Report for The Red Squirrel Trust Wales

The Impact of Pine Marten Predation on Red Squirrel Conservation

A Case Study of Three Priority Regions in Wales

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Executive Summary

This project extended a spatial modelling approach to examine the potential spread and impact of pine martens on resident red and grey squirrels in three areas: the island of Anglesey; the forest of Clocaenog and the Bangor area of Gwynedd. The project report provides maps of predicted distributions for the three species in North Wales which can be used to guide future monitoring programs including the identification of likely grey squirrel incursion routes at Clocaenog Forest, the likely expansion routes of pine marten and consequent red squirrel range expansion. The key results are:

- Simulations of red and grey squirrel competition in the absence of grey squirrel control and pine martens indicate that grey squirrels would re-invade and colonise Anglesey and that grey squirrels would expand their presence in Clocaenog with only a 50% likelihood of red squirrel population survival after 40 years (see Figure 7).

- The inclusion of squirrelpox as a factor in model simulations led to a marginal increase in the rate of red squirrel replacement along with a reduction in the size of the region in which red squirrels could persist.

- Simulations of pine marten spread due to migration from established populations in Mid Wales indicate that there was little range expansion for the first 10 years of simulation, due to low starting densities that occur due to the time taken for dispersing marten to establish new source populations. After 10 years pine marten become established in regions around Tremadog Bay, Gwydir Forest Park and Clocaenog Forest and by 15 to 20 years they start to inhabit the Bangor area, the Llŷn peninsula and areas along the English border. In the real world this will depend on local starting densities, additional pine marten mortality (e.g. road traffic mortality) and reproductive success.

- The model simulations strongly suggest that, when pine marten are assumed to migrate from Mid Wales only, pine martens would fail to establish in high enough densities to impact grey squirrel populations on Anglesey for almost four decades. Grey squirrels would therefore continue to out-compete and replace red squirrels in the Bangor area and on Anglesey.

- Limited predation of grey squirrels as a result of pine marten absence or low presence leads to red squirrel extinction through competition in the Bangor area. Model simulations (Figures 10 - 12) therefore suggest that a pine marten release in the Bangor region could be key to safeguarding the red squirrel population near Bangor and on Anglesey.

- A pine marten release in the Bangor region, combined with migration from Mid Wales, leads to more rapid pine marten spread and a quicker increase in pine marten density. Consequently, there are increased impacts on local grey squirrel population control and red squirrel recovery and range expansion.

- Pine marten release in the Bangor region, combined with migration from Mid Wales, leads to range expansion across much on North Wales within 20-25 years. Pine marten expand their range from Bangor across the northern coast and down the Conwy river valley, as

well as into the region north of Clocaenog. Expansion from Mid Wales sees pine marten occupying the region to the south of Clocaenog.

- The model suggests that the intensity of pine marten predation (Fig. 15) is a key factor in determining the future distribution of red and grey squirrels. Even low predation rates are likely sufficient to allow red squirrel survival at Clocaenog Forest but could, for example, on their own not prevent grey squirrel colonisation of Anglesey; whereas high rates of marten predation would allow red squirrels to dominate the Anglesey and Bangor area. Monitoring will therefore be required to determine what (if any) additional grey squirrel control may be needed in the future to maintain (or expand) red squirrel presence in Wales.

- Pine martens will also predate on red squirrels. The model results indicate that this will not lead to red squirrel population extinction but, if pine marten predation of red squirrels is high, can lead to reduced densities locally and reduced range expansion in the assumed absence of grey squirrels.

- Pine martens also have an additional ecosystem service effect in terms of disease management. Model simulations indicate that squirrelpox virus may fade out, within 40 years of pine marten release, as grey squirrel density is reduced, due to pine marten predation, below the threshold value necessary to maintain the disease.

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1 Background

The Eurasian red squirrel (*Sciurus vulgaris*) is under threat in the United Kingdom, with recent estimates (Mathews et al., 2018) indicating that just over 80% of the remaining populations are now thought to live exclusively in Scotland. The remaining populations survive in isolated forests or offshore islands throughout England and Wales (Mathews et al., 2018). The decline of red squirrel populations has arisen due to the spread and disease-mediated competition with the North American grey squirrel (*Sciurus carolinensis*) which was introduced into the UK in the 19th century (Middleton, 1930). 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 (Santicchia et al., 2018; Bertolino et al., 2014; Gurnell et al., 2004; Wauters et al., 2002). Grey squirrels are also a reservoir host of squirrelpox virus (SQPV) that is asymptomatic and endemic in grey squirrels but fatal to reds with observed mortality rates of $> 80\%$ (Chantrey et al., 2014). The replacement rate of red squirrels occurs significantly faster in areas where SQPV is present (Tompkins et al., 2003; Rushton et al., 2006).

Efforts to re-introduce red squirrels into Wales have encompassed a number of translocations, initially beginning with the release of small groups of red squirrels into specific regions of Anglesey, with released numbers kept low to avoid the risk of a large-scale SQPV outbreak. These releases coincided with a programme of grey squirrel eradication on the island of Anglesey which has resulted in Anglesey becoming a red squirrel stronghold that supports a viable population (Schuchert et al., 2014). Current management to prevent the re-invasion of Anglesey by grey squirrels is guided by modelling that uses the framework that is utilised in this report (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 the forest at Clocaenog, a 5,000-hectare upland commercial spruce plantation. The coniferous forest in Clocaenog provides a competitive advantage to red squirrels, with grey squirrels struggling to maintain sufficient population density when only coniferous resources are available. However, grey squirrels reach high densities in forests containing oak, hickory and walnut (Koprowski, 1994), which is similar to their native habitat in North America. Consequently, the red squirrel population at Clocaenog is threatened by grey squirrels that have become established in neighbouring regions that contain a higher proportion of broadleaved trees. The red squirrel population in Clocaenog is also under threat from squirrelpox that can spread from adjacent grey squirrel populations (White et al., 2014). Current UK efforts to aid the conservation of the red squirrel aim to tackle the different aspects of the competitive interactions. They include targeted grey squirrel control (Gill, 2019) to prevent grey squirrel range expansion and reduce disease transmission (e.g. see Highland Boundary Line, *Saving Scotland's red squirrels* 2019 or Schuchert et al., 2014) as well as the designation and management of 'stronghold' forests that are intended to provide refuge for red squirrels against the incursion of, and competition by grey squirrels (e.g. see Forestry Commission Scotland, 2012).

Pine marten (*Martes martes*) are generalist predators that have been shown to preferentially predate on grey squirrels compared to red squirrels (Twining et al., 2020). A recent resurgence in pine marten density has resulted in an expansion of their distribution in Scotland, Northern Ireland and the Republic of Ireland. This expansion has seen a concurrent reduction, and in some instances the extirpation, of grey squirrels that has allowed the re-establishment of red squirrels (Sheehy and Lawton, 2014; Sheehy et al., 2018; Twining et al., 2020). The reintroduction of pine marten into Wales could act to reduce grey squirrel density and potentially lead to predator mediated recovery of red squirrels. Previous pine marten 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 the creation of a viable pine marten population in Mid Wales, with future plans to release pine marten into the Bangor region in North Wales.

1.1 Aims

This project will extend established spatial modelling approaches that represent the interactions of red and grey squirrels and SQPV in realistic landscapes to include the impact of pine marten predation and dispersal. The model system will be used to examine the potential spread and impact of pine marten on resident red squirrel populations on the island of Anglesey and to examine the potential spread and impact of pine marten on red and grey squirrel interactions and SQPV in the Clocaenog forest and Bangor area of Gwynedd. The results will inform red squirrel conservation management and the Heritage Fund OL-18-06694 Magical Mammals project.

1.1.1 Objectives

1. To examine the potential spread and impact of pine marten on resident red squirrel populations on the island of Anglesey.

   As a result of grey squirrel control and red squirrel re-introduction (between 2005-2013) there is now a viable, resident population of red squirrels on the island of Anglesey. Ongoing conservation efforts prevent the successful re-establishment of grey squirrels. We will use the model to examine whether Anglesey could provide suitable habitat for pine marten, to understand the potential impact of pine marten on the density and viability of resident red squirrels and the effect of pine marten on the conservation effort required to prevent grey squirrel re-invasion of Anglesey from adjacent mainland populations.

2. To examine the potential spread and impact of pine marten on red and grey squirrel interactions and SQPV in the (a) Clocaenog forest and (b) Bangor area of Gwynedd.

   There is the potential for re-establishment of pine marten in many regions in Wales. This may be of particular significance in Clocaenog forest where a population of red squirrels has managed to persist in the face of the threat from grey squirrels and in Bangor and the surrounding area which is adjacent to a source of red squirrels on the island of Anglesey. We note that pine martens have occasionally been recorded in Clocaenog (2017-2019) following the Mid Wales translocation, and there are plans to release pine marten into the Bangor region in North-West Wales. We will use the model to examine whether these regions could provide suitable habitat for pine marten and to understand the potential impact of pine marten predation on competition and disease mediated interactions between red and grey squirrels. In particular, could preferential predation of pine marten on grey squirrels lead to the loss of their competitive advantage over red squirrels and a subsequent increase in red squirrel abundance and an expansion of their distribution.

3. Provide maps of predicted mammal distribution which can be used to develop future mammal monitoring programs including identifying key grey squirrel incursion routes at Clocaenog.

2 Mathematical Model

We extend established modelling frameworks to represent the population density of red and grey squirrels, the prevalence of the SQPV infection, and the population density of pine marten in a specific geographic region. The model represents the dynamics on a discretised, 1 km by 1 km grid square, basis. These grid squares are linked via dispersal (since individual squirrels and pine marten can move freely between adjacent areas) with the carrying capacity of each grid square defined using land cover data in order to suitably approximate the heterogeneous landscape of North Wales.

2.1 Model Framework

The mathematical model used in this report is based on previous models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches (Tompkins et al., 2003) to develop a spatial, stochastic model (Jones et al., 2016; White et al., 2016; White and Lurz, 2014). The deterministic approach underpinning the model (see equations 1 and 2) allows the key population processes to be defined and understood. However, deterministic models do not include the randomness and variability that is exhibited by real systems. We develop a stochastic version of the deterministic model, in which the probability of birth, death, infection, recovery, predation and dispersal of individuals is used to determine the population dynamics. Hence, the stochastic model includes the variability seen in real systems and provides essential realism when squirrel numbers become low which gives a better representation of population extinction and the fade-out of infection. The underlying deterministic system represents the population density and infection status (with regard to squirrelpox) 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^x). The model we use is:

$$\begin{aligned}
\frac{\mathrm{d}S_G}{\mathrm{d}t} &= A_G(t) - bS_G - \beta S_G(I_G + I_R) - \mu_G S_G P^x \\
\frac{\mathrm{d}I_G}{\mathrm{d}t} &= \beta S_G(I_G + I_R) - bI_G - \gamma I_G - \mu_G I_G P^x \\
\frac{\mathrm{d}R_G}{\mathrm{d}t} &= \gamma I_G - bR_G - \mu_G R_G P^x \\
\frac{\mathrm{d}S_R}{\mathrm{d}t} &= A_R(t) - bS_R - \beta S_R(I_G + I_R) - \mu_R S_R P^x \\
\frac{\mathrm{d}I_R}{\mathrm{d}t} &= \beta S_R(I_G + I_R) - bI_R - \alpha I_R - \mu_R S_R P^x \\
P(t) &= P^x
\end{aligned} \tag{1}$$

where

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

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 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 $c_R = 0.61$ (Bryce et al., 2002). SQPV is transmitted (both within and between each squirrel species) with coefficient β that can take either a low value of 0.83 or a high value of 1.1 (White and Lurz, 2018). 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^x, q_G^x) are set to ensure the average density over one year is equal to the 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 2.3 below). The superscript x indicates that the value is grid-square dependent. We assume a pine martin population, P^x, that depends on birth and death and can reach a maximum carrying determined by habitat in each grid square. Pine marten can predate on squirrels with predation rates given by μ_i, with $\mu_R = 0.2\mu_G$, reflecting that pine marten preferentially predate on grey squirrels. Predation is unaffected by squirrel infection status. Further details of the formulation and parametrisation of the pine marten aspects of the model can be found in Section 2.2. All parameter values assume an annual time-scale.

2.2 Pine Marten

Pine marten are generalist omnivores that exhibit intra-sexual territoriality, which means that the home ranges of same sex individuals do not overlap but opposite sex ranges do overlap (Birks, 2020), with seasonally stable home ranges (O'Mahony, 2014). Consequently, pine marten density is primarily space, rather than resource, limited. Thus, pine marten are assumed to reach a maximum density in any grid-square, with the carrying capacity of that square being dependent on habitat. The model framework considers the birth, death and dispersal of pine marten as well as the predation of squirrels by pine marten.

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 gender ratio with an average annual litter size of 2. Thus, the expected number of newborns is given by:

$$\begin{aligned}\text{Newborns} &= \frac{\text{Average Lifespan} - \text{Maturity Age}}{\text{Average Age}} \times (\text{Litter Size} \times \text{Gender Split}) \\ &= 0.6\text{per individual.}\end{aligned}$$

This 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, natural death rate $b_P = 0.2$. 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 (based on pers. comms. from X. Lambin) which gives $\mu_G = 1.5$. This will be altered, using 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. Red squirrel predation rate $\mu_R = 0.2\mu_G$ (Sheehy and Lawton, 2014; Twining et al., 2020).

