Grey squirrel control along the highland line: A model analysis

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Executive Summary

This report details the findings from a mathematical modelling study to examine the realistic, spatial dynamics of red and grey squirrels and squirrelpox when grey squirrels are subject to population control through trapping and removal. In particular the report assesses the viability of grey squirrel control along the 'highland line' which runs from Loch Lomond in the west to Montrose in the east of Scotland and which represents the northern interface between red and grey squirrels in Scotland. The key findings from the study are:

- Grey squirrel control along the highland line is an effective method of preventing northwards grey squirrel range expansion.

  The model highlights key control regions and indicates the level of control that is required to prevent the range expansion of grey squirrels. The suggested successful levels of control in the model are in line with current estimates of the control effort on the ground (SWT pers. comm.) and therefore indicates that the current effort should be continued if the red – grey squirrel interface at the highland line is to be maintained.

- Medium to high intensity grey squirrel control should be applied in response to grey squirrel observations (where medium equates to 92 and high 137 trap days per 1km by 1km per year – see main text for full details).

  This has the effect of (largely) clearing the control region of grey squirrels and focussing control on the southern boundary of the control region (although control is still required in the interior of the control regions in response to grey squirrel observations and sporadic grey squirrel dispersal).

- Squirrelpox does not impact on red squirrel conservation to the north when grey squirrels are controlled at the highland line.

  When control is applied to prevent grey squirrels from expanding their range beyond the highland line then squirrelpox is also contained to the south of the highland line. Here, since trapping and removal of grey squirrels in the control regions prevents grey squirrel establishment it also prevents the establishment of squirrelpox. In line with previous research (Lurz et al. 2015) the model predicts that squirrelpox will not spread through established red squirrel populations along or to the north of the highland line.

- If resources for grey squirrel control in Scotland are reduced, preventing the range expansion of grey squirrels in Angus and Aberdeenshire should be a priority, but a watching brief should be instituted in other potential areas of dispersal.

  The model evaluation indicates that much of the region north of the highland line is disconnected from regions where red squirrels are currently observed in Highland Scotland. Therefore, red squirrel populations in the Cairngorm National Park (and further north and west) may not be threatened by a direct northwards expansion of grey squirrels beyond the highland line. However, dispersal through Angus and Aberdeenshire could offer a long-term route for grey squirrel dispersal and establishment in the Highlands. This therefore highlights the need for the continued effort to remove grey squirrels from Aberdeenshire and for grey control to prevent their expansion through Angus. Expansion of grey squirrels into Argyll over the very long term may still be a possibility, particularly if new habitat networks are established or habitat restructured to favour native woodland.

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. In southern Scotland, the virus persists at endemic levels in the widespread and established grey squirrel populations. Red squirrels still persist widely across the region and the conservation strategy is to defend prioritised 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, White and Lurz 2014) 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).

In northern Scotland red squirrel conservation is aimed at protecting red squirrel populations in the Highlands, Argyll, north-east Scotland, northern Tayside and Stirling where there are currently no grey squirrels (SNH 2015). To do this grey squirrel control is implemented at the interface between red and grey squirrels, currently running approximately along the Highland Boundary Fault. This major fault zone cuts across Scotland like a geological knife, north-east to south-west from coast to coast. A few narrow passes and river or coastal corridors create potential routes for grey squirrel dispersal between the lowlands and highlands. Along the highland red squirrel protection line, (see Fig. 1.1) grey squirrel control is implemented with the aim of preventing the northwards range expansion of grey squirrels. The ‘highland line’ is extensive, from Helensburgh in the west to Montrose in the east and therefore grey control along the highland line is a resource intensive task. Mathematical modelling can be used as a tool to improve the coordination and effectiveness of this control and in this study we undertake large-scale model simulations to predict the likely rate of the future invasion of greys into red squirrel-only populations north of the highland line. The mathematical model includes grey squirrel control and can therefore indicate the location and level of control required to maintain the red-grey squirrel interface along the highland line. This will help answer a key question of ‘where and how much’ control should be applied and therefore inform future policy and resource utilisation of ongoing conservation projects.

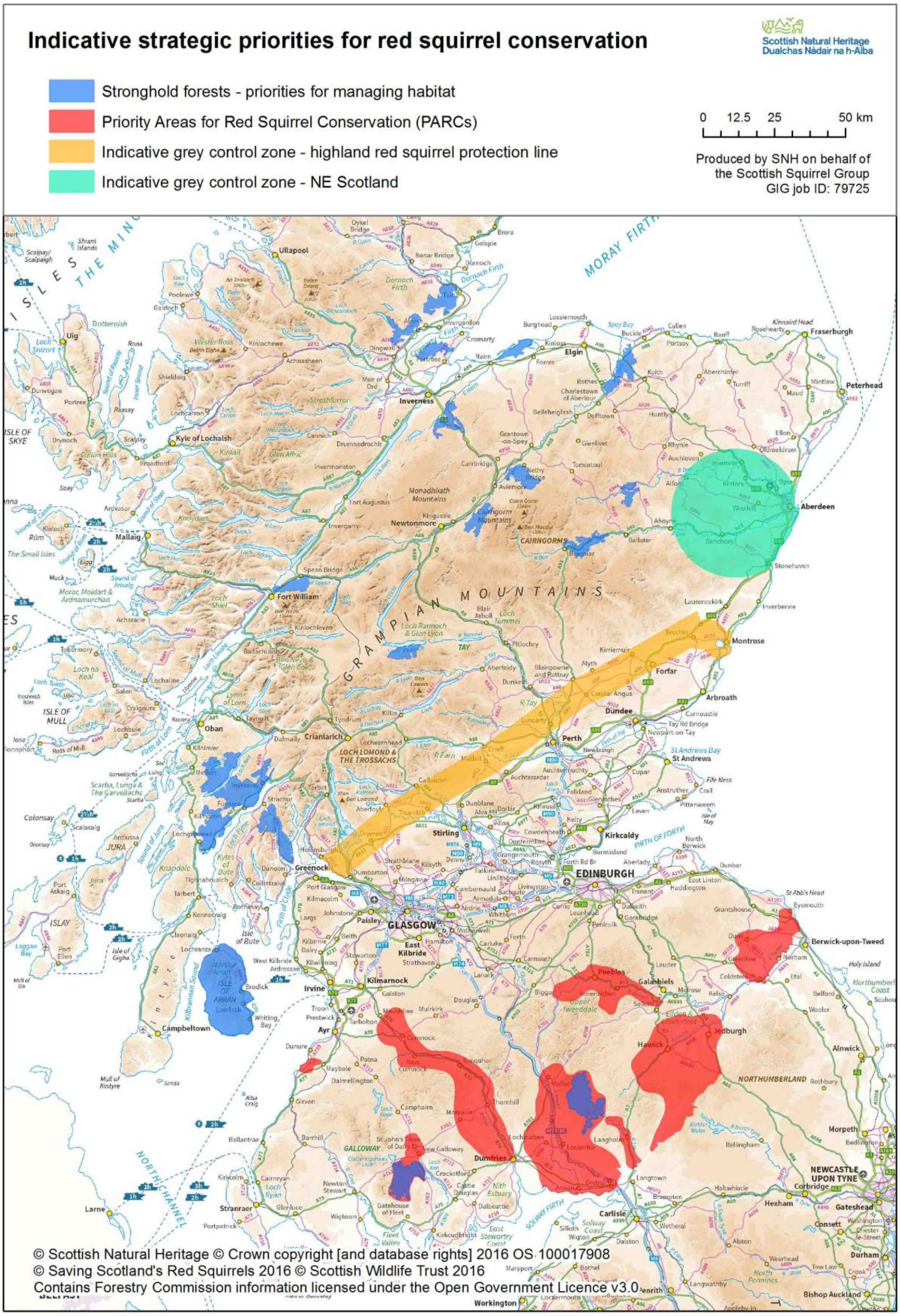

Figure 1.1: A map highlighting key areas for red squirrel protection in Scotland (SNH 2015). Priority areas for conservation of red squirrels in southern Scotland are shown in red. The highland line, which is an interface with red squirrel populations in the absence of greys to the north of this line and red and grey squirrel populations to the south, in shown in yellow.

