Mathematical Modelling for Red Squirrel Conservation

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Abstract

In this thesis we develop mathematical models to understand the impact of forest management and pine marten predation on red and grey squirrel disease-mediated competitive dynamics. Our work extends a well-tested, spatially-explicit, stochastic model framework to assess the impact of forest management plans undertaken in designated red squirrel stronghold forests in Scotland. We determine the impact of the forest management on the population viability of red squirrels, when threatened by grey squirrel invasion. The model framework is further extended to identify natural strongholds - forest sites that act as red squirrel strongholds without the need for specific forest composition plans or grey squirrel control. The results have direct implications for forest management practice and will inform an upcoming review of red squirrel conservation policy on the future of designated strongholds.

The stochastic model framework was modified to include pine marten dynamics in order to assess the impact of pine marten predation on red and grey squirrel interactions. Over the last few decades pine marten have seen a recovery in their density and range in Scotland and Ireland, and this has coincided with a reduction in grey squirrel density and the recovery of red squirrels. We use the model to assess the impact of pine marten trans-locations into North Wales, with particular attention paid to the red squirrels resident on Anglesey and in Clocaenog (a forest site in North Wales). The thesis also develops a deterministic model framework to understand how a temporal refuge from predation can mediate the interactions of competing prey species. This deterministic framework is extended to consider the red and grey squirrel and pine marten system, where a temporal refuge can occur when pine marten predation is focussed on the peak phase of vole density cycles. The refuge from predation has the potential to reverse the beneficial advantage of pine marten for red squirrels, and provides a necessary note of caution for the role of pine marten as grey squirrel control agents.

The work in this thesis highlights how important mathematical models are in understanding the potential impact of conservation policy on focal species in Scotland and Wales.

I dedicate this thesis to my grandpa, Roy Pound, who is sadly no longer with us.

Without his encouragement, and occasional (gentle) browbeating, I would not have begun nor gained my degree in Mathematics and would never have begun, let alone finished, a PhD.

As he used to say "You've got a brain, so use it!".

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Contents

Chapter 1

Introduction

Rodents (*Rodentia*) are the most successful order of the class Mammalia, with around 40% of all mammals being rodents [58]. The order *Rodentia* is comprised of five sub-orders, one of which is *Sciuromorpha* which means squirrel-like. This sub-order contains three living (and three extinct) families [22], including the family *Sciuridae*. This family can be further divided into five sub-families, one of which is the sub-family *Sciurinae*, which consists of the Eurasian, North and South American tree squirrels as well as the flying squirrels. This sub-family is comprised of two separate tribes, with the flying squirrels being part of the tribe *Pteromyini*, and the rest belonging to the tribe *Sciurini*. The tribe *Sciurini* consists of five sub-genera. One sub-genus, known as *Sciurus* (whose name is derived from two Greek words: *skia*, meaning shadow, and *oura*, meaning tail, which references the ancient belief that squirrels used their tails to shelter themselves from the sun [15]) contains the majority of the common, bushy-tailed squirrels in Europe, temperate Asia as well as in North, Central and Southern America [145] (though a recent paper by de Abreu-Jr et al. [36] suggests that the genus *Sciurus* be split into multiple new genera). Of interest here are the Eurasian red squirrel (*Sciurus vulgaris*) and North American Eastern grey squirrel (*Sciurus carolinensis*), both of which belong to the sub-genus *Sciurus*.

1.1 Eurasian red squirrel (*Sciurus vulgaris*)

The Eurasian red squirrel, henceforth simply the red squirrel, resides in the northern temperate regions of the Eurasian continent (Figure 1.1). The red squirrel colonised the British Isles around the end of the last ice age (12,500 - 10,000 years ago [15]) and were the only species of squirrel on the islands until relatively recently. However, red squirrels are under threat in the United Kingdom, Ireland and also northern Italy, with recent estimates for the UK [79] 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 in England and Wales [79]. The decline of red squirrel populations has arisen due to the spread of, and competition with, the North American grey squirrel (*Sciurus carolinensis*).

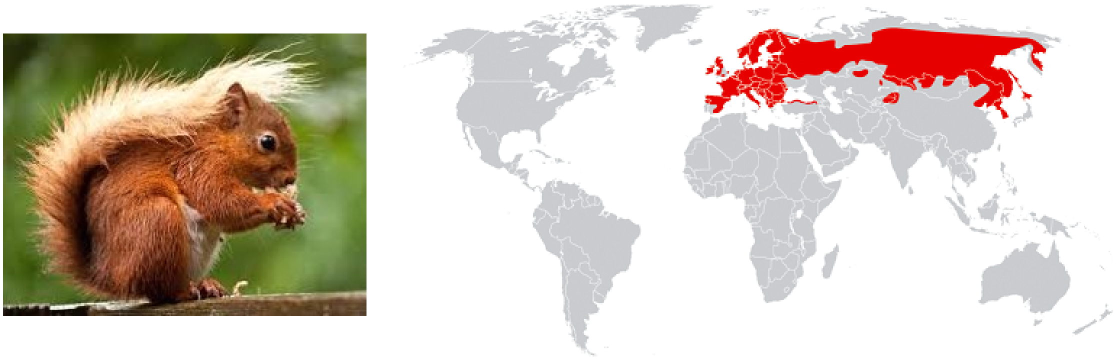


Figure 1.1: Eurasian red squirrel and the historic extent of its territory. Squirrel picture from [71]. Territory picture from [4]

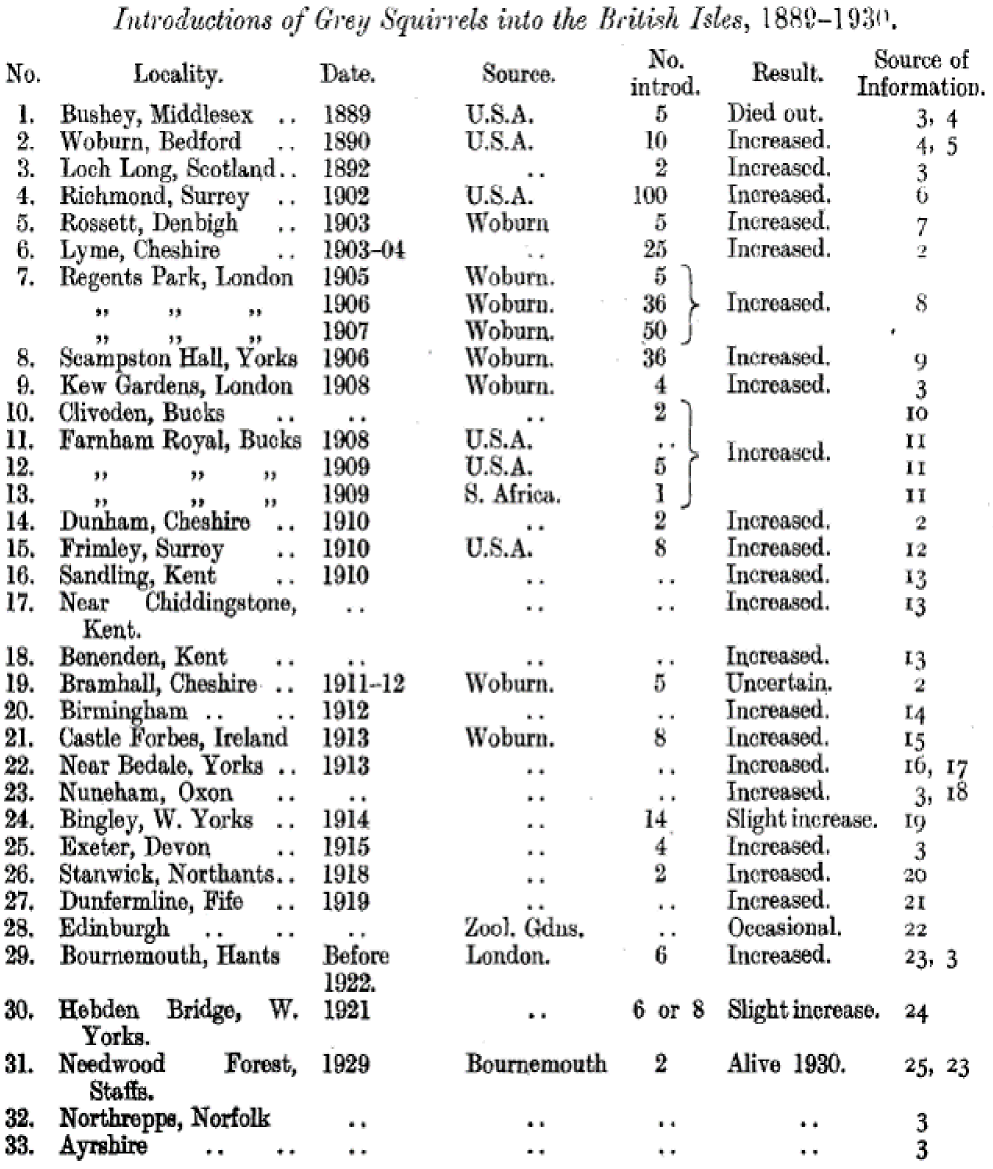
1.2 North American eastern grey squirrel (*Sciurus carolinensis*)

The North American Eastern grey squirrel, henceforth known simply as the grey squirrel, is a species of tree squirrel whose historic territory range is to be found in eastern and central North America (Figure 1.2). Grey squirrels were introduced into the United Kingdom in the 19th century, with the first verifiable introduction occurring in 1876 when Mr. T. U. Brocklehurst released grey squirrels, that he kept in a cage as a curiosity, into Henbury park, Cheshire after losing interest in them [86]. There is anecdotal evidence of grey squirrels being present earlier than

Figure 1.2: North American Eastern grey squirrel and the historic extent of its territory. Squirrel picture from [81]. Territory picture from [169]

this, with one sighting in North Wales being reported in 1830, however verifiable evidence is missing [86]. Grey squirrels were introduced into Ireland in 1913 [126]. There were numerous introductions of grey squirrels into the UK from the USA, with modern grey squirrel populations believed to be descended from introductions that began in 1890. Grey squirrels were also trans-located within the British Isles, with newly established populations being released in previously grey free territory. Figure 1.3 shows a non-exhaustive list of introductions that was compiled by Middleton [86], with many of the grey squirrel introductions originating from populations in Woburn, Bedford. Grey squirrels were also introduced into Australia, South Africa and Northern Italy. The squirrels introduced into South Africa and Australia did not survive but the population introduced into Piedmont in northern Italy in 1948 became established [86]. Further introductions into Genoa in the 1960s and trans-locations into Lombardy in the late 1990s have led to an expansion of grey squirrel range into Central Italy as well as north across the Po plain, with a real risk of future expansion into France and Switzerland [76, 78, 128].

When grey squirrels were introduced into the British Isles it was assumed they would co-exist with the native red squirrel. However, as is now well known, the introduction of a non-indigenous species into an area can have negative consequences for biodiversity and the native ecosystem [67, 131]. The impact of invasive on native species has been well documented [131], and the decline in red squirrel populations has coincided with the introduction, and range increase, of grey squirrels in the United Kingdom (Figure 1.4).



Introductions of Grey Squirrels into the British Isles, 1889–1930.

No.	Locality.	Date.	Source.	No. introd.	Result.	Source of Information.
1.	Bushey, Middlesex	1889	U.S.A.	5	Died out.	3, 4
2.	Woburn, Bedford	1890	U.S.A.	10	Increased.	4, 5
3.	Loch Long, Scotland	1892	..	2	Increased.	3
4.	Richmond, Surrey	1902	U.S.A.	100	Increased.	6
5.	Rossett, Denbigh	1903	Woburn	5	Increased.	7
6.	Lyme, Cheshire	1903–04	..	25	Increased.	2
7.	Regents Park, London	1905	Woburn.	5	Increased.	8
	,, ,, ,,	1906	Woburn.	36		
	,, ,, ,,	1907	Woburn.	50		
8.	Scampston Hall, Yorks	1906	Woburn.	36	Increased.	9
9.	Kew Gardens, London	1908	Woburn.	4	Increased.	3
10.	Cliveden, Bucks	..	..	2	Increased.	10
11.	Farnham Royal, Bucks	1908	U.S.A.	..		11
12.	,, ,, ,,	1909	U.S.A.	5		11
13.	,, ,, ,,	1909	S. Africa.	1		11
14.	Dunham, Cheshire	1910	..	2	Increased.	2
15.	Frimley, Surrey	1910	U.S.A.	8	Increased.	12
16.	Sandling, Kent	1910	..	..	Increased.	13
17.	Near Chiddingstone, Kent.	..	..	..	Increased.	13
18.	Benenden, Kent	..	..	..	Increased.	13
19.	Bramhall, Cheshire	1911–12	Woburn.	5	Uncertain.	2
20.	Birmingham	1912	..	..	Increased.	14
21.	Castle Forbes, Ireland	1913	Woburn.	8	Increased.	15
22.	Near Bedale, Yorks	1913	..	..	Increased.	16, 17
23.	Nuneham, Oxon	..	..	..	Increased.	3, 18
24.	Bingley, W. Yorks	1914	..	14	Slight increase.	19
25.	Exeter, Devon	1915	..	4	Increased.	3
26.	Stanwick, Northants	1918	..	2	Increased.	20
27.	Dunfermline, Fife	1919	..	..	Increased.	21
28.	Edinburgh	..	Zool. Gdns.	..	Occasional.	22
29.	Bournemouth, Hants	Before 1922.	London.	6	Increased.	23, 3
30.	Hebden Bridge, W. Yorks.	1921	..	6 or 8	Slight increase.	24
31.	Needwood Forest, Staffs.	1929	Bournemouth	2	Alive 1930.	25, 23
32.	Northrepps, Norfolk	..	..	..	..	3
33.	Ayrshire	..	..	..	..	3

Figure 1.3: A list of known grey squirrel introduction into and within the British Isles [86]

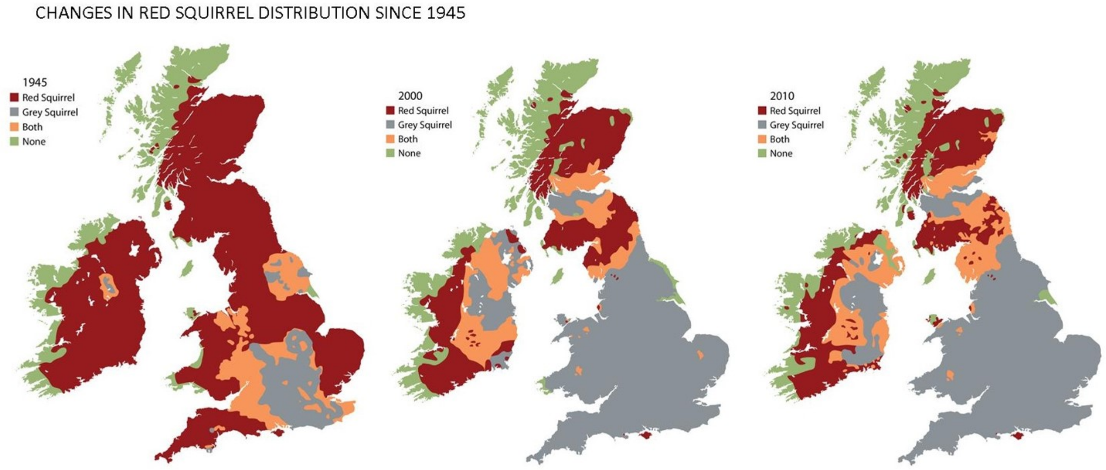


Figure 1.4: The change in the territorial expanse of red and grey squirrels in the United Kingdom [168]

1.3 Competition hypothesis

Several theories have been put forward to explain the replacement of red squirrels by grey squirrels. One theory is encapsulated by the Interference Competition Hypothesis (ICH) which suggests three possible forms of interference: (1) direct aggressive interaction, such as the chasing and attacking of red squirrels by grey squirrels, including the killing of young red squirrels in the nest, (2) the interruption of red squirrel mating chases by grey squirrels, and (3) forcing red squirrels to avoid areas intensively used by grey squirrels [159]. Regarding the first suggestion, there is no evidence of red squirrels acting aggressively towards grey squirrels and only one recorded instance of a grey squirrel being aggressive towards a red squirrel. There is also no evidence to support the possibility of grey squirrels killing young red squirrels in the nest. As Figure 1.5 shows, the majority of red-grey interactions are non-aggressive in nature. Likewise, there is no evidence that grey squirrels interfere in the mating chases of red squirrels. Furthermore, there is no evidence to support the idea that grey squirrels are intimidating red squirrels to such an extent that they actively avoid areas used by grey squirrels [159].

A second theory for red squirrel replacement states that increased interaction time between red and grey squirrels reduces the foraging time for red squirrels which leads to them being less successful at gaining the necessary food to survive. Observations suggest that, on average, a red squirrel will only spend around 2 minutes

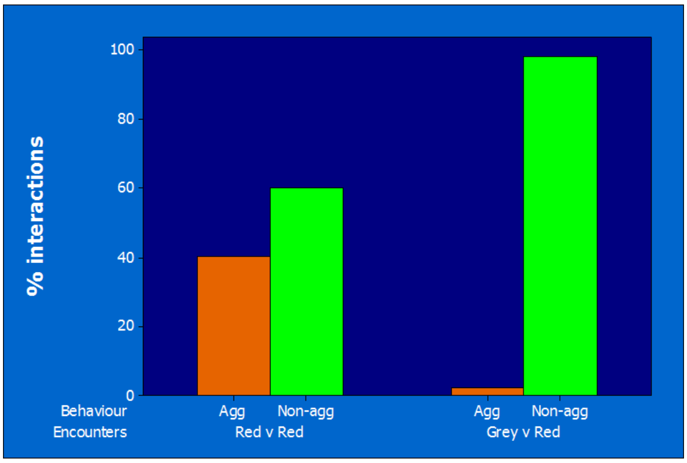


Figure 1.5: The percentage of red-red and red-grey interactions that are aggressive and non-aggressive, redrawn using tables 1 & 2 from [159]

per day in winter and around 1 minute per day in summer interacting with grey squirrels. Observations also indicate that whenever a red and grey squirrel cross paths the red squirrel will freeze in place for around 1 minute whilst the grey squirrel passes by, generally without even noticing the red squirrel, with the red squirrel continuing on as normal once the grey squirrel has passed. Hence, it is unlikely that such a small increase in squirrel-squirrel interactions significantly impacts the ability of red squirrels to gather food [159]. Thus the ICH does not explain the replacement of red squirrels that has been observed.

An alternative hypothesis states that grey squirrels are simply better at surviving. In their native range, grey squirrels inhabit the deciduous woodlands of eastern North America with highest densities in forests containing oak, hickory and walnut [68]. This specialisation on deciduous habitats and their types of tree seeds is thought to be key in the ability of grey squirrels to cope with phytotoxic polyphenols in acorns. While red squirrels do feed on acorns, their digestive efficiency of acorns is only 59% compared to grey squirrels, giving the latter a food refuge and, coupled with their high densities a decisive, competitive advantage in deciduous-dominated forest landscapes [64]. The theory states that, since grey squirrels have a competitive food advantage they put on more body mass during the autumn in preparation for winter. The increased body mass leads to more grey squirrels surviving until the spring to reproduce - thus leading to a higher growth rate in the population. However, despite the advantage gained by grey squirrels due to increased densities in deciduous habitat, the difference in change in body mass is not deemed to be of significance due to the differing foraging strategies of the squirrels. One study observes that red squirrels spend around 67% of their time, throughout the year, in the tree canopy whereas grey squirrels spend only around 14% of their time in the canopy. Thus, in this instance, having a larger body mass would not be advantageous for the red squirrels due to them being required to traverse the thin tree branches that are found in the canopy [65]. There is, however, evidence that grey squirrels will steal food that red squirrels have cached for the winter months. This theft of food means that the overall body mass of the red squirrels is reduced and, more importantly, the body mass of the female red squirrels is reduced, with potential consequences for litter size and reproductive success. It has also been noted that, in forests where red squirrels co-habit with grey squirrels, red squirrels tend to be smaller than those that live in red only forests. This suggests that red squirrel juveniles and sub-adults are in direct competition with grey juveniles and sub-adults and, since grey squirrels grow faster than their red counterparts, the red squirrels are at a competitive disadvantage and lose out with respect to foraging and resource intake [54]. This then leads to a reduction in the recruitment of red squirrel juveniles into the adult population [15] when grey squirrels are present. Therefore the presence of grey squirrels is likely to reduce the red squirrel litter size, the number of annual litters as well as juvenile recruitment into the red squirrel population [11, 53, 114, 161]. These effects can thus manifest themselves as grey squirrels exerting a competitive effect on the red squirrels which, from a modelling perspective, reduces their average reproductive rate.

1.3.1 *An outline of the mathematical models describing red and grey squirrel competition*

To try and verify the competition hypothesis mathematical models have been developed to simulate and explain the interactions between the two species of squirrel. The first model study was reported by Okubo et al. [91] who developed a deterministic diffusion-competition model that consists of a system of two coupled reaction-diffusion equations. These equations (1.1) are population equations of the

Lotka-Volterra type that include isotropic diffusion.

$$\frac{\partial S_1}{\partial T} = D_1 \nabla^2 S_1 + a_1 S_1 (1 - b_1 S_1 - c_1 S_2) \tag{1.1a}$$

$$\frac{\partial S_2}{\partial T} = D_2 \nabla^2 S_2 + a_2 S_2 (1 - b_2 S_2 - c_2 S_1) \tag{1.1b}$$

In the above system S_i denotes the population densities, D_i are the diffusion coefficients, a_i the net birth rates, $1/b_i$ the carrying capacities, c_i are competition coefficients, T is the time, and $i = \{1, 2\} = \{\text{grey}, \text{red}\}$ denotes the species of squirrel. Competition is assumed to occur via indirect competition for resources, hence the competition term serves to reduce the growth rate of the other species. Furthermore, it is assumed that grey squirrels outperform red squirrels, which manifests itself by ensuring that $b_2 > c_1$ and $c_2 > b_1$.

The solutions to this model predicted that the grey squirrels would expand in waves across the domain of interest and replace red squirrels through a process of competitive exclusion at the wave-front. The wave speed in the two species competitive system suggested by Okubo et al. [91] is similar to the expansion rate noted by Reynolds [101], who recorded annual records of the presence of each squirrel species near Norfolk, eastern England, between 1960 and 1981. Reynolds discretised the area around Norfolk into 5 km squares and recorded if either or both species of squirrel was present in a particular grid square. The data showed a clear increase of grey squirrels and a corresponding decrease of red squirrels which resulted in the near eradication of red squirrels from the study site. It should be noted that the diffusion coefficients used by Okubo et al. are somewhat larger than suggested by field data. The rate of grey squirrel expansion calculated by Okubo et al. is slower than the speed that would be observed for a single species expanding in the absence of competition.

This model is not without issue. The model is fully deterministic which, despite allowing the easy identification of individual parameter effects, means that population sizes have to be large enough to allow stochastic effects to be ignored. However, the context of the model requires small population numbers to be considered which means that stochastic effects cannot be assumed to be negligible. The model assumes that the squirrel populations are homogeneously dispersed across the domain and that they diffuse isotropically in a homogeneous environment. Given that the forest landscape of the British Isles is fragmented and consists of a variety of species of tree these assumptions would appear to be an over-simplification which could overly smooth the resultant dispersal and density profiles.

An alternative model was suggested by Rushton et al. [107]. They designed a spatially explicit population dynamics model (SEPM) that integrated geographic information system (GIS) data to describe the domain. The model was separated into two components. One used the GIS data, which stored information on the environment, habitat as well as population information such as carrying capacities, to define habitat blocks, where each block corresponded to a given geographic area and was separated from neighbouring blocks by areas of uninhabitable land. This gives the model the spatial heterogeneity that was lacking in Okubo et al. [91]. The second part of the model simulates the changing dynamics of the squirrel populations, with competition assumed to be present whenever both species of squirrel were present in a specific block. Competition was assumed to be uni-directional, with red squirrels having no competitive effect on grey squirrels, and was instituted by a linear reduction effect. If the grey squirrel population was at $x\%$ of the grey squirrel carrying capacity in a given block then the red squirrel carrying capacity for that block, the reproductive success of the red squirrel, as well as the adult population would be reduced by $x\%$. Thus the model assumes that competition occurs according to the interference hypothesis that has been mentioned previously. The model also incorporated population dispersal by allowing members of a species present in a given habitat block to move to a different, neighbouring, block. Dispersion within each block was not considered.

Rushton et al. [107] compared the model results with data published by Reynolds [101]. Rushton's model did manage to re-create the observed data with a good degree of accuracy, however as Rushton et al. noted in their conclusion, in order to obtain these results the parameter values for grey squirrel mortality and fecundity needed to be outside of the observed averages, with mortality being lower and fecundity higher. This suggests that the competition model is not sufficient to explain the observed decline in red squirrel density. In fact, as noted previously, the interference hypothesis that is assumed here does not have a strong enough evidence base to justify its use as an explanation for the replacement of red squirrels by grey squirrels. Alongside this, the model is complex and rules based (Figure 1.6), therefore it is difficult to assess the effects of individual parameters and to explain the key drivers of the population dynamics.

Tompkins et al. [147] adapted the deterministic model presented by Okubo et al., by considering a temporal differential equation model of red and grey squirrel competition (equation 1.2). This model represents the dynamics between the two species in linked grid squares that allowed the results to be compared with those of Rushton et al. [107]. The temporal model that was used by Tompkins et al. is

$$\frac{\mathrm{d}S_G}{\mathrm{d}T} = [a_G - q_G(S_G + c_R S_R)]S_G - bS_G \tag{1.2a}$$

$$\frac{\mathrm{d}S_R}{\mathrm{d}T} = [a_R - q_R(S_R + c_G S_G)]S_R - bS_R \tag{1.2b}$$

where S_i represents the population density, a_i the birth rate, q_i the susceptibility to crowding, c_i the competition coefficient and b the adult mortality rate for $i = \{G, R\}$ denoting grey and red squirrels respectively.

The results of this model are shown in Figure 1.7. As can be seen, whilst the model does reproduce the qualitative elements of the replacement of the red squirrels by grey squirrels, this replacement does not occur on the correct time-scale. This result is in accordance with the results from Okubo et al. [91] and Rushton et al. [107] which suggests that competition alone is an insufficient explanation for the rate of squirrel replacement observed by Reynolds [101].

1.4 Squirrelpox virus

Mathematical models suggest that competition alone is unable to reproduce the rate at which red squirrels are replaced by grey squirrels. This implies that other processes may be occurring that drive the rate of red squirrel decline. It was noted by Middleton [86] that there had been instances of disease epidemic that led to a dramatic reduction in the local red squirrel population. Middleton even went as far as to suggest a disease, carried by grey squirrels, to which the grey squirrel was immune and that was fatal to red squirrels. This idea proved to be controversial

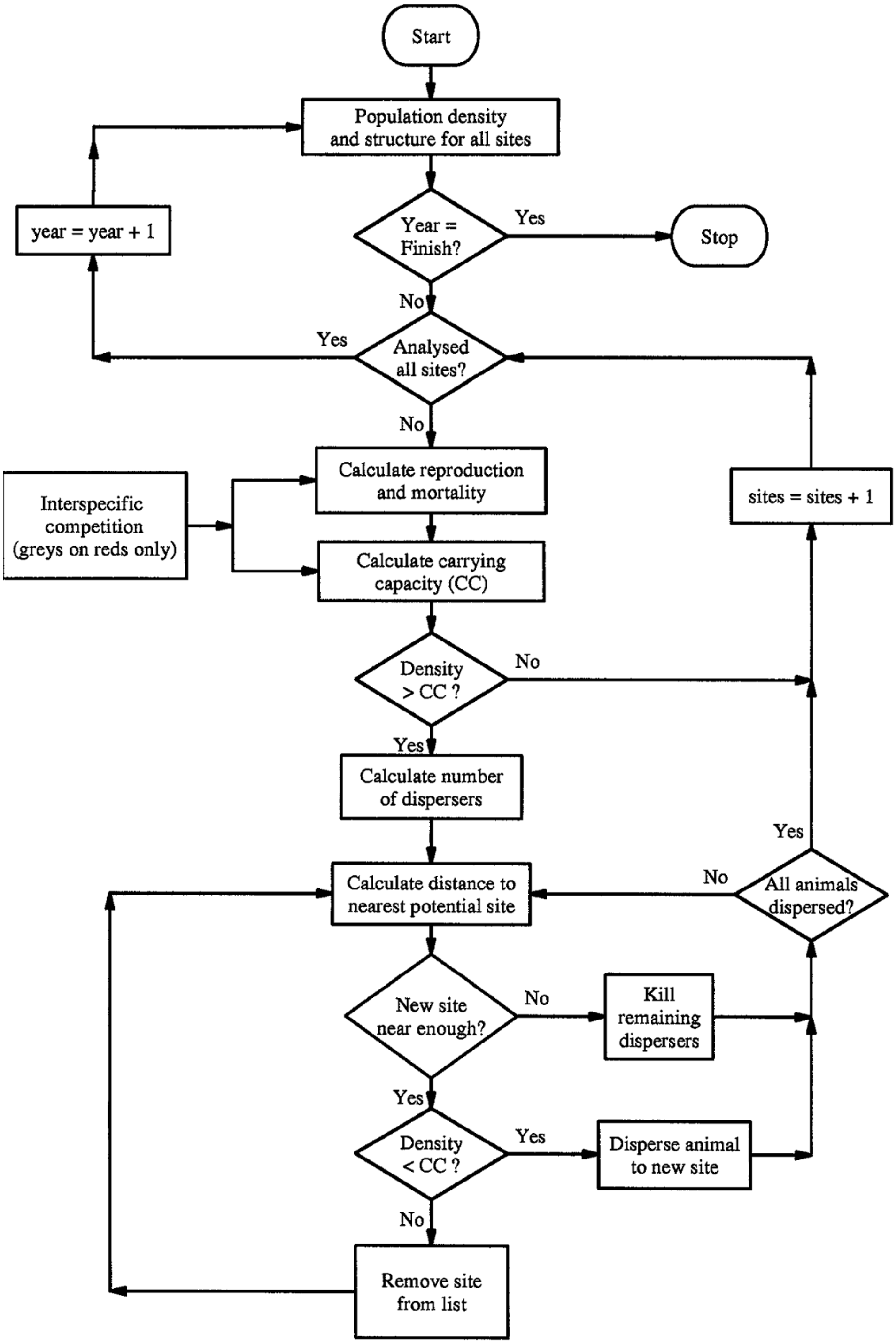


Figure 1.6: Flow diagram for the stochastic competition model proposed by Rushton et al. [107]

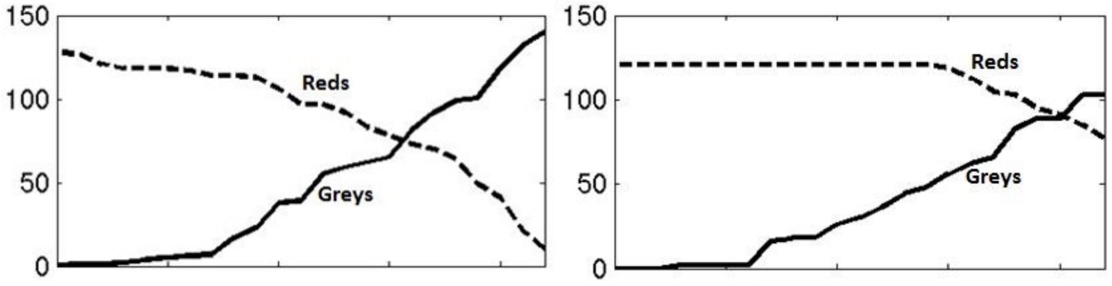


Figure 1.7: Left: Results from Reynolds [101] observed data showing the number of grid squares where red and grey squirrels are present. Right: Results from the competition only model suggested by Tompkins et al. [147]

and was heavily contested by his contemporaries, with many noting that population collapse due to disease had occurred in the red squirrel population before the introduction of the grey squirrel, which Middleton attributed to population fluctuations that are common in rodents. As such, disease was not considered to be a contributing factor in the replacement of red squirrels by grey squirrels. This view began to change with the publication of a paper by Edwards [40] in 1962 which documented the near eradication of the local red squirrel population in Shropshire from a disease that was later to be recognised as a virus [83]. In fact, this is the earliest accepted documentation of the disease that is now known as squirrelpox.

Squirrelpox is a member of the poxvirus family of viruses that include diseases such as smallpox and cowpox. The common symptoms of squirrelpox include skin lesions and scabs around the face, hands and feet, and genitals, as well as lethargy. The pox virus was first identified in red squirrel lesions in Norfolk in 1984, and the causal link between infection with squirrelpox and the development of skin lesions was confirmed by Thomas et al. [143] in 2003. Squirrelpox is a highly virulent disease for red squirrels, with mortality due to the virus being almost certain [147]. Despite the impact of squirrelpox on red squirrels, there was no evidence to implicate grey squirrels as the vector of disease. This changed in 2000 with the publication of a paper by Sainsbury et al. [110] in which he used the Enzyme-Linked Immunosorbent Assay (ELISA) method to identify the presence of squirrelpox antibodies, which would indicate that the squirrel being tested had at some point contracted the squirrelpox virus. Of the squirrels he tested, 61% of the 223 apparently healthy grey squirrels tested positive, indicating that they had been exposed to the squirrelpox

Figure 1.8: A red squirrel with the scabs and skin lesions symptomatic of squirrelpox [168]

virus whilst only 2.86% of the 140 (4/140) red squirrels had the antibody present. Furthermore, 3 of the squirrels that tested positive for the antibodies had a poxvirus associated disease. According to Crouch et al. [35], a species can be considered as a reservoir host of a poxvirus if the prevalence of the related antibodies exceeds 8-12% of the population, assuming that the virus remains present in the host and can be transmitted to other species. Thus, that 61% of the grey squirrels tested by Sainsbury et al. [110] had the antibodies present suggests strongly that the grey squirrel may be a host species for the squirrelpox virus. This relationship was confirmed by Tompkins et al. [146] when grey squirrels that had been deliberately infected with the squirrelpox virus failed to catch the disease, although antibodies were developed by the squirrels in all cases. McInnes et al. [82] also found evidence of the virus, and the corresponding antibodies, in grey squirrels in North America, where there have been no recorded instances of death due to the virus [82].

Strauss et al. [138] outlines the various scenarios that can occur when there is a disease that is shared between a native and a non-native species. The scenario of relevance here is the spill-over scenario in which the invasive organism carries the infectious disease which can infect native competitors. When the introduced disease has a higher virulence amongst the native population than it does with the invasive species then the disease can act as a biological weapon, which can lead to a disease-mediated invasion. Disease-mediated invasions are relatively common [138], and are important factors in explaining the replacement of native species by invasive species that are phylogenetically similar, which is the case with regards to red and grey squirrels. Moreover, the invasive species and the introduced disease can benefit from an indirect mutualism, whereby the invasive species acts as a host for the disease, which allows the disease to spread amongst the native species, which in turn helps the invasive species out-compete the native. Anderson [2] outlines two possible outcomes, either the disease manifests itself as a stable endemic infection which exerts a steady influence over time, or the disease manifests as recurrent epidemics in the native population, with sometimes unpredictable intervals between epidemics. In either case, the disease has the effect of impairing the native population which creates an opportunity that the invasive species can exploit to increase its range and population size, which in turn benefits the disease. Therefore the existence of the disease could tip the competitive balance in favour of the invasive species [138].

1.4.1 *An outline of the mathematical models describing the epidemiological interaction between red and grey squirrels*

One of the first attempts to understand the role, if any, that the squirrelpox virus played in the replacement of red squirrels by grey squirrels was undertaken by Rushton et al. [108]. The SEPM competition only model [107] that has been outlined above was extended to include the spread of a poxvirus. The model assumed that the disease spread amongst fragmented populations due to the dispersal of infected animals and included the probability of encounters between infected and non-infected animals, the chance of exposure to the virus and the subsequent mortality that is a consequence of the virus.

The results of this model suggest that the squirrelpox virus could explain the rate of expansion of grey squirrels via a disease-mediated, apparent competition dynamic. In particular, the grey squirrel expansion rate, the disease infection rate as well as the encounter rates between the two species of squirrel were outlined as key factors that determine the rate of red squirrel extermination. Furthermore, the model suggested that the virus was possibly too virulent to be able to spread effectively across the landscape, thus infection is localised into separate outbreaks with the expansion of the grey squirrel triggering new outbreaks that lead to replacement. However, the results generated for the epidemiological model were similar to those for the competition only model, which means that either the competition or the disease mediated apparent competition could be used as an explanation for the replacement of the red squirrels. The work was further updated by Rushton et al. [109] in 2006 and used the competition and disease model [108] to try and recreate the known decline of the red squirrels in Cumbria between 1993 and 2003. The main finding of this paper came from empirical observations found by comparing known distributions of red and grey squirrel with and without disease. The finding was that the inclusion of the disease led to replacement rates that were between 17 and 25 times faster than those found for competition alone. While the disease dynamics can accelerate the replacement of red squirrels, it should be noted that this does not mean that competition between the species should be discounted as a factor altogether.

An alternative to the individual based model pursued by Rushton et al. [108] was developed by Tompkins et al. [147]. This model extended the deterministic competition only model (equation 1.2) and consists of a susceptible-infected (SI) model for the red squirrel population along with a susceptible-infected-recovered (SIR) model for the grey squirrels (see equations 1.3 below).

$$\frac{\mathrm{d}S_G}{\mathrm{d}t} = [a_G - q_G(H_G + c_R H_R)]H_G - bS_G - \beta S_G(I_G + I_R) \tag{1.3a}$$

$$\frac{\mathrm{d}I_G}{\mathrm{d}t} = \beta S_G(I_G + I_R) - bI_G - \gamma I_G \tag{1.3b}$$

$$\frac{\mathrm{d}R_G}{\mathrm{d}t} = \gamma I_G - bR_G \tag{1.3c}$$

$$\frac{\mathrm{d}S_R}{\mathrm{d}t} = [a_R - q_R(H_R + c_G H_G)]H_R - bS_R - \beta S_R(I_G + I_R) \tag{1.3d}$$

$$\frac{\mathrm{d}I_R}{\mathrm{d}t} = \beta S_R(I_G + I_R) - (\alpha + b)I_R \tag{1.3e}$$

where H_i is the total population of the red and grey squirrels, denoted by R, G respectively.

The model assumes that there is a common infection rate β, with cross species infection occurring in both directions. Competition is still present in this model, with the competition coefficients c_R and c_G being the same as defined for the competition only model (equation 1.2). The key assumptions of this model can be seen in the parameters α and γ. The parameter α is the death rate due to disease, with only the red squirrels suffering mortality due to the disease. The parameter γ is the rate of recovery from the disease, with only grey squirrels recovering and gaining immunity from the disease. This dynamic is encapsulated in the fact that the recovered individuals can not become re-infected or re-enter the susceptible pool. Thus, the infection is fatal to red squirrels but has no effect on grey squirrel mortality. These assumptions are somewhat stronger than what has been observed in nature, with there being at least one instance of a grey squirrel dying from a poxvirus and a red squirrel recovering from squirrelpox under laboratory conditions [143] but they do conform to the pattern of relative effects that are known to be associated with the squirrelpox virus.

To incorporate spatial dynamics the model used the same scheme as the competition only model, with a proportion of the population in a given grid-square dispersing into neighbouring squares at the end of a years simulation. The results of this model closely matched those that were produced by Reynolds [101] (Figure 1.9). Furthermore, the model suggests that the disease acts to reduce the red squirrel population via a local disease outbreak which then provides an opportunity for the expansion of the grey squirrels due to reduced competition from the lower density red population. The results are therefore in accordance with those produced by Rushton et al. [108]. The model of Tompkins et al. [147] was also robust to parameter change and thus the notion that the inclusion of disease dynamics increases the rate at which replacement of the red squirrels occurs is reinforced. The main drawback of this model is that it is fully deterministic and therefore does not consider the possibility of stochastic extinction or disease fade-out which may be important since the population numbers are small and eradication events are being considered.

The models considered so far have either been fully deterministic or individual based stochastic models. Both model types have their respective positive and negative aspects which means that neither should be discounted. To try and harness the

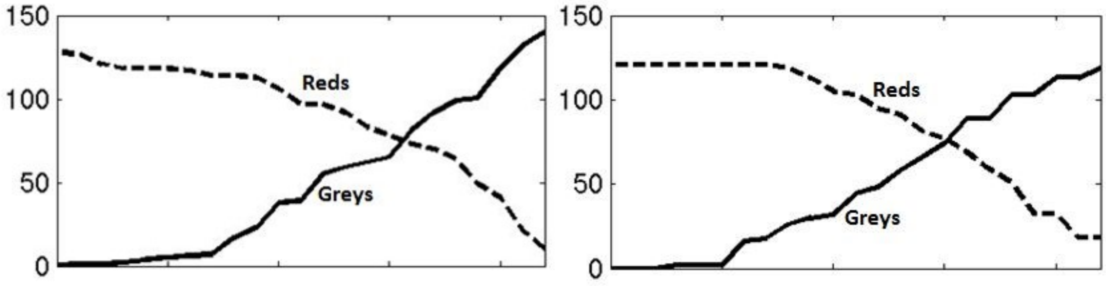


Figure 1.9: Left: Results from Reynolds [101] observed data showing the number of grid squares where red and grey squirrels are present. Right: Results from the epidemiological model suggested by Tompkins et al. [147]

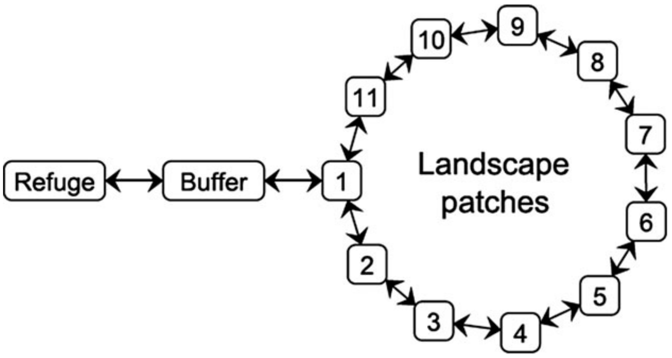


Figure 1.10: The spatial domain chosen by White et al. [164] that encompasses a ring of habitat patches and a single buffer and refuge patch

positive aspects of both of these frameworks White et al. [164] took the epidemiological model presented by Tompkins et al. [147] and transformed it into a stochastic model by viewing each event probabilistically using the approach of Gillespie [47]. An outline of the probabilities of the events that pertain to grey squirrels are shown in table 1.1 below. Similar probabilities are also used for the events involving red squirrels.

Spatial dynamics were added as in the model presented by Tompkins et al. [147], with a proportion of the population moving to an adjacent spatial patch. The spatial domain consisted of 3 types of patch, which were 11 standard landscape patches, 1 buffer zone patch and finally a refuge patch. The 11 landscape patches were organised in a ring, with the movement of individuals allowed between adjacent patches. This ring of patches was then connected to the buffer zone patch and refuge patch as shown in Figure 1.10.

The probability of dispersal between different patches is governed by the follow-

Event	**Population Change**	**Probability of Event**
Birth of S_G	$S_G \to S_G + 1$	$[(a_G - q_G(H_G + c_R H_R))H_G]/R$
Natural Death of S_G	$S_G \to S_G - 1$	$[bS_G]/R$
Infection of Grey	$S_G \to S_G - 1, I_G \to I_G + 1$	$\Big[\beta S_G\Big((I_G + I_R) + \theta \sum_{Adjacent} (I_G + I_R) + \theta^2 \sum_{Corner} (I_G + I_R)\Big)\Big]/R$
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	$R_G \to R_G - 1$	$[bR_G]/R$
Sum of Rates		$R = \Sigma[\text{rates}]$

Table 1.1: Stochastic probabilities of events involving grey squirrels. Events involving red squirrels are similar, except with subscripts R, G interchanged.

ing: for a grey squirrel in the susceptible class S_G, the probability of it moving to a different patch is given by $P(S_G \to S_G - 1) = [mS_G F(H_G, H_R)]/R$, where m is the long range dispersal rate, $F(H_G, H_R) = (H_G + c_R H_R)^2/(K_G)^2$ is a function representing saturation dispersal and R is the sum of all the rates present in the model. The time period between events is the same as that used by Rushton et al. [107], namely that the time between events is exponentially distributed, with $T_{event} = -\ln(\sigma)/R$ and σ being a random number drawn from a uniform $U[0, 1]$ distribution.

The results of this model further support the hypothesis that the disease acts by creating a population collapse due to a virus outbreak rather than through constant infection. This means that the rate of replacement in a disease free environment is slower than that for an environment where the squirrelpox disease is present, with the increased rate due primarily to the population crashes that are induced by the outbreaks of disease. The model also notes the dependence of the rate of red squirrel replacement on the carrying capacity of the grey squirrels in the buffer and refuge zones. This suggests that there may be a minimum density of grey squirrel necessary to ensure replacement.

The red/grey squirrel model was subsequently modified and used by White et al. [166] to show that applied grey squirrel control methods in the Borders region of England and Scotland were insufficient to prevent the northward spread of squirrelpox due to multiple and complex dispersal routes for disease spread and insufficient available resources for disease management. This result led to a shift in Scottish conservation policy from disease control at the landscape level in southern Scotland to protecting priority red squirrel populations in the region [120]. Jones et al. [63] used the model in conjunction with a 16-year field data set on grey squirrel control to parameterise and validate a model framework that was used to inform the best strategy to protect red squirrels on the island of Anglesey from grey squirrel re-invasion. Jones et al. [62] adapted the model of red and grey squirrel interactions to assess differing forest design plan scenarios at the local forest scale to ensure continued red squirrel population viability in the Kidland-Uswayford Forest System, Northern England. Following the research, a renewed monitoring programme based on feeding signs was set up in the forest in 2017 and red squirrel presence is monitored annually [73]. These later studies highlight how mathematical modelling has had an impact on a range of red squirrel conservation initiatives.

1.5 Conservation efforts

The models outlined in the previous section reproduce field data with a good degree of accuracy. Thus it is possible that a mathematical model could be used to investigate different control strategies in order to aid the conservation and survival of the red squirrel in Great Britain. There are a number of different strategies that are available, and a selection shall be outlined here.

The first option when it comes to species conservation and control is to do nothing. This strategy assumes that the native and invasive species will reach a natural equilibrium with both species present at a stable population. This strategy also assumes that the red squirrels will gain immunity to the squirrelpox virus over time, leading to them becoming a host species for the virus along with the grey squirrels. However, this strategy is not feasible for the red/grey squirrel system being considered in this thesis. The scale of decline in the red squirrel population has so far been dramatic, with red squirrels becoming nearly extinct in England and Wales. There is a stable population in Central and Northern Scotland, but the assumption that this population will remain viable in the long term is not backed up by a strong enough evidence base and therefore the total eradication of the red squirrel in the British Isles could occur.

A different possibility is the use of a vaccine to eradicate the squirrelpox virus. Vaccinating wildlife species has previously been done, with a vaccine used to eradicate fox rabies in Europe. However the strategy to vaccinate squirrels in the UK has two issues that render it non-viable. The first is that competition only models, such as that proposed by Tompkins et al. [147], still lead to the replacement of red squirrels by grey, albeit on a longer time frame. It is possible that geographic and forest composition factors could lead to a red squirrel population remaining stable in Scotland, mainly due to a reduced carrying capacity of grey squirrels leading to the competitive effect of greys not being sufficient to completely remove the red squirrels, but this fact has not been established and therefore has considerable risk. A more prominent issue with this strategy is the difficulty and efficacy of the administration of a vaccine. Vaccines are produced in one of two ways, either by the use of a related virus, for example the cowpox virus which was successfully used as a smallpox vaccine, or by the deliberate weakening of the virus in a laboratory in order to reduce its lethality and enable an effective immune response to be established. The issue here is that the squirrelpox virus appears to be the sole virus on its particular branch of the poxvirus tree. This means that a weakened form would have to be used. However, given the virility of the disease in red squirrels, and the inability to control exact doses that are administered to individual squirrels, there is a possibility that this route could serve to introduce virus outbreaks into areas where they had previously been absent. Thus it is possible that the attempt at vaccination could in fact cause the outbreaks that lead to the eradication of the species. Lastly, even if a viable vaccine that could be administered in unregulated doses was created, it would need to be used on a large proportion of the red and grey squirrels in order to introduce herd immunity and is likely to prove financially prohibitive.

Tangential to this idea is the possibility of administering birth control to grey squirrels in order to suppress the birth rate [171]. Such a move would reduce the population density of grey squirrels in the UK which could cause squirrelpox to become eradicated due to insufficient host density. The reduced population density of grey squirrels would also reduce the competitive pressure on reds and, potentially, allow them to survive. This strategy has a number of issues. Primarily is the availability of suitable birth control - ideally one that has little to no impact on other forest species. Other issues concern the scale of control, which would have to be UK wide to have a meaningful impact, as well as financial cost that could prove prohibitive. Despite these concerns, a birth control trial has been vocally supported by government in the UK [105].

This leaves us with a more direct control strategy - the capture and removal of grey squirrels. The direct intervention of humans in the control of the grey squirrel population is not new. Middleton [86] notes the existence of ‘squirrel clubs’ that would meet with the intention of hunting grey squirrels. Jones et al. [63] also document the successful program of grey squirrel removal that occurred on Anglesey, beginning in 1998, which resulted in the total eradication of the grey squirrel on the island. The grey squirrel removal was subsequently followed up by the reintroduction of the red squirrel in the 2000s. The effects of trapping as a control method was also considered by Rushton et al. [109], White et al. [164] and White et al. [166]. Rushton et al. concluded that in order to effectively ensure the survival of the red squirrel, around 60% of the grey squirrels would need to be eradicated. The results obtained by White et al. [164] suggested that only around 25% of the grey squirrel population would need to be removed annually, although this model focussed on the removal of individuals from the refuge and buffer zones only, with the aim of maintaining a red squirrel population in the refuge zone. White et al. [166] also suggested that the trapping of grey squirrels along specific geographic corridors could prevent the spread of squirrelpox.

Current efforts to protect red squirrels in Scotland are focused on defending priority populations of red squirrels [120] across their Scottish range. This is achieved mainly through grey squirrel control that aims to prevent grey squirrel expansion northwards across a chosen boundary line (a line approximately between Helensburgh and Montrose [120], henceforth called the grey squirrel control boundary). There are also efforts to protect red squirrels in priority regions that lie south of the grey squirrel control boundary. Red squirrel conservation policy also recommends conservation action through sympathetic forest management in selected forest sites (strongholds), which are meant to provide refuge for red squirrels against the incursion and competition from grey squirrels [119]. An examination of the efficacy of a selection of these strongholds constitutes Chapter 2. An extension of the stronghold idea is 'natural strongholds'. These are forest sites that can maintain a viable red squirrel population, despite competitive pressure from greys outside of the stronghold, without the need for specific forest management. The identification of 'natural strongholds' is considered in Chapter 3.

