Applying remotely sensed habitat descriptors to assist reintroduction programmes: a case study in the hazel dormouse

Running title

Habitat descriptors assisting reintroductions

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Key words

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

Target audience

Researchers and practitioners who are interested in assisting reintroduction programmes, through site selection and population analysis.

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1. Authors' Contributions

ELC and MB contributed equally to the study. MB conceived and led the habitat suitability component of the paper and ELC conceived and led the reintroduction population component, with ELC and MB carrying out the related data analysis. ELC and MB contributed equally to writing of the original draft, with input from PS. PS and JLH provided supervision and secured funding. IW provided the NDMP data and guidance on dormouse ecology and reintroduction programmes. AP, BG and MV 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.

2. Ethics Statement

All NDMP data was collected under dormouse handling licence.

3. Data Accessibility 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 (Table S1 – S4, Fig. S1 – S6).

4. Conflict of Interest

The authors declare no conflict of interest.

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Abstract

For reintroduction programmes 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 programme in the UK. The programme 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 hypothesised 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 generalised 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 prioritise 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.

Key Words

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

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 et al. 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 et al. 2009, Matthews et al. 2014, Díaz et al. 2019). *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 (Seddon et al. 2007, IUCN 2013).

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 et al. 1989). Reintroduction sites need high quality habitat that is preferably located within the historical range of the species (Griffith et al. 1989, Wolf et al. 1996, Wolf et al. 1998, IUCN 2013, Bubac et al. 2019), with the original cause of decline removed (Fischer & Lindenmayer 2000, Bubac et al. 2019). However, many reintroductions do not meet these conditions, and reintroduction successes could be as low as 23% (Griffith et al. 1989, Wolf et al. 1996, Fischer & Lindenmayer 2000). To improve the chances of success, potential reintroduction programmes should be thoroughly assessed at the outset, and target sites should meet species-specific habitat requirements and implement any necessary ongoing habitat management programmes (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 modelling 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 erythrorhynchus*, Kalle et al. 2016), eastern barred bandicoot (*Perameles gunnii,* Cook et al. 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 modelling approaches to assist reintroduction planning (Seddon et al. 2007).

The arboreal hazel dormouse, *Muscardinus avellanarius*, has typically been associated with diverse ancient woodlands (Bright & Morris 1990, Bright et al. 1994, Harris et al. 1995), due to relying on a variety of seasonal foods, such as flowers, fruits and invertebrates (Richards et al. 1984, Bright & Morris 1993). 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, Juškaitis & Šiožinyte 2008; Goodwin et al. 2018a). 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 (Hurrell & McIntosh 1984, Bright & Morris 1996). This is thought to be due to habitat fragmentation, deterioration and loss, and changes in habitat management practices (Bright & Morris 1990, 1996, Bright et al. 1994, Mortelliti et al. 2011).

Since the early 1990s, dormice have been monitored via a co-ordinated programme 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 maximise 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. Favoured vegetation types vary depending on geographic location (Ramakers et al. 2014). In Germany and Lithuania, dormice inhabit spruce-dominated mixed forests with overgrown clearings (Wuttke et al. 2012, Juškaitis 2007), whereas in the Netherlands well-developed deciduous forests and hedgerows are favoured (Foppen et al. 2002). In England, dormouse presence has historically been associated with ancient coppiced woodlands (Goodwin et al. 2018b). However, ancient woodlands have declined in abundance and size, covering only 2.6% of England and Wales and 87% are less than 20 ha (Spencer & Kirby 1992, Bright et al. 1994, Mitchell-Jones & White 2009). 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 programme (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 et al. 2002, 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 et al. 2006). The approach has been successfully used across diverse taxa (Engler et al. 2004, Galparsoro et al. 2009, Neupane et al. 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 eco-geographical 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 generalised linear mixed modelling 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.

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-25th), with at least one pre-breeding survey (May/June) and one post-breeding 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).

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-Maderia), using the British National Grid co-ordinate reference system, into a Boolean raster map of the study area (England) to a resolution of one hectare. This resolution was chosen to match the home range of dormice, as the size of monitoring sites varies across locations (Bright & Morris 1991, Mortelliti et al. 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, Fig. 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, Fig. 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 300m 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 100m 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 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 specialisation 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.

