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Article

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology

WILEY

Current and future climate suitability for the hazel dormouse in the UK and the impact on reintroduced populations

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Abstract

Reintroductions are increasingly being used as a conservation tool to restore species to areas where they once existed. Unfortunately, many reintroduction projects fail to establish viable populations. Climate suitability at release sites is thought to be important in determining reintroduction outcomes, and future climate change is an essential consideration for effective reintroduction planning. Climate change threatens species in a variety of ways, such as by impacting life history traits or causing spatial and temporal distribution mismatches of interdependent species. Hibernating species, such as the hazel dormouse (*Muscardinus avellanarius*), may be particularly susceptible to changes in climate. For example, milder winters may increase the number of interbout arousals during hibernation, which are energetically costly. Timing of food availability may also be impacted by changing climates, potentially causing mismatches between activity and feeding opportunities. Here, we use species distribution models (SDMs) to map climate suitability for dormice in the UK. We also investigate the impact of climate suitability on a long-running dormouse reintroduction programme, providing the first such investigation for a reintroduced mammal. We find that higher levels of current climate suitability increase the probability of reintroduction success. We find no effect of climate suitability on adult dormouse counts at reintroduction sites, but dormouse counts decline with time since reintroduction. Future projections predict that climate change may lead to more widespread climate suitability for dormice in the UK, reflecting predicted changes in seasonality, winter temperature and precipitation. Our work demonstrates the importance of understanding changing climate suitability for reintroduction planning, with potential widespread applications of SDMs for conservation projects of low-dispersing mammals.

KEYWORDS
climate change, conservation planning, mammals, predictive modeling, remote sensing, threatened species

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1 | INTRODUCTION

Climate change is contributing to global biodiversity loss by impacting all levels of biodiversity from organism to biome (IPBES, 2019; Parmesan, 2006). Changing climate can directly impact species, for example those that are living at thermal limits, or act by compromising life history traits. It is also indirectly impacting species that rely on certain habitats or food sources, leading to mismatches in distribution or timings of food availability (Line Bellard et al., 2012). There is limited evidence as to the number of species that have been lost directly due to climate change, but it is expected that it will surpass habitat destruction as the biggest global threat to biodiversity (Leadley et al., 2010). The future impacts on species will depend on the trajectory of various climate change scenarios.

In response to the biodiversity crisis, rising numbers of reintroductions are taking place every year (Armstrong et al., 2019; Seddon et al., 2007). Unfortunately, despite increasing research, reintroduction programmes still have a low chance of success (Bubac et al., 2019), so it is important to understand the factors impacting reintroduction outcomes. Some of the key factors thought to increase the risk of failure include unsuitable habitat (Berger-Tal et al., 2020; Germano & Bishop, 2009; Wolf et al., 1996), not removing the initial cause of decline (Bubac et al., 2019; Fischer & Lindenmayer, 2000; Kleiman, 1989) and an insufficient number of individuals released (Fischer & Lindenmayer, 2000; Wolf et al., 1998). Reintroductions are generally more successful if the species is released within its historical range (Berger-Tal et al., 2020; Bubac et al., 2019; Griffith et al., 1989; Wolf et al., 1998). However, if the climate has changed, some areas of the historical range may no longer be suitable.

A recent study demonstrated the importance of assessing climate suitability in translocations of ectothermic taxa, finding that project outcomes were better in areas with higher predicted climate suitability (Bellis et al., 2020). Furthermore, predicted climate suitability was the strongest determinant of success when compared to other more conventional predictors of translocation outcome, such as the number of individuals released and the origin of the source population (Bellis et al., 2020). However, few reintroduction programmes utilize climate suitability estimates for planning, instead relying on known previous occupancy (but see Rusconi et al., 2022). Given the low success rates of reintroductions, limited conservation funding and dealing with species of conservation concern, it is essential to understand the potential impacts of current climate suitability and climate change.

The IUCN reintroduction guidelines (IUCN, 2013) recommend that "the climate requirements of the focal species should be understood and matched to current and/or future climate at the destination site." Species distribution models (SDMs) are recommended to locate suitable release sites effectively and rapidly (IUCN, 2013; Osborne & Seddon, 2012). Species distribution models identify statistical relationships between species presence data and environmental descriptors, such as climate or habitat, and are a useful tool for aiding reintroduction site selection (Bellis et al., 2020; Di Febbraro et al., 2018).

Hibernating species may be particularly susceptible to climate change (Lane et al., 2012; Rézouki et al., 2016). In response to poor environmental conditions, around half of all mammalian orders contain species that enter a multiday torpor (Geiser & Ruf, 1995; Turbill et al., 2011). During hibernation, animals will reduce body temperature and metabolic rate to conserve energy. Hibernation is generally associated with slow life-history strategies (Turbill et al., 2011) and can increase chances of survival by reduced starvation, and in some species, reduced predation (Ruf & Bieber, 2023; Turbill et al., 2011). Costs associated with hibernation include reduced immune function, increased telomere degradation and increased predation in some species (Estók et al., 2010; Nowack et al., 2019; Predergast et al., 2002). These costs can be reduced by occasional arousal from hibernation, known as interbout arousals (Humphries et al., 2003). Interbout arousals are themselves energetically costly, so their frequency should be optimized (Boyles et al., 2020).

