Report to Forestry and Land Scotland

Modelling the impact of tree removal due to *Phytophthora ramorum* on red squirrels (*Sciurus vulgaris*) in the Cowal Peninsula

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Contents Page

Executive Summary

I. This model study investigated the likely impacts of proposed larch removal affected by Phytophthora, based on supplied felling plans, on red squirrel density and population persistence in the forest of Glenbranter and the Cowal peninsula as a whole.

II. The model simulated two different replanting schemes over a period of 75 years into the future: a like-for-like replanting and an enhanced replanting scheme. In both scenarios larch was replaced by other species.

III. For the like-for-like replanting scheme the model predicted a maximum of 180 and a minimum of 25 red squirrels for Glenbranter. While red squirrel numbers can get very low and the species may be absent for a period of time in parts of Glenbranter during the restructuring, none of the model simulations predicted extinction. For the Cowal peninsula as a whole the model predicted a maximum of 1185 and a minimum of 245 red squirrels.

IV. Importantly, the model predicted a species recovery in the like-for-like replanting scheme with an average population of 795 (down from 955 currently) red squirrels for the Cowal peninsula since some of the replanted forest has not reached seed bearing age and matured. The loss and replacement of larch, a tree species that supports good densities of red squirrels, also leads to a reduced maximum average population for this replanting scheme.

V. For the hypothetical enhanced replanting scheme which replaces the lost larch and a small proportion of Sitka spruce with tree species that favour red squirrels and biodiversity (PAWS) the model predicted a maximum of 215 and a low of 40 individuals for Glenbranter. For the Cowal peninsula as a whole the model predicted a maximum of 1420 and a minimum of 400 red squirrels.

VI. Under the enhanced replanting scheme the model predicted re-colonisation of Glenbranter and recovery in the Cowal peninsula following the replanted trees becoming mature. Furthermore, the decline in the red squirrel population was less severe in this scenario, which in part may relate to seed food becoming available sooner through the planting of hazel in suitable locations as well as through the provision of tree species that support higher densities of red squirrels.

VII. There are no grey squirrels in the Cowal peninsula and a combination of recovering pine marten populations and grey squirrel control (if needed) may allow a larger enhanced replanting scheme than the cautious one simulated here. However, care would have to be taken that the overall tree species composition is not shifted too far in the favour of grey squirrels. Nevertheless, the simulated, enhanced replanting scheme illustrates that there is scope to potentially improve red squirrel carrying capacity and biodiversity with respect to forest restocking on the Cowal peninsula.

VIII. In conclusion, the model study suggested that while felling to remove larch affected by Phytophthora is likely to lead to very low numbers in all but periphery regions of Glenbranter and will reduce red squirrel density throughout the Cowal Peninsula, the current felling and replanting plans do not place resident red squirrels at risk of extinction in the Cowal peninsula and that populations will recover as the replanted forest mature.

1. Introduction

Larch tree disease is caused by the highly destructive water mould *Phytophthora ramorum*. The mould is known to cause damage and death in over 150 plant species in Europe and North America, including many forest shrub and tree species such as *Rhododendron ponticum*, oak (e.g. *Quercus agrifolia*), alder (*Alnus glutinosa*) or larch (e.g. *Larix kaempferi*; Brasier, 1999; Purse et al., 2013; Hansen, 2015; Harris & Webber, 2016; Forestry Commission, 2021).

Symptoms of the disease in larch such as blackened needles, wilted shoots or bleeding lesions (e.g. Forestry Commission 2021) illustrate that water moulds of the genus *Phytophthora* are aptly named, with the scientific name being derived from the Greek words for 'plant' (*phytón*) and 'destroyer' (*phthorá*) (Wiktionary, 2021). While initial concern in the UK was focused on, for example, Sweet chestnut (*Castanea*) and *Phytophthora cambivora* or *P. cinnamomi*, the impacts of *Phytophthora* species have been increasing since the 1990s (Brasier, 1999). Over short distances, the mould can be spread by air currents or along watercourses and by rain splash. Over longer distances, it can also be spread on footwear, equipment as well as vehicles, including mountain-bike wheels (Forestry Commission 2021). Long distance transport of the pathogen is often via soil or plant material (Brasier, 1999). Furthermore, a recent survey for *P. ramorum,* covering more than 4000 samples from 2002-2009 in Scotland, also indicated that *Phytophthora* was frequently found in trade premises highlighting the role of the plant trade in its spread (Schlenzig et al., 2014).

Invasion prevention would clearly represent the best strategy to protect against *Phytophthora* species (e.g. Hansen, 2015). However, once *Phytophthora* has become established, management to safeguard the wider landscape focuses on the reduction or prevention of spread. This involves removal of affected shrubs or trees (Statutory Plant Health Notices, sanitation felling), as well as restrictions on the movement and planting of vulnerable species in designated risk zones where climatic conditions favour *Phytophthora* growth and spread (Forestry Commission 2021).

Larger-scale forest removals inevitably carry the risk of negative impacts on local biodiversity, food webs and endangered species. *Phytophthora* therefore not only represents a threat to UK forest ecosystems, but also to native woodland species relying on specific tree species for food, shelter, and survival. Restrictive replanting policies with an emphasis on tree species that hinder spore production are therefore also likely to have unwanted, additional side effects on local population densities of species in affected woodland ecosystems. This can, for example, occur through potential impacts on local carrying capacity and thus population density and survival. A species that is reliant on forest habitat is the endangered red squirrel (*Sciurus vulgaris*) and Shuttleworth et al. (2012) highlighted the need for an integration of their habitat requirements with the management of pathogenic tree diseases in commercial forests in the UK.

Here, in collaboration with Forestry and Land Scotland (FLS) we have applied an established mathematical model (Jones et al. 2016; Slade et al. 2020, 2021) of the red squirrel population dynamics in realistic landscapes to assess the impact of forest management to remove infected larch in the Cowal peninsula on red squirrel viability. Specifically, we simulated the impact of proposed felling plans, which aim to remove all of the infected larch trees (but will, by necessity, also fell other tree species) in the Glenbranter stronghold and the wider Cowal peninsula on red squirrel density and population persistence.

1.1 Objectives

1: *Determine red squirrel viability under planned forest removal and 'like-for-like' replanting in Glenbranter.*

The model will be used to assess red squirrel density and viability under the proposed scenarios of forest removal and replanting in Glenbranter. The species mixture in replanted regions will use the same relative species proportions as those prior to removal – but larch will not be replanted. The mathematical model will include seed crop patterns and reflect the time for replanted trees to reach maturity and thereby provide a resource for red squirrels. This will highlight the impact of forest management on short-term and long-term red squirrel viability.

2: *Determine red squirrel viability under planned forest removal and 'like-for-like' replanting in the Cowal peninsula.*

The forest regions out-with FLS control will also require larch removal due to infection. Therefore, the set-up in objective (1) will be modified to additionally include a representation of felling and replanting in non-FLS managed forests in the Cowal peninsula. We will approximate the felling rate in non-FLS managed forests (for which data is not available) by assuming is has the same rate of felling, over the same proportional area as in FLS managed regions. This scenario is important as red squirrel viability will be affected by the availability of adjacent suitable habitat.

3: *Determine red squirrel viability under planned forest removal and replanting with 'enhanced' species diversity in Glenbranter.*

This scenario is the same as that in objective (1) except it is assumed that the felled regions are replanted with a tree species mixture that has enhanced diversity (with the enhanced diversity, tree species mixture determined in collaboration with FLS). An assessment of the impact of enhanced diversity on long-term red squirrel viability will be undertaken by comparing red squirrel density and variability under 'enhanced' replanting with the results for 'like-for-like', commercial conifer dominated, replanting from objective (1).

4: *Determine red squirrel viability under planned forest removal and replanting with 'enhanced' species diversity in the Cowal peninsula.*

This scenario is the same as that in objective (2) except it is assumed that all felled regions are replanted with a tree species mixture that has enhanced diversity.

2. Methods

2.1 Tree Species Information

The tree species composition and felling plans for Glenbranter were supplied by FLS. In total there are 15 different tree species used in the model, with a full list being provided in Table 1 (see Figure 1 for the initial tree species composition).

The forest composition of the Cowal peninsula is initially generated using the National Forest Inventory (2016) dataset, which includes information on the location of broadleaf and coniferous trees. The Inventory dataset also includes ‘mixed, mainly broadleaf’ - which we set as 65% broadleaf and 35% conifer, ‘mixed mainly conifer’ – which we set as 65% conifer and 35% broadleaf, as well as ‘assumed woodland’ which we set as 50% broadleaf and 50% conifer. The tree species composition of the Glenbranter stronghold is superimposed upon the National Forest Inventory data, which provides a more detailed forest landscape in the Cowal peninsula. This assumes that the wider Cowal peninsula has the same broadleaf and conifer tree species proportions as the Glenbranter stronghold. In the wider Cowal peninsula the forest inventory data does not provide information on the location of larch and so the proportion of tree species that would be designated as larch trees are instead classified as ‘Other Conifer’ (which has similar carrying capacity characteristics as larch, see Table 1), and it is assumed that any larch that is felled in the wider Cowal peninsula will be replaced either by an alternative coniferous tree species that has a similar carrying capacity, or by the ‘enhanced’ species (a simulated scenario with greater emphasis on PAWS species with improved biodiversity impacts). Given that neutral species do not contribute to the red squirrel carrying capacity, they have been omitted from the imposition. See Figure 2 for the initial forest composition of the Cowal peninsula (excluding the Glenbranter stronghold).

2.2 Felling

We use the data provided by FLS to determine the extent of felling over the next 75 years. The data indicates that a maximum of 4.75% and a minimum of 0% of the forest of Glenbranter is felled each year (see Figure 3a(i)). On average, 1.03% of the total forest density is felled annually. In total, 77.37% of the forest in the Glenbranter stronghold is felled and replanted over the 75 year study period (see Figure 3b(i)). The felling location is highly variable from year to year, which suggests an effort to avoid over-felling any one region. The felling regions do not correspond directly to the 1km^2 grid used in the model, so felling removes a proportion of the grid-square, based on the amount of forest that should be felled.

The felling in the wider peninsula is based on the felling plans for the Glenbranter stronghold. There is a maximum of 4.53% and a minimum of 0% of the forest to be felled each year (see Figure 3a(ii)). On average 1.05% of the total forest density is felled annually. In total 78.43% of the forest in the Cowal peninsula, not including the Glenbranter stronghold, is felled and replanted over the 75 year study period (see Figure 3b(ii)). The choice of what regions of mature forest to fell is chosen at random, meaning the felling plans match the 1km^2 grid. Once a grid square has been felled it cannot be felled again for the next 40 years, as this is the felling age of Sitka spruce, which is the dominant species. A snapshot of the felling regions is shown in Figure 4.

Table 1- Tree Species Carrying Capacity, Mast Interval and Maturity Information (Slade et. al, 2020). Maturity indicates how many years of growth are required before a tree species starts reliably producing seeds.

Tree Species	**Mast CC (ha^{-1})**	**Non-Mast CC (ha^{-1})**	**Mast Interval (Years)**	**Age of Maturity (Years)**
Beech	110	28	7	50
Hazel	85	85	1	5
Sycamore	0	0	2	25
Oak	100	25	4	40
Other Broadleaf	92	23	5	30
Neutral Species	0	0	N/A	N/A
Secondary Species	10	2	1	1
Larch	38	21	4	15
Lodgepole Pine	21	16	2	15
Scots Pine	83	33	2	15
Corsican Pine	110	28	3	25
Douglas Fir	16	4	5	30
Norway Spruce	58	25	4	30
Sitka Spruce	20	2	4	30
Other Conifer	35	14	3	25

2.3 Tree Replacement

We consider two replanting schemes – a like-for-like replanting and an enhanced, 'biodiversity' replanting scheme where the PAWS component is enhanced:

I.) The like-for-like replanting scheme assumes that felled species are replaced like-for-like – excluding larch whose density in Glenbranter is split evenly between the other species. Any larch in the wider Cowal peninsula is included in the 'Other Conifer' group and assumed to be replaced by a non-larch species that has a similar carrying capacity.