Pine marten dispersal occurs on a 5 km by 5 km gridded scale which has a defined habitat dependent carrying capacity (see section 2.3). When the pine marten population exceeds the carrying capacity 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 the carrying capacity the dispersing pine marten are removed. This simulates the inter-species pressure that can see dispersing juveniles killed by adults who wish to protect their home range. In addition to local dispersal we assume rare long distance dispersal 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). 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 Wales have been recorded over 200 miles away from the point of release, after several years have passed.

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 patch level abundance (Renshaw, 1993). Each simulation is run for 50 years.

2.3 Carrying Capacities

We have used the National Forest Inventory Woodland Wales 2018 dataset, which includes information on whether the primary species 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. These data sets are at high resolution (25 m by 25 m) and the information is converted into a proportion of each habitat type in a 1 km x 1 km grid square. The full 25 m by 25 m feature map can be seen in Figure 1. This information can be used in conjunction with squirrel and pine marten carrying capacity values for broadleaf and conifer habitat to give carrying capacity values for each 1 km grid-square. Figure 2(a) shows the red squirrel carrying capacity map, Figure 2(b) the grey squirrel carrying capacity map and 2(c) the pine marten capacity map. The pine marten carrying capacity values are used to create the 5 km by 5 km carrying capacity values that are used to trigger dispersal. The broadleaf, conifer and urban squirrel capacity values are the medium values from the Anglesey study conducted by Jones et al. (2016). In line with recent studies for Scotland (Slade et al., 2020) we assume red squirrels have a competitive advantage over grey squirrels in 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). Open land is any region that does not have a named feature. The small pine marten carrying capacity for this feature indicates that, whilst pine marten cannot

Event	**Population Change**	**Probability of Event**
Birth of S_G	$S_G \to S_G + 1$	$[(a_G - q_G^x(H_G + c_R H_R))H_G]/R$
Natural Death of S_G	$S_G \to S_G - 1$	$[bS_G]/R$
Infection of Grey	$S_G \to S_G - 1, I_G \to I_G + 1$	$\left[\beta S_G \left((I_G + I_R) + \theta \sum_{Adjacent} (I_G + I_R) + \theta^2 \sum_{Corner} (I_G + I_R)\right)\right]/R$
Natural Death of I_G	$I_G \to I_G - 1$	$[bI_G]/R$
Recovery of Grey	$I_G \to I_G - 1, R_G \to R_G + 1$	$[\gamma I_G]/R$
Natural Death of R_G	$R_G \to R_G - 1$	$[bR_G]/R$
Birth of S_R	$S_R \to S_R + 1$	$[(a_R - q_R^x(H_R + c_G H_G))H_R]/R$
Natural Death of S_R	$S_R \to S_R - 1$	$[bS_R]/R$
Infection of Red	$S_R \to S_R - 1, I_R \to I_R + 1$	$\left[\beta S_R \left((I_G + I_R) + \theta \sum_{Adjacent} (I_G + I_R) + \theta^2 \sum_{Corner} (I_G + I_R)\right)\right]/R$
Natural/Diseased Death of Red	$I_R \to I_R - 1$	$[(b + \alpha)I_R]/R$
Dispersal of S_G	$S_G \to S_G - 1, S_G^* \to S_G^* + 1$	$\left[mS_G\left(\frac{(H_G + c_R H_R)^2}{(K_G)^2}\right)\right]/R$
Predation of S_G	$S_G \to S_G - 1$	$[\mu_G S_G P^x]/R$
Birth of P^x	$P^x \to P^x + 1$	$[a_P P^x]/R$
Natural Death of P^x	$P^x \to P^x - 1$	$[b_P P^x]/R$
Dispersal of P^x	$P^x \to P^x - 1, P^{x*} \to P^{x*} + 1$	$[d_P P^x]/R$

Table 1: State transitions and their probabilities in the stochastic model. A full table legend can be found overleaf.

Table 1: (Previous page.) Stochastic model events that govern the dynamics that occur within each 1 km grid square. The parameters representing squirrel control and dispersal were fitted with observed data on the Island of Anglesey (Jones et al., 2017). 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. 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. 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 potential density. 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). 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. Further details of the model framework and the calculation of parameter values can be found in (Jones et al., 2017).

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 Anglesey and the mainland. 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.

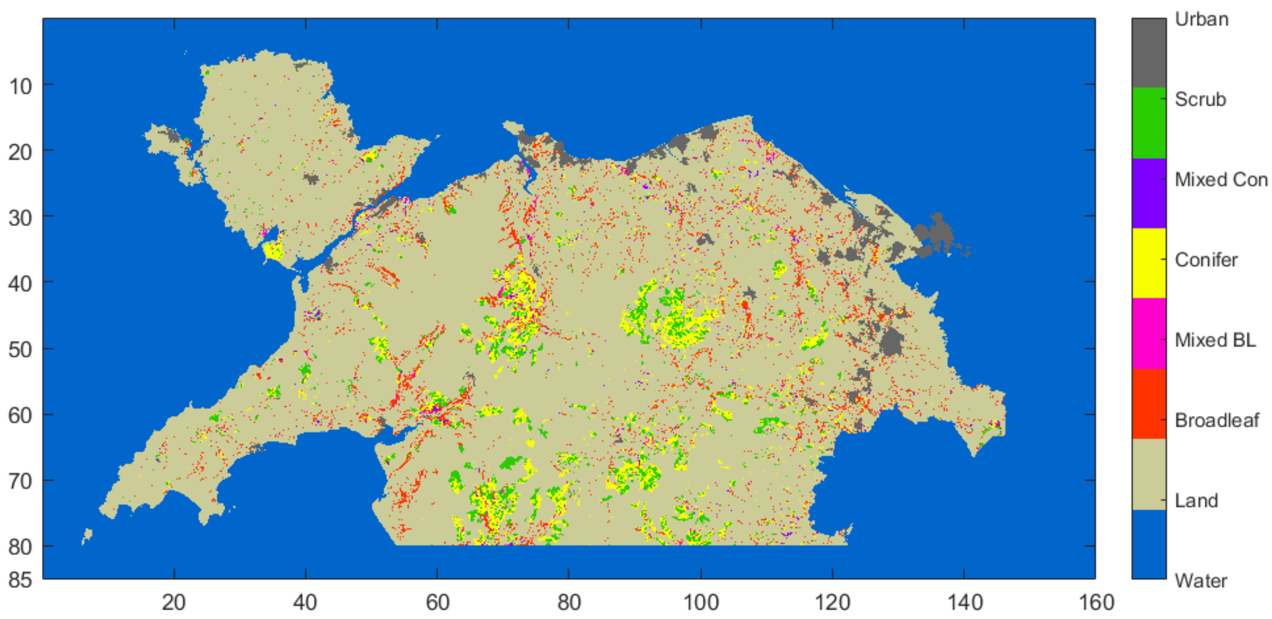

Figure 1: High resolution (25 m by 25 m) feature map for North Wales. The colour scale indicates which feature is the predominant one in any given 25 m by 25 m square. The axes values indicate the distance in kilometres.

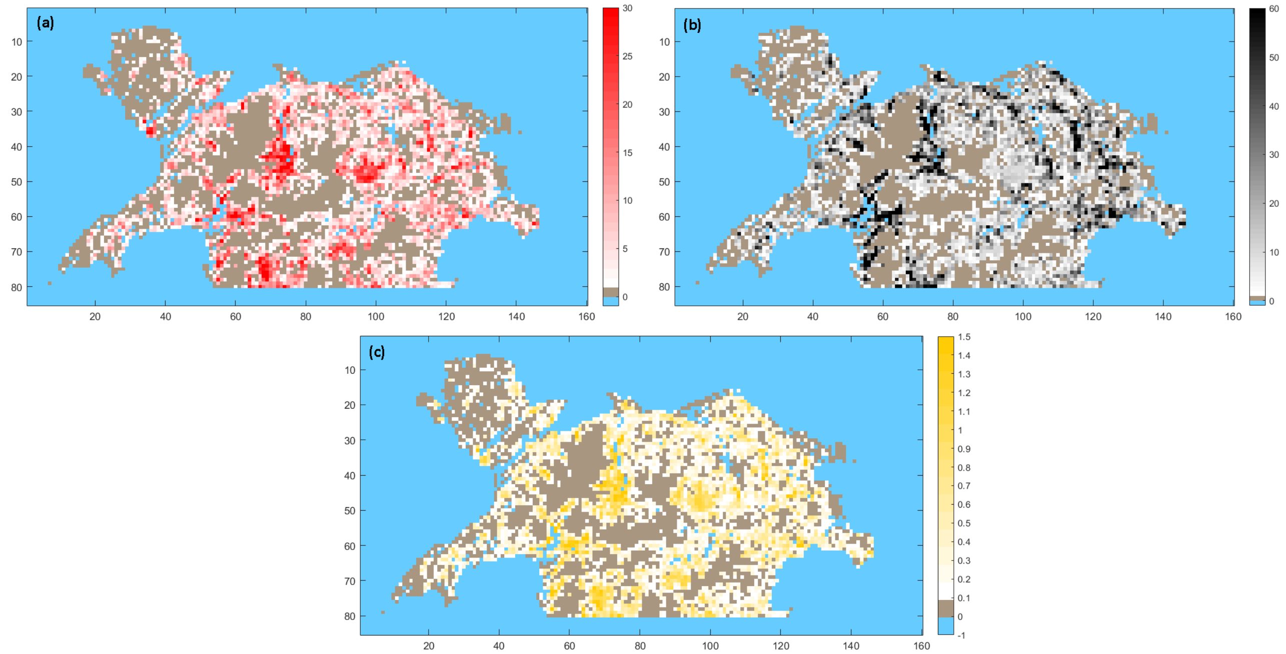

Figure 2: Carrying capacity maps for (a) red squirrels, (b) grey squirrels and (c) pine marten. All capacity values are per km^2.

	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

Table 2: Red and grey squirrel, and pine marten carrying capacity values for different habitat types. Squirrel values are the medium level values used by Jones et al. (2016). Pine marten carrying capacity values are authors estimates based on personal communications with J. Twining and D. Tosh.

2.4 Initial Conditions

Currently, red squirrels are resident in the forest at Clocaenog and on the island of Anglesey, with some red squirrels dispersing from Anglesey into the Bangor region. Grey squirrels are established across the the entirety of North Wales except Anglesey. Given the absence of detailed density data we assume grey squirrels are not present in the Clocaenog region. Thus, the model results will simulate the replacement of red squirrels due to dispersal from nearby known grey squirrel populations. The squirrel initial conditions therefore assume that red squirrels are at their carrying capacity in Anglesey and Clocaenog, red and grey squirrels are at half their car-

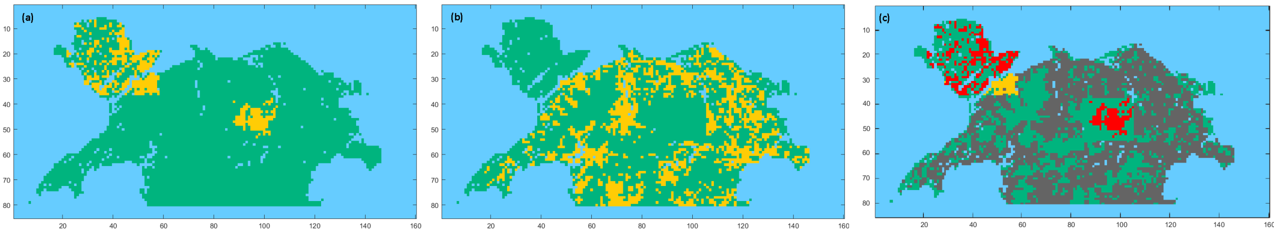

Figure 3: Initial condition for (a) red squirrels, which are initialled at Clocaenog, Anglesey and Bangor, and (b) grey squirrels which are initialled in all suitable habitat except Clocaenog and Anglesey. Image (c) shows the initial occupancy where grey regions indicate grey presence, red regions red presence and yellow regions indicate the presence of both red and grey squirrels.

rying capacity in the Bangor region and grey squirrels are at their carrying capacity in all other regions (as indicated in Figure 3). We consider a range of pine marten initial conditions that simulate different scenarios. The first initial condition (Figure 4(a)) assumes that pine marten resident in South and Mid Wales migrate north, with the initial population located in suitable habitat in Mid Wales, set at a quarter of the carrying capacity. The second initial condition (Figure 4(b)) models the potential release of 20 pine marten into the area surrounding Bangor. The release will occur in one of three ways: either (i) all 20 pine marten are released at the beginning of the simulation, (ii) 10 pine marten are released initially with 10 more released one year later or (iii) 5 pine marten are released initially with 5 more being released every year for the next 3 years. The third initial condition is a combination of the first two, with pine marten being initially located in Mid Wales as well as Bangor (Figure 4(c)), and the final initial condition assumes pine marten are fully established in North Wales and at their carrying capacity in every viable grid-square (Figure 4(d)). This last condition is used to simulate the long-term dynamics under the assumption that pine marten have expanded their range to all suitable habitat. To generate the SQPV initial conditions, the model was simulated for 10 years with only grey squirrels present. We assume two different infection transmission coefficients, β. A β value of 0.83 represents the infection rate needed to ensure 74% seroprevalence (Sainsbury et al., 2000; Schuchert et al., 2014) in a homogeneous population of 80 individuals in a 1 km by 1 km grid-square (equivalent to a grey squirrel density of 0.8 ha^{-1}). A value of $\beta = 1.11$ is the infection rate required to get 74% seroprevalence in a homogeneous population of 60 individuals. The values of 60 and 80 individuals are representative for grey squirrel density (per km^2) in regions in North Wales where squirrelpox has been reported (Sainsbury et al., 2000; Schuchert et al., 2014). The prevalence of squirrelpox, for the different transmission values, is shown in Figure 5 and indicates that the model predicts variability in the prevalence of squirrelpox, which is strongly linked to grey squirrel density across North Wales.

