Report for Forest Enterprise Scotland

Part 1: Evaluation of Red Squirrel Stronghold Forest Management

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Executive Summary

This report uses mathematical modelling to assess the viability of red squirrels in 6 stronghold regions, as designated by the Forestry Commission Scotland, both with and without the presence of grey squirrels. In particular we assess red and grey squirrel abundance and thereby red squirrel viability under two forest management scenarios: the Stronghold Management strategy, as outlined in [7], and the UK Forestry Standard scenario, as outlined in [10]. The timing of the change to the Stronghold Management strategy and the potential threat from the squirrelpox virus are also considered. The key findings are:

- In the absence of grey squirrels, all 6 strongholds can sustain a viable red squirrel population under the UK Forestry Standard, although the population at Leanachan is predicted to become vulnerable during years of poor seed crop.
- The transition from the UK Forestry Standard to the Stronghold Management strategy reduces the red squirrel abundance in all strongholds during the period of transition, however this reduction is temporary and the population level returns to pre-transition levels in the long-term.
- The size of the reduction is dependent on the scale of alteration needed for transition, with greater alteration leading to larger reductions. Greater diversity in tree species in the stronghold forest can help mitigate the size of the reduction.
- Transition from the UK Forestry Standard to the Stronghold Management strategy offers no discernible benefit in the absence of grey squirrels and is thus unnecessary.
- Grey squirrels can persist in all 6 strongholds under both management strategies, however the Stronghold Management strategy does achieve its key aim of reducing the grey squirrel population size (and thus competition) resident in the stronghold.
- Coexistence of red and grey squirrels is possible only in 2 of the strongholds under the UK Forestry Standard (Eskdalemuir and Daviot Loch Moy) although the red squirrel populations can still become vulnerable in years of bad seed crop. The number of strongholds where coexistence is possible increases to 4 (Daviot Loch Moy, Fleet Basin, Balmoral to Invar and Eskdalemuir) under the Stronghold Management strategy, with Balmoral to Invar and Fleet Basin becoming vulnerable in bad seed crop years.
- The strongholds at Leanachan and Glenbranter cannot support red and grey squirrel coexistence under either management strategy and as such do not constitute ideal locations for strongholds.
- A good stronghold is one that is comprised of tree species that are favourable to red squirrels compared to grey squirrels, has limited access routes for grey squirrel incursion and is located in a wider region that cannot maintain a sizeable grey squirrel population.
- Grey squirrels cannot be removed from the strongholds via management strategy alone due to the surrounding regions acting as reservoirs for grey squirrel immigration. However, local geography could be utilised along with grey squirrel trapping to reduce the level of grey squirrel incursion into the strongholds which will improve red squirrel viability in all of the strongholds.

- Long term population levels are in close agreement regardless of whether the transition to the Stronghold Management strategy is undertaken prior to, or at the instance of grey squirrel arrival in the region surrounding the stronghold. However, given the reduction in red squirrel abundance during the transition, it may be wise to complete the transition before grey squirrel arrival or alternatively supplement the transition with grey squirrel control to reduce competitive effects if the transition is initiated once grey squirrels have arrived.

- The grey squirrel abundance in the 6 strongholds that are examined is not sufficiently large to support the squirrelpox virus, thus the threat to red squirrels within the strongholds from squirrelpox in negligible.

- The Stronghold Management strategy provides an advantage to red squirrels over grey squirrels when compared to the UK Forestry Standard and is therefore preferable in the presence of grey squirrels. In the absence of grey squirrels, the UK Forest Standard is sufficient to maintain viable red squirrel populations.

Contents

1 Background

The Eurasian red squirrel is under threat in the United Kingdom due to the expansion of, and resultant competition from, the North American grey squirrel which was introduced into the British Isles in the 19^{th} century [1]. Scotland has a special responsibility in the conservation of red squirrels in a UK. Recent estimates [2] indicate that nearly 80% of the remaining UK populations are now 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 occurs due to disease-mediated competition and red squirrel decline is significantly faster in areas where grey squirrels are carriers of the squirrelpox virus (SQPV) ([3],[4]). The virus is currently present in some parts of southern and central Scotland and efforts to stem its spread in the south of Scotland have managed to slow, but not prevent, SQPV spread [5]. 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 [6]. One critical aspect of this strategy that is employed nationally in Scotland in order to aid the conservation of red squirrels is the creation and management of designated stronghold regions [7].

1.1 Strongholds

Strongholds are defined by the Forestry Commission Scotland as "large areas of coniferous and mixed forest identified as having the potential to sustain resilient and healthy populations of red squirrels...over the long-term". Management of these strongholds aims to provide red squirrels with a competitive advantage over grey squirrels through the selective felling and replacement of large-seeded broadleaved trees by coniferous tree species that are believed to be disadvantageous to grey squirrels compared to red squirrels (evidence for this viewpoint comes from field studies e.g. at Craigvinean forest, Perthshire, [8],[9]). Such management may allow red squirrel populations to be resilient against incursion by grey squirrels, meaning that the strongholds act as refuge zones for the red squirrels, even if the surrounding region becomes dominated by grey squirrels. There are currently 19 stronghold regions throughout Scotland (Figure 1), partially or fully on National Forest Estate land. The strongholds in the south and west comprise mainly Sitka spruce dominated forests whilst the northern and eastern strongholds are largely Scots pine forest. The island of Arran is also designated as a stronghold due to the advantages inherent in an island habitat [7].

1.1.1 Stronghold Management Strategies

There are currently two guidance schemes regarding forestry management in Scotland that are relevant to the stronghold programme. The stronghold guidance policy outlined in the Forestry Commission Scotland practice note [7] and the UK Forestry Standard [10].

Scottish Stronghold Management Strategy [7]

The Scottish Stronghold Management strategy stipulates that (if necessary) the forest composition should be altered incrementally over a period of roughly 30 years such that a maximum of

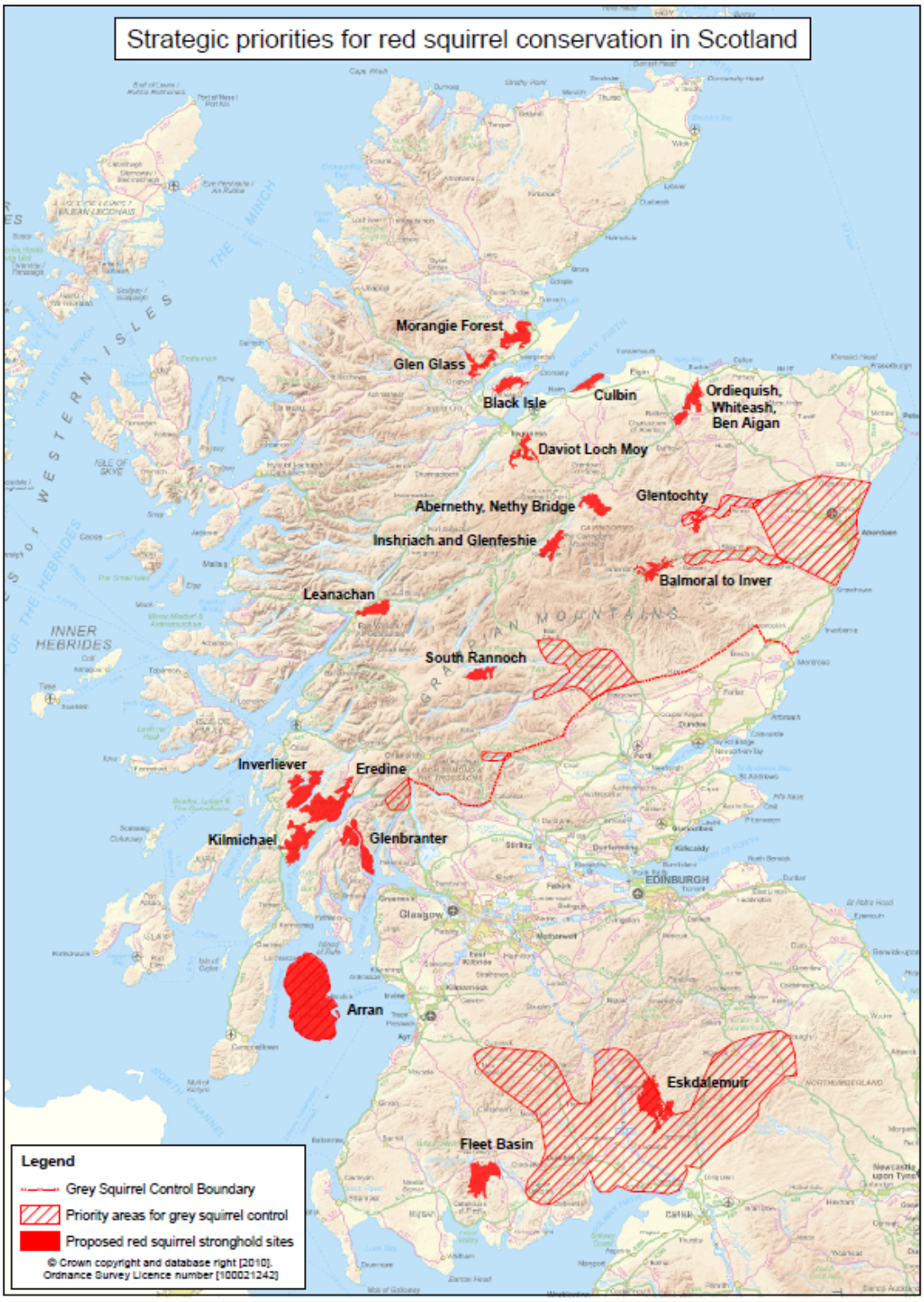

Figure 1: Map of Scotland with the 19 stronghold regions shown in solid red. The map also includes the northern most extent of the grey squirrels as well as regions that are the focus for grey squirrel control. Image courtesy of Scottish Natural Heritage

5% of tree density is comprised of large-seeded broadleaved trees, due to the favourable nature of these tree species to grey squirrels. The removed broadleaved trees are to be replaced by coniferous trees that ideally provide an advantage to red squirrels through the discouragement of grey squirrels (see Table 1 for list of favourable and discouraged tree species). The strategy also encourages the diversification of coniferous tree species, with no single non-native species constituting more than 80% of the forest. This is due to the advantageous nature of a diverse forest regarding the provision of a more continuous resource supply, which in turn increases the viability of a stable red squirrel population. Furthermore, native woodland should diversify using other native tree species. Alongside this, forestry management should aim to create an age structure that has ideally less than one third of trees be classed as young (not of seed bearing age) and the other two-thirds or more consisting of thicket and mature trees.

Favoured	**Secondary**	**Neutral**	**Discouraged**
Douglas Fir	*Bird Cherry*	*Alder*	Beech
Larch	*Blackthorn*	*Ash*	Chestnuts
Scots Pine	*Bramble*	*Aspen*	*Hazel*
Corsican Pine	*Dog Rose*	*Birches*	*Oaks*
Lodgepole Pine	*Hawthorn*	*Cypress*	Sycamore
Norway Spruce	*Wild Cherry*	Other Firs	
Sitka Spruce	*Wych Elm*	*Holly*	
Yew		*Juniper*	
		Rowan	
		Western Hemlock	
		Western Red Cedar	
		Willows	

Table 1: Tree species that benefit red squirrels (favoured), trees and shrubs that provide some benefit to red squirrels (secondary), trees and shrubs that offer no advantage to either red or grey squirrels (neutral) and tree species that offer grey squirrels a competitive advantage (discouraged). Species that are native to Scotland are italicised.

UK Forestry Standard [10]

The UK Forestry Standard stipulates that there should be a maximum of 75% of a single species in a forest, there should be a minimum of 10% of other tree species along with a minimum 5% broadleaved trees and shrub. The remaining land should constitute either open ground or ground managed for conservation and enhancement of biodiversity. Alongside this, diversification should be pursued if possible. Almost all of the current stronghold regions in Scotland, and all of the strongholds considered in this report, meet these guidelines. Therefore the species composition in each stronghold can remain unchanged under this regime.

Based on these different strategies a subset of the 19 stronghold regions have been selected for study in this report, with the main factor driving the decision to include a region being whether there is a noticeable difference in forest composition under the two regimes. The chosen strongholds are also geographically dispersed to allow different regional compositions to be investigated. The full list of strongholds to be studied is given in Table 2.

Region	Stronghold
East	Balmoral to Invar
	Daviot Loch Moy
Central	Leanachan
West	Glenbranter
South	Fleet Basin
	Eskdalemuir

Table 2: Strongholds to be studied in this report, grouped by geographic location (see Figure 1)

1.2 Aims

This assessment aims to apply established mathematical models ([11],[12]) of the red-grey-squirrelpox system that includes grey squirrel control to examine red and grey squirrel habitat suitability and potential management needs to ensure a long-term future for native red squirrels in Scottish forests. Specifically, this assessment shall assess the efficacy of the current stronghold regions in maintaining a resilient and healthy red squirrel population under the stronghold forest management guidelines.

1.2.1 Objectives

1. Use the model to examine red squirrel viability under the principles of Stronghold Management practice and compare this to the UK Forestry Standard management practice which is used for commercial objectives for the chosen case study stronghold regions.

2. Use the model to identify suitable forest regions for red squirrel conservation that exist on the National Forest Estate that could supplement the existing stronghold regions. Suitable regions north of the highland line, where there are no grey squirrels present, could act as 'safe havens' for red squirrels whilst regions south of the highland line shall be ranked according to the level of grey squirrel control required to ensure red squirrel persistence.

3. Determine the impact of squirrelpox on red squirrel persistence in the suitable forest regions identified as part of objective (2).

4. Provide general recommendations and insight into management strategies for the conservation best practice in Scotland. These strategies will be applicable to the conservation of red squirrels in the UK and Ireland where red squirrels are under threat from grey squirrel replacement.

1.2.2 Agreed Outputs

The output will take the form of an intermediate and final project report. Objective (1) will be delivered by 31 March 2019 followed by a meeting with FES\FCS to discuss preliminary findings and to obtain feedback. Objectives (2)-(4) will be delivered by 31 March 2020.

2 Mathematical Model

A mathematical model is used to represent the population density of red and grey squirrels, as well as the prevalence of the squirrelpox infection, in a specific geographic region that is discretised into 1km by 1km grid squares. These grid squares are linked via dispersal (since individual squirrels can move freely between adjacent areas) with the carrying capacity of each grid square defined using land cover data in order to suitably approximate the heterogeneous landscape of Scotland. The changes to the land cover that occur under the differing forest management scenarios are also included.

2.1 Changing Forest Composition

The initial forest composition was attained by using the GRASS GIS software package (`https://grass.osgeo.org`) along with the National Forest Inventory Scotland 2016 and National Forest Estate Scotland 2017 digital land cover datasets (supplied by Forestry Commission Scotland) to extract information on the primary tree species in a 25m by 25m area. The National Forest Estate Scotland dataset contains information regarding the tree species outlined in Table 1 whereas the National Forest Inventory Scotland dataset contains information only as to whether the trees are either broadleaf or conifer. This data was then supplemented by information from the Scottish Natural Heritage 2007 dataset which has information about the urban environment. The relevant sections of these three datasets were combined which resulted in a 1km by 1km scale grid map of Scotland that details the proportion of land covered by each of the features in the datasets. In order to alter the composition of the forest in a stronghold region, broadleaf trees (those species denoted 'Discouraged' in Table 1) are removed from each grid square of the map that contain broadleaf trees in sufficient volumes such that, after 30 years, the stronghold will contain a maximum of 5% broadleaf in any given grid square. This method leads to the possibility of a particular stronghold having less than 5% broadleaf as a measure of the total tree density, however it will ensure that there are no regions within the stronghold that could support a grey squirrel population. Once the broadleaf trees have been removed, it is assumed that they are replaced by favoured conifers in the same year, with the density of each conifer species that is planted in a given grid square being inversely proportional to the existing species densities across the entire stronghold. This is done to increase the diversity of species in the stronghold, although new species, and species that account for less than $1/16^{th}$ of the forested area in the given grid square, are not introduced. It is assumed that the planted conifers require a fixed time period, dependent on the species (see Table 3), before they reach seed bearing age and contribute to the forests carrying capacity. Once the trees have reached maturity and are seed producing, no distinction between them and pre-existing trees of the same species is made. The age structure is assumed to be fixed (See Table 3) such that only a percentage of the tree density in a given grid square contributes to the carrying capacity. No changes were made to the forest outside of the stronghold regions where UK Forest Standards are assumed to apply.

2.2 Carrying Capacity

The forest composition data can be combined with estimates of squirrel density in different habitat types to produce a carrying capacity for each 1km grid square for red (K_R) and grey

Broadleaf	**Seed Bearing Age (Years)**	**Seed Bearing Proportion (2 d.p.)**
Beech	50	0.50
Chestnut	40	0.60
Hazel	1	1.00
Sycamore	25	0.65
Oak	40	0.60
Conifer	**Seed Bearing Age (Years)**	**Seed Bearing Proportion (2 d.p.)**
Larch	15	0.68
Lodgepole Pine	15	0.70
Scots Pine	15	0.73
Corsican Pine	25	0.50
Douglas Fir	30	0.50
Norway Spruce	30	0.54
Sitka Spruce	30	0.40
Other	**Seed Bearing Age (Years)**	**Seed Bearing Proportion (2 d.p.)**
Neutral Species	N/A	N/A
Secondary Species	1	1.00
Other Broadleaf	30	0.63
Other Conifer	25	0.50

Table 3: All the tree species that are considered in this model. Only the density of favourable and discouraged species are altered, hence the secondary and neutral species are grouped together. Other Broadleaf and Other Conifer refer to National Forest Inventory data which does not specify individual tree species. Hence, the values for these species are calculated as the average of the other broadleaf or conifer trees respectively. Seed bearing age refers to the age at which they start producing seeds whilst seed bearing proportion is the fraction of trees that are seed bearing, which is found using the equation $\frac{F-M}{F}$ where F is the age at which these trees are either felled commercially or the age at which they stop producing reliable seed crops and M is the age at which they start to bear seeds. Neutral species do not contribute to the carrying capacity for red or grey squirrels, hence the data is not included. All data from Aldhous [13] except age of felling data which comes from Savill [14].