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. Gridsquares are linked by dispersal and the potential squirrel density in each grid square is based on landcover data and therefore approximates the real heterogeneous habitat of Scotland. Following discussions with Saving Scotland's Red Squirrels (SSRS) and Scottish Natural Heritage (SNH), we focus on the region of Scotland above the central belt that includes the highland grey squirrel protection line (Fig. 2.1).

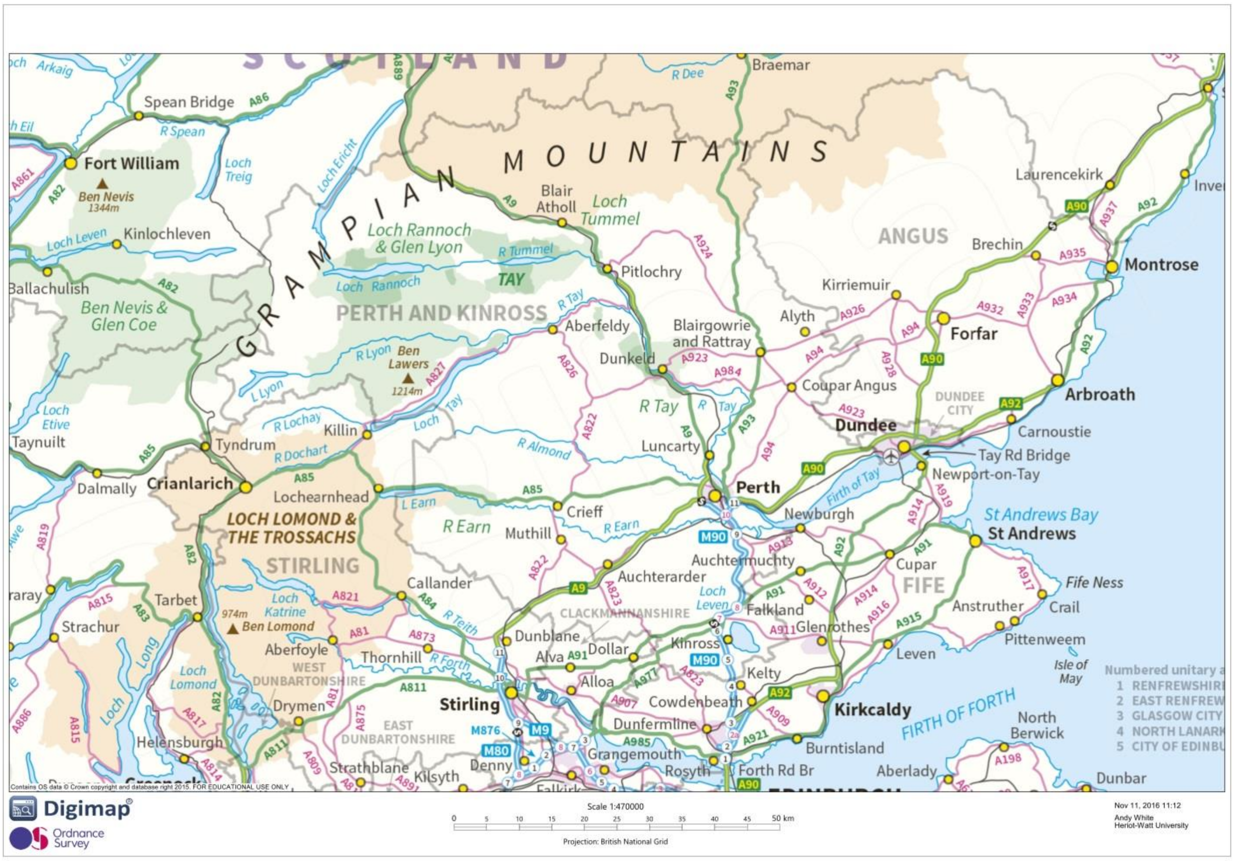

Figure 2.1: An OS map of the region considered in model simulations on which we examine the level of grey control required along the highland line (© Digimaps).

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 landcover datasets (supplied by the Forestry Commission) to extract coniferous, broadleaf, shrub and Sitka spruce (*Picea sitchensis*) habitat types and used the Scottish Natural Heritage 2007 dataset to extract urban habitat types at a 25 m by 25 m scale. This data was combined with estimates of squirrel densities in different habitat types (Table 2.1) and summed to obtain the potential density of red and grey squirrels at a 1km x 1km patch level that could be supported in the landscape. This scale and approach have been used successfully to model the UK squirrel system in previous studies (Macpherson et al 2016; White et al. 2015, 2016).

Habitat Type	Default (density /ha)	
	Red	Grey
Broadleaf	0.81	1.96
Conifer	0.5	0.53 (or 0.16 for **poor** in conifer scenario)
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 (and the lower potential density for grey squirrels if we assume that conifer offers a poor habitat, see section 3.3 later).

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 consider a spatial, stochastic model, (Macpherson et al 2016; White et al. 2014, 2015, 2016). Here, the deterministic underpinning allows the key population dynamical processes to be understood and the stochastic adaptation provides essential realism when squirrel numbers become low and therefore the chance of extinction and the fade-out of infection are represented.

To generate the stochastic model, the rates in the deterministic model are converted to probabilities of events that account for changes in individual grid cell level abundance. We consider the abundance of susceptible, infected and recovered grey squirrels, (S_G, I_G, R_G), and susceptible and infected reds, (S_R, I_R), respectively. The probabilities are given in Table 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/). 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 near Strathblane and Denny in central Scotland (to represent the spread of infection from central Scotland, where infected grey squirrels have been observed).

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

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 2km 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 represents the rate of 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

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 undertake simulations for 3 scenarios: in the absence of squirrelpox, with squirrelpox introduced in the central Scotland, and with squirrelpox introduced in central Scotland and with grey squirrel density at poor levels in conifer.

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 as taken from the NBN observed data. After 5 years grey squirrel expansion has occurred to regions of nearby suitable habitat and the 'highland line' is indicated by the northern extent of the light orange gridcells. It is clear that without grey control grey squirrels expand their range northwards into regions previously occupied by red squirrels only, causing loss of red squirrel range to the north of the highland line. The expansion is most pronounced in eastern regions to the north of Montrose and in the central Highlands north of Dunkeld and Blairgowrie. The expansion is less pronounced in the west in Argyll, around Loch Lomond, Loch Earn and the western extent of Loch Tay, but is possible over a longer timescale.

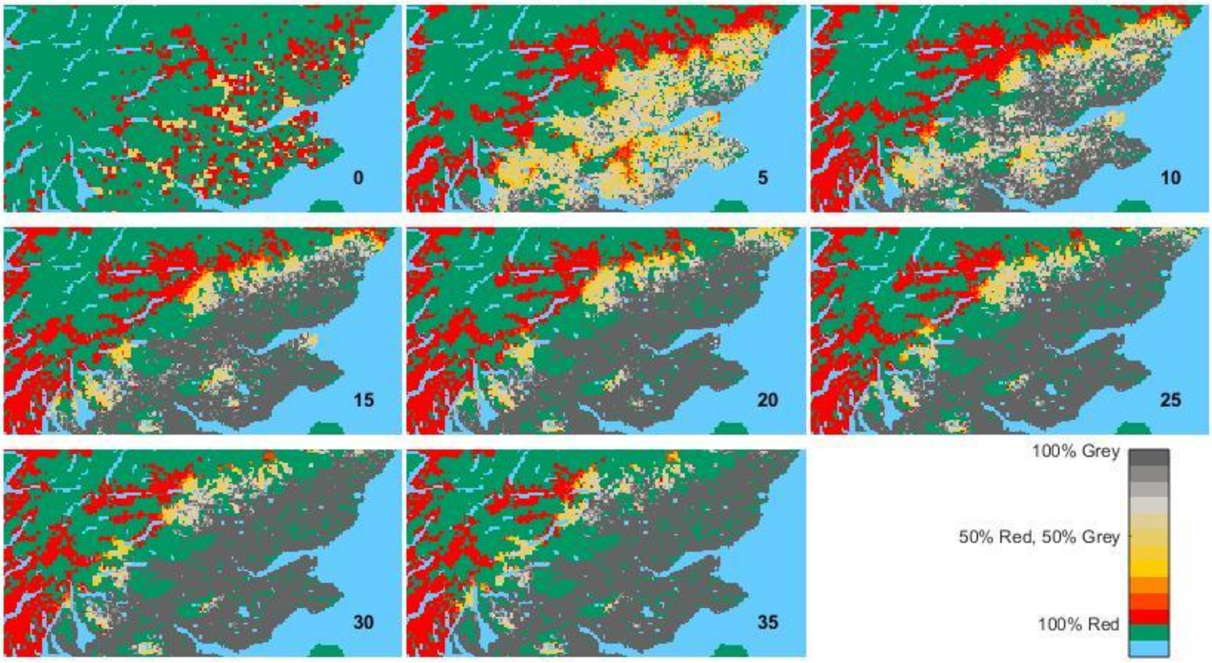

Figure 3.1: Model simulations under default parameter values in the absence of grey squirrel control and squirrelpox showing the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