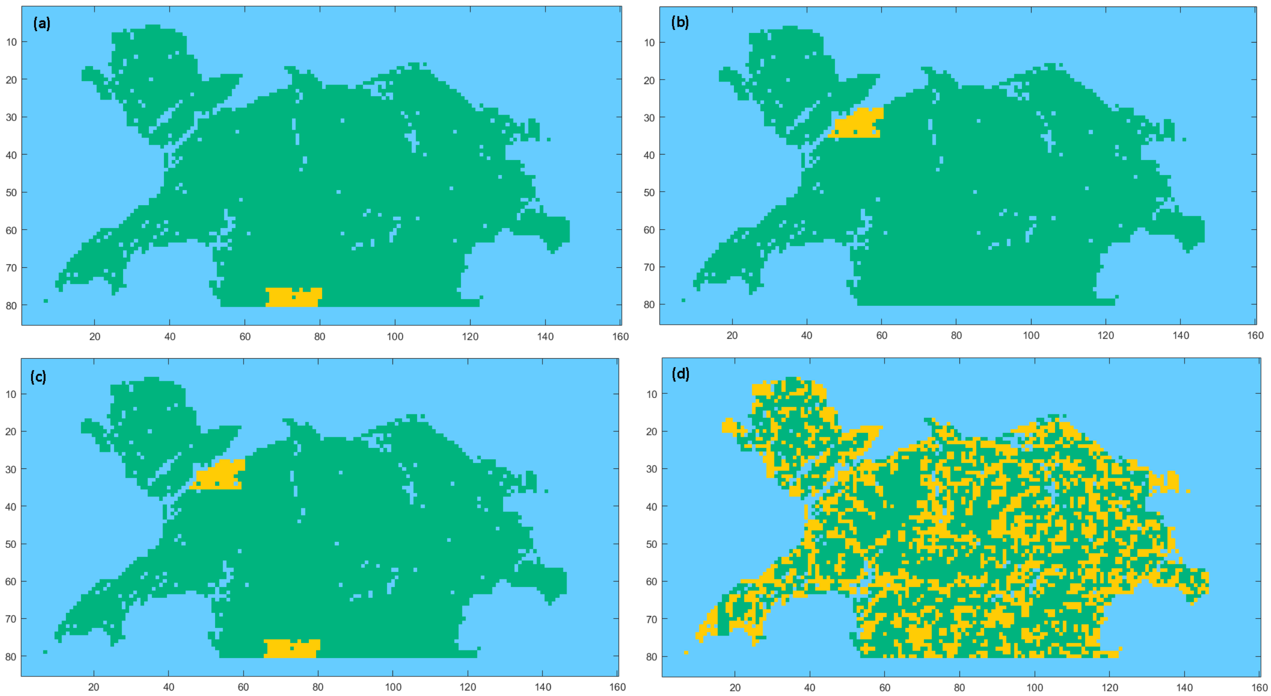

Figure 4: Initial conditions for pine marten. Here (a) shows the location of pine marten that are assumed to have migrated north from Mid Wales, (b) shows the Bangor region where different release scenarios were tested, (c) is a combination of the Bangor and Mid Wales introduction sites and (d) has pine marten being introduced, at full carrying capacity, into every available grid-squares.

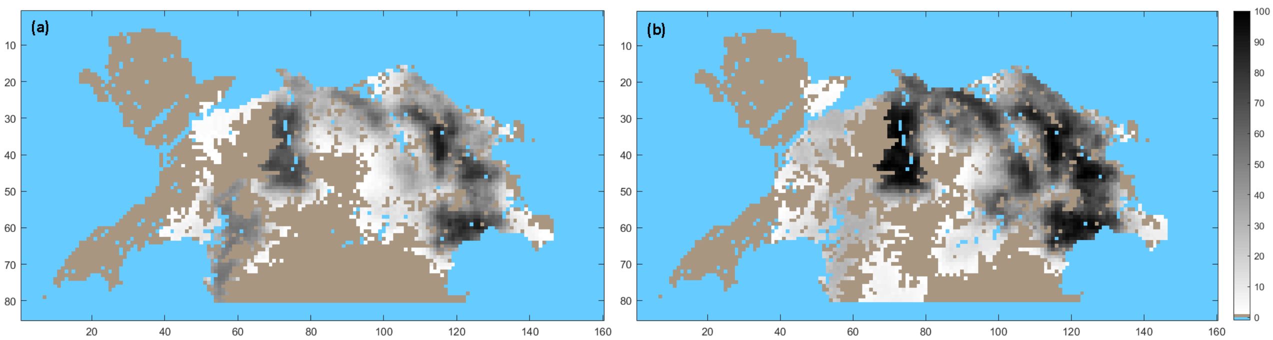

Figure 5: Squirrelpox prevalence in grey squirrels, shown as the percentage of the population that has previously been infected with the disease, when the infection rate is (a) $\beta = 0.83$ and (b) $\beta = 1.11$. These results are the outcome of a 10-year model spin-up with only grey squirrels present.

3 Results

The model results are presented as follows. Section 3.1 will outline the red and grey squirrel dynamics, both with and without squirrelpox, in the absence of pine marten in order to identify the grey squirrel incursion routes into Anglesey and Clocaenog. Section 3.2 will outline the red and grey squirrel dynamics, in the presence of squirrelpox and pine marten, which will show the impact of pine marten on red and grey squirrel interactions in North Wales. Section 3.3 will detail the impact of pine marten on squirrelpox, as well as the impact of pine marten on red squirrel density and Section 3.4 will highlight key expansion routes for pine marten in North Wales.

3.1 Red/Grey/Squirrelpox Interactions in the Absence of Pine Marten

Figure 6 shows red and grey squirrel occupancy over a 40 year time frame, in the absence of pine marten, with (a) the absence of squirrelpox, (b) the presence of squirrelpox with an infection transmission coefficient of $\beta = 0.83$, and (c) the presence of squirrelpox and with an infection transmission coefficient of $\beta = 1.11$. A comparison of Figure 6 a-c indicates that the inclusion of squirrelpox has a marginal impact on the red and grey squirrel occupancy dynamics. There is a reduction in the range of red squirrel occupancy in Clocaenog, but little impact of squirrelpox on the rate of grey squirrel invasion on Angelsey (as also reported in Jones et al. 2017). Therefore while squirrelpox may have played a role in the historic expansion of grey squirrels and replacement of red squirrels across Wales, our model results indicate that it does not have a marked impact on the replacement of remaining red squirrel populations on Anglesey and in Clocaenog.

The model does not assume grey squirrel control and so grey squirrels can invade Anglesey and replace resident red squirrels. Grey squirrel expansion into Anglesey occurs within 10 years in the model simulation via the Britannia bridge. Once established on the island, grey squirrels expand their range north and west into the interior of the island, with replacement of all red squirrels except those on the west coast occurring within 40 years. This time-frame is similar to the historic replacement of red squirrels by grey squirrels that occurred on Anglesey from the 1960s (Shuttleworth, 2003).

Grey squirrels invade and continually disperse into the Clocaenog region which removes red squirrel dominance in Clocaenog. However, there is 50% probability of red squirrel survival after 40 years. The chance of survival and the region over which red squirrels can persist is reduced (slightly) as the squirrelpox transmission increases. These results are in broad agreement with the observation of low density red squirrel populations in Clocaenog that has occurred after the expansion of grey squirrels into North Wales. Figure 7 shows the routes of invasion for grey squirrels into Clocaenog. Grey squirrel incursion occurs from all directions, except from the west. Consequently, the region of red squirrel dominance in Clocaenog is reduced over time and increasingly located in the west of Clocaenog, though these regions also allow grey squirrel incursion after 10 years of simulation.

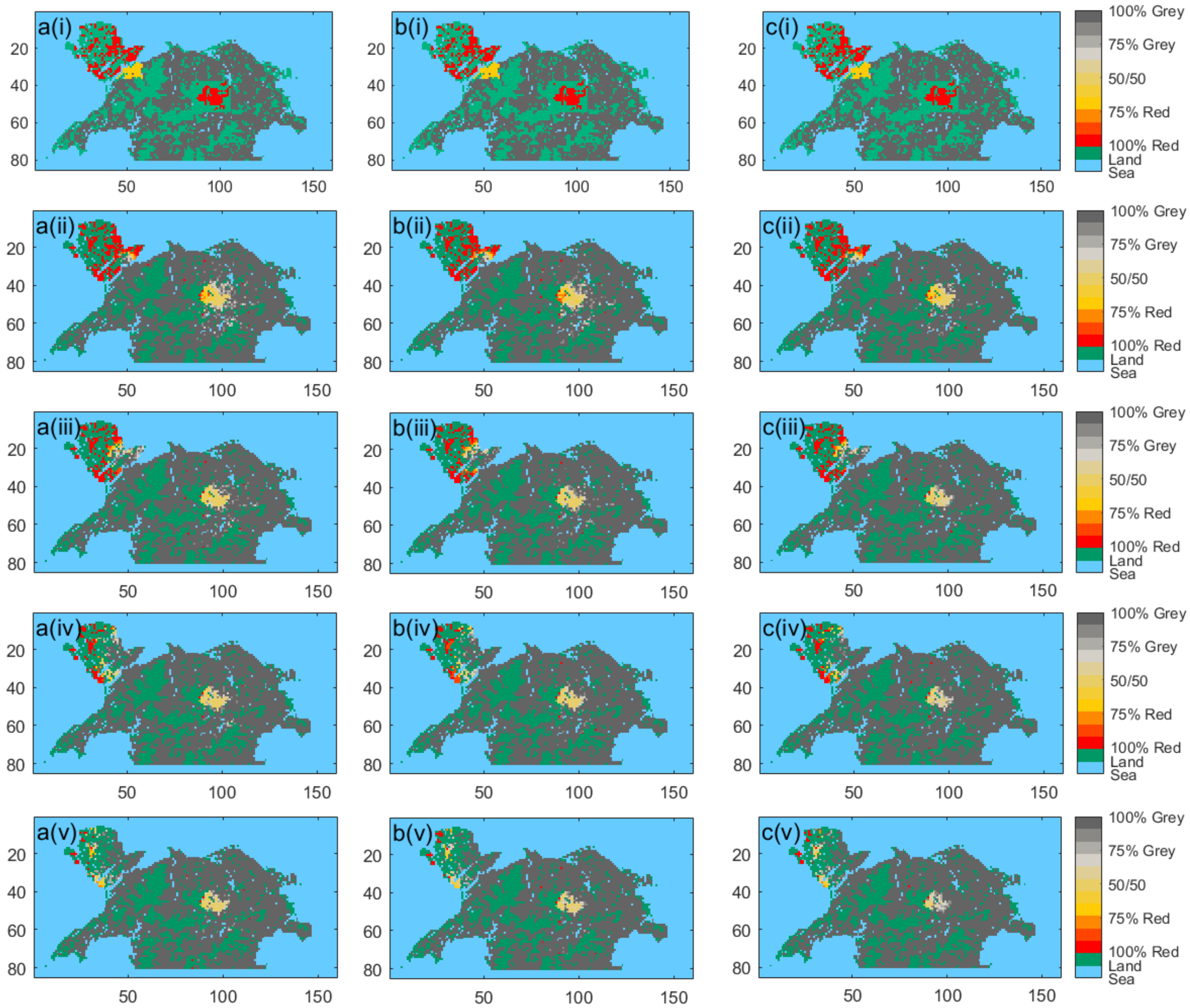

Figure 6: Occupancy results for red and grey squirrels in the absence of pine marten. Here (a) shows the results when there is no squirrelpox present, (b) shows the results when squirrelpox is included with transmission coefficient $\beta = 0.83$ and (c) shows the results when squirrelpox is included with transmission coefficient $\beta = 1.11$. Image (i) denotes the initial conditions, (ii) denotes the results after 10 years of simulation, (iii) denotes the results after 20 years, (iv) denotes the results after 30 years, and (v) denotes the results after 40 years of simulation. 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.