(K_G) squirrels which signifies the potential population density that the landscape can support. At this stage seed crop dynamics can be introduced. It is known that trees have mast years during which they produce a higher than average yield of seeds and that these mast years are largely cyclical and occur simultaneously for the majority of trees within a single species that are present in a local, connected forest. During mast years a tree species can support a higher squirrel population density than in non-mast years. During the non-mast years the trees can either undergo 'intermediate' or 'poor' years in terms of cone or seed production, which introduces variability into the availability of seed food and thus squirrel densities (and how many squirrels a forest patch can support), squirrel reproductive success and survival [15], [16]. The intermediate and poor years have been averaged in this modelling framework to produce a single non-mast value for each species. This value therefore represents a combined average of poor and intermediate seed years in order to simulate red squirrel population dynamics in

years of reduced seed food availability. Where data were available in the literature for specific tree species these have been used (Table 4); where they were not available they have been conservatively set at being one quarter of the mast values. The latter estimate is based on data from Spadeadam Forest, Northern England [17], an analysis of 16 years of cone crop data for Sitka spruce and Scots pine at Kidland Forest, Northern England [18] and an examination of a 25 year cone data set for Scots pine [19].

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

Table 4: Carrying capacities for red and grey squirrels, in individuals per hectare, for mast and non-mast years for each of the tree species considered in the model. Values for Other Broadleaf and Other Conifer are averages of the known broadleaf or conifer trees. The last column is the (average) interval between mast years. Mast interval data is based on Aldhous [13].

2.3 Model Framework

The model framework is based on previous mathematical models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches [3] to develop a spatial, stochastic model, ([20]; [21]; [5]; [22]; [23]; [12]). 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):

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

where

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

represents the periodic birth rate of grey squirrels. This expression assumes that births only occur in the first 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 [3] the two species have the same rate of adult mortality ($b = 0.9$: [25]) but different rates of maximum reproduction ($a_R = 3, a_G = 3.4$ adapted from [3] 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 $c_R = 0.61$ [9]. Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient $\beta = 1.1$ [24]. Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ [3]. The susceptibilities to crowding (q_R, q_G) are set to ensure the average density over one year is equal to the carrying capacity in each grid square for that year. 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 [26]. 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 5.

2.4 Initial Conditions

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

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

Table 5: Stochastic model events that govern the dynamics that occur within each 1km grid square. The parameters representing control and dispersal were fitted with observed data on the Island of Anglesey [20]. 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 [20].

3 Results

3.1 Daviot Loch Moy

The Daviot Loch Moy stronghold is located between the town of Daviot and Loch Moy, both of which are to the south-east of Inverness (Figure 2). The stronghold, approximately 89 km^2, is part of the National Forest Estate and as such species specific information about its composition is available which reveals a diverse forest with no single dominant species (Figure 3).

Figure 2: Map of the the region surrounding the Daviot Loch Moy stronghold. The stronghold is the forested region south-east of the B851 (see Figure 4 for stronghold outline). Image from Digi-Maps, Crown copyright and database rights 2018 Ordinance Survey

According to the available land cover data, the regions to the east and south of the stronghold are mountainous and so do not provide suitable habitat. The remainder of the region is capable of supporting both red and grey squirrels (Figure 4). The effect on the carrying capacity of the changes to the forest composition that are necessary to transition to the Stronghold Management strategy can be seen in Figure 5. The main point of note is the reduction in grey squirrel carrying capacity, with the large spikes in capacity that are apparent in the UK Forestry Standard strategy being removed under the Stronghold Management strategy. There is little alteration to the carrying capacity for red squirrels.

The red squirrel population dynamics can be seen in Figure 6 which show a reduction in the red squirrel abundance, up to a maximum reduction of approximately 6.5%, during the period that the forest is undergoing alteration to its composition. The size of the reduction, and the fact that the two management strategies have the same long-term abundance levels (approx. 305 individuals), occurs due to the Daviot Loch Moy stronghold having a good tree species diversity which helps to mitigate the effects of the changes. This trend is highlighted by Figure 7 which shows the difference in population density between the two management strategies.

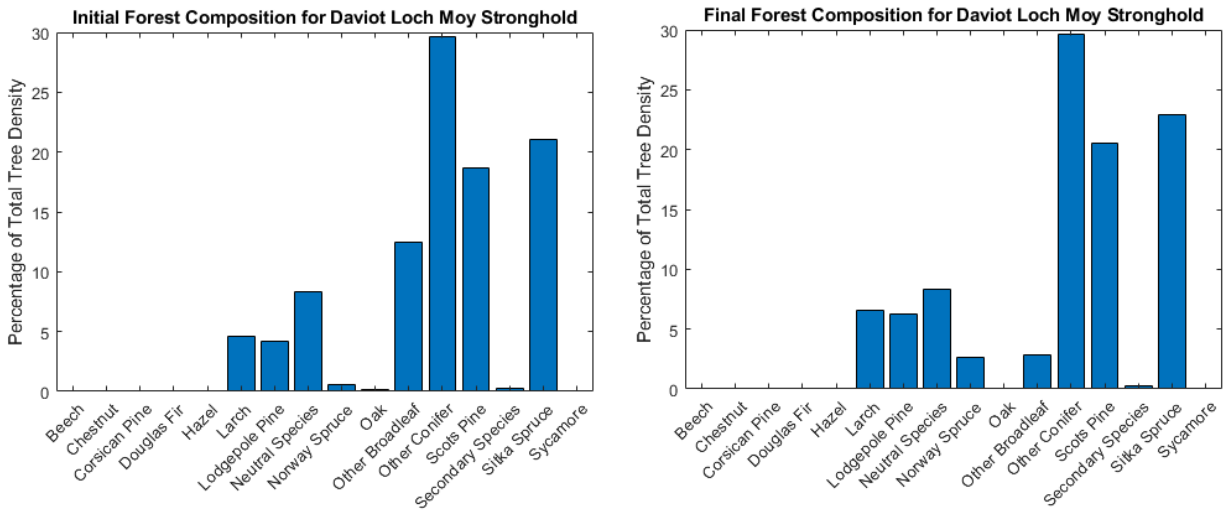

Figure 3: Initial and final forest composition for the Daviot Loch Moy stronghold. All values are percentages of total tree cover.

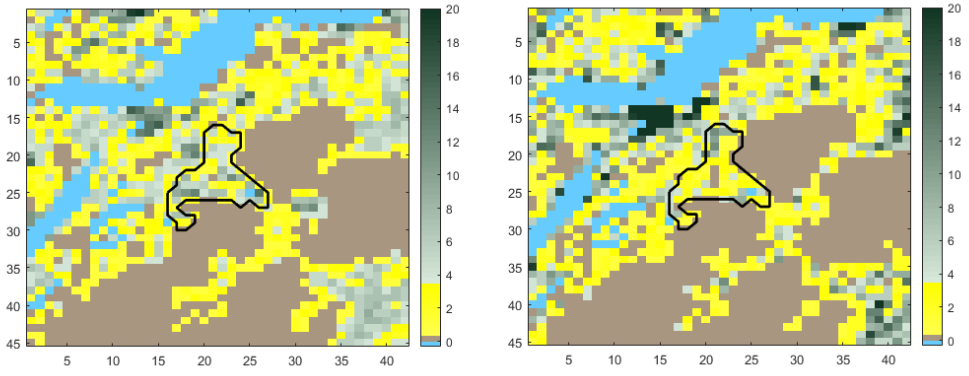

Figure 4: Carrying capacity for red (left) and grey (right) squirrels in the region of Daviot Loch Moy. The stronghold region is outlined in black.

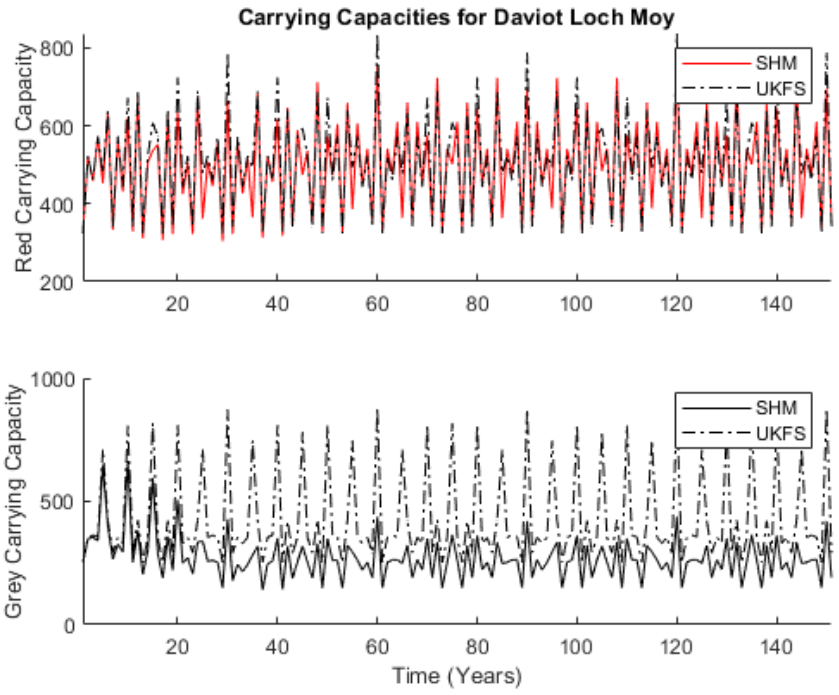

Figure 5: Yearly carrying capacity under Stronghold Management and UK Forestry Standard strategies. The dynamics each strategy undergoes is due to seed crop dynamics and the difference between the two lines (solid and dashed) are due to the changes in forest composition.

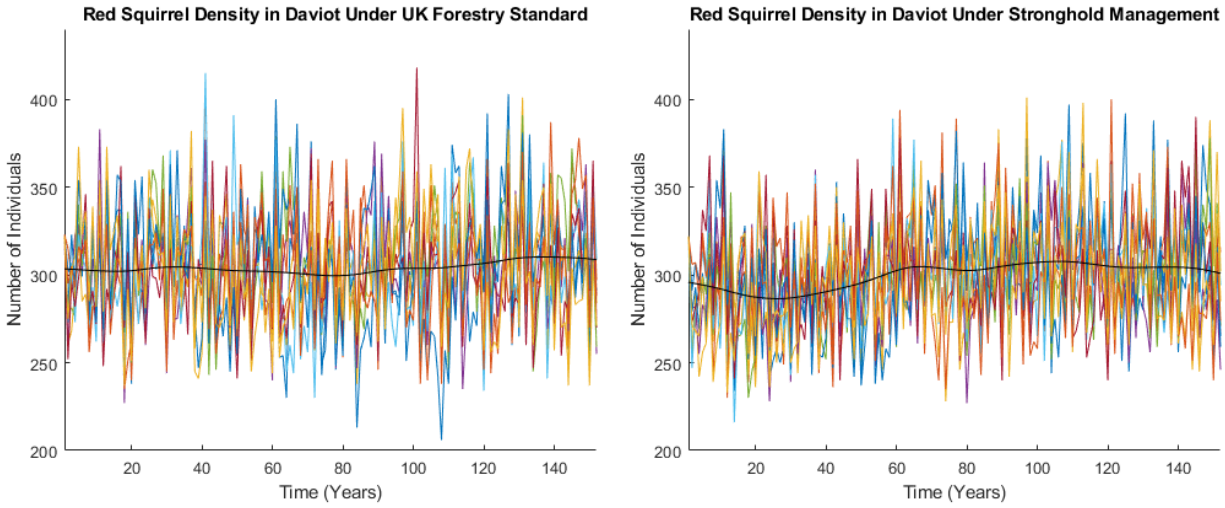

Figure 6: Red squirrel density under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. All 10 simulations are shown simultaneously.

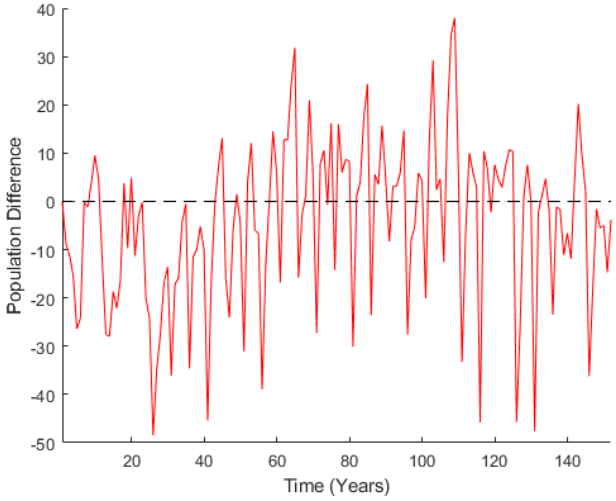

Figure 7: The difference in the average population density of red squirrels in the Daviot Loch Moy stronghold. The plot shows the population under the Stronghold Management strategy minus the population under the UK Forestry Standard strategy. Thus negative values indicate that the population is higher under the UK Forestry Standard strategy and positive values indicate that the population is higher under the Stronghold Management strategy.

3.1.1 Introduction of Grey Squirrels

There are currently no grey squirrels in the region of Daviot Loch Moy, with the northern extent of grey squirrels indicated by the grey squirrel control line which can be seen in Figure 1. Thus the model can be used to assess the potential impact of grey squirrels on red squirrel viability if grey squirrels were to enter the region and become a threat. To do this grey squirrels were introduced into the model in a region around the stronghold and the effects of the changing forest composition on the competitive interaction between red and grey squirrels was examined. Grey squirrels were introduced at the start of the simulation in three regions around the stronghold, to the north-east, north-west and south-east, as can be seen in Figure 8 which shows the density and geographic spread of grey squirrels. Grey squirrels were introduced into a specific grid square if the carrying capacity of that square was greater than 5 individuals, with the number of individuals introduced being equal to half of the carrying capacity (rounded down). Figure 9 shows the impact of the two forest management strategies for red and grey squirrels. The red squirrel population fares better under the Stronghold Management strategy, and the grey squirrel population conversely fares worse. Figure 10 shows the population sizes for red and grey squirrels under the two forestry management strategies. The Stronghold Management strategy leads to a red squirrel population that is approximately 45% larger than that under the UK Forestry Standard (average of 120 individuals under the UK Forestry Standard and 175 individuals under the Stronghold Management strategy). Conversely the Stronghold Management strategy leads to an approximate decline of 55% in the grey squirrel population compared to the UK Forestry Standard (average of 190 individuals under UK Forestry Standard compared to 85 under the Stronghold Management strategy). However, the Stronghold Management strategy does not prevent grey squirrels from residing in the stronghold, primarily due to continuous dispersal into the stronghold from larger grey squirrel populations in the wider region.

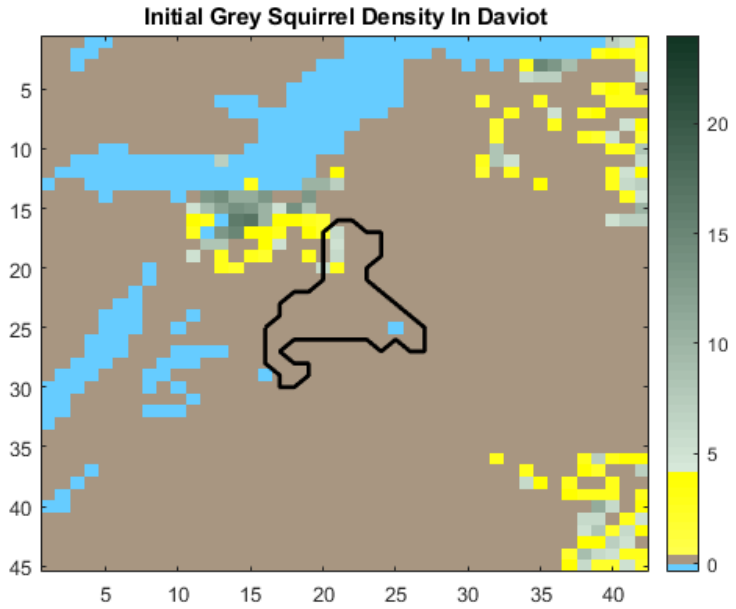

Figure 8: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the stronghold at Daviot Loch Moy

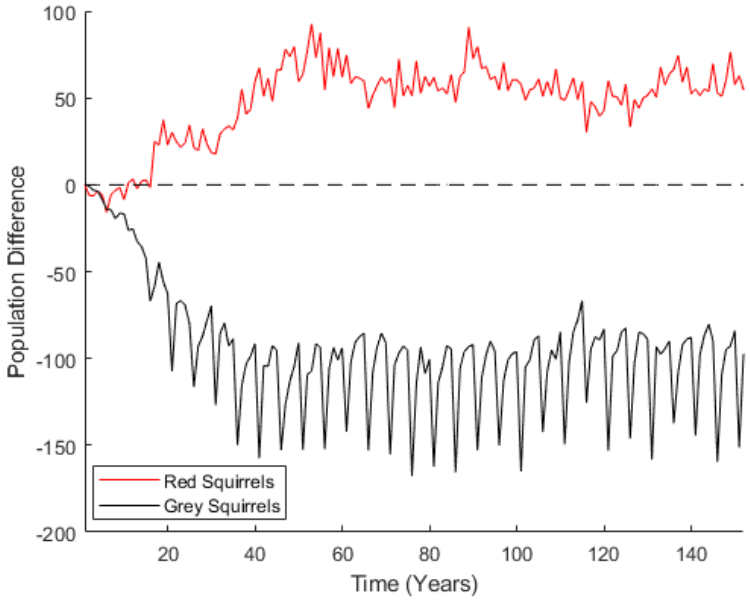

Figure 9: Difference in population density for Daviot Loch Moy for the introduction of grey squirrels at the beginning of the simulation. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

