Grey squirrel control in Southern Scotland: A model analysis

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Contents

Executive Summary

This report assesses the viability of grey squirrel control in southern Scotland in order to inform and maximise the efficiency and cost effectiveness of Forest Enterprise Scotland (FES) funded management. In particular, the report details the findings from a mathematical modelling study to examine the realistic, spatial dynamics of red and grey squirrels and squirrelpox (SQPV) when grey squirrel are subject to population control through trapping and removal.

The modelling study also undertook a 'proof of concept' study into the potential impact of pine marten predation on red and grey squirrel abundance, and the potential of pine marten to reduce grey squirrel density and therefore the level of grey squirrel control required to protect red squirrels. This illustrates the potential ecosystem service pine martens could provide with respect to grey squirrel management.

Key findings are as follow

- The control of grey squirrels is required in broadleaf dominated habitats and corridors that are adjacent to conifer dominated regions in which red squirrels can persist. Here, grey squirrel control prevents their expansion into red squirrel strongholds/PARCS. If grey squirrel control is at a sufficiently high level it allows red squirrels to return to broadleaf habitats and therefore to be visible in key populated regions and tourist sites. In high density areas, control also reduces disease transmission and risk of disease outbreaks (White & Lurz 2014).

- A key assumption of the model in this study is that red squirrels can persist and out-compete grey squirrels in conifer dominated habitats. This assumption is based on evidence from the field that grey squirrels have not invaded and replaced red squirrels in large conifer forests even though they have been present in adjacent habit for many years (e.g. Bryce 2000; Bryce et al. 2002; authors own observations). This means that there are likely to be large regions in southern Scotland in which red squirrels can persist in the absence of grey squirrel control. These regions are typically Sitka spruce dominated forests (or other large conifer plantations) and would support low red squirrel densities (and so red squirrels would not be easily visible). A key question that requires future research is what composition of conifer species and forest structure and size is required to allow red squirrels to outcompete grey squirrels and maintain viable populations in the long term.

- An initial 'proof of concept' study that assumes pine marten would preferentially predate on grey squirrels indicates that the current, low density, presence of pine marten in Dumfries and Galloway could reduce the level of grey squirrel control required to exclude greys from key regions without unduly affecting red squirrel density. It also raises the research question on UK forest ecosystems of what community composition in terms of tree species, seed predators and predators favours the long-term survival of red squirrels. Should red squirrel conservation be widened and encompass ecosystem diversity and habitat quality and in special cases the enhancement of the diminished UK predator fauna?

- Comparing results for Dumfries and Galloway, Eskdalemuir and the Peebles region it is apparent that low levels of grey squirrel control would allow grey squirrels to dominate and expand and red squirrels would be restricted to large and often remote conifer blocks. Survival of red squirrels would therefore depend on suitable forest management in conifer blocks with respect to tree species composition and age-structure to maintain long-term viable populations.

- With low levels of grey squirrel control SQPV would also remain endemic in the Eskdalemuir (southeast) and in the Peebles area. SQPV is not predicted to play a significant role in Dumfries and Galloway as most of the habitat here supports only low density squirrel populations which cannot sustain prolonged SQPV outbreak.

- Medium to high intensity levels to control grey squirrels would arrest grey squirrel expansion and can remove grey squirrels from most of the areas where control takes place. This protects red squirrels in the wider area and leads to an expansion of red squirrel in to habitat previously occupied by grey squirrels.

- A key conclusion here is that the effort of control expended will therefore influence where red squirrels are seen. Red squirrels are likely to survive over the next 30 years in all three regions at <u>low density</u> in the larger, remote conifer areas (subject to tree species composition, age structure and local forest management plans). Conservation of red squirrels in populated areas, which include high levels of deciduous forest and that can support high density squirrel populations, would require medium to high intensity control of grey squirrels.

- The presence of red squirrels in the deciduous habitats resulting from medium to high levels of grey squirrel control would also increase overall red squirrel population viability. Red squirrel populations in conifer forests experience large fluctuations in abundance as a result of significant, natural annual changes in seed food availability (seed crop cycles). Their presence in the mixed-deciduous habitats as a result of grey squirrel control will create red squirrel source populations in years when resource availability in conifer forests is low or absent due to poor seed crops.

- If targeted grey squirrel control around red squirrel strongholds and PARCs can be sustainably devolved to local red squirrel groups then (at medium to high intensity effort) it offers a way to protect red squirreel in southern Scotland, and to make them visible in mixed-deciduous woodland that are in close proximity to populated areas where people can enjoy them.

1. Background

The native red squirrel is under threat as a result of the expansion of the introduced North American grey squirrel. Scotland has a special responsibility for red squirrels in a UK context, as an estimated 75% of the remaining UK populations are thought to live in Scotland. The red squirrel has already disappeared from a large part of its former Scottish range in central and south-eastern Scotland. Replacement of red squirrels by grey squirrels takes the form of disease-mediated competition and decline is significantly faster in areas where grey squirrels act as carriers of squirrelpox virus (Tompkins et al. 2003). The virus is currently present in some parts of southern and central Scotland and efforts to stem its spread in the south of Scotland managed to slow but not prevent SQPV spread (White & Lurz 2014). In southern Scotland, the virus persists at endemic levels in the widespread and established grey squirrel populations. Red squirrels still persist in isolated areas and the conservation strategy is to defend these red squirrel populations from the threat of replacement by grey squirrels (SNH 2015). Recent research (Chantrey et al. 2014; Lurz et al. 2015) and modelling work, by Heriot-Watt University (White et al. 2014, 2015) has provided insights and valuable lessons on how to manage red squirrel populations to potentially "live" with the threat of the virus in priority regions for the conservation of red squirrels (see Fig. 1.1).

The red squirrel conservation project in southern Scotland, coordinated by Saving Scotland's Red Squirrels (SSRS), is in its 3rd phase and aims to save red squirrels in key areas. It also attempts to manage the impact of squirrelpox virus, and to monitor and establish a long-term, cost effective means of controlling grey squirrels (SSRS 2017). Key issues with respect to red squirrel conservation in southern Scotland are the presence of squirrelpox virus, large oak-dominated deciduous woodlands important for biodiversity and conservation (e.g. south-west Scotland around Fleet Basin) that are ideal for grey squirrels, forest management of extensive Sitka spruce (*Picea sitchensis*) dominated conifer forests used for timber production that are potential refuges for red squirrels, as well as the presence of pine martens in the Galloway Forest and surrounding areas.

1.1 Project aim:

In order to assist with red squirrel conservation efforts in southern Scotland the current mathematical modelling project in collaboration with Forest Enterprise Scotland aims to apply established mathematical models (Jones et al. 2017; White et al. 2017) of the red-grey-squirrelpox system that includes grey squirrel control to assess the location and level of control required to protect red squirrels in three priority regions in the Dumfries and Galloway and Scottish Borders Forest Districts. The three priority regions are as follows (see also Figure 1.1)

A. Galloway forest park (partly an FCS squirrel stronghold)
B. Eskdalemuir (FCS/privately owned squirrel stronghold)
C. Peebles (Priority Area for Red Squirrel Conservation (PARC))

1.2 Objectives

I. Determine the level of grey squirrel control required to protect red squirrels in the Galloway Forest Park. The model will determine the location and level of grey squirrel control required to prevent grey squirrel expansion into the Galloway Forest Park. In particular it will highlight key dispersal corridors on which focussed grey squirrel control should be applied.

II. Undertake a preliminary investigation of the potential role of pine marten on reducing grey squirrel density in the Galloway Forest Park. Adapt the model framework to include preferential predation of grey squirrels by pine marten to provide and assessment of the potential of pine marten to reduce grey squirrel density. The results will be interpreted in terms of the potential reduction in the level of grey squirrel control required in comparison to when pine marten are not included in the model (objective (I)) and therefore highlight the potential of pine marten to offset some of the costs associated with grey squirrel trapping.

III. Determine the level of grey squirrel control to protect red squirrels in the priority regions (ii)-(iii). Use the methods of objective (I) to undertake an assessment of the location and level of grey squirrel control required to prevent grey squirrel expansion in priority regions (ii)-(iii).

IV. Provide a cost/benefit analysis of the three priority regions. Assess the level of grey squirrel control required in the three priority regions relative to the predicted density and population survival of red squirrels within these regions. This will inform on the characteristics that provide the most suitable areas for red squirrel protection. By determining the cost of grey squirrel control this work can direct future resource allocation.

1.3 Agreed outputs

The output will take the form of an intermediate and final project report.
Objectives (I) and (II) will be delivered by 1 September 2017 followed by a meeting with FES to discuss preliminary findings and to obtain feedback. Objectives (III) and (IV) will be delivered by 31 March 2018.

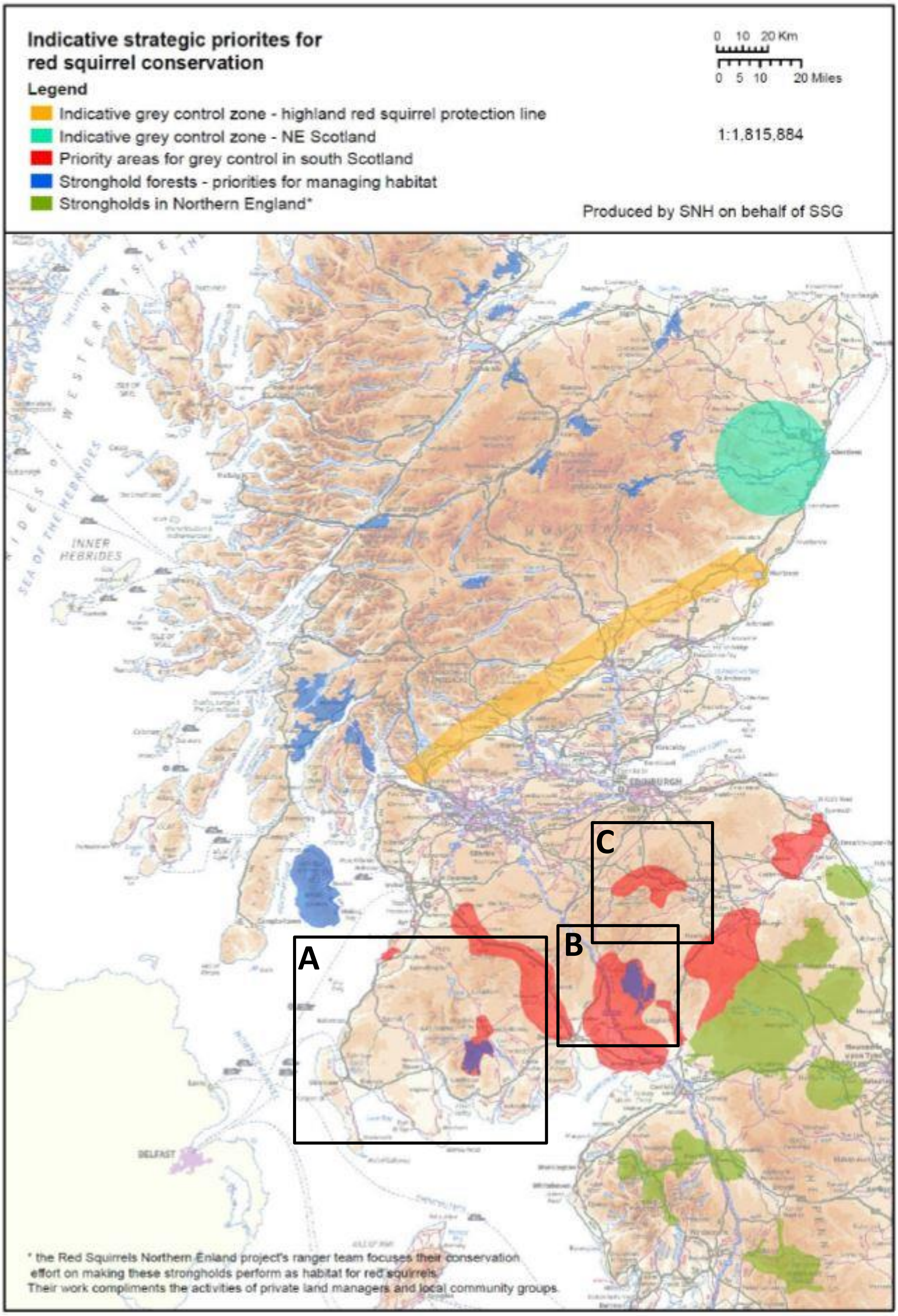
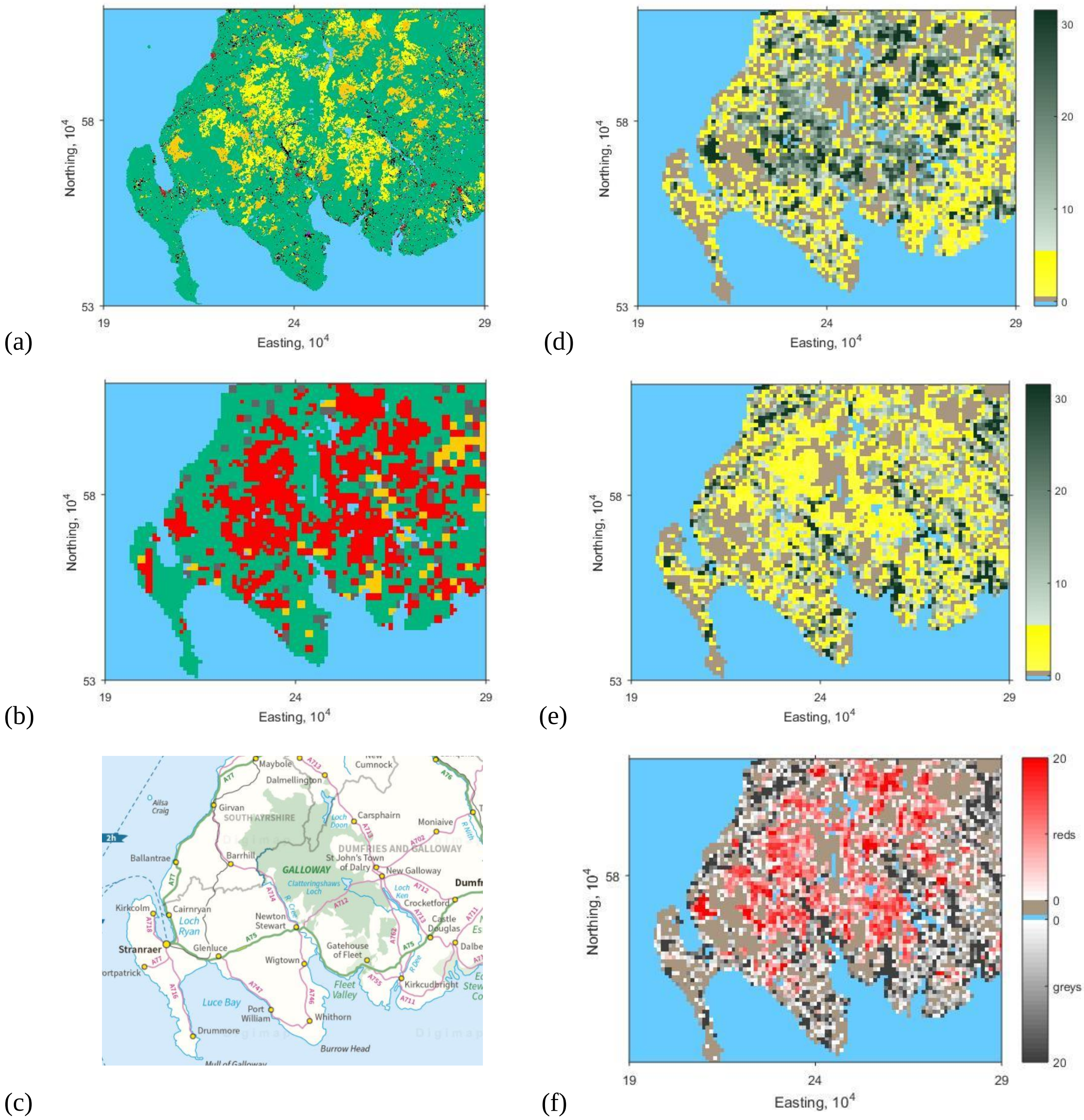


Figure 1.1: A map highlighting key areas for red squirrel protection in Scotland and northern England (SNH 2015). Priority areas for conservation of red squirrels in southern Scotland are shown in red (and blue), similar areas in England are shown in green. The three regions studied here are (A) Dumfries and Galloway, (B) Eskdalemuir and (C) Peebles.

