Applying remotely sensed habitat descriptors to assist reintroduction programs: A case study in the hazel dormouse

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Abstract

For reintroduction programs to succeed, it is vital to identify suitable release sites. This is especially true for low dispersing habitat specialists, which are at particular risk from habitat fragmentation. The habitat specialist Muscardinus avellanarius (hazel dormouse) is part of a large-scale reintroduction program in the UK. The program began in 1993 and has so far had varying levels of long-term success across 24 sites. Although the causes of population persistence at reintroduction sites are not well understood, continued habitat suitability is hypothesized to play an important role. Here, we establish broad-scale habitat descriptors associated with the current distribution of natural hazel dormouse populations in England, using ecological niche factor analysis and remotely sensed, open-source maps. We also apply generalized linear mixed effects models to long-term monitoring data for reintroduced hazel dormouse populations, revealing that broad-scale habitat factors strongly influence the number of animals present in nest boxes. To aid conservation practitioners in future site selection, we illustrate the practical application of habitat suitability mapping to help prioritize the most appropriate woodlands for future hazel dormouse reintroductions, using the county of Cheshire as an example. Although demonstrated here for the hazel dormouse, this approach to reintroduction site selection could be beneficial to a broad range of species.

KEYWORDS
CENFA, GIS, habitat suitability analysis, hazel dormouse, Muscardinus avellanarius, population analysis, reintroduction, species distribution models

1 | INTRODUCTION

Despite global conservation efforts and targets to reduce the rate of biodiversity loss, pressures on biodiversity are increasing and the rate of loss has not slowed (Butchart
et al., 2010). Habitat fragmentation and reduced connectivity is accelerating the rate of biodiversity loss at local and regional scales (Horváth, Ptacnik, Vad, & Chase, 2019). Habitat specialists are at particular risk from increased fragmentation and declines in habitat quality, experiencing greater habitat losses and reduced adaptability than habitat generalists (Colles, Liow, & Prinzing, 2009; Díaz et al., 2019; Matthews, Cottée-Jones, & Whittaker, 2014). In situ conservation measures, such as habitat management and protected areas, can help to protect remaining populations (Soulé & Orians, 2001). However, the intentional movement of species, termed translocation, is increasingly carried out to restore or augment populations (IUCN, 2013; Seddon, Armstrong, & Maloney, 2007).

Defined as the intentional release of an organism inside the indigenous range from which it has disappeared (IUCN, 2013), reintroductions should ideally lead to self-sustaining populations (Griffith, Scott, Carpenter, & Reed, 1989). Reintroduction sites need high quality habitat that is preferably located within the historical range of the species (Bubac, Johnson, Fox, & Cullingham, 2019; Griffith et al., 1989; IUCN, 2013; Wolf, Garland, & Griffith, 1998; Wolf, Griffith, Reed, & Temple, 1996), with the original cause of decline removed (Bubac et al., 2019; Fischer & Lindenmayer, 2000). However, many reintroductions do not meet these conditions, and reintroduction successes could be as low as 23% (Fischer & Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996). To improve the chances of success, potential reintroduction programs should be thoroughly assessed at the outset, and target sites should meet species-specific habitat requirements and implement any necessary ongoing habitat management programs (Seddon, 1999).

According to IUCN reintroduction guidelines, a detailed feasibility assessment should be carried out before a reintroduction takes place, where even simple models can support decision-making (IUCN, 2013). The guidelines also highlight the importance of habitat in reintroduction planning, stating that “matching habitat suitability and availability to the needs of candidate species is central to feasibility and design” (IUCN, 2013). With increasingly accessible spatial data, geographic information systems (GIS) can be a useful tool to assist reintroduction planning. Using species distribution data and landscape habitat maps, habitat suitability modeling evaluates the likelihood that a location can accommodate a target species (Di Febbraro et al., 2018). This technique has been successful in aiding reintroductions, including for the red-billed oxpecker (Buphagus erythrorynchus, Kalle, Combrink, Ramesh, & Downs, 2017), eastern barred bandicoot (Perameles gunnii, Cook, Morgan, & Marshall, 2010) and Eurasian lynx (Lynx lynx, Schadt et al., 2002). Models such as these allow conservation practitioners to more easily identify potential target sites for reintroduction, thus reducing survey times and offering time cost savings, whilst also answering calls for incorporation of modeling approaches to assist reintroduction planning (Seddon et al., 2007).

The arboreal hazel dormouse, Muscardinus avellanarius, has typically been associated with diverse ancient woodlands (Bright, Mitchell, & Morris, 1994; Bright & Morris, 1990; Harris, Morris, Wray, & Yalden, 1995), due to relying on a variety of seasonal foods, such as flowers, fruits and invertebrates (Bright & Morris, 1993; Richards et al., 1984). A well-structured understorey is preferred, comprising early to mid-successional stages of woody vegetation such as dense areas of scrub or woodland edge (Capizzi et al., 2002; Goodwin, Hodgson, Bailey, Bennie, & McDonald, 2018; Juškaitis & Šioložinyte, 2008). Across Europe and Asia minor, hazel dormice are considered Least Concern on the IUCN Red List (Hutterer et al., 2016). Once widespread in England and Wales, the species is classified as vulnerable in the UK, declining by 5.8% annually (Goodwin et al., 2017; Mathews et al., 2020), and has been lost from much of northern England (Bright & Morris, 1996; Hurrell & McIntosh, 1984). This is thought to be due to habitat fragmentation, deterioration and loss, and changes in habitat management practices (Bright et al., 1994; Bright & Morris, 1990, 1996; Mortelliti et al., 2011).

Since the early 1990s, dormice have been monitored via a co-ordinated program and reintroduced to 24 sites (White, 2012; White, 2019), aiming to re-establish the historic range (Mitchell-Jones & White, 2009). Despite short-term success reported at many of the reintroduction sites (with dormice surviving the first two winters), approximately half have not maintained dormouse populations for longer than 10 years (White, 2019). To maximize the chances of reintroduction success, there should be strong evidence that the original threats have been removed or reduced (IUCN, 2013). Available evidence for dormouse reintroductions indicates that habitat suitability, continued habitat management and connectivity impact reintroduction success (White, 2019).

Increasing the chance of future reintroduction success requires a thorough understanding of dormouse habitat preferences and population drivers. Favored vegetation types vary depending on geographic location (Ramakers, Dorenbosch, & Foppen, 2014). In Germany and Lithuania, dormice inhabit spruce-dominated mixed forests with overgrown clearings (Juškaitis, 2007; Wuttke, Büchner, Roth, & Böhme, 2012), whereas in the Netherlands well-developed deciduous forests and hedgerows are favored (Foppen, Verheugen, & Boonman, 2002). In England, dormouse presence has historically been associated with ancient coppiced woodlands (Goodwin et al., 2018). However, ancient woodlands have declined in abundance and size, covering only
2.6% of England and Wales and 87% are less than 20 ha (Bright et al., 1994; Mitchell-Jones & White, 2009; Spencer & Kirby, 1992). Woodland management has also been abandoned in many areas, resulting in an 83% decline of coppiced woodlands (Hopkins & Kirby, 2007). The decline in ancient and coppiced woodlands presents a challenge for locating suitable reintroduction sites in England, with few potential sites meeting the criteria outlined in the reintroduction program (White, 2019). A better understanding of the habitats occupied by the remnant UK dormouse population, and of the factors influencing populations at current reintroduction sites, could therefore help to identify suitable potential sites for future reintroductions.

Here we aim to investigate habitat suitability for hazel dormice in England, UK, and to identify the key ecological factors driving population differences at current dormouse reintroduction sites. Ecological niche factor analysis (ENFA) can be used for habitat suitability mapping, requiring presence only data (Hirzel, Hausser, Chessel, & Perrin, 2002; Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006). ENFA avoids problems caused by false absences in species distribution data, which likely occur for the cryptic hazel dormouse, which lives at low population densities (Bright, Morris, & Mitchell-Jones, 2006).