Specialisation 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 specialisation.

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.

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 (Fig. S3, Table S3).

Analysis of habitat factors explaining population trends in reintroduced dormouse populations

We used generalised linear mixed models (GLMMs) to analyse the factors most strongly influencing dormouse population size across current reintroduction sites. GLMMs were run using the package lme4 (Bates et al. 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 standardised 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) (Burham & 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).

Identifying suitable future reintroduction sites

To demonstrate the practical application of ENFA modelling, 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 & Morris 1992, Bright et al. 1994).

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.

Results

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 specialisation factors 1-4, which contribute to the total specialisation score, along with the other specialisation factors) account for 50% of the total specialisation (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 300m 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). Specialisation 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 specialisation factor derived accounts for 24.7% of specialisation 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 specialisation factor accounts for 11.0% of specialisation; 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 300m 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.

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 (Fig. 1a, approximately 1 in 13 chance one year after reintroduction compared to approximately 1 in 80 chance 25 years after reintroduction). We also found evidence of seasonal population trends (Fig. 1b), with a Tukey test revealing significantly greater chances of finding adult dormice in nest boxes in autumn than in spring ($p< 0.001$) and summer ($p< 0.001$), but no difference between spring and summer ($p= 0.563$). 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 (Fig. 1c). Similarly, the chance of finding adult dormice in a nest box decreased with an increased slope gradient in the region (Fig. 1d) and with an increasing proportion of arable land nearby (Fig. 1e). Lastly, the further east the site, the higher the chance of finding adult dormice in nest boxes (Fig. 1f).

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 (Fig. 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, $\chi^2 = 502.31$, df = 2, $p < 0.001$, Fig. S4). Natural populations occupy sites with significantly better suitability scores compared to both the rest of England ($p < 0.001$) and reintroduction sites ($p < 0.001$). Current habitat suitability scores at reintroduction sites are more similar to the scores of the rest of England, but still differ significantly ($p = 0.015$).

Can habitat suitability modelling help identify suitable future reintroduction sites?

Here, we focus on one county in the UK (Cheshire) to demonstrate the potential practical application of ENFA modelling. 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 (Fig. 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 (Fig. 3). By contrast, the 1996 Cheshire reintroduction is currently in 'least suitable' habitat, according to our model.

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 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 et al. 2016). The model further highlights the importance of broadleaved woodlands to hazel dormice (Sanderson et al. 2004, Goodwin et al. 2018a), 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 et al. 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, Bright, & Trout 2004, Schulz et al. 2012, Trout et al. 2018). Whilst presence-only data has advantages, when creating a species distribution model, it is more prone to sampling bias (Stolar & Nielsen 2015, Støa et al. 2018). 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 & Morris 1993, Bright 1998, 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 et al. 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 et al. 2018a). 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 et al. 2018a). 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 et al. 2018a). 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 urbanisation (Hopkins & Kirby 2007). Assessments of ancient woodlands have identified common topographical features such as ravines, rock outcrops and gullies (Pryor et al. 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 favoured by the edible dormouse, *Glis glis*, in Austria (Cornils et al. 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 two weeks (Gyan & Woodell 1987, Goodwin et al. 2018b).

Despite long-term conservation efforts, natural hazel dormouse populations are still declining in the UK (Wembridge et al. 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 (Griffith et al. 1989, Wolf et al. 1996, Wolf et al. 1998, Fischer & Lindenmayer 2000), 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 were 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 behavioural responses to climate conditions, where they can maintain sufficient body mass even during periods of more frequent arousal, but food availability remains vital (Pretzlaff et al 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 (Morris et al. 1990, Juškaitis 2005). 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 (Panchetti et al. 2004, Juškaitis & Büchner 2013). 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 & Morris 1990, Bright et al. 1994, 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 colonisation at potential reintroduction sites (Dietz et al. 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 (Griffith et al. 1989, Wolf et al. 1996, Wolf et al. 1998, Bubac et al. 2019).