1.6 Pine marten (*Martes martes*)

In addition to human led control of grey squirrels recent studies have indicated that a resurgence of a native predator, the pine marten (*Martes martes*) could act to reduce grey squirrel density. The pine marten is a generalist arboreal predator that belongs to the family *Mustelidae* which is part of the order *Carnivora.* The *Mustelidae* is the largest, and most diverse, family of carnivorous mammals [13] that includes animals such as otter, mink and weasel. The pine marten is a member of the genus *Martes* which contains 8 species of marten, although only the pine marten is native to the United Kingdom [13] (see Birks [13] for a discussion on the stone marten whose position as a native species is disputed). Fossil and genetic evidence suggest the genus *Martes* arose is the tropical forests of south-west Eurasia during the Miocene period (23 to 5.3 million years ago), with divergence from other mustelids occurring around 12 million years ago. The pine marten appeared around 120,000 years ago [13], with colonisation of the UK believed to have occurred after the most recent ice age (around 18,000 years ago). However, anthropogenic forest clearing, and predation by humans, either for their fur (which was highly desired across Europe [13]) or due to gamekeepers protecting wild game, has seen the population of pine marten collapse to the point where, at its nadir, the pine marten were resident only in the north-west of Scotland and a few isolated locations in England and Wales [70]. Since the 1920s the population numbers of pine marten have started to increase in Scotland, a trend which was aided by the Wildlife and Countryside Act 1981 and reforestation efforts that have seen forestry cover increase from 5% in 1900

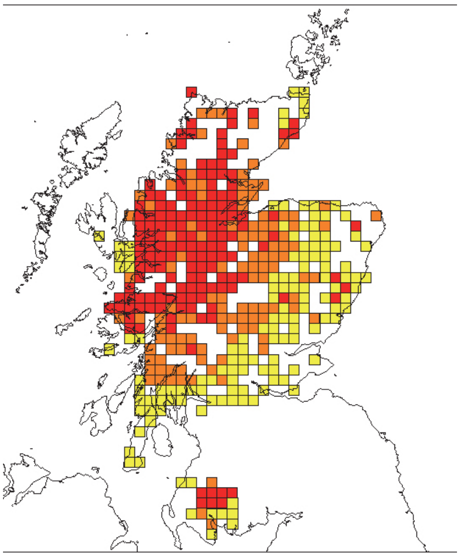


Figure 1.11: Distribution of pine marten in Scotland. The red squares are hectads with pine marten presence in 1980-1982, orange squares are for 1994 and yellow squares are those hectads that have positive pine marten presence in 2012. Image taken from Croose et al. [34]

to 18% in 2007 [120]. The pine marten diet relies heavily on the field vole (*Microtus agrestis*) although they will eat other small mammals (inc. squirrels), small birds, invertebrates, carrion and fruit [13, 149].

In 2014 Sheehy and Lawton [122] confirmed anecdotal evidence that linked the decline in local grey squirrel populations to the resurgence of the pine marten population in Ireland. Their main finding was that, at a woodland level, there is a strong negative correlation between the presence of pine marten and grey squirrels, alongside a positive correlation between pine marten and red squirrel densities at a landscape level. Grey squirrel population numbers were reported to undergo a crash in 9,000km^2 of their former territory, with a crash defined as a reduction in numbers nearing 90% in c30 years. These same territorial ranges that have been vacated by the grey squirrels have subsequently been recolonised by red squirrels, who have been absent from these areas for up to 30 years. One possible cause for the difference in correlation between the squirrel species is attributed to the difference in predation frequency. The red squirrel is noted as only comprising between 0 and 3% of the pine marten diet, as measured by frequency of occurrence (FO%), whereas the grey squirrel is believed to account for between 15 and 17% of the pine marten diet, with Sheehy et al. [123] suggesting that predation rates for pine marten mirror those of the American marten in the grey squirrels natural home territory at 15.6%.

This differential predation, as well as FO% for each species, is further reinforced by Twining et al. [151] who conducted a literature review, alongside their own data, that corroborated the values given by Sheehy and Lawton [122].

More evidence for the correlations between the squirrel species and the pine marten was presented by Sheehy et al. [124] in which a strong negative correlation between grey squirrel occupancy and pine marten density weighted connectivity (DWC) was proved in Scotland. The paper used DWC rather than population density because DWC gives a measure of how intensely the pine marten use the landscape, and can thus be taken as a candidate measure of the impact of the pine marten predation on the grey squirrels. The paper also found a positive correlation between red squirrel occupancy and pine marten DWC, which again is in accordance with the results from Sheehy and Lawton [122]. Furthermore, the results suggested that the grey squirrels were maladapted to the presence of pine marten. In areas where pine marten were known to be present the detection rates of red squirrels decreased dramatically, which suggests that the red squirrels are actively avoiding the pine marten which is to be expected of a prey species that has co-evolved with a predator. The grey squirrels on the other hand had a higher detection rate when pine marten were present. One possible reason for this is that the grey squirrels were exploiting the absence of the red squirrels whilst having no response to the pine marten, which would consequently lead to higher predation rates amongst grey squirrels. Thus, given that the only competitor to the grey squirrel is the red squirrel, and grey squirrels will out-compete red squirrels both with and without the presence of squirrelpox, it can be concluded that the pine marten is the cause of the decline in grey squirrel numbers. However, pine marten are not that numerous. It was noted by Sheehy and Lawton [122] that pine marten in Ireland have an average population density of 3.3 per km^2, which is higher than has been reported for the rest of Europe, and so it is not initially clear that predation alone is the sole cause of the decline of the grey squirrels. An alternative hypothesis for the reduction in grey squirrel density is the ‘climate of fear’ whereby the presence of a pine marten causes the grey squirrels to vacate an area due to fear [13], however this hypothesis is difficult to quantify and a study by Twining et al. [150] introduced pine marten scent into squirrel feeding stations and the results indicate that grey squirrels present no antipredator behaviours in response to the pine marten scent - whereas red squirrels actively avoided the feeding stations. This indicates that preferential predation, rather than fear, is the primary cause of the grey squirrel decline. Twining et al. [152] developed a multi-species presence/absence occupancy model that confirmed the negative correlation between pine marten and grey squirrels. The model also suggested that, whilst the predator mediated replacement of grey squirrels by red squirrels could occur in Scotland, Ireland and Northern England, it would be unlikely in southern England due to increased grey squirrel densities that occur in the resident broadleaf forests. We extend the stochastic model framework to consider the impact of pine marten introductions on red and grey squirrel interactions for a region in North Wales in chapter 4 of this thesis.

1.6.1 *Temporal refuge*

Pine marten are generalist predators [13, 25, 93] whose primary prey species in the UK, field voles (*Microtus agrestis*), undergo multi-annual cycles in their population density [69]. When vole density is high, pine marten will increasingly focus their predation efforts on voles, a classical functional response. This will reduce the predation pressure on red and grey squirrels, providing them with a temporal refuge from predation. Therefore, the ability of a native predator to control an invasive prey species may be weakened by the intermittent use of refugia by the prey species, which in turn may be dependent on the availability of a predators primary prey species. The impact of a temporal refuge on predator-mediated competition in interacting prey species with a case study examining its impact on the replacement of red squirrels by grey squirrels is explored in Chapter 5.

1.7 Outline of thesis

This thesis is organised as follows:

Chapter 2 utilises a spatially explicit stochastic model of red and grey squirrel competitive interactions to assess the impact of specific forest management plans on red squirrel viability in designated stronghold forests in Scotland.

Chapter 3 extends the study in Chapter 2 to identify forest regions, termed natural strongholds, that can maintain a red squirrel population despite grey squirrel presence without the need for specific forest management.

Chapter 4 modifies the stochastic model of red and grey squirrel interactions to include pine marten dynamics. The model is used to assess the impact of pine marten trans-locations on red and grey squirrel interactions in 3 priority regions in Wales: Anglesey, Bangor and Clocaenog.

Chapter 5 develops an ODE system with 2 competing prey species and 1 predator with variable predation in order to assess the impact of a temporal refuge from predation on the predators ability to shape prey dynamics.

Chapter 6 discusses the key findings and impact of the thesis.

Chapters 2 and 3 have been published in peer-reviewed research publications.

Chapter 5 is undergoing peer-review at the time of thesis submission.

It is intended that Chapter 4 will be submitted for publication at a later date.

Chapter 2

An assessment of long-term forest management policy options for red squirrel conservation in Scotland

This chapter is based on the peer reviewed manuscript:

Slade, A., White, A., Kortland, K. and Lurz, P.W.W. 2020. An assessment of long-term forest management policy options for red squirrel conservation in Scotland. Hystrix, the Italian Journal of Mammology **31**(2).`https://doi.org/10.4404/hystrix-00351-2020`

The chapter is presented as the published version of the paper. I undertook all the modelling work and played a lead role in developing the project objectives and writing the manuscript.

Abstract

A spatially explicit mathematical model was developed to assess the population viability of red squirrels (Sciurus vulgaris) in designated forest strongholds in Scotland under the implementation of two forest management policies: a specific Stronghold Management for red squirrel conservation (SM) compared to the multi-purpose UK Forestry Standard (UKFS) for sustainable forest management. The study showed

that, in the presence of grey squirrels (Sciurus carolinensis), the SM policy provides an advantage to red squirrels over grey squirrels when compared to the UKFS, and its implementation supports red squirrel conservation efforts. When grey squirrels are not present, there is no discernible benefit in the SM policy compared to the UKFS. The model results therefore indicate that species-specific forest management for red squirrel conservation in the absence of sympatric grey squirrels would not be required. This would allow less prescriptive forest management options that maintain viable red squirrel populations to be explored. The study also identified forest regions that, due to their composition, are capable of sustaining a viable red squirrel population, in the presence of grey squirrels, without the application of specific forest management policy. They can be considered 'natural strongholds'. Selecting such natural strongholds may afford more flexibility to conserve red squirrel populations whilst simultaneously delivering other multi-species conservation and forest management objectives. We review our finding in terms of criteria that were used in the original stronghold designation in Scotland and discuss how our work can be used to inform a forthcoming review of stronghold management policy by Scottish Forestry. Furthermore, the findings can inform red squirrel conservation strategies in other regions and the modelling techniques can be adapted to a wide range of conservation settings.

2.1 Introduction

Multi-objective forests are managed to meet a range of aims in addition to wood production. These include the long-term sustainability of the forest as well as the maintenance of species diversity [29, 38]. For this to be successful it will require the integration of wildlife conservation policy with other objectives of forest management [8, 99]. Changes to forest composition, once set in motion, can take decades to be completed. It is therefore critical to assess the potential impacts of forest compositional management plans on species viability prior to large-scale implementation. Mathematical models can be used to explore the suitability of potential habitat-management strategies. Model results can help inform policies that combine commercial and conservation interests. Models can combine accurate habitat information, such as satellite-derived land-cover information and data on a species' ecology obtained from field studies, with dynamic modelling approaches to predict population change over time. They have successfully been used to assess the impact of habitat change in species conservation and applications consist of different modelling frameworks that cover a range of organisms and purposes. For example, Watkins et al. [157] used an agent-based model to explore the interaction of jaguar (*Panthera onca*) and their landscape, Heikkinen et al. [60] used a spatially-explicit population dynamics model to simulate the potential success of the trans-location of specialist grassland butterfly (*Maniola jurtina*) and Broome et al. [17] combined a statistical linear mixed effects model with forest yield models to evaluate the effect of forest thinning on capercaillie (*Tetrao urogallus*).

A group of species suited for mathematical modelling approaches are tree squirrels such as the Eurasian red squirrel (*Sciurus vulgaris*), since its forest habitat can easily be mapped and its ecology is well understood [12]. Red Squirrels are under threat in the United Kingdom, Ireland and northern Italy and recent estimates for the UK [79] indicate that just over 80% of the remaining populations are now thought to live exclusively in Scotland. The rest survive in isolated forests or offshore islands in England and Wales [79]. The decline of red squirrel populations has arisen due to the spread and competition with the North American grey squirrel (*Sciurus carolinensis*). In the British Isles the grey squirrel was introduced in the 19th century and trans-located from Britain to Ireland [86]; whereas the Italian populations stem from separate 20th century introductions (e.g. see overview by Martinoli et al. [78]). The competitive interactions between the two species can lead to stress in red squirrels, reduced body size and fecundity, as well as measurable reductions in local juvenile recruitment rates [11, 53, 114, 161].

In the UK, survival of red squirrel populations in the presence of grey squirrels has been longest in large, conifer-dominated forests and decline and their disappearance fastest in deciduous woodlands (e.g. Bryce et al. [20], Bosch and Lurz [15]). In their native range, grey squirrels inhabit the deciduous woodlands of eastern North America with highest densities in forests containing oak, hickory and walnut [68]. This specialisation on deciduous habitats and their types of tree seeds is thought to be key in the ability of grey squirrels to cope with phytotoxic polyphenols in acorns. While red squirrels do feed on acorns, their digestive efficiency of acorns is only 59% compared to grey squirrels, giving the latter a food refuge and coupled with their high densities a decisive, competitive advantage in deciduous-dominated forest landscapes [64].

This is not the whole story. In contrast with Italy, the populations in the British Isles have also had to contend with the squirrelpox virus (SQPV). The virus is endemic but harmless in greys, yet lethal to red squirrels with observed mortality rates of $> 80\%$ [26]. This has resulted in disease-mediated competition between red and grey squirrels that significantly increases the speed of replacement of red squirrels by grey squirrels [109, 147].

Current UK efforts to aid the conservation of the red squirrel therefore encompass the different aspects of the competitive interactions. They include (i) targeted grey squirrel control [46] to reduce disease transmission and regional spread (e.g. see Highland Boundary Line, [116]), (ii) research on the development of contraceptives that would be applied to grey squirrels (e.g. Yoder et al. [171], Nichols [90]), as well as (iii) the designation and management of 'stronghold' forests (see Figure 2.A1) that are intended to provide refuge for red squirrels against the incursion of, and competition by, grey squirrels [44].

The use of mathematical models to help inform conservation efforts for red squirrels has evolved and developed over time. The early model frameworks considered competitive interactions between red and grey squirrels [91], but the model results could not match the rate of replacement of red squirrels observed in England and Wales. Rushton et al. [108] and Tompkins et al. [147] adapted the competition models to additionally focus on the role of squirrelpox (SQPV). Their model results highlighted the critical role of disease in the replacement of red squirrels, an aspect that up to then had been underestimated in its impact and scale [109]. The model frameworks were further developed to help inform evolving conservation priorities. White and Lurz [162] and White et al. [166] showed that applied grey squirrel control methods in the Borders region of England and Scotland were insufficient to prevent the northward spread of squirrelpox due to multiple and complex dispersal routes for disease spread and insufficient available resources for disease management. This led to a shift in Scottish conservation policy from disease control at the landscape level in southern Scotland to protecting priority red squirrel populations in the region [120]. Jones et al. [63] used a 16-year field data set on grey squirrel control to parameterise and validate a model framework that was used to inform the best strategy to protect red squirrels on the Island of Anglesey from grey squirrel re-invasion. Jones et al. [62] used a model of red and grey squirrel interactions to assess differing forest design plan scenarios at the local forest scale to ensure continued red squirrel population viability in the Kidland-Uswayford Forest System, Northern England. Following the research, a renewed monitoring programme based on feeding signs was set up in the forest in 2017 and red squirrel presence is monitored annually [73]. These studies highlight how mathematical modelling has had an impact on a range of red squirrel conservation initiatives. Our paper extends these previous model frameworks in order to inform national forest management policy options for red squirrel conservation areas (termed strongholds) in Scotland. We assess the potential impacts of two different forest management policies, namely, the stronghold management policy and the UK Forestry Standard policy, on red squirrel population viability both in the presence and the absence of grey squirrels.

The stronghold forest management policy provides species specific recommendations on forest management for red squirrels [44]. Based on research findings with respect to red-grey squirrel interactions, it makes recommendations on tree species composition and age structure to prevent or reduce grey squirrel competition. In contrast, the UK Forestry Standard policy [42] has wider economic, environmental and social objectives. It provides recommendations for tree species composition and age structure to preserve and enhance biodiversity and sets guidelines for sustainable forest management.

In collaboration with Forestry and Land Scotland (FLS), the government agency managing national forests, our principal aim was to assess red squirrel population viability, here defined as 125 individuals in a connected forest (Scottish Natural Heritage, pers. comm.), in designated strongholds under the stronghold management policy [44] compared to the UK Forestry Standard. A further aim was to outline general guidance on what determines a suitable stronghold (protected area) for red squirrels. Forestry and Land Scotland (who advise on national policy for forest management) are about to embark on a review of red squirrel strongholds and the presented findings are intended to underpin this review. The methods and findings presented here are not specific to the Scottish system. They compare two different forest management policies that stipulate general rules for tree species composition which we apply to our mathematical model. Hence, they can be used to inform red squirrel conservation strategies for other regions where red squirrels are under threat. Hence, this paper provides an important case study of how mathematical models can assist forest-management practice and future planning to help protect endangered species, with the techniques being adaptable to a wide range of conservation settings.

2.2 Methods

In this study we will use mathematical modelling to assess the viability of red squirrels under two forest management policies: UK Forestry Standard policy (UKFS) [42] and Stronghold Management policy (SM) [44].

2.2.1 *UK Forestry Standard*

The UK Forestry Standard [42], the UK standard guidance on sustainable forest management, stipulates that there should be a maximum of 75% of a single tree species present in a forest, there should be a minimum of 10% of other tree species along with a minimum 5% broadleaved trees and shrub. The remaining land should constitute either open ground or ground managed for conservation and enhancement of biodiversity. Alongside this, diversification should be pursued if possible. Note that the UKFS is defined as sustainable forest management in the Forestry and Land Management (Scotland) Act 2018.

2.2.2 *Stronghold management policy*

When the stronghold policy was developed it was assumed that grey squirrel expansion would continue into northern Scotland and eventually threaten the existence of red squirrels in Scotland. Consequently, 19 stronghold areas were proposed, based on the work by Poulsom [95] and other stakeholders, with the intention of creating red squirrel safe havens in order to safeguard the population against incursion by grey squirrels. The main recommendations were that potential stronghold areas should be large (> 20 km^2), defendable, not under immediate threat from grey squirrels, geographically representative of the then red squirrel distribution, and that the area of semi-natural or ancient woodland within the stronghold and in the area around it should be compatible with red squirrel management objectives (e.g. see Forestry Commission Scotland [44]).

The Scottish Stronghold Management policy [44] outlines forest management guidelines and stipulates that (if necessary) the forest composition inside strongholds should be altered incrementally over a period of roughly 30 years. It suggests that (i) a maximum of 5% of tree density is comprised of large-seeded broadleaved trees (discouraged trees, Table 2.1), and (ii) that the trees that are removed during normal forest operations should be replaced by coniferous trees (favoured trees, Table 2.1) that ideally provide a habitat advantage to red squirrels. Whilst coniferous tree species support lower densities of both squirrel species, they can provide a competitive advantage to red squirrels due to low grey densities. Large-seeded broadleaved trees do provide a plentiful food supply that can maintain higher population densities of both squirrel species compared to coniferous trees, but they give a selective advantage to grey squirrels [64, 161].

Seed mast intervals with good and bad seed years differ between conifer species, thus conifer species diversity reduces the likelihood of cone crop failures. The SM policy therefore also encourages the diversification of coniferous tree species to ensure a dependable tree seed supply, with no single non-native species constituting more than 80% of the forest. Local, native deciduous woodland should be diversified using native small-seeded tree species that do not provide grey squirrels with a competitive advantage over red squirrels. Forestry management should also aim to create an age structure that has ideally less than one third of trees be classed as young (not of seed bearing age) and the other two-thirds or more consisting of thicket and mature trees, as this would ensure that there is always some forest habitat that can support red squirrels since, on average, it takes more than 25 years for trees to regularly seed [61].

In this study, we do not consider the impact of SM policy on wider forest biodiversity, though we accept that the SM policy will have a negative impact that would need to be assessed if the SM policy were to be taken forward and implemented across Scotland. The results presented therefore provide a comparative assessment of the two management policies and allow us to test scenarios that would not be possible in field studies (such as the impact of introducing grey squirrels where they are currently absent). This study also does not consider the impact of climate change on forest composition. Climate driven compositional changes could distort the impact of the forest management policy which would render any comparison unreliable. Hence, the results should not be viewed as predictive with regards to exact squirrel densities and competitive outcomes in a specific location (which would require detailed information on the forest management techniques such the silviculture system or felling practice).

2.2.3 *Study area*

Strongholds are defined by Scottish Forestry as "large areas of coniferous and mixed forest identified as having the potential to sustain resilient and healthy populations of red squirrels...over the long-term" [44]. There are currently 19 stronghold regions throughout Scotland (Figure 2.A1).

We consider three strongholds in this study (results for a further three are presented in the supplementary information), one in north-east Scotland, one in north-west Scotland and one in south Scotland. These strongholds are chosen as they encompass the different geographic regions, habitat structure and threats from grey squirrel invasion found in Scotland. Habitat in the west of Scotland is predominantly comprised of Sitka Spruce, whereas eastern habitats tend to be drier and more predominated by pine trees. The north of Scotland is currently free of grey squirrels whilst the south of Scotland has had a resident grey squirrel population for several decades.

The Eastern Stronghold is approximately 89 km^2, is located on the Balmoral Estate in the Cairngorms National Park and is mainly threatened by grey squirrels migrating west from Aberdeen. The Western Stronghold encompasses approximately 63 km^2 in the FLS West Region to the east of Fort William on the western coast of Scotland. Neither of these strongholds currently have resident grey squirrels. Habitat in the south of Scotland (south of the Central Belt of Edinburgh and

Glasgow) does have grey squirrels present. The Southern Stronghold encompasses approximately 180 km^2 of the western section of the Eskdalemuir forest, which is located in south east Dumfries and Galloway. All three strongholds are predominated by conifers, primarily Sitka spruce in the west along with Scots pine, larch, lodgepole pine and Norway spruce but also contain broadleaved trees at levels that exceed those recommended under the current Stronghold Management policy. All three stronghold have a resident red squirrel population. Note, the strongholds considered in this study all comply with UKFS but do not comply with SM policy.

2.2.4 *Determining habitat composition*

The mathematical model uses forest habitat information obtained from the National Forest Estate 2017 (available at: `https://data-forestry.opendata.arcgis.com/datasets/`) and National Forest Inventory 2016 (available at: `https://data.gov.uk/dataset/`) land cover data sets and is supplemented by the Scottish National Heritage (available at: `https://www.nature.scot/`) dataset which contains information on the urban landscape of Scotland. The data was used to create a map consisting of a 1 km^2 resolution grid with each grid square containing the proportion of land covered by each tree species as well as the proportion of urban environment. The age structure of a forest cannot be accurately included in a 1 km^2 scale model. Instead, it is assumed that a proportion of each tree species is not mature and so does not provide resources for squirrels (given by the age of maturity divided by the expected lifetime of the species, Table 2.1). The proportion of each tree species in a given grid square can be altered incrementally to simulate the felling and replanting needed to allow the region to comply with SM policy. In this case study we impose the condition that all transitions to SM forest management occur incrementally over 30 years. In particular, the proportion of each tree species that needs to be replaced in order for a stronghold to comply with SM policy is calculated and 1/30th of this amount is removed every year. The removed trees are replaced by favoured coniferous tree species, with the specific species of conifer being chosen to increase tree diversity in the stronghold. Trees that are replanted do not provide a resource for squirrels until they have matured (Table 2.1).

2.2.5 *Determining the carrying capacity for red and grey squirrels*

The link between squirrel density, habitat and tree seed crops is well evidenced (e.g. Gurnell [51, 52], Lurz et al. [75], See also Table 2.A.8). Thus, the gridded habitat data is combined with estimates of squirrel density in different habitat types. This produces a red and grey squirrel carrying capacity value for each 1 km grid square. These values signify the potential population density that the landscape can support. In the model the carrying capacity is not fixed but instead fluctuates due to forest compositional changes and seed crop dynamics which assumes that tree species undergo a mast year with a defined period, producing higher yield of seed crops that can support increased squirrel densities (Table 2.1) [15, 52]. These mast years are largely cyclical and occur simultaneously for the majority of trees within a single species that are present in a local, connected forest. During the non-mast years, the trees can either undergo 'intermediate' or 'poor' years in terms of cone or seed production which have been averaged in this modelling framework to produce a single non-mast value for each species. Each tree species undergoes a period of non-mast and mast years at regular intervals (with the period defined in Table 2.1). The starting point for this period was chosen at random for each tree species at the beginning of the simulation. Carrying capacity values for each tree species were updated every year, using the relevant values in Table 2.1, to account for tree felling, replanting and maturity changes as well as seed crop dynamics, which allowed the forests carrying capacity dynamics to be incorporated into the model. The seed crop dynamics lead to large temporal changes in carrying capacity (see Figure 2.2).

	Red Squirrel CC		**Grey Squirrel CC**					
	Mast	**Non-Mast**	**Mast**	**Non-Mast**	**Mast Int**	**SBA**	**AF**	**SBP**
Favoured								
Larch	38	21	38	10*	4	15	47	0.68
Lodgepole Pine	21	5*	8	2*	2	15	50	0.70
Scots Pine	83	33	31	8*	2	15	55	0.73
Corsican Pine	110	28*	110	28*	3	25	50	0.50
Douglas-Fir	21	5*	8	2*	5	30	60	0.50
Norway Spruce	58	25	33	8*	4	30	65	0.54
Sitka Spruce	20	2	0	0	4	30	50	0.40
Discouraged								
Beech	110	28*	149	37*	7	50	100	0.50
Chestnut	100	25*	340	85*	4	40	100	0.60
Hazel	85	85	200	200	1	1	N/A	1.00
Sycamore	0	0	149	10	2	25	70	0.65
Oak	100	25*	340	85*	4	40	100	0.60
Other								
Other Broadleaf	78	19	245	61	5	30	80	0.63
Other Conifer	40	15	20	5	3	25	50	0.50
Neutral Species	0	0	0	0	N/A	N/A	N/A	N/A
Secondary Species	10	2	10	2	1	1	N/A	1.00
Urban	19	8	40	11	N/A	N/A	N/A	N/A

Table 2.1: Red and grey squirrel carrying capacity (CC) per km^2 for mast and non-mast years, the mast interval (Mast Int, years), seed bearing age (SBA, years), age at felling or average age (AF, years) and seed bearing proportion (SBP). Full details can be found in section 2.A.10.

2.2.6 *Mathematical model*

The mathematical model used here is based on previous models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches [147] to develop a spatial, stochastic model [62, 162, 166] (see appendix 2.B for more details). The deterministic approach underpinning the model (see equations 2.1 and 2.2) 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 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, which assumes the existence of a shared disease, represents the dynamics of red squirrels who are susceptible (S_R) to the disease and those that are already infected (I_R) by the disease. The model also includes susceptible (S_G) and infected (I_G) grey squirrels as well as grey squirrels that have recovered (R_G) from the disease. The model we use is:

$$\begin{aligned}
\frac{\mathrm{d}S_G}{\mathrm{d}t} &= A_G(t) - bS_G - \beta S_G(I_G + I_R) \\
\frac{\mathrm{d}I_G}{\mathrm{d}t} &= \beta S_G(I_G + I_R) - bI_G - \gamma I_G \\
\frac{\mathrm{d}R_G}{\mathrm{d}t} &= \gamma I_G - bR_G \\
\frac{\mathrm{d}S_R}{\mathrm{d}t} &= A_R(t) - bS_R - \beta S_R(I_G + I_R) \\
\frac{\mathrm{d}I_R}{\mathrm{d}t} &= \beta S_R(I_G + I_R) - bI_R - \alpha I_R
\end{aligned} \tag{2.1}$$

where

$$A_G(t) = \begin{cases} (a_G - q_G(H_G + c_R H_R))H_G & 0 \le t < 0.5 \\ 0 & 0.5 \le t < 1 \end{cases} \tag{2.2}$$

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 $b = 0.9$ [5] 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 $a_G = 3.4$ [147]. 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 $c_R = 0.61$ [20]. Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient $\beta = 1.1$ [163]. Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ [147]. The susceptibilities to crowding (q_R, q_G) 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 taken from the values derived in section 2.2.5 above. All parameter values assume an annual time-scale. We provide a description of the model terms in terms of birth, death, infection, recovery and dispersal rates in the supplementary information (see Table 2.A2). To generate the stochastic model (Table 2.2), the rates in the deterministic model are converted into probabilities of events that account for changes in individual patch level abundance [100].

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	$S_G \rightarrow S_G - 1, I_G \rightarrow I_G + 1$	$\left[\beta S_G \left((I_G + I_R) + \theta \sum\limits_{Adjacent} (I_G + I_R) + \theta^2 \sum\limits_{Corner} (I_G + I_R)\right)\right]/R$
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	$S_R \rightarrow S_R - 1, I_R \rightarrow I_R + 1$	$\left[\beta S_R \left((I_G + I_R) + \theta \sum\limits_{Adjacent} (I_G + I_R) + \theta^2 \sum\limits_{Corner} (I_G + I_R)\right)\right]/R$
Natural/Diseased Death of Red	$I_R \rightarrow I_R - 1$	$[(b + \alpha)I_R]/R$
Dispersal of S_G	$S_G \rightarrow S_G - 1, S_G^* \rightarrow S_G^* + 1$	$\left[mS_G \left(\frac{(H_G + c_R H_R)^2}{(K_G)^2}\right)\right]/R$

Table 2.2: Stochastic model events that govern the dynamics that occur within each 1 km grid square. Full details can be found in section 2.A.11

2.2.7 *Model initialisation*

The model was initialled with observed data for the presence of red and grey squirrels between 2014 - 2017 (using the National Biodiversity Network (NBN) Gateway (`http://data.nbn.org.uk`) – see Figure 2.A2). In regions where only one squirrel species was observed the model was initialised at the respective carrying capacity for that grid-square, based on available habitat types. In regions where both squirrel species were observed the model was initialised with red and grey squirrel densities at half their respective potential carrying capacities. Once initialised, the model was run for 10 years in order to allow for changes in density in grid-squares with both squirrels present and for squirrels to expand into nearby available habitat.

In total we present results for four different scenarios for each stronghold. The first two scenarios outline the red squirrel dynamics, in the absence of grey squirrels, under UKFS and then SM policy. The remaining two scenarios detail both red and grey squirrel population dynamics under UKFS and SM policy, with both squirrel species being present at the start of the simulations. This stipulation will later be relaxed and we will consider scenarios where grey squirrels are introduced after 50 years in the model simulation in order to simulate the scenario where grey squirrels colonise during the transition from UKFS to SM policy. To generate results each scenario was simulated 10 times, with each simulation of the model being run for 150 years each to ensure that enough time was allowed for forest management plans to be implemented and their effects to be fully realised. The UKFS results were gained by maintaining the initial forest composition for the 150-year simulations. SM policy simulations actively altered forest composition, as described in section 2.2.4 and 2.2.5, for each simulation. For each scenario we show results for each of the 10 simulations and this gives an indication of the variability between each model realisation. We also show the average of the 10 simulations in order to give a representative trend in population density for each scenario.

Note, in the stronghold regions we examine in this paper grey squirrel densities were not large enough to support an endemic infected population. Consequently, squirrelpox does not play a role in determining red and grey squirrel population dynamics in our study regions and so is not a factor in the results presented below. Evidence supporting this choice is presented in section 2.3.5 (and see section 2.A.6).

2.3 Results

2.3.1 *Eastern stronghold*

The tree species distribution at the Eastern Stronghold (Figure 2.A1) complies with the UKFS but not with SM policy (Figure 2.1.a(i)). The application of the SM policy would reduce the proportion of broadleaved trees present from around 18% to less than 5% (Figure 2.1.b(i)) and replaces them with favoured species, primarily larch, lodgepole pine and Sitka spruce. The changes to the forest composition do not significantly alter the red squirrel carrying capacity (Figure 2.2.a(i)) whereas the grey squirrel carrying capacity (Figure 2.2.a(ii)) is noticeably reduced.

Currently, there are no grey squirrels in the region of the Eastern Stronghold (see Figure 2.A2). In the absence of grey squirrels, the red squirrel population in the Eastern Stronghold is stable when the forest complies with UKFS, with an average size of 315 individuals (Figure 2.1.a(ii)), which equates to approximately 3.5 red squirrels per km^2. Under the SM policy the red squirrel population initially falls to an average of 290 individuals (3.3 individuals per km^2) during the transition from the UKFS to the SM, which takes 30 years to complete. The reduction occurs as a result of the forest restructuring to comply with the SM policy and the concomitant lag in carrying capacity until planted trees reach coning age. Consequently, red squirrel density begins to recover once the replanted trees start to reach maturity (after 15 years in this study). The population size recovers in the long term to an average of 315 individuals (Figure 2.1.b(ii)).

Although grey squirrels are not currently a threat to red squirrels at this stronghold, the rationale of the SM policy is to provide a safe haven for red squirrels should they be threatened by grey squirrels. We therefore examine the viability of red squirrels when grey squirrels are introduced to locations adjacent to the stronghold (Figure 2.A3). Under UKFS the red squirrel population abundance collapses from its initial value (315) to an average of 20 individuals (Figure 2.1.a(iii)), which is an average of 0.2 individuals per km^2. This population level is likely to be too small to be viable and long-term population extinction would be expected (and occurs in some model realisations). The grey squirrel population under the UKFS grows to a stable average of 340 individuals (3.8 ind. per km^2) (Figure 2.1.a(iv)). When the SM policy is implemented the red squirrel population initially falls to an average of 160 individuals (1.8 ind. per km^2) during the transition from UKFS to SM policy but recovers in the long term to an average of 215 individuals (2.4 ind. per km^2) which we assume is large enough to be viable (Figure 2.1.b(iii)). The grey squirrel population under SM (Figure 2.1.b(iv)) initially grows to an average of 135 (1.5 ind. per km^2) but is reduced to an average of 70 individuals (0.8 ind. per km^2) once the SM policy changes have been fully implemented. The population density and geographic spread of red and grey squirrels in the Eastern Stronghold and the surrounding area under UK Forestry Standard and Stronghold Management policy can be found in Figure 2.A5. Thus, the introduction of the SM policy and the linked changes to the forestry that this entails serves to reduce the grey squirrel population in the stronghold and allow the red squirrel population to survive and be more viable.

2.3.2 *Western stronghold*

The forest at the Western Stronghold (Figure 2.A1) complies with the UKFS but not with SM policy (Figure 2.3.a(i)). The application of the SM policy reduces the proportion of broadleaved trees present from around 14% to less than 5% (Figure 2.3.b(i)) and replaces them with favoured species, primarily Norway spruce and Scots pine. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure 2.2.b(i)) whereas the grey squirrel carrying capacity (Figure 2.2.b(ii)) is noticeably reduced.

Currently, there are no grey squirrels in the region of the Western Stronghold (see Figure 2.A2). In the absence of grey squirrels the red squirrel population under UKFS is stable with an average size of 170 individuals (2.7 ind. per km^2) (Figure 2.3.a(ii)), whereas under the SM policy the red squirrel population initially falls to an average of 150 individuals (2.4 ind. per km^2) during the transition from the UKFS to the SM but the population size recovers in the long term to an average of 175 individuals (2.8 ind. per km^2) (Figure 2.3.b(ii)). It is interesting to note that, even in the absence of grey squirrels, the red squirrel population is relatively small, due to the small stronghold area, and potentially vulnerable to extinction even after the SM policy is implemented.

Grey squirrels are not currently a threat to red squirrels at this stronghold - but

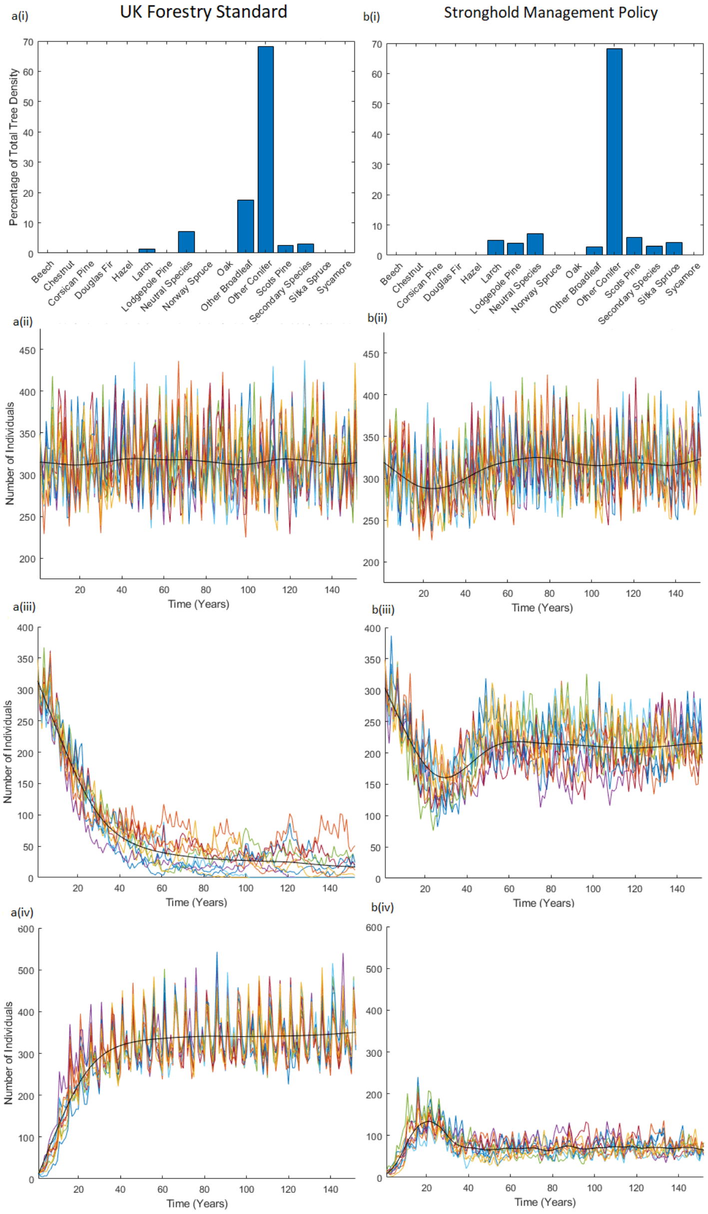


Figure 2.1: Results for the Eastern Stronghold. Images a(i-iv) illustrate the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition (after SM policy has been implemented in (b)), (ii) shows the red squirrel population time series when no grey squirrels are present, (iii) shows the red squirrel population time series when grey squirrels are present and (iv) shows the grey squirrel population time series (when red squirrels are present). The results for the 10 model realisations are shown and the darker lines indicate the average population trend for the 10 realisations.

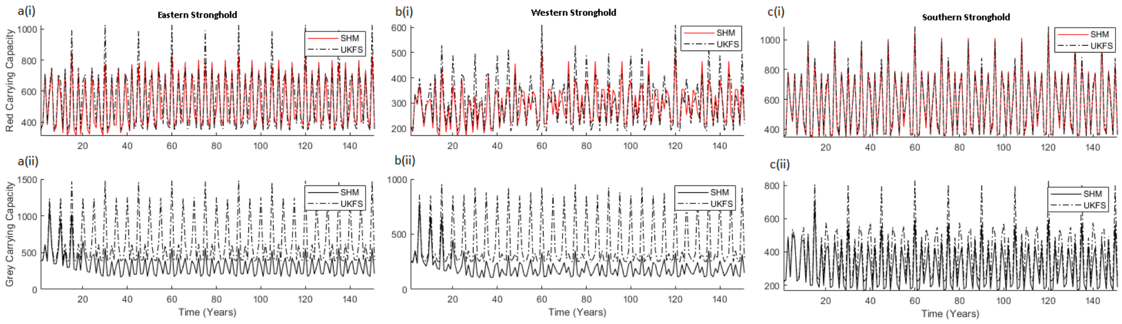


Figure 2.2: Changes in carrying capacity over the 150 year simulation for (i) red and (ii) grey squirrels at (a) the Eastern Stronghold, (b) the Western Stronghold and (c) the Southern Stronghold. Each image shows the capacity under the UK Forestry Standard (dashed line) and the Stronghold Management (solid line).

as with the Eastern Stronghold we examine impact on red squirrel viability of grey squirrels. When grey squirrels are introduced into regions adjacent to the stronghold (Figure 2.A4) the red squirrel population under UKFS collapses to an average of 5 individuals (<0.1 ind. per km^2) (Figure 2.3.a(iii)) with population extinction in some model simulations. The grey squirrel population under the UKFS grows to a stable average of 230 individuals (3.7 ind. per km^2) (Figure 2.3.a(iv)). When the SM policy is implemented the red squirrel population undergoes a similar dynamic as under UKFS, with the population collapsing during the first 20 years of simulation. The average population size under SM policy is 20 individuals (0.3 ind. per km^2) (Figure 2.3.b(iii)), and again extinction occurs in some model simulations. The long-term grey squirrel population abundance under SM is 120 individuals (1.9 ind. per km^2) (Figure 2.3.b(iv)). The population density and geographic spread of red and grey squirrels in the Western Stronghold and the surrounding area under UK Forestry Standard and Stronghold Management policy can be found in Figure 2.A6. Thus, the introduction of the SM policy and the changes to the forestry that this entails would serve to reduce the resident grey squirrel population to just over half of its size under UKFS. However, despite red squirrel abundance being four times as large under SM policy than UKFS, the implementation of SM policy is insufficient to allow the red squirrel population to become viable. This suggests that the forest composition at the Western Stronghold is unsuitable as a red squirrel stronghold.

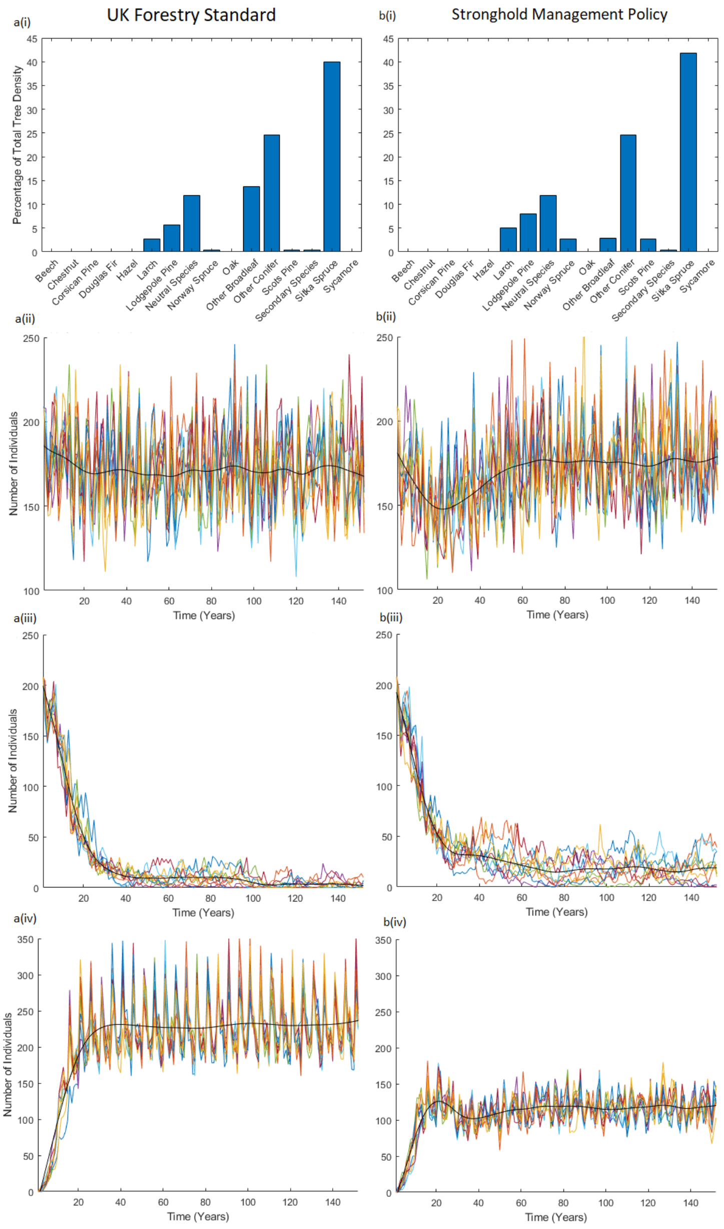


Figure 2.3: Results for the Western Stronghold. Images a(i-iv) illustrate the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition (after SM policy has been implemented in (b)), (ii) shows the red squirrel population time series when no grey squirrels are present, (iii) shows the red squirrel population time series when grey squirrels are present and (iv) shows the grey squirrel population time series (when red squirrels are present). The results for the 10 model realisations are shown and the darker lines indicate the average population trend for the 10 realisations.

2.3.3 *Southern stronghold*

The forest at the Southern Stronghold (Figure 2.A1) complies with the UKFS but not with SM policy (Figure 2.4.a(i)). The SM policy reduces the proportion of broadleaved trees from just over 5% to less than 5% (Figure 2.4.b(i)) and replaces them with favoured species, primarily Scots pine, larch and lodgepole pine. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure 2.2.c(i)) and leads to a minor reduction in grey squirrel carrying capacity (Figure 2.2.c(ii)).

There are currently grey squirrels present in the Southern Stronghold (see Figure 2.A2). In order to allow a better comparison between the three strongholds outlined in this paper the Southern Stronghold was initially simulated without grey squirrels being present. In the absence of grey squirrels, the red squirrel population in the Southern Stronghold has an average population size of 280 individuals (1.6 ind. per km^2) under UKFS and SM policy (Figure 2.4.a(ii) & b(ii)). The reduction in population size during the transition from UKFS to SM policy shown in the Eastern and Western Strongholds is not seen here since the transition removes only a small amount of broadleaved trees.

As previously mentioned, grey squirrels are present in the wider landscape in southern Scotland. To assess their impact on red squirrel viability we initialise the model with the observed distribution of red and grey squirrels. Under UKFS this leads to a long-term average of 160 red squirrels and 110 greys squirrels (0.9 and 0.6 ind. per km^2 respectively) (Figure 2.4.a(iii) & b(iii)). Under SM policy the red squirrel population increases to a stable average population size of 250 individuals (1.4 ind. per km^2) (Figure 2.4.a(iv)) and the grey squirrel population is reduced to an average of around 15 individuals (<0.1 ind. per km^2) (Figure 2.4.b(iv)). The population density and geographic spread of red and grey squirrels in the Southern Stronghold and the surrounding area under the UK Forestry Standard and Stronghold Management policy can be found in Figure 2.A7. Thus, the introduction of the SM policy would reduce the resident grey squirrel population and be sufficient to allow the red squirrel population to increase in number and improve viability.

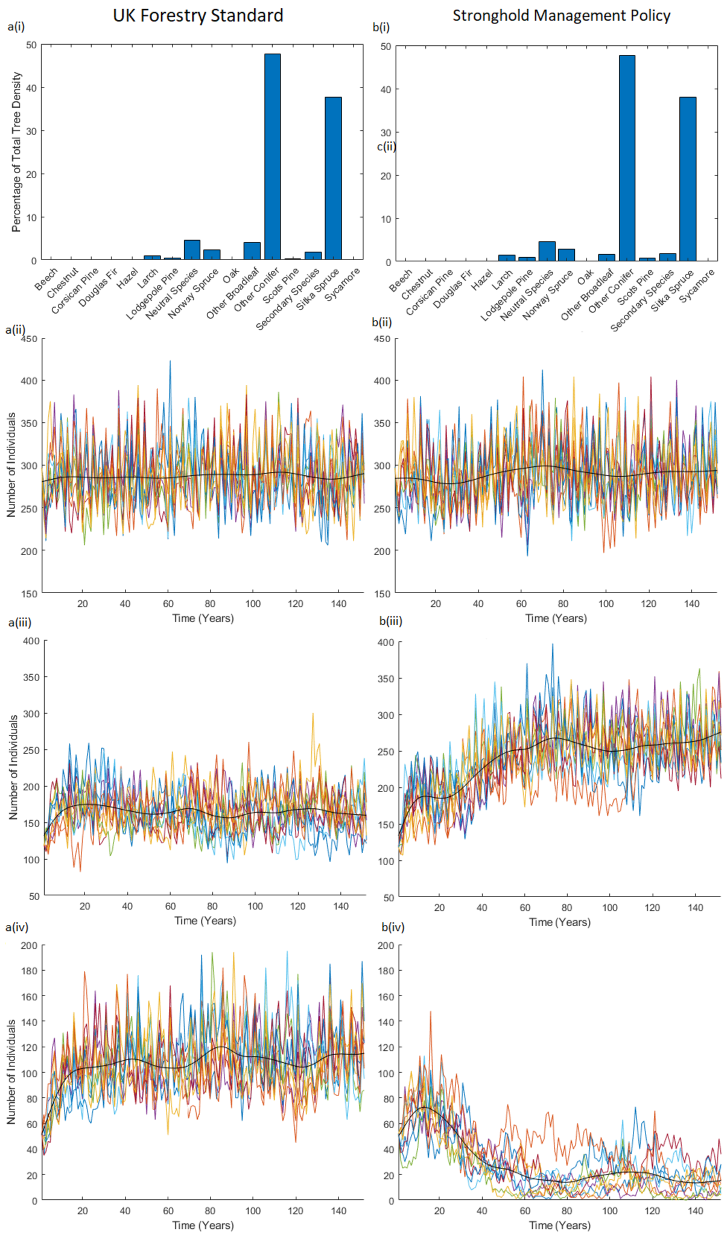


Figure 2.4: Results for the Southern Stronghold. Images a(i-iv) illustrate the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition (after SM policy has been implemented in (b)), (ii) shows the red squirrel population time series when no grey squirrels are present, (iii) shows the red squirrel population time series when grey squirrels are present and (iv) shows the grey squirrel population time series (when red squirrels are present). The results for the 10 model realisations are shown and the darker lines indicate the average population trend for the 10 realisations.

2.3.4 *Implementing SM policy before grey squirrel arrival*

The above results for the Eastern and Western Strongholds assume that the transition from UKFS to SM policy and the introduction of grey squirrels occurs simultaneously. We consider the introduction of grey squirrels at year 50 of the simulation (Figures 2.A8 & 2.A9), which corresponds to the forest management being implemented in advance of grey squirrel arrival. During the transition from UKFS to SM grey squirrels are not present and the results are similar to those above when grey squirrels were not introduced (Figure 2.1.b(ii) & Figure 2.3.b(ii)) whereas the long-term results are similar to those above when grey squirrels are present (Figure 2.1.b(iii) & Figure 2.3.b(iii)). This implies that, for strongholds in the north of Scotland where grey squirrels do not currently reside and SM policy allows a stable red squirrel population to exist, the implementation of SM policy can be delayed until grey squirrels are a more pressing threat. Since grey squirrels are already present in the region surrounding the Southern Stronghold this scenario does not apply there.

2.3.5 *Impact of the squirrelpox virus*

Squirrelpox can be supported in grey squirrel populations and from there transmitted to adjacent red squirrels in which it causes a high level of mortality [26, 111]. It is therefore important to assess the potential impact of squirrelpox on the viability of red squirrel strongholds. To do this we simulated the introduction of infected grey squirrels in regions around the strongholds that could support grey squirrels. In many of these regions the density of grey squirrels was insufficient to maintain squirrelpox which led to it dying out before it could become established in the wider population. Moreover, within the strongholds squirrelpox could not be supported, due to low squirrel density, and so had no impact on the ability of a stronghold to maintain a viable red squirrel population.

The density of infected grey squirrels in the Eastern Stronghold is shown in Figure 2.A10 when infected grey squirrels were introduced to the wider environment in years 10, 15 and 20 showing that the disease does not persist. This result holds for all strongholds considered in this study.

2.4 Discussion

		Red Squirrels					
		No Greys		*With Greys*		**Grey Squirrels**	
		UKFS	**SM**	**UKFS**	**SM**	**UKFS**	**SM**
Eastern Stronghold	Avg	315	315	20	215	340	70
(89 km^2)	Min	225	225	0	75	225	25
	Max	440	425	100	325	545	135
Western Stronghold	Avg	170	175	5	20	230	120
(63 km^2)	Min	110	105	0	0	165	75
	Max	245	270	30	60	355	180
Southern Stronghold	Avg	280	280	160	260	110	15
(180 km^2)	Min	205	195	80	160	45	0
	Max	425	410	260	365	195	75

Table 2.3: Red and grey squirrel average abundance at the end of the model simulations, rounded to nearest 5 individuals, under the UK Forestry Standard (UKFS) and Stronghold Management (SM) strategies.

