Is Britain still Great for Pine Marten? A Habitat Suitability Assessment

Ella Lewis[1] Amy Fitzmaurice[1] Kirsty Swinnerton[1], Rachel Gardner[2], Lawrence Ball[1], Neal Armour-Chelu[3]

[1]Kent Wildlife Trust Group, Tyland Barn, Chatham Rd, Sandling, Maidstone ME14 3BD

[2]Forestry England, National Office, 620 Bristol Business Park, Coldharbour Lane, BS16 1EJ

[3]Forestry England, East Forest District, Santon Downham, Brandon, Suffolk IP27 0TJ

Key words: Pine Marten, reintroduction, feasibility, species distribution model, habitat suitability, BIOMOD2

Abstract

Species distribution models are used to predict habitat suitability for a species, by quantifying the environmental characteristics which allow a species to occupy a geographical area. The abundance and range of Pine Marten *(Martes martes)* has declined substantially in Great Britain, with the remaining populations restricted to Scotland. Here, we perform species distribution modelling to determine habitat suitability, and identify potential reintroduction sites, for Pine Marten in Great Britain. Using a global range dataset of 4,189 occurrences, and seven environmental variables, ensemble species distribution models were used to predict habitat suitability across Europe at 1 km resolution and Great Britain at 100 m resolution. High habitat suitability was identified across substantial areas in the South East, East of England and South West, with pockets of suitable habitat along the West Coast of Britain. The results indicate that elevation and land cover are important drivers of suitability.

Introduction

Pine Marten *(Martes martes)* are a mustelid species that typically occupy woodland habitats, distributed across mainland Europe extending to Western Siberia (Buskirk, 1992; Delibes,1983). In Britain, Pine Marten were once abundant, however their populations suffered severe decline during the late 1800's due to habitat loss and hunting practices, particularly predator control for game birds (Langley and Yalden, 1977). The species is classified as critically endangered in England and Wales according to the Red List for British Mammals (Mathews and Harrower, 2020). It is a priority species in the UK Biodiversity Action Plan and has been fully protected since 1988 under Schedule 5 of the Wildlife and Countryside Act 1981. The remaining populations are restricted to north-west Scotland and the north of England and Wales. As a generalist apex predator, their diet is comprised of small mammals, particularly voles, small birds, berries and insects (Twining et al., 2019). They play an important role within a woodland ecosystem as a mesopredator, by providing several functions including seed dispersal and balancing prey populations (Paine 1969; Hastings et al. 2007). In Scotland for example, they have been shown to suppress non-native invasive Grey Squirrel (*Sciurus carolinensis*) populations (Sheehy et al., 2018; Vincent Wildlife Trust, 2020). This in turn, allows indirect benefits for vegetation recovery due to reductions in tree damage, and Red Squirrel (*Sciurus vulgaris*) population recovery by reducing interspecific competition with Grey Squirrel (Sheehy et al. 2018; Schaumann and Heinken, 2002; Crowley et al., 2018).

Pine Martens are considered a keystone species for woodland ecosystems, where their presence can indicate a biologically diverse ecosystem in good condition (Buskirk, 1992; JNCC, 2021). As a flagship species, Pine Marten can act as an effective conservation tool, not only for reintroduction approaches, but also to promote conservation of woodland habitats. Woodland

covers only 13% of land in Britain (Forest Research, 2022), compared to the European average of 34% (Forestry Commission 2010), therefore woodland recovery is a national priority (Defra, 2022). Reintroduction programmes are a key strategy for population recovery and Pine Marten reintroductions have already occurred across Britain in the Forest of Dean, Wales, Devon and Cumbria (MacPherson et al., 2014; Stringer et al., 2015). However, they require extensive research, primarily around social and ecological feasibility pre-release, population genetics, disease risk, dispersal potential, and post-release monitoring (Kirkwood, 2013; Klein and Arts, 2021; Armstrong and Seddon, 2008; 2019).

This research aims to identify areas in Britain with sufficient suitable habitat to support viable breeding populations of Pine Marten. Current populations in southern England are small and fragmented and thus are considered highly vulnerable to environmental, genetic and demographic factors (MacPherson et al., 2014) which could potentially lead to an extinction vortex (MacPherson et al., 2014; Gilpin and Soulé, 1986). Interventions, including translocation and reintroduction projects, are therefore necessary for the long-term viability of these populations (MacPherson and Wright, 2021). Previous feasibility assessments for the reintroduction of Pine Marten to Britain have used occurrence records from the populations in Scotland, Ireland and the Netherlands only (Stringer et al., 2015; MacPherson et al., 2014). Our methodology uses occurrence data indiscriminately, from across their global range, to predict suitability at 100 m resolution in Britain. Pine Marten populations in the UK and Ireland have likely been driven to suboptimum, or ‘refuge’, areas due to anthropogenic disturbance, with loss of forest cover as a main contributor (European Environment Agency, 2018a). Across mainland Europe, we assume that Pine Marten can more easily disperse and occupy the most suitable areas. Therefore, we anticipate our model predictions, which are based on their global range, will more closely reflect the optimal habitat suitability requirements of Pine Marten.

Species distribution models (SDM), sometimes referred to as environmental niche models (ENM) or habitat suitability models (HSM), are a useful tool to identify suitable habitats or environments for a species. SDMs estimate the relationship between observed species occurrences and the environmental conditions at these locations, to characterise the environmental conditions that are suitable for that species. These estimated relationships are then used to identify where suitable environments are distributed in space, in the form of a habitat suitability map (Anderson et al., 2003; Elith and Leathwick 2009).

A key application for SDMs is to identify sites with high suitability for a species, as an informative tool for conservation planning (Guisan et al., 2006). For example, they can be used to assist in identifying priority areas for conservation management that will have the most impact, based on species richness and suitability. SDMs are also used to predict species' distributional changes over time and space (Mammola et al., 2021), for instance, to understand how species will respond to future climatic conditions (Raes and Aguirre-Gutiérrez, 2018).

SDMs use a single statistical technique to predict habitat suitability for a species. However, the field of habitat suitability mapping has evolved rapidly, giving access to more complex and potentially reliable approaches (Meller et al., 2014). One approach is ensemble species distribution models (eSDMs), which use an assemblage of statistical models to produce suitability predictions. This method has been shown to improve the accuracy of model predictions compared to individual models (Kwon, 2014; Araújo and New 2007; Hao et al., 2020). Given that there is often significant variation in the predictions across model techniques and there is no single outstanding model algorithm, it is sensible to combine several, well-performing techniques in order to generate accurate predictions (Meller et al., 2014). In addition, ensemble forecasting has become more widely used for its ability to combat the limitations of

individual algorithms, whilst allowing for comparisons between the performance of different algorithms (Araújo & New, 2007).

This research aimed to use eSDMs to map environmental suitability for Pine Marten, to inform the selection of optimum release site locations for reintroductions in Britain.

Methods

BIOMOD2 v 4.2, a widely used ‘ensemble platform for species distribution modelling’ available in the R statistical programming language (R Development Core Team, 2020; Thuiller et al., 2016), was used to build eSDMs with 9 algorithms, 4,189 occurrences and 7 environmental variables, at a 1 km resolution across Europe. They were ensembled based on a threshold model evaluation score, and weighted according to these scores, then ensembled predictions of habitat suitability were projected across Europe at 1 km resolution and Great Britain at 100 m resolution. The fine scale (100 m) predictions for Britain provide a more detailed view of habitat suitability to facilitate understanding of habitat fragmentation and connectivity at local scales to support conservation practice.

Environmental predictors

SDMs are based on the ecological niche concept, which posits that species occupy spatial ranges with suitable environmental conditions for their existence. Thus, the environmental variables used to predict suitability herein are chosen based on the ecological requirements of Pine Marten. It is hypothesised that the suitability of a habitat for Pine Marten is determined by risks of mortality, food availability, and availability of denning sites (Stringer et al., 2018;

MacPherson et al., 2014). Seven environmental variables were chosen based on these factors, derived from open data sources (Table 1). Processing of environmental predictors was conducted in QGIS v3.22 (QGIS.org, 2021). All environmental variables were reprojected to ETRS89-extended /LAEA Europe, resampled to a resolution of 1 km (nearest neighbour for categorical variables and bilinear for continuous variables using WARP tool in QGIS), cropped to the same extent of Europe and aligned. Four of these environmental variables were used for the British projection, whilst the remainder were sourced from different datasets (Table 1). Pre-processing of these environmental variables followed the same aforementioned workflow.

Multicollinearity was tested between environmental variables using Pearson's r-correlation test with r >0.7 considered as unacceptably collinear. Collinear variables cannot be included in statistical models because it would be impossible to determine the unique effect of each variable (Dormann et al., 2013; Brun et al., 2019; Glon et al., 2017). This process led to the removal of four environmental variables: average monthly maximum and minimum temperature (°C), and northness and eastness. Removal of these variables was not a concern, as average mean annual temperature was retained, whilst northness and eastness were not assumed to influence Pine Marten habitat preference.

During the iterative process, two environmental variables were removed from the eSDM due to spatial autocorrelation of sampling efforts (sampling bias); distance to roads and urban areas. Distance to roads was derived from a shapefile subset to major roads (A and B roads) using UN Spatial Data Infrastructure Transport (UNSDI-T) v2 (CIESIN, 2013). Distance to urban areas was derived from a shapefile from North American Cartographic Information Society (Patterson et al., 2012). Both urban areas and major roads vector layers were rasterized, and distance was calculated from the proximity (raster distance) tool, both derived from GDAL in QGIS.

139

Environmental predictor	Source	Original resolution (m)	Resolution for European modelling (m)	Resolution for UK modelling (m)	Processing	Justification for inclusion
Elevation	SRTM DEM WorldClim database v2.1 (Fick and Hijmans, 2017)	1000	1000			Elevation is strongly correlated with climatic conditions. Pine Martens avoid thermal stresses and lack of prey abundance at high altitudes (Vergara et al., 2015).
Slope	WorldClim database v2.1 (Fick and Hijmans, 2017)	1000	1000		GDAL geoprocessing tool in QGIS.	Slope is closely linked to soil nutrients, water-holding capacity and erosion, which in turn influence vegetation communities and Pine Marten prey abundance (particularly small-rodents) and availability of denning sites (Krebs, 2009; Lee et al., 2020).
Topographic Position Index (TPI)	WorldClim database v2.1 (Fick and Hijmans, 2017)	1000	1000		GDAL geoprocessing tool in QGIS.	TPI is used to classify slope position and landform types. It is a powerful proxy for local geology, hydrology, nutrient availability, and topoclimatic conditions which in turn influence ecological communities. High values represent hilltops and valley shoulders, whilst lower values represent valley beds and depressions (Ball and Tzanopoulos, 2020). TPI also influences the mobility of animals with implications for species interactions (Sultaire et al., 2022)..
Normalised Difference Vegetation Index (NDVI)	Landsat satellite imagery (USGS, 2022)	30	1000		Calculated in Google Earth Engine as the mean annual maximum greenest pixel from 2010 to 2022 (USGS, 2022).	NDVI indicates vegetation greenness (relative plant biomass). Pine Martens prefer habitat with high vegetation cover fraction (Storch et al.,1990).
Forest cover density (%)	Copernicus land monitoring (European Environment Agency, 2018b)	100	1000		Secondary mapping product. Percentage tree density per pixel.	Pine Martens are predominantly found in diversely-structured deciduous and coniferous woodland, which provide a combination of abundant food resources, well-insulated denning sites and protection from predators (Buskirk, 1992;

						Delibes,1983; Balestrieri et al., 2015; Virgos et al., 2012).
Land cover	CORINE 2018 (European Environment Agency, 2018a)	100	1000		Consisting of 44 land cover type categories amalgamated into 17 broad categories that align as far as possible with UK recognised habitat nomenclature (Appendix 3).	Pine Marten have been shown to avoid open habitat and urban areas (Brainerd and Rolstad, 2002; Storch et al.,1990; Vergara et al., 2015). Certain land cover types support the dispersal of Pine Marten, for example riparian corridors and hedgerows allow range expansion in landscapes dominated by urbanisation and agriculture (Balestrieri et al., 2016). Land cover distinguishes coniferous, deciduous and mixed woodland categories.
Canopy height (mm)	GLAS and ICESat satellite imagery (Simard et al., 2011)	1000	1000		Secondary mapping product	Pine Marten prefer taller spruce-dominated forest for protection from predators and for den and resting sites within the forest canopy (Brainerd and Rolstad, 2002).
Average monthly temperature (°C)	WorldClim database v2.1 (Fick and Hijmans, 2017)	1000	1000		Averaged across 1970 to 2000.	Pine Martens deal poorly with thermal stress, with small fat reserves, poor fur insulation and high low critical temperatures, so avoid areas of extreme temperature ranges (Harlow, 1994). Snow also reduces prey catching efficiency (Jedrzejewski et al., 1993).
Average monthly precipitation (mm)	WorldClim database v2.1 (Fick and Hijmans, 2017)	1000	1000		Averaged across 1970 to 2000.	Rainfall strongly influences vegetation abundance, which in turn influences prey abundance.
Elevation (DEM)	Japan Aerospace Exploration Agency, using ALOS satellite (JAXA, 2021)	30		100		
Topographic Position Index (TPI)	Japan Aerospace Exploration Agency, using ALOS satellite (Japan Aerospace Exploration Agency, 2021)	30		100	GDAL geoprocessing tool in QGIS.	
Slope	Japan Aerospace Exploration Agency, using ALOS satellite (JAXA, 2021)	30		100	GDAL geoprocessing tool in QGIS.	
Land cover	UKCEH 2020 (Morton et al., 2021)	25		100	Consisting of 21 land type categories, amalgamated into the same 17 broad	

	land categories as the Europe raster (Appendix 4).

