usdm (Naimi et al., 2014). To reduce collinearity, candidate models with more than one landscape variable only included variables with VIF (variable inflation factor) <4. The best supported models were identified based on AICc and Bayesian information criterion (BIC) evidence weights.

2.6 | Approximate Bayesian computation inference of demographic history

To identify evidence of historic changes in population size, we reconstructed the demographic history of the British barbastelle populations using the approximate Bayesian computation approach (Beaumont, 2010) implemented in DIYABC-RF (Collin et al., 2021) (Appendix S1). Generation length was estimated at 2 years because females commonly reach sexual maturity in their second year (age 1.25 years), but some may become fertile in their first autumn when only a few months old (Russo et al., 2020).

We first ran a preliminary analysis to determine whether the British population is increasing or decreasing. We divided the dataset into two populations, Britain and Iberia, removing Portugal because it was unlikely to be the source of colonisation for the British population. We compared three demographic history scenarios (Figure S1): a null model of no change in the British population size since splitting from Iberia (S1.1); a British population increase since splitting from Iberia (S1.2); and a recent decline in the British population (S1.3). The results of this preliminary analysis were used to inform the development of scenarios for the second analysis.

In the second analysis, we divided the dataset into three populations: Britain South, Britain North and Iberia (excluding Portugal) based on the results of the population structure analysis (see Results section). We compared four demographic history scenarios (Figure S2): a null model of no change in population size since the British population split into north and south populations (S2.1); a recent population decline in both south and north British populations (S2.2); a recent population decline in only the south British population with no change in north (S2.3); and a recent population decline in the north British population with no change in the south (S2.4).

The following priors were used to inform the models: Iberian and British population split dates ranged from pre- to post-Last Glacial Maximum (1000–1,000,000 generations ago), split of the British population was set at 100–10,000 to reflect the postglacial colonisation of Britain, and recent decline dates were set at 10–1000 generations ago. The range of split time between the Iberian and British populations covers more ancient split times to reflect the findings of Rebelo et al. (2012) that Iberia did not contribute to postglacial colonisation of Britain.

3 | RESULTS

3.1 | Population structure

We identified three population clusters. The main population split was between British and Iberian samples (PCA Axis 1: 5%; DAPC Axis 1: 92.6%). Within Britain, there was a further split between north (Bedfordshire, Nottinghamshire and Warwickshire) and south (Sussex and Devon) population clusters (PCA Axis 2: 2.4%; DAPC Axis 2: 4.7%). Within the northern cluster, the most differentiated samples were from the northernmost colony, Nottinghamshire (Figure 1c; Figure S3 for ancestry coefficient plots; Figure S4 for DAPC). Difference in the per cent variance accounted for by each axis based on PCA and DAPC results relate to differences in what they measure, variance in a genomic dataset of tens of thousands of SNPs versus per cent of the variance captured by each axis. Levels of genetic differentiation among colonies were moderate (mean $F_{ST}=0.048\pm0.02$), with highest values ($F_{ST}>0.07$) between British colonies and southern Spain and Portugal, and lowest levels ($F_{ST}<0.015$) between Iberian colonies (Table S3).

3.2 | Landscape drivers of genetic diversity

The British colonies, with the exception of Nottinghamshire, had the highest levels of genetic diversity (heterozygosity) and the lowest levels of inbreeding (Table S4). In the full dataset, genetic diversity was strongly negatively correlated with levels of inbreeding (Spearman correlations: $S=420$, $p<0.0001$, $r=-0.909$; weighted correlation: $wr=-0.912$; Figure S5), meaning that colonies that had high levels of genetic diversity had low levels of inbreeding. Therefore, only results for inbreeding are shown here. Levels of inbreeding were negatively correlated with per cent broadleaf woodland cover around the colony location ($S=410$, $p=0.0012$, $r=-0.864$, wr $=-0.864$), broadleaf woodland aggregation ($S=408$, $p=0.0016$, $r=-0.854$, wr $=-0.858$) and contemporary habitat diversity ($S=390$, $p=0.008$, $r=-0.773$, wr $=-0.772$; Figure 2a–c).

In the British dataset, levels of inbreeding decreased with increasing broadleaf woodland cover ($S=100$, $p=0.048$, $r=-0.786$, wr $=-0.745$) and tended to decrease with broadleaf woodland aggregation ($S=98$, $p=0.066$, $r=-0.750$, wr $=-0.744$). Genetic diversity showed a trend of increasing with per cent forest cover around the colony (LM: $F=6.34$, $p=0.053$, $r=0.748$; weighted Spearman correlation: wr $=0.394$; Figure 2d–f). Low levels of inbreeding and high levels of heterozygosity were found in areas with >20% broadleaf woodland cover (Figure 2; Tables S5 and S6).

3.3 | Landscape drivers of genetic connectivity

Genetic differentiation among British colonies was highly correlated with geographic distance (isolation by distance; $F=126.8$, $R^2=0.869$, $p=0.0008$). The landscape variables most strongly affecting genetic connectivity between British barbastelle colonies were the extent of artificial lights ($R^2=0.432$, AICcmin $=0.256$; connectivity decreased with increasing artificial lights), followed by the combination of rivers and broadleaf woodland cover ($R^2=0.411$, AICcmin $=0.217$; connectivity increased with river and broadleaf cover). The confidence intervals of both models did not overlap zero, supporting their effect on gene flow (Table 2). Movement density maps based on the impacts of artificial lights show limited landscape connectivity around London and other large cities (Figure 3).