Mathematical modelling is increasingly being applied to predict likely future distributions, density and population dynamics of native and introduced species. Model results can be used to assist with policy decisions, conservation and management - particularly in relation to non-native species [12]. Recent successful applications of a spatial mathematical modelling approach [162, 163, 165–167] has enabled a re-evaluation of existing red squirrel conservation policy. This has recommended new management guidelines in Scotland in relation to the current distribution of introduced North American grey squirrels. This paper outlines the model results which investigated the viability of red squirrels in three stronghold regions (with results for three more in the supplementary information), as designated by Scottish Forestry, both with and without the presence of grey squirrels. In particular, we assess red and grey squirrel abundance and thereby potential red squirrel viability under two forest management policies: The Stronghold Management policy [44], and the UK Forestry Standard policy [42].

Our model results indicate that grey squirrels could persist in the Eastern and Western Strongholds, and the surrounding regions (which we assume meet UKFS criteria), under both the SM and UKFS scenarios. However, the SM policy reduces grey squirrel abundance, and consequently increases red squirrel abundance and thus population viability inside the stronghold. This means that the SM policy provides an advantage to red squirrels over grey squirrels when compared to the UKFS (Table 2.3). Therefore, the SM policy does satisfy its intended objective of providing a forest habitat that is beneficial to red squirrels over greys. Hence, the SM policy would support red squirrel conservation in areas where grey squirrels have the potential to invade red squirrel habitat (such as below the grey squirrel control boundary (Figure 2.A1)). At the time of publication, the SM policy has not been enacted in a stronghold and so there is no data to test the model results.

Our model findings also indicate that some of the currently designated strongholds (e.g. Western Stronghold) cannot support viable red squirrel populations in the presence of grey squirrels under either UKFS or SM practice (Table 2.3). These strongholds have neighbouring habitat that provides a source of grey squirrels that can disperse into the strongholds and prevent the maintenance of a viable red squirrel population. The model study therefore suggests that, despite SM policy improving these forests for red squirrels, they are unsuitable strongholds. This highlights the importance of considering red squirrel conservation management at the wider landscape scale compared to the local (stronghold) scale. It also highlights the potential need for a review of the existing stronghold sites that were originally selected over a decade ago [43]. Landscapes are not static and forest cover is subject to change in terms of felling and replanting operations as well as in terms of longer-term climatic changes. The latter, for example, is predicted to affect suitability for the planting of certain tree species in parts of Scotland (e.g. Sitka spruce, *Picea sitchensis*; [98]) in the near future.

Furthermore, the model suggests that the Southern Stronghold can support red squirrels in the presence of greys under both UKFS and SM practice, with SM policy supporting a higher red population (Table 2.3). These regions are therefore capable of sustaining a viable red squirrel population, in the presence of grey squirrels, without the application of a specific forest composition management policy or grey squirrel control and can be considered ‘natural strongholds’. The reasons for this are two-fold. The Southern Stronghold is comprised primarily of Sitka spruce which, while a poor habitat for red squirrels, is generally unsuitable for grey squirrels. It therefore provides a red squirrel stronghold despite the stronghold being well connected with the surrounding area. Conversely, a stronghold that has a more diverse range of favoured conifer species (such as the East2 Stronghold; see section 2.A.7) as well as a limited number of access points into the stronghold (which reduces the potential dispersal of grey squirrels from neighbouring forests) can also maintain a viable red squirrel population in the presence of grey squirrels under both SM and UKFS. Hence, SM policy could be applied differentially and focus on strongholds, such as the Eastern Stronghold, which can only support a viable red squirrel population under SM policy. Our model study also found other potential natural strongholds such as regions east of the Western Stronghold (Figure 2.A6) and north east of the Southern Stronghold (Figure 2.A7). The current model study could thus be extended to examine the location and forest properties that promote natural strongholds that would require no or minimal additional management due to their tree species composition, size or geographic factors. These findings could then be utilised by forest managers to ensure that standard forestry practice either maintains these regions or that efforts to increase biodiversity and forest resilience do not undermine the ability of the forests to act as natural red squirrel strongholds.

Our model results also indicate that, in the absence of grey squirrels, sustainable red squirrel populations (defined as having above 125 individuals in a connected forest region, Scottish Natural Heritage, pers. comm.) are viable in all strongholds under the UKFS management practice. The transition from the UKFS to the SM policy reduces the red squirrel abundance in all strongholds during the transition period, with the size of the reduction being dependent on the scale of alteration required for transition. Thus, greater levels of alteration lead to larger reductions in population size. Conversely, a greater variety of tree species in a stronghold mitigates the population reduction. Following the transition between forest composition management strategies, red squirrel abundance is comparable under the UKFS and the SM scheme (Table 2.3). A key result therefore is that, in the absence of grey squirrels, there is no discernible benefit for red squirrels in the SM policy compared to the UKFS. It should be noted that other red squirrel conservation practice and mitigation, beyond the management of tree species composition, is applied during forest operations and therefore red squirrel viability may be enhanced above that predicted for the UKFS scenarios. Moreover, the focus of UKFS on enhancing biodiversity could lead to a more diverse forest ecosystem that may have been disrupted due to the implementation of the SM policy [7, 8, 42, 103]. Since the northern extent of grey squirrels in Scotland has been contained for the past 30 years [19] this result suggests that species-specific management for red squirrels in the absence of sympatric grey squirrels would not be required. This would allow a more biodiversity-oriented management approach in currently designated strongholds that lie north of the grey squirrel control boundary (Figure 2.A1).

Grey squirrels are not only a threat to red squirrels in the United Kingdom. Grey squirrels were first introduced into Piedmont in northern Italy in 1948 and in Genoa in the 1960s with further trans-locations to Lombardy in the late 1990s. They have since expanded their range south into Central Italy as well as north across the Po plain with a real risk of future expansion into France and Switzerland [76, 78, 128]. This increase in range has led to a parallel and significant reduction in red squirrel density. In much of the UK red squirrel replacement is primarily driven by disease-mediated competition. However, the squirrelpox virus, carried by grey squirrels and lethal to native red squirrels in the UK, is not present in Italy [104, 109, 147]. In Italy red replacement is due to food competition and increased red squirrel stress due to the presence of greys [11, 53, 114]. Our findings for Scotland suggest that the virus does not play a critical role in red squirrel replacement inside strongholds since densities are too small to sustain the squirrelpox virus. This means our results and the situation in Scotland may be representative of the red and grey squirrel interactions in Italy. Furthermore, like Scotland, northern Italy has regions that favour grey squirrels in the deciduous forests at lower elevations and red squirrels in the more conifer dominated forests higher up in the mountains. We therefore think that our approach and findings hold lessons for the situation in Italy and could be used to inform management and conservation decisions. Notwithstanding, we recognise that the situation in Italy is much richer, complex and scientifically challenging, in that in addition to grey squirrels, there are also other introduced squirrel species present (see Mazzamuto et al. [80]) and the natural predator populations are not as depauperate as they are in the UK [124]. This could form the basis of a new study.

Our model study also considers the impact of squirrelpox virus on the potential of strongholds to support red squirrels. There is consensus that squirrelpox played a key role in the competition and disease mediated invasion of red squirrels when greys squirrels expanded through England and Wales [15, 147]. Here the habitat consisted of broadleaved or mixed stands that could support high squirrel densities. Our modelling study showed that the impact of squirrelpox on red squirrel viability in strongholds was negligible. Viable strongholds under either UKFS or SM practice (or natural strongholds) contain predominately coniferous habitat that only supports low density red squirrel populations and minimises grey squirrel competition. Our study is in line with previous studies that show squirrelpox cannot be supported in red squirrel populations [39, 63, 162], that red squirrels can therefore 'live' with the threat from squirrelpox and that squirrelpox is unlikely to play a key role in grey squirrel invasion and replacement in low density populations in Scotland [77]. Outside of Scotland we expect squirrelpox to be a key factor in the red and grey squirrel competitive dynamics. Other factors could, however, impact on the ability of forest regions to act as strongholds for red squirrels. Coordinated grey squirrel control has acted to reduce grey squirrel density which in turn can reduce grey squirrel expansion [43]. Furthermore, recent studies have suggested that a shared predator, the pine marten (*Martes martes*), may modify the competitive interaction between red and grey squirrels [124, 151]. The presence of pine marten has been shown to correlate with the absence of grey squirrels. This leads to an indirect positive affect on red squirrel presence. Pine martens are currently expanding their geographic range and population density in Scotland [34] and so may play a key role in determining the future distribution of red and grey squirrels and therefore affect the requirement for forest management to protect red squirrels.

While we recognise that it will become an increasingly important factor, we did not include the impact of climate change in our study. Including climate change impacts in population models is a complex process and we felt it could obscure the direct comparison of the two forest management policies that were the key focus of our study. We nevertheless discuss its potential impact here. Climate change would influence tree species composition [89], the time to maturity as well as mast intervals [14]. All these effects would have as yet difficult to predict impacts on squirrel distribution, ecology and local population viability. A primary consequence of climate change is likely to be the increase in broadleaved trees, either through in situ expansion or species migration northwards [89]. In Scotland, winters are likely to become milder and wetter, and summers warmer and drier with predicted benefits to some deciduous species such as beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*; e.g. see Ray [98]). Given the competitive advantage grey squirrels have in broadleaved habitat, an expansion of deciduous tree species will lead to higher grey squirrel densities in Scotland. Higher grey squirrel densities may be able to sustain endemic squirrelpox that, when coupled with greater competitive pressure, could lead to a more rapid decline and local or regional red squirrel extinction [109, 147]. Whilst some authors predicted an increase in woodland cover [98], climate change conversely could also increase the proportion of Scotland that is viable for agricultural use. An expansion in agricultural land could necessitate a reduction in the forested area, which in turn could reduce the connectivity of Scottish forests [48]. A more fragmented forest landscape could aid red squirrels by reducing the ability of grey squirrels to expand their range. However, a more fragmented landscape would also isolate red squirrel populations, reduce genetic diversity and increase the risk of local population extinction. Given the threat climate change poses to red squirrels, suitable forest management may need to be instituted in order to safeguard them in Scotland [21].

2.4.1 *Policy implications*

Our model study has examined the effectiveness of SM practice in protecting red squirrels from grey invasion. It has shown that, despite SM policy improving red squirrel abundance when compared to UKFS, some currently designated strongholds would not successfully achieve the objective of protecting red squirrels. This highlights the importance of careful site selection in terms of stronghold and landscape composition.

The study has also identified the potential of other regions to act as ‘natural’ strongholds. It is therefore worthwhile to review some of the criteria that were used in the stronghold designation, their current suitability and management plans. The original policy (outlined in section 2.2.2) assumed that grey squirrel expansion would continue into northern Scotland and eventually threaten the existence of red squirrels in the whole of Scotland. Consequently, the Red Squirrel Action Plan [43], which originally called for the establishment of stronghold areas, set out the provision of funds for grey squirrel control officers to prevent grey squirrel range expansion in strategic areas. This objective has since been successfully implemented by Saving Scotland's Red Squirrels and the strongholds established based on work by Poulsom [95].

With hindsight, it is apparent that the final selection of strongholds (Figure 2.A1) did not accomplish all these objectives (e.g. some strongholds have significant areas of deciduous woodland within and surrounding them). More importantly, the Action Plan, while building in a review process for Squirrel Conservation Officers, did not envisage a review of stronghold sites. This would be critical for several key reasons: i) there is a need to review if selected sites meet and can maintain the criteria set out in the Action Plan and ii) successful control operations would alter predicted expansion of grey squirrels in northern Scotland and potentially affect forest design plans in strongholds. This then highlights the need for rigorous scientific underpinning, combined with robust policy reviews, when embarking on conservation policy that has significant implications for a commercial sector.

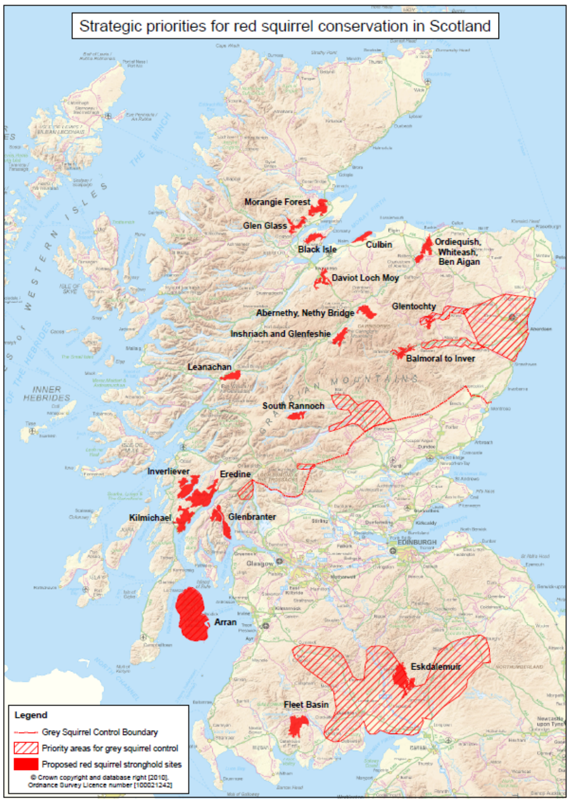
Scottish Forestry intend to undertake a review of SM policy and the results presented here will form part of this review. For Forestry and Land Scotland (FLS), reconciling the SM policy with other management objectives, fluctuating timber markets and wind-blow events, requires significant additional management input and can affect income from timber sales. Furthermore, the single species focus of the SM policy has consequences for other environmental work. For example, restrictions on planting or regenerating oak (*Quercus* spp.) puts limits on FLS efforts to further the conservation of biodiversity. The results of this study are therefore important for FLS and will influence management across large parts of the national forest estate. A future focus on natural strongholds under the UKFS approach will afford more flexibility to conserve red squirrel populations whilst simultaneously delivering other forest management objectives.

Appendix 2.A Supplementary information

The information in this Appendix was included as Supplementary Information in the published version of this work [132].

2.A.1 *Map of Current Scottish Red Squirrel Strongholds*

Currently there are 19 regions of forest, primarily in publicly-owned forests, that are designated as red squirrel strongholds which are coloured solid red in Figure 2.A1. The three strongholds that are examined in the main paper are at Balmoral to Inver (Eastern Stronghold), Leanachan (Western Stronghold) and Eskdalemuir (Southern Stronghold). Three more strongholds will be examined in this document. They are at Daviot Loch Moy (East2 Stronghold) located south of Inverness, Glenbranter (West2 Stronghold) located in southern Argyll and Bute and Fleet Basin (South2 Stronghold) in western Dumfries and Galloway.



Grey squirrel control will aim to eliminate any populations to the north of this line and prevent new populations from becoming established.
The extent of the grey squirrel control area is as published in the draft Grey Squirrel Control Strategy (SNH, 2010) and is subject to review over time.

Figure 2.A1: Map of Scotland with the 19 stronghold regions shown in solid red. The map also includes the grey squirrel control boundary which is the northern most extent (excluding Aberdeen) of the grey squirrels as well as regions that are the focus for grey squirrel control (hatched area). Image courtesy of Scottish Natural Heritage

2.A.2 *Current Distribution of Red and Grey Squirrels*

The following image outlines the current distribution of red and grey squirrel in Scotland.

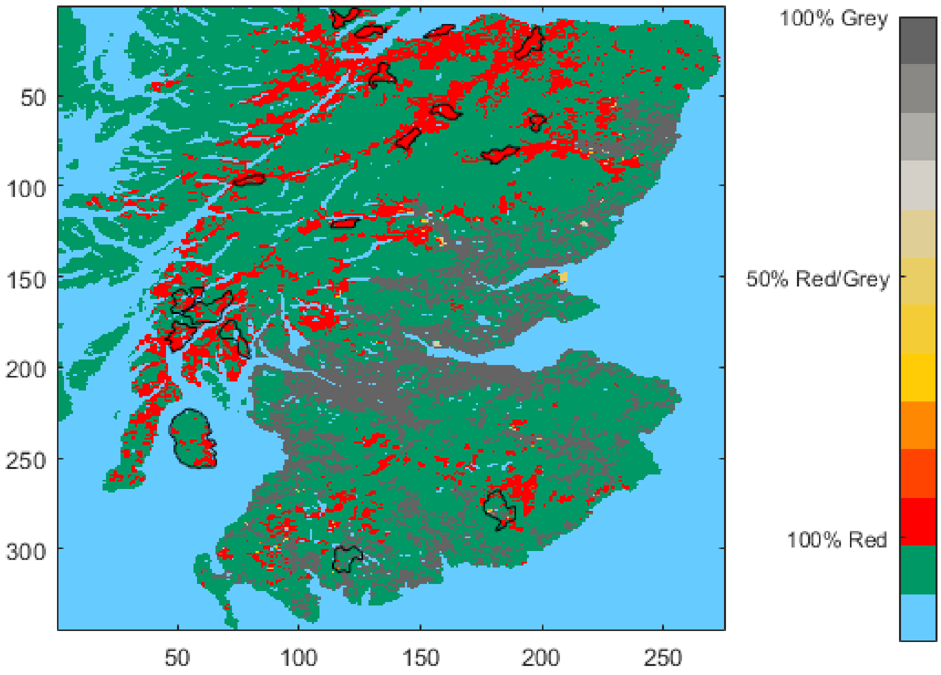


Figure 2.A2: Current distribution of red and grey squirrels in Scotland. The northern extent of the grey squirrel distribution is defined by the Highland Protection Boundary (not including the population at Aberdeen). The 19 stronghold regions are outlined in black.

2.A.3 *Map of Grey Squirrel Introductions at the Eastern & Western Strongholds*

To test if the strongholds located north of the grey squirrel control boundary are capable of acting as strongholds in the event that grey squirrels colonise the surrounding region, grey squirrels were artificially introduced in grid squares with carrying capacity of 5 or more that were located in the area surrounding the Eastern Stronghold (Figure 2.A3) and at the Western Stronghold (Figure 2.A4).

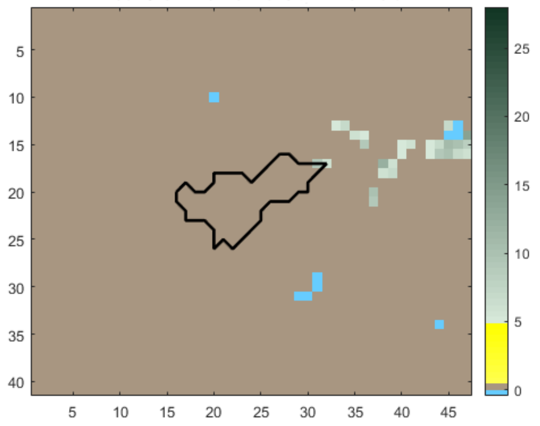


Figure 2.A3: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the Eastern Stronghold. Colour scale to the right indicates the number of individuals per square kilometre.

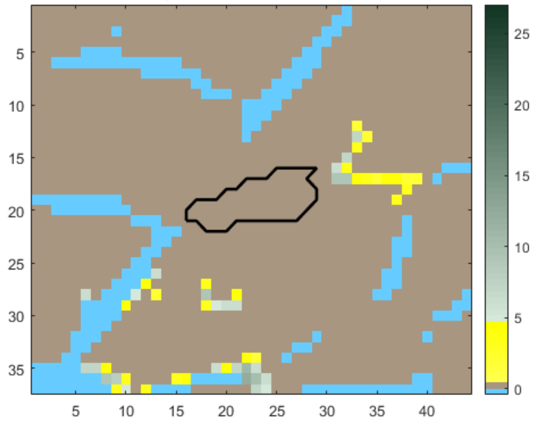


Figure 2.A4: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the Western Stronghold.

2.A.4 *Density Maps for the Eastern, Western & Southern Strongholds*

The following are the maps showing the red and grey squirrel density at the Eastern, Western and Southern Strongholds under the UK Forestry Standard and the Stronghold Management strategy.

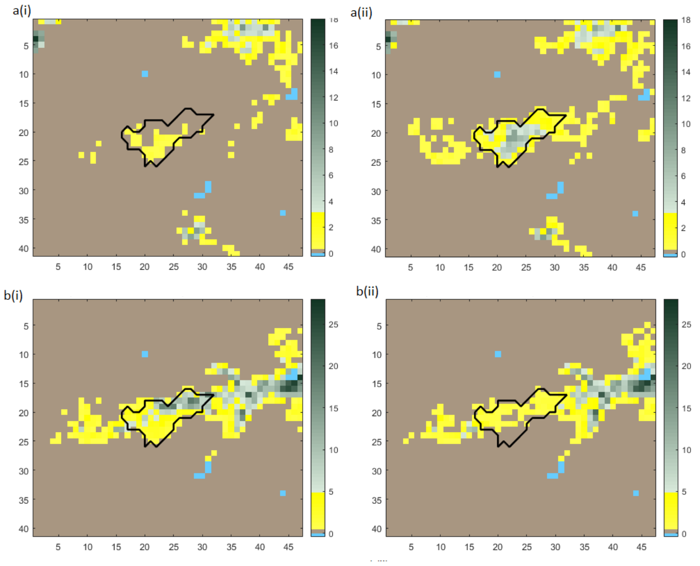


Figure 2.A5: Population density (animals per grid square) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the Eastern Stronghold at the end of the 150 year model simulation.

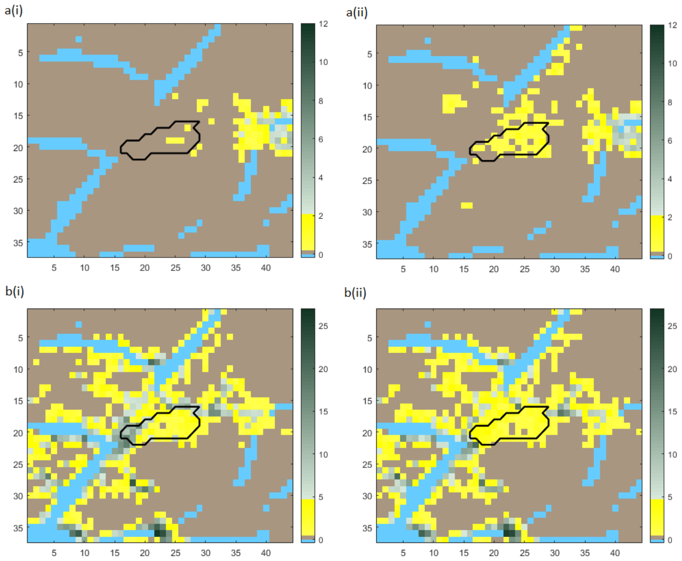


Figure 2.A6: Population density (animals per grid square) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the Western Stronghold at the end of the 150 year model simulation.

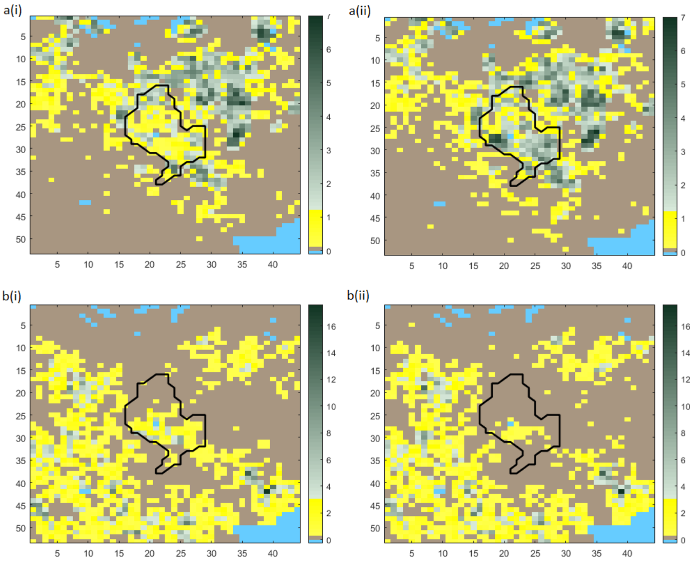


Figure 2.A7: Population density (animals per grid square) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the Southern Stronghold at the end of the 150 year model simulation.

2.A.5 *Results for Grey Squirrel Introduction at Year 50 of the Simulation*

All of the results in the main paper assume that the transition in the stronghold from UK Forestry Standard to the Stronghold Management policy occurs simultaneously with the arrival of grey squirrels into the area surrounding the stronghold. This need not be the case as grey squirrel expansion could be predicted based on grey squirrel monitoring and the Stronghold Management policy be implemented in a stronghold before the arrival of the grey squirrels. This ensures that the reduction in the red squirrel abundance that occurs due to the transition between forest management polices is not compounded by competition from grey squirrels. Figure 2.A8 shows the results with greys introduced at year 50 in the Eastern Stronghold whilst Figure 2.A9 shows the same results for the Western Stronghold.

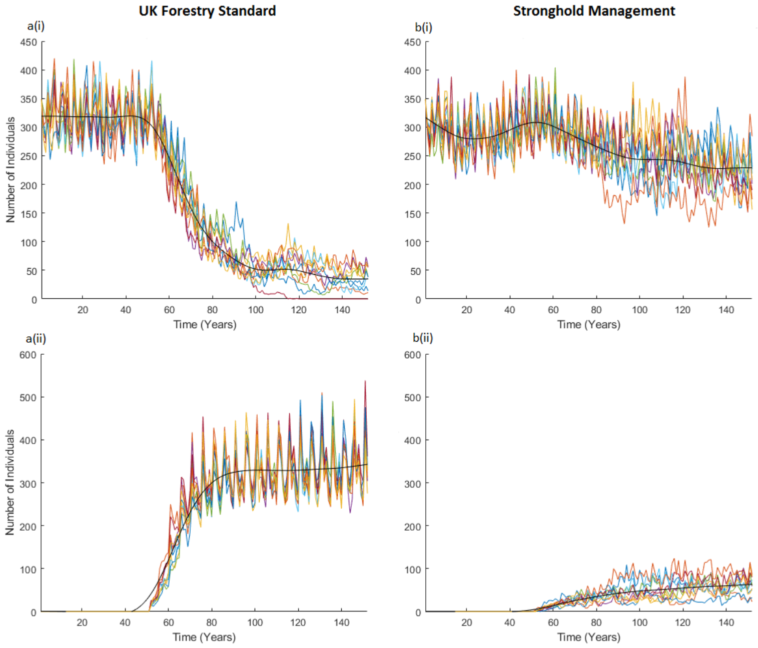


Figure 2.A8: Time series data for the Eastern Stronghold when grey squirrels were introduced at year 50 of the simulation under (a) UK Forestry Standard and (b) Stronghold Management policy. Here (i) shows the red squirrel populations and (ii) shows the grey squirrel populations. The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

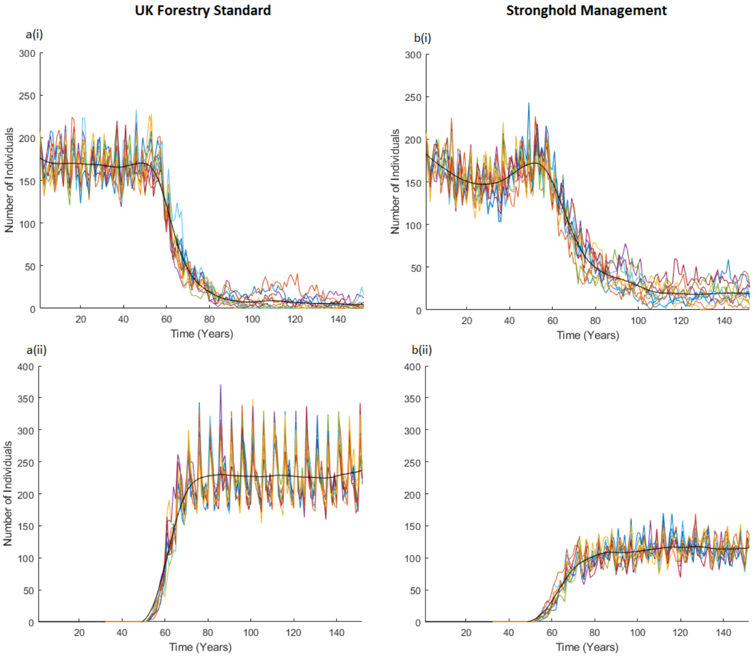


Figure 2.A9: Time series data for the Western Stronghold when grey squirrels were introduced at year 50 of the simulation under (a) UK Forestry Standard and (b) Stronghold Management policy. Here (i) shows the red squirrel populations and (ii) shows the grey squirrel populations. The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

2.A.6 *Results for the Introduction of Squirrelpox Virus*

Squirrelpox can remain endemic in a resident grey squirrel population if the population density is high enough to ensure its survival. In this study we introduced infected grey squirrels in regions surrounding the strongholds in years 10, 15 and 20. Within the strongholds this led to short-lived outbreaks of squirrelpox but the disease did not persist within either grey or red squirrels in the long-term (Figure 2.A10). Hence, squirrelpox did not play a significant role in the population dynamics within the stronghold at any of the 6 stronghold locations considered in this study.

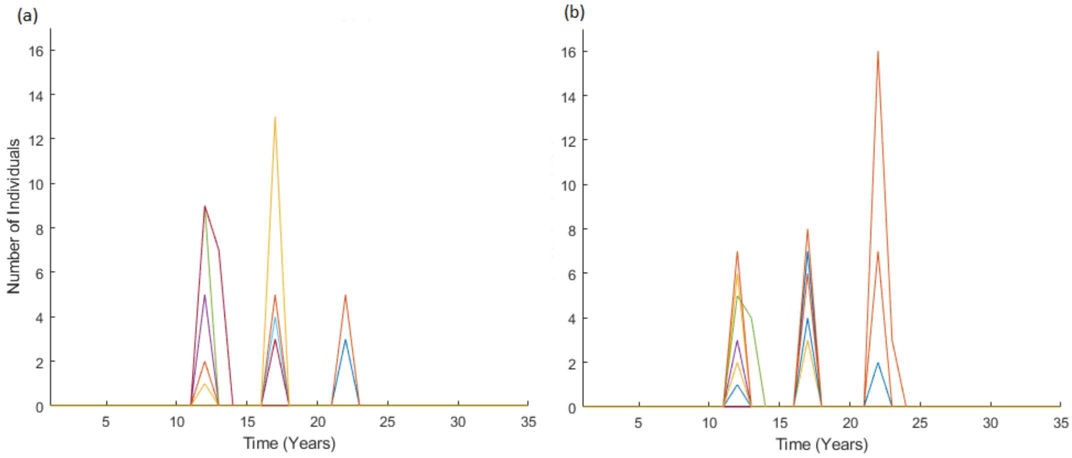


Figure 2.A10: The abundance of infected grey squirrels in the Eastern Stronghold under (a) UK Forestry Standard and (b) Stronghold Management policy. The results for the 10 model simulations are shown.

2.A.7 *Results for the Three Remaining Strongholds*

East2 Stronghold

The forest at the East2 Stronghold, located at Daviot Loch Moy which is just south of Inverness (Figure 2.A1), complies with the UK Forestry Standard (UKFS) but not with Stronghold Management (SM) policy (Figure 2.A11.a(i)). The application of the SM policy reduces the amount of broadleaved trees present from around 13% to less than 5% (Figure 2.A11.b(i)) and replaces them with favoured species: Norway spruce, larch, lodgepole pine, Sitka spruce and Scots pine. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure 2.A12.a(i)) whereas the grey squirrel carrying capacity (Figure 2.A12.a(ii)) is noticeably reduced.

Currently there are no grey squirrels resident in this stronghold. In the absence of grey squirrels the red squirrel population under UKFS is stable with an average size of 305 individuals (Figure 2.A11.a(ii)), whereas under the SM policy the red squirrel population initially falls to an average of 290 individuals during the transition from the UKFS to the SM, which takes 30 years, but the population size recovers in the long term to an average of 305 individuals (Figure 2.A11.b(ii)). This reduction is smaller than that at Eastern or Western Strongholds primarily due to the increased diversity of tree species present at the East2 Stronghold.

Grey squirrels are not currently a threat to red squirrels at this stronghold - but as with the Eastern and Western Strongholds we examine the impact grey squirrels have on red squirrel viability. When grey squirrels are introduced into regions adjacent to the stronghold the red squirrel population under UKFS collapses from its initial value (300) to an average of 120 individuals (Figure 2.A11.a(iii)) which is close to being a large enough population to ensure viability of the stronghold (we assume a viable population needs to be larger than 125 individuals). The grey squirrel population under the UKFS grows to a stable average of 190 individuals (Figure 2.A11.a(iv)). When the SM policy is implemented the reduction in red squirrel population abundance is reduced, with the average population size under SM policy being 175 individuals (Figure 2.A11.b(iii)). The long term grey squirrel population abundance under SM is 85 individuals (Figure 2.A11.b(iv)). The population density and geographic spread of red and grey squirrels in the East2 Stronghold and the surrounding area under UK Forest Standard and Stronghold Management policy can be found in Figure 2.A13. Thus the introduction of the SM policy and the changes to the forestry that this entails serves to reduce the resident grey squirrel population to just over half of its size under UKFS which allows the red squirrel population to increase to a level that has the potential to be viable.

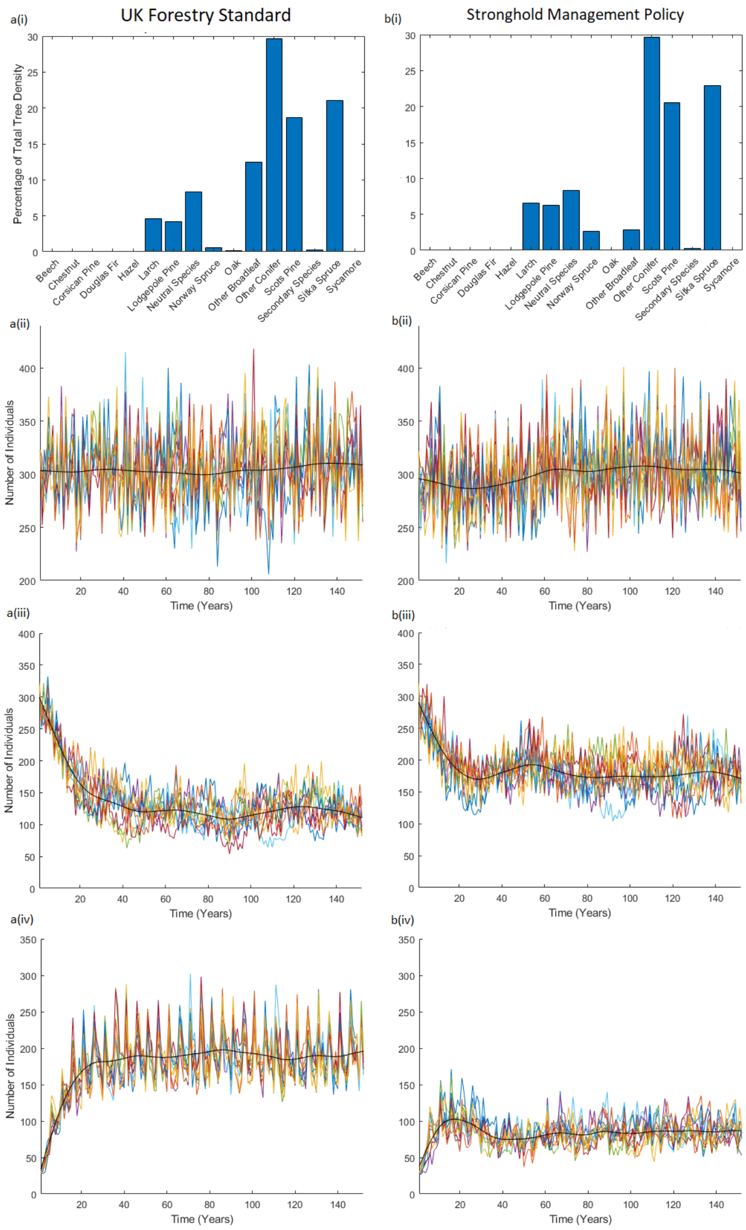


Figure 2.A11: Results for the stronghold at East2 Stronghold. Images a(i-iv) are the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition, (ii) shows the red squirrel population time series when no grey squirrels are present, (iii) shows the red squirrel population time series when grey squirrels are present and (iv) shows the grey squirrel population time series (when red squirrels are present). The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

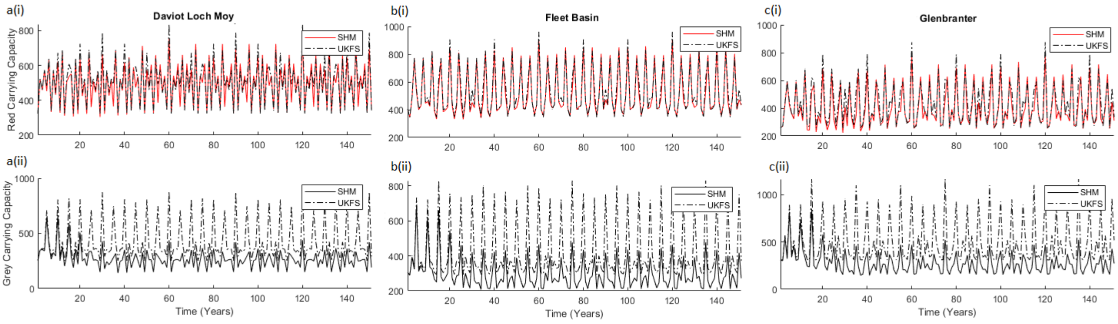


Figure 2.A12: Changes in carrying capacity over the 150 year simulation for (i) red and (ii) grey squirrels at the (a) East2 Stronghold, (b) South2 Stronghold and (c) West2 Stronghold. Each image shows the capacity under the UK Forestry Standard (dashed line) and the Stronghold Management (solid line).

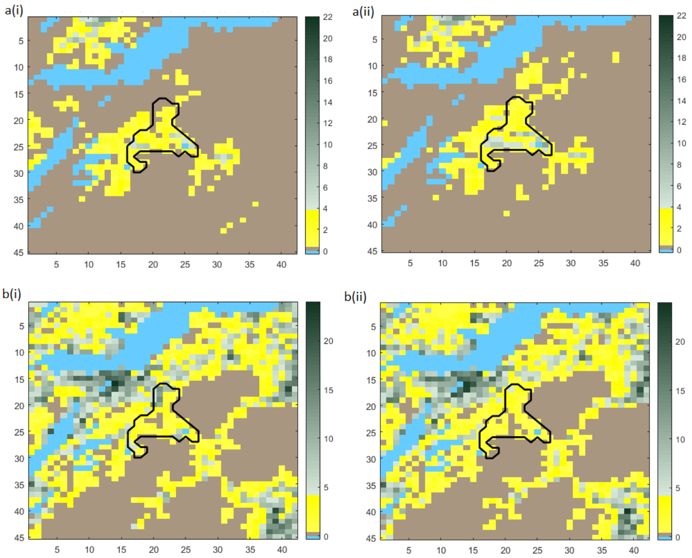


Figure 2.A13: Population density (animals per grid square) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the East2 Stronghold at the end of the 150 year model simulation.

South2 Stronghold

The forest at the South2 Stronghold, located at Fleet Basin in south-west Dumfries and Galloway (Figure 2.A1), complies with the UKFS but not with SM policy (Figure 2.A14.a(i)). The SM policy reduces the amount of broadleaved trees from just over 5% to less than 5% (Figure 2.A14.b(i)) and replaces them with favoured species. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure 2.A12.b(i)) whereas the grey squirrel carrying capacity (Figure 2.A12.b(ii)) is noticeably reduced.

There are currently grey squirrels resident in the landscape surrounding the South2 Stronghold. However, we initially examine a scenario where grey squirrels are absent. In the absence of grey squirrels the red squirrel population in the South2 Stronghold has an average population size of 280 individuals under UKFS and SM policy (Figure 2.A14.a(ii) & b(ii)). The reduction in population size during the transition from UKFS to SM policy is small, with the population falling form 280 individuals to 260 individuals, due to only a small amount of broadleaved trees being removed.

Grey squirrels are present in the wider landscape in southern Scotland. To assess their impact on red squirrel viability we initialise the model with the observed distribution of red and grey squirrels. Under UKFS this leads to a long-term average of 45 red squirrels and 195 greys squirrels (Figure 2.A14.a(iii) & b(iii)). Under SM policy the red squirrel population increases to a stable average population size of 105 individuals (Figure 2.A14.a(iv)) and the grey squirrel population is reduced to an average of around 115 individuals (Figure 2.A14.b(iv)). The population density and geographic spread of red and grey squirrels in the South2 Stronghold and the surrounding area under UK Forest Standard and Stronghold Management policy can be found in Figure 2.A15. Thus the introduction of the SM policy would not significantly reduce the resident grey squirrel population due to the many access points into the stronghold for grey squirrels resident in the wider landscape. This means that the SM policy would be insufficient on its own to allow the red squirrel population to increase to a level that would be viable.

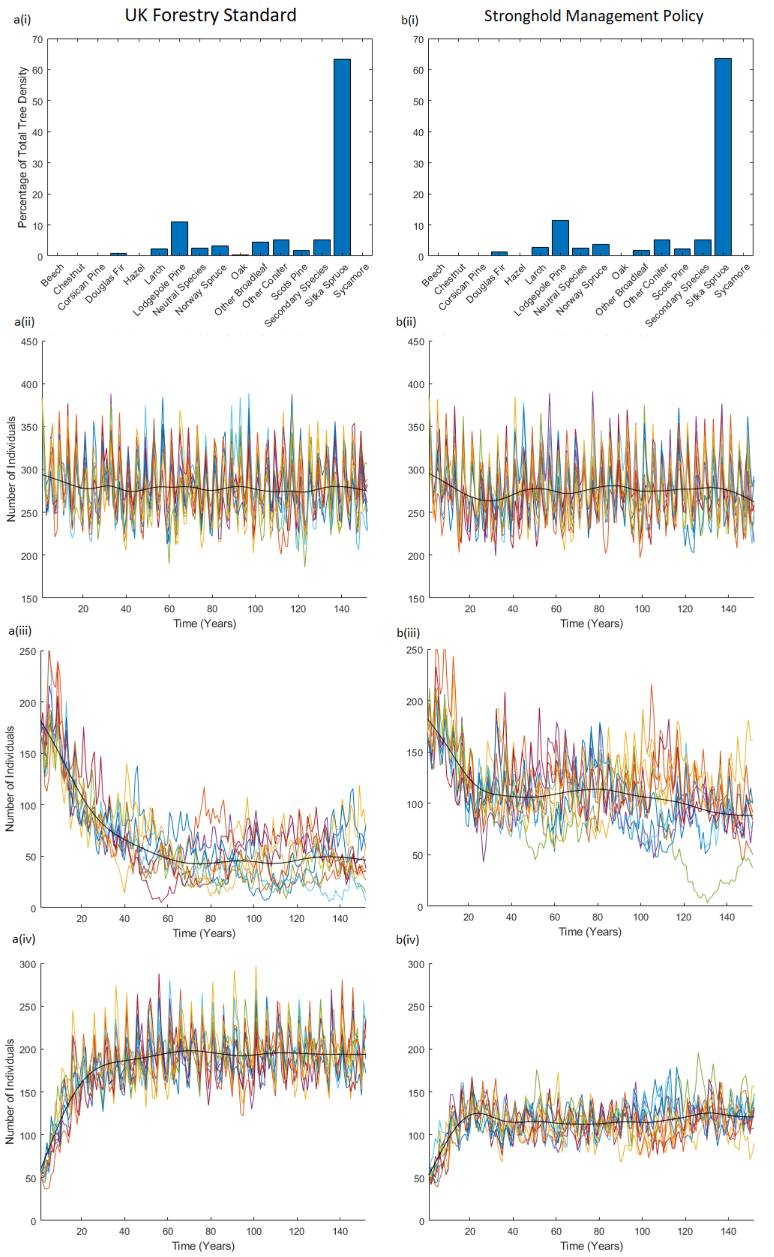


Figure 2.A14: Results for the South2 Stronghold. Images a(i-iv) are the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition, (ii) shows the red squirrel population time series when no grey squirrels are present, (iii) shows the red squirrel population time series when grey squirrels are present and (iv) shows the grey squirrel population time series (when red squirrels are present). The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

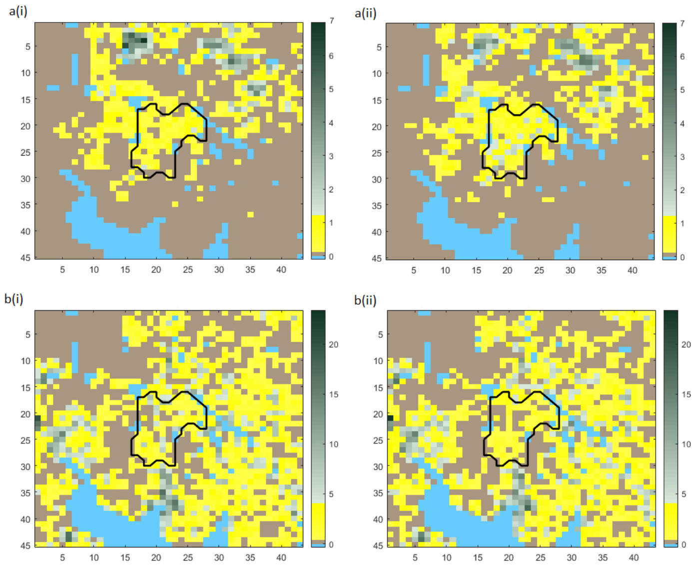


Figure 2.A15: Population density (animals per grid square) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the South2 Stronghold at the end of the 150 year model simulation.

West2 Stronghold

The forest at the South2 Stronghold, located at Glenbranter in southern Argyll and Bute (Figure 2.A1), complies with the UKFS but not with SM policy (Figure 2.A16.a(i)). The SM policy reduces the amount of broadleaved trees from around 10% to less than 5% (Figure 2.A16.b(i)) and replaces them with favoured species. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure 2.A12.c(i)) whereas the grey squirrel carrying capacity (Figure 2.A12.c(ii)) is noticeably reduced.

There are currently no grey squirrels in this stronghold, however they are resident in the wider landscape due to the strongholds proximity to the grey squirrel control boundary. In the absence of grey squirrels the red squirrel population in the West2 Stronghold has an average population size of 200 individuals under UKFS and SM policy (Figure 2.A16.a(ii) & b(ii)). During the transition from UKFS to SM policy the red squirrel population falls to an average of 175 individuals, but recovers after the transition between forest management policies is completed.

Grey squirrels are present in the wider landscape in southern Scotland. To assess their impact on red squirrel viability we initialise the model with the observed distribution of red and grey squirrels. Under UKFS this leads to a long-term average of 20 red squirrels and 205 greys squirrels (Figure 2.A16.a(iii) & b(iii)), with some simulations seeing red squirrel extinction. Under SM policy the red squirrel population does not stabilise and continues its downwards trajectory at the end of the 150 year simulation (Figure 2.A16.a(iv)). The population size at the end of the simulation is approximately 30 individuals which indicates that the introduction of the SM policy does not significantly increase the population size and as such extinction is still a strong possibility. The grey squirrel population is reduced to an average of around 100 individuals (Figure 2.A16.b(iv)). The population density and geographic spread of red and grey squirrels in the West2 Stronghold and the surrounding area under UK Forest Standard and Stronghold Management policy can be found in Figure 2.A17. Thus, similar to the Western Stronghold, the introduction of the SM policy and the changes to the forestry that this entails serves to reduce the resident grey squirrel population to just over half of its size under UKFS however this is insufficient to allow the red squirrel population to become viable and suggests that the West2 Stronghold is unsuitable as a red squirrel stronghold.

Comparison

The East2 Stronghold, located at Daviot Loch Moy, is similar to the Southern Stronghold at Eskdalemuir in that red squirrels are supported under UKFS and the implementation of the SM policy increases the resident red squirrel abundance and improves viability (Figures 2.A11 & 2.A13). The South2 Stronghold at Fleet Basin is similar to the Eastern Stronghold at Balmoral to Inver since red squirrels are vulnerable under UKFS but are viable under SM policy (Figures 2.A14 & 2.A15). The West2 Stronghold at Glenbranter is similar to the Western Stronghold at Leanachan with the stronghold under both UKFS and SM policy being unable to support a viable red squirrel population, despite SM policy increasing red squirrel abundance compared to UKFS, and extinction being likely (Figures 2.A16 & 2.A17). From this we can state that access into the stronghold is a key feature of a successful red squirrel stronghold, with the Southern and East2 Strongholds having limited access points and a consequent ability to maintain a red squirrel population under

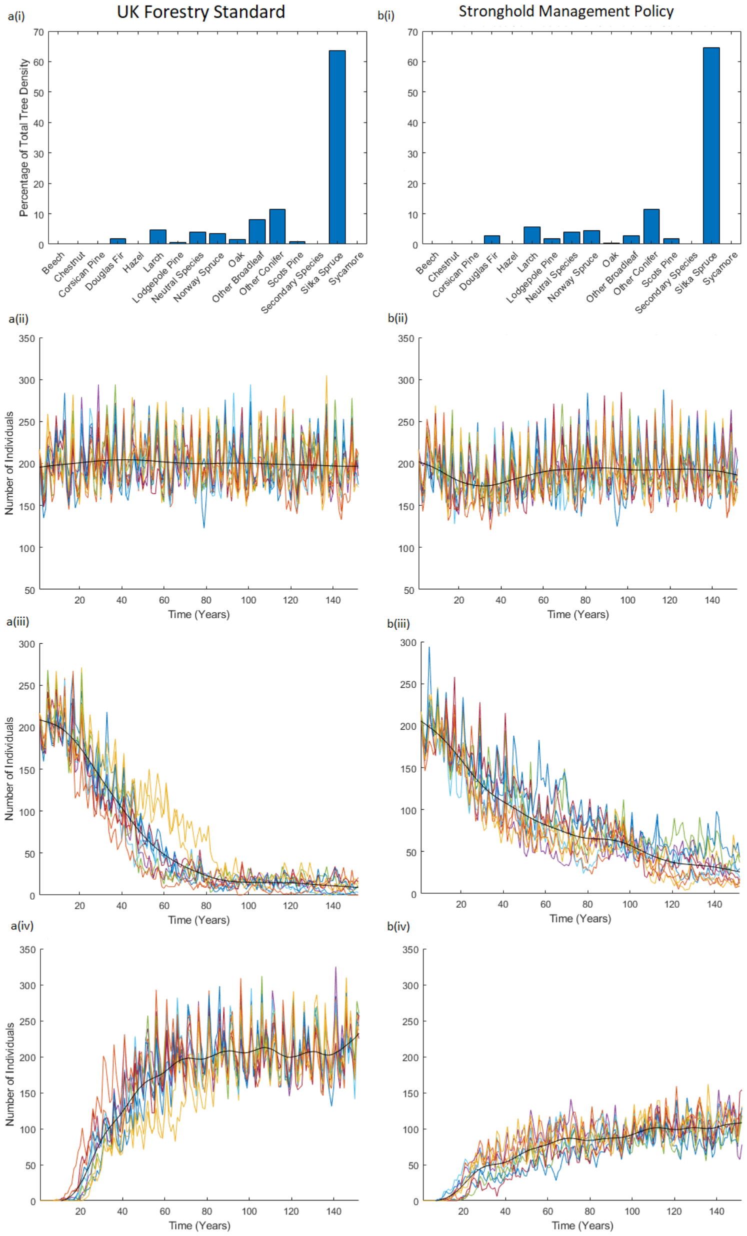


Figure 2.A16: Results for the West2 Stronghold. Images a(i-iv) are the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition, (ii) shows the red squirrel population time series when no grey squirrels are present, (iii) shows the red squirrel population time series when grey squirrels are present and (iv) shows the grey squirrel population time series (when red squirrels are present). The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

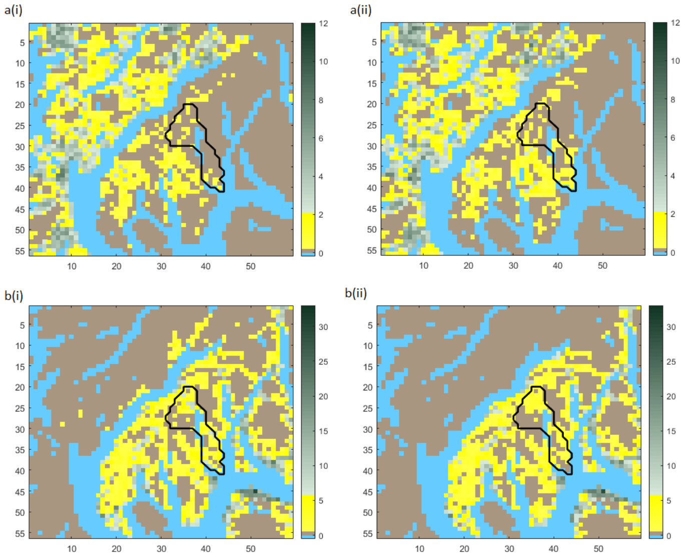


Figure 2.A17: Population density (animals per grid square) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the West2 Stronghold at the end of the 150 year model simulation.

