Article:

Hobson, K.J., Sutherland, C., Waggershauser, C.N. et al. (2026) Both forest cover and land management practices explain variation in recovering pine marten densities. Wildlife Biology. e01594. ISSN: 1903-220X

https://doi.org/10.1002/wlb3.01594

WILDLIFE BIOLOGY

Research Article

Both forest cover and land management practices explain variation in recovering pine marten densities

Keziah J. Hobson[1,2], **Chris Sutherland**[3], **Cristian Navarro Waggershauser**[1,4], **Deborah A. Dawson**[2], **Gavin J. Horsburgh**[2], **Lucy S. Knowles**[2] and **Xavier Lambin**[1]

[1]School of Biological Sciences, University of Aberdeen, Aberdeen, UK
[2]NERC Environmental Omics Facility, School of Biosciences, University of Sheffield, Sheffield, UK
[3]Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, UK
[4]University of the Highlands and Islands, Inverness, UK

Correspondence: Xavier Lambin (x.lambin@abdn.ac.uk)

Wildlife Biology
2026: e01594
doi: 10.1002/wlb3.01594
Subject Editor:
Jean-Francois Robitaille
Editor-in-Chief: Ilse Storch
Accepted 26 December 2025

Robust monitoring of wildlife populations to guide interventions is fundamental to conservation and wildlife management. Understanding how landscape characteristics are influencing predator population dynamics is often vital to inform recovery strategies, management, and policy. The pine marten *Martes martes* is recovering in the UK; however, population spread has occurred at different rates across the country. We investigated how spatial variation in density of recovering pine marten populations is influenced by key habitat and human-related factors. We genotyped non-invasively collected pine marten hair samples collected through standardised surveys covering four landscapes in Scotland over three seasons. We applied a multi-session, sex-structured, spatial capture–recapture model to estimate within- and between-landscapes spatial variation in density. We identify larger areas being used by individuals in recently recolonised areas compared to more established populations. We find significant differences in the spatial variation of density across landscapes ranging from 0.05 marten km^{-2} (95% CI: 0.03–0.07) in the recently colonised Borders region of southern Scotland to 0.21 marten km^{-2} (95% CI: 0.10–032) in the Trossachs region of central Scotland. There was substantial variation in pine marten density within landscapes. The amount of forest had a positive effect on population density, but not in the most recently recolonised population. Closer proximity to large gamebird shoots had a significant negative effect on pine marten density in one landscape suggesting that, despite being protected in law, pine martens suffer sufficiently elevated mortality close to some pheasant pens to locally depress their density. We did not find an effect of distance to nearest major road on spatial variation in population density in any landscape. While the mechanistic processes driving these patterns are not clear, our work highlights the importance of elucidating the processes underlying these effects of forest and land management.

Keywords: pine marten, population density, recovering predator, spatial capture–recapture

NORDIC SOCIETY OIKOS

www.wildlifebiology.org

Introduction

Over the centuries, many predators have been driven to very low densities or regional extinction through a combination of recreational hunting, (over)harvesting for trophies or fur, or deliberate eradication in response to perceived human–wildlife conflicts. While environmental change (climate and land use) has contributed to declines, many declines have been driven predominantly by the impact of persecution (Langley and Yalden 1977). In recent decades, however, many predators have recovered in parts of Europe following legal protections (Chapron et al. 2014).

The return of mammalian predators can provide socio-ecological and economic benefits (Gregr et al. 2020, Twining et al. 2022a) and challenges (Dickman 2010, Ritchie et al. 2012, Marshall et al. 2016), yet little is known about the process of recolonisation in historical native ranges that are now modified from their original state. Specifically, it is unknown whether recovering native species undergoing rapid range expansion will temporarily reach abnormally high abundance and overshoot notional carrying capacities in the same way that establishing invasive species do (Strayer et al. 2017). Rising abundance from low recent historical baselines may contribute to both a social perception of overabundance of predators (Hobson et al. 2024), but also sensitive prey populations may be tipped into declines (Marshall et al. 2016, Bamber et al. 2024). Substantiating or dispelling those concerns requires estimating the density of the predator.

Substantial efforts have been made to overcome the challenges of density estimation of scarce, elusive large carnivores using spatial capture–recapture models (SCR; Efford et al. 2009, Royle et al. 2018). In the context of recovering European carnivores, this has best been achieved though non-invasive genetic sampling (e.g. brown bears *Ursus arctos*, wolves *Canis lupus*, and wolverines *Gulo gulo* in Scandinavia (Bischof et al. 2020), and wolves in Spain (López-Bao et al. 2018)). Where available, such density estimates guide management actions such as conservation performance payments in Sweden that are given to reindeer herders based on the estimated number of predators and the associated predation pressure (Zabel and Holm-Müller 2008, Pekkarinen et al. 2020). The reinstatement of traditional protective measures such as livestock protection dogs is also informed by density estimates (Gehring et al. 2010). In the absence of evidence, however, perceptions about over-abundance of recovering predators may be based on qualitative impressions, anecdotal evidence, and individuals' perceptions and attitudes towards the species (Fischer et al. 2014, Hobson et al. 2024). Further, spatial variability in the density of recovered predators could result in areas where conflict involving predators is heightened (Miller 2015). Therefore, understanding the determinants of spatial variation in predator population density is particularly important for guiding and targeting more effective and appropriate policies, and management strategies, and conservation efforts.

The European pine marten *Martes martes* is recovering on mainland Britain after severe population declines and range contraction in the 18th and 19th centuries (Croose et al. 2013, Sainsbury et al. 2019). Its historical decline is attributed to both loss of forest cover, whereby widespread woodland clearance reduced forest to just 5% in the early 1900s, and to persecution due to perceptions of pine martens as pests (anti-predator gamekeeping practices, and fur trapping) (reviewed by O'Reilly et al. 2024). The southward expansion from its remnant range in northwest Scotland followed legal protection in 1988, large-scale reforestation increasing tree cover from 5.0% in the early 1900s to 18.5% in 2018 in Scotland, and both licensed and unlicensed reintroductions (Forestry Commission 2003, Mergey et al. 2011, Croose et al. 2013, Hobson 2023, MacPherson et al. 2024).

Although pine martens are generally associated with forest habitat, they can also occupy landscapes with low forest cover and exploit forest edges (Moll et al. 2016). Indeed, population density (based on home range size derived from radio-tracking) has been documented to be higher in moderately fragmented habitats compared to contiguous forests, suggesting a complex relationship between forest amount and density (Mergey et al. 2011, Caryl et al. 2012a), and at lower density in conifer plantations and agricultural landscapes lacking arboreal denning sites than in native woodland (Twining et al. 2020).

The recovery of the pine marten population reflects improved conditions, but there is also evidence that some old threats endure, and new threats have emerged in parts of the landscape. Novel sources of mortality for pine marten include vehicle collisions, indiscriminate predator control practices resulting in accidental killing, and direct persecution linked to shooting of small game. Roads are known to affect pine marten spread and distribution, and potentially cause high individual turnover (Mergey et al. 2011, Hobson 2023, MacPherson et al. 2024). It is not known to what extent immigration and recruitment, which will vary with stage of population recovery, compensate these sources of mortality and explain spatial variation in pine marten densities (Moore et al. 2023). Several studies in the UK and Ireland have documented the influence of forest cover, fragmentation, and habitat type on pine marten population density (Caryl et al. 2012a, Kubasiewicz et al. 2017, Twining et al. 2020), but to date no studies have considered the influence of roads and land management practices on density and spatial variation in density, but rather only on the presence of pine martens (Weber et al. 2018, MacPherson et al. 2024).

To address these knowledge gaps, we quantity the relative effects of habitat, potential persecution, and infrastructure on spatial variation in recovering pine marten populations. We apply SCR methods to individual pine marten capture histories obtained from non-invasive DNA genotyping of hair samples from standardised surveys covering four landscapes across Scotland over three seasons.

Material and methods

Survey design

We collected hair samples in four survey areas (landscapes hereafter) in Scotland between January 2018 and July 2019. These landscapes were selected to each have similar amount and distribution of forest cover, proximity to large pheasant release pens, and variation in road density, but that spanned a gradient in times since recolonisation by pine martens (Table 1). Small remnant pine marten populations held on in several areas across Scotland, and therefore we estimated times since recolonisation based on multiple hectads (10 × 10 km grid cells) having positive pine marten records in the following surveys. Pine marten records from past distribution surveys were conducted in 1980–1982 (Velander 1983), 1994 (Balharry et al. 1996), 2012 (Croose et al. 2013), and 2013 (Croose et al. 2014) and compiled by Croose et al. (2014). Our four focal landscapes were Highlands (HI, region = Cairngorms, eastern Highlands) which has been recolonised the longest, followed by the Trossachs (TR, region = west-central Scotland), then Aberdeenshire (AB, region = northeast Scotland), and the most recently recolonised Borders (BO, region = Scottish Borders and Dumfries and Galloway, southern Scotland) (Table 1).