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 analysing 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 centre and east of Cheshire (Fig. 3). The potential of a reintroduction site should be analysed 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 modelling 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 programmes 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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Table 1. A set of 55 eco-geographical variables (EGV) for Ecological Niche Factor Analysis (ENFA). EGVs ending in '_FQ' are frequency variables and '_DT' are distance variables. EGVs highlighted with '*' were found to have high correlation with other EGVs and were removed from the final ENFA model.

Class	Eco-Geographical Variable	Source
Land Cover	Acid Grassland_DT	UKCEH
	Acid Grassland_FQ	UKCEH
	Arable Horticulture_DT	UKCEH
	Arable Horticulture_FQ	UKCEH
	Bare Ground/ Rock_DT	FC
	Bare Ground/ Rock_FQ	FC
	Broadleaved Woodland_DT	UKCEH
	Broadleaved Woodland_FQ	UKCEH
	Calcareous Grassland_DT	UKCEH
	Calcareous Grassland_FQ	UKCEH
	Coniferous Woodland_DT	UKCEH
	Coniferous Woodland_FQ	UKCEH
	Coppice_DT	FC
	Coppice_FQ	FC
	Felled Trees_DT	FC
	Felled Trees_FQ	FC
	Heather Grassland_DT	UKCEH
	Heather Grassland_FQ	UKCEH
	Heather_DT	UKCEH
	Heather_FQ	UKCEH
	Improved Grassland_DT	UKCEH
	Improved Grassland_FQ	UKCEH
	Inland Rock_DT	UKCEH
	Inland Rock_FQ	UKCEH
	Low Density Forest_DT	FC
	Low Density Forest_FQ	FC
	Neutral Grassland_DT	UKCEH
	Neutral Grassland_FQ	UKCEH
	Shrub_DT	FC
	Shrub_FQ	FC
	Young Trees_DT	FC
	Young Trees_FQ	FC

Class	Eco-Geographical Variable	Source
Anthropogenic	*Buildings_DT	OS
	Major Towns and Cities_DT	ONS
	Railways_DT	OS
	Roads_DT	OS
	Suburban_DT	UKCEH
	Suburban_FQ	UKCEH
	Urban_DT	UKCEH
	Urban_FQ	UKCEH
Hydrography	Canal_DT	OS
	Coast_DT	OS
	Inland Rivers_DT	OS
	Lakes_DT	OS
	*Tidal Rivers_DT	OS
Topography	Aspect	OS
	Elevation	EDD
	Slope	OS
	*Terrain	EDD
Other	Agricultural Land Classification	NE
	Ecological Status	UKCEH
	Local Nature Reserves_FQ	NE
	National Nature Reserves_FQ	NE
	Sites of Special Scientific Interest_FQ	NE
	*Special Areas of Conservation_FQ	NE

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).

Table 2. The top 10 eco-geographical variables (EGVs) for each of the first three factors (a) marginality, (b) specialisation 1 and (c) specialisation 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[e]
Broadleaved Woodland_FQ	2.32
Slope	0.95
Arable Horticulture_FQ	-0.60
Broadleaved Woodland_DT	-0.58
Felled Trees_DT	-0.56
Coniferous Woodland_DT	-0.51
Coppice_FQ	0.49
Agricultural Land Classification	0.43
Heather_DT	-0.42
Coast_DT	-0.39

(b)

EGV	Specialisation 1[f]
Urban_FQ	-0.93
Broadleaved Woodland_DT	0.36
Arable Horticulture_FQ	-0.05
Heather_DT	-0.05
Major Towns and Cities_DT	-0.04
Improved Grassland_DT	0.03
Improved Grassland_FQ	-0.03
Suburban_DT	0.03
Agricultural Land Classification	-0.03
Coniferous Woodland_DT	-0.02

(c)

EGV	Specialisation 2[f]
Arable Horticulture_DT	0.55
Improved Grassland_DT	0.44
Arable Horticulture_FQ	-0.36
Urban_FQ	0.23
Improved Grassland_FQ	-0.22
Acid Grassland_FQ	-0.22
Canal_DT	0.18
Urban_DT	0.17
Coniferous Woodland_DT	-0.16
Heather_DT	-0.14

(d)

EGV	Sensitivity[g]
Urban_FQ	27.75
Broadleaved Woodland_DT	16.91
Arable Horticulture_FQ	10.51
Arable Horticulture_DT	9.87
Acid Grassland_FQ	8.16
Improved Grassland_DT	7.47
Improved Grassland_FQ	7.41
Canal_DT	5.97
Heather_DT	5.33
Suburban_DT	5.26

Factors ending in '_FQ' or '_DT' indicate frequency and distance measures, respectively.