UKFS. The western coast of Scotland appears to be unsuitable as red squirrel territory, as evidenced by the Western and West2 Strongholds both failing to support a red squirrel population under either UKFS or SM policy. The Eastern and South2 Strongholds are key candidates for the application of SM policy as red squirrels can reside n the strongholds under SM policy but not under UKFS.

2.A.8 *References for Tree Species Carrying Capacities*

The following outlines the references used for the carrying capacity associated with each tree species. Full references are to be found below the table.

Tree Species	**References**
Beech	Wauters et al. 2000, Münch 1998, Jones et al. 2017
Chestnut	Author's estimate
Hazel	Tonkin 1983, Holm 1990, Kenward et al. 1998, Magris 1998, Wauters et al. 1990
Sycamore	Authors' estimate
Oak	Tonkin 1983, Holm 1990, Kenward et al. 1998 Magris 1998, Wauters et al. 1990, Gurnell 1996
Other Braodleaf	Author's estimate based on combined data
Neutral Species	Not food plants for either species, do not support population in absence of other species
Secondary Species	Authors' estimate based on combined data
Larch	Halliwell 1997, Jones et al. 2016
Lodgepole Pine	Lurz et al. 1998, Lurz 2012
Scots Pine	Tittensor 1970, Moller 1986, Halliwell 1997, Cartmel 2000, Kenward et al. 1998, Smith 1999
Corsican Pine	Authors' estimate, Smith 1999
Douglas Fir	Jones et al. 2016
Norway Spruce	Halliwell 1997, Lurz et al. 1995, 1998, Cartmel 2000
Sitka Spruce	Lurz et al. 1995, 1998, Lurz 2012, Shuttleworth pers. comm.
Other Conifer	Authors' estimate based on combined data
Urban	Authors' estimate

Table 2.A1: References for the link between tree species and squirrel carrying capacity.

- Cartmel, S. (2000). Squirrel ecology in a conifer forest in North Wales. PhD Thesis, Queen Mary and Westfield College, University of London
- Gurnell, J. (1996). The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. Journal of Applied Ecology 33: 325-338.
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- Jones, H.,A. White, P. Lurz, & C. Shuttleworth (2017). Mathematical models for invasive species management: Grey squirrel control on Anglesey. Ecological

Modelling 359: 276-284.

- Jones, E. H., A. White, N. Geddes, P. Clavey, J. Farries, T. Dearnley, M. Boots & P. W. W. Lurz (2016). Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel. Hystrix doi:10.4404/hystrix-27.1-11673
- Kenward, R. E., Hodder, K. H., Rose, R. J., Walls, C. A., Parish, T., Holm, J. L., Morris, P. A., Walls, S. S. & Doyle, F. I. (1998). Comparative demography of red squirrels (Sciurus vulgaris) and grey squirrels (Sciurus carolinensis) in deciduous and conifer woodland. Journal of Zoology 244: 7-21.
- Lurz, P. W. W., P. J. Garson & S. P. Rushton (1995). The ecology of squirrels in spruce dominated plantations: implications for forest management. Forest Ecology & Management 79: 79-90.
- Lurz, P.W.W., Garson P.J. & Ogilvie J.F. (1998) Conifer species mixtures, cone crops and red squirrel conservation. Forestry 71: 67-71.
- Lurz, P. W. W. (2012) Kidland Squirrel Monitoring Report. Report to Forestry Commission, Kielder Forest District.
- Magris, L. (1998). The ecology and conservation of the red squirrel (Sciurus vulgaris) on Jersey. PhD Thesis, Queen Mary and Westfield College, University of London.
- Münch, S. (1998). Eichhörnchen im Bergwald. PhD-Thesis Friedrich-Schiller University, Jena, Germany
- Smith, D. F. E. (1999). Grey squirrel, Sciurus carolinensis, population dynamics and feeding in a conifer forest. Ph. D. Thesis, University of London.
- Tittensor, A. M. (1970). The red squirrel (Sciurus vulgaris) in relation to its food resource. PhD Thesis, University of Edinburgh.
- Tonkin, J. M. (1983). Ecology of the red squirrel (Sciurus vulgaris L.) in mixed woodland. PhD Thesis, University of Bradford.
- Wauters L. & Dhondt A. A. (1990) Red squirrel (Sciurus vulgaris Linnaeus, 1758) population dynamics in different habitats. Zeitschrift für Saeugetierkunde 55:161-175
- Wauters, L.A., Lurz, P.W.W. & Gurnell, J. (2000). The interspecific effects of grey squirrels (Sciurus carolinensis) on the space use and population dynamics

of red squirrels (S. vulgaris) in conifer plantations. Ecological Research 15: 271-284.

2.A.9 *Description of Model Terms*

Table 2.A2: The following is a written explanation of the model terms that appear in the manuscript.

Change in susceptible grey density	=	Birth of grey squirrels (a_G)	-	death of susceptible grey squirrels (b)	-	infection of susceptible grey squirrels (β)
Change in infected grey density	=	Infection of susceptible grey squirrels (β)	-	death of infected grey squirrels (b)	-	recovery from infection of infected grey squirrels (γ)
Change in recovered grey density	=	Recovery from infection of grey squirrels (γ)	-	death of recovered grey squirrels (b)		
Change in susceptible red density	=	Birth of red squirrels (a_R)	-	death of susceptible red squirrels (b)	-	infection of susceptible red squirrels (β)
Change in susceptible red density	=	Infection of susceptible red squirrels (β)	-	death of infected red squirrels (b)	-	disease induced mortality of infected red squirrels (α)

Table 2.A2: In addition to these terms it is assumed that the birth of squirrels occurs during the breeding season only (6 months, April-September) and that the maximum birth rate is reduced due to intra- and inter-specific competition between squirrels for resources. These equations underpin the stochastic model which represents changes to the abundance of the different classes of red and grey squirrels within 1 km by 1 km grid squares. In the stochastic model squirrels can undertake long distance dispersal to neighbouring grid squares within a 2 km range. See section 2.B for more details.

2.A.10 *Details for Table 2.1*

Favourable trees are those deemed to provide red squirrels with a competitive advantage over grey squirrels. Discouraged trees are large-seeded broadleaved trees that are favourable to grey squirrels. Other Broadleaf and Other Conifer refer to National Forest Inventory data which does not specify individual tree species. The values for these species are calculated as the average of the other broadleaf or conifer trees respectively. The seed bearing age (SBA) is the age at which the trees start producing seeds, AF denotes either the age at which the trees are felled commercially or their average age whilst SBP refers to the Seed Bearing Proportion which is the proportion of a trees life that is seed bearing, which is found using the equation $SBP = (AF - SBA)/AF$ with AF and SBA defined as above. Given the lack of information regarding the age structure of the forest, we use SBP as a proxy for the proportion of trees of a given species that are seed bearing. Neutral species do not contribute to the carrying capacity for red or grey squirrels, hence the data is not included. Secondary species are trees and bushes that provide no benefit to one squirrel species over the other and have thus been grouped together. SBA and Mast Int. data is from Aldhous [1972] and AF data comes from Savill [2013]. References for species carrying capacities can be found in section 2.A.8. Where data for non-mast year carrying capacities was available in the literature for specific tree species these have been used; where they were not available they have been conservatively set at being one quarter of the mast values (denoted by *). The latter estimate is based on data from Spadeadam Forest, Northern England [74], an analysis of 16 years of cone crop data for Sitka spruce and Scots pine at Kidland Forest, Northern

England [72] and an examination of a 25 year cone data set for Scots pine [18].

2.A.11 *Details for Table 2.2*

The parameters representing control and dispersal were fitted with observed data on the Island of Anglesey [63]. The events are assumed to be exponentially distributed with the time between events given by $dt = -\ln(z)/R$ where z is a uniform random number between 0 and 1 and $R = \sum[\text{rates}]$ (the sum of all the parameter values). 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 dispersal term is 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). Further details of the model framework and the calculation of parameter values can be found in [63].

Appendix 2.B Details of the Stochastic Model

The stochastic model, whose model events are outlined in Table 2.2, utilises the Gillespie algorithm [47] to choose which event occurs in a given grid square as well as the time interval between events. The following will describe the stochastic model that is implemented to produce the model results shown in the main part of this chapter.

2.B.1 Parameter values

Parameter values that relate to red and grey squirrels system are required to give specific values to the events described in Table 2.2. These are reported in the main text (see section 2.2.6) but repeated here for completeness. The natural rate of adult mortality $b = 0.9/\mathrm{yr}$ is the same for both red and grey squirrels. We assume births occur only during the squirrel breeding season (April-September) with maximum red squirrel birth birth rate $a_R = 3/\mathrm{yr}$ and grey squirrel birth rate $a_G = 3.4/\mathrm{yr}$. In the 6 month non-breeding season the birth rate for red and grey squirrels is set to zero. The maximum birth rate is modified due to crowding where the susceptibilities to crowding ($q_R; q_G$) are set to ensure the average density over one year is equal to the carrying capacity in each grid square for that year (see section 2.B.1 for a detailed derivation). 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 $c_R = 0.61$. Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient $\beta = 1.1$. It is assumed that squirrels have a 'core' range, here denoted as a circle with radius $\theta = 0.15\mathrm{km}$. This core range can cross grid square boundaries, meaning infection can occur if squirrelpox is present in an adjacent square. Infected red squirrels die due to the disease at rate $\alpha = 26/\mathrm{yr}$ and infected greys recover at rate $\gamma = 13/\mathrm{yr}$.

Derivation of intra-specific competition coefficients

To derive the intra-specific competition parameters q_R and q_G we start with the following seasonal model for a single population N:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(r - qN) \qquad \text{if } 0 \leq t < \frac{1}{s}, \tag{2.3}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -bN \qquad \text{if } \frac{1}{s} \leq t < 1, \tag{2.4}$$

where $r = as - b$ is the growth rate and a, b, and q are the birth, death and intra-species competition parameters respectively. The parameter s ($s \geq 1$) is related to the breeding season length such that the breeding season is a fraction, $1/s$ of a year.

We can solve equation (2.3) using partial fractions and integration to give:

$$N = \frac{C_1 r \exp{(rt)}}{1 + C_1 q \exp{(rt)}}, \qquad 0 \leq t < \frac{1}{s} \tag{2.5}$$

where $C_1 = \frac{N_0}{r-qN_0}$, and $N_0 = N(0)$ is the initial condition. Hence, at the end of the breeding season (when $t = \frac{1}{s}$) we have:

$$N\left(\frac{1}{s}\right) = N_s = \frac{C_1 r \exp\left(\frac{r}{s}\right)}{1 + C_1 q \exp\left(\frac{r}{s}\right)}. \tag{2.6}$$

If we now solve equation (2.4) we get:

$$N = C_2 \exp(-bt), \qquad \frac{1}{s} \leq t < 1.$$

When $t = \frac{1}{s}$, $N = N_s = C_2 \exp\left(-\frac{b}{s}\right)$, and so $C_2 = N_s \exp\left(\frac{b}{s}\right)$ which gives us:

$$N = N_s \exp\left(-b\left(t - \frac{1}{s}\right)\right), \qquad \frac{1}{s} \leq t < 1. \tag{2.7}$$

At the end of the year (when $t = 1$) equation (2.7) becomes:

$$N(1) = N_s \exp\left(-b\left(1 - \frac{1}{s}\right)\right). \tag{2.8}$$

We require $N(1) = N(0)$ which means

$$N(0) = N_s \exp\left(-b\left(1 - \frac{1}{s}\right)\right). \tag{2.9}$$

Substituting the expression for N_s given by equation (2.6), as well as the expression for the constant C_1, into equation (2.9) and rearranging yields:

$$N_0 = \frac{r\left(1 - \exp\left(\frac{r}{s}\right)\exp\left(-b\left(1 - \frac{1}{s}\right)\right)\right)}{q\left(1 - \exp\left(\frac{r}{s}\right)\right)} \tag{2.10}$$

Hence we now have expressions for the initial condition N_0 (equation (2.10)), the density at the end of the breeding season/beginning of the non-breeding season (N_s, equation (2.6)) as well as the constant of integration $C_1 = \frac{N_0}{r-qN_0}$.

We now wish to find the average density N_{avg}. To find the average density, we integrate equation (2.5) over the interval $[0, \frac{1}{s}]$ and add the integral of equation (2.7) over the interval $[\frac{1}{s}, 1]$. Thus,

$$N_{avg} = \int_0^{\frac{1}{s}} \frac{C_1 r \exp{(rt)}}{1 + C_1 q \exp{(rt)}} \mathrm{d}t + \int_{\frac{1}{s}}^{1} N_s \exp\left(-b\left(t - \frac{1}{s}\right)\right) \mathrm{d}t, \tag{2.11}$$

$$= \left[\frac{1}{q} \ln(1 + C_1 q \exp(rt))\right]_0^{\frac{1}{s}} + \left[-\frac{N_s}{b} \exp\left(-b\left(t - \frac{1}{s}\right)\right)\right]_{\frac{1}{s}}^{1}. \tag{2.12}$$

Substituting all the constants into equation (2.12) and rearranging gives:

$$N_{avg} = \frac{1}{q}\left[(a-b) + \frac{(as-b)(\exp(a-b)-1)(\exp(b(1-\frac{1}{s}))-1)}{b(\exp(\frac{as-b}{s})-1)}\right] \tag{2.13}$$

We now equate the average density with the carrying capacity (such that $N_{avg} = K$) and rearrange to give the intra-species competition coefficient:

$$q = \frac{1}{K}\left[(a-b) + \frac{(as-b)(\exp(a-b)-1)(\exp(b(1-\frac{1}{s}))-1)}{b(\exp(\frac{as-b}{s})-1)}\right] \tag{2.14}$$

Note, when $s = 1$ we recover the standard expression for the intra-species competition coefficient $q = \frac{a-b}{K}$. The expression for q_R (q_G) is thus attained by using equation (2.14) with $a = a_R$ and $K = K_R$ ($a = a_G$ and $K = K_G$). The carrying capacity will vary with habitat and this means that q_R (q_G) will vary spatially. We explain how the carrying capacity is determined in the next section.

2.B.2 Annual carrying capacity

Heterogeneous habitat is included via the use of a 1 km by 1 km gridded landscape upon which the spatial model is run. The choice of a 1 km^2 spatial scale is made as this area encompasses the core range of red and grey squirrels [166]. Each 1 km grid square contains forest composition information, obtained from the National Forest Estate 2017 (available at: `https://data-forestry.opendata.arcgis.com/datasets/`) and National Forest Inventory 2016 (available at: `https://data.gov.uk/dataset/`) land cover data sets which is supplemented by the Scottish National Heritage (available at: `https://www.nature.scot/`) dataset which contains information on the urban landscape of Scotland, that details the proportion of the 1 km^2 region that each tree species occupies. Tree felling is enacted via a reduction in a given tree species proportion. Replanted trees are added to the grid square proportions only after the required maturity time has passed in order to simulate the fact that immature trees do not provide a usable resource for squirrels. The annual changes in forest composition is combined with known red and grey squirrel carrying capacities for each tree species (see Table 2.1 for capacity values and Table 2.A.8 for references) to create an annual carrying capacity map that encompasses habitat variation due to felling and seed masting events. Seed masting events are largely cyclical and occur simultaneously for the majority of trees within a single species that are present in a local, connected forest. During the non-mast years, the trees can either undergo 'intermediate' or 'poor' years in terms of cone or seed production which have been averaged in this modelling framework to produce a single non-mast value for each species. Each tree species undergoes a period of non-mast and mast years at regular intervals (with the period defined in Table 2.1). The starting point for this period was chosen at random for each tree species at the beginning of the simulation. It is assumed that all trees are felled, replanted, reach maturity and undergo masting events at the beginning of the year, with the year beginning in April, which is the start of the squirrel breeding season. Consequently, the carrying capacity value for a given grid square is updated at the beginning of each year and remains constant for that year. The carrying capacity value for each squirrel species in each grid square then determines the value of q_R (q_G) in each grid square.

2.B.3 Initial squirrel distribution

The initial squirrel distribution, which is generated using the National Biodiversity Network atlas database for 2014-2017 (`http://data.nbn.org.uk`) and a 10 year 'spin-up' period, indicates which grid squares have either red or grey squirrels, both or neither squirrels present. This data is used to generate the initial squirrel populations. Grid squares that have sole squirrel occupancy are initialised at full carrying capacity and grid squares that have both squirrels present are initialised at half of their respective capacity for each species.

2.B.4 Choosing an event

With the parameter values and the initial squirrel densities in each grid square specified, the event rates of each event across all the grid squares are summed to give the value R in Table 2.2. Dividing each event rate by R gives the probability that an event occurs. We use the Gillespie algorithm [47] to determine the time between events and the specific event that will occur. The value R is used to determine the time to the next event as $dt = -\ln(z)/R$, where $z \in \mathrm{U}(0, 1]$ is a uniformly distributed random number between zero and one. This choice of time step ensures that the time between events follow an exponential distribution. A different uniform random number between zero and one is used to choose the the specific event (which also specifies the grid square in which the event occurs). The population change in a specific grid square for each event is shown in Table 2.2. If the event involves birth, death, infection or recovery from infection then the appropriate population change is made to the specific grid square in which the event occurs. If the dispersal event is chosen, the grid square into which the squirrel will disperse needs to be determined and the appropriate population change in the grid square where the squirrel disperses from, and to, needs to be made. The dispersal event is outlined in detail in section 2.B.4.1. Once an event has been chosen and the population values are updated, the value of R is updated, and then the individual probabilities for each event in each grid square are updated. The process above is then repeated to choose the time to the next event and the next event that occurs.

Dispersal Event

When a dispersal event is chosen we assume a squirrel can disperse to a grid square that is within a 2 km radius of the focal grid square from which the squirrel disperses. Dispersal is assumed to be a saturating function such that individuals are more likely to disperse as the local population increases [63]. The choice of the dispersal rate $m = 2b = 1.8$ and the 2 km dispersal distance is also taken from [63] which fitted the model to known rates of grey squirrel expansion as they replaced red squirrels on Anglesey between 1966 to 1998. The choice of which grid square a squirrel disperses to is determined by calculating the dispersal probabilities of each grid square which is found using the weighted average of the area of each 1 km by 1 km grid square that is within 2 km of the center of the focal grid square from which dispersal occurs. The destination grid square is checked against a water map, which indicates which grid squares are impassible due to water. A grid square is impassible if water must be crossed to reach the destination grid square. When water impedes dispersal, movement occurs up to the water boundary and then along the water boundary.

2.B.5 Ending the year

The above process is used to run individual model realisations with the model stopped once the total time reaches a specified value. In chapter 2, ten model realisations are run to provide information on the average and variation in the model results (see, for example, Figure 2.1).

Chapter 3

Natural strongholds for red squirrel conservation in Scotland

This chapter is based on the peer reviewed manuscript:

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The chapter is presented as the published version of the paper. I undertook all the modelling work and played a lead role in developing the project objectives and writing the manuscript.

Abstract

The Eurasian Red Squirrel (*Sciurus vulgaris*) is under threat from the invasive North American Eastern Grey Squirrel (*Sciurus carolinensis*) with 80% of the remaining red squirrel populations in the British Isles found in Scotland. In this study we develop a spatially explicit mathematical model of the red and grey squirrel system and use it to assess the population viability of red squirrels across Scotland. In particular we aim to identify existing forests - natural strongholds for red squirrels - that can successfully support red squirrels under UK Forestry Standard management and protect them from potential disease-mediated competition from grey

squirrels. Our model results indicate that if current levels of grey squirrel control, which restrict or reduce the distribution of grey squirrels, are continued then there will be large expanses of forests in northern Scotland that support viable red squirrel populations. Model results that represent (hypothetical) scenarios where grey squirrel control no longer occurred indicated that grey squirrel range expansion and the process of red squirrel replacement would be slow. Model results for an assumed worst-case scenario where grey squirrels have expanded to all regions in Scotland identified forest regions - denoted natural strongholds - that could currently support red squirrels under UK Forestry Standard management practice. The results will be used to inform forest management policy and support a strategic review of red squirrel management by land management agencies and other stakeholders.

3.1 Introduction

The Eurasian red squirrel (*Sciurus vulgaris*) is under threat in the British Isles. Recent estimates [79] indicate that just over 80% of the remaining British populations are now thought to live exclusively in Scotland. The decline of red squirrel populations has arisen due to the expansion of, and resultant disease-mediated competition from, the North American Eastern grey squirrel (*Sciurus carolinensis*) which was introduced into the British Isles in the 19th century [86, 109, 147].

Current efforts to protect red squirrels in Scotland are focused on defending priority populations of red squirrels [120] across their Scottish range. This is achieved mainly through grey squirrel control that aims to prevent grey squirrel expansion northwards across a chosen boundary line (a line approximately between Helensburgh and Montrose [120], henceforth called the grey squirrel control boundary). There are also efforts to protect red squirrels in priority regions that lie south of the grey squirrel control boundary. Red squirrel conservation policy also recommends conservation action through sympathetic forest management in selected forest sites (strongholds), which are meant to provide refuge for red squirrels against the incursion and competition from grey squirrels [119]. The native habitat of the grey squirrel is the broadleaved forests of Eastern North America, meaning grey squirrels are broadleaf specialists. Consequently, they enjoy a significant competitive advantage over native Eurasian red squirrels in deciduous but not coniferous woodland. Strongholds tend to therefore be large, conifer-dominated forests [44, 53].

There are currently 19 sites throughout Scotland that have been designated as strongholds [44, 119]. Forest management guidance in these strongholds aims to "use woodland management to maintain healthy self-sustaining populations of red squirrels" [44]. The guidance is based on five key principles: (i) the maintenance of a dependable tree seed food supply, (ii) a resolution of conflicts with other management objectives, (iii) planning for red squirrels at the landscape scale, (iv) long term planning to sustain resilience and (v) the establishment of a monitoring system. Whilst the guidance acknowledges that stronghold sites should have been chosen to minimise conflicts (e.g. sites with a low proportion of broadleaved trees that favour grey squirrels), it recognised the challenge for forest managers to integrate red squirrel conservation with other forest management objectives.

A recent study has examined red squirrel viability in designated strongholds under recommended stronghold forest management compared to UK Forestry Standard (UKFS) management for strongholds in Scotland [132]. The findings showed that forest management policy specifically designed to reduce competition has little benefit in the absence of grey squirrels. Thus the rationale for managed strongholds north of the grey squirrel control boundary could be reconsidered to account for the distribution of grey squirrels. However, when grey squirrels are present the strongholds perform as intended, with stronghold forest management benefiting red squirrels at the expense of grey squirrels. The study [132] also highlighted that some designated strongholds could not protect red squirrels from potential grey squirrel invasion regardless of forest management policy - largely due to the high connectivity of these strongholds to habitat that is favourable for grey squirrels. These designated strongholds are therefore unsuitable for red squirrel protection and reflect an unwise choice in stronghold site selection. Furthermore, the study also described the potential for natural strongholds, where red squirrel populations would persist under UKFS management [42] despite the threat from grey squirrel expansion. Management of the designated strongholds requires resources and additional management time. Therefore, the identification of natural strongholds north of the grey squirrel control boundary, within which red squirrels can persist under UKFS management, even in the presence of grey squirrels, would free resources and management time that could be deployed elsewhere.

Mathematical models that combine accurate habitat information, such as land-cover information provided by GIS data and data on a species' ecology from field studies, with dynamic modelling to capture the population dynamics and species interaction can be utilised to inform conservation policy [17, 24, 60]. Such model frameworks have been successfully employed to inform red squirrel conservation, with models being used to examine the potential spread of squirrelpox in Scotland [166], to assess the importance of grey squirrel control to protect red squirrel populations on Anglesey [63], to determine how forest management practice affects red squirrel viability in the absence of grey squirrels [62] and in designated red squirrel strongholds in Scotland [132]. In collaboration with Forestry and Land Scotland (FLS), the Scottish Government agency responsible for managing Scotland's publicly-owned forests and land, we extend the established spatially explicit mathematical modelling framework for the red and grey squirrel system [62, 63, 132, 166] and use it to assess the population viability of red squirrels across Scotland. In particular we aimed to identify existing forests, natural strongholds for red squirrels, that can successfully support red squirrels against potential disease-mediated competition from greys under UK Forestry Standard management. The results will be used to inform forest management policy, and support a strategic review of red squirrel management by FLS and other stakeholders.

3.2 Methods

In this study we have developed a mathematical model to assess the long-term viability of red squirrels in Scotland. The model is based on previous models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches [147] to develop a spatial, stochastic model [62, 132, 162, 166]. The deterministic approach underpinning the model (see equations 3.1 and 3.2) 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 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, which assumes the existence of a shared disease, represents the dynamics of red squirrels who are susceptible (S_R) to the disease and those that are already infected (I_R) by the disease. The model also includes susceptible (S_G) and infected (I_G) grey squirrels as well as grey squirrels that have recovered (R_G) from the disease. The model we use is:

$$\begin{aligned}
\frac{\mathrm{d}S_G}{\mathrm{d}t} &= A_G(t) - bS_G - \beta S_G(I_G + I_R)\\
\frac{\mathrm{d}I_G}{\mathrm{d}t} &= \beta S_G(I_G + I_R) - bI_G - \gamma I_G\\
\frac{\mathrm{d}R_G}{\mathrm{d}t} &= \gamma I_G - bR_G\\
\frac{\mathrm{d}S_R}{\mathrm{d}t} &= A_R(t) - bS_R - \beta S_R(I_G + I_R)\\
\frac{\mathrm{d}I_R}{\mathrm{d}t} &= \beta S_R(I_G + I_R) - bI_R - \alpha I_R
\end{aligned} \tag{3.1}$$

where

$$A_G(t) = \begin{cases} (a_G - q_G(H_G + c_R H_R))H_G & 0 \leq t < 0.5 \\ 0 & 0.5 \leq t < 1 \end{cases} \tag{3.2}$$

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, $H_G = S_G + I_G + R_G$ and $H_R = S_R + I_R$ represent the total populations for grey and red squirrels respectively. The natural rate of adult mortality $b = 0.9$ [5] 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 $a_G = 3.4$ [147]. 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 $c_R = 0.61$ [20].

Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient $\beta = 1.1$ [166]. Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ [147]. The susceptibilities to crowding (q_R, q_G) are set to ensure the average density over one year is equal to the carrying capacity in each grid square for that year, with carrying capacities being habitat dependent (see section 3.A.1). All parameter values assume an annual time-scale. To generate the stochastic model, the rates for birth, death, infection, recovery etc., in the deterministic model are converted into probabilities of events that account for changes in individual 1 km by 1 km patch level abundance [100] - see section 3.A.2 for full description. The stochastic model also includes events that allows for dispersal of individuals between patches (see Table 3.A2 for details) as well as the possibility of control through the removal of grey squirrels (see section 3.A.4).

The stochastic model is used in conjunction with landscape information, primarily forest composition data and information on masting, which gives forest capacity dynamics. These data provides estimates for red and grey squirrel carrying capacity at the 1 km^2 level (see Chapter 3.A for further details).

In this paper we considered the following scenarios:

(i) The natural expansion of red and grey squirrel populations beyond the grey squirrel control boundary. This allows an examination of the threat to current red squirrel population from ‘natural’ grey squirrel expansion.

For this scenario the model was initialled with observed data for the presence of red and grey squirrels between 2014-2017 (using the National Biodiversity Network (NBN) Gateway, `http://data.nbn.org.uk`). In regions where only one squirrel species was observed the model was initialised at the respective carrying capacity for that grid-square, based on available habitat types. In regions where both squirrel species were observed the model was initialised with red and grey squirrel densities at half their respective potential carrying capacities. Once initialised, the model was run for 10 years in order to allow for changes in density in grid-squares with both squirrels present and for squirrels to expand into nearby available habitat.

(ii) The assumption that grey squirrels initially occupy all viable habitat in Scotland. This allows the model to predict the composition and location of current natural strongholds in Scotland in which viable red squirrel populations would persist when faced with the threat from grey squirrels.

For this scenario the model was initiated by assuming red squirrel occupancy is as in Figure 3.1(a) and that grey squirrels are present at their carrying capacity in all grid squares in which the grey squirrel carrying capacity is greater than, or equal to, 5 km^{-2} (and therefore this scenario assumes that grey squirrels have dispersed to all regions in Scotland).

To generate results each scenario was simulated 10 times, with each simulation of the model being run for 150 years each to ensure that the model is predicting the long-term population dynamics. Habitat, carrying capacity and occupancy maps were generated using MATLAB R2018b. Simulations were run using Fortran90.

3.3 Results

Figure 3.1(a) shows the initial distribution of red and grey squirrels used in the model simulations and is indicative of the current distribution in Scotland. This highlights how red squirrels currently occupy suitable habitat in the north of Scotland (above the grey squirrel control boundary) as well as in isolated populations in southern and central Scotland. Grey squirrels typically dominate habitat south of the grey squirrel control boundary as well as habitat in Aberdeen and surrounding areas. The grey squirrel population at Aberdeen has persisted since a separate introduction in the 1970s [117]. At present, grey squirrel control, coordinated by Saving Scotland's Red Squirrels [120] aims to prevent grey squirrels from expanding northwards beyond the grey squirrel control boundary, to reduce the distribution of greys in Aberdeen and the surrounding area and to defend the isolated red populations in southern and central Scotland.

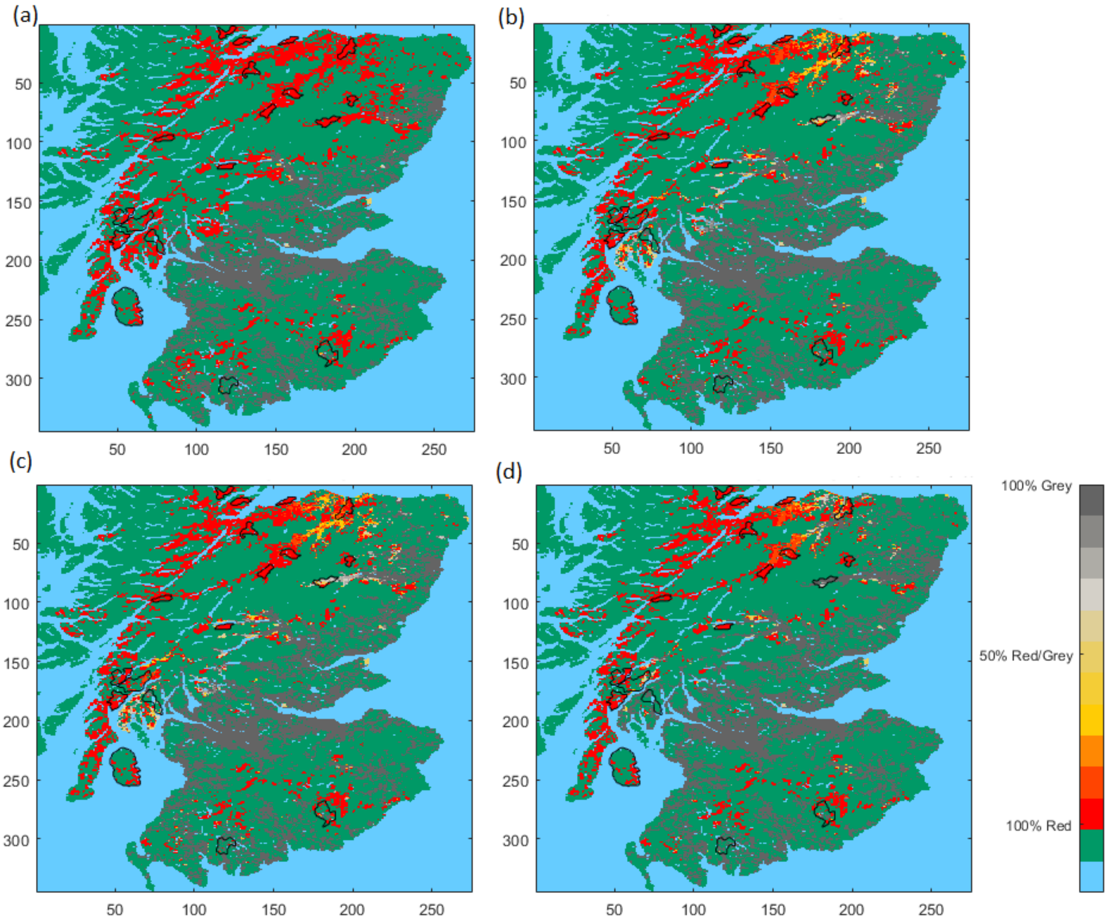

Figure 3.1: Results showing the relative occupancy of each 1 km grid-square. Here (a) shows the initial occupancy as maintained by trapping at the grey squirrel control boundary, (b) shows an average occupancy of the first 30 years of the simulation after grey squirrels are allowed to disperse freely, (c) shows the average occupancy results for years 65 to 95 of the simulation where grey squirrels are allowed to disperse freely, and (d) shows the long-term occupancy (150 years after the simulation begins) of red and grey squirrels after greys have been allowed to disperse freely. A grid square is classed as being occupied if there are 2 or more individuals of any species present. The scale bar indicates the proportion of the 10 simulations that ended with either red or grey squirrel occupancy. For example, 75% red occupancy in a given grid-square indicates that 75% of the simulations that ended in occupancy were occupied by red squirrels. The 19 designated strongholds [119] are outlined in black.

3.3.1 *Red squirrel viability when grey squirrels naturally expand their range of occupancy*

Figure 3.1(a-d) shows occupancy maps for 150 years of model simulation when squirrels can disperse beyond their current distribution. Findings show that grey squirrels swiftly expand their range into the north-east of Scotland, with consequent loss of red squirrel populations. The range expansion of grey squirrels into the north-east beyond the initial expansion (through habitats in Moray and along the river Spey) is slow.

There is limited expansion in grey squirrel distribution across the grey squirrel control boundary and into red squirrel occupied regions in central and southern Scotland. In the model this range expansion occurs within the first 30 years and the grey distribution remains relatively fixed thereafter. The mathematical model has been fitted to qualitatively reproduce observed rates of red and grey squirrel expansion through suitable habitat [62]. Therefore, the absence of grey squirrel expansion north of the grey squirrel control boundary is due to a lack of suitably connected habitat in relation to the assumed and validated grey squirrel dispersal ability.

Much of northern Scotland, above the grey squirrel control boundary, remains occupied by viable red squirrel populations (maps of average squirrel density for the these simulations can be found in Figure 3.B1). This is primarily due to the inability of grey squirrels to disperse to suitable habitat in northern Scotland. Isolated red squirrel populations persist in central and southern Scotland and indicate that these regions are natural strongholds for red squirrels. Here red squirrel populations persist in conifer-dominated regions even though grey squirrels occupy neighbouring habitat.

3.3.2 *Identifying natural red squirrel strongholds in Scotland*

Results showing the occupancy of red and grey squirrels at the end of the model simulations, when grey squirrel are assumed to initially occupy all viable habitat, are shown in Figure 3.2 (see also Figure 3.B2). The regions where red squirrels persist in Figure 3.2 can be defined as natural strongholds that would support red squirrel populations under a worst-case scenario of grey squirrel expansion across the whole of Scotland. The density of red and grey squirrels for this scenario are shown in Figure 3.3a(i)-c(i). There are numerous natural strongholds but they are often isolated and support low-density red squirrel populations. The qualitative nature of the simulations do not allow us to decide which strongholds would support viable red squirrel populations. The habitat composition for red-dominated regions (natural strongholds) and grey-dominated regions in Figure 3.2 is shown in Figure 3.4. Natural red squirrel strongholds are predicted for regions composed of conifer and pine species with a general absence of broadleaf and urban habitat. This is typical of large forest plantations in Scotland. Grey squirrel dominated regions contain broadleaf species and urban habitat and grey squirrels can occupy conifer and pine habitats where they are adjacent to broadleaf and urban habitats.

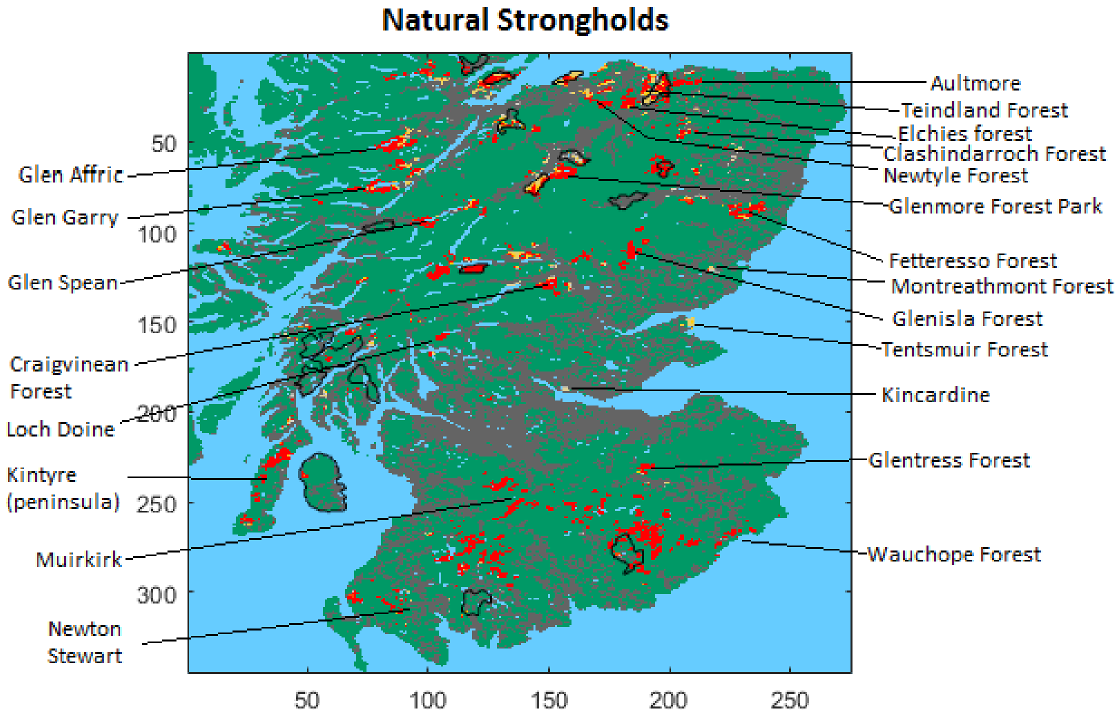

Figure 3.2: Relative occupancy of red and grey squirrels when grey squirrels have been introduced everywhere. The names are of the forests that the model predicts can act as natural strongholds. The 19 designated strongholds [119] are outlined in black.

Figure 3.3a(ii)-c(ii) shows red and grey squirrel densities, as well as squirrel occupancy, when grey squirrel trapping is applied in grid-squares that contain a grey squirrel population. The amount of trapping applied is equivalent to 18 trap-days per year in each grid cell. The results show that this level of grey squirrel trapping does not reveal new red squirrel strongholds, but does reinforce and enlarge existing natural strongholds. Increases in trapping effort further enhances this effect.

3.4 Discussion

In this study we have developed a spatial mathematical model that includes the competitive and disease interactions between red and grey squirrels in realistic habitats across Scotland to assess the viability of red squirrel populations under several scenarios of grey squirrel expansion. The current strategy for red squirrel conservation in Scotland aims to restrict or reduce the distribution of grey squirrels and to maintain viable red squirrel populations in priority areas for red squirrel conservation [120]. If this conservation strategy is successful (which observations suggest is currently the case [88]) then the model predicts that there will be large expanses of forest north of the grey squirrel control boundary that support viable red squirrel populations.

The model allowed us to test 'what if' scenarios for red squirrel conservation and predicted that if current levels of grey squirrel control, which aim to restrict grey squirrels to their current distribution, were to end and grey squirrels were allowed to expand their range, then the process of red squirrel replacement would be slow. This would allow time for red squirrel conservation management policy to be implemented. Furthermore, during the period of grey squirrel expansion there would still remain large expanses of forest in north and north west Scotland that would support viable red squirrel populations. In the absence of control, grey squirrels are predicted to expand northwards, most notably along the north-east and northern coast, with their expansion directly north curtailed by geographical constraints (such as the Cairngorm mountains). Our results support the current grey squirrel control efforts aimed at containing and removing grey squirrels from Aberdeen and the surrounding area [120] as this will prevent grey squirrel expansion around the north-east and northern coast of Scotland. Expansion of grey squirrels into central or western Scotland is also impeded by the geography, with the Southern Highland mountains forcing grey squirrels to migrate along the west coast which provides poor habitat.

Since large-scale grey squirrel range expansion beyond their current distribution is prevented by geographical constraints on natural migration, it will be important to provide public information regarding the threat of grey squirrels to prevent artificial dispersal, whether accidental or intentional, across geographical barriers by members of the public. History shows that grey squirrel range expansion was facilitated by humans (e.g. see Signorile et al. [129]). Grey squirrels were introduced into Aberdeen and its surroundings via separate introductions, and considerable resources and effort has been required to keep these populations under control, with the goal of eradication occurring in the future [120]. Further evidence of the risks inherent in the deliberate introduction of grey squirrels can be found in Italy. Grey squirrels were introduced into Piedmont in northern Italy in 1948. Subsequent introductions into Genoa in the 1960s and trans-locations into Lombardy in the late 1990s have led to further grey squirrel expansion southwards into central Italy as well as northwards across the Po plain, where future expansion into France and Switzerland is a real possibility [76, 78, 128]. This increase in grey squirrel range in Italy has led to a corresponding reduction in red squirrel density and highlights the need for public information campaigns that detail the risks and consequences of trans-locations to native wildlife and forestry.

An assumed worst-case scenario where grey squirrels have expanded to all regions in Scotland identified a range of forest regions across Scotland that could support red squirrels under UKFS management practice. We define these forest sites as natural strongholds (see Figure 3.2). Several forest sites in the north of Scotland are able to maintain a viable red squirrel population, despite the presence of grey squirrels. However, these sites are relatively small and isolated, with densities of around 2 red squirrels km^{-2}, potentially placing the red squirrel populations resident in the natural strongholds at risk due to stochastic extinction and loss of genetic diversity [160]. To overcome this problem, the disparate forests could either be physically connected via forest management, or the genetic viability of the populations could be managed and enhanced by periodic trans-locations of red squirrels. It should be noted that the density of red squirrels in natural strongholds under UKFS management are in line with those predicted in model studies for the designated strongholds under stronghold forest management [132]. The study by [132] also showed that the additional forest management required (above that of UKFS) to satisfy the designated stronghold policy [44, 119] may have little benefit to red squirrel viability in the absence of grey squirrels. Moreover, it was predicted that some of the designated strongholds could not protect red squirrels from the threat of grey squirrel invasion even when their composition was modified to satisfy designated stronghold policy. The model results presented in this paper also show that the locations of the natural strongholds does not match the locations of the 19 designated forest strongholds in Scotland (the designated strongholds are outlined in black in Figure 3.2). Our findings suggests that natural strongholds could offer similar or improved protection to red squirrels if threatened by grey squirrel invasion as offered by the designated strongholds.

A potential red squirrel conservation strategy could employ grey squirrel control to reinforce the ability of natural strongholds to sustain a red squirrel population. Figure 3.3 a-c(ii) shows results for squirrel density and occupancy when grey squirrel trapping is applied in all regions where grey squirrels are present (see also section 3.B.2). Grey squirrel trapping is applied to all grid squares in which greys are present with approximately 18 trap-days per year per grid square. Although it is unrealistic to apply grey squirrel control across all regions, the model results highlight whether grey squirrel trapping would improve red squirrel viability in natural strongholds. North of the grey squirrel control boundary, grey squirrel trapping leads to an expansion of the regions of red squirrel occupancy and an increase in red squirrel density. There is a small expansion of red squirrel occupied regions in southern Scotland. This indicates that grey squirrel control around natural strongholds can lead to red squirrel expansion and improved population viability.

An analysis of the available land-cover data indicated that the forest composition of natural strongholds is comprised predominantly of Sitka spruce in southern Scotland and Sitka spruce, Scots and lodgepole pine in northern Scotland combined with an absence of broadleaf and urban habitat. This forest composition is already met by forest plantations in the north of Scotland, which consequently act as natural strongholds. Management would still be required to maintain a suitable tree species composition and age structure, in the face of normal timber and harvesting operations, to provide an advantage to red squirrels over grey squirrels and to maintain a viable population in the long term. Nevertheless, a review and potential change in management policy for some designated strongholds in northern Scotland may allow current efforts and resources to be reassigned to focus on vulnerable red squirrel populations that are threatened by incursions of grey squirrels. Note, whilst broadleaf and urban habitats are suitable to support viable (high-density) red squirrel populations these habitats favour grey squirrels who out-compete red squirrels. This analysis is supported by a recent statistical occupancy model for red and grey squirrels in Northern Ireland. This study used data collected by citizen science to show that red squirrel occupancy was positively correlated with coniferous woodland and negatively correlated with urban habitat. Likewise, grey squirrels were positively correlated with broadleaved forests and urban habitat and negatively correlated with coniferous habitat [151].

There is consensus that squirrelpox played a key role in the competition and disease mediated invasion of red squirrels when greys squirrels expanded through England and Wales [15, 147], where the habitat consisted of broadleaved or mixed stands that could support high squirrel densities. The natural strongholds predicted in this study are dominated by coniferous habitats that generally support low-density red squirrel populations. The impact of squirrelpox on the location of, and red squirrel density in, natural strongholds was negligible. This is in line with previous studies that show squirrelpox cannot be supported in low-density red squirrel populations [63, 162] and that red squirrels can therefore ‘live’ with the threat from squirrelpox. Hence, squirrelpox is unlikely to play a key role in grey squirrel invasion in low-density populations in Scotland [77].

In this study we did not consider the impact of climate change on forest composition as it went beyond the scope of this project. However, we recognise that it will be an increasingly important factor in the red/grey squirrel dynamics and therefore red squirrel conservation in the future. Natural strongholds in Scotland largely coincide with managed forest plantations, due to their tree species composition. Thus, incorporating climate change into the model to identify natural strongholds would require knowledge of detailed future forest management plans. Climate change will influence the tree species composition in forests, maturation time and seed mast cycles [14, 89] and will likely favour an increase in broadleaf trees through range expansion and species migration [89]. Grey squirrels have a competitive advantage in broadleaved habitat and can reach higher densities which may be able to support endemic squirrelpox virus [109, 147]. This could make natural strongholds vulnerable to grey squirrel invasion and threaten red squirrel viability. Studies also suggest that climate change may lead to an increase in woodland cover [98]. This could increase the avenues northwards, above the grey squirrel control boundary, which would facilitate and increase the rate at which grey squirrels can colonise the remainder of Scotland. Conversely, the mountainous habitat that lies directly north of the control boundary could remain resistant to reforestation by climate change. Alternatively, climate change could increase the proportion of land in Scotland that is viable for agricultural use, which in turn could reduce the connectivity of Scottish forests [48]. This could aid red squirrels by reducing the ability of grey squirrels to expand their range, but such isolation may reduce genetic diversity and increase the risk of local population extinction. The impact of climate change on red squirrel conservation should therefore be the focus of future research efforts to help sustain viable populations in the long term.

3.5 Conclusion

Our findings highlight the existence of forest areas (natural strongholds) north of the grey squirrel control boundary that would currently support viable red squirrel populations without the need for species specific management. Natural strongholds, which often correspond to large commercial forest plantations, are managed according to UKFS policy and are typically composed of Sitka spruce and other conifer and pine species. Our predictions suggest grey squirrel dispersal and expansion will likely be slow even in the absence of grey squirrel control, due to geography in northern Scotland forming a barrier between the current distribution of red and grey squirrels. Together with recently published results [132] our findings here support a policy review to better target effort and resources for red squirrel conservation in Scotland.

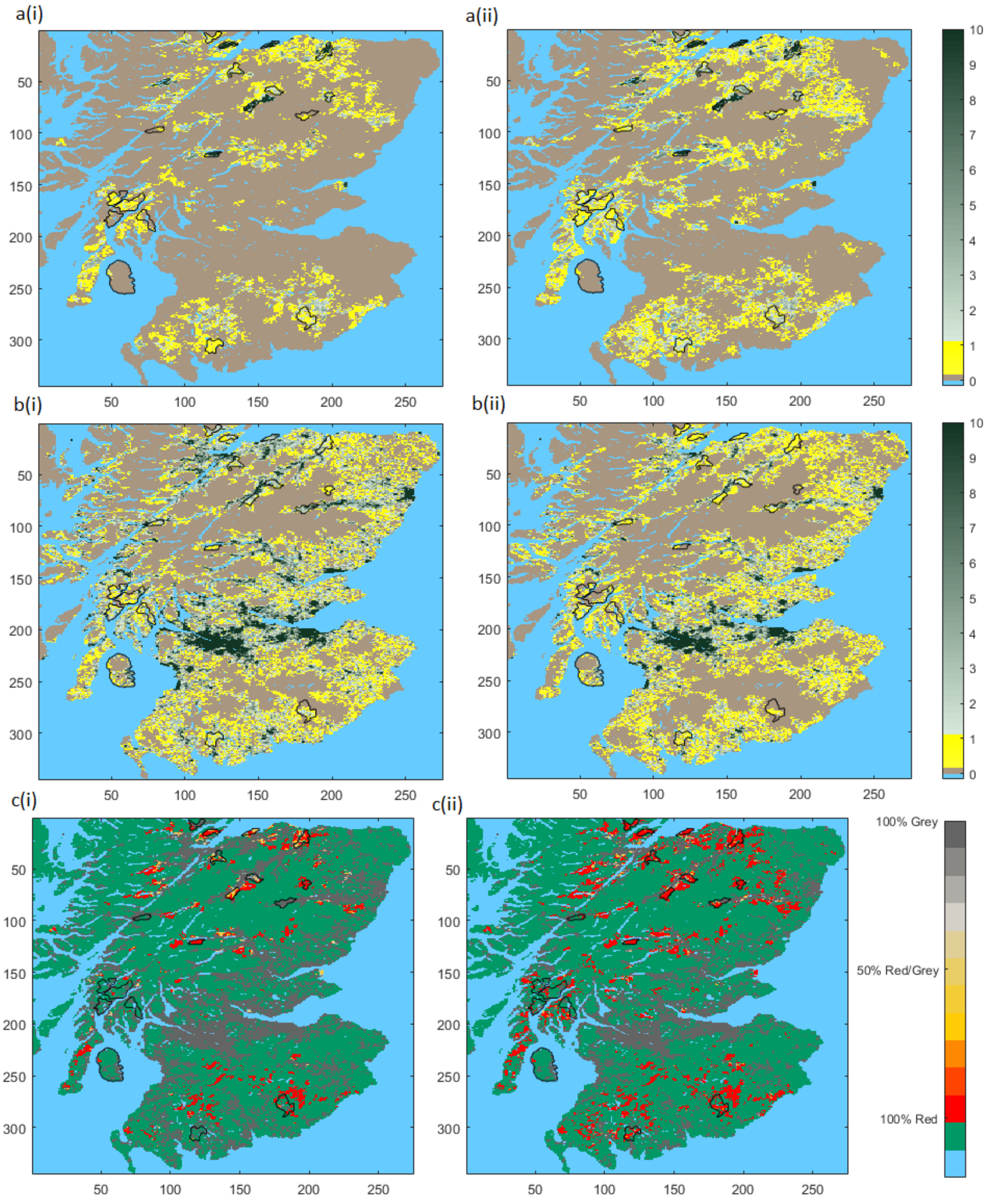

Figure 3.3: Density and occupancy results when grey squirrels have been introduced everywhere in Scotland. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the occupancy results for (i) the simulation where no grey squirrel trapping was applied and (ii) the simulation where grey squirrel trapping (approx. 18 trap days per year) is applied to each grid square that contains grey squirrels. The 19 designated strongholds [119] are outlined in black.