Table 1: Environmental predictors used in the modelling or removed after multicollinearity assessment, with their justification for inclusion based on ecological relevance.

Occurrence data

The occurrence data was collated from the Global Biodiversity Information Facility (GBIF, 2023), which holds a vast array of georeferenced species occurrence records, and the NBN Atlas (NBN, 2023), the UK's main biodiversity data centre. GBIF provided 26,277 presence records across Europe (https://doi.org/10.15468/dd.32w6qw), and NBN Atlas provided 11,048 records across Britain and Ireland (Supplementary material 1). Although these databases hold large datasets, many records may be subject to bias from uneven sampling or inaccurate georeferencing (Glon et al., 2017; Beck et al., 2014). For example, certain areas may be the focus of targeted Pine Marten surveys (Austin, 2007).

Data cleaning is essential so that models are built on robust and spatially-uniform data. To clean the GBIF data we followed the methodology of Zizka et al (2019) and used the 'CleanCoordinates' package v2.0-11 (Zizka et al., 2019). This included removing records made prior to 1945 (which have low accuracy), removing duplicate records, removing coordinates assigned to country and province centroids, removing records with 0,0 coordinates, coordinates at sea, and coordinates assigned to biodiversity institutions. We incorporated additional cleaning steps to the remaining data including removing records with coordinate uncertainty of above 1 km, , removing records of unknown source, records derived from fossil specimens, and records with noted geospatial issues. After data cleaning, 32,000 out of 37,325 records were retained (Figure 1).

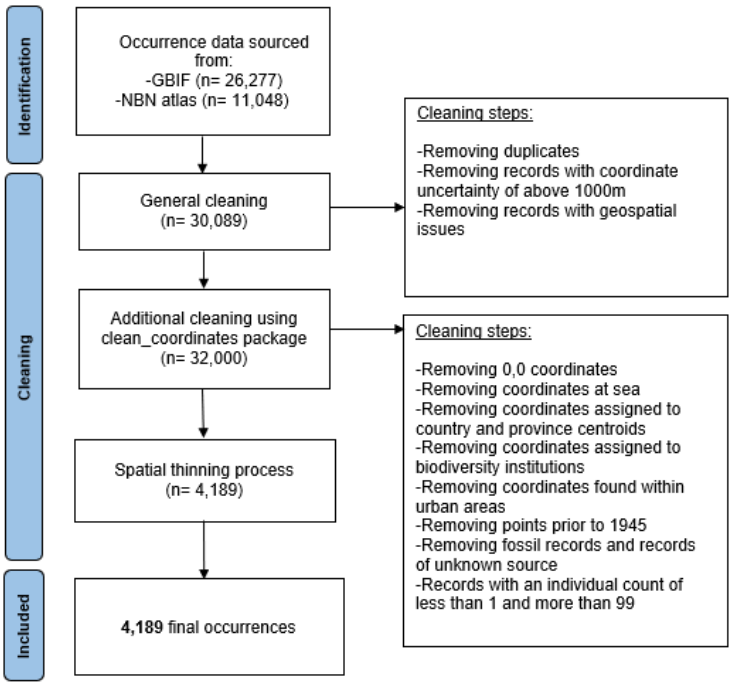


Figure 1: PRISMA diagram illustrating the necessary cleaning steps with the number (n) of occurrences remaining after each cleaning process.

Sampling bias can skew model accuracy, as it may not reflect the complete species' range of environmental conditions and may over-represent environmental conditions associated with regions of higher sampling (Kadmon et al. 2004; Anderson and Gonzalez, 2011; Duque-Lazo et al., 2016). To reduce the influence of spatial bias, occurrence data should undergo spatial thinning. To do so, the 'spThin' function in R was applied to the cleaned occurrences, which used a randomised approach to remove occurrence points within 10 km of one another, making sure the maximum number of occurrence points were returned (Aiello-Lammens et al., 2015). We identified 10 km as an appropriate thinning distance by visually inspecting a variogram of the environmental variables (Figure 2). The variogram shows the variation in environmental conditions with increasing Euclidian distance between points. Therefore, the distance at which

the variance ceases to increase and begins to plateau can inform the distance at which occurrences are geospatially independent from one another, and therefore the distance to use for thinning (Anderson and Gonzalez, 2011; Bio et al., 2002). After data cleaning and spatial thinning, 4,189 occurrences were retained for use in the modelling (Figure 3).

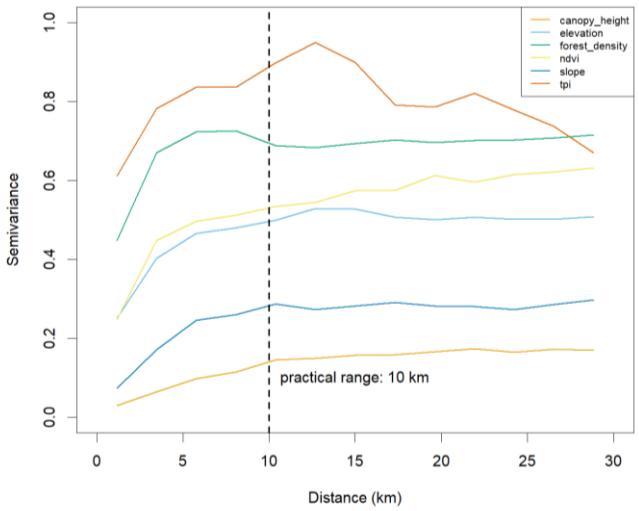


Figure 2: The variogram shows that the semivariance reached a plateau after 10 km from points. This ‘practical range’ was used to thin the occurrence data in order to remove spatial autocorrelation, but retain the most occurrence data.

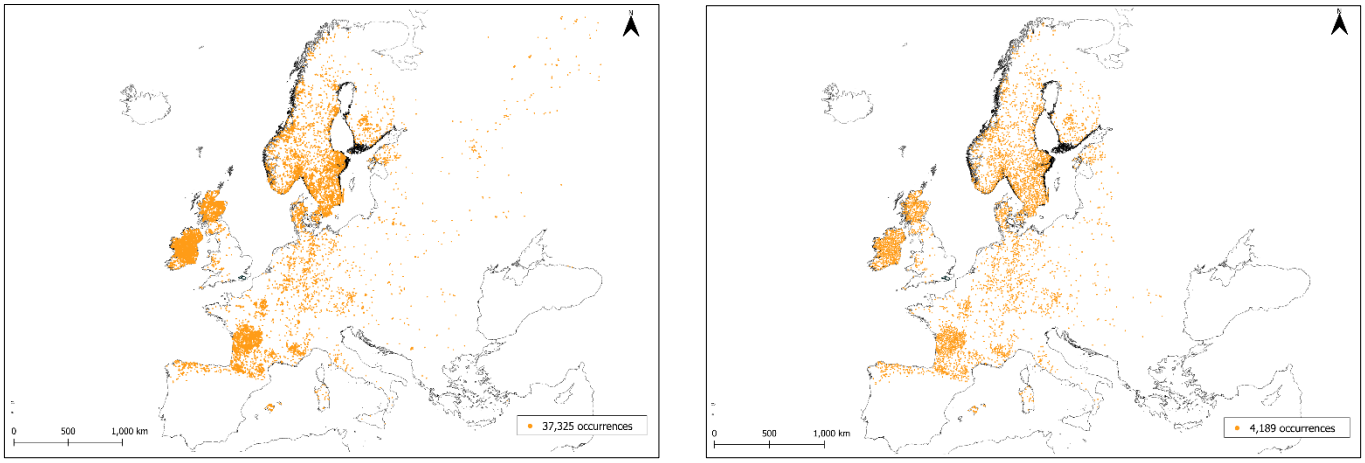


Figure 3: The locations of occurrence records before (left) and after (right) cleaning and spatial thinning.

Modelling

Model algorithms:

For the ensemble model, we used 9 algorithms within the BIOMOD2 package in R (R Core Development Team, 2014). These were generalised linear model (GLM), generalised boosted regression model (GBM), generalised additive model (GAM), classification tree analysis (CTA), artificial neural networks (ANN), flexible discriminant analysis (FDA), multivariate adaptive regression splines (MARS), random forest (RF), and maximum entropy model (MaxEnt), using the default parameters specific to each algorithm.

Pseudo absences:

Most SDM algorithms require both presence and absence data. For many species, true absence data is rarely available or unreliable and so presence-only models are used, wherein artificial absence data, known as pseudo-absences, are generated (Barbet-Massin et al., 2012).

They aid the model's ability to differentiate the environmental conditions under which the species occurs (Brown and Yoder, 2015). We used a large number of pseudo absences, equally weighted to presences (4,189), as has been shown to produce the most accurate predictions (Barbet-Massin et al., 2012). Pseudo-absences are randomly generated within the entire study area. We used BIOMOD's disk method to prohibit pseudo-absence generation within 5 km of occurrence points, respective of a typical Pine Marten home range for females (Stringer et al., 2018). This random assignment of geographically stratified pseudo-absences is recommended for machine-learning and classification methods (Barbet-Massin et al., 2012). To reduce bias towards a single distribution of pseudo-absences, five sets were generated (Guisan et al., 2017). Prevalence was assigned as 0.5, where presences and pseudo-absences have the same weighting in the model calibration process (Liu et al., 2005).

Model evaluation:

In order to test model accuracy when no independent data is available, cross-validation is performed, where the data is randomly partitioned into a set of training data and testing data (Raes and Aguirre-Gutiérrez, 2018). For our analysis, data was randomly partitioned to 70% for training and 30% for testing using repeated split samples. This cross-validation process was repeated 10 times for each modelling run (Yu et al., 2024). We chose the widely used repeated random cross-validation method. Model quality was evaluated based on kappa statistic (Cohen, 1960), the area under the receiver operating characteristic curve (AUC), and the true skill statistic (TSS) (Allouche, et al., 2006). Only single models with a TSS score greater than the upper quartile (0.324) of TSS scores (0%: 0.218, 25%: 0.286, 50%: 0.307, 75%: 0.324, 100%: 0.368) were retained for the final ensemble and ensemble projections (Tanaka et al., 2020; Hill

et al., 2017). TSS corresponds to the sum of sensitivity and specificity minus one (Barbet-Massin et al., 2012). TSS scores can be classified according to Ben Rais Lasram et al., (2010) as excellent (TSS > 0.8), good (TSS = 0.6–0.8), fair (TSS = 0.4–0.6), poor (TSS = 0.2–0.4), and no predictive ability (TSS < 0.2). We chose TSS to evaluate model accuracy for inclusion in the ensemble models as it is a threshold-dependent measure of model accuracy and independent of prevalence (the ratio of presence to pseudo-absence data in the presence-absence predictions) (Allouche et al., 2006).