Climate change may impact hibernating species in multiple ways, but the direction and magnitude of impact is likely to vary across mammalian species (Findlay-Robinson et al., 2023). Hibernation is thought to be an energy-saving mechanism during periods of poor environmental conditions, therefore the changing climate is likely to have strong impacts. Climatic cues affect the timing of emergence from hibernation and warming air temperatures are associated with earlier emergence in species groups such as Rodentia, which can lower chances of survival (Findlay-Robinson et al., 2023; Turbill & Prior, 2016). Timing of food availability may not be driven by the same cues as those which lead to emergence from hibernation, which could lead to limited resources when animals enter their active period (Lane et al., 2012). If winters are milder, interbout arousals may increase (Findlay-Robinson et al., 2023), causing energetic costs and depleting fat reserves. Early emergence from hibernation would lead to reallocation of energy resources, which is likely to influence other life-history traits, such as litter size, parturition date and offspring survival rates, in turn impacting individual and population fitness (Findlay-Robinson et al., 2023;

Maldonado-Chaparro et al., 2017). Conversely, there are also suggestions that hibernators may be more adaptable to climate change and climatic extremes, due to having more plastic energetic requirements (Geiser & Turbill, 2009).

The hazel dormouse (*Muscardinus avellanarius*) is a hibernating rodent, with a current distribution across Europe and Asia Minor (Hutterer et al., 2021). In the UK, dormice were historically found across England and Wales, but are now mostly restricted to southern England and parts of Wales, having lost over half of their range (Bright & Morris, 1996; Hurrell & McIntosh, 1984). The population is in decline and reduced by 72% between 1993 and 2014 (Goodwin et al., 2017), leading to a Red List status of Vulnerable (Mathews & Harrower, 2020). Dormice are generally associated with diverse deciduous and mixed woodland, with a well-developed understorey (Bright et al., 1994; Bright & Morris, 1990; Harris et al., 1995). It is thought their decline is linked to habitat loss, fragmentation and a change in woodland management practices, with previous work also suggesting that climate change is likely to have had an impact (Bright et al., 2006; Bright & Morris, 1996; Goodwin, Suggitt, et al., 2018).

Dormice are monitored in the UK as part of the National Dormouse Monitoring Programme (NDMP; White, 2012) and ad hoc records are kept in the National Dormouse Database, which is maintained by the People's Trust for Endangered Species (PTES). The NDMP currently comprises over 400 sites, including around 30 reintroduction sites, so generates a large amount of data. At every site, nest boxes are surveyed at least twice a year by licensed volunteers, who record evidence of dormice (animals or dormouse nests present). Any animals that are present are counted, sexed, and weighed, providing information on demographics at each site through time.

The dormouse reintroduction programme has been running since 1993 and releases have taken place almost annually since (White, 2019); however, it has been reported to be very difficult to select appropriate release sites (White, 2014). The aim of the programme is to re-establish dormouse populations within the historic range; therefore, most of the sites are in central and northern England. According to NDMP monitoring, even though short-term success has been reported at the majority of sites (with dormice surviving the first two winters), around half have failed to maintain viable populations for longer than 10 years (White, 2019). Currently, reintroduction planning is focused on selecting suitable locations based on habitat and access (White, 2014), so there is a need for more detailed understanding of how climate impacts dormice (Phillips et al., 2022), both now and under future climate change scenarios.

Existing evidence indicates that reintroduction sites are performing better in eastern England, with larger populations, which was suggested to be due to more climate stability in these regions (Cartledge et al., 2021). Dormice benefit from warmer, drier, sunnier springs, summers, and autumns, as well as colder, drier winters (Bright et al., 1996; Combe et al., 2022; Goodwin, Suggitt, et al., 2018). Climate change in the UK is likely to lead to warmer winters and hotter summers, with periods of flooding and drought (Defra, 2022), all of which may be detrimental to remaining populations. Dormouse interbout arousals increase with warmer winters, which is costly (Pretzlaff & Dausmann, 2012). Despite these concerns, there is evidence that dormice might be adaptable to changing climate (Pretzlaff et al., 2021; Pretzlaff & Dausmann, 2012) and even now in some climates, dormice have a limited hibernation period or do not hibernate at all (Panchetti et al., 2004).

In this study, we investigate current and future climate suitability for hazel dormice in the UK. We explore whether current climate suitability impacts reintroduced dormouse populations, both in terms of reintroduction outcome and adult nest box counts. To investigate the impacts of climate change on dormice, we project climate suitability into the future (2050 and 2070) and discuss what this may mean for dormouse conservation and the reintroduction programme.

2 | METHODS

All data analysis was carried out in R version 4.2.1 (R Core Team, 2022). We projected all spatial data into the WGS84 co-ordinate reference system (latitude/longitude, EPSG code 4326), unless stated otherwise.

2.1 | Dormouse presence data

Dormice are currently monitored in woodlands in England and Wales, as part of the NDMP, which began in 1988 (White, 2012). Since its inception, the NDMP has collected data on 671 sites, with around 400 sites currently being actively monitored. National Dormouse Monitoring Programme surveys are undertaken by licensed volunteers and take place up to once a month, but with at least one survey before breeding (May/June) and one after breeding (September/October). Further information on NDMP surveys can be found online (PTES, 2017). Alongside this monitoring scheme, the PTES collects ad hoc dormouse records, which are not restricted to woodland sites, and may incorporate public records. This ad hoc data combined with the NDMP is known as the National Dormouse Database (NDD;

PTES, 2022). Records within the NDD date back to 1969 and are graded according to the reliability of the source. Therefore, most of the occurrence data is derived from dormice that use nest boxes. Monitoring techniques such as this likely only capture a subset of the population. For example, if there are other traits that are associated with this nest box use, this could potentially influence the model output by leading to incorrect presence estimates. However, by incorporating data from the NDD, our study maximizes the use of occurrence data from all potential sources.