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. The expansion of grey squirrels beyond the highland line initially occurs at a similar rate to that in the absence of squirrelpox (Fig. 3.1), but then occurs at a slightly faster rate from year 20 onwards, with grey range expansion increased in central highlands from year 25 onwards (compare Fig. 3.1 and 3.2). This is due to the absence of squirrelpox in central Highlands regions until year 20 (Fig. 3.3) and so prior to this red replacement has been due to competitive effects only (and therefore Fig. 3.1 and Fig. 3.2 are very similar till year 20 in these regions). After year 20 the expansion of greys in the central Highlands is more rapid when squirrelpox is present and therefore further highlights that squirrelpox plays a key role in the rate of replacement of red squirrels by greys. In regions around Loch Lomond and the Trossochs squirrelpox is present after approximately 10 years (Fig. 3.3). However the expansion of grey squirrels in these regions does not seem to be enhanced by the presence of squirrelpox. This is likely to be due to the relatively poor habitat at the north of Loch

Lomond that makes grey squirrel establishment difficult, potentially keeps densities low and makes the persistence of squirrelpox within grey populations unlikely.

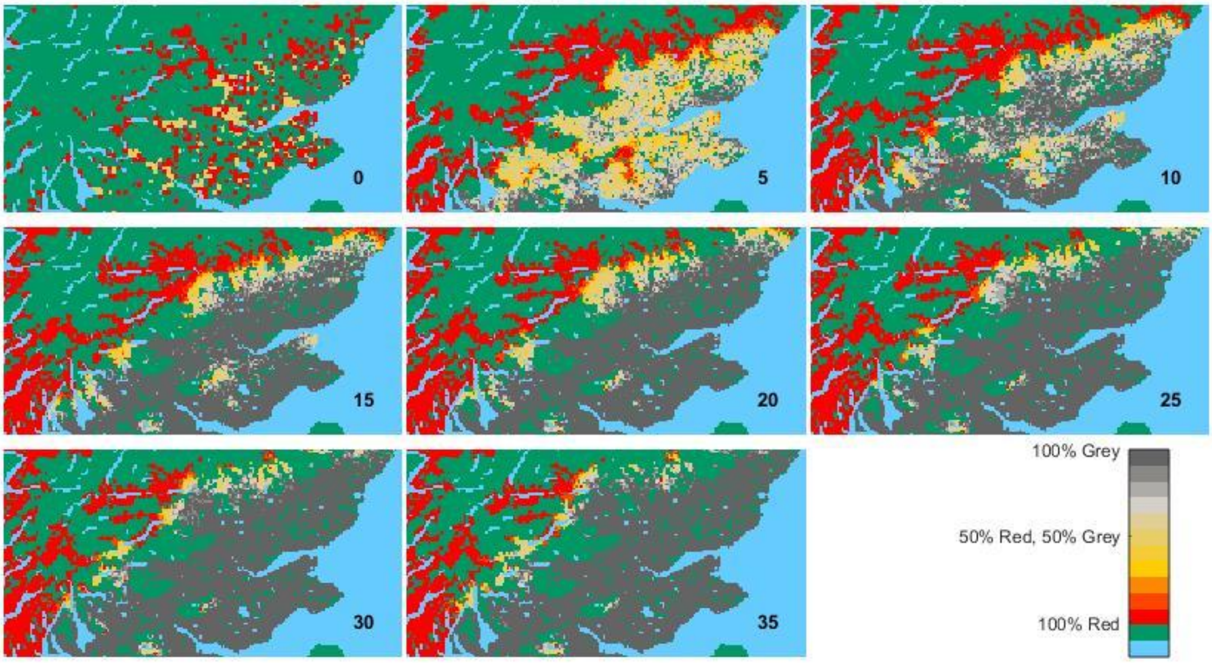

Figure 3.2: Model simulations under default parameter values with squirrelpox in the absence of grey squirrel control showing the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

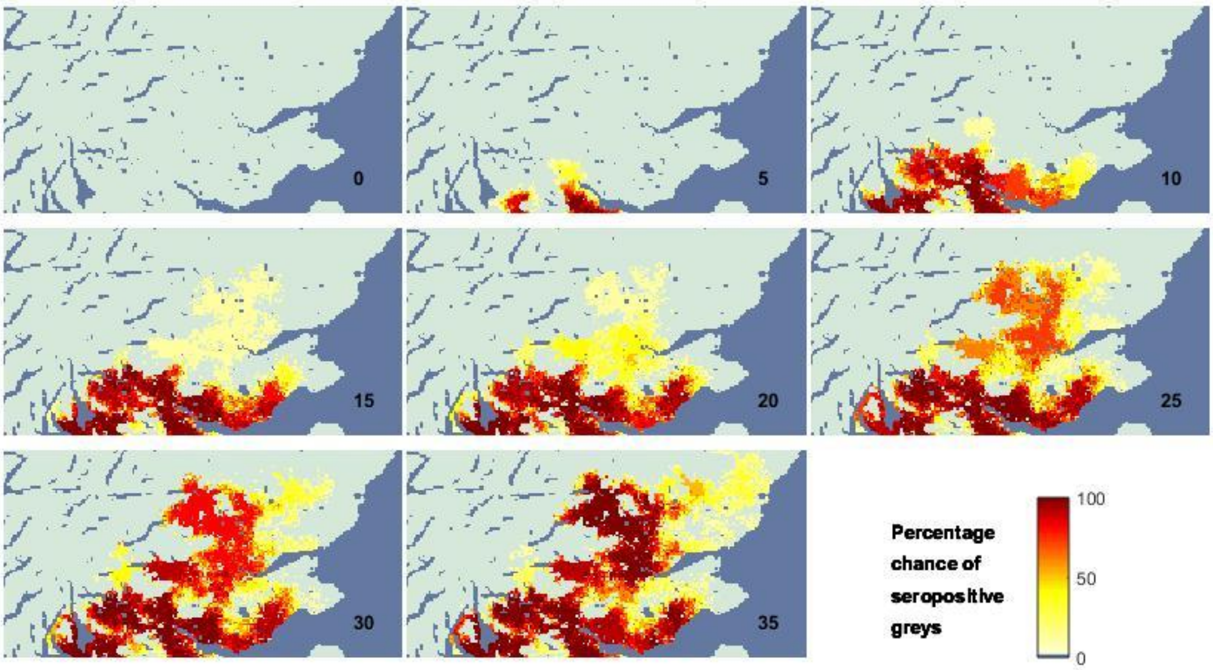

Figure 3.3: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 3.2.

3.3. Grey expansion with squirrelpox and with conifer as a poor habitat for grey squirrels (with no grey squirrel control)

Results for grey squirrel expansions when we assume that conifer offers a poor habitat for grey squirrels are shown in Figure 3.4, with the associated spread of squirrelpox in Figure 3.5. Under this scenario the expansions of grey squirrels is slightly reduced (compare Fig. 3.4 with Fig. 3.2). Moreover, there is an increase in the regions in which red and grey squirrels coexist. Some of these regions reflect areas where red squirrels are currently observed in central Scotland (e.g. north east Fife, Kinross and Perthshire) and suggests that more information on the suitability of coniferous habitat in Scotland for grey squirrels is required (the empirical data for grey squirrel potential density on conifer largely comes from studies in English and Welsh habitat, see Smith 1999, Cartmel 2000).