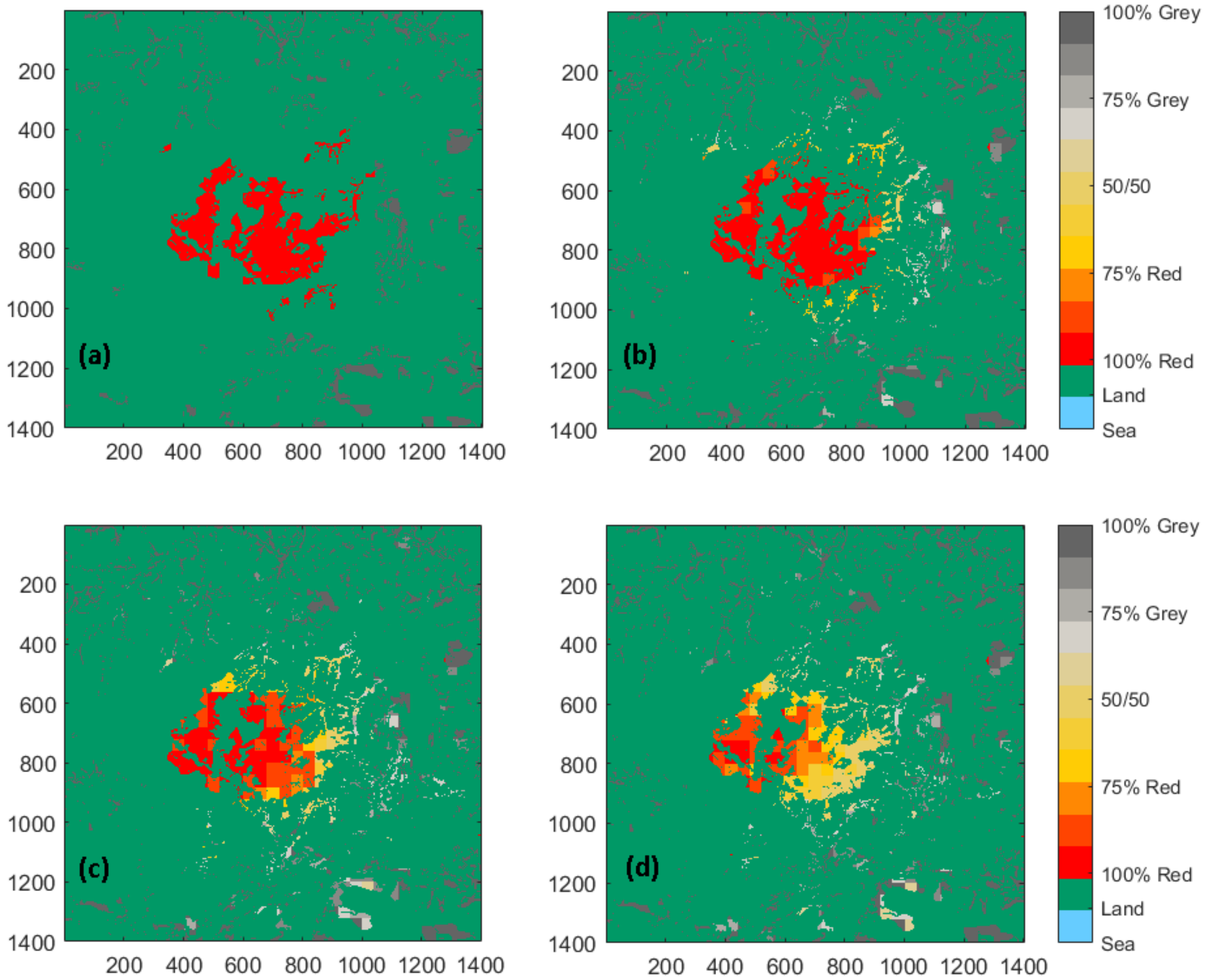

Figure 7: High resolution (25 m by 25 m) red and grey squirrel occupancy results, in the absence of pine marten, that demonstrate the available colonisation routes for grey squirrels into Clocaenog. Here (a) shows the initial occupancy, (b) shows the results after 2 years, (c) shows the results after 4 years, and (d) shows the results after 6 years of simulation. The results include squirrelpox with transmission coefficient $\beta = 0.83$.

3.2 Red/Grey/Squirrelpox Interactions in the Presence of Pine Marten

3.2.1 Pine Marten Migration from Mid Wales

Figure 8 outlines the range expansion routes for pine marten that are assumed to have migrated north from South and Mid Wales. Initially - for the first 10 years - there is very little expansion in pine marten range due to the initial condition being set at a quarter of the carrying capacity. Once the density is large enough to allow regular dispersal we see expansion into regions connected with the initial introduction area, as well as long range dispersal events which seed populations into North Wales. The three primary regions of pine marten expansion are Tremadog Bay, Gwydir Forest Park and Clocaenog. Once these regions have established pine marten populations - which occurs approximately 15 to 20 years into the simulation - pine marten start to inhabit territory in the Bangor region, the Llŷn peninsula, as well as along the English border.

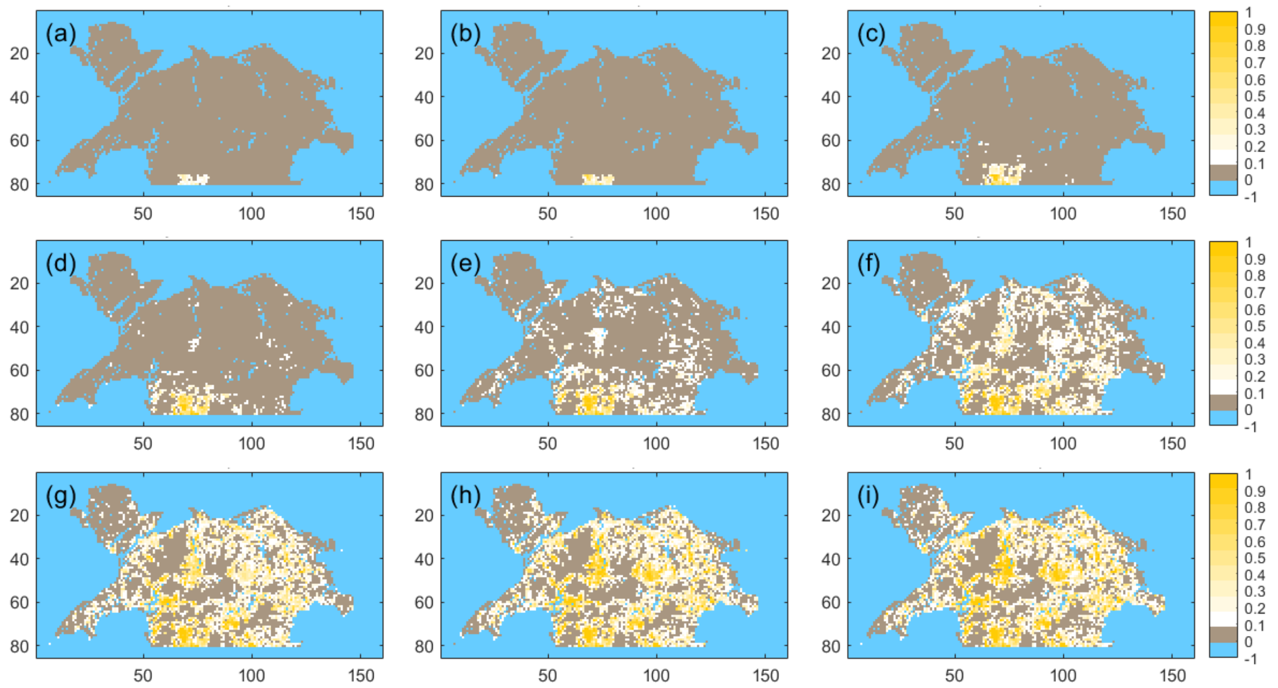

Figure 8: Pine marten range expansion when they are released into Mid Wales only, at a quarter of the carrying capacity. Here (a) shows the initial condition, (b) the pine marten range expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

Figure 9 shows the squirrel occupancy results when pine marten are assumed to migrate from Mid Wales. As shown in Figure 8, the rate of pine marten expansion to the north of Wales takes time and this means grey squirrels can out-compete and replace red squirrels in the Bangor regions and colonise Anglesey. Pine marten fail to establish at high density on Anglesey by the end of the 40 year model simulation and therefore grey squirrels continue to expand and replace red squirrels on Anglesey. However, comparing Figure 6 (the absence of pine marten) and Figure 9 (where pine marten are present) does show that red squirrels occupy a larger region on Anglesey when pine marten are present. The presence of pine marten does allow red squirrels to expand their region of occupancy from Clocaenog southwards into Mid Wales. This occurs for all three rates of pine marten predation, with the size of red occupied region being larger with increasing predation rate. The higher predation rates also cause a removal of grey squirrels from the region south of Snowdonia, without a concurrent increase of red squirrels in the area, due to there being no adjacent population source of red squirrels.

3.2.2 Pine Marten Introduction into the Bangor Region

Figure 10 shows the impact that the different pine marten release schemes into the Bangor region have on pine marten dispersal. The difference in release schemes on pine marten dispersal in minimal and so for further results we focus on one release scheme only (when two releases of 10 pine marten are undertaken in consecutive years).

Figure 11 shows pine marten range expansion in 5 year intervals when pine marten are released in the Bangor region. The primary routes for range expansion occur along the north coast and down the river Conwy as well as southwards into the Tremadog bay region. Once the population in the Conwy region is large enough, pine marten can expand southwards and eastwards into the rest of North Wales. Pine marten expansion into Anglesey occurs by year 10 of the simulation. Comparing Figure 8 with Figure 11, the key difference between pine marten range expansion when they are released into the Bangor region or when dispersing from Mid Wales occur in the first 20 years following their release. After this period pine marten have largely dispersed across their full range - although it takes further time for them to reach their carrying capacity density.

Figure 12 shows the impact of pine marten range expansion and predation on the occupancy of red and grey squirrels. The results show that the assumed rate of predation by pine marten has an impact on red squirrel occupancy and survival. When the predation rate is low ($\mu_g = 0.75$), red squirrels are unable to survive in the Bangor region and grey squirrels successfully colonise the majority of Anglesey, although the red population at Clocaenog is able to survive and potentially expand southwards. For medium and high rates of pine marten predation, red squirrels are able to persist in the Bangor region, and more extensively on Anglesey. It takes time for pine marten dispersal and the consequent increases in their density to have an impact on red and grey squirrel competition, but from year 20 onwards the preferential predation of pine marten on grey squirrels leads to increased occupancy of red squirrels in Clocaenog which then facilitates red squirrel range expansion.

3.2.3 Pine Marten Introduction into the Bangor Region and Migration from Mid Wales

Figure 13 outlines the expansion routes for pine marten that are have been released into the Bangor region as well as pine marten that are assumed to migrate from Mid Wales. The combined effect of pine marten 'release' into both regions is that pine marten range expansion is more rapid and the time frame for pine marten to reach their carrying capacity density is reduced. Pine marten expansion from Bangor occurs primarily across the North Wales coast and down the river Conwy. The pine marten in Mid Wales primarily disperse via Clocaenog. Pine marten expansion into Anglesey occurs by year 10 of the simulation.

Figure 14 shows the impact of pine marten range expansion from the Bangor and Mid Wales region on the occupancy of red and grey squirrels. The results are similar to those in Figure 12, which indicates that the pine marten release in the Bangor region is potentially key to safeguarding the red squirrel population near Bangor and on Anglesey. The release of pine marten in the Bangor region is also sufficient (at medium and high predation rates) to support the range expansion of red squirrels from Clocaenog. The expansion of pine marten from Mid Wales does have an impact on grey squirrel occupancy in Mid, and North-West Wales as here pine marten reach high density. However, red squirrel range expansion into these regions does not occur within 40 years in the model simulations.

3.2.4 Pine Marten Introduction into All Regions

Figure 15 shows the results when pine marten have been introduced, at their carrying capacity, into all suitable regions of North Wales. This scenario is intended to simulate the long-term impact of pine marten on red and grey squirrel interactions. At the low predation rate of $\mu_G = 0.75$, the impact of pine marten predation is sufficient to safeguard the red squirrel population in Clocaenog. Pine marten predation can also allow moderate expansion of the red squirrel range to the south of Clocaenog, but it cannot prevent the expansion of grey squirrels onto Anglesey. A medium predation rate of $\mu_G = 1.5$ renders the majority of central North Wales viable for red squirrels. Grey squirrels still dominate the border regions, as well as the Llŷn peninsula, but the regions around and to the south of Clocaenog, as well as the island of Anglesey, are dominated by red squirrels. When the grey squirrel predation rate is at its highest value ($\mu_G = 2.25$) pine marten can eradicate the majority of grey squirrels from North Wales, with only the English border and the Llŷn peninsula (as well as a small region to the west of Clocaenog) allowing grey squirrel survival. Red squirrels dominate Anglesey and Bangor with this predation rate, as well as the wider region in central North Wales. Grey squirrels are removed from the regions south of Snowdonia to Mid Wales and red squirrels are unable to colonise this region during the 40 year model simulation time-frame.

3.2.5 Impact of Pine Marten on Red Squirrels

Pine marten presence is detrimental to grey squirrels, with local extirpation being predicted by the model for medium and high predation rates across many parts of North Wales. This could results in red squirrel range expansion and ultimately the coexistence of red squirrels and pine marten in many regions. Thus it is prudent to examine the impact of pine marten predation on red squirrel density and viability in the absence of grey squirrels. Figures 16a and 16b outline the red squirrel expansion, over 100 years, when pine marten are introduced into every available grid-square for predation rates of $\mu_G = 0.75, 1.5, 2.25$ with $\mu_R = 0.2\mu_G$. As can be seen, red squirrels are able to survive, and even expand their range of occupancy from Anglesey and Clocaenog, with red squirrels successfully occupying the majority of available habitat when the predation rate is low. As expected, increasing the predation rate reduces the red squirrel density, as well as their geographic spread. The rate of expansion is much slower when the high predation rate is used, with Snowdonia and the south-west area of North Wales remaining unoccupied. Red squirrels density and range is also reduced on Anglesey as the pine marten predation rate increases. These results should be interpreted in conjunction with the findings on red and grey squirrel occupancy in the presence of pine marten (sections 3.2.1-3.2.4) which indicates that medium or high levels of pine marten predation are required to sufficiently reduce grey squirrel density to a level where red squirrels can have a predator mediated advantage over grey squirrels across more extensive regions in North Wales.