2. Mathematical Model

The modelling framework represents the abundance of red and grey squirrels and squirrelpox infection in 1 km by 1 km grid squares. Grid squares are linked by dispersal (since individual squirrels can disperse from one grid square to the adjacent squares), and the potential squirrel density in each grid square is based on land cover data. This approximates the real heterogeneous habitat of Scotland. We initially focus on the Dumfries and Galloway region of Scotland (Fig. 2.1).



(a) (b) (c) (d) (e) (f)

Figure 2.1: (a) The key habitat types considered in the model for this region (Sitka spruce – yellow, conifer – orange, mixed conifer – purple, broadleaf – black, urban – red). (b) The initial distribution of red and grey squirrels used in the model (red squirrels – red, grey squirrels – grey, both red and grey squirrels – orange). (c) An OS map of the region considered in the model simulations (© Digimaps). The carrying capacity (/km^2) based on landsurface data and estimates in Table 2.1 for (d) red squirrels and (e) grey squirrels. In (f) the value of $K_R - c_G K_G$ for parameter values in Table 2.1 is plotted indicating regions where red squirrels have an advantage (red) and where grey squirrels have an advantage (grey).

2.1. Determining Potential Density

Using GRASS GIS software (https://grass.osgeo.org/) we used National Forestry Inventory Scotland 2014 and Forest Estate Scotland 2014 digital land cover datasets (supplied by Forestry Commission Scotland) to extract coniferous, broadleaf, shrub and Sitka spruce habitat types and used the Scottish Natural Heritage 2007 dataset to extract urban habitat types at a 25 m by 25 m scale (Fig. 2.1a). This data was combined with estimates of squirrel densities in different habitat types (Table 2.1) and summed to obtain the carrying capacity of red (K_R) and grey (K_G) squirrels at a 1km x 1km patch level that could be supported in the landscape (see Figs 2.1d,e). A key assumption in this study is that the potential density for greys squirrels in conifer is lower than the potential density of red squirrels. Evidence for this comes from field sites in which grey squirrels do not invade and replace red squirrels in conifer dominated forests even though they have been in adjacent mixed/broadleaf habitat for some time (e.g. at Craigvinean forest, Perthshire, Bryce 2000, Bryce et al. 2002). This scale and approach have been used successfully to model the UK squirrel system in previous studies (Jones et al. 2017; Macpherson et al 2016b; White et al. 2015, 2016, 2017).

Habitat Type	Default (density /ha)	
	Red	Grey
Broadleaf	0.81	1.96
Conifer	0.5	0.16
Mixed Conifer	0.5	0.53
Sitka	0.2	0.02
Shrub	0.06	0.06
Urban/suburban	0.14	0.26

Table 2.1: The default parameters used to generate the potential density for red and grey squirrels at the 1km by 1km patch level in the model simulations (values taken from White et al. 2017). Note, we assume that red squirrels can reach higher densities than grey squirrels in pure conifer and Sitka spruce habitats.

2.2. Model Framework

We base our model framework on previous mathematical models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches (Tompkins et al. 2003) to develop a spatial, stochastic model, (Jones et al 2017; Macpherson et al 2016b; White et al. 2014, 2015, 2016, 2017). Here, the deterministic underpinning allows the key population dynamical processes to be understood. In addition, the stochastic adaptation provides essential realism when squirrel numbers become low and therefore provides a better representation of population extinction and the fade-out of infection. The underlying deterministic system which represents the dynamics of susceptible and infected reds (S_R, I_R) and susceptible, infected and immune greys (S_G, I_G, R_G) is as follows (see the Appendix for an explanation of the terms in the model):

$$\frac{dS_G}{dt} = A_G(t) - bS_G - \beta S_G(I_G + I_R)$$
$$\frac{dI_G}{dt} = \beta S_G(I_G + I_R) - bI_G - \gamma I_G$$
$$\frac{dR_G}{dt} = \gamma I_G - bR_G \qquad (2.1)$$
$$\frac{dS_R}{dt} = A_R(t) - bS_R - \beta S_R(I_G + I_R)$$
$$\frac{dI_R}{dt} = \beta S_R(I_G + I_R) - bI_R - \alpha I_R$$

where

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

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 squirrel populations. In Tompkins et al. (2003) the two species have the same rate of adult mortality (b=0.9: Barkalow et al. 1970) but different rates of maximum reproduction (a_R=3, a_G=3.4 adapted from Tompkins et al. 2003 to account for seasonality). The competitive effect of grey squirrels on red squirrels is denoted by c_G=1.65, whilst that of red squirrels on grey squirrels is denoted by c_R=0.61 (Bryce et al. 2001). Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient β=1.1. Infected red squirrels die due to the disease at rate α=26 and infected greys recover at rate γ=13 (Tompkins et al. 2003). 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 (as shown in Fig. 2.1 d & e). To generate the stochastic model, the rates in the deterministic model are converted to probabilities of events that account for changes in individual patch level abundance (Renshaw 1991). The relationship between the terms in Equation (2.1) and (2.2), the different events (birth, death, infection, dispersal, etc), the change on population abundance and the probability of each event in the stochastic model are given in Table 2.2.

2.3. Initial Conditions

The model was initialled with observed data for the presence of red and grey squirrels between 2012-2014 (using the National Biodiversity Network's (NBN) Gateway, http://data.nbn.org.uk/) and by using a model spin-up to allow red squirrels to expand into available habitat prior to the initialisation of the model (Fig. 2.1b). 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. In model runs that included the impact of squirrelpox, infected grey squirrels were introduced each year in grid cells that represent regions in which SQPV seropositive grey squirrels have been reported (at locations that are approximately Dalbeattie, New Galloway and Maybole).

Note that an indication of the long-term distribution of red and grey squirrels can be approximated from an examination of the carrying capacity data only. In Figure 2.1(f) we calculate $K_R - c_G K_G$ for each grid square and this indicates regions in which red or grey squirrels are likely to dominate in the absence of grey control. In particular red squirrels are likely to be vulnerable in the following regions: around Loch Ken, the Glenkens, Gatehouse of Fleet (and north along the water of Fleet), Newton Stewart to Glentrool (along the river Cree), Pinwherry to Glentrool (along the river Duisk), and from Glentrool to Loch Trool to Loch Neldricken. It is also worth noting that an assumption of the model in this study is that red squirrels have a competitive advantage over grey squirrels in large areas of the Galloway forest park where the habitat is dominated by Sitka spruce or conifer species.

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

Table 2.2: The stochastic model within each 1km by 1km grid square indicating the probability of different events. In particular the parameters representing control and dispersal were fitted with observed data on the Island of Anglesey (Jones et al. 2017). Here $R = \sum[rates]$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (6 months from the start of April to the end of September) and are set to zero otherwise. Transmission can occur from infected squirrels within the focal grid square and also from the 8 neighbouring grid cells due to daily movement within a core range of radius, $\theta = 0.15$km. The 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). 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 gridcell per day). Further details of the model framework and the calculation of parameter values can be found in Jones et al. (2017).

3. Baseline results without grey squirrel control in Dumfries and Galloway

We initially undertook simulations of the model without grey control. This allowed an assessment of the potential spatial expansion of grey squirrels in the absence of control (and what would happen if the grey control programme was ended). We undertook simulations for two scenarios: one in the absence of squirrelpox, and one with squirrelpox introduced at the eastern edge of the study area in which SQPV seropositive grey squirrels have been reported.

3.1. Grey expansion in the absence of squirrelpox (with no grey squirrel control)

Figure 3.1 shows the model results for default parameters (Table 2.1) in the absence of squirrelpox. Results at time zero indicate the initial conditions used in the study.

Figure 3.1: Model simulations using default parameter values in the absence of grey squirrel control and squirrelpox. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations) for different model years. Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha).

The figure indicates that grey squirrels can spread around the northern and southern coastal habitats and also expand inland at from Gatehouse of Fleet, along Loch Ken and at Newton Stewart in the south and along the river Stinchar and river Duisk in the north.

A key result is that red squirrels can persist and grey squirrels are not predicted to invade in the large Sitka spruce and conifer dominated forests at Glentrool, east of the Merrick (west Glenkens), in the Fleet basin and from Loch Doon (Carsphairn forest) to Loch Urr (Dalmacallam forest). In the Kirroughtree forest, the east of Loch Ken and west of Newton Stewart red and grey squirrels are predicted to cooccur. In these regions grey squirrels can thrive along broadleaf dominated river valleys and disperse into surrounding areas. They do not exclude red squirrels from the neighbouring conifer dominated forests, but the constant dispersal of greys from broadleaf source populations leads to large regions where red squirrels may be at risk.

3.2. Grey expansion with squirrelpox (with no grey squirrel control)

Figure 3.2 shows the model results for the occupancy of red and grey squirrels for default parameters when squirrelpox is included and Figure 3.3 shows the associated spread of squirrelpox. It does not spread extensively through Dumfries and Galloway (Fig. 3.3). In particular, squirrelpox does not spread through the grey squirrel populations that dominate along the southern and northern coastal regions, and importantly it does not spread through the established red squirrel populations. This is supported by field evidence (SSRS Pers. Comm.), since squirrelpox was not reported in these regions when testing for squirrelpox was undertaken (from 2016 squirrelpox testing was ceased to the south of Glasgow). As predicted by previous studies (Lurz et al. 2015; Jones et al. 2016; White et al. 2017) squirrelpox fails to spread in low density squirrel population. In poor, low-density habitats the infection appears to burn out in the absence of sufficient squirrel numbers. For this reason squirrelpox does not play a key role in the potential invasion and replacement dynamics in this region and so the model results with and without the inclusion of squirrelpox look similar.

Figure 3.2: Model simulations using default parameter values with squirrelpox in the absence of grey squirrel control. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha).

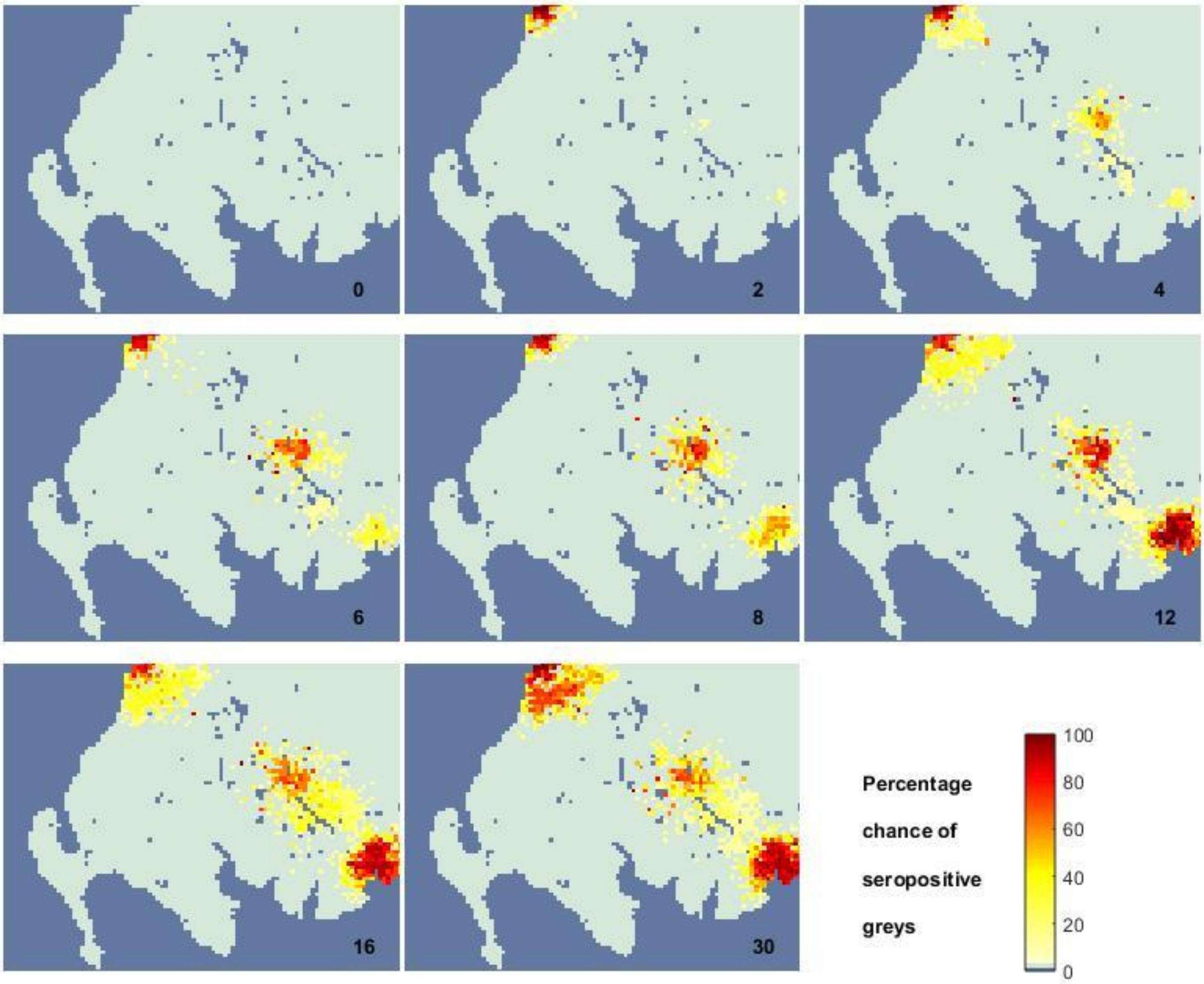


Figure 3.3: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 3.2.