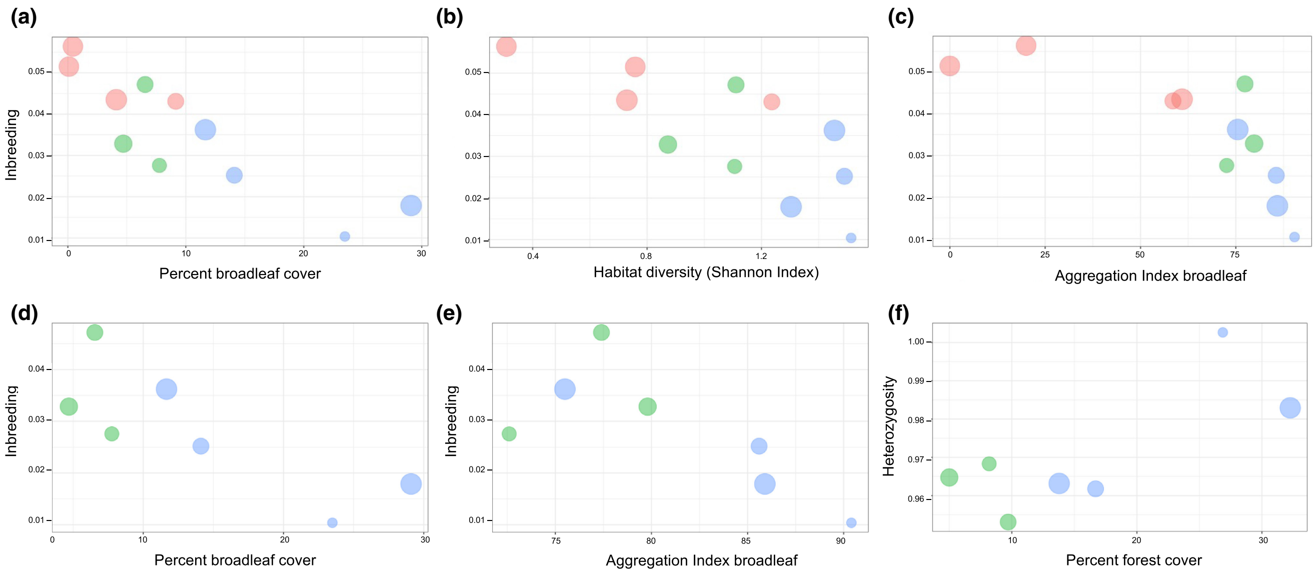

FIGURE 2 Environmental drivers of genetic diversity in the barbastelle. The relationship between the average levels of inbreeding in British and Iberian colonies and per cent broadleaf forest cover (a), current levels of habitat diversity (b) and broadleaf forest aggregation index (c) within the colony home range; and between average levels of inbreeding in British bat colonies and per cent broadleaf forest cover (d) and broadleaf forest aggregation index (e), and heterozygosity in British bat colonies and overall forest cover (f). Symbol size represents the number of individuals in each colony, and symbol colour represents the population cluster individuals from the colony belong to (pink—Iberia, blue—Britain south and green—Britain north).

TABLE 2 Results of the maximum likelihood population effect models comparing resistance costs based on different landscape variables to levels of genetic connectivity (F_{ST} corrected for geographic distance) between British barbastelle colonies.

Model	R^2	AICc weights	BIC weights	CI 2.5%	CI 97.5%
Broadleaf woods	0.363	0.169	0.165		
Min temp autumn	0.338	0.067	0.065		
River + woods	**0.411**	**0.217**	**0.212**	4.47E-05	0.0002
River	0.353	0.114	0.111		
Artificial lights	**0.432**	**0.256**	**0.250**	5.70E-05	0.0003
Land cover	0.339	0.078	0.076		
River + woods & Lights	0.453	0.068	0.083		
Woods & Tmin	0.386	0.031	0.038		

Note: Significance for bold values $p<0.01$.