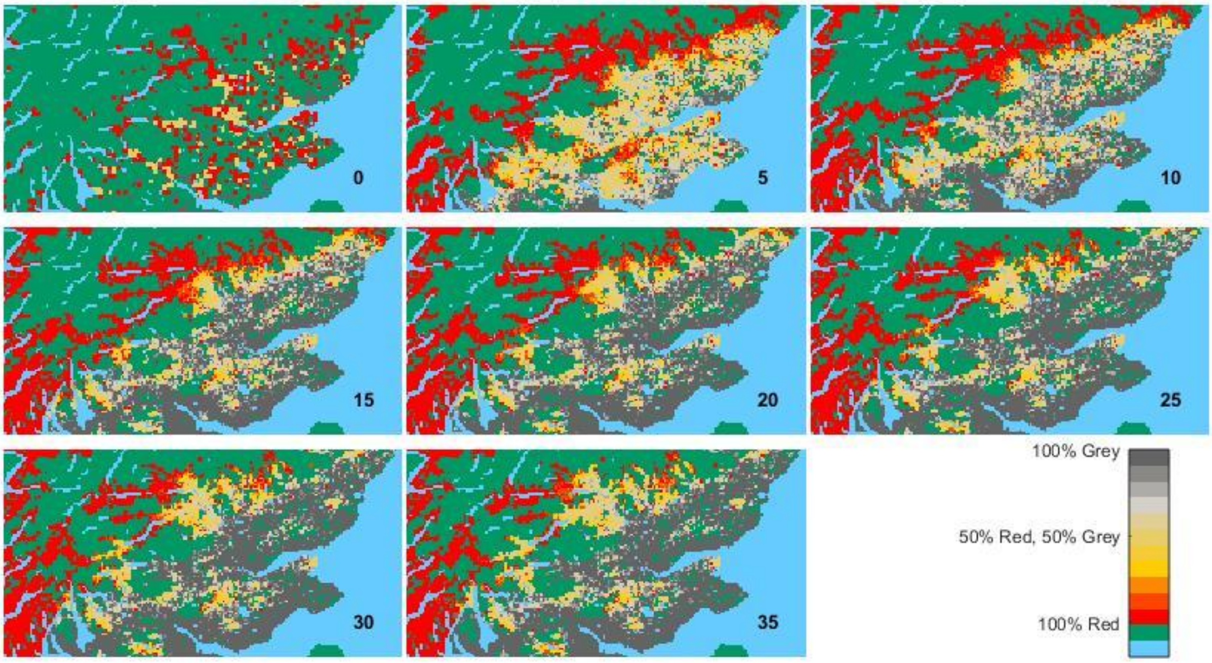

Figure 3.4: Model simulations under parameter values in which conifer offers a poor habitat for grey squirrels and with squirrelpox in the absence of grey squirrel control showing the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations). Notice the persistence of reds as far south as Clackmannanshire and Fife.

Squirrelpox spread is contained in central Scotland when conifer offers a poor habitat for grey squirrels (Fig. 3.5). This is due to grey squirrel density being suppressed to levels that do not support endemic persistence of squirrelpox in grey squirrel populations between central Scotland and northern Fife, Kinross-shire and southern Stirlingshire. This has implications if future woodland management favours restructuring towards native woodland species.

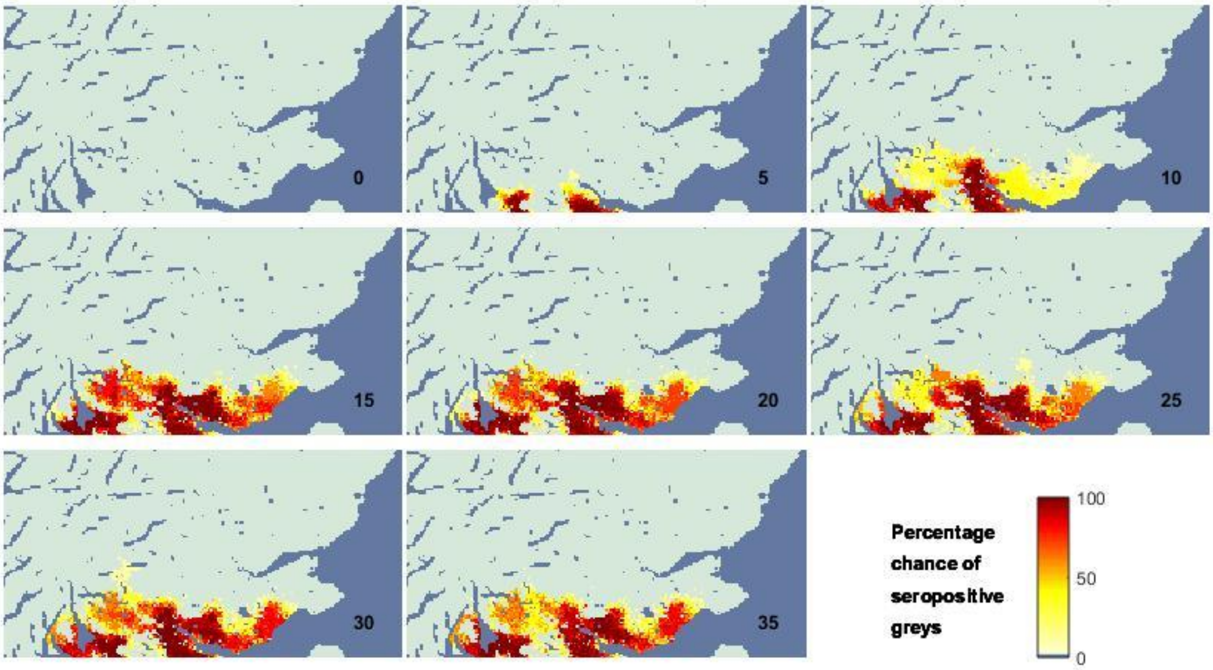

Figure 3.5: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 3.4.

4. Results with grey control along the highland line

The results in the absence of control were used to isolate key regions in which control should be included in an attempt to prevent the northwards expansion of grey squirrels beyond the highland line. The control regions are shown in Figure 4.1. 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). We chose to undertake the model simulations that include control for the default parameter setting (Table 2.1) and in which squirrelpox is included. This represents a worst case scenario and should provide an upper bound on the level of grey control required to maintain red squirrel protection along the highland line.

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 in the regions (typically 10km by 10km) outlined in Figure 4.1. In specified 1km by 1km gridcells within these regions control is applied with a trap intensity of T_D traps per day. An analysis of when control was applied in the field was undertaken for a reduced region in Tayside (data for the Tayside demonstration area was provided by SWT, results not shown). This indicated that the majority of grey squirrel control occurs between 1 April and 30 September. Therefore in the model we assume control can occur for up to 6 months, from 1 April – 30 September (183 days) which is split into three 61 day (2 month) control periods. At the start of the first control period trapping is applied in gridsquares in which grey squirrels are present and in gridsquares in a 2km buffer zone around these gridsquares. Control is maintained at this level for 61 days. The same procedure is applied to determine the gridcells 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. This means that within any control region the level of trapping can increase or decrease from year to year as it depends on the grey squirrel presence within the control regions (which varies over time and in response to previous trapping). We run the model for three levels of trap intensity (T_D = 0.3 – low; 0.5 – medium; 0.75 – high). To aide interpretation, a low intensity of trapping equates to a maximum of 0.3x183 = 55 trapdays per year in a 1km by 1km gridsquare (and equates to 92 and 137 trap days per year per gridsquare for medium and high intensity trapping respectively).

