Declining invasive grey squirrel populations may persist in refugia as native predator recovery reverses squirrel species replacement

Joshua P. Twining1 | W. Ian Montgomery1 | David G. Tosh2

1School of Biological Sciences, Queen's University of Belfast, Belfast, UK
2National Museums NI, Cultra, UK

Abstract

1. Invasive species pose one of the most serious global threats to biodiversity. Investigations into the interactions of native and non-native species focus on the impacts of single species, despite being embedded in a network of direct and indirect interactions between multiple species and their environments.

2. We developed 1-km² resolution, single-species and multi-species occupancy models using quantitative camera trap data collected by citizen scientists at 332 sites in a regional survey comprising the 14,130 km² of Northern Ireland.

3. Recent research suggests that native red and invasive grey squirrels in Britain and Ireland are linked by resource and disease-mediated competition, and by a shared enemy, the European pine marten. We demonstrate that the presence of the pine marten reverses red squirrel replacement by grey squirrels on a regional basis, with red squirrel occupancy positively affected by exposure to pine marten. In contrast, the grey squirrel has a strongly negative response to the presence of pine marten.

4. Modelling habitat suitability of pine marten and both squirrel species suggests that, despite the potentially strong effect of a recovering population of pine martens in controlling grey squirrel distribution, the latter is likely to persist in urban refugia that are either inaccessible or avoided by the pine marten.

5. Synthesis and applications. Sustainable recovery of both the red squirrel and the pine marten across the wider landscapes of Ireland, Scotland and Northern England seems probable, while in Southern England and Wales, although possible, chances are more remote. Increasing native woodland cover on a landscape scale to facilitate pine marten recovery may assist in realizing this scenario. Despite the ongoing recovery of the pine marten, and resultant declines in grey squirrels, isolated populations are likely to persist in urban areas. Human-lead control of grey squirrel populations in urban refugia requires urgent funding and implementation to avoid the development of novel genotypes in grey squirrel source populations that enable the species to better avoid predation by the pine marten.
Modelling whether recovery of a native predator results in complete or partial extirpation of an invasive species depends on the specific interactions of each species and the extent to which the species co-occur (Bonsall & Hassell, 1997). If an invasive prey species has access to refugia which are permanently inaccessible to or avoided by a recovering predator, the former may survive and potentially disperse outwards again facilitating the spread of novel genotypes which are more difficult for the predator to deal with.

Despite the role of three-species interactions with respect to a global increase in the occurrence of invasive species, demonstrating the influence of a shared predator interaction involving native and invasive species, and predicting outcomes, is quantitatively challenging. The spatial scale on which to base models, for example, may be critical. Furthermore, the high standard of evidence required to shape policy with respect to control of invasive species hinges on the need to account for imperfect detectability rather than using indices of abundance (Hayward & Marlow, 2014). This necessitates well-designed surveys that record detections and non-detections over the region of interest (e.g. presence–absence data), using a standardized sampling programme to remove spatial bias (Thompson, White, & Gowan, 1998). The presence–absence (PA) approach provides high-quality occupancy data (Kéry, Gardner, & Monnerat, 2010) as it enables calculations that account for imperfect detection of species (MacKenzie et al., 2002). Occupancy models constructed using PA data enable researchers to investigate multi-species interactions but also to predict habitat suitability of such species when projected across landscape into unsampled areas. Although this approach allows robust conclusions to be made, its inherent expense (both economically and time demands) constrains researchers to small areas often unrepresentative of a species’ geographical range. However, recent investigations have enlisted ‘citizen scientists’ to collect data at spatial and temporal scales that would not be feasible by any other method (Dickinson, Zuckerberg, & Bonter, 2010). This raises issues regarding analyses of the data due to variable effort and incomplete detections (Altwegg & Nicols, 2019). For example, as reported in south-western Australia, where volunteer biases and resultant variable sampling efforts were observed to lead to skewed and therefore inaccurate representations of bird communities (Tulloch & Szabo, 2012). Conclusions based on citizen scientists’ data that do not account for these factors may result in biased and erroneous inferences (Isaac, van Strein, August, de Zeeuw, & Roy, 2014).

The most common errors arising from citizen science projects originate from false negatives, that is, failing to report a species that occurs in a specific grid cell (Altwegg & Nicols, 2019). This is due to the low probability of detecting species, even common ones, during a single visit to a site (Kéry & Schmidt, 2008). This is exacerbated in low density or elusive species (Tyre et al., 2003). False positives resulting from misidentification of species is also a recognized issue.
within citizen scientist projects (MacKenzie et al., 2018). The variability of sampling effort in citizen science projects also fluctuates considerably across space (Altwegg & Nicols, 2019), as easily accessible sites generally receive more effort than more remote sites, as do those species and locations that are deemed interesting versus non-interesting (Tulloch & Szabo, 2012). Recent advances in remote sensing based on affordable, more sophisticated camera traps, however, have improved data-collection protocols using citizen scientists (Dickinson et al., 2010; Wearn & Glover-Kapfer, 2017). The use of camera traps removes concerns regarding variable effort and inconsistent detections, permitting more robust statistical inference based on high-quality occupancy data without the associated high costs of PA surveys.