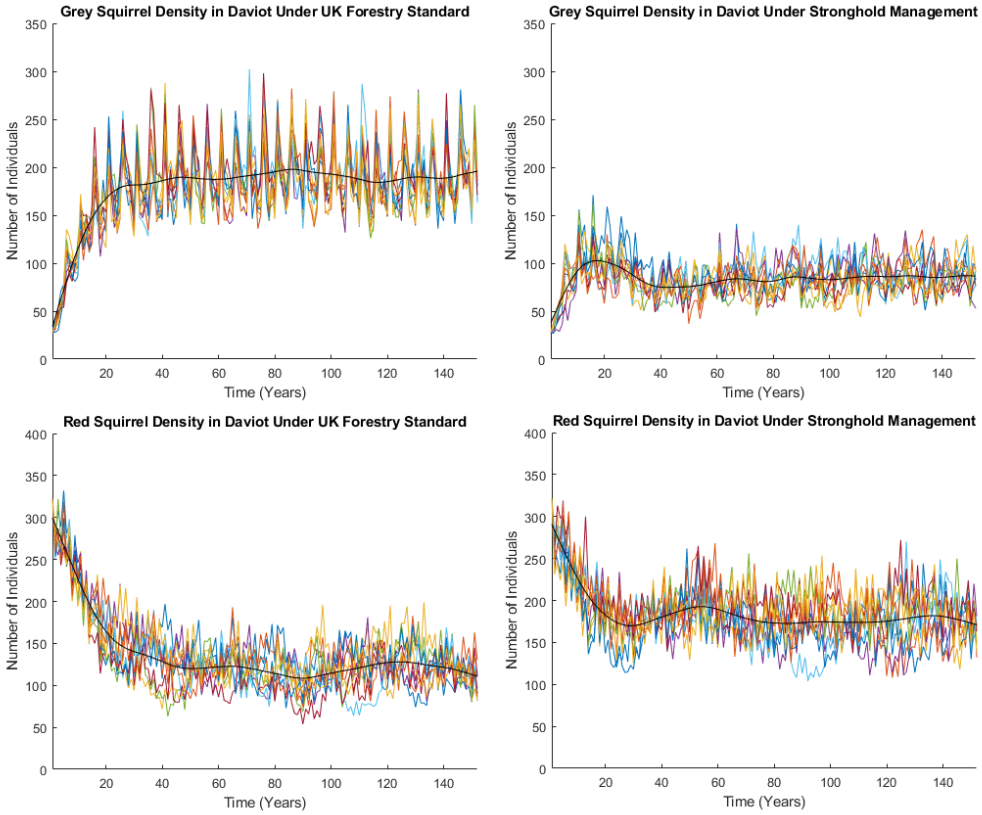

Figure 10: Population density for grey (top) and red (bottom) squirrels in Daviot Loch Moy stronghold that have been introduced during the first year of the simulation. Black curve indicates average density. It has been suggested that a minimum viable red squirrel population size is 125 individuals (SNH pers. comm.). The red squirrel population size under the UK Forestry Standard strategy is approximately 120 individuals, thus the possibility of red squirrel extinction in Daviot Loch Moy under the UK Forestry Standard should not be dismissed. Despite the grey squirrel population averaging only 85 individuals, there is no risk of the Stronghold Management strategy leading to grey squirrel extinction in the stronghold due to continuous dispersal from the wider region.

Figure 11 shows the density of each squirrel species under both management strategies at the end of the 150 year simulation. As can be seen, the Stronghold Management strategy reduces the number of grey squirrels that can reside in the north of the stronghold, which in turn leads to a higher red squirrel population in that region. Figure 12 shows the population dynamics when grey squirrels are introduced after 50 years of simulation. These results are similar to the findings when grey squirrels are introduced prior to forest alterations in the Stronghold Management scenario (Figure 10). This indicates that it may not be necessary to complete the forest alterations before grey squirrels are present in the area surrounding the stronghold.

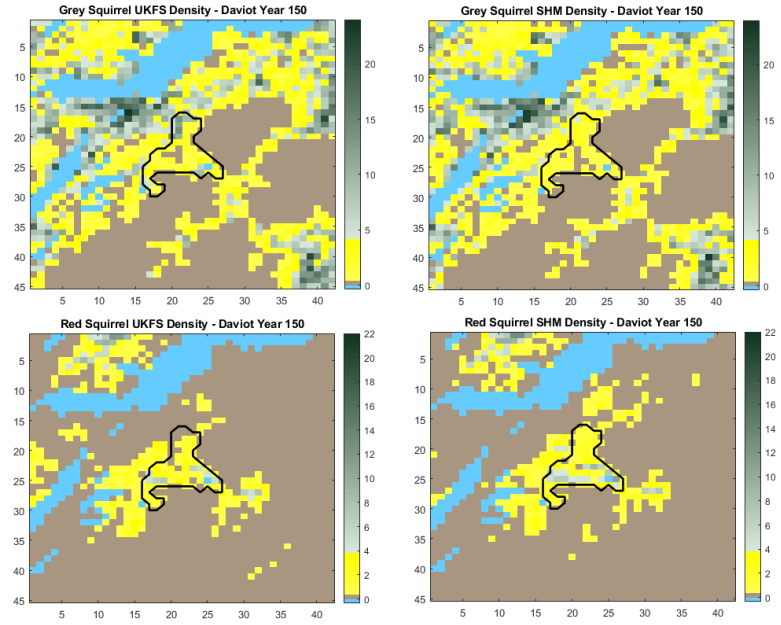

Figure 11: Population density for grey (top) and red (bottom) squirrels under the UK Forestry Standard (left) and Stronghold Management (right) strategies. Note that red squirrels survive in the stronghold and in nearby regions under the UK Forestry Standard scenario, indicating that Daviot Loch Moy acts as a natural stronghold (assuming that the population is large enough to be viable (SNH pers. comm.)).

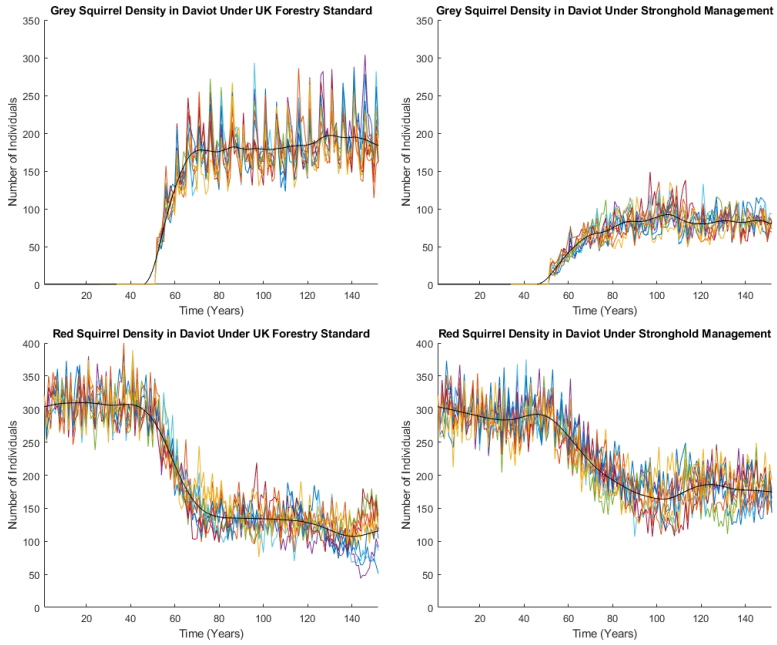

Figure 12: Population density for grey (top) and red (bottom) squirrels in Daviot Loch Moy stronghold that have been introduced during year 50 of the simulation. Black curve indicates average density.

3.1.2 Introduction of Infection

If grey squirrels were to become established within the stronghold and the surrounding area then the potential risk of squirrelpox outbreaks would increase. Thus grey squirrels that are infected with squirrelpox are introduced into the region surrounding the stronghold in order to assess how the differing management strategies affect the spread and severity of the virus. A pair of infected grey squirrels were introduced in years 10, 15 and 20 of the simulation into two adjacent grid squares in each of the regions where non-infected grey squirrels were introduced in order to provide the infection with a good chance of becoming established. Figure 13 shows how the population size for red and grey squirrels differs under the different management strategies. As can be seen, the difference in population is remarkably similar to that in Figure 9, which has no infection, including in terms of numbers of individuals. This result can be explained by Figure 14 which shows that, despite there being an initial epidemic of infection following the introduction of the infected individuals, the disease fades out in the stronghold (and in the neighbouring wider populations) under both forest management strategies which indicates that the population density of grey (and red) squirrels is insufficient to support a stable infected population (a result that has been reported in other model studies ([27], [11])). Consequently, the population size and geographic spread of each squirrel species, and the changes introduced by the Stronghold Management strategy, follow the same trend as in Figure 10 (see Figure 15).

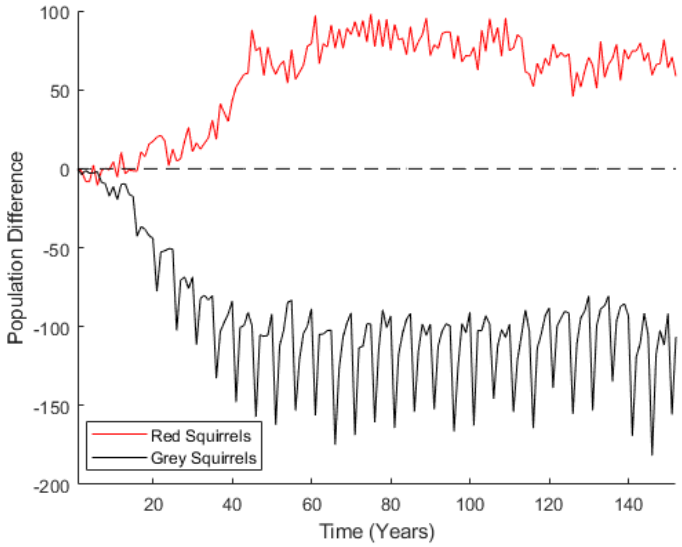

Figure 13: Difference in population density for Daviot Loch Moy where susceptible grey squirrels were introduced at the beginning of the simulation, as above, along with infected grey squirrels that were introduced in pairs in years 10, 15 and 20, with a total of 12 infected greys added each year. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

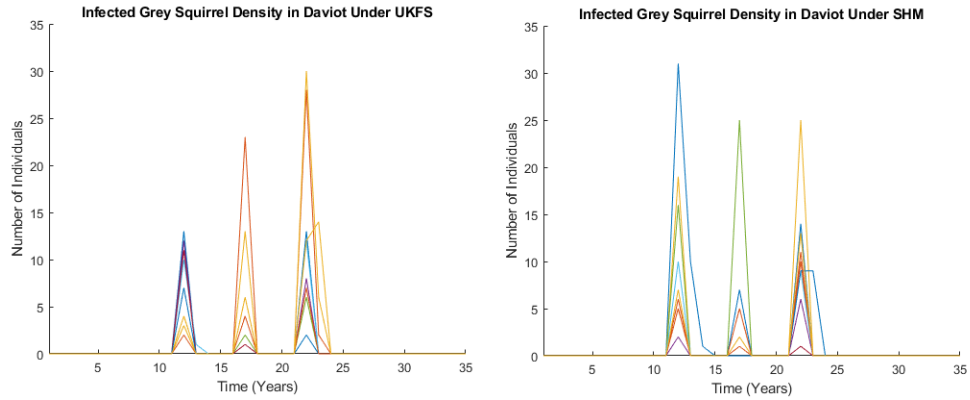

Figure 14: Population dynamics of infected grey squirrels in Daviot Loch Moy stronghold under the UK Forestry Standard (left) and Stronghold Management (right) strategies.

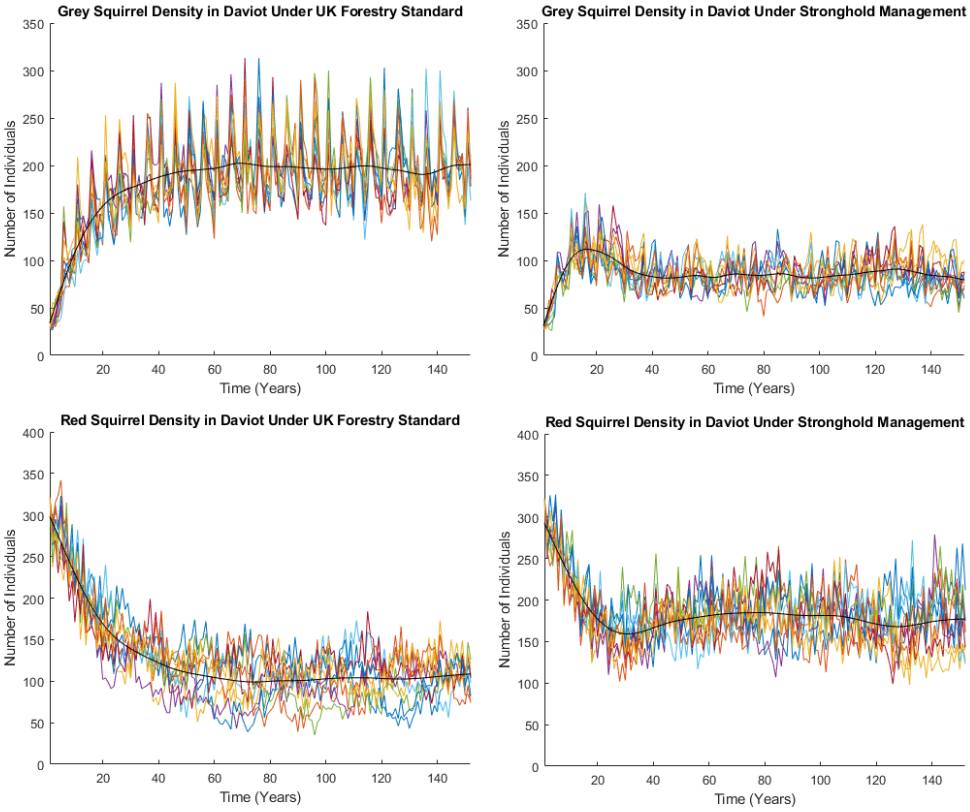

Figure 15: Population density for grey (top) and red (bottom) squirrels in Daviot Loch Moy stronghold that have been introduced in the first year of the simulation, along with infected grey squirrels introduced in years 10, 15 and 20. Black lines indicate average population size.

3.2 Balmoral to Invar

The Balmoral to Invar stronghold, which is approximately 89km^2 in area, is located on the Balmoral Estate (Figure 16), a private estate owned by the British royal family, which in turn is located in the Cairngorms National Park. The primary tree species in the stronghold is listed as Other Conifer due to the private ownership of the land which means that only National Forest Inventory data is available. The initial and final forest composition in the stronghold can be found in Figure 17.

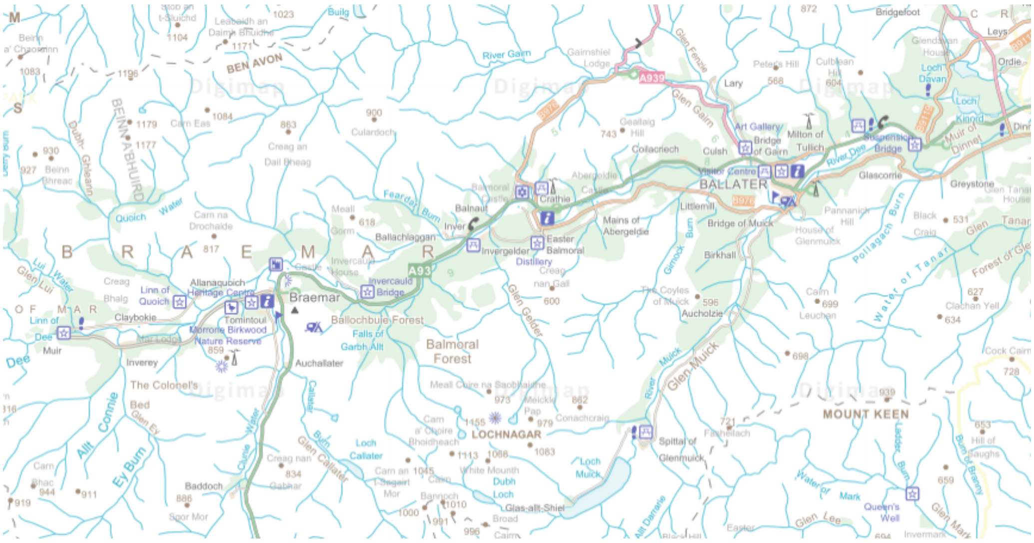

Figure 16: Map of the Balmoral Estate (see Figure 18 for stronghold outline). Image from Digi-Maps, Crown copyright and database rights 2018 Ordinance Survey

The strongholds position within the Cairngorms and along the Dee river valley lead to the carrying capacity of the region being restricted to the valley, as can be seen in Figure 18 which shows the carrying capacity for red and grey squirrels before any changes have been made to the forest composition. The effect on the carrying capacity of the changes to the forest composition that are necessary to transition to the Stronghold Management strategy can be seen in Figure 19 which tracks the changes to the strongholds carrying capacity under the Stronghold Management strategy compared to the UK Forestry Standard strategy for both red and grey squirrels. The change in the grey squirrel carrying capacity is easily discerned, with the large spikes in carrying capacity (due to broadleaved trees undergoing mast years) being absent under the Stronghold Management strategy. Conversely, the carrying capacity for red squirrels does not undergo such a noticeable change, with the reduction in the magnitude of the intermittent spikes in capacity being the only change of note. The dynamics of the red squirrel population under the Stronghold Management and the UK Forestry Standard strategies can be seen in Figure 20. During the period of forest alteration the red squirrel population is reduced under the Stronghold Management strategy by a maximum of approximately 12.5% which is larger than was seen at Daviot Loch Moy, primarily due to the greater species diversity at Daviot Loch Moy compared to Balmoral to Invar. However the population subsequently recovers to a level comparable to that under the UK Forestry Standard (approx. 315 individuals).