We used a clustered sampling design, where a site within landscapes was defined as a cluster of detectors (mean: 8, range: 3–19) deployed, with multiple sites in each of the four landscapes (AB: 24, BO: 15, HI: 5, TR: 6 sites; Fig. 1). The cluster approach maximised spatial representation and spatial recaptures while also ensuring sampling effort was efficient (Royle et al. 2018, Dupont et al. 2021). The specific sampling sites were chosen by selecting locations with forest, mainly plantation commercial conifers, that were accessible, and where access permission was granted, while also ensuring wide coverage of each landscape.

Sampling of pine martens

We used wooden squirrel feeder boxes attached to trees at ~ 1.5 m high and baited them with a mixture of maize, peanuts, and sunflowers as detectors. Two adhesive tape hair traps were fixed to the underside of the lid of each detector. These detectors have proven to be effective for surveying pine

Table 1. Summary data for landscapes. Time since colonisation based on distribution surveys, and Recolonisation categories – from longest (1) to shortest (4) time since recolonisation. Area – total area of each region calculated using a 10 km dissolved buffer from all detectors used in a landscape, Number of detectors – number of detectors placed within each landscape, Hair samples collected – total number of hair samples collected during all 3 surveys, Pine marten hair samples – number of hair samples identified as pine marten using morphological characteristics, Hair samples DNA extracted from – number of hair samples DNA was extracted from (as not all could be analysed due to funding constraints), Consensus genotype at 7 or more loci – total number of hair DNA samples that had a consensus genotype at 7 or more loci following PCR replicates using the 3 microsatellite multiplexes, Matched to individuals – number of hair DNA samples matched to unique individuals, Unique individuals – total number of individuals detected across all surveys, with number of males and females identified, Forest cover – mean proportion of forest cover across landscapes, Distance to large road – mean distance to nearest major road (motorway or A roads), Distance to large pen – mean distance to the nearest large pheasant pens from each detector in a landscape, and across all landscapes, and Number of large pens – number of large pens within a 10 km dissolved buffer from all detectors in the landscape.

	Landscape				
	AB	BO	HI	TR	
Pine marten records from past distribution surveys	Potential remnant population to south of monitoring area with records from 1980 to 1982. More positive hectads in 2012 and 2013	Few positive hectads in 2012 that were isolated from occupied areas to the north	Few positive hectads 1980–1982, more hectads positive in 1994	Potential remnant population to north of monitoring area with records from 1980 to 1982. More positive hectads in 1994 and 2012	
Estimated time since recolonisation	~ 12–13 years	~ 12 years	~ 30–45 years	~ 13–31 years	
Recolonisation categories	Short (3)	Shortest (4)	Longest (1)	Long (2)	
					Total
Area (km^2)	1779.0	2680.5	1088.4	1070.7	6618.6
No. of detectors	167	120	59	66	412
Hair samples collected	714	540	244	393	1891
Pine marten hair samples	559	444	226	307	1536
Hair samples DNA extracted from	382	345	148	231	1106
Consensus genotype at 7 loci or more	210	193	113	136	652
Matched to individual	170	173	102	114	559
Unique individuals	30	27	16	20	93
Sex: males	18	14	8	3	49
Sex: females	11	8	3	4	26
Sex: uncertain	1	5	5	7	18
					Mean
Forest cover	0.31	0.31	0.23	0.28	0.3
Distance to large road (km)	6.1	5.8	7.7	5.1	6.2
Distance to large pen (km)	9.3	15.4	18	30.2	18.2
No. of large pens	4	3	1	0	2

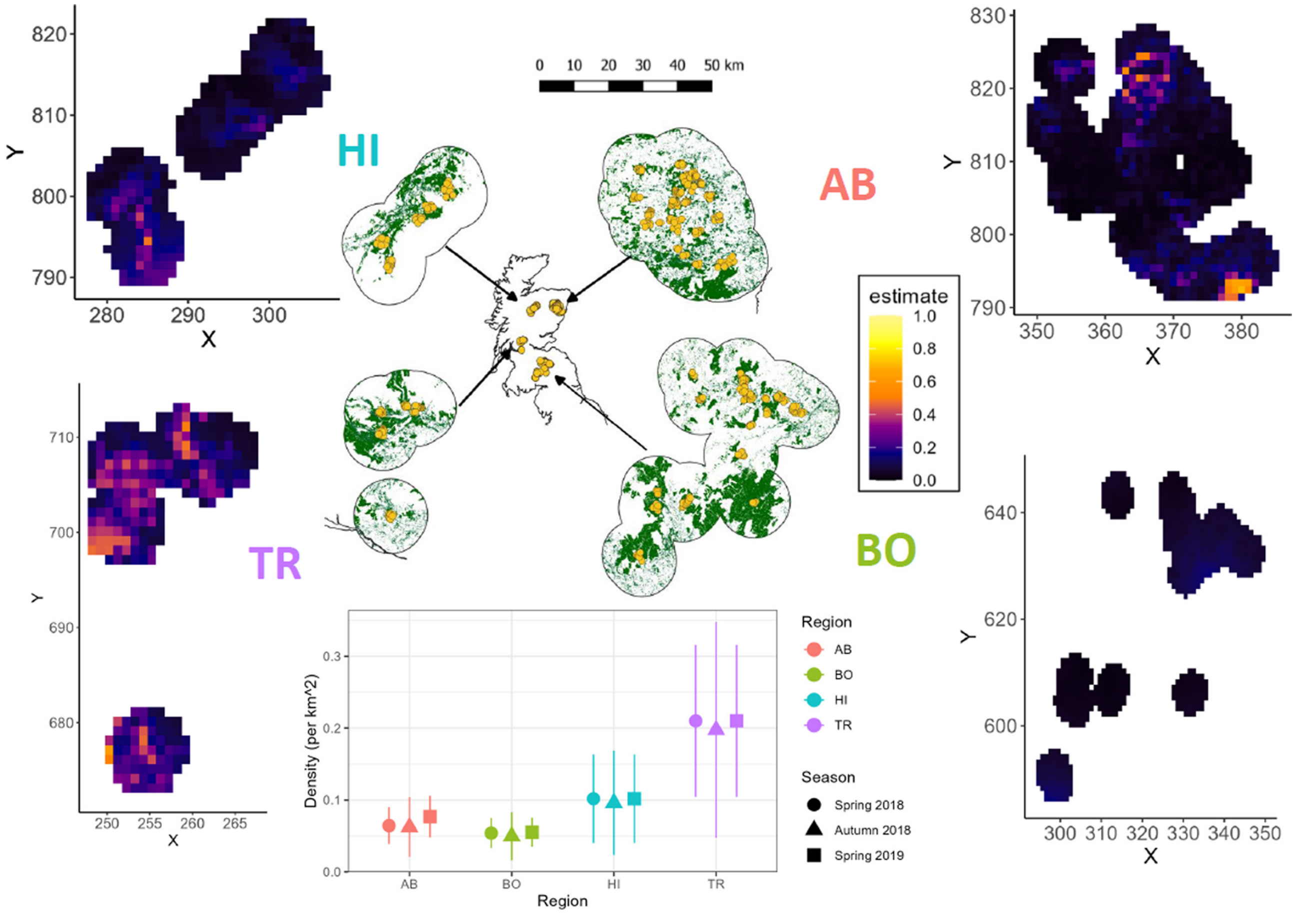

Figure 1. Spatial variation in pine marten density across the four regions. The most northwest region was located in the in the Scottish Highlands in the Cairngorms National Park (HI, 57.1 N, −3.8 W), the northeast region in Aberdeenshire (AB, 57.2 N, −2.5 W), the western region in Loch Lomond and the Trossachs National Park and Mugdock Country Park (TR, northern part 56.2 N, −4.3 W, southern area 56.0 N, −4.3 W), and the most southern region in the Scottish Borders and Dumfries and Galloway (BO, 55.4 N, −3.2 W). Estimated spatial variation density maps from the spring 2019 survey (AB, BO, HI, TR). Centre map showing the location of the landscapes in the UK, yellow points represent detectors grouped in clusters at sampling sites, green shading represents forest cover (broadleaved and conifer forest combined – UKCEH Land Cover Map 2020, resolution 10 m), contains Ordnance Survey data Crown Copyright 2007, Licence no. 100017572. Insert shows density estimates at the scale of landscapes and 95% CI across each region for each of the surveys (spr18 – spring 2018, aut18 – autumn 2018, spr19 – spring 2019).

martens and collecting hair samples (Sheehy et al. 2018). Within each site, detectors were placed at mean spacing of 425 m (min 61 m, max 1450 m). Thus, based on previous estimates of space use, individuals were exposed to detection in multiple detectors (Sheehy et al. 2018), a prerequisite of our chosen analytical method, spatial capture–recapture.