II.) The enhanced replanting scheme assumes that the felled larch, along with 5% of the felled Sitka spruce in the Glenbranter forest, is replaced by hazel, Scots pine, and Other Broadleaf in a 20:30:50 ratio. This, in effect, simulates a PAWS focused scenario (e.g. see Thompson et al. 2003) to increase both red squirrel density in what would have been the original red squirrel woodland habitat in the UK in the absence of grey squirrels combined with a wider biodiversity enhancement. PAWS planting is being undertaken in some regions of Glenbranter (Forest and Land Scotland, pers. comm.). The combined larch and 5% of the felled Sitka spruce are replaced as follows: 20% is replaced by hazel, which is a fast growing species that can help maintain red squirrel density during the period of felling operations, 30% is replaced with Scots pine, which is a native conifer that will improve biodiversity and the remaining 50% is replaced by 'Other Broadleaf' which reflects the possibility that a range of broadleaf species could be planted to improve biodiversity and tree species diversity. The remaining species and 95% of the felled Sitka spruce are replaced like-for-like. Any larch in the wider Cowal peninsula is included in the Other Conifer group. Initially 5% of the Glenbranter forest is larch and 1% is Other Conifer, making a total of 6%. Thus, we assume that 5/6th of the Other Conifer category in the wider Cowal peninsula is comprised of larch, which will be replaced with hazel, Scots pine and Other Broadleaf at the same proportions outlined above. The same proportion of felled Sitka spruce (5%) is also replaced with the enhanced species in the Cowal peninsula.

Each species has a growth period during which it does not contribute to the red squirrel carrying capacity (see Age of Maturity, Table 1). This simulates the time required for a tree to grow and start bearing seeds.

There are currently no grey squirrels, and consequently no squirrelpox disease and no competition between the two squirrel species in the Cowal peninsula. Hence, we only need to model the population dynamics of red squirrels without squirrelpox being present. The squirrel dynamics are modelled using an established and well-tested stochastic model that links squirrel population dynamics to habitat (White et al. 2016; Jones et al. 2016) and has previously been used to model the implementation of forest felling and replanting in selected stronghold forests in Scotland (Slade et. al. 2020, 2021).

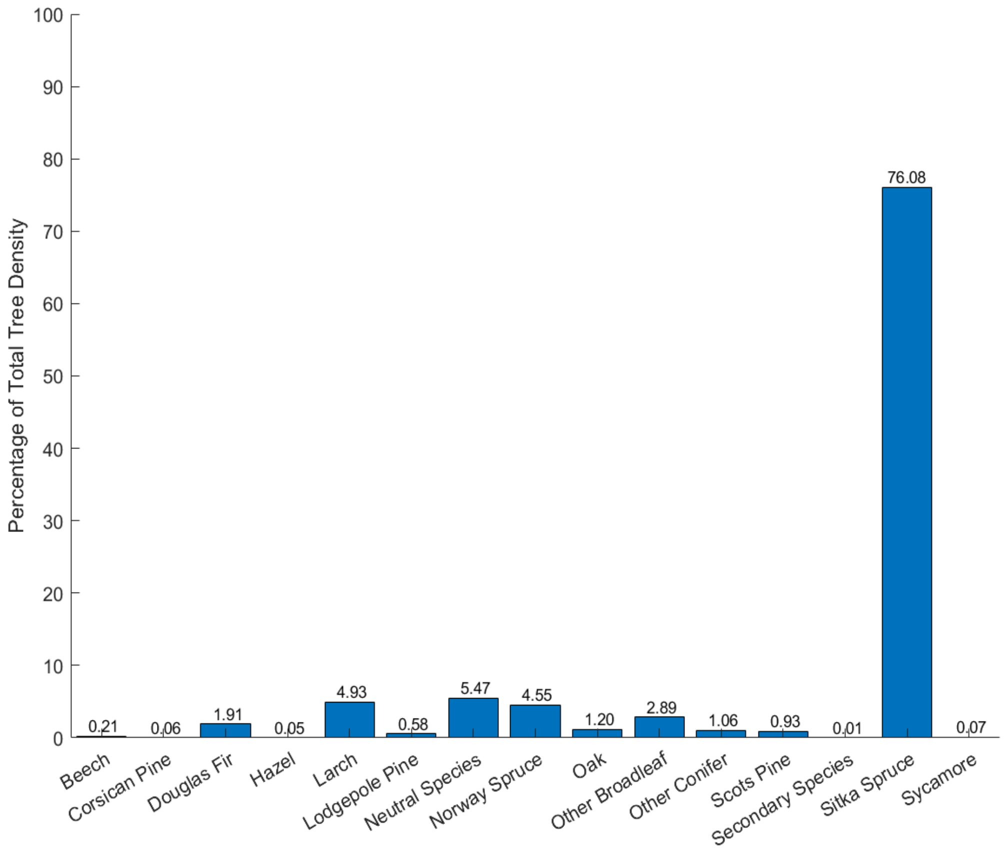

Figure 1- Initial tree species composition in the Glenbranter stronghold. Values above each bar indicate the percentage of the forest, as a proportion of the total forest density, that each tree species makes up.

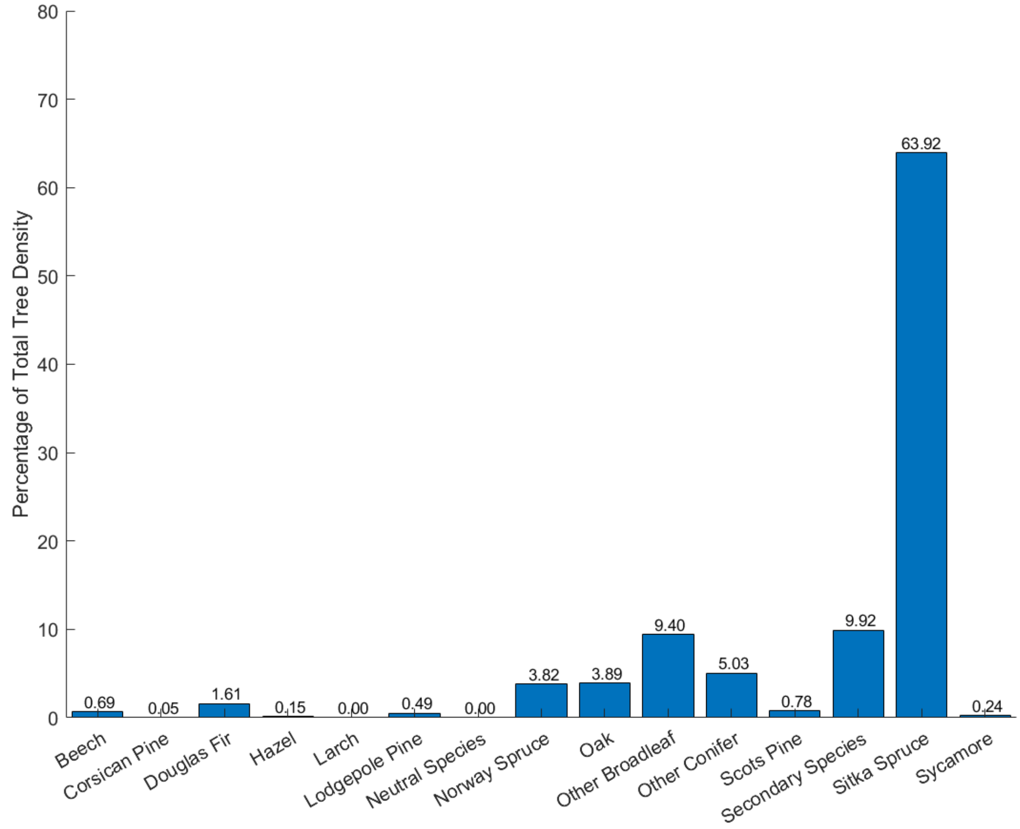

Figure 2 - Initial tree species composition in the Cowal peninsula. Values above each bar indicate the percentage of the forest, as a proportion of the total forest density, that each tree species makes up.

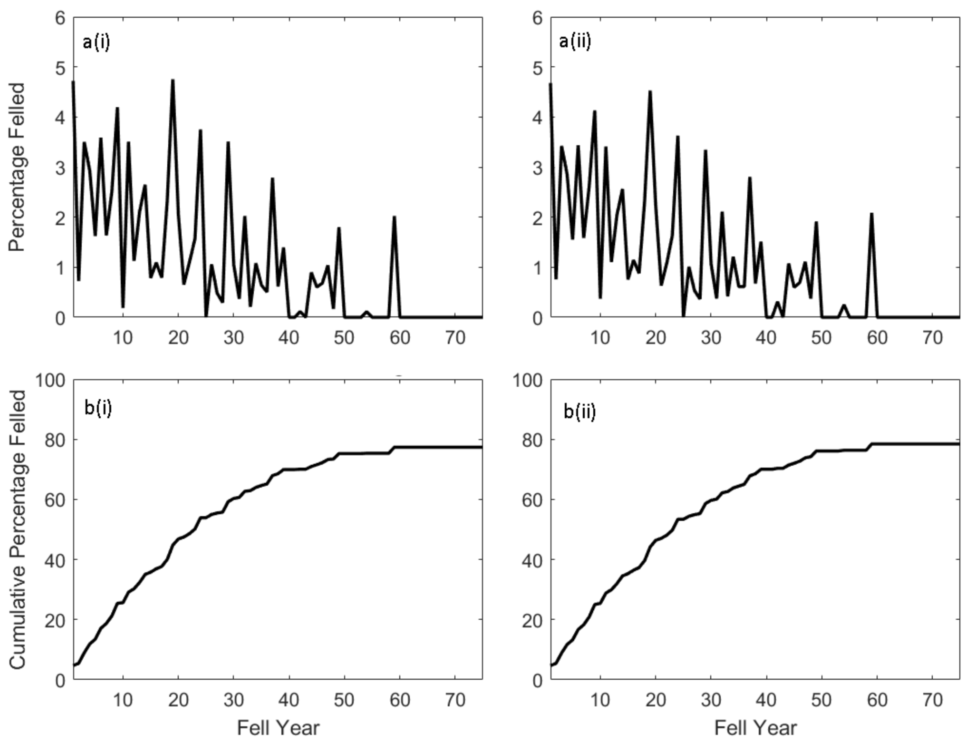

Figure 3 - Annual and cumulative felling percentages. Here (a) shows the annual felling amount and (b) the cumulative felling whilst (i) shows the felling for Glenbranter and (ii) the felling for the whole Cowal peninsula, without Glenbranter. Year 0 in the image indicates the year 2022.

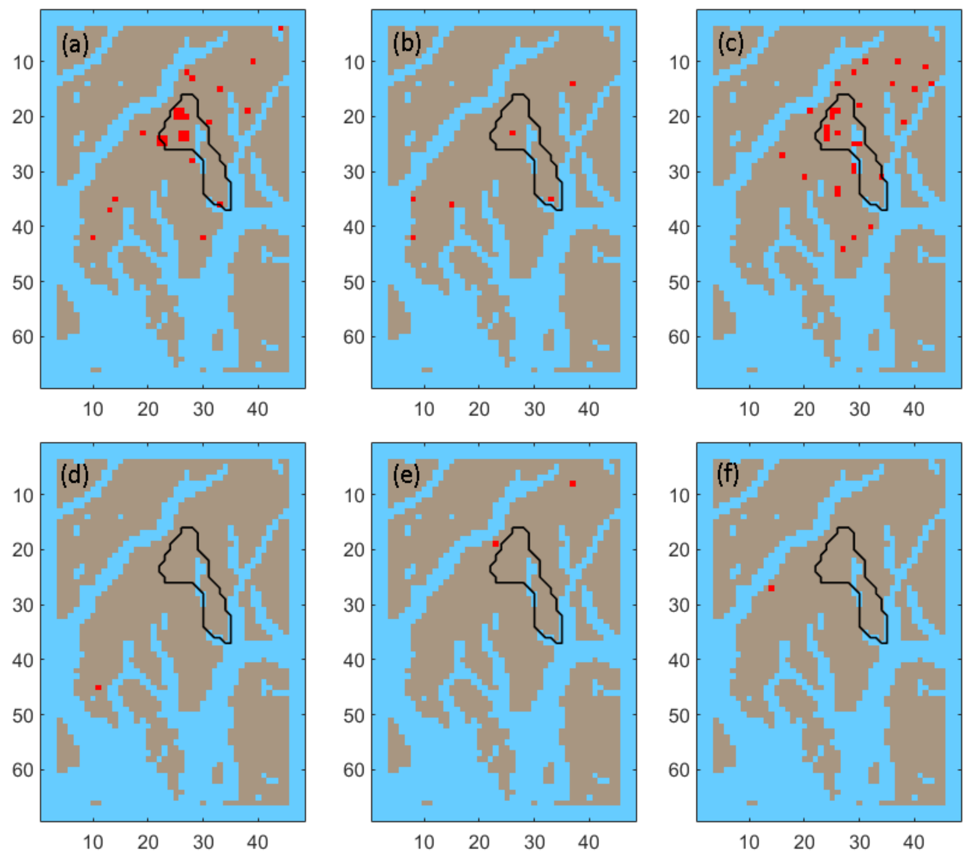

Figure 4 - Felling locations in the Cowal peninsula, indicated by red squares, in years (a) 5, (b) 10, (c) 20, (d) 40, (e) 60, and (f) 70.