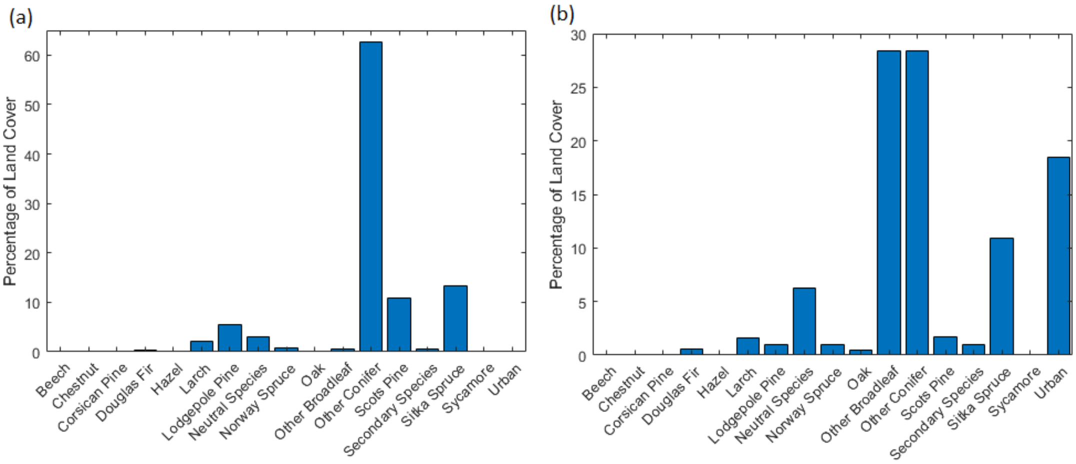

Figure 3.4: Habitat composition in regions where (a) red squirrels have greater than 80% occupancy and (b) grey squirrels have greater than 80% occupancy. Named species are from the National Forest Estate 2017 dataset whilst Other broadleaf and Other conifer data is from the National Forest Inventory 2016 dataset.

Appendix 3.A Mathematical model

The information in this Appendix was included as Supplementary Information in the published version of this work [133].

In this section we outline how detailed habitat information is used to determine squirrel carrying capacities and we detail the stochastic model that is generated from the deterministic model in the main paper.

3.A.1 *Carrying capacity*

The mathematical model uses forest habitat information obtained from the National Forest Estate 2017 (available at: https://data-forestry.opendata.arcgis.com/datasets/) and National Forest Inventory 2016 (available at: https://data.gov.uk/dataset/) land cover data sets and is supplemented by the Scottish National Heritage (available at: https://www.nature.scot/) dataset which contains information on the urban landscape of Scotland. Primary tree species information for each 25 m by 25 m area was extracted from these datasets using the GRASS GIS software package (https://grass.osgeo.org). This data was used in MATLAB to create a map consisting of a 1 km^2 resolution grid with each grid square containing the proportion of land covered by each tree species as well as the proportion of urban environment.

The link between squirrel density, habitat and tree seed crops is well evidenced [51, 52, 75]. Thus, the gridded habitat data is combined with estimates of squirrel density in different habitat types. This produces a red and grey squirrel carrying capacity value for each 1 km grid square. These values signify the potential population density that the landscape can support. In the model the carrying capacity is not fixed but instead fluctuates due to seed crop dynamics which assumes that tree species undergo a mast year with a defined period, producing higher yield of seed crops that can support increased squirrel densities (Table 3.A1) [15, 52]. These mast years are largely cyclical and occur simultaneously for the majority of trees within a single species that are present in a local, connected forest. During the non-mast years, the trees can either undergo ‘intermediate’ or ‘poor’ years in terms of cone or seed production which have been averaged in this modelling framework to produce a single non-mast value for each species. Each tree species undergoes a period of non-mast and mast years at regular intervals (with the period defined in Table 3.A1). The starting point for this period was chosen at random for each tree species at the beginning of the simulation. Carrying capacity values for each tree species were updated every year, using the relevant values in Table 3.A1, to account for seed crop dynamics, which allowed the forests carrying capacity dynamics to be incorporated into the model. Where data were available in the literature for specific tree species these have been used (Table 3.A1); where they were not available they have been conservatively set at being one quarter of the mast values. The latter estimate is based on data from Spadeadam Forest, Northern England [74], an analysis of 16 years of cone crop data for Sitka spruce and Scots pine at Kidland Forest, Northern England [72] and an examination of a 25 year cone data set for Scots pine [18].

	Red Squirrel		**Grey Squirrel**		
Tree Species	**Mast**	**Non-Mast**	**Mast**	**Non-Mast**	**Mast Interval**
Beech	1.10	0.28	1.49	0.37	7
Chestnut	1.00	0.25	3.40	0.85	4
Hazel	0.85	0.85	2.00	2.00	1
Sycamore	0.00	0.00	1.49	0.10	2
Oak	1.00	0.25	3.40	0.85	4
Other Broadleaf	0.78	0.19	2.45	0.61	5
Neutral Species	0.00	0.00	0.00	0.00	N/A
Secondary Species	0.10	0.02	0.10	0.02	1
Larch	0.38	0.21	0.38	0.10	4
Lodgepole Pine	0.21	0.05	0.08	0.02	2
Scots Pine	0.83	0.33	0.31	0.08	2
Corsican Pine	1.10	0.28	1.10	0.28	3
Douglas Fir	0.21	0.05	0.08	0.02	5
Norway Spruce	0.58	0.25	0.33	0.08	4
Sitka Spruce	0.20	0.02	0.00	0.00	4
Other Conifer	0.40	0.15	0.20	0.05	3
Urban	0.19	0.08	0.40	0.11	N/A

Table 3.A1: Carrying capacities for red and grey squirrels, in individuals per hectare, for mast and non-mast years for each of the tree species considered in the model. Values for Other Broadleaf and Other Conifer are averages of the known broadleaf or conifer trees. The last column is the (average) interval between mast years. Mast interval data is based on [1].

3.A.2 *Model framework*

To generate the stochastic model, the different rates in the deterministic model are converted into probabilities of events that account for changes in individual patch level abundance [100]. To do this, we calculate the relevant rate for each event by adding/multiplying the relevant parameter values together. For example, the rate associated with the natural death of a susceptible grey squirrel (S_G) is given by $b \times S_G$, where $b = 0.9$ and S_G is the susceptible grey squirrel density in the relevant grid square. When each event has an associated rate, these are added together to give the parameter R. By dividing each event rate by R we attain the probability of each event occurring. The relationship between the terms in the model equations, the different events (birth, death, infection, dispersal, etc.), the change in population abundance and the probability of each event in the stochastic model are given in Table 3.A2. The time between events can be determined as $T_{event} = -ln(\sigma)/R$ where R is defined above and σ is a random number drawn from a uniform distribution between 0 and 1 (which assumes that the time to the next event is an exponentially distributed random variable). The events are incremented at random with the associated probabilities updated due to changes in population density after each event. Individual simulations can be undertaken in FORTRAN90 using a Gillespie algorithm and provide information of the behaviour in a single realisation. Ten realisations are run for each scenario, and averages taken. For further information see [100].

In this framework, the birth terms shown in Table 3.A2 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 dispersal term is shown in Table 3.A2 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 control of squirrels is shown for class S_G only but is similar for all other classes (although when a red squirrel is caught there is no change in red squirrel abundance to reflect the fact that it is released unharmed). Here, $c = 3.5$, represents the rate of successfully trapping a squirrel and T_D is the trap intensity (trap effort per grid-cell per day). Further details of the model framework and the calculation of parameter values can be found in [63].

Event	**Population Change**	**Probability of Event**
Birth of S_G	$S_G \to S_G + 1$	$[(a_G - q_G(H_G + c_R H_R))H_G]/R$
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	$S_R \to S_R + 1$	$[(a_R - q_R(H_R + c_G H_G))H_R]/R$
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	$S_G \to S_G - 1, S_G^* \to S_G^* + 1$	$\left[mS_G \left(\frac{(H_G + c_R H_R)^2}{(K_G)^2}\right)\right] /R$
Control of Grey	$S_G \to S_G - 1$	$[cT_D S_G]/R$

Table 3.A2: Stochastic model events that govern the dynamics that occur within each 1 km grid square. The parameters representing control and dispersal were fitted with observed data on the Island of Anglesey [63]. See section 3.A.2 for full details.

3.A.3 *Initial conditions*

The model was initialled with observed data for the presence of red and grey squirrels between 2014-2017 (using the National Biodiversity Network's (NBN) Gateway, `http://data.nbn.org.uk`) and by using a model spin-up to allow red and grey squirrels to expand into available habitat prior to the initialisation of the model. In regions where only one squirrel species was predicted the model was initialised at the respective potential density based on available habitat types. In regions where both squirrel species were predicted the model was initialised by assuming that reds and greys had access to half the habitable area in each grid cell.

3.A.4 *Grey squirrel trapping*

Grey squirrel trapping is included in every square that has a grey squirrel population. Geographically, this level of trapping is unrealistic and much more comprehensive than what is currently applied. However, given that the location of natural strongholds is unknown a priori, trapping cannot be targeted. Hence, occupancy results that include trapping should be viewed according to local effects. Of particular interest is whether the use of trapping can either expand existing regions, or create new regions, where red squirrels persist compared to scenarios where trapping is absent. Grey squirrel trapping is only included during the squirrel breeding season (1 April - 30 September), which is 183 days. A trapping coefficient $T_D = 0.1$ [163] is used and this is equivalent to 18 trap-days per year per 1 km grid square.

Appendix 3.B Additional results

3.B.1 *Results when grey squirrels naturally expand their range*

Figure 3.B1 shows the results for squirrel density and occupancy when grey squirrels are allowed to expand their range.

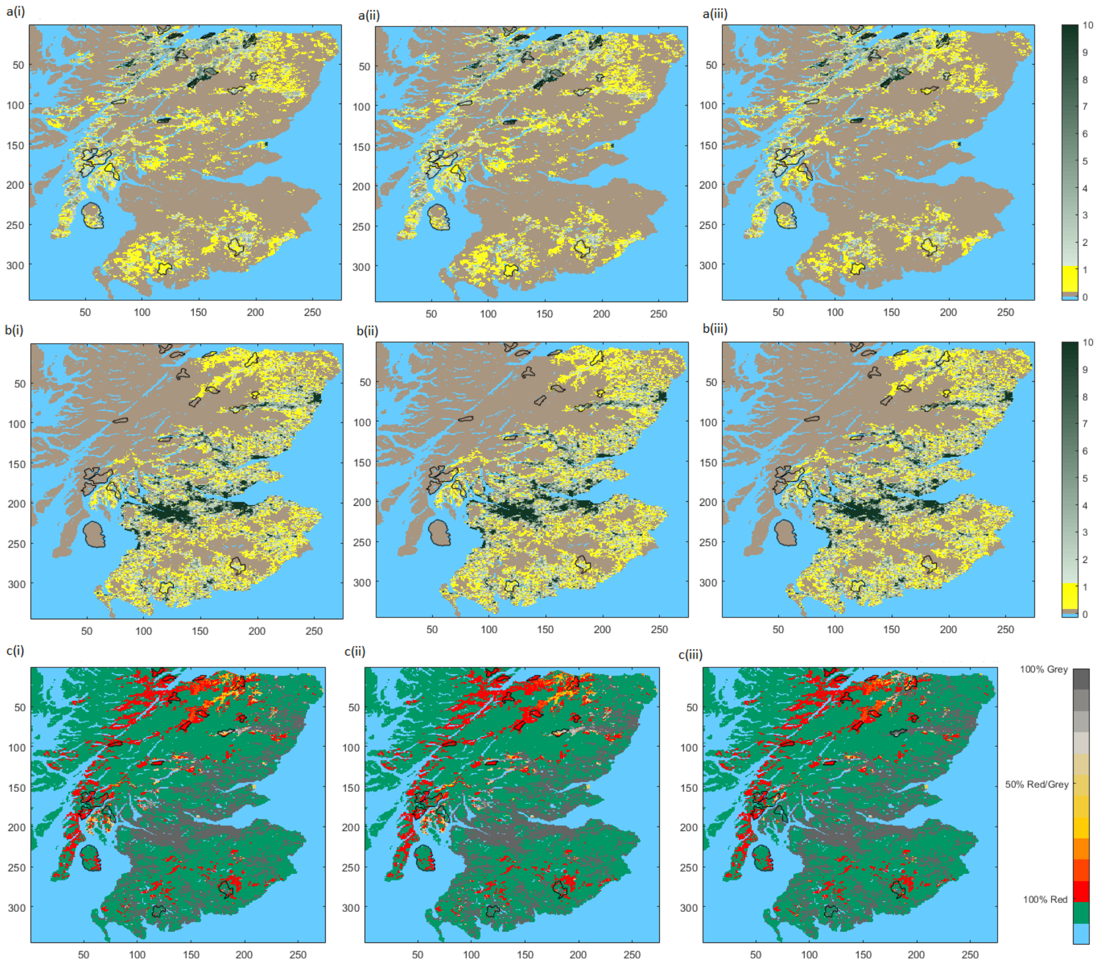

Figure 3.B1: Results for the scenario where red and grey squirrels are allowed to disperse and compete freely. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The 19 designated strongholds are outlined in black.

3.B.2 *Results when grey squirrels occupy the entirety of Scotland*

Results without grey squirrel trapping

Figure 3.B2 shows results for squirrel density and occupancy for the scenario where grey squirrels have been introduced everywhere and grey squirrel trapping has not been included.

In central Scotland the regions of forest at Rannoch, which includes the forest of South Rannoch as well as the forest that lies directly west, would constitute good red squirrel strongholds. Furthermore, given the lack of grey squirrel occupancy in this region, these two forests could potentially be connected, using appropriate planting that give an advantage to red squirrels over greys, to create a single, larger, connected natural stronghold which would aid population viability. The forest to the east of Rannoch, just north of Loch Tummel, is contested between red and grey squirrels, with some simulations ending with grey squirrels present and some ending without grey squirrels, despite being connected to an area of grey squirrel occupancy. The forest of Craigvinean, to the south of Rannoch near Dunkeld, also acts as a natural red squirrel stronghold which suggests that trapping around Dunkeld could isolate the natural red squirrel strongholds at Rannoch due to geographic factors that prevent grey squirrel incursion via other routes. To the east of this region lies Glenisla forest which also acts as a natural red squirrel stronghold due to its relative isolation and lack of connectivity.

In the east of Scotland the region that includes the forest at Glentochty, which lies to the west of Aberdeen, is a natural stronghold. Directly south of Aberdeen is Fetteresso forest which also makes a good natural stronghold, especially given its proximity to Aberdeen.

Along the northern coast of Scotland there is a significant region of forest that either has sole red occupancy or is contested. In the centre of this region is the forest of Ordiequish, to the east lies the forest of Aultmore whilst Teindland forest lies directly to the west, all of which either have sole red squirrel occupancy or contested occupancy, despite the wider region being grey dominated, which suggests that trapping could safeguard these forests for red squirrels. Sole red squirrel occupancy occurs at Elchies forest which lies to the south-west of Ordiequish. To the west of Elchies forest is the forests of Newtyle, Dallas and Monaughty, all of which can be found further west along the north coast, to the south-east of the forest at Culbin, and all of which see some grey squirrel incursion, but not dominance, during the simulations. The forest at Culbin is also contested between red and grey squirrels but is separated from the other three forests by a region of grey squirrel occupancy at Darnaway forest and the city of Elgin. However, trapping at Elgin could prevent grey squirrel expansion further west along the northern coast, which would isolate the region south of Culbin allowing red squirrel occupancy, due to the limited number of migration routes available to grey squirrels.

The river Spey is also in this region and includes the forests of Inshriach and Glenfeshie, which is a region that sees grey squirrel incursions, and Abernethy which only allows red squirrel occupation in part of the forest. However, the forest in between these two regions, Glenmore Forest Park, makes a good natural stronghold which suggests that this and the two adjacent forests could potentially be combined to create a single natural stronghold. Furthermore, given limited grey squirrel access routes imposed by the geography, trapping further along the Spey river, to the south of Ordiequish for example, could isolate the region and prevent grey squirrels entering from the north-east.

Further north the forest of Black Isle, which lies to the north of Inverness, makes for a good natural stronghold. The forests around Glen Affric and Glen Garry, which lie on the opposite side of Inverness from Black Isle, also act as natural strongholds. To the south of Glen Garry there is a region of red squirrel occupancy around Glen Spean, which lies to the east of Fort William, which makes a good natural stronghold.

The peninsula of Kintyre in west Scotland allows both red and grey squirrel occupation, with segregation occurring naturally and red squirrels occupying the west and grey squirrels the east of the peninsula. There is also a small region that could act as a natural stronghold at the western edge of Loch Doine, however the west of Scotland appears to offer little in the way of natural red squirrel stronghold.

In the south of Scotland the regions of red squirrel occupancy are the same as the current observational data, due to the current existence of grey squirrels in the region. Thus in the Scottish Borders the eastern section of the forest at Eskdalemuir allows sole red occupancy. The forest to the north of Eskdalemuir, at Glentress forest, as well as Wauchope forest at the border with England, which is connected to the stronghold at Kielder forest which is approx. 5000 km^2 in area and is dominated by Sitka spruce, also act as natural red squirrel strongholds.

In Dumfries and Galloway the urban area at Gatehouse of Fleet as well as deciduous regions along the river valley to the north provide good grey squirrel habitat. The forests to the north of the Gatehouse of Fleet, east of the Waters of Ken, are better suited to be natural strongholds. Further north, near the town of Muirkirk, there are a number of small regions of forest that can act as red squirrel strongholds. There is also a region of forest, near the town of Newton Stewart, that can act as a natural stronghold.

Beyond this there are a few small regions, such as Tentsmuir forest, Kincardine and Montreathmont forest, that see both red and grey squirrel occupancy during the simulations, which suggests that trapping could exclude grey squirrels, despite these regions being surrounded by sole grey occupancy regions.

Results with grey squirrel trapping

Figure 3.B3 shows results for squirrel density and occupancy for the scenario where grey squirrels have been introduced everywhere and grey squirrel trapping is included. Grey squirrel trapping is applied to all grid squares in which greys are present with approximately 18 trap-days per year per grid square. The inclusion of grey squirrel trapping does not reveal new natural strongholds, though some regions that allow both red and grey squirrels to compete at low densities, such as the area on the north coast, only allow red squirrel occupancy when trapping is introduced. Existing natural strongholds are reinforced by the trapping, with some expanding slightly, but the results are not dramatic. Regions where red squirrels can survive despite grey squirrel competition are regions where grey squirrels cannot reside in large numbers. Thus the poorness of the habitat that allows red squirrels to survive also hinders their potential expansion when grey squirrel abundance is reduced via trapping.

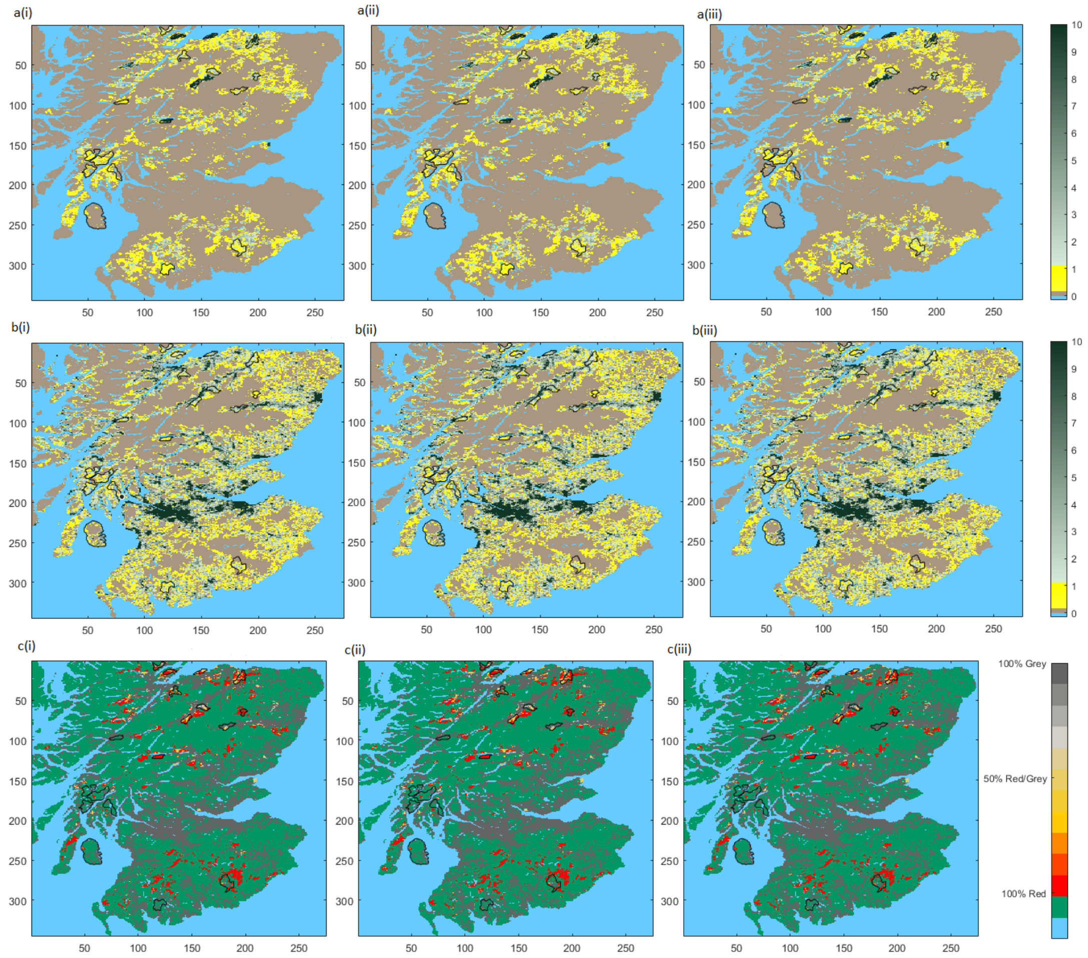

Figure 3.B2: Results for the scenario where grey squirrels have been introduced everywhere, in order to simulate a situation where grey squirrels have successfully colonised the entirety of Scotland. These results have no grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The 19 designated strongholds are outlined in black.

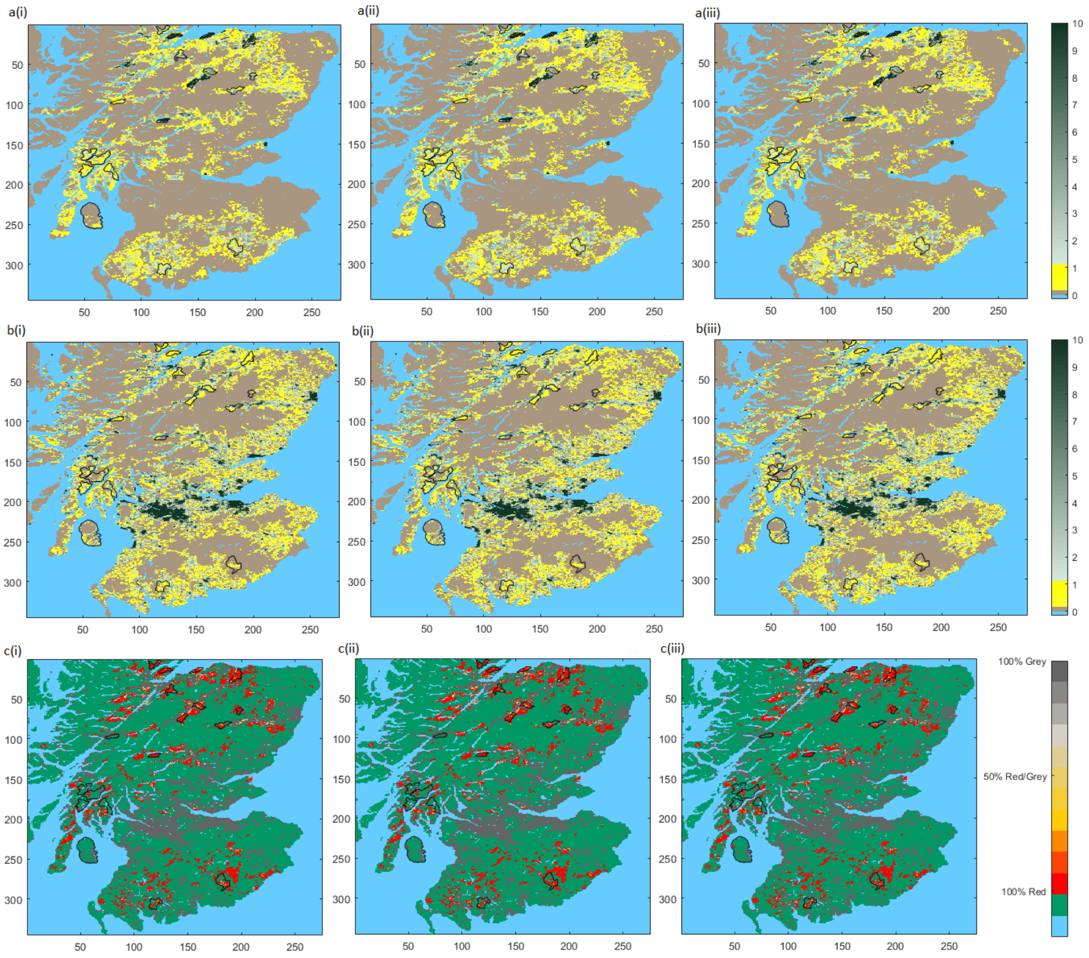

Figure 3.B3: Results for the scenario where grey squirrels have been introduced everywhere, in order to simulate a situation where grey squirrels have successfully colonised the entirety of Scotland. These results include grey squirrel trapping (approx. 18 trap-days per year per grid-square in which greys are present). Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The 19 designated strongholds are outlined in black.

Chapter 4

The impact of pine marten predation on red squirrel conservation in North Wales

This chapter is based on the commission report for the Red Squirrel Trust Wales:

Slade, A., White, A. and Lurz, P.W.W. 2021. The impact of pine marten predation on red squirrel conservation: A case study of three priority regions in Wales.

We aim to turn this report into a manuscript for submission to 'Ecological Modelling'. I undertook all the modelling work and played a lead role in developing the project objectives and writing the report.

4.1 Introduction

The Eurasian red squirrel (*Sciurus vulgaris*) is under threat in the United Kingdom, with recent estimates [79] 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 [79]. 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 [86]. 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 [11, 53, 114, 161]. 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 $> 80\%$ [26]. The replacement rate of red squirrels occurs significantly faster in areas where SQPV is present [109, 147].

Efforts to re-introduce red squirrels into Wales have encompassed a number of trans-locations, 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 [118]. 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 [63]. 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 [68], 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 [164]. 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 [46] to prevent grey squirrel range expansion and reduce disease transmission (e.g. see Highland Boundary Line, [116] or [118]) 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 [44]).

Pine marten (*Martes martes*) are generalist predators that have been shown to preferentially predate on grey squirrels compared to red squirrels [152]. 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 [122, 124, 152]. 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. [112]), 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.

In this chapter we aim to 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. Our specific objectives are as follows:

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 trans-location, 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.

4.2 Mathematical model

We extend established modelling frameworks that represent the population density of red and grey squirrels, the prevalence of the SQPV infection (see Chapters 2 and 3), to include 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.

4.2.1 *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 [147] to develop a spatial, stochastic model [62, 162, 166]. The deterministic approach underpinning the model (see equations 4.1 and 4.2) 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:

$$
\begin{aligned}
\frac{\mathrm{d}S_G}{\mathrm{d}t} &= A_G(t) - bS_G - \beta S_G(I_G + I_R) - \mu_G S_G P^x \\
\frac{\mathrm{d}I_G}{\mathrm{d}t} &= \beta S_G(I_G + I_R) - bI_G - \gamma I_G - \mu_G I_G P^x \\
\frac{\mathrm{d}R_G}{\mathrm{d}t} &= \gamma I_G - bR_G - \mu_G R_G P^x \\
\frac{\mathrm{d}S_R}{\mathrm{d}t} &= A_R(t) - bS_R - \beta S_R(I_G + I_R) - \mu_R S_R P^x \\
\frac{\mathrm{d}I_R}{\mathrm{d}t} &= \beta S_R(I_G + I_R) - bI_R - \alpha I_R - \mu_R I_R P^x \\
P(t) &= P^x
\end{aligned}
\tag{4.1}
$$

where

$$A_G(t) = \begin{cases} (a_G - q_G^x(H_G + c_R H_R))H_G & 0 \le t < 0.5 \\ \\ 0 & 0.5 \le t < 1 \end{cases} \tag{4.2}$$

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 $b = 0.9$ [5] 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 $a_G = 3.4$ [147]. 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 $c_R = 0.61$ [20]. 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 [163]. Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ [147]. 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 A1 (See also Section 4.2.3 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 4.2.2. All parameter values assume an annual time-scale.

4.2.2 *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 [13], with seasonally stable home ranges [92]. 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:

$$\text{Newborns} = \frac{\text{Average Lifespan} - \text{Maturity Age}}{\text{Average Lifespan}} \times (\text{Litter Size} \times \text{Gender Split})$$

$$= 0.6 \text{ per individual.}$$

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 $\mu_R = 0.2\mu_G$ [122, 152].

Pine marten dispersal occurs on a 5 km by 5 km gridded scale which has a defined habitat dependent carrying capacity (see section 4.2.3). 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 (see Appendix). 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 4.1), the rates in the deterministic model are converted into probabilities of events that account for changes in individual patch level abundance [100]. Each simulation is run for 50 years.

Event	Population Change	Probability of Event
Birth of S_G	$S_G \to S_G + 1$	$[(a_G - q_G(H_G + c_R H_R))H_G]/R$
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	$S_R \to S_R + 1$	$[(a_R - q_R(H_R + c_G H_G))H_R]/R$
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 4.1: State transitions and their probabilities in the stochastic model. A full table legend can be found overleaf.

Table 4.1: (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 [63]. 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 [63].

4.2.3 *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 4.1. 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 4.2(a) shows the red squirrel carrying capacity map, Figure 4.2(b) the grey squirrel carrying capacity map and 4.2(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. [62]. In line with recent studies for Scotland [132] 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 [62]. 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 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 A1.

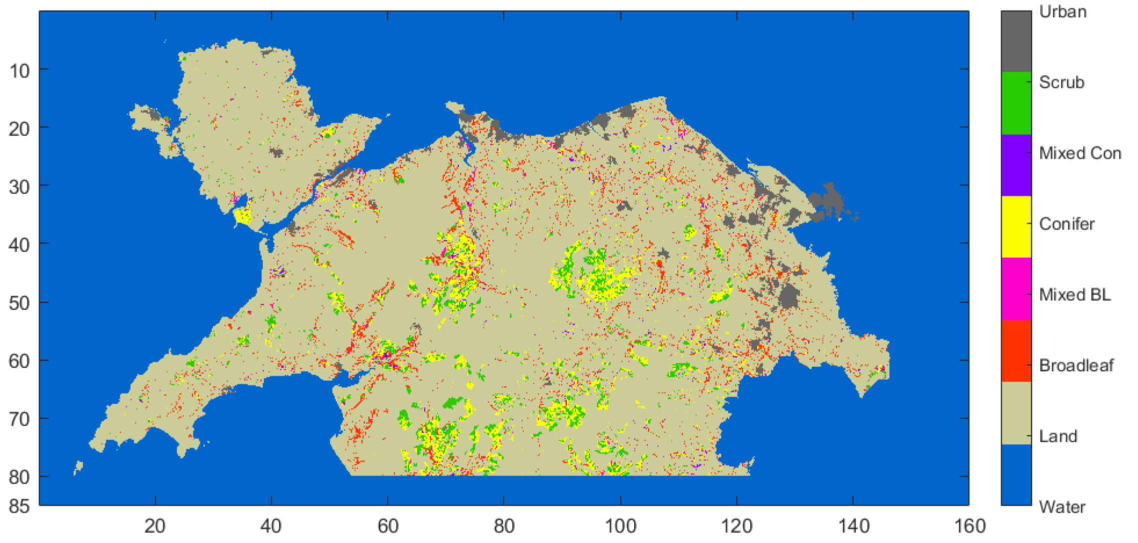

Figure 4.1: High resolution (25 m by 25 m) feature map for North Wales. The colour scale indicates which feature is the predominant one in any given 25 m by 25 m square. The axes values indicate the distance in kilometres.

4.2.4 *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

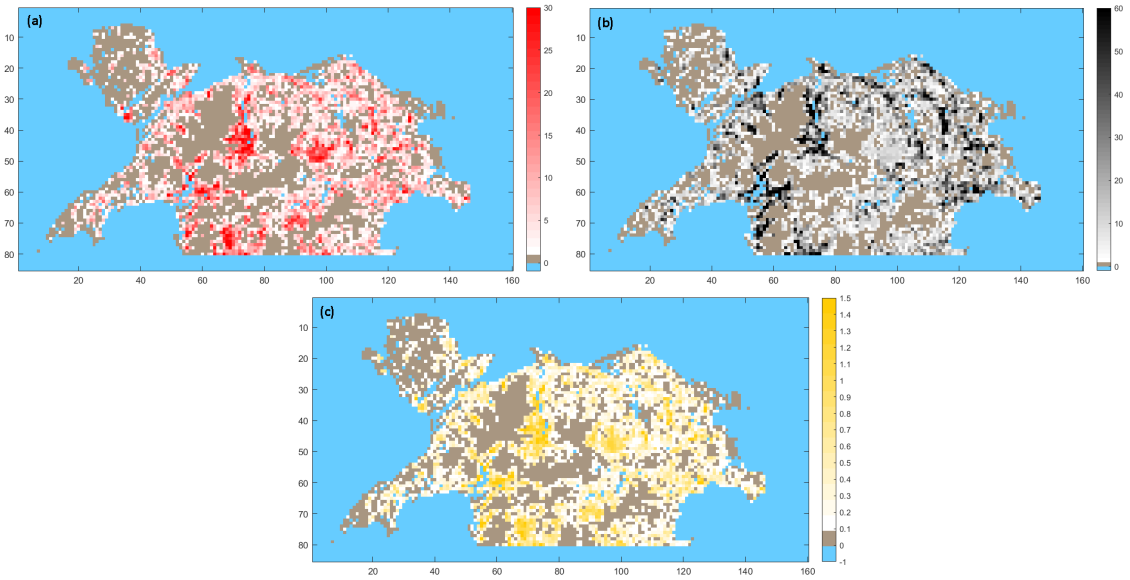

Figure 4.2: Carrying capacity maps for (a) red squirrels, (b) grey squirrels and (c) pine marten. All capacity values are per km^2.

	Red CC	**Grey CC**	**Marten CC**
Broadleaf	65	250	3.49
Conifer	35	15	1.15
Mixed Mainly Broadleaf	55	168	2.67
Mixed Mainly Conifer	46	97	1.97
Scrub	6	6	1.15
Urban	32	95	0.05
Britannia Bridge	32	95	0.05
Open Land	0	0	0.05

Table 4.2: Red and grey squirrel, and pine marten carrying capacity values, per km^2, for different habitat types. Squirrel values are the medium level values used by Jones et al. [62]. Pine marten carrying capacity values are authors estimates based on personal communications with J. Twining and D. Tosh.

capacity in Anglesey and Clocaenog, red and grey squirrels are at half their carrying capacity in the Bangor region and grey squirrels are at their carrying capacity in all other regions (as indicated in Figure 4.3). We consider a range of pine marten initial conditions that simulate different scenarios. The first initial condition (Figure 4.4(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 4.4(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

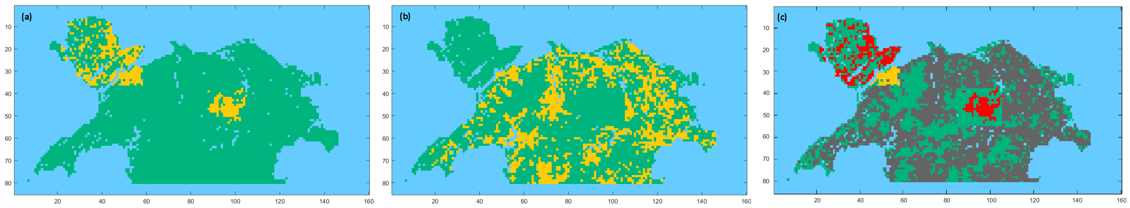

Figure 4.3: Initial condition for (a) red squirrels, which are initialled at Clocaenog, Anglesey and Bangor, and (b) grey squirrels which are initialled in all suitable habitat except Clocaenog and Anglesey. Image (c) shows the initial occupancy where grey regions indicate grey presence, red regions red presence and yellow regions indicate the presence of both red and grey squirrels.

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 4.4(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 4.4(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 [110, 118] in a homogeneous population of 80 individuals in a 1 km by 1 km grid-square (equivalent to a grey squirrel density of 80 km^{-2}). 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 [110, 118]. The prevalence of squirrelpox, for the different transmission values, is shown in Figure 4.5 and indicates that the model predicts variability in the prevalence of squirrelpox, which is strongly linked to grey squirrel density across North Wales.

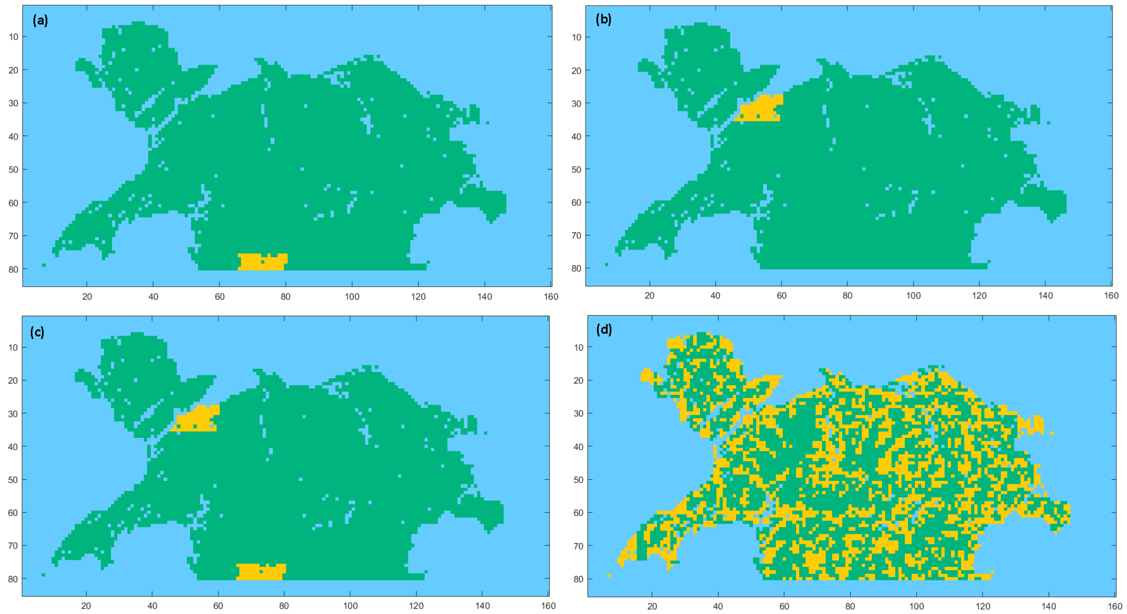

Figure 4.4: Initial conditions for pine marten. Here (a) shows the location of pine marten that are assumed to have migrated north from Mid Wales, (b) shows the Bangor region where different release scenarios were tested, (c) is a combination of the Bangor and Mid Wales introduction sites and (d) has pine marten being introduced, at full carrying capacity, into every available grid-squares.

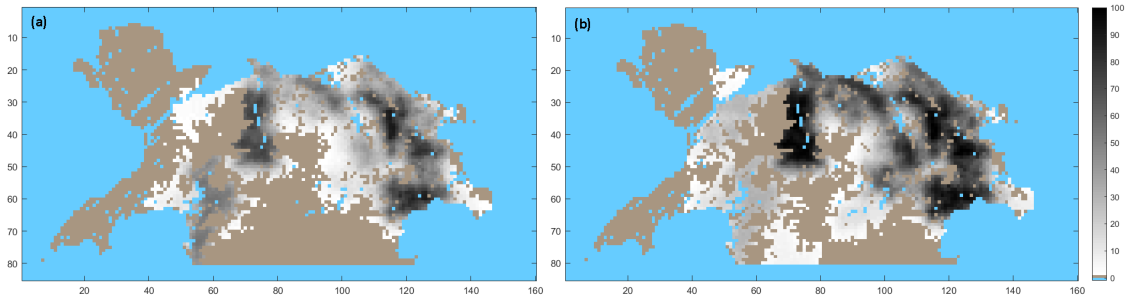

Figure 4.5: Squirrelpox prevalence in grey squirrels, shown as the percentage of the population that has previously been infected with the disease, when the infection rate is (a) $\beta = 0.83$ and (b) $\beta = 1.11$. These results are the outcome of a 10-year model spin-up with only grey squirrels present.

4.3 Results

The model results are presented as follows. Section 4.3.1 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 4.3.2 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 4.3.3 will detail the impact of pine marten on squirrelpox, as well as the impact of pine marten on red squirrel density and Section 4.3.4 will highlight key expansion routes for pine marten in North Wales.

4.3.1 *Red/grey/squirrelpox interactions in the absence of pine marten*

Figure 4.6 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 4.6 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. [63]). 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 [125].

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 4.7 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.

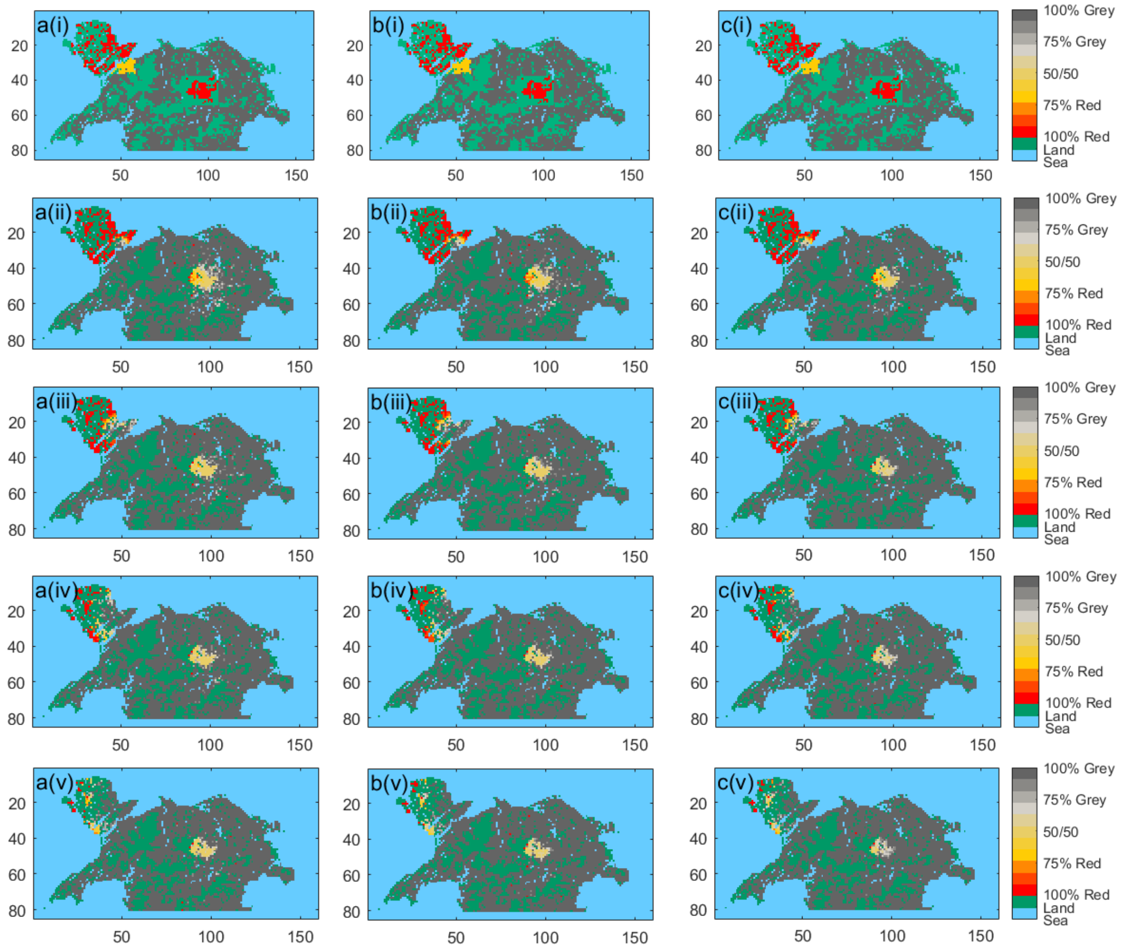

Figure 4.6: Occupancy results for red and grey squirrels in the absence of pine marten. Here (a) shows the results when there is no squirrelpox present, (b) shows the results when squirrelpox is included with transmission coefficient $\beta = 0.83$ and (c) shows the results when squirrelpox is included 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.

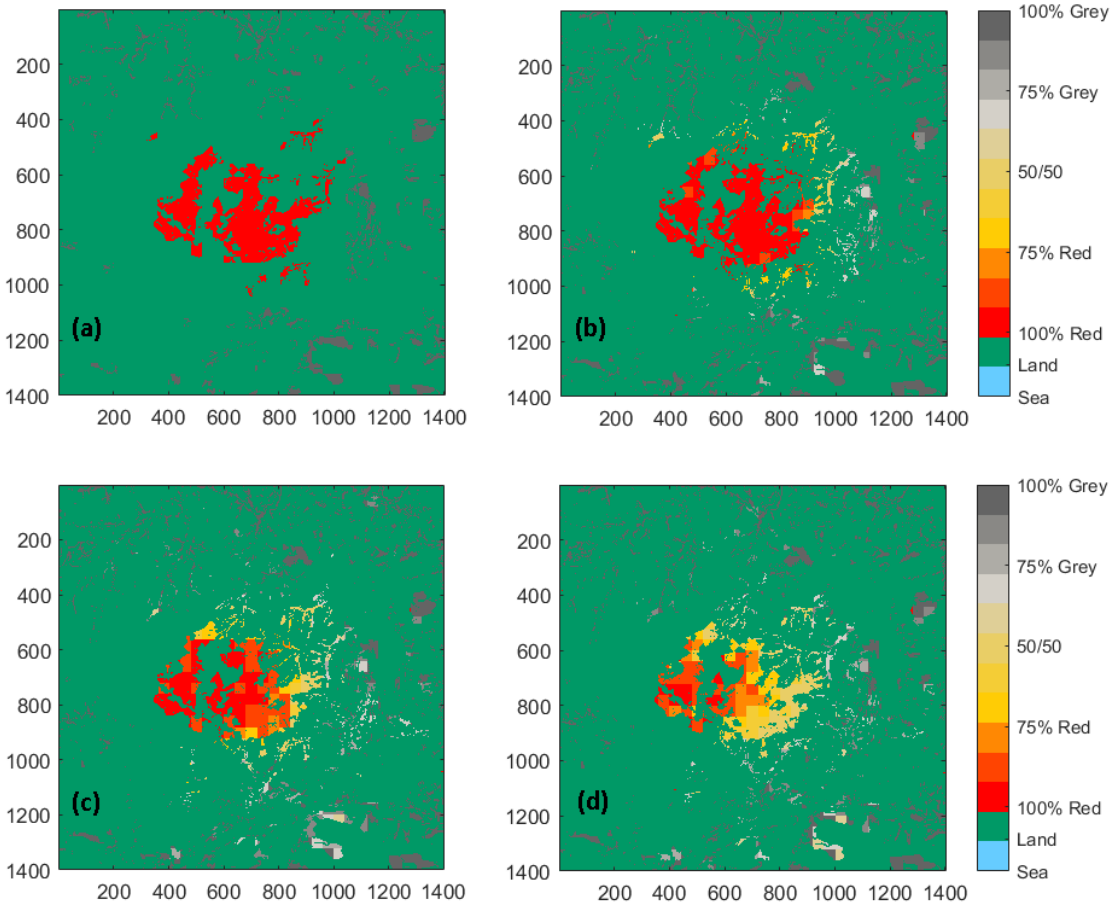

Figure 4.7: High resolution (25 m by 25 m) red and grey squirrel occupancy results, in the absence of pine marten, that demonstrate the available colonisation routes for grey squirrels into Clocaenog. Here (a) shows the initial occupancy, (b) shows the results after 2 years, (c) shows the results after 4 years, and (d) shows the results after 6 years of simulation. The results include squirrelpox with transmission coefficient $\beta = 0.83$.

4.3.2 *Red/grey/squirrelpox interactions in the presence of pine marten*

Pine marten migration from Mid Wales

Figure 4.8 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.