In each landscape, sampling was conducted in winter–spring 2018 (January to July), autumn 2018 (October to December), and winter–spring 2019 (March to May 2019). Detectors were checked between two and seven times (median 5 visits) per survey period at approximately 2-week intervals. During each visit, data were collected on whether bait was taken and if a hair sample was present. Hair traps were collected (retaining the hairs on the adhesive tape) and replaced, and detectors rebaited or topped up. Hair samples were sealed in separate labelled zip lock plastic bags and dried at the end of the day by opening the top of the zip lock bag and placing it on top of a radiator or in a warm room for a few hours. The dry hair samples (still on the adhesive tape) were then frozen (−20°C) within approximately 5 days of collection.

Genetic identification of pine marten individuals

Each hair sample was examined using a dissection microscope at ×40 magnification and identified to species or group; pine marten, red squirrel, grey squirrel, or rodent species, based on morphology including colour, size, and shape. If only a few hairs were collected on the hair trap or it was not possible to confirm the species identification between red squirrel and pine marten, the hair samples were retained and included in the next stage of DNA extraction and genotyping to confirm and maximise the number of pine marten samples included in the analysis. Genotyping, which included multiple pine marten-specific nuclear markers, made it possible to later conclude if the hair belonged to pine marten or not. Genomic DNA was extracted from a single hair rather than a clump of hairs to avoid extracting DNA from more than one individual, as it is possible that more than one pine marten can visit a feeder during a sampling session (Supporting information).

Three microsatellite multiplex sets were used to genotype the hair DNA samples, which included 18 markers including 2 sex markers, 1 squirrel marker, and 15 pine marten autosomal microsatellite markers (Supporting information). Of these markers, we included 4 newly developed *Martes* microsatellite markers, and new pine marten sex marker primer sets, designed using the sequences provided by Campbell et al. (2010) for the American marten *M. americana* and Pacific marten *M. caurina* that were amplified using the Lut-SRY primer set (Dallas et al. 2000; Supporting information). The 15 autosomal pine marten microsatellite loci were confirmed autosomal by their amplification in females (XX) as well as males (XY), ruling out Y-linked markers, and the observation of heterozygotes in some males (as well as some females) for each locus, ruling out X-linked markers.

Each multiplex PCR reaction was replicated two to five times for each sample in order to adopt the comparative-multiple tube approach developed by Frantz et al. (2003), adapted from Taberlet et al. (1996)'s standard multiple-tubes approach and accommodate any poor or failed PCR reactions. A consensus genotype was assigned based on the rule that each differently sized allele of a heterozygous genotype must be observed ≥ 2 times, whereas homozygous genotypes must be observed ≥ 3 times to confirm a homozygous genotype (Frantz et al. 2003). The amplification success of each DNA sample was considered, and only samples where 50% or more loci amplified in the marker's expected size range for the first PCR reaction were retained and used for further repeat PCR reactions towards obtaining a complete profile (by detecting allelic dropout, revealing heterozygotes and confirming homozygotes) (Supporting information).

Identifying individuals from consensus genotypes

A 48-well capillary Applied Biosystems 3730 DNA Analyser was used to separate the PCR product fragments by size using capillary electrophoresis and the output fragment size data analysed. The allele sizes were scored for each locus using GENEMAPPER ver. 3.7 (Applied Biosystems). The 'ConGenR' R package (ver. 3.4.1; Lonsinger and Waits 2015) was used to assign consensus genotypes using 13 of the 15 pine marten and cross species markers (2 were excluded: Mvis354 and PMcons_gr845) and calculate genotyping error rates, including allelic dropout (ADO) and false alleles (FA; Supporting information). Seventy samples (13% of the 556 samples with a consensus genotype at 9 loci or more that possessed near-complete or complete consensus genotypes (missing alleles ≤ 1 or 2 loci) from sites across the 4 landscapes were identified as most likely unique individuals based on comparing their genotypes. These 70 samples were selected to validate the power and performance of the marker set by assessing allele frequencies, estimating the frequency of null alleles, calculating polymorphic information content (PIC) using the program CERVUS (Kalinowski et al. 2007) and used with the GenAlEx software to estimate the probability of identity (PID, 7 loci or more for PID < 0.001) and probability of identity between siblings ($PI_{Sibs,}$ 9 loci for $PI_{Sibs} < 0.01$; Peakall and Smouse 2006).

Matching samples to unique individuals was completed using the R package 'Allelematch' and an iterative process to enable missing alleles; due to dropout, for example, to be interpolated from matching profiles, which helped to retain samples with missing data within the analysis (Galpern et al. 2012; Supporting information). A maximum of two mismatches was allowed, with the sex markers added after the third iteration to check the grouping of samples to unique individuals and assign sex. Each sample was classed as male, female, or uncertain based on the percentage of PCR replicates per individual that amplified with the Y-linked 130 bp product of the MSRY134 sex marker. Allelic dropout of the 130 bp Y-linked product would lead to the incorrect assigned of a real male individual as a female. To avoid potential error caused by allelic dropout in sex assignments, a sample was assigned as male if 66% or more replicates had been assigned as male (due to amplifying the 130 bp Y-linked MSRY134 amplicon), and as female if 33% or less replicates had amplified the 130 bp Y-linked product, and sex classed as uncertain for samples with more than 33% and less than 66% of replicates amplifying the 130 bp product (Supporting information). A unique individual pine marten was assigned male if over 75% of the grouped multiple samples genotyped (which had been assigned to the same unique individual) were classed as male, female if 75% or more of the samples were assigned as female, and grouped samples where the percentage of replicates classed as either male or female was less than 75% and were classified as 'uncertain'.

Spatial capture–recapture

We used spatial capture–recapture to estimate the variability in pine marten density within and between each landscape as a function of spatial covariates including key habitat and human-related landscape characteristics (Efford 2004, Royle et al. 2018). The theoretical framework of spatial SCR is that the activity centres of individuals within a population are distributed uniformly or non-uniformly across an area (Efford 2004). By sampling the population with detectors, the probability of encountering an individual can be modelled as a function of the distance between the detector and individual's activity centre (Efford 2004). The scale parameter 'sigma' allows for heterogeneity in individual activity centres by altering the distance over which detection probability decreases and allowing this to vary for sexes if home range sizes differ (Sutherland et al. 2019). We used full model inference, whereby all covariates to model detection probability, sigma, and density are included in a model and inference made on the relative effects and significance determined using p-values. We make predictions on the covariate effects on density, and map spatial variation in density across each landscape to understand key habitat and human-related landscape characteristics influencing the recovery of a native predator in the UK.

Statistical analysis

We used the spatially explicit individual encounter histories of all uniquely identified pine martens ($n=93$) from 559 genotyped hair samples at each detector to fit a multi-session, sex-structured, spatial capture–recapture model (SCR). Given the detection-non-detection nature of hair snares, we used a binomial encounter model (Sutherland et al. 2019). The multi-session model allowed us to jointly analyse data from all four landscapes and both sexes to test hypotheses about between landscape differences in density and space use. As many mustelid species display strong behavioural responses to baited detectors (i.e. trap happiness; Linden et al. 2017), and sex-specific space-use and resource requirements (Powell 1979, Bartolommei et al. 2016), we included a behavioural response on detectability over time (Sutherland et al. 2019) and modelled detection parameters (p0 and sigma) as sex-specific.

We used, as a starting point, a (biologically informed) base model allowing for: variation in detection by landscape and by season, including also a behavioural response as additive effect; additive season and landscape effects on the space use parameter, sigma; and a constant density model where density was assumed constant within and between landscapes. We refer to this base model as our null model against which variation in density, both between landscape and within landscape as a function of spatial covariates, are assessed. To estimate the effect of forest cover, major roads, and land managed for large gamebird shoots on spatial variation in pine marten density across and between the four landscapes, we fitted one single full model which included covariates for detection and sigma, as well as sex, and the proportion of forest cover, distance to nearest large road, and distance to large gamebird pen modelled in separate interactions with landscape.