3.3 The Impact of Pine Marten On Squirrelpox

Squirrelpox is currently endemic in the grey squirrel populations of North Wales. Figure 17 outlines the impact of pine marten predation on squirrelpox, for the scenario where pine marten have been introduced into the Bangor region (10 per year for 2 years) as well as Mid Wales. As pine marten expand their range and increase in density (Figure 13), predation of grey squirrels reduces the grey squirrel density (Figure 18) to levels that cannot support squirrelpox (Figure 17). Higher predation rates lead to greater, more rapid, reduction in squirrelpox prevalence. There is no squirrelpox in either Bangor or on the island of Anglesey after 10 years of model simulation. After 20 years of model simulation, there emerges two distinct regions where squirrelpox remains endemic - one region stretches from the north to the west coast whilst the other region is in the north-east of North Wales. Squirrelpox is largely absent from Clocaenog by year 20 in the model and, by year 30 of the model simulation, the majority of North Wales is predicted to be squirrelpox free. Squirrelpox is largely eradicated under all three predation rate scenarios by year 40 of the simulation. Notice that extinction of squirrelpox does not require the extinction of grey squirrels (compare Figures 17 and 18), but instead requires that grey squirrel density is reduced below a threshold value. Pine marten predation therefore has an additional ecosystem benefit in terms of disease management, even when predation does not lead to species eradication.

3.4 High Resolution Pine Marten Range Expansion Images

Figure 19 details the high resolution (25 m by 25 m) maps displaying pine marten expansion, where pine marten have been introduced into the Bangor region as well as Mid Wales. Expansion mainly occurs during the first 20 years of simulation, with pine marten expanding their range from Bangor across the northern coast and down the Conwy river valley, as well as into the region north of Clocaenog. Expansion from Mid Wales sees pine marten occupying the region to the south of Clocaenog, which is also a primary red squirrel expansion route. After 20 years of simulation, pine marten occupancy mirrors the high resolution habitat map (Figure 1), with potentially high density populations occurring in the fragmented broadleaf habitat and lower density populations residing in the larger regions of coniferous habitat. Consequently, pine marten could potentially be found anywhere in North Wales 20 years after release.

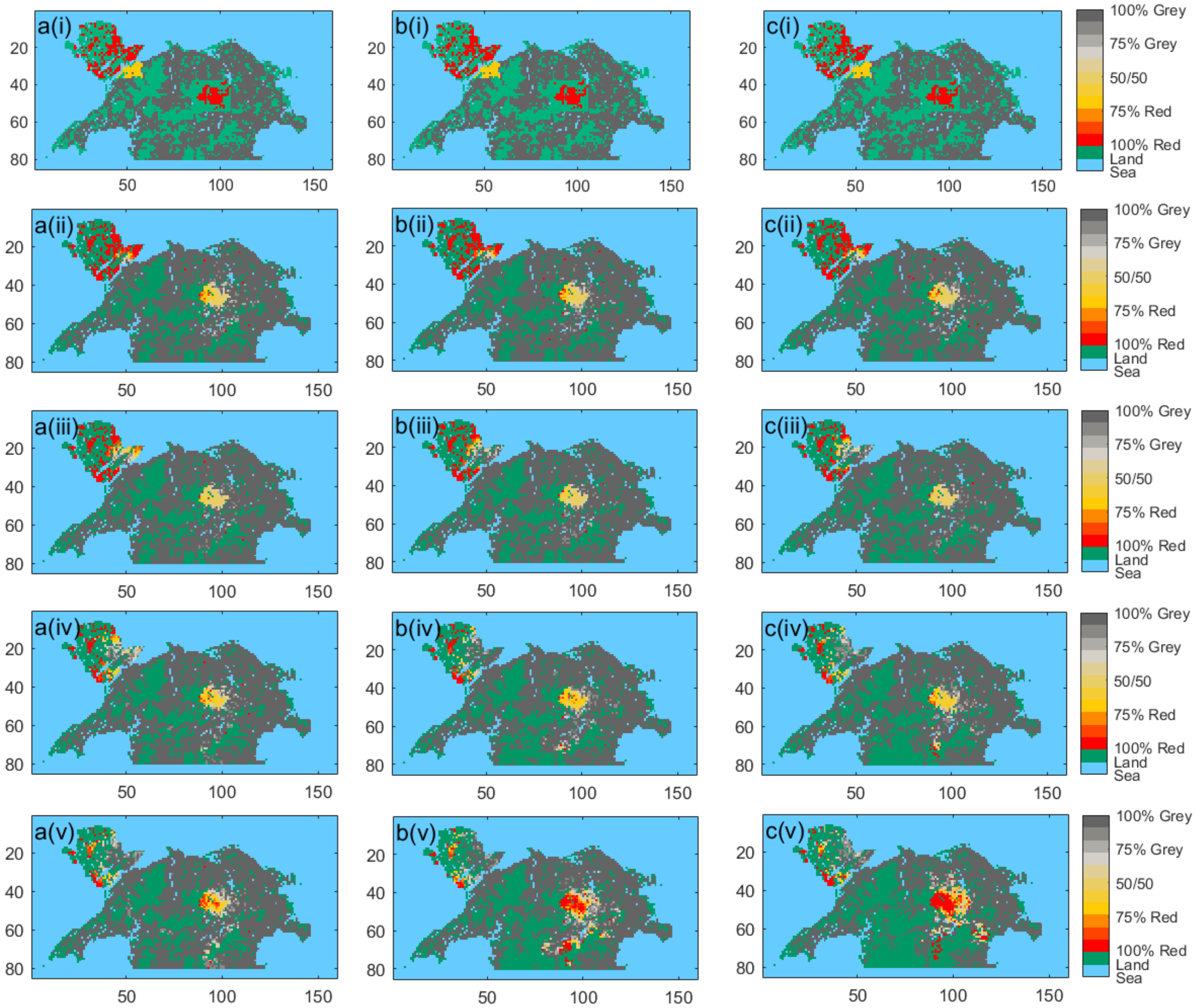

Figure 9: Red and grey squirrel occupancy results when pine marten are introduced into Mid Wales at a quarter of the carrying capacity (see Figure 4(a)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. Here (a) shows the results when the grey squirrel predation 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) shows the results after 20 years, (iv) shows the results after 30 years, and (v) shows the results after 40 years of simulation. 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.

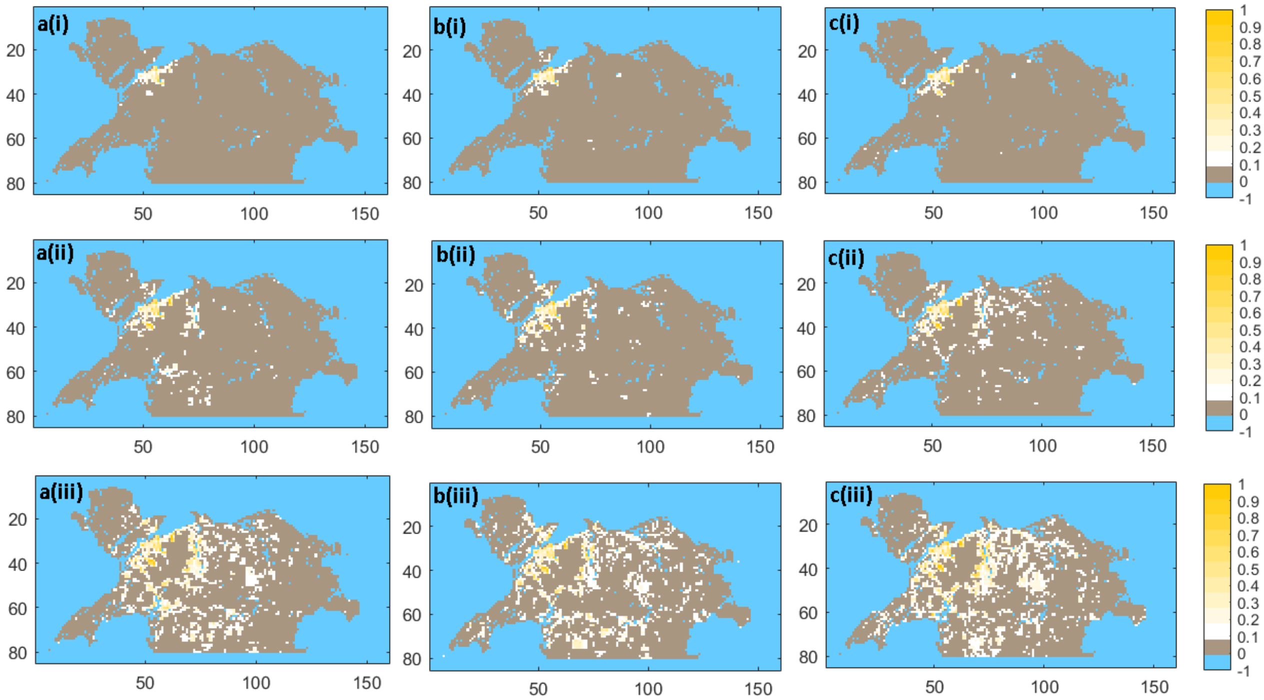

Figure 10: Pine marten expansion when pine marten are released into the Bangor region (see Figure 4(a)) in (a) 4 groups of 5 individuals, over 4 years, (b) 2 groups of 10 over 2 years and (c) a single group of 20 individuals at the start of the simulation. Image (i) shows the dispersal after 7 years, (ii) shows the dispersal after 15 years, and (iii) shows the expansion after 21 years of simulation.

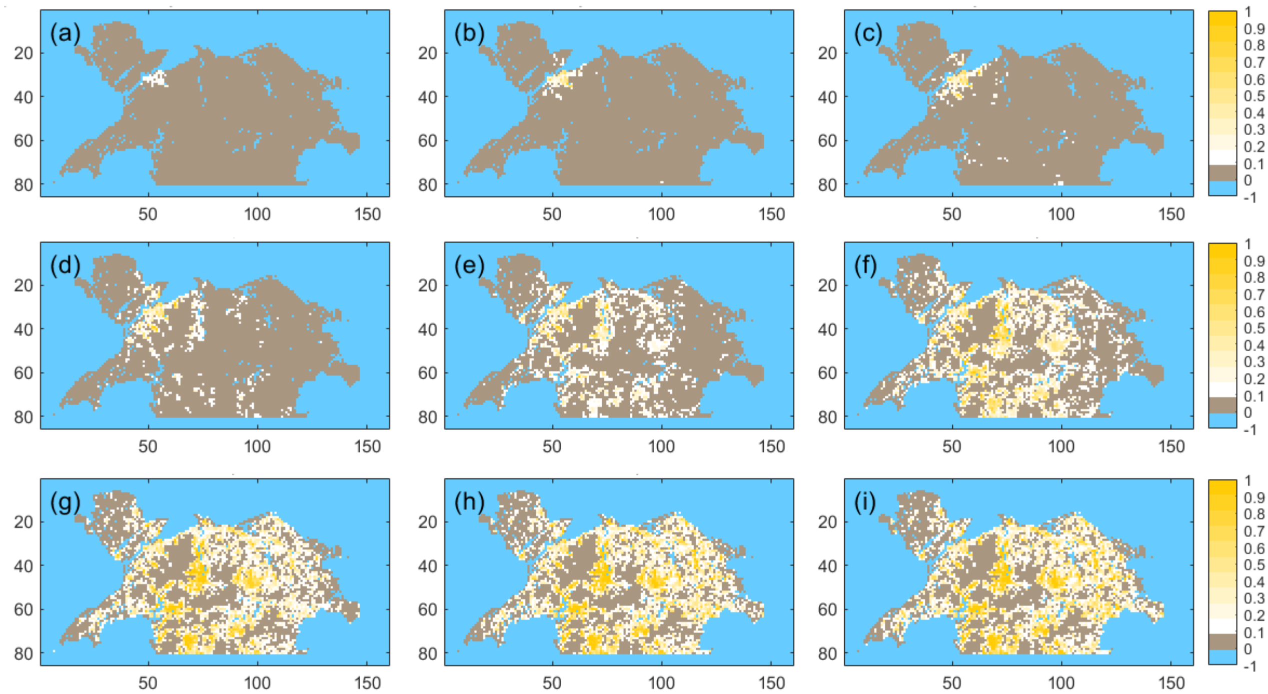

Figure 11: Pine marten range expansion when they are released into the Bangor region as two groups of 10 individuals in consecutive years. Here (a) shows the initial condition, (b) the pine marten expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