We combined the single models into ensemble models based on mean, median and weighted average. Mean and median produce the ensemble results by averaging or taking the median of the single model probability of suitability values, respectively, whereas weighted mean weights the individual models based on their cross-validation performance, in our case the TSS values (Marmion et al., 2009; Thuiller et al., 2009). For the ensemble model evaluation, TSS, ROC and Kappa were used to assess model performance. The method used to combine the models that performed best, should be used to present the projection results. The ensemble model included 111 single models out of 450 individual models.

To evaluate the relative importance of each environmental variable (the variable importance), a simple Pearson's correlation *r* was calculated between predictions of the full model and a model with each variable removed (Thuiller *et al.*, 2009). We also generated species response curves, which show how suitability for Pine Marten changes as a given environmental variable changes.

Habitat suitability projections:

We generated single and weighted mean ensemble model projections in Britain using the 100 m resolution environmental predictors. Suitability index has been re-scaled 0 to 100, where larger values indicate higher suitability.

Results

The mapped relative probability of habitat suitability in Europe show markedly low habitat suitability for Pine Marten at high altitudes in the Alps and the Scandinavian Mountains, in heavily-modified and farmed landscapes, in dry and arid zones including much of Spain, and over open water bodies. Higher habitat suitability occurs in areas with woody vegetation cover, in lowlands, low topographic positions, and notably along Europe's West coast (Figure 4).

The cartographic outputs of relative probability of habitat suitability in Great Britain show high suitability across substantial areas in the South East, East of England and South West, with pockets of suitable habitat along the West Coast of Britain. Suitability is greatest in wooded landscapes and lower in urban and intensively farmed areas. Substantial areas of the Scottish Highlands and central Wales show relatively low suitability (Figure 5).

In the South East, where the feasibility of a reintroduction is currently being assessed, highest suitability was in woodland habitats and other areas with tree cover (Figure 6). Notable hotspots of suitability were in the South Downs National Park, the High Weald AONB, and the western end of the Kent Downs AONB. Low-lying coastal agricultural areas of low suitability include Thanet, Romney, Dungeness, and along the North Kent coast, as well as agricultural areas around Andover. Greater London and other urban centres are unsuitable, however, those along

the south coast such as Southampton, Portsmouth and Eastbourne are closely neighboured by areas of high suitability. Across the region, highest suitability was in woodland habitats and other areas with tree cover.

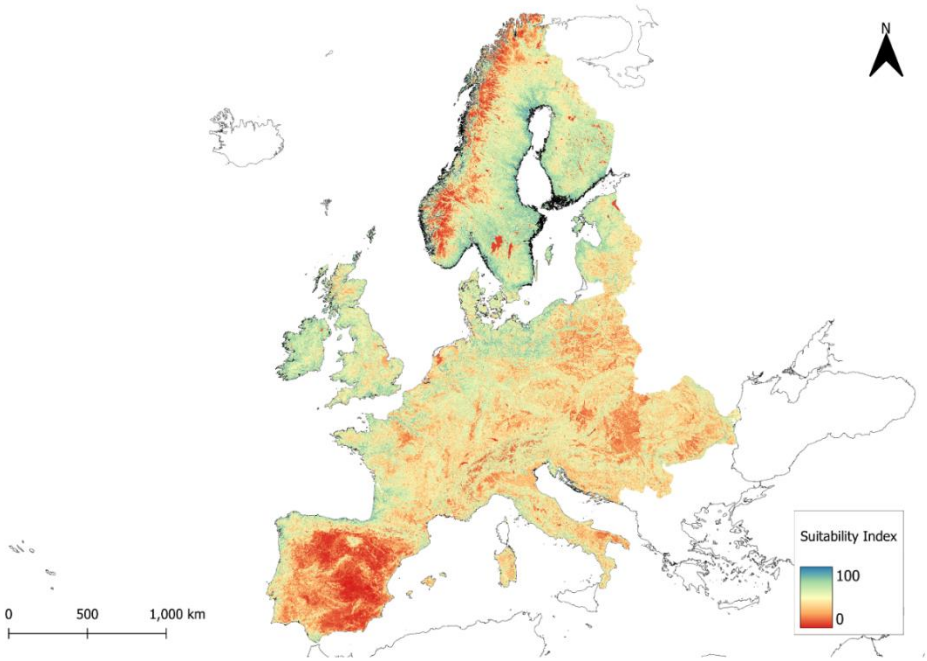


Figure 4: Habitat suitability map indicating Pine Marten suitability across Europe at a resolution of 1km x 1km. Suitability index ranged from 0 to 100, where larger values indicate higher suitability.

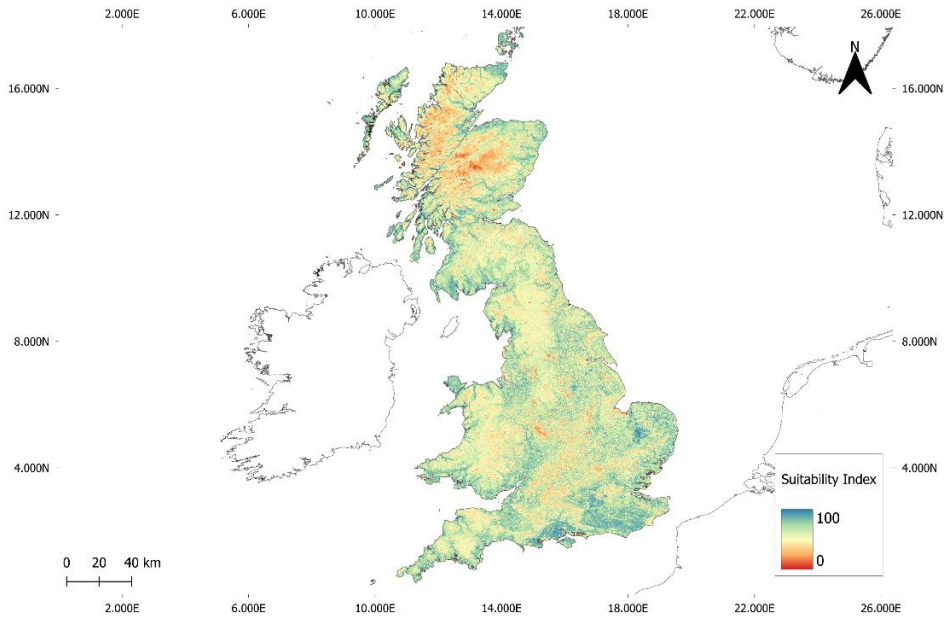


Figure 5: Habitat suitability map indicating Pine Marten suitability across Great Britain at a resolution of 100 x 100 m. Suitability index ranged from 0 to 100, where larger values indicate higher suitability.

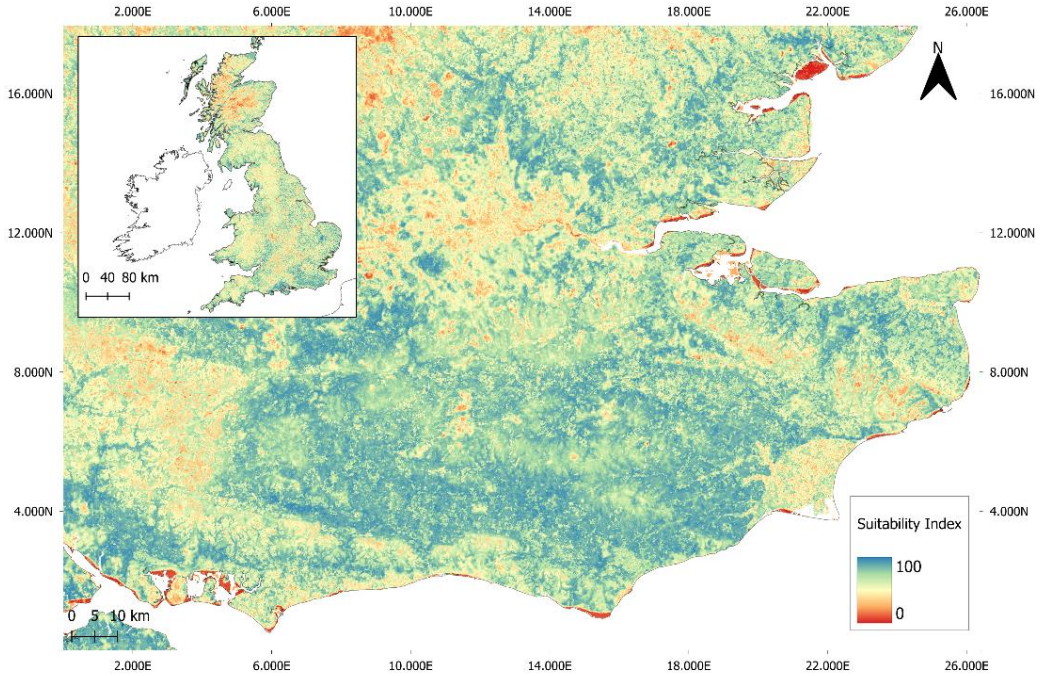


Figure 6: Habitat suitability map indicating Pine Marten suitability across the South East of England, at a resolution of 100 x 100 m. Suitability index ranged from 0 to 100, where larger values indicate higher suitability

TSS and ROC validation scores were used to assess the performance of the models. The mean TSS value of the single models was 0.3046 (Min: 0.218, Q1: 0.286, Median: 0.307, Q3: 0.324, Max: 0.368). The mean ROC value of the single models was 0.7087 (Min: 0.628, Q1: 0.698, Median: 0.713, Q3: 0.723, Max: 0.756). The calibration scores for the mean ensemble model were TSS = 0.425 and ROC = 0.786. The calibration scores for the median ensemble model were TSS = 0.361 and ROC = 0.751. The calibration scores for the weighted-mean ensemble model were TSS = 0.426 and ROC = 0.786.

The ensemble model variable importance results, averaged across the ensemble types, showed elevation was the strongest predictor of suitability, followed by land cover, vegetation greenness (NDVI) and slope, but to a lesser degree. TPI and canopy height were of relatively low importance, with forest density being of least importance (Figure 7).

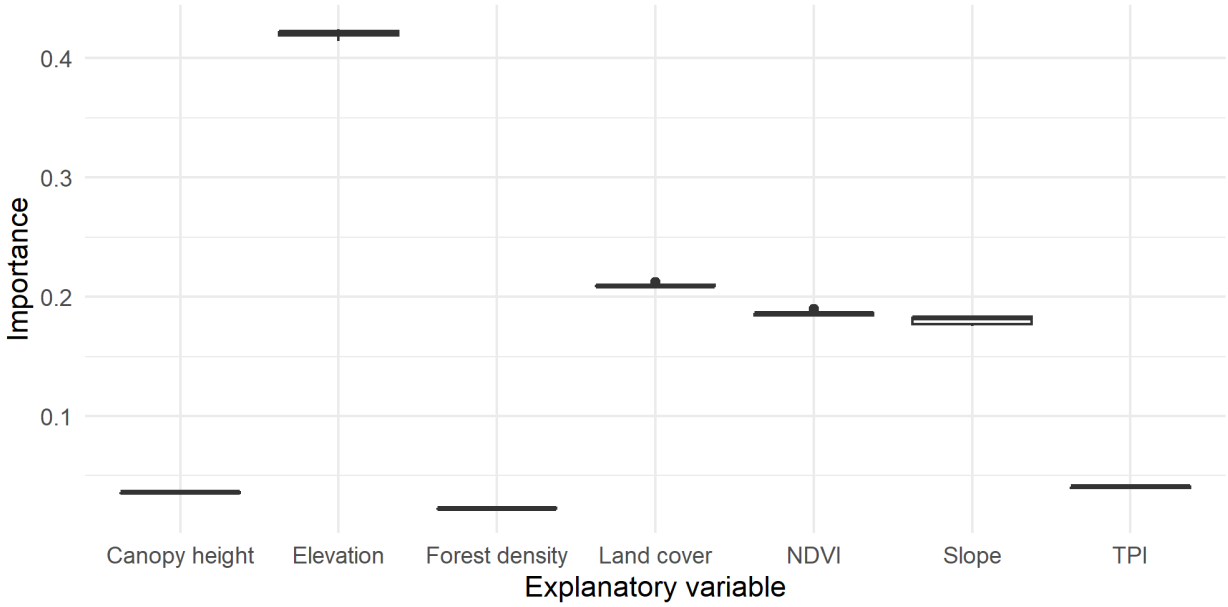


Figure 7: Box plot showing the ensemble variable importance, across the mean, median and weighted mean.