We created a state-space in oSCR, which is a core element of an SCR model that defines the area where individuals with non-zero capture probability are assumed to live and therefore includes their activity centres (Sutherland et al. 2019). We used data from three spatially referenced covariate rasters to create the state-space, which allowed us to include spatially referenced covariates to model spatial variation in density (i.e. an inhomogeneous point process; Sutherland et al. 2019). First, we defined the area of the state space using a 10 km dissolved buffer around all detectors used within each landscape, considering the maximum plausible sigma, which was divided into 30 × 30 m pixels. Covariate values for each pixel were extracted from the following covariate rasters: proportion of forest cover, with broadleaved and conifer forest combined, using the UKCEH Land Cover Map 2020 (raster, 10 m resolution; Morton et al. 2021) distance to the nearest major road (motorways and A roads) using the Ordnance Survey Strategi dataset (Ordnance Survey (GB) 2015); and distance to the nearest large gamebird pens using the APHA Poultry Register (2008 to 2020). At the time of the study it was compulsory to report pheasant and partridge pens with over 10 000 stock to the register (https://keptbirdregister.service.gov.scot). All covariates were standardised (centred to 0 and scaled to the standard deviation) to the global mean of all landscapes and scaled to 1 km^2 in the state space. These spatially varying covariates were included as interactions with the landscape covariate in the final model fitted to the data to test whether their influence on density differed between landscapes.

Analyses were performed using R (www.r-project.org) and packages: 'sf' and 'raster' for extracting covariates and mapping (Hijmans 2025). The 'oSCR' R package was used for spatial capture–recapture for inference about spatial ecological processes (Sutherland et al. 2019), and 'ggplot2' for plotting results (Wickham 2016). QGIS was used for extracting covariates and mapping (QGIS Development Team 2023). The data and code are available in Hobson et al. (2025a).

Results

A total of 93 individuals were identified from hair samples collected at 412 detectors, with 26 females and 49 males identified, and 18 individuals where sex was undetermined, distributed across the four landscapes covering an area of approximately 6619 km^2 (Table 1). Recapture rates were relatively high: the mean number of times an individual was encountered was 3.1 (min 1.4, max 6.2), and the mean number of spatial locations individuals were encountered at was 2.4 (min 1.4, max 4.1). The mean maximum Euclidean distance between detectors used by an individual was 1.2 km (min 0.4, max 2.5). Detectors in AB and BO were in landscapes with the highest forest cover, and those in HI were furthest from large roads (Table 2). TR detectors were furthest from large gamebird pens (mean 30.2 km) with no large pens within 10 km of detectors, whereas HI had one, BO three, and AB four large pens (Table 2).

There was substantial between-landscape variation in total density (estimated number of animals divided by the size of the state-space: Fig. 1, Table 2). Total density was highest in TR (Spring 2018: mean 0.21 marten km^{-2}, min 0.05, max 0.62, SD 0.11), followed by HI (all sampling occasions: 0.10 marten km^{-2}, min 0.01, max 0.49, SD 0.07), and lowest across the recently recolonised BO landscape (Spring 2018: mean 0.05 marten km^{-2}, min 0.01, max 0.15, SD 0.03;). Total density was also low for AB (Spring 2018: mean 0.07 marten km^{-2}, min 0.01, max 0.71, SD 0.08); however, spatial variation in density was acute, with very high densities predicted in two blocks of state-owned forest areas to the north and south of the AB landscape, and much lower densities where small blocks of forest were interspersed with farmland and large pheasant pens (Fig. 1).

The full SCR model improved the null model parsimony by 40.3 AIC. The detection and sigma components of the SCR model indicated pine martens were substantially more likely to be detected following a first detection (behaviour effect on detection probability: 1.4 ± 0.2 SE), and detection

Table 2. Estimated 'total density' of pine martens, which is the number of individuals in the landscape, as predicted from a spatially varying density model that relies on covariates, divided by the area over which these predictions are made (i.e. the state space) for all 12 region-season-year combinations and corresponding uncertainty (95% confidence intervals) and areas of the state spaces, which is the area over which spatially explicit predictions are made. Region: AB: Aberdeenshire, BO: Borders, HI: Highlands, TR: Trossachs.

Region	Season	Year	State space area (km^2)	Density marten km^{-2}	Lower95	Upper95
AB	Spring	2018	640	0.06	0.04	0.09
AB	Autumn	2018	665	0.06	0.02	0.10
AB	Spring	2019	841	0.08	0.05	0.11
BO	Spring	2018	791	0.05	0.03	0.07
BO	Autumn	2018	778	0.05	0.02	0.08
BO	Spring	2019	720	0.06	0.04	0.08
HI	Spring	2018	357	0.10	0.04	0.16
HI	Autumn	2018	357	0.10	0.02	0.17
HI	Spring	2019	357	0.10	0.04	0.16
TR	Spring	2018	288	0.21	0.10	0.32
TR	Autumn	2018	289	0.20	0.05	0.35
TR	Spring	2019	288	0.21	0.10	0.32

probability was significantly higher in the spring (0.8 ± 0.4; Table 3). Probability of detection was similar for males and females (−0.4 ± 0.2 SE). Sigma was larger for males compared to females (males 0.5 ± 0.1; females −0.6 ± 0.2) and in the recently colonised low density BO landscape (0.4 ± 0.1). The sex ratio (proportion of males) was estimated as 51.1% across all landscapes.

The SCR model revealed pine marten density increased with forest cover in all landscapes except for BO (Table 3, Fig. 2). The relationship between pine marten density and distance from large gamebird pens varied in sign and magnitude between landscapes. In TR, where pine marten density was nearly uniformly high, but no detector was closer than 18 km from the small number of present pens in the region

Table 3. Parameter estimates from the fitted multi-session sex-structured spatial capture–recapture model for probability of detection, sigma, and density. Regions: Region: AB: Aberdeenshire, BO: Borders, HI Highlands, TR: Trossachs. Abbreviations: SE – standard errors, z – z score. P(>|z|) – p value, : interaction.

	Parameter	Estimate	SE	z	P(>|z|)
Detection	(Intercept)	−1.8	0.4	−4.3	< 0.001
	Sex (male)	−0.4	0.2	−1.6	0.106
	RegionBO	0.5	0.3	1.6	0.113
	RegionHI	0.7	0.4	1.8	0.074
	RegionTR	0.5	0.3	1.6	0.113
	Season (Spring)	0.8	0.4	2.1	0.040
	Behavioural effect	1.4	0.2	7.6	< 0.001
Sigma	(Intercept)	−0.6	0.2	−3.1	0.002
	Sex (male)	0.5	0.1	5.1	< 0.001
	RegionBO	0.4	0.1	3.5	< 0.001
	RegionHI	0	0.1	0.1	0.892
	RegionTR	−0.2	0.1	−1.6	0.104
	Season (Spring)	0.1	0.2	0.7	0.464
Density	(Intercept)	−2.1	0.5	−4.2	< 0.001
	RegionBO	−1.1	0.6	−2	0.046
	RegionHI	−0.7	0.8	−0.8	0.426
	RegionTR	−0.5	1	−0.5	0.612
	Season (Autumn)	−0.1	0.3	−0.2	0.850
	Proportion of forest	1.1	0.4	2.8	0.004
	Distance to large pen	1.2	0.5	2.6	0.009
	Distance to major road	−0.1	0.2	−0.4	0.674
	RegionBO:forest	−1.2	0.5	−2.5	0.014
	RegionHI:forest	−0.3	0.7	−0.4	0.664
	RegionTR:forest	−0.3	0.6	−0.5	0.600
	RegionBO:dist large pen	−2.1	0.5	−3.8	< 0.001
	RegionHI:dist large pen	−2	0.6	−3.4	0.001
	RegionTR:dist large pen	−0.7	0.6	−1.2	0.248
	RegionBO:dist major road	0	0.3	0	0.964
	RegionHI:dist major road	1.1	0.6	1.8	0.069
	RegionTR:dist major road	−0.3	0.4	−0.7	0.513
Sex ratio	psi.constant	0.044	0.2	0.2	0.846

