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A modelling assessment of the population dynamics of red squirrels in the Kidland and Uswayford forest, Northumbria, in relation to proposed forest design plans.

 

A modelling assessment of the population dynamics of red squirrels in the Kidland and Uswayford forest, Northumbria, in relation to proposed forest design plans.

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Executive Summary

This report is the outcome of a partnership between the Forestry Commission, Prof Andrew White, Hannah Jones (Heriot-Watt University) and Peter Lurz (Ecological Consultant) and through collaboration with Prof Mike Boots. The objective of the project was to apply mathematical modelling techniques to assess the current levels of red squirrel population abundance in Kidland and Uswayford and to assess the impact of predicted felling and restocking regimes on future population levels.

A spatially explicit, stochastic model was developed to represent the population dynamics of red squirrels based on the techniques outlined in Tompkins et al. (2003) and White et al. (2014). The red squirrel carrying capacity was calculated for each forestry commission compartment based on suitable habitat types in the landscape which was determined from digital landcover maps. The carrying capacity in each compartment could change over time based on forest design plans to fell and replant certain areas. The model analysis assessed how red squirrel abundance would change as a result of forest design plans and proposed strategies to improve red squirrel viability. The Forestry Commission provided their proposed forest design plans (Scenario A) in February 2014. As a result of the model analysis the Forestry Commission provided three further forest design plans (Scenario B, October; Scenario C, November 2014; Scenario D, February 2015) aimed at improving red squirrel viability in the Kidland and Uswayford forest regions.

Main findings:

- Model results that approximate current conditions in Kidland and Uswayford in which the seed crop can alternate between good and bad years indicate that a squirrel population can persist but with population abundance closely linked to resource availability. The model indicates that abundance peaks at around 150 and troughs at around 30 squirrels for Kidland and Uswayford (this is supported by data from the annual Kidland red squirrel monitoring).

- Model simulations that use the Forestry Commission's Scenario A forest design plans indicate that in the high carrying capacity scenario (which assumes each year is a good seed year), red squirrel populations in Kidland never go extinct, while in Uswayford they may become extinct as the carrying capacity becomes very small between 2040 and 2052 as a result of harvesting operations and replanted stock taking up to 30 years to become a seed producing age. In the 3 high, 1 low carrying capacity scenario (where 3 good seed years are followed by a bad seed year) red extinctions occur in Kidland in some model realisations, leading to total population extinction in 2% of the realisations. In Uswayford, 84% of the realisations predict that red squirrels will become extinct by 2052.

- The model indicated that under the Scenario A forest design plan, squirrel populations are simultaneously low in both Kidland and Uswayford forests between 2032-2052. Adjusting the forest management plans so that low carrying capacities are out of phase in each forest would limit the likelihood of total population extinction. Considering Kidland and Uswayford forests as one system was desirable and would increase the overall viability of red squirrels. Therefore, if the connection between Kidland/Tilhill and Uswayford was improved, this would allow either forest to act as a source of squirrels if temporary extinctions were to occur in one of the forests. The Forestry Commission used this information to develop new forest design plans with the aim of increasing red squirrel population viability.

- The new forest design plans aim to increase the amount of suitable habitat in Uswayford (Scenario B) and additionally reduce the felling rate in Kidland (Scenario C). Economical restocking with delayed felling is given by Scenario D. Model simulation under the new scenarios indicate that there is a reduced chance of population extinction at Uswayford, with Scenario D having the least probability of extinction and Scenario C having the highest total squirrel densities. While the new scenarios have therefore led to an improvement in red squirrel viability compared to Scenario A, population levels can still drop to low levels with a risk of extinction in Uswayford.

- When a dispersal corridor between the forests at Tilhill and Uswayford is included in (Scenarios B, C and D), the chance of extinction is reduced further (compared to when the corridor is absent), being lowest when the link is considered to be mature enough to provide suitable cover for the squirrels 10 years after planting. Population extinction can still occur in Uswayford when the dispersal corridor is included but in all of these cases the model predicts Uswayford will be re-populated by 2066. Therefore, the dispersal corridor reduces the chance of extinction and significantly improves the re-population of Uswayford if extinction does occur.