There is growing evidence that the recovery of a native predator, the European pine marten, Martes martes, influences the occupancy of native red squirrel Sciurus vulgaris and invasive grey squirrels S. carolinensis in Britain and Ireland. The interactions of these sciurids are well documented and are driven by exploitative competition and disease-mediated competition (Gurnell, Wauters, Lurz, & Tosi, 2004; McLennan et al., 2012; Tompkins, Sainsbury, Nettleton, Buxton, & Gurnell, 2002). The three-species interaction, involving invasive and native squirrels and the predator, was reported initially in Ireland (Carey, Hamilton, Poole, & Lawton, 2007; Lawton, Flaherty, Goldstein, Sheehy, & Carey, 2015; Reilly, 1997; Teangana, Reilly, Montgomery, & Rochford, 2001). Since the legal protection of the European pine marten in Ireland in 1976 under the Irish Wildlife Act, and 1981 in Northern Ireland under the Wildlife and Countryside Act, the pine marten has started recovering. This has resulted in the species returning to many counties from which it had previously been extirpated (O’Mahony et al., 2017; O’Sullivan, 1983). Sheehy and Lawton (2014), following anecdotal reports and Carey et al. (2007) and Lawton et al. (2015) based on incidental sightings, found a negative spatial correlation between pine marten presence and grey squirrel occurrence. A more recent study, again based on incidental reports and sightings directed at the regional demise of the grey squirrel in Ireland, highlighted the potential role of the pine marten as the most important factor (Flaherty & Lawton, 2019). A quantitative investigation, using hair tube sampling with camera trapping in three locations in Scotland, confirmed the negative spatial correlation of pine marten and grey squirrel and showed this relationship to be density-dependant (Sheehy et al., 2018). Pine marten connectivity (occupancy adjusted for detection probabilities and nearby occurrence) above a minimum threshold was positively correlated with red squirrel occurrence, and strongly negatively correlated with grey squirrel occurrence (Sheehy et al., 2018). Thus, it was hypothesized that the pine marten suppresses grey squirrel populations when present, although the mechanism of the relationship remained unexplored until recently (Twining, Montgomery, Price, Kunc, & Tosh, 2020; Twining, Montgomery, & Tosh, 2020b). The future of such an interaction has yet to be modelled in an applied context and, thus, it is not clear whether pine martens will provide enduring, wide scale control of the invasive grey squirrel. For example, it is not certain that grey squirrel numbers and distribution will be reduced to extinction where pine martens occur, or across the entire area of both Britain and Ireland.

The aim of this study is to investigate the habitat suitability and interactions among the native predator, the pine marten, native prey species, the red squirrel, and invasive prey species, the grey squirrel, within a region of the United Kingdom, Northern Ireland. This regional approach, using citizen scientists, allows for the collection of consistent, high-quality data on a scale (14,130 km²) which encompasses habitat and landscape effects within a single jurisdiction responsible for conservation within the European Union. Thus, we elucidate the potential of a recovering predator to control an invasive prey species on a landscape scale. We first construct landscape scale probability of occupancy models for the study species from single-species occupancy models (MacKenzie et al., 2018). Multi-species models (Rota et al., 2016) are then used to predict species co-occurrence across the region. Finally, generalized linear models are used to investigate the effect of pine marten occupancy on the occupancy of the two squirrel species. Collectively, these models predict the future distributions of three species and can be used to inform policy with respect to the ability of the recovering predator population to control the invasive grey squirrel at a regional level. Results suggest that red squirrel and pine marten populations will have coinciding distributions in forests in the wider landscape while grey squirrels will persist in isolated woods and parklands around more urban areas and not become regionally extinct.

2 | MATERIALS AND METHODS

A survey documenting the presence of pine marten and grey and red squirrel was conducted in 2015 at 332 sites throughout Northern Ireland by citizen scientists using camera traps (Figure 1). In each site, a single Bushnell HD Trophy Camera Trap was deployed at a randomly selected point. Cameras were installed at head height on a tree overlooking a wooden squirrel feeder baited with peanuts and sunflower seeds. Cameras were set to take three images per trigger with a 60 s reset time. Traps were deployed for a minimum of 7 days at each location after which cameras were retrieved and SD cards containing photographs were returned to DT/JT for species identification, data collation and analysis. Detection records were created for each species over 7 days of recording.