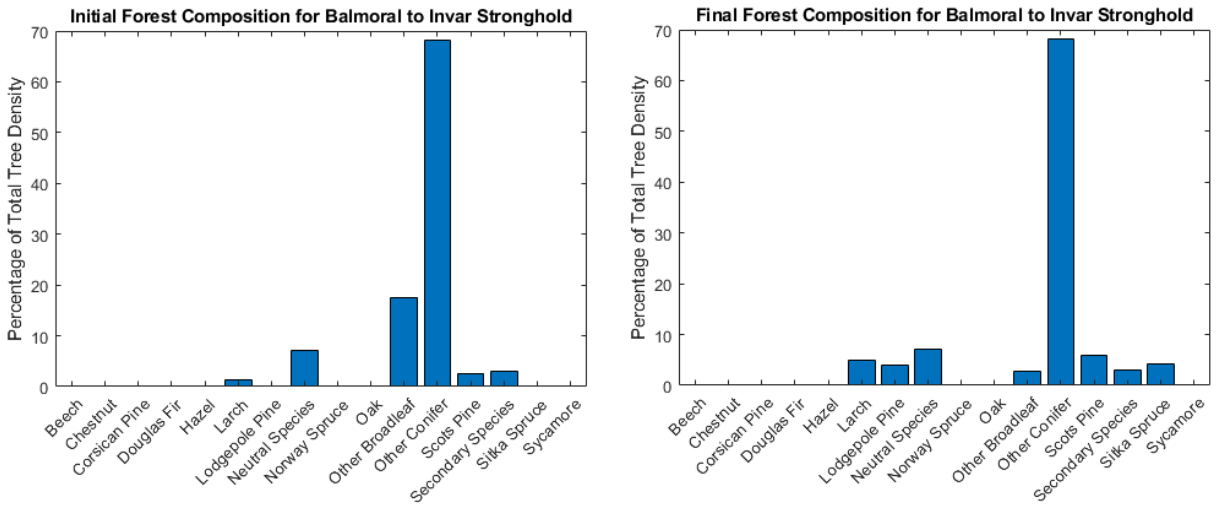

Figure 17: Initial and final forest composition for the Balmoral to Invar stronghold. All values are percentages of total tree cover. Note, Lodgepole pine and Sitka spruce densities are above the threshold value in the initial composition despite not being visible in the image.

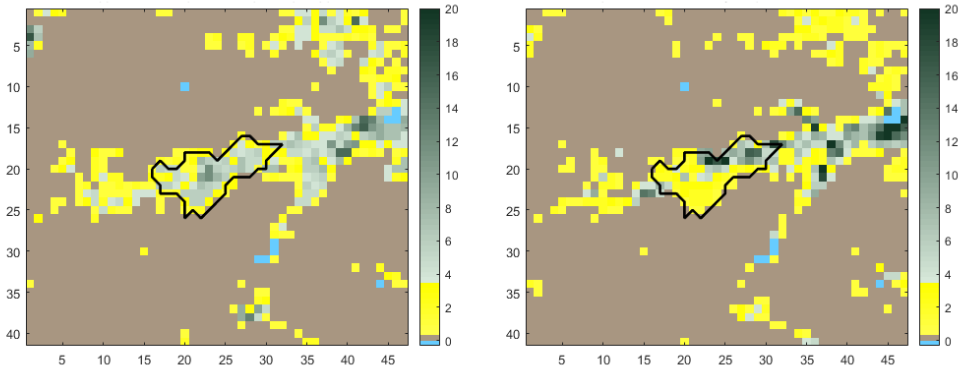

Figure 18: Carrying capacity for red (left) and grey (right) squirrels in the region of Balmoral. The stronghold region is outlined in black.

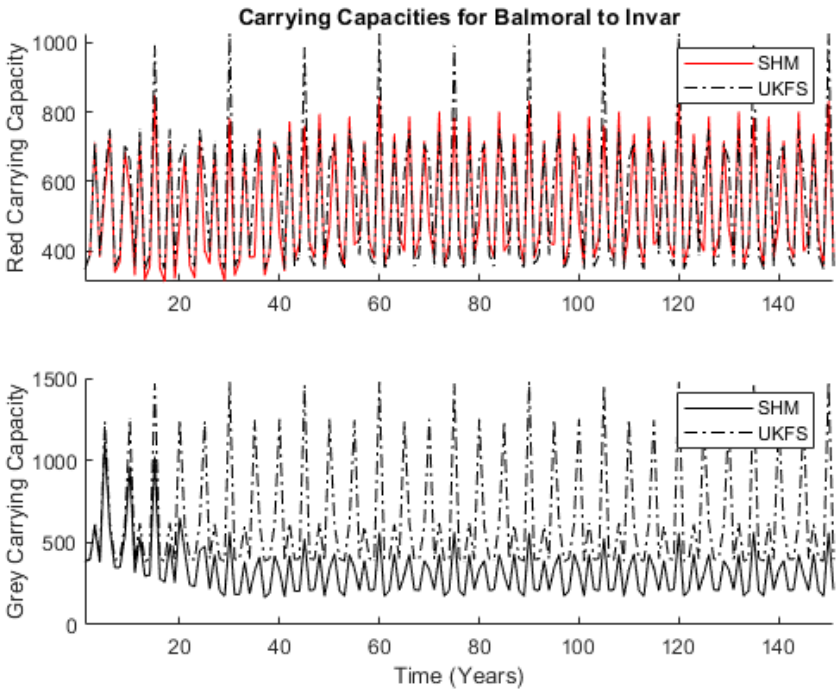

Figure 19: Yearly carrying capacity under Stronghold Management and UK Forestry Standard strategies. The dynamics each strategy undergoes is due to seed crop dynamics and the difference between the two lines (solid and dashed) are due to the changes in forest composition.

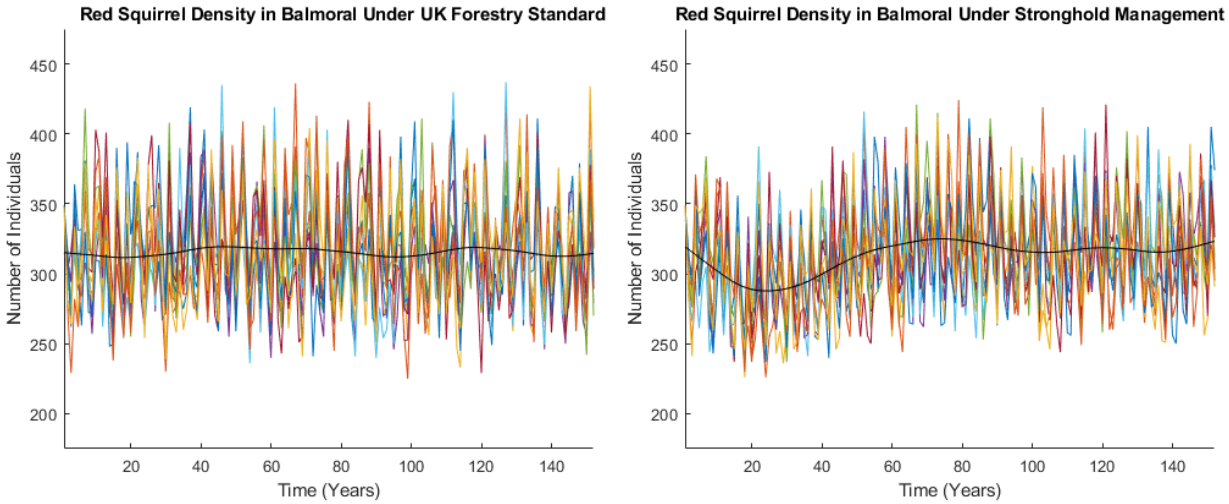

Figure 20: Red squirrel density under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. All 10 simulations are shown simultaneously.

3.2.1 Introduction of Grey Squirrels

There are currently no grey squirrels present in the region of Balmoral to Invar, however Figure 1 indicates that the region to the east of the stronghold (encompassing the Dee valley and the area around Aberdeen) are priority areas for grey squirrel control. Grey squirrels were introduced in the model in order to assess the effect of the changing forest composition on the competitive interaction between red and grey squirrels in the Balmoral to Invar stronghold. Grey squirrels are introduced into the region to the east of the stronghold in the same manner as for Daviot Loch Moy, with Figure 21 showing the areas where grey squirrels were introduced.

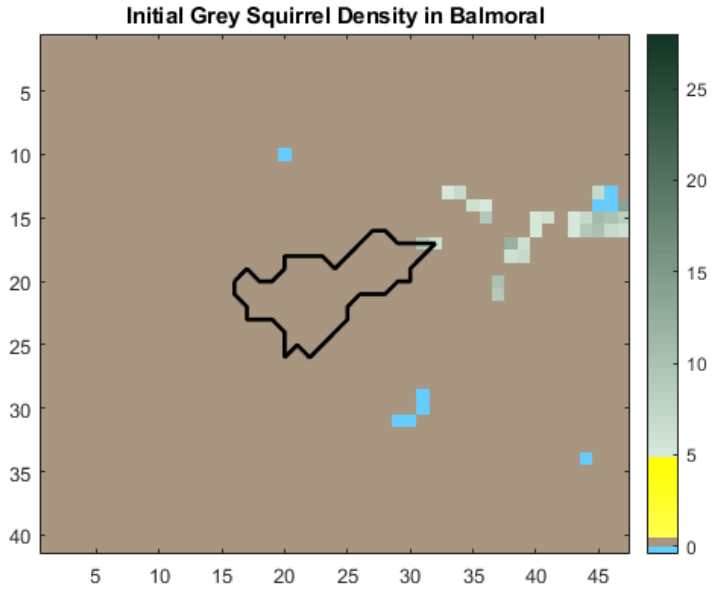

Figure 21: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the stronghold at Balmoral to Invar.

Figure 22 shows the impact of the management strategies on the population density of red and grey squirrels suggesting that the Stronghold Management scheme leads to a higher red squirrel population and a lower grey squirrel population. Figure 23 shows the population densities for grey and red squirrels under both management schemes. Under the UK Forestry Standard the red squirrel abundance falls to around 20 individuals which, given that a minimum viable population is believed to be 125 individuals (SNH pers. comm.), means that extinction of red squirrels is possible (and indeed red squirrel extinction in the stronghold occured in 30% of the simulations, with 20% leading to single figure population sizes). Under the Stronghold Management strategy the red squirrel population stabilises at around 215 individuals, although the population during the transition falls to around 100 individuals in some simulations. The increased viability of red squirrels under the stronghold management scenario is primarily due to the decline in grey squirrel numbers, with the stronghold management policy leading to a 79% reduction in grey squirrel abundance compared to the UK Forestry standard strategy (340 individuals under UK Forestry Standard compared to 70 individuals under the Stronghold Management strategy).

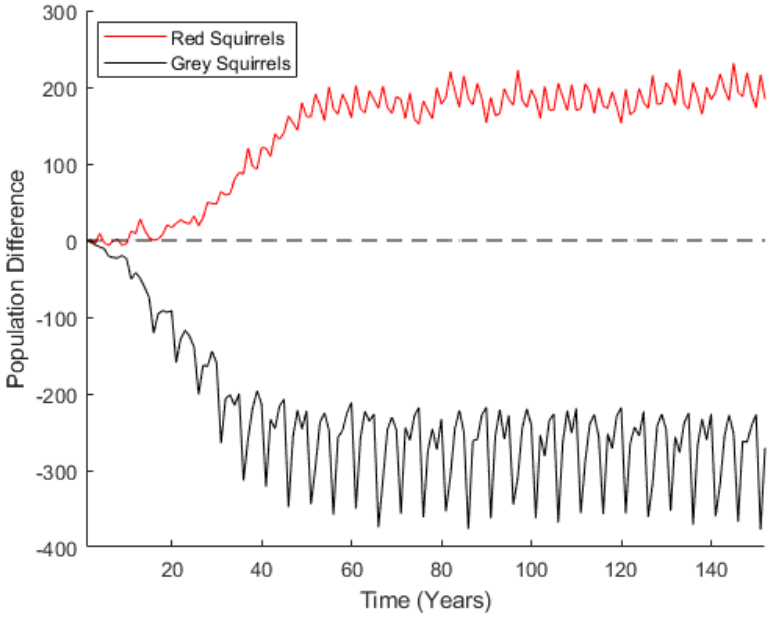

Figure 22: Difference in population density for Balmoral to Invar for the introduction of grey squirrels at the beginning of the simulation. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

Figure 24 shows a map of squirrel densities under both management strategies and indicates that the northern region of the stronghold is where the main change in carrying capacity for grey squirrels occurs. This reduced carrying capacity appears to prevent grey squirrels from becoming established in the rest of the stronghold which allows red squirrels to reside at greater densities.

These results are reproduced when grey squirrels are introduced 50 years into the simulation (Figure 25). Here the long-term results are similar to when grey squirrels were introduced at the start of the simulation (Figure 23). It is worth noting that red squirrels do not drop to vulnerable levels, with the minimum value for red squirrels being approximately 150 individuals (Figure 25).

3.2.2 Introduction of Infection

In the simulations where infected grey squirrels were introduced to the north east of the stronghold the disease did not persist. Thus, similar to the results in Daviot Loch Moy, squirrelpox does not play a significant role in red squirrel viability in the Balmoral to Invar stronghold.

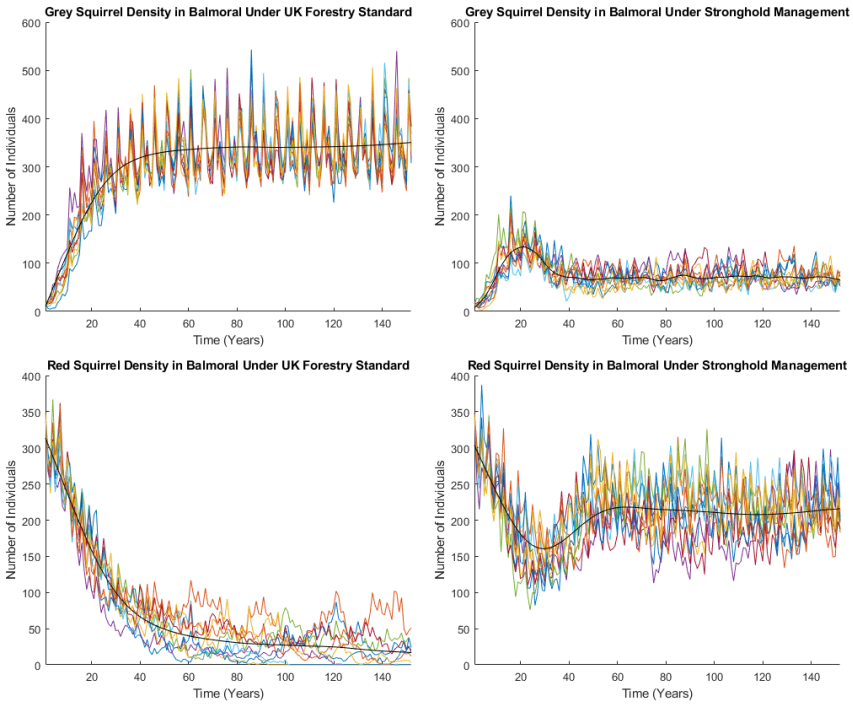

Figure 23: Population density for grey (top) and red (bottom) squirrels in Balmoral to Invar stronghold that have been introduced at the beginning of the simulation. The black lines indicate the average population size.

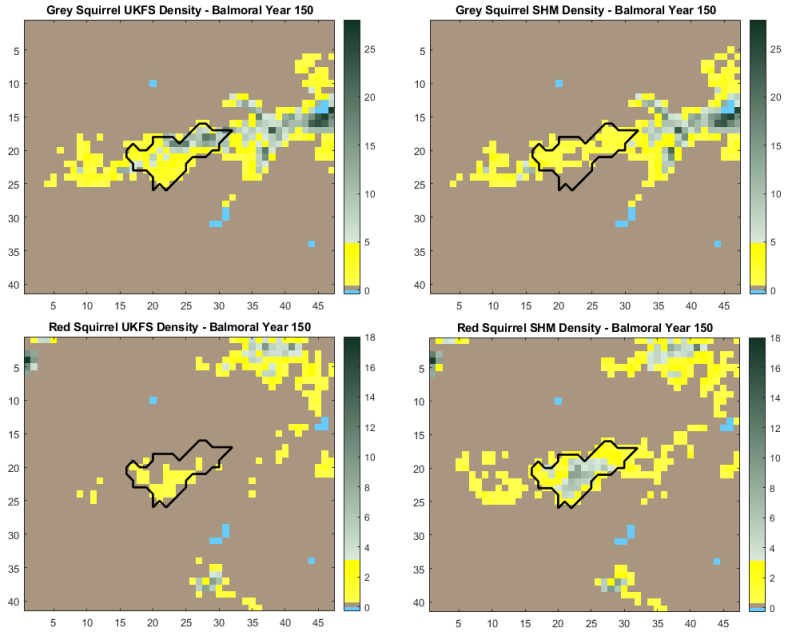

Figure 24: Population density for grey (top) and red (bottom) squirrels under the UK Forestry Standard (left) and Stronghold Management (right) strategies at Balmoral to Invar.