The approach has been successfully used across diverse taxa (Engler, Guisan, & Rechsteiner, 2004; Galparsoro, Borja, Bald, Liria, & Chust, 2009; Neupane, Kwon, Risch, & Johnson, 2020). We use presence data taken from the National Dormouse Monitoring Programme (NDMP), which has been monitoring dormice in woodlands since 1988 (White, 2012), combined with remotely sensed habitat variables, known as ecogeographical variables (EGVs), from a range of open access data sources. Using ENFA, we determine which EGVs best describe the natural range of dormice in England and estimate habitat suitability by creating a sensitivity map. Using the key habitat descriptors and other variables relating to dormouse reintroductions, we use generalized linear mixed modeling to identify the factors that best explain population numbers in dormouse reintroduction sites. Finally, we demonstrate the practical application of habitat mapping as an aid to identify potential reintroduction sites in Cheshire, England.

2 | METHODS

Dormouse populations are currently monitored at over 400 woodlands throughout England and Wales, as part of the National Dormouse Monitoring Programme (NDMP PTES, 2017). These include the sites of 24 reintroductions, which have taken place almost annually since 1993, and are mainly concentrated in northern England. NDMP sites are surveyed up to once a month (between 15th and 25th), with at least one prebreeding survey (May/June) and one postbreeding survey (September/October) each year. Licensed volunteers collect count data from a grid of nest boxes, with a minimum of 50 nest boxes per site, and record age, weight and sex of any animals present (see the NDMP guidelines [PTES, 2017] for further details).

2.1 | Habitat analysis of sites where natural hazel dormouse populations are present

Presence at an NDMP site in England was recorded if adult dormice had been found between 2014 and 2019, with 410 sites matching the selection criteria (PTES, 2020). Grid references for these sites were transformed in QGIS (v3.4.15-Madera), using the British National Grid co-ordinate reference system, into a Boolean raster map of the study area (England) to a resolution of 1 ha. This resolution was chosen to match the home range of dormice, as the size of monitoring sites varies across locations (Bright & Morris, 1991; Mortelliti, Santarelli, Sozio, Fagiani, & Boitani, 2013). Presence cells were valued at one, with remaining cells valued at zero.

To describe the various habitat gradients across England, an extensive search of open-source databases was carried out. An unbiased approach was taken to selecting variables with the aim of identifying previously overlooked habitat descriptors and to clarify existing knowledge of dormouse habitat preferences. Overall, we collated data for 55 EGVs from open-source databases (Table 1, Table S1, Figure S1). These were then tested in all combinations for spatial correlation, using a recommended $R$ value threshold of 0.7 (Green, 1979) to ensure that the effect of an EGV was not overestimated due to collinearity issues. The results revealed six combinations of high correlation ($R$ value > 0.7; Table S2, Figure S2), which led to the removal of four EGVs from further analysis: distance from tidal rivers, terrain, distance to buildings and special areas of conservation frequency.

EGVs were classified into five categories: land cover, anthropogenic, hydrography, topography and other. Some variables are directly quantitative, such as the frequency land cover data from the UKCEH and topographic data (Table 1). Where necessary, variables were transformed into frequency or distance maps (QGIS.org, 2020). Frequency maps were Boolean, consisting of ones for presence and zeros for absence of each environmental factor. Populations are likely to be influenced by their home range habitat and surrounding area, so we...
calculated a moving average using the GDAL grid function. Frequency scores therefore describe the proportion of cells within a 300 m radius of the focal cell. Distance maps were calculated as the Euclidean distance from any cell in England to the closest focal cell of the habitat variable, using the GDAL proximity (raster distance) function. ENFA requires EGVs to have the same co-ordinate reference system, resolution, extent, and spatial unit. All maps used the British National Grid (OSGB 1936). All EGV maps were then re-sampled to the extent of the presence map at a 100 m resolution, using the GDAL warp (reproject) function. The 51 EGVs were compressed into a raster brick format using the GDAL merge function. Dormouse presence and EGVs were used in an updated version of ENFA called Climate Niche Factor Analysis (CENFA), to identify habitat requirements of

| Class            | Eco-geographical variable       | Source       | Class            | Eco-geographical variable       | Source       |
|------------------|---------------------------------|--------------|------------------|---------------------------------|--------------|
| Land cover       | Acid Grassland_DT               | UKCEH        | Anthropogenic    | *Buildings_DT                   | OS           |
|                  | Acid Grassland_FQ               | UKCEH        | Major towns and Cities_DT | ONS               |
|                  | Arable Horticulture_DT          | UKCEH        | Railways_DT      | OS                              |
|                  | Arable Horticulture_FQ          | UKCEH        | Roads_DT         | OS                              |
|                  | Bare ground/Rock_DT            | FC           | Suburban_DT      | UKCEH                          |
|                  | Bare ground/Rock_FQ            | FC           | Suburban_FQ      | UKCEH                          |
|                  | Broadleaved Woodland_DT         | UKCEH        | Urban_DT         | UKCEH                          |
|                  | Broadleaved Woodland_FQ         | UKCEH        | Urban_FQ         | UKCEH                          |
|                  | Calcareous Grassland_DT         | UKCEH        | Hydrograph       | Canal_DT                       | OS           |
|                  | Calcareous Grassland_FQ         | UKCEH        | Coast_DT         | OS                              |
|                  | Coniferous Woodland_DT          | UKCEH        | Inland Rivers_DT | OS                              |
|                  | Coniferous Woodland_FQ          | UKCEH        | Lakes_DT         | OS                              |
|                  | Coppice_DT                      | FC           | *Tidal Rivers_DT | OS                              |
|                  | Coppice_FQ                      | FC           | Topography        | OS                              |
|                  | Felled Trees_DT                 | FC           | Aspect            | OS                              |
|                  | Heather Grassland_DT            | UKCEH        | Elevation         | EDD                            |
|                  | Heather Grassland_FQ            | UKCEH        | Slope             | OS                              |
|                  | Heather_DT                      | UKCEH        | *Terrain          | EDD                            |
|                  | Heather_FQ                      | UKCEH        | Other             | NE                              |
|                  | Improved Grassland_DT           | UKCEH        | Agricultural land classification | NE |
|                  | Improved Grassland_FQ           | UKCEH        | Ecological status | UKCEH                          |
|                  | Inland Rock_DT                  | UKCEH        | Local nature Reserves_FQ | NE |
|                  | Inland Rock_FQ                  | UKCEH        | National nature Reserves_FQ | NE |
|                  | Low density Forest_DT           | FC           | Sites of special scientific Interest_FQ | NE |
|                  | Low density Forest_FQ           | FC           | *Special areas of Conservation_FQ | NE |
|                  | Neutral Grassland_DT            | UKCEH        |                  |                                 |
|                  | Neutral Grassland_FQ            | UKCEH        |                  |                                 |
|                  | Shrub_DT                        | FC           |                  |                                 |
|                  | Shrub_FQ                        | FC           |                  |                                 |
|                  | Young Trees_DT                  | FC           |                  |                                 |
|                  | Young Trees_FQ                  | FC           |                  |                                 |

Note: Sources are coded as follows: UK Centre for Ecology and Hydrology (UKCEH), the Forestry Commission (FC), Ordnance Survey (OS), Office for National Statistics (ONS), Edinburgh Data Share (EDD) and Natural England (NE).
dormice in England (Rinnan & Lawler, 2019; Rinnan, 2020; R version 4.0.0 R Core Team, 2020). CENFA is not climate specific, so will hereafter be referred to as ENFA. ENFA uses factor analysis, to examine a species’ habitat requirements extracted from EGVs. This results in the production of two uncorrelated factors: marginality and sensitivity. The latter is a variation of the overall index of specialization outlined by Hirzel et al. (2002). Marginality describes the difference between the species optimum habitat conditions and the mean habitat for the study area, in our case England, therefore describing the location of the species niche (Santos et al., 2006). The model produces an overall marginality score and a score for each EGV. A value above one on the overall marginality score indicates that the species prefers a significantly different habitat to the study area (Hirzel et al., 2002), while the absolute value of the score for the individual EGVs describes the ecological distance of the species mean from the habitat mean. For each EGV, a positive marginality score indicates the species mean is above the study area mean, whilst a negative score indicates the species mean is below the study area mean.