The response curves, averaged across the ensemble results (Figure 8), indicate that Pine Marten favour lower elevations, with a sharp decline in suitability at elevations above 500 m above sea level (a.s.l.).

Woodland was favoured over other land cover typed, with mixed woodland as the most suitable, followed by broadleaf woodland and coniferous woodland (Figure 8). Preference for arable and pasture land cover was lower, with suitability values below 0.5. Urban greenspace, sclerophyllous vegetation and peat bogs were the least favoured land cover type.

There is a fairly consistent medium probability of occurrence of Pine Marten across all values of tree density, although at low densities (<25% tree cover) probability starts to decrease, and at very low densities (<6% tree cover), the probability of occurrence drops sharply from about 0.42

to 0.36 (Figure 8). NDVI showed a weak positive correlation with suitability, such that the probability of occurrence of Pine Marten increased slightly with increasing vegetation greenness. Between NDVI values of 0.55 and 0.8 the probability of occurrence exceeds 0.4 (Figure 8). The probability of occurrence of Pine Marten is fairly consistent across values of canopy height, although above a canopy height of 20 m, there is a slight decrease in the probability of occurrence, from 0.4 at 25 m, to 0.3 at 35 m (Figure 8).

The species response curve for TPI, indicates a preference of Pine Marten for lower topographic positions within valleys and depressions (Figure 8). The probability of occurrence of Pine Marten is fairly consistent across all values of slope, apart from a slight decrease in very flat areas (Figure 8).

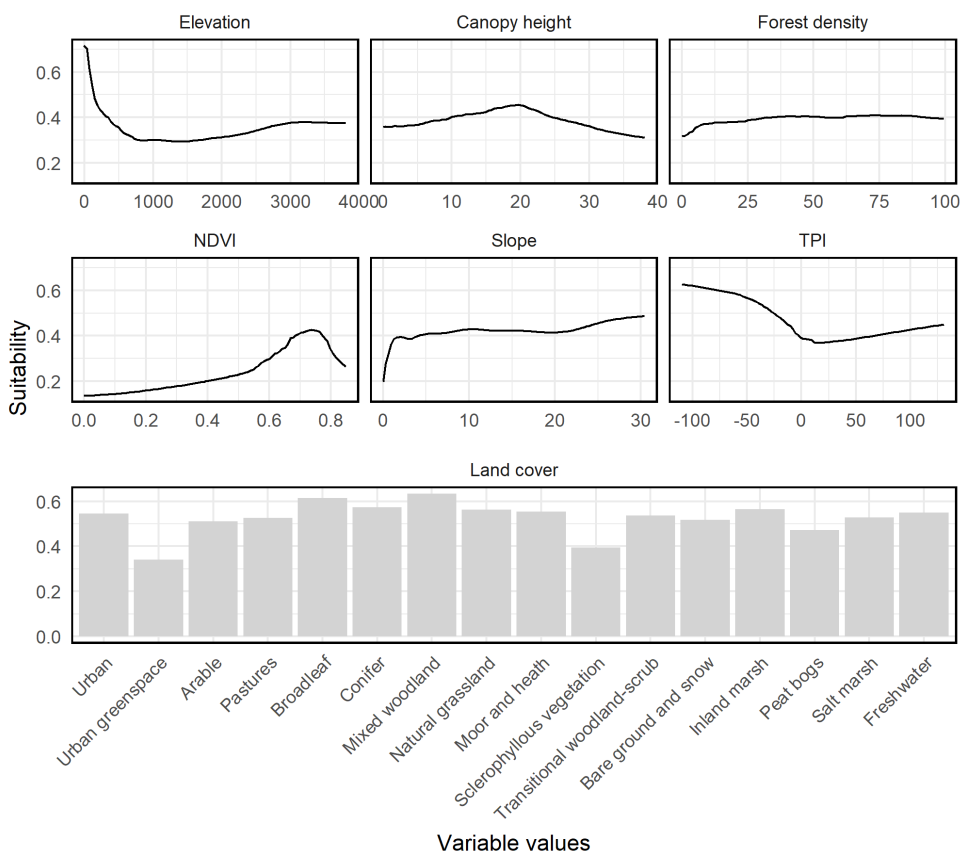


Figure 8: The response curves, averaged from the final ensemble models. Probability of suitability is on a 0-1 scale.

Discussion

In this study, eSDMs were used to map environmental suitability for Pine Marten in Great Britain, to inform conservation and restoration of the species, with a focus on reintroduction site suitability. Across the extent of Europe, the results indicate high suitability in the British isles, northern parts of continental Europe including France, Denmark and Germany and lower altitudes of Scandinavia. Low suitability regions were often found at lower latitudes including the Mediterranean regions such as large parts of the Iberian Peninsula and South East Italy, as well as areas of high altitudes including the Alps, the North Western Highlands across Norway and Sweden and extents of the Scottish Highlands (Figure 4). Across Britain, the results indicated high suitability in most regions of Northern and Republic of Ireland and lower altitudes of Scotland as well as parts of South West of England, North Yorkshire, South Cumbria and North and South Wales (Figure 5). In the South East, we found areas of high suitability to be extensively wooded environments in protected areas (National Landscapes and NPs), with lowest suitability in urban especially low-lying coastal areas (Figure 6). Hotspots of suitability were in the South Downs National Park, the High Weald AONB, and the western end of the Kent Downs AONB, which may serve as suitable reintroduction locations. The South East region holds the second highest density of woodland in the UK with 22.1% forest cover (Forest Research, 2023), which suggests why a large proportion of the landscape indicates medium to high suitability. Evaluation scores indicated an overall moderate performance of model accuracy, likely due to the limitation of mapping at a fine scale with a large spatial extent.

The variable importance results showed that elevation is the strongest predictors of habitat suitability for Pine Marten across its global range. Our results show substantially higher probability of Pine Marten habitat suitability at lower elevations (< 500 m a.s.l). We expect that elevation acts as a proxy for the complex nuances around the characteristics of woodland habitats across Europe, with the preference for lower elevations likely being associated with = their preference for broadleaved woodland habitats which typically occur at lower altitudes (Harmer et al., 2010; Portoghesi, 2006). Coniferous woodlands and alpine tundra and meadows generally occur at higher altitudes, but lack the abundance of prey and denning sites required by Pine Marten (Fonda et al., 2021). Based on our results, which we assume to be free of sampling bias with altitude, we see that Pine Marten are unlikely to occur in substantial populations at altitudes above 2000 m a.s.l. In the South East of England, the maximum elevation is 276m, and thus the altitude of the region is highly suitable for Pine Marten.

Although its relative importance was low, the response curve indicates that Pine Marten prefer lower topographic positions, representing environments within valleys and depressions. We expect this preference is linked to the greater presence of woody vegetation in these locations compared to sparser tree cover that tends to occur in higher topographic positions, on ridges and valley shoulders. Interestingly, the areas with highest suitability for Pine Marten in the South East of England were in topographically complex areas (Appendix 1).

Land cover is the second strongest predictor of suitability, with mixed, broadleaf and coniferous woodland being highly favoured (Figure 8). As forest-dwellers, Pine Marten are found primarily in well-structured deciduous and coniferous woodland, with well-insulated denning sites and abundant food resources, and with a complex understorey providing a low-risk of predation (Buskirk, 1992, Virgo et al., 2012; Delibes,1983; Balestrieri et al., 2015). The results show a lower preference for coniferous woodland compared to mixed and broadleaf woodland, which

could reflect their preference towards more structurally diverse woodland systems. Planted coniferous woodland is often thinned and structurally uniform, which serves as a poor habitat for Pine Marten due to the lack of diverse ground flora and foraging opportunities. Interestingly, arable, pasture and grassland land cover types were found to be moderately favoured, contradicting previous models which have shown that they avoid open habitats (Brainerd and Rolstad, 2002; Storch et al.,1990; Vergara et al., 2015; Wereszczuk and Zalewski, 2015). This may be explained by the species' ecological flexibility and ability to occupy heterogenous landscapes. Evidence suggests that diverse habitats can promote higher diversity of food resources than a continuous forest habitat (Rosalino and Santos-Reis, 2009; Vergara et al., 2015). For instance, we know that pine marten travel up to150 m from woodland edge to forage for prey species such as voles, provided there is some low-level vegetation cover (Caryl, 2008).

Linear or small habitat features will be underrepresented in our model due to the analytical resolution of the modelling (1x1 km). For example, shrub or hedge features within a grassland or arable pixel will not be represented. These features can serve as important facilitators of connectivity for pine martens to move through the landscape to access other patches of woodland, therefore our model likely underpredicts habitat suitability. Notably, urban greenspace, sclerophyllous vegetation and peat bogs land cover types indicated the lowest suitability. These land types are rare which may explain why they indicate significantly lower suitability compared to other land types. Amalgamating the land categories into 17 classes may have led to increased background noise within the environmental data creating biased habitat predictions. An improvement to the methodology would be to further reduce the total number of categories in the model by conducting pairwise correlations between the broad land cover types to identify highly correlated categories (Buckley and Lundy, 2012).

NDVI (vegetation greenness) was the third strongest predictor of suitability because Pine Marten inhabit woodland and adjacent edge habitat. As well as providing denning sites and shelter, vegetation greenness is also strongly correlated with prey abundance. For example, rodent density is strongly correlated with net productivity of ground vegetation (Zalewski et al., 2004). The response curve showed a peak in suitability around 0.55-0.8 NDVI which indicates high vegetation cover fraction like that of closed-canopy woodland.

Our results also suggested that Pine Marten will occupy a broad range of forest densities, with a consistent medium probability of occurrence of Pine Marten across all values of tree density (Figure 8). We expect this links strongly with their ability to adapt to possibly sub-optimum environments (MacPherson et al., 2014). For example, South Europe populations can be found across ancient woodland, coppiced woodland and cultivated land with forest fragments, where they are not restricted to dense woodland cover (Pittiglio, 1996). Even within countries, the adaptation to varying vegetation structures is evident. For example, French populations have genetically diverged to occupy varying woodland cover. In the Bressie region, individuals occupy human-dominated landscapes with fragmented forest whilst in the Ariège region individuals occupy densely forested habitat (Larroque et al., 2015).

The results show canopy height was a relatively unimportant variable. Suitability increased with increasing canopy height, up to 20 m, where it then decreased with increasing canopy height Pine Marten favour taller spruce-dominated forest for protection from predators and access to den and resting sites within the forest canopy (Brainerd and Rolstad, 2002).

Mean average monthly temperature (°C) and mean average monthly precipitation (mm) were removed from the eSDM. While these variables have high predictive power at the European scale, we know that Great Britain has a highly favourable climate for Pine Martens, and thus the predictive dominance of the climatic variables in the model were unfavourable for mapping

suitability in Great Britain. In previous model versions, mean average monthly temperature (°C) was the strongest (37%), and mean average monthly precipitation (mm) (17%), the third strongest predictor of suitability. Model performance evaluation metrics were also higher (mean single model validation TSS of ~0.43) when these variables were included. Mean average monthly precipitation (mm) was also collinear with vegetation greenness (NDVI) and elevation.