2.1 | Habitat covariates

Eight biophysical variables were identified as potentially important predictors of the three study species distributions and occurrence in Northern Ireland. The variables were generated for each 1-km² cell. Values were derived from GIS shape files supplied for the Land Cover Map, 2007 (LCM, 2007). Prior to model building, the strength of correlation coefficients between pairs of variables was assessed; if variables were highly correlated...
(r > 0.6), a randomly selected variable in each pair was removed (Zuur, Leno, Walker, Saveliev, & Smith, 2009). No evidence of multicollinearity amongst the identified variables was observed. Table 1 presents the variables used. Previous research has shown that climatic variables such as mean temperature and precipitation have no significant effect on the presence of martens (Zub, Kozieł, Siluch, Bednarczyk, & Zalewski, 2018). Although such clear evidence is not available for squirrels, the relatively homogeneous, mild climatic conditions of Northern Ireland and absence of extreme weather events (McCarthy, Gleeson, & Walsh, 2015; Peel, Finlayson, & McMahon, 2007) would suggest that environmental effects within the region on the species occurrence are minimal. Addition of variables not supported by evidence can lead to aberrant and misleading results, due to over-parameterization of models. Finally, accurate data pertaining to rainfall was not available on the required spatial scale being used (1 km²). Thus, due to the combination of these factors, environmental variables such as temperature and rainfall were not included in this regional analysis.

### 2.2 Single-species occupancy models

We estimated pine marten, red squirrel and grey squirrel occupancy (ψ) using a likelihood-based, single season, occupancy model (MacKenzie et al., 2002). For each camera site, species detections were coded binomially (1 = detection of target species, 0 = no detection of target species). Records were transformed into detection histories for each site ($X_i$), which were used with a product, multinomial, likelihood model to estimate occupancy parameters as follows (MacKenzie et al., 2018):

$$L(p_i | n, y) = \left( \frac{n}{y} \right) p_1^{y_1} p_2^{y_2} p_3^{y_3} \ldots p_7^{y_7},$$  \hspace{1cm} (1)

where $P_i$ is the probability of encounter history $i$, $n$ is the number of sites sampled and $y$ is the frequency of each type of encounter history.

We ran analyses using PRESENCE 12.26 for three single species, single season models (MacKenzie et al., 2002). For each model, we considered seven sampling occasions, one for

### Table 1 Habitat covariates used in occupancy models

| Covariate | Description | References |
|-----------|-------------|------------|
| Built | Proportion of built-up areas and gardens both urban and suburban | Balestrieri et al. (2018) and Lombardini et al. (2015) |
| Broadleaf | Proportion of broadleaved and mixed woodlands | Lawton et al. (2015), Rushton et al. (1997) and Zub et al. (2018) |
| Coniferous | Proportion of coniferous woodland | Carey et al. (2007), Caryl et al. (2012) and Zub et al. (2018) |
| People | Number of people per km²² | Balestrieri et al. (2018) |
| Dwarf | Proportion of dwarf shrub heath (heather and heather grassland) | Caryl et al. (2012), Clevenger (1994) and Lombardini et al. (2015) |
| River | All freshwater rivers and streams (km) | Carey et al. (2012), Clevenger (1994) and Lombardini et al. (2015) |
| Latitude | Decimal degrees latitude of location | Flaherty and Lawton (2019) |
| Longitude | Decimal degrees longitude of location | Flaherty and Lawton (2019) |
each 24-hr period of continuous sampling. The data were ana-
ysed using a two-step approach (Sarmento, Cruz, Eira, & Fonseca, 2011). First, we calculated the outcome of our covari-
ates on detection probabilities while keeping occupancy con-
stant (i.e. \( p(\cdot), p(\text{covariate}) \)). Next, we used the best fitting model
for detection probabilities and combined it with a set of a priori
models integrating covariates to explain observed patterns of
occupancy based on knowledge from the literature (Figure 2; Balesstrieri, Mori, Menchetti, Ruiz-Gonzalez, & Milanesi, 2018; Caryl, Quine, & Park, 2012; Zub et al., 2018). The ranking of
candidate models was conducted using Akaike information cri-
terion (AIC) corrected for sample size by calculating their Akaike
weights (\( \Delta \text{AIC} \); Burnham, Anderson, & Huyvaert, 2011). Those
models with \( \Delta \text{AIC} \) values <2 when compared with the most
parsimonious model were classified as robust. Akaike weights
were used to determine the relative importance of indepen-
dent variables in each model. Likelihood ratio tests were used
to compare models representing the hypothesis tested by com-
paring the difference in deviance between pairs of models to
the critical value of the Chi square distribution. The selected
models allowed the calculation of the average estimates of oc-
cupancy and detection probabilities. Calculation of detection
probabilities ensures that heterogeneity in detection prob-
abilities caused by environmental or temporal factors (i.e. availabil-
ity of alternative resources, time of sampling) are not falsely
interpreted as changes in occurrence (MacKenzie, 2005; Royle
& Nichols, 2003). Anticipating heterogeneity in detection prob-
ability, and minimizing its effects through careful study design,
and via the use of relevant covariate data are essential for good
performance of occupancy models (MacKenzie et al., 2018). We
used habitat covariate data present for all of Northern Ireland
to extrapolate to predicted probability of occupancy values for
all 14,402 km\(^2\) (land area minus major water bodies) of Northern
Ireland for all three species.