2.4 Carrying Capacity

The carrying capacity of the forest features, which denote the maximum allowable red squirrel population (assuming all regions are occupied at maximum capacity), are generated using the values supplied in Table 1. Seed crop dynamics have been included that provide a higher carrying capacity in mast years compared to non-mast years. The initial condition (mast/non-mast) of each species is decided randomly, and the same initial condition is used across all simulations to remove it as a stochastic factor. The change between mast and non-mast values is governed by the mast interval, which is pre-defined for each tree species (Table 1). We only use the habitat types outlined in Table 1 when calculating the red squirrel carrying capacity. In particular, we do not include urban areas, where supplementary feeding may take place.

Figure 5 shows the red squirrel carrying capacity, with both replanting schemes and without felling, in the Glenbranter stronghold. The annual fluctuation in capacity due to seed crop dynamics sees a maximum capacity of 500 and a minimum of 145 individuals when there is no felling, with an average capacity of 260. When felling is included and tree species replanted like-for-like, Glenbranter has a maximum carrying capacity of 435, a minimum capacity of 95 individuals and an average between 160 and 250 individuals resident in the stronghold. At its lowest level, the average carrying capacity is reduced by 40% due to felling in the stronghold. When the felled species are replanted according to the enhanced scheme Glenbranter has a maximum capacity of 525, a minimum capacity of 135 individuals and an average between 200 and 330 individuals resident in the stronghold. At its lowest level, the average capacity is reduced by 23%. The average carrying capacity when there is no felling is greater than the average capacity under the like-for-like replacement for the entire simulation, and greater than the enhanced replacement for the first 42 years of simulation only. The enhanced replanting scheme ends the simulations with an increase in average capacity of 25% compared to when there is no felling. The average capacity under the enhanced replanting is greater than that for the like-for-like replanting for the entire simulation.

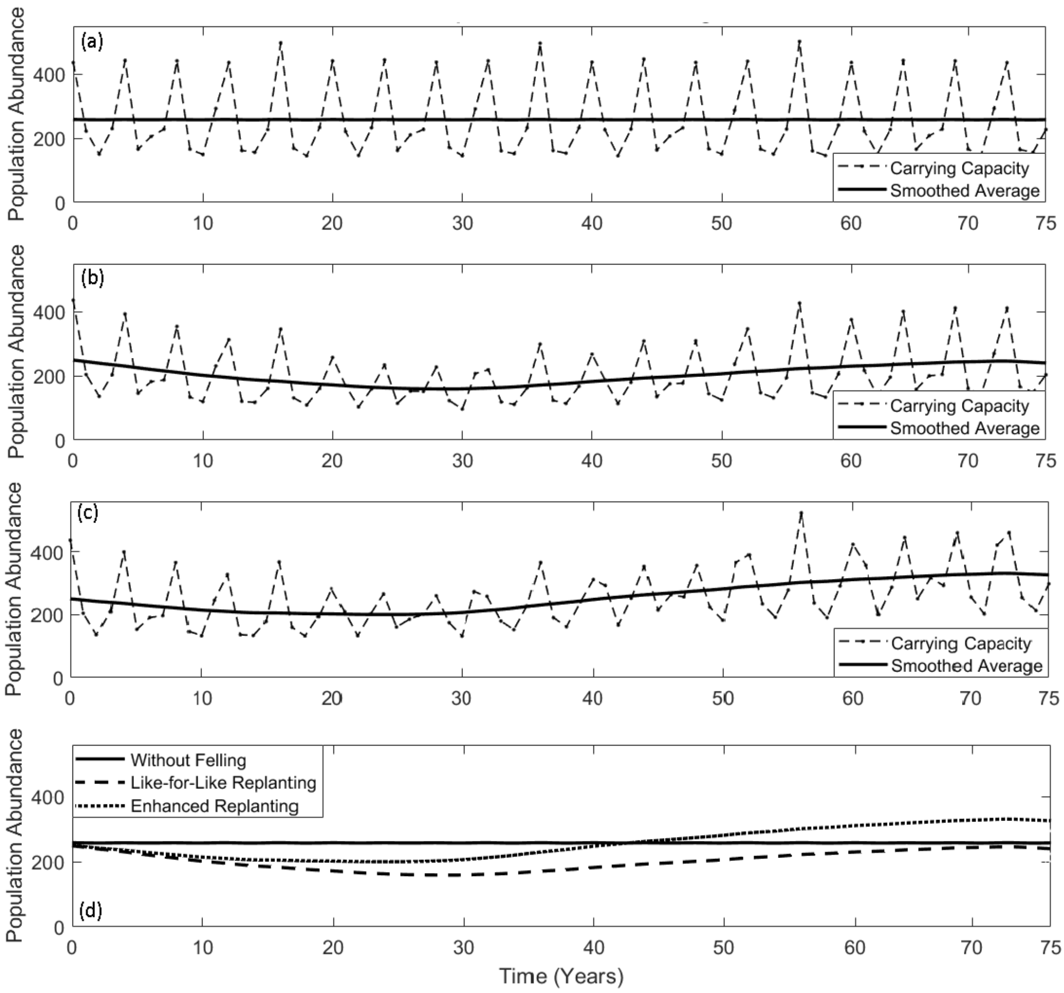

Figure 5 - Carrying capacity in Glenbranter (a) without felling, (b) with felling and like-for-like replanting and (c) with felling and an enhanced replanting. Image (d) shows a comparison of the smoothed averages for the 3 scenarios. Year 0 of the image represents the year 2022.

Figure 6 below shows the red squirrel carrying capacity, with both replanting schemes and without felling, for the whole Cowal peninsula, which includes the Glenbranter stronghold. The maximum capacity without felling is 4625, the minimum capacity is 1310 and the average carrying capacity is 2185 individuals. When felling is included and tree species replanted like-for-like, there is a maximum carrying capacity of 3880, a minimum capacity of 680 individuals and an average between 1090 and 2120 individuals resident in the stronghold. At its lowest level, the average carrying capacity is reduced by 50% due to felling in the stronghold. When the felled species are replaced according to the enhanced scheme there is a maximum capacity of 4755, a minimum capacity of 900 individuals and an average between 1365 and 2485 individuals resident in the stronghold. At its lowest level, the average capacity is reduced by 38%. The average carrying capacity when there is no felling is greater than the average capacity under the like-for-like replanting scheme for the entire simulation and is greater than the enhanced replacement for the first 59 years of the simulation. The enhanced replanting scheme ends the simulations with an increase in average capacity of 14%. The average capacity is greater under the enhanced replanting than the like for like replacement for the whole simulation. Note, not all replanted trees will have reached maturity at the end of the simulation, thus the final capacity may not be the long-term average.

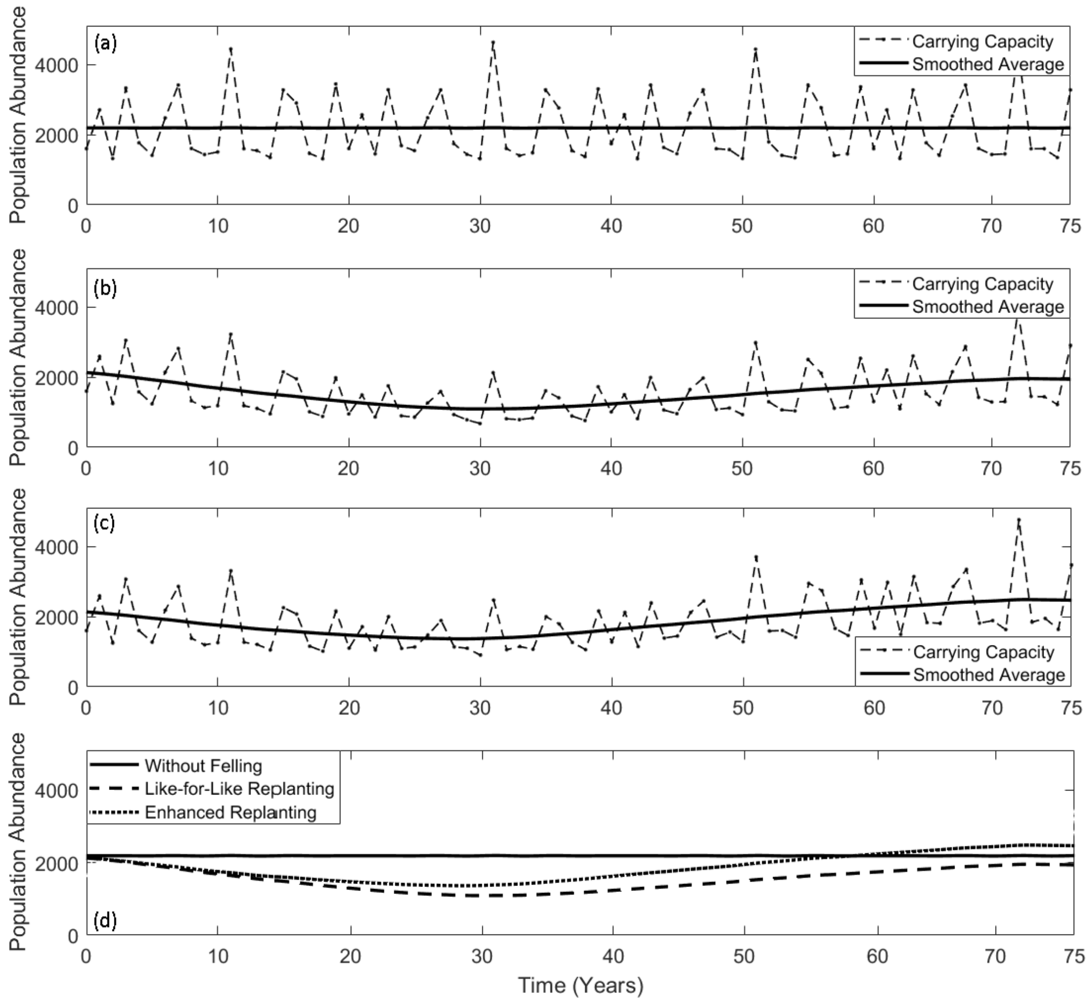

Figure 6 - Carrying capacity in the Cowal Peninsula (a) without felling, (b) with felling and like-for-like replanting and (c) with felling and enhanced replanting. Image (d) shows a comparison of the smoothed averages for the 3 scenarios. Year 0 of the image indicates the year 2022.

Figure 7 shows maps of the Cowal peninsula, without felling, which highlights the variability in carrying capacity as well as the regions that are unable to support red squirrels. It is worth noting that Glenbranter supports lower density squirrel populations compared to regions in the wider Cowal peninsula.

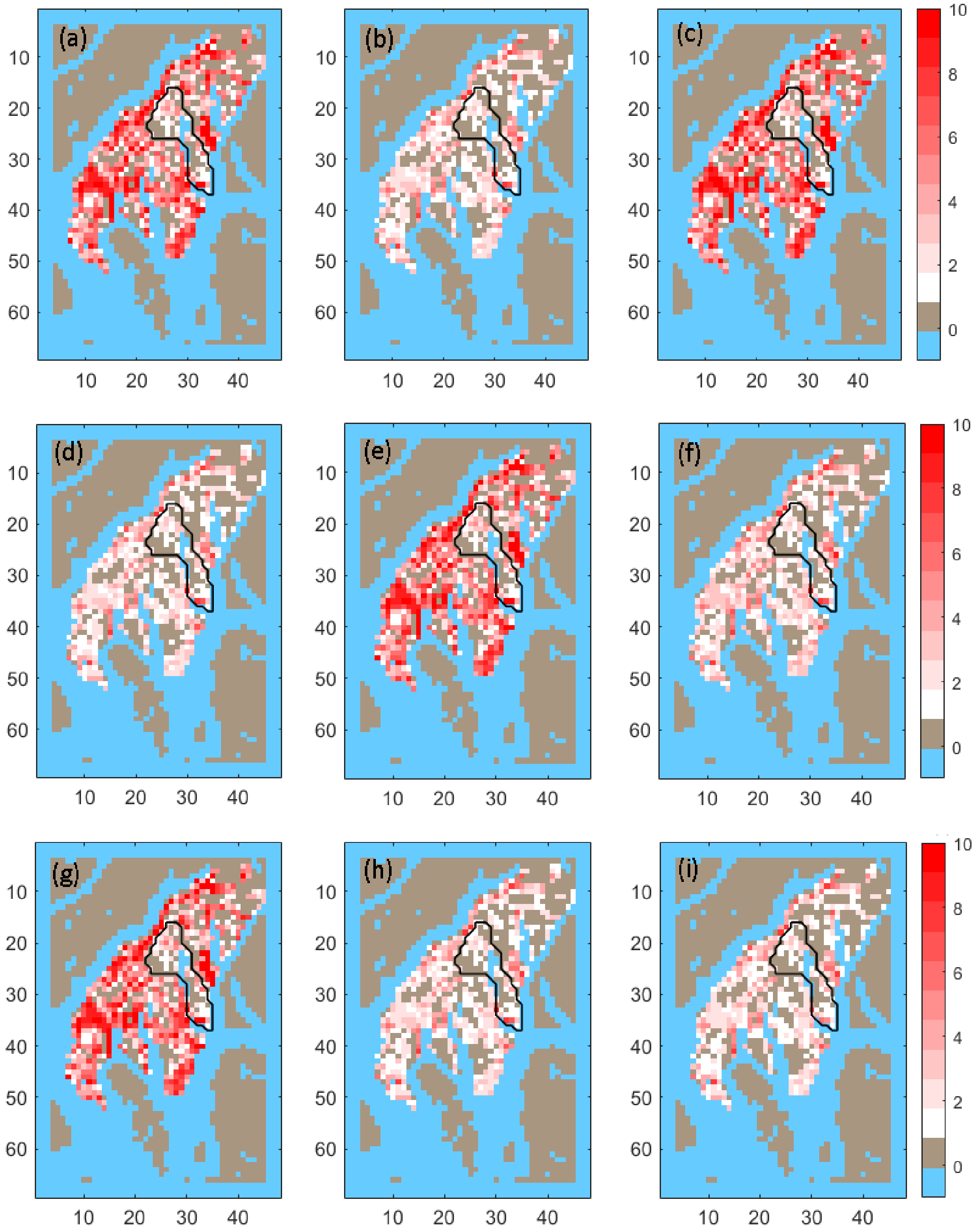

Figure 7 - Carrying capacity maps, without felling, for years (a) 0, (b) 10, (c) 20, (d) 30, (e) 40, (f) 50, (g) 60, (h) 70, & (i) 75. Regions outside the Cowal peninsula have had their carrying capacity artificially set to zero for imaging purposes only.