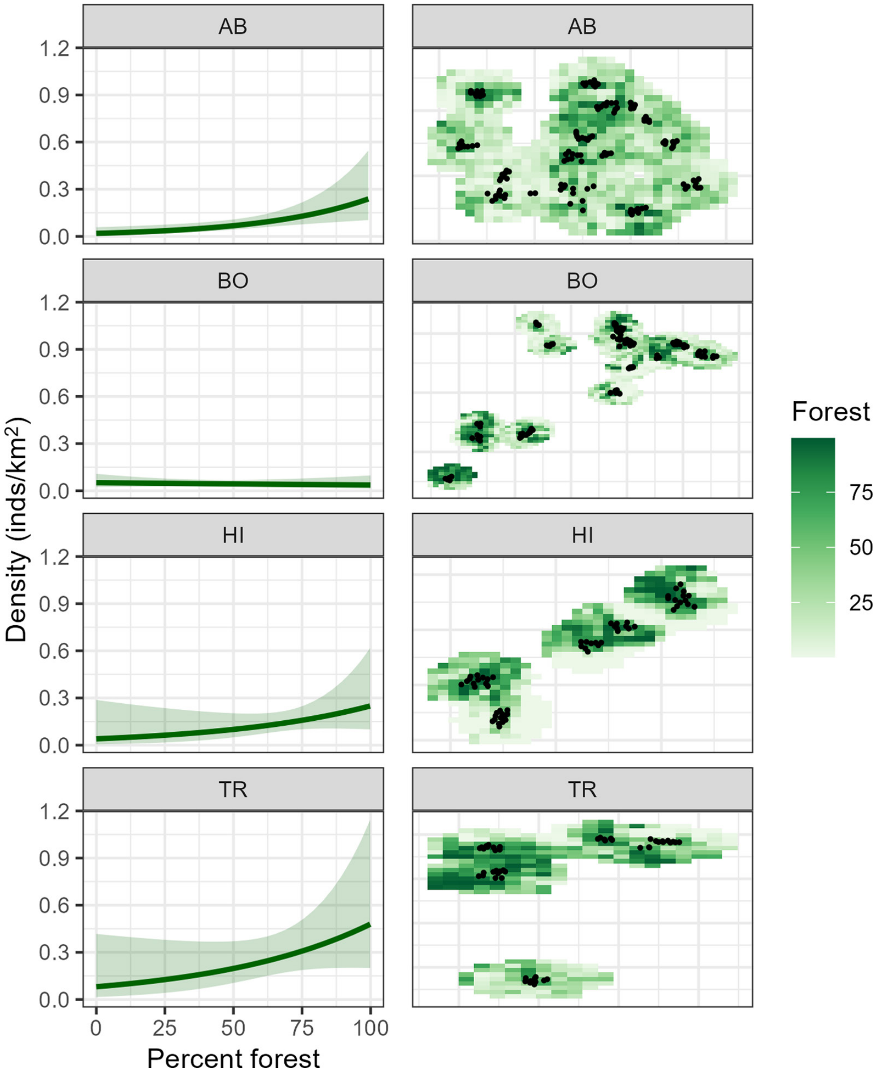

Figure 2. Left: the effect of forest cover on spatial variation of pine marten population density with 95% confidence intervals in the four study regions (AB: Aberdeenshire, BO: Borders, HI Highlands, TR: Trossachs). The distance to the nearest large gamebird pen (km) and distance to major roads were set to the region-specific means for the purpose of prediction. Right: location of detectors (black dots) in each region with colours showing the proportion of forest (broadleaved and conifer forest combined) recorded in the UKCEH land cover map 2020, resolution 10m.

and located well outside the state space where information on pine marten density is available, there was no relationship between pine marten density and distance to game pens (slope: 0.496, 95% CI: −0.321 to 1.314, Table 3, Fig. 1 and 3). In AB, where pine martens prevailed at high density in subsets of the landscapes managed by Forestry Land Scotland and lower density elsewhere, pine marten density increased with distance from large gamebird pens, with effect size of similar magnitude as that of proportion of forest (AB slope: 1.222, 95% CI: 0.302–2.142, Table 3, Fig. 1 and 3). In the HI and BO, the proximity effects were statistically significant but weaker. The influence of distance to large gamebird pens in the BO landscape was negative (slope: −0.846, 95% CI: −1.401 to −0.292), noting there were only 3 pens within 10 km and a mean distance between detectors and pens of 15.4 km, as was the case in the HI landscape (slope: −0.740, 95% CI: −1.409 to −0.071) where there was a single gamebird pen within 10 km of detectors and a mean distance of 18 km between the pen and detectors (Table 1, 3, Fig. 1, 3). There was no evidence that pine marten densities varied with distance to the nearest major road in any landscape (Table 3).

Discussion

We applied a multi-session, sex-structured spatial capture–recapture model to detections of pine martens from four landscapes of Scotland with similarly low (29%) forest cover. Pine martens were individually identified using non-invasively collected hair samples that we DNA genotyped. We found that, surprisingly, the amount of forest and the distance to locations managed for large gamebird shoots, a

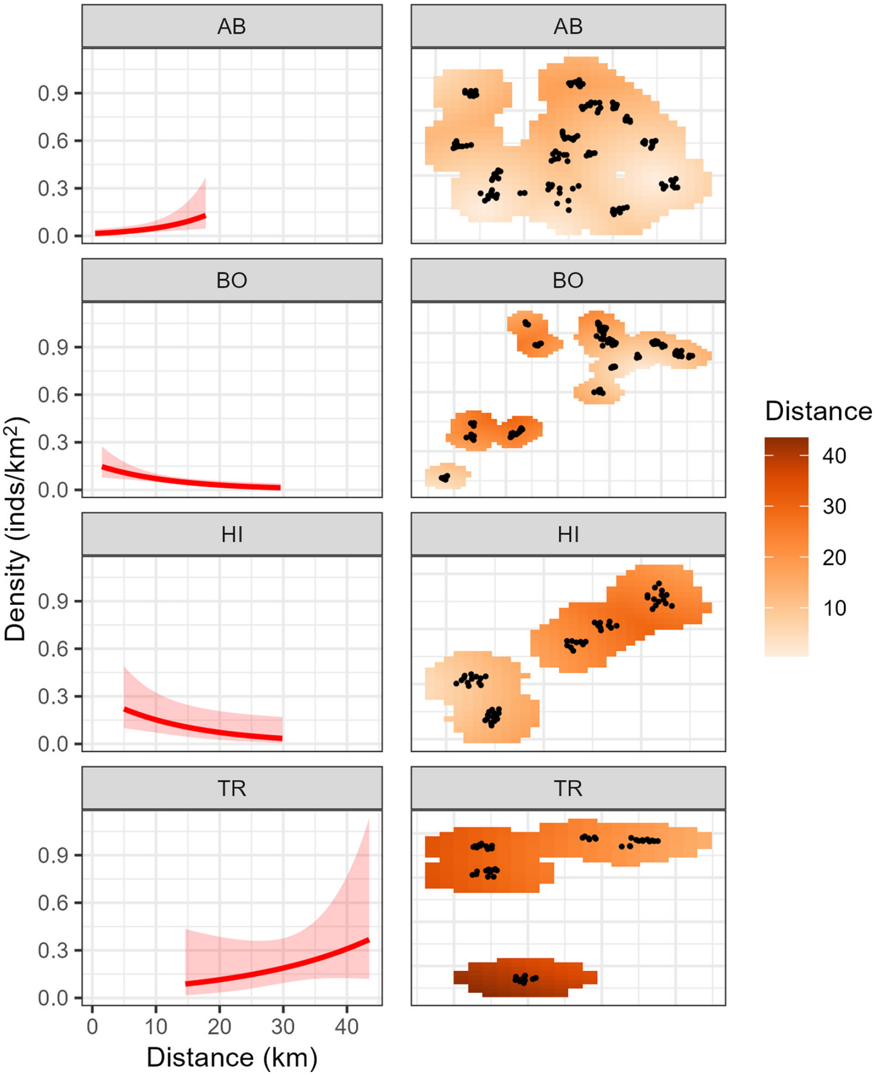

Figure 3. Left: the effect of distance to the nearest large gamebird pen (km) on spatial variation in pine marten population density with 95% confidence intervals in the four study regions (AB: Aberdeenshire, BO: Borders, HI Highlands, TR: Trossachs). The proportion of forest and distance to major roads were set to the region-specific means for the purpose of prediction. Internal guidelines (light red) are 10 km apart for predictions. Right: Location of detectors (black dots) in each region with colours showing the distance (in km) between detectors and the nearest large pheasant pen recorded in the APHA register.

proxy for persecution, had influences of similar magnitude on spatial variation in population density in two landscapes. The effect of forest cover was expected and visible in all the landscapes apart from the most recently colonised Borders region of Scotland (BO). Pine marten densities in partially forested areas and in the absence of likely persecution we deemed associated to the presence of pheasant pens were comparable with those estimated elsewhere for UK mainland populations using similar methodologies, supporting the validity of our results and methodology. Density was moderately low, and largely unchanged over 7 to 8 years since a previous SCR pine marten study in the sampling area for the HI landscape (Kubasiewicz et al. 2017). Forest cover was low at the landscape scale (30%) relative to cover in mainland Europe studies (Zalewski and Jedrzejewski 2006) and density is predicted to rise to up to approximately 0.40 individuals km^{-2} where forest cover reaches 100%, according to the SCR model (Fig. 2).