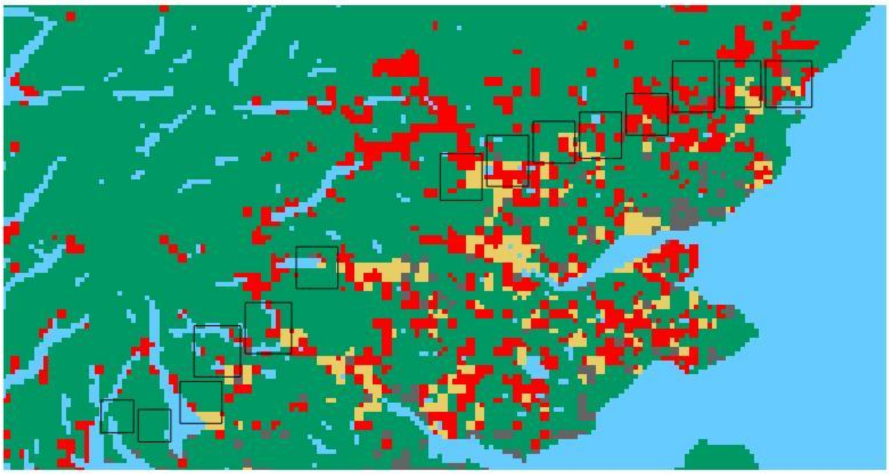

Figure 4.1: The initial distribution of red and grey squirrels and the regions in which control is applied in the model along the highland line (see Table 8.1 for further details of the location of the control regions).

4.1. Low intensity trapping (T_D = 0.3).

Low intensity trapping fails to prevent the expansion of grey squirrels beyond the highland line (Fig. 4.2). The highland line is breached in the north east (between Montrose and Brechin) and in the central Highlands (around Dunkeld) after 10 years, potentially threatening the Red Squirrel Stronghold forest at Rannoch, and by year 30 also north of Blairgowrie and Kirriemuir in the Highlands and Strathyre in the Trossachs. By the end of the 35 year model simulation greys are present to the north of all the control regions. Note, however, that grey expansion was significantly reduced when a low level of control was applied compared to when no control was applied (compare Fig. 4.2 with Fig. 3.2).

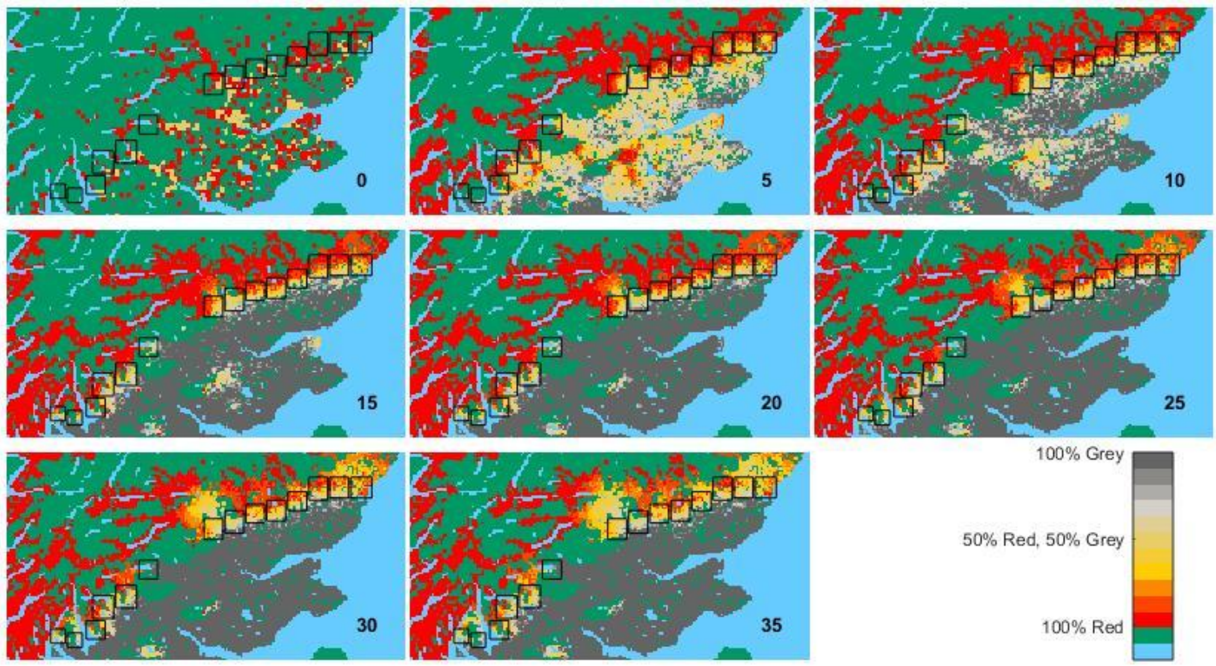

Figure 4.2: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a low trapping intensity. Maps show the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

4.2. Medium intensity trapping (T_D = 0.5).

A medium intensity level of control prevents grey expansion beyond the highland line in the majority of simulations. However, in some control regions greys manage to evade capture and spread northward (this happens in 1 out of the 10 realisations after 10 years and in a further realisation after 30 years). This occurs in regions north of Dunkeld and north of Blairgowrie (as seen by the orange colour above the control regions in Figure 4.3). This suggests that medium intensity control would suffice in most regions but additional control may be required in regions around Dunkeld and Blairgowrie.

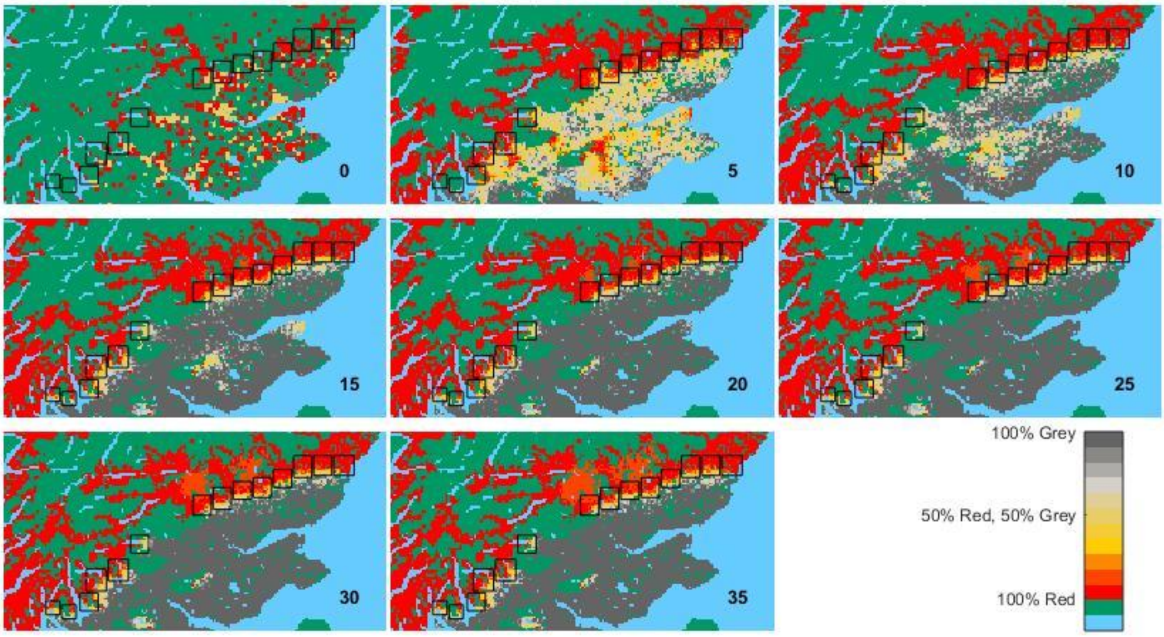

Figure 4.3: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a medium trapping intensity. Maps show the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

4.3. High intensity trapping (T_D = 0.75).

High intensity trapping prevented grey squirrels from expanding beyond the highland line in all model realisations (Fig. 4.3). This therefore suggests that a combination of medium intensity trapping in most control regions with high intensity trapping around Dunkeld and Blairgowrie (regions 7-10, see table 4.1 below) would prevent the northward expansion of grey squirrels and protect red squirrels above the highland line.