When mapping current dormouse occurrence, we considered dormice to be present at any of the 671 NDMP sites within England and Wales that had recorded dormice at least once, or at locations of dormouse recordings in the NDD since 1980, with reliability scores of "good" (thus removing all "poor" and "fair" assessments). With occurrence data taken up to February 2022, this totaled 4218 locations where dormice had been recorded. These records were then combined and thinned to a resolution of 1 km². To create the set of dormouse occurrence data, we then removed the reintroduction sites and any dormouse presence records within 2 km of the reintroduction site (to remove records of any dispersed reintroduced dormice). We chose 2 km as it is thought that the majority of dormice disperse no further than 2 km (Juškaitis & Büchner, 2013; Schulze, 1987). This meant we could focus on climatic suitability based upon naturally remaining dormouse populations. After this, the total number of dormouse occurrence records was 2522 1-km² grid cells (Figure 1a).
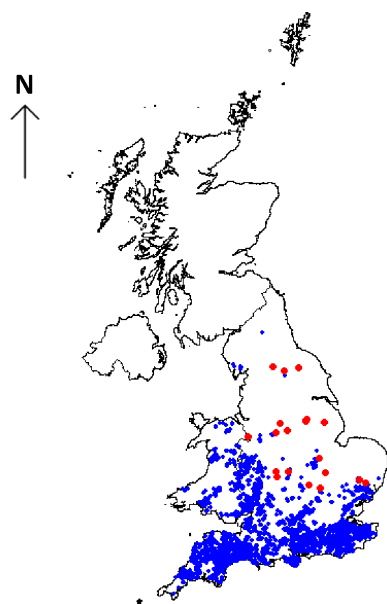
FIGURE 1 The dormouse presence points used as presence data in our current SDMs, after thinning down to 1 km² (current: 1980–2021). Red points represent reintroduction site locations used for analysis in this study (up to 2015).

2.2 | Climate data

We downloaded current and future climate data from the World Clim Database (Fick & Hijmans, 2017) at a 30 arc-sec resolution, which approximately equates to 1 km² at the equator. All species are influenced by factors at multiple scales and dormice specifically have some fine-scale needs. For example, microclimate is thought to have an impact on dormouse habitat use (Bright & Morris, 1996). At a 1 km scale, our SDMs do not take into account these fine-scale effects of climate suitability on dormice, but they offer a valuable oversight of how climate suitability can affect dormice at a macro scale.

Bioclimatic variables for the current period are averaged across 1970–2000. Using a climate normal (a three-decade average of climatic variables), our approach is robust to short-term anomalies and allows us to fit multivariate models, such as the SDMs used here. The future climate data was downloaded for 2050 and 2070 (which are each an average across 2041–2060 and 2061–2080, respectively). We used the CMIP5 data with the CCSM4 Global Climate Model, using the RCP8.5 high greenhouse gas climate change scenario (Gent et al., 2011), as we wished to explore the potential effects of the climate at the most extreme likely scenario, to model the possible extent of change. Of the 19 standard bioclimatic variables, we selected the variables that most likely influence dormouse distribution (Table 1). We checked for collinearity between these bioclimatic variables, using the variance inflation factor (VIF) and correlation checks, ensuring there were no variables with a VIF higher than 10 (which would indicate strong collinearity) and correlations were lower than 0.7 (Green, 1979; Quinn & Keough, 2002). As a result, the variables selected for further analysis were temperature seasonality, mean temperature of coldest quarter and precipitation of coldest quarter (Table 1). Temperature seasonality was selected

TABLE 1 The bioclimatic variables utilized from the WorldClim database, selected due to likely impacts on dormice.

Bioclim number	Variable
Bio1	Annual mean temperature
Bio4	Temperature seasonality (standard deviation of average daily mean temperature per month × 100)[a]
Bio6	Minimum temperature of coolest month
Bio10	Mean temperature of warmest quarter
Bio11	Mean temperature of coldest quarter[a]
Bio18	Precipitation of warmest quarter
Bio19	Precipitation of coldest quarter[a]

[a]Selected for running SDMs, after collinearity checks.

to investigate the effects of temperature variation across a year. Temperature and precipitation of the coldest quarter was chosen due to expected influence on dormouse ecology, given that dormice prefer cooler, drier winters (Bright et al., 1996; Combe et al., 2022; Goodwin, Suggitt, et al., 2018). All climate rasters were masked to the UK, using a shapefile downloaded from the geoBoundaries Global Administrative Database (Runfolaid et al., 2020).