- The forest design plan represented by Scenario C provides the most viable habitat for red squirrels, with Scenario D providing an economical alternative supporting slightly lower overall densities. Model results indicate that Scenario C supports the highest abundance of squirrels while Scenario D has the least chance of population extinction in Uswayford. However, while Scenario D is more economical, the tree species composition is dominated by Sitka spruce. If Sitka has a poor seed year this would affect the whole region and impact detrimentally on squirrel numbers. The minimum viable population size for red squirrels has been estimated to be 200 [10] and therefore the enhanced population sizes predicted for Scenario C are closer to this estimate.

- Considering Kidland and Uswayford as a combined, linked, system would offer increased flexibility with respect to timber extraction and maintaining a balanced forest age structure in the future. This would mitigate forest management impacts and help maintain squirrel numbers above levels that present an extinction risk. This is why Scenarios C and D show increased levels of squirrel survival.

Contents

1 Background

Since its introduction into the UK, the grey squirrel has replaced the native red squirrel throughout most of England and Wales, and in parts of Scotland and Ireland. There are now only certain regions in which the red squirrel survives and maintaining these populations is a major conservation priority. Red squirrel strongholds have been employed in the UK to conserve red squirrel populations. These strongholds are local forest regions that are large enough to sustain viable red squirrel populations over the long-term, and in which habitat composition and management offers native red squirrels a competitive advantage over greys. Strongholds may be isolated from surrounding (grey squirrel) populations (through poor connectivity or poor adjoining habitat) or grey squirrel density may be controlled through trapping and removal. To date, there are 18 strongholds in Scotland and 17 in the North of England managed by Government, Non-Government, private landowners and Charitable organisations (such as the Forestry Commission, Scottish Natural Heritage and the Wildlife Trust).

The Kidland and Uswayford forests in Northumberland are designated strongholds that are managed by the Forestry Commission (Kielder Forest District). They are composed predominantly of Sitka spruce and other conifer species and monitoring for red squirrels at Kidland Forest has occurred for the last 14 years on an annual basis . The forests are managed for timber with large sections periodically felled for wood production and then re-planted. The forest habitat is suitable for red squirrels and thought to be unsuitable for greys. The Kidland and Uswayford forests are also relatively isolated and therefore the likelihood of invasion by grey squirrels will be low. A key determinant of red squirrel abundance in these regions will be resource availability and this will depend on the availability of mature seed producing trees suitable for red squirrels (which varies depending on felling and restocking strategies) and seed crop abundance (which varies annually due to climate patterns, weather and phenology).

The objective of this assessment was to apply mathematical modelling techniques to assess the current levels of red squirrel population abundance in Kidland and Uswayford and to assess the impact of predicted felling and restocking regimes on future population levels. A spatially explicit, stochastic model was developed to represent the population dynamics of red squirrels based on the techniques outlined in Tompkins et al. (2003) and White et al. (2014). The red squirrel carrying capacity was calculated for each Forestry Commission compartment based on suitable habitat types in the landscape which was determined from digital landcover maps. The carrying capacity in each compartment could change over time based on forest design plans to fell and replant certain areas. The model analysis assessed how red squirrel abundance would change as a result of forest design plans and proposed strategies to improve red squirrel viability.

The forest design plans were produced and supplied by the Forestry Commission. The initial design plan (Scenario A) was supplied in Febuary 2014 and included details of habitat/tree type and year of planting at the 25m by 25m scale for both Kidland and Uswayford regions from 2012 to 2052. The model results indicated that squirrel abundance may fall to low levels under this scenario and so a further two scenarios, B and C, were proposed in October and November 2014 (respectively) to try to reduce the chance of extinction and increase the number of red squirrels supported by the forests. The different forest design plans are summarised in Table 1.

Scenario	Date received	Summary
A	24/2/14	Original forest design plans
B	14/10/14	Updated plans to improve potential density in Uswayford
C	17/11/14	Updated plans with a reduced felling rate in Kidland
D	12/2/15	Economical restocking with delayed felling as in Scenario C

Table 1: A summary of the three forest design plans

2 Model Set-up

Based on the published models of Tompkins et al (2003), [13] and White et al (2014), [14], a spatially explicit, stochastic model has been developed to represent the population dynamics of red squirrels in Kidland and Uswayford. The model will represent the dynamics in subpopulations (compartment level) in which species specific habitat details are available (from the Forestry Commission subcompartment dataset).

