Indirect effects of pine marten recovery result in benefits to native prey through suppression of an invasive species and a shared pathogen

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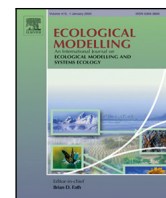
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ABSTRACT

Invasive species pose a major threat to native species, both through direct interactions, such as competition for resources, and indirect interactions, such as when the invasive species acts as a reservoir host for a virulent pathogen. Recent research has indicated that the recovery of native predators can benefit native prey species that compete with invasive prey, in circumstances where predation is more pronounced on the naïve invasive species. We use the native red squirrel (*Sciurus vulgaris*), invasive grey squirrel (*Sciurus carolinensis*) and shared squirrelpox virus (SQPV) system in North Wales, UK, as a case study system to assess the impact of a recovering, native predator of both squirrel species, the pine marten (*Martes martes*), on community structure. We develop a stochastic, spatial model that represents the habitat structure, distribution, and connectivity in North Wales and models the interactions of red and grey squirrels, SQPV, and pine marten to examine the indirect effect of native predator recovery on competitively linked native-invasive prey species and a viral pathogen. Our model demonstrates the potential role of native predators in reversing the replacement of a threatened native prey through the regulation of the invasive prey species due to sustained predation, and the resultant extirpation of a viral pathogen, which otherwise catalyses the replacement of the native red squirrel by the invasive grey squirrel. Our findings have system specific applied conservation implications, but moreover demonstrate the critical role of native predators in mitigating the impacts of invasive species and, indirectly, the infectious diseases they harbour.

1. Introduction

The introduction of, and invasion by, non-native species is recognised as a major threat to native species persistence and biodiversity (Simberloff, 2011; Bellard et al., 2016; Seebens et al., 2017). Replacement of native species can occur as a result of direct interactions, such as through predation and interspecific competition for resources, as well as through indirect effects, such as when the invasive species acts as a reservoir host for a virulent pathogen of the native species (Bellard et al., 2016; Strauss et al., 2012). The impact of introduced non-native species and their pathogens on the population dynamics of native species communities has uncovered the importance of both direct and indirect interactions across trophic levels in driving system outcomes (Tompkins et al., 2003; Hilker and Schmitz, 2008; Roberts and Heesterbeek, 2021). Pathogens and predators are key elements in many different systems, with their impact dependent on

community configuration (Hatcher et al., 2006; Lafferty, 2004; Ritchie and Johnson, 2009; Cortez and Duffy, 2020). Competitively linked prey species can share both predators and pathogens, meaning the presence and impact on one host/prey species cannot be determined without understanding the indirect interactions that arise due to the presence of a different predator, pathogen, or prey species (Holt and Bonsall, 2017). For example, declines in populations of the native water vole (*Arvicola terrestris*) in the United Kingdom have been demonstrated to be driven indirectly through apparent competition with an invasive competitor (European rabbit, *Oryctolagus cuniculus*) which serves as the staple prey item of their shared invasive predator (American mink, *Neovison vison*, (Oliver et al., 2009)). Knowledge of the impacts of indirect effects between predators and competitors is growing. However, a key challenge remains in comprehending the effects of the combined indirect interactions between both predators and pathogens on prey.
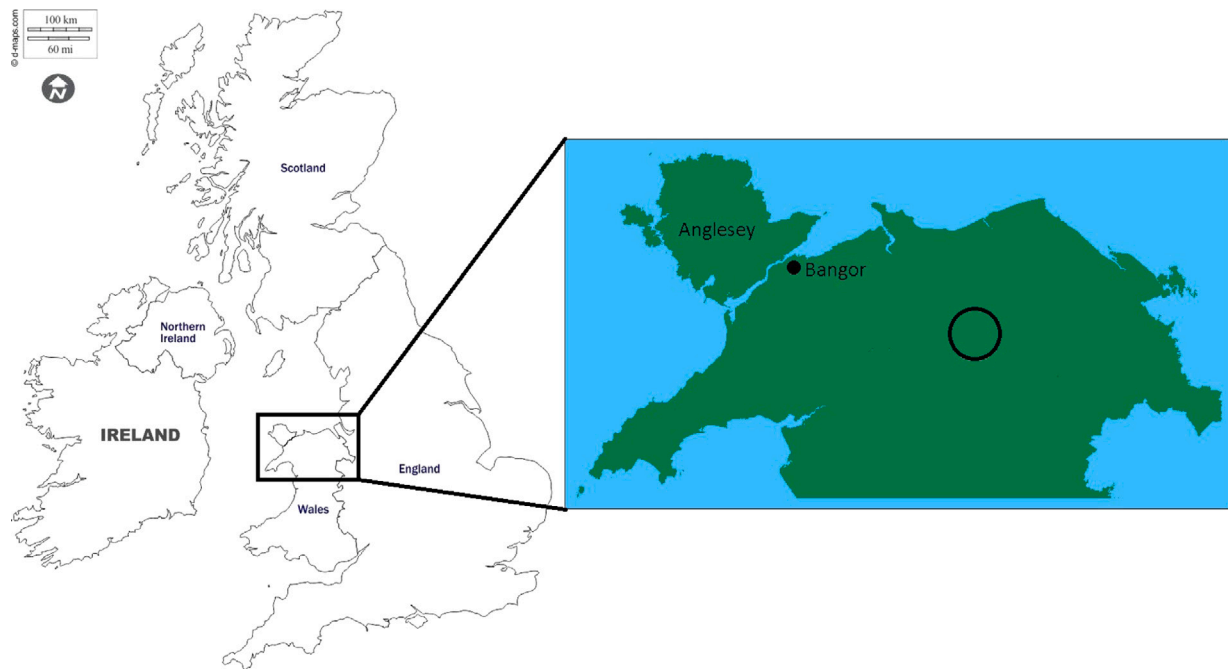
Fig. 1. Left: A map of the United Kingdom, with the study area of North Wales highlighted. Right: A map of North Wales highlighting the key site of Anglesey, an island off the north coast of Wales, which is connected to the mainland via the Britannia bridge across the Menai Strait at the coastal city of Bangor. The large circle indicates the approximate location of the upland conifer plantation that has a resident red squirrel population.

The Eurasian red squirrel (*Sciurus vulgaris*), which is native to Great Britain and Ireland, is threatened by the introduced, invasive, North American grey squirrel (*Sciurus carolinensis*). The red squirrel has become extinct in large parts of Great Britain and Ireland, and it is estimated that just over 80% of the remaining populations in Great Britain are in Scotland, with the rest found in isolated forests or offshore islands in England and Wales (Mathews et al., 2018). The decline of red squirrel populations has arisen due to the spread of, and disease-mediated competition with, the North American grey squirrel which, since its introduction at the turn of the 20th century, has replaced red squirrels throughout most of England and Wales and parts of Scotland and Ireland (Middleton, 1930; White et al., 2016). The competitive interactions between the two species can lead to increased stress in red squirrels, reduced body size and fecundity, as well as measurable reductions in local juvenile red squirrel recruitment rates (Wauters et al., 2002; Gurnell et al., 2004; Bertolino et al., 2014; Santicchia et al., 2018). Grey squirrels are a reservoir host of squirrelpox virus (SQPV) that is asymptomatic and endemic in grey squirrels but fatal to red squirrels (Chantrey et al., 2014). The replacement of red squirrels has been reported to occur up-to twenty-five times faster in areas where SQPV is present (Tompkins et al., 2003; Rushton et al., 2006).

Recent research has indicated that the recovery of native predators can benefit native prey species that compete with invasive prey in circumstances where predation is more pronounced on the naïve invasive species (Sheehy and Lawton, 2014; Twining et al., 2022b). Pine martens (*Martes martes*) are generalist semi-arboreal predators, native to Great Britain and Ireland, that have been reported to prey upon grey squirrels at a greater frequency compared to red squirrels (Twining et al., 2020c), which is believed to occur due to evolutionary naïvety and a lack of anti-predator behaviours in grey squirrels (Twining et al., 2020a). Recent legal protection has led to the on-going recovery of pine marten that has led to the recolonisation of much of their historical range in Scotland and Ireland. This recovery has resulted in landscape scale declines of established grey squirrel populations that has allowed the re-establishment of red squirrels in regions where they have previously been excluded (Sheehy and Lawton, 2014; Twining et al., 2022b, 2020c; Sheehy et al., 2018; Bamber et al., 2020). There

remains a paucity of information on the impact of pine marten recovery on the prevalence of SQPV in squirrel populations (but see Roberts and Heesterbeek, 2021).

Current red squirrel conservation efforts aim to mitigate the impacts of grey squirrels on red squirrels (Gill et al., 2019; Schuchert et al., 2014; Saving Scotland's red squirrels, 2019; Scotland, 2012). They include targeted squirrel control to remove or reduce the density of established populations of grey squirrels (Gill et al., 2019; Schuchert et al., 2014) to prevent further grey squirrel range expansion and reduce disease transmission (White et al., 2016; Saving Scotland's red squirrels, 2019). Conservation efforts also include the designation and management of 'stronghold' forests that are intended to provide refuge for red squirrels against the incursion of grey squirrels (Scotland, 2012; Slade et al., 2020). In Wales, like elsewhere, the arrival and range expansion of grey squirrels led to widespread replacement of red squirrels (Mathews et al., 2018). Efforts to re-introduce red squirrels have included translocations, with releases occurring on Anglesey (an island off the north coast of Wales, see Fig. 1) after a programme of grey squirrel eradication. Monitoring and grey squirrel control, guided by mathematical modelling, is used to protect the re-established red squirrel populations in Wales (Jones et al., 2017). Red squirrels have also maintained a limited presence, via the use of population reinforcement in an attempt to prevent extinction, in a 5,000-hectare upland commercial conifer plantation in central North Wales. Previous pine marten reinforcement translocations, whereby 51 pine marten were captured in Scotland and released into Mid Wales between 2015 and 2017 (Vincent Wildlife Trust, unpub. data; (Sainsbury et al., 2019)), has resulted in regional population establishment in Mid Wales, whilst a programme to release pine marten into North Wales near the coastal city of Bangor (see Fig. 1) has recently begun. The reinforcement of pine marten populations in Wales could act to reduce SQPV prevalence and grey squirrel density, and potentially lead to the predator mediated recovery of red squirrels.