2.3 | Species distribution models

For current species distribution models (SDMs), we used an ensemble modeling technique to minimize uncertainty associated with each algorithm (Buisson et al., 2010). The ensemble included generalized additive models (GAMs), generalized boosted models (GBMs), random forests (RFs), and MaxEnt models, run using the biomod2 package (Thuiller et al., 2021) in R version 4.2.1 (R Core Team, 2022). These models require presence and absence data to generate projections (although it is possible to run MaxEnt without absence data). To compensate for a lack of reliable data on known absences, pseudoabsences were generated at random from the background extent of the UK, whereby 2500 points were selected, to balance with the number of presence points. We evaluated model performance by using the NbRunEval function which used 70% training and 30% testing splits of the data five times. We calculated variable importance for all three runs of each SDM algorithm and calculated the mean for each algorithm. We evaluated the discrimination capacity of the SDMs by using the evaluation statistics KAPPA, TSS (total sum of squares) and AUC (area under receiver-operating characteristic curve ROC: Allouche et al., 2006; Swets, 1988). Ensemble models for current time period were constructed by using the weighted mean based on the four SDM algorithms, five testing/training runs and the three pseudoabsence selections. An ensemble model framework has been previously recommended to increase SDM reliability (Buisson et al., 2010). All models (Figure S1, Supporting Information) with scores as follows were included in the ensemble models: KAPPA ≥0.4, TSS ≥0.5, and AUC ≥0.7 (Araujo et al., 2005). After running the ensemble model for current dormouse climate suitability predictions, we then incorporated the future climate data and used the "BIOMOD_EnsembleForecasting" function to predict future changes in climate suitability for dormice. Next, we ran a plausibility check for each SDM algorithm, including the ensemble models, by plotting the response curves for each bioclimatic variable. These plots estimate the probability of dormouse occurrence across the range of each variable.

2.4 | Climate suitability and dormouse reintroduction sites

We gathered the reintroduction site data from the NDMP (between 1993 and 2015). Using generalized linear models (GLMs), we investigated the impact of predicted climate suitability on reintroduction outcome and reintroduced populations. To study the impact on reintroduction outcome, we extracted the predicted current climate suitability scores from the reintroduction sites that have been categorized as successful or not. This includes all reintroductions that took place at least 10 years ago (19 sites), according to the PTES system of identifying successful reintroductions, where a reintroduction is categorized as successful if dormouse populations are stable or increasing (White, 2019). To test whether climate suitability impacts reintroduction success, we ran a binomial GLM with climate suitability as a predictor and compared it to a null model. We then investigated climate suitability at reintroduction sites when compared to natural sites, both currently and in the future, using the 2050 climate predictions. To assess differences between the natural and reintroduction sites, both now and in the future, we ran a two-way ANOVA followed by a Tukey post hoc test.

When investigating whether climate suitability impacted reintroduced population counts, we used a negative binomial generalized linear mixed model (GLMM) with the number of nest boxes as an offset variable, to account for differing survey effort, and site as a random effect. In this part of the analysis, 22 sites were included (all reintroductions that took place between 1993 and 2015), including the 19 sites used in the binomial model. Predictor variables for these models included different combinations of predicted climate suitability scores, the number of releases, the number of dormice released, survey season and time since reintroduction, mirroring the non-habitat variables used in Cartledge et al. (2021). Population counts (used as the response variable) were taken from NDMP surveys and included all adult dormice recorded during a particular survey at each site. Adult counts were used because adults are the most consistently recorded age bracket and most likely to contribute towards population trends (Juškaitis & Büchner, 2013). The number of adults is more stable, with juveniles having a higher mortality rate during hibernation (Juškaitis, 1999). Model selection was carried out by ranking Akaike's information criterion corrected for small sample size (AICc; Burnham & Andersen, 2002). The best-fitting models were selected as the most parsimonious from within the top two ΔAICc scores (Burnham & Andersen, 2002). Results and error margins were visualized using the effect plot function in the R package jtools (version 2.2.0; Long, 2022).

3 | RESULTS

3.1 | Species distribution models

The ensemble SDM was of high quality and had high predictive power, with the current climate suitability SDM having an AUC score of 0.949 (+/−0.003 standard deviation). For the ensemble model and each SDM algorithm considered for the ensemble model, the AUC scores plotted against the TSS scores can be found in Figure S2.