3 Kidland and Uswayford Compartments

Kidland and Uswayford are part of Kielder Forest, in Northumberland, England. They were planted post 1960 and are commercially managed. Kidland is 2050 ha, 1190ha of which are managed by the Forestry Commission, the rest managed by private landowners, while Uswayford is approximately 1000ha, all managed by the Forestry Commission, [3]. The two forests are separated by less than 1km of open land, but are relatively isolated from other forested regions.

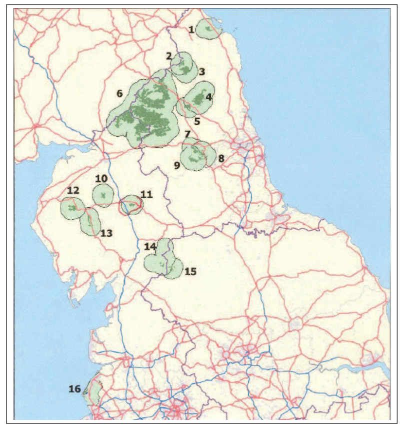

Figure 1: Map of the Forestry Commission red squirrel reserve areas in northern England. Uswayford is labelled as 2 and Kidland is labelled as 3. [8]

Using Forestry Commission data we extract the compartments that represent Kidland and Uswayford (these are compartments 6221-6248 for Kidland and 6249-6266 for Uswayford, see Figure 2). A further large forest region (Tilhill) links to Kidland and Uswayford, but is not managed by the Forestry Commission (see red region in Figure 2).

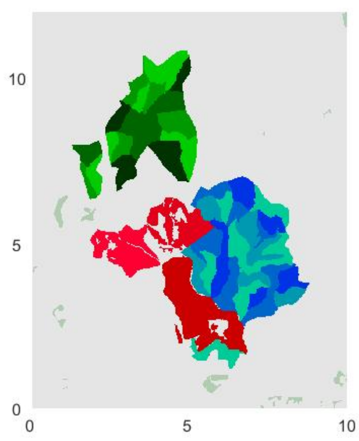

Figure 2: Map of the Forestry Commission compartments in Kidland (blue) and Uswayford (green) and the privately managed forest by Tilhill (red).

4 Carrying Capacity

The carrying capacity in each compartment can be determined using Forestry Commission data (or Forest Inventory records for Tilhill) to provide species specific habitat information within each compartment. This is combined with published estimates of red squirrel abundance for each tree species (Table 2). It is assumed that it takes 30 years for trees to reach maturity and provide suitable, regular resources for red squirrels. As felling plans for the adjacent, privately managed, forest area of Tilhill are not known, the land was taken to be one third felled, one third immature and one third mature. This allows the project to focus on assessing the impacts of any proposed Forestry Commission design plans only, without confounding the results with changes to the structure of adjacent woodland. Tilhill was split into three compartments with 80% of the trees taken to be Sitka Spruce and 20% Lodgepole pine. We determine a high and low carrying capacity to reflect good and poor seed years for each compartment.

Red Squirrel Density (/ha)		
Tree Species	High	Low
Ash	0	0
Birch	0	0
Douglas fir	0.45	0.17
European larch	0.38	0.21
Grand fir	0	0
Hybrid larch	0.38	0.21
Japanese larch	0.38	0.21
Lodgepole pine	0.4	0.04
Mixed broadleaf	1	0.62
Norway spruce	0.58	0.25
Oak	1	0.62
Scots pine	0.4	0.04
Sitka spruce	0.11	0.011
Sycamore	0	0
Western hemlock	0	0
Other conifer	0.45	0.17
Other spruce	0.2	0.02
Mixed conifer	0.45	0.17

Table 2: Estimated red squirrel carrying capacities. The data was derived from a variety of references, see [2],[5],[7],[9],[15].

In Figure 3 we show the carrying capacity estimates based on 2012 Forestry Commission data for the high and low carrying capacity scenarios. Under the high carrying capacity scenario the number of red squirrels is predicted to be 100 for Kidland, 99 for Uswayford and 41 for Tilhill, whereas under the low scenario the predictions are 29 for Kidland, 25 for Uswayford and 5 for Tilhill. Using the forest design plans supplied by the Forestry Commission, it is possible to calculate the carrying capacity in each compartment, annually, between 2012 and 2052. In Figure 4, we combine these estimates to show how the carrying capacity will change over time in Kidland and Uswayford.