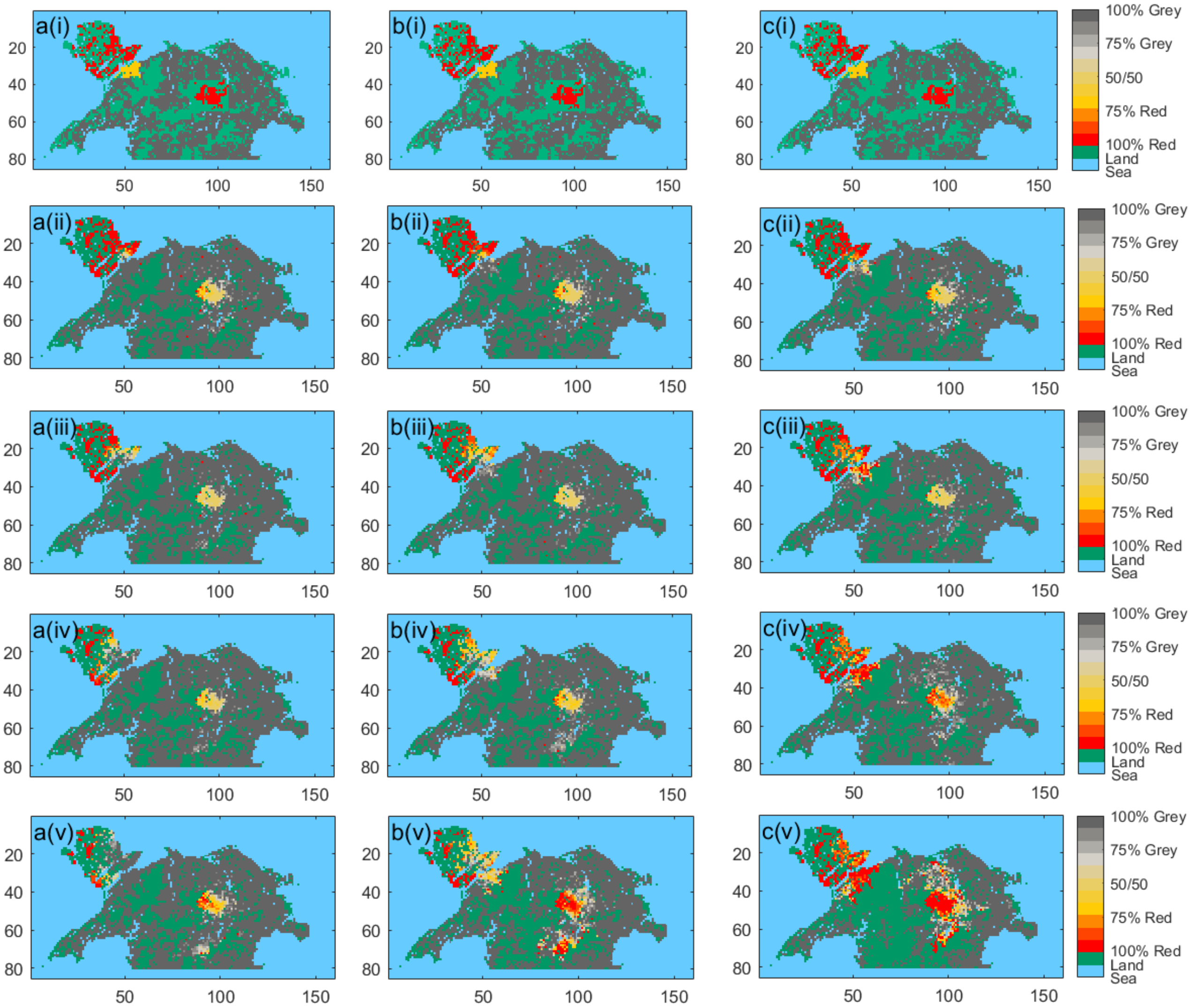

Figure 12: Red and grey squirrel occupancy results when pine marten are introduced into the Bangor region as two groups of 10 individuals in consecutive years (see Figure 4(b)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. Here (a) shows the results with 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) the results after 20 years, (iv) the results after 30 years and (v) the results after 40 years of simulation. 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.

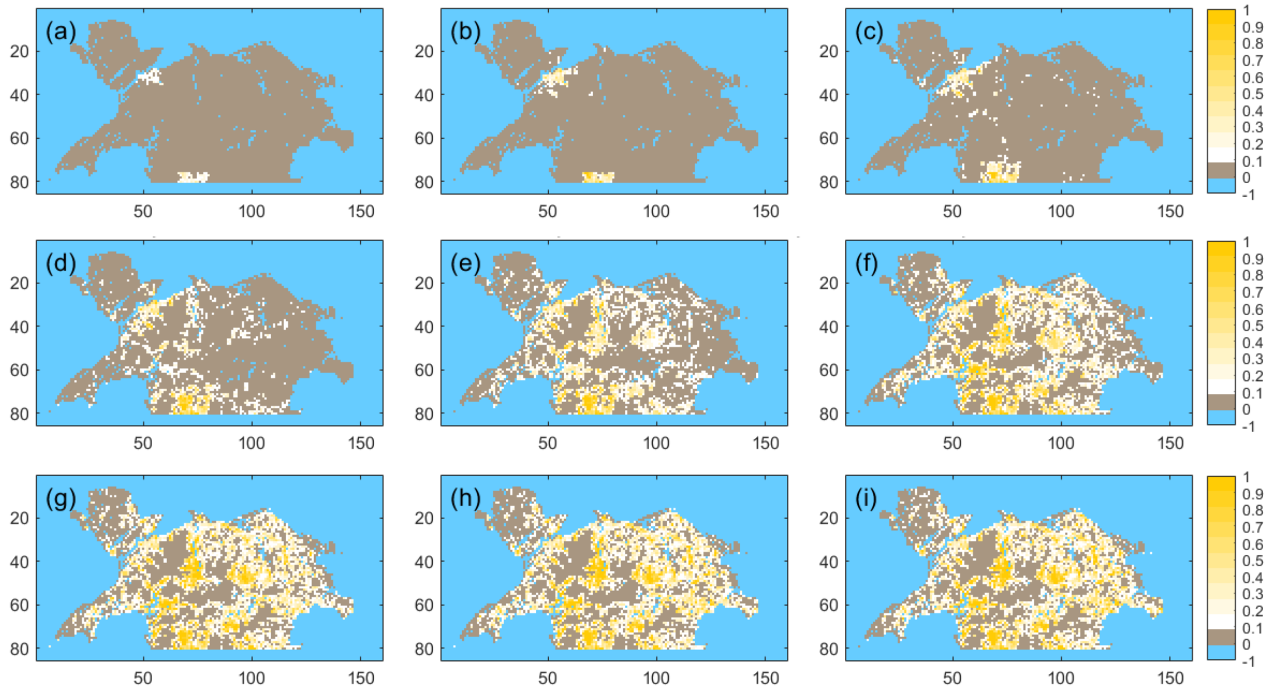

Figure 13: Pine marten range expansion when they are released into the Bangor region as two groups of 10 individuals in consecutive years, and into Mid Wales at a quarter of the carrying capacity (see Figure 4(c)). Here (a) shows the initial condition, (b) the pine marten expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

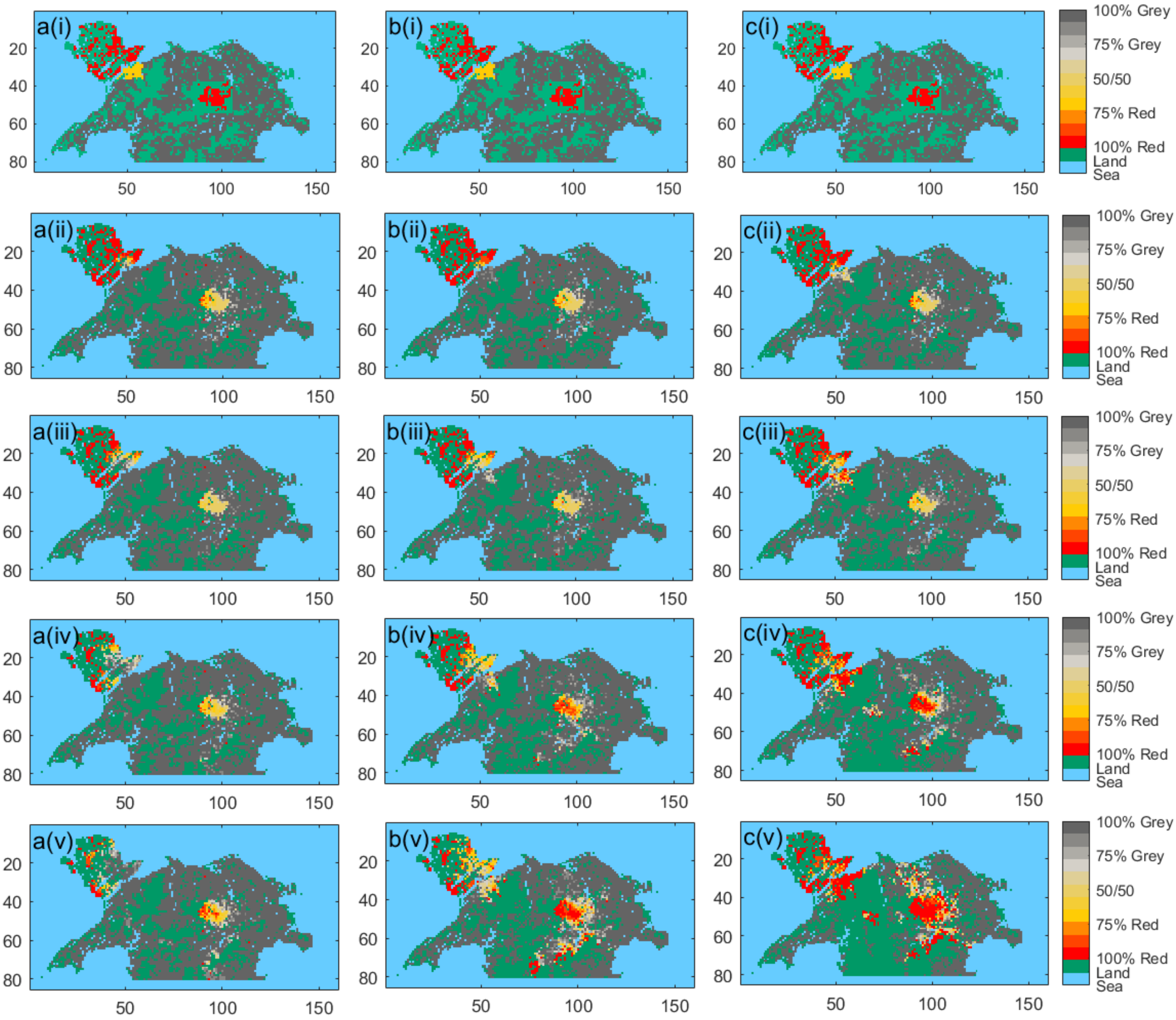

Figure 14: Red and grey squirrel occupancy results when pine marten are introduced into the Bangor region, as two groups of 10 individuals in consecutive years, and into Mid Wales at a quarter of the carrying capacity (see Figure 4(c)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. 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) the results after 20 years, (iv) the results after 30 years and (v) the results after 40 years of simulation. 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.

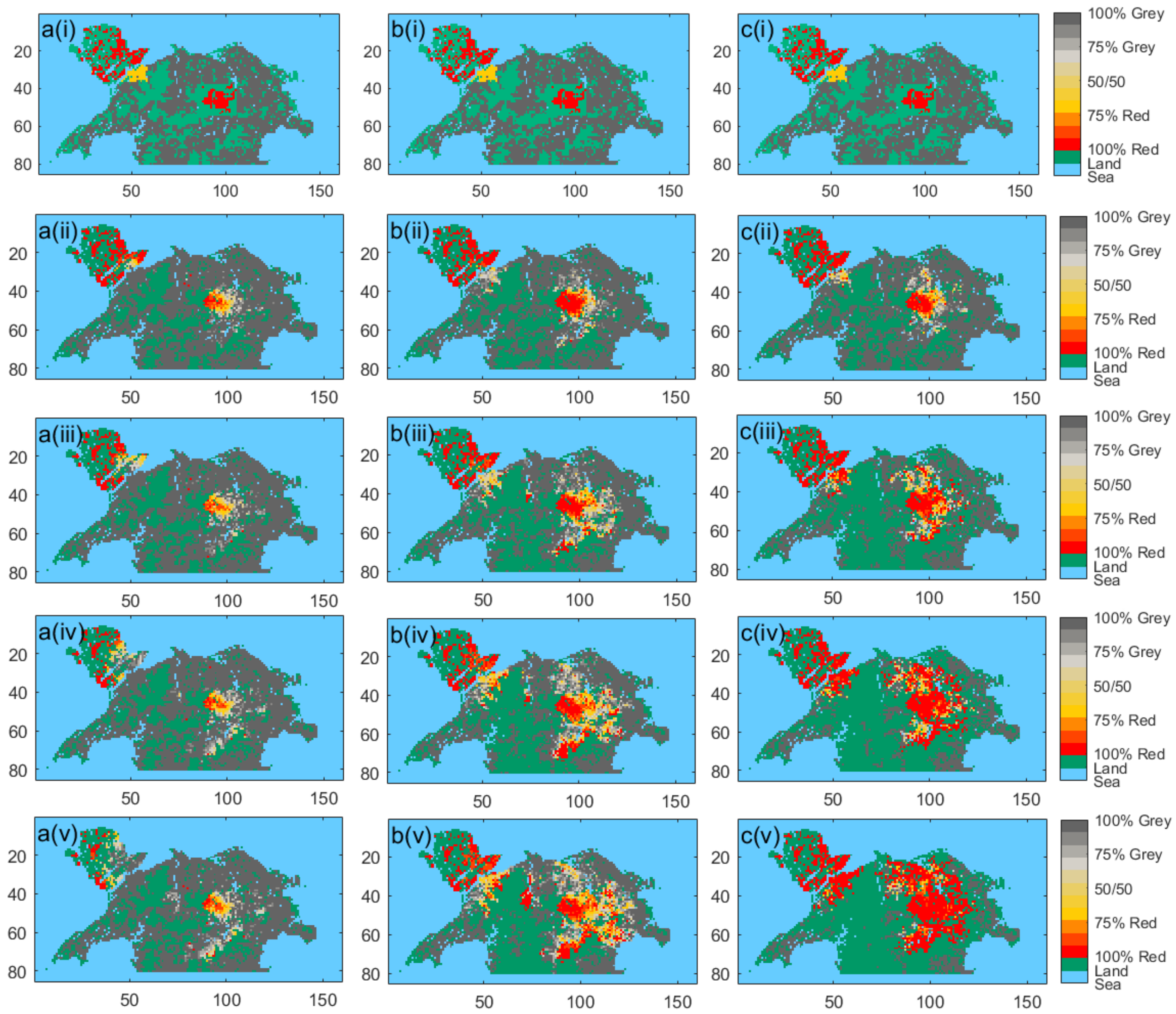

Figure 15: Red and grey squirrel occupancy results when pine marten are introduced into all available regions of North Wales at full carrying capacity (see Figure 4(d)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. Here (a) shows the results with predation 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) the results after 20 years, (iv) the results after 30 years and (v) the results after 40 years of simulation. 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.