The highest level of current climate suitability for dormice can be found in southern England, with some highly suitable areas also present in southern Wales and the north west of England (Figure 2a). The response plots from the current SDM indicate that dormice are more likely to occur where temperature seasonality (standard deviation of average daily mean temperature per month × 100) is higher than 400, the mean temperature of the coldest quarter is above 3°C and the precipitation of the coldest quarter is above 200 mm (with a drop-off
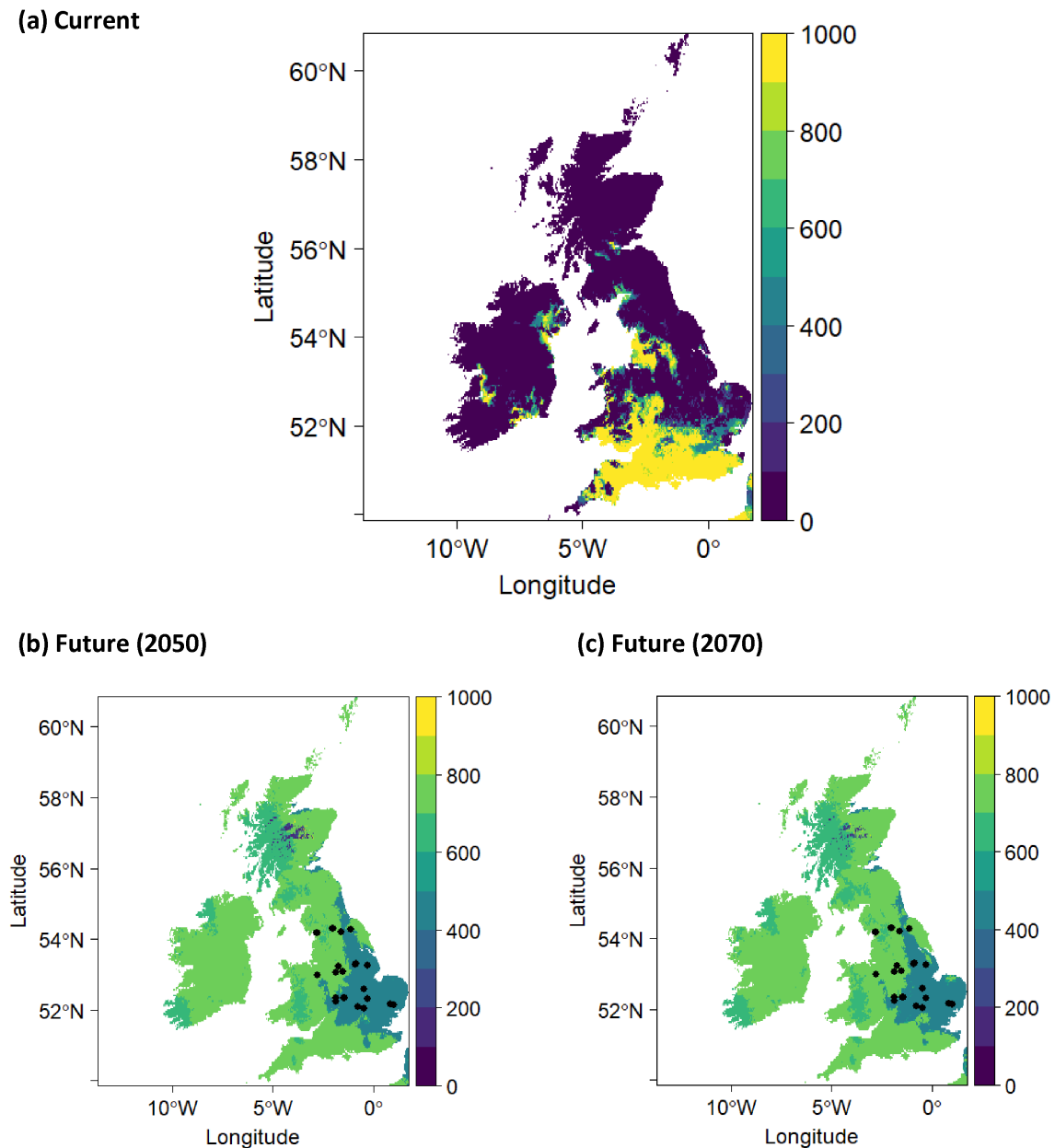
FIGURE 2 Ensemble SDM projections across the UK and Ireland. Color codes represent level of climate suitability, with yellow representing the most climatically suitable areas for dormice. Darker colors represent the least climatically suitable areas. Climate suitability is projected across various time periods, with projections across (a) current, (b) future (2050) and (c) future (2070) periods. Future SDMs were based upon the CCSM4 Global Climate Model and RCP8.5 greenhouse gas scenario. Black points indicate locations of dormouse reintroduction sites.
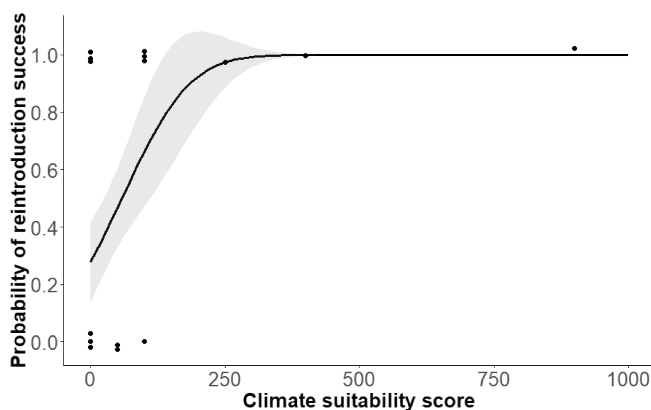
around 400 mm: Figure S3). The average variable importance across each SDM algorithm revealed that temperature seasonality ranked first in all algorithms, followed by the mean temperature of coldest quarter and finally the precipitation of the coldest quarter (Figure S4).

When projecting into the future, there is more widespread predicted climatic suitability for dormice in the UK, with similar projections in 2050 and 2070 (Figure 2b,c). There are also major changes in climate suitability for dormice in the Republic of Ireland and Northern Ireland, where dormice are not native. Although current climate suitability is spatially limited, future projections indicate extensive climate suitability for dormice in Ireland and Northern Ireland. However, the highest levels of climate suitability as projected for the current range (shown in yellow in Figure 2) are not predicted to persist in future scenarios. In the future, the maximum climate suitability is projected to be markedly lower than it is currently.