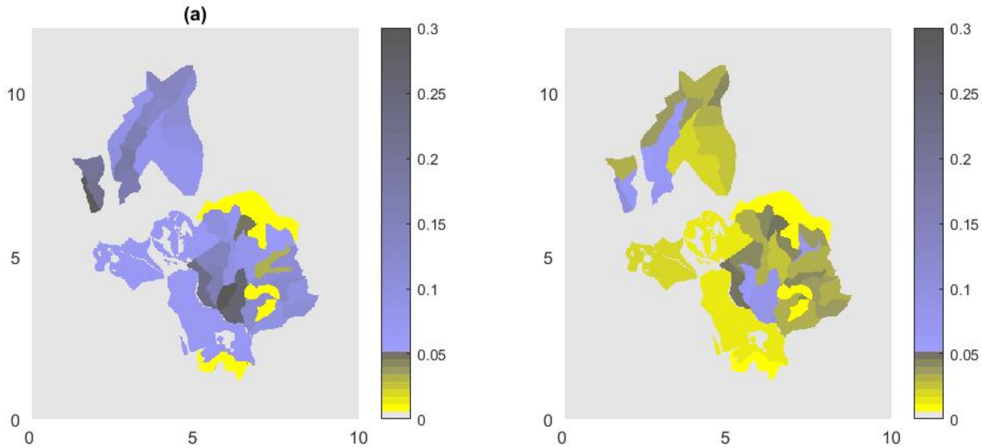

Figure 3: Red squirrel carrying capacities for Scenario A in 2012 for the high (left) and low (right) density estimates (units are squirrels per hectare).

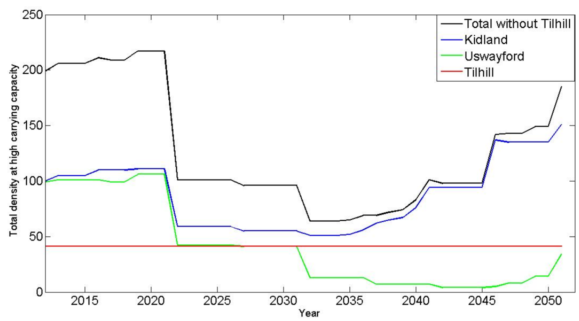

Figure 4: Changes in red squirrel carrying capacity using the high density estimates between 2012-2052 for Scenario A

5 Model

The underlying deterministic framework represents the density of red squirrels using the following differential equation

$$\begin{aligned} \frac{dN}{dt} &= aN\left(1 - \frac{N}{K_1}\right) - bN\left(\frac{N}{K}\right) \qquad && t_n \leq t < t_{n+1} + 0.5 \\ \frac{dN}{dt} &= -bN\left(\frac{N}{K}\right) && t_n + 0.5 \leq t < t_{n+1} \end{aligned} \tag{5.1}$$

We assume birth and death are density dependent and birth only occurs for a 6 month breeding season (representing 2 litter periods between May-Oct), whereas death can occur throughout the year. The natural mortality rate is $b = 0.9\text{yr}^{-1}$, [1], and the birth rate is $a = 3.0\text{yr}^{-1}$, [13]. The carrying capacity, K , is determined using Forestry Commission data for each compartment in Kidland and Uswayford. The density dependent parameter that scales the birth rate, $K_1 = 2.6K$, is calculated to ensure that the average population density over a year is equal to the carrying capacity K.

The deterministic model is turned into an individual based stochastic model by turning the rates for births and deaths in Equation 5.1 into probabilities of a birth or death "event". We also need to consider the dispersal of individuals. We assume saturation dispersal such that individuals are more likely to disperse as the local population increases [11]. Individuals disperse randomly up to a distance of 1km and therefore could move to any compartment that is within this distance. The spatial stochastic model is therefore

Event	Outcome	Probability
Birth (breeding season)	$N \to N+1$	$[aN(1-N/K_1)]/R$
Death	$N \to N-1$	$[bN(N/K)]/R$
Dispersal	$N_i \to N_i - 1, N_j \to N_j + 1$	$[m(N/K)^2]/R$

Table 3: Possible events and their outcomes in a particular compartment i, with dispersal occurring to compartment j. The rates from Equation 5.1 are turned into probabilities by dividing by $R = \sum[\text{rates}]$.