Specialization factors are computed from the marginality factor and assess the variance of each EGV. Only the absolute values of these factors are important, as the signs are arbitrary (Hirzel et al., 2002). These are then averaged to produce the second main factor, sensitivity (Rinnan & Lawler, 2019). A value above one for the overall index of sensitivity indicates the tolerance for habitat conditions of the target species, whereas the individual EGV sensitivity scores describe the degree of sensitivity to shifts away from the species mean for each EGV mean and allows interpretation of the size of the species niche relative to the study area. These values range from zero to infinity and a value above one for each sensitivity score indicates some form of specialization.

2.2 | Habitat suitability mapping

We projected sensitivity scores to produce a raster map of England in R, indicating areas of high and low habitat suitability for dormice. All cells across the map were given a suitability score, with lower values indicating more suitable habitat (Rinnan & Lawler, 2019). To examine the difference in habitat suitability between natural dormouse populations and the rest of England, and how well reintroduction sites currently match the natural habitats of the dormice, we extracted suitability scores for reintroduction sites, natural dormouse sites and for the whole of England from this map. We used the point sampling plugin in QGIS, which takes a grid reference and extracts the habitat suitability score from the corresponding pixel on the map. Scores were compared to assess whether reintroduction sites are currently in similar habitat conditions to those of natural dormice population using a Kruskal–Wallis test, followed by post-hoc pairwise comparisons using Mann–Whitney U tests.

2.3 | Model validation

A jack-knife model validation technique was used to evaluate the performance of the model (Fielding & Bell, 1997). The presence data was split into 10 equal groups of 41 sites. The model was calibrated using nine of these groups, with the last group used to extract habitat suitability scores from the sensitivity map. This was repeated 10 times, leaving out a different group each time. The medians of the full model (the model produced using all 410 monitoring sites) and validation model for each site were compared. We also calculated the absolute difference at each site for the two scores and compared the overall median.

This jack-knife model validation technique showed that predicted habitat suitability scores of natural dormouse population produced values slightly higher than the full model (validation median = 1.43 [IQR = 0.48], full model median = 1.37 [IQR = 0.47]). The absolute difference between habitat suitability score of monitoring sites in the validation and full model produced a median of 0.045 (IQR = 0.077). Here, 75% of validation monitoring sites produced suitability scores within 0.1 of the full model (Figure S3, Table S3).

2.4 | Analysis of habitat factors explaining population trends in reintroduced dormouse populations

We used generalized linear mixed models (GLMMs) to analyze the factors most strongly influencing dormouse population size across current reintroduction sites. GLMMs were run using the package lme4 (Bates, Maechler, Bolker, & Walker, 2015) in R version 4.0.2 (R Core Team, 2020). Models were run with a negative-binomial distribution, with log link, as this produced the best fitting models, while reducing overdispersion. Dormouse count data was obtained from NDMP reintroduction site surveys (between 1993 and 2015), with adult counts per survey session used as the response variable. Adult counts are the most consistently recorded age bracket and adults are most likely to contribute to population trends (Juškaitis & Büchner, 2013). Their
numbers are more stable, with juveniles having a higher mortality rate during hibernation (Juškaitis, 1999). The number of nest boxes per site was used as an offset variable, to take account of effort in surveys. Survey site was included as a random effect. Where there were multiple survey sections within one woodland, these were grouped into one site to reduce the non-independence of samples.

From the NDMP data, we included as predictor variables the time since reintroduction, number of animals reintroduced, the number of reintroductions that took place, the season when survey data was collected (spring, summer, autumn), site co-ordinates and size of each reintroduction site. The top 10 most important habitat factors featured in the marginality and sensitivity ENFA results (Table 2) were also added, using a point sampling tool in QGIS to extract values for each reintroduction site. Continuous variables were standardized to help with model convergence. Candidate models included combinations of these predictor variables and model selection was carried out by ranking Akaike’s information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). Using the AICcmodavg R library (Mazerolle, 2020), the best fitting model was selected as the most parsimonious from the top two ΔAICc scores (Burnham & Anderson, 2002).

### Table 2: The top 10 eco-geographical variables (EGVs) for each of the first three factors (a) marginality, (b) specialization 1 and (c) specialization 2 and (d) the sensitivity factor produced by the Ecological Niche Factor Analysis (ENFA) model. These are most likely to describe the habitat where hazel dormice are naturally found

| (a) EGV                  | Marginality a | (b) EGV              | Specialization 1 b |
|-------------------------|--------------|----------------------|---------------------|
| Broadleaved Woodland_FQ | 2.32         | Urban_FQ             | −0.93               |
| Slope                   | 0.95         | Broadleaved Woodland_DT | 0.36               |
| Arable Horticulture_FQ  | −0.60        | Arable Horticulture_FQ | −0.05               |
| Broadleaved Woodland_DT | −0.58        | Heather_DT            | −0.05               |
| Felled Trees_DT         | −0.56        | Major towns and Cities_DT | −0.04           |
| Coniferous Woodland_DT  | −0.51        | Improved Grassland_DT | 0.03                |
| Coppice_FQ              | 0.49         | Improved Grassland_FQ | −0.03               |
| Agricultural land classification | 0.43 | Suburban_DT             | 0.03                |
| Heather_DT              | −0.42        | Agricultural land classification | −0.03 |
| Coast_DT                | −0.39        | Coniferous Woodland_DT | −0.02               |

| (c) EGV                  | Specialization 2 b | (d) EGV              | Sensitivity c |
|-------------------------|---------------------|----------------------|--------------|
| Arable Horticulture_DT  | 0.55                | Urban_FQ             | 27.75        |
| Improved Grassland_DT   | 0.44                | Broadleaved Woodland_DT | 16.91        |
| Arable Horticulture_FQ  | −0.36               | Arable Horticulture_FQ | 10.51        |
| Urban_FQ                | 0.23                | Arable Horticulture_DT | 9.87         |
| Improved Grassland_FQ   | −0.22               | Acid Grassland_FQ     | 8.16         |
| Acid Grassland_FQ       | −0.22               | Improved Grassland_DT | 7.47         |
| Canal_DT                | 0.18                | Improved Grassland_FQ | 7.41         |
| Urban_DT                | 0.17                | Canal_DT             | 5.97         |
| Coniferous Woodland_DT  | −0.16               | Heather_DT            | 5.33         |
| Heather_DT              | −0.14               | Suburban_DT           | 5.26         |

Note: Factors ending in “_FQ” or “_DT” indicate frequency and distance measures, respectively.

*aMarginality describes the difference between the species optimum conditions and the mean habitat for the reference area. An absolute value above one indicates a significant difference in habitat from the reference area (England). Factors are ranked by their absolute score value and sign indicates whether the habitat value is above or below the reference area mean.

*bSpecialization scores are built off the marginality score and only absolute values are important.

*cSensitivity scores ranging from zero to infinity describe the degree of sensitivity to shifts away from the species mean: scores above one indicates some form of sensitivity.
2.5 | Identifying suitable future reintroduction sites

To demonstrate the practical application of ENFA modeling, a map of Cheshire, England, was extracted from the overall habitat suitability map. A dormouse reintroduction took place in Cheshire in 1996 but the population failed to persist, with no dormice recorded for the NDMP since 2017 (PTES, 2020). It is thought that the site has become more unsuitable over time, with woodland management only taking place once in 2017 (White, 2019). Potential new reintroduction sites were assessed using locations of broadleaved woodlands, as identified from the National Forest Inventory Woodland England 2018 dataset. Habitat suitability values for each woodland were calculated using the QGIS zonal statistics tool, taking the mean of the habitat suitability scores within the woodland area. Sites were then divided into most suitable (<median), marginal (>median, <third quartile) and least suitable habitats (>third quartile) based on the median of all 410 NDMP natural population sites. In addition to habitat suitability, the size of the site was also considered. Previous studies suggest that reintroduced dormouse populations require at least 20 ha of suitable habitat or connected via hedgerows or tree lines (Bright et al., 1994; Bright & Morris, 1992). However, it has also been suggested that this value should be over 50 ha (Bright, 1996; Mitchell-Jones & White, 2009) and some dormouse populations have been maintained at reintroduction sites of 10 ha (White, 2019). Any woodland of less than 10 ha was therefore removed from analysis and the remaining sites were classified into three categories: 10–19, 20–49 and 50–80 ha. Sites having above 10 ha of habitat classified as “most suitable” were highlighted for further consideration.