Mathematical models have successfully been used to elucidate the mechanisms that underpin red squirrel replacement, highlighting that disease-mediated competition from grey squirrels and predation by shared predators are key factors (Tompkins et al., 2003; Roberts and

Heesterbeek, 2021). They have been adapted to inform conservation strategies to protect red squirrels, suggesting that grey squirrel control, which has been empirically shown to reduce SQPV prevalence (Schuchert et al., 2014), may be insufficient to prevent the spatial spread of SQPV (White et al., 2016). Furthermore, models have been used to outline control strategies that can result in local grey squirrel extinction and prevent the re-invasion of grey squirrels into red squirrel strongholds (Jones et al., 2017; Croft et al., 2021). In this paper we extend established spatial modelling approaches that represent the interactions of red and grey squirrels and SQPV in realistic landscapes (White et al., 2016; Jones et al., 2017) to include the dynamics of pine marten and examine the indirect effect of pine marten predation on red and grey squirrel interactions and the prevalence and persistence of a viral pathogen (SQPV) in the prey populations. The model system will incorporate habitat information from land-cover datasets for North Wales and will therefore be representative of realistic landscapes (see Fig. 1). Using the model, we will examine the potential spread of pine marten from populations in Mid Wales as well as from populations introduced into North Wales. Our aim will be to assess the likely impact of pine marten predation on red and grey squirrel abundance and the prevalence and persistence of SQPV in North Wales. While we recognise that model results are at best an approximation of reality, they allow key scenarios to be tested and compared, and can provide a starting point for wider scientific debate and further studies. Specifically, the model results presented in this study will provide a key platform for informing applied conservation practice in Great Britain and Ireland, including guiding the decision to support the translocation of pine marten into North Wales. Furthermore, the findings from the model system are also applicable in general, highlighting how the recovery of native predators may act to control invasive species and, indirectly, the infectious diseases they harbour.

2. Materials and methods

2.1. Model framework

The mathematical model adapts previous models of the red and grey squirrel system, which used classical deterministic approaches (Tompkins et al., 2003) to develop a spatial, stochastic model in realistic landscapes (White et al., 2016; Jones et al., 2017), to include pine marten population dynamics. The model simulates the demographics of red squirrels, grey squirrels, pine marten, and SQPV infection, along with intra and inter-specific competition between squirrels and predation from pine marten on squirrels. The model runs on an array of 1 km by 1 km grid-squares linked by dispersal. To approximate the real, heterogeneous landscape of North Wales the model uses landcover data, in conjunction with carrying capacity estimates associated with specific tree species, to estimate species carrying capacities in each grid-square.

The deterministic model for the system, upon which the stochastic model is based, highlights the key population processes that we consider. The deterministic system represents the population density and infection status (with regard to SQPV) for susceptible (S_R) and infected (I_R) red squirrels, susceptible (S_G), infected (I_G) and recovered (R_G) grey squirrels as well as the density of pine marten (P). The model is as follows:

$$
\begin{aligned}
\frac{dS_G}{dt} &= A_G(t) - bS_G - \beta S_G(I_G + I_R) - \mu_G S_G P \\
\frac{dI_G}{dt} &= \beta S_G(I_G + I_R) - bI_G - \gamma I_G - \mu_G I_G P \\
\frac{dR_G}{dt} &= \gamma I_G - bR_G - \mu_G R_G P \\
\frac{dS_R}{dt} &= A_R(t) - bS_R - \beta S_R(I_G + I_R) - \mu_R S_R P \\
\frac{dI_R}{dt} &= \beta S_R(I_G + I_R) - bI_R - \alpha I_R - \mu_R I_R P \\
\frac{dP}{dt} &= M(t)
\end{aligned}
\tag{1}
$$

where

$$
A_G(t) = \begin{cases} (a_G - q_G(H_G + c_R H_R))H_G & 0 \le t < 0.5 \\ 0 & 0.5 \le t < 1 \end{cases}
\tag{2}
$$

$$
M(t) = \begin{cases} (a_P - b_P)P & P \le P_{CC}^{1km} \\ 0 & P > P_{CC}^{1km} \end{cases}
\tag{3}
$$

The model framework that we use to represent the dynamics of red and grey squirrels and SQPV has been used in previous studies and yields results that are a good match with empirical data (see White et al., 2016; Jones et al., 2017). Here, $A_G(t)$ represents the periodic birth rate of grey squirrels which assumes births occur for only half of the year (between March and September each year, representing observed peak litter periods and periods with no breeding activity). The term for $A_R(t)$ is equivalent to $A_G(t)$ with the subscripts for R and G interchanged. Note, $H_R = S_R + I_R$ and $H_G = S_G + I_G + R_G$ represent the total populations for red and grey squirrels respectively. The natural rate of adult mortality $b = 0.9$ (Barkalow Jr. et al., 1970) is assumed to be the same for both red and grey squirrels but the rates of maximum reproduction differ with red squirrel birth rate $a_R = 3$ and grey squirrel birth rate $a_G = 3.4$ (Tompkins et al., 2003). The competitive effect of grey squirrels on red squirrels is denoted by $c_G = 1.65$, whilst that of red squirrels on grey squirrels is denoted by $c_R = 0.61$, highlighting the asymmetry in competitive outcome (Bryce et al., 2002). SQPV is transmitted (both within and between each squirrel species) in a density dependent manner with transmission coefficient $\beta = 0.83$ (see Section 2.3 below). Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ (Tompkins et al., 2003). The susceptibilities to crowding (q_R, q_G), which are specific to each grid-square, are set to ensure the average density over one year is equal to the estimated carrying capacity in each grid-square for that year, with the carrying capacity being defined using tree species information that is given in Table 2 (see also Section 2.2 below).

Pine marten are generalist omnivores whose density is also driven by resource limitation. Pine martens, like most mustelids, display intrasexual territoriality with resident animals of the same sex having non-overlapping, stable home ranges (O'Mahony, 2014; Birks, 2020). Consequently, we assume pine marten density, P, can reach its local maximum value in any 1 km grid-square, which we denote P_{CC}^{1km}, with the carrying capacity of that square being dependent solely on habitat (see Table 2). Thus, we assume that, as generalists, pine marten density is not dependent on local squirrel availability. For the pine marten birth rate, we assume an average lifespan of 5 years, with sexual maturity occurring after 2 years. We assume a 50/50 sex ratio with an average annual litter size (which ranges between 1 and 5 kits per litter) of 2 (Birks, 2020). This leads to 0.6 new-borns per year, per individual which translates into an annual birth rate of 0.47. We assume a 6-month breeding season and therefore the births occur at a constant rate $a_P = 0.94$ for 6 months and $a_P = 0$ for the rest of the year. For the death rate, we use the inverse of the average life span which yields a constant, annual death rate (due to all possible factors) of $b_P = 0.2$. The predation rate of pine marten on grey squirrels, μ_G, is defined such that a pine marten density of 0.36 km^{-2} will cause a 30% drop in grey squirrel density (a conservative estimate given empirical evidence that grey squirrels can be eradicated by pine marten at densities that are found in Scotland and Ireland (Twining et al., 2022b, 2020c; Sheehy et al., 2018)) which gives a value of $\mu_G = 1.5$. Given the uncertainty in this value, the predation rate will be altered, with a lower value of $\mu_G = 0.75$ and a high value of $\mu_G = 2.25$, to explore the impact of the predation rate on the squirrel dynamics. The average frequency of occurrence of red squirrels in pine marten diet (2.5% (Sheehy and Lawton, 2014), 3.7% (Twining et al., 2020c)) has been reported to be lower than that of grey squirrels (15.6% (Sheehy and Lawton, 2014; Twining et al., 2020c)) and therefore we set $\mu_R = 0.2\mu_G$ to reflect the higher occurrence of grey squirrels in pine marten diet. Whilst we recognise that frequency of occurrence does not directly

Table 1

Stochastic model events that govern the dynamics that occur within each 1 km grid-square. Here $R = \sum [rates]$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (6 months from the start of April to the end of September) and are set to zero otherwise. Disease transmission can occur from infected squirrels within the focal grid-square and also from the 8 neighbouring grid-cells due to daily movement within a core range of radius, $\theta = 0.15$ km. The predation and dispersal terms are shown for the class S_G only but is similar for all other classes of both red and grey squirrels. The star superscript indicates the relevant population abundance in the grid-square into which dispersal occurs. The parameters representing squirrel dispersal were estimated such that model results agree with observed data on the Island of Anglesey (Jones et al., 2017). The model assumes density dependent dispersal such that squirrel dispersal increases as density increases and the dispersal rate is $m = 2b$ when the patch density is equal to the carrying capacity. Therefore, individuals undergo long distance dispersal on average twice in their lifetime and relocate to a different patch up to a distance of 2 km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). In the stochastic model, pine marten abundance, P, and carrying capacity, P_{CC}, are defined on the 5 km grid square level. The pine marten abundance at the 5 km scale is distributed across the relevant 1 km grid squares according to the relative carrying capacity of each 1 km grid square to give the pine marten density at the 1 km grid square level, $P^{1\,km}$. The pine marten dispersal only concerns the long-distance dispersal events, with parameter $d_P = 0.05$. Dispersal due to space filling occurs when a pine marten birth event causes the population to exceed the carrying capacity. Pine marten that attempt to disperse into a grid square at or above its capacity are assumed to die. Further details of the model framework and the calculation of parameter values can be found in Jones et al. (2017).