[e] Marginality 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.

[f] Specialisation scores are built off the marginality score and only absolute values are important.

[g] Sensitivity 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.

Table 3. Top five generalised 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[a]	**K**	**ΔAICc**
[b] Time since reintroduction + season + broadleaved woodland FQ + slope gradient + arable horticulture FQ + longitude *<u>Best-fitting model equation:</u>* *Number of adult dormice = -1.656 - 0.065 (time since reintroduction) - 0.781 (spring) - 0.866 (summer) - 0.206 (broadleaved woodland FQ) - 0.513 (slope) - 1.043 (arable horticulture FQ) + 0.797 longitude + (1 | site)*	10	0.00
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

[a] 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.

[b] Best-fitting model.

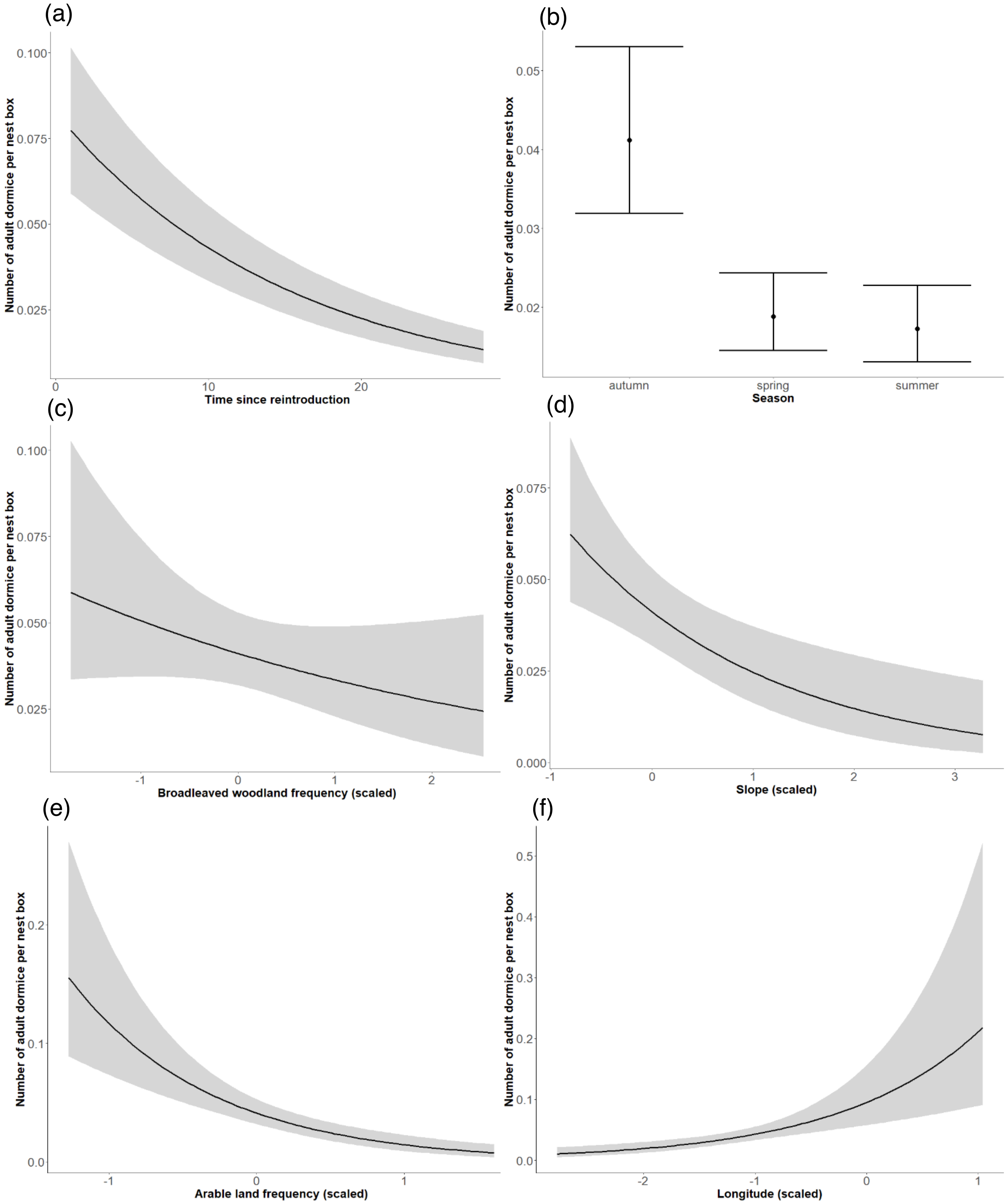
Figure 1. The factors that best describe the number of hazel dormice at reintroduction sites, based on GLMM analyses. The number of adult dormice per nest box is shown, according to (a) time since reintroduction, (b) season, (c) broadleaved woodland frequency, (d) slope, (e) arable land frequency, (f)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