Figure 8 shows maps of the Cowal peninsula, when felling has occurred and the trees are replaced like-for-like, which highlights the regions that are unable to support red squirrels due to the felling regime.

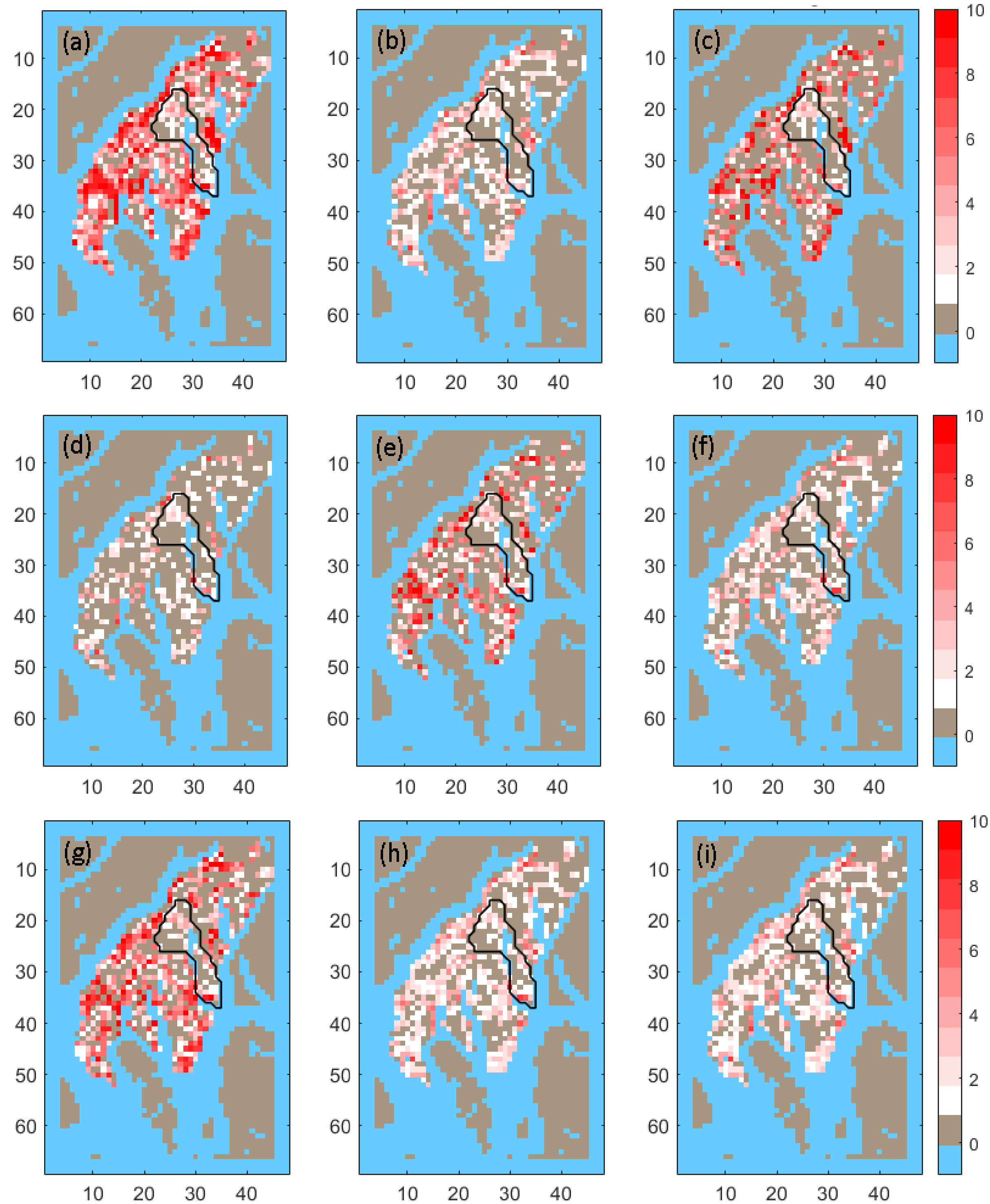

Figure 8 - Carrying capacity maps, with felling and like-for-like replacement, for years (a) 0, (b) 10, (c) 20, (d) 30, (e) 40, (f) 50, (g) 60, (h) 70, & (i) 75. Regions outside the Cowal peninsula have had their carrying capacity artificially set to zero for imaging purposes only.

Figure 9 shows maps of the Cowal peninsula, when felling has occurred and the trees are replaced with an enhanced mixture, which highlights the regions that are unable to support red squirrels due to the felling regime.

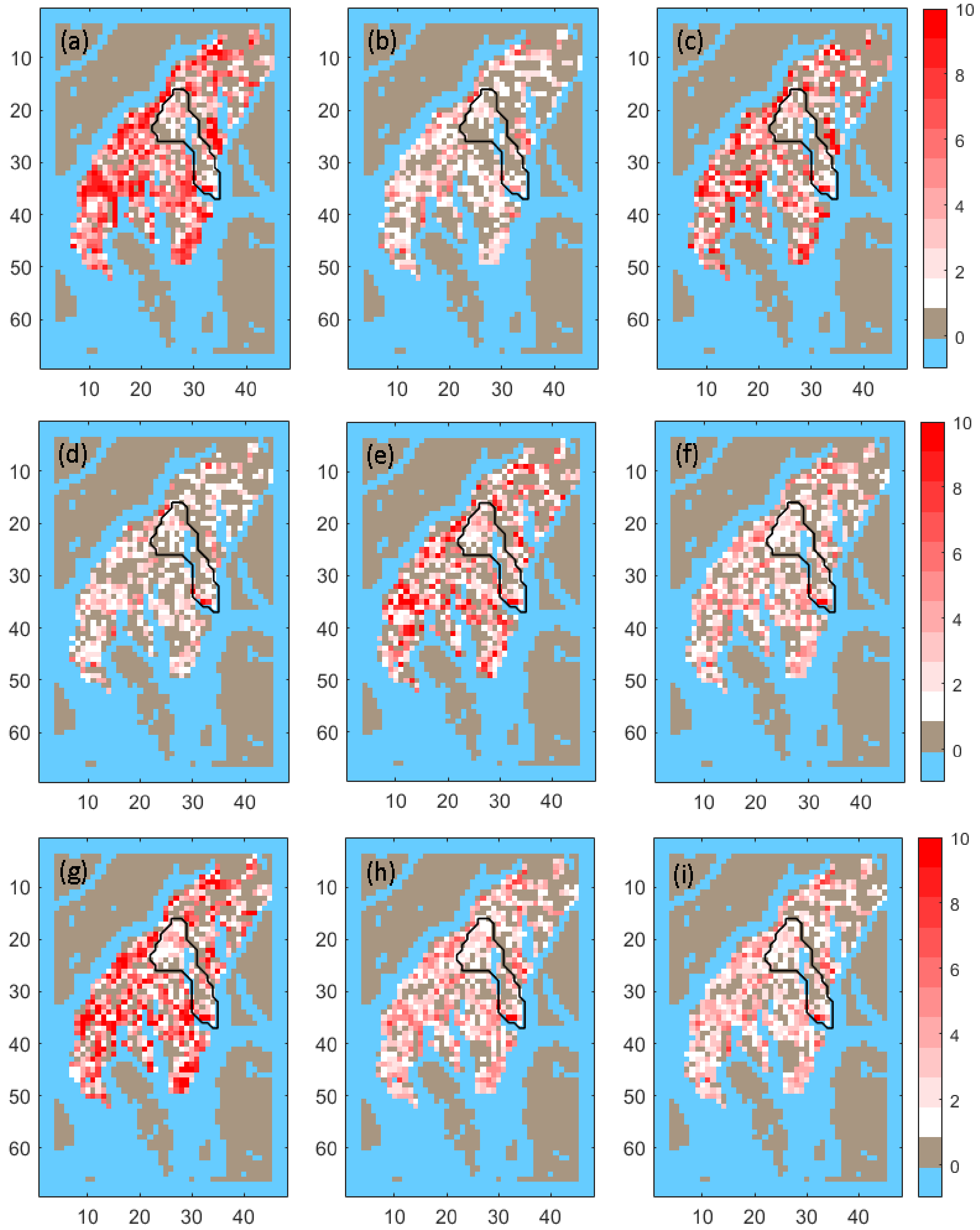

Figure 9 - Carrying capacity maps, with felling and enhanced replanting, for years (a) 0, (b) 10, (c) 20, (d) 30, (e) 40, (f) 50, (g) 60, (h) 70, & (i) 75. Regions outside the Cowal peninsula have had their carrying capacity artificially set to zero for imaging purposes only.

2.5 Red Squirrels

Red squirrels are currently resident in the Cowal peninsula. The proposed felling will impact the population dynamics of all species that inhabit the forest, but only red squirrels shall be simulated in this report. Using information from Slade et. al. (2020, 2021) we created a stochastic model that simulates the population dynamics of red squirrels. The stochastic model is based on an underlying ODE model (equation 1) for the density of red squirrels (R)

$$\frac{dR}{dt} = a(t)(1 - qR)R - bR \qquad (1)$$

where a(t) is the birth rate which equals 3.0 during the squirrel breeding season (between March and September) and zero otherwise, b=0.9 is the natural death rate and q denotes the susceptibility to crowding, which is grid-square dependent and is directly linked to the carrying capacity (K) in each grid-square. This model is used in conjunction with the Gillespie algorithm to generate a stochastic model of the red squirrel population dynamics (see Table 2). Spatial dynamics are included in the stochastic model – by allowing red squirrels to disperse between grid-squares – which allows the impact of the felling on the geographic dynamics of red squirrels to be assessed. The stochastic model is simulated for 75 years, with 10 model realisations being produced for each scenario which captures the variability inherent in stochastic models.

Table 2 - State transitions and their probabilities in the stochastic model. S=sum of all the rates. The asterisk denotes the grid-square that is being dispersed into

Event	Population Change	Probability of Event
Birth	$R \to R+1$	$[a(1-qR)R]/S$
Death	$R \to R-1$	$[bR]/S$
Dispersal	$R \to R-1, R^* \to R^*+1$	$\left[mR\left(\frac{R^2}{K^2}\right)\right]/S$

3. Results

3.1 Red Squirrel Abundance

3.1.1 No Felling

Figure 10 shows the red squirrel density in (a) Glenbranter and (b) the whole Cowal peninsula when felling does not occur. Figure 10(a) indicates that the average, smoothed, population density (solid line) in Glenbranter varies between 90 and 100 individuals, whereas the unsmoothed average (dashed line) has a high value of 150 and a low value of 75. The maximum and minimum of any single realisation is 200 and 50 respectively. No model realisation reaches zero during the simulation. Figure 10(b) indicates that the average, smoothed, population density in the Cowal peninsula varies between 950 and 1000 individuals. The unsmoothed average has a high of 1200 and a low of 800 individuals. The maximum and minimum of any single realisation is 1325 and 680 respectively. No model realisation for the entire peninsula reaches zero during the simulation. Note, squirrel density is consistently lower than the expected carrying capacity. On average, 19% of grid-squares with a carrying capacity are empty as abundance is low and the grid-squares are isolated which increases the chance of local extinction. Also, the squirrel density cannot respond quickly to the large increases in capacity during high resource years. Nevertheless, we capture the variation in squirrel abundance due to seed crop variation.