3 | RESULTS

3.1 | Habitat analysis of sites where natural hazel dormouse populations are present

Habitat occupied by natural dormouse populations differed substantially from the mean habitat for England, with an overall marginality score of 3.11 (see Table S4 for full model output). Moreover, an overall sensitivity score of 1.98 indicates a relatively restrictive tolerance of dormice to variation in the habitat condition. The first five factors of the model output (marginality and specialization factors 1–4, which contribute to the total specialization score, along with the other specialization factors) account for 50% of the total specialization (Table S4). Marginality scores describe the difference between the mean habitat conditions naturally occupied by dormouse populations and the mean habitat across England, showing that natural dormouse populations in England are concentrated in regions with a higher than average proportion of hectares nearby (within a 300 m radius) containing broadleaved woodland (2.32, Table 2a), reflecting the NDMP dataset which monitors dormice in woodlands. These NDMP sites are found in regions with a higher than average slope gradient (0.95) and proportion of hectares nearby containing coppicing (0.49), lower than average proportion of nearby hectares containing arable horticulture (−0.60), and closer to broadleaved woodlands (−0.58), coniferous woodlands (−0.51) and felled trees (−0.56). Specialization assesses the variance of each EGV in areas naturally occupied by dormice relative to the variance of habitat suitability scores for England, for each factor derived by ENFA (Table 2b,c). The first specialization factor derived accounts for 24.7% of specialization and indicates a high sensitivity to the proportion of land nearby that is urban (absolute score = 0.93) and distance to broadleaved woodlands (0.36, Table 2b). The second specialization factor accounts for 11.0% of specialization; the main factors are distance to and frequency of arable horticulture (absolute scores 0.55 and 0.36 respectively), and improved grassland frequency (0.44, Table 2c). Sensitivity scores describe the degree of sensitivity to shifts away from the species mean. Dormice are particularly sensitive to the proportion of hectares nearby containing urban habitat (sensitivity score = 27.75) and broadleaved woodland (16.91; Table 2d). Both the distance to and proportion of hectares containing arable horticulture within 300 m produced high sensitivity scores of 9.87 and 10.51, respectively. These EGVs had negative marginality scores, indicating that dormouse habitats are below the England average.

3.2 | Analysis of habitat factors explaining population trends in reintroduced dormouse populations

The number of adult dormice at reintroduction sites was best described by a model that included the fixed effects of time since reintroduction, season, the proportion of nearby hectares containing broadleaved woodland and arable land, slope, and longitude, with site included as a random effect (see Table 3 for full equation and AIC model selection). Consistent with an overall pattern of population decline, the longer the time since reintroduction, the lower the chance of finding adult dormice in a nest box (Figure 1a, approximately 1 in 13 chance 1 year after reintroduction compared to
approximately 1 in 80 chance 25 years after reintroduction). We also found evidence of seasonal population trends (Figure 1b), with a Tukey test revealing significantly greater chances of finding adult dormice in nest boxes in autumn than in spring (*p < .001*) and summer (*p < .001*), but no difference between spring and summer (*p = .563*). Taking these factors into account, we found several habitat factors were significantly related to the size of dormouse populations. In contrast to our results based on the presence or absence of natural dormouse populations, here we found that the chance of finding adult dormice in nest boxes decreased as the proportion of surrounding hectares containing broadleaved woodland increased, but with a large margin of error (Figure 1c). Similarly, the chance of finding adult dormice in a nest box decreased with an increased slope gradient in the region (Figure 1d) and with an increasing proportion of arable land nearby (Figure 1e). Lastly, the further east the site, the higher the chance of finding adult dormice in nest boxes (Figure 1f).

### 3.3 Comparing habitat in current reintroduction sites with areas occupied by natural populations

Based on the ENFA sensitivity scores for England, the majority of suitable habitat can be found in the south of England, with larger, more connected areas (Figure 2). The 24 reintroduction sites are more northerly than most existing natural populations. Sensitivity values extracted from the habitat suitability map indicate a significant difference in habitat suitability between natural sites, reintroduction sites and habitat across the rest of England (Kruskal–Wallis, \( \chi^2 = 502.31, \text{df} = 2, p < .001 \), Figure S4). Natural populations occupy sites with significantly better suitability scores compared to both the rest of England (*p < .001*) and reintroduction sites (*p < .001*). Current habitat suitability scores at reintroduction sites are more similar to the scores of the rest of England, but still differ significantly (*p = .015*).

### 3.4 Can habitat suitability modeling help identify suitable future reintroduction sites?

Here, we focus on one county in the UK (Cheshire) to demonstrate the potential practical application of ENFA modeling. Using the habitat suitability map, 246 woodlands in Cheshire were identified as broadleaved woodlands over 10 ha, meeting one of the basic requirements of current reintroduction schemes (Figure 3). Of these, 45 sites were considered to contain suitable habitat and 16 sites were in the largest site area classification (50–80 ha). Only one site matched the top classifications for both site area and habitat suitability (Figure 3). By contrast, the 1996 Cheshire reintroduction is currently in “least suitable” habitat, according to our model.

### 4 Discussion

We have identified regions across England that are likely to contain broadly suitable habitats for hazel dormice. Our habitat suitability map reflects the current natural

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**Table 3** Top five generalized linear mixed models describing the number of adult dormice found in nest boxes at reintroduction sites according to delta AIC scores, with K degrees of freedom. The full equation is shown for the best-fitting GLMM. Null model is also shown.

| Variables included in model* | K | \( \Delta \text{AICc} \) |
|-----------------------------|---|-------------------|
| Time since reintroduction + season + broadleaved woodland FQ + slope gradient + arable horticulture FQ + longitude + latitude | 11 | 1.62 |
| Time since reintroduction + season + broadleaved woodland FQ + slope gradient + arable horticulture FQ | 9 | 10.04 |
| Time since reintroduction + season + broadleaved woodland FQ + slope gradient + arable horticulture FQ + latitude | 10 | 10.82 |
| Time since reintroduction + season + broadleaved woodland FQ + slope gradient + arable horticulture FQ + distance to felled trees | 10 | 10.95 |
| Null model | 3 | 295.48 |

*Reintroduction site was included as a random factor in all models and nest box number was included as an offset variable. All models were run with a negative binomial distribution, with log link, and all continuous variables were scaled to help with model convergence. FQ = frequency.

*Best-fitting model.

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The factors that best describe the number of hazel dormice at reintroduction sites, based on GLMM analyses. The number of adult dormice per nest box is shown, according to (a) time since reintroduction, (b) season, (c) broadleaved woodland frequency, (d) slope, (e) arable land frequency, (f) longitude. Habitat variables and longitude have been scaled.

**FIGURE 1** The factors that best describe the number of hazel dormice at reintroduction sites, based on GLMM analyses. The number of adult dormice per nest box is shown, according to (a) time since reintroduction, (b) season, (c) broadleaved woodland frequency, (d) slope, (e) arable land frequency, (f) longitude. Habitat variables and longitude have been scaled.

range of dormice in England, with suitable habitat present mostly in southern England and lacking in the Midlands and northern England (Bright & Morris, 2002; Wembridge, Al-Fulaij, & Langton, 2016). The model
further highlights the importance of broadleaved woodlands to hazel dormice (Goodwin, Hodgson, et al., 2018; Sanderson, Bright, & Trout, 2004), as broadleaved woodland frequency is identified as the EGV with the greatest difference between mean habitat conditions at dormouse sites and the rest of England.