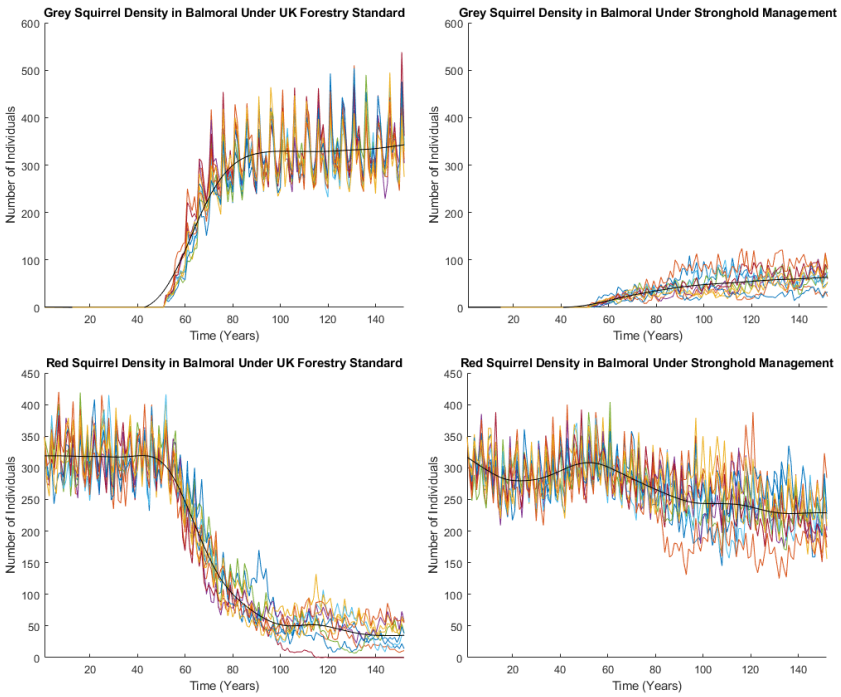

Figure 25: Population density for grey (top) and red (bottom) squirrels in Balmoral to Invar stronghold that have been introduced during year 50 of the simulation. Black curve indicates average density.

3.3 Leanachan

The Leanachan stronghold is part of an active working forest in the Lochaber forest district. It encompasses approximately 63km^2 of forest and is located in western central Scotland with the town of Fort William to the east and Ben Nevis to the south of the stronghold. To the north of the stronghold is the river Lochy, which flows out of Loch Lochy (Figure 26).

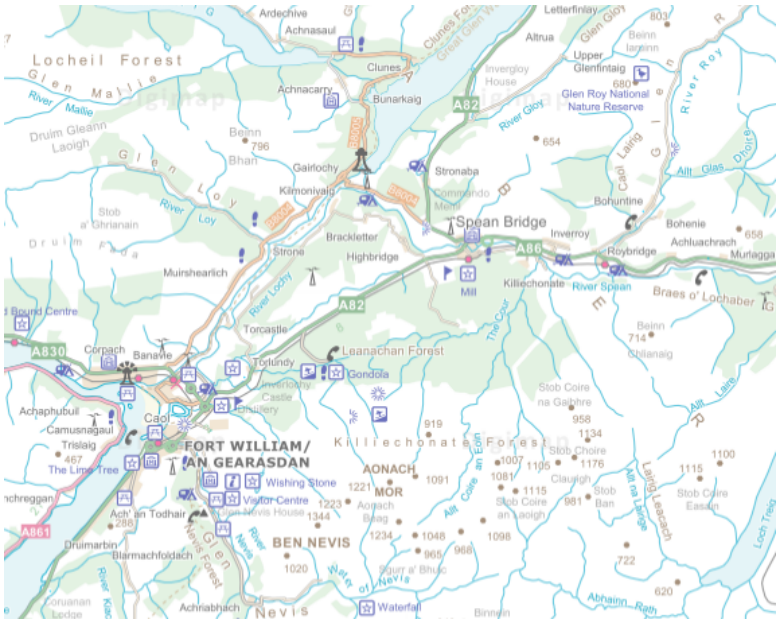

Figure 26: Map of the Leanachan Forest (see Figure 28 for stronghold outline). Image from Digi-Maps, Crown copyright and database rights 2018 Ordinance Survey

The primary tree species in the stronghold is Sitka spruce and 'Other Conifer' (Figure 27). The initial carrying capacity for red and grey squirrels in the region is shown in Figure 28.

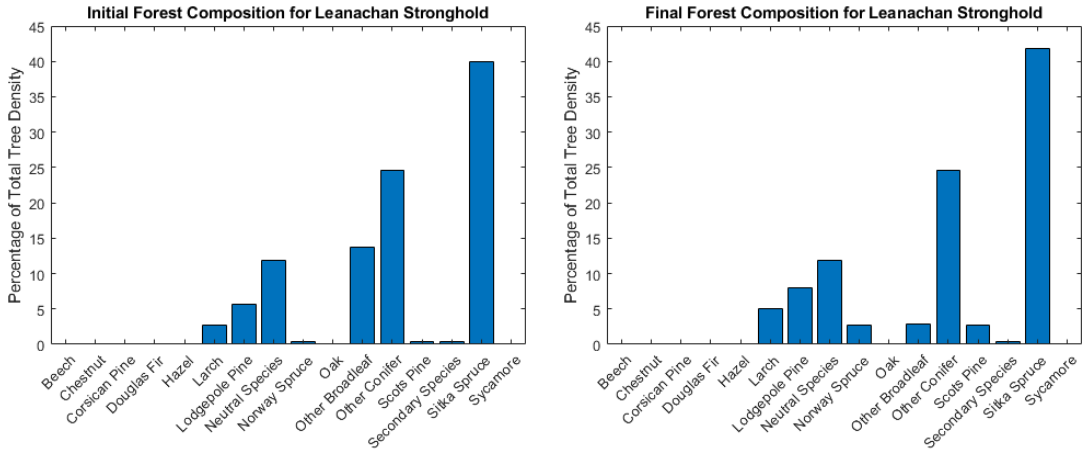

Figure 27: Initial and final forest composition for the Leanachan stronghold. All values are percentages of total tree cover.

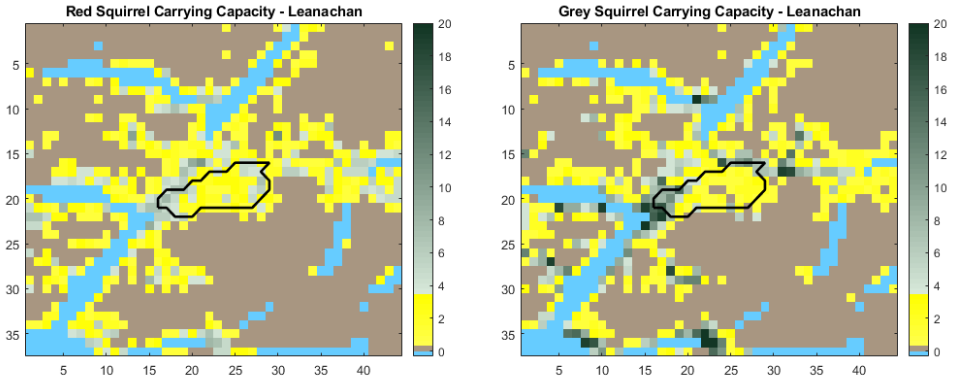

Figure 28: Carrying capacity for red (left) and grey (right) squirrels in the region of Leanachan. The stronghold region is outlined in black.

The effect on the carrying capacity of the changes to the forest composition that are necessary to transition to the Stronghold Management strategy can be seen in Figure 29. The effect of the forest composition changes on the red squirrel abundance can be seen in Figure 30 which shows that the transition from the UK Forestry Standard to the Stronghold Management strategy causes a short-term decline in red squirrel population size, however this decline is not permanent and the the population size recovers to a level comparable to that under the UK Forestry Standard (average of 170 under UK Forestry Standard and 175 under Stronghold Management, with a minimum average of 150 during the transition).

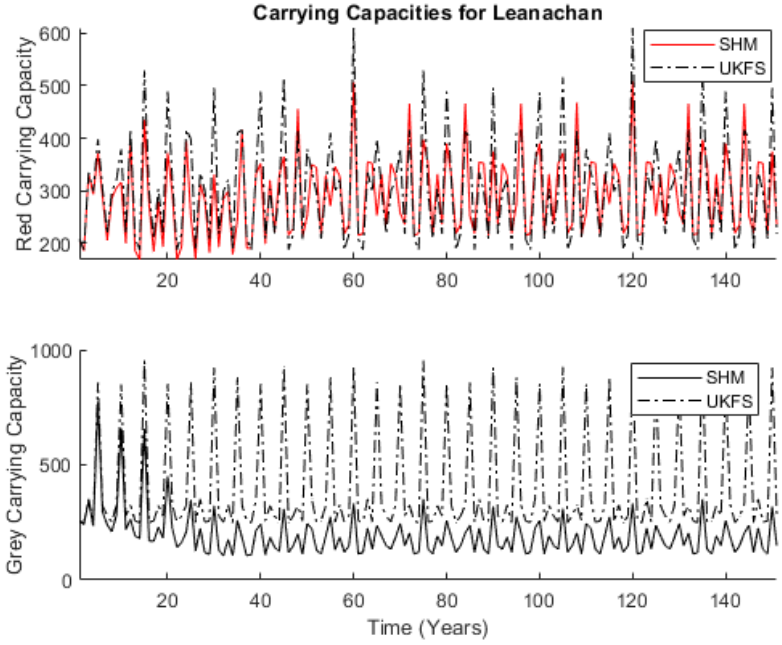

Figure 29: Yearly carrying capacity under Stronghold Management and UK Forestry Standard strategies. The dynamics each strategy undergoes is due to seed crop dynamics and the difference between the two lines (solid and dashed) are due to the changes in forest composition.

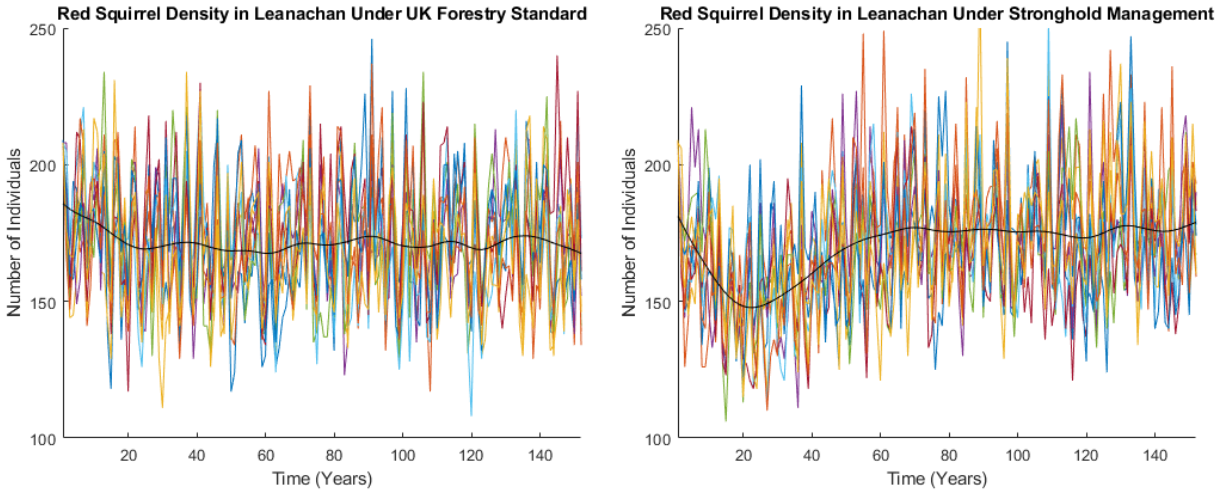

Figure 30: Red squirrel density under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. All 10 simulations are shown simultaneously.

3.3.1 Introduction of Grey Squirrels

Currently there are no grey squirrels in the Leanachan stronghold or in the surrounding region. Thus grey squirrels are artificially introduced to assess the effect of the Stronghold Management policy on grey (and red) squirrel viability in Leanachan. The initial areas of introduction are shown in Figure 31.

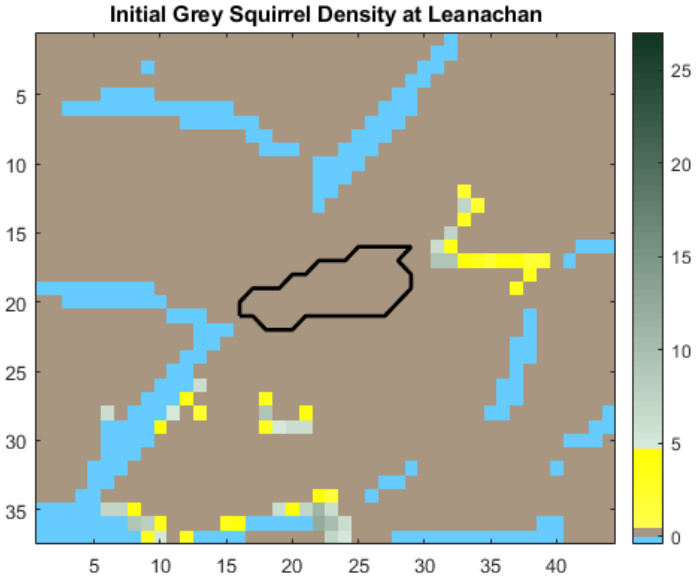

Figure 31: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the stronghold at Leanachan.

Figure 32 shows how the population size of red and grey squirrels change due to the different management strategies and, whilst the grey squirrel abundance is noticeably reduced, this does not translate into a significant increase in the red squirrel numbers.

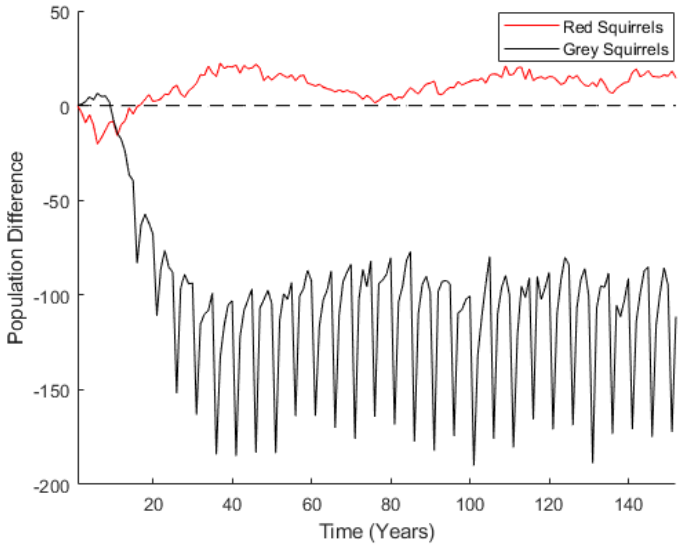

Figure 32: Difference in population density for Leanachan for the introduction of grey squirrels at the beginning of the simulation. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

This can also be seen in Figure 33 which shows that the grey squirrel population incurs a reduction in abundance of approximately 48% (from 230 individuals under UK Forest Standard to 120 individuals under the Stronghold Management strategy). The red squirrel population is low under both the Stronghold Management (average of 20 individuals) and UK Forestry Standard (average of 5 individuals) and is likely to go extinct (Figure 33). This, and Figure 34, suggest that the stronghold at Leanachan is ill-suited to the task of maintaining a viable red squirrel population when grey squirrels are present. Figure 34 does suggest that the region to the east of the stronghold, near Glen Spean, could be a better candidate for a red squirrel stronghold (potential stronghold sites will be examined in the second part of this project). The results for when grey squirrels are introduced after 50 years of simulation (near the completion of the changes to the forest composition) are similar to those presented in Figures 33 & 34.

3.3.2 Introduction of Infection

Grey squirrels infected with the squirrelpox virus were introduced in pairs in years 10, 15 and 20 of the simulation into 2 grid squares that have carrying capacities sufficiently high as to provide the infection with a good chance of becoming established in the region. However, as with the results for previous strongholds, the grey squirrel density is not large enough to support an infected population and as such the infection dies out roughly 5 years after its introduction.

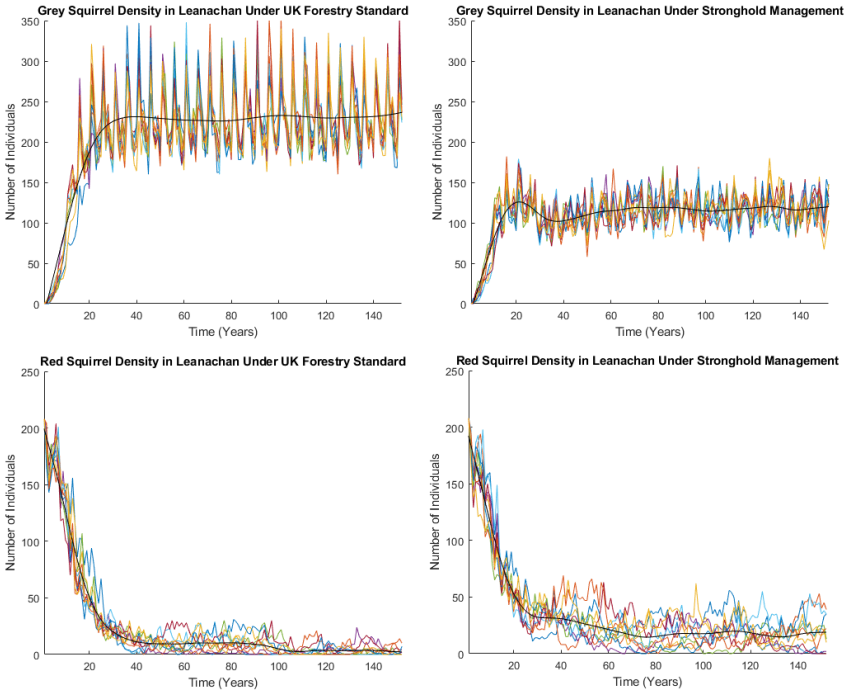

Figure 33: Population density for grey (top) and red (bottom) squirrels in the Leanachan stronghold that have been introduced at the beginning of the simulation. The black lines indicate the average population size.