We use a Gillespie algorithm [4] to select each event and update the number of individuals (and therefore the probabilities) after each event. The time between each event is given by $dt = -\ln(\theta)/R$ where θ is a uniform random number between 0 and 1 (which assumes the next event is an exponentially distributed random variable,[12]).

6 Model predictions of current red squirrel abundance

Model simulations using the high and low carrying capacities for 2012 were undertaken for 25 model realisations (over a simulated 100 year period) to assess the viability and variability of population levels. In Figure 5 we show the results using the high carrying capacity. All realisations persist over the 100 year period, with there being little variation between the realisations. A clear annual signal with an increase in abundance during the breeding season followed by a decrease in the non-breeding season is shown. Towards the end of the breeding season the population exceeds the carrying capacity, which will trigger dispersal and increased mortality. When the population drops below the carrying capacity the probability of dispersal and mortality are reduced. This reflects the key life history characteristics of the natural red squirrel system [2].

In Figure 6 we show the results using the low carrying capacity. In all realisations the population becomes extinct within 40 years. Whilst a sustained period of "poor seed years" is highly unrealistic, this demonstrates that in low density populations, good seed years are vital to sustain low red squirrel populations in these spruce-dominated habitats. It also highlights the importance of maintaining a diverse forest to promote a dependable seed food supply.

Since the population is not viable with the low carrying capacity, and a sequence of only poor (or good) years is highly unrealistic, we also tested scenarios in which the carrying capacity varied between high and low levels as is typical for Kidland and Uswayford (for example see [6]). In Figure 7 we show results when three good seed years (high) are followed by one poor seed year (low), termed the 3 high, 1 low carrying capacity scenario. In this scenario the population can persist (in all realisations) but the population abundance does decline to low levels during the poor seed year (this is supported by data from the annual Kidland red squirrel monitoring). The model indicates that abundance peaks at around 150 and troughs at around 30 squirrels in Kidland and Uswayford (with numbers split approximately 50-50 between the two forest region) These predicted red squirrel population sizes are supported by the monitoring of feeding remains carried out at Kidland for the last 14 years (see Lurz 2014, [6]).

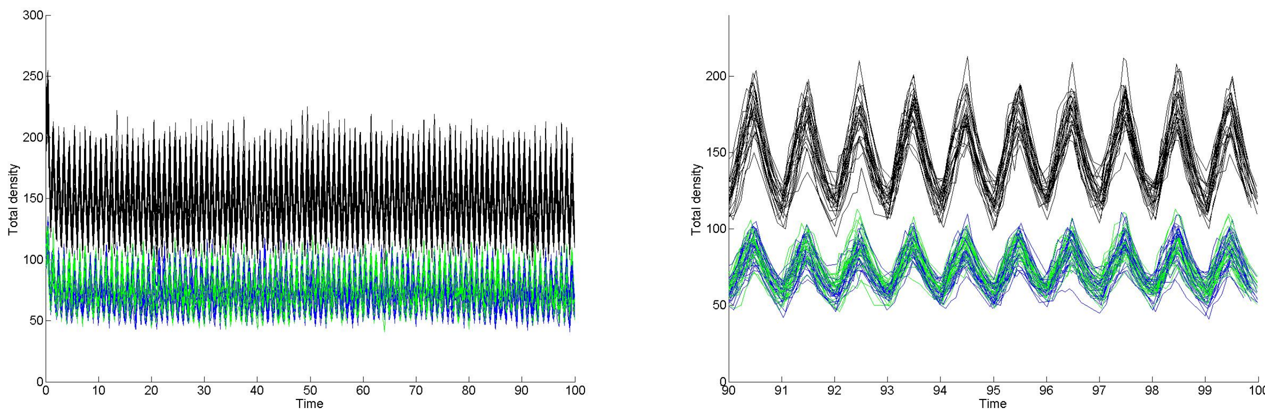

Figure 5: 25 model realisations using the high carrying capacity for 2012 in Kidland (blue), Uswayford (green) and both (black).