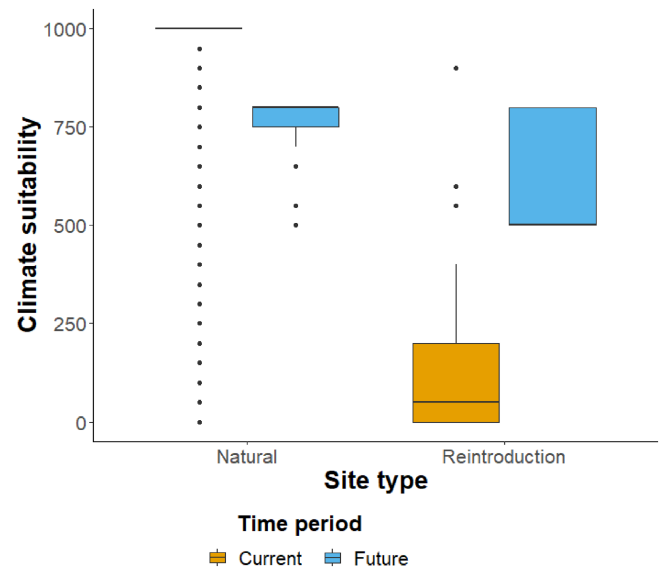## 3.2 | Climate suitability and dormouse reintroduction sites

We find a positive relationship between the predicted climate suitability of reintroduction sites (based upon the current SDM) and the probability of dormouse reintroduction success (Figures 3 and S5). Average climate suitability is higher at successful reintroduction sites, when compared to failed reintroduction sites.

Climate suitability is significantly lower at reintroduction sites when compared to natural dormouse sites (Tukey test $p < 0.001$; Figure 4). It is predicted to increase at the existing reintroduction sites by 2050 and become more similar to natural dormouse sites, although reintroduction sites will remain significantly less climatically suitable than natural sites (Tukey test $p < 0.001$). However, the average climate suitability at natural dormouse sites is predicted to decline (Tukey test $p < 0.001$).

FIGURE 4 Current and future climate suitability scores compared across natural dormouse sites and reintroduction sites (2503 and 22 sites, respectively). Color represents time period, either from the current SDM or future projection (2050). Boxes show interquartile range, horizontal lines are medians, whiskers show 1.5 × interquartile range and points are outliers.
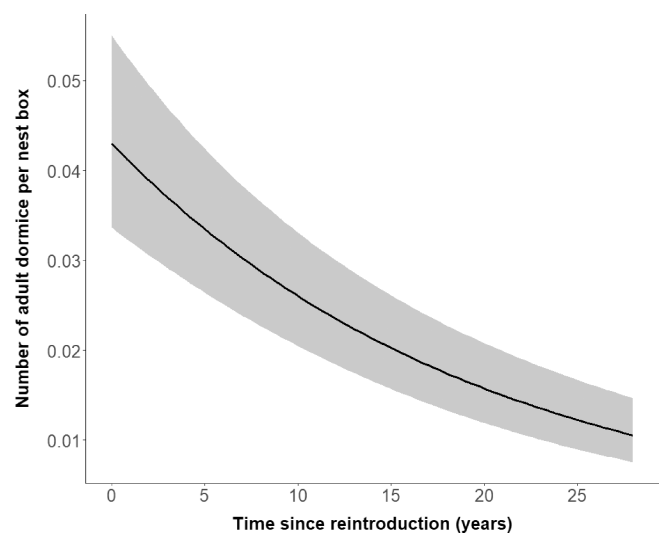

FIGURE 3 The relationship between current climate suitability and the probability of reintroduction success, as calculated by a binomial generalized linear model. Gray shading shows standard error margins. Points represent raw data used in the model.

FIGURE 5 Number of adult dormice per nest box plotted against time since reintroduction, as predicted by negative binomial generalized linear models. Reintroduction site was included as a random effect and number of nest boxes as an offset variable. Gray shaded area represents 95% confidence interval (calculated using the jtools R package).

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When investigating the impact of climate on reintroduced adult population counts, we find that the best-fitting model included time since reintroduction as the only predictor variable, with an estimated decline of 5.03% each year (Figures 5 and S6). The number of adult dormice per nest box declines in the years after a reintroduction is carried out, but other predictor variables (such as current climate suitability, site size, number of releases and number of dormice released) do not have an impact on our dataset.

4 | DISCUSSION

We used ensemble SDMs to predict current and future climate suitability for hazel dormice in the UK. Investigating the climate suitability for dormice reveals some interesting trends. The extent of areas projected to be highly climatically suitable increases in future climate change projections; however, the very highest levels of climate suitability, based on current projections, are predicted to decline to a slightly lower level of suitability in future scenarios.

The majority of highly suitable climate for dormice is currently located in the south of England, with some areas in the east and west, and southern and eastern Wales. There are also some small, isolated patches of climatically suitable areas in Ireland, Northern Ireland and Scotland, where dormice are non-native. There are no records in these countries, apart from a handful of sightings in County Kildare in Ireland (Sheehy & Lawton, 2015), but this is in an area of low predicted climate suitability. There is also a patch of suitable climate in the northwest of England, where there is now one remaining natural population (White, 2012).

Given that our SDMs are built with data from the current dormouse range, which is predominantly distributed in southern England, it is unsurprising that the current climate suitability map shows a bias towards higher predicted suitability in this area. For example, it is easy to assume that the remaining dormouse populations are located in ideal areas, in terms of habitat or climate, as a "refuge species" (Kerley et al., 2012). Therefore, it is important to be cautious when drawing conclusions about ideal climate suitability, as the models likely represent a combination of climate suitability and other factors which allowed dormice to remain in the southern sites.