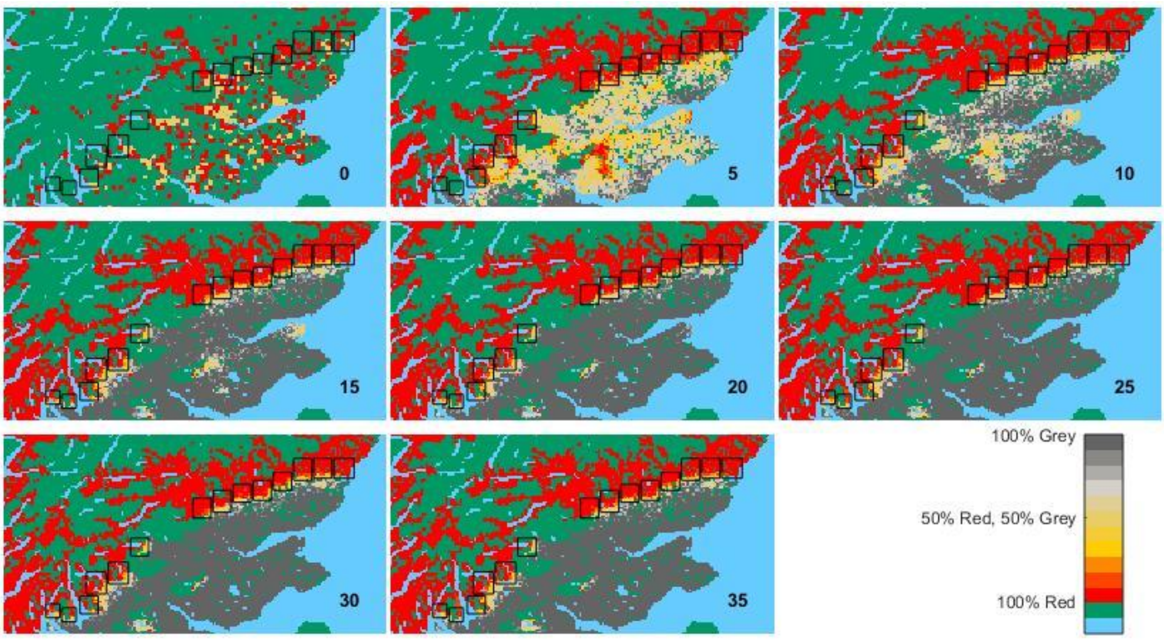

Figure 4.3: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a high trapping intensity. Maps show the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

4.4. A comparison on trap effort for different trapping intensity

Table 4.1 shows the trap effort, in trap days per year, for three different levels of trap intensity. The modelling results suggest that if medium trapping intensity is undertaken in regions 1-6 and 11-14 and high trapping intensity in regions 7-10 then grey squirrel range expansion beyond the highland line will be prevented. This implies that the number of trap days per year in each region should range from 1831 to 7494. The associated number of grey squirrel caught in each region is shown in Table 4.2. Note, in general as the intensity of trapping is increased the number of grey squirrels caught (from year 5 onwards) decreases. This is because at low intensity trapping grey squirrels can disperse throughout the control regions and so trapping is required across the whole control region and there are abundant greys to catch. Trapping, in effect, represents a kind of harvesting and greys persist indefinitely. As trap intensity increases the control regions are cleared of grey squirrels and so most grey captures will occur at the interface with regions in which greys are not controlled (typically at the southern boundaries of the control regions). This also explains why the trap effort in control regions can decrease over time. For example there is a decrease in trap effort in region 14 (Montrose) as greys are removed from the majority of the region and therefore control becomes focussed on the southern boundary. These results highlight the importance of undertaking grey squirrel control with a sufficient trap intensity to prevent their dispersal within and beyond the control regions. In practical terms this involves employing traps in the highland line control zone in locations where grey squirrels are observed (and in a buffer zone around these regions). According to model results the trap intensity should be either 92 (medium) or 137 (high) trap days per 1km by 1km per year.

	Regions and corresponding trap effort (trapdays per year)													
	Reg 1	**Reg 2**	**Reg 3**	**Reg 4**	**Reg 5**	**Reg 6**	**Reg 7**	**Reg 8**	**Reg 9**	**Reg 10**	**Reg 11**	**Reg 12**	**Reg 13**	**Reg 14**
Year	**Low intensity trapping scenario**													
0	29	238	1433	2212	2580	1389	3120	4154	3794	2180	1680	2652	4311	3883
5	1168	1274	2181	3259	3281	1497	4112	4370	4022	3296	3115	3429	4570	4187
10	1728	1652	2337	3876	3676	1651	4161	4399	4427	4165	3797	3501	4507	4030
15	1799	1779	2280	3779	3773	1715	4291	4469	4397	4494	3999	3558	4674	3838
20	1867	1795	2395	3911	3896	1717	4419	4570	4467	4582	4504	3691	4813	3693
25	1936	1812	2421	4052	3971	1733	4882	4529	4615	4776	4621	3821	5082	3825
30	1907	1812	2406	4092	4132	1746	4932	4650	4785	4859	4559	4394	5463	3795
35	1980	1812	2511	4308	4299	1819	5082	4643	4839	4842	4698	4344	5479	4134
Year	**Medium intensity trapping scenario**													
0	55	451	2334	3579	4203	2336	5259	6944	6323	3605	2918	4228	7041	6254
5	1970	2102	3308	4320	4728	2364	5046	6695	5256	4836	3606	3508	4898	4303
10	2653	2443	3304	4551	5183	2535	3782	5908	5162	5496	4510	2633	4606	2144
15	2598	2562	3547	5099	5237	2590	3637	5836	5387	5639	4998	3937	5060	2162
20	2678	2529	3480	5044	5162	2574	3441	6126	5527	6173	5586	4182	5317	1983
25	2672	2526	3492	4523	5088	2611	3596	5886	5692	6329	5655	4365	5195	2042
30	2751	2534	3575	4621	5073	2602	3826	5947	6083	6485	5441	4486	5314	2004
35	2912	2541	3474	4887	5405	2538	3928	6438	5950	6133	5572	4474	5292	1831
Year	**High intensity trapping scenario**													
0	73	608	3340	5234	6172	3454	7412	10230	9443	5421	4072	6039	10504	9406
5	2576	3061	4095	5211	6281	3033	4246	7832	5197	6140	4223	1084	4296	2553
10	3518	3212	4653	5673	6469	3463	4053	7412	6323	7764	5298	2718	5920	1775
15	3532	3450	4795	5980	6556	3605	4140	7585	7000	7713	6762	5206	6597	2288
20	3582	3381	4872	6387	7087	3514	3870	7412	6574	7498	6776	5696	6657	2246
25	3756	3605	4895	5961	6949	3687	4085	7453	6382	7489	6986	5765	6565	2265
30	3893	3399	4831	6126	6812	3605	3857	7384	6981	7942	7059	5664	6670	2347
35	3742	3418	4822	5838	6895	3550	4104	7494	6378	7508	7123	5687	6689	2297

Table 4.1: The average trap effort for a model realisation (trap days per year) for the different control regions for the low, medium and high intensity trapping scenarios. The 14 trap regions are indicated in Figures 4.1-4.4 starting on the left with region 1 and moving to region 14 on the right. To aid interpretation of the trap regions we provide approximate geographical location as follows. Region 1 – Garelochhead, Region 2 – Arden, Region 3 – Rowardennen forest, Region 4 – Loch Ard/Achray forest, Region 5 – Strathyre forest, Region 6 – Eastern Loch Earn, Region 7 – Dunkeld (west), Region 8 – Dunkeld (east), Region 9 – Blairgowrie, Region 10 – Alyth, Region 11 – Kirriemuir, Region 12 – Finavon , Region 13 – Brechin, Region 14 – Montrose. Note, in some regions trapping is initially low as there is a low initial presence of grey squirrels (see Figure 4.1).