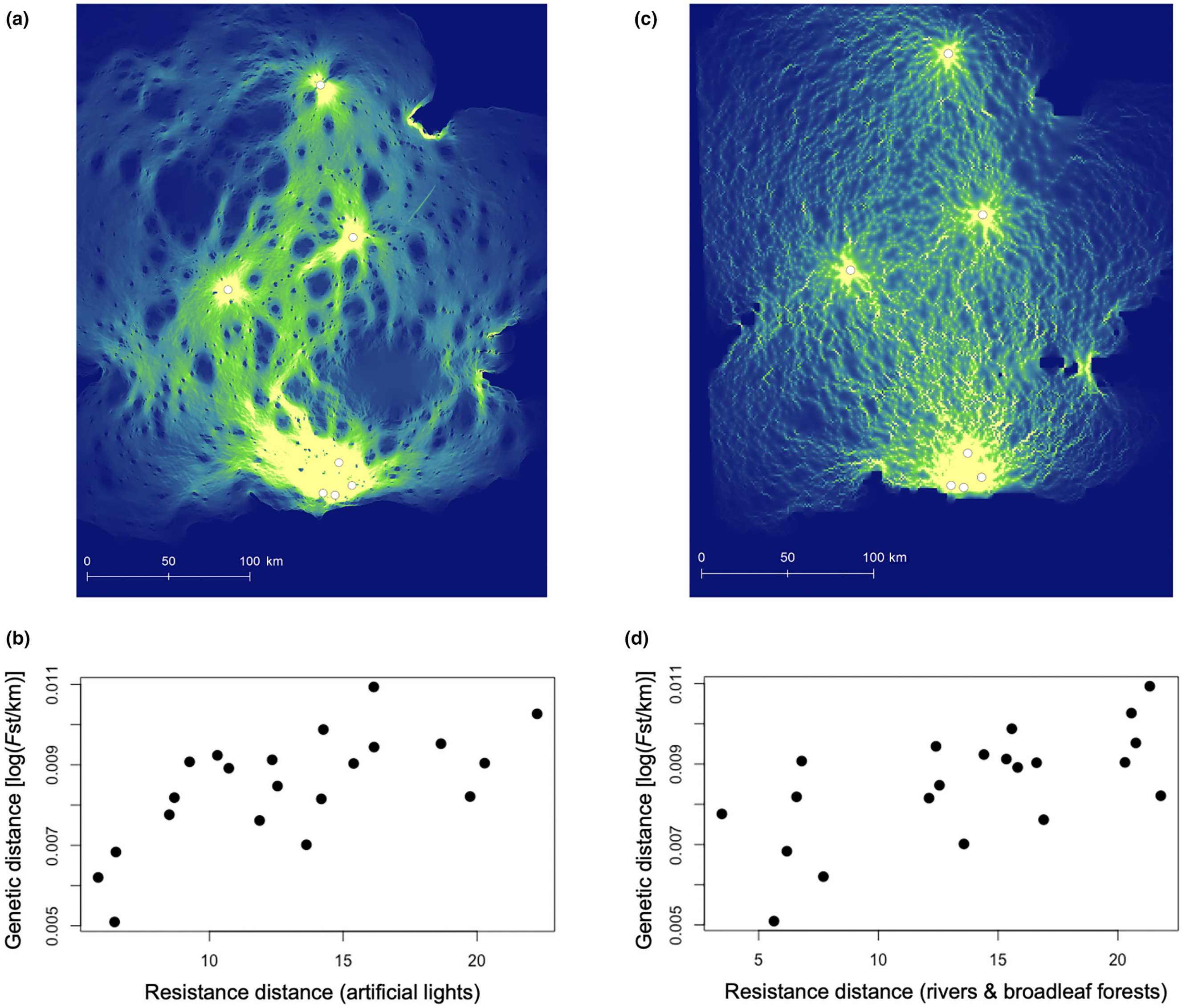

FIGURE 3 Results of the landscape genetics analysis. Predicted movement density potential between British barbastelle colonies based on the effect of landscape resistance due to (a) the intensity of artificial lights at night and (c) rivers and broadleaf woodland cover. Maps show electric currents crossing the matrix between pairs of colonies based on the resistance surfaces generated for landscape variables included in the analysis. Colours represent the probability of movement across the landscape, ranging from low probability in dark blue to high in yellow. White circles denote colony locations. (b) and (d) show the relationship between genetic connectivity (F_{ST} corrected for geographic distance) among British barbastelle colonies and the two landscape resistance distances.

3.4 | Model-based inference of demographic history

The best supported scenario in the preliminary analysis was a recent decline of the British population (scenario S1.3; posterior probability = 0.720; Table S7). The best supported scenario for the second analysis was a recent population decline in both British populations (scenario S2.2; posterior probability = 0.573). The observed data fell within the cloud of simulated datasets (Figure S6). The southern and northern Britain populations were estimated to have declined by 99% around a median of 548 years ago (90% credibility intervals: 126–1066 years ago) and 330 years ago (72–816), respectively. The British population was estimated to have split from the Iberian population a median of 57,682 years ago, while the two British populations split a median of 8432 years ago (Table 3; Figure 4).

4 | DISCUSSION

We show how genomic approaches can be applied to inform conservation status and identify evidence of population declines in response to anthropogenic land-use changes. Applying landscape genetics tools to the threatened barbastelle bat, we show that genetic composition and population connectivity are affected by broadleaf woodland cover and the extent of artificial lights at night. Applying genetically informed demographic history models, we

TABLE 3 Parameter estimation based on the best supported scenario (S2.2) in the second DIYABC-RF model-based inference analysis provided as median and 95% credible intervals.

Parameter	Explanation	Median	5% quantile	95% quantile
Na	Britain S current effective population size	7590	1502	9872
Nb	Britain N current effective population size	6711	1627	9873
N3	Iberian effective population size	357,295	98,634	892,148
N5	Britain S past effective population size	660,935	208,182	975,551
N6	Britain N past effective population size	532,039	61,783	967,252
t3	Split time Iberia & Britain	57,682	15,980	122,004
t4	Split time Britain S & N	8432	1602	19,438
t5	Decline time Britain S population	548	126	1066
t6	Decline time Britain N population	330	72	816

Note: Time is calculated as number of years ago.