Dormice have also recently been associated with conifer woodlands and plantations (Trout, Brooks, Combe, & Rudlin, 2018), which was reflected in the results of our ENFA model. It is important to note that the NDMP monitors woodlands almost exclusively (PTES, 2017), and mainly broadleaved sites, so our model may not capture the full variety of sites where dormice are present such as roadsides and coniferous woodlands (Sanderson et al., 2004; Schulz, Ehlers, Lang, & Büchner, 2012; Trout et al., 2018). Whilst presence-only data has advantages, when creating a species distribution model, it is more prone to sampling bias (Stoa, Halvorsen, Mazzoni, & Gusarov, 2018; Stolar & Nielsen, 2015). Hence, we would advise caution if a conservation practitioner wished to reintroduce dormice into a habitat type other than broadleaved woodland, the focus of the NDMP. In this case, another model would be beneficial to include data from sites with the desired habitat characteristics.

Exploration of additional remotely sensed habitat descriptors, such as slope, urban areas, arable horticulture, and felled trees, revealed some other important characteristics that correlate with the natural presence of dormice. Dormice are arboreal and depend on linear wooded areas for dispersal and survival, which may explain why urban areas are not suitable for this species (Angold et al., 2006). Dormice will travel through arable land, but the botanical diversity does not meet their breeding or feeding requirements (Bright, 1998; Bright & Morris, 1993; Mortelliti et al., 2013). The decline in hedgerows across the UK has likely further reduced the possibility of arable land supporting dormice and therefore their association in our model (Staley, Amy, Facey, & Pywell, 2012). It is thought that hedgerows provide valuable connectivity between suitable habitat patches.
Bright, 1998; Capizzi et al., 2002; Mortelliti et al., 2011), with lower abundance associated with more isolated woodland fragments (Goodwin, Hodgson, et al., 2018). Hedgerows likely improve the viability of maintaining dormouse metapopulations within an area, through mitigating against habitat degeneration within patches.

The ENFA model also indicates a connection to felled trees, reflecting the dormouse requirement of diverse woodlands with a range of tree heights (Goodwin, Hodgson, et al., 2018). Although the initial effects of felling can increase mortality to dormice, the subsequent stages of forest regrowth can provide the mid-successional woodlands that dormice require (Bright & Morris, 1990; Goodwin, Hodgson, et al., 2018). Coppicing, which is beneficial to dormice in a similar way (Bright & Morris, 1992), is not highlighted to the same extent in our analysis. However, UK coppicing has mostly been discontinued (Sanderson et al., 2004) and where small-scale projects take place at reintroduction sites, the maps used in this study are unlikely to identify these areas.

Ancient woodlands have declined in England and many flat woodlands have been cleared for agriculture or urbanization (Hopkins & Kirby, 2007). Assessments of ancient woodlands have identified common topographical features such as ravines, rock outcrops and gullies (Pryor, Curtis, & Peterken, 2002), thus remaining dormouse sites are likely sloped woodlands. However, sloped locations might provide additional benefits for dormice, as evidence suggests that moderate slopes are favored by the edible dormouse, *Glis glis*, in Austria (Cornils, Hoelzl, Rotter, Bieber, & Ruf, 2017). Topography could increase the variability of shade and sun, aiding hazel dormice by creating microclimates with a greater plant diversity (Bright & Morris, 1996). Furthermore, bramble is often associated with stable dormouse populations and a range of sunlight can increase the seasonal availability of bramble fruit by up to 2 weeks (Goodwin, Suggitt, et al., 2018; Gyan & Woodell, 1987).

Despite long-term conservation efforts, natural hazel dormouse populations are still declining in the UK (Wembridge, White, Al-Fulaij, Marnham, & Langton, 2019; White, 2019), and our findings indicate that reintroduced populations are also declining. Consistent with the most important EGVs in our ENFA models, the best model describing reintroduced population numbers included the proportion of nearby hectares containing...
broadleaved woodland or arable land and slope. The number of individuals reintroduced, the number of reintroductions and the area of the reintroduction site were not retained as factors in the model. This was unexpected based on published findings for other reintroduced species (Fischer & Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996; Wolf et al., 1998), but further highlights the importance of habitat characteristics for the long-term success of dormouse reintroductions. Nonetheless, it is possible that the number of individuals released, the number of reintroductions per site and the site area may be important to the success of reintroduced dormouse populations, but were not identifiable from this dataset.

The number of adult dormice found in nest boxes at reintroduction sites was also related to season and longitude. Consistent with these results, populations are known to peak in autumn (Juškaitis & Büchner, 2013), as numbers include mature animals born earlier in the year and dormice are more likely to be using nest boxes, possibly due to changes in the use of the habitat across seasons. Longitude may also be an important factor, with dormouse numbers found to increase as reintroduction sites get further east. This may be due to more stable climatic conditions in the east of England, with colder winters and more suitable remnant habitat, but this needs further study. Colder winters are thought to be preferable for dormice, by reducing the chances of arousal during hibernation (Pretzlaff & Dausmann, 2012). Interestingly, a recent study has found that dormice have flexibility in physiological and behavioral responses to climate conditions, where they can maintain sufficient body mass even during periods of more frequent arousal, but food availability remains vital (Pretzlaff, Radchuk, Turner, & Dausmann, 2021). Latitude was another factor which was not retained in the best-fitting model. This may seem surprising, as our maps reveal more suitable habitat in the south, however the 24 reintroduction sites used in the model are mostly located in northerly regions.

Comparing the remotely sensed habitat descriptors predicting dormouse presence within their remaining natural range with those predicting numbers found in reintroduced populations reveals some interesting differences. Notably, although our ENFA models indicate that dormice prefer broadleaved woodland and steeper slopes, our models for reintroduction sites suggest that these factors are associated with smaller populations. This apparent contradiction highlights the need to better understand dormouse nest box use. There is evidence that nest boxes increase nest site availability, in turn increasing the carrying capacity of a site (Juškaitis, 2005; Morris, Bright, & Woods, 1990). Therefore, nest box use may also vary across habitat types and quality, such that population numbers in nest boxes might be relatively higher in less suitable habitat because there are fewer natural nesting opportunities. Nest boxes are also more likely to be occupied in wet weather and deserted when temperatures are too high (Juškaitis & Büchner, 2013; Panchetti, Amori, Carpaneto, & Sorace, 2004). Further, the habitat frequency measures used in these models reflect the local area surrounding the reintroduction sites. Finding fewer animals at the central reintroduction site, with a higher frequency of surrounding woodland, could indicate higher levels of dispersal, but this needs to be investigated further. Given that dormice are thought to prefer certain successional stages of woodland development, it could be that over time nearby woodlands offer more optimal habitat, highlighting the importance of connectivity between sites. We also note that our models use broad scale habitat factors recorded at one time point, while the hazel dormouse has complex requirements, preferring particular woodland structure and diversity (Bright et al., 1994; Bright & Morris, 1990; Harris et al., 1995), and the variables used in our study do not reflect the quality or structure of the habitat or temporal changes.