4. Results with grey control in Dumfries and Galloway

The results in the absence of control were used to isolate and target key regions in which control should be included in an attempt to prevent expansion of grey squirrels. The control regions were determined by studying the grey squirrel expansion paths in Figure 3.2 and by undertaking model simulations with a range of control regions to determine their best size and location (results not shown). These regions also correspond to the locations where grey squirrels have a competitive advantage over reds squirrels as indicated in Figure 2.1 (f). The control regions are shown in Figure 4.1 and they correspond to habitats that are dominated by broadleaf forests or broadleaf corridors that run along river valleys. We chose to undertake the model simulations that include control for the default parameter setting (Table 2.1) and in which squirrelpox is included.

Figure 4.1: The regions in which control is applied in the model superimposed over the map that shows the outcome of competition (K_R - $c_G K_G$) between red and grey squirrels based on their carrying capacity. These control regions correspond to broadleaf corridors. Clockwise from the top right are labelled: Glenkens, Loch Ken, Gatehouse of Fleet, Newton Stewart, Glentrool, Barrhill (see also Table 4.1).

To understand the results that follow, it is important to understand the method in which grey squirrel control is implemented in the model. Control is only applied within the regions outlined in Figure 4.1. In specified 1km by 1km grid cells within these regions control is applied with a trap intensity of T_D traps per day. Control can occur during the breeding season only (6 months from 1 April – 30 September, 183 days). Data from a grey squirrel control demonstration region in Tayside indicated that the majority of control occurred during this period (see Appendix, Figure A1). The control period is split into three 61 day (2 month) control periods. At the start of the first control period trapping is applied in grid squares in which grey squirrels are present and in grid squares in a 2km buffer zone around these grid squares. Control is maintained at this level for 61 days. The same procedure is applied to determine the grid cells in which greys squirrels are present (and the buffer zone) at the start of the second and third control period. This way trapping can react to grey squirrel dispersal and observations of grey squirrels throughout the trapping period. We run the model for three levels of trap intensity (T_D = 0.1 – low; 0.25 – medium; 0.5 – high). For clarity, low intensity of trapping equates to a maximum of 0.1x183 = 18 trap days per year in a 1km by 1km gridsquare (and equates to a maximum of 46 and 92 trap days per year per gridsquare for medium and high intensity trapping respectively).

4.1. Low intensity trapping ($T_D = 0.1$).

Low intensity trapping fails to prevent the expansion of grey squirrels within the control regions (Fig. 4.2). Here the density of grey squirrels in the trap regions increases over time and the trap regions either become dominated by grey squirrels, or lead to both species being present if some local habitat areas are favourable to reds (with grey squirrels dominating in broadleaf habitats and red squirrels persisting in neighbouring coniferous habitat).

Figure 4.2: Model simulations using default parameter values with squirrelpox when grey squirrel control is applied with a low trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 4.1.

4.2. Medium intensity trapping (T_D = 0.25).

A medium intensity level of control reduces the level of grey expansion within the majority of the control regions and can prevent grey squirrels from establishing in some control regions (Fig. 4.3. This level of trapping would provide protection for red squirrels from grey squirrel expansion into the Galloway forest region.

Figure 4.3: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a medium trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 4.1.

4.3. High intensity trapping (T_D = 0.5).

High intensity trapping prevented grey squirrels from expanding within all control regions (Fig. 4.4). This level of control would provide protection for red squirrels in the Galloway forest region and allow red squirrel recovery and grey exclusion in the control areas. Thus, red squirrels are likely to be visible in some key populated regions, such as Gatehouse of Fleet and Newton Stewart and around tourist sites at Loch Ken and Glentrool.

Figure 4.4: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a high trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 4.1.

4.4. A comparison on trap effort for different trapping intensity

A comparison of the red and grey squirrel occupancy at the end of the model simulations is shown in Figure 4.5. The control effort needed (in trap days per year) in the three trap-intensity scenarios (low, medium and high) is shown in Table 4.1. As indicated above low-intensity trapping did not prevent grey squirrel dispersal across suitable habitat in the region. This finding may be important with respect to grey squirrel control carried out by local volunteers and stresses the importance of consistent trap effort to protect red squirrels.

Medium level grey squirrel control did protect the Galloway Forest and high intensity control prevented grey squirrel expansion and retained red squirrels in populated areas for people to see and experience in their gardens. Of note is that the highest levels of control needed (high-intensity scenario) were the control regions at Newton Stewart, Gatehouse of Fleet and Barrhill. It is noteworthy that the trap effort at Glenkens was higher in the medium compared to the high-intensity scenario. This was due to trapping effort around Loch Ken, which in the high-intensity scenario reduced grey squirrel dispersal to Glenkens. The latter also illustrates that trapping in one square has impacts on grey squirrel abundance in adjacent squares.

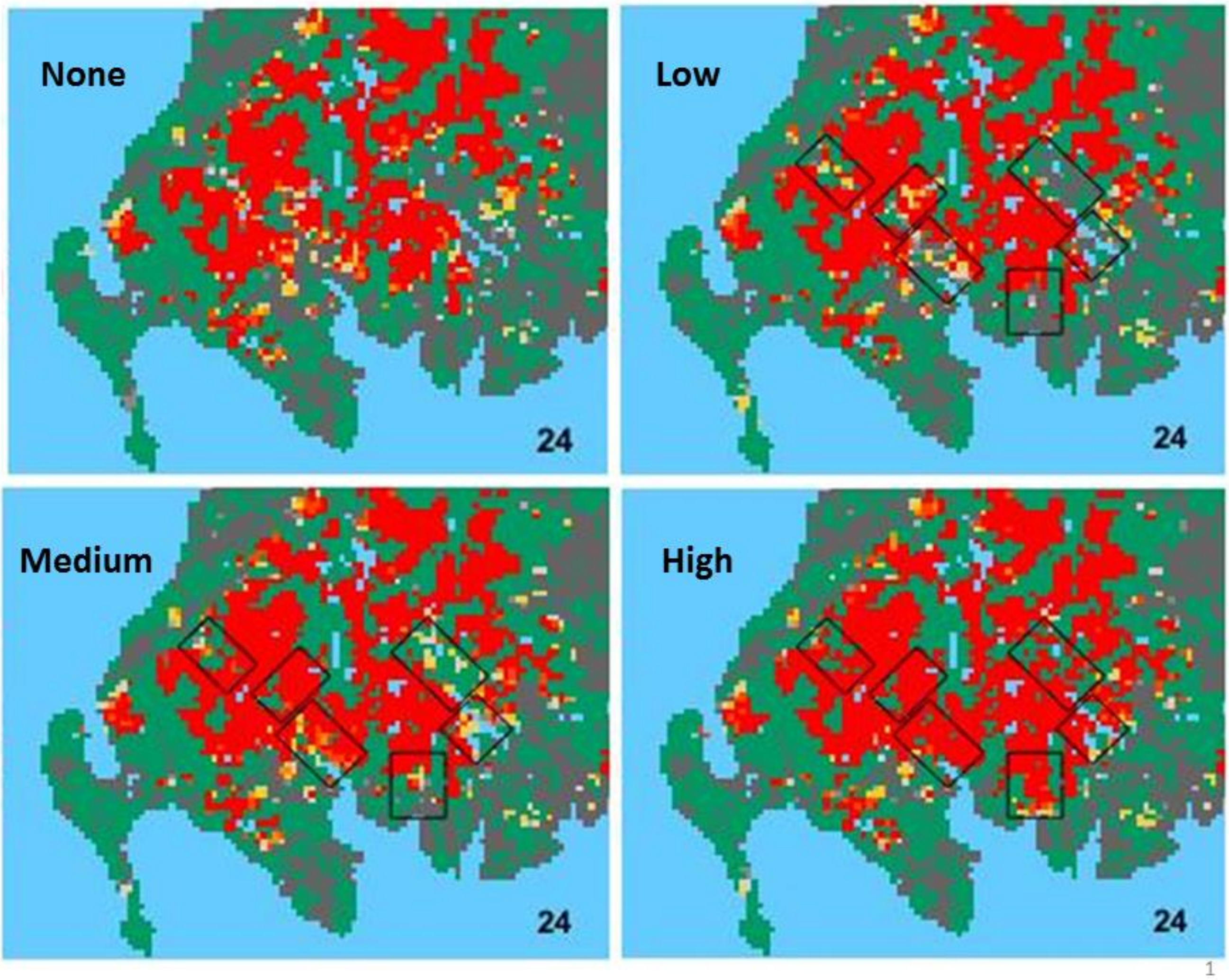


Figure 4.5: A comparison of the red and grey squirrel occupancy after 24 simulated years for different control intensities for Dumfries and Galloway.

Trapping Region	Trap days per year		
	Low	Medium	High
Glenkens	1884	4619	4324
Loch Ken	1208	2987	5096
Gatehouse of Fleet	1591	3885	6495
Newton Stewart	2031	4718	6998
Glentrool	1367	1537	2357
Barrhill	1456	3285	5529

Table 4.1: A comparison of the amount of trapping applied under the different trap intensity levels (in trap days per year per region, with regions shown in Figure 4.1).

5. The impact of pine marten on the level of grey squirrel control in Dumfries and Galloway.

Following the publication of the findings by Sheehy and Lawton (2014) who investigated the decline of grey squirrels in the Irish Midlands, much has been speculated on the potential suppressant effect of pine martens on grey squirrels. Often, and without any attempt to question the underlying causes, the findings have been generalised and the pine marten has been lauded as a natural solution to the grey squirrel problem (e.g. Monbiot 2015). Whilst pine martens are clearly implicated in the dramatic decline of grey squirrels in Ireland, it is important to understand the factors and underlying mechanisms that led to grey squirrel populations crashing over an area of 9000 km^2, and to determine how representative the Irish situation is.

Macpherson et al. (2016a) argue that studies in the UK and from elsewhere indicate that marten-squirrel interactions are complex. Direct predation is perhaps the obvious interaction between pine martens and grey squirrels, but less direct interactions may also occur and create what has been termed a "landscape of fear" (Macpherson et al. 2016a; see also Laundré et al. 2001). Small mammals (e.g. field voles which are a key prey species in Scotland) are the most important food for pine martens, followed by birds, which comprise a large proportion of their diet in spring. Other prey items include eggs, insects, fruit, nuts, fungi, amphibians, lizards as well as leftovers from bird tables and bins (Balharry et al. 2008; Macpherson et al. 2016a). They will predate on red squirrels and Halliwell (1997) observed that in established pine marten areas in Scotland, red squirrel densities were lower than in equivalent habitats where they were absent.

On first principles, key factors determining the likely interactions and impacts of pine martens on grey and red squirrels are likely to be:

- local abundance of pine martens (influenced by habitat, den availability etc.)
- availability and abundance of non-squirrel prey throughout the year (lack of other prey may lead to switching to squirrels including reds)
- reductions in grey squirrel abundance may additionally alter squirrelpox virus impacts in medium to high density squirrel habitats by reducing both transmission probability and increasing the chance of disease burn out as a result of lower densities of susceptibles.

Here we undertake a proof of principle, preliminary modelling investigation on the potential role of pine marten predation on reducing grey squirrel density (see section 1.3 Objectives).

5.1 Modelling pine marten predation on squirrels

We included pine marten predation by assuming there is a constant pine marten density in all 1km grid cells that are contained in the larger 10km by 10km regions in which pine marten have been observed between 2010-2014 (Fig. 5.1 constructed using Croose et al. 2014 and the NBN Gateway). The pine marten density is taken to be 0.08 per km^2, a value that is similar to the average density in the Sottish Borders where pine marten density is low or recovering and which is a similar to the level expected in Dumfries and Galloway (Birks, Sheehy and Lambin pers. comm.). The predation rate is set by considering a simplified model of grey squirrel dynamics that represents birth, death and pine marten predation as follows:

$$\frac{dH_G}{dt} = A_G(t)H_G(1-q_G H_G) - bH_G - ePH_G \qquad (5.1)$$

We select the predation coefficient e such that grey squirrels are excluded (in regions with a grey squirrel carrying capacity density of 30 per km^2) when the pine marten density is 0.36 per km^2 (as pine marten have been linked to the absence of grey squirrels in the Loch Lomond region where the average density is 0.36 per km^2 Sheehy and Lambin (pers. comm.)). This sets the predation coefficient $e = 2.2$ for grey squirrels (and we assume that the value for red squirrel is 20% of the value for grey squirrels based on red squirrels forming 2.5% and grey squirrels 15% of pine marten diet (Sheehy and Lawton 2014)). Using this value for the predation coefficient a representation of pine marten predation is added to the full red/grey/squirrelpox model (Table 2.2) to assess how predation may interact with grey squirrel control in efforts to protect red squirrels in Dumfries and Galloway.

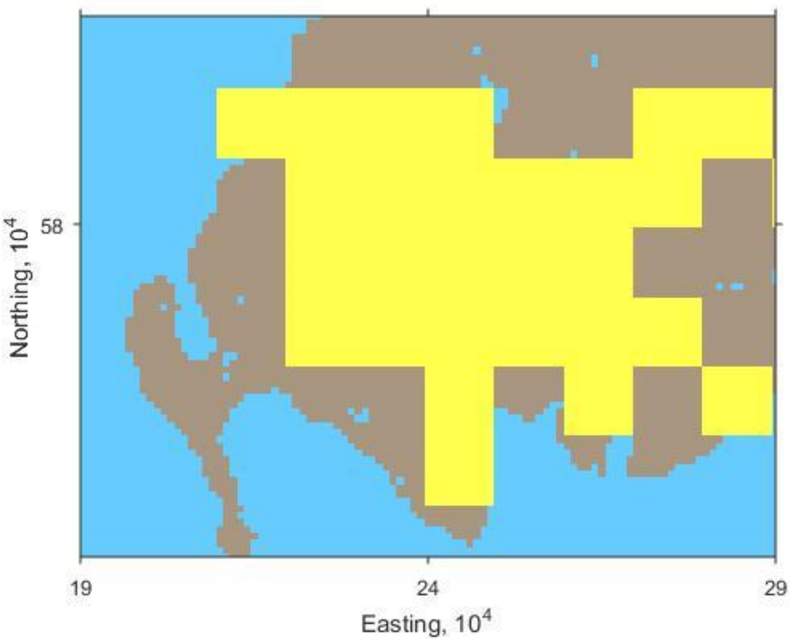


Figure 5.1: The 10km by 10km regions where pine marten have been observed between 2010-2014 in the Dumfries and Galloway study region. The data is taken from Croose et al. (2014) and the NBN gateway.

5.2 Grey squirrel control and pine marten interactions

Figure 5.2 shows the results for the different control levels with and without the inclusion of predation by pine marten. The level of control required under the different control scenarios is shown in Table 5.1 and indicates that predation by pine marten has the effect of reducing the level of grey control needed. Recall that in Dumfries and Galloway pine marten are at low density and would not be predicted to exclude grey squirrels in the absence of control! Nevertheless, pine marten still have utility in reducing the effort required to control grey squirrels. There is only a small reduction in trapping levels in the presence of pine marten at low intensity trapping. This is because this level of trapping is insufficient to prevent the establishment of grey squirrels. At medium and high levels of trap intensity (where trap levels restrict grey establishment) pine marten reduce the grey control effort required in all regions by an average of approximately 30% (but by up to 70% under the high scenario in Glentrool).