Sampling bias is a major challenge for species distribution modelling, and we identified disproportionate sampling effort in our dataset. Specifically, Pine Marten occurrence records were more common near urbanised areas and roads, possibly linked to accessibility for recorders (Araújo and Guisan, 2006). This could lead to spatial bias in the model, misrepresenting the environmental conditions which reflect suitability. We therefore decided to remove the distance to roads and urban areas variables to prevent the influence of spatial autocorrelation. One may also argue that roads and urban areas should not be included as they serve as barriers rather than predictors of suitable habitat. In other words, Pine marten do not deliberately choose to be close to or far from roads, rather, territory is chosen based on predominantly the abundance of woodland for denning potential and availability of prey. The impacts of roads and urban areas on habitat suitability and connectivity are better examined using connectivity modelling to quantify the intensity of movement barriers, which includes analysing the risks of mortality and how it effects overall population viability. Whilst comprehensive efforts have been made to reduce bias in the occurrence data, other causes of bias may still be present. For instance, we identified low environmental suitability at high altitudes, which may be due to a lower number of observations in these difficult to reach locations, as well as low importance of canopy height which may be linked to fewer observations of Pine Marten high in the canopy.

Our models did not perform to a good or excellent standard, which may be due to the large spatial extent of our analysis (Europe), which can lead to the selection of a higher proportion of less informative background points (Barbet-Massin et al. 2012). This can lead to difficulties detecting commission and omission errors (false presences and false absences), leading to low-moderate model performance. Moreover, climatic predictor variables were removed which had the strongest predictive power. Due to these imitations, the suitability maps should be used to guide further ecological feasibility research to assess suitability in the local context.

Raster data with higher resolutions than is typical for this type of study were used for a number of reasons. Firstly, higher resolution environmental variables provide more accurate information about the environment, whereas down-sampled environmental variables average across neighbouring cells, often leading to a poor measure of local conditions. This is particular pertinent in highly fragmented landscapes, where environmental predictors which change over small spatial distances may become meaningless if a coarse resolution averages a broad range of values. Secondly, high-resolution projections provide suitability estimates for smaller land areas, which is particularly important in highly fragmented landscapes such as in England. At the 100m scale, the results show substantial connected suitable habitat in the South East, particularly in the High Weald National Landscape. Moreover, it is expected that Nature Recovery Networks will increasingly connect fragmented habitat patches in future years.

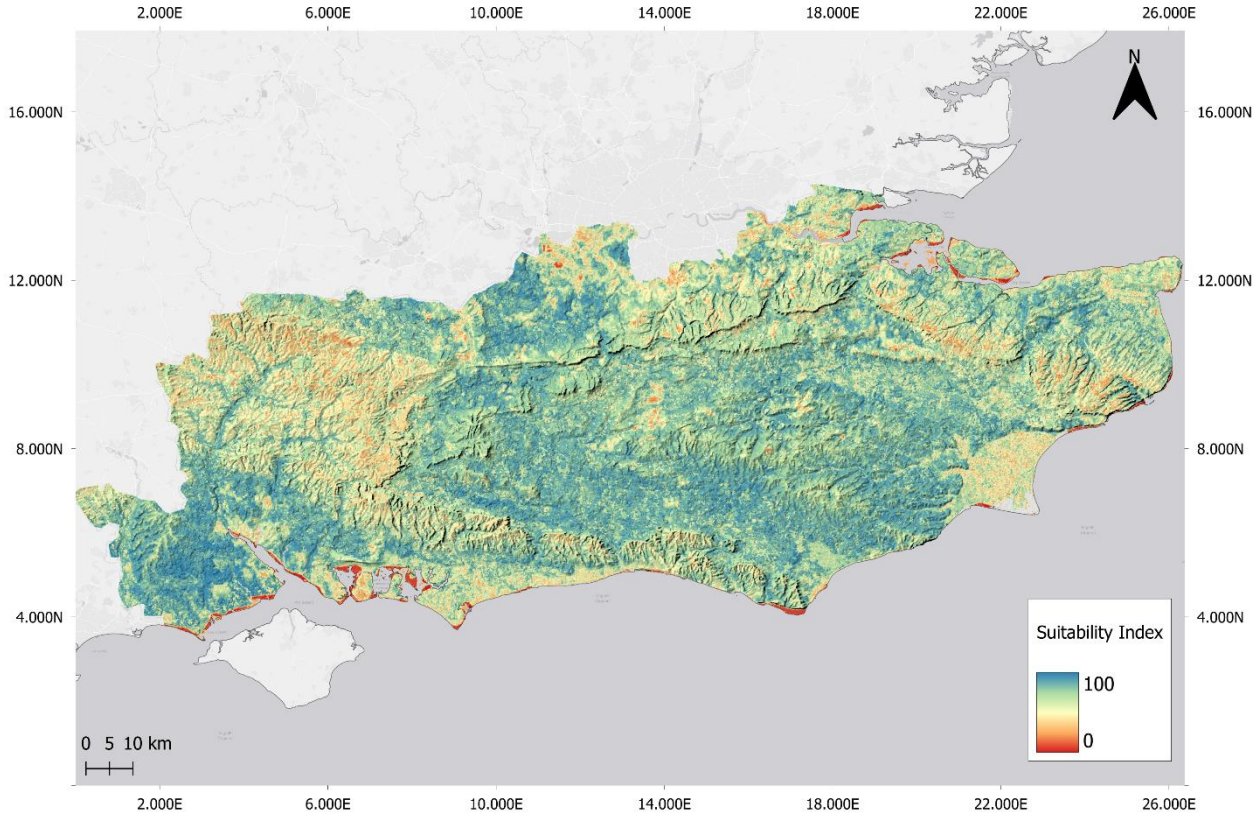
Our results reveal contiguous areas of suitable habitat in the South East and East of England. These results must be coupled with further research into connectivity and road mortality to inform the viability of a reintroduction. Since male Pine Martens hold large territories, ranging from 2 km^2 to up to 25 km^2 (Zalewski and Jędrzejewski, 2006; Balestrieri et al. 2010), the requirement for connectivity between highly suitable habitat areas is essential for their long-term establishment (McNicol et al., 2020) and should therefore be investigated. Through the

connectivity modelling, we can also assess proximity to existing populations, for example in the New Forest, which is important for ensuring genetic diversity and the long-term viability of the reintroduced populations. Additionally, MacPherson and Wright's (2021) 'Long-term strategic recovery plan for Pine Martens in Britain' report recommends further research into the effects of roads on risk of mortality in more densely-populated parts of the Great Britain, like the South East region. The South East has the second highest density of woodland (Forest Research, 2023), but also the highest traffic levels in the UK (Department for Transport, 2023). Our suitability models do not account for roads, and therefore further research into road mortality is essential prior to restoration activity.

Appendices

Appendix 1:

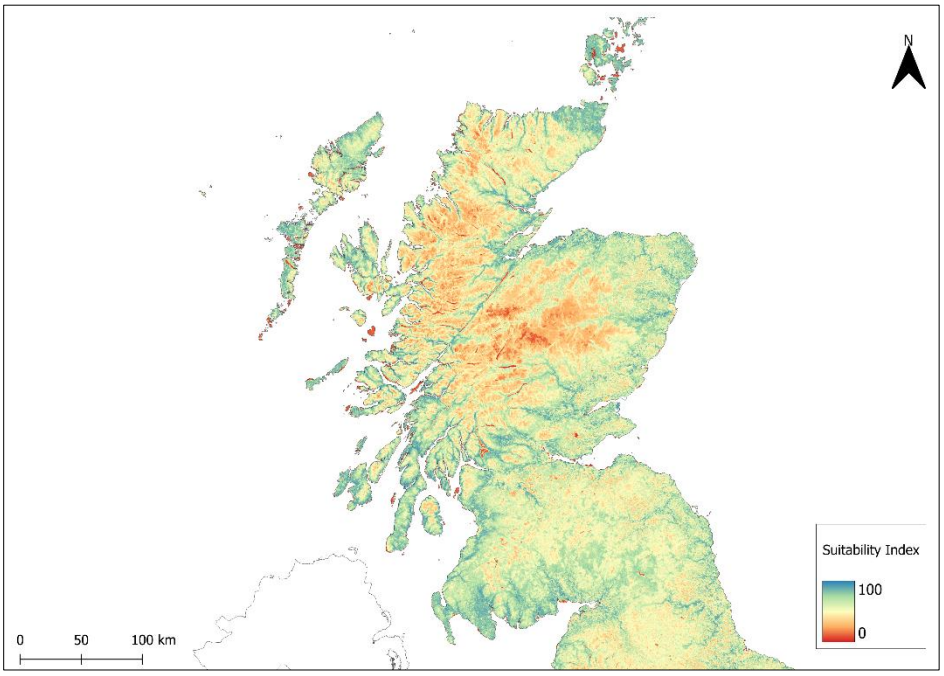
Habitat suitability map indicating Pine Marten suitability across the Southeast of England overlayed with DEM Terrain model 30m (Jaxa, 2021), at a resolution of 100 x 100 m. Suitability index ranged from 0 to 100, where larger values indicate higher suitability



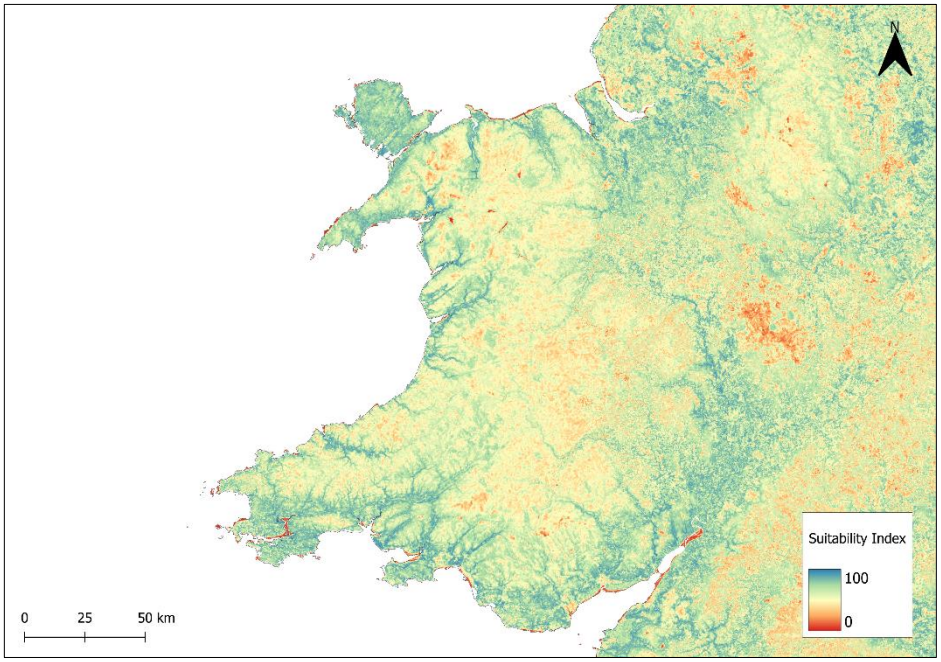
Appendix 2:

Habitat suitability map indicating Pine Marten suitability across regions of Scotland, England and Wales at a resolution of 100 x 100 m. Suitability index ranged from 0 to 100, where larger values indicate higher suitability.