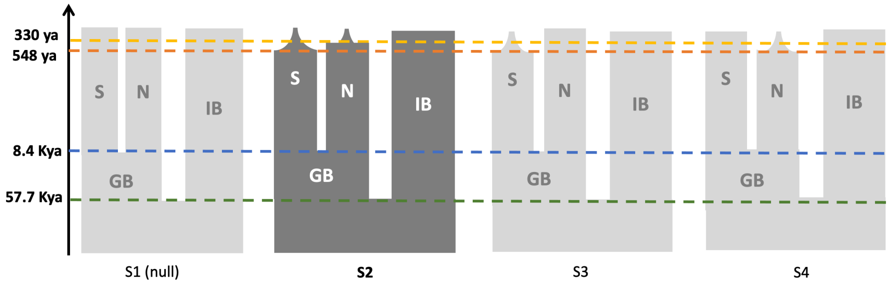

FIGURE 4 Graphical representation of the four demographic history scenarios compared in the second barbastelle demographic history analysis (Figure S2 for full scenario representation), with the best supported scenario (S2) in dark grey. The median parameter estimations for the best supported scenario are displayed along the *y*-axis (IB, Iberian; GB, British; S, British south; N, British north populations) (Table 3 for parameter estimation).

identify alarming levels of decline in British barbastelle populations, likely attributed to woodland loss and declining habitat quality in woodlands and the surrounding matrix. This decline corresponds to the broader pattern of severe vertebrate population declines across the globe, with 40% of studied European mammals showing ≥80% range contractions in the past century (Ceballos et al., 2017).

4.1 | Impacts of anthropogenic land-use change on genetic composition

The barbastelle can disperse over distances of up to 75 km and rarely up to 290 km (Hutterer et al., 2005). Barbastelles have relatively long wings and high wing loading values (Norberg & Rayner, 1987), which enables them to fly fast for relatively long distances. We found evidence for the presence of isolation by distance among barbastelle colonies in Britain, supporting the relatively sedentary nature of this bat (Russo et al., 2020) despite its longer distance dispersal ability.

Our landscape genetics analysis identified the combination of rivers and broadleaf woodland cover as a key landscape variable facilitating genetic connectivity between British barbastelle colonies. Barbastelles tend to commute to foraging grounds following natural tree lines along watercourses (Greenaway, 2004; Zeale et al., 2012), likely avoiding open areas due to predation risk (Russo et al., 2020). Longer distance dispersal may be limited by the strong association of barbastelles with old-growth mature broadleaf woodlands for roosting and foraging (Russo et al., 2004; Zeale et al., 2012), a habitat type that is particularly rare and fragmented in Britain (Reid et al., 2021).

Genetic connectivity between colonies is also affected by the extent of artificial lights at night. Artificial lights are a key threat to nocturnal biodiversity, like bats, that can have negative physiological and demographic consequences (Gaston et al., 2015; Voigt et al., 2021). Barbastelles tend to avoid artificially lit areas and their activity is reduced when foraging or drinking sites are artificially illuminated (Russo et al., 2017). Artificial lights can also affect insect densities (Owens & Lewis, 2018) and consequently prey availability for bats. Hence, the continuing expansion of artificial lights in Britain may fragment barbastelle populations, impede genetic connectivity and affect foraging success. Artificial lights can be a proxy for other aspects of human disturbance, such as the expansion of urban areas and roads, habitats avoided by the barbastelle (Zeale et al., 2012). Lower levels of urbanisation and light pollution across the Iberian Peninsula could explain the higher gene flow rates among Iberian colonies.

Broadleaf woodland cover and aggregation are key variables associated with patterns of genetic diversity and inbreeding in barbastelle colonies. Genetic diversity increases and levels of inbreeding decrease with increasing broadleaf woodland cover and aggregation around the colony, suggesting that a higher extent of broadleaf woodland cover and more connected woodlands within the colony home range supports larger population sizes. Summer maternity colonies are mainly found in tree cavities, often in standing dead trees. Barbastelles select relatively tall and wide deciduous trees, usually oak (*Quercus* spp.) or beech (*Fagus sylvatica*), for roosting (Russo et al., 2020). Maternity colonies on average switch roosts every 3.5 days and therefore require several large trees that can form an expansive roosting network (Russo et al., 2005). Hence, large mature broadleaf woodlands are needed to support a large enough population to avoid inbreeding and loss of genetic diversity. Many native woodlands have been lost or replaced by plantation forests across Europe, and the remaining woodlands are fragmented and degraded (Estreguil et al., 2012). This situation is even more acute in Britain, where the proportion of native and ancient woodlands is particularly low due to historic losses (Reid et al., 2021).

Genetic diversity also increases with increasing habitat diversity across the landscape. We would expect levels of inbreeding to be lower in colonies found in good-quality habitats that can support larger populations because inbreeding is associated with small populations. Barbastelles forage in a variety of habitats across the wider landscape, including woodlands, riparian habitats, freshwater wetlands and unimproved grasslands (Zeale et al., 2012). Hence, negative correlations between inbreeding and habitat diversity mean that colonies are likely to be larger in areas with a diversity of foraging habitats that can support high densities of moths, their main prey (Goerlitz et al., 2010).

4.2 | Broadleaf woodland loss as a driver of population decline

For the first time, using our genomic dataset and demographic history models, we were able to provide evidence that confirms suspected historic population declines in the barbastelle. Our models show that both the northern and southern British populations have declined by 99% in the past 330 and 548 years, respectively. Despite these severe population declines, contemporary levels of inbreeding are low in British colonies and heterozygosity is high relative to Iberian colonies, indicating that effective population size is still high enough to prevent substantial losses of genetic diversity (Frankham et al., 2014). Moreover, levels of heterozygosity in the British colonies are higher than in British colonies of the grey long-eared bat, *Plecotus austriacus*, which has experienced similarly high levels of population decline in the past century (Razgour et al., 2018).