Consistent with well-monitored large carnivores in mainland Europe, there is now a good range of pine marten density estimates that use spatially explicit capture–recapture approaches where abundance is scaled to an appropriate sampling area where detectability is above zero. Density estimates from past SCR studies in Scotland, including some in the same location as this study, range from 0.07 to 0.38 individuals km^{-2} (Kubasiewicz et al. 2017), compared to our estimates ranging from 0.05 to 0.21. Pine marten density estimates from Ireland and northern Ireland are generally higher, averaging around 0.7 individuals km^{-2} (O'Mahony et al. 2017, Twining et al. 2022b) despite the absence of field voles *Microtus agrestis*, a key prey species of pine marten in mainland UK (Caryl et al. 2012b).

Our estimates from four landscapes with similar forest cover but contrasting recolonisation histories suggest that pine marten density increases only gradually with years since recolonisation, as expected given their relatively slow life history. Pine martens occurred at low density and ranged most widely (larger sigma parameter) in the recently colonised BO landscape. Pine martens occurred at consistently higher density across the TR landscape recolonised 13 to 31 years ago, suggesting a strong and established population (Fig. 1, Table 2). They attained the highest density of 0.62 individuals km^{-2} in some 1 × 1 km cells in state-managed forest plantation in subsets of the AB landscape, which was recolonised around 12 to 13 years ago, but were scarce in other parts of that landscape where smaller blocks of forest are interspersed with pastures and where there is high gamebird shooting activity (Fig. 1, 3).

The density across the HI region, a landscape comprising ancient Caledonian pine *Pinus sylvestris*-dominated woodland rich in natural arboreal denning sites and planted forests bordered by heather moorland rather than pastures with linear tree features, was lower than might be expected for an area that has been re-colonised for a longer duration than the other landscapes (30–45 years ago). The same landscape had been surveyed 6 to 7 years prior to this study, using similar field, laboratory, and analytical methodologies with density estimates ranging from 0.07 km^2 (95% CI 0.03–0.16) to 0.38 km^2 (95% CI 0.11–1.07) in 2011 and 2012, strikingly similar to the low densities we recorded of 0.10 km^2 (min 0.01, max 0.49) in 2018 and 2019. Thus, despite reports that a mostly uncalibrated index of pine marten abundance based on scat abundance (Kubasiewicz et al. 2017) had increased 3.9-fold from 1995 to 2009 in a nearby area (Baines et al. 2013), our statistically robust density estimates show neither evidence of further population growth between 2012 and 2019, nor evidence that pine martens reach high densities post-recolonisation of their hitherto lost range. Thus, claims that pine marten populations are rising out of control and their impact on declining capercaillie *Tetrao urogallus* will escalate (Bamber et al. 2025) are not supported by evidence.

Forest cover in Scotland has increased from just 5% in the early 1900s to approximately 30% in our sampled landscapes (Forestry Commission 2003; Table 2) with mostly grazed pastures in between. Although pine martens are known to readily occupy areas with low forest cover (Moll et al. 2016), our study provides strong evidence that population density increases with forest cover within landscapes (Fig. 1). However, there was no evidence that forest cover influenced pine marten density within the most recently recolonised and still sparsely populated landscape BO, where the population is thought to arise predominantly from reintroductions (O'Reilly et al. 2024) and many well-forested parts of the region are not yet occupied (Fig. 1).

Despite evidence that mortality on roads affects pine marten spread (Hobson 2023), occurrence (MacPherson et al. 2024), and population structure (Mergey et al. 2011), we did not detect an effect of distance to nearest large roads on the spatial variation of pine marten population density. This is despite nearly all detectors being within 5 km of a major road (Table 1). A compensatory process may negate the effect of road mortality and impart a degree of resilience to established pine marten populations. Alternatively, our study design without detectors distant from major roads nearby may be statistically under-powered and other covariates maybe better suited to capturing the subtle influence of road configuration and habitat on road mortality (Moore et al. 2023).

We detected contradictory relationships between pine marten density and the proximity to large pheasant release pens. Given the correlative nature of the data, care is required when considering whether these statistical associations might reflect causation rather than the influence of unmeasured environmental gradients. Importantly, both positive and negative influences of pheasant pens on local pine marten density could occur at a spatial scale commensurate with the mobility of pine martens. A positive influence might be mediated by the massive increase in prey biomass resulting from the release of 1000s of captive-reared exotic birds. A negative influence might be mediated by increased pine marten mortality reflecting actions by a subset of gamekeepers willing to break wildlife protection laws to protect their stock. It is possible that the killing of established individuals pine martens holding territories might have resulted in vacant territories being colonised by new individuals, and thus potentially inflating local density estimates. Should this have occurred, it would have led to underestimation of the impact of pheasant release pens on pine marten density. However, relating individual turnover to the prevalence of shooting and illegal action by a subset of shoot managers over the 3–7-month-long sampling occasions would require substantially larger sample size than available. On that basis, the lack of any association in one of 3 regions (TR) is unsurprising as none of the pine martens detected lived in the vicinity of pheasant release pens. The negative, statistically significant influences of pens in BO and HI, regions with overall low pine marten density and a single cluster of detectors within 5 to 8 km of nearest pheasant pen, are likely not causal, even if (weakly for HI) statistically significant. There was, however, a well-defined relationship between the distance between clusters of detectors and the nearest large pheasant pen in the AB landscape with a high number of pheasant pens in proximity to detectors and highly contrasting local pine marten densities within the landscape (Fig. 1), hence with statistical power to detect a relationship. This evidence suggests that, despite being protected in law, pine martens suffer sufficiently elevated mortality close to some pheasant pens to overcome compensatory processes such as the replacement of territory holders by juveniles and locally depress their density given their low reproductive rates (Sainsbury et al. 2019). Pheasant release pens with more than 10 000 birds are indicative of large, often commercially run shoots, and such sites may be areas where conflicts involving predator impacts and human interests are heightened. Lawful predator control through shooting and trapping targeted at foxes, small mustelids, and corvids by professional gamekeepers are likely intensified in those areas. There is, however, ample evidence that some gamekeepers deliberately and unlawfully kill protected predators such as birds of prey and likely pine marten, to maximise the number of gamebirds shot (Newton 2021, Ewing et al. 2023). Deliberate pine marten killing by a subset of gamekeepers willing to break the law in the vicinity of some of the gamebird pens is a plausible explanation for the strong spatial variability in pine marten density and low density in proximity to pheasant release pens in the AB landscape. A non-exclusive explanation comes from the evidence of pervasive contamination of predators such as American mink *Neovison vison*, polecats *Mustela putorius*, and birds of prey by anticoagulant rodenticides (Ruiz-Suarez et al. 2016, Sainsbury et al. 2019) that were lawfully used until 2024 to control rats attracted to food dispensed for pheasants before and after they are released from pens, through deliberate or careless secondary poisoning.

Pheasant shoots in the UK can vary dramatically in size, from small shoots where > 3000 birds are released, usually family-run or small collaborative syndicates, to large commercial shoots on estates where over 10 000 birds are reared and released into the environment (Mason et al. 2020). Increased raptor persecution is suggested to be linked with increased economic pressures on gamekeepers of commercial shoots to produce high gamebird numbers (Burnside et al. 2021). Therefore, this persecution may extend to other predators that pose a risk to the birds but is also likely to vary between different commercial operations. A large-scale questionnaire survey revealed that tolerance to the impacts of pine marten and other recovering species was lowest for stakeholders with strong interests in shooting and little to no interest in wildlife conservation, yet tolerance increased for those who had strong interests in both shooting and wildlife conservation (Hobson et al. 2024).