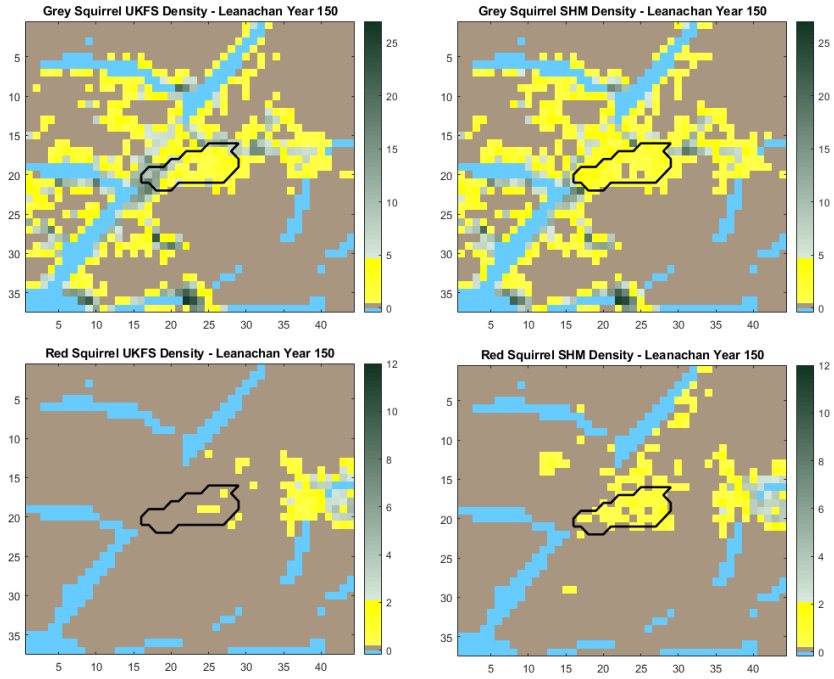

Figure 34: Population density for grey (top) and red (bottom) squirrels under the UK Forestry Standard (left) and Stronghold Management (right) strategies at Leanachan.

3.4 Eskdalemuir

The stronghold at Eskdalemuir encompasses the western section of the Eskdalemuir forest (approx. 180km^2), with the eastern edge of the stronghold defined by the B709, as well as the Castle O'er forest to the south. The forest is located in south east Dumfries and Galloway and is named after the village of Eskdalemuir which lies in the forested region (Figure 35).

Figure 35: Map of the Eskdalemuir Forest. Image from Digi-Maps, Crown copyright and database rights 2018 Ordinance Survey. An outline of the stronghold is shown in Figure 39

The stronghold is primarily comprised of Sitka spruce although, as Figure 36 shows, the most numerous tree species is Other Conifer (as defined by the National Forest Inventory database).

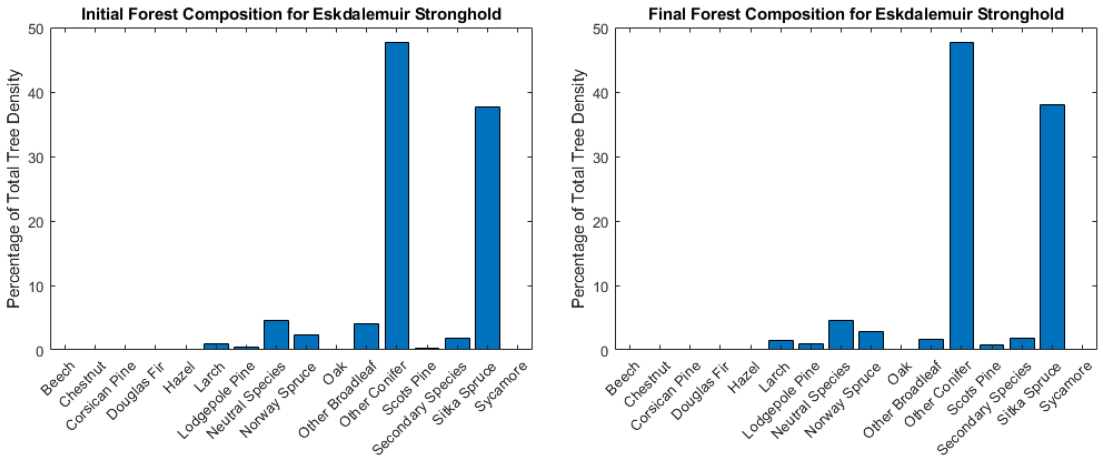

Figure 36: Initial and final forest composition for the Eskdalemuir stronghold. All values are percentages of total tree cover.

Given that the stronghold is dominated by Sitka spruce and Other Conifer, the effect on red and grey carrying capacity due to the changes to the forest composition that are necessary to transition to the Stronghold Management strategy is limited (Figure 37). Therefore, the transition from the UK Forestry Standard to the Stronghold Management strategy has little effect on the red squirrel density during or following the transition (Figure 38).

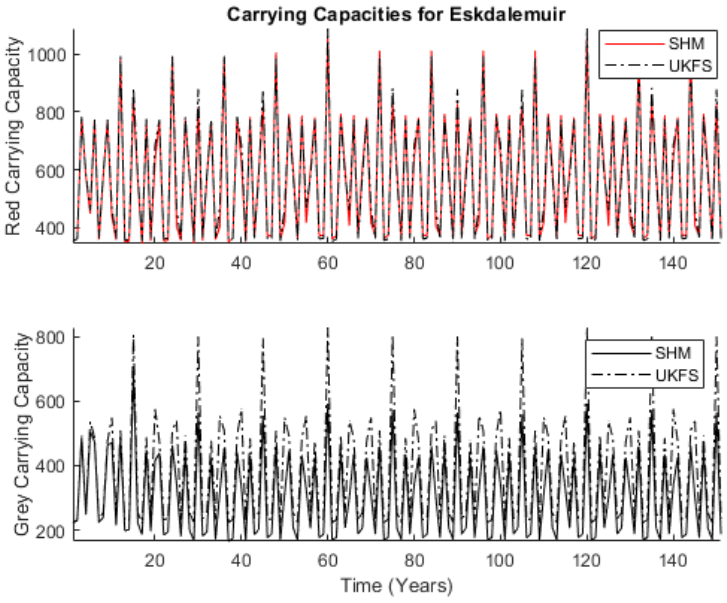

Figure 37: Yearly carrying capacity under Stronghold Management and UK Forestry Standard strategies. The dynamics each strategy undergoes is due to seed crop dynamics and the difference between the two lines (solid and dashed) are due to the changes in forest composition.

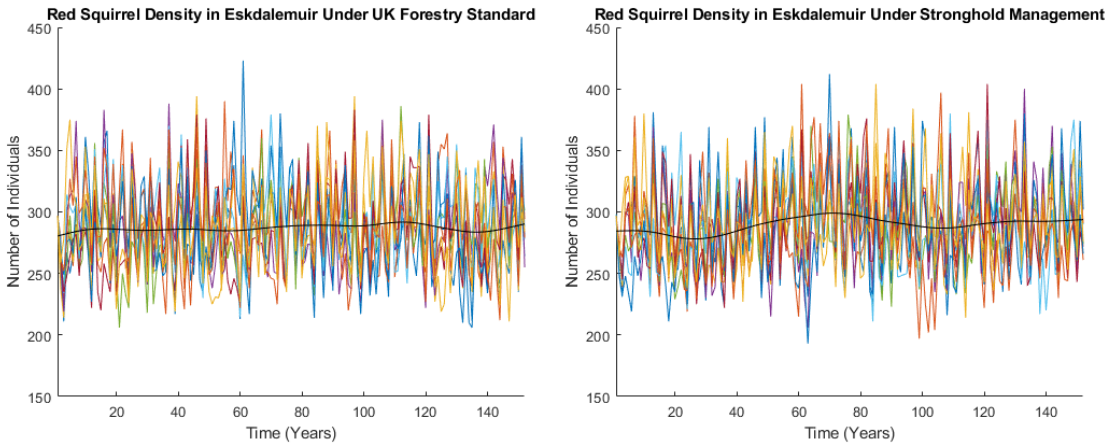

Figure 38: Red squirrel density under UK Forestry Standard (left) and Stronghold Management (right) strategies in the absence of grey squirrels with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. Average population size under both strategies is approximately 280 individuals. All 10 simulations are shown simultaneously.

However, the Eskdalemuir stronghold is situated south of the Highland line (Figure 1) and so there are grey squirrels that reside in the region. Figure 39 shows that grey squirrels are primarily concentrated in the center of the stronghold, near the Black Esk reservoir, and the small reduction in carrying capacity that is a consequence of the forestry changes is sufficient to restrict the presence of grey squirrels in the stronghold.

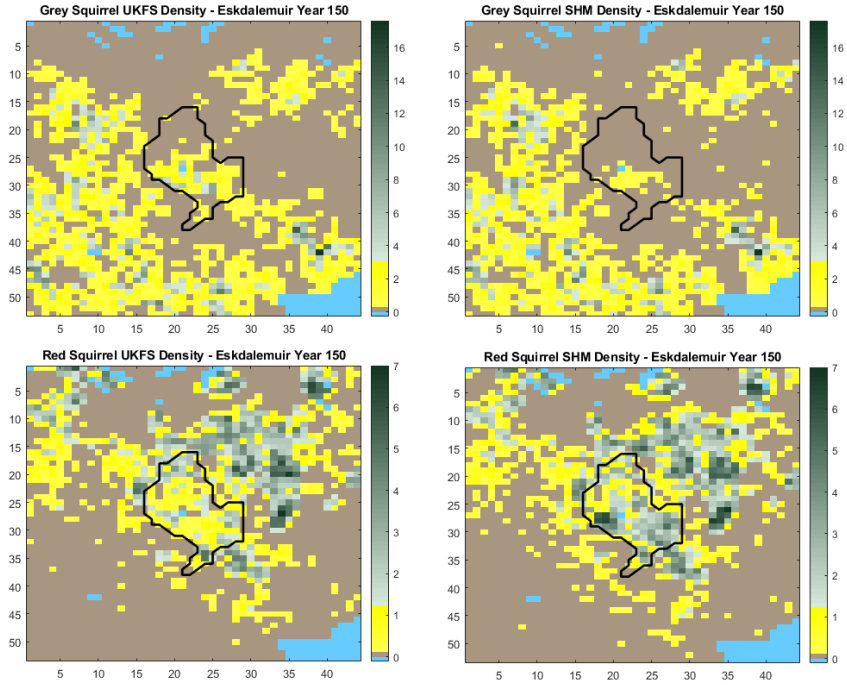

Figure 39: Population density for grey (top) and red (bottom) squirrels under the UK Forestry Standard (left) and Stronghold Management (right) strategies at Eskdalemuir.

Thus, as can be seen in Figure 40, the changes introduced under the Stronghold Management strategy lead to a reduction in the grey squirrel population, from an average of approximately 110 individuals under the UK Forestry Standard to an average of around 15 individuals under the Stronghold Management strategy (a decline of 86%). The decline in the grey squirrel abundance reduces the competitive effect on red squirrels which consequently leads to an increase in the red squirrel abundance, from 160 individuals under UK Forestry Standard to 260 under Stronghold Management strategy, which is an increase of 62.5%. This result is further highlighted by Figure 41 which indicates the relative change in population due to the different management strategies.

3.4.1 Introduction of Infection

The density of grey squirrels in the stronghold at Eskdalemuir, as well as in the surrounding region, is low and therefore the disease does not remain endemic. Thus the squirrelpox virus does not have an impact on the red squirrel viability in the stronghold.

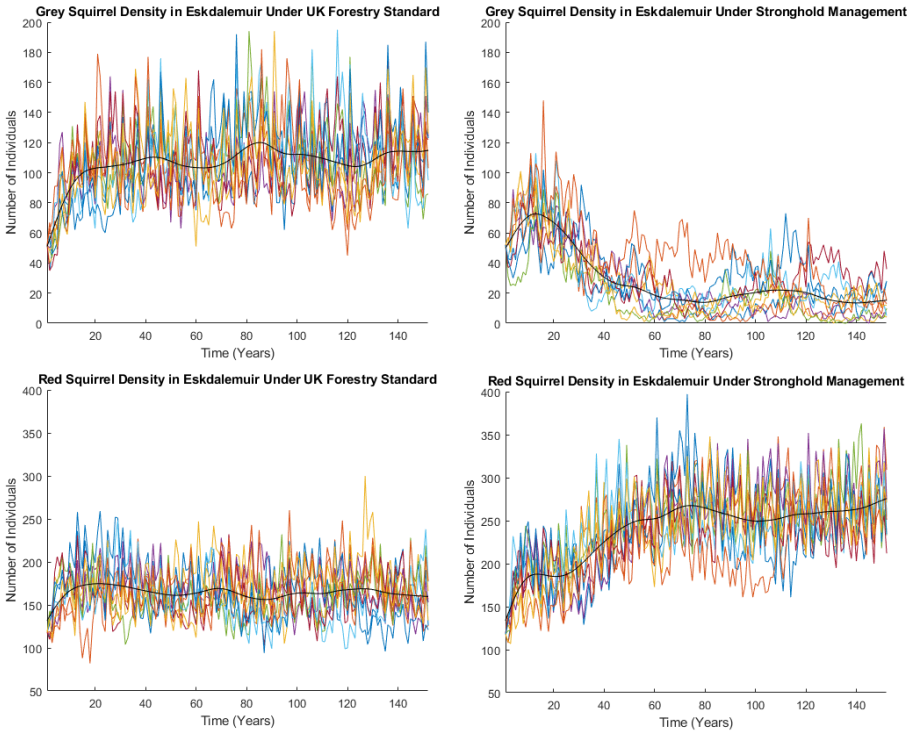

Figure 40: Population density for grey (top) and red (bottom) squirrels in the Eskdalemuir stronghold under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. All 10 simulations are shown simultaneously.

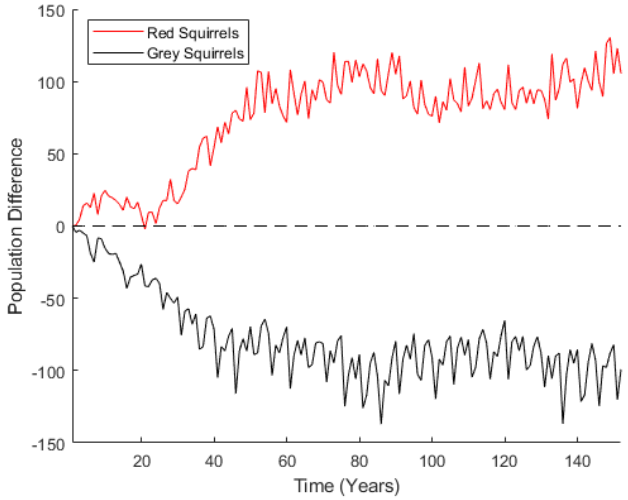

Figure 41: Difference in population density for Eskdalemuir. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

3.5 Fleet Basin

The stronghold at Fleet basin is to be found at the south east of the Galloway forest park in Dumfries and Galloway, SW Scotland. The stronghold encompasses 131km^2 of the region that is south of the A712, north of the Gatehouse of Fleet and east of Loch Grannoch (Figure 42). The stronghold is primarily comprised of Sitka spruce (Figure 43).

Figure 42: Map of the Fleet Basin Forest. Image from Digi-Maps, Crown copyright and database rights 2018 Ordinance Survey

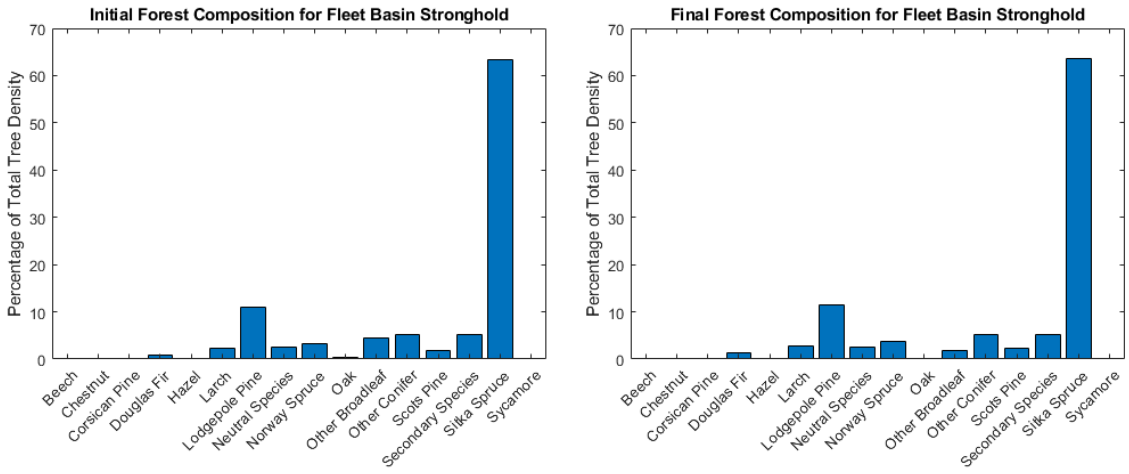

Figure 43: Initial and final forest composition for the Fleet Basin stronghold. All values are percentages of total tree cover.

The effect on the carrying capacity of the changes to the forest composition that are necessary to transition to the Stronghold Management strategy can be seen in Figure 44. Grey squirrel capacity is reduced, most notably with the removal of the large spikes in capacity generated by the large seeded broadleaved trees undergoing mast years.

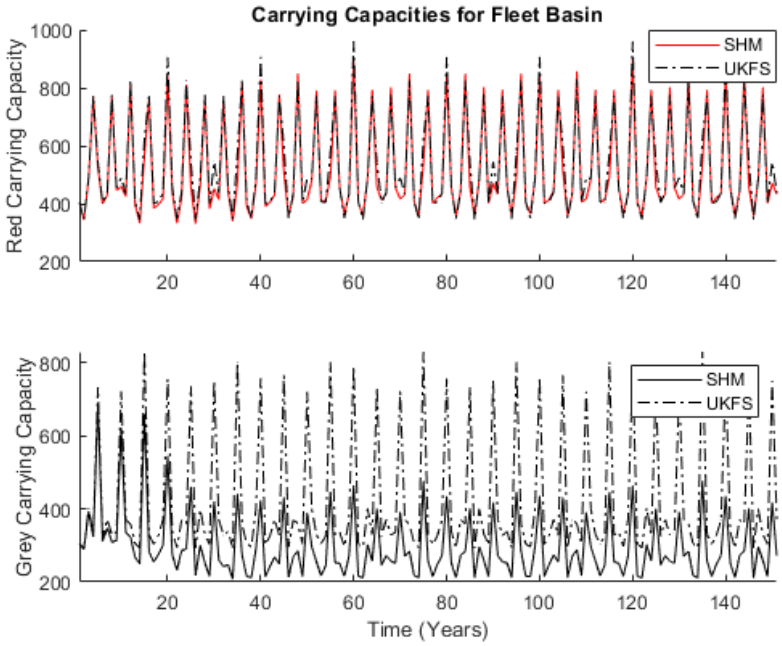

Figure 44: Yearly carrying capacity under Stronghold Management and UK Forestry Standard strategies. The dynamics each strategy undergoes is due to seed crop dynamics and the difference between the two lines (solid and dashed) are due to the changes in forest composition.