2.3 | Multi-species occupancy models

We estimated species co-occurrence probabilities of the pine
marten, the red squirrel and the grey squirrel, as a function of
habitat covariates using single-species occupancy model theory
(MacKenzie et al., 2002). We generalized this theory to three
species, by assuming the latent occupancy state is a multivariate
Bernoulli random variable (Rota et al., 2016). For each camera site,
species detections were coded multinomially (00 = no detection
of target species, 01 = detection of species one, 02 = detection of
species two, 03 = detection of species one and two, 04 = detection of
species three, 05 = detection of species one and three, 06 = detec-
tion of species two and three). These were used as the dependen-
ty/response variable in a multinomial logit model to estimate occu-
pancy parameters as above. Odds ratios (OR) were used for specific
occurrence and co-occurrence of species as follows (MacKenzie
et al., 2018):

\[
\text{OR} = \frac{\text{odds}_{BA}}{\text{odds}_{BD}} = \frac{\psi_{AB}/(\psi_{A} - \psi_{AB})}{(\psi_{B} - \psi_{AB})/(1 - \psi_{A} - \psi_{B} + \psi_{AB})} = \frac{\psi_{AB}(1 - \psi_{A} - \psi_{B} + \psi_{AB})}{(\psi_{A} - \psi_{AB})(\psi_{B} - \psi_{AB})} = \frac{\psi_{AB}(1 - \psi_{AD} - \psi_{DB} - \psi_{AB})}{\psi_{AD}\psi_{DB}},
\]

where OR is the odds ratio for species B is present given species A is
absent (MacKenzie et al., 2018), uppercase letters indicate presence of
species, that is, \( \psi_{AB} \) is the probability of occupancy of both species A
and B both being present. 0 indicates absence of the species, that is,
\( \psi_{0B} \) is sites occupied by only species B.

3 | RESULTS

Sampling effort overall was 2,296 trap days (24-hr periods) across
332 sites with 757 independent detections comprising pine martens
(\( n = 217 \)), red squirrels (\( n = 208 \)) and grey squirrels (\( n = 332 \)). Only
one detection for each species was allowed per 24-hr period of sam-
ping to ensure data independence. Grey squirrels were detected at
the most sites (78) but were not found to co-occur with pine martens
and only co-occurred with red squirrels at a single site. Pine martens
were detected at 63 sites, co-occurring with red squirrels at 20 sites.
Red squirrels occurred at 55 sites.

3.1 | Single-species occupancy models

Detection probabilities (i.e. the probability of detecting a species
given it is present in the sampling area) were significantly different
between species (Figure 3a; ANOVA: \( F_2 = 30.42, p < 0.001 \)); grey
squirrels had the highest mean detection probability, followed by
pine martens, and then red squirrels which had the lowest detection probability. For both grey and red squirrels, the covariates coniferous, broadleaf and number of people were considered the most important in determining detection probability. For grey squirrels, broadleaf and number of people decreased detection probability (Broadleaf: $-1.351 \pm 0.608$; People: $-0.003 \pm 0.002$), while coniferous woodland increased detection probability (Coniferous: $2.429 \pm 0.672$). For red squirrels, both coniferous and broadleaf habitats decreased detection probability (Broadleaf: $-1.224 \pm 0.518$; Coniferous: $-0.672 \pm 0.347$), while detection probability increased slightly with human population (People: $0.003 \pm 0.002$). For the European pine marten, both coniferous and broadleaf were important for determining detection probability, with both habitats decreasing detection probability (Broadleaf: $-1.093 \pm 0.447$; Coniferous: $-0.713 \pm 0.325$).

**FIGURE 3** (a) Mean (±SE) detection probabilities (p) for the grey squirrel, pine marten and red squirrel. (b) Mean (95% CI) probability of occupancy (ψ) values for the grey squirrel, pine marten and red squirrel

**TABLE 2** Comparison of models exploring land cover metrics on occupancy of the European pine marten, the grey squirrel and the red squirrel. Only models with ΔAIC < 2 are shown

| Model | -2logL | No. parameters | AIC  | ΔAIC  | AICwt |
|-------|--------|----------------|------|-------|-------|
| Pine marten |         |                |      |       |       |
| $ψ$(Coniferous, Broadleaf, Built, Lat, Long), $p$(Broadleaf, Coniferous) | 985.56 | 8 | 1,001.56 | 0.00 | 0.460 |
| $ψ$(Coniferous, Broadleaf, Built, Lat, Dwarf), $p$(Broadleaf, Coniferous) | 985.10 | 9 | 1,003.10 | 1.54 | 0.213 |
| Red squirrel |        |                |      |       |       |
| $ψ$(Built, Coniferous), $p$(Broadleaf, People, Coniferous) | 927.10 | 6 | 939.10 | 0.00 | 0.205 |
| $ψ$(Built, Coniferous, Broadleaf), $p$(Broadleaf, People, Coniferous) | 925.41 | 7 | 939.41 | 0.31 | 0.176 |
| $ψ$(Built), $p$(Broadleaf, People, Coniferous) | 929.98 | 5 | 939.98 | 0.88 | 0.132 |
| $ψ$(Built, Coniferous, River), $p$(Broadleaf, People, Coniferous) | 926.86 | 7 | 940.86 | 1.76 | 0.085 |
| $ψ$(Built, Coniferous, Lat), $p$(Broadleaf, People, Coniferous) | 926.90 | 7 | 940.90 | 1.80 | 0.084 |
| $ψ$(Built, Coniferous, Long), $p$(Broadleaf, People, Coniferous) | 926.97 | 7 | 940.97 | 1.87 | 0.080 |
| $ψ$(Coniferous), $p$(Broadleaf, People, Coniferous) | 931.07 | 5 | 941.07 | 1.97 | 0.076 |
| Grey squirrel |          |                |      |       |       |
| $ψ$(Built, Coniferous, Broadleaf, Lat), $p$(Broadleaf, Coniferous) | 1,174.92 | 8 | 1,190.92 | 0.00 | 0.496 |
| $ψ$(Built, Coniferous, Lat), $p$(Broadleaf, Coniferous, People) | 1,178.06 | 7 | 1,192.06 | 1.14 | 0.281 |
| $ψ$(Built, Lat, Coniferous, River), $p$(Broadleaf, Coniferous, People) | 1,176.58 | 8 | 1,192.58 | 1.66 | 0.217 |