Event	Population change	Probability of event
Birth of S_G	$S_G \rightarrow S_G + 1$	$[(a_G - q_G(H_G + c_R H_R))H_G]/R$
Natural death of S_G	$S_G \rightarrow S_G - 1$	$[bS_G]/R$
Infection of grey	$S_G \rightarrow S_G - 1, I_G \rightarrow I_G + 1$	$\left[\beta S_G \left((I_G + I_R) + \theta \sum_{Adjacent}(I_G + I_R) + \theta^2 \sum_{Corner}(I_G + I_R)\right)\right]/R$
Natural death of I_G	$I_G \rightarrow I_G - 1$	$[bI_G]/R$
Recovery of grey	$I_G \rightarrow I_G - 1, R_G \rightarrow R_G + 1$	$[\gamma I_G]/R$
Natural death of R_G	$R_G \rightarrow R_G - 1$	$[bR_G]/R$
Birth of S_R	$S_R \rightarrow S_R + 1$	$[(a_R - q_R(H_R + c_G H_G))H_R]/R$
Natural death of S_R	$S_R \rightarrow S_R - 1$	$[bS_R]/R$
Infection of red	$S_R \rightarrow S_R - 1, I_R \rightarrow I_R + 1$	$\left[\beta S_R \left((I_G + I_R) + \theta \sum_{Adjacent}(I_G + I_R) + \theta^2 \sum_{Corner}(I_G + I_R)\right)\right]/R$
Death of I_R	$I_R \rightarrow I_R - 1$	$[(b + \alpha)I_R]/R$
Dispersal of S_G	$S_G \rightarrow S_G - 1, S_G^* \rightarrow S_G^* + 1$	$\left[mS_G \left(\frac{(H_G + c_R H_R)^2}{(K_G)^2}\right)\right]/R$
Predation of S_G	$S_G \rightarrow S_G - 1$	$[\mu_G S_G P^{1\,km}]/R$
Birth of P	$P \rightarrow P + 1$ if $P < P_{CC}$ $P^* \rightarrow P^* + 1$ if $P \geq P_{CC}$ & $P^* < P_{CC}^*$ $P \rightarrow P, P^* \rightarrow P^*$ Otherwise	$[a_P P^{1\,km}]/R$
Natural death of P	$P \rightarrow P - 1$	$[b_P P^{1\,km}]/R$
Dispersal of P	$P \rightarrow P - 1, P^* \rightarrow P^* + 1$ if $P^* < P_{CC}^*$ $P \rightarrow P - 1, P^* \rightarrow P^*$ if $P^* \geq P_{CC}^*$	$[d_P P^{1\,km}]/R$

imply differences in predation rates, we believe that the dietary data, which is taken from a wide and representative sample that includes both allopatric and sympatric populations of red and grey squirrels at various densities, is a suitable proxy for the difference in predation given the lack of quantitative data on the functional response of the pine marten to these two prey species. Predation is assumed to be unaffected by squirrel infection status. All parameter values assume an annual time-scale.

To generate the stochastic model (Table 1), the rates in the deterministic model are converted into probabilities of events that account for changes in individual grid-square level abundance (Renshaw, 1993). We also add squirrel and pine marten dispersal in the stochastic model to represent movement between grid-squares. For both squirrel species the model assumes density-dependent dispersal, such that squirrel dispersal increases as density increases (see Jones et al., 2016 and Table 1 legend for more details). Pine marten dispersal occurs on a 5 km by 5 km gridded scale which has a defined habitat dependent carrying capacity, P_{CC}, that is the sum of the carrying capacities of the 25 1 km grid squares that are contained within the 5 km region (see Section 2.2). When the pine marten population exceeds P_{CC} the excess individuals are assumed to disperse into one of the 8 neighbouring 5 km by 5 km regions. If the pine marten density in the chosen destination region is

at or above P_{CC}, the dispersing pine marten are assumed to die, and are thus removed. This ensures pine marten do not disperse continuously when densities are high across the landscape. In addition to local dispersal, we assume rare long distance dispersal, that can occur at any time, with dispersal rate $d_P = 0.05$, which was chosen to fit the pine marten expansion rate that has been observed in Northern Ireland (J. Twining, unpub. data; see also Twining et al., 2022b). During the long-range dispersal event, pine marten can disperse to any grid-square, chosen at random, within a 50 km radius. This reflects observations in which tracked individuals who were previously released into Mid Wales have been recorded over 103 km away from the point of release after approximately 6 months (McNicol et al., 2020). In the model we assume all grid squares outside the study area have zero carrying capacity. Consequently, neither squirrel nor pine marten can disperse into these grid squares. In the model, Anglesey and mainland Wales are considered as different gridded maps, with the transition between these maps being governed by a single grid square that is designated as the Britannia bridge, which represents the primary expansion route for grey squirrels onto Anglesey. Movement between Anglesey and the mainland requires squirrels/martens to disperse via the grid square designated as the Britannia bridge. This ensures that the 5 km by 5 km pine marten regions do not overlap both Anglesey and the mainland

Table 2

Red and grey squirrel, and pine marten carrying capacity values for different habitat types. Red and grey squirrel carrying capacity values for broadleaf trees are from Jones et al. (2016). Red squirrel carrying capacity for conifer is from Jones et al. (2016), whereas the grey squirrel carrying capacity value for conifer is based on that in Slade et al. (2020). Urban carrying capacity for red and grey squirrels is equal to the capacity used for gardens in Jones et al. (2016). Scrub carrying capacities for red and grey squirrels is based on the Secondary species values in Slade et al. (2020). Mixed mainly broadleaf is assumed to be 65% broadleaf and 35% conifer, whereas mixed mainly conifer is assumed to be 65% conifer and 35% broadleaf. Pine marten carrying capacity values are authors estimates.

	Red CC (ha^{-1})	Grey CC (ha^{-1})	Marten CC (km^{-2})
Broadleaf	0.65	2.50	3.49
Conifer	0.35	0.15	1.15
Mixed mainly broadleaf	0.55	1.68	2.67
Mixed mainly conifer	0.46	0.97	1.97
Scrub	0.06	0.06	1.15
Urban	0.32	0.95	0.05
Britannia bridge	0.32	0.95	0.05
Open land	0.00	0.00	0.05

2.2. Carrying capacities

To estimate plausible carrying capacities for each grid-square we use the National Forest Inventory Woodland Wales 2018 dataset, which includes information on whether the primary tree species in a given area is broadleaf or conifer, the Urban Wales 2015 dataset, which outlines the urban habitat, as well as a Major Rivers dataset, which locates the main rivers in Wales, to create a map detailing the proportion of each habitat type in a 1 km by 1 km grid-square. This information can be used, in conjunction with fixed estimates of squirrel and pine marten density values for broadleaf and conifer habitat (Table 2), to generate carrying capacity estimates for each species for each 1 km grid-square in the model (see Figure S1 in the Supp. Info. for carrying capacity maps). We use constant estimates of pine marten and squirrel carrying capacity, thereby ignoring factors such as seasonal variation and seed crop cycles that are inherent in the real system. Croft et al. (2021) (Croft et al., 2021) suggest this is appropriate for mixed species woodland where asynchrony in tree species masting maintains a more stable food resource, and consequently reduces amplitude in squirrel density variation, than would be expected in woodland with lower tree diversity. This also allows us to compare different model scenarios without the added complication that variation in resources would impose on the dynamics. The grid-square level pine marten carrying capacity values are used to create the 5 km by 5 km carrying capacity values that in-turn are used to trigger pine marten dispersal. The broadleaf, conifer and urban squirrel capacity values are the medium values from the Anglesey study conducted by Jones et al. (2016). However, in line with recent studies for Scotland (Slade et al., 2020; Twining et al., 2020c), we assume red squirrels have a competitive advantage over grey squirrels in purely coniferous habitat. Mixed mainly broadleaf carrying capacity consists of 65% broadleaf capacity + 35% conifer carrying capacity, whilst mixed mainly conifer is 65% conifer capacity + 35% broadleaf capacity. The carrying capacity values for scrub have been set at a low value to indicate that, whilst neither squirrels nor pine marten would reside in this habitat, they will utilise it and move through it to reach other habitats (Jones et al., 2016; Caryl et al., 2012; Twining et al., 2020b). Open land is any region that does not have a named feature. The small pine marten carrying capacity associated with open land indicates that, whilst pine marten cannot reside in these regions, they can cross these areas and reach available habitat beyond them. The Britannia bridge is the only available dispersal route between the island of Anglesey and mainland Wales. This grid-square has been given the same carrying capacity as the urban regions to allow free movement of squirrels and pine marten. All carrying capacity values can be found in Table 2.

2.3. Initial conditions

Currently, red squirrels are resident in an upland conifer plantation in central North Wales and on the island of Anglesey, with some red squirrels dispersing from Anglesey across the Britannia bridge into the region surrounding the city of Bangor (see Fig. 1). Grey squirrels are established across the entirety of North Wales except the island of Anglesey. Given the absence of detailed density data, we assumed grey squirrels are not present in the conifer plantation. Thus, the model results will simulate the replacement of red squirrels due to dispersal from nearby known grey squirrel populations. The squirrel initial conditions in the model therefore assume that red squirrels are at their carrying capacity in the regions where they are sole residents, red and grey squirrels are at half their carrying capacity in the area around the city of Bangor, where they both reside, and grey squirrels are at their carrying capacity in all other regions of North Wales (as indicated in Figure S2 in the Supp. Info.). In the model we consider two scenarios for pine marten initial conditions. The first assumes that pine marten resident in Mid Wales migrate north, with the initial population located in suitable habitat in Mid Wales (which is the southern edge of our study region), set at a quarter of the carrying capacity (Figure S3(a)). The second initial condition assumes the potential release of 20 pine marten (10 pine marten released in consecutive years at the start of the model simulation) into the area surrounding the city of Bangor (Figure S3(c)), in addition to dispersal from Mid Wales. The release site at Bangor is chosen as there have been recent releases of pine marten into the area surrounding the city with the aim of conserving red squirrels on the island of Anglesey. Results where pine marten have been released into the region surrounding Bangor only (Figure S3(b)), as well as a long-term scenario whereby pine marten have colonised the entirety of Wales (Figure S3(d)) are included in the supplementary information.