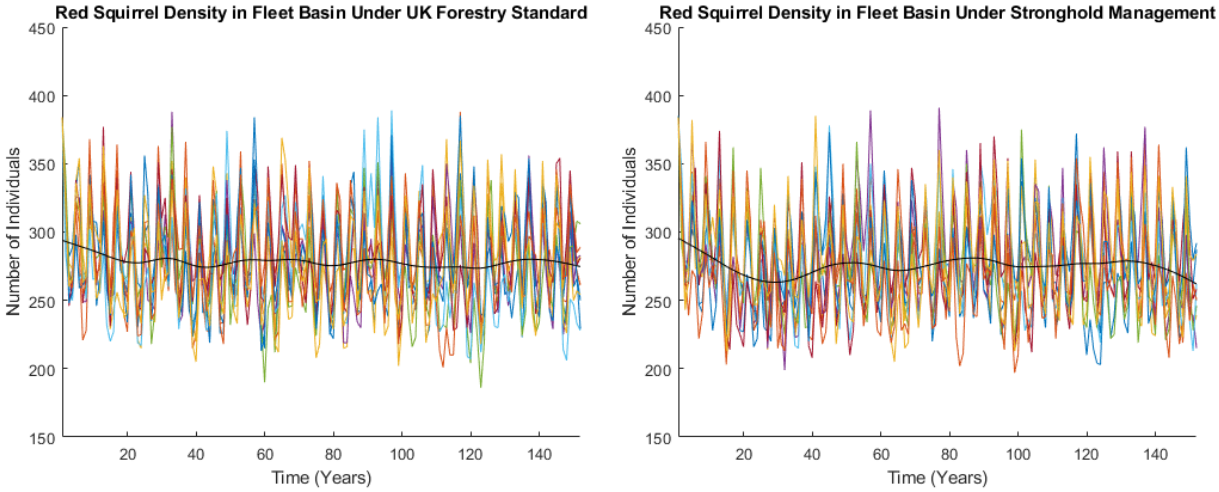

Figure 45: Red squirrel density under UK Forestry Standard (left) and Stronghold Management (right) strategies in the absence of grey squirrels with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. Average population size under both strategies is approximately 280 individuals. All 10 simulations are shown simultaneously.

The effect on red squirrel carrying capacity however is limited, which is shown in Figure 45. The red squirrel abundance under the UK Forestry Standard is approximately 280 individuals whereas the Stronghold Management strategy sees an initial reduction in abundance, to ap-

proximately 260 individuals during the period of transition, with the population recovering in the long-term to the level it was at prior to the transition.

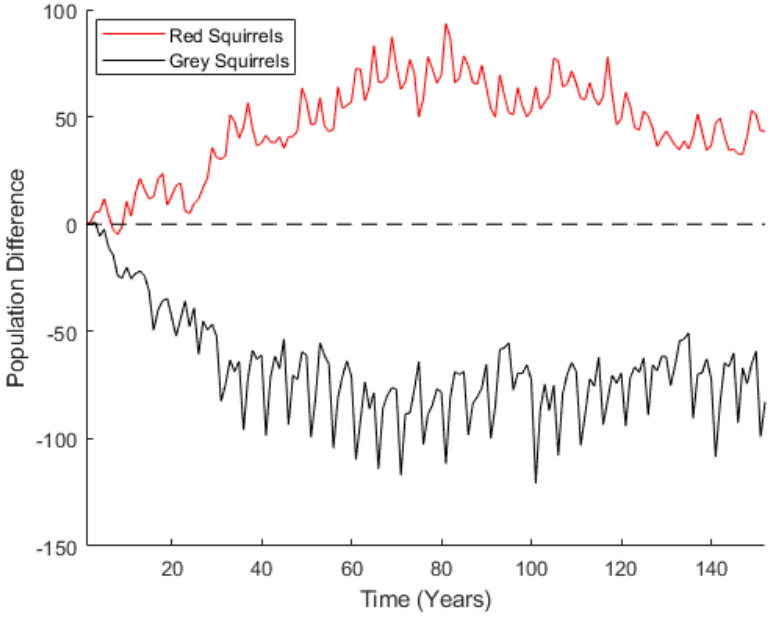

Figure 46: Difference in population density for Fleet Basin. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

The stronghold at Fleet Basin is located to the south of the Highland line, and as such there are currently grey squirrels present in the region. The implementation of the Stronghold Management strategy reduces the grey squirrel abundance by around 40% (from 195 individuals under UK Forestry Standard to 115 under Stronghold Management strategy) and increases the red squirrel abundance by 230% (from 45 individuals under UK Forestry standard to 105 under Stronghold Management strategy) (Figure 47). Note that under both UK Forestry Standard and Stronghold Management strategies the red squirrel density can fall to low levels in the presence of grey squirrels. Overall, the red squirrel abundance is larger under the Stronghold Management strategy but it is still small enough that extinction is a threat in the Fleet Basin stronghold. The grey squirrel population in the stronghold is supplemented by regions of high grey squirrel density outside of the stronghold, most notably to the south (Figure 48).

3.5.1 Introduction of Infection

Squirrelpox was introduced into the region along with grey squirrels in the region surrounding the stronghold. Despite the high grey squirrel density to the south of the stronghold which can act as a reservoir of infection that could lead to the infection intermittently entering the stronghold, the grey squirrel population inside the stronghold is insufficient in abundance to support a viable population of infected individuals. Thus the presence of the squirrelpox infection has little impact on red squirrel abundance in the stronghold under either management scenarios with the dynamics being similar to those shown in Figure 47.

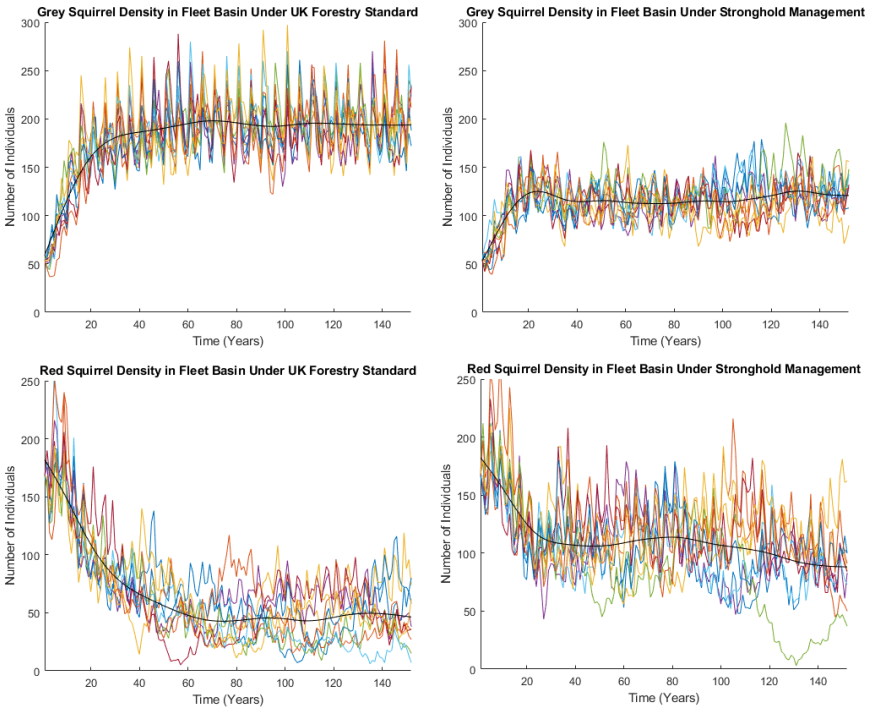

Figure 47: Population density for grey (top) and red (bottom) squirrels in the Fleet Basin stronghold under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. All 10 simulations are shown simultaneously.

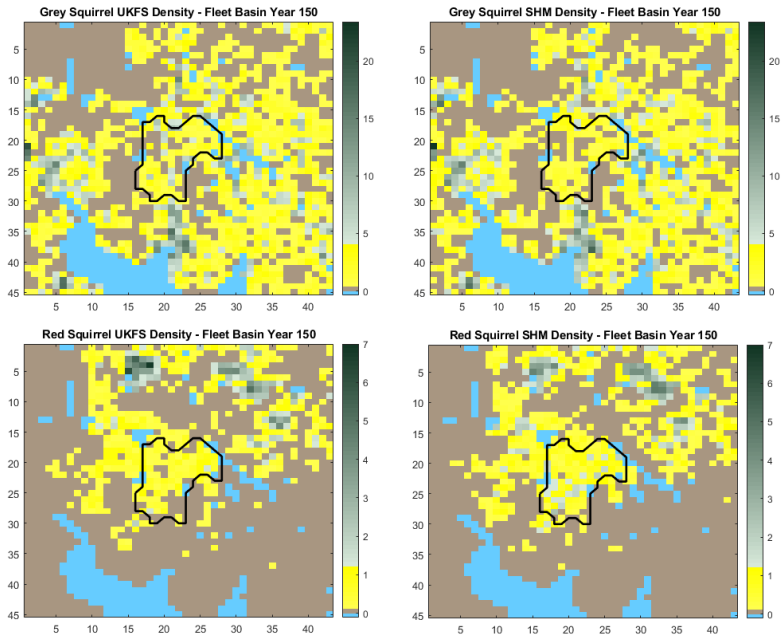

Figure 48: Population density for grey (top) and red (bottom) squirrels under the UK Forestry Standard (left) and Stronghold Management (right) strategies at Fleet Basin.

3.6 Glenbranter

The Glenbranter stronghold is located in the Argyll Forest Park which can be found on the Cowal peninsula, Argyll and Bute, in the west of Scotland. The stronghold encompasses 133 km^2 of the peninsula and includes the Glenbranter forest as well as Loch Eck and forest regions to either side of the Loch (Figure 49). The stronghold is primarily comprised of Sitka spruce (Figure 50).

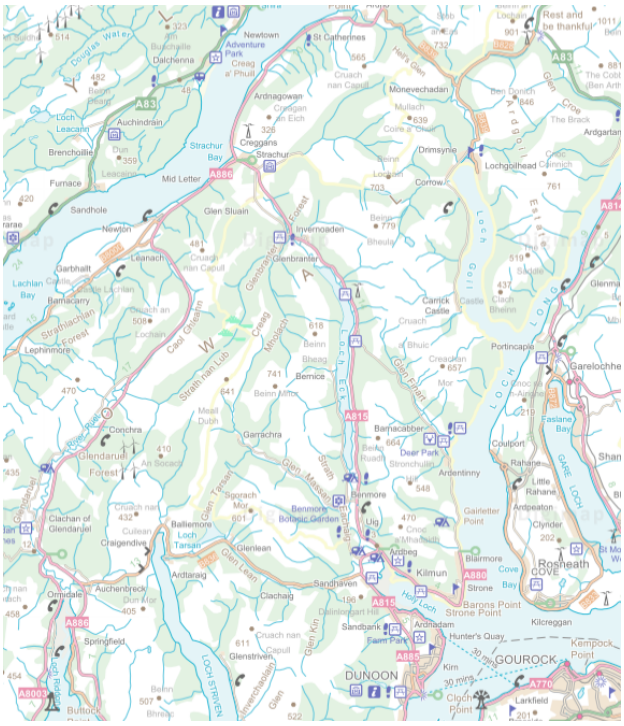

Figure 49: Map of the Glenbranter Forest (see Figure 51 for stronghold outline). Image from Digi-Maps, Crown copyright and database rights 2018 Ordinance Survey

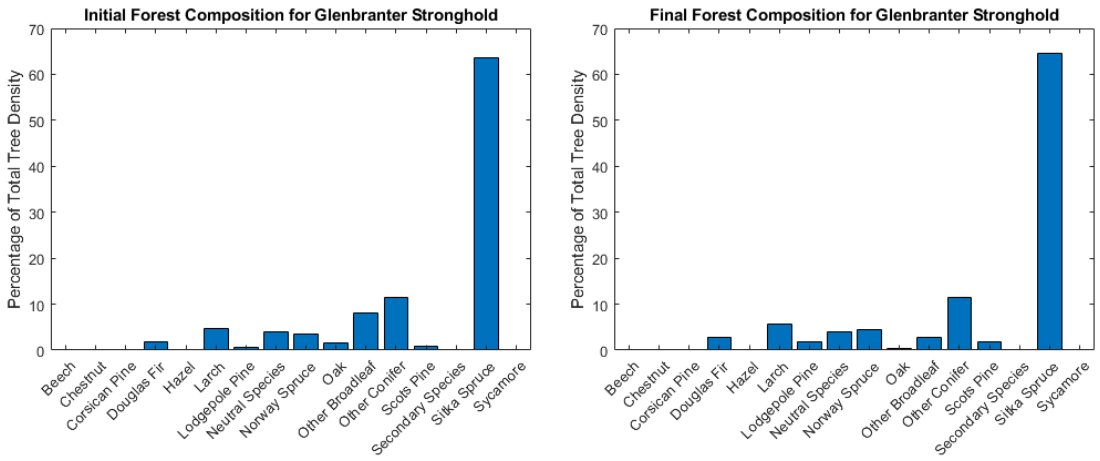

Figure 50: Initial and final forest composition for the Glenbranter stronghold. All values are percentages of total tree cover.

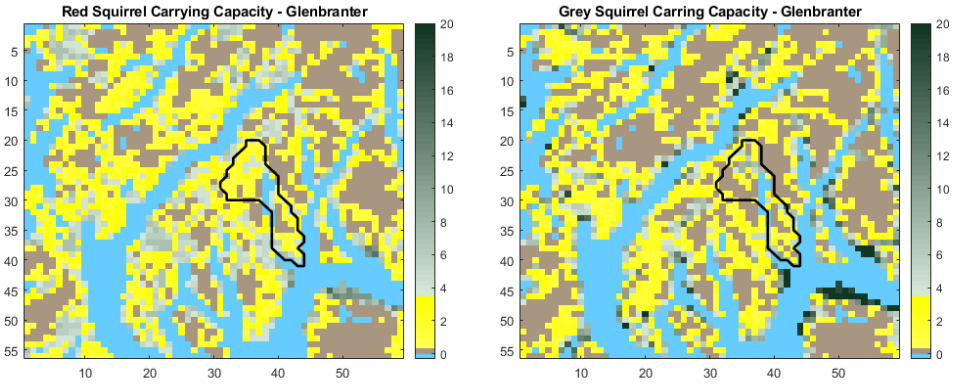

Figure 51: Carrying capacity for red (left) and grey (right) squirrels in the region of Glenbranter. The stronghold region is outlined in black.

The effect on the carrying capacity of the changes to the forest composition that are necessary to transition to the Stronghold Management strategy can be seen in Figure 52. The grey squirrel carrying capacity sees an average reduction alongside a more noticeable reduction in the large spikes in capacity that are due to the large seeded broadleaved trees undergoing mast years.

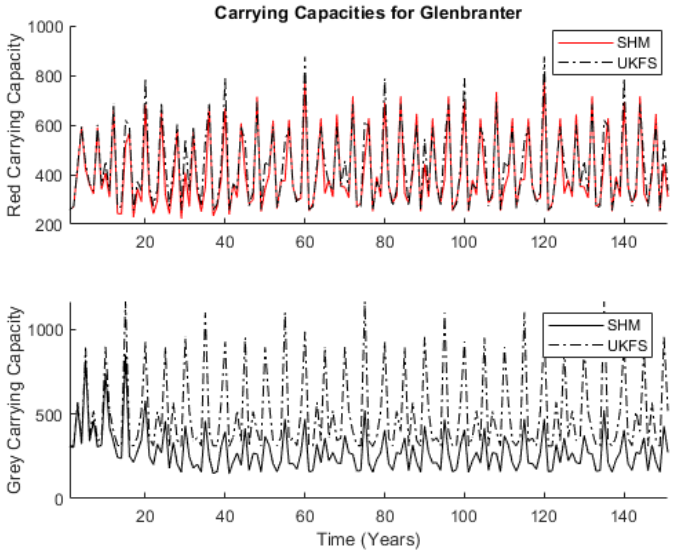

Figure 52: Yearly carrying capacity under Stronghold Management and UK Forestry Standard strategies. The dynamics each strategy undergoes is due to seed crop dynamics and the difference between the two lines (solid and dashed) are due to the changes in forest composition.

In the absence of grey squirrels the red squirrel abundance under the UK Forestry Standard is approximately 200 individuals whereas the Stronghold Management strategy sees an initial reduction in abundance, to roughly 175 individuals during the period of transition to the new strategy, but this is not maintained in the long term and the population level recovers to be equivalent to that under the UK Forestry Standard (Figure 53).