Probability of occupancy (i.e. the probability the sampling area was occupied by study species) was significantly different between species (Figure 3b; ANOVA: $F_2 = 7.456, p < 0.001$); grey squirrels had the highest probability of occupancy, followed by red squirrels, followed by pine martens. Occupancy was mainly explained by a small number of covariates (Table 2; Figure 4). Pine marten occurrence was positively correlated with broadleaf and coniferous woodlands, and negatively correlated with buildings (Figure 4). Pine marten occurrence was negatively correlated with both longitude and latitude meaning martens are more likely to occur in the south-west of Northern Ireland, that is, West-Fermanagh, South-Armagh. Red squirrel occurrence was also negatively correlated with buildings and positively correlated with coniferous woodland (Figure 4). Red squirrel occurrence was not correlated with longitude or latitude. Finally, grey squirrel occurrence was positively correlated with buildings, and broadleaf forest but negatively affected by coniferous woodland (Figure 4). Grey squirrel occurrence was
positively correlated with latitude, meaning they are more likely to occur in the north.

Figure 5 illustrates the heat maps showing predictive outputs from the models for the whole region. Each map presents the distribution of estimated probability of occupancy for each species across all of Northern Ireland. Hitherto, M1 will refer to the best models according to its AIC value including habitat covariates only (Figure 5a–c), while M2 will refer to the best occupancy model with all possible covariates as according to its AIC value (Figure 5d–f; M2 models may contain latitude and longitude as covariates, M1 models do not). M2 models are of interest as they take into account current distribution of the species, but for future predictions of species distribution M1 models which only account for the habitat covariates available may be more useful. Both M1 and M2 predict grey squirrels to have the highest probability of occupancy ($\psi = 0.84–0.99$) in areas of human habitation including both urban and suburban areas throughout Northern Ireland, with areas adjacent to cities and towns also having a high, albeit slightly lower probability of occupancy ($\psi = 0.44–0.62$). Grey squirrels have the lowest probability of occupancy in large coniferous plantation blocks which make up the majority of forest cover in Northern Ireland ($\psi \leq 0.01$). The M2 model differs for the grey squirrel from the M1 model as it takes into account latitude, demonstrating that grey squirrels have a higher probability of occurrence in the north of the region ($\psi = 0.34–0.44$), than the centre ($\psi = 0.19–0.27$), or south ($\psi = 0.1–0.19$). The importance of latitude for grey squirrels is likely to stem from the fact pine martens have recovered from populations in the Irish midlands and are at the highest densities in the south-west of Northern Ireland, that is, the counties of Fermanagh, South Armagh and South Down. The pine marten shows the reverse of this pattern in both M1 and M2 models, with the highest probability of occupancy restricted to coniferous plantations and broadleaf woodlands ($\psi = 0.44–0.62$). Pine martens have the lowest probability of occupancy in human inhabited locations, that is, cities and towns, and adjacent areas ($\psi \leq 0.01$). The M2 model differs from the M1 model for pine marten as they take into account both latitude and longitude, showing the pine marten has the highest probability of occupancy in the south-west of the region ($\psi = 0.19–0.61$), with the lowest probability of occupancy in the north of the region ($\psi \leq 0.01–0.1$), and reduced probability of occupancy in the centre of the region ($\psi = 0.1–0.19$). The red squirrel displays a very similar pattern in probability of occupancy to the pine marten, with the highest probability of occupancy in the same coniferous forest blocks as the pine marten ($\psi = 0.44–0.62$), with the lowest probability of occupancy ($\psi \leq 0.01$) in cities and large towns. Adjacent areas to human inhabitation have a slightly higher, but still low ($\psi = 0.09–0.19$) probability of occupancy for red squirrels. M1 and M2 model results for the red squirrel are the same, as latitude and longitude were not important in determining probability of occupancy (Table 2).
3.2 | Multi-species occupancy models

The probability of grey squirrel occupancy is dramatically reduced in the presence of the pine marten ($\psi_{GSPM}$; $\beta = -16.79 \pm 976.39$), with the two species not co-occurring at a single site resulting in a very high standard error for the beta value. In contrast, the probability of the red squirrels occurring increased when pine martens were present ($\psi_{RSPM}$; $\beta = 0.575 \pm 0.418$). Finally, red and grey squirrels are less likely to occur when the other species is present ($\psi_{GSRS}$; $\beta = -2.95 \pm 1.40$).