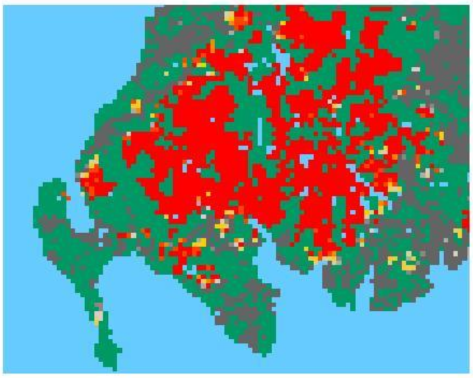
Trapping	Trap days per year					
Region	Low	Low+PM	Medium	Med+PM	High	High+PM
Glenkens	1884	1874	4619	3140	4324	2522
Loch Ken	1208	1207	2987	2608	5096	4487
Gatehouse of Fleet	1591	1580	3885	3474	6495	6003
Newton Stewart	2031	1997	4718	3328	6998	4880
Glentrool	1367	724	1537	620	2357	647
Barrhill	1456	1320	3285	2751	5529	4382

Table 5.1: A comparison of the amount of trapping applied under the different trap intensity levels (in trap days per year per region, with regions shown in Figure 4.1) when pine marten (PM) are included in the model with a density of 0.08 per km^2 in regions shown in Fig. 5.1.

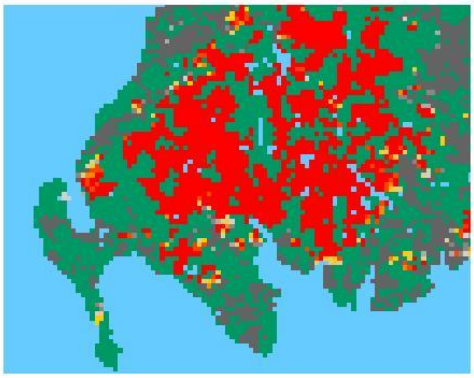
Whilst these are very preliminary model results, it is interesting to note that despite the model allowing pine martens to predate red squirrels as well as grey squirrels, red squirrel numbers are higher in the low and medium control intensity scenarios in the presence of pine marten (Table 5.2, Fig. 5.2). This is most likely the result of a balance between some loss due to pine marten predation and a gain as a result of reduced competition with grey squirrels. Note that in the high-intensity control scenario most greys will be removed by control and pine martens slightly reduce the red squirrel population. Whilst pine martens can reduce red squirrel populations (see Halliwell 1997), current anecdotal evidence from a pine marten survey in Galloway forest (Lurz, P. pers. obs; Fig. 5.3) and data from scat analyses from the region (Ventress & Hayward 2017) both indicate that current levels of red squirrel predation are very low.

	Low	Low+PM	Medium	Med+PM	High	High+PM
Total trap days	9537	8702	21031	15921	30799	22921
Increase in Red Squirrel Abundance	1725	2094	3036	3154	4308	4029

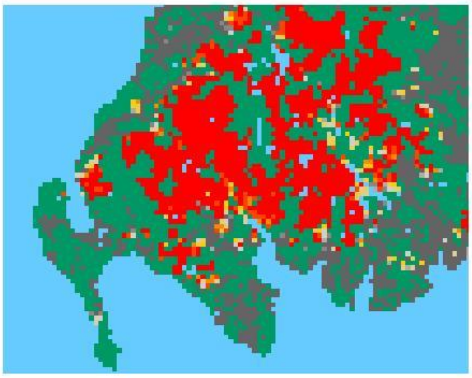
Table 5.2: A comparison of the total trap days per year and the increase in the abundance of red squirrels (compared to the absence of trapping) with and without pine marten (PM).



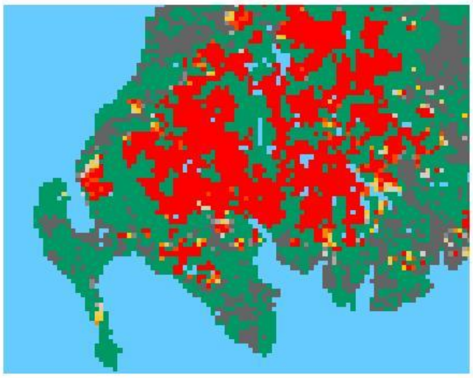
(a)



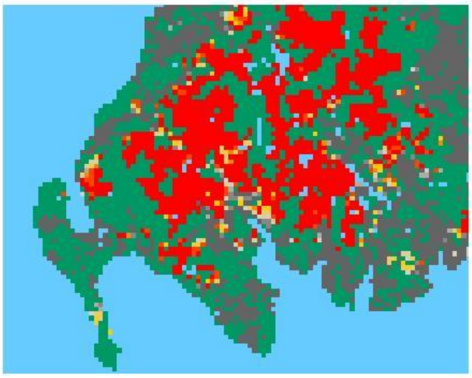
(b)



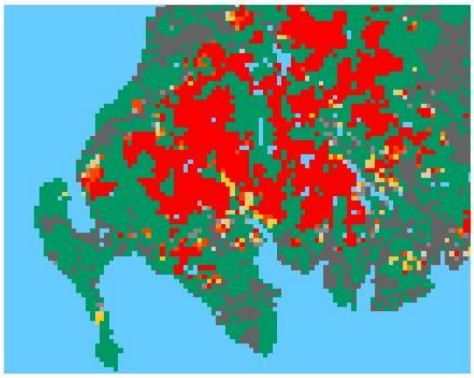
(c)



(d)



(e)



(f)

Figure 5.2: Model simulations after 24 model years under default parameter values with squirrelpox when grey squirrel control is applied with (a) high intensity, (b) high intensity with pine marten, (c) medium intensity, (d) medium intensity with pine marten, (e) low intensity and (f) low intensity with pine marten. The colour scheme is the same as in Fig. 3.1.

5.3 Summary of the Impact of Pine Marten on Grey Squirrel Control

This preliminary investigation highlights the potential of pine marten predation to reduce the level of grey squirrel trapping required to protect red squirrels in the Galloway forest park. We should stress that the model assumes preferential predation of grey squirrels with reduced (at 20% of the level) predation on red squirrels. Macpherson et al. (2016a) argue that pine marten-squirrel interactions are complex and alternative interactions beyond predation are not considered in the model. Furthermore, the impact of pine marten predation on grey squirrels has not as yet been rigorously studied. Nevertheless, under our assumptions the model does show that pine marten predation could reduce the effort required to control grey abundance without having a negative impact of red squirrel abundance.

Figure 5.3a Nest box for pine martens in Galloway Forest

Figure 5.3b One of two cubs present in the box

Figure 5.3c All prey remains found in the box and around the nestbox tree. Prey items are dominated by birds with a handful of small mammals and amphibians. No red squirrel remains were found at this study site.

6. Eskdalemuir and surrounding regions

We now assess the level of grey control required to protect red squirrels in Eskdalemuir forest and the surrounding region (Fig. 6.1 and see Fig. 1.1).

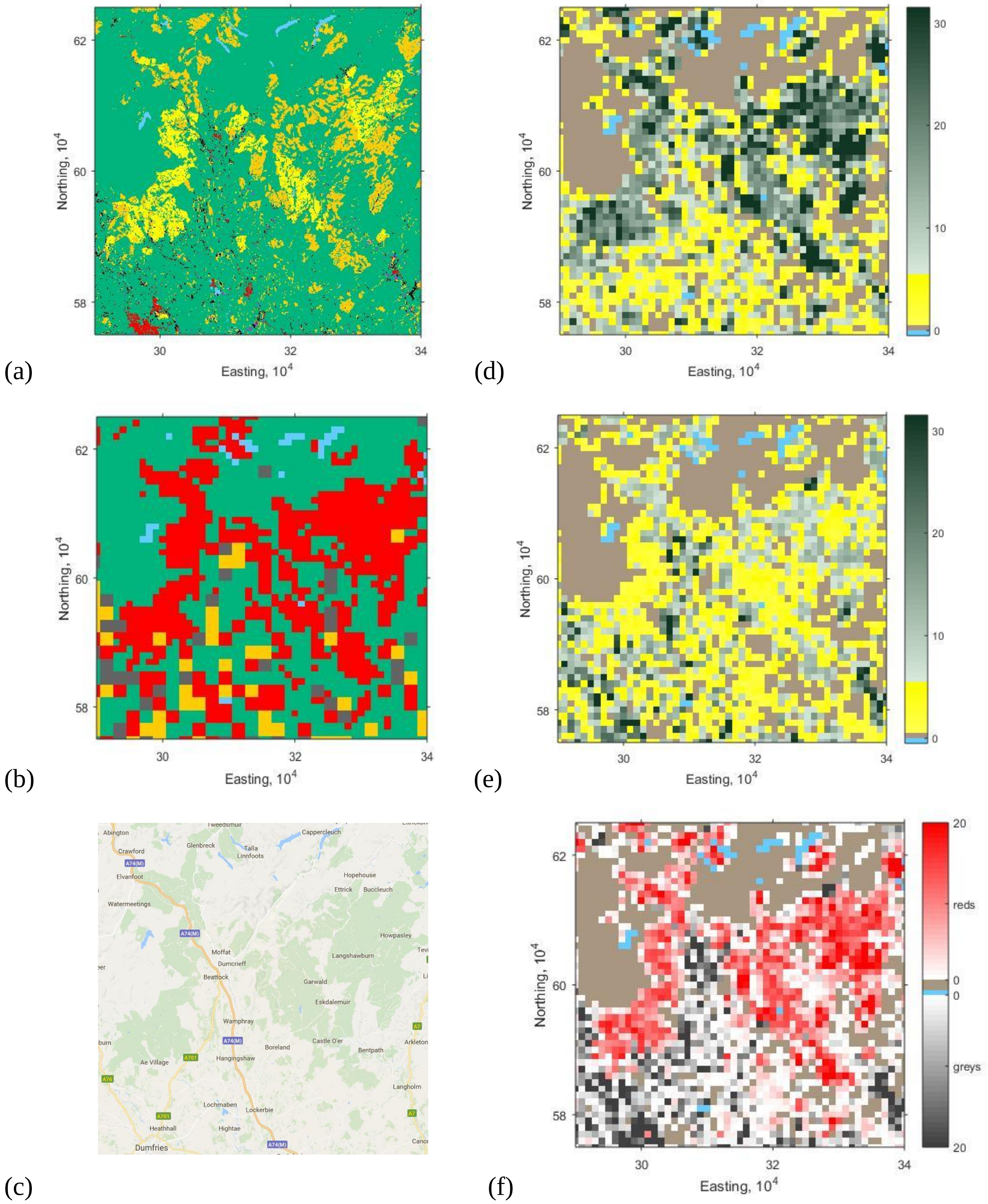


Figure 6.1: (a) The key habitat types considered in the model for this region (Sitka spruce – yellow, conifer – orange, mixed conifer – purple, broadleaf – black, urban – red). (b) The initial distribution of red and grey squirrels used in the model (red squirrels – red, grey squirrels – grey, both red and grey squirrels – orange). (c) An OS map of the region considered in the model simulations (© Digimaps). The carrying capacity (/km^2) based on landsurface data and estimates in Table 2.1 for (d) red squirrels and (e) grey squirrels. In (f) the value of $K_R - c_G K_G$ for parameter values in Table 2.1 is plotted indicating regions where red squirrels have an advantage (red) and where grey squirrels have an advantage (grey).

6.1 Baseline results without grey control in the Eskdalemuir test region

Figure 6.2 shows the model results for the occupancy of red and grey squirrels for default parameters when squirrelpox is included in the absence of grey squirrel control and Figure 6.3 shows the associated spread of squirrelpox. In the absence of grey control red squirrels can persist and dominate in large conifer plantations including Eskdalemuir, Craik, Castle O'er and Ae forests. Grey squirrels dominate and reds are excluded along the river Annan and Nith valley, which includes many populated areas (Fig. 6.2). Squirrelpox remains endemic in the south east of the study region (near Canonbie) but does not spread northwards to any great extent (Fig. 6.3).

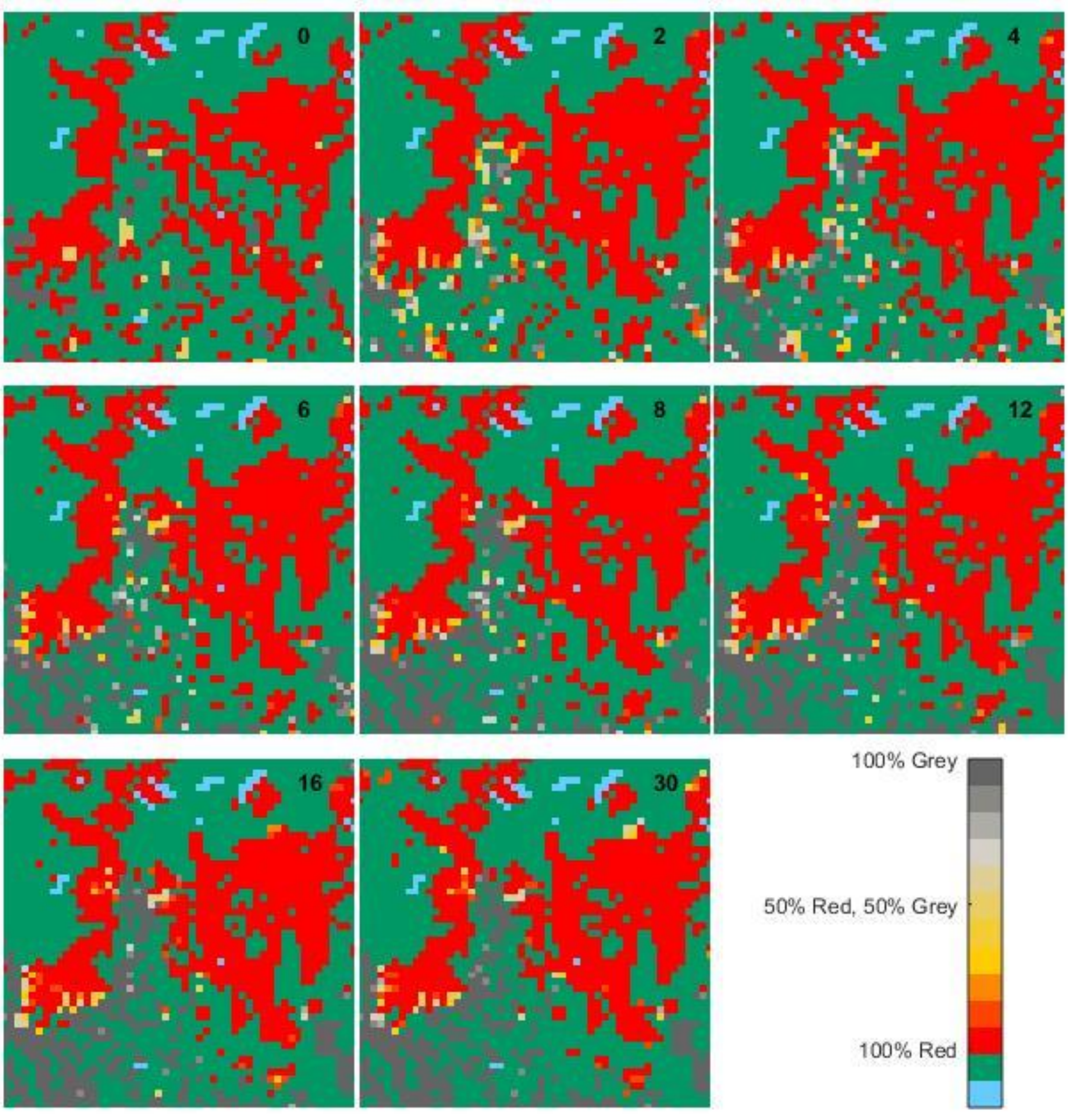


Figure 6.2: Model simulations using default parameter values with squirrelpox in the absence of grey squirrel control. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha).