To generate the SQPV initial conditions, the model was simulated for 10 years with only grey squirrels present. The value of $\beta = 0.83$ was used as this leads to a seroprevalence of 74% in grey squirrels (Schuchert et al., 2014; Sainsbury et al., 2000) in a homogeneous population of 80 individuals in a 1 km by 1 km grid-square, which is representative of grey squirrel density (per km^2) in regions in North Wales where SQPV has been reported (Schuchert et al., 2014; Sainsbury et al., 2000). The initial condition of SQPV (shown in Figure S4 in the Supp. Info.) indicates that the model predicts variability in the prevalence of SQPV, which is strongly linked to grey squirrel density across North Wales.

2.4. Model realisations

Each model realisation follows a Gillespie algorithm (Gillespie, 1977). Here, the time between events is an exponentially distributed random variable that can be determined as $T_{event} = -\ln(\sigma)/R$ where σ is a random number drawn from a uniform distribution between zero and one and R is the sum of the event rates, as defined in Table 1 (see also Renshaw, 1993). The event (see Table 1) which occurs at each time step is also chosen at random, based on the relative event rates,
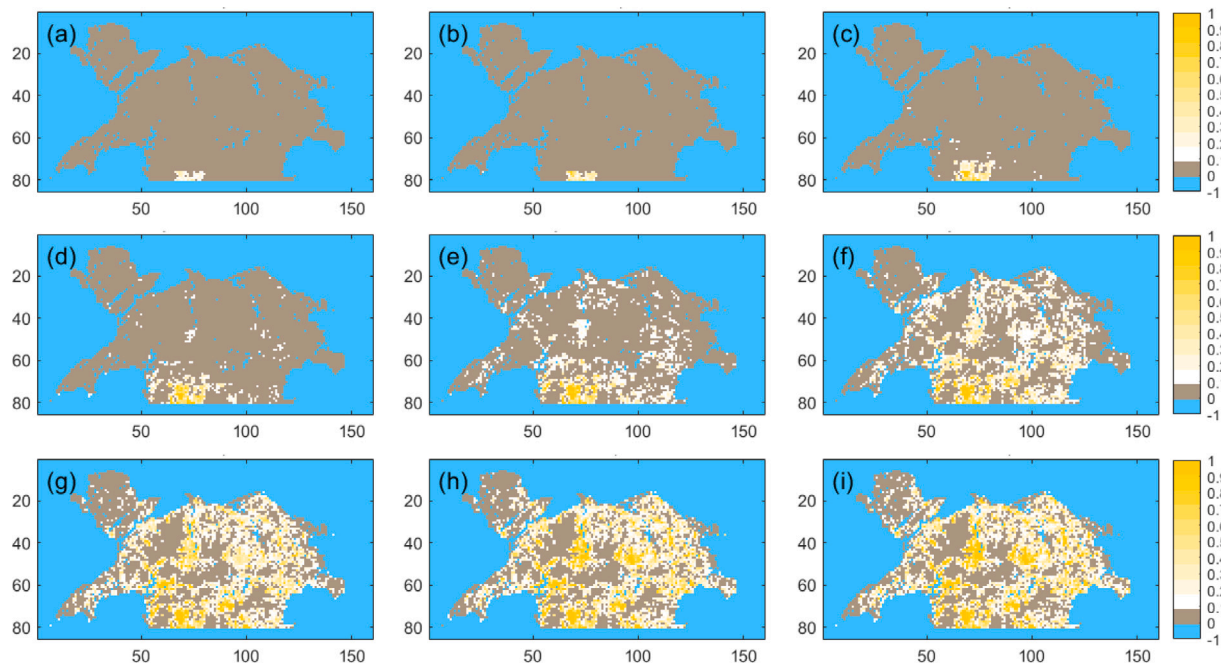
Fig. 2. Average pine marten density (km⁻²), as predicted by the stochastic model, for initial conditions of pine marten at one quarter carrying capacity in Mid Wales only (see Figure S3(a)). Here (a) shows the initial condition, (b) the pine marten density after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

with changes in density and the associated probabilities updated after each event. We run each realisation for 40 (model) years and run 10 realisations of the stochastic model for each scenario that we test.

3. Results

3.1. Pine marten migration from mid Wales

There is little expansion in pine marten range during the first 10 years of simulation as it takes time for pine marten abundance to increase to levels that trigger local dispersal (Fig. 2). Thereafter, local and rare long-distance dispersal leads to pine marten range expansion into North Wales, and subsequent increases in density, within 30 years. Such wide-scale and rapid expansion matches real-world scenarios and has, for example, been observed in Northern Ireland (Twining et al., 2022b).

As shown in Fig. 2, the model suggests that pine marten expansion into North Wales will take time, thus allowing grey squirrels the opportunity to out-compete and replace red squirrels in north-west Wales, which could lead to the re-colonisation of the island of Anglesey (as would be the case if grey squirrel control efforts were stopped (Jones et al., 2016), Fig. 3). Pine martens fail to establish at high density on the island Anglesey by the end of the 40 year model simulation, likely due to a lack of suitable habitat on the island as well as a lack of connectivity between the island and the mainland. Consequently, grey squirrels continue to expand and replace red squirrels on the island. A comparison between Fig. 3 and results showing red and grey squirrel occupancy in the absence of pine marten (Figure S5 in the Supp. Info.) indicate that red squirrel replacement on the island of Anglesey is predicted to be reduced when pine marten are present. The presence of pine marten leads to the reduction of grey squirrel density (Fig. 4), particularly from year 30 of the simulation onwards, which coincides with the increase in pine marten density that occurs following dispersal (Fig. 2). The suppression of grey squirrel density due to pine marten presence allows red squirrels resident in large conifer plantations to expand their range into neighbouring forests, where they previously were excluded. This occurs for all three rates of pine marten predation, with the expansion of the red occupied region

increasing with increasing predation rate. The higher predation rates also lead to a removal of grey squirrels from regions where there is not a concurrent increase in red squirrel occupancy due to the lack of adjacent red squirrel populations (Fig. 4(b) & (c)).

3.2. Pine marten reinforcement in North Wales and migration from Mid Wales

The combined effect of pine marten 'release' into both North and Mid Wales is that pine marten range expansion is predicted to be more rapid as the time frame for the northern populations of pine marten to reach their carrying capacity is reduced (Fig. 5). In particular, the range expansion of pine marten across the north coast, and south from these populations, is now pronounced (compare Figs. 2(e) and 5(e)). Where pine marten establish and recover to sufficient density, they reduce grey squirrel density (Fig. 7). Pine marten populations in the north-west of Wales, and later on the island of Anglesey, reduce the impact of grey squirrel expansion onto Anglesey. Therefore, the model system predicts that the pine marten release into North Wales, as opposed to the migrating pine marten from Mid Wales, is potentially key to safeguarding the red squirrel population in North Wales and on the island of Anglesey (especially for medium and high predation rates, Fig. 6(b) & (c)). The release of pine marten into North Wales is also predicted to support an increase in red squirrel expansion from the resident population in the large conifer plantation, and at high predations rates to facilitate the establishment of red squirrel populations into regions where they are excluded when pine marten migrate from Mid Wales alone.