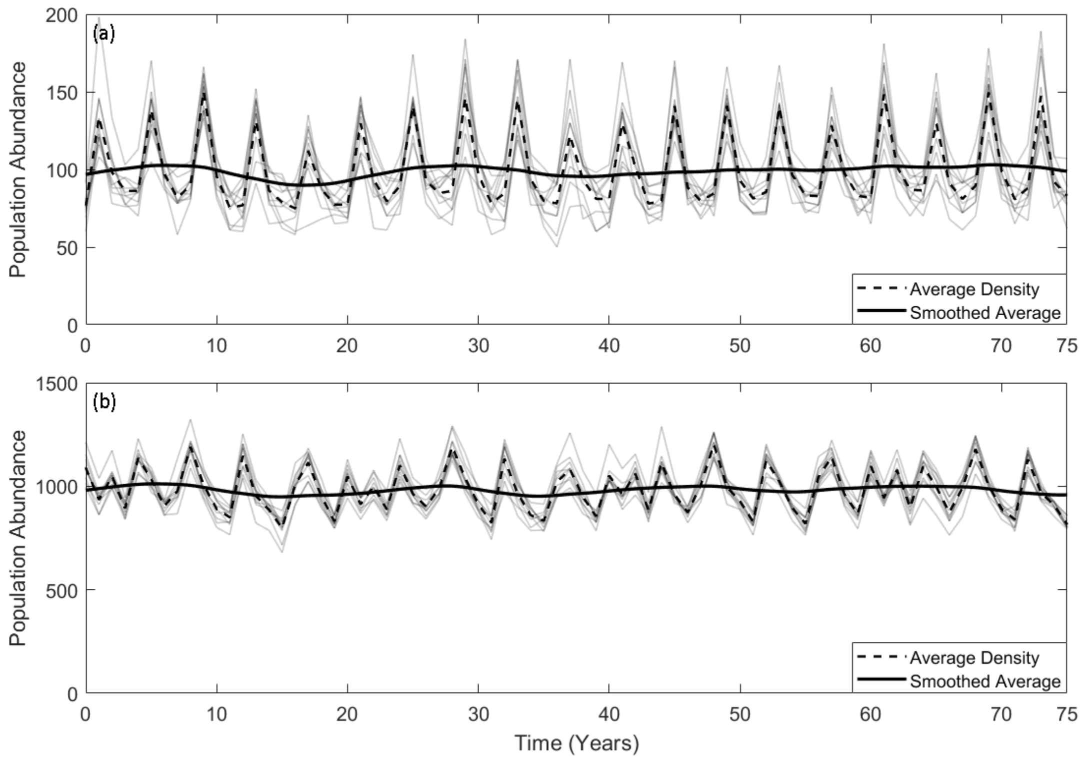

Figure 10 - Red squirrel density in (a) Glenbranter and (b) the Cowal Peninsula when no felling has occurred. The solid line is the smoothed average, the dashed line indicates the unsmoothed average of the 10 model realisations and the grey lines are the 10 model realisations. Year 0 of the image indicates the year 2022.

Figure 11 shows density maps for years 0, 10, 20, 30, 40, 50, 60, 70 and 75 of the simulation. Given there is no felling, all the geographic differences in red squirrel density are due to seed crop dynamics. The maps indicate that there are regions in the Cowal peninsula that cannot support long-term red squirrel populations.

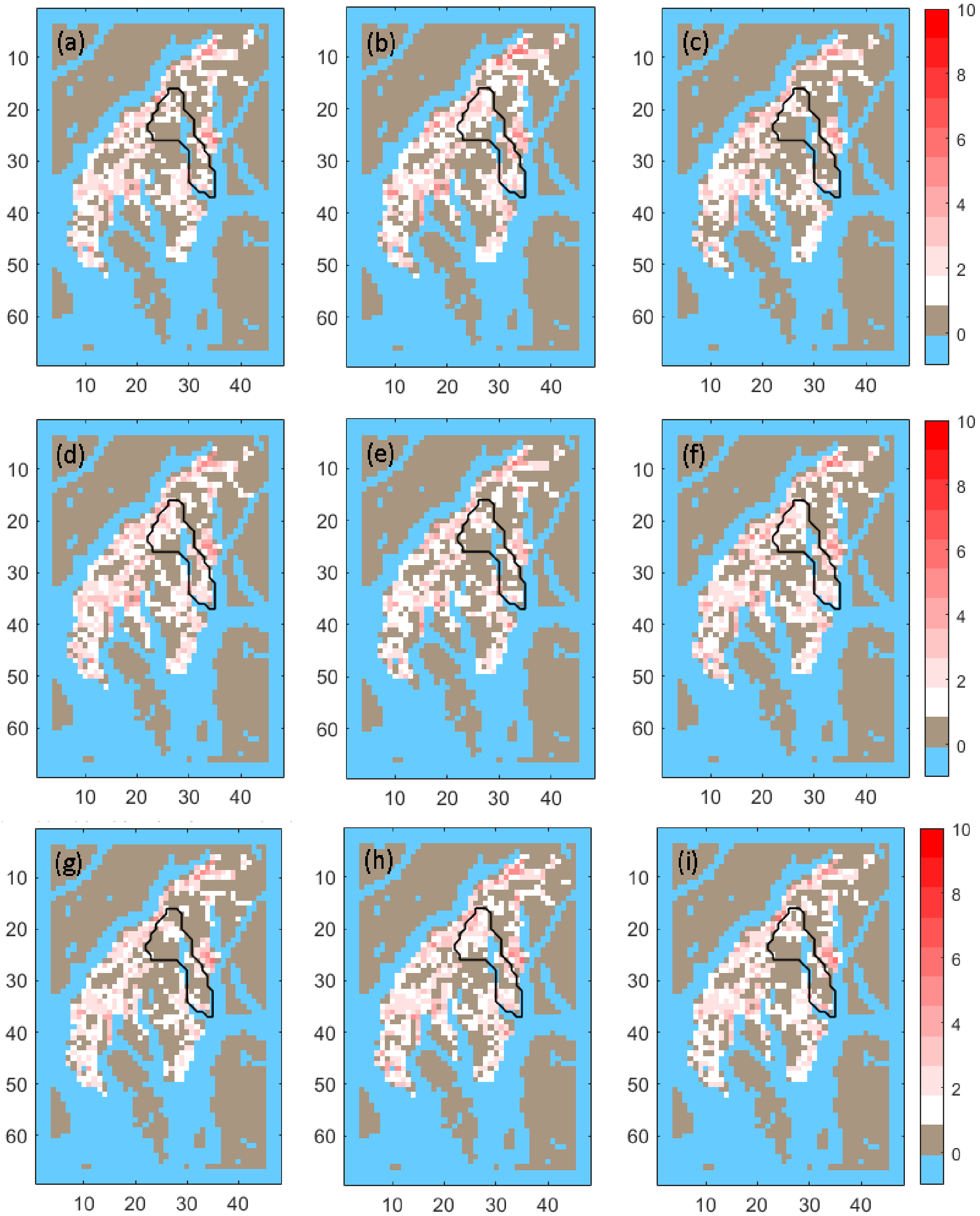

Figure 11 - Maps showing red squirrel density and location, when no felling has occurred, for years (a) 0, (b) 10, (c) 20, (d) 30, (e) 40, (f) 50, (g) 60, (h) 70, & (i) 75. Regions outside the Cowal peninsula have had their carrying capacity artificially set to zero for imaging purposes only.

3.1.2 Like-for-Like Replanting Scheme

Figure 12 shows the red squirrel density in (a) Glenbranter and (b) the whole Cowal peninsula when felling and like-for-like replanting occurs. Figure 12(a) indicates that the average, smoothed, population density in Glenbranter begins at 100, reaches a low of 55 in year 38 of the simulation and ends the simulation at 85 individuals. The unsmoothed average has a high of 140 and a low of 45 individuals. The maximum and minimum of any single realisation is 180 and 25 respectively. None of the 10 simulation realisations reach zero population during the 75 year simulation. Figure 12(b) indicates that the average, smoothed, population density in the Cowal peninsula begins at 955, reaches a low of 375 in year 38 of the simulation and ends the simulation at 795 individuals. The unsmoothed average has a high of 1060 and a low of 335 individuals. The maximum and minimum of any single realisation is 1185 and 245 respectively. No model realisation for the entire peninsula reaches zero during the simulation.

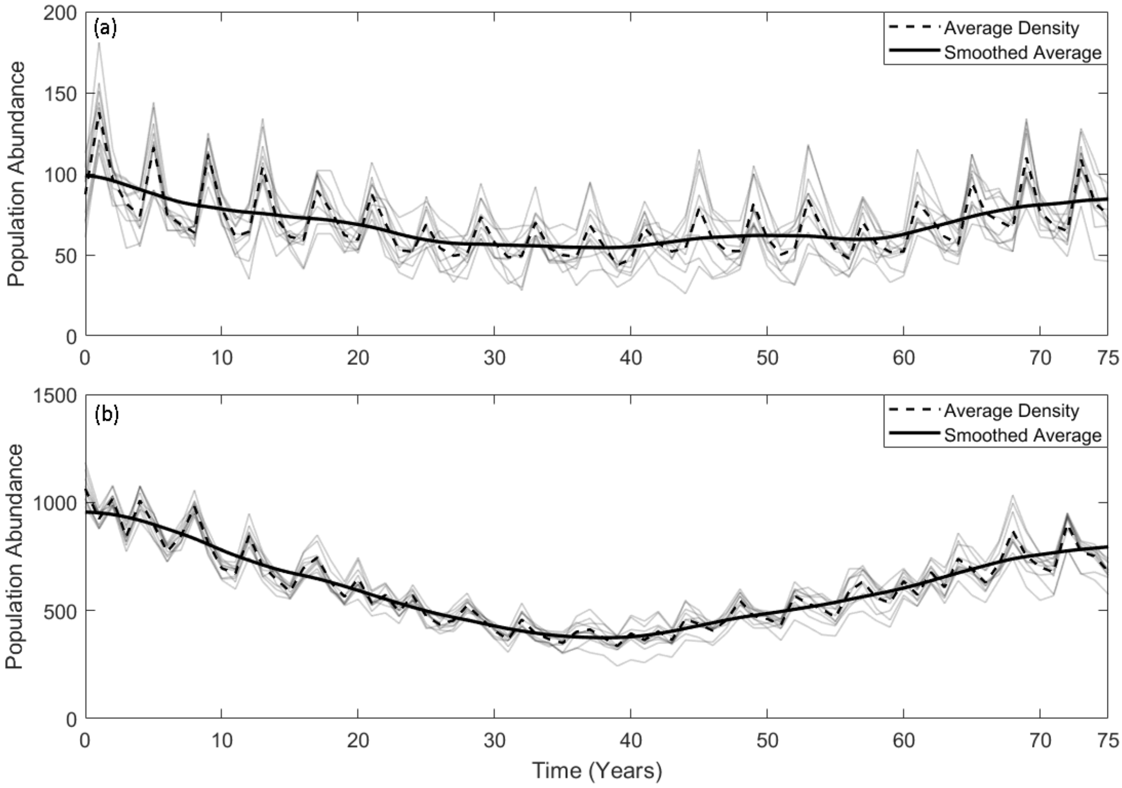

Figure 12 - Red squirrel density in (a) Glenbranter and (b) the Cowal Peninsula when felling and like-for-like replanting has occurred. The solid line is the smoothed average, the dashed line indicates the unsmoothed average of the 10 model realisations and the grey lines are the 10 model realisations. Year 0 in the image indicates the year 2022.

Figure 13 shows density maps for years 0, 10, 20, 30, 40, 50, 60, 70 and 75 of the simulation when there is felling and like-for-like replanting. The geographic spread of red squirrels in the Cowal peninsula becomes patchier when felling is included, though red populations persist in several regions. The density in Glenbranter is reduced by the felling, with the majority of the stronghold having no red squirrels present for many years. However, red squirrels are able to re-colonise the stronghold from the wider peninsula when the forest in Glenbranter is able to support them again.