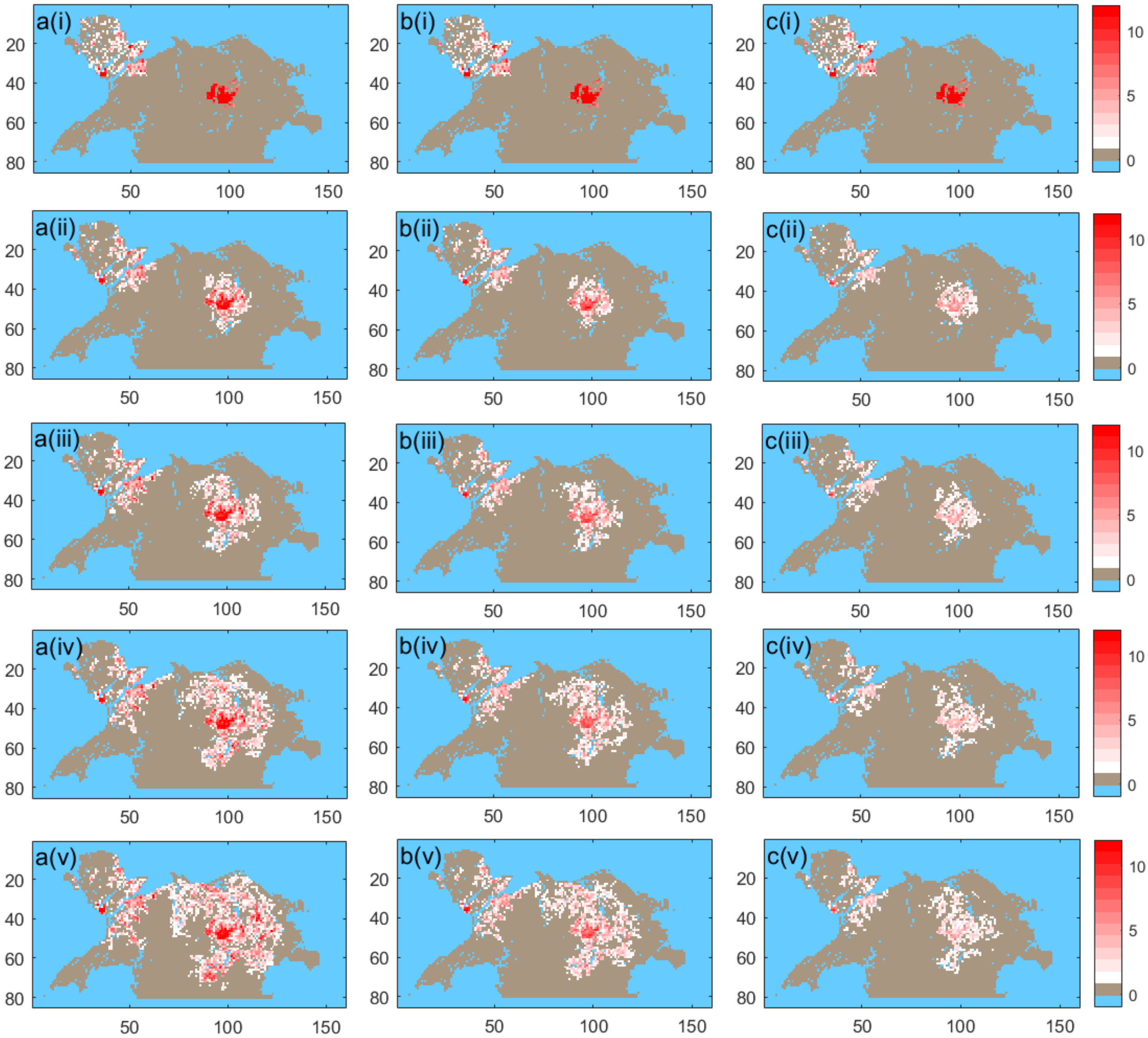

Figure 16a: Red squirrel density results when only red squirrels and pine marten are included in the model, with red squirrels being introduced into Clocaenog and Anglesey and pine marten being introduced into all available habitat, at carrying capacity. Here (a) shows the results when the grey squirrel predation rate $\mu_G = 0.75$, (b) shows the results when the grey squirrel predation rate is $\mu_G = 1.5$, and (c) shows the results when the grey squirrel predation rate is $\mu_G = 2.25$. Image (i) shows the initial condition, (ii) the results after 10 years, (iii) the results after 20 years, (iv) the results after 30 years and (v) the results after 40 years of simulation. The red squirrel predation rate $\mu_R = 0.2\mu_G$.

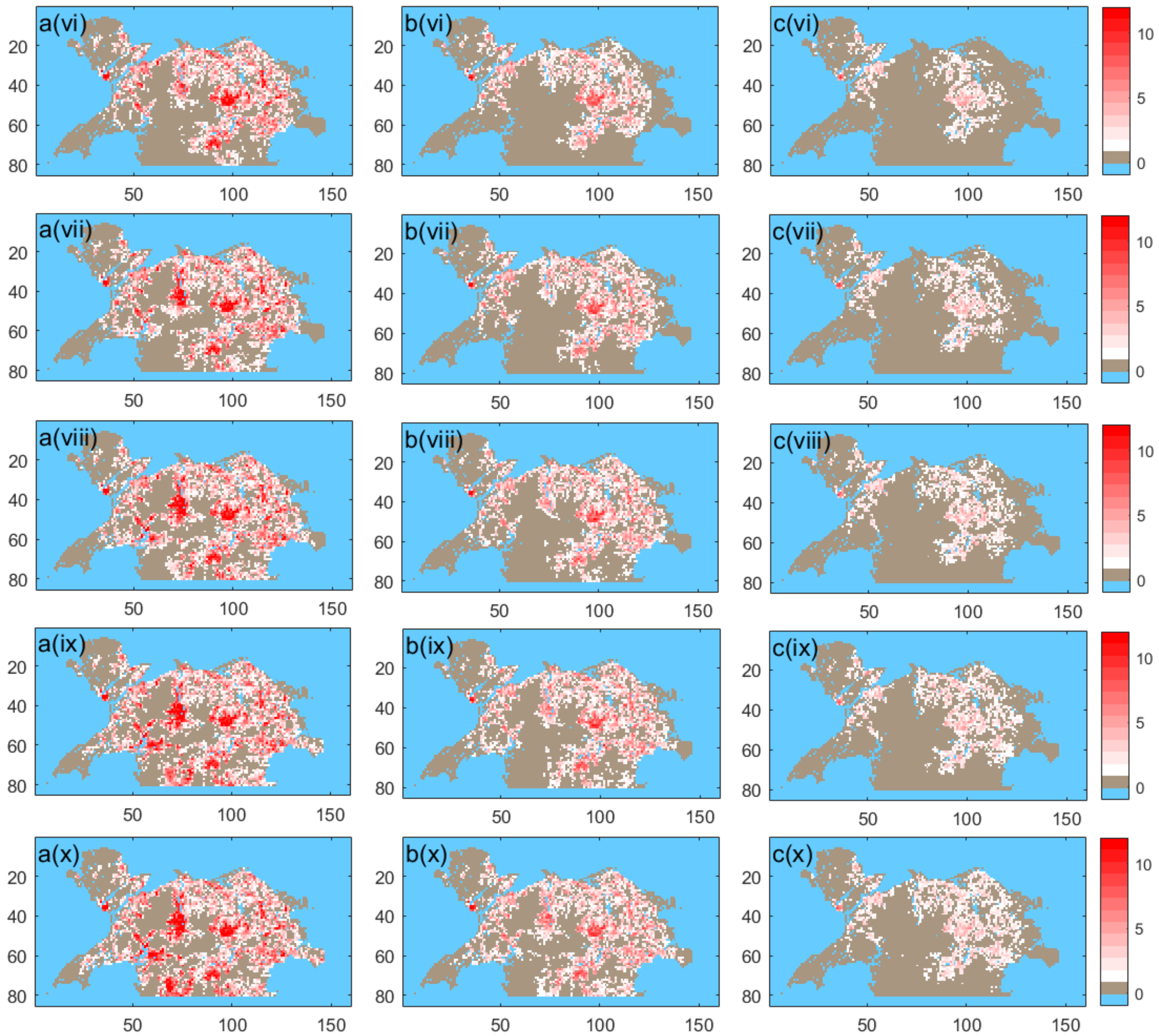

Figure 16b: Red squirrel density results when only red squirrels and pine marten are included in the model, with red squirrels and pine marten being introduced into all available habitat, at carrying capacity. Here (a) shows the results when the grey squirrel predation rate $\mu_G = 0.75$, (b) shows the results when the grey squirrel predation rate is $\mu_G = 1.5$, and (c) shows the results when the grey squirrel predation rate is $\mu_G = 2.25$. Image (vi) shows the results after 50 years, (vii) the results after 60 years, (viii) the results after 70 years, (ix) the results after 80 years and (x) the results after 90 years of simulation. The red squirrel predation rate $\mu_R = 0.2\mu_G$.

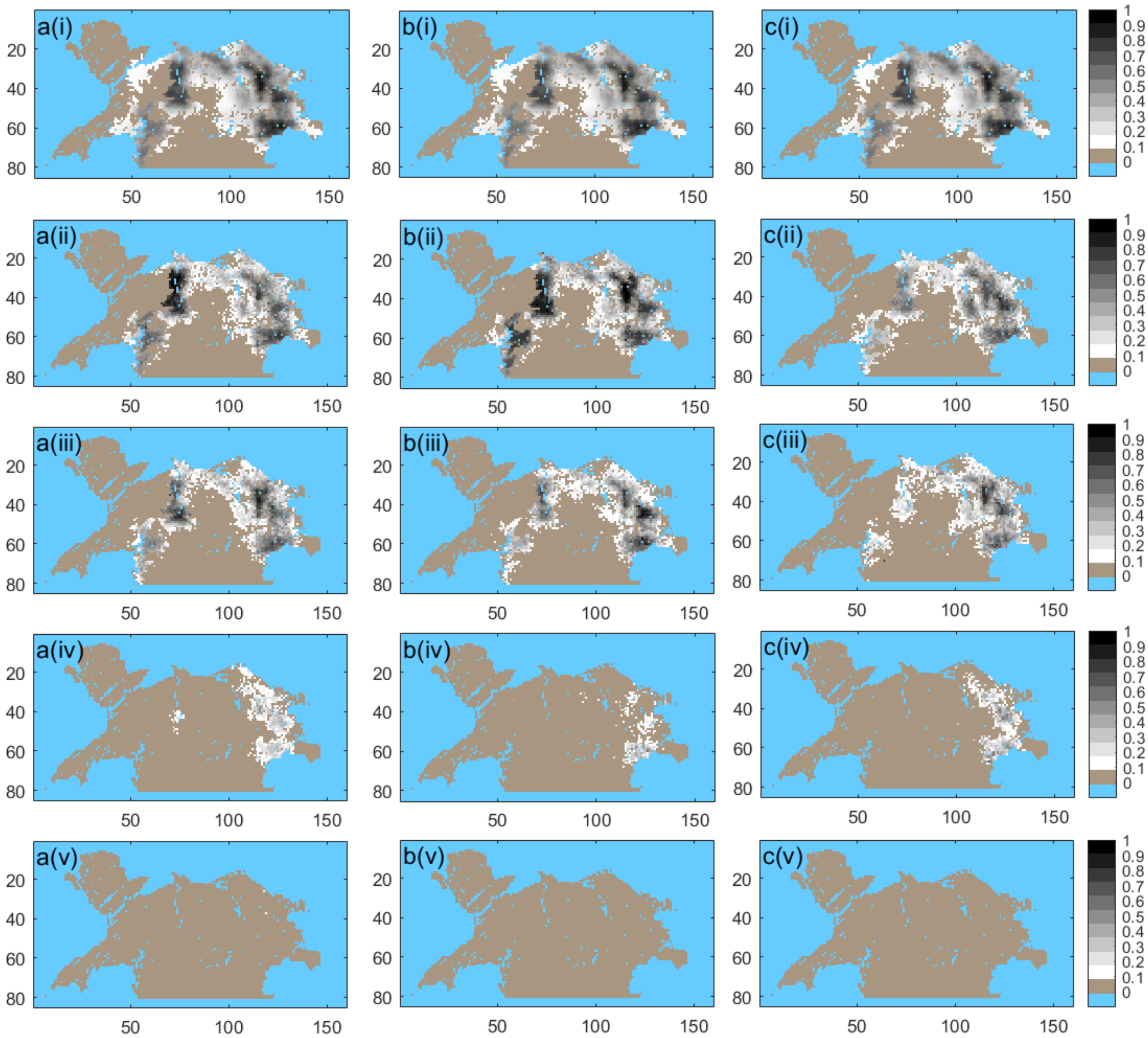

Figure 17: Changes in the prevalence of squirrelpox in grey squirrels over time, with infection transmission coefficient $\beta = 0.83$ and with pine marten being introduced into the Bangor region in two sets of 10 individuals and into Mid Wales at a quarter of the carrying capacity. Here (a) shows the 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) shows the results after 20 years of simulation, (iv) shows the results after 30 years of simulation, and (v) shows the results after 40 years of simulation.