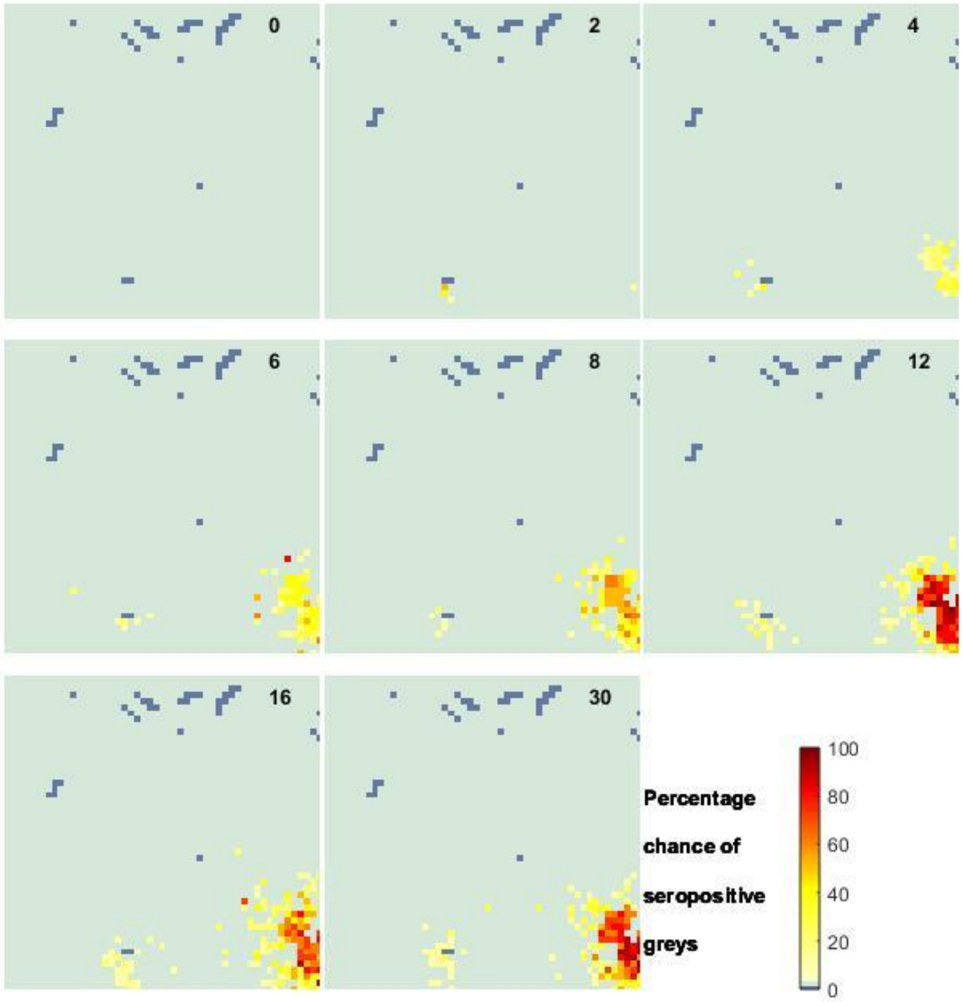


Figure 6.3: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 6.2. Squirrelpox was introduced in 1km by 1km grid squares along the southern edge of the study area in regions which represent Canonbie and south of Locherbie.

6.2 Results with grey control in the Eskdalemuir stronghold

The control regions were determined by studying the grey squirrel expansion paths in Figure 6.2 and through consultation with SSRS to reflect the historical and ongoing control effort in this region. The control regions focus along the river Anna valley and are shown in figure 6.4.

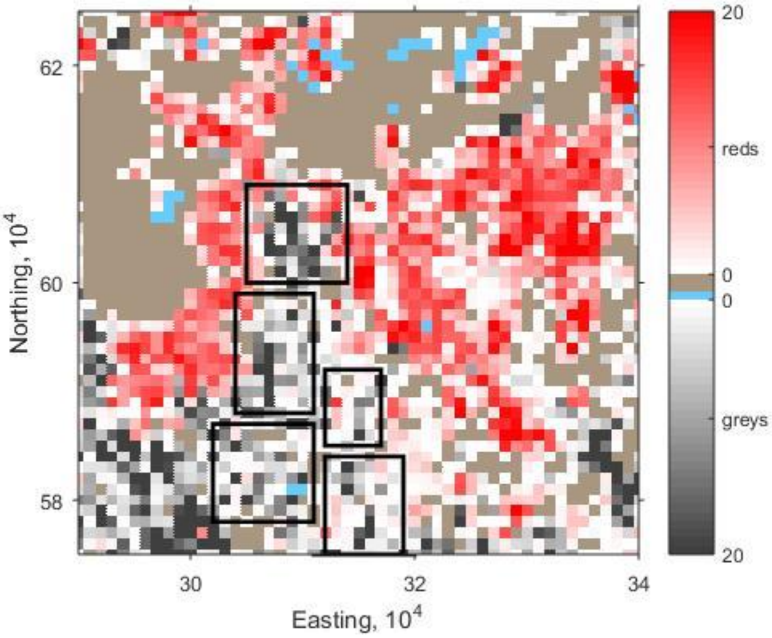


Figure 6.4: The regions in which control is applied in the model superimposed over the map that shows the outcome of competition (K_R - $c_G K_G$) between red and grey squirrels based on their carrying capacity. Control regions are labelled: Moffat (top), Johnstonebridge (middle left), Lochmaben (bottom left), Locherbie (bottom right) and Dryfe Water (middle right) (see also Table 6.1).

6.2.1 Low intensity trapping (T_D = 0.1).

Low intensity trapping fails to prevent the expansion of grey squirrels within the control regions (Fig. 6.5). Here the density of grey squirrels in the trap regions increases over time and the trap regions either become dominated by grey squirrels, or allow the co-occurrence of red and grey squirrels (with grey squirrels dominating in broadleaf habitats and red squirrels persisting in neighbouring coniferous habitat).

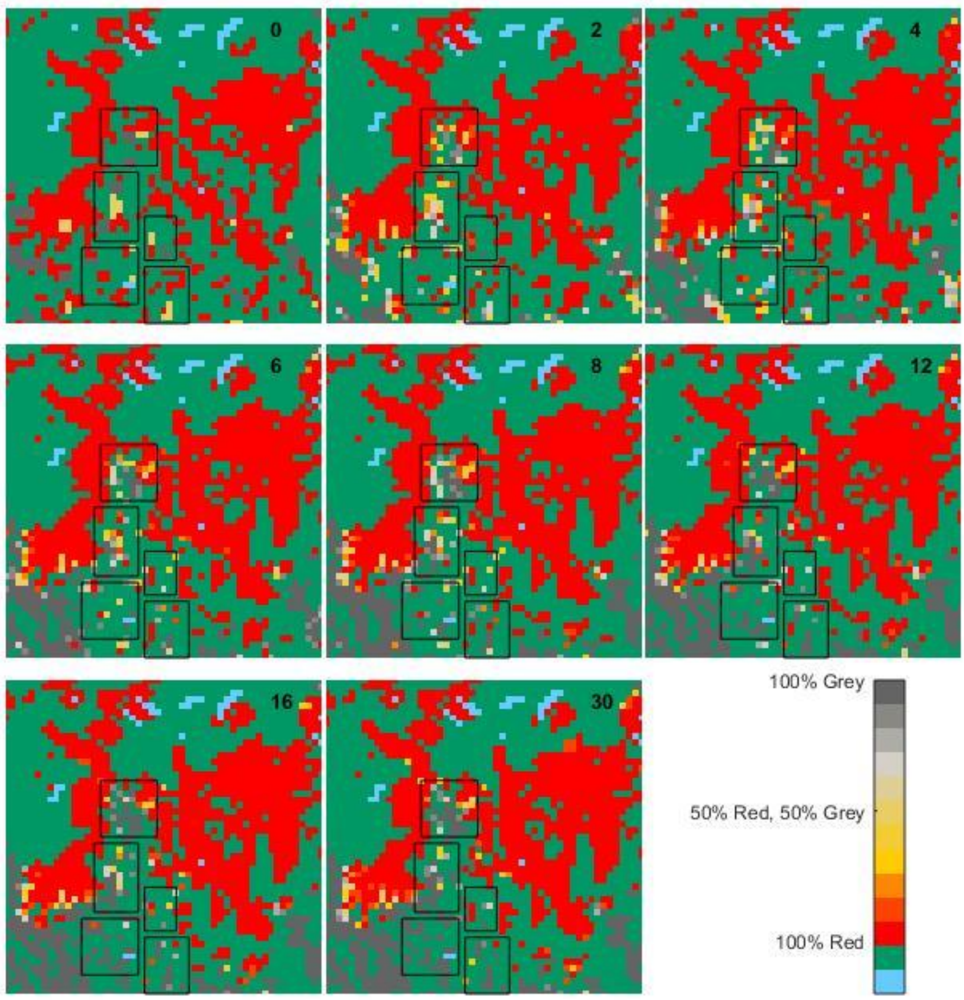


Figure 6.5: Model simulations using default parameter values with squirrelpox when grey squirrel control is applied with a low trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 6.1.

6.2.2 Medium intensity trapping (T_D = 0.25).

A medium intensity level of control reduces the level of grey presence within two of the control regions and can prevent grey squirrels from establishing in some control regions ((Lochmaben, Dryfe Water; Fig. 6.6).

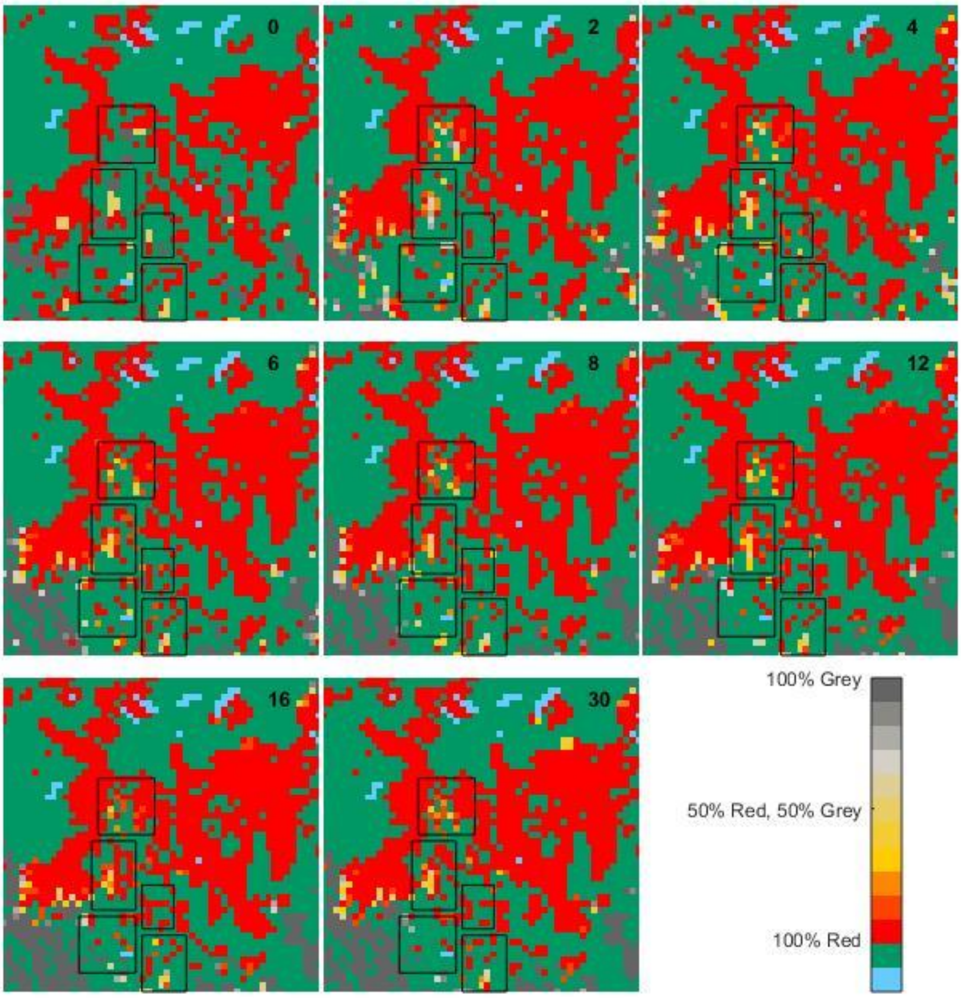


Figure 6.6: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a medium trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 6.1.

6.2.3 High intensity trapping (T_D = 0.5).

High intensity trapping prevented grey squirrels from expanding within all control regions (Fig. 6.7). This level of control would remove grey squirrels from the river Annan valley north of Locherbie and allow the re-establishment of red squirrels. The distribution of both squirrels under high intensity trapping would switch to a mostly red squirrel distribution with a small presence of grey squirrels in a handful of areas where habitat is highly suitable for grey squirrels just beyond the control zone (e.g. see final map Johnstonebridge square, bottom left corner).