The estimated median time of the start of the British barbastelle population declines is set at the mid-15th to late 17th century. This period in European history is referred to as the 'Age of Discovery' representing the first wave of European colonialism. Extensive shipbuilding to support colonial explorations and wars required vast quantities of wood (Davey, 2011), especially 'outsized' mature oak trees (Melby, 2012), the same trees favoured by barbastelles for roosting (Russo et al., 2020). Historic documents from that period raise concerns about wood shortage in Britain (Warde, 2006). An Act of Parliament from 1503 states that the woodlands in England had been 'utterly destroyed' due to increased demand for timber for shipbuilding, houses and iron smelting, linked to the development of overseas trade and expanding human population (Holmes, 1975). The 15th–early 17th century saw extensive oak woodland loss due to naval expansion (Childs, 2009), corresponding to the estimated decline time of the British south population. Losses continued throughout the 17th–18th centuries, corresponding to the estimated decline time of the British north population, with government policy trying to restrict felling oak to supplying timber to the Navy (Holmes, 1975). Across England, woodland cover decreased from an estimated 15% in 1086 to 8% in the 17th Century and down to 5.1% in 1924, before increasing to 10.2% by 2022 (Forest Research, 2022). Therefore, the severe decline of the British barbastelle populations may be attributed to the loss of maternity colony roosts following the felling of large oak trees for shipbuilding to support colonial explorations and the overall decline in woodland cover that continued until the late 20th Century. More recently, agricultural intensification and insect declines in open landscapes and inside forests (Seibold et al., 2019) likely impede the recovery of this and other bat species.

4.3 | Applying genomic approaches to assess historic population declines

Genomic data can improve the accuracy and precision of estimates of population size and demographic history and provide higher power than genetic markers, meaning that the analysis is less limited by sample size (Shafer et al., 2015). Although more work is needed to assess when approaches to estimate effective population size are reliable (Hoban et al., 2014), genetic estimates can accurately reflect declines in population size (Pierson et al., 2018), even when declines are not as severe as those identified in this study (Razgour et al., 2021). A comparison of museum specimens to contemporary samples can improve the estimation of historic population sizes and genetic changes in populations over time (Habel et al., 2014) for species with adequate collections and when sufficient funding is available.

Previous studies applied genomic approaches to identify more ancient wildlife population declines from the last glaciation period, for example in the Scandinavian wolverine population (Ekblom et al., 2018) and the giant panda, which also experienced a subsequent decline around 2800 years ago (Zhao et al., 2012). Our study shows that genomic approaches can identify recent historic population declines, occurring in the last few hundred years, and therefore can be relevant for informing current conservation management.

4.4 | Applying genomic approaches to inform policy and conservation management

Genomic approaches can inform our understanding of the historic context of current population estimates and timelines for changes, as well as help identify reasons for declines in population size, reduced genetic diversity and increased inbreeding. While research in the last 20 years (reviewed in Russo et al. (2020)) has revealed some key landscape, habitat and roosting requirements of the barbastelle, these all represent the species survival in an anthropogenically changed landscape. We need a longer-term understanding of how species inhabit the landscape and how they have been affected by landscape changes. As we show in this study, genomic data can offer this longer-term perspective. Genomic data can be combined with ecological data on demography, reproductive success and behaviour to provide a broader perspective on how populations are responding to environmental changes.

The findings of this study are currently being applied in conservation management of the barbastelle and used to inform policy to support British bats. This study helps place current and future estimates of British barbastelle population sizes, trends and indices into historic context. Understanding this along with the associated drivers of historic change is vital in producing Favourable Conservation Status definitions. The findings of this study are currently being used to inform the Favourable Conservation Status definition which awaits publication by Natural England. This work also directly informs other key national and local policies such as targets for species recovery and mapping importance in Local Nature Recovery strategy priorities and the focus of agri-environmental schemes. The impact of these actions is measured based on the Favourable Conservation Status definition. The lack of a robust historic context and associated drivers of change has compromised the evaluation of the conservation status of bats and other priority species. This gap in our knowledge has serious implications for not only practical actions and targets for species recovery but also for the appropriateness and applicability of national policy and related schemes and initiatives. This study shows that genomic approaches have an important role in overcoming omissions in current conservation policy and in applications used in species recovery programmes.

5 | CONCLUSIONS

Genomic approaches can be applied to inform conservation status and identify evidence of historic population declines in response to anthropogenic land-use change. For the first time, we provide evidence that confirms suspected historic population declines in the barbastelle bat. Our models show that both the northern and southern British populations have declined by 99% in the past few hundred years and this decline is likely related to the loss of mature broadleaf woodlands, possibly linked to shipbuilding and woodland loss during the early colonial period. These alarming results place current and future British barbastelle population sizes, trends and indices into context and are being used to inform recovery targets for this species.

Despite their promises, genomic approaches have not been widely applied in conservation management due to challenges associated with translation into conservation practices and insufficient engagement between academic researchers generating the genomic tools and conservation practitioners (Shafer et al., 2015). This study shows how we can bridge the implementation gap, as well as the disciplinary and thematic gaps, which limit the contribution of science to conservation (Habel et al., 2013). Through co-designing studies with conservation practitioners, we can address evidence needs identified by practitioners and co-develop evidence-based management targets and recommendations. Therefore, this study contributes to better integration of genomic data into national reporting on biodiversity conservation targets and monitoring (Hoban et al., 2022; O'Brien et al., 2022).