	Regions and corresponding grey squirrels caught (squirrels per year)													
	Reg 1	Reg 2	Reg 3	Reg 4	Reg 5	Reg 6	Reg 7	Reg 8	Reg 9	Reg 10	Reg 11	Reg 12	Reg 13	Reg 14
Year	**Low intensity trapping scenario**													
0	0	1	25	59	91	37	106	160	31	13	7	42	64	48
5	12	55	39	111	89	42	104	198	44	24	27	31	64	40
10	49	119	63	157	166	118	115	268	72	61	47	33	90	44
15	81	118	81	191	267	154	132	317	89	79	70	55	139	51
20	88	138	87	225	294	178	153	345	110	94	93	73	160	50
25	85	161	93	240	326	181	221	363	118	107	98	81	187	64
30	90	184	103	265	319	191	285	366	127	113	111	100	197	62
35	103	198	104	261	333	195	332	399	136	114	140	101	212	70
Year	**Medium intensity trapping scenario**													
0	0	2	36	84	140	50	149	236	52	17	11	63	89	68
5	16	72	25	69	52	34	37	124	24	21	23	9	31	14
10	49	128	64	101	114	104	41	190	53	48	34	8	61	16
15	55	125	79	146	179	133	36	209	66	63	46	42	93	18
20	49	138	77	156	220	142	43	219	68	63	59	49	111	17
25	50	125	81	148	215	152	52	211	79	68	56	56	114	19
30	52	138	84	153	221	138	67	215	78	64	55	56	106	18
35	51	129	82	155	207	150	72	234	79	71	52	55	102	17
Year	**High intensity trapping scenario**													
0	0	3	44	105	169	62	187	297	57	22	12	74	111	87
5	18	80	25	50	43	29	14	73	18	18	18	2	18	5
10	36	129	57	81	89	88	30	156	47	47	32	6	48	8
15	43	131	63	100	148	114	36	179	58	46	43	35	83	16
20	36	126	80	117	164	115	39	184	57	56	47	44	80	15
25	42	137	71	112	170	122	34	188	53	53	45	40	80	13
30	34	138	71	113	169	115	38	183	60	60	45	49	81	14
35	44	135	70	117	178	111	33	188	49	56	47	45	87	16

Table 4.2: The average trap number of grey squirrels caught for a model realisation for the different control regions for the low, medium and high intensity trapping scenarios. For a description of the location of each of the control regions see Table 4.1.

5. Long term expansion of grey squirrels in northern Scotland in the absence of grey squirrel control.

A key question for red squirrel conservation management is what would be the impact of a reduction or removal of grey squirrel control along the highland line? In Figures 3.2 and 3.4 we highlight the medium term impact (over 35 years) of grey expansion in regions beyond the highland line. In this section we consider grey squirrel expansion over a longer time scale and assess the impact on currently thriving populations of red squirrels in the Highlands of Scotland. To achieve this we extended the region over which the model simulations were undertaken (see Fig. 8.1) and expand the time scale to 70 years (for the default model parameters, see Table 2.1, and where squirrelpox was included). The results are shown in Figure 5.1. This indicates that much of the region north of the highland line is disconnected from regions where red squirrels are currently observed in Highland Scotland. For instance, the Grampian Mountains north of Blair Athol, Glen Shee, Glen Isla, Glen Prosen and Glen Clova prevent grey squirrel expansion into suitable habitat in the Cairngorm National Park (which is home to well-established populations of red squirrels). However, grey squirrel expansion through Angus and into Aberdeenshire does provide a potential long-term route for grey squirrels to enter the Cairngorm National Park. This could occur via a route north of Aberdeen, through Huntly, Dufftown and then along the river Spey valley. This confirms the rationale and highlights the need for the continued effort to remove grey squirrels from Aberdeenshire and for grey control to prevent their expansion through Angus. In the west of Scotland grey squirrel range expansion is less rapid, taking approximately 30 years to spread beyond Crianlarich, the north of Loch Long and Loch Lomond. Red squirrel control (at a medium intensity) could be employed in these regions to protect red squirrel populations in the West Highlands, on the Cowal Penisula and the Mull of Kintyre.

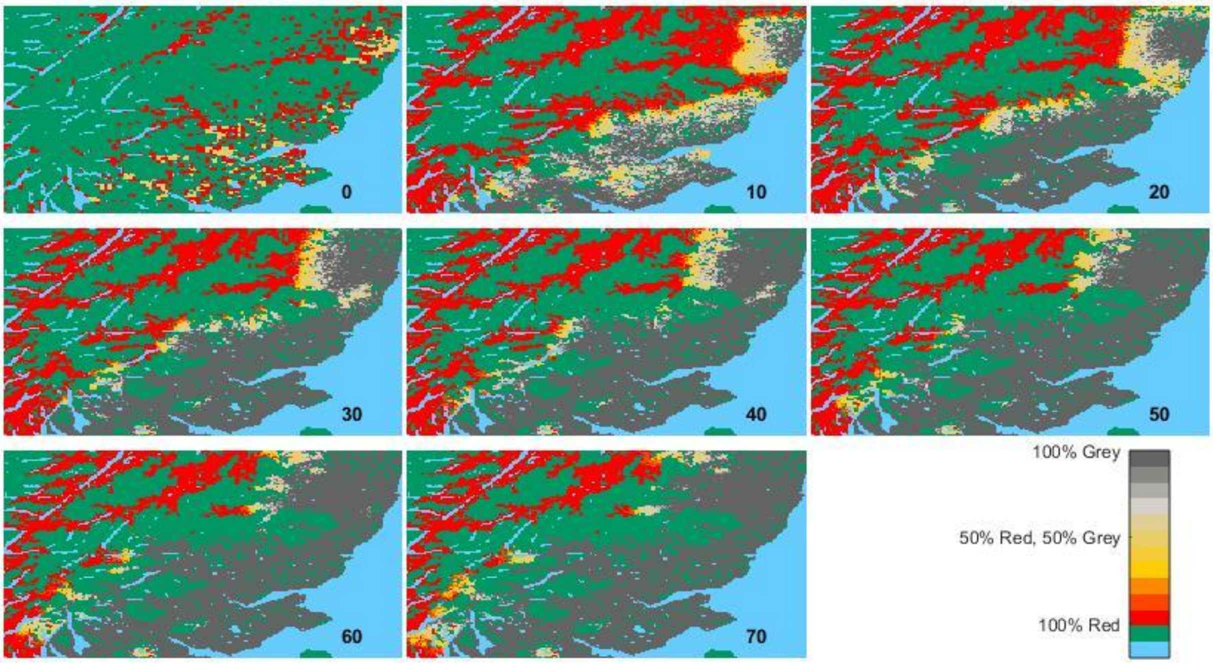

Figure 5.1: Model simulations under default parameter values with squirrelpox in the absence of grey squirrel control showing the percentage occupancy of red and grey squirrels at 10 year intervals (based on ten model realisations). Results are comparable to Figure 3.2 but here we have expanded the geographical region over which the model simulations are undertaken and show results over a longer time period.

6. Conclusions

In this report we used have shown how mathematical modelling that represents realistic, spatial dynamics of red and grey squirrels can be used as a tool to improve the coordination and effectiveness of grey squirrel control to prevent the range expansion of grey squirrels into Highland Scotland. The key findings from the study are:

- Grey squirrel control along the highland line is an effective method of preventing northwards grey squirrel range expansion.

  The model highlights key control regions and indicates the level of control that is required to prevent the range expansion of grey squirrels. The suggested successful levels of control in the model are in line with current estimates of the control effort on the ground (SWT pers. comm.) and therefore indicates that the current effort should be continued if the red – grey squirrel interface at the highland line is to be maintained.

- Medium to high intensity grey squirrel control should be applied in response to grey squirrel observations (where medium equates to 92 and high 137 trap days per 1km by 1km per year – see main text for full details).

  This has the effect of (largely) clearing the control region of grey squirrels and focussing control on the southern boundary of the control region (although control is still required in the interior of the control regions in response to grey squirrel observations and sporadic grey squirrel dispersal).

- Squirrelpox does not impact on red squirrel conservation to the north when grey squirrels are controlled at the highland line.

  When control is applied to prevent grey squirrels from expanding their range beyond the highland line then squirrelpox is also contained to the south of the highland line. Here, since trapping and removal of grey squirrels in the control regions prevents grey squirrel establishment it also prevents the establishment of squirrelpox. In line with previous research (Lurz et al. 2015) the model predicts that squirrelpox will not spread through established red squirrel populations along or to the north of the highland line.