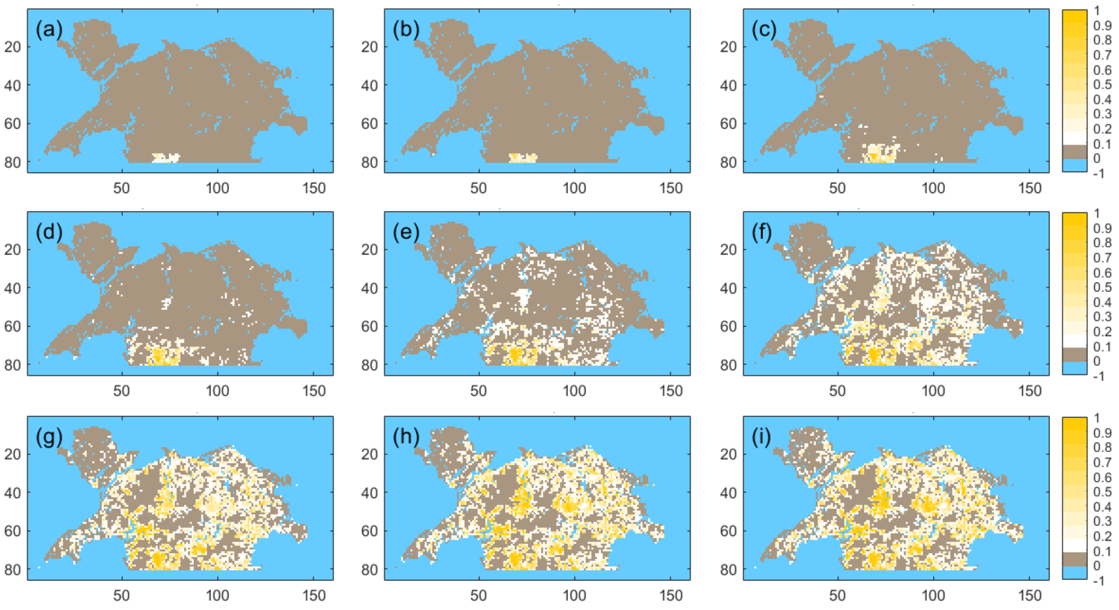

Figure 4.8: Pine marten range expansion when they are released into Mid Wales only, at a quarter of the carrying capacity. Here (a) shows the initial condition, (b) the pine marten range expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

Figure 4.9 shows the squirrel occupancy results when pine marten are assumed to migrate from Mid Wales. As shown in Figure 4.8, 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 4.6 (the absence of pine marten) and Figure 4.9 (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.

Pine marten introduction into the Bangor region

Figure 4.10 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 4.11 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 4.8 with Figure 4.11, 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 4.12 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.

Pine marten introduction into the Bangor region and migration from Mid Wales

Figure 4.13 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 4.14 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 4.12, 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.

Pine marten introduction into all regions

Figure 4.15 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.

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 4.16a and 4.16b 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 presented above 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.

4.3.3 *The impact of pine marten on squirrelpox*

Squirrelpox is currently endemic in the grey squirrel populations of North Wales. Figure 4.17 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 4.13), predation of grey squirrels reduces the grey squirrel density (Figure 4.18) to levels that cannot support squirrelpox (Figure 4.17). 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 4.17 and 4.18), 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.

4.3.4 *High resolution pine marten range expansion images*

Figure 4.19 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 4.1), 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.

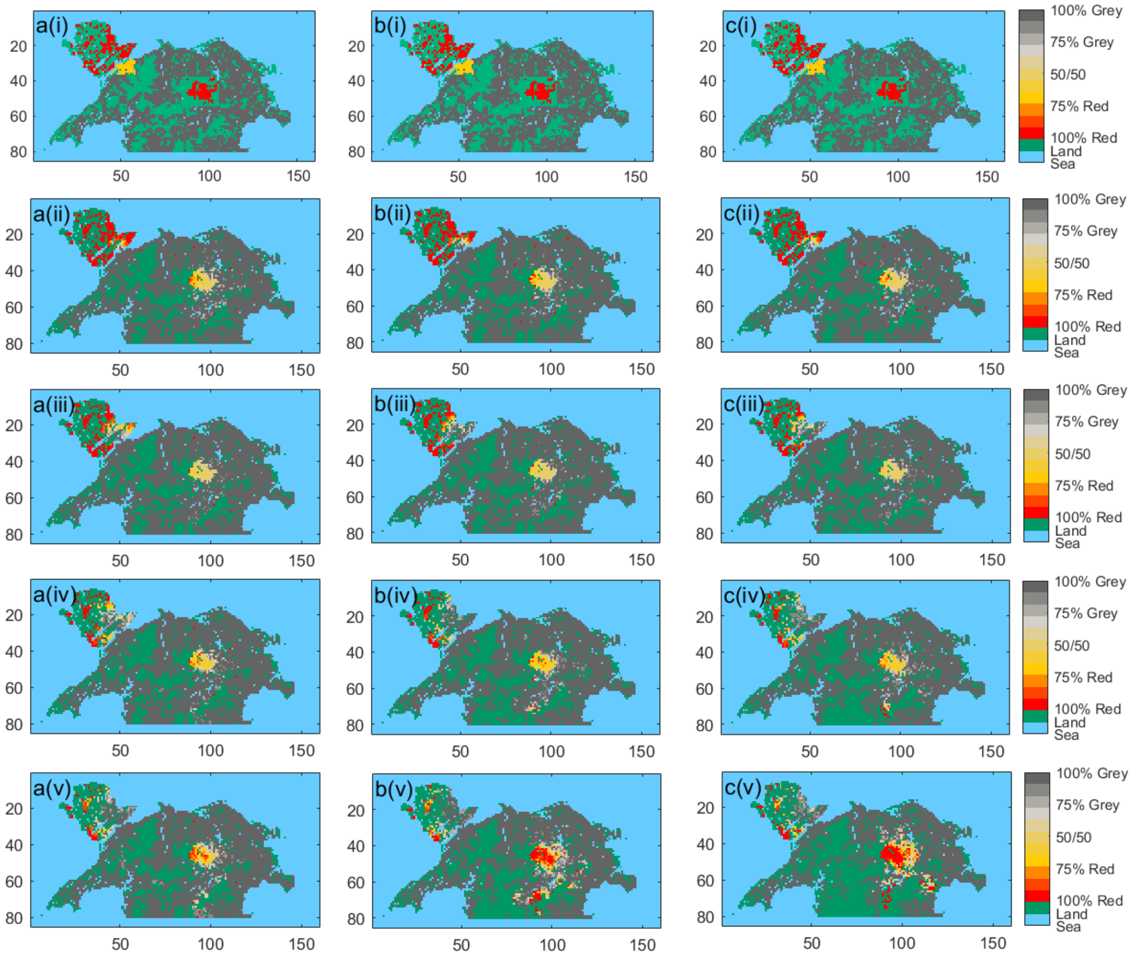

Figure 4.9: Red and grey squirrel occupancy results when pine marten are introduced into Mid Wales at a quarter of the carrying capacity (see Figure 4.4(a)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. Here (a) shows the results when the grey squirrel 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.

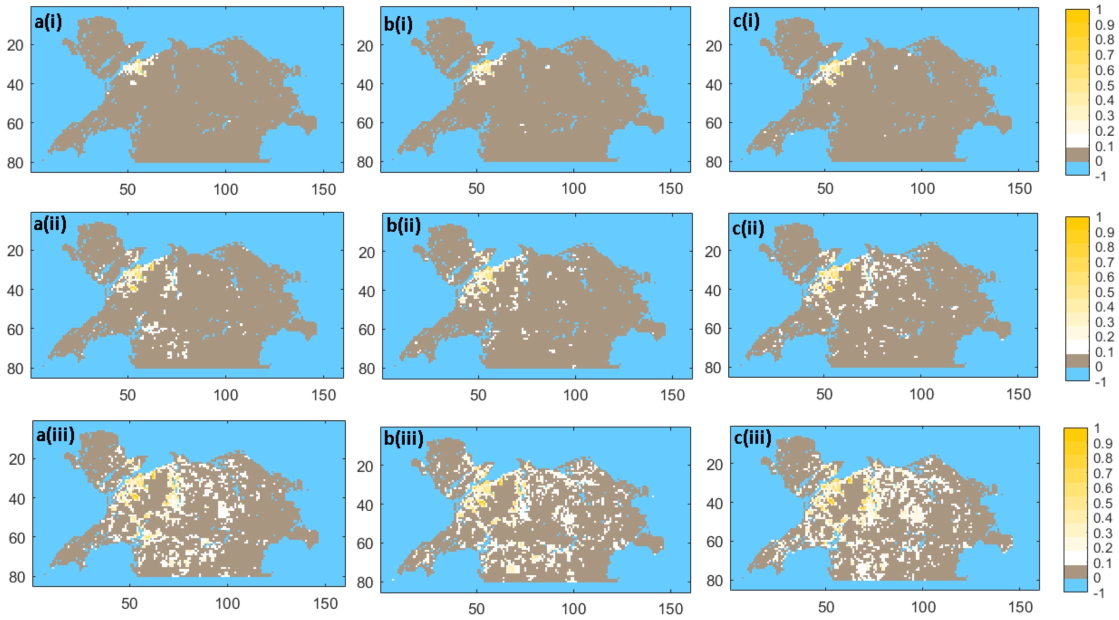

Figure 4.10: Pine marten expansion when pine marten are released into the Bangor region (see Figure 4.4(a)) in (a) 4 groups of 5 individuals, over 4 years, (b) 2 groups of 10 over 2 years and (c) a single group of 20 individuals at the start of the simulation. Image (i) shows the dispersal after 7 years, (ii) shows the dispersal after 15 years, and (iii) shows the expansion after 21 years of simulation.

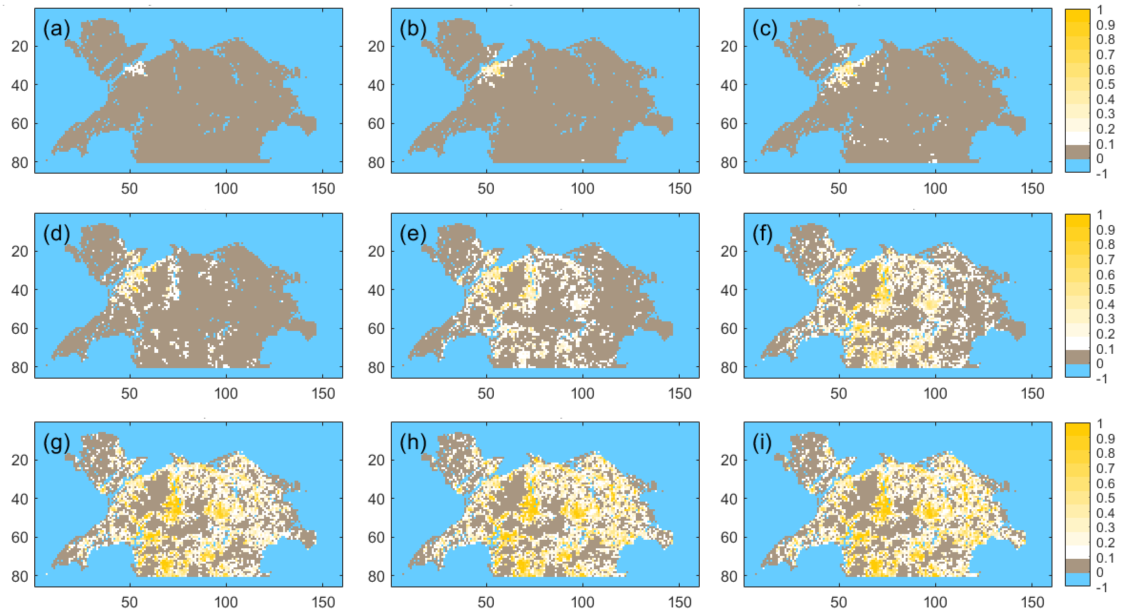

Figure 4.11: Pine marten range expansion when they are released into the Bangor region as two groups of 10 individuals in consecutive years. Here (a) shows the initial condition, (b) the pine marten expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

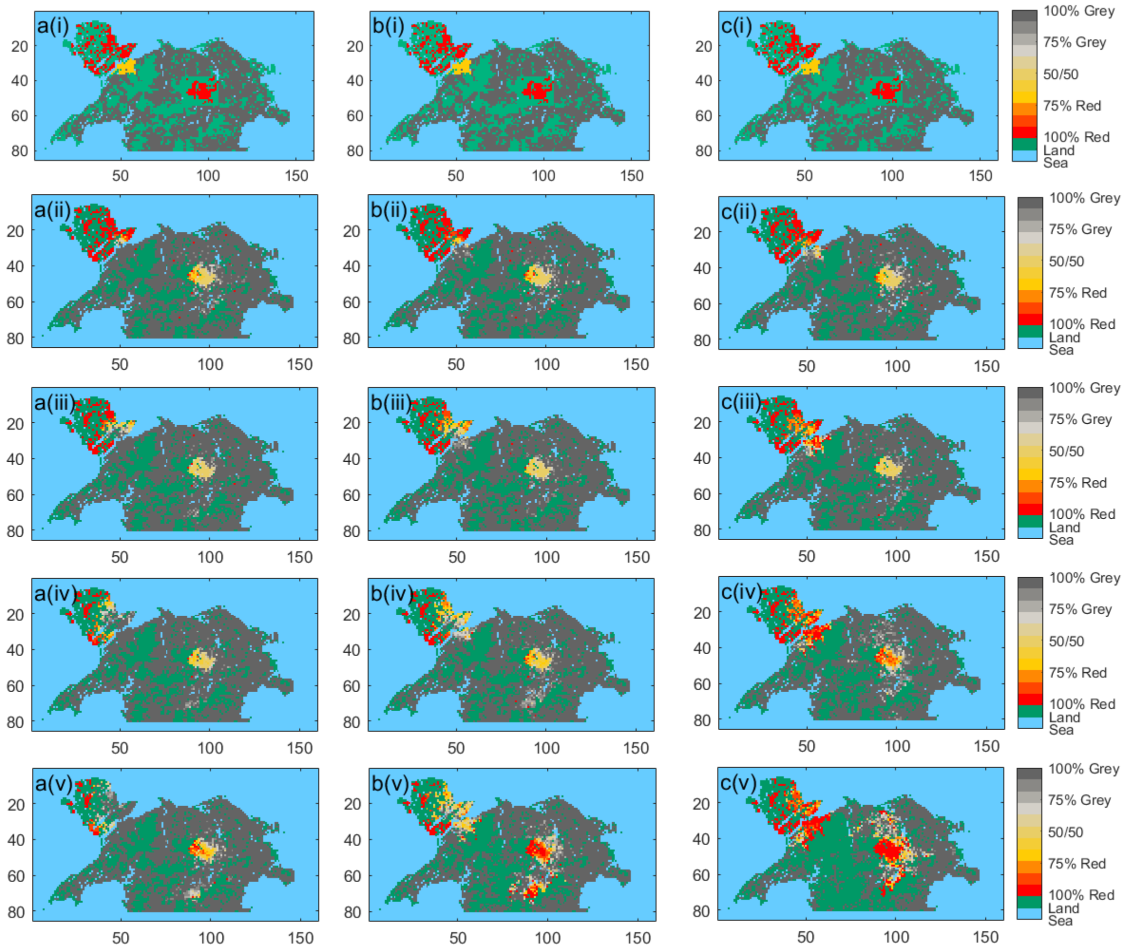

Figure 4.12: Red and grey squirrel occupancy results when pine marten are introduced into the Bangor region as two groups of 10 individuals in consecutive years (see Figure 4.4(b)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. Here (a) shows the results 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.

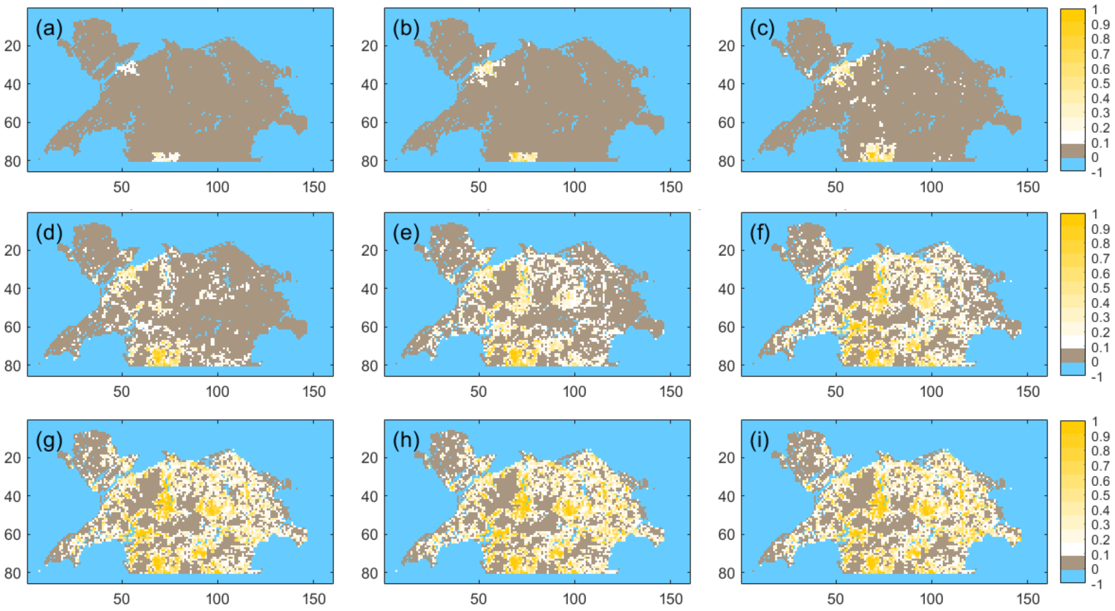

Figure 4.13: Pine marten range expansion when they are released into the Bangor region as two groups of 10 individuals in consecutive years, and into Mid Wales at a quarter of the carrying capacity (see Figure 4.4(c)). Here (a) shows the initial condition, (b) the pine marten expansion after 5 years, (c) 10 years, (d) 15 years, (e) 20 years, (f) 25 years, (g) 30 years, (h) 35 years and (i) 40 years.

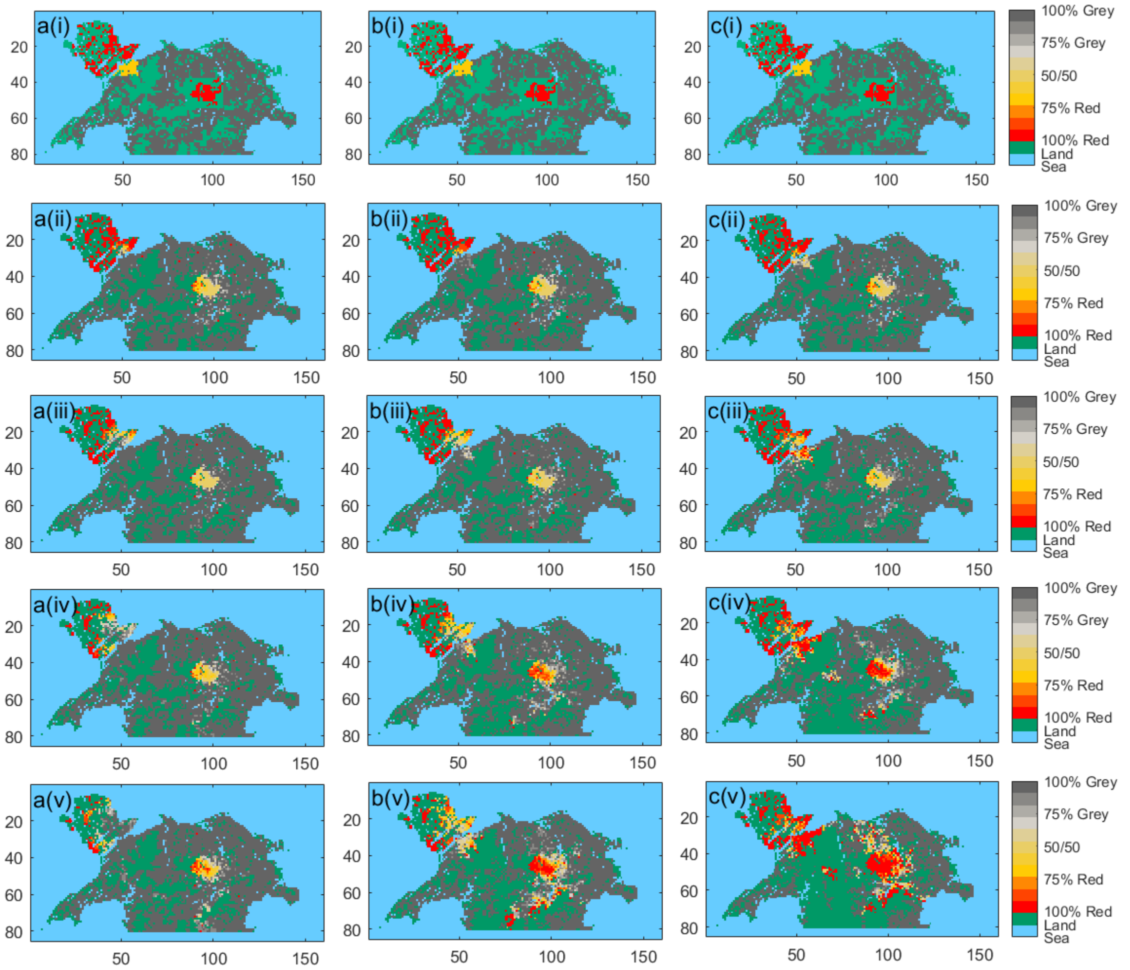

Figure 4.14: Red and grey squirrel occupancy results when pine marten are introduced into the Bangor region, as two groups of 10 individuals in consecutive years, and into Mid Wales at a quarter of the carrying capacity (see Figure 4.4(c)). The results include squirrelpox with a infection transmission 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.

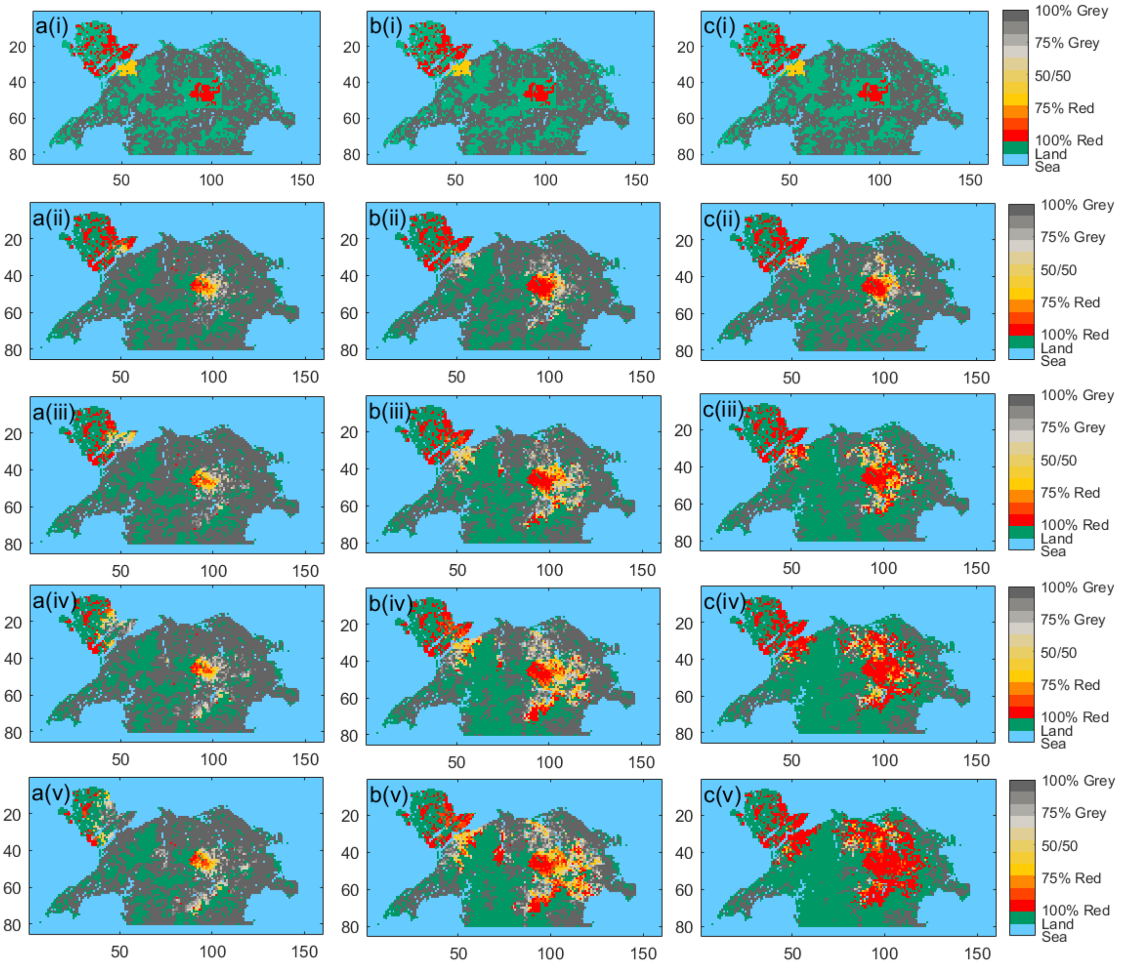

Figure 4.15: Red and grey squirrel occupancy results when pine marten are introduced into all available regions of North Wales at full carrying capacity (see Figure 4.4(d)). The results include squirrelpox with a infection transmission coefficient of $\beta = 0.83$. Here (a) shows the results with predation 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.

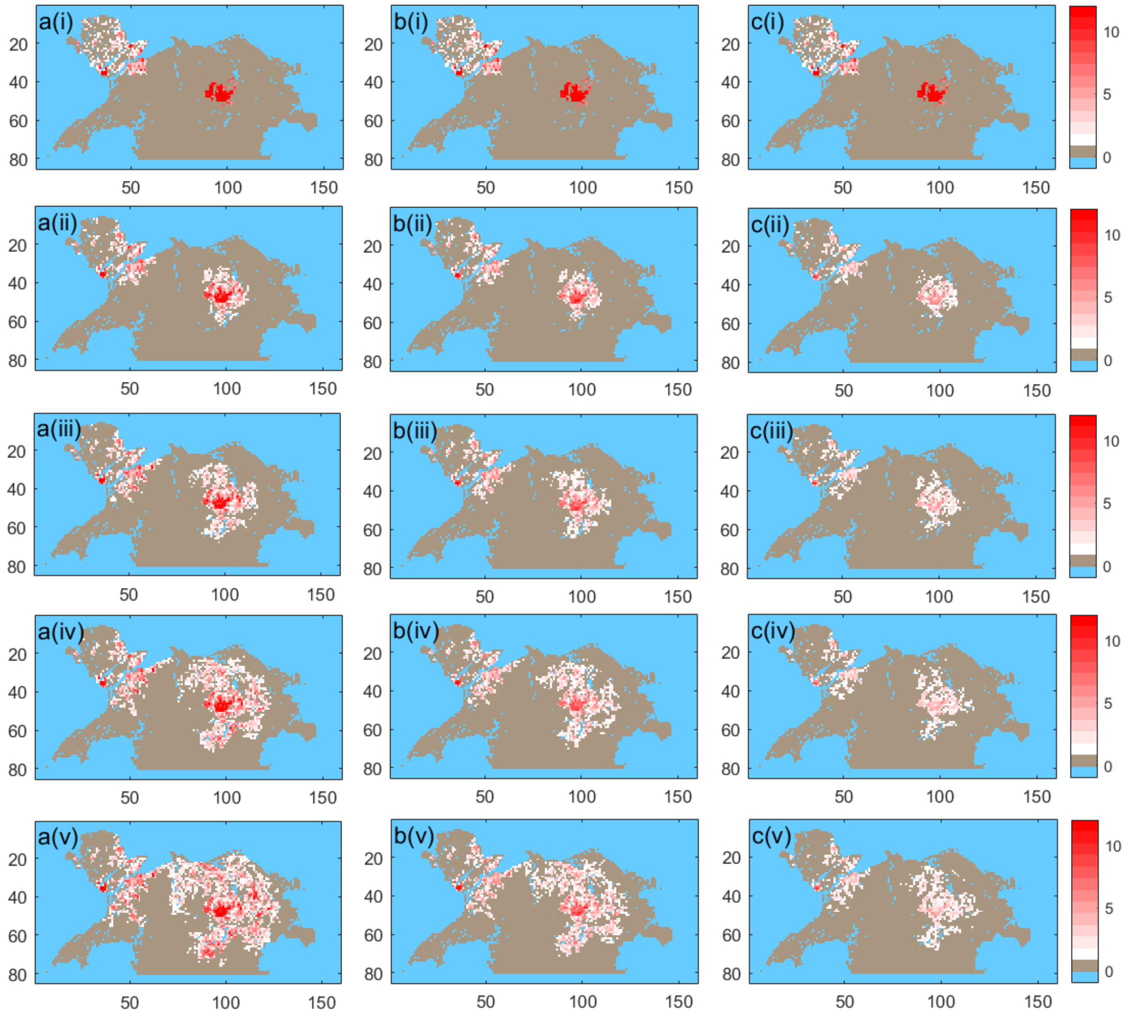

Figure 4.16a: Red squirrel density results when only red squirrels and pine marten are included in the model, with red squirrels being introduced into Clocaenog and Anglesey and pine marten being introduced into all available habitat, at carrying capacity. Here (a) shows the results when the grey squirrel 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 $\mu_R = 0.2\mu_G$.

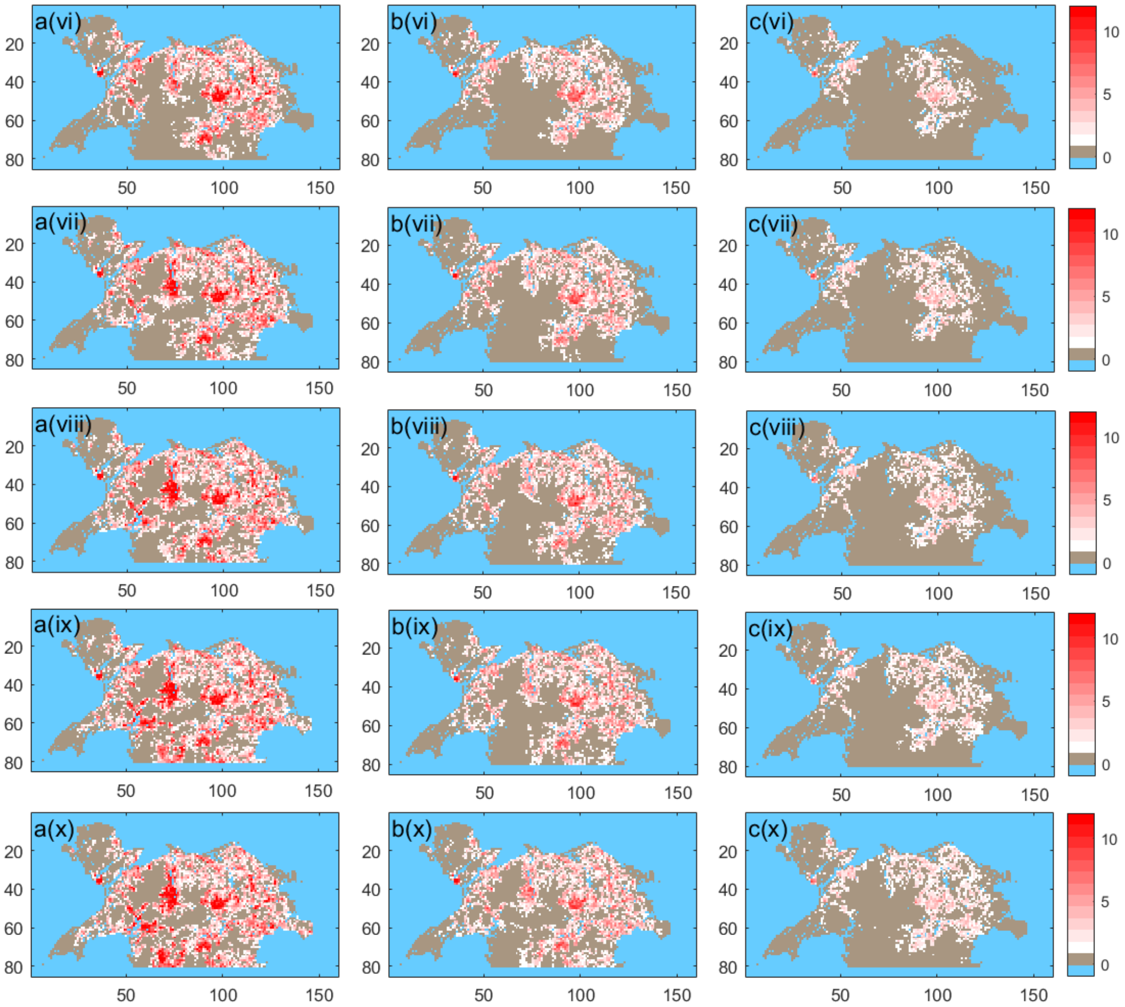

Figure 4.16b: Red squirrel density results when only red squirrels and pine marten are included in the model, with red squirrels and pine marten being introduced into all available habitat, at carrying capacity. Here (a) shows the results when the grey squirrel predation rate $\mu_G = 0.75$, (b) shows 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 $\mu_R = 0.2\mu_G$.

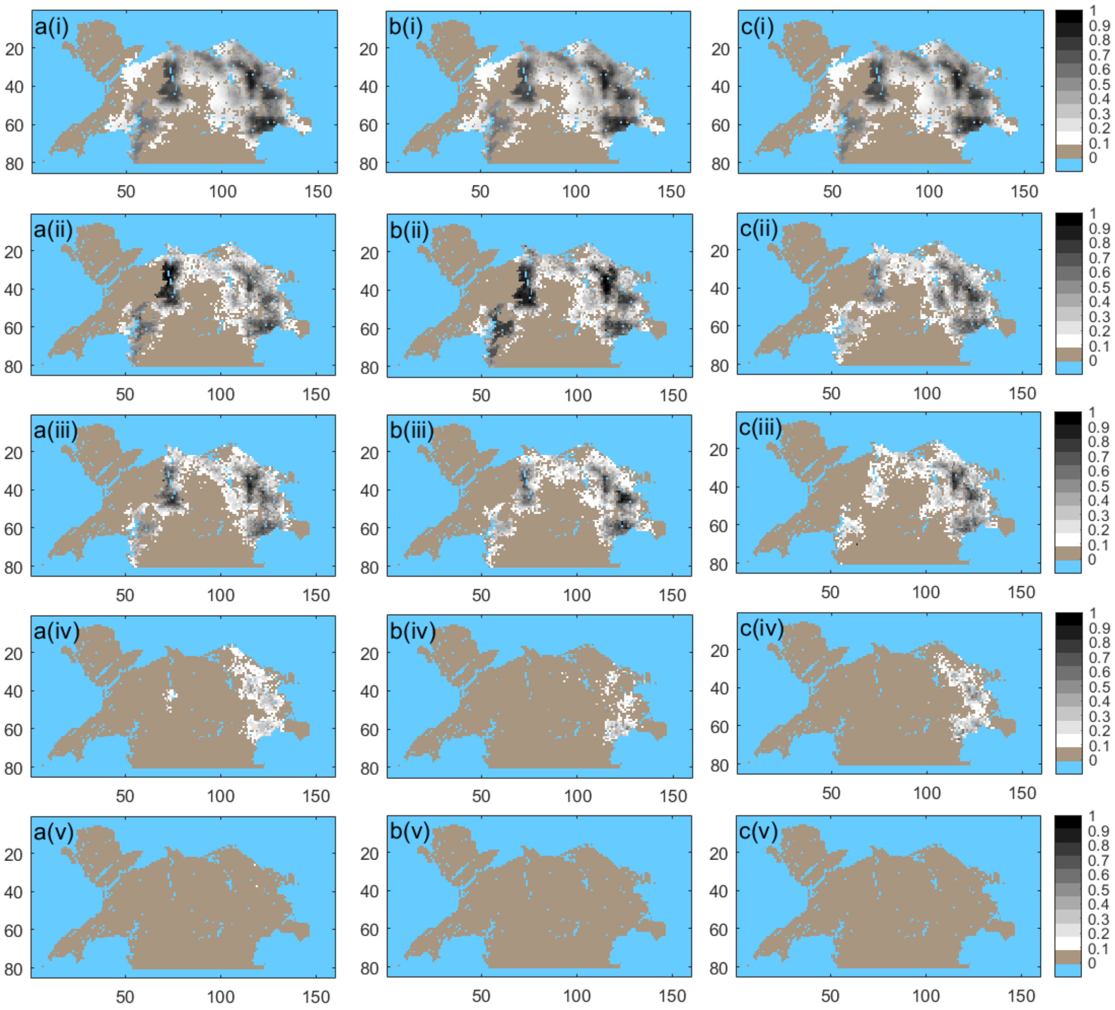

Figure 4.17: Changes in the prevalence of squirrelpox in grey squirrels over time, with infection transmission coefficient $\beta = 0.83$ and with pine marten being introduced into the Bangor region in two sets of 10 individuals and into Mid Wales at a quarter of the carrying capacity. Here (a) shows 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.

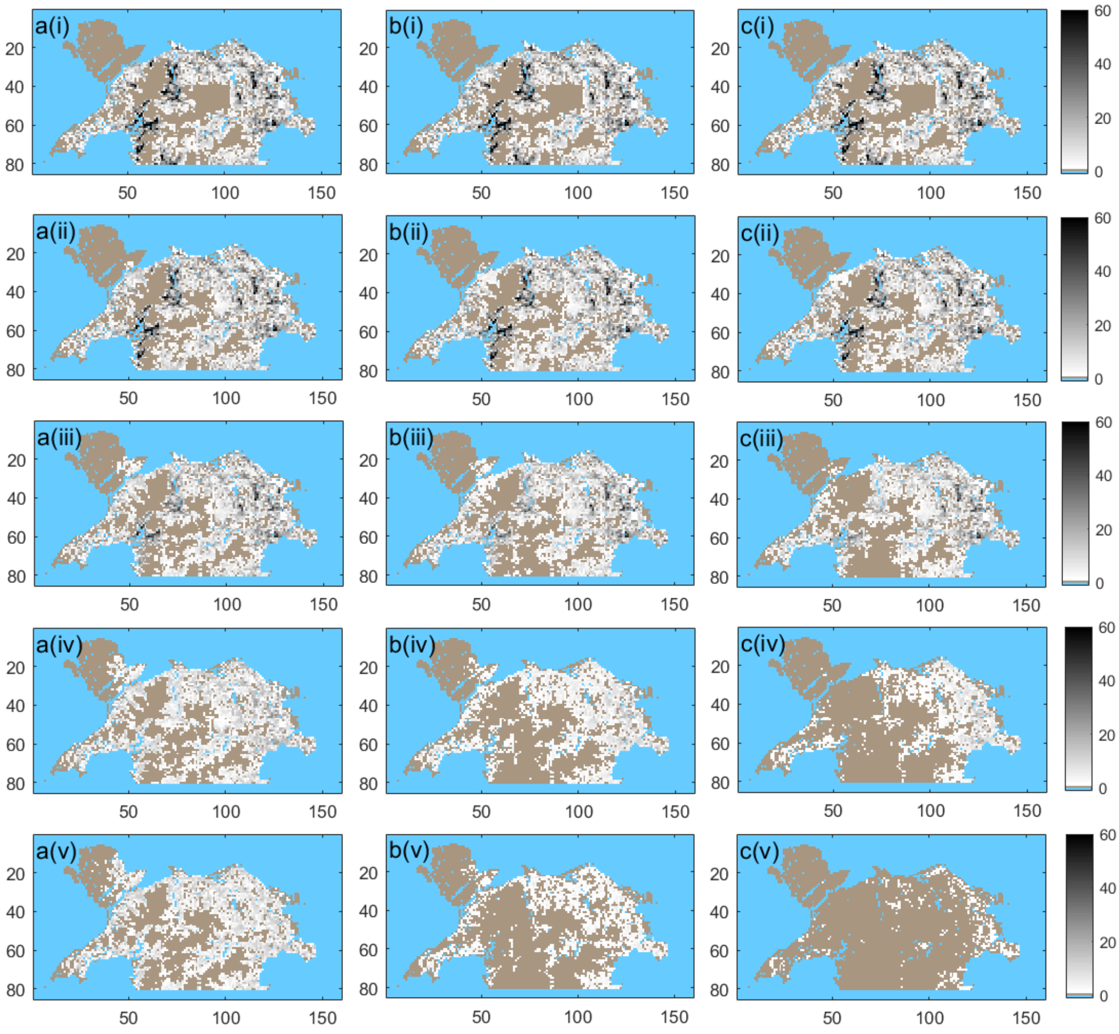

Figure 4.18: Grey squirrel density with infection transmission coefficient $\beta = 0.83$ and pine marten being introduced in 2 groups of 10 into the Bangor region and at a quarter of their carrying capacity into Mid Wales. Here (a) shows the results with predation parameter $\mu_G = 0.75$, (b) shows 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.

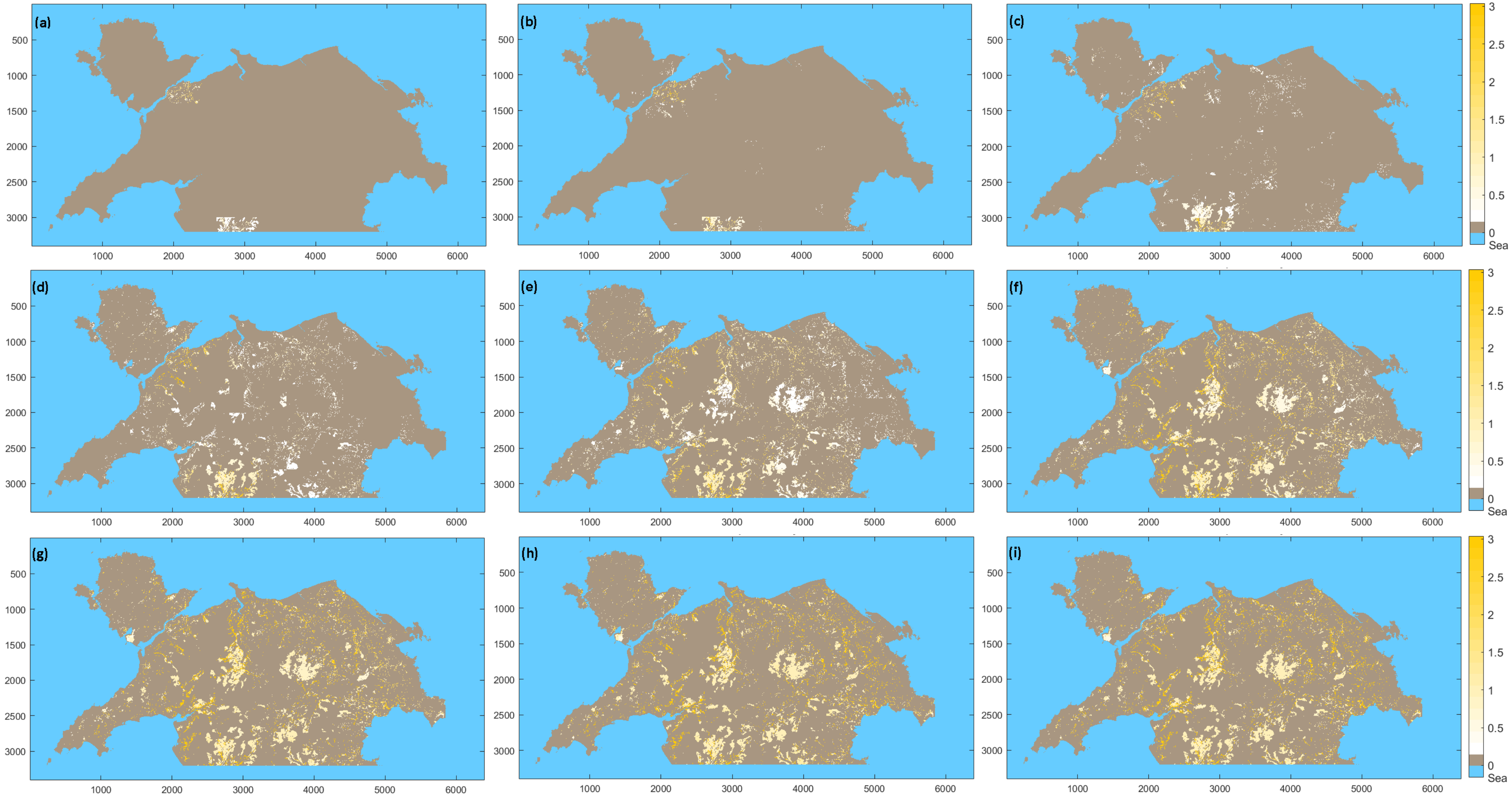

Figure 4.19: High resolution (25 m by 25 m) images showing pine marten expansion. The results are presented for (a) the initial conditions, (b) year 5, (c) year 10, (d) year 15, (e) year 20, (f) year 25, (g) year 30, (h) year 35, and (i) year 40 of the simulation. The colour-bar indicates the representative 1 km^2 density. Only densities greater than 0.14 km^{-2} are included.

4.4 Discussion

In this study we have extended an established mathematical model of the red and grey squirrel system with squirrelpox [62, 63, 132, 166] 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 Clocaenog 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.

The results presented in this chapter agree with previous results that show a negative correlation between grey squirrels and pine marten, as well as a corresponding positive correlation between red squirrels and pine marten. Sheehy and Lawton [122] corroborated anecdotal evidence of grey squirrel decline, and subsequent red squirrel revival, due to pine marten resurgence in Ireland which suggested either a ‘climate of fear’ [13] or preferential predation as the cause of the grey squirrel decline. The study was repeated for populations in Scotland [124], with a similar outcome. Twining et al. [151] confirmed that pine marten preferentially predate on grey squirrels, with grey squirrel remains occurring 5 times as much as red squirrel in pine marten diet (measured via frequency of occurrence in scat). Furthermore, Twining et al. [150] suggested that the impact of pine marten on grey squirrels is due to direct predation rather than due to climate of fear, by assessing the behavioural response of red and grey squirrels to pine marten scent. The results of this study reaffirm the primary results of these papers - that pine marten predation can reduce grey squirrel density sufficiently to benefit red squirrels, with asymmetric predation due to a lack of grey squirrel behavioural response to pine marten presence being the assumed cause. Our results further confirm that pine marten could play a key role in red squirrel population recovery and the results presented in this chapter will inform red squirrel conservation management coordinated by the Red Squirrel Trust Wales and the Heritage Fund OL-18-06694 Magical Mammals project.

Appendix 4.A Pine marten dispersal mechanism and parameter fitting

While detailed pine marten observational data is not available for Wales, it is available for Northern Ireland (J. Twining pers. comms.). We use this data to define a set of criteria that needs to be recreated by the dispersal mechanism which will then be used to refine the parameter value for the pine marten dispersal mechanisms in the model. The data outlines the regions where pine marten have been observed over a 12 year period, from 2007 to 2019, including data for 2012. The data suggests that there should be extensive pine marten dispersal from the focal sites, but that the pine marten populations remain predominantly in the East and West of Northern Ireland. There should be a gap in pine marten distribution that runs from north to south roughly along Lough Neagh. We also know that long-range dispersal events can occur for pine marten, thus we would expect there to be isolated pine marten in the region in-between the main population blocks that would not occur without extra dispersal being included.

The information for 2007 was used to generate initial conditions data for pine marten which can be used to represent the situation in Northern Ireland (Figure A1). We assume that pine marten were initially at either a quarter or a half of their carrying capacity. Habitat information for Northern Ireland, generated using the Land Cover Map 2015 dataset for Northern Ireland which outlines the feature proportion of each 1 km grid-square, is used in conjunction with pine marten carrying capacity information to create a 1 km by 1 km gridded carrying capacity map (Figure A2). The pine marten carrying capacity information is used to create the 5 km by 5 km carrying capacity values that are used to trigger dispersal. A full list of the different habitat features, and associated pine marten carrying capacities, can be found in Table A1.

We model the birth, death and dispersal of pine marten as described in the main text (Table 1) and consider the case where dispersal is local (space-filling) only ($d_P = 0$) and where rare long distance dispersal is additionally included ($d_P > 0$).

Figure A3 outlines the pine marten dispersal when the space-filling dispersal mechanism is used ($d_P = 0$). The initial populations expand radially, remaining

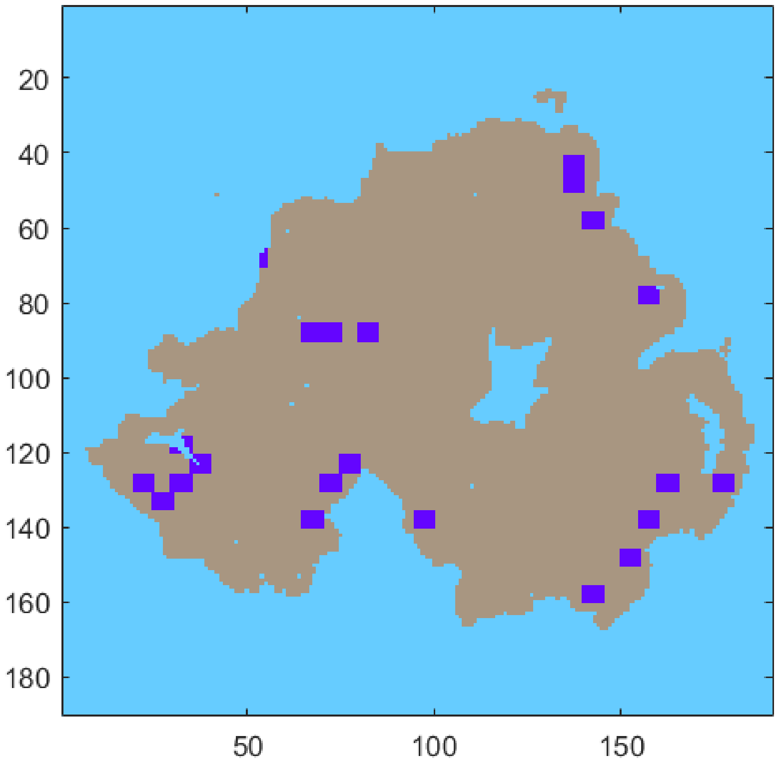

Figure A1: Initial Occupancy map for pine marten in Northern Ireland, based on occupancy data for 2007 in Northern Ireland.

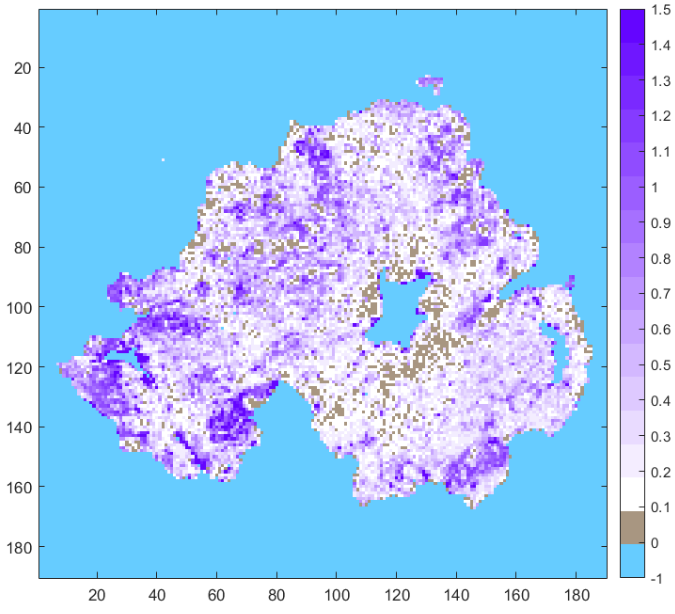

Figure A2: Pine marten carrying capacity map for Northern Ireland. Land-cover information is combined with carrying capacity estimates (see Table A1) to create this 1 km by 1 km map of potential pine marten density.