Our results suggest that where suitable habitat exists outside of the current natural range of hazel dormice, it is patchy and often near less suitable habitat, which could have contributed to the original range retraction. Habitat patches in northern England may pose a threat to dormouse dispersal and colonization at potential reintroduction sites (Dietz, Büchner, Hillen, & Schulz, 2018), as dormice are reluctant to cross open spaces (Bright & Morris, 1996). Smaller woodlands are less likely to contain the high plant diversity and complex habitat structures that dormice require (Bright, 1996; Ehlers, 2012), leaving reintroduction populations vulnerable to stochastic processes (Bright et al., 1994; Mortelliti et al., 2014). Assessment of reintroduction sites, using values extracted from our habitat suitability map, further suggest that many of these specific locations are less suitable than natural sites or have become more unsuitable since reintroduction. For example, in our Cheshire analysis, the original 1996 reintroduction site is currently within the least suitable habitat category and is relatively isolated from other sites. A lack of continued habitat suitability may help to explain why long-term success at these reintroduction sites does not always occur (White, 2019) and reinforces the importance of both carefully assessing habitat descriptors at potential reintroduction sites and continued habitat management. This concurs with broader findings in reintroduction biology, with habitat factors frequently associated with unsuccessful reintroductions across taxa (Bubac et al., 2019; Griffith et al., 1989; Wolf et al., 1996; Wolf et al., 1998).
With the importance of habitat to reintroduced populations, EGVs could be used to assist reintroduction site selection, thus bridging the gap between expert-based and model-based habitat selection (Di Febbraro et al., 2018). Using Cheshire as a case study, we have demonstrated how habitat suitability mapping could be used to identify potential areas for future reintroductions. By analyzing the results of the habitat suitability model and the basic requirements as described by PTES (White, 2019), woodlands can be identified for further assessment as potential reintroduction sites. In our Cheshire analysis, there are more than 50 broadleaved woodlands meeting the highest category of habitat suitability and one of these sites, in the east, is larger than 50 ha. This site could be considered as a potential reintroduction site. Interestingly, in the past, the south of Cheshire was recommended for future reintroductions (Chanin, 2014). However, we found clusters of suitable woodlands, within the center and east of Cheshire (Figure 3). The potential of a reintroduction site should be analyzed within the context of the local landscape, with clusters of connected woodland providing the opportunity of setting up metapopulations, thus improving the chance of long-term persistence via reducing the extinction risk (Hanski, 1982).

Potential sites identified by habitat suitability maps should be used alongside expert opinion and on-the-ground checks to ensure the site is appropriate for reintroduction. For example, the presence of important habitat descriptors at a site does not necessarily reflect quality of habitat for dormice, but can be used as a starting point for further investigation. More detailed assessment should aim to determine if additional requirements exist, such as diversity of plant species, ability to continue woodland management and considerations of the connectivity potential of the site within the landscape. During reintroduction planning, once target sites have been identified, the next challenge is selecting suitable individuals for release. As highlighted in the IUCN reintroduction guidelines, the genetics of individuals for release should be suited to the target location (IUCN, 2013). Particularly for dormice, reintroductions should aim to preserve local adaptive genetic variation, as suggested by Combe et al. (2016).

Future studies could take advantage of the climate tools offered by the CENFA R package (Rinnan, 2020). This is particularly important when reintroductions are aimed at increasing the range of the hazel dormouse into the north of England, since dormouse distribution is likely constrained regionally by habitat and climate (Bright & Morris, 1996) and may be impacting the long-term success rates of reintroductions. Strong correlations between dormouse incidence and the climatic gradient along the south–north axis have been observed (Bright, 1996). The model could be further refined by adding other factors such as site connectivity, plant species composition, woodland management levels and temporal changes, as well as the addition of dormouse presence data outside of broadleaved woodlands. In addition to assisting with reintroduction planning, habitat models such as these can be applied to identify areas most likely to contain dormice. This is potentially an important application, especially for protected species such as the hazel dormouse, which require surveys for mitigation purposes during building and development.

In conclusion, the methods used here could assist in identifying suitable sites for hazel dormouse reintroductions. We have shown that dormouse distribution is correlated with a range of remotely sensed broad-scale habitat factors, including broadleaved woodlands, urban areas, arable horticulture, and slope. Habitat factors explain the most variation in the number of individuals found at reintroduction sites, further highlighting the need to identify high-quality sites to increase the chance of reintroduction success. Importantly, the flexibility of our habitat suitability modeling approach provides potential for further refinement as more data become available. It also offers the opportunity to identify areas which may be more likely to contain natural dormouse populations, aiding the survey process for mitigation purposes. The model could be used to assist other UK reintroduction programs across various taxa, by changing the presence data map for the species of interest. Through identifying the key EGVs preferred by natural populations and providing a habitat suitability map, ENFA offers a useful tool for reintroduction planning and population monitoring.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.
**AUTHOR CONTRIBUTIONS**
Emma L. Cartledge and Melanie Baker contributed equally to the study. Melanie Baker conceived and led the habitat suitability component of the paper and Emma L. Cartledge and Melanie Baker carrying out the related data analysis. Emma L. Cartledge and Melanie Baker contributed equally to writing of the original draft, with input from Paula Stockley. Paula Stockley and Jane L. Hurst provided supervision and secured funding. Ian White provided the NDMP data and guidance on dormouse ecology and reintroduction programs. Andrea Powell, Ben Gregory, and Martin Varley provided support via a CASE partnership, with input from a conservation practitioner perspective. All authors contributed to the reviewing and editing stage of writing the manuscript.

**DATA AVAILABILITY STATEMENT**
NDMP data including exact locations for dormouse monitoring sites and reintroductions cannot be distributed without prior permission from the People’s Trust for Endangered Species. EGV maps, ENFA model outputs and code for ENFA is included in the Supporting Information (Tables S1–S4, Figures S1–S6).

**ETHICS STATEMENT**
All NDMP data was collected under dormouse handling license.

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**REFERENCES**
Angold, P. G., Sadler, J. P., Hill, M. O., Pullin, A., Rushton, S., Austin, K., ... Thompson, K. (2006). Biodiversity in urban habitat patches. *Science of the Total Environment*, 360, 196–204.

Bates, D., Maechler, 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

Blackwood, C. (2017). England land-form PANORAMA® DTM. EDINA. https://doi.org/10.7488/ds/1756

Bright, P., Morris, P., & Mitchell-Jones, T. (2006). *The dormouse conservation handbook: Working towards Natural England for people, places and nature* (2nd ed.). Peterborough: English Nature.

Bright, P. W. (1996). Status and woodland requirements of the dormouse in England (English Nature Research Report No. 166). Peterborough: English Nature Retrieved from http://publications.naturalengland.org.uk/publication/156001

Bright, P. W. (1998). Behaviour of specialist species in habitat corridors: Arboreal dormice avoid corridor gaps. *Animal Behaviour*, 56, 1485–1490.

Bright, P. W., Mitchell, P., & Morris, P. A. (1994). Dormouse distribution: Survey techniques, insular ecology and selection of sites for conservation. *Journal of Applied Ecology*, 31, 329–339.

Bright, P. W., & Morris, P. A. (1990). Habitat requirements of dormice *Muscardinus avellanarius* in relation to woodland management in Southwest England. *Biological Conservation*, 54, 307–326.

Bright, P. W., & Morris, P. A. (1991). Ranging and nesting behaviour of the dormouse *Muscardinus avellanarius*, in diverse low-growing woodland. *Journal of Zoology*, 224, 177–190.

Bright, P. W., & Morris, P. A. (1992). Ranging and nesting behaviour of the dormouse *Muscardinus avellanarius*, in coppice-with-standards woodland. *Journal of Zoology*, 226, 589–600.

Bright, P. W., & Morris, P. A. (1993). Foraging behaviour of dormice *Muscardinus avellanarius* in two contrasting habitats. *Journal of Zoology*, 230, 69–85.

Bright, P. W., & Morris, P. A. (1996). Why are dormice rare? A case study in conservation biology. *Mammal Review*, 26, 157–187.

Bright, P. W., & Morris, P. A. (2002). Putting dormice back on the map. *British Wildlife*, 14, 91–100.

Bubac, C. M., Johnson, A. C., Fox, J. A., & Cullingham, C. I. (2019). Conservation translocations and post-release monitoring: Identifying trends in failures, biases, and challenges from around the world. *Biological Conservation*, 238, 108239.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.

Butchart, S. H. M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., ... Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, 328, 1164–1168.

Capizzi, D., Battistini, M., & Amori, G. (2002). Analysis of the hazel dormouse, *Muscardinus avellanarius*, distribution in a Mediterranean fragmented woodland. *Italian Journal of Zoology*, 69(1), 25–31.