3.3 | Marten squirrel interactions

| FIGURE 5 | Predicted probability of occurrence of the (a) grey squirrel, (b) the pine marten and (c) the red squirrel based on M1 single-species models (no latitude or longitude), (d) grey squirrel, (e) the pine marten and (f) the red squirrel based on M2 (may contain latitude or longitude) single-species models extrapolated to 14,401 1-km² grids of Northern Ireland, based on best rated occupancy models from the 332 sampling sites |

F I G U R E 6  Model predictions of the relationship between pine marten probability of occupancy and the probability of occupancy of (a) grey squirrel and (b) red squirrel in Northern Ireland

$p < 0.001$). Significant portions of variance in red squirrel probability of occupancy were also explained by pine marten probability of occupancy. However, this relationship was reversed with probability of red squirrel occupancy increasing with increasing probability of occupancy of the pine marten (Figure 6; GLM, $F_{14400} = 161.4$, $p < 0.001$).
4 | DISCUSSION

We provide robust evidence on a regional landscape scale that a recovering native predator is able to provide biological control of an invasive prey species. This increases the resilience of an ecosystem to invaders by reversing the typical outcome of pairwise interaction between the invasive and native prey species. The impact of the recovering predator was relatively symmetrical, having a negative effect on the invasive species, and a positive effect on the native species. Despite evidence that the recovery of a native predator has resulted in a large-scale decline of the invader, the results also indicate that recovery of the native predator alone will not be sufficient to cause complete extirpation of the invasive species. The predicted outcome of pine marten recovery, will instead, results in fugitive coexistence due to the presence of refugia suitable to the invader, and not accessible, or avoided by the native predator, that is, parklands in and around towns and cities.

Our evidence is observational rather than experimental, but it is derived from a planned and structured survey design, incorporating key species and habitat covariates, using a method that allows for variable detectability of target species. Integral to the survey design was the high sampling resolution of the project which enabled collection of quantitative data on species occurrence at 332 different sites across different habitats and topographies on a regional scale made possible via collaboration with citizen scientists. We accounted for concerns surrounding use of citizen scientists through the use of camera traps with a standardized protocol and all analysis counted for concerns surrounding use of citizen scientists through the use of camera traps with a standardized protocol and all analysis conducted by a single experienced researcher negating concerns about data quality due to varied recorder bias and effort (Dickinson et al., 2010).

4.1 | Habitat suitability

The results confirm pine marten to be woodland specialists in Ireland concurring with previous work in Italy (Balestrieri et al., 2018), the Iberian Peninsula (Virgos, 2003) and Scotland (Caryl et al., 2012). The presence of both coniferous plantation and broadleaf and mixed forests influenced species occupancy positively. Our results expand upon previous habitat suitability studies (Balestrieri et al., 2018; Zub et al., 2018) demonstrating broadleaf and mixed habitats are more suitable than coniferous woodlands, with broadleaf having a stronger positive effect on marten occurrence. This demonstrates that although commercial coniferous plantations provide suitable habitat for the European pine marten, they are less suitable in comparison to deciduous woodlands. This is likely due to the fact that over 75% of coniferous plantations in Ireland are immature (<30 years old; Department of Agriculture, Food, & the Marine, 2018), and are monotypic stands of exotic tree species, which lack the structural complexity and biodiversity associated with natural native woodlands (Caryl et al., 2012). These results may be particular to regions which are currently undergoing afforestation schemes driven by Government forestry bodies and timber production as in Ireland and Britain (Mitchell, 2000). In these regions, over three quarters, total forest cover are formed from such monotypic plantations of exotic, low-biodiversity supporting species, for example, Sitka spruce Picea sitchensis subject to 30-year cycles of rotational logging (Department of Agriculture, Food, & the Marine, 2018; Forestry Commission, 2019). Present results may have less relevance where young forests of non-native species are not predominant, for example, in Scandinavia where natural old-growth boreal forest is common.

Our results also demonstrate the strong avoidance pine marten have for human settlements in Ireland, as the ‘urban’ covariate had the strongest effect of any of the habitat covariates. The European pine marten was not found to occur in any urban areas in our study. Although avoidance of urban areas by the pine marten has been previously acknowledged (Balestrieri et al., 2018; Vergara, Cushman, Urra, & Ruiz-González, 2015), our analyses demonstrate that the species’ lack of tolerance for human disturbance is key in shaping their pattern of distribution in Ireland.