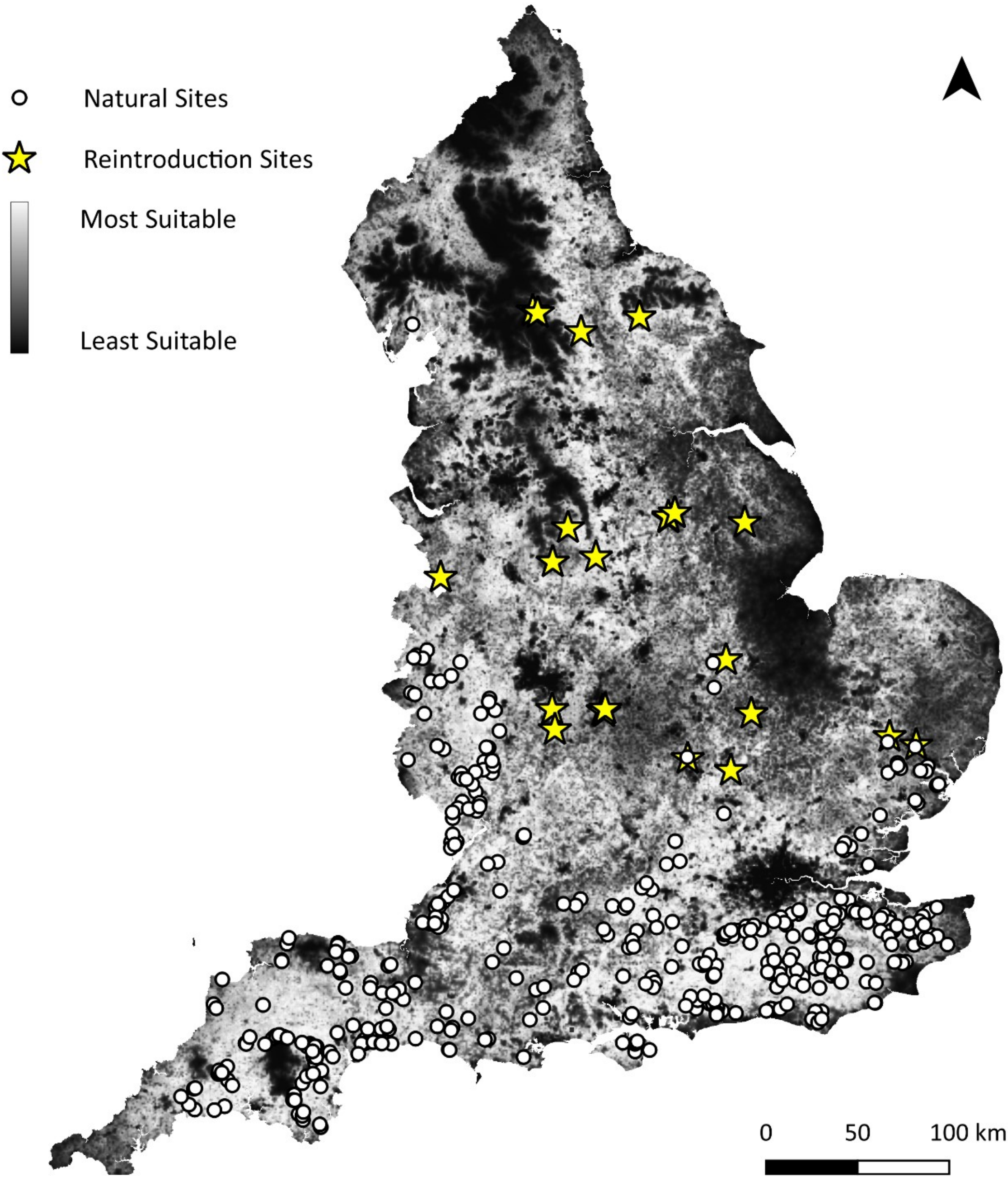
Figure 2. Habitat suitability map for hazel dormice in England UK. Lighter regions indicate more suitable habitats and darker regions indicate less suitable habitats. Small open circles indicate locations of 410 sites where natural dormice populations are monitored. Large yellow stars indicate locations of 24 sites where hazel dormice have been reintroduced. Where open circles and yellow stars overlap on the map, the symbols represent different sites that are geographically close together. The map contains, or is based on, information supplied by: The Forestry Commission (© Crown copyright and database right 2020 Ordnance Survey. License number: 100021242); Natural England (© Natural England copyright. Contains Ordnance Survey data © Crown copyright and database right [2020]); Ordnance Survey (Ordnance Survey data © Crown copyright and database right 2020); UKCEH (Dyer and Oliver, 2016, Rowland et al. 2017 - LCM2015 © and database right NERC (CEH) 2017. All rights reserved. Contains Ordnance Survey data © Crown copyright and database right 2007); Edinburgh Data Share (Blackwood, 2017, Pope, 2017).