AUTHOR CONTRIBUTIONS

Orly Razgour, Katherine Boughey and Daniel Whitby conceived and designed the study. Orly Razgour, Daniel Whitby, Javier Juste, Carlos Ibáñez, Hugo Rebelo and Gareth Jones contributed to sample collection. Francesca Festa, Sandra Afonso, Orly Razgour and Michael Bekaert generated the genomic data. Orly Razgour and Cecilia Montauban analysed the data. Orly Razgour, Carol Williams and Katherine Boughey led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Orly Razgour is a trustee, and Carol Williams and Katherine Boughey are employees of the Bat Conservation Trust (BCT). While this paper details vital findings which will support the conservation work of BCT, there is no source of conflict of interest, financial or otherwise. Orly Razgour was an associate editor of the *Journal of Applied Ecology* at the time of submission, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Raw sequencing reads of all libraries are available from EBI/ENA via the project PRJEB61793: https://www.ebi.ac.uk/ena/browser/view/PRJEB61793 (Institute of Aquaculture, 2023). Study locations are presented in Table 1. SNP datasets in vcf format are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.wstqjq2qd (Razgour, 2023).

ORCID

Orly Razgour https://orcid.org/0000-0003-3186-0313
Carlos Ibáñez https://orcid.org/0000-0003-1181-7641

REFERENCES

Barlow, K. E., Briggs, P. A., Haysom, K. A., Hutson, A. M., Lechiara, N. L., Racey, P. A., Walsh, A. L., & Langton, S. D. (2015). Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation*, *182*, 14–26. https://doi.org/10.1016/j.biocon.2014.11.022

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beaumont, M. a. (2010). Approximate Bayesian computation in evolution and ecology. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 379–406. https://doi.org/10.1146/annurev-ecolsys-102209-144621

Beichman, A. C., Huerta-Sanchez, E., & Lohmueller, K. E. (2018). Using genomic data to infer historic population dynamics of nonmodel organisms. *Annual Review of Ecology and Systematics*, *49*, 433–456. https://doi.org/10.1146/annurev-ecolsys-110617

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(30), E6089–E6096. https://doi.org/10.1073/PNAS.1704949114/SUPPL_FILE/PNAS.1704949114.SAPP.PDF

Childs, D. (2009). *Tudor sea power: The foundation of greatness*. Pen and Sword Books.

Collin, F., Durif, G., Raynal, L., Lombaert, E., Gautier, M., Vitalis, R., Marin, J., & Estoup, A. (2021). Extending approximate Bayesian computation with supervised machine learning to infer demographic history from genetic polymorphisms using DIYABC Random Forest. *Molecular Ecology Resources*, *21*(8), 2598–2613. https://doi.org/10.1111/1755-0998.13413

Davey, J. (2011). Securing the sinews of sea power: British intervention in the Baltic 1780–1815. *The International History Review*, *33*(2), 161–184. https://doi.org/10.1080/07075332.2011.555384

Ekblom, R., Brechlin, B., Persson, J., Smeds, L., Johansson, M., Magnusson, J., Flagstad, Ø., & Ellegren, H. (2018). Genome sequencing and conservation genomics in the Scandinavian wolverine population. *Conservation Biology*, *32*(6), 1301–1312. https://doi.org/10.1111/COBI.13157

Estreguil, C., Caudullo, G., de Rigo, D., & San Miguel, J. (2012). *Forest landscape in Europe: Pattern, fragmentation and connectivity*. https://forest.jrc.ec.europa.eu/media/filer_public/8e/d2/8ed29884-6f0d-423b-9c8e-b3afebb8edc2/2012_eur25717.pdf

Forest Research. (2022). *Forestry statistics 2022: A compendium of statistics about woodland, forestry and primary wood processing in the United Kingdom*. Forestry Commission.

Frankham, R., Bradshaw, C. J. A., & Brook, B. W. (2014). Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation*, *170*, 56–63. https://doi.org/10.1016/j.biocon.2013.12.036

Frichot, E., & François, O. (2015). LEA: An R package for landscape and ecological association studies. *Methods in Ecology and Evolution*, *6*(8), 925–929. https://doi.org/10.1111/2041-210X.12382

Gaston, K. J., Visser, M. E., & Hölker, F. (2015). The biological impacts of artificial light at night: The research challenge. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *370*(1667), 20140133. https://doi.org/10.1098/rstb.2014.0133

Goerlitz, H. R., ter Hofstede, H. M., Zeale, M. R. K., Jones, G., & Holderied, M. W. (2010). An aerial-hawking bat uses stealth echolocation to counter moth hearing. *Current Biology*, *20*(17), 1568–1572. https://doi.org/10.1016/j.cub.2010.07.046

Greenaway, F. (2004). Advice for the management of flightlines and foraging habitats of the barbastelle bat *Barbastella barbastellus*. Research Reports EN Report no 657.

Habel, J. C., Gossner, M. M., Meyer, S. T., Eggermont, H., Lens, L., Dengler, J., & Weisser, W. W. (2013). Mind the gaps when using science to address conservation concerns. *Biodiversity and Conservation*, *22*(10), 2413–2427. https://doi.org/10.1007/s10531-013-0536-y

Habel, J. C., Husemann, M., Finger, A., Danley, P. D., & Zachos, F. E. (2014). The relevance of time series in molecular ecology and conservation biology. *Biological Reviews*, *89*(2), 484–492. https://doi.org/10.1111/brv.12068

Hanna, J. (2021). *Favourable conservation status definitions. Natural England technical information note, TIN180*. Natural England.