In a fragmented and heavily modified landscape, such as is present in Ireland, it may be expected that open habitats, like heather and scrubland, would positively affect pine marten occurrence. Several studies in other parts of the pine martens’ range have observed the use of such open habitats in the absence of old-growth forest e.g. Minorca (Clevenger, 1994), Italy (Balestrieri et al., 2018; Lombardini et al., 2015) and Scotland (Caryl et al., 2012). However, this was not the case in the present study region. This does not preclude the pine marten from making use of such habitats in degraded woodlands such as coniferous plantations but does suggest that open habitats are only suitable and/or used when adjacent to woodland.

For sciurid species, the present results confirm previous research into their habitat suitability. Grey squirrels were positively correlated with urban areas, and broadleaf and mixed habitats, and negatively correlated with coniferous plantations. The converse was true of red squirrels. This supports earlier research that showed grey squirrels prefer broadleaf habitat and will outcompete red squirrels in deciduous and mixed woodlands (Gurnell et al., 2004; Lawton et al., 2015; Wauters, Lurz, & Gurnell, 2000). Although this resulted in red squirrels being largely confined to large coniferous plantations where grey squirrels are less capable of outcompeting the native sciurid (Lawton et al., 2015), grey squirrels have historically replaced red squirrels throughout many smaller coniferous forests as well.

Examples of coniferous plantations where declines in grey squirrels and the return of red squirrels, following recolonization by the pine marten are found across Northern Ireland (e.g. West Fermanagh, South Armagh, South Down). This is likely due to conifer plantations being the predominant forest type across Northern Ireland (Forestry Commission, 2019), rather than these plantations being more suitable to red squirrels than broadleaf forests. Both coniferous plantations and broadleaf forests are suitable for red squirrels where pine martens are present and reverse the typical competitive outcome between reds and greys (Sheehy et al., 2018). It is interesting to note that grey squirrels have more tolerance of human activity and that this is more important than the presence of broadleaved trees
in determining their occupancy. This may be a collateral effect of predation by pine martens, which occur in broadleaf habitats, but strongly avoid areas of human inhabitation.

The detection probabilities of each of the species provide additional support of the habitat suitability for all three study species. As forest cover (both coniferous and deciduous) increased, detection probability of both pine marten and red squirrel decreased. This suggests when feeders are in larger forests, the greater availability of exploitable resources in both types of forest lowers the advantages of visiting the feeder and likelihood of detection. This supports findings elsewhere that show, in the absence of grey squirrels, both broadleaf and coniferous woodland are suitable habitat for red squirrels (Cagnin, Aloise, Fiore, Oriolo, & Wauters, 2000; Magris & Gurnell, 2002). The confounding, negative effects of grey squirrel presence serve to explain why broadleaved woodland is not selected for as an occupancy covariate in the most parsimonious model for red squirrel occurrence.

The contrasting effects of broadleaf and coniferous woodlands on grey squirrel detection probability also provide additional support for the ecological preferences of the species (Lawton et al., 2015; Rushton, Lurz, Fuller, & Garson, 1997). Coniferous woodland increased detection of grey squirrels, whilst broadleaf woodlands decreased probability of detection. This demonstrates that in broadleaf woodland, grey squirrels are comparatively less likely to visit the feeders. Again, this is likely linked to the exploitability of resources present in the environment to the grey squirrel. Grey squirrels are well adapted to broadleaf woodland and its large seed resources (Moller, 1983), and less well suited to exploiting the small cone seeds of coniferous woodlands (Lawton et al., 2015).

4.2 | Predicted outcome of impact of native predator on invasive species

The present analyses provide insights into previously unaddressed questions on the potential outcome of native predator recovery in the invasive–native prey interaction at a landscape scale. In consensus with previous investigations into the effect of the European pine martens on grey and red squirrels, we confirm the pine marten appears to suppress invasive grey squirrel populations (Carey et al., 2007; Lawton et al., 2015; Sheehy & Lawton, 2014; Sheehy et al., 2018). Where the pine marten has recovered within the last decade, for example, West Fermanagh, South Armagh, South Down, grey squirrels are now absent where they were previously common (Carey et al., 2007; Lawton et al., 2015). In addition, grey squirrels now only have high probability of occupancy in areas where pine martens are absent, for example, urban areas of Belfast and the Lagan Valley. Furthermore, multi-species occupancy models predict near zero co-occurrence of pine marten and grey squirrel. However, due to lack of species co-occurrence in the survey, and resulting high standard errors, conclusions based on multi-species models must be used cautiously. The error overlapping zero could result in a conclusion of independence (C. Rota, pers. comm.). However, the lack of co-occurrence of these species in this survey is likely a by-product of the biogeographical situation in Ireland where pine martens and grey squirrels only co-occur ephemerally when pine martens recover in an area, making detection of co-occurrence events a rarity (Flaherty & Lawton, 2019). Despite pine marten recovery resulting in apparent wide-scale declines of the invasive grey squirrel, the latter will likely persist in urban areas due to the pine martens’ current inability to occupy such habitats.