Of the three bioclimatic variables used in our SDMs, temperature seasonality had most impact on the probability of dormouse occurrence, with dormice preferring a value higher than 400 (a standard deviation of >4°C in average daily mean temperature per month across the year). This variable therefore represents locations with higher temperature variability, indicating larger seasonal differences. This fits with previous studies suggesting that dormice prefer warmer springs and summers, and cooler winters (Combe et al., 2022; Goodwin, Suggitt, et al., 2018). However, when investigating the impact of the temperature of the coldest quarter, dormice preferred locations with a mean temperature above 3°C, so there may be a required threshold for winter temperatures. We also found that dormice may have a required winter precipitation threshold of around 200 mm, but that the probability of dormouse occurrence declines at a threshold of around 400 mm. This is consistent with some previous studies that have found dormice prefer drier winters (Combe et al., 2022), but that they need to ensure they do not desiccate during hibernation (Bright & Morris, 1996).

We found that higher current climate suitability, as estimated by SDMs, increases the probability of dormouse reintroduction success. It has been suggested to use SDMs to assist reintroduction site selection (IUCN, 2013; Osborne & Seddon, 2012). Recently, it has been shown quantitatively for the first time that SDMs can be used to select climatically suitable sites for ectotherms and that climate is a key influencer of reintroduction outcome (Bellis et al., 2020). Here, we find that this is also true for a mammalian species. Existing reintroductions sites are on average found in areas of lower climate suitability than natural dormouse sites, but there are fewer areas of climate suitability in northern England, which is the current target of the dormouse reintroduction programme (Mitchell-Jones & White, 2009).

Although we found that reintroduction success was more likely in areas of higher climate suitability, there are likely to be other factors playing an important role in reintroduction outcome, as we see that some sites have succeeded even with low climate suitability. For example, it is thought that habitat suitability plays a key role in reintroduction success (Berger-Tal et al., 2020; Germano & Bishop, 2009; Wolf et al., 1996) and that dormice are particularly susceptible to habitat changes (Bright & Morris, 1996; Morris, 2003). When using ecological-niche factor analysis, Cartledge et al. (2021) found that reintroduction sites had lower habitat suitability on average when compared to natural sites and that some habitat factors influence adult dormouse counts at reintroduction sites (such as frequency of broadleaved woodland and arable land). It would be interesting to include other variables in our binomial climate suitability models, such as these habitat variables, the number of releases, number of dormice released and site size. At this point, there are not enough reintroduction sites where the outcome has been assessed at the 10-year mark to create these more complex models, but in the future, it would be possible to add the reintroduction outcome of

other sites. Currently, the release site decision is based on observational judgments of habitat suitability and accessibility, and more recently, the possibility of setting up metapopulations (Chanin, 2014; White, 2014). Our results suggest that it is also important to consider climate suitability at proposed dormouse release sites.

When investigating the variables that impact population counts for reintroduced adult dormice, we found that current climate suitability was not included in the best-fitting model. Of the variables tested, only time since reintroduction influenced population counts. That is, as time since reintroduction increases, dormouse population counts decline, which was also found in a previous dormouse habitat suitability study (Cartledge et al., 2021). The rate of decline estimated in the current study (5.0% per year) is similar to the background decline at wider NDMP dormouse sites, which has been calculated as an average of 5.8% per year between 1993 and 2014 (Goodwin et al., 2017). Initially, this may seem to contradict our results from the binomial reintroduction model, which found that climate suitability strongly influenced reintroduction outcome. It has previously been suggested that nest box counts may not reflect true population size (Cartledge et al., 2021), as it is known that dormice alter nest box use according to various factors such as season or natural nest site availability (Chanin & Woods, 2003; Juškaitis & Büchner, 2013). The results of our population count model may also indicate imperfect nest box counts, where population trends or even dormouse presence can be masked by other factors. With most of our presence points resulting from nest box surveys, there may be hidden biases which impact the model outcomes.

There are likely finer-scale impacts of climate suitability that we could not detect with our model. This may occur due to the climate suitability scores being calculated from each of the variable averages across 1970–2000, so it would not necessarily be expected to closely match changing populations over time. Dormice have very specific requirements for habitat and food availability, which may be impacted by local-scale climate differences across time and space. There could also be differences in how climate influences population establishment or persistence at reintroduction sites. The key factors influencing long-term reintroduction success are not always the same as those determining initial population establishment (Armstrong & Seddon, 2008). Climate suitability may be more closely linked to establishment of dormouse populations and thus influence initial reintroduction success, but may not be as important at regulating population persistence. When considering population regulation, other factors may be more important. However, previous research has found that dormouse population numbers respond in a density-dependent way to

climate, but these models used occupancy methods to account for imperfect detection (Combe et al., 2022).

When considering the success of dormouse reintroduction sites, there are likely unknown impacts of the founder source populations. It has previously been shown that dormice are genetically structured across the UK; however, there is evidence that at least one reintroduction site in northern England has resident dormice with genetics most like a southern cluster on the Isle of Wight (Combe et al., 2016). This likely traces back to the individuals originally sourced for reintroduction; however, the impacts of dormouse genetics on local adaptation has not yet been studied. For example, there is a possibility that historical northern dormouse population were climate adapted and became extinct for reasons other than climate. There are potentially many factors affecting reintroduction success that were not the focus of this study. However, it is worth noting that we still found a clear relationship between climate suitability and reintroduction success.