3.3. The impact of pine marten on SQPV

SQPV is currently endemic in the grey squirrel populations of North Wales. Fig. 8 outlines the predicted impact of pine marten predation on SQPV, for the scenario where pine marten have been introduced into North Wales as well as migrated from Mid Wales. As pine marten expand their range and increase in density (Fig. 5), predation of grey squirrels reduces the grey squirrel density (Fig. 7) to levels that cannot support SQPV (Fig. 8). Higher predation rates lead to greater, more
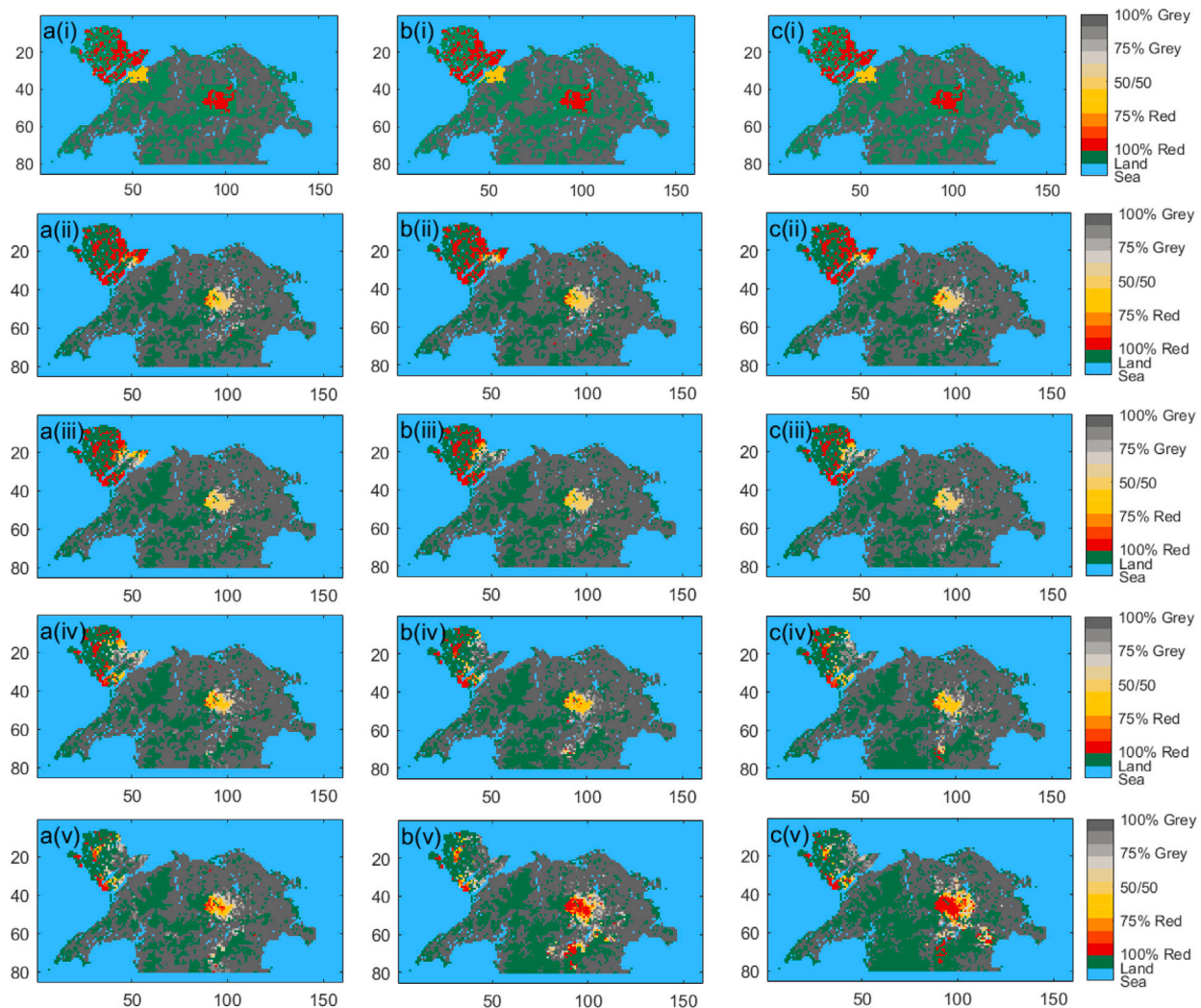
Fig. 3. Red and grey squirrel occupancy results as predicted by the stochastic model, for initial conditions of pine marten at one quarter carrying capacity in Mid Wales only (see Figure S3(a)). Here (a) shows the results when the grey squirrel predation rate $\mu_G = 0.75$, (b) shows the results when the grey squirrel predation rate $\mu_G = 1.5$, and (c) shows the results when the grey squirrel predation rate $\mu_G = 2.25$. Image (i) shows the initial condition, (ii) shows the results after 10 years, (iii) 20 years, (iv) 30 years, and (v) 40 years. Occupancy is determined by the number of simulations that have squirrel presence at a particular point in time. Thus, 70% red occupancy indicates that 7 out of the 10 simulations had red squirrel presence in that particular 1 km by 1 km grid-square, at the respective time point.

rapid, reductions in SQPV prevalence. The model predicts that SQPV will be eradicated from north-west Wales, and from the island of Anglesey, after 10 years. After 20 years of model simulation, there emerges two distinct regions where SQPV remains endemic — one region stretches from the north coast to the west coast whilst the other region is in the north-east of North Wales (adjacent to the border between England and Wales). SQPV is largely absent from the conifer plantation by year 20 in the model and, by year 30 of the model simulation, the majority of North Wales is predicted to be SQPV free. SQPV is largely eradicated under all three predation rate scenarios by year 40 of the simulation. Notice that extinction of SQPV does not require the extinction of grey squirrels (compare Figs. 7 and 8), but instead requires that grey squirrel density is reduced below a threshold value. Pine marten predation could therefore have an additional ecosystem benefit in terms of disease management, even when predation does not lead to species eradication.

3.4. Alternative model scenarios

We undertook a model scenario in which pine marten were released into North Wales only (with no expansion from Mid Wales). The results are shown in the Supplementary Information (Figures S6 & S7). The

results are similar to those in Fig. 6, although the potential red squirrel range expansion into Mid Wales is more rapid when pine marten dispersal also occurred from Mid Wales. Nevertheless, this indicates that the release of pine marten into North Wales could be key to safeguarding the red squirrel population on the island of Anglesey, and to supporting the range expansion of red squirrels across North Wales. We also tested different pine marten release strategies in North Wales (our default of 10 individuals in two consecutive years, or 20 individuals in one year, or 5 individuals in four consecutive years) but this had a minimal impact on the results.

We also considered a scenario where pine marten have been introduced, at their carrying capacity, into all suitable regions of North Wales, to simulate the long-term impact of pine marten on red and grey squirrel interactions (Figures S8, S9 & S10). At the low predation rate of $\mu_G = 0.75$, the impact of pine marten predation is predicted to be sufficient to safeguard the red squirrel population resident in the conifer plantation and support moderate expansion of the red squirrel range to the south of the plantation. However, low levels of predation cannot prevent the expansion of grey squirrels onto the island of Anglesey. At medium and high predation rates, the higher frequency of predation by pine marten on grey squirrels protects red squirrels on Anglesey and the model suggests that the majority of central North Wales could be viable
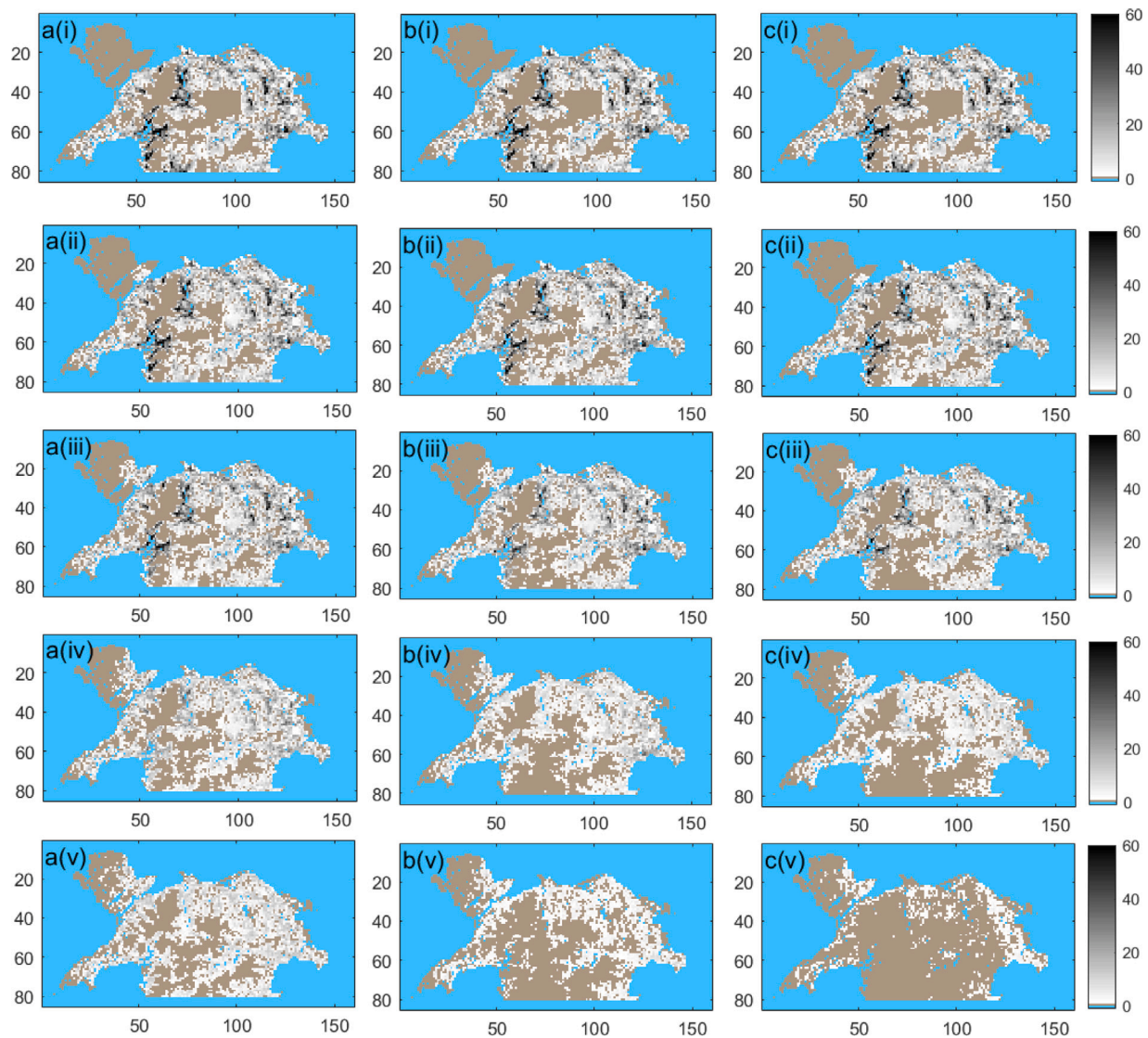
Fig. 4. Average grey squirrel density as predicted by the stochastic model, for initial conditions of pine marten at one quarter carrying capacity in Mid Wales only (see Figure S3(a)). Here (a) shows the results with predation parameter $\mu_G = 0.75$, (b) shows the results with predation parameter $\mu_G = 1.50$, and (c) shows the results with predation parameter $\mu_G = 2.25$,. Image (i) shows the initial conditions, (ii) the results after 10 years, (iii) 20 years, (iv) 30 years and (v) 40 years.

for red squirrel occupation. Model results indicate that grey squirrels will still dominate the border region between England and Wales (the eastern border of our study region), as well as the western peninsula (Llŷn peninsula), due to the fragmented habitat which provides limited access routes into the peninsula from the rest of North Wales.