Chanin, P. (2014). *The Dormouse Reintroduction Programme: A review* (NECR144). UK: Natural England. Retrieved from http://publications.naturalengland.org.uk/publication/5914082255306752

Colles, A., Liow, L. H., & Prinzing, A. (2009). Are specialists at risk under environmental change? Neoeccological, paleoecological and phylogenetic approaches. *Ecology Letters*, 12, 849–863.

Combe, F., Ellis, J., Lloyd, K. L., Cain, B., Wheeler, C. P., & Harris, W. E. (2016). After the Ice Age: The impact of post-glacial dispersal on the phylogeography of a small mammal, *Muscardinus avellanarius*. *Frontiers in Ecology and Evolution*, 4, 1–12.

Cook, C. N., Morgan, D. G., & Marshall, D. J. (2010). Re-evaluating suitable habitat for reintroductions: Lessons learnt from the eastern barred bandicoot recovery program. *Animal Conservation*, 13, 184–195.

Cornils, J. S., Hoelzl, F., Rotter, B., Bieber, C., & Ruf, T. (2017). Edible dormice (*Glis glis*) avoid areas with a high density of their preferred food plant—the European beech. *Frontiers in Zoology*, 14, 23.

Di Febbraro, M., Sallustio, L., Vizzarri, M., De Rosa, D., De Lizio, L., Loy, A., ... Marchetti, M. (2018). Expert-based and correlative models to map habitat quality: Which gives better
support to conservation planning? Global Ecology and Conservation, 16, e00513.

Diaz, S., Settele, J., Brondizio, E. S., Ngo, H. T., Agard, J., Arneth, A., ... Garibaldi, L. A. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. Science, 366, 6471.

Dietz, M., Büchner, S., Hillen, J., & Schulz, B. (2018). A small mammal’s map: Identifying and improving the large-scale and cross-border habitat connectivity for the hazel dormouse Muscardinus avellanarius in a fragmented agricultural landscape. Biodiversity and Conservation, 27, 1891–1904.

Dyer, R. & Oliver, T. (2016). UK ecological status map version 2. NERC Environmental Information Data Centre. Retrieved from https://doi.org/10.5285/58b248a8-6e34-4fbb-ae32-3744566399a2.

Ehlers, S. (2012). The importance of hedgerows for hazel dormice (Muscardinus avellanarius) in Northern Germany. Peckiana, 8, 41–47.

Engler, R., Guisan, A., & Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology, 41, 263–274.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24, 38–49.

Fischer, J., & Lindenmayer, D. B. (2000). An assessment of the published results of animal relocations. Biological Conservation, 96, 1–11.

Foppen, R., Verheggen, L. S. G. M., & Boonman, M. (2002). Biology, status, and conservation of the hazel dormouse (Muscardinus avellanarius) in The Netherlands. Lutra, 45, 147–154.

Galparsoro, I., Borja, A., Bald, J., Liria, P., & Chust, G. (2009). Predicting suitable habitat for the European lobster (Homarus gammarus), on the Basque continental shelf (Bay of Biscay), using ecological-Niche factor analysis. Ecological Modelling, 220, 556–567.

Goodwin, C. E. D., Hodgson, D. J., Al-Fulaij, N., Bailey, S., Langton, S., & Mcdonald, R. A. (2017). Voluntary recording scheme reveals ongoing decline in the United Kingdom hazel dormouse Muscardinus avellanarius population. Mammal Review, 47, 183–197.

Goodwin, C. E. D., Hodgson, D. J., Bailey, S., Bennie, J., & McDonald, R. A. (2018). Habitat preferences of hazel dormice Muscardinus avellanarius and the effects of tree-felling on their movement. Forest Ecology and Management, 427, 190–199.

Goodwin, C. E. D., Suggitt, A. J., Bennie, J., Silk, M. J., Duffy, J. P., Al-Fulaij, N., ... McDonald, R. A. (2018). Climate, landscape, habitat, and woodland management associations with hazel dormouse Muscardinus avellanarius population status. Mammal Review, 48, 209–223.

Green, R. H. (1979). Sampling design and statistical methods for environmental biologists. New York: Wiley.

Griffith, B., Scott, J. M., Carpenter, J. W., & Reed, C. (1989). Translocation as a species conservation tool. Science, 245, 477–480.

Gyan, K. Y., & Woodell, S. R. J. (1987). Nectar production, sugar content, amino acids, and potassium in Prunus spinosa L., Crataegus monogyna Jacq. and Rubus fruticosus L. at Wytham, Oxfordshire. Functional Ecology, 1, 251–259.

Hanski, I. (1982). Dynamics of regional distribution: The core and satellite species hypothesis. Oikos, 38, 210–221.

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. UK: Joint Nature Conservation Committee 216 pp.

Hirzel, A. H., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology, 83, 2027–2036.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling, 199, 142–152.

Hopkins, J. J., & Kirby, K. J. (2007). Ecological change in British broadleaved woodland since 1947. Ibis, 149, 29–40.

Horváth, Z., Ptacnik, R., Vad, C. F., & Chase, J. M. (2019). Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. Ecology Letters, 22, 1019–1027.

Hurrell, E., & McIntosh, G. (1984). Mammal society dormouse survey, January 1975–April 1979. Mammal Review, 14, 1–18.

Hutterer, R., Krystufek, B., Yigit, N., Mitsain, G., Meinig, H. & Juškaitis, R. (2016). Muscardinus avellanarius (errata version published in 2017). The IUCN Red List of Threatened Species 2016. Retrieved from https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T13992A22222242.en.

IUCN. (2013). Guidelines for reintroductions and other conservation translocations (Vol. 1). Gland, Switzerland: IUCN SSC.

Juškaitis, R. (1999). Winter mortality of the common dormouse (Muscardinus avellanarius) in Lithuania. Folia Zoologica, 48, 11–16.

Juškaitis, R. (2005). The influence of high nestbox density on the common dormouse Muscardinus avellanarius population. Acta Theriologica, 50, 43–50.

Juškaitis, R. (2007). Peculiarities of habitats of the common dormouse, Muscardinus avellanarius, within its distributional range and in Lithuania: A review. Folia Zoologica, 56, 337.

Juškaitis, R., & Büchner, S. (2013). The hazel dormouse (1st ed.). Hohenwarsleben: Westarp Wissenschaften.

Juškaitis, R., & Šiožiūnyte, V. (2008). Habitat requirements of the common dormouse (Muscardinus avellanarius) and the fat dormouse (Glis glis) in mature mixed forest in Lithuania. Ekologia Bratislava, 27(2), 143–151.

Kalle, R., Combrink, L., Ramesh, T., & Downs, C. T. (2017). Re-establishing the pecking order: Niche models reliably predict suitable habitats for the reintroduction of re-billed oxpeckers. Ecology and Evolution, 7, 1974–1983.

Mathews, F., Harrower, C., & Mammal Society. (2020). IUCN-compliant Red List assessment for Britain’s terrestrial mammals. Peterborough: Natural England.

Matthews, T. J., Cottee-Jones, H. E., & Whittaker, R. J. (2014). Habitat fragmentation and the species-area relationship: A focus on total species richness obscures the impact of habitat loss on habitat specialists. Diversity and Distributions, 20, 1136–1146.

Mazerolle, M. J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. Retrieved from https://cran.r-project.org/package=AICcmodavg.
Mitchell-Jones, A. J., & White, I. (2009). Using reintroductions to reclaim the lost range of the dormouse, Muscardinus avellanarius, in England. *Folia Zoologica, 58*, 341–348.

Morris, P. A., Bright, P. W., & Woods, D. (1990). Use of nestboxes by the dormouse Muscardinus avellanarius. *Biological Conservation, 51*, 1–13.

Mortelliti, A., Amori, G., Capizzi, D., Cervone, C., Fagiani, S., Pollini, B., & Boitani, L. (2011). Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. *Journal of Applied Ecology, 48*, 153–162.