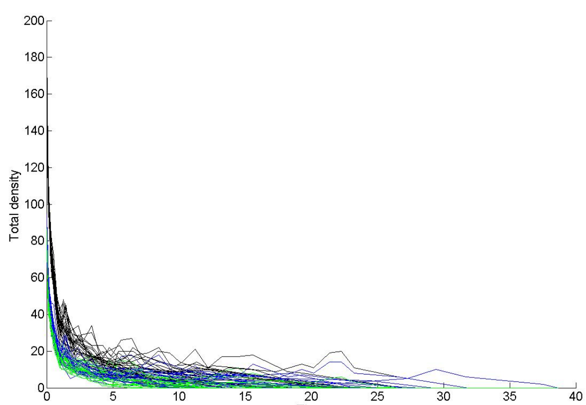

Figure 6: 25 model realisations using the low carrying capacity for 2012 in Kidland (blue), Uswayford (green) and both (black).

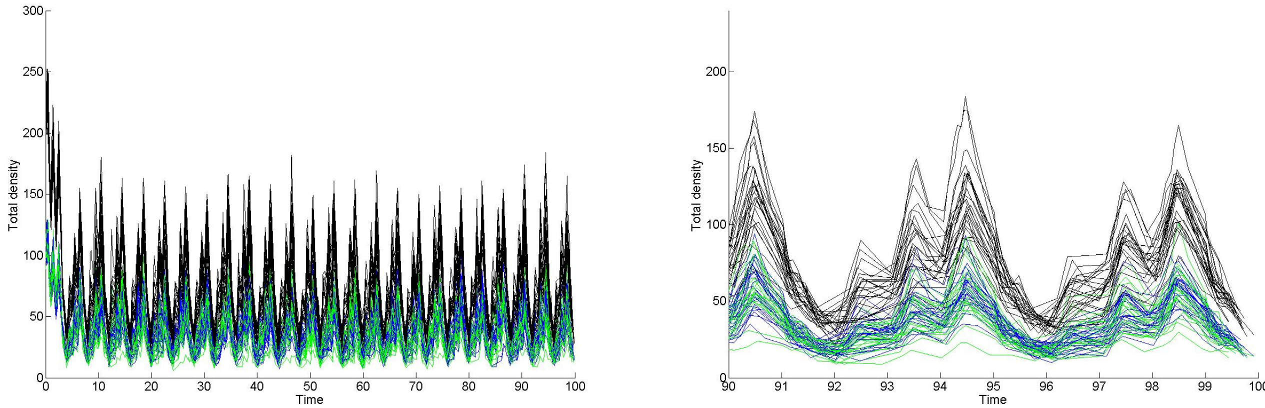

Figure 7: 25 model realisations using 3 good seed years followed by 1 poor year for 2012 in Kidland (blue), Uswayford (green) and both (black)

Changes in red squirrel abundance under the Scenario A forest design plan

Following the 100 year spin up period, 50 realisations of the model were run for a further 40 years, with the carrying capacity being updated yearly depending on the felling and replanting strategy of the Scenario A forest design plan (see Figures 8-9 for maps of the carrying capacities at 2 year intervals for the high and low carrying capacity scenarios).