In our SDM future projections to 2050 and 2070, under the most extreme climate change scenario, high levels of climate suitability for dormice become much more widespread, expanding further into all countries of the UK. However, there are some areas in central and eastern England and central Scotland that are predicted to remain relatively low in terms of climate suitability. The highest level of climate suitability in the south of England declines, but still remains relatively high. We found that the climate at existing reintroduction sites is set to improve and become closer to the levels of climate suitability currently found at natural dormouse sites, but still significantly lower. Generally, this is good news for the future of the reintroduction programme, as the targeted areas in northern and central England (Mitchell-Jones & White, 2009; White, 2014) will increase in climate suitability. However, we have demonstrated that the *current* climate suitability will impact reintroduction outcome for the release sites, so reintroduction planning should not rely on future climatic improvements. We also found that climate suitability will decline at the remaining natural sites, but still remain relatively high.

Despite the relatively positive outlook on future climate suitability for dormice in the UK, there may be other more nuanced impacts of climate change. Our SDMs are based on presence records of dormice, which reliably represents dormouse occurrence in the UK. However, it does not consider impacts on dormouse population dynamics, which are likely to be altered by changing climates, with warmer and wetter winters likely contributing to lower survival rates (Combe et al., 2022). Life history traits, such as hibernation, may be altered with warmer climates, for example with increased

interbout arousals during winter or earlier emergence in the spring, which will both have energetic costs (Boyles et al., 2020; Findlay-Robinson et al., 2023; Maldonado-Chaparro et al., 2017). Timing of food availability may be impacted by changing climates and it is not clear whether this will cause mismatches in dormouse activity and feeding opportunities. Alternatively, if dormice reduce hibernation times or do not hibernate at all, as in some Mediterranean locations, there may be very limited feeding opportunities through the winter. Climate change may impact other factors too, such as increasing pests and disease to dormice or their habitats, therefore more research should be conducted in this area (Phillips et al., 2022). The presence of dormice is also strongly driven by non-climatic habitat factors (Cartledge et al., 2021; Goodwin, Hodgson, et al., 2018; Goodwin, Suggitt, et al., 2018), meaning that even with suitable climate, viable dormouse populations are unlikely to be supported if the habitat is unsuitable.

It may be possible for dormice to adapt life history traits (Findlay-Robinson et al., 2023). For example, in the Mediterranean, dormice hibernate for short periods or not at all (Panchetti et al., 2004). If dormice emerge earlier there may be the opportunity to breed earlier or multiple times, leading to more offspring and potentially more time to fatten up for hibernation, as long as food is available (Pretzlaff et al., 2021; Pretzlaff & Dausmann, 2012). Data from captive populations of dormice may offer the opportunity to investigate the impacts of climate on hibernation immergence and emergence dates, as well as frequency of interbout arousals, and how this is linked to body condition and breeding success.

Our study focuses on the climate suitability for dormice within the UK and does not consider the whole dormouse distribution. Whilst this provides useful regional insights for the UK, future work should consider the impacts of climate change across the full current distribution. At the moment, dormice are considered Least Concern by the IUCN Red List (Hutterer et al., 2021), but if climate suitability shifts northwards, there may be cause for concern for existing population strongholds.

SDMs do not always represent the actual species range, as there may be limits on dispersal or biotic interactions (Svenning & Sandel, 2013). For example, dormice are thought to be particularly limited by habitat fragmentation, due to low dispersal ability (Bright & Morris, 1996). Even where there is predicted suitable climate, dispersal and other factors such as suitable habitat or food availability will influence where the species occurs. With complex interactions between these factors (Williams et al., 2022), it can be difficult to tease apart the impacts of each independently. Other limitations with SDMs relate to the method of selecting pseudoabsence, for example different SDM algorithms have optimal numbers of pseudoabsence points and runs (Barbet-Massin et al., 2012). Further, we chose three bioclimatic variables, based on our own understanding of dormouse ecology, but there may be others which influence dormouse distribution. For example, we investigated the effects of precipitation in winter, but the levels of precipitation in spring and summer are also likely to impact dormice (Bright et al., 2006). We chose only one of these variables due to a strong correlation between them, but it would be possible to undertake a principal component analysis on the bioclimatic variables and use the resulting principal components.

Overall, our results suggest that climate suitability in the UK may become more widespread with climate change, with the loss of some high levels of suitability. However, it is important to consider that this analysis has focused on climate suitability at a low resolution, with further fine-scale impacts not considered. This may impact the long-term sustainability of dormouse populations within these areas, alongside any other changes in habitat or food availability. We found that the outcome of dormouse reintroductions is influenced by current climate suitability, where the probability of successfully maintaining populations for over 10 years increases with increasing climate suitability. We find no evidence that climate suitability impacts adult dormouse population counts, when using nest box records, but we find that dormouse counts decline in the time since reintroduction at a similar rate to the population decline found at natural sites (Goodwin et al., 2017). Future analysis could investigate climate impacts on dormouse populations at natural sites, for example population numbers, litter size and weight. There are also some sites where dormice are tagged for individual identification, offering the potential to study climate impacts on survival probability. We note that it has previously been highlighted by dormouse conservation practitioners that a greater understanding of the potential impacts of climate change on dormice is required (Phillips et al., 2022). We provide the first projection and evidence that climate suitability for dormice, at a $1 km^2$ scale, in the UK may increase with climate change, highlighting the importance of considering current climate in reintroduction planning.

AUTHOR CONTRIBUTIONS

and guidance on dormouse ecology and reintroduction programs. E.L.C. wrote the original draft manuscript and all authors contributed to revising and editing the final draft.

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SUPPORTING INFORMATION

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