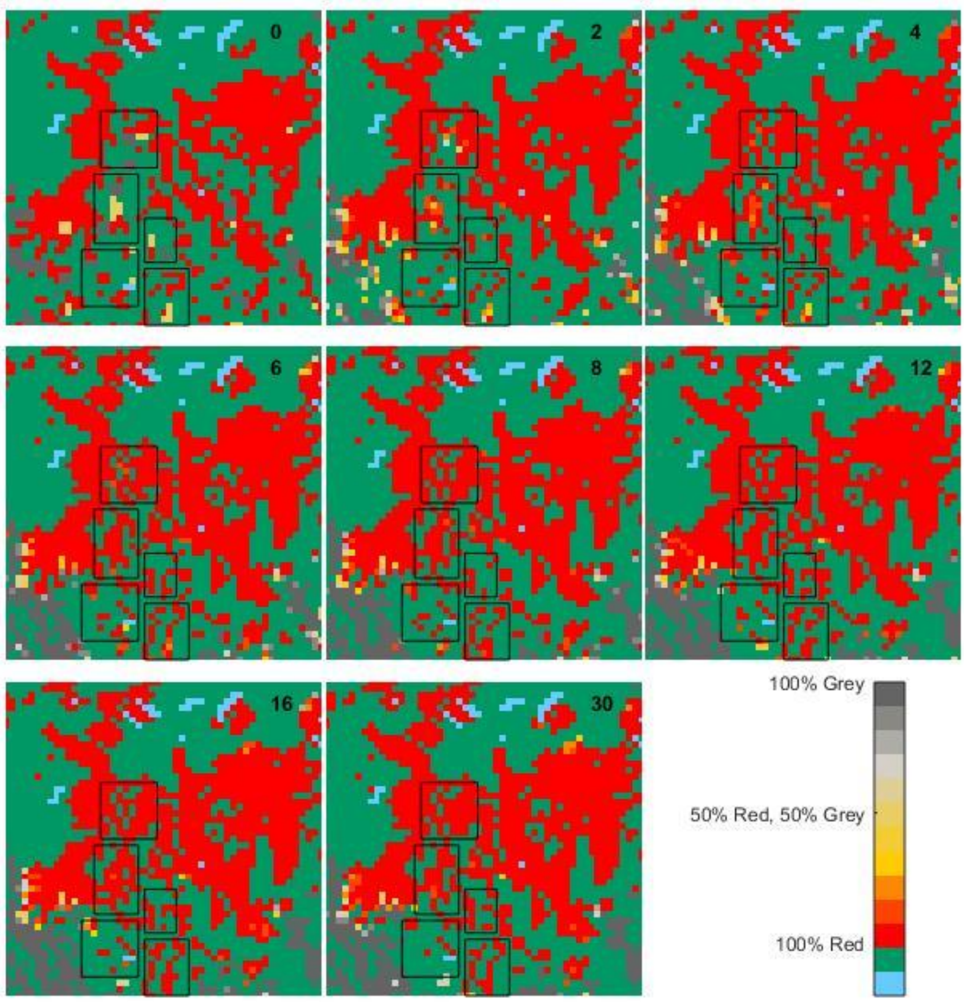


Figure 6.7: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a high trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 6.1.

6.3. A comparison of trap effort for different trapping intensity in Eskdalemuir

A comparison of the red and grey squirrel occupancy at the end of the model simulations is shown in Figure 6.8. Table 6.1 shows the control effort needed (in trap days per year) in the three trap-intensity scenarios (low, medium and high). As indicated above low intensity trapping did not prevent grey squirrel dispersal across suitable habitat in the region. Note, in the high intensity scenario, relatively small levels of control are required in the long-term around Moffat and along the Dryfe water as efforts in other control regions can reduce or even prevent the dispersal of greys squirrels to these regions. This highlights how the river Annan corridor is a suitable region for grey control since once cleared, grey squirrel expansion can be focussed on the southern region around Lochmaben and Locherbie. Also, trapping at a high intensity that removes grey squirrels from the northern region of the river Annan valley results in a significant increase in red squirrels for a relatively modest increase in trap effort (see difference in effort for medium and high; Table 6.2).

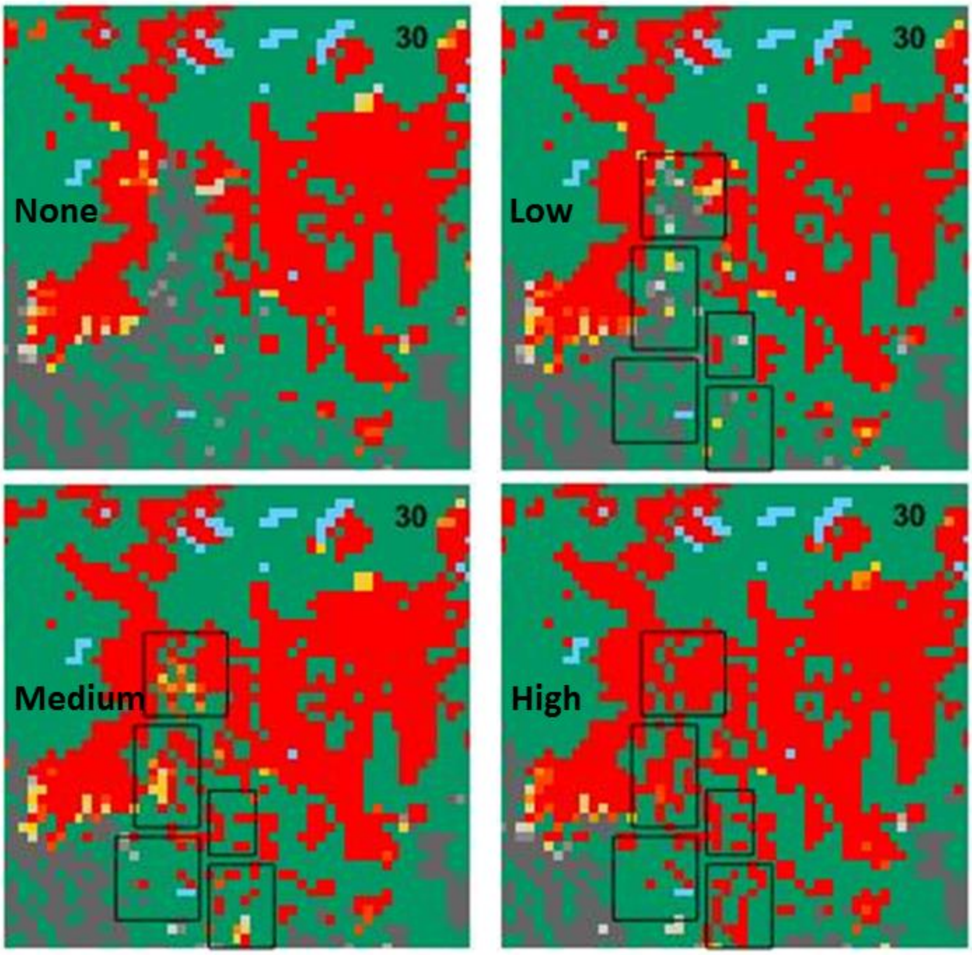


Figure 6.8: A comparison of the red and grey squirrel occupancy after 30 simulated years for different control intensities for Eskdalemuir and the surrounding areas.

Trapping	Trap days per year		
Region	Low	Medium	High
Moffat	1645	2875	471
Johnstonebridge	1500	3527	3877
Lochmaben	1519	3745	6362
Locherbie	1318	3218	4881
Dryfe Water	787	1316	885

Table 6.1: A comparison of the amount of trapping applied under the different trap intensity levels (in trap days per year per region, with regions shown in Figure 6.4).

	Low	Med	High
Total trap days	6769	14681	16476
Increase in Red Squirrel Abundance	593	1351	2060

Table 6.2: A comparison of the total trap days per year and the increase in the abundance of red squirrels (compared to the absence of trapping).

7. Peebles and the surrounding region

We also assess the level of grey control required to protect red squirrels in the region around Peebles which is a priority area for red squirrel conservation (Fig. 7.1).

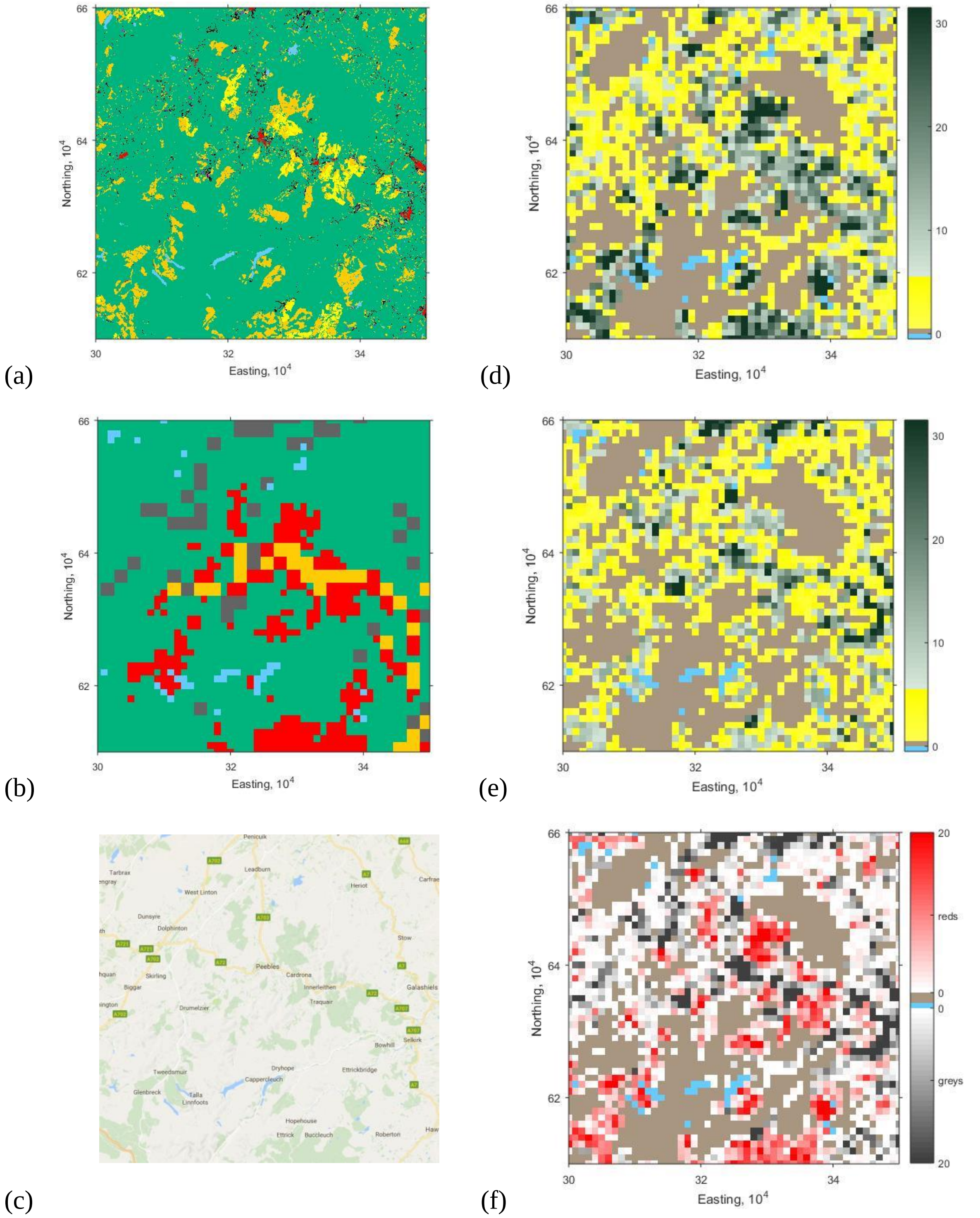


Figure 7.1: (a) The key habitat types considered in the model for this region (Sitka spruce – yellow, conifer – orange, mixed conifer – purple, broadleaf – black, urban – red). (b) The initial distribution of red and grey squirrels used in the model (red squirrels – red, grey squirrels – grey, both red and grey squirrels – orange). (c) An OS map of the region considered in the model simulations (© Digimaps). The carrying capacity (/km^2) based on landsurface data and estimates in Table 2.1 for (d) red squirrels and (e) grey squirrels. In (f) the value of $K_R - c_G K_G$ for parameter values in Table 2.1 is plotted indicating regions where red squirrels have an advantage (red) and where grey squirrels have an advantage (grey).

7.1 Baseline results without grey control in the Peebles stronghold

Figure 7.2 shows the model results for the occupancy of red and grey squirrels for default parameters in the absence of grey squirrel control when squirrelpox is included. Figure 7.3 shows the associated spread of squirrelpox. In the absence of grey control red squirrels can persist and dominate in large conifer plantations including Glenntress, Cardrona, Eilbank and Traquair forests that are adjacent to the Tweed valley between Peebles and Selkirk. Red can also persist in conifer forests west of Edelston, around Tweedsmuir and in the Craik forest. Grey squirrels dominate and reds are excluded along the Tweed valley travelling east from Dawyck to Peebles to Innerleithen. There is a region of red and grey co-occurrence east of Innerleithen in the Eilbank and Traquair forest but further east greys once more dominate around Selkirk and Galashiels (Fig. 7.2). Habitat in that area would support higher densities of squirrels and the model predicts that squirrelpox remains endemic in the Selkirk and Dawyck region. There are also occasional outbreaks along the Tweed valley between these regions (Fig. 7.3).

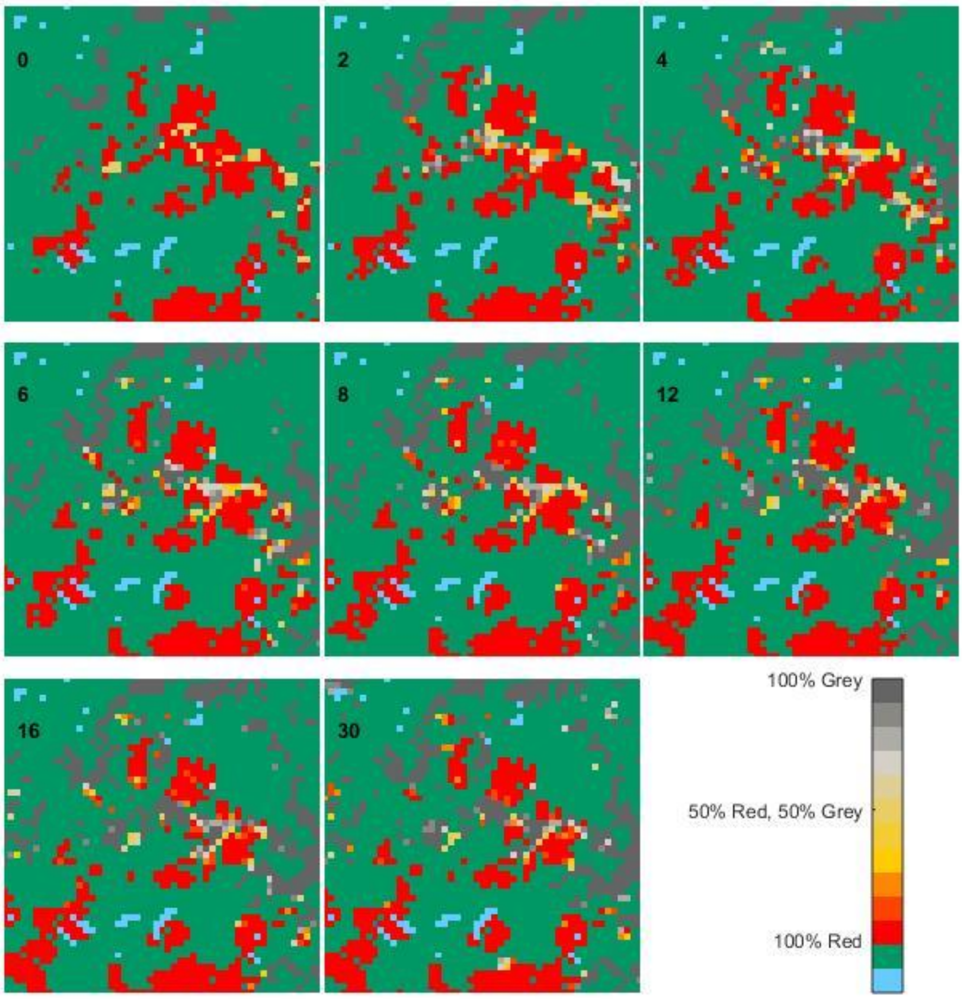


Figure 7.2: Model simulations using default parameter values with squirrelpox in the absence of grey squirrel control. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha).