Hoban, S., Archer, F. I., Bertola, L. D., Bragg, J. G., Breed, M. F., Bruford, M. W., Coleman, M. A., Ekblom, R., Funk, W. C., Grueber, C. E., Hand, B. K., Jaffé, R., Jensen, E., Johnson, J. S., Kershaw, F., Liggins, L., MacDonald, A. J., Mergeay, J., Miller, J. M., … Hunter, M. E. (2022). Global genetic diversity status and trends: Towards a suite of essential biodiversity variables (EBVs) for genetic composition. *Biological Reviews*, *97*(4), 1511–1538.

Hoban, S., Arntzen, J. A., Bruford, M. W., Godoy, J. A., Rus Hoelzel, A., Segelbacher, G., Vilà, C., & Bertorelle, G. (2014). Comparative evaluation of potential indicators and temporal sampling protocols for monitoring genetic erosion. *Evolutionary Applications*, *7*(9), 984–998. https://doi.org/10.1111/eva.12197

Hohenlohe, P. A., Funk, W. C., & Rajora, O. P. (2021). Population genomics for wildlife conservation and management. *Molecular Ecology*, *30*, 62–82.

Holmes, G. D. (1975). History of forestry and forest management. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *271*(911), 69–80. https://doi.org/10.1098/rstb.1975.0035

Hutson, T., Spitzenberger, F., & Aulagnier, S. (2007). *Barbastella barbastellus* (Europe assessment). The IUCN Red List of Threatened Species 2007: e.T2553A9453283.

Hutterer, R., Ivanova, T., Meyer-Cords, C., & Rodrigues, L. (2005). *Bat migration in Europe: A review of banding data and literature*. Naturschutz und Biologische Vielfault Heft 28. Federal Agency for Nature Conservation.

Institute of Aquaculture. (2023). Data from: Applying genomic approaches to identify historic population declines in European forest bats. *EBI/ENA via the project PRJEB61793*: https://www.ebi.ac.uk/ena/browser/view/PRJEB61793

IPCC. (2022). *Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC.

Jombart, T. (2008). Adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*(11), 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Keenan, K., Mcginnity, P., Cross, T. F., Crozier, W. W., & Prodöhl, P. A. (2013). DiveRsity: An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, *4*(8), 782–788. https://doi.org/10.1111/2041-210X.12067

Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, *18*(4), 189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

Mathews, F., Kubasiewicz, L. M., Gurnell, J., Harrower, C. A., McDonald, R. A., & Shore, R. F. (2018). *A review of the population and conservation status of British mammals*. A report by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. www.gov.uk/natural-england

McRae, B. H. (2006). Isolation by resistance. *Evolution*, *60*(8), 1551. https://doi.org/10.1554/05-321.1

Melby, P. (2012). *Insatiable shipyards: The impact of the Royal Navy on the World's forests, 1200–1850*. Western Oregon University.

Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, *37*(2), 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Nazareno, A. G., Bemmels, J. B., Dick, C. W., & Lohmann, L. G. (2017). Minimum sample sizes for population genomics: An empirical study from an Amazonian plant species. *Molecular Ecology Resources*, *17*(6), 1136–1147. https://doi.org/10.1111/1755-0998.12654

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, B: Biological Sciences*, *316*(1179), 335–427. https://doi.org/10.1098/rstb.1987.0030

Nunziata, S. O., & Weisrock, D. W. (2018). Estimation of contemporary effective population size and population declines using RAD sequence data. *Heredity*, *120*(3), 196–207. https://doi.org/10.1038/s41437-017-0037-y

O'Brien, D., Laikre, L., Hoban, S., Bruford, M. W., Ekblom, R., Fischer, M. C., Hall, J., Hvilsom, C., Hollingsworth, P. M., Kershaw, F., Mittan, C. S., Mukassabi, T. A., Ogden, R., Segelbacher, G., Shaw, R. E., Vernesi, C., & MacDonald, A. J. (2022). Bringing together approaches to reporting on within species genetic diversity. *Journal of Applied Ecology*, *59*, 2227–2233. https://doi.org/10.1111/1365-2664.14225

Owens, A. C. S., & Lewis, S. M. (2018). The impact of artificial light at night on nocturnal insects: A review and synthesis. *Ecology and Evolution*, *8*(22), 11337–11358. https://doi.org/10.1002/ece3.4557

Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS ONE*, *7*(5), e37135. https://doi.org/10.1371/journal.pone.0037135

Pierson, J. C., Graves, T. A., Banks, S. C., Kendall, K. C., & Lindenmayer, D. B. (2018). Relationship between effective and demographic population size in continuously distributed populations. *Evolutionary Applications*, *11*(7), 1162–1175. https://doi.org/10.1111/EVA.12636

Piraccini, R. (2016). *Barbastella barbastellus*. The IUCN Red List of Threatened Species 2016: e.T2553A22029285. IUCN Red List. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T2553A22029285.en

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., Maller, J., Sklar, P., de Bakker, P. I. W., Daly, M. J., & Sham, P. C. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *The American Journal of Human Genetics*, *81*(3), 559–575. https://doi.org/10.1086/519795

Racey, P. A., & Stebbings, R. E. (1972). Bats in Britain—A status report. *Oryx*, *11*(5), 319–327. https://doi.org/10.1017/S0030605300010322

Razgour, O. (2023). Data from: Applying genomic approaches to identify historic population declines in European forest bats. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.wstqjq2qd