The results presented here are averages of the ten model realisations that were generated using the stochastic model. The results should not be viewed as definitive predictions of pine marten and squirrel population dynamics. In particular, the initial pine marten dispersal can vary due to the assumed random nature of the long-distance dispersal. This variability results in different initial patterns of pine marten dispersal in different model realisations, and these variations can have a greater or lesser impact on squirrel interactions, dependent on the distance between pine marten and squirrel populations. This can subsequently impact the timing of certain squirrel events, such as the transition onto Anglesey by grey squirrels. Similarly, given the competitive interactions that occur at the boundary between red and grey squirrel populations, the variation at these sites is naturally higher than in single species regions where competition between species does not occur. Nevertheless, in the long-term pine marten become established across the entirety of the study region in all realisations and so their impact on squirrels becomes consistent.

4. Discussion

In this study we provide theoretical evidence, through empirically devised mathematical modelling, of the impacts of the recovery of a native predator on the densities of two competitively linked prey species, along with the prevalence of a virulent pathogen that mediates the replacement of the native species by the invasive competitor. In the absence of pine marten, SQPV led to the loss of around 80% of the red squirrel mainland population in an area of North West Wales in 2020/21 (Shuttleworth et al., 2022). However, the model findings indicate that the recovery of the pine marten could result in the eradication of SQPV from the landscape, thus reducing the threat of replacement of red squirrels by the invasive grey squirrel. We demonstrate a viable mechanism for this, which occurs through the predation and regulation of the host reservoir below the threshold for pathogen persistence. Results from the spatially explicit mathematical model developed here indicate that pine marten recovery will benefit native red squirrels in Wales, reversing the typical outcome of disease mediated competition between the two prey species. The model indicates that empirically supported higher predation by the native predator of grey squirrels, compared to red squirrels, could safeguard current red squirrel populations and allow red squirrels to expand their range in North Wales, as
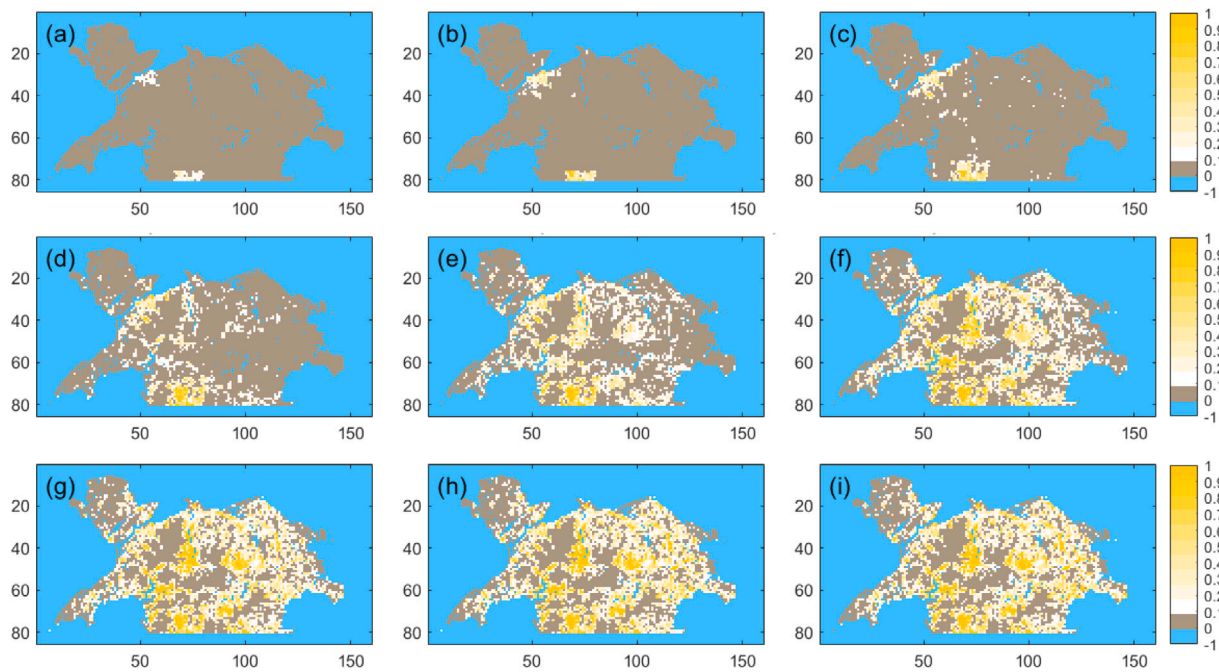
Fig. 5. Average pine marten range expansion, as predicted by the stochastic model, when they are released into the Bangor region as two groups of 10 individuals in consecutive years, and into Mid Wales at a quarter of the carrying capacity (see Figure S3(c)). Here (a) shows the initial condition, (b) the pine marten expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

has been observed in both Scotland and Ireland. Thus, the model results demonstrate that the potential impacts of native predator recovery on native prey are multi-faceted, occurring through several linked indirect pathways; through the predation of an invasive competitor and the subsequent suppression, and extirpation, of a virulent pathogen that is a key factor in species replacement.

In consensus with real-world empirical data from other ecosystems (Twining et al., 2022b, 2020c; Sheehy et al., 2018), this modelling study indicates that the population recovery of pine marten can lead to reductions in grey squirrel density, or extirpation of grey squirrels, and the recovery and range expansion of red squirrels on a landscape scale. The key mechanism that underpins this result is that pine marten prey upon grey squirrels at a higher frequency than red squirrels, which has been observed in the field (Sheehy and Lawton, 2014; Twining et al., 2020c). Prey regulation and persistence is sensitive to the force of predation, which can occur at the individual level through a predator's functional response (Holling, 1959), or at the population level through predator aggregation (Solomon, 1949). We see this in our model with the combination of the predation coefficient and predator density driving grey squirrel extirpation. While the predation coefficient is difficult to estimate, observations of the extirpation of grey squirrels following pine marten establishment (Twining et al., 2022b, 2020c; Sheehy et al., 2018) offers support that the model results shown for medium and high predation rates are reflective of the real system. The model also suggests that grey squirrel extirpation could occur more rapidly in regions where pine marten recovery is adjacent to source populations of red squirrels. For example, grey extirpation is pronounced in large areas of coniferous forest where predation combines with inter-specific competition from red squirrels (Roberts and Heesterbeek, 2021; Slade et al., 2022). In general, the model results concur with findings from field and observational studies in Northern Ireland and Scotland that indicate that pine marten can reverse the typical competitive outcome between red and greys squirrels in forest habitats (Twining et al., 2022b, 2020c; Sheehy et al., 2018). We acknowledge that model studies are abstractions of the real systems and should not be used as definitive predictive tools, particularly due to the difficulty inherent in assigning constant values to variable quantities such as predation

rates and carrying capacities. However, model studies can be used to understand the qualitative dynamics, elucidate critical mechanisms, and predict potential outcomes of complex species interactions. The model study here suggests that the range expansion and increase in density of pine marten in the UK could have significant benefits for the conservation of red squirrels that are threatened by grey squirrels, both through lowering the density of the invasive competitor and reducing the prevalence of disease (SQPV in this example).