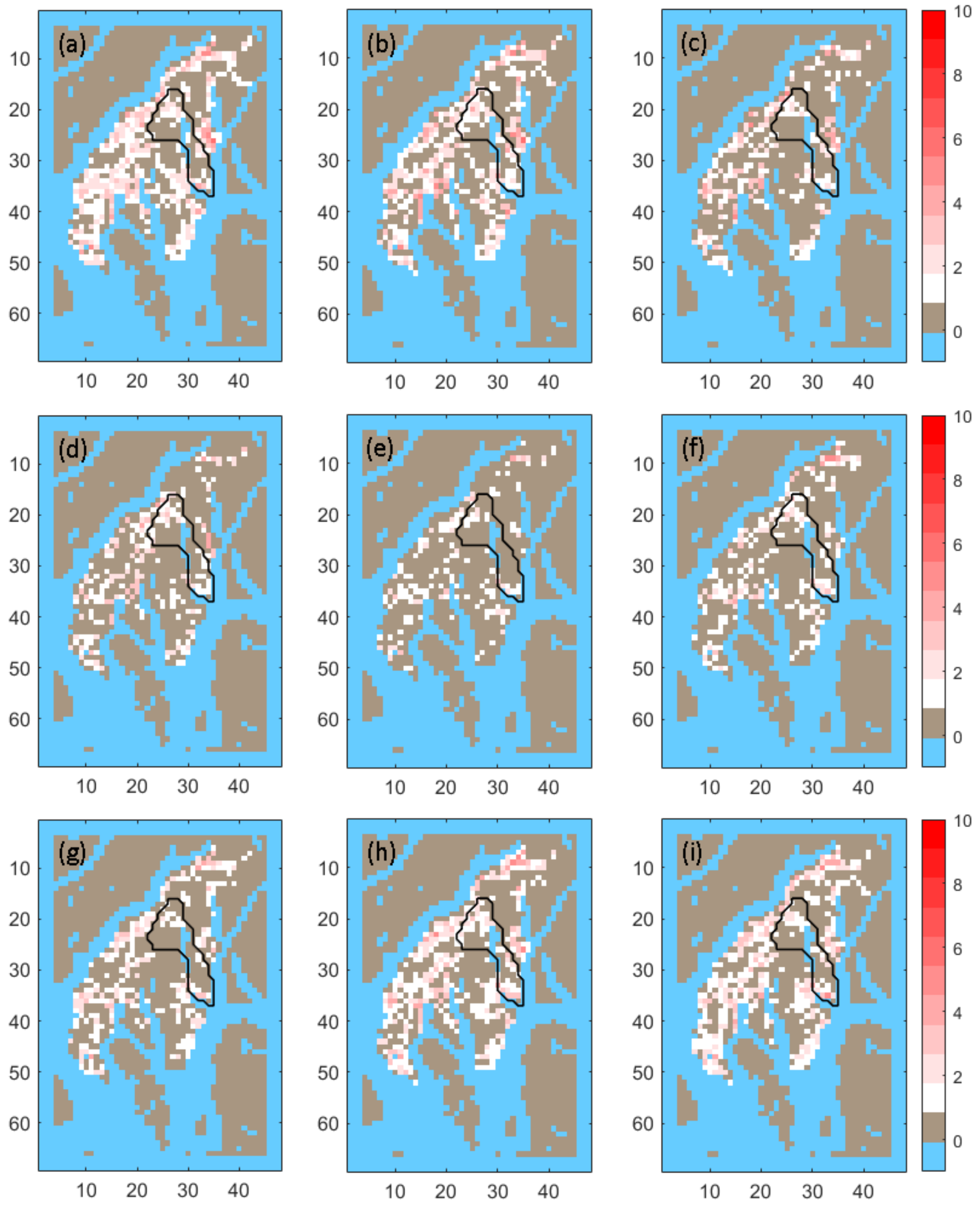

Figure 13 - Maps showing red squirrel density and location, when felling and like-for-like replanting has occurred, for years (a) 0, (b) 10, (c) 20, (d) 30, (e) 40, (f) 50, (g) 60, (h) 70, & (i) 75. Regions outside the Cowal peninsula have had their carrying capacity artificially set to zero for imaging purposes only.

3.1.3 Enhanced Replanting Scheme

Figure 14 shows the red squirrel density in (a) Glenbranter and (b) the whole Cowal peninsula when felling and enhanced replanting occurs. Figure 14(a) indicates that the average, smoothed, population density in Glenbranter begins at 100, reaches a low of 70 in year 30 of the simulation and ends the simulation at 140 individuals. The unsmoothed average has a high of 190 and a low of 60 individuals. The maximum and minimum of any single realisation is 215 and 40 respectively. This indicates that density is higher in this scenario compared to the like-for-like replanting and illustrates the effects of increased tree-species diversity could have on red squirrels in the absence of grey squirrels. None of the 10 simulation realisations reach zero population during the 75 year simulation. Figure 14(b) indicates that the average, smoothed, population density in the Cowal peninsula begins at 985, reaches a low of 515 in year 33 of the simulation and ends the simulation at 1190 individuals. The unsmoothed average has a high of 1355 and a low of 460 individuals. The maximum and minimum of any single realisation is 1420 and 400 respectively. No model realisation for the entire peninsula reaches zero during the simulation.

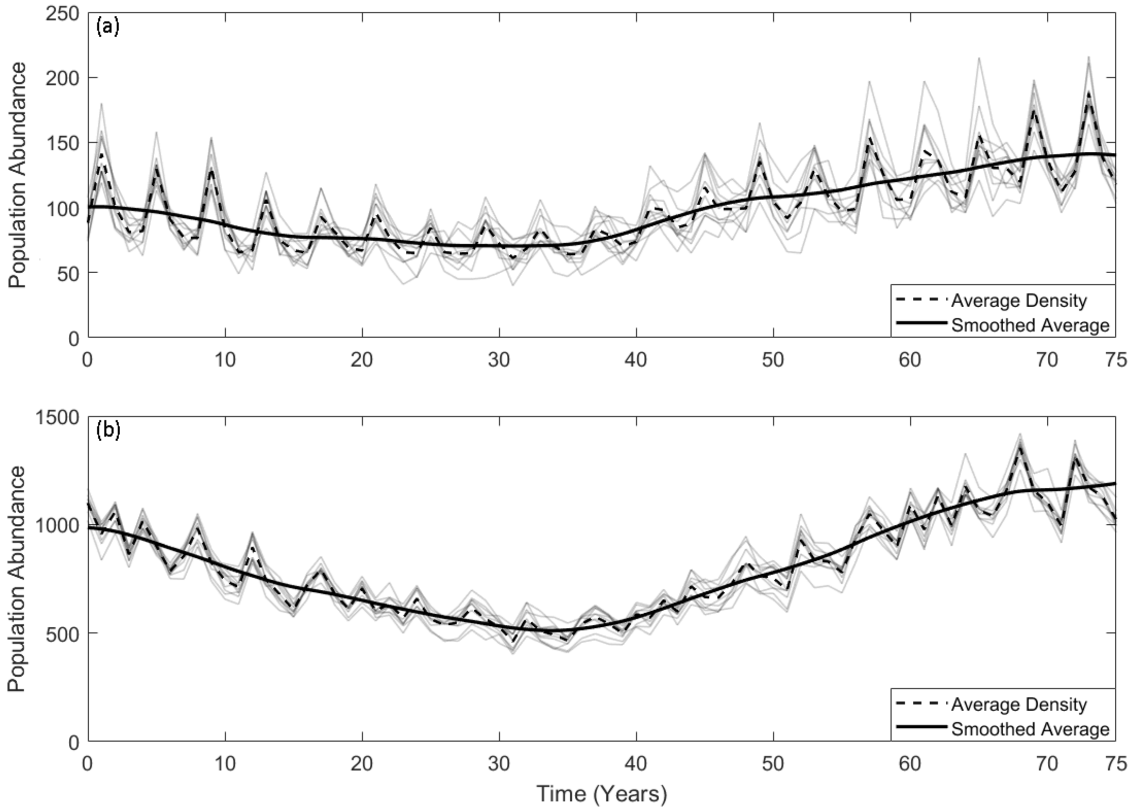

Figure 14 - Red squirrel density in (a) Glenbranter and (b) the Cowal Peninsula when felling and enhanced replanting has occurred. The solid line is the smoothed average, the dashed line indicates the unsmoothed average of the 10 model realisations and the grey lines are the 10 model realisations. Year 0 in the image indicates the year 2022.

Figure 15 shows density maps for years 0, 10, 20, 30, 40, 50, 60, 70 and 75 of the simulation when there is felling and enhanced replanting. The geographic spread of red squirrels in the Cowal peninsula becomes patchier but not to the extent seen under the like-for-like replanting. The density in Glenbranter is reduced by the felling but recovers more quickly that under the like-for-like scenario. Red squirrels are able to re-colonise the stronghold from the wider peninsula when the forest in Glenbranter is able to support them again. Note, the density of red squirrels is higher and more widespread under the enhanced replanting scenario (Figure 15) than under the like-for-like replanting scenario (Figure 13) and the final density and distribution of red squirrels is enhanced to a level beyond that prior to felling.

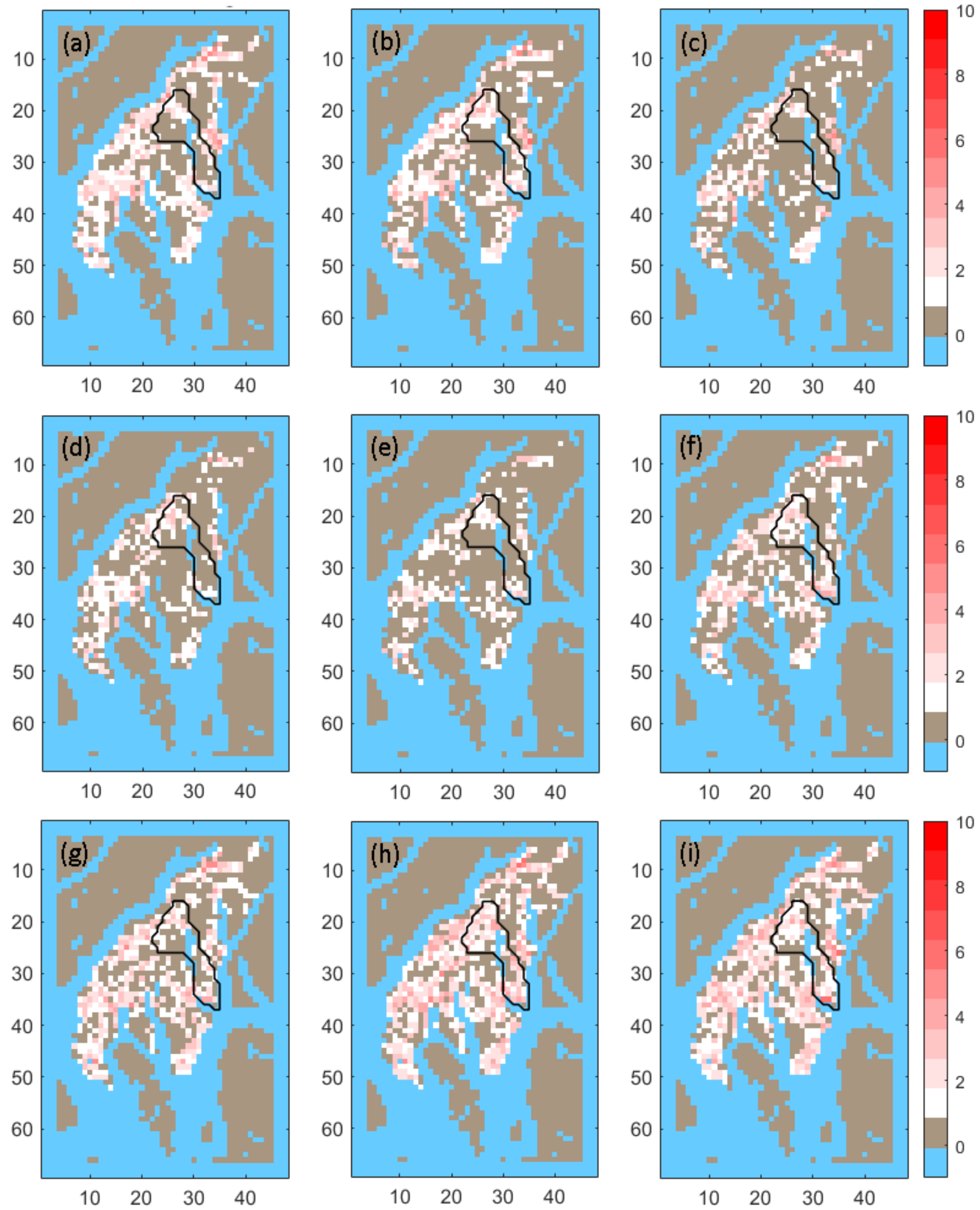

Figure 15 - Maps showing red squirrel density and location, when felling and enhanced replanting has occurred, for years (a) 0, (b) 10, (c) 20, (d) 30, (e) 40, (f) 50, (g) 60, (h) 70, & (i) 75. Regions outside the Cowal peninsula have had their carrying capacity artificially set to zero for imaging purposes only.