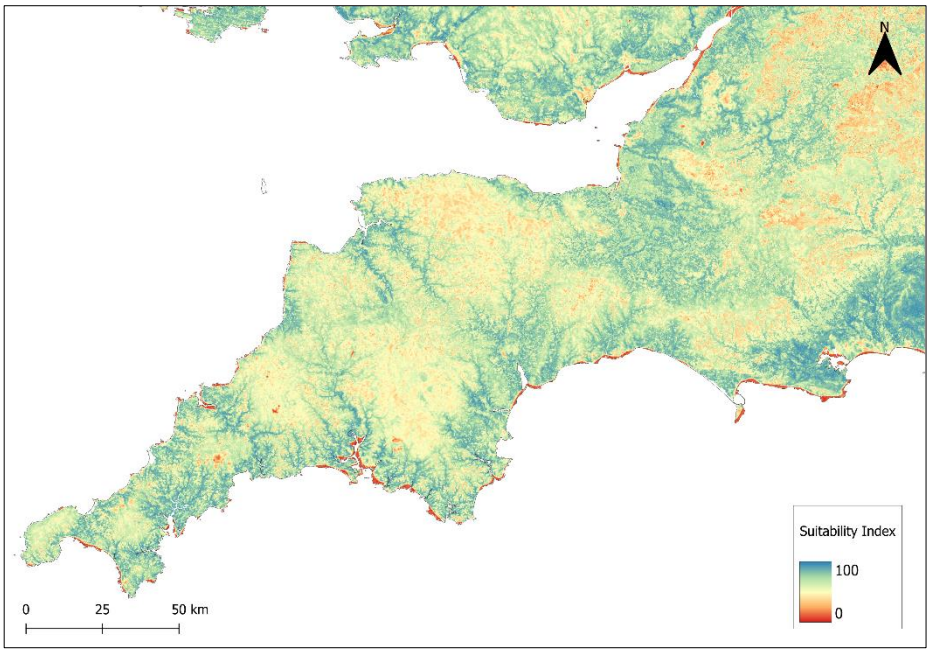
Scotland



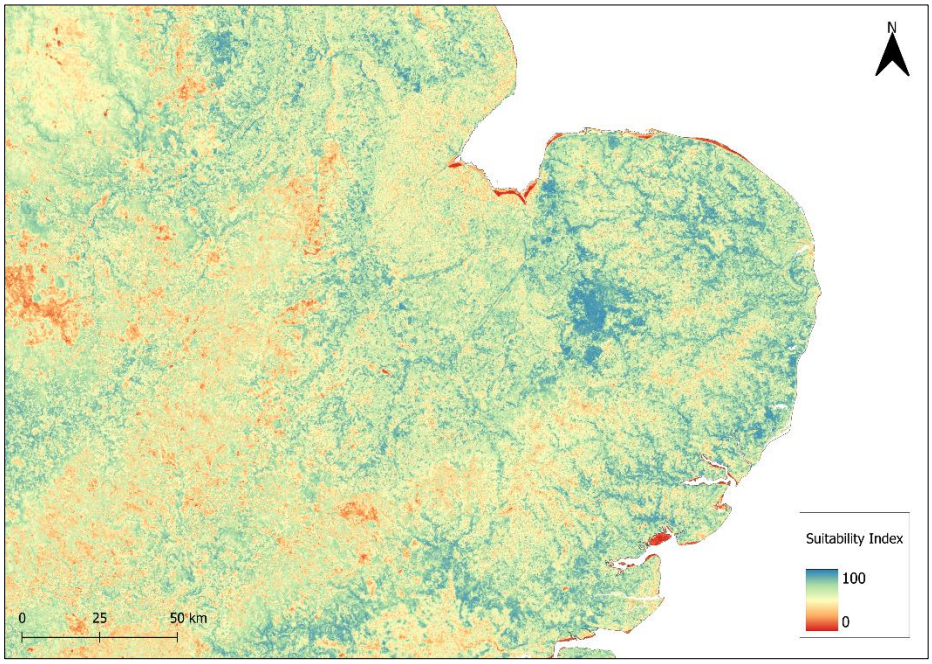
Wales



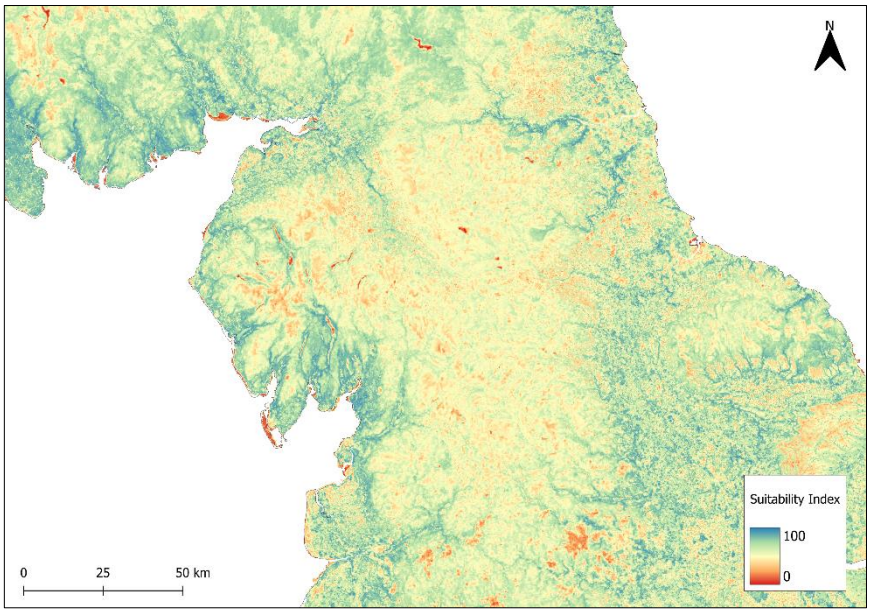
Southwest England



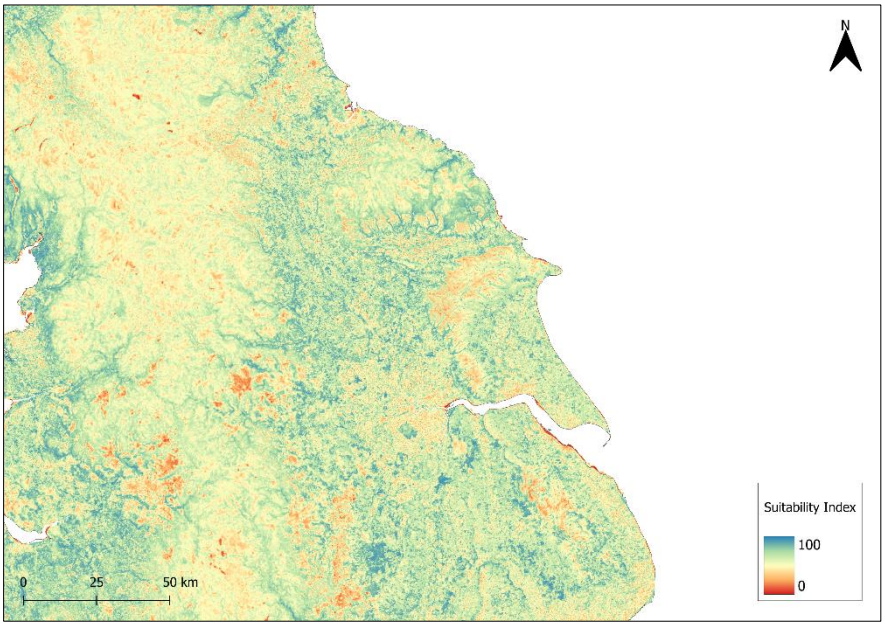
East Anglia



South Cumbria



North Yorkshire



Appendix 3:

Reclassification of CORINE land classes and UKCEH land classes to form 17 land classifications. NA indicates the categories which were not available in the UKCEH layer.

UKCEH land class number	**Alternative layer for UKCEH land class**	**CORINE land class number**	**Merged land class categories (combined CORINE and UKCEH)**	**Classification code of combined categories**
20		1 to 9, 11	Urban	1
NA	OS Open Greenspace (Ordnance Survey, 2022)	10	Urban green	2
3		12, 19 to 22	Arable	3
NA		18	Pastures	4
1		23	Broadleaf	5
2		24	Conifer	6
NA		25	Mixed woodland	7
4 to 7		26	Natural grassland	8
9		27	Moor and heath	9
NA		28	Sclerophyllous vegetation	10
NA		29	Transitional woodland-scrub	11
12		30 to 34	Bare (bare rock/sparse veg/burnt area/glacial/perpetual snow)	12
8		35	Inland marsh	13
11		36	Peat bogs	14

19		37	Salt marsh	15
13, 15, 16		38 to 39, 42 to 44	Coastal	16
14		40 to 41	Freshwater	17

Appendix 6:

Ensemble model evaluation results from the ensemble model outputs, indicating model performance across TSS, ROC and Kappa evaluations.

	filtered.by	algo	metric.eval	cutoff	sensitivity	specificity	calibration	validation	evaluation
1	TSS	EMmean	ROC	496.5	76.940	65.643	0.786	NA	NA
2	TSS	EMmean	TSS	491.0	78.133	64.327	0.425	NA	NA
3	TSS	EMmean	KAPPA	597.0	51.444	84.548	0.323	NA	NA
4	TSS	EMmedian	ROC	493.5	70.972	65.294	0.751	NA	NA
5	TSS	EMmedian	TSS	491.0	71.545	64.595	0.361	NA	NA
6	TSS	EMmedian	KAPPA	607.0	44.235	85.094	0.273	NA	NA
7	TSS	EMwmean	ROC	494.5	77.894	64.734	0.786	NA	NA
8	TSS	EMwmean	TSS	493.0	78.205	64.241	0.426	NA	NA
9	TSS	EMwmean	KAPPA	600.0	51.516	84.558	0.323	NA	NA

Appendix 7:

Ensemble variable importance results from ensemble model outputs across mean, median and weighted average evaluations.

	filtered.by	algo	expl.var	rand	var.imp
1	TSS	EMmean	elevation	1	0.424409
2	TSS	EMmean	canopy_height	1	0.036039
3	TSS	EMmean	forest_density	1	0.022745
4	TSS	EMmean	ndvi	1	0.184354
5	TSS	EMmean	slope	1	0.183473
6	TSS	EMmean	tpi	1	0.040790
7	TSS	EMmean	land_cover	1	0.210616
8	TSS	EMmean	elevation	2	0.419510
9	TSS	EMmean	canopy_height	2	0.036504

10	TSS	EMmean	forest_density	2	0.022720
11	TSS	EMmean	ndvi	2	0.184362
12	TSS	EMmean	slope	2	0.184106
13	TSS	EMmean	tpi	2	0.040971
14	TSS	EMmean	land_cover	2	0.209221
15	TSS	EMmean	elevation	3	0.414192
16	TSS	EMmean	canopy_height	3	0.036326
17	TSS	EMmean	forest_density	3	0.023042
18	TSS	EMmean	ndvi	3	0.185699
19	TSS	EMmean	slope	3	0.182867
20	TSS	EMmean	tpi	3	0.040130
21	TSS	EMmean	land_cover	3	0.209279
22	TSS	EMmedian	elevation	1	0.419994
23	TSS	EMmedian	canopy_height	1	0.035677
24	TSS	EMmedian	forest_density	1	0.022718
25	TSS	EMmedian	ndvi	1	0.189380
26	TSS	EMmedian	slope	1	0.176616
27	TSS	EMmedian	tpi	1	0.039820
28	TSS	EMmedian	land_cover	1	0.208859
29	TSS	EMmedian	elevation	2	0.419096
30	TSS	EMmedian	canopy_height	2	0.035526
31	TSS	EMmedian	forest_density	2	0.022522
32	TSS	EMmedian	ndvi	2	0.186160
33	TSS	EMmedian	slope	2	0.177070
34	TSS	EMmedian	tpi	2	0.039465
35	TSS	EMmedian	land_cover	2	0.209999
36	TSS	EMmedian	elevation	3	0.418853
37	TSS	EMmedian	canopy_height	3	0.035591
38	TSS	EMmedian	forest_density	3	0.022522
39	TSS	EMmedian	ndvi	3	0.187979
40	TSS	EMmedian	slope	3	0.175561
41	TSS	EMmedian	tpi	3	0.038905
42	TSS	EMmedian	land_cover	3	0.212062
43	TSS	EMwmean	elevation	1	0.422913
44	TSS	EMwmean	canopy_height	1	0.036650
45	TSS	EMwmean	forest_density	1	0.022307
46	TSS	EMwmean	ndvi	1	0.184124
47	TSS	EMwmean	slope	1	0.181986
48	TSS	EMwmean	tpi	1	0.040894
49	TSS	EMwmean	land_cover	1	0.208688
50	TSS	EMwmean	elevation	2	0.424065
51	TSS	EMwmean	canopy_height	2	0.035704
52	TSS	EMwmean	forest_density	2	0.022511
53	TSS	EMwmean	ndvi	2	0.185314
54	TSS	EMwmean	slope	2	0.183928
55	TSS	EMwmean	tpi	2	0.040741
56	TSS	EMwmean	land_cover	2	0.207191
57	TSS	EMwmean	elevation	3	0.420573
58	TSS	EMwmean	canopy_height	3	0.036186
59	TSS	EMwmean	forest_density	3	0.022882
60	TSS	EMwmean	ndvi	3	0.186369
61	TSS	EMwmean	slope	3	0.182078
62	TSS	EMwmean	tpi	3	0.040748
63	TSS	EMwmean	land_cover	3	0.209171

References

1.Langley, P.J.W. & Yalden, D.W. (1977) The decline of the rarer carnivores in Great Britain during the nineteenth century. Mammal Review, 7, 95-116

2.Twining, J.P., Montgomery, I., Fitzpatrick, V., Marks, N., Scantlebury, D.M. and Tosh, D.G. (2019). Seasonal, geographical, and habitat effects on the diet of a recovering predator population: the European Pine Marten (Martes martes) in Ireland. European Journal of Wildlife Research, 65(3).