Pine marten are generalist predators and so will prey upon both red and grey squirrels (Twining et al., 2020c; Halliwell, 1997) (as well as other native species), and therefore pine marten recovery could threaten red squirrel viability where populations are fragmented or in habitats such as commercial conifer plantations that support low abundance of alternate prey species (Twining et al., 2022b). Our model study assumes pine marten predation rates that are constant across all habitat types. Model results suggest that, for pine marten densities that are in line with those from field observations from Great Britain and Ireland (Twining et al., 2022b, 2020c; Sheehy et al., 2018), increasing levels of predation (in the absence of grey squirrels) will reduce red squirrel population density. However, the model results suggest red squirrels can persist in the presence of pine marten predation in all habitat types, albeit at low densities in conifer dominated habitat (including when pine marten have recovered to carrying capacity levels, see Figure S8). Red squirrels have been observed to persist at significantly lower densities where they co-occur with pine marten in Scotland (Halliwell, 1997). Additionally, empirical evidence from landscape scale monitoring and multi-species occupancy modelling demonstrated a positive influence of pine marten recovery on red squirrel occurrence at a landscape scale. This is especially evident in broadleaf habitats, where pine marten allow red squirrels to recover following the local extirpation of grey squirrels (Twining et al., 2022b, 2020c), even though pine martens reduce the occurrence of red squirrels in areas dominated by conifer plantations in Northern Ireland (Twining et al., 2022b). These differences may highlight an unrealistic assumption in our model, with habitat mediation of the interactions between native predator and prey being likely linked to the seasonal abundance or lack of alternate resources, resulting in potentially increased predation pressure at certain times
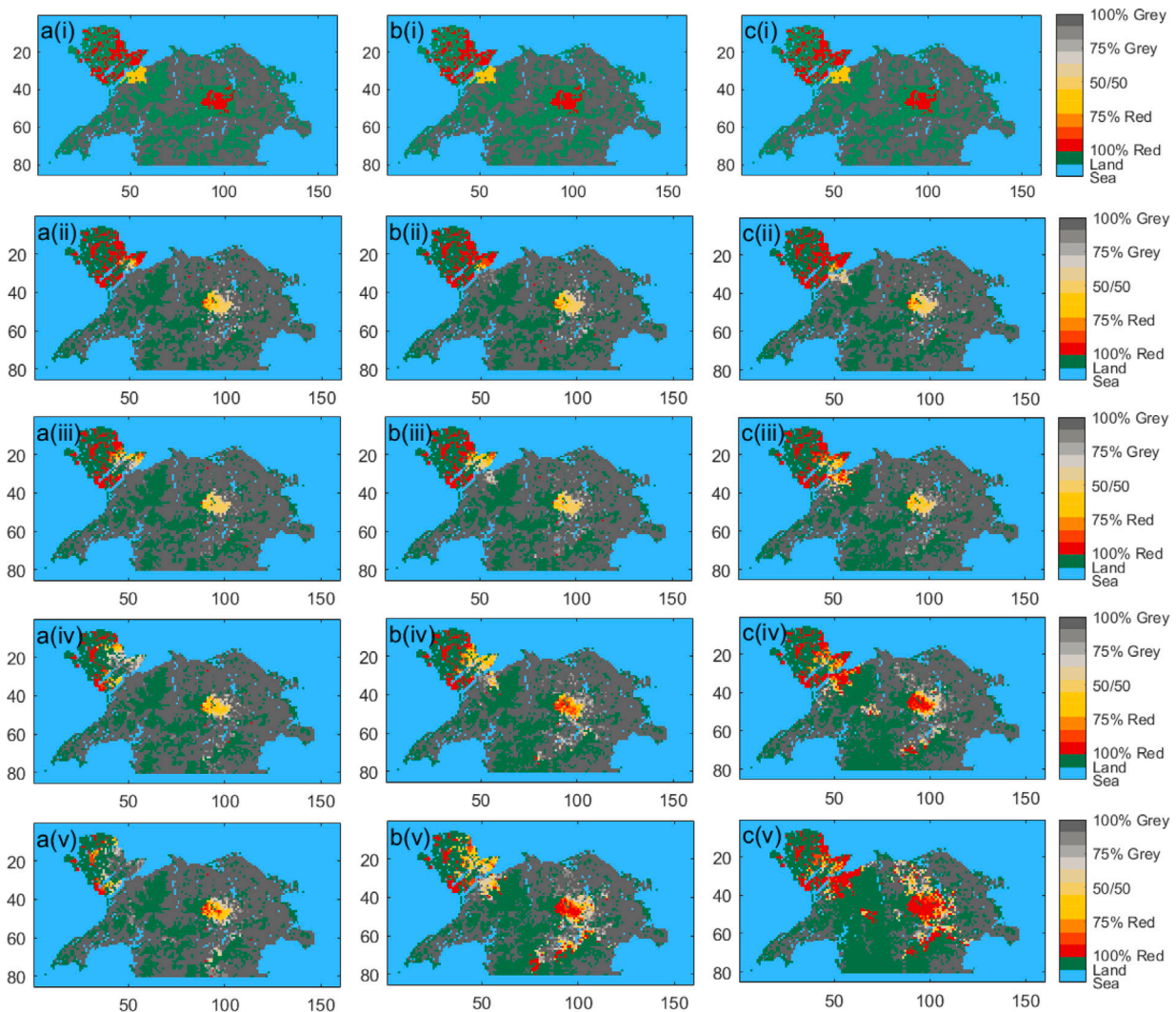
Fig. 6. Red and grey squirrel occupancy results, as predicted by the stochastic model, when pine marten are introduced into the Bangor region, as two groups of 10 individuals in consecutive years, and into Mid Wales at a quarter of the carrying capacity (see Figure S3(c)). Here (a) shows the results with predation parameter $\mu_G = 0.75$, (b) shows the results with predation parameter $\mu_G = 1.50$, and (c) shows the results with predation parameter $\mu_G = 2.25$. Image (i) shows the initial conditions, (ii) the results after 10 years, (iii) 20 years, (iv) 30 years and (v) 40 years. Occupancy is determined by the number of simulations that have squirrel presence at a particular point in time. Thus, 70% red occupancy indicates that 7 out of the 10 simulations had red squirrel presence in that particular 1 km by 1 km grid-square, at the respective time point.

in some habitats (Twining et al., 2022b). The threat to red squirrels in conifer plantations may be reduced in Great Britain, where the presence of numerically dominant field voles (*Microtus agrestis*) results in distinct dietary differences between Ireland and Great Britain. Field voles, which are often a key prey item in diet studies in Great Britain (e.g. Caryl et al., 2012), undergo inter-annual cycles in abundance. Whilst pine marten diet during nadirs in these cycles appear relatively similar (Caryl et al., 2012; Twining et al., 2019), theoretical modelling suggests that peaks in vole population cycles may provide temporal refuges for both squirrel species, thus mediating the impacts of pine marten recovery on both species (Slade et al., 2022). Whilst these hypotheses remains empirically unvalidated, we can draw inference from the better studied invasive species. Despite the presence of field voles in Scotland and their potential to diffuse the population impacts of pine marten recovery on both prey species (Slade et al., 2022), a quantitative investigation in Scotland has demonstrated that even low-density marten populations depress the occurrence of invasive grey squirrels, with local extirpation of grey squirrels predicted (Sheehy et al., 2018). The ubiquity of the impacts of pine marten recovery on grey squirrels across both systems, both in the presence and absence of field voles (Scotland and Ireland respectively), raises expectations for similarity in the impacts on red squirrels between the two systems.

Given the potential risk to red squirrel viability in conifer dominated habitats, there is a need for more research on the relative impacts of pine martens on red squirrels in different contexts and ecological communities.

Prey species may harbour infectious pathogens which can persist at endemic levels if, for instance, prey density exceeds a threshold that can support the pathogen (Lloyd-Smith et al., 2005). The population recovery of predators can result in the regulation of prey populations when predation occurs across a range of observed prey densities (Turchin, 1995). We considered a variety of different, sustained, predation rates on prey/host populations and the threshold for disease persistence, and we demonstrate the capacity for native predators to have significant impacts on pathogen prevalence and persistence in certain scenarios (Moore et al., 2010). In our study system grey squirrels are a reservoir for SQPV that has little effect on grey squirrel health but leads to a deleterious infection in red squirrels and has been demonstrated as a key driver of species replacement in Great Britain and Ireland (Tompkins et al., 2002). Our model results indicate that pine marten predation could be sufficient to reduce grey squirrel density to levels that cannot support endemic SQPV. The reduced risk of transmission of SQPV from grey squirrels to neighbouring, re-establishing, red squirrels would prevent the potential crash of local red squirrel populations due to
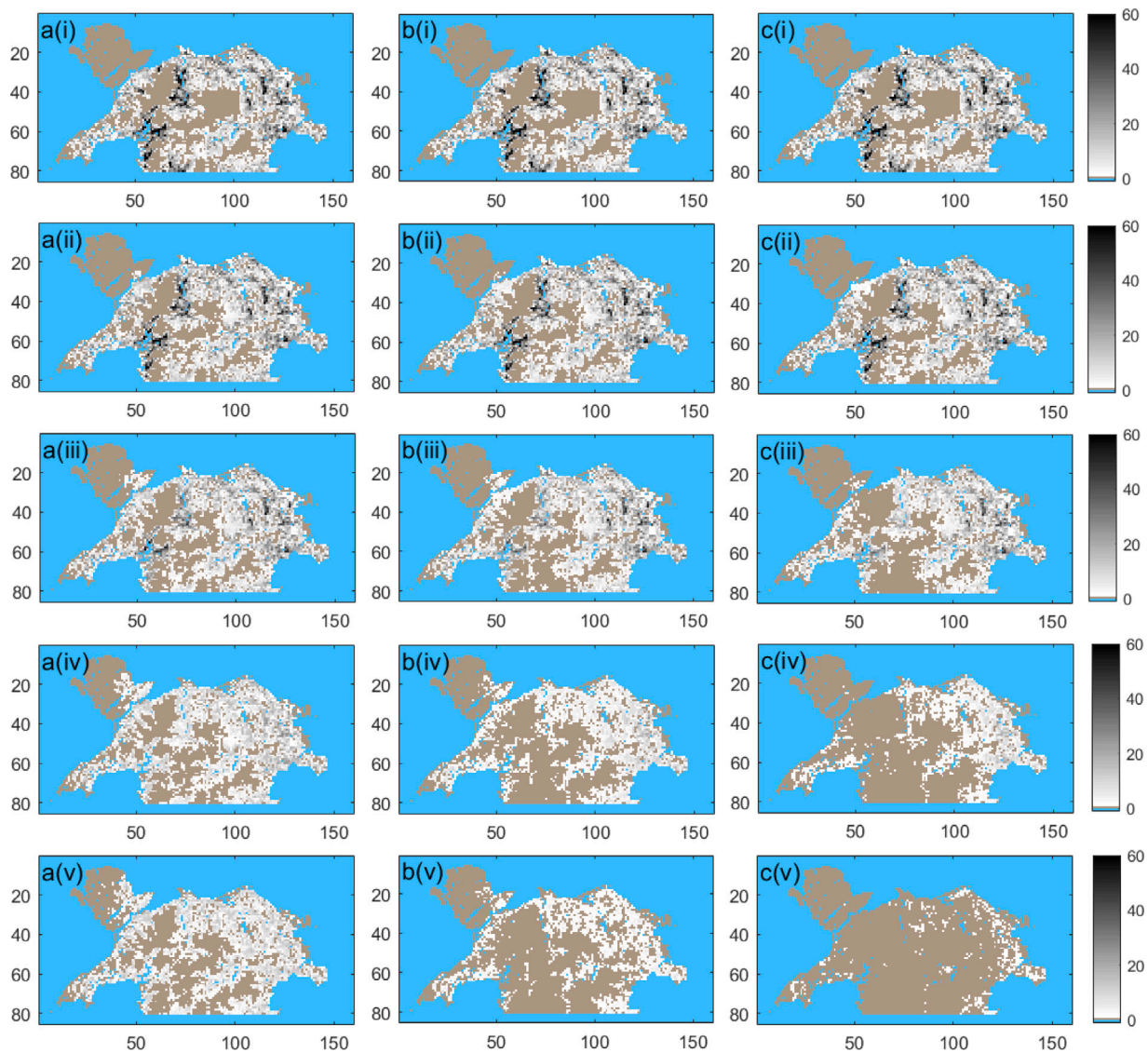
Fig. 7. Average grey squirrel density, as predicted by the stochastic model, with infection transmission coefficient $\beta = 0.83$ and pine marten being introduced in 2 groups of 10 into the Bangor region and at a quarter of their carrying capacity into Mid Wales (see Figure S3(c)). Here (a) shows the results with predation parameter $\mu_G = 0.75$, (b) shows the results with predation parameter $\mu_G = 1.50$, and (c) shows the results with predation parameter $\mu_G = 2.25$,. Image (i) shows the initial conditions, (ii) the results after 10 years, (iii) 20 years, (iv) 30 years and (v) 40 years.

a SQPV epidemic outbreak (Chantrey et al., 2014; White and Lurz, 2014; Shuttleworth et al., 2022). The model results therefore provide a key example of how the recovery and re-establishment of native predators can have an impact on both invasive species and pathogen persistence. This provides additional support to recent work suggesting that increased predator diversity and density can reduce parasite transmission, thereby highlighting the importance of predator communities for disease dynamics and ecosystem stability (Rohr et al., 2015).