Figure 3. Application of the model for identifying potential reintroduction sites. Each filled circle on the map represents a woodland, larger than 10 ha, within the county of Cheshire, UK. The size of the circles represents the relative total area of each woodland (small = 10-19ha, medium = 20-49ha and large = 50-80ha) and their colour represents habitat suitability of each woodland calculated as a mean of the raw habitat suitability scores found within the area of the woodland (red = least suitable, amber = marginal, green = most suitable). Habitat suitability categorisation was based upon the distribution of suitability values for all 410 NDMP sites with most suitable (< median), marginal (> median, < third quartile) and least suitable habitats (> third quartile). Sites meeting the highest category for size and suitability are indicated by a star. Note that the reintroduction which took place in 1996 is currently in least suitable habitat, but is not indicated on the map due to a confidentiality agreement with the landowner. The background maps habitat

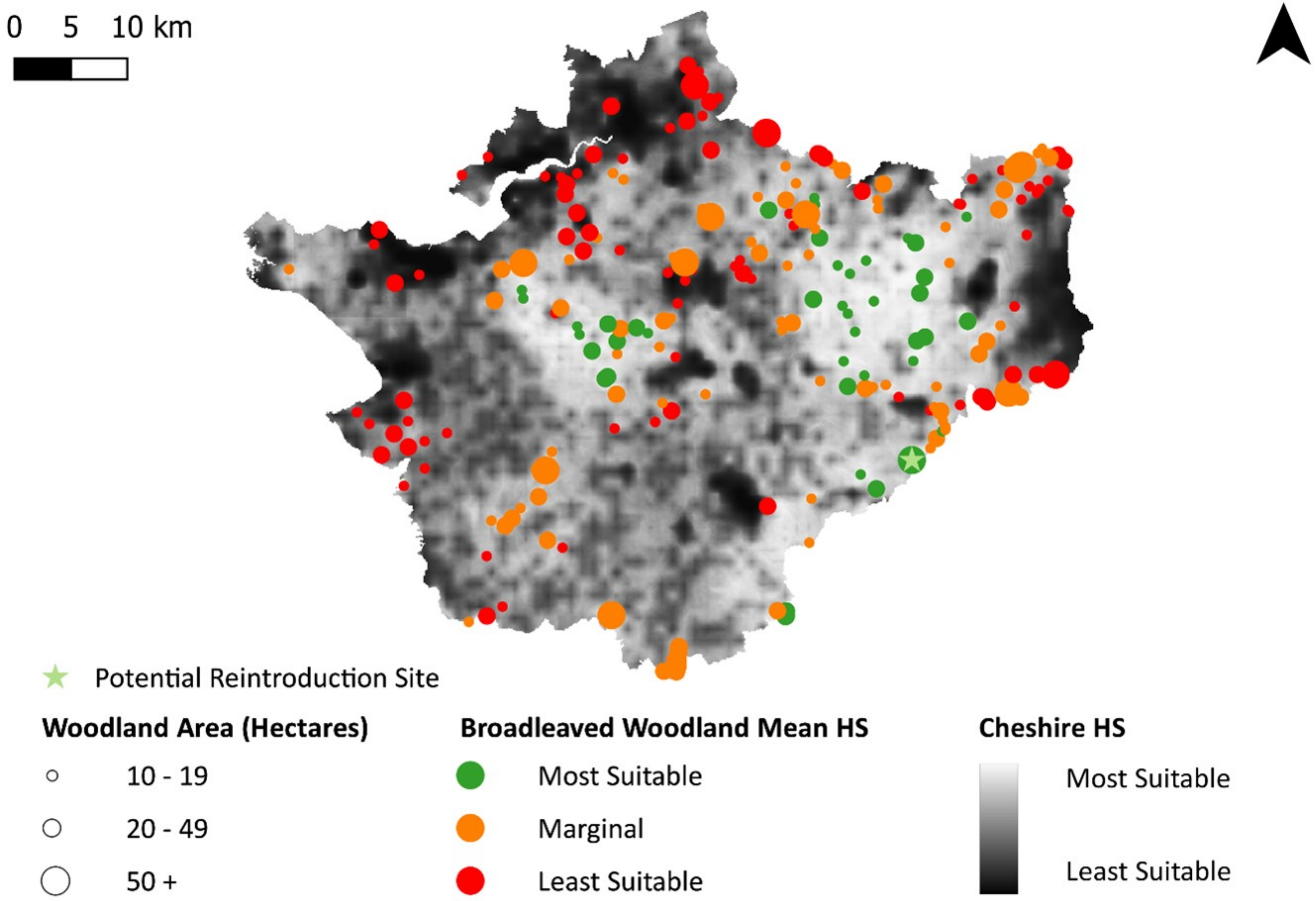