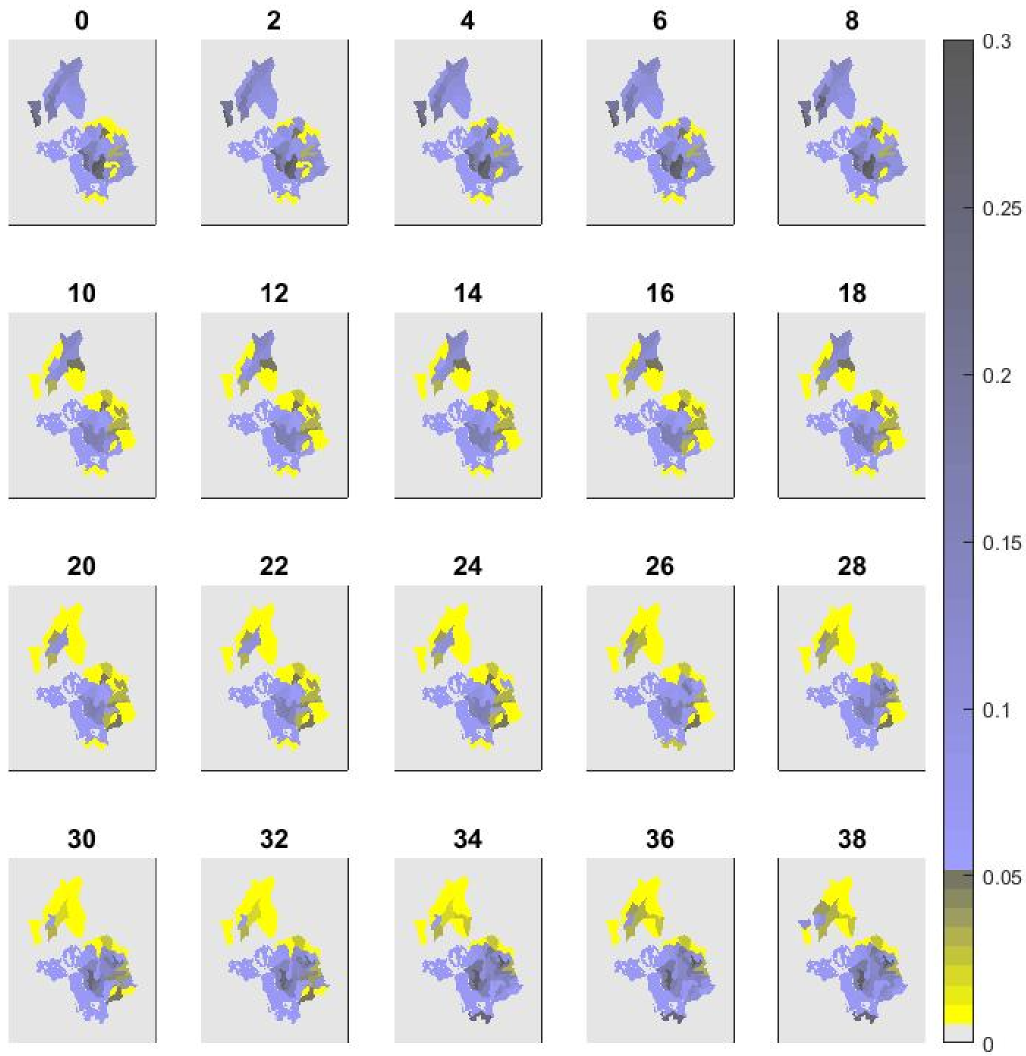

Figure 8: Carrying capacity estimates (as a density of squirrels/ha) in the Kidland and Uswayford compartments under Scenario A at 2 year intervals starting in 2012 for the high carrying capacity estimates.

Figure 9: Carrying capacity estimates (as a density of squirrels/ha) in the Kidland and Uswayford compartments under Scenario A at 2 year intervals starting in 2012 for the low carrying capacity estimates.

The predicted squirrel population abundance in the high carrying capacity scenario is shown in Figure 10. Population abundance follows a similar trend as the carrying capacities profile for the next 40 years, Figure 4. Squirrel numbers in Kidland drop to low levels between 2022 - 2038 due to loss of mature forest habitat. The numbers in Kidland increase after 2038 as previously felled and replanted regions become mature. There are no extinctions in Kidland in the 50 simulations. In Uswayford, squirrel numbers drop from 2022 onwards with very low populations by 2052. In 2052, 68% of the realisations predict red squirrel extinction in Uswayford. There is potential for recovery from low numbers since the carrying capacity for Uswayford in 2052 is 34. One might expect dispersal from the more abundant population in Kidland and Tilhill to induce recovery in Uswayford (since dispersal is possible between these forest regions). When simulations are run for a further 20 years with 2052 carrying capacities results indicate that while the population in Kidland stabilises in all cases, the population in Uswayford recovers in a few realisations only (Figure 11).

The model was also run using the predicted 2012-2052 carrying capacities for the 3 high, 1 low scenario, Figure 10. Complete extinction of red squirrels in both Kidland and Uswayford was observed in 2% of the realisations. In 2052, 84% of the realisations predicted red squirrel extinction in Uswayford. When an additional 20 years was simulated (Figure 11) the density at Kidland stabilises but there is little recovery of squirrel numbers in Uswayford. As in the high carrying capacity case, Uswayford does not appear to be being restocked by squirrels dispersing from Kidland, even though there is suitable habitat in Uswayford to support squirrel populations.