Landscape-scale pine marten population density is higher in more forested landscapes; however, it is also influenced by the density of large gamebird shoots, the stage of recovery of the populations, and likely differences in land use captured partly by our landscape factor in this study. Recently recolonised areas may take considerable time to establish and reach densities equivalent to those in more established populations. Yet, population densities should not be assumed to be highest in areas where the species is most established, as pine martens show strong spatial heterogeneity in density across some landscapes strongly associated statistically to gamebird shooting. Even though pine marten densities obviously rose substantially from zero where they had been extirpated in a few decades, our methodologically robust estimates should alleviate concerns that this increase in density has been unbounded. Martens have returned to moderately forested landscapes and now exist at moderately low density. They provide a valued biological control ecosystem service on non-native grey squirrels without impacting native red squirrels (Sheehy et al. 2018). Validated technical solutions now exist to mitigate their impact on ground-nesting birds (Bamber et al. 2025) where it is deemed excessive for conservation or commercial considerations.

Acknowledgements – We are grateful to all the individuals, organisations, land managers, and owners that granted access and permissions for the surveys, with a special thanks to all the dedicated volunteers that helped conduct the surveys, Eve Schulte, Dr Emma Sheehy, Jackie Cumberbirch, Kenny Kortland, Forestry and Land Scotland, Bennachie Mammal Group Bailiffs, Cairngorms Connect, National Trust Scotland, Saving Scotland's Red Squirrels Project (SSRS), John Muir Trust, Egger Forestry, Till Hill, and Mugdock Country Park/Council. We thank the team at the NEOF Visitor Facility for support of the marker development, DNA extraction and genotyping. Comments by Tim Hofmeester and Siow Yan Jennifer Angoh improved the paper.

Funding – KJH was supported by a NERC studentship grant (NE/N008960/1) at the School of Biological Sciences at the University of Aberdeen, in partnership with Forestry England, Vincent Wildlife Trust, Forest Research, RSNE, and CONFOR. XL was in receipt of a Leverhulme fellowship RF-2024-363. The genotyping of pine marten hair samples was supported by the Natural Environment Research Council (NERC) with additional funding provided by Forestry and Land Scotland and performed at the NERC Environmental Omics Facility (NEOF, previously NERC Biomolecular Analysis Facility, NBAF) Visitor Facility at Sheffield [NBAF1063].

Conflict of interest – The authors declare no conflict of interest.

Author contributions

Keziah J. Hobson: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (equal); Project administration (equal); Software (equal); Visualization (lead); Writing – original draft (lead). **Chris Sutherland**: Conceptualization (supporting); Formal analysis (equal); Methodology (supporting); Software (equal); Writing – review and editing (equal). **Cristian Navarro Waggershauser**: Data curation (supporting); Investigation (supporting); Resources (supporting); Writing – review and editing (supporting). **Deborah A. Dawson**: Formal analysis (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Gavin J. Horsburgh**: Data curation (supporting); Investigation (supporting); Methodology (supporting). **Lucy S. Knowles**: Investigation (supporting); Resources (supporting). **Xavier Lambin**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (equal); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01594.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.17605/OSF.IO/FK27V (Hobson et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Baines, D., Aebischer, N., Macleod, A. and Woods, J. 2013. Pine marten *Martes martes* and red fox *Vulpes vulpes* sign indices in Scottish forests: population change and reliability of field identification of scats. – Wildl. Biol. 19: 490–495.

Balharry, E. A., McGowan, G. M., Kruuk, H. and Halliwell, E. 1996. Distribution of pine martens in Scotland as determined by field survey and questionnaire. – Scottish Natural Heritage Research, Survey and Monitoring Report, No. 48.

Bamber, J. A., Kortland, K., Sutherland, C., Payo-Payo, A. and Lambin, X. 2024. Evaluating diversionary feeding as a method to resolve conservation conflicts in a recovering ecosystem. – J. Appl. Ecol. 61: 1968–1978.

Bamber, J. A., Sutherland, C. and Kortland, K. 2025. Bridging the implementation gap: from predator control to non-lethal impact-based intervention. – J. Appl. Ecol. 62: 2082–2088.

Bartolommei, P., Manzo, E. and Cozzolino, R. 2016. Seasonal spatial behaviour of pine marten *Martes martes* in a deciduous oak forest of central Italy. – Mamm. Res. 61: 319–326.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., Ordiz, A., de Valpine, P., Turek, D., Royle, J. A., Gimenez, O., Flagstad, Ø., Åkesson, M., Svensson, L., Brøseth, H. and Kindberg, J. 2020. Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. – Proc. Natl Acad. Sci. USA 117: 30531–30538.

Burnside, E., Pamment, N. and Collins, A. 2021. "If it flies, it dies": profit, workplace pressure and bird of prey persecution. – J. Rural Stud. 86: 54–61.

Campbell, G. M., Pauli, J. N., Thomas, J. G. and Mcclean, T. 2010. Accuracy in molecular sexing of martens (*Martes americana* and *Martes caurina*) varies among sample types. – Mol. Ecol. Resour. 10: 1019–1022.

Caryl, F. M., Quine, C. P. and Park, K. J. 2012a. Martens in the matrix: the importance of nonforested habitats for forest carnivores in fragmented landscapes. – J. Mammal. 93: 464–474.

Caryl, F. M., Raynor, R., Quine, C. P. and Park, K. J. 2012b. The seasonal diet of British pine marten determined from genetically identified scats. – J. Zool. 288: 252–259.

Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – Science 346: 1517–1519.

Croose, E., Birks, J. D. S. and Schofield, H. W. 2013. Expansion zone survey of pine marten (*Martes martes*) distribution in Scotland. – Scottish Natural Heritage Commissioned Report, No. 520.

Croose, E., Birks, J. D. S., Schofield, H. W. and O'Reilly, C. 2014. Distribution of the pine marten (*Martes martes*) in southern Scotland in 2013. – Scottish Natural Heritage Commissioned Report, No. 740.

Dallas, J. F., Carss, D. N., Marshall, F., Koepfli, K. P., Kruuk, H., Bacon, P. J. and Piertney, S. B. 2000. Sex identification of the Eurasian otter *Lutra lutra* by PCR typing of spraints. – Conserv. Genet. 1: 181–183.

Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. – Anim. Conserv. 13: 458–466.

Dupont, G., Royle, J. A., Nawaz, M. A. and Sutherland, C. 2021. Optimal sampling design for spatial capture–recapture. – Ecology 102: e03262.

Efford, M. 2004. Density estimation in live-trapping studies. – Oikos 106: 598–610.

Efford, M. G., Dawson, D. K. and Borchers, D. L. 2009. Population density estimated from locations of individuals on a passive detector array. – Ecology 90: 2676–2682.

Ewing, S. R., Thomas, C. E., Butcher, N., Denman, B., Douglas, D. J. T., Anderson, D. I. K., Anderson, G. Q. A., Bray, J., Downing, S., Dugan, R., Etheridge, B., Hayward, W., Howie, F., Roos, S., Thomas, M., Weston, J., Smart, J. and Wilson, J. D. 2023. Illegal killing associated with gamebird management accounts for up to three-quarters of annual mortality in hen harriers *Circus cyaneus*. – Biol. Conserv. 283: 110072.

Fischer, A., Selge, S., Van Der Wal, R. and Larson, B. M. H. 2014. The public and professionals reason similarly about the management of non-native invasive species: a quantitative investigation of the relationship between beliefs and attitudes. – PLoS One 9: e105495.

Forestry Commission 2003. Forestry statistics 2003. – https://www.forestresearch.gov.uk/publications/forestry-statistics-2003/

Frantz, A. C., Pope, L. C., Carpenter, P. J., Roper, T. J., Wilson, G. J., Delahay, R. J. and Burke, T. 2003. Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. – Mol. Ecol. 12: 1649–1661.

Galpern, P., Manseau, M., Hettinga, P., Smith, K. and Wilson, P. 2012. Allelematch: an R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. – Mol. Ecol. Resour. 12: 771–778.

Gehring, T. M., Vercauteren, K. C. and Landry, J. M. 2010. Livestock protection dogs in the 21st century: is an ancient tool relevant to modern conservation challenges? – J. Biosci. 60: 299–308.

Gregr, E. J., Christensen, V., Nichol, L., Martone, R. G., Markel, R. W., Watson, J. C., Harley, C. D. G., Pakhomov, E. A., Shurin, J. B. and Chan, K. M. A. 2020. Cascading social-ecological costs and benefits triggered by a recovering keystone predator. – Science 368: 1243–1247.