Habitat Feature	**Pine Marten CC (km^{-2})**
Arable Land	0.05
Bog	0.05
Broadleaved Woodland	3.49
Built-up Areas	0.05
Coniferous Woodland	1.15
Dwarf Shrub Heath	1.15
Grassland	0.05

Table A1: Pine marten carrying capacity values for different habitat types, as defined in the Land Cover Map 2015 dataset. The Grasslands feature includes all grassland types that occur in the dataset (acid, neutral etc.). The minimum carrying capacity value of 0.05 is chosen to simulate the fact that, whilst pine marten can use these features, they do not reside there. Pine marten carrying capacity values are authors estimates based on personal communications with J. Twining and D. Tosh.

separate, until the leading front of the expanding waves of pine marten dispersal meet. Comparing Figure A3 to the dispersal criteria set out above suggests that starting with pine marten at quarter carrying capacity (Figure A3a(i-ii)) does not disperse sufficiently with the different populations remaining entirely separate. Having pine marten begin at full carrying capacity (Figure A3c(i-ii)) leads to too much dispersal with the pine marten creating a single population that spans the entire region. Figure A3b(i-ii), which has pine marten start at half carrying capacity, meets the criteria regarding the population blocks, however it does not have long-range dispersal which we know occurs.

Figure A4 shows the results when, in addition to local dispersal, pine marten can disperse into any available grid-square that falls within a 50 km radius of the initial grid-square. The results after 12 years of simulation when the initial density is set at half the carrying capacity (Figure A4a-d(iv)) show pine marten occupying the entirety of Northern Ireland, which does not agree with the observational data. When the initial density is set at a quarter of the carrying capacity the results show pine marten dispersal primarily occurs through the local space-filling mechanism but the random dispersal allows some pine marten to enter the regions in between the primary population blocks which more closely represents the observational data (i.e. vanguard populations that arrive before the main populations are connected). As the long distance dispersal parameter in increased it begins to dominate over the local dispersal and leads to low density well dispersed populations. Observational records include rare sightings of pine marten at significant distances from their source population (up to 200 km). Since the model results provide the best comparison to the observation data when local space filling dispersal is included and long distance dispersal is rare ($d_P = 0.05$) we set this as the default parameters for pine marten dispersal in the main study.

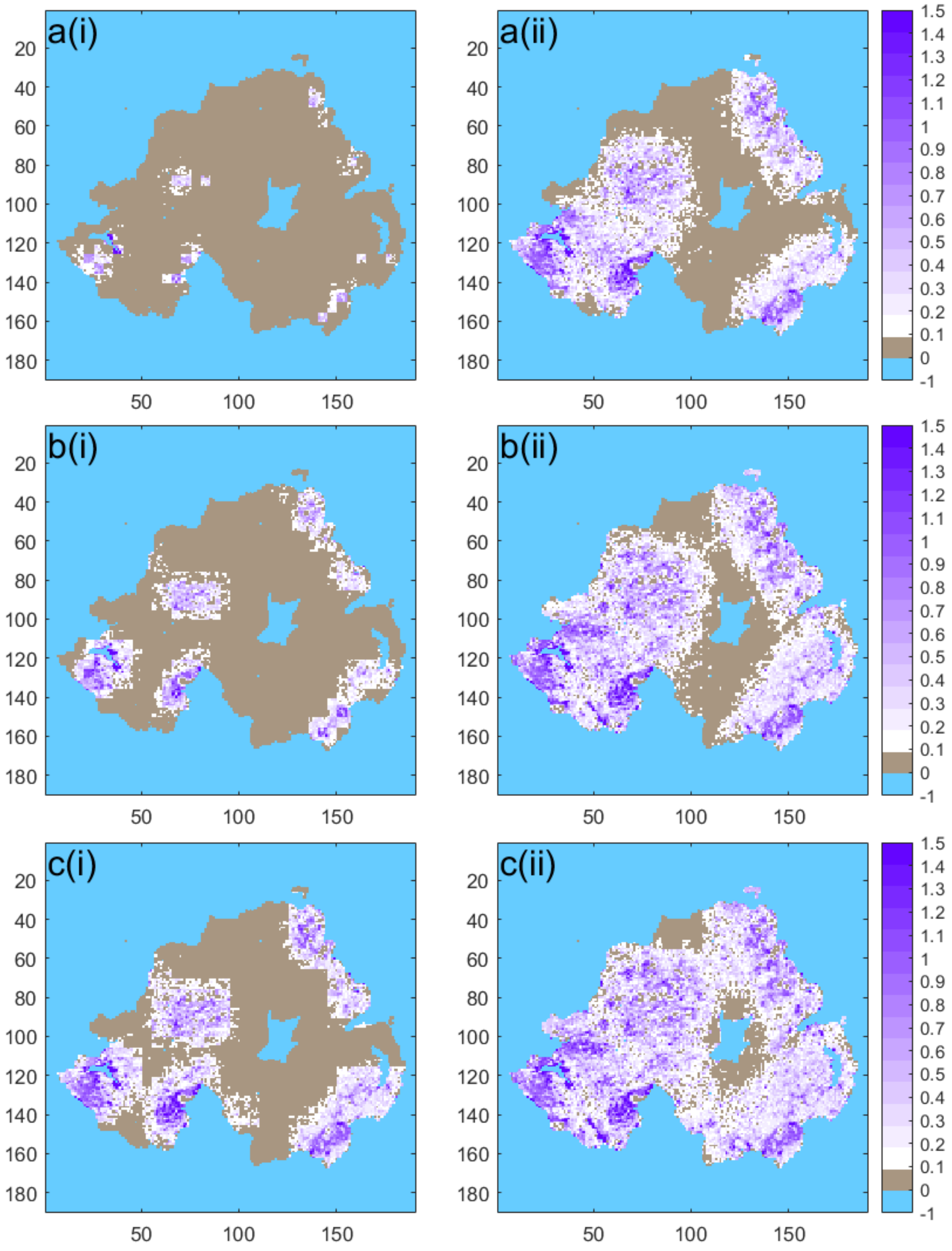

Figure A3: Results showing pine marten dispersal at year (i) 5, and (ii) 12 of the simulation when there is no extra dispersal allowed ($d_P = 0$). The initial pine marten density was set at (a) quarter carrying capacity, (b) half carrying capacity, and (c) full carrying capacity. Pine marten density is in km^{-2}.

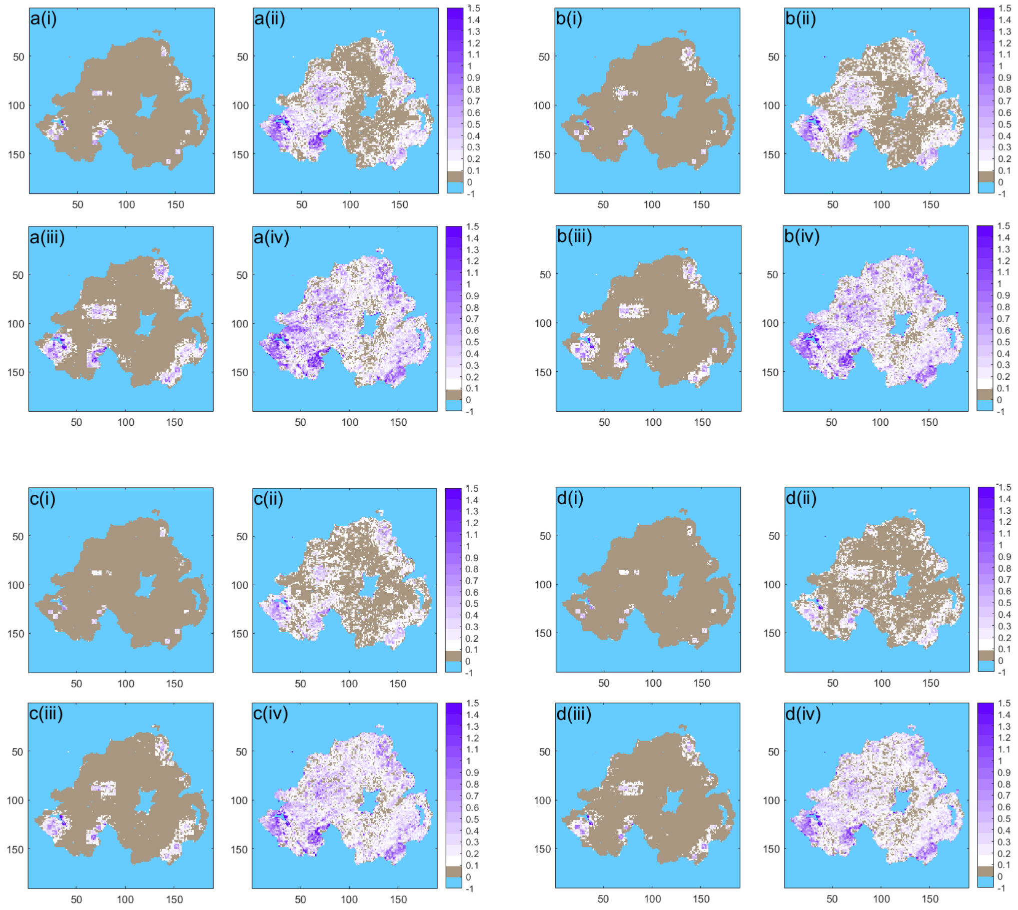

Figure A4: Results showing pine marten dispersal when the extra dispersal occurs to any grid-square within a 50 km radius of the origin square. The dispersal parameter is (a) $d_P = 0.05$, (b) $d_P = 0.1$, (c) $d_P = 0.15$ and (d) $d_P = 0.2$. Image (i) shows the results after 5 years and (ii) shows the results after 12 years of model simulation when the initial condition is set at a quarter of the carrying capacity. Image (iii) shows the results after 5 years and (iv) shows the results after 12 years of model simulation when the initial condition is set at half of the carrying capacity. Pine marten density is in km^{-2}.

Chapter 5

The impact of a temporal refuge on predator mediated prey species competition

This chapter is based on the submitted manuscript:

Slade, A., White, A., Lurz, P.W.W., Shuttleworth, C. and Lambin, X. 2021. The impact of a temporal refuge on predator mediated prey species competition. Submitted to Oikos.

The chapter is presented as the submitted version of the paper. I undertook all the modelling work and played a lead role in developing the project objectives and writing the manuscript.

Abstract

We develop mathematical theory to assess how a temporal refuge from predation could affect prey population dynamics. The theory combines the processes of prey switching by generalist predators with that of a prey's ability to utilise a refuge to avoid predation. We show that a temporal refuge can play a key role in determining species persistence and ecosystem structure, and that the duration of the refuge is fundamental for determining the outcome of predator mediated competition. Our

model results provide new insight on the influence of alternative prey dynamics, such as multi-annual cycles, on species coexistence. The general theoretical framework was extended to consider a key case study system of pine marten predation on red and grey squirrels in which a temporal refuge for both squirrel species arises due to prey switching in years of abundant density of field voles. The length of the temporal refuge, hence vole cycle length, is a critical factor in the ability of pine marten to suppress grey squirrel density and allow red squirrel recovery. Our findings therefore provide important insights for the conservation of the endangered red squirrel in the UK and the Republic of Ireland.

5.1 Introduction

Predator-prey dynamics are a dominant theme in ecology and form part of a complex web of inter-species relationships that occur across a given ecosystem [9]. There exists a rich body of empirical and theoretical work that capture the essential components of predator-prey interactions which uncover the key drivers of the predator-prey population dynamics [6]. It is recognised that predators play an important role in regulating ecosystems and sustaining biodiversity [102]. Their role in shaping ecosystem composition and the promotion of the persistence of predator-prey systems can depend on the capacity of predators to switch to more abundant prey species [87, 153] as well as the prey's ability to avoid predation via the use of a spatial or temporal refuge [10, 130].

A refuge, which is seen as an integrating concept in trophic ecology [10], is created when a threat to a given species, such as predation, is reduced or removed. Refugia have been the focus for theoretical study due to their well-known contribution to the stability of predator-prey interactions [10, 106, 130], with the proportion of prey that utilises the refuge being a key determinant of predator-prey dynamics. Refugia can become established due to the creation of enemy-free space by, for example, shelter, restrictions in movement or group living [10]. A refuge can also occur implicitly through prey switching, whereby a predator focusses on alternative prey species which creates a temporal refuge for a focal prey species [45], with theoretical assessments typically limited to switching between two prey species [87, 153]. There are numerous examples of refuge use by prey species [102]. For example, African wild dogs (*Lycaon pictus*) alter their daily behaviour to avoid the spatial locations and active time periods of predatory lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) [102, 113] which provides a spatial and temporal refuge that allows the wild dogs to coexist in the same habitat as the two predators. A refuge can exist over different temporal and spatial scales. For the wild dogs, the duration of temporal refuge is dictated by the daily circadian rhythms of the lions and hyenas. Consequently, the temporal refuge lasts only for a number of hours per day, but is repeated on a daily basis. Thus, the wild dogs spend a substantial proportion of time in the refuge. A key property of a temporal refuge is that it is quantifiable, which allows an assessment of how a temporal refuge may alter the dynamics and persistence of interacting species, including those between invasive and native species, and therefore play a key role in determining ecosystem structure [41].

The impact of invasive species is of global concern due to their role in biodiversity loss in native ecosystems [67, 131] with the rate of invasions continuing to increase [121]. It is well documented that invasive species may out-compete native species and therefore be considered harmful from a conservation perspective [131]. Invasive species will, however, provide a resource for native predators and consumers with examples including the consumption of non-native plants by herbivores [85, 148], fruit of alien plants by frugivores [49, 170], and non-native animals by native and non-native predators [37, 57, 84, 136]. Native predators can therefore play a key role in the regulation of invasive species and the overexploitation of native predators could help facilitate biological invasions [23]. Examples include the common celebes toad (*Ingerophrynus celebensis*), an endemic predator, that controls the population density of the invasive yellow crazy ant (*Anoplolepis gracilipes*) which positively affects the diversity of native ant species on the Indonesian island of Sulawesi [155]. Hence, predation reduces the density of, and therefore the competitive pressure from, the invasive species on the native species which allows the native species to persist. There are also wide ranging examples of the introduction of predators for biological control of introduced pest species [135], such as the control of insect pests by parasitoids [32].

The ongoing reintroduction and recovery of native predators [59] can regulate native and invasive prey species that utilise a temporal refuge. These processes require further investigation since the interactions can lead to complex population dynamics and changes to ecosystem structure. A case study example of the impact of refugia on predator-prey interactions is the effect of predation by the Eurasian pine marten (*Martes martes*) on the native Eurasian red squirrel (*Sciurus vulgaris*) and invasive North American grey squirrels (*Sciurus carolinensis*) [122, 124, 151], a pair of competing prey species that share a common predator. The Eurasian red squirrel has been replaced by the invasive grey squirrel in much of the UK and the Republic of Ireland due to disease-mediated competitive replacement, with over 80% of the remaining UK red squirrel populations now exclusively found in Scotland [79]. A resurgence in pine marten density, and an expansion of their distribution in Scotland, Northern Ireland and the Republic of Ireland, has seen a concurrent reduction, and in some instances the extirpation, of invasive grey squirrels that has allowed the re-establishment of the native red squirrel [122, 124, 152]. It is suggested that pine marten preferentially predate on grey squirrels [122, 152], with naivety of the invasive species regarding the predator being cited as a cause [155]. However, pine marten are generalist predators [25, 93] whose primary prey species in the UK, field voles (*Microtus agrestis*), undergo multi-annual cycles in their population density [69]. When vole density is high, pine marten will increasingly focus their predation efforts on voles, a classical functional response. This will reduce the predation pressure on red and grey squirrels, providing them with a temporal refuge from predation. Therefore, the ability of a native predator to control an invasive prey species may be weakened by the intermittent use of refugia by the prey species, which in turn may be dependent on the availability of a predators primary prey species. At present we lack a strategic understanding of how the outcome of such interactions depend upon the characteristics of the temporal refuge.

In this study, we will develop a general theoretical framework to assess the impact of predation on two, competitively interacting, prey species. We will assess how a temporal refuge from predation could affect prey population dynamics and the outcome of predator mediated competition. We will extend the model framework to consider the case study system of pine marten predation on red and grey squirrels.

This case study will assess the impact of a temporal refuge from predation for both squirrel species due to prey switching in years of abundant density of field voles, the primary prey species of pine marten. Our model results will lead to general ecological hypotheses on the role of temporal refuges in determining species persistence and ecosystem structure and provide important insights for the conservation of the endangered red squirrel in the UK and the Republic of Ireland.

5.2 The impact of predation on competing prey species

We outline a model to represent the dynamics of two competing prey species that are subject to predation. The model is based on the classical Lotka-Volterra framework for competing species [156]. The model represents the densities of prey species X_1 and X_2 at time t as follows:

$$\begin{aligned}\frac{\mathrm{d}X_1}{\mathrm{d}t} &= (a_1 - q_1(X_1 + c_2X_2))X_1 - B_1X_1, \\ \frac{\mathrm{d}X_2}{\mathrm{d}t} &= (a_2 - q_2(X_2 + c_1X_1))X_2 - B_2X_2,\end{aligned} \tag{5.1}$$

where the death rate B_i is defined as:

$$B_i = \begin{cases} b_i & \text{if } \mu_i = 0, \\ b_i + \mu_i\, K_P & \text{if } \mu_i \neq 0, \end{cases} \tag{5.2}$$

with μ_i being the predation rates and K_P the population density of the predator, which we assume is fixed at its carrying capacity. Defining the death rate in this manner allows the two-species competition model to represent a scenario in which prey compete in the absence ($\mu_i = 0$) and presence ($\mu_i > 0$) of predation. By setting $\mu_1 \neq \mu_2$ we can account for different levels of predation on different species, thus reflecting prey susceptibility and predator preference/attack rate. We assume for simplicity that predation occurs according to a linear functional response (thus we are assuming a generalist predator whose predation does not saturate). We assume a maximum birth rate (a_i) for each species. The birth rate for species i is modified by intra-specific competition from species i, denoted by q_i, and by inter-specific competition from species j, given by c_j. We assume constant natural death rates, b_i.

This system has four steady states: extinction of both X_1 and X_2; species X_1 in the absence of species X_2; species X_2 in the absence of species X_1 and the coexistence of species X_1 and X_2. We ignore the trivial steady state where both populations are extinct which imposes a requirement that $a_i > B_i$. We define K_i^* as follows:

$$K_i^* = \begin{cases} K_i = \frac{a_i - b_i}{q_i} & \text{if } \mu_i = 0, \\ H_i = K_i - \frac{\mu_i K_P}{q_i} & \text{if } \mu_i \neq 0, \end{cases} \tag{5.3}$$

where K_i is the carrying capacity for species i in the absence of predation and H_i denotes the predation-suppressed density for species i, in the absence of species j. The steady states, and associated stability conditions, are outlined in Table 5.1(i).

Table 5.1: Steady states and stability conditions for the model represented by equation (5.1) which (i) does not include a temporal refuge and (ii) does include a temporal refuge.

	Steady State	**Stability Condition(s)**
(i) Without Temporal Refuge	$(K_1^*, 0)$	$K_2^* - c_1 K_1^* < 0$
	$(0, K_2^*)$	$K_1^* - c_2 K_2^* < 0$
	$\left(\frac{K_1^* - c_2 K_2^*}{1 - c_1 c_2}, \frac{K_2^* - c_1 K_1^*}{1 - c_1 c_2}\right)$	$K_1^* - c_2 K_2^* > 0$ $K_2^* - c_1 K_1^* > 0$ $0 < c_1 c_2 < 1$
(ii) With Temporal Refuge	$(X_1^*, 0)$	$K_2 - \frac{K_P \mu_2}{q_2}(1 - \frac{T_c}{T}) < c_1 \frac{1}{T} \int_0^T X_1^* \mathrm{d}t$
	$(0, X_2^*)$	$K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T}) < c_2 \frac{1}{T} \int_0^T X_2^* \mathrm{d}t$

Note, K_i^* is defined in equation (5.3). The coexistence steady state does not exist when $c_1 c_2 = 1$ (except when $K_1^* = c_2 K_2^*$ and $K_2^* = c_1 K_1^*$ which is unstable) and is unstable when $c_1 c_2 > 1$. X_i^* is the stable periodic solution for species i in the absence of species j. We assume the predator switches between no predation on species 1 and 2 ($\mu_i = 0$) for $0 \leq t < T_c$ and predation on species 1 and 2 ($\mu_i > 0$) for $T_c \leq t < T$ in a periodic manner (with period T). The prey species benefit from a temporal refuge for a length of time T_c (during each period). The term $1/T \int X_i^* dt$ denotes the average density of species i over one period of length T. If neither $(X_1^*, 0)$ or $(0, X_2^*)$ are stable, we expect coexistence of both species in the periodic system.

The stability conditions are such that each steady state is mutually exclusive. However, the introduction of predation can allow a scenario where an unstable steady state becomes stable and changes the competitive outcome of the dynamics. For example, if we assume the $(0, K_2^*)$ steady state is stable without predation, meaning $K_1 - c_2K_2 < 0$ and $K_2 - c_1K_1 > 0$, then the steady state will change to the $(K_1^*, 0)$ steady state with predation if $H_1 - c_2H_2 > 0$ and $H_2 - c_1H_1 < 0$. Furthermore, due to the exclusivity of the steady states, the system can move between the steady states that include predation, such as from the coexistence steady state to a single species steady state, via a change in either the predator density or predation rates (assuming the carrying capacities and competition coefficients are fixed). Hence, predation can alter the outcome of prey species interactions and therefore change ecosystem diversity.

5.2.1 *Predation induced temporal refuge*

To consider a temporal refuge from predation we assume the dynamics are represented by equation (5.1) with the following criteria for the predation parameter:

$$\mu_i \begin{cases} = 0 & \text{for } 0 \le t < T_c, \\ > 0 & \text{for } T_c \le t < T. \end{cases} \tag{5.4}$$

The predator continuously switches predation off and on for species 1 and 2 in a periodic manner, with period T. The length of the temporal refuge is given by T_c during each period. This represents the scenario whereby the predator feeds on alternative prey species during the first part of the period and so does not predate on species 1 and 2 for a length of time T_c for each period.

With this set-up, standard techniques for stability analysis of steady states do not apply. Instead we need to examine the existence and stability of time varying solutions using Floquet theory [66]. Here we provide a summary of the stability analysis (which is detailed in full in section 5.B). It can be shown that a periodic solution for species 1, in the absence of species 2, exists and can be defined explicitly. We denote this periodic solution as $(X_1^*, 0)$. Floquet theory can be used to assess the stability of this periodic solution. It can be shown that $(X_1^*, 0)$ is stable if

$$K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T}) < 2\frac{1}{T}\int_0^T X_1^* \mathrm{d}t, \tag{5.5}$$

which is the condition that species 1 does not go extinct in the absence of species 2 (analogous to $a_1 > B_1$ above, which we assume holds) and if

$$K_2 - \frac{K_P \mu_2}{q_2}(1 - \frac{T_c}{T}) < c_1\frac{1}{T}\int_0^T X_1^* \mathrm{d}t, \tag{5.6}$$

where $1/T \int_0^T X_1^* \mathrm{d}t$ is the average density of species 1 over 1 time period.

An equivalent analysis can be undertaken to assess the stability of a periodic solution $(0, X_2^*)$ for species 2 in the absence of species 1. The stability conditions are summarised in Table 5.1 (ii).

Note, it is possible to recover the results for the non-periodic version of the model (Table 5.1 (i)) from the periodic results (Table 5.1 (ii)). If $T_c = T$ then the above stability conditions revert to those for the system without predation (Eqn. (5.1), $B_i = b_i$), whilst if $T_c = 0$ then the conditions revert to those for the predator-prey system (Eqn. (5.1), $B_i = b_i + \mu_i K_P$). Thus, these two scenarios provide the limiting cases for the temporal refuge. Therefore, the duration of the temporal refuge may be a key determinant to the outcome of predator mediated competition between prey species. In particular the length of the temporal refuge, which is dependent on the population dynamics of the predators alternative prey species, could lead to a switch from one solution to the other.

To explore how the temporal refuge can change the prey interaction we can make an approximation to the integral defined in equation (5.6). We approximate the average density over one period by assuming the prey species is at its carrying capacity K_i when there is no predation ($0 \le t < T_c$) and that it is at its predation-suppressed density H_i when there is predation ($T_c \le t < T$) which gives the following relationship:

$$\frac{1}{T}\int_0^T X_i^* \mathrm{d}t = K_i - \frac{\mu_i K_P}{q_i}(1 - \frac{T_c}{T}). \tag{5.7}$$

Equations (5.6) and (5.7) can be used to determine the critical length, T_{crit}^1, of the temporal refuge that is required for the steady state $(X_1^*, 0)$ to be stable as

$$T_{crit}^1 = T\left(1 - \frac{q_1 q_2 (K_2 - c_1 K_1)}{K_P(\mu_2 q_1 - c_1 \mu_1 q_2)}\right). \tag{5.8}$$

Under the assumption that $(X_1^*, 0)$ is stable in the presence of predation $(T_c = 0)$ and that $(0, X_2^*)$ is stable in the absence of predation $(T_c = T)$, the expression for T_{crit}^1 provides the maximum duration of temporal refuge that allows species 1 to exclude species 2 due to predator mediated competition.

An equivalent expression can be derived for the critical length of the temporal refuge, T_{crit}^2, to ensure that $(0, X_2^*)$ is stable. This expression is:

$$T_{crit}^2 = T\left(1 - \frac{q_1 q_2 (K_1 - c_2 K_2)}{K_P(\mu_1 q_2 - c_2 \mu_2 q_1)}\right). \tag{5.9}$$

Hence, if $(X_1^*, 0)$ is stable with predation $(T_c = 0)$ and $(0, X_2^*)$ is stable without predation $(T_c = T)$, and assuming $T_{crit}^1 < T_{crit}^2$, then the $(X_1^*, 0)$ solution is stable for $T_c \leq T_{crit}^1$, species X_1 and X_2 would coexist with a temporally varying solution for $T_{crit}^1 < T_c < T_{crit}^2$ and the $(0, X_2^*)$ solution is stable for $T_c \geq T_{crit}^2$ (see Figure 5.B2 for numerical solutions that confirm this result). Alternatively, equations (5.8) and (5.9) can be rearranged to give the predator density needed to ensure stability for a fixed length of temporal refuge. If the inter-specific competition parameters are such that $c_1 c_2 = 1$ then $T_{crit}^1 = T_{crit}^2$ and the coexistence steady state does not occur in the deterministic system.

5.3 Case study

We modify and expand the general model framework (Eqns. (5.1)) to represent the key case study system of the impact of pine marten predation on its primary prey species, field voles, and two of its secondary prey species, grey and red squirrels.

The model considers the competitive interaction between red and grey squirrels, as described by [147], and additionally includes predation by pine marten where the rate of predation is a function of field vole density. The model is represented by the following equations:

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= (a_R - q_R(R + c_G G))R - b_R R - \mu_R\, g(V)\, R\, P, \\
\frac{\mathrm{d}G}{\mathrm{d}t} &= (a_G - q_G(G + c_R R))G - b_G G - \mu_G\, g(V)\, G\, P, \\
P &= K_P, \\
V &= V(t),
\end{aligned} \tag{5.10}$$

which represents the density of red (R) and grey (G) squirrels. We assume pine marten (P) are maintained at a fixed density K_P, which can be altered to explore the effects of pine marten density on squirrel competitive interactions. The rate of predation of pine marten is a function of field vole density, V, which can vary over time. We assume the density of field voles (V) is a periodic function, with the periodicity of the fluctuations being based on observed data.

The model assumes a maximum birth rate for red and grey squirrels a_i (where i is equal to R for red and G for grey squirrels respectively) which is modified due to intra-specific competition with coefficient q_i and due to inter-specific competition between red and grey squirrels with coefficient c_i. The natural death rate is b_i. We assume grey squirrels out-compete red squirrels under equally suitable habitats ($c_R < c_G$, with $c_G = 1.65 = 1/c_R$). The parameter values are as in [147], except q_i which can be modified for each squirrel species to represent different habitat composition and, due to the link between habitat and squirrel density, different squirrel carrying capacities K_i, since $q_i = (a_i - b_i)/K_i$. Red and grey squirrel carrying capacities are taken from [132] and are representative of habitats in Scotland and Northern England. The carrying capacities are assumed to be 0.31 per km^2 in 100% broadleaf forests and 0.23 per km^2 in 100% conifer forests for red squirrels and 0.98 per km^2 in broadleaf and 0.10 per km^2 in conifer forests for grey squirrels. Predation of red and grey squirrels is assumed to occur linearly according to the constant parameter μ_i, with $\mu_G = 1.5$ (such that a pine marten density of 0.36 km^{-2} reduces the grey squirrel population by approximately 30%), and $\mu_R = 0.2\mu_G$ (based on [152] which states that red and grey squirrels constitute an average of

3.3% and 15.6% of pine marten diet respectively).

The predation rate of pine marten on squirrels is also assumed to depend on vole density, with pine marten focusing predation on voles when they are at high density. The prey switching mechanism is encapsulated in the function $g(V)$ (Figure 5.1) (note, we undertake a sensitivity analysis with respect to the predation parameters at the end of the results section).

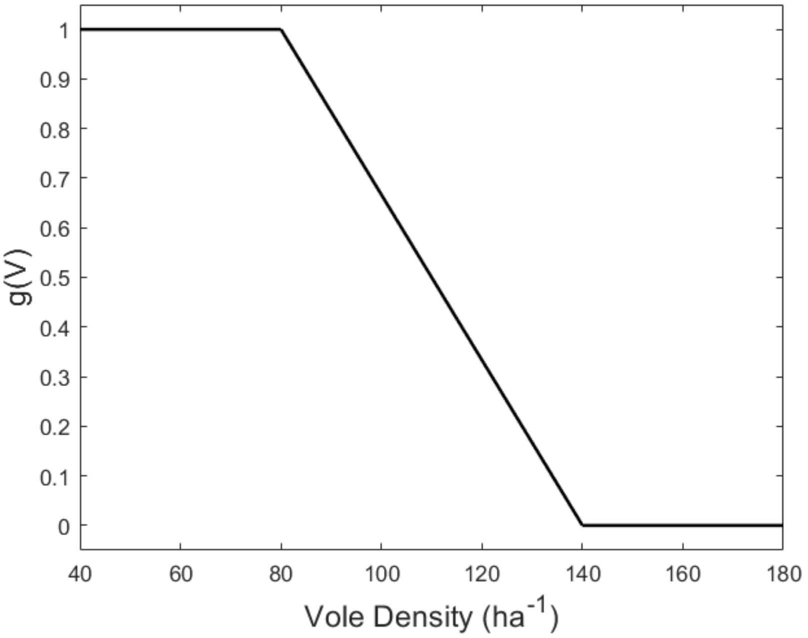

Figure 5.1: The functional response of the predator, which is dependent on field vole density. Here, the predation function $g(V)$ is set to one when the vole population is below a minimum threshold value $V_0 = 80$ voles per ha and $g(V)$ is set to zero when the vole population is larger than a maximum threshold value $V_x = 140$ voles per ha. These values are based on the inter-quartile ranges of the 3 and 4 year field vole population cycles at Kielder forest [69]. Sensitivity analysis suggests little change in results for different values of V_0 and V_x (see supplementary information Figure 5.C1(d) for details). The value of the predation function $g(V)$ decreases linearly from one to zero as the vole population increases from V_0 to V_x.

5.3.1 *Vole density*

Field vole populations are known to exhibit high amplitude periodic fluctuations, with 3 to 4 year periodicity [56, 69, 137], and pine marten prey switching, which focuses predation on voles when their density increases, will offer a temporal refuge from predation for red and grey squirrels. We wish to examine how this temporal refuge will affect the predator-mediated competitive interaction between red and grey squirrels. We initially consider idealised periodic dynamics for vole density, where we assume a three year cycle ($T = 3$) where vole density is at a high density for one or two years ($T_c = 1$ or 2) and vole density is low otherwise (Figure 5.2 (b),(c)). When vole density is high in these scenarios, it is assumed that there is no pine marten predation. This set-up provides a direct analogue to the general theoretical results. We then consider the vole dynamics that correspond to 3-year (Figure 5.2 (d)) and 4-year (Figure 5.2 (e)) cycles as observed in long-term field studies in Kielder Forest, England [69]. We finally consider the vole dynamics as described by the full Kielder Forest dataset (Figure 5.2 (f)).

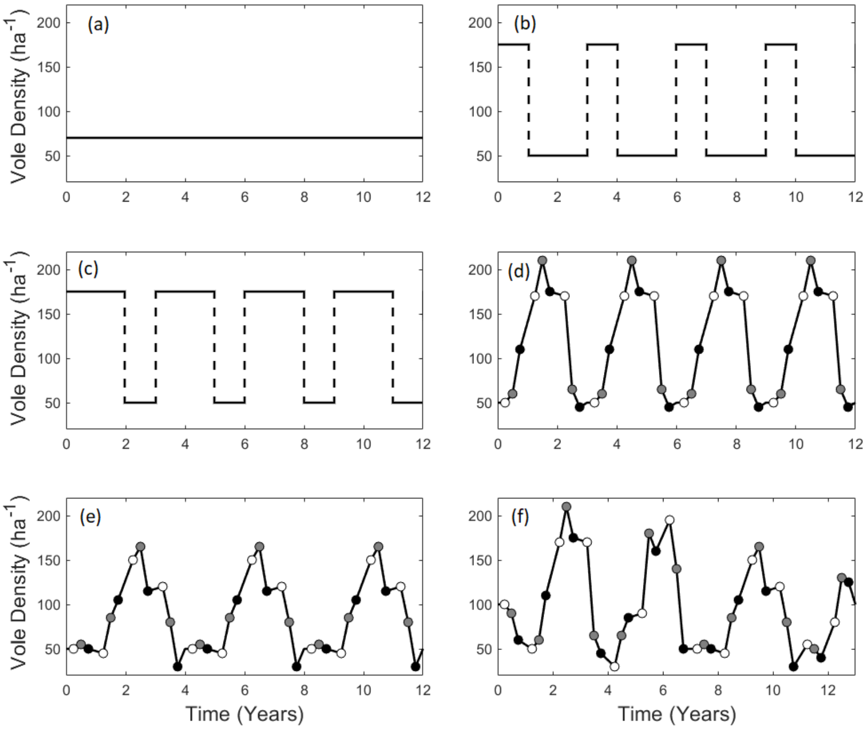

Figure 5.2: Field vole densities. Here (a) shows a constant field vole density that is less than V_0, (b) denotes the idealised 3-year periodic field vole density with temporal refuge of length $T_c = 1$, (c) denotes the idealised 3-year periodic field vole density with a temporal refuge of length $T_c = 2$, (d) denotes the 3-year periodic vole density based on real vole densities at Kielder Forest [69]. The cycle is set-up by extracting the observed data for years 1986-88 and repeating these values to provide periodic data with a 3-year cycle. (e) denotes the 4-year periodic vole density based on real vole densities from Kielder forest [69]. The cycle is set-up by extracting the observed data for years 1992-95 and repeating these values to provide periodic data with a 4-year cycle. (f) denotes the full Kielder Forest data set [69], which we assume repeats periodically. Spring, summer and autumn vole density information from Kielder Forest is given by white, grey and black circles respectively.

5.3.2 *Results*

We present model results for a range of scenarios for the case study system. We have used best estimates for parameters where possible and report findings in terms of indicative species densities to allow qualitative comparison between different scenarios.

Figure 5.3 presents the average red and grey squirrel population density at the end of the simulation, which has been run sufficiently long to ensure a stable periodic solution is reached, for a habitat with 15% broadleaved trees, for different, fixed, pine marten densities (K_P). In Figure 5.3(a) the vole dynamics are as in Figure 5.2(a) and there is no temporal refuge and constant predation. At low pine marten density grey squirrels out-compete red squirrels. As pine marten density is increased grey squirrel density decreases, and at a pine marten threshold density of 0.23 km^{-2} red squirrels can exclude greys squirrels due to predator mediated competition. Note, in this case study system $c_G c_R = 1$ and so there is no possibility of coexistence between red and grey squirrels. It is also important to note that grey squirrels are not excluded in the absence of red squirrels for pine marten densities less than 0.53 km^{-2} (which may be greater than expected pine marten densities in Scotland and northern England, meaning pine marten alone may not lead to the extirpation of grey squirrels). Exclusion of grey squirrels requires their density to be suppressed by pine marten that preferentially predate on grey squirrels, to a level where red squirrels have a competitive advantage. For pine marten densities above the threshold for grey squirrel exclusion, red squirrels persist and their density decreases as pine marten density increases. Pine marten can also exclude red squirrels but only when their density is greater than 3 km^{-2}, which is greater than pine marten densities observed in Scotland to date. In Figure 5.3(b) the vole dynamics are as in Figure 5.2(b), leading to 1 year out of every 3 years being a temporal refuge. The results are similar to those in Figure 5.3(a) except that the pine marten threshold density that leads to predator mediated competitive exclusion of grey squirrels by red squirrels is 1.5 times greater at 0.35 km^{-2}. In Figure 5.3(c) the vole population is as in 5.2(c), with 2 years out of every 3 years being a temporal refuge. The results are similar to Figure 5.3(a),(b) except that the pine marten threshold density that leads to predator mediated competitive exclusion of grey squirrels by red squirrels has increased twofold to 0.7 km^{-2}, a value in excess of what has thus far been observed in Scotland. An increase in the length of the temporal refuge therefore reduces the ability of pine marten to mediate the replacement of grey squirrels by red squirrels.

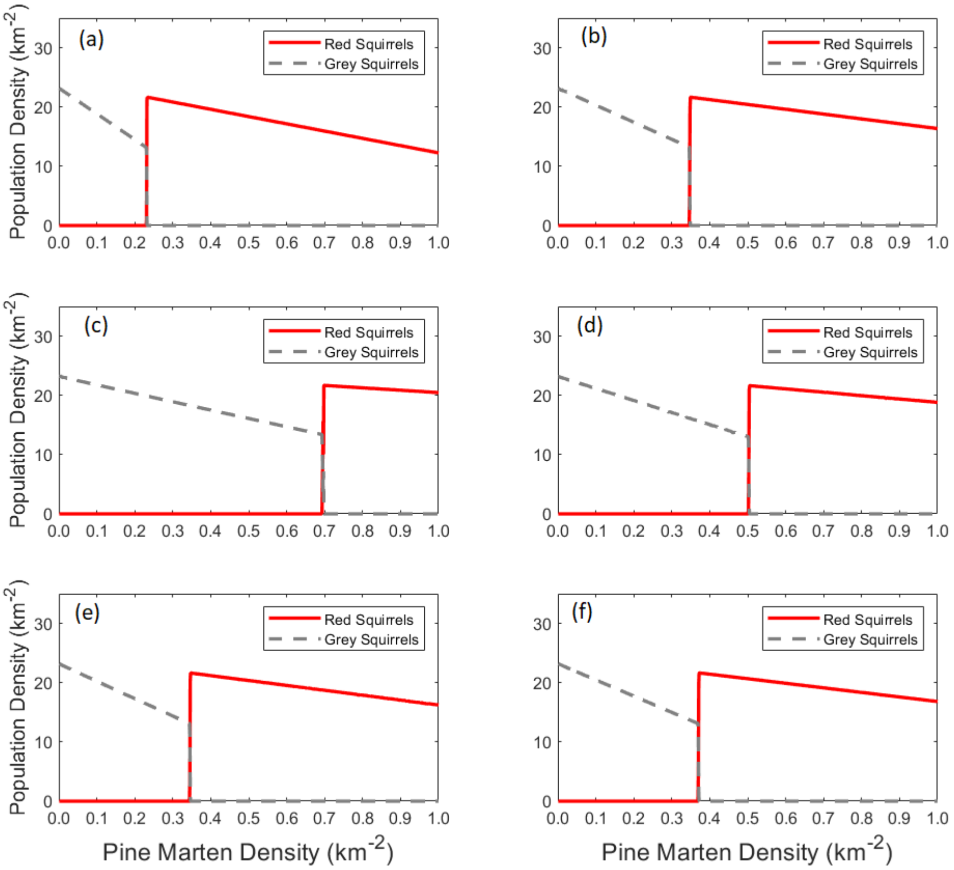

Figure 5.3: Average population density results for the red and grey squirrel and pine marten model (Equation (5.10)) that has reached equilibrium in a habitat with 15% broadleaved trees, with the remainder being coniferous trees, for a range of pine marten densities. Here (a) shows the baseline results without temporal refuge (vole dynamics are defined by Figure 5.2(a)), (b) shows the results when 1 year out of every 3 years is a temporal refuge (the vole dynamics are defined by Figure 5.2(b)), (c) shows the results when 2 years out of every 3 years is a temporal refuge (the vole dynamics are defined by Figure 5.2(c)), (d) shows the results when the vole dynamics follow the 3-year cycle based on the Kielder Forest data (Figure 5.2(d)), (e) shows the results when the vole dynamics follow the 4-year cycle based on the Kielder Forest data (Figure 5.2(e)) and (f) shows the results when the vole dynamics follow the full Kielder Forest dataset (1984-1998) (Figure 5.2(f)).

The results shown in Figure 5.3 (d),(e), which uses vole population dynamics that follow a periodic solution derived from the data observed in Kielder Forest (Figure 5.2 (d),(e)), are similar to the results in Figure 5.3 (a)-(c). The solution with a 3-year cycle requires a pine marten density of 0.5 km^{-2} (Figure 5.3 (d)) and the 4-year cycle requires a pine marten density of 0.35 km^{-2}, which is 30% lower, (Figure 5.3 (e)) to mediate grey squirrel exclusion. This indicates that the 3-year cycle offers a longer temporal refuge against pine marten predation than the 4-year cycle - which arises as vole densities are higher for a more sustained length of time (over each period) in the 3-year cycle. While the 4-year vole population cycle may allow red squirrels to exclude grey squirrels at a lower pine marten density it is worth noting that when red squirrels persist, their density is lower for a fixed pine marten density under the 4-year cycle compared to the 3-year vole cycle. Figure 5.3(f) shows the results when the full Kielder Forest dataset is used (Figure 5.2(f)) which requires a pine marten density of 0.37 km^{-2} to exclude grey squirrels. Given that the full dataset is comprised of the 3 and 4-year cycles, which leads to different predator mediated competitive outcomes due to differences in the duration in the temporal refuge (compare Figure 5.3(d) and 5.3(e)), then it may be expected that coexistence between red and grey squirrels could occur. However, coexistence does not occur in this instance, with pine marten predation and competition from red squirrels leading to the exclusion of grey squirrels. Thus, the dynamics are more heavily influenced by the 4-year cycles (and the associated shorter temporal refuge duration) than the 3-year cycles.

Figure 5.4 shows the density of red and grey squirrels over time, for a fixed habitat of 15% broadleaved trees and highlight the dynamics that occur for a fixed pine marten density of 0.4 per km^2 in Figure 5.3. These results show how the inclusion of a temporal refuge can change the competitive outcome and further emphasises how the duration of temporal refuge from pine marten predation can alter the population dynamics and persistence of red and grey squirrels. In particular, when the temporal refuge is short, red squirrels can exclude grey squirrels through predator mediated competition. If the temporal refuge is sufficiently long, the impact of predation on squirrels is reduced and therefore grey squirrels can exclude red squirrels as greys are better competitors with low levels, or no, predation. A key point to note is that different, observed, patterns of vole population fluctuations can lead to different outcomes in terms of red and grey squirrel persistence.

Figure 5.5 shows the pine marten density needed to ensure predator mediated

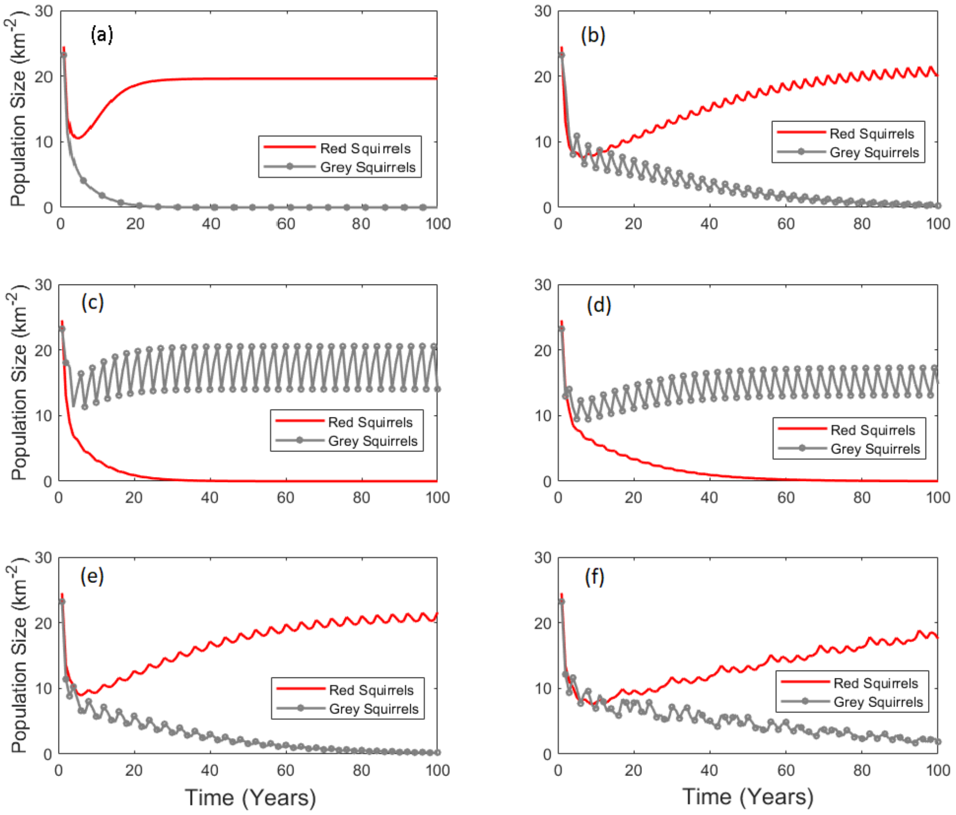

Figure 5.4: The population density over time for red and grey squirrels for the model defined by equation (5.10) with a habitat comprised of 15% broadleaved trees and a pine marten density of 0.4 per km^2. Here (a) shows the results when there is no temporal refuge (the vole dynamics are defined by Figure 5.2(a)), (b) shows the results when 1 year out of every 3 years is a temporal refuge (the vole dynamics are defined by Figure 5.2(b)), (c) shows the results when 2 years out of every 3 years is a temporal refuge (the vole dynamics are defined by Figure 5.2(c)), (d) shows the results when the vole dynamics follow the 3-year cycle based on the Kielder Forest data (Figure 5.2(d)), (e) shows the results when the vole dynamics follow the 4-year cycle based on the Kielder Forest data (Figure 5.2(e)) and (f) shows the results when the vole dynamics are defined by the full Kielder Forest dataset (Figure 5.2(f)).

exclusion of grey squirrels by red squirrels for different habitats, defined by their proportion of broadleaved trees (with the remainder of the habitat being coniferous), when there is either no temporal refuge ($T_c = 0$), or a temporal refuge of either 1 or 2 years. For habitats with less than 5% broadleaved trees, the model predicts that red squirrels out-compete grey squirrels, without the need for pine marten predation (and so the pine marten density required for grey exclusion is zero in Figure 5.5). When the habitat is greater than 5% broadleaved trees, grey squirrels will out-compete red squirrels in the absence of pine marten, with grey squirrels having an increasing competitive advantage over red squirrels as the percentage of broadleaved trees increases. The threshold in pine marten density required for grey squirrel exclusion increases as the percentage of broadleaved habitat increases. Thus, a pine marten density that may exclude grey squirrels in conifer dominated habitats may be insufficient in broadleaf dominated habitats. For each habitat the threshold in pine marten density also increases as the length of the temporal refuge increases (and note that the theoretical result shown in equation 5.8 is a close fit to the numerical result for the vole density trajectories represented by Figure 5.2 a-c.)

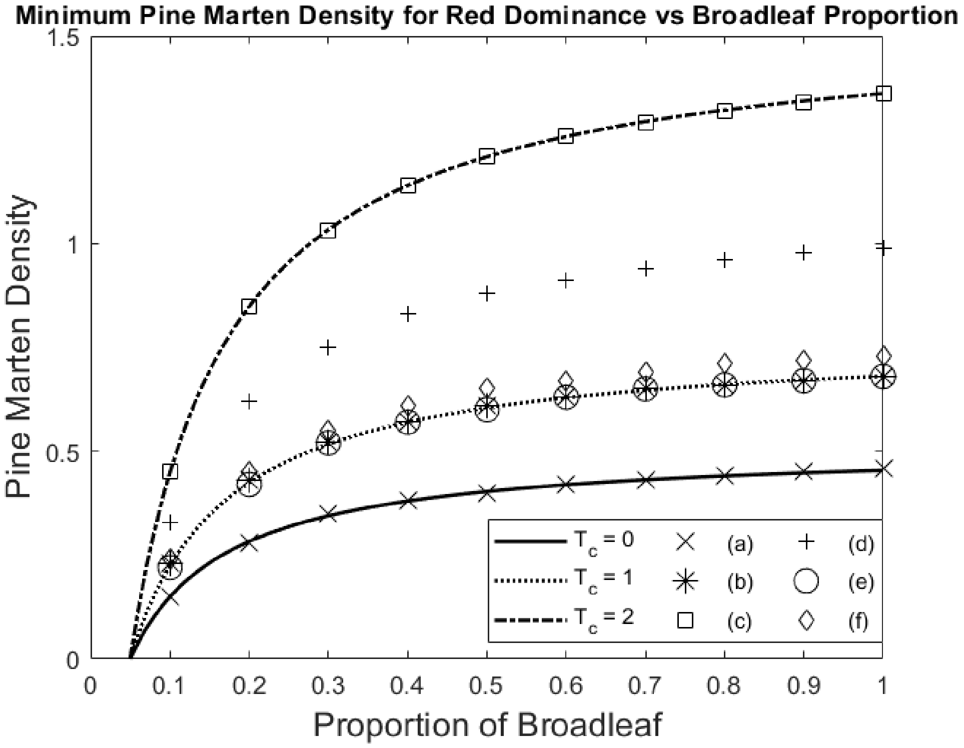

Figure 5.5: Graph of the theoretical pine marten density, calculated in Eqn. (5.8), along with numerical results required to ensure red squirrel survival. T_c defines the length of the temporal refuge (in years) with the time period T being 3 years. The pine marten density reaches zero when broadleaf proportion is 5% since under our model set-up red squirrels out-compete grey squirrels in habitats with less than 5% broadleaved trees. Here (a) shows the simulation results when there is no temporal refuge (the vole dynamics are defined by Figure 5.2(a)), (b) shows the simulation results when every 1 out of every 3 years being a temporal refuge (the vole dynamics are defined by Figure 5.2(b)), (c) shows the simulation results when every 2 out of 3 years is a temporal refuge (vole density as in Figure 5.2(c)), (d) shows the simulation results when the vole dynamics follow the 3-year cycle based on the Kielder Forest data (Figure 5.2(d)), (e) shows the simulation results when the vole dynamics follow the 4-year cycle based on the Kielder Forest data (Figure 5.2(e)) and (f) shows the simulation results when the vole dynamics follow the full Kielder Forest dataset (Figure 5.2(f)).

We acknowledge that the available data to parametrise the predation terms in the model is scarce. We therefore undertake a sensitivity analysis of the impact of the predation rate and characteristics of prey switching function $g(V)$ on our key findings (see section 5.C). Results show that, if the overall predation rate is reduced or if the preferential predation rate of pine marten on grey squirrels is less pronounced (μ_R/μ_G is increased), then a higher density of pine marten is required for predator mediated exclusion of grey squirrels by reds. However, the trends in pine marten density that lead to grey squirrel exclusion as the length of the temporal refuge is increased are robust to changes in pine marten predation parameters.