Although theory typically envisages predators suppressing disease as we predict here, there is also striking evidence of predators increasing the chance of a disease outbreak (Strauss et al., 2016). A key mechanism in determining potential predator effects on disease has been suggested to be the coupling of predator–prey population dynamics and the selectivity of predation (Duffy and Hall, 2008). If pathogen infected individuals are more vulnerable to predation (Dick et al., 2010; Tanner et al., 2019), predators may dramatically reduce disease in host populations. However, the opposite can also be true. If susceptible individuals are more prone to predation, then predation could increase disease prevalence in a population (Hatcher and Dunn, 2011). In the absence of empirical data on the selectivity of predation

in the model system, we assumed equal predation of infected and susceptible individuals and, with this estimate for the selectivity of predation, predators still suppress the infection. Thus, we observe that the potential of predators to positively or negatively impact disease are not equal, and we demonstrate that it is more likely that predators will reduce disease, as only in special contexts, e.g. when infected prey become much less susceptible to predation, which is likely a rare occurrence, that predation will have the potential to increase disease prevalence.

Our model results predict that it will take approximately 5–10 years for pine marten density to increase to levels that are sufficient to provide a source for local dispersal, with limited long distance dispersal occurring during this period. Thereafter, local and rare long-range dispersal of pine marten provides new source populations which leads to further, more rapid, range expansion such that North Wales is largely occupied by pine marten after approximately 25–30 years. This is likely to be a conservative estimate with recolonisation of all 32 counties in Ireland, without additional reinforcement, occurring within a shorter time frame (Carey et al., 2007; Lawton et al., 2015, 2020; Twining et al., 2022a). When the 'natural' expansion of pine marten from populations in Mid Wales (in the south of our study region) is supplemented
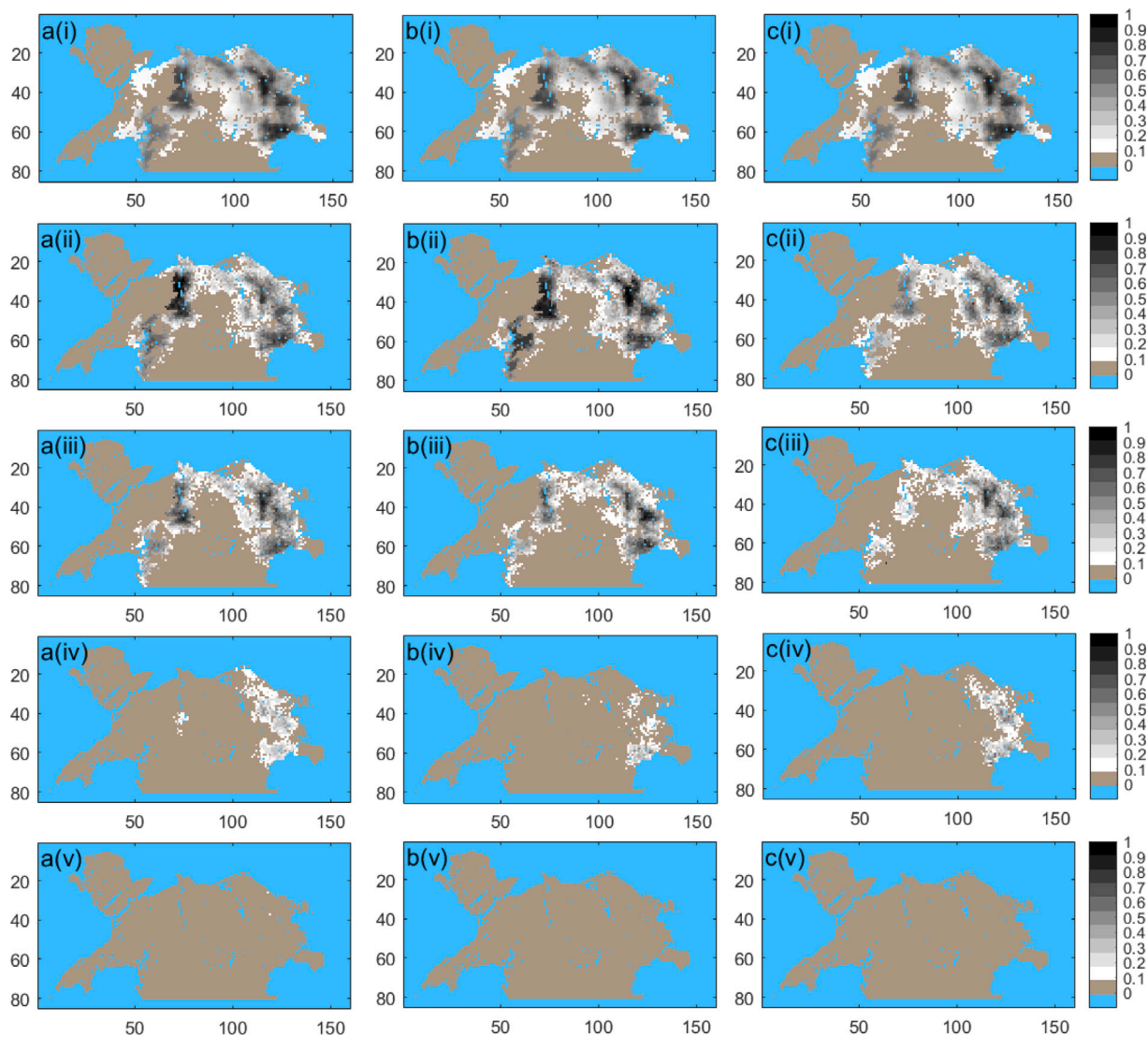
Fig. 8. Average changes in the prevalence of squirrelpox in grey squirrels over time, as predicted by the stochastic model, with pine marten being introduced into the Bangor region in two sets of 10 individuals and into Mid Wales at a quarter of the carrying capacity (see Figure S3(c)). Here (a) shows the results when the predation rate is $\mu_G = 0.75$, (b) the results when the predation rate is $\mu_G = 1.50$ and (c) the results when the predation rate is $\mu_G = 2.25$. Image (i) shows the initial condition, (ii) shows the results after 10 years of simulation, (iii) 20 years, (iv) 30 years, and (v) 40 years.

by the targeted release of pine marten into North Wales the range expansion of pine marten is more rapid. Our model results therefore lend support to the use of translocated and captive-bred founders to increase the rate of recovery and dispersal (and genetic variability) of native predator populations that can form part of the conservation approach to reduce the impact of invasive species (Bamber et al., 2020).

Our model findings provide key information, such as the creation of a scenario framework and the identification of uncertainties, on the potential impact of pine marten re-introductions in North Wales. The findings have been used to support pine marten translocations in North Wales, which will contribute to the delivery of the regional squirrel management strategy. Pine marten recovery has the potential to contribute to grey squirrel decline. Assuming, for example, that changes in grey squirrel behaviour, or some adaptive response to predator presence, does not act to reduce the proportionally higher predation of grey squirrels compared to red squirrels, then pine marten recovery potentially offers a long-term sustainable mechanism that could reverse the fortunes of the red squirrel. It is recognised that monitoring, and where necessary coordinated grey squirrel control (i.e., via trapping or shooting), must continue. The parallel detection and removal of animals that disperse onto the island of Anglesey will also need to be

maintained in these periods (Shuttleworth et al., 2020). Progressively therefore, such interventions may become even more targeted, e.g., at localised grey squirrel populations inhabiting key habitats where pine marten density may be low, or their presence ephemeral or infrequent (such as urban parkland, for example). This type of integrated conservation management offers a dynamic and cost effective landscape scale approach to predator-mediated control of invasive species (Dunn and Marzano, 2015).

5. Conclusion

In this study we demonstrate the potential role native predators may have in reversing the replacement of a threatened native prey species by an established invasive species. Our model highlights a potential mechanism: regulation of the invasive prey species through sustained predation over a range of densities, and the resultant extirpation of a viral pathogen which otherwise catalyses the replacement of the native species by the invasive species. This body of research has not only key system specific applied implications to inform future conservation policy and management strategy, but also demonstrates the critical role of native predators in mitigating the impacts of disease and invasive species as well as supporting ecosystem stability.

CRediT authorship contribution statement

Andrew Slade: Conceptualization, Methodology, Software, Visualization, Writing – original draft Writing – review & editing. **Andy White:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Peter W.W. Lurz:** Writing – original draft, Writing – review & editing. **Craig Shuttleworth:** Conceptualization, Writing – original draft, Writing – review & editing. **David G. Tosh:** Writing – original draft, Writing – review & editing. **Joshua P. Twining:** Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecolmodel.2022.110216. The supplementary information contains maps outlining the different carrying capacities and initial conditions of red and grey squirrels, and pine marten. The supplementary information also contains results where pine marten are introduced into north Wales only, results where pine marten are introduced into all suitable habitat, and results showing the impact of pine marten predation on red squirrels only.

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