3.2 Forest Composition After Felling & Replanting

3.2.1 Like-for-Like Replanting Scheme

The proportion of larch in Glenbranter is reduced from 4.93% to 1.65% as a result of the proposed felling and like-for-like replanting (see Figure 16). The proportion of all other species is increased as it is assumed that larch is replaced by other current species in equal quantities.

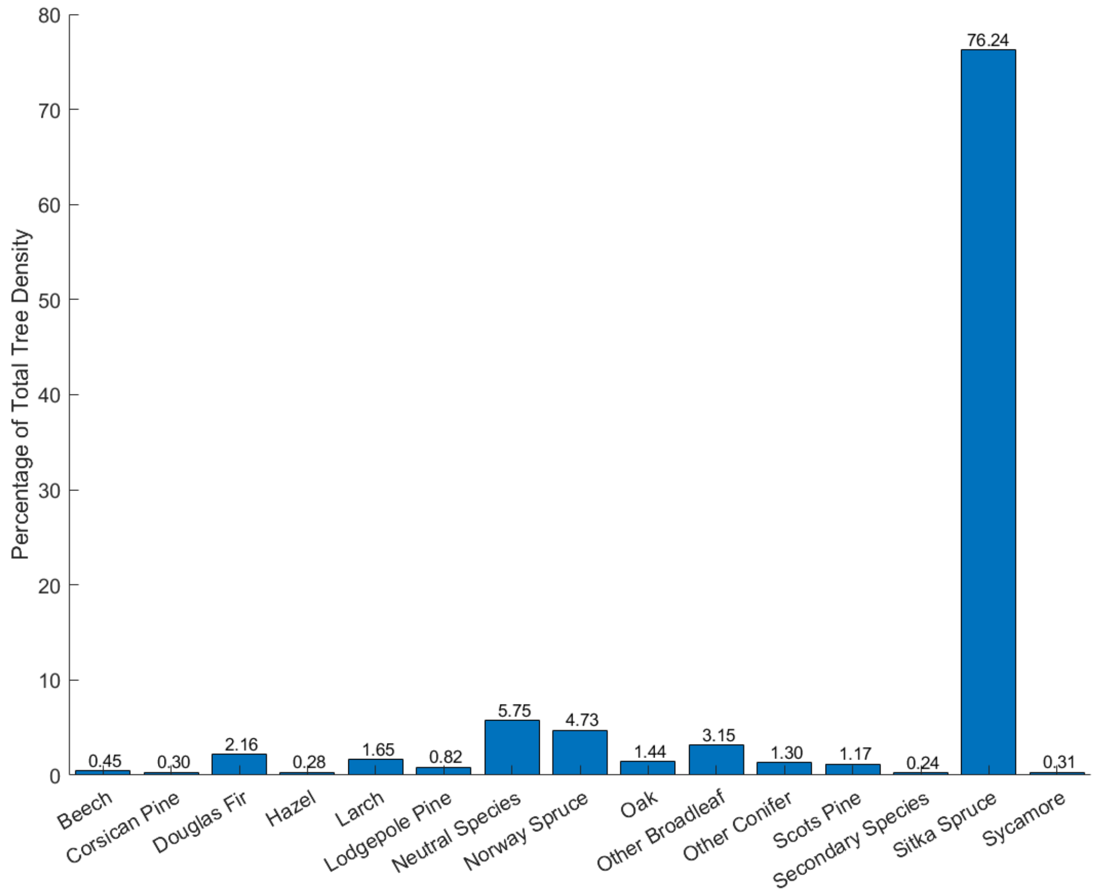

Figure 16 - Final forest composition, at year 75 of the simulation, in the Glenbranter stronghold when felled trees are replanted like-for-like. Values above each bar indicate the percentage of the forest, as a proportion of the total forest density, that each tree species makes up.

The final forest composition in the Cowal peninsula (Figure 17) is slightly different than the initial composition, due to computational rounding errors. The final composition is the same as the initial composition due to larch being included in the Other Conifer category, with the replacement of larch by other species being the primary reason for compositional changes in Glenbranter. Thus, we are assuming in this scenario that any larch is removed and replaced by a different Other Conifer species that has the same (or at least very similar) carrying capacity.

Both Glenbranter and the whole Cowal peninsula remain dominated by Sitka spruce under the like-for-like replanting scheme.

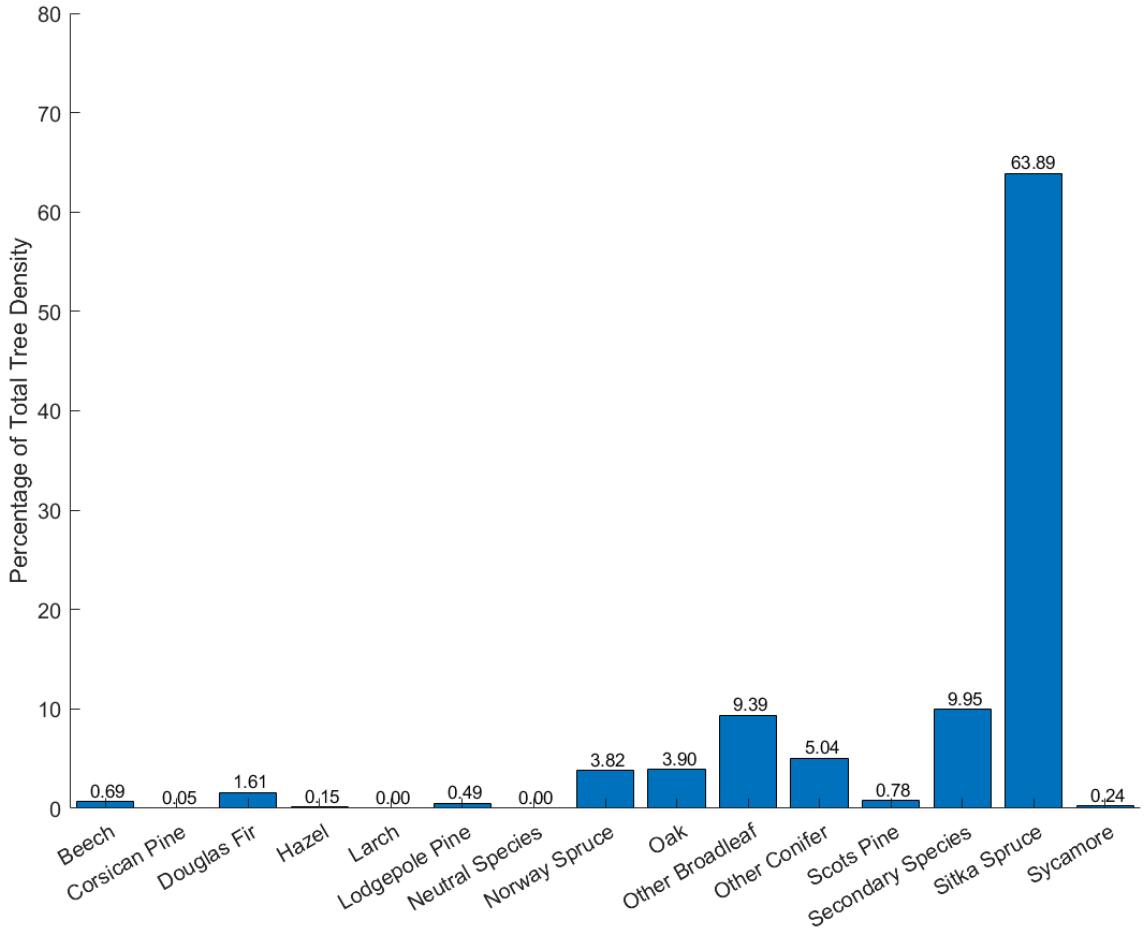

Figure 17 - Final forest composition, in year 75 of the simulation, in the Cowal peninsula when trees are felled and replanted like-for-like. This does not include the forests in the Glenbranter stronghold. Values above each bar indicate the percentage of the forest, as a proportion of the total forest density, that each tree species makes up.

3.2.2 Enhanced Replanting Scheme

The proportion of larch in Glenbranter is reduced from 4.93% to 1.65% as a result of the proposed felling and enhanced replanting (see Figure 18). The proportion of Sitka spruce is reduced from 76.08% to 72.70% due to the mandated reductions under the enhanced replacement scheme, which sees 5% of the felled Sitka replaced by enhanced species (note the drop in Sitka spruce in the whole of Glenbranter is not 5% as not all regions are felled). The proportion of hazel is increased from 0.05% to 1.37%, Other Broadleaf from 2.89% to 6.21% and Scots pine is increased from 0.93% of the Glenbranter forest to 2.92%. The remaining tree species are at similar proportions to the initial forest composition due to them being replanted like for like.

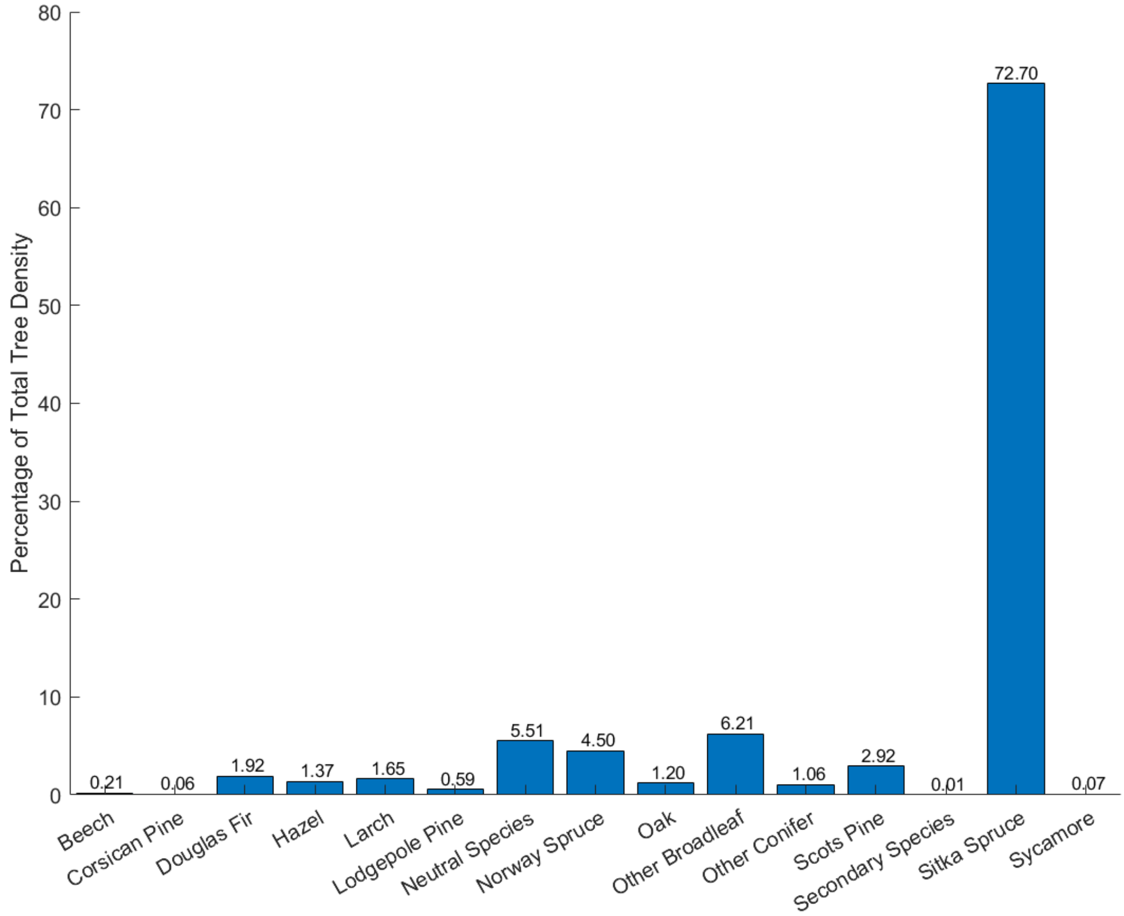

Figure 18 - Final forest composition, at year 75 of the simulation, in the Glenbranter stronghold when felled trees are replanted with an enhanced mixture of species. Values above each bar indicate the percentage of the forest, as a proportion of the total forest density, that each tree species makes up.

The final forest composition in the Cowal peninsula (Figure 19) sees the proportion of Sitka spruce reduced from 63.92% to 62.63% due to 5% of the felled Sitka being replaced. The proportion of Other Conifer, of which we assume 5/6th is larch, is reduced from 5.03% to 3.50% of the forest in the Cowal peninsula. The proportion of hazel is increased from 0.15% to 0.71%, Other Broadleaf is increased from 9.40% to 10.78% and Scots pine is increased from 0.78% to 1.63% of the forest. The remaining species end the simulation at similar proportions to the beginning of the simulation.