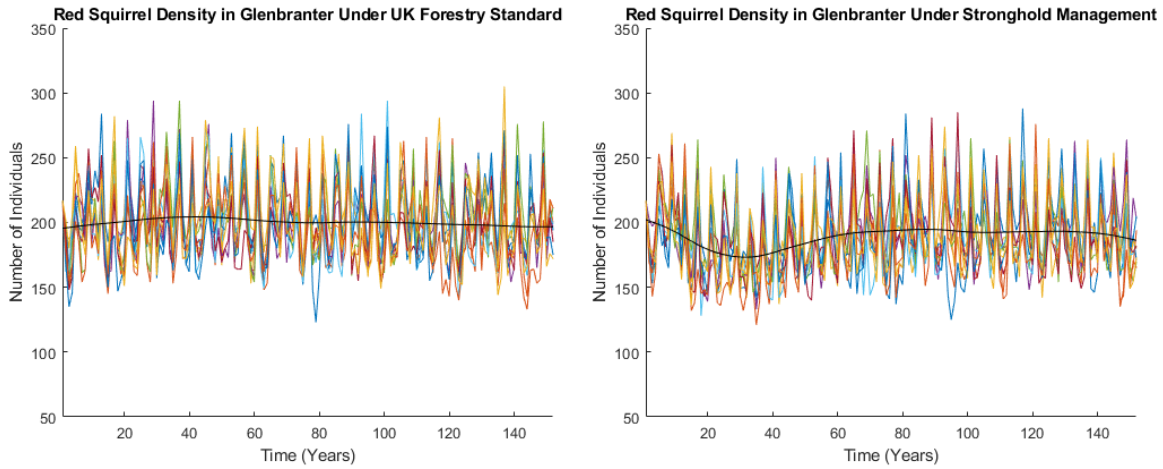

Figure 53: Red squirrel density under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. Average population size under both strategies is approximately 200 individuals. All 10 simulations are shown simultaneously.

As with Eskdalemuir and Fleet Basin, the Glenbranter stronghold is south of the Highland line, and as such there are currently grey squirrels present in the region. The implementation of the Stronghold Management strategy reduces the grey squirrel abundance by around 51% (from 205 individuals under UK Forestry Standard to 100 under Stronghold Management strategy). The red squirrel abundance under the UK Forestry Standard is around 20 individuals, although some of the simulations do lead to extinction. Under the Stronghold Management strategy the red squirrel abundance does not stabilise during the 150 years of simulation. It is possible that the dynamics would stabilise after an extended period of time however, given the trend shown in Figure 55, it is unlikely that the population level would be sufficiently high to ensure viability in the Glenbranter stronghold.

Thus the results suggest that the Glenbranter stronghold is not able to support the coexistence of red and grey squirrels, with red squirrels becoming extinct (Figure 57). The poor viability of red squirrels under both forest management scenarios suggests that an alternative course of action could be to utilise the geography of the Cowal peninsula to prevent grey squirrels entering the region and to remove those that do disperse into the area.

3.6.1 Introduction of Infection

As with Eskdalemuir and Fleet Basin, the infected grey squirrels were introduced into the region as part of the initial conditions. However, the grey squirrel population inside the stronghold as well as in the wider region appears to be insufficient in abundance to support a viable population of infected individuals. Thus the presence of the squirrelpox infection has little impact on the results due to forest management.

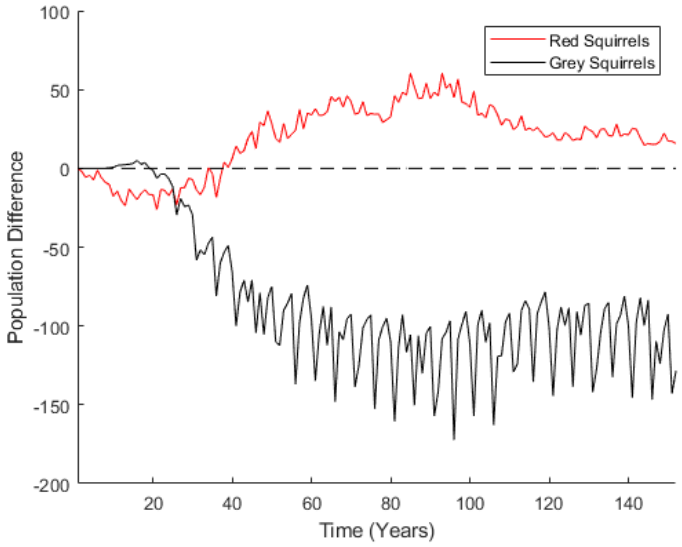

Figure 54: Difference in population density for Glenbranter. The plots show the difference between the two management strategies for both red and grey squirrels. Positive values indicate a higher population under the Stronghold Management scheme, whilst negative values a higher population under the UK Forestry Standard strategy.

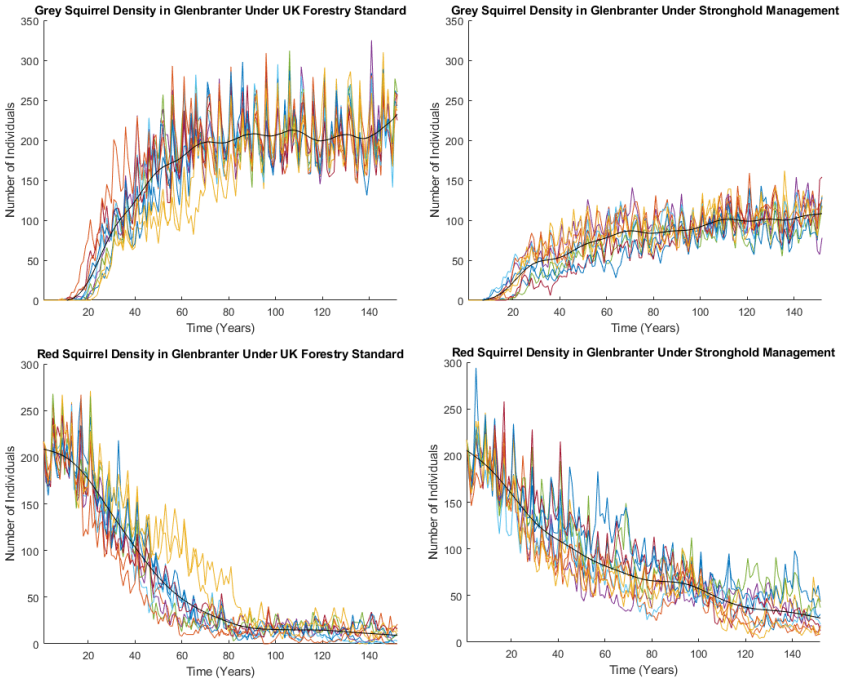

Figure 55: Population density for grey (top) and red (bottom) squirrels in the Glenbranter stronghold under UK Forestry Standard (left) and Stronghold Management (right) strategies with the inclusion of a smooth fitted curve (black line) that shows the average population trend without the inclusion of variation due to seed crop dynamics. All 10 simulations are shown simultaneously.

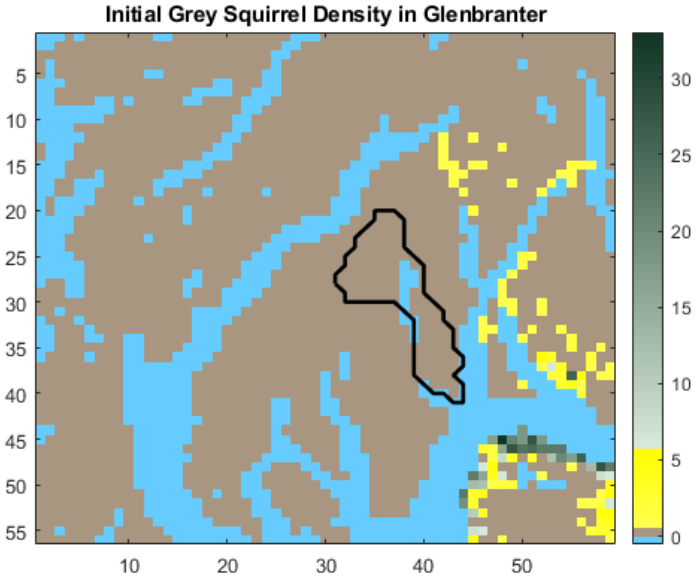

Figure 56: Initial population density for grey squirrels at Glenbranter. Note that there are no grey squirrels initially present on the Cowal peninsula.

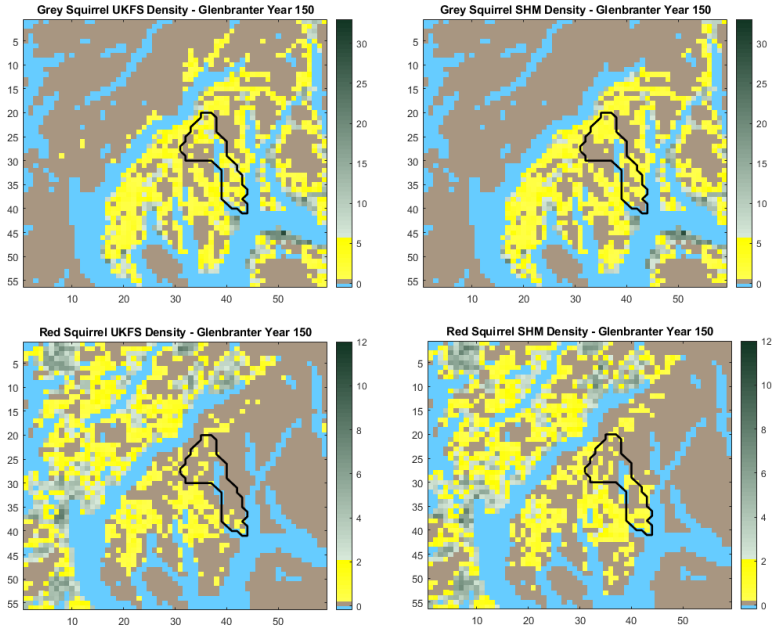

Figure 57: Population density for grey (top) and red (bottom) squirrels under the UK Forestry Standard (left) and Stronghold Management (right) strategies at Glenbranter.

4 Conclusion

The impact of different forest management strategies on the abundance of red and grey squirrels in selected strongholds in Scotland has been examined and the findings across the strongholds is summarised in Table 6.

		Red Squirrels					
		No Greys		*With Greys*		**Grey Squirrels**	
		UKFS	**SHM**	**UKFS**	**SHM**	**UKFS**	**SHM**
	Avg	305	305	120	175	190	85
DLM	Min	205	215	55	105	125	40
(89km^2)	Max	420	400	200	270	300	140
	Avg	315	315	20	215	340	70
BtI	Min	225	225	0	75	225	25
(89km^2)	Max	440	425	100	325	545	135
	Avg	170	175	5	20	230	120
Lean	Min	110	105	0	0	165	75
(63km^2)	Max	245	270	30	60	355	180
	Avg	280	280	160	260	110	15
Esk	Min	205	195	80	160	45	0
(180km^2)	Max	425	410	260	365	195	75
	Avg	280	280	45	105	195	115
FB	Min	185	200	5	50	120	70
(131km^2)	Max	390	390	120	210	300	180
	Avg	200	200	20	40	205	100
GB	Min	125	120	0	10	130	60
(133km^2)	Max	305	290	40	100	325	160

Table 6: Red and grey squirrel abundance, rounded to nearest 5 individuals, under the UK Forestry Standard (UKFS) and Stronghold Management (SHM) strategies at Daviot Loch Moy (DLM), Balmoral to Invar (BtI), Leanachan (Lean), Eskdalemuir (Esk), Fleet Basin (FB) and Glenbranter (GB).

Table 6 shows that in the absence of grey squirrels all stronghold are capable of supporting viable red populations, although the populations at Leanachan and Glenbranter do become vulnerable during years of minimum population. The model results show that there is little difference in red squirrel abundance between the UK Forestry Standard and Stronghold Management strategies. Therefore in the absence of grey squirrels there does not seem to be evidence supporting the implementation of the Stronghold Management strategy.

A clear finding of the model, as shown in Table 6, is that the red squirrel population does better, in terms of population size, under the Stronghold Management strategy than under

the UK Forestry Standard in the presence of grey squirrels. Furthermore, Table 6 also shows that the grey squirrel population size is reduced under the Stronghold Management strategy compared to the UK Forestry Standard.

In Daviot Loch Moy, Balmoral to Invar and Eskdalemuir the transition to the Stronghold Management strategy ensures that the average population remains above 125 (and in most cases the minimum population also stays above 125) which is taken as sufficient for population viability. The strongholds at Daviot Loch Moy and Balmoral to Invar are located in regions that have a limited number of routes available for grey squirrel incursion. Hence the number of individuals that can enter the stronghold is limited. The implementation of the Stronghold Management strategy reduces the amount of preferable habitat for grey squirrels in the stronghold, which leads to a noticeable decline in grey squirrel population which in turn prevents the decline in the already resident red squirrels. The stronghold at Eskdalemuir is dominated by Sitka spruce, which is poor habitat for grey squirrels. The stronghold Management strategy removes the small number of large seeded broadleaf trees that the grey squirrels were relying on, meaning that the viable grey squirrel population size falls dramatically. Furthermore, the surrounding area is also poor grey squirrel habitat which limits the number of grey squirrels that can enter the stronghold. This reduces the competitive pressures on red squirrels thereby allowing the population size to increase.

In Fleet Basin the average red squirrel population size, in the presence of grey squirrels, is close to being viable under the Stronghold Management strategy. Thus if the management strategy is supplemented with targeted catching and removal of grey squirrels in the surrounding area this stronghold could become viable. Such trapping would be required to the south of the stronghold and may have the advantage of allowing red squirrels to expand into populated areas such as the Gatehouse of Fleet [24]. In Glenbranter and Leanachan the population levels are low and red squirrels are likely to become extinct if the Stronghold Management strategy is the only conservation strategy imposed. The stronghold at Leanachen has multiple access points for grey squirrel incursion, including a number of nearby towns which provide good grey squirrel habitat, which limits the impact of the forestry management. Whereas the stronghold at Glenbranter encompasses on a proportion of the interconnected forest on the Cowal peninsula which again allows for easy incursion routes for grey squirrels from regions that have not undergone management plans in-line with the Stronghold Management strategy.

According to this study regions of forest that are relatively isolated with limited access points for grey squirrel incursion make for a good stronghold, e.g. Daviot Loch Moy and Balmoral to Invar. Forests that are dominated by Sitka spruce and that contain no continuous regions of large seeded broadleaf trees, such as at Eskdalemuir, can also support red squirrels and exclude grey squirrels, but red squirrel density is likely to be low in Sitka dominated forests. Conversely, forests that are located near to urban areas, such as Leanachan, and forests that comprise only a limited section of a larger contiguous forest region, such as Glenbranter, generally make for poor strongholds due to the obvious opportunity for grey squirrels to invade the stronghold in sufficient numbers over prolonged periods of time. The stronghold viability can be further increased through the use of targeted trapping of grey squirrels. This is most evident in Daviot Loch Moy and Balmoral to Invar, where the limited access points provide natural pinch-points for trapping that could prevent grey squirrel incursion entirely, likewise Glenbranter has a

natural pinch-point near the base of the Cowal peninsula, where it meets the mainland, which could lead to the entire peninsula becoming a stronghold region. For more information on the possible effects of trapping at Fleet Basin and Eskdalemuir see [22][24].

The key findings from the study are summarised below:

4.1 Forest Management in the Absence of Grey Squirrels

- Sustainable red squirrel populations (above 125 individuals) are viable in all strongholds under the UK Forestry Standard management practice, although the population does become vulnerable at Leanachan during years of minimum population.
- The transition from the UK Forestry Standard to the Stronghold Management strategy reduces the red squirrel abundance in all strongholds during the transition period.
- The size of the reduction is dependent on the scale of alteration required for transition, with greater alteration leading to larger reductions.
- A greater variety of tree species in a stronghold can help mitigate the population reduction, such as in Daviot Loch Moy.
- Following forest transition, red squirrel abundance is comparable under the UK Forestry Standard and the Stronghold Management scheme (Table 6).
- In the absence of grey squirrels, there is no discernible benefit in the Stronghold Management strategy compared to the UK Forestry Standard.

4.2 Forest Management in the Presence of Grey Squirrels

- Grey squirrels can persist in the strongholds and the surrounding regions under both the Stronghold Management strategy and the UK Forestry Standard.
- The Stronghold Management strategy reduces the grey squirrel abundance, which in turn leads to an increase in red squirrel abundance. Therefore the Stronghold Management strategy provides an advantage to red squirrels over grey squirrels when compared to the UK Forestry Standard (Table 6) and is therefore favourable in the presence of grey squirrels.
- Red and grey squirrels can coexist in the Daviot Loch Moy, Balmoral to Invar, Eskdalemuir and Fleet Basin strongholds at a reasonable level of abundance (above 100 individuals, see Table 6) under the Stronghold Management scenario and at Eskdalesmuir and Daviot Loch Moy under UK Forestry Standard. This suggests that Eskdalemuir and Daviot Loch Moy are good natural strongholds because they could support red squirrels without forest management changes. The risk of red squirrel extinction is a possibility in all four of these strongholds but this risk is reduced under the Stronghold Management strategy (particularly in Eskdalemuir and Balmoral to Invar).
- Extinction of grey squirrels in the strongholds under the Stronghold Management practice is unlikely due to dispersal into the strongholds from the wider region.

- Red squirrels cannot coexist with grey squirrels in the Leanachan and Glenbranter strongholds. The location of the strongholds, with neighbouring habitat that provides a source of grey squirrels, allows greys to disperse into the strongholds. The model study suggests that these are therefore not good natural strongholds.

- The long term results regarding red and grey squirrel abundance are in close agreement regardless of whether the grey squirrels are introduced at the beginning of the simulation (before the transition to the Stronghold Management scheme) or in year 50 of the simulation (near the completion of the transition), however the red squirrel population can become vulnerable during the period of transition when grey squirrels are present, in which case the transition should either be completed before grey squirrels arrive in the region or grey squirrel control should be enacted during the transition to reduce grey squirrel numbers.

- In all scenarios the grey squirrel population that can coexist within the strongholds is not sufficiently large to support squirrelpox virus meaning that the threat to red squirrels due to squirrelpox is small.

- A good stronghold is one that is comprised of tree species that are favourable to red squirrels compared to grey squirrels, has limited access routes for grey squirrel incursion and is located in a wider region that cannot maintain a sizeable grey squirrel population.

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A Description of Model Terms in Equation 2.1

The following is a written explanation of the model terms that correspond to the terms in equation 2.1, in the same order as they appear in equation 2.1.

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

In addition to these terms it is assumed 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 5) which represents changes to the abundance of the different classes of red and grey squirrels within 1km by 1km grid squares. In the stochastic model squirrels can undertake long distance dispersal to neighbouring grid squares within a 2km range.