Hijmans, R. 2025. Raster: geographic data analysis and modeling. – R package ver. 3.6-32, https://rspatial.org/raster.

Hobson, K. 2023. Recovering native predators in multi-use landscapes: an ecological and social case study of the pine marten in the UK. – PhD thesis, University of Aberdeen, UK.

Hobson, K. J., Stringer, A., Gill, R., MacPherson, J. and Lambin, X. 2024. Interests, beliefs, experience and perceptions shape tolerance towards impacts of recovering predators. – People Nat. 6: 117–133.

Hobson, K. J., Sutherland, C., Waggershauser, C. N., Dawson, D. A., Horsburgh, G. J., Knowles, L. S. and Lambin, X. 2025. Data and code for: Both forest cover and land management practices explain variation in recovering pine marten densities. – OSF Digital Repository, https://osf.io/fk27v.

Kalinowski, S. T., Taper, M. L. and Marshall, T. C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. – Mol. Ecol. 16: 1099–1106.

Kubasiewicz, L. M., Quine, C. P., Summers, R. W., Coope, R., Cottrell, J. E., A'Hara, S. W. and Park, K. J. 2017. Non-invasive genotyping and spatial mark–recapture methods to estimate European pine marten density in forested landscapes. – Hystrix Ital. J. Mammal. 28: 265–271.

Langley, P. J. W. and Yalden, D. W. 1977. The decline of the rarer carnivores in Great Britain during the nineteenth century. – Mamm. Rev. 7: 95–116.

Linden, D. W., Fuller, A. K., Royle, J. A. and Hare, M. P. 2017. Examining the occupancy–density relationship for a low-density carnivore. – J. Appl. Ecol. 54: 2043–2052.

Lonsinger, R. C. and Waits, L. P. 2015. ConGenR: rapid determination of consensus genotypes and estimates of genotyping errors from replicated genetic samples. – Conserv. Genet. Resour. 7: 841–843.

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., Palacios, V. and Jiménez, J. 2018. Toward reliable population estimates of wolves by combining spatial capture–recapture models and non-invasive DNA monitoring. – Sci. Rep. 8: 2177.

MacPherson, J., Wright, P., Schumaker, N., Watkins, S., Birks, J., Croose, E., Gilbert, J. and Hofmeester, T. 2024. Use of multi-modelling methods to inform conservation and reintroductions of pine marten *Martes martes* in Britain. – Stacks J: 24004, https://doi.org/10.60102/stacks-24004.

Marshall, K. N., Stier, A. C., Samhouri, J. F., Kelly, R. P. and Ward, E. J. 2016. Conservation challenges of predator recovery. – Conserv. Lett. 9: 70–78.

Mason, L. R., Bicknell, J. E., Smart, J. and Peach, W. J. 2020. The impacts of non-native gamebird release in the UK: an updated evidence review. – RSPB research report 66. RSPB Centre for Conservation Science.

Mergey, M., Helder, R. and Roeder, J. J. 2011. Effect of forest fragmentation on space-use patterns in the European pine marten (*Martes martes*). – J. Mammal. 92: 328–335.

Miller, J. R. B. 2015. Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. – Biodivers. Conserv. 24: 2887–2911.

Moll, R. J., Kilshaw, K., Montgomery, R. A., Abade, L., Campbell, R. D., Harrington, L. A., Millspaugh, J. J., Birks, J. D. S. and Macdonald, D. W. 2016. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: a case study with a recovering mesocarnivore. – J. Zool. 300: 177–185.

Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E. and Yarnell, R. W. 2023. Demographic effects of road mortality on mammalian populations: a systematic review. – Biol. Rev. 98: 1033–1050.

Morton, D., Marston, C., O'Neil, A. and Rowland, C. 2021. Land Cover Map 2020 (10 m classified pixels, GB). – NERC environmental information data centre, https://doi.org/10.5285/35c7d0e5-1121-4381-9940-75f7673c98f7.

Newton, I. 2021. Killing of raptors on grouse moors: evidence and effects. – Ibis 163: 1–19.

O'Mahony, D. T., Powell, C., Power, J., Hanniffy, R., Marnell, F., Turner, P. and O'Reilly, C. 2017. Non-invasively determined multi-site variation in pine marten *Martes martes* density, a recovering carnivore in Europe. – Eur. J. Wildl. Res. 63: 48.

O'Reilly, C., Sheehy, E., MacPherson, J., Birks, J., Martin, J., Croose, E., Fletcher, K., Lambin, X., Curran, T., Synnott, R. and O'Meara, D. 2024. Genetic lag in a demographically recovering carnivore: the case of the British pine marten (*Martes martes*). – Conserv. Genet. 26: 165–181.

Peakall, R. and Smouse, P. E. 2006. GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. – Mol. Ecol. Notes 6: 288–295.

Pekkarinen, A. J., Kumpula, J. and Tahvonen, O. 2020. Predation costs and compensations in reindeer husbandry. – Wildl. Biol. 2020: 1–14.

Powell, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. – Z. Tierpsychol. 50: 153–165.

QGIS Development Team 2023. QGIS geographic information system. – Open Source Geospatial Foundation Project, https://qgis.org.

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G. and McDonald, R. A. 2012. Ecosystem restoration with teeth: what role for predators? – Trends Ecol. Evol. 27: 265–271.

Royle, J. A., Fuller, A. K. and Sutherland, C. 2018. Unifying population and landscape ecology with spatial capture–recapture. – Ecography 41: 444–456.

Ruiz-Suárez, N., Melero, Y., Giela, A., Henríquez-Hernández, L. A., Sharp, E., Boada, L. D., Taylor, M. J., Camacho, M., Lambin, X., Luzardo, O. P. and Hartley, G. 2016. Rate of exposure of a sentinel species, invasive American mink (*Neovison vison*) in Scotland, to anticoagulant rodenticides. – Sci. Total Environ. 569–570: 1013–1021.

Sainsbury, K. A., Shore, R. F., Schofield, H., Croose, E., Campbell, R. D. and Mcdonald, R. A. 2019. Recent history, current status, conservation and management of native mammalian carnivore species in Great Britain. – Mamm. Rev. 49: 171–188.

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. – Proc. R. Soc. B 285: 20172603.

Strayer, D. L., D'Antonio, C. M., Essl, F., Fowler, M. S., Geist, J., Hilt, S., Jarić, I., Jöhnk, K., Jones, C. G., Lambin, X., Latzka, A. W., Pergl, J., Pyšek, P., Robertson, P., von Schmalensee, M., Stefansson, R. A., Wright, J. and Jeschke, J. M. 2017. Boom–bust dynamics in biological invasions: towards an improved application of the concept. – Ecol. Lett. 20: 1337–1350.

Sutherland, C., Royle, J. A. and Linden, D. W. 2019. oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. – Ecography 42: 1459–1469.

Taberlet, P., Griffin, S., Goossens, B., Questiau, S., Manceau, V., Escaravage, N., Waits, L. P. and Bouvet, J. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. – Nucleic Acids Res. 24: 3189–3194.

Twining, J. P., Montgomery, W. I., Reid, N., Marks, N., Tosh, D. G. and Scantlebury, D. M. 2020. All forests are not equal: population demographics and denning behaviour of a recovering small carnivore in human modified landscapes. – Wildl. Biol. 2020: 1–10.

Twining, J. P., Lawton, C., White, A., Sheehy, E., Hobson, K., Montgomery, W. I. and Lambin, X. 2022a. Restoring vertebrate predator populations can provide landscape-scale biological control of established invasive vertebrates: insights from pine marten recovery in Europe. – Global Change Biol. 28: 5368–5384.

Twining, J. P., McFarlane, C., O'Meara, D., O'Reilly, C., Reyne, M., Montgomery, W. I., Helyar, S., Tosh, D. G. and Augustine, B. C. 2022b. A comparison of density estimation methods for monitoring marked and unmarked animal populations. – Ecosphere 13: e4165.

Velander, K. A. 1983. Pine marten survey of Scotland, England and Wales 1980–1982. – Vincent Wildlife Trust.

Weber, D., Roth, T., Tesini, C. and Thiel, D. 2018. Widespread distribution of pine martens (*Martes martes*) in a fragmented suburban landscape. – Mamm. Res. 63: 349–356.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer-Verlag, https://ggplot2.tidyverse.org.

Zabel, A. and Holm-Müller, K. 2008. Conservation performance payments for carnivore conservation in Sweden. – Conserv. Biol. 22: 247–251.

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: 31–43.