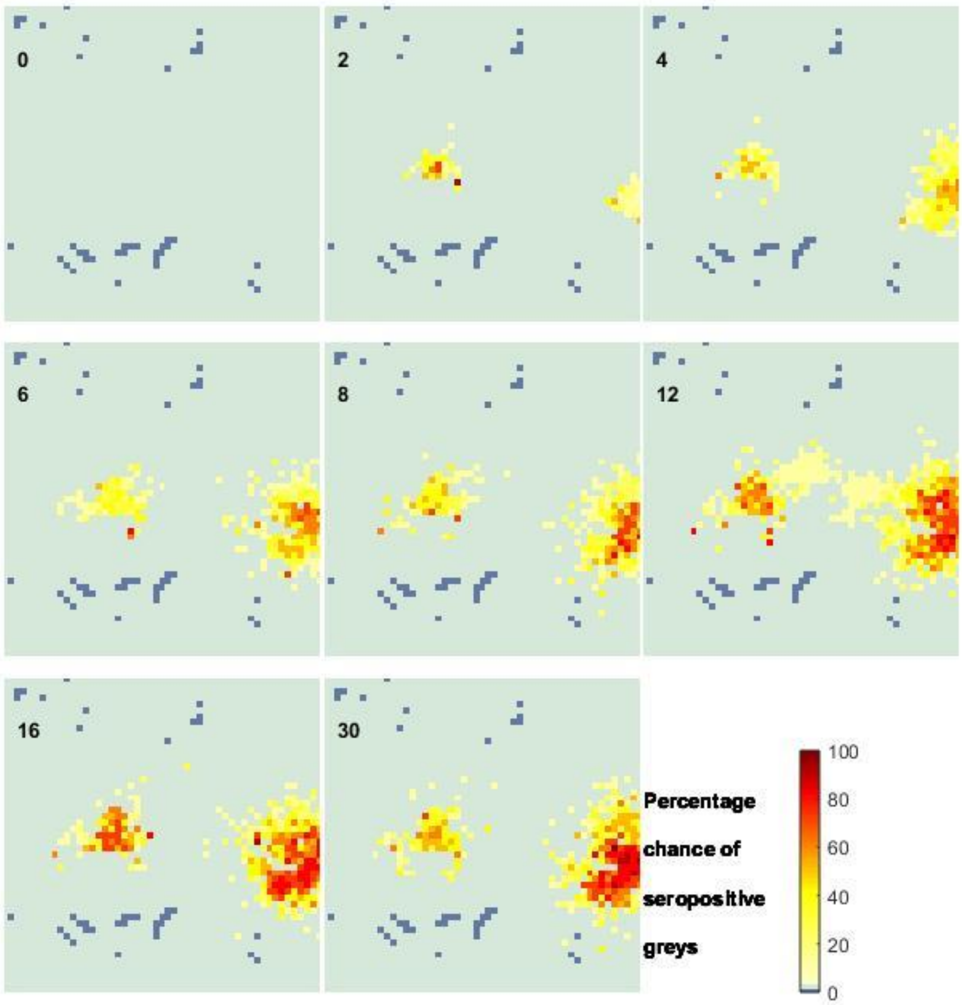


Figure 7.3: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 7.2. Squirrelpox was introduced in 1km by 1km grid squares in regions which represent Selkirk and Dawyck.

7.2 Results with grey control for the Peebles test region

The control regions were determined by studying the grey squirrel expansion paths in Figure 7.2 and through consultation with SSRS to reflect the historical and ongoing control effort in this region. The control regions focus along the Tweed valley and are shown in figure 7.4.

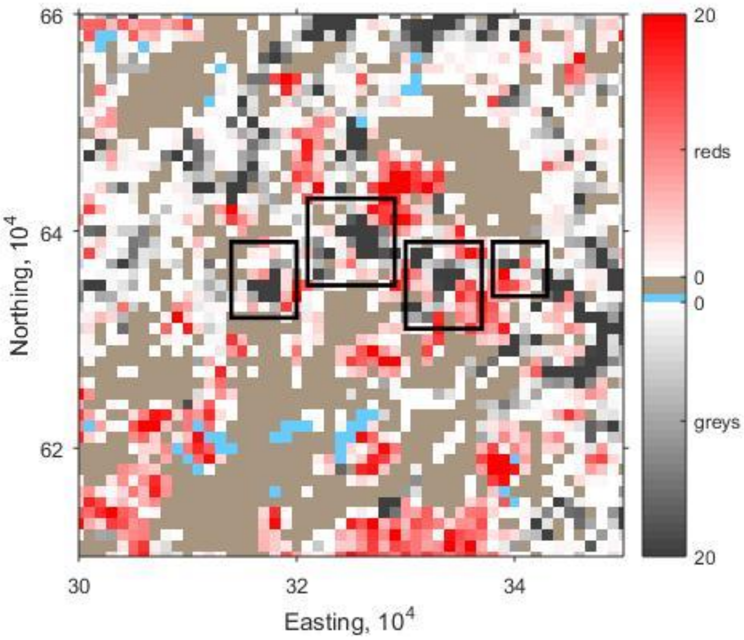


Figure 7.4: The regions in which control is applied in the model superimposed over the map that shows the outcome of competition (K_R - c_GK_G) between red and grey squirrels based on their carrying capacity. Control regions are labelled from left to right as Dawyck, Peebles, Innerleithen, Thornylee (see also Table 7.1).

7.2.1 Low intensity trapping (T_D = 0.1).

Similar to the other regions, low intensity trapping fails to prevent the expansion of grey squirrels within this control regions (Fig. 7.5). However, the low trapping intensity leads to a slightly increased red squirrel distribution compared with no control. Thus, even a low level of trapping has some impact in this area.

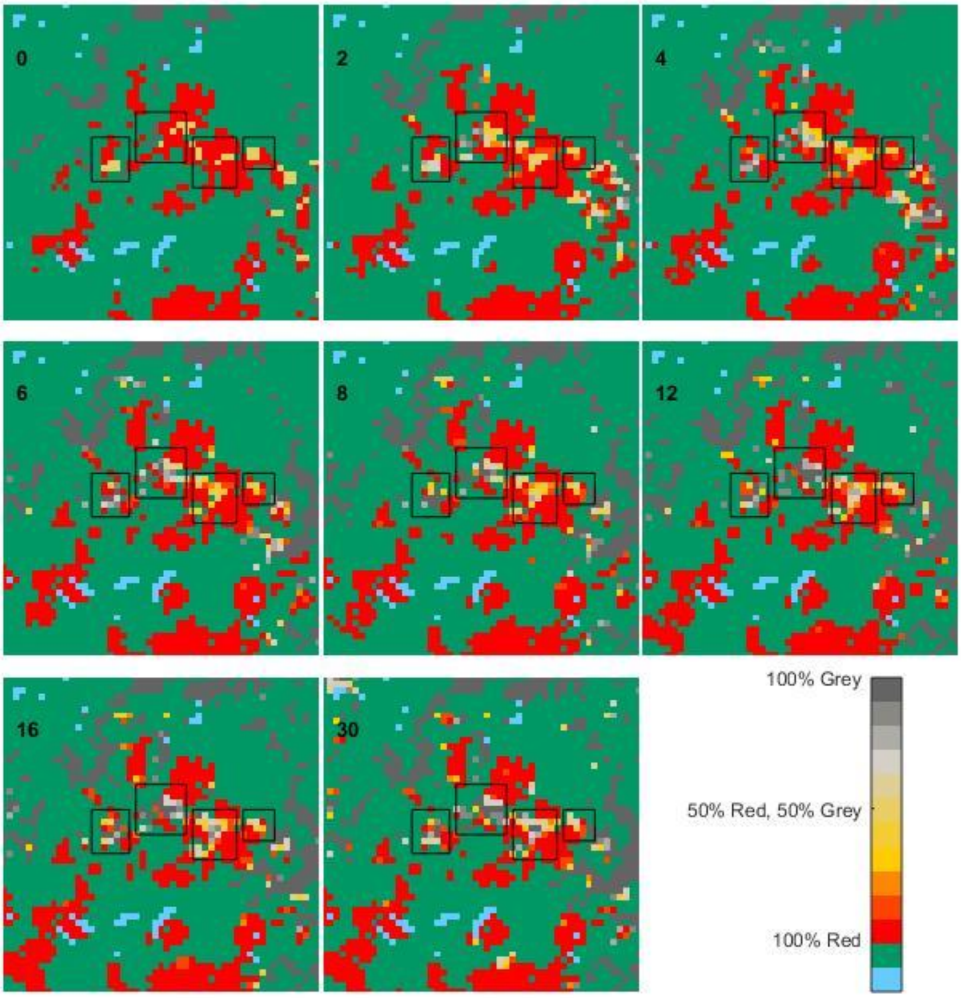


Figure 7.5: Model simulations using default parameter values with squirrelpox when grey squirrel control is applied with a low trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 7.1.

7.2.2 Medium intensity trapping (T_D = 0.25).

A medium intensity level of control reduces the level of grey expansion within the majority of the control regions, but grey squirrels are still present (up to 50%) in some squares within the Dawyk, Peebles and Thornylee control regions and have a reduced and very low presence in the Innerleithen square (Fig. 7.6).

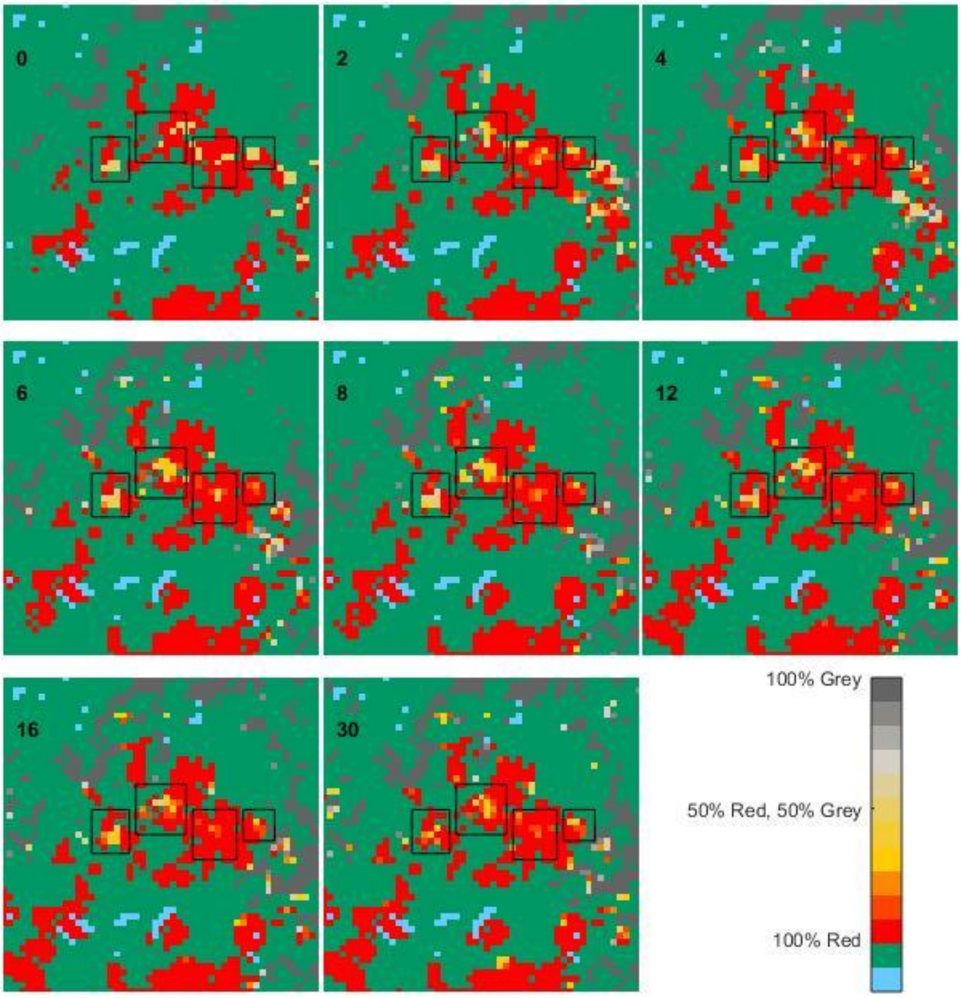


Figure 7.6: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a medium trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 7.1.

7.2.3 High intensity trapping (T_D = 0.5).
High intensity trapping prevented grey squirrels from expanding within all control regions (Fig. 6.7). This level of control would essentially allow red squirrels to dominate in the Peebles region PARC with grey squirrels being present outside control regions. Note that there will be large grey squirrel dominated areas beyond the control regions to the east and north which will act as a continuous source of immigration.

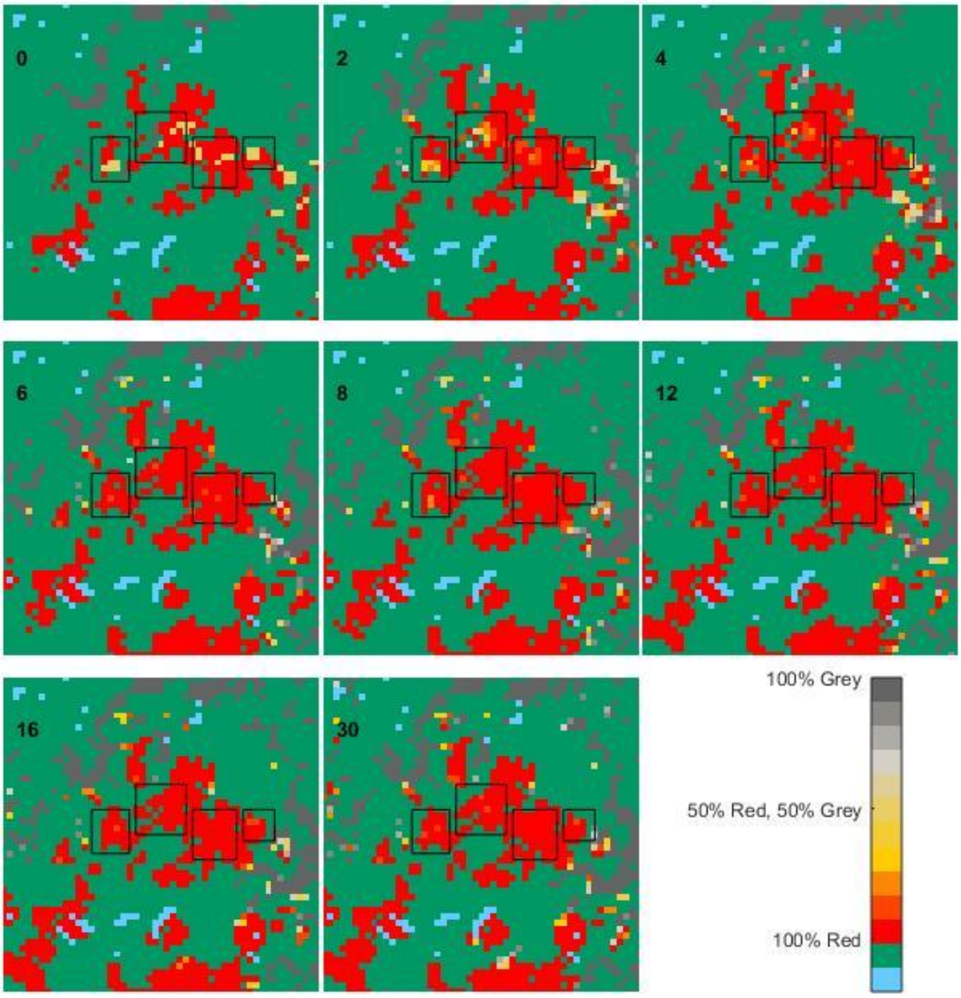


Figure 7.7: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a high trapping intensity. Maps show the percentage occupancy of red and grey squirrels (based on ten model realisations). Occupancy is defined as a density ≥ 5 squirrels per km^2 (0.05 squirrels/ha). The average level of trapping (trap days per year) in the different trapping regions is shown in Table 7.1.