suitability values for hazel dormice across Cheshire, ranging from the most suitable areas (light coloured) to the least suitable (dark coloured) as produced by the model. Woodland data were obtained from the National Forest Inventory Woodland England 2018. See Figure 2 for data copyright statements.

Figure 1.


(a)
0.100
0.075
0.050
0.025
Number of adult dormice per nest box
0
10
20
Time since reintroduction
(b)
0.05
0.04
0.03
0.02
Number of adult dormice per nest box
autumn
spring
summer
Season
(c)
0.100
0.075
0.050
0.025
Number of adult dormice per nest box
-1
0
1
2
Broadleaved woodland frequency (scaled)
(d)
0.075
0.050
0.025
0.000
Number of adult dormice per nest box
-1
0
1
2
3
Slope (scaled)
(e)
0.2
0.1
0.0
Number of adult dormice per nest box
-1
0
1
Arable land frequency (scaled)
(f)
0.5
0.4
0.3
0.2
0.1
0.0
Number of adult dormice per nest box
-2
-1
0
1
Longitude (scaled)



Natural Sites
Reintroduction Sites
Most Suitable
Least Suitable
0
50
100 km


0 5 10 km
Potential Reintroduction Site
Woodland Area (Hectares)
10 - 19
20 - 49
50 +
Broadleaved Woodland Mean HS
Most Suitable
Marginal
Least Suitable
Cheshire HS
Most Suitable
Least Suitable