Razgour, O., Kasso, M., Santos, H., & Juste, J. (2021). Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. *Evolutionary Applications*, *14*(3), 794–806. https://doi.org/10.1111/eva.13161

Razgour, O., Taggart, J. B., Manel, S., Juste, J., Ibáñez, C., Rebelo, H., Alberdi, A., Jones, G., & Park, K. (2018). An integrated framework to identify wildlife populations under threat from climate change. *Molecular Ecology Resources*, *18*(1), 18–31. https://doi.org/10.1111/1755-0998.12694

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*(11), 2761–2774. https://doi.org/10.1111/J.1365-294X.2012.05566.X

Reid, C., Hornigold, K., McHenry, E., Nichols, C., Townsend, M., Lewthwaite, K., Elliot, M., Pullinger, R., Hotchkiss, A., Gilmartin, E., White, I., Chesshire, H., Whittle, L., Garforth, J. G., Reed, T., & Hugi, M. (2021). *State of the UK's woods and trees 2021*. Woodland Trust. https://www.woodlandtrust.org.uk/media/49731/state-of-the-uks-woods-and-trees-2021-the-woodland-trust.pdf

Russo, D., Cistrone, L., & Jones, G. (2005). Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats *Barbastella barbastellus*. *Ecography*, *28*(6), 769–776. https://doi.org/10.1111/j.2005.0906-7590.04343.x

Russo, D., Cistrone, L., Jones, G., & Mazzoleni, S. (2004). Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: Consequences for conservation. *Biological Conservation*, *117*(1), 73–81. https://doi.org/10.1016/S0006-3207(03)00266-0

Russo, D., Cistrone, L., Libralato, N., Korine, C., Jones, G., & Ancillotto, L. (2017). Adverse effects of artificial illumination on bat drinking activity. *Animal Conservation*, *20*(6), 492–501. https://doi.org/10.1111/acv.12340

Russo, D., Salinas-Ramos, V. B., & Ancillotto, L. (2020). Barbastelle Bat *Barbastella barbastellus* (Schreber, 1774). In K. Hackländer & F. E. Zachos (Eds.), *Handbook of the mammals of Europe* (pp. 1–21). Springer Nature.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674. https://doi.org/10.1038/s41586-019-1684-3

Shafer, A. B. A., Wolf, J. B. W., Alves, P. C., Bergström, L., Bruford, M. W., Brännström, I., Colling, G., Dalén, L., de Meester, L., Ekblom, R., Fawcett, K. D., Fior, S., Hajibabaei, M., Hill, J. A., Hoezel, A. R., Höglund, J., Jensen, E. L., Krause, J., Kristensen, T. N., … Zieliński, P. (2015). Genomics and the challenging translation into conservation practice. *Trends in Ecology & Evolution*, *30*(2), 78–87. https://doi.org/10.1016/j.tree.2014.11.009

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*(17), 3576–3591. https://doi.org/10.1111/j.1365-294X.2010.04657.x

van der Meij, T., van Strien, A. J., Haysom, K. A., Dekker, J., Russ, J., Biala, K., Bihari, Z., Jansen, E., Langton, S., Kurali, A., Limpens, H., Meschede, A., Petersons, G., Presetnik, P., Prüger, J., Reiter, G., Rodrigues, L., Schorcht, W., Uhrin, M., & Vintulis, V. (2015). Return of the bats? A prototype indicator of trends in European bat populations in underground hibernacula. *Mammalian Biology*, *80*(3), 170–177. https://doi.org/10.1016/J.MAMBIO.2014.09.004

van Strien, M. J., Keller, D., & Holderegger, R. (2012). A new analytical approach to landscape genetic modelling: Least-cost transect analysis and linear mixed models. *Molecular Ecology*, *21*(16), 4010–4023. https://doi.org/10.1111/j.1365-294X.2012.05687.x

Voigt, C. C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens, H. J. G. A., Mathews, F., Rydell, J., Spoelstra, K., & Zagmajster, M. (2021). The impact of light pollution on bats varies according to foraging guild and habitat context. *BioScience*, *71*(10), 1103–1109. https://doi.org/10.1093/biosci/biab087

Warde, P. (2006). Fear of wood shortage and the reality of the woodland in Europe, c.1450–1850. *History Workshop Journal*, *62*(1), 28–57. https://doi.org/10.1093/HWJ/DBL009

WWF. (2022). *Living planet report 2022—Building a Nature Positive Society*. WWF.

Zeale, M. R. K., Davidson-Watts, I., & Jones, G. (2012). Home range use and habitat selection by barbastelle bats (*Barbastella barbastellus*): Implications for conservation. *Journal of Mammalogy*, *93*(4), 1110–1118. https://doi.org/10.1644/11-MAMM-A-366.1

Zhao, S., Zheng, P., Dong, S., Zhan, X., Wu, Q., Guo, X., Hu, Y., He, W., Zhang, S., Fan, W., Zhu, L., Li, D., Zhang, X., Chen, Q., Zhang, H., Zhang, Z., Jin, X., Zhang, J., Yang, H., … Wei, F. (2012). Whole-genome sequencing of giant pandas provides insights into demographic history and local adaptation. *Nature Genetics*, *45*(1), 67–71. https://doi.org/10.1038/ng.2494

SUPPORTING INFORMATION

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

Appendix S1: Supporting methods.

Appendix S2: Supporting results.

Appendix S3: Supporting figures.

Appendix S4: Supporting tables.

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