7.3. A comparison of trap effort for different trapping intensity in the Peebles test region

A comparison of the red and grey squirrel occupancy at the end of the model simulations is shown in Figure 7.8. Table 7.1 illustrates control effort needed (in trap days per year) in the three trap-intensity scenarios (low, medium and high). Table 7.2 shows the increase in red squirrel density under the three control scenarios. Of note for this region is that a low level of control can lead to a significant relative increase in red abundance. Higher intensity levels of control do see further increases in red squirrel abundance but the gains are relatively small compared to the increase in control effort.

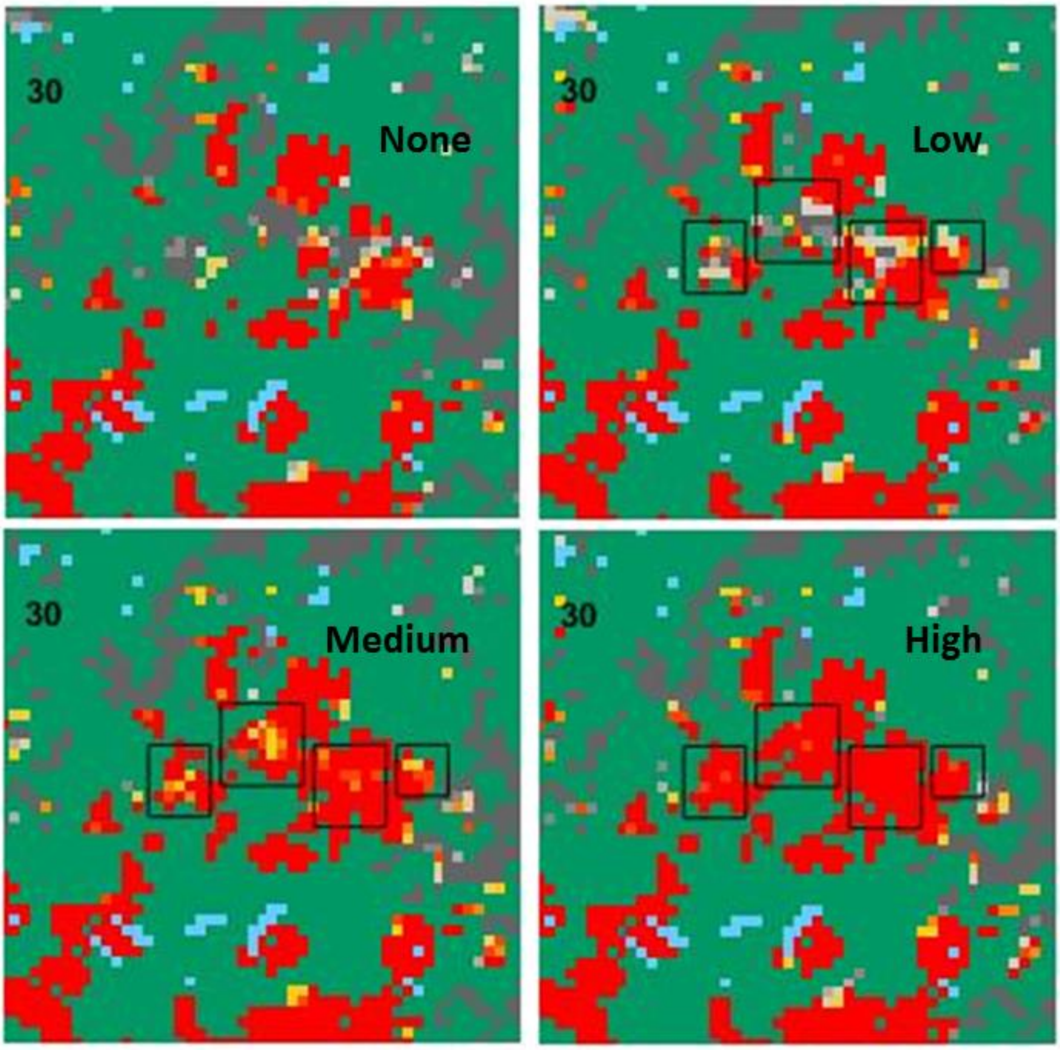


Figure 7.8: A comparison of the red and grey squirrel occupancy after 30 simulated years for different control intensities for Peebles the surrounding areas.

Trapping Region	Trap days per year		
	Low	Medium	High
Dawyck	714	1775	2728
Peebles	1263	3119	4370
Innerleithen	1226	2939	4391
Thornylee	567	1418	2793

Table 7.1: A comparison of the amount of trapping applied under the different trap intensity levels (in trap days per year per region, with regions shown in Figure 7.4).

	Low	Med	High
Total trapdays	3770	9251	14282
Increase in Red Squirrel Abundance	847	1120	1342

Table 7.2: A comparison of the total trap days per year and the increase in the abundance of red squirrels (compared to the absence of trapping).

8. A Comparisons of grey squirrel control for the 3 different test regions.
The modelling study predicts that there are likely to be large regions within the study areas (see Fig. 1.1), which are typically Sitka spruce dominated forests or other large conifer plantations, which would allow red squirrels to persist over the short to medium term in the absence of grey squirrel control. Grey squirrel control has been and continues to be applied within the study areas and so stopping control would result in a decline of red squirrel density, their disappearance from many populated areas and their restriction to large, and often remote conifer forests at low densities. Their continued survival in these conifer dominated areas would then depend on favourable forest management (e.g. see Anonymous 2012; Jones et al. 2016). A key question that requires future research is what composition of conifer species, forest structure and size is required to allow red squirrels to outcompete grey squirrels and maintain viable populations in the long term.

Squirrelpox virus is predicted to remain endemic in parts of the Eskdalemuir and the Peebles study region in medium to high density grey squirrel populations in the absence of control. In the predominantly low density habitats of Dumfries and Galloway the model predicts that SQPV will not play a significant role in red-grey squirrel interactions.Where squirrelpox remains endemic there is a risk of spread from grey squirrel populations to red populations. However, since red squirrel density is low the model predicts that squirrelpox will not spread through red squirrel populations. Squirrelpox outbreaks in red squirrels will be isolated to the inteface between red and grey squirrels and will burn out rapidly in red squirrel populations (Lurz et al. 2015; White et al. 2014). The model study therefore suggests that grey squirrel control should be focussed on redcuing grey squirrel density in key locations rather than focussing on preventing the spread of squirrelpox.

Model simulations predict that trapping, at all of the three levels considered in this study, will increase red squirrel abundance and distribution. However, low intensity trapping efforts fail to prevent grey squirrel expansion and establishement in any of the the three regions (Table 8.1) and grey squirrels will dominate in the Peebles, and parts of the Eskdalemuir and Galloway regions over time. Whilst red squirrels will have a refuge in large parts of, for example, the Galloway Forest, greys would dominate in suitbale habitat areas such as the area around Gatehouse of Fleet. This findings stresses that if grey squirrel control is undertaken for red squirrel conservation, it needs to be carried out systematically with sufficient effort to have effect. With medium to high intensity control efforts we report a significant reduction of grey squirrel presence or outright disappearance of grey squirrels within control regions (see Table 8.1). The latter provides not only protection of red squirrels in the wider area and increases their overall presence, but also produces synergistic effects, in that trapping on some squares reduced dispersal and immigration of grey squirrels.

Control of grey squirrels in regions close to large conifer forests that have been designated as red squirrel protection areas will lead to expansion of red squirrels into the wider landscape as grey squirrel abundance declines. However, these efforts would have to be maintanined to prevent subsequent contraction and decline. Control also has a wider benefit to red squirrel population dynamics and survival. Red squirrel populations in conifer forests experience large fluctuations due to significant, natural annual changes in seed food availability there (mast crop cycles; e.g. see Lurz et al. 1995). Enabling red squirrels to colonise neighbouring mixed-deciduous habitats as a result of grey squirrel control will create red squirrel source populations that could support the populations in conifer forest following years with poor seed crops and increase overall population viability. Further model studies that include the seed crop fluctuations could test the vulnerability of red squirrels in conifer forests and benefit of nearby sink populations in mixed-deciduous habitat.

If targeted grey squirrel control around red squirrel strongholds and PARCs can be sustainably devolved to local red squirrel groups then (at medium to high intensity effort) it offers a way to protect red squirrels in southern Scotland, and to make them visible in mixed-deciduous woodland that are in close proximity to populated areas where people can enjoy them.

Dumfries and Galloway	No control: Reds predicted to survive in large conifer areas. SQPV has no great impact in the low density habitats.
	Low: Fails to prevent grey expansion over time. Reds survive in conifer areas.
	Medium: Removes greys from majority of areas where controlled and provides protection for wider area.
	High: No grey squirrel expansion in the control regions. Wider area protected and grey dispersal between control regions reduced.
Eskdalemuir	No control: Grey squirrels dominate, reds excluded from deciduous habitats e.g. along river valleys (Nith, Annan). Reds survive in large conifer plantations. SQPV remains endemic in greys in south-east of study area.
	Low: Fails to prevent expansion of grey squirrels. Control regions become dominated by greys over time. Reds survive in conifer areas.
	Medium: Reduces grey squirrel expansion in 2 of the 5 control regions (Lochmaben, Dryfe Water).
	High: No grey squirrel expansion within control regions. Increased red squirrel distribution within landscape. Grey squirrels persist beyond control areas.
Peebles	No control: SQPV remains endemic around Dawyk and Peebles with additional outbreaks along Tweed valley. Reds predicted to survive in larger conifer areas.
	Low: Fails to prevent grey squirrel expansion but increases red squirrel distribution slightly.
	Medium: Reduces grey squirrel presence in the control regions; especially the Innerleithen control region.
	High: Prevents grey squirrel expansion and removes grey squirrels form all control regions. This level of control allows red squirrels to dominate within the Peebles region.

Table 8.1 Overview of the impact of control in the 3 regions. For further details see individual result sections.

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Appendix

In this appendix we include some additional results that compliment the findings reported in the main text.

In Figure A1 we show data for the number of trapdays per year in the Tayside demonstration area (data provided by SSRS). This indicates that the majority of trapping occurs between March and September. This corresponds to the breeding season in the model.

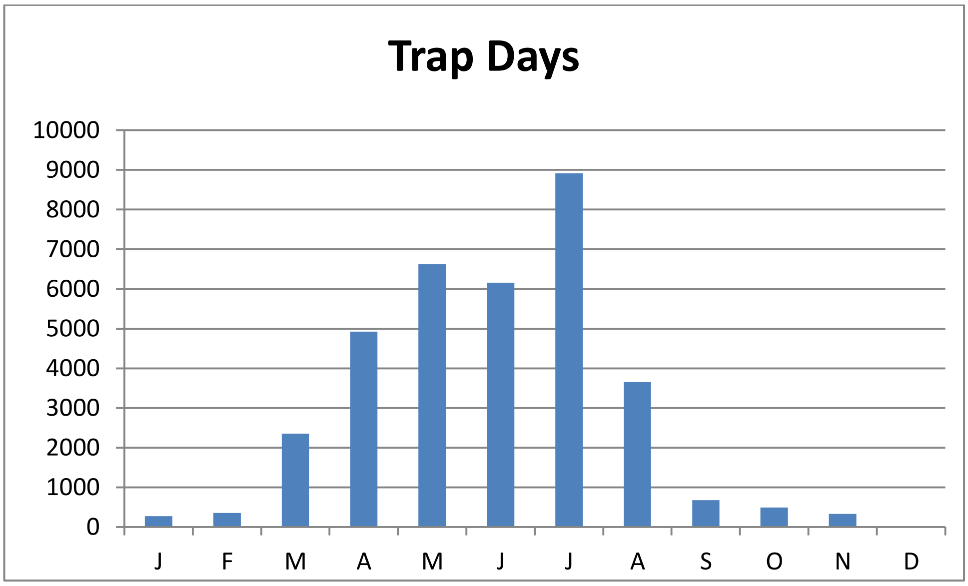

Figure A1. The number of trapdays per year in the Tayside demonstration area.

Explanation of the terms in the red-grey-squirrelpox model (equation 2.1).

Below we explain the model terms that correspond to the terms in equation (2.1) in words (and in the same order as they appear in equation 2.1)

Change in susceptible grey density	=	+ Birth of grey squirrels (max birth rate a_G)	- death of susceptible grey squirrels (death rate b)	- infection of susceptible grey squirrels (transmission rate β)
Change in infected grey density	=	+ infection of susceptible grey squirrels (transmission rate β)	- death of infected grey squirrels (death rate b)	- recovery from infection of grey squirrels (recovery rate γ)
Change in recovered grey density	=	+ recovery from infection of grey squirrels (recovery rate γ)	- death of recovered grey squirrels (death rate b)	
Change in susceptible red density	=	+ Birth of red squirrels (max birth rate a_R)	- death of susceptible red squirrels (death rate b)	- infection of susceptible red squirrels (transmission rate β)
Change in infected red density	=	+ infection of susceptible red squirrels (transmission rate β)	- death of infected red squirrels (death rate b)	- disease induced mortality of infected reds (virulence α)

In addition to these terms we assume that the birth of squirrels occurs during the breeding season only (6 months, March-September) and that the maximum birth rate is reduced due to intra- and inter-specific competition between squirrels for resources (see equation 2.2). These equations underpin the stochastic model (Table 2.2) which represents changes to the abundance of the different classes of red and grey squirrels within 1km by 1km gridsquares. In the stochastic model squirrels can undertake long distance dispersal to neighbouring gridsquares within a 2km range and grey squirrel control can be applied to remove grey squirrels.