3.Thuiller, W. (2014). Editorial commentary on ‘BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change’. Global Change Biology, 20(12), pp.3591–3592.

4.Raes, N.; Aguirre-Gutiérrez, J. A (2018) Modeling framework to estimate and project species distributions in space and time. In Mountains, Climate and Biodiversity; Hoorn, C., Perrigo, A., Antonelli, A., Eds.; John Wiley & Sons: Chichester, UK

5.Dormann, C.F., Elith, J., Bacher, S. and Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography,* 36(1), pp.27-46

6.Allouche, O., Tsoar, A. and Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43(6), pp.1223–1232.

7.Anderson R. P. et al. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecol. Model.* 162, pp.211– 232.

8.Brown, J.L. and Yoder, A.D. (2015). Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution*, 5(6), pp.1131–1142.

9.Forest Research. (2022). Woodland Statistics - Forest Research. Available at: https://www.forestresearch.gov.uk/tools-and-resources/statistics/statistics-by-topic/woodlandstatistics/#:~:text=The%20area%20of%20woodland%20in,and%209%25%20in%20Northern%20Ireland. [Accessed 31 Jan. 2023].

10.Araújo, M. & New, M. (2007) Ensemble forecasting of species distributions. Trends in Ecology & Evolution. 22 (1), 42–47.

11.Elith, J and Leathwick, J.R (2009) Species Distribution Models Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics 40(1),pp. 677-697

12.Kwon, H. S. (2014) 47. Species Distribution Modeling of Endangered Mammals for Ecosystem Services Valuation - Focused on National Ecosystem Survey Data**.** Journal of the Korean Society of Environmental Restoration Technology 17(1) pp. 111-122

13.Araújo, M. B., and M. New. (2007). Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22:42–47.

14. Yu B, Dai W, Li S, Wu Z, Wang J. (2024) A new threshold selection method for species distribution models with presence-only data: Extracting the mutation point of the P/E curve by threshold regression. Ecological Evolution. 14(4):e11208.

15.Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J.J. and Elith, J. (2021). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. Ecological Monographs, 92(1).

16.Hughes-Oliver, J. M. (2018). Population and empirical PR curves for assessment of ranking algorithms. *ArXiv* abs/1810.08635

17.Barbet-Massin, M., Jiguet, F., Albert, C.H. and Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, 3(2), pp.327–338.

18. Rosalino, Luís and Santos-Reis, Margarida. (2009). Fruit consumption by carnivores in Mediterranean Europe. Mammal Review. 39. 67 - 78.

19. Glon, H.E., Heumann, B.W., Carter, J.R., Bartek, J.M. and Monfils, A.K. (2017). The contribution of small collections to species distribution modelling: A case study from Fuireneae (Cyperaceae). Ecological Informatics, 42, pp.67–78.

20.Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling, 200(1-2), pp.1–19.

21.Thuiller, W. et al. (2009) 'BIOMOD - A platform for ensemble forecasting of species distributions', Ecography, 32(3), pp. 369–373.

22. Liu, C., Berry, P.M., Dawson, T.P. and Pearson, R.G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. Ecography, 28(3), pp.385–393.

23.Cohen, J. (1960) A coefficient of agreement of nominal scales. Education and Psychological Measurement, 20, pp.37-46.

24.Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. Ecography, 32, 369–373.

25. Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., and Anderson, R. P. (2015). spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545.

26. Kadmon, R, Farber, O, and Danin, A (2004). Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. – Ecological Applications. 14, pp. 401–413.

27.Anderson, R. P. and Gonzalez, I. J. (2011). Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. – Ecological Modelling. 222, pp-2796–2811.

28. Duque-Lazo, J., van Gils, H., Groen, T.A. and Navarro-Cerrillo, R.M. (2016). Transferability of species distribution models: The case of Phytophthora cinnamomi in Southwest Spain and Southwest Australia. Ecological Modelling, 320, pp.62–70.

29. R Core Development Team. R: A Language and Environment for Statistical Computing R Foundation for Statistical Computing, Vienna, Austria (2014)

30. Bio, A.M.F. Becker, P.T, Bie, E.D., and Wassen, M.J. (2002). Prediction of plant species distribution in lowland river valleys in Belgium: Modelling species response. Biodiversity and Conservation, 11(12), pp.2189-2216

31.Sheehy, E., Sutherland, C., O'Reilly, C. and Lambin, X. (2018) The enemy of my enemy is my friend: native Pine Marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations. Proceedings of the Royal Society B: Biological Sciences, 285, 20172603.

32.Schaumann, F. and Heinken, T. (2002). Endozoochorous seed dispersal by martens (Martes foina, M. martes) in two woodland habitats. Flora - Morphology, Distribution, Functional Ecology of Plants, 197(5), pp.370–378.

33. Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12), 4302-4315.

34. Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMC, Aspinall R, Hastie T. (2006) Making better bio-geographical predictions of species' distributions. Journal of Applied Ecology. 43, 386–392.

35.Meller L, Cabeza M, Pironon S, Barbet-Massin M, Maiorano L, Georges D, Thuiller W. (2014) Ensemble distribution models in conservation prioritization: from consensus predictions to consensus reserve networks. Diversity Distribution. 20(3):309-321.

36. Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geo-graphic distributions. Ecological Informatics, 19, 10–15

37.Aarts, G., Fieberg, J., Brasseur, S. and Matthiopoulos, J. (2013). Quantifying the effect of habitat availability on species distributions. Journal of Animal Ecology, 82(6), pp.1135–1145.

38. Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15 (1), 59–69

39. S.J. Phillips, R.P. Anderson, R.E. (2006) Schapire Maximum entropy modelling of species geographic distributions Ecological Modelling, 190 (3–4), pp. 231-259,

40. Guisan, A., Thuiller, W., and Zimmermann, N. (2017). The Biomod2 Modeling Package Examples. In Habitat Suitability and Distribution Models: With Applications in R (Ecology, Biodiversity and Conservation, pp. 357-400). Cambridge: Cambridge University Press.

41.Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V. and Antonelli, A. (2019). CoordinateCleaner : Standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution, 10(5), pp.744–751.

42. Ball and Tzanopoulos (2020) Interplay between topography, fog and vegetation in the central South Arabian mountains revealed using a novel Landsat fog detection technique, Remote Sensing in Ecology and Conservation 6(4): 498-513.

43.Paine, R.T. (1969) A note on trophic complexity and community stability. The American Naturalist, 103:91–93.

44.Hastings, A., Byers J.E, Crooks J.A, Cuddington K, Jones C.G, Lambrinos J.G, Talley T.S, Wilson W.G. (2007) Ecosystem engineering in space and time. Ecology Letters 10, pp.153–164.

45. Crowley, S.L, Hinchliffe S, McDonald R.A. (2018) Killing squirrels: Exploring motivations and practices of lethal wildlife management. Environment and Planning E: Nature and Space 1, pp.120–143.

46. Sandom C, Donlan C.J, Svenning J.C, Hansen D (2013) Rewilding. Key topics in conservation biology. Wiley-Blackwell, Chichester, UK. pp.430–451

47.Davies H.T, Du Toit J.T. (2004) Anthropogenic factors affecting wild dog Lycaon Pictus reintroductions: A case study in Zimbabwe. Oryx. 38, pp. 32–39

48. Simard, M., Pinto, N., Fisher, J.B. and Baccini, A. (2011). Mapping forest canopy height globally with spaceborne lidar. Journal of Geophysical Research, 116(G4).

49. Brus, D.J., Hengeveld, G.M., Walvoort, D.J.J., Goedhart, P.W., Heidema, A.H., Nabuurs, G.J. and Gunia, K. (2011). Statistical mapping of tree species over Europe. European Journal of Forest Research, 131(1), pp.145–157.

50.Morton, R.D.; Marston, C.G.; O'Neil, A.W.; Rowland, C.S. (2021). Land Cover Map 2020 (25m rasterised land parcels, GB). NERC EDS Environmental Information Data Centre

51. F. Ben Rais Lasram, F. Guilhaumon, C. Albouy, S. Somot, W. Thuiller, D. Mouillot (2010), The Mediterranean Sea as a "cul-de-sac" for endemic fishes facing climate change Global Change Biol., 16. pp. 3233-3245,

52.W. Thuiller, D. Georges, R. Engler, F. Breiner biomod2: ensemble platform for species distribution modeling R package version, 3 (2016), pp. 3-7

53. Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R.O., Wang, Z. and Zimmermann, N.E. (2019). Model complexity affects species distribution projections under climate change. Journal of Biogeography, 47(1), pp.130–142.

54. Duan, R.Y., Kong, X.Q., Huang, M.Y., Fan, W.Y. and Wang, Z.G. (2014). The Predictive Performance and Stability of Six Species Distribution Models. PLoS ONE, 9(11), p.e112764.

55.A.T. Peterson, J. Soberón, R.P. Anderson, R.G. Pearson, E. Martínez-Meyer, M. Nakamura, M.B. Araújo Ecological Niches and Geographic Distributions: A Modeling Perspective Princeton University Press, Princeton (2012) 328 pp.

56.Hao, T., Elith, J, Lahoz-Monfort, J.J.,Guillera-Arroita, G. (2020) Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. Ecography 2020, 43, pp.549–558.

57. Buskirk, S.W (1992) Conserving circumboreal forests for martens and fishers. Conservation Biology 6, pp.318–320

58.Delibes, M (1983) Interspecific competition and the habitat of the stone marten Martes foina (Erxleben 1777). Environmental Science. 174, pp. 229–231

59. Pittiglio, C (1996). Differential use of food and habitat by sympatric carnivores in the eastern Italian Alps. Journal of Zoology, 75(2), pp. 173–184

60. Storch I, Lindström E.R, Jounge,J (1990) Diet and habitat selection of the Pine Marten in relation to competition with the red fox. Acta Theriologica 35, pp.311–320

61. Balestrieri A, Remonti L, Ruiz-González A, Gómez-Moliner B.J, Vergara M, Prigioni, C (2010) Range. expansion of the Pine Marten (Martes martes) in an agricultural landscape matrix (NW Italy). Mammal Biology 75, pp. 412–419

62. Zalewski, A., Jedrzejewski, W. and Jedrzejewski, B. (2004). Mobility and home range use by Pine Martens (Martes martes) in a Polish primeval forest. Écoscience, 11(1), pp.113–122.

63. Jedrzejewski, W., A. Zalewski and B. Jedrzejewska, (1993) Foraging by pine marten Martes martesin relation to foodresources in Bialowieza National Park, Poland. ActaTheriologica, 38, pp.405-426

64. Harlow, H.J. (1994). Trade-offs associated with the size and shape of American martens. Pages 391-403 inS. W.Buskirk, A. S. Harestad, M. G. Raphael & R. A. Powell(eds.). Martens, Sables, and Fishers: Biology and Conservation. Cornell University Press, Ithaca, New York.