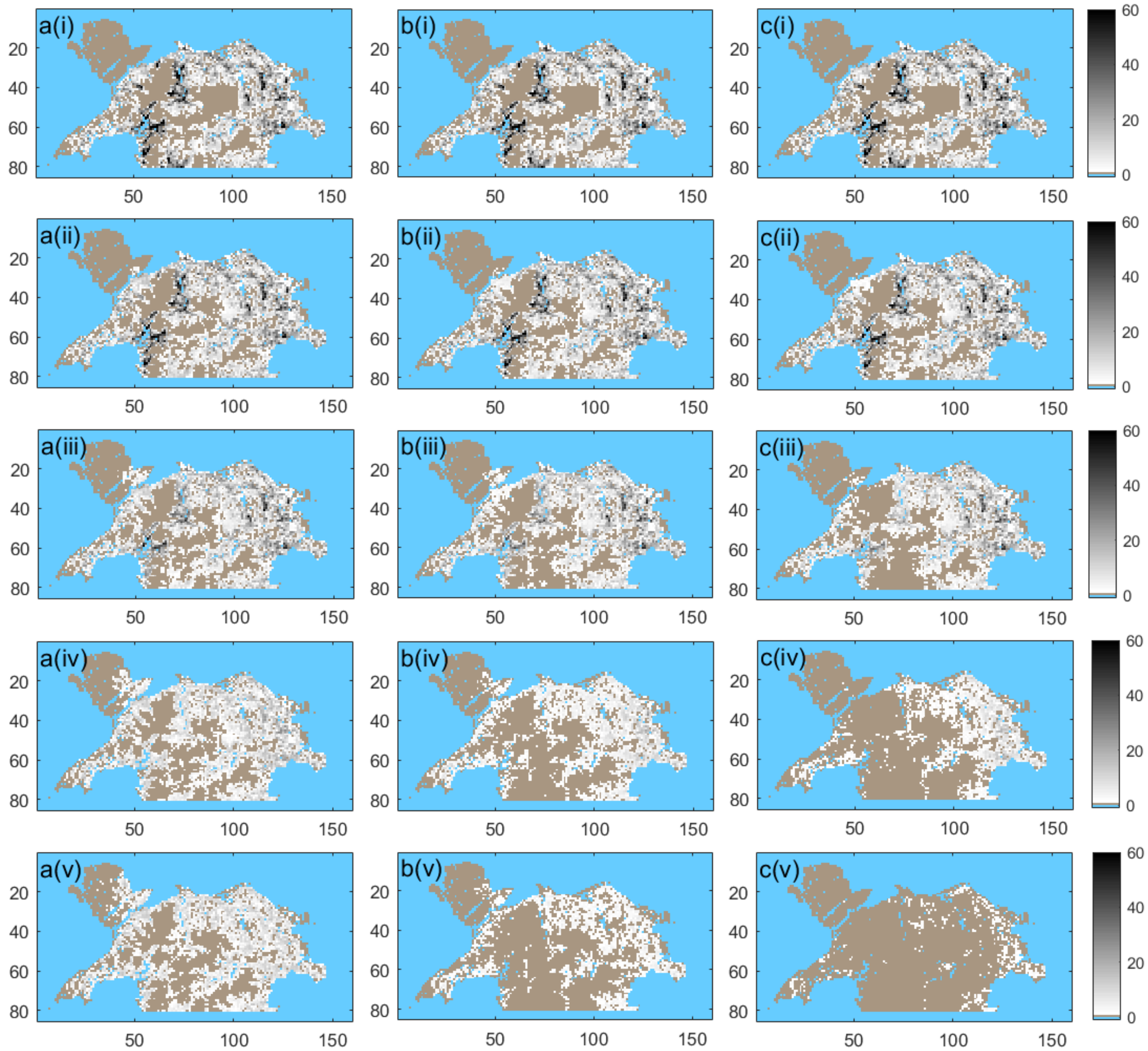

Figure 18: Grey squirrel density with infection transmission coefficient $\beta = 0.83$ and pine marten being introduced in 2 groups of 10 into the Bangor region and at a quarter of their carrying capacity into Mid Wales. Here (a) shows the results with predation parameter $\mu_G = 0.75$, (b) shows the 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) the results after 20 years, (iv) the results after 30 years and (v) the results after 40 years of simulation.

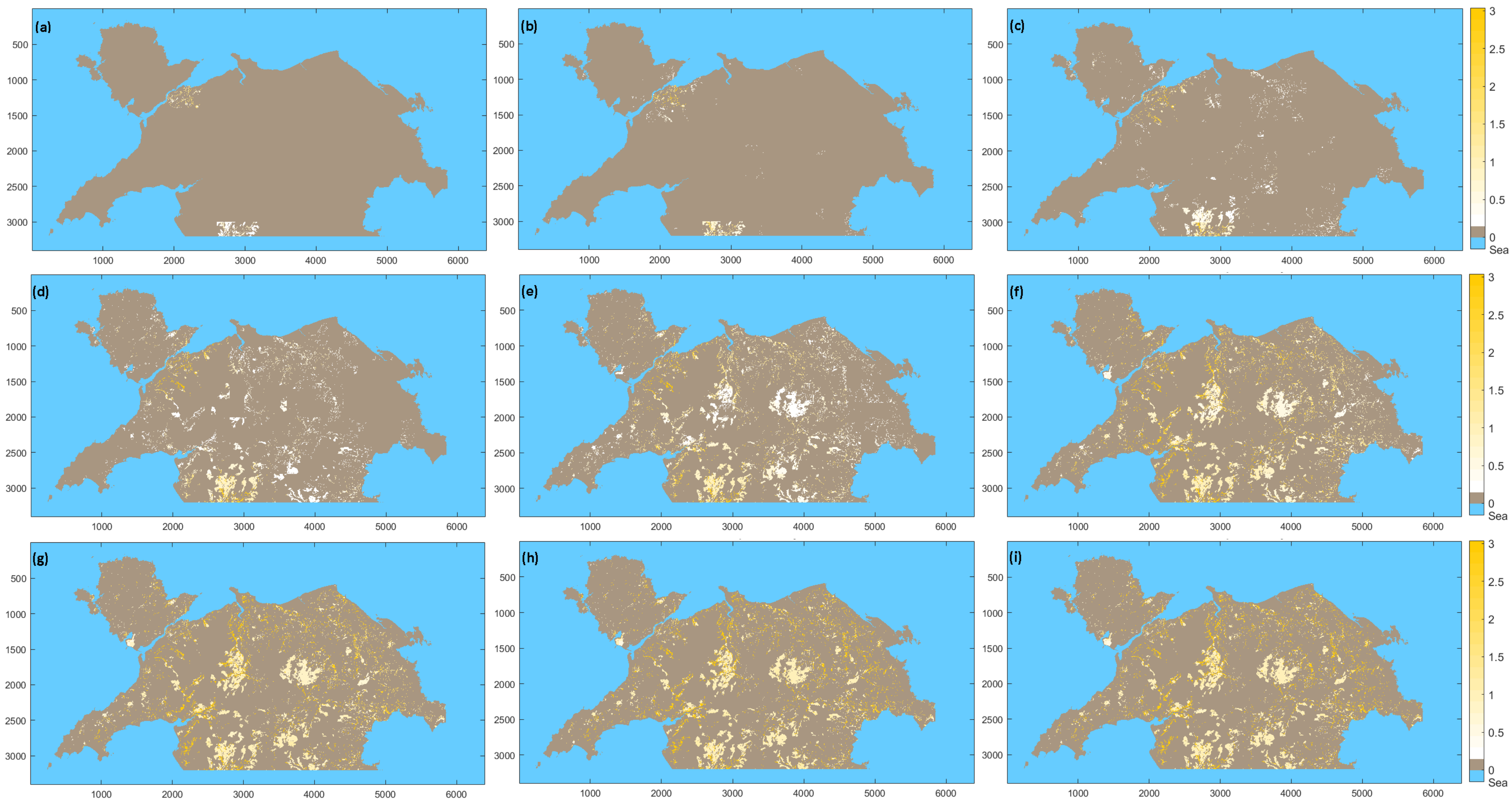

Figure 19: High resolution (25 m by 25 m) images showing pine marten expansion. The results are presented for (a) the initial conditions, (b) year 5, (c) year 10, (d) year 15, (e) year 20, (f) year 25, (g) year 30, (h) year 35, and (i) year 40 of the simulation. The colour-bar indicates the representative 1 km^2 density. Only densities greater than 0.14 km^{-2} are included.

4 Summary

We have extended a mathematical model of the red and grey squirrel system with squirrelpox, which uses a realistic representation of the landscape and habitat of North Wales, to assess the impact of pine marten predation on the squirrel occupancy and squirrelpox persistence. The model results compare scenarios in which pine marten are absent, where pine marten are assumed to migrate from Central Wales, where pine marten are released in the Bangor region and for the combined migration from Central Wales and release in the Bangor region.

In the absence of pine marten (and the absence of any other forms of intervention/grey squirrel control) grey squirrels can disperse onto Angelsey, via the Britannia bridge, and replace red squirrels across much of the island within the 40 year model time frame. Isolated populations of red squirrels survive primarily in the west of Anglesey, suggesting that the habitat in some regions of Anglesey is unsuitable for grey squirrels. Grey squirrels can also invade Clocaenog, primarily from the east, when pine marten (and other forms of grey squirrel control) are absent. A reduced population of red squirrels can persist in Clocnaenog for the 40 year model simulations, indicating that some of the habitat in Clocaenog is unsuitable for grey squirrels. The remaining red squirrel population in Clocaenog is subject to competition from grey squirrels dispersing from neighbouring regions of more suitable grey squirrel habitat.

When pine marten are included in the model, their dispersal is initially slow. It takes approximately 5-10 years for pine marten density to increase to levels which is sufficient to provide a source for dispersal. Thereafter, local and rare long distance dispersal of pine marten provides new source populations which leads to further range expansion such that North Wales is largely occupied by pine marten after approximately 25-30 years. When pine marten were released into the Bangor region (only) their initial range expansion occurs along the north coast of Wales, with expansion to the whole of North Wales occurring after 25-30 years. This range expansion profile was unaffected by the different pine marten release scenarios tested in the model. For assumed medium and high predation rates pine marten predation was sufficient to protect the majority of the red populations on Anglesey and promote red squirrel range expansion from Anglesey and Clocaenog.

When pine marten range expansion is assumed to occur through natural migration from pine marten populations in Mid Wales (only), pine marten do not disperse onto Anglesey until 20-25 years in the model. This allows grey squirrels to invade and disperse on Anglesey with red squirrel populations surviving along the west coast of Anglesey only. This suggests that the pine marten release into the Bangor region could play an important role in red squirrel conservation on Anglesey. The red squirrel populations in Clocaenog is protected under this scenario but the range expansion of red populations is reduced compared with the scenario of pine marten release into the Bangor region.

The combination of pine marten release into the Bangor region and natural migration from Mid Wales led to a marginal increase in the rate of pine marten range expansion with a consequent increase in the rate of red squirrel range expansion. The results are similar to when pine marten are released in the Bangor region only and therefore suggest that this proposed programme of release could have a significant impact on pine marten recovery and red squirrel conservation. In the long term pine marten density reaches high levels in regions between the south of Snowdownia and Mid Wales, with pine marten concentrations at Gwydir Forest park and Tremadog bay. Here predation is sufficient to eradicate grey squirrels. Red squirrels are capable of recolonising these regions within 100 years for low and medium predation values and thereby could become re-established in the majority of regions in North Wales. The slow rate of red squirrel re-establishment in some regions following grey squirrel extirpation is due to poor connectedness to viable red squirrel populations. Here, red squirrel trans-locations could improve the re-establishment rate.

The model predicts that the range expansion and increase in density of pine marten is sufficient to reduce grey squirrel density below the threshold that supports squirrelpox. Therefore, pine marten predation could drive the eradication of squirrelpox from North Wales within 40 years. Pine marten therefore could offer an ecosystem service in terms of disease management.

Red squirrels can survive and expand their current range in the presence of pine marten even though they are also subjected to pine marten predation (albeit at a reduced predation rate compared to grey squirrels). In the first 40 years of the model simulations red squirrel range expansion is focused around the Bangor and Clocaenog regions, though the majority of North Wales can be colonised by red squirrels within 100 years.

It is important to note that there is uncertainty in model generated results and in particular in the rate at which pine marten predate on red and grey squirrels. To examine this we simulated three different predation rates and this did have a significant impact on the results. For the scenarios tested, the impact of pine marten predation on reducing grey density and expanding red squirrel range increased as the predation rate increased. The model results clearly support the potential role that pine marten predation could play in reversing predator mediated competitive interactions between red and grey squirrels, as well as promoting the recovery of native red squirrel populations in North Wales.

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