Both Glenbranter and the whole Cowal peninsula remain dominated by Sitka spruce under the enhanced replanting scheme.

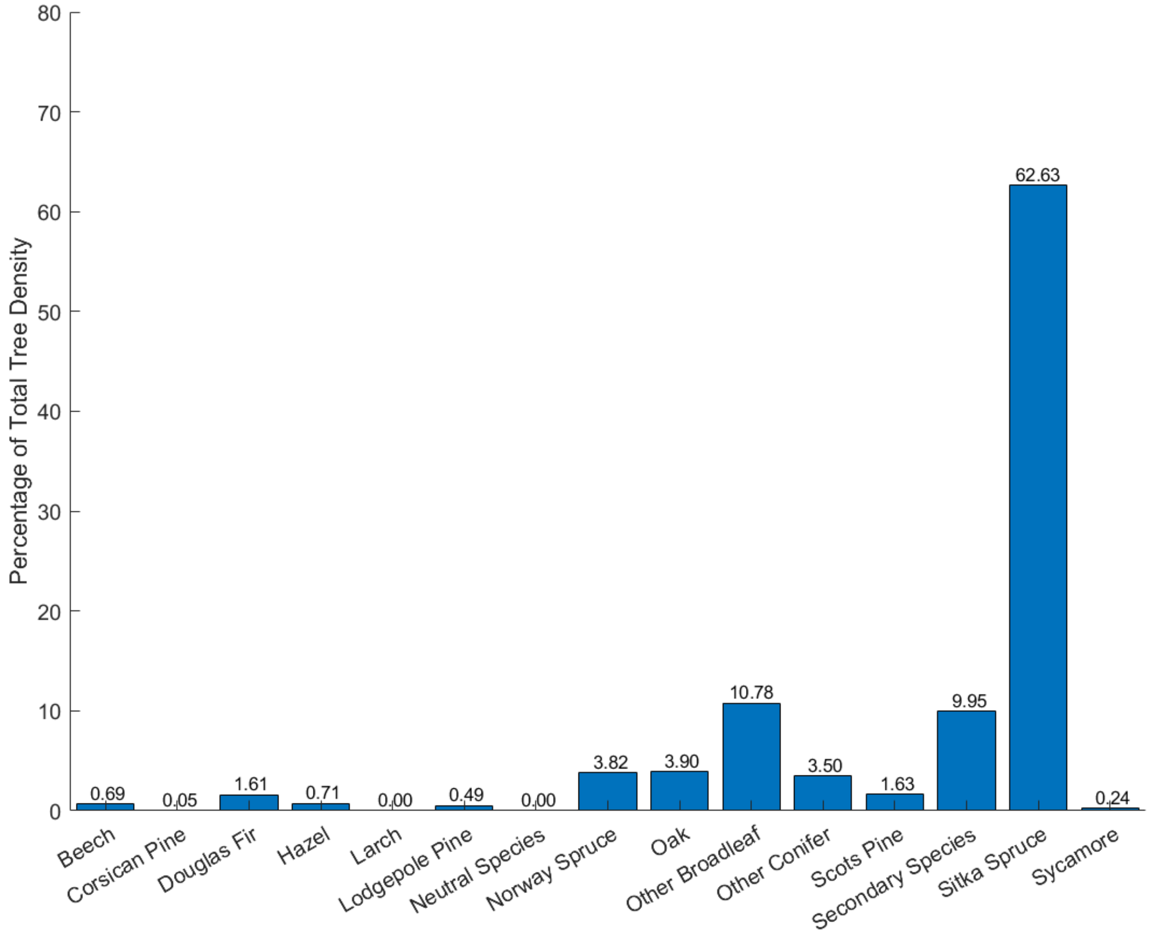

Figure 19 - Final forest composition, in year 75 of the simulation, in the Cowal peninsula when trees are felled and replanted with an enhanced mixture of species. This does not include the forests in the Glenbranter stronghold. Values above each bar indicate the percentage of the forest, as a proportion of the total forest density, that each tree species makes up.

4. Summary of results and conclusion

Current red squirrel abundance

Based on current forest composition and simulated tree seed crop cycles, we estimate that the Cowal peninsula holds between 800 and 1200 red squirrels. The red squirrel population at Glenbranter is predicted to be between 75 and 150. The relatively low estimate is due to the high proportion of Sitka spruce which generally supports only low numbers of red squirrels.

The red squirrel population in Glenbranter consists of 3 largely separate groups, one in the north and two in the south, all of which are connected to larger populations in the wider Cowal peninsula. The best areas for red squirrels on the Cowal peninsula appear to lie outside of Glenbranter, primarily in the west (see predicted red squirrel density Figs. 13 & 15), and red squirrels would be able to recolonise Glenbranter from the Cowal peninsula if local extinction in Glenbranter were to occur, as soon as the habitat is suitable again (see replanting scenarios).

Change in carrying capacity due to felling and replanting

There is a clear reduction in carrying capacity (i.e. the number of squirrels both the Cowal Peninsula as a whole and Glenbranter will support based on tree species composition, tree seed cycles, and age structure) for a period of time following the sanitation felling. Under the like-for-like replanting scheme the carrying capacity decreases for the first 30 years and then begins to increase as the level of felling is reduced and replanted trees mature. Under the enhanced planting scheme there is less of a reduction in carrying capacity and a more rapid recovery, due to the increase of fast growing species that provide a more sustained seed resource. The final carrying capacity under the enhanced replanting scenario is greater than the like-for-like scenario because a proportion of the Sitka Spruce is replaced by native species that provide an increased resource for squirrels.

Red squirrel abundance under felling like-for-like replanting

Red squirrel density on the Cowal peninsula is reduced for a period during the felling and restructuring, with the lowest population level occurring around year 40 of the simulation. The population is predicted to recover to pre felling levels under the like-for-like replanting scheme and at no point is the population likely to fall below a minimum viable population threshold.

Red squirrel density at Glenbranter is predicted to fall to very low numbers (<50 in some simulations) and becomes localised to the north and south, with connections to the wider Cowal peninsula. Therefore, red squirrels may become scarce in Glenbranter and there is a small risk that squirrels will disappear at Glenbranter (Figures 12 and 13). Red squirrels are predicted to recover in Glenbranter once the replanted trees have reached maturity and start providing a usable resource.

Red squirrel abundance under felling and enhanced diversity replanting

Red squirrel density on the Cowal peninsula is reduced for a period during the felling and restructuring, with the lowest population level occurring around year 35 of the simulation. The population is predicted to recover and exceed pre-felling levels under the enhanced replanting scheme due to the increase in Scots pine, hazel and Other Broadleaf. These species replace 5% of Sitka spruce which supports only low densities of red squirrels. At no point is the population likely to fall below a minimum viable population threshold.

Red squirrel density at Glenbranter undergoes only a small reduction due to the enhanced felling scenario, likely due to the increased use of hazel in the replanting which produces high energy seeds after only a few years and thus provides a more consistent resource that prevents a population crash. The red squirrel population becomes localised to the north and south in the first 40 years of simulation, however the local populations appear more resilient than those under the like-for-like replanting scheme and red squirrels occupy the majority of Glenbranter for the last 30 years of the simulation. Therefore, it is possible that red squirrels may become scarce in Glenbranter during the initial felling period, but there is little risk that squirrels will disappear from Glenbranter (Figures 14 and 15). The red squirrel density in Glenbranter recovers and exceeds the pre-fell average due to the inclusion of hazel, Scots pine and tree species in the Other Broadleaf category that support higher densities of red squirrels.

Planted ancient Woodlands (PAWS)

In the enhanced replanting scenario, the proportion of hazel, Scots pine and Other Broadleaf is increased in place of the felled larch and some of the Sitka spruce. The Other Broadleaf category was chosen as a facsimile for a range of broadleaf species that could be introduced as part of the Planted Ancient Woodlands (PAWS) scheme (Thompson, 2003) which intends to restore ancient woodlands that have been previously turned into plantation. While the enhanced replanting scheme is hypothetical, it illustrates the effects of likely changes in woodland composition with a shift towards more deciduous species due to climate change or biodiversity considerations. The proportion of Sitka spruce plantation that is replaced by PAWS species could therefore be increased beyond what has been suggested in this study (currently there are a total of 583.76 ha of potential PAWS areas at Glenbranter; K. Kortland pers. comm.), which would lead to a greater increase in the long-term carrying capacity for red squirrels (in the absence of grey squirrels), above what is reported in this study. Likewise, the reduction in red squirrel density that is caused by the felling could be further reduced by the planting of more hazel (e.g. as screen plantings or along water courses) and other fast maturing species that provide a more dependable seed crop resource in the short term. Conversely, a reduction in the amount of PAWS replanting would see density results closer to those in the like-for-like scenario.

Given that there are currently no grey squirrels in the Cowal peninsula, it is possible that a larger enhanced replanting scheme could be conducted in the Cowal peninsula. This would benefit local red squirrel abundance and may help red squirrel populations in adjacent areas. However, care must be taken to ensure corridors of high quality habitat are not created which could provide a refuge for grey squirrels which would negatively affect red squirrels in the Cowal peninsula or that the overall species composition is shifted too much in favour of grey squirrels which are broadleaf specialists. Conversely, pine marten are currently resurgent in Scotland, and an increase in semi-natural ancient woodland could increase densities and pine marten may help protect resident red squirrels against possible grey squirrel incursion and competition.

Conclusions

Clear felling to remove larch affected by Phytophthora is likely to reduce red squirrel abundance. It is likely to lead to very low numbers in all but periphery regions of Glenbranter and will reduce red squirrel density throughout the Cowal Peninsula. However, red squirrels are predicted to persist in the Cowal peninsula and will recover and disperse to occupy replanted regions once the trees are mature and seed producing. The predicted reduction in red squirrel abundance can be mitigated by replanting with an increased proportion of a fast maturing, more stable resource – such as hazel in suitable locations as well as by replanting with an increased proportion of native species, potentially in line with PAWS guidance. Most importantly, the model study suggests that the current felling plans do not place resident red squirrels at risk of extinction in the Cowal peninsula and that populations will recover as the replanted forest matures.

5. References

Brasier, C., 1999. *Phytophthora* Pathogens of Trees: Their Rising Profile in Europe. Forestry Commission Information Note 30: 1-6, Forestry Commission, Edinburgh, UK.

Forestry Commission, 2021. Resources: Ramorum disease (Phytophthora ramorum). https://www.forestresearch.gov.uk/tools-and-resources/fthr/pest-and-disease-resources/ramorum-disease-phytophthora-ramorum/ (accessed 8.7.2021).

Hansen, E.M., 2015. *Phytophthora* species emerging as pathogens of forests. Current Forestry Report 1: 16-24

Harris, A., R., Webber, J., F., 2016. Sporulation potential, symptom expression and detection of *Phytophthora ramorum* on larch needles and other foliar hosts. Plant Pathology 65: 1441-1451.

Jones, H., White, A., Geddes, N., Clavey, P., Farries, J., Dearnley, T., Boots, M. & Lurz, P. W. W. 2016. Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel. Hystrix, the Italian Journal of Mammalogy 27, 1.

Jones, H., White, A., Lurz, P.W.W, Shuttleworth C.M., 2017. Mathematical models for invasive species management: Grey squirrel control on Anglesey. Ecological Modelling 359: 276-284.

Purse, B., V., Graeser, P., Searle, K., Edwards, C., Harris, C., 2013. Challenges in predicting invasive reservoir hosts of emerging pathogens: mapping *Rhododendron ponticum* as a foliar host for *Phytophthora ramorum* and *Phytophthora kernoviae* in the UK. Biological Invasions 15: 529-545.

Schlenzig, A., Campbell, R., Chard, J., 2014. *Phytophthora* species infecting hardy ornamentals in nurseries and the managed environment in Scotland. Journal of Phytopathology 163: 686-689.

Shuttleworth, C.M., Lurz, P.W.W., Geddes, N., Browne, J., 2012. Integrating red squirrel (*Sciurus vulgaris*) habitat requirements with the management of pathogenic tree disease management in the UK. Forest Ecology and Management 279: 167-175.

Slade, A., White, A., Kortland, K. and Lurz, P.W.W. 2020. An assessment of long-term forest management policy options for red squirrel conservation in Scotland. Hystrix, the Italian Journal of Mammalogy 31(2):137–147

Slade, A., White, A., Kortland, K. and Lurz, P.W.W. 2021. Natural strongholds for red squirrel conservation in Scotland. Nature Conservation 43: 93-108.

Thompson, R., Humphrey, J., Harmer, R. & Ferris, R. 2003. Restoration of Native Woodland on Ancient Woodland Sites. Forestry Commission Practice Guide.
Forestry Commission, Edinburgh. i–iv + 1–52 p

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.

Wiktionary 2021. Phytophthora. https://en.wiktionary.org/wiki/phytophthora (accessed 4.7.2021).