Mortelliti, A., Santarelli, L., Sozio, G., Fagiani, S., & Boitani, L. (2013). Long distance field crossings by hazel dormice (Muscardinus avellanarius) in fragmented landscapes. *Mammalian Biology, 78*, 309–312.

Mortelliti, A., Sozio, G., Driscoll, D. A., Bani, L., Boitani, L., & Lindenmayer, D. B. (2014). Population and individual-scale responses to patch size, isolation and quality in the hazel dormouse. *Ecosphere, 5*, 1–21.

Neupane, D., Kwon, Y., Risch, T. S., & Johnson, R. L. (2020). Changes in habitat suitability over a two-decade period before and after Asian elephant recolonization. *Global Ecology and Conservation, 22*, e01023.

Panchetti, F., Amori, G., Carpaneto, G. M., & Sorce, A. (2004). Activity patterns of the common dormouse (Muscardinus avellanarius) in different Mediterranean ecosystems. *Journal of Zoology, 262*, 289–294.

People’s Trust for Endangered Species (PTES). (2017). *National Dormouse Monitoring Programme (NDMP): Survey guidelines and recordings forms*. Retrieved from https://ptes.org/wp-content/uploads/2014/06/NDMP-guidelines-and-forms-2017.pdf.

People’s Trust for Endangered Species (PTES). (2020). *National Dormouse Monitoring Programme (NDMP) Hazel Dormouse Nest Box Dataset*. People’s Trust for Endangered Species. Unpublished.

Pope, A. (2017). *SRTM slope DEM for Great Britain*. University of Edinburgh. Retrieved from https://doi.org/10.7488/ds/1720.

Pretzlaff, I., & Daussmann, K. H. (2012). Impact of climatic variation on the hibernation physiology of Muscardinus avellanarius. In T. Ruf, C. Bieber, W. Arnold, & E. Millesi (Eds.), *Living in a seasonal world*. Berlin, Heidelberg: Springer.

Pretzlaff, I., Radchuk, V., Turner, J. M., & Daussmann, K. H. (2021). Flexibility in thermal physiology and behaviour allows body mass maintenance in hibernating hazel dormice. *Journal of Zoology, 314*, 1–11.

Pryor, S. N., Curtis, T. A. & Peterken, G. F. (2002). Restoring plantations on ancient woodland sites. The Woodland Trust. Retrieved from https://pdfs.semanticscholar.org/2de9/526c1882e7912f9fc7521d56557b56ce9bf.pdf.

QGIS.org. (2020). *QGIS Geographic Information System*. v3.4.15-Maderia. Open Source Geospatial Foundation Project. Retrieved from http://qgis.org.

R Core Team. (2020). *R: A language and environment for statistical computing. Version 4.0.0 and Version 4.0.2*. [Computer Programme]. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Ramakers, J. J., Dorenbosch, M., & Foppen, R. P. (2014). Surviving on the edge: A conservation-oriented habitat analysis and forest edge manipulation for the hazel dormouse in The Netherlands. *European Journal of Wildlife Research, 60*, 927–931.

Richards, C. G. J., White, A. C., Hurrell, E., & Price, F. E. F. (1984). The food of the common dormouse, Muscardinus avellanarius, in South Devon. *Mammal Review, 14*(1), 19–28.

Rinnan, D. S. (2020). *CENFA: Climate and Ecological Niche Factor Analysis*. R package version 1.1.0.9000. Retrieved from https://CRAN.R-project.org/package=CENFA.

Rinnan, D. S., & Lawler, J. (2019). Climate-niche factor analysis: A spatial approach to quantifying species vulnerability to climate change. *Ecography, 42*, 1494–1503.

Rowland, C. S., Morton, R. D., Carrasco, L., McShane, G., O’Neil, A. W. & Wood, C. M. (2017). *Land Cover Map 2015 (1km percentage aggregate class, GB)*. NERC Environmental Information Data Centre. Retrieved from https://doi.org/10.5285/7115bc48-3ab0-475d-84ae-fd3126c20984.

Sanderson, F., Bright, P., & Trout, R. (2004). Management of broadleaved and coniferous woodland to benefit hazel dormice. In C. Quine, R. Shore, & R. Trout (Eds.), *Managing woodlands and their mammals*. Proceedings of a symposium organised jointly by the Mammal Society and the Forestry Commission (pp. 19–24). Edinburgh: Forestry Commission.

Santos, X., Brito, J. C., Sillero, N., Pleguezuelos, J. M., Llorente, G. A., Fahd, S., & Parellada, X. (2006). Inferring habitat-suitability areas with ecological modelling techniques and GIS: A contribution to assess the conservation status of Vipera latastei. *Biological Conservation, 130*, 416–425.

Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczynski, P., Breitenmoser, U., ... Stanisła, C. (2002). Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology, 39*, 189–203.

Schulz, B., Ehlers, S., Lang, J., & Büchner, S. (2012). Hazel dormice in roadside habitats. *Peckiana, 8*, 49–55.

Seddon, P. J. (1999). Persistence without intervention: Assessing success in wildlife reintroductions. *Trends in Ecology & Evolution, 14*, 503.

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology, 21*, 303–312.

Soulé, M., & Orians, G. (2001). *Conservation biology: Research priorities for the next decade*. Washington: Island Press.

Spencer, J. W., & Kirby, K. J. (1992). An inventory of ancient woodlands and their mammals. Proceedings of a symposium organised jointly by the Mammal Society and the Forestry Commission (pp. 19–24). Edinburgh: Forestry Commission.

Stoa, B., Halvorsen, R., Mazzoni, S., & Gusarov, V. I. (2018). Sampling bias in presence-only data used for species distribution modelling: Theory and methods for detecting sample bias and its effects on models. *Sommerfeltia, 38*(1), 1–53.

Stolar, J., & Nielsen, S. E. (2015). Accounting for spatially biased sampling effort in presence-only species distribution modelling. *Diversity and Distributions, 21*(5), 595–608.

Trout, R. C., Brooks, S., Combe, F. J., & Rudlin, P. (2018). The different effects of periodic experimental tree removal patterns on the population demography of the hazel dormice (Muscardinus avellanarius) in a conifer plantation. *Folia Zoologica, 67*(2), 110–119.
Wembridge, D., Al-Fulaij, N. & Langton, S. (2016). The State of Britain’s Dormice 2016. People’s Trust for Endangered Species. Retrieved from https://ptes.org/wp-content/uploads/2016/09/State-of-Britains-Dormice-2016.pdf.

Wembridge, D., White, I., Al-Fulaij, N., Marnham, E. & Langton, S. (2019). The State of Britain’s Dormice 2019. People’s Trust for Endangered Species. Retrieved from https://www.launcestonparishwildlife.org.uk/wp-content/uploads/2019/12/SoBD-2019.pdf.

White, I. (2012). The National Dormouse Monitoring Programme in Britain. *Peckiana, 8*, 89–93.

White, I. (2019). *Hazel Dormouse Reintroduction Sites Report 2019*. People’s Trust for Endangered Species. Retrieved from https://ptes.org/wp-content/uploads/2019/07/20190717_Dormouse-Reintroduction-Report-2019.docx.pdf.

Wolf, C. M., Garland, T., & Griffith, B. (1998). Predictors of avian and mammalian translocation success: Reanalysis with phylogenetically independent contrasts. *Biological Conservation, 86*, 243–255.

Wolf, C. M., Griffith, B., Reed, C., & Temple, S. A. (1996). Avian and mammalian translocations: Update and reanalysis of 1987 survey data. *Conservation Biology, 10*, 1142–1154.

Wuttke, N., Büchner, S., Roth, M., & Böhme, W. (2012). Habitat factors influencing the distribution of the hazel dormouse (*Muscardinus avellanarius*) in the Ore Mountains, Saxony, Germany. *Peckiana, 8*, 21–30.

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Additional supporting information may be found in the online version of the article at the publisher’s website.

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