4.3 | Policy implications

These results have direct policy implications for Ireland, the United Kingdom and mainland Europe. The models demonstrate the ability of the pine marten to positively influence the conservation of the red squirrel which has been in decline since the grey squirrel’s introduction to Ireland and Britain. However, the ability of the pine marten to extirpate the grey squirrel from Ireland and Britain is constrained by two things: refugia in the form of urban areas and the lack of forest cover on the islands. Our study shows woodland to be the preferred habitat of pine marten; however, Britain and Ireland have some of the lowest forest cover in Europe (10.5% in Ireland; Department of Agriculture, Food, & the Marine, 2018; 13% in UK, with Northern Ireland having the lowest cover of 8%, Forestry Commission, 2019). This means the pine marten’s sphere of influence is limited by lack of suitable habitat. This, combined with the fact the pine marten usually does not occupy urban areas anywhere within its European range, will likely mean the species is not the sole solution to complete grey squirrel control. Despite this, the models suggest the potential for a future in which, if suitable habitat is provided, red squirrel and pine marten populations may recover and coexist in the wooded landscapes of Ireland and Britain.

The models predict a likely future scenario where, even assuming continued recovery of pine marten populations, grey squirrel populations will remain in urban areas. Urban populations could subsequently act as sources for reinforcement of populations in the wider landscape. This scenario could aid the development of novel genotypes that may infer an awareness of pine marten, thus reducing predation. The potential of such a situation altering the pine marten’s ability to control grey squirrels cannot be ignored. Current research indicates that the pine marten’s ability to suppress grey squirrel populations may be linked to a lack of anti-predator behaviours in the latter to the former (Twining, Montgomery, Price, et al., 2020). Naive prey species can develop anti-predator behaviours to novel predators within a few generations (e.g. Anson & Dickman, 2012). However, novel predators have also caused extinction of naive prey species prior to adaptation (Saunders et al., 2010). Thus, the grey squirrel’s ability to adapt, over time, to pine marten presence is unknown. If grey squirrels learn to avoid predation by the pine marten, the invasive species may return to its previous, wider distribution, recolonizing and replacing red squirrels. To avoid this scenario, grey squirrel control should be undertaken in human-populated areas to ensure total extirpation of the invasive. Despite the possible
scenarios above, there is an added risk of negative public perception prohibiting attempts to control grey squirrels in human-populated areas, as demonstrated in Italy (Lioy et al., 2019). Public outreach and education programmes in urban grey squirrel hotspots should be initiated immediately to gauge public perception and create preparedness in anticipation of control programmes.

Legislative action must be taken to ensure a future for two of Britain and Ireland’s native fauna. This would necessitate an increase in forest cover comprising native trees and connectivity in the Irish and British landscapes which would facilitate the expansion of both pine marten and red squirrel populations. Afforestation schemes such as the £50 million Woodland Carbon Guarantee in the United Kingdom are not only beneficial in terms of carbon sequestration but also integral to the conservation of our native biodiversity. Both broadleaf and coniferous woodlands should be managed with the suitability of the habitat for pine marten in mind. Individually, and collectively, the following policies will work to restore old-growth structural characteristics to forests increasing their suitability to the pine marten: provisioning of arboreal denning locations which are typically limited in coniferous woodlands, through artificial den box schemes (Croose, Birks, & Martin, 2016; Twining, Birks, Martin, & Tosh, 2018); interplanting of native, cavity producing species, for example, oak Quercus robur; applying long-term retention protocols for veteran trees; and implementing continuous forest cover principles, that is, avoiding clear felling, to provide continuity of forested habitat (Denman, 2015). Policies that increase the suitability of woodlands will increase the potential of the pine marten to occupy areas and limit numbers of invasive grey squirrels.

Britain has suffered more from grey squirrel invasion than Ireland (Lloyd, 1968), but grey squirrels have been largely kept out of central and northern Scotland by the presence of the European pine marten (Sheehy et al., 2018). Managing woodland and forest provision in southern Scotland and northern England may assist in reducing grey squirrel numbers and allow for further recovery of pine marten and red squirrel populations. In southern Britain, the human population is much higher, and the pine marten is generally absent (apart from small localized populations e.g. New Forest, J. Palmer, pers. comm.). Reintroductions of the pine marten in Wales and Northern England (Vincent Wildlife Trust, 2020) may prove successful but additional investment, and human-led action will be required with respect to populated urban areas of southern Britain to work towards a future scenario where it is a possible for the red squirrel to recover in any meaningful way.

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**AUTHORS’ CONTRIBUTIONS**

D.G.T. conceived ideas and designed sampling methodology; J.P.T. and D.G.T. collected data and performed analysis; J.P.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**DATA AVAILABILITY STATEMENT**

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.pzgmsbc7 (Twining, Montgomery, & Tosh, 2020a).

**ORCID**

Joshua P. Twining [https://orcid.org/0000-0002-0881-9665](https://orcid.org/0000-0002-0881-9665)

W. Ian Montgomery [https://orcid.org/0000-0001-9715-4767](https://orcid.org/0000-0001-9715-4767)

David G. Tosh [https://orcid.org/0000-0001-5210-6358](https://orcid.org/0000-0001-5210-6358)

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.