5.4 Discussion

We have developed new mathematical theory that combines the processes of prey switching by a generalist predator with that of a prey's ability to utilise a refuge to avoid predation. We show that temporal refugia can play a key role in determining species persistence and ecosystem structure, and that the duration of the refuge is fundamental for determining the outcome of predator mediated competition.

Previous studies have shown that the proportion of a prey population that utilises a refuge, defined as either a fixed proportion of the total population or a fixed number of individuals (regardless of population size), is a key parameter in determining the stability and persistence of predator-prey interactions [10, 106, 130]. These spatial refugia offer constant refuge from predation by safeguarding a segment of the population, thereby making extinction less likely [10]. Our study develops new theory to show that the length of time spent in a temporal refuge from predation, relative to the length of time when predation occurs, is a key factor in determining the outcome of predator-prey dynamics. A temporal refuge occurs when the predator switches its focus onto an abundant alternative prey species, which either reduces or alleviates predatory pressure on the focal prey species for a fixed period of time. Building on a model of enemy mediated apparent competition, we derived explicit criteria that determines how the length of the temporal refuge governs the outcome of the interaction between competing prey species and a shared predator. This explicit solution is an advance on previous analytical considerations of refuges from predation for which the proportion of prey that benefits from a spatial refuge does not have an obvious biological interpretation. It opens the way for considering the influence of different alternative prey dynamics on species coexistence.

Previous theoretical assessments examining how prey switching can determine the stability and persistence of predator prey systems have typically been limited to switching between two focal prey species [87, 94, 153]. These studies have found prey switching occurs more readily in species that have a strong preference for one prey species over the other. When there is a weak preference, predation proportions are more likely to follow abundance ratios, as would be expected with generalist predators. Thus, prey switching is not a sufficient condition for prey species stabilisation [87], with the promotion of prey persistence via the creation of stable limit cycles, as opposed to stable equilibria, being a more likely theoretical outcome [153]. There is ample empirical evidence of prey switching shaping predator-mediated indirect interactions, but relatively little theoretical treatment to support generalisations. For instance, the long-standing Alternative Prey Hypothesis [3] posits that a change in predatory impact on alternative prey, caused by a functional response of generalist predators, synchronises the fluctuations of cyclic primary and alternative preys. Accordingly, increased predatory impact by red foxes (*Vulpes vulpes*) and pine martens that exploit cyclically fluctuating vole populations, their main prey when they are abundant, has a negative effect on ground nesting willow ptarmigan (*Lagopus lagopus*) growth rates and breeding success when vole abundances are low. However, they exert little influence on alternative prey species, e.g. ptarmigan, when the main prey densities are high (e.g. see Breisjøberget et al. [16]). The alternative prey hypothesis does not consider directly competing species but shares with the scenario explored here that shifting patterns of predation reflect exogenous changes in the abundance of the main prey.

We extend the prey switching theory to consider how a predator can mediate the interaction between two focal prey species that are in competition, and how this is affected by the predator switching to an alternative prey that generates a temporal refuge for the focal prey. We highlight the utility of the theory for the well-documented 3-4 years of multi-annual cyclic dynamics in small rodents that are a key driver of predator-prey relationships involving vertebrates. An important feature of a temporal refuge described in our model study is that the unequal predatory impact on the competing focal prey is reinstated dynamically as the abundance of the cyclic alternative prey collapses. Hence, the refuge from predation diminishes and predation of the focal competing prey resumes, potentially disproportionally to their relative abundances. Our general theory shows that, when there is differential predation on the focal prey species the predator can mediate the outcome of competition and allow an inferior competitor to persist if it suffers less from the impact of predation. When the predator switches to an alternative abundant prey, the focal prey species in our study benefits from a temporal refuge which can lead to renewed competition and the loss of the inferior competitor. The theory also allows coexistence between the competing species to occur, depending on the relative competitive and predation pressures. Thus, unlike a spatial refuge, the temporal refuge does not reduce the chance of extinction during times of active predation. Instead it allows greater population growth during times of refuge, which can bolster the population size, making them resilient to the effects of predation. Hence, predators, and their prey-switching behaviour, can play a key role in ecosystem structure [23] and the temporal impacts, in addition to the spatial component, should be considered.

Our general theoretical framework was extended to consider a key case study system in which two prey species – the endangered Eurasian red squirrel which is subject to competition from, and potential exclusion by, the invasive North American grey squirrel – are subject to predation from the native pine marten. Pine marten population density is recovering in the UK and the Republic of Ireland following historical decline as a result of persecution associated with the growth of the sporting-estate and habitat loss due to deforestation [70]. Pine martens predate on both red and grey squirrels, but grey squirrels typically compose a greater proportion of pine marten diet than red squirrels, as measured by frequency of occurrence [122, 152]. This preferential predation of pine marten on grey squirrels has been linked to the decline of grey squirrels and the recovery of native red squirrels in the Republic of Ireland and Scotland [122, 124, 152]. Our theoretical results indicate that preferential predation on grey squirrels can counter their enhanced competitive ability and allow red squirrels to exclude greys. However, pine martens are opportunistic predators that target locally abundant resources [149] and, in particular, may focus predation efforts on field vole populations which are known to exhibit multi-year cycles in population abundance [69]. This has the potential to lead to a temporal refuge from predation for both squirrel species and our results indicate that, if the duration of the temporal refuge is suitably long, the predator mediated advantage for red squirrels is diminished and may prevent red squirrel recovery.

Field vole cycles documented in Scotland and northern England may also be present in Wales and the rest of England [31, 69, 142]. These population cycles have variable period length, with the 3-year cycles that have prevailed since 2013 offering greater refuge for grey squirrels than the lower amplitude 4-year cycles [33]. We find that 3-year cycles, which provide a relatively longer refuge, require a 40% higher threshold in pine marten density, compared to the 4-year cycle, to ensure predator mediated exclusion of grey squirrels. We note that the threshold values of marten density that yield predator mediated exclusion in our strategic models fall within the observed range of density values recorded using statistically robust methods, but often sparse data. However we recognise that the appropriate use of our findings is for the qualitative comparison of model scenarios rather than for quantitative interpretation. Nevertheless our results imply that our necessarily parameter rich multi species model broadly captures the essence of the biology of the species and effectively uses empirical evidence, despite strong simplifying assumptions [63, 132, 166].

The strategic model developed to assess the case study system highlights the importance of a range of potential processes that could influence the ability of pine marten to promote the recovery of red squirrels. Assuming that pine marten preferentially predates on grey squirrels compared to red squirrels [152], a key finding is that the pine marten density required for red squirrels to exclude greys is habitat, and hence squirrel carrying capacity, dependent, with higher carrying capacities requiring greater marten densities for exclusion to occur. Required pine marten density also increases by a factor of 1.5 to 2 as the relative length of the temporal refuge increases (e.g. 3 vs 4-year cycles). Note that, while we considered the known influence of the proportion of coniferous and deciduous tree cover on squirrel species carrying capacity, we implicitly held constant the amount of field vole habitat. Field voles inhabit rough grasslands, rather than forest understorey and clear-felled areas in short rotation conifer plantations. These conditions prevail in northern Britain and support abundant field vole populations, as do unplanted river margins and ungrazed meadows. However, plantation forests lack tree cavities, which North American research indicates could confer higher survival rates for grey squirrels relative to dreys, which may limit both grey squirrel and marten densities [127]. Determining how habitat properties in the UK and Republic of Ireland affect the four interacting species considered in our case study system is an important applied endeavour beyond the scope of this modelling exercise.

Our results indicate that the pine marten density required to exclude grey squirrels is higher in the absence of red squirrels (compare Figure 5.C1 b and c) which suggests that grey squirrel decline, mediated by pine marten predation, is likely to be most pronounced in regions that are contiguous with red squirrel populations. Thus, the influence of pine marten may spread as a slowly expanding wave front as red squirrel recovery enhances the impact of pine marten on grey squirrel population declines. Pine marten also predate on red squirrels [55] and there is concern that pine marten recovery may threaten red squirrel viability. Despite our strong caveats on the interpretation of modelled pine marten densities, our study reflects the results from field observations [124, 152] that suggest that, at the level of pine marten density observed in the UK and Republic of Ireland, the impact of pine marten predation on red squirrel density is low. It is noteworthy that cyclically fluctuating field vole populations are altogether absent from the island of Ireland, where bank voles (*Myodes glareolus*) and wood mice (*Apodemus sylvaticus*) are the primary prey of pine marten [149]. Those species exhibit irregular outbreaks in density linked to tree seed masting events [97], however they do not reach the densities exhibited by field voles in mainland UK [134]. Thus, the impact of a temporal refuge may be more pronounced in Scotland and northern England than in Ireland, which may explain why the grey squirrel decline that has coincided with the recovery of pine marten in Ireland has been rapid [122, 152].

The mathematical model developed to examine predator mediated interactions between red and grey squirrels did not consider the role of squirrelpox, a shared pathogen that has little impact on grey squirrel mortality but is generally lethal to red squirrels [26, 110]. Squirrelpox has been shown to increase the rate of replacement of red squirrels by greys when they expanded through much of the UK and Ireland [109, 147]. Squirrelpox persists in grey squirrel populations leading to outbreaks in adjacent red squirrel populations [162]. However, squirrelpox may not be supported in low density red and grey squirrel populations associated with conifer dominated habitat in Scotland [77, 132, 166]. This indicates that, as with pine marten and grey squirrels, there is a threshold density for squirrelpox persistence. Since pine marten predation reduces grey squirrel density, it may lead to the eradication of squirrelpox in advance of the potential replacement of grey squirrels by recovering red squirrels, as was observed during grey eradication and red recovery on Anglesey [118]. This suggests a potential role for pine marten, and predators in general, in the control of infectious disease [140]. This is a topic for future study and would further highlight how strategic models can be used to develop new hypothesis that extend the debate on the role of the reintroduction and conservation of natural predators to control invasive species and disease and to maintain ecosystem diversity [102].

Appendix 5.A Steady state analysis

The information in this Appendix was included as Supplementary Information in the submitted version of this work.

5.A.1 *Two-species competition model with predation*

We outline a model to represent the dynamics of two competing prey species that are subject to predation. The model is based on the classical Lotka-Volterra framework for competing species. The model represents the densities of prey species X_1 and X_2 at time t as follows:

$$\frac{\mathrm{d}X_1}{\mathrm{d}t} = (a_1 - q_1(X_1 + c_2X_2))X_1 - B_1X_1, \tag{5.A1}$$

$$\frac{\mathrm{d}X_2}{\mathrm{d}t} = (a_2 - q_2(X_2 + c_1X_1))X_2 - B_2X_2,$$

where the death rate B_i is defined as:

$$B_i = \begin{cases} b_i & \text{if } \mu_i = 0, \\ b_i + \mu_i\, K_P & \text{if } \mu_i \neq 0, \end{cases} \tag{5.A2}$$

with μ_i being the predation rates and K_P the population density of the predator, which we assume is fixed at its carrying capacity. Defining the death rate in this manner allows the two-species competition model to represent a scenario in which prey compete in the absence ($\mu_i = 0$) and presence ($\mu_i > 0$) of predation. By setting $\mu_1 \neq \mu_2$ we can account for different levels of predation on different species, thus reflecting prey susceptibility and predator preference/attack rate. We assume for simplicity that predation occurs according to a linear functional response (thus we are assuming a generalist predator whose predation does not saturate). We assume a maximum birth rate (a_i) for each species. The birth rate for species i is modified by intra-specific competition from species i, denoted by q_i, and by inter-specific competition from species j, given by c_j. We assume constant natural death rates, b_i.

5.A.2 *Steady states*

The steady states are found by setting the derivatives in system (5.A1) to zero and solving the resultant system of equations. There are four steady states in total, which are:

$$\begin{aligned}
(X_1, X_2) &= (0, 0) \\
(X_1, X_2) &= (K_1^*, 0) \qquad (5.\text{A}3) \\
(X_1, X_2) &= (0, K_2^*) \\
(X_1, X_2) &= \left(\frac{K_1^* - c_2 K_2^*}{1 - c_1 c_2}, \frac{K_2^* - c_1 K_1^*}{1 - c_1 c_2} \right)
\end{aligned}$$

where

$$K_i^* = \begin{cases} K_i & \text{if } \mu_i = 0, \\ H_i & \text{if } \mu_i \neq 0, \end{cases} \qquad (5.\text{A}4)$$

with $H_i = K_i - K_P \mu_i / q_i$ being the predation suppressed carrying capacity for prey species i.

5.A.3 *Stability*

To assess the stability of the steady states we require the Jacobian matrix for system (5.A1).

$$J_{(X_1, X_2)} = \begin{pmatrix} a_1 - B_1 - q_1(2X_1 + c_2 X_2) & -q_1 c_2 X_1 \\ & \\ -q_2 c_1 X_2 & a_2 - B_2 - q_2(2X_2 + c_1 X_1) \end{pmatrix}$$

The following are the eigenvalues and stability conditions for the steady states given in Eqn. (5.A3):

Steady State	**Eigenvalues**	**Stability Cond.**
(0,0)	$\lambda_1 = a_1 - B_1$	$a_1 < B_1$
	$\lambda_2 = a_2 - B_2$	$a_2 < B_2$
(K_1^*,0)	$\lambda_1 = B_1 - a_1$	$a_1 > B_1$
	$\lambda_2 = a_2 - B_2 - q_2 c_1 K_1^*$	$K_2^* - c_1 K_1^* < 0$
(0,K_2^*)	$\lambda_1 = a_1 - B_1 - q_1 c_2 K_2^*$	$K_1^* - c_2 K_2^* < 0$
	$\lambda_2 = B_2 - a_2$	$a_2 > B_2$
$\left(\frac{K_1^* - c_2 K_2^*}{1 - c_1 c_2}, \frac{K_2^* - c_1 K_1^*}{1 - c_1 c_2}\right)$	$\lambda_{1,2} = \frac{1}{2}[-(q_1 X_1^* + q_2 X_2^*) \pm \sqrt{(q_1 X_1^* + q_2 X_2^*)^2 - 4 q_1 q_2 X_1^* X_2^* (1 - c_1 c_2)}]$	$K_1^* - c_2 K_2^* > 0$
		$K_2^* - c_1 K_1^* > 0$
		$0 < c_1 c_2 < 1$

Note: For the coexistence steady state, X_i^* denotes the steady state for species i. Furthermore, the steady state is unconditionally unstable when $c_1 c_2 > 1$ and does not exist when $c_1 c_2 = 1$. The other two stability conditions are required for biological realism (positive population sizes).

Appendix 5.B Temporal Refuge analysis

To consider a temporal refuge from predation we assume the dynamics are represented by equation (5.A1) with the following criteria for the predation parameter:

$$\mu_i \begin{cases} = 0 & \text{for } 0 \leq t < T_c, \\ > 0 & \text{for } T_c \leq t < T. \end{cases} \tag{5.B1}$$

The predator continuously switches predation off and on for species 1 and 2 in a periodic manner, with period T. The length of the temporal refuge is given by T_c during each period. This represents the scenario whereby the predator feeds on alternative prey species during the first part of the period and so does not predate on species 1 and 2 for a length of time T_c for each period.

With this set-up, standard techniques for stability analysis of steady states do not apply. Instead we need to examine the existence and stability of time varying solutions using Floquet theory.

5.B.1 *Existence of a periodic solution*

Before we can assess the stability of the solution using Floquet theory, we first need to check that a periodic solution exists. For this, we need to solve the ODE system. We shall use the combined system using the variables B_i and K_i^*:

$$\frac{\mathrm{d}X_1}{\mathrm{d}t} = (a_1 - q_1(X_1 + c_2X_2))X_1 - B_1X_1, \tag{5.B2}$$

$$\frac{\mathrm{d}X_2}{\mathrm{d}t} = (a_2 - q_2(X_2 + c_1X_1))X_2 - B_2X_2.$$

We are interested in solutions, and stability conditions, that ensure the survival of species X_1, which we previously defined as the native species that is out-competed by the invasive species X_2. If we consider the periodic steady state $(X_1^*, 0)$ with initial conditions $(X_1(0), 0)$, we can ignore the second equation, which gives us:

$$\frac{\mathrm{d}X_1}{\mathrm{d}t} = (a_1 - B_1 - q_1X_1)X_1, \tag{5.B3}$$

which is a separable equation. We use partial fractions to give:

$$\int \left(\frac{1}{X_1} + \frac{q_1}{a_1 - B_1 - q_1 X_1} \right) \mathrm{d}X_1 = (a_1 - B_1) \int \mathrm{d}t. \tag{5.B4}$$

The above integral needs to be split into 2: one integral for $\mu_1 = 0$ and another when $\mu_1 \neq 0$ with:

$$B_i = \begin{cases} b_i & \text{for } 0 \leq t \leq T_c \\ \hat{b}_i & \text{for } T_c \leq t \leq T \end{cases} \tag{5.B5}$$

where $\hat{b}_i = b_i + K_P \mu_i$, T_c denotes the time when predation is switched on, and T is the period of the periodic solution (thus $T > T_c$).

Thus we have:

$$\int_{X_1(0)}^{X_1(t)} \left(\frac{1}{X_1} + \frac{q_1}{a_1 - b_1 - q_1 X_1} \right) \mathrm{d}X_1 = (a_1 - b_1) \int_0^t \mathrm{d}t, \tag{5.B6}$$

and

$$\int_{X_1(T_c)}^{X_1(t)} \left(\frac{1}{X_1} + \frac{q_1}{a_1 - \hat{b}_1 - q_1 X_1} \right) \mathrm{d}X_1 = (a_1 - \hat{b}_1) \int_{T_c}^t \mathrm{d}t. \tag{5.B7}$$

These integrals can be solved, and rearranged, to give us our periodic solution:

$$X_1(t) = \begin{cases} \frac{r_1 X_1(0) e^{r_1 t}}{r_1 + X_1(0) q_1 (e^{r_1 t} - 1)} & \text{for } 0 \leq t \leq T_c, \\ \\ \frac{\hat{r}_1 X_1(T_c) e^{\hat{r}_1 (t - T_c)}}{\hat{r}_1 + X_1(T_c) q_1 (e^{\hat{r}_1 (t - T_c)} - 1)} & \text{for } T_c \leq t \leq T, \end{cases} \tag{5.B8}$$

where $r_1 = a_1 - b_1$ and $\hat{r}_1 = a_1 - \hat{b}_1$. If we instead choose species X_2 as the surviving species, the derivation would result in a similar expression for the periodic solution, except with the indices $\{1, 2\}$ switched.

Figure 5.B1 shows a single time period for X_1.

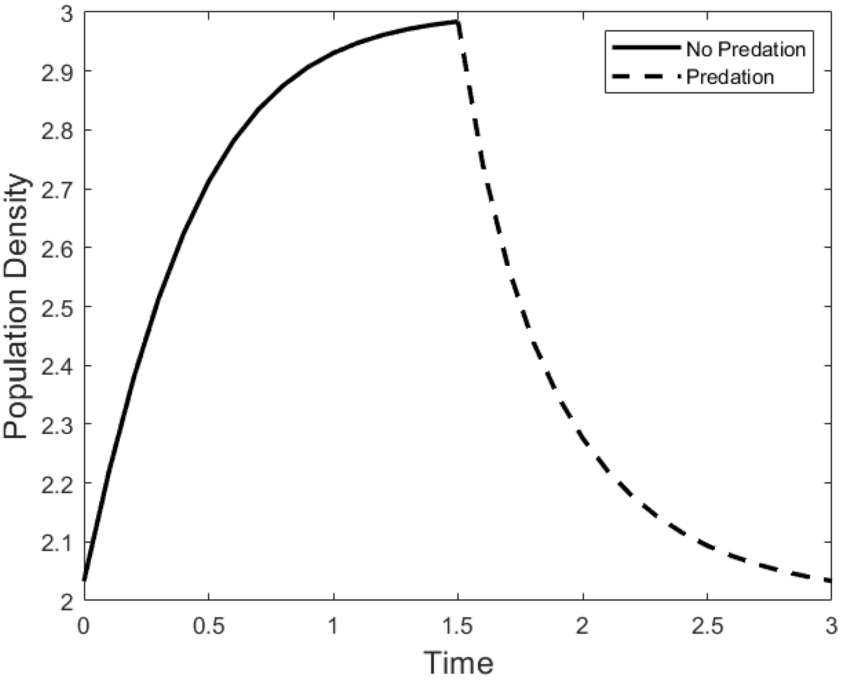

Figure 5.B1: Plot of the analytic solution for the periodic population density for prey species X_1 (Eqn. 5.B8). Constants were: $r1 = 3$, $\hat{r}_1 = 2$ (thus $K_P\mu_1 = 1$), $q_1 = 1$, $X_1(0) = 2.033$ and $T_c = 1.5$. As can be seen, the final solution $X_1(T)$ reaches the same value as the initial condition, as expected.

5.B.2 ***Stability analysis***

Now that we have a periodic solution, we need to assess its stability. To do this, we need to linearise (5.B2) about the periodic steady state $(X_1^*, 0)$. If we substitute $(X_1, X_2) = (X_1^* + \epsilon\tilde{X}_1, 0 + \epsilon\tilde{X}_2)$, $\epsilon << 1$, into (5.B2) we get:

$$\frac{\mathrm{d}\tilde{X}_1}{\mathrm{d}t} = (a_1 - B_1 - 2q_1X_1^*)\tilde{X}_1 - q_1c_2X_1^*\tilde{X}_2, \tag{5.B9}$$

$$\frac{\mathrm{d}\tilde{X}_2}{\mathrm{d}t} = (a_2 - B_2 - q_2c_1X_1^*)\tilde{X}_2.$$

From (5.B9) we can find solutions and create the following matrix:

$$M = \begin{pmatrix} \tilde{X}_1^a(T) & \tilde{X}_1^b(T) \\ \tilde{X}_2^a(T) & \tilde{X}_2^b(T) \end{pmatrix},$$

where $\tilde{X}_i^a(T)$ denotes solutions after one period of length T with initial conditions $(\tilde{X}_1(0), \tilde{X}_2(0)) = (1, 0)$ and $\tilde{X}_i^b(T)$ the corresponding solutions when the initial conditions are $(\tilde{X}_1(0), \tilde{X}_2(0)) = (0, 1)$. Floquet theory tells us that the steady state $(X_1^*, 0)$ is stable if the eigenvalues of M are less than 1.

For initial conditions $(\tilde{X}_1^a, \tilde{X}_2^a) = (1, 0)$ we know $\tilde{X}_2^a(T) = 0$. Consequently, this means that the eigenvalues of M are given by $\tilde{X}_1^a(T)$ and $\tilde{X}_2^b(T)$. Hence, the following derives an expression for $\tilde{X}_1^a$ and so assesses the stability of the steady state to perturbations in X_1.

Applying the initial condition gives us:

$$\frac{\mathrm{d}\tilde{X}_1^a}{\mathrm{d}t} = (a_1 - B_1 - 2q_1X_1^*)\tilde{X}_1^a. \tag{5.B10}$$

This is a separable equation that yields:

$$\int_1^{\tilde{X}_1^a(T)} \frac{\mathrm{d}\tilde{X}_1}{\tilde{X}_1} = \int_0^T (a_1 - B_1 - 2q_1X_1^*)\mathrm{d}t, \tag{5.B11}$$

whose solution is:

$$\boxed{\tilde{X}_1^a(T) = e^{\int_0^T a_1 - B_1 - 2q_1X_1^* \mathrm{d}t}.} \tag{5.B12}$$

If we now set our initial conditions to $(\tilde{X}_1^b, \tilde{X}_2^b) = (0, 1)$ we can find a solution for $\tilde{X}_2^b$, which gives us:

$$\frac{\mathrm{d}\tilde{X}_2^b}{\mathrm{d}t} = (a_2 - B_2 + q_2c_1X_1^*)\tilde{X}_2^b, \tag{5.B13}$$

which is also a separable equation that gives:

$$\int_1^{\tilde{X}_2^b(T)} \frac{\mathrm{d}\tilde{X}_2}{\tilde{X}_2} = \int_0^T (a_2 - B_2 - q_2c_1X_1^*)\mathrm{d}t, \tag{5.B14}$$

whose solution is:

$$\boxed{\tilde{X}_2^b(T) = e^{\int_0^T a_2 - B_2 - q_2c_1X_1^* \mathrm{d}t}.} \tag{5.B15}$$

We know that the eigenvalues of the matrix M are given by $\tilde{X}_1^a(T)$ and $\tilde{X}_2^b$(T). Hence, the steady state $(X_1^*, 0)$ is stable if:

$$\tilde{X}_1^a(T) = e^{\int_0^T a_1 - B_1 - 2q_1X_1^* \mathrm{d}t} < 1, \tag{5.B16}$$

and

$$\tilde{X}_2^b(T) = e^{\int_0^T a_2 - B_2 - q_2 c_1 X_1^* \mathrm{d}t} < 1. \tag{5.B17}$$

These conditions are met if:

$$\int_0^T a_1 - B_1 - 2q_1 X_1^* \mathrm{d}t < 0, \tag{5.B18}$$

and

$$\int_0^T a_2 - B_2 - q_2 c_1 X_1^* \mathrm{d}t < 0. \tag{5.B19}$$

which, given the split between the model where the predator is present and where it isn't present, gives:

$$\int_0^{T_c} a_1 - b_1 - 2q_1 X_1^* \mathrm{d}t + \int_{T_c}^T a_1 - b_1 - K_P\mu_1 - 2q_1 X_1^* \mathrm{d}t < 0, \tag{5.B20}$$

and

$$\int_0^{T_c} a_2 - b_2 - q_2 c_1 X_1^* \mathrm{d}t + \int_{T_c}^T a_2 - b_2 - K_P\mu_2 - q_2 c_1 X_1^* \mathrm{d}t < 0. \tag{5.B21}$$

Rearranging these 2 expressions gives us our 2 stability conditions:

$$K_1 - \frac{K_P\mu_1}{q_1}(1 - \frac{T_c}{T}) < 2\frac{1}{T}\int_0^T X_1^* \mathrm{d}t, \tag{5.B22}$$

$$K_2 - \frac{K_P\mu_2}{q_2}(1 - \frac{T_c}{T}) < c_1\frac{1}{T}\int_0^T X_1^* \mathrm{d}t \tag{5.B23}$$

where $\frac{1}{T}\int_0^T X_1^* \mathrm{d}t$ is the average value of the periodic solution over 1 time period.

Again, if we assume that species 2 survives instead of species 1, then the above analysis can be repeated to give the corresponding set of stability conditions with indices $\{1, 2\}$ swapped.

Note. If $T_c = T$ then the above stability conditions revert to those for the system without predation (Eqn. 5.A1, $B_i = b_i$), whilst if $T_c = 0$ then the conditions revert to those for the predator-prey system (Eqn. 5.A1, $B_i = b_i + K_P\mu_i$). Thus, these two scenarios provide the limiting cases for the temporal refuge.

5.B.3 *Analysis of stability conditions*

The above stability conditions require us to know the average population density of either species 1 or 2 (depending on which species survives) when it is at its steady state.

If we assume that the prey density instantaneously switches from its higher value (K_1) to its lower value (H_1), thus introducing a step function when the critical value (T_c) is reached (when predation is turned on), the the average value for the density of species 1 is:

$$\frac{1}{T}\int_0^T X_1^* \mathrm{d}t = \frac{1}{T}\int_0^{T_c} K_1 \mathrm{d}t + \frac{1}{T}\int_{T_c}^T H_1 \mathrm{d}t$$

$$= K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T}). \tag{5.B24}$$

Hence, the first stability condition (equation 5.B22) becomes:

$$K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T}) < 2(K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T})). \tag{5.B25}$$

This can be rearranged to give:

$$K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T}) > 0. \tag{5.B26}$$

Thus, the first stability condition requires the temporal and predation reduced carrying capacity to be positive.

The second stability condition (equation 5.B23) becomes:

$$K_2 - \frac{K_P \mu_2}{q_2}(1 - \frac{T_c}{T}) < c_1(K_1 - \frac{K_P \mu_1}{q_1}(1 - \frac{T_c}{T})). \tag{5.B27}$$

This can be rearranged to give:

$$\frac{T_c}{T} > 1 - \frac{q_1 q_2 (c_1 K_1 - K_2)}{K_P(c_1 \mu_1 q_2 - \mu_2 q_1)}. \tag{5.B28}$$

Using some basic algebra we can show the above inequality holds in both direction (i.e. $T_c > \cdots$ and $T_c < \cdots$) which means we can assume the equality to give us:

$$\boxed{T^1_{crit} = T\left(1 - \frac{q_1 q_2(K_2 - c_1 K_1)}{K_P(\mu_2 q_1 - c_1\mu_1 q_2)}\right),} \tag{5.B29}$$

as the critical value of temporal refuge needed to ensure the survival of prey species X_1. Specifically, if $c_1 > c_2$ then T^1_{crit} is the minimum value required whilst if $c_1 < c_2$ then T^1_{crit} is the maximum temporal refuge allowed.

The above analysis can be repeated for the survival of prey species 2 which gives analogous stability conditions - except with the indices 1 and 2 switched. This gives the following expression:

$$\boxed{T^2_{crit} = T\left(1 - \frac{q_1 q_2(K_1 - c_2 K_2)}{K_P(\mu_1 q_2 - c_2\mu_2 q_1)}\right).} \tag{5.B30}$$

If the competition coefficients are such that $c_1 c_2 = 1$ then coexistence is impossible. In this case expressions 5.B29 and 5.B30 are equivalent ($T^1_{crit} = T^2_{crit}$) and they denote the maximum/minimum temporal refuge needed to exclude species 2 for the benefit of species 1. If $c_1 c_2 < 1$ then the two expressions are not equivalent and the difference in values gives the range of temporal refuge length that allows coexistence. When $c_1 c_2 > 1$ the values of T^1_{crit} and T^2_{crit} are such that the better competitor will always out-compete the lesser competitor with no coexistence possible due to the steady state being unstable.

Furthermore, equations 5.B29 and 5.B30 can be rearranged to give the predator density needed for species survival under a fixed length of temporal refuge.

5.B.4 *Example of varying solutions as temporal refuge length changes*

The steady states associated with Equation 5.A1 are mutually exclusive and suggest a smooth transition between states as certain parameters change. Given the periodic model (equation 5.B2) is based on the deterministic model (equation 5.A1) we would expect this behaviour to also apply to the periodic setting.

If we assume $c_1 c_2 < 1$, meaning coexistence is possible, the solution $(X_1^*, 0)$ is stable with predation ($T_c = 0$) and $(0, X_2^*)$ is stable without predation ($T_c = T$), and assuming $T^1_{crit} < T^2_{crit}$, then the $(X_1^*, 0)$ steady state should be stable for $T_c \leq T^1_{crit}$, species X_1 and X_2 would coexist with a temporally varying solution for $T^1_{crit} < T_c < T^2_{crit}$ and the $(0, X_2^*)$ steady state would be stable for $T_c \geq T^2_{crit}$.

Let $K_1 = 24.51$, $q_1 = 0.0245$, $c_1 = 1/1.65$, $\mu_1 = 0.3$, $K_2 = 23.2$, $q_2 = 0.0345$, $c_2 = 1.2$, $\mu_2 = 1.5$, $K_P = 0.4$ and $T = 3$. These parameters yield $T^1_{crit} = 1.26$ and $T^2_{crit} = 2.37$.

Figure 5.B2(a) shows the average population density of species 1 and 2 as the length of the temporal refuge is increased from $T_c = 0$ to $T_c = 3$. The results clearly demonstrate that species 1 is dominant when $T_c < T^1_{crit}$, species 2 is dominant when $T_c > T^2_{crit}$ and that there is coexistence when $T^1_{crit} < T_c < T^2_{crit}$. Figures 5.B2(b-d) show specific instance results for each of these scenarios which affirms the periodic nature of the resultant densities.

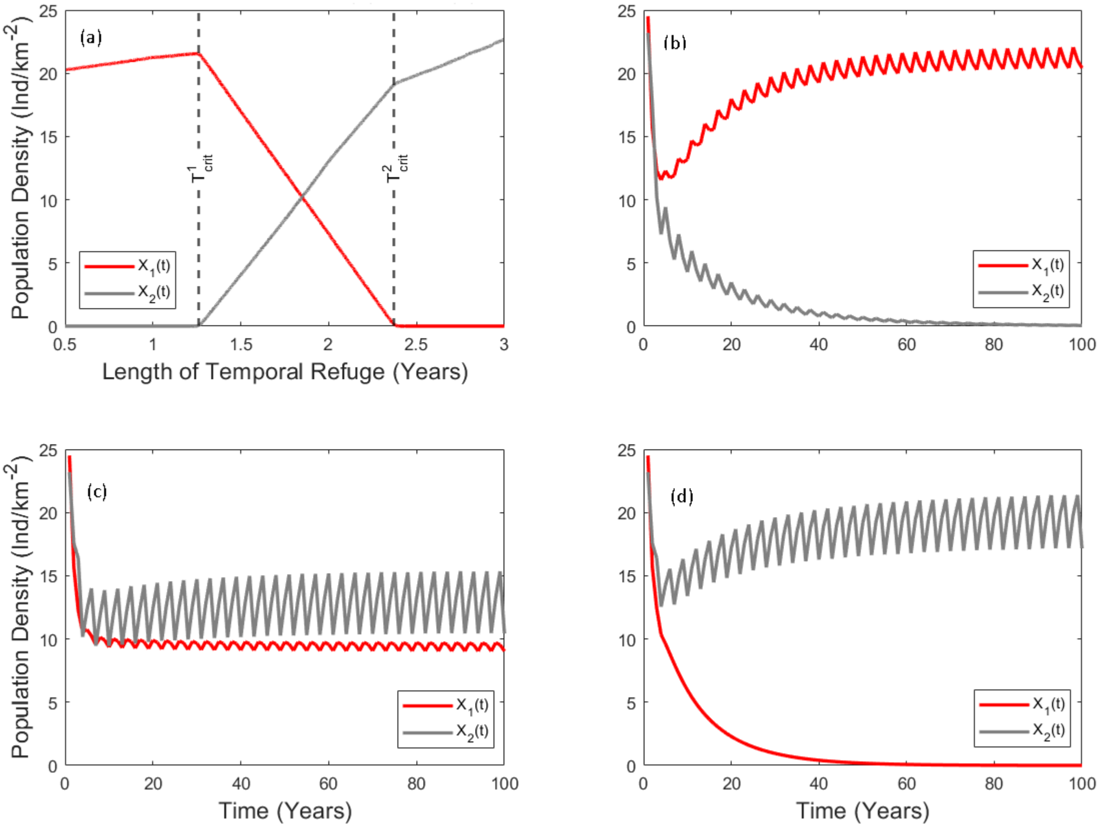

Figure 5.B2: Average population density results for prey species 1 and 2 for the periodic model (Equation 5.B2) that has reached equilibrium in a habitat with 15% broadleaved trees, with the remainder being coniferous trees, and a predator density of 0.4 km^{-2}. Here (a) shows the overall change in prey density as the length of temporal refuge in increased from $T_c = 0$ to $T_c = 3$. Dashed lines for $T^1_{crit} = 1.26$ and $T^2_{crit} = 2.37$ (as defined by Equations 5.B29 and 5.B30) are included. Image (b) shows a specific result with $T_c = 1$ ($T_c < T^1_{crit}$) which shows prey species 1 out-competing species 2, (c) shows the coexistence results when $T_c = 1.89$ ($T^1_{crit} < T_c < T^2_{crit}$ and (d) shows the result when $T_c = 2.7$ ($T_c > T^2_{crit}$) which shows species 2 out-competing species 1.

Appendix 5.C Sensitivity analysis

Figure 5.C1 shows results of a sensitivity analysis into the predation rates μ_R and μ_G as well as the functional response values V_0 and V_x. The pine marten density required to exclude one species in the absence of another (Figure 5.C1(a),(b)) decreases as the predation rate increases. The pine marten density required to exclude grey squirrels when both squirrels are present (Figure 5.C1(c)) increases as the red squirrel predation rate μ_R converges towards the grey squirrel predation rate μ_G. This occurs due to greater predation on red squirrels reducing the competitive pressure on grey squirrels.

In all three instances increased duration of temporal refuge requires greater pine marten density for exclusion.

Figure 5.C1(d) shows how the pine marten density required for grey squirrel exclusion in the presence of red squirrels changes as the functional response parameters, $V_0 = 110 - \delta$ and $V_x = 110 + \delta$, change as δ changes from zero to 110. When $\delta = 0$ the functional response is a step function and exactly models our theoretical derivation. When $\delta = 110$ the functional response is a linear gradient with no regions of constant response. The pine marten density required to exclude grey squirrels begins at 0.375 km^{-2} when $\delta = 0$, drops to 0.37 km^{-2} when $\delta = 20$ before increasing almost linearly upto a maximum density just over 0.415 km^{-2} when $\delta = 110$. Hence, the change in density needed is robust against the change in functional response.

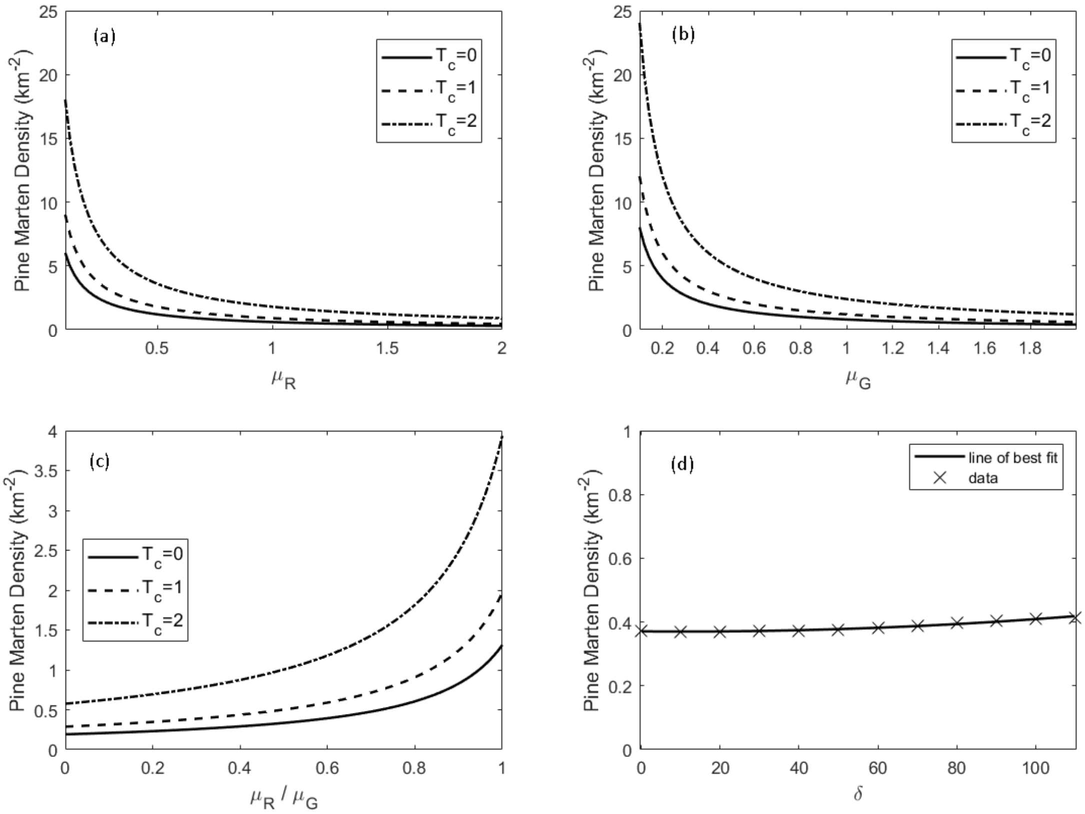

Figure 5.C1: Sensitivity analysis of the pine marten predation rates and functional response. Here (a) shows the pine marten density needed to exclude red squirrels when there are no grey squirrels present, (b) shows the pine marten density needed to exclude grey squirrels when red squirrels are absent, (c) shows the pine marten density needed to exclude grey squirrels when both squirrels are present in the model and (d) shows the pine marten density needed to exclude grey squirrels, using the full Kielder Forest vole dynamics, as the functional response parameters V_0 and V_x are altered by the parameter δ, with $V_0 = 110 - \delta$ and $V_x = 110 + \delta$. All results gained using a habitat of 15% broadleaved trees (the remainder being conifers) and the associated red and grey squirrel carrying capacities.

Chapter 6

Conclusions

Each chapter of this thesis is a distinct piece of work with the majority of the chapters having either been published or submitted for publication. Consequently, each chapter has its own detailed discussion. Therefore, this discussion briefly recaps key methodology and findings and highlights the impact of the work as well as areas for future research.

6.1 Forest management for red squirrel conservation

Chapters 2 and 3 use a well-established model framework [62, 162, 166] that consists of a spatially-explicit stochastic model of red and grey squirrel competitive interactions, along with squirrelpox infection, on realistic landscapes generated from forest inventory data sets. This model is based on an established ODE framework, meaning the dynamic interactions are well understood. The added realism of the 'real' heterogeneous landscape and stochastic dynamics allows us to assess the importance of grey squirrel dispersal and the potential spread of squirrelpox on red squirrel viability. A key result is that, when grey squirrels are present in the local landscape, specific forest management which promotes coniferous trees over broadleaved trees does improve the viability of red squirrels in Scotland [132]. However, the forest management offers no discernible long-term benefit to red squirrels in the absence of grey squirrels. Squirrelpox does not affect red squirrel viability, primarily due to the low grey squirrel densities in the north of Scotland which cannot support an endemic infection. This supports previous studies that have suggested that squirrelpox will have only a minor impact on red squirrel viability in Scotland [77, 166]. The modelling also suggests that some forest sites currently designated as strongholds are unsuited to the task, regardless of forest management.

The modelling used to assess the viability of designated strongholds highlighted regions that could maintain a red squirrel population without specific stronghold forest management. We used the model framework to identify regions that could support red squirrels despite grey squirrel competition and named them natural strongholds [133]. The main findings were that, if the current grey squirrel distribution were maintained, the north of Scotland would act as a stronghold - due to the absence of grey squirrels. If the current grey squirrel distribution were to expand and cover the entirety of Scotland then there remains a number of regions that can support red squirrels against grey squirrel incursion. The modelling also correctly identified natural strongholds in central and southern Scotland, such as Tentsmuir, which provides credibility to the predicted natural strongholds in northern Scotland.

6.1.1 The impact of our work for forest management and red squirrel conservation

Our work which highlights that conifer dominated forests can provide strongholds for red squirrels [132, 133] is given further support by Tamura et al. [139] who use our study to support the use of specific forest management that favours coniferous tree species for red squirrel conservation due to the different chemical contents of various tree seeds, which shapes the preferred tree seed diets of red and grey squirrels due to their different evolutionary histories. Furthermore, Wauters and Martinoli [158] use our studies [132, 133] as the basis for a proposal to identify forests in Italy whose composition is favourable to red squirrels. These forests are intended to help restrict the expansion of grey squirrel populations in Italy and is thus similar to the stronghold management plan. Stronghold forest management is currently a topic of much debate both in the press (the natural stronghold results received press coverage in over 25 print and online international articles) and in the Scottish forestry industry (K. Kortland, pers. comm.) and it is expected that our work will be central to a policy update on how to manage forest regions in Scotland for red squirrel conservation.

The modelling conducted in the assessment of specific forest management highlights how mathematical modelling can be combined with forest inventory datasets to assess the impact of forest management policy on conservation goals. Furthermore, the predictive nature of mathematical models allows the potential impact of proposed management policy to be assessed, with the model results being available for use in refining management and conservation policy. For example, the natural strongholds identified by the model are not large, and are also generally isolated. Hence, the model results indicate that, under a worst case scenario where grey squirrels inhabit the entirety of Scotland, conservation policy would need to be amended to include human intervention to either expand the natural strongholds (via tree planting or grey squirrel control) or mandate red squirrel trans-locations to ensure genetic viability. The modelling work can also be used to assess the impact of more intrusive forest management on red squirrel viability. In collaboration with Forestry and Land Scotland we intend to use the model to assess red squirrel population viability in response to emergency, large scale felling that is required due to Phytopthora Ramorum infection of larch trees in the Cowal peninsula in south-eastern Scotland. The model can be also be used to test alternative replanting strategies following felling to provide a more immediate and stable resource for red squirrels and to increase tree species diversity in line with the proposals to restore ancient native woodlands [144].

6.2 The impact of pine marten predation on red squirrel recovery

The stochastic model of red and grey squirrel and squirrelpox interactions was extended to include potential predation of squirrels by pine marten. The model estimated demographic and dispersal parameters for pine marten from data and represents the observed preferential predation of pine marten on grey squirrels compared to red squirrels [150]. The model was used to assess the potential impact of pine marten trans-location and subsequent range expansion on red and grey squirrel competitive interactions in North Wales. In the absence of pine marten and grey squirrel control the model showed that grey squirrels would replace red squirrels in much of North Wales, including re-invading and replacing red squirrels on the island of Angelsey. The main findings were that pine marten migrating northwards from central Wales, where pine marten are already established, are insufficient to prevent grey squirrel dominance of Bangor and Anglesey - a region that is currently managed for red squirrel conservation. Pine marten releases into the Bangor area of North Wales would help conserve red squirrels in the region via a reduction in grey squirrel density due to predation. Red squirrels would also expand their range from Clocaenog under the Bangor release strategy. A key output of this modelling project is the ability - via the production of high resolution density maps - to locate pine marten and squirrels in the landscape which can aid resource allocation for monitoring programs that assess the spread of pine marten and their impact on grey squirrel population reductions and red squirrel recovery. Our modelling work will direct policy and practice of the Red Squirrel Trust Wales to protect and enhance red squirrel populations.

The pine marten case study system was used as the motivation for a general study that developed a classical ODE framework with temporal forcing that analysed the impact of predation on competing prey species. In particular we showed how the duration of a refuge from predation (arising through prey switching) may alter the outcome of predator-mediated prey competition. Hence, the inclusion of a temporal refuge indicates that predator-mediated changes in competitive outcome may not be a straight-forward relationship, with refugia a complicating factor. A key output of our study is that our theory can be tested in real systems since temporal refuges from predation that are linked to alternative prey species abundance can be measured in the field.

6.2.1 The role of predation in shaping ecosystem structure

Our work shows that predators can shape species diversity in the landscape, due to differences in predation rates and variations in prey species behavioural responses to predator presence. This can be particularly acute when dealing with invasive-native species competitive interactions, and predation may allow alternate competitive outcomes to persist that would otherwise not occur. These outcomes can equally promote, or reduce, biodiversity in the landscape with the impact on species diversity being a consequence of the interaction of predation and competition [28, 30]. For example, in our case study the asymmetric predation of grey squirrels that occurs due to the lack of grey squirrel behavioural response to pine marten scent counteracts the competitive edge grey squirrels have over red squirrels which allows red squirrels to persist under circumstances that would otherwise see their eradication. This acts to improve biodiversity at the landscape scale, even though it only alters the diversity at a local level. A review of 39 field experiments concluded that predation acts to reduce the level of competitive interactions between species which improves the growth prospects of the less-competitive species [50] which can even lead to species coexistence under circumstances that would normally result in competitive exclusion.

The work regarding pine marten-squirrel interactions shows that predators can be utilised to control invasive species, which can have tangential benefits for native species. Invasive species are recognised as a major threat to species biodiversity across the globe [67, 131], and the removal of native predators is seen as a key reason for the proliferation of non-native species [154]. Thus, the reintroduction of native predators is seen as a way of reducing the impact of invasive species, with the lack of behavioural response of invasive species to predator presence being a key driver in the suppression of invasive species by native predators. However, caution should be advised as predator interactions with invasive species will not necessarily conform to expected behavioural patterns due to the novel interaction of predator and prey [96].

The modelling study assessing the impact of pine marten on red squirrel conservation also highlighted important new findings in terms of disease control. Grey squirrel density in North Wales is higher than in most parts of Scotland and so in North Wales squirrelpox is endemic [27, 82, 110]. Pine marten act to reduce grey squirrel density to levels where squirrelpox can no longer be supported - even though grey squirrels can still persist. This suggests that pine marten could act as natural disease control agents, with the control a consequence of grey squirrel density depression due to predation. The consequent increase in red squirrel density can therefore be attributed to a reduction in competition from grey squirrels but also a lack of disease induced mortality for red squirrels [141]. In our case study, reduction of disease alone would not suffice to allow red squirrels to out-compete grey squirrels and so the lack of mortality of grey squirrels due to squirrelpox is a key element in the predator mediated control of squirrelpox. Our work therefore highlights a general mechanism in which predators may contribute to disease management. This is in agreement with a study in Asturias in northern Spain where it has been shown that predation by wolves (*Canis lupus*) on wild boar (*Sus scrofa*) can reduce infection of animal tuberculosis (TB). A mathematical model confirmed field results and showed that prevalence of TB was reduced in areas with resident wolves compared to areas without wolves and therefore that wolves may reduce the risk of spillover of TB from the wildlife reservoir to livestock [140]. A novel area for future research could consider general mathematical frameworks that examine the role of predators in controlling infectious disease and the implication for ecosystem structure.

6.3 Areas for improvement

No piece of work is perfect. All work can be improved upon through enhancements in data quality and availability as well as updated and improved methodologies. The reports that comprise Chapters 2 and 3 would be improved through an increased accuracy in forest compositional data. The stronghold project used National Forest Estate data for the forest composition inside the strongholds which includes information on individual species. However, the regions outside the strongholds, as well as the locations of the natural strongholds, relies on National Forest Inventory information which only has information on the amount of broadleaved and coniferous trees that are present. Having specific tree species information for the forest regions outside Scottish Government owned land would greatly increase the accuracy of the carrying capacities which would allow for much more accurate predictions of red squirrel viability across the landscape. The inclusion of forest compositional changes due to climate change would enhance long-term model output and improve the predictive power of the model results that are used to inform conservation policy.

The work in Chapter 4 would benefit from better data availability for pine marten parameter value estimation. Currently the birth and death parameters are based on general life history information, such as gender split, average life span and litter size. Having information on region specific birth and death rates would improve pine marten modelling accuracy. Likewise, more accurate and regional dispersal information would improve the ability of the model to predict the range expansion of pine marten. This would allow better targeting of conservation resources. Lastly, more detailed information on pine marten predation rates and preference would increase model accuracy. Currently, pine marten predation rates for squirrels are based on limited studies and the frequency of occurrence of squirrel remains in pine marten scat. This method assumes all food sources remain identifiable in animal scat, which cannot be guaranteed. Thus, predation rates that do not rely on this method would be preferable as these would better represent the impact pine marten predation has on local squirrel populations.

6.4 Future work

The work in this thesis has shown how modelling frameworks can be used to understand complex species interactions and shape management and policy related to protecting endangered species. The stochastic model framework can be employed as a tool to aid many future studies. For instance, as forest management across Scotland is altered to cope with the spread of tree diseases such as Phytophthora Ramorum, which adversely affects larch trees, the model can be used to assess the impact of increased felling on red squirrel viability as well as suggesting the optimal tree species composition that should be replanted to enhance biodiversity more generally. The model also has potential uses in assessing how population isolation affects genetic diversity and fitness of red squirrel populations. Pine marten are currently increasing their density and range in the United Kingdom and Ireland. The model used in this thesis could be used to assess future marten distributions across the UK, as well as their impact on various prey species which includes red and grey squirrels. The work in this thesis has also shown how properties observed in case study ecological systems can be the motivation for general modelling studies that lead to new, testable, ecological hypotheses and highlight the utility of mathematical models for the development of ecological theory.

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