65. Vergara M, Cushman S.A, Urra F, Ruiz-González A. (2015) Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (Martes martes and Martes foina) in the northern Iberian Peninsula. Landscape Ecology. 31, pp.1241–1260

66. Wereszczuk, A, Zalewski, A. (2015) Spatial Niche Segregation of Sympatric Stone Marten and Pine Marten– Avoidance of Competition or Selection of Optimal Habitat? PLOS ONE. 10(10)

67. Virgos E, Zalewski A, Rosalino L, Mergey M (2012) Habitat ecology of genus Martes in Europe: a review of the evidences. In: Aubry KB, Zielinski WJ, Proulx G, Buskirk SW (eds) Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, New York, pp. 255–266

68. Balestrieri A, Remonti L, Ruiz-Gonza´lez A, Zenato M, Gazzola A, Vergara M, Detorri E.E, Saino N, Capelli E, Go´mezMoliner BJ, Guidali F, Prigioni C (2015) Distribution and habitat use by Pine Marten Martes martes in a riparian corridor crossing intensively cultivated lowlands. Ecological Research, 29(6), pp.1-10

69. JNCC (2021) UK Biodiversity Indicators 2021. JNCC.

70. Mammola, S., Pétillon, J., Hacala, A., Monsimet, J., Marti, S., Cardoso, P. and Lafage, D. (2021). Challenges and opportunities of species distribution modelling of terrestrial arthropod predators. Diversity and Distributions, 27(12), pp.2596–2614.

71. European Environment Agency (2018a) CORINE land cover 2018--copernicus land monitoring services https://land.copernicus.eu/pan-european/corine-land-cover/clc2018

72. European Environment Agency (2018b) Tree Cover Density 2018--copernicus land monitoring services https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/status-maps/tree-cover-density-2018

73. QGIS Development Team, 2021. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

74.Li X, Wang Y. (2012) Applying various algorithms for species distribution modelling. Integral Zoology. 8, pp.124–135

75. Zalewski, A. and Jędrzejewski, W. (2006) Spatial organisation and dynamics of the Pine Marten Martes martes population in Białowieza Forest (E Poland) compared with other European woodlands. Ecography, 29,pp. 31-43.

76. McNicol, C.M., Bavin, D., Bearhop, S., Bridges, J., Croose, E., Gill, R., Goodwin, C.E.D., Lewis, J., MacPherson, J., Padfield, D., Schofield, H., Silk, M.J., Tomlinson, A.J. and McDonald, R.A. (2020). Postrelease movement and habitat selection of translocated Pine Martens Martes martes. Ecology and Evolution, 10(11), pp.5106–5118.

77.Caryl, F.M. (2008). Pine Marten diet and habitat use within a managed coniferous forest. Ph. D. Thesis. University of Stirling Available at: https://dspace.stir.ac.uk/bitstream/1893/2261/1/Fiona%20Mae%20Caryl.%20Pine%20Marten%20Diet%20%26%20Habitat%20Use%20Within%20A%20Managed%20Coniferous%20Forest.pdf (Accessed 7th July 2023)

78. Forest Research (2023) The canopy cover Webmap of the United Kingdom's towns and cities. Available at: https://www.forestresearch.gov.uk/publications/the-canopy-cover-webmap-of-the-united-kingdoms-towns-and-cities/ Accessed 23 Mar 2024]

79. Department for Transport (2023) Road Traffic Statistics. Available at: https://roadtraffic.dft.gov.uk/regions Accessed 23 Mar 2024]

80. Buckley, D.J. and Lundy, M. (2012). The current distribution and potential for future range expansion of feral ferret Mustela putorius furo in Ireland. European Journal of Wildlife Research, 59(3), pp.323–330

81. Kirk T.A and Zielinski W.J (2009) Developing and testing a landscape habitat suitability model for the American marten (Martes americana) in the Cascades mountains of California. Landscape Ecology 24, pp.759–773

82.Carroll C, Zielinski W.J, Noss R.F (1999) Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath region, USA. Conservation Biology, 13, pp.1344–1359

83. O'Mahony, D.T. (2017). A species distribution model for Pine Marten (Martes martes) in the least forested region of Europe. Mammal Research, 62(2), pp.195–200.

84. McPherson J, Jetz W, Rogers D.J (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? Journal of Applied Ecology 41, pp.811–823

85. GDAL/OGR contributors (2022). GDAL/OGR Geospatial Data Abstraction software Library. Open Source Geospatial Foundation. URL: https://gdal.org

86. USGS (2022) *Landsat 8 Collection 1 Tier 1 Landsat 8 Collection 1 Tier 1 Annual Greenest-Pixel TOA Reflectance.* Available at: https://developers.google.com/earth-engine/datasets/catalog/LANDSAT_LC08_C01_T1_ANNUAL_GREENEST_TOA [Accessed 28 Mar. 2023]

87. GBIF Secretariat. GBIF Backbone Taxonomy. Checklist dataset. Available at: https://www.gbif.org/dataset/d7dddbf4-2cf0-4f39-9b2a-bb099caae36c2023-09-01. [Accessed 28 Mar 2023]

88. National Biodiversity Network (NBN) Trust (2023). The National Biodiversity Network (NBN) Atlas. Available at: https://ror.org/00mcxye41 [Accessed 28 Mar 2023].

89. 75. Seddon, P.J, Armstrong, D.P (2019) The role of translocation in rewilding. In: du Toit JT, Pettorelli N, Durant SM (eds) Rewilding (pp. 303-324). Cambridge University Press, Cambridge

90. Klein, L. and Arts, K. (2021). Public participation in decision-making on conservation translocations: the importance and limitations of a legislative framework. Restoration Ecology, 30(1).

91. Kirkwood, J. (2013). Guidelines for reintroductions and other conservation translocations. Animal Welfare, 22(4), pp.489–490

92. D.P. Armstrong, P.J. and Seddon (2008) Directions in reintroduction biology. Trends in Ecology and Evolution, 23, pp. 20-25

93. Mathews F, and Harrower C. (2020). IUCN – compliant Red List for Britain's Terrestrial Mammals. Assessment by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough ISBN 978-1-78354-485-1

94. MacPherson, J. (2014) Feasibility assessment for reinforcing Pine Marten numbers in England and Wales. Vincent Wildlife Trust. Available at: https://www.vwt.org.uk/wp-content/uploads/2015/04/Feasibility-Assessment-for-Reinforcing-Pine-Martens-in-England-and-Wales.pdf [Accessed 28 Mar 2023]

95. Stringer, A. P., MacPherson, J., Carter, S., Gill, R., Ambrose-Oji, B. and Wilson, R.(2015). The Feasibility of Reintroducing Pine Martens (Martes martes) to the Forest of Dean and Lower Wye Valley. Herefordshire: Forestry Commission England, Gloucestershire Wildlife Trust, Vincent Wildlife Trust.

96. MacPherson, J., Croose, E., Bavin, D., O'Mahony, D., Somper, J. and Buttriss, N. (2014). Feasibility assessment for reinforcing Pine Marten numbers in England and Wales. Ledbury, UK: Vincent Wildlife Trust.

97. MacPherson, J. and Wright, P. (2021) Long-term strategic recovery plan for Pine Martens in Britain. The Vincent Wildlife Trust, Natural England, NatureScot. pp.1-72.

98. Gilpin, M.E. and Soulé, M.E. (1986) Minimum viable populations: processes of species extinction. Conservation Biology: the science of scarcity & diversity (eds M.E. Soulé & M.A. Sunderland), pp. 19-34. Sinauer Associates.

99. Birks, J.D. (2020) Pine Martens. Whittet Books Ltd, Essex, UK. Reprint (with updates)

100. Lariviere, S. & Jennings, A.P. (2009). European Pine Marten (Martes martes). Family Mustelidae (Weasels and Relatives). In: D.E. Wilson & R. A. Mittermeier (Eds), Handbook of the Mammals of the World. Volume 1: Carnivores. Lynx Edicions, Barcelona, Spain.

101. Brainerd, S.M. and Rolstad, J. (2002). Habitat selection by Eurasian Pine Martens *Martes martes* in managed forests of southern boreal Scandinavia. Wildlife Biology, 8(4), pp.289–297.

102. Lee, J.-K., Hwang, H.-S., Eum, T.-K., Bae, H.-K. and Rhim, S.-J. (2020). Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Animal Biology, 70(2), pp.203–213.

103. Krebs, C.J. (2009) *Ecology: the Experimental Analysis of Distribution and Abundance*. 6th Edition. Pearson Benjamin Cummings, San Francisco, CA, USA.

104. Báez, S., Fadrique, B., Feeley, K. and Homeier, J. (2022). Changes in tree functional composition across topographic gradients and through time in a tropical montane forest. PLOS ONE, 17(4), p.e0263508.

105. Sultaire, S.M., Millspaugh, J.J., Jackson, P.J. and Montgomery, R.A. (2022). The influence of fine-scale topography on detection of a mammal assemblage at camera traps in a mountainous landscape. *Wildlife Biology*, 2023(2).

106. Balestrieri, A., Bogliani, G., Boano, G., Ruiz-González, A., Saino, N., Costa, S. and Milanesi, P. (2016). Modelling the Distribution of Forest-Dependent Species in Human-Dominated Landscapes: Patterns for the Pine Marten in Intensively Cultivated Lowlands. *PLOS ONE*, 11(7), p.e0158203.

107. DEFRA (2022). Keepers of time: ancient and native woodland and trees policy in England Government's statement on England's ancient and native woodland and ancient and veteran trees. Available at: https://www.gov.uk/government/publications/keepers-of-time-ancient-and-native-woodland-and-trees-policy-in-england/keepers-of-time-ancient-and-native-woodland-and-trees-policy-in-england [Accessed 28 Mar 2023]

108. Ferrier, S. and Guisan, A. (2006) 'Spatial modelling of biodiversity at the community level', *Journal of Applied Ecology*, 43(3), pp. 393–404.

109. Japan Aerospace Exploration Agency (JAXA) (2021). ALOS World 3D 30 meter DEM. V3.2, Jan 2021. Distributed by OpenTopography. https://doi.org/10.5069/G94M92HB. [Accessed 23 Mar 2023]

110. R Development Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

111. Center for International Earth Science Information Network - CIESIN (2013)- Columbia University, and Information Technology Outreach Services - ITOS - University of Georgia. 2013. Global Roads Open Access Data Set, Version 1 (gROADSv1). Palisades, New York: NASA Socioeconomic Data and Applications Center (SEDAC). Available at: https://doi.org/10.7927/H4VD6WCT. [Accessed 23 Mar 2023]

112. Patterson, Tom. Kelso, Nathaniel Vaughn. (2012). World Urban Areas, 1:10 million [Shapefile]. North American Cartographic Information Society. Available at: https://maps.princeton.edu/catalog/stanford-xg070wh7159. [Accessed 23 Mar 2023]

113.Araújo, M.B. and Guisan, A. (2006). Five (or so) challenges for species distribution modelling. Journal of Biogeography, 33(10), pp.1677–1688.

114. Stringer A.P, MacPherson, J , Carter, S , Gill, R , Ambrose-Oji, B , Wilson, R , Kelsall, P, Feirn, W.G, Galbraith, L.C, Hilário CM, Parry, G and Taylor, A (2018) The feasibility of reintroducing pine martens (Martes martes) to the Forest of Dean and lower Wye Valley. Gloustershire Wildlife Trust Report

115. Fonda, F., Chiatante, G., Meriggi, A.. (2021) Spatial distribution of the pine marten (*Martes martes*) and stone marten (*Martes foina*) in the Italian Alps. Mammal Biology 101, pp.345–356

116. Croitor, R and Brugal J.P, (2010) Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. Quaternary International, 212, pp.98–108.

117. Harmer, R., Kerr, G. and Thompson, R. (2010) Managing Native Broadleaved Woodland. The Stationary Office, Edinburgh

118. Portoghesi L, (2006). European Forest Types. Categories and types for sustainable forest management reporting and policy. Forest 3 (4): 462-463

119. Allaby,, M.(2006) Biomes of the Earth: Temperate Forests. New York, NY: Chelsea House

120. Ordnance Survey (2022) *OS Green Open Greenspace*. Available at: https://www.ordnancesurvey.co.uk/products/os-open-greenspace

121.Vincent Wildlife Trust (2020) Red squirrels making comeback as return of native pine marten spells bad news for invasive grey squirrel. Available at: https://www.vincentwildlife.ie/news/red-squirrels-making-comeback-as-return-of-native-pine-marten-spells-bad-news-for-invasive-grey-squirrel

122. Larroque, J., Ruette, S., Vandel, J.-M. and Devillard, S. (2015) *Landscape Ecology*, 31(3), pp. 517–531. doi: 10.1007/s10980-015-0281-6.