- If resources for grey squirrel control in Scotland are reduced, preventing the range expansion of grey squirrels in Angus and Aberdeenshire should be a priority, but a watching brief should be instituted in other potential areas of dispersal.

  The model evaluation indicates that much of the region north of the highland line is disconnected from other regions in Highland Scotland where red squirrels are currently observed. Therefore, red squirrel populations in the Cairngorm National Park (and further north and west) may not be threatened by a direct northwards expansion of grey squirrels beyond the highland line. However, dispersal through Angus and Aberdeenshire could offer a long-term route for grey squirrel dispersal and establishment in the Highlands, potentially threatening several red squirrel stronghold forests. This therefore highlights the need for the continued effort to remove grey squirrels from Aberdeenshire and for grey control to prevent their expansion through Angus. In addition, expansion of grey squirrels into Argyll over the very long term may still be a possibility, particularly if new habitat networks are established or habitat restructured to favour native woodland.

7. References

Cartmel, S. 2000. Squirrel ecology in a conifer forest in North Wales. Ph. D. Thesis University of London

Chantrey, J., Dale, T. D., Read, J. M., White, S., Whitfield, F., Jones, D., McInnes, C. J., Begon, M. 2014. European red squirrels population dynamics driven by squirrelpox at a grey squirrel invasion interface. Ecol. Evol. 4: 3788-3799.

Jones, H.E., White, A., Lurz, P.W.W. Shuttleworth, C. 2017. Mathematical models for invasive species management: Grey squirrel control on Anglesey. (Submitted).

Lurz, P.W.W., White, A., Meredith, A., McInnes, C., Boots, M. 2015. Living with pox project: Forest management for areas affected by squirrelpox virus. Forestry Commission Scotland Report.

Macpherson, M. F., Davidson, R. S., Duncan, D. B., Lurz, P. W., Jarrott, A., White, A. 2016. Incorporating habitat distribution in wildlife disease models: conservation implications for the threat of squirrelpox on the Isle of Arran. Anim. Conserv. 19: 3–14.

Signorile, A. L., Reuman, D. C., Lurz, P. W. W., Bertolino, S., Carbone, C. & Wang, J. 2016. Using DNA profiling to investigate human-mediated translocation of an invasive species. Biological Conservation 195: 97-105.

Smith, D. F. E. 1999. Grey squirrel, Sciurus carolinensis, population dynamics and feeding in a conifer forest. Ph. D. Thesis, University of London.

SNH 2015. Scottish Strategy for Red Squirrel Conservation. SNH publication. http://www.snh.gov.uk/docs/A1465416.pdf

Tompkins, D.M., White, A.R., Boots, M. 2003. Ecological replacement of native red squirrels by invasive greys driven by disease. Ecol. Lett. 6: 189–196.

White, A., Bell, S.S., Lurz, P.W., Boots, M. 2014. Conservation management within strongholds in the face of disease-mediated invasions: red and grey squirrels as a case study. J. Appl. Ecol. 51: 1631–1642.

White, A., Lurz, P.W.W., Jones, H.E., Boots, M., Bryce, J., Tonkin, M., Ramoo, K., Bamforth, L., Jarrott, A. 2015. The use of mathematical models in red squirrel conservation: Assessing the threat from grey invasion and disease to the Fleet basin stronghold. In: Red Squirrels: Ecology, Conservation & Management in Europe. C.M. Shuttleworth, P.W.W. Lurz, Warrington-Hayward, M. eds. European Squirrel Initiative, Woodbridge, Suffolk, England.

White, A., Lurz, P. W. W., Bryce, J., Tonkin, M., Ramoo, K., Bamforth, L., Jarrott, A. & Boots, M. 2016. Modelling disease spread in real landscapes: Squirrelpox spread in Southern Scotland as a case study. Hystrix, the Italian Journal of Mammalogy 27, 1.

8. Supplementary Information

8.1 Locations of the grey squirrel control regions along the highland line

We provide easting and northing reference locations for the grey squirrel control regions used in this study.

	Control Region	Lower left		Upper right	
		Easting	Northing	Easting	Northing
Garelochhead	1	221000	687000	228000	694000
Arden	2	229000	685000	236000	692000
Rowardennen forest	3	238000	689000	247000	698000
Loch Ard/Achray forest	4	241000	699000	251000	710000
Strathyre forest	5	252000	704000	262000	715000
Eastern Loch Earn	6	263000	718000	272000	727000
Dunkeld (west)	7	294000	737000	303000	747000
Dunkeld (east)	8	304000	740000	313000	751000
Blairgowrie	9	314000	745000	323000	754000
Alyth	10	324000	746000	333000	756000
Kirriemuir	11	334000	751000	343000	760000
Finovan	12	344000	756000	353000	767000
Brechin	13	354000	757000	363000	767000
Montrose	14	364000	757000	374000	767000

Table 8.1: The lower left and upper right grid location for the control regions used in this study (see Fig. 4.1).

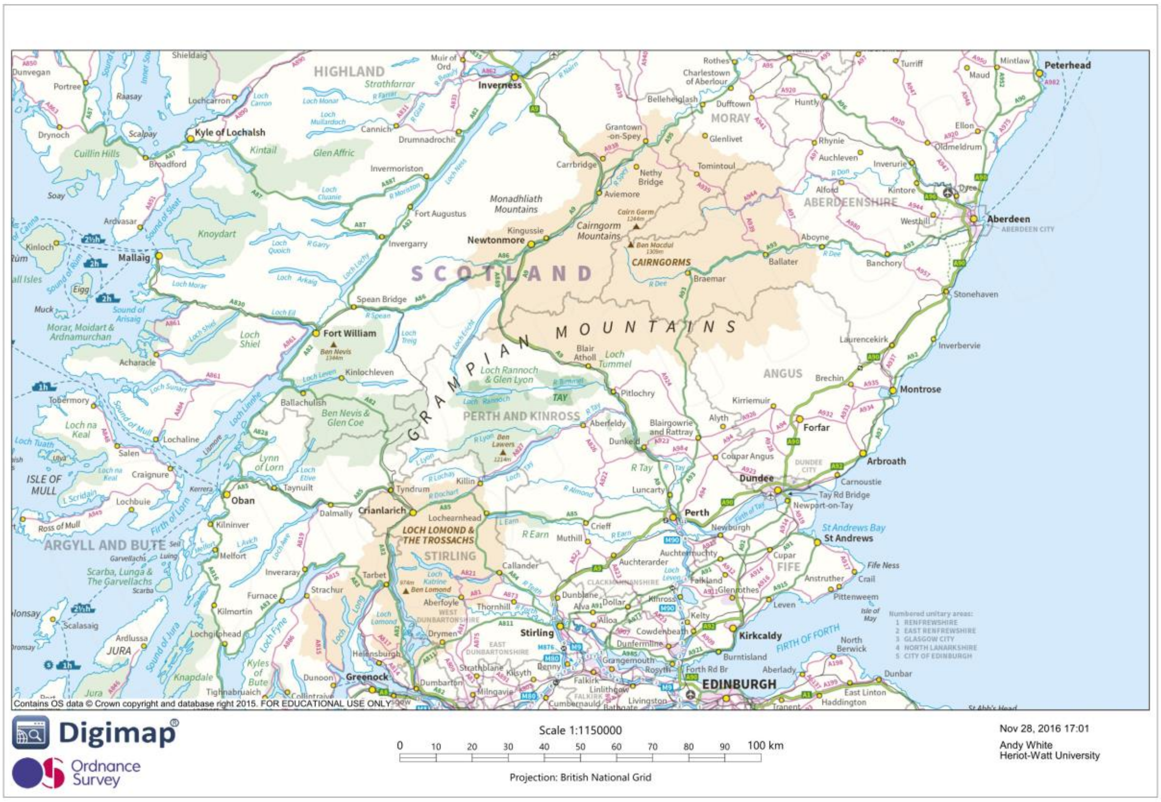

Figure 8.1: A map of the extended region considered in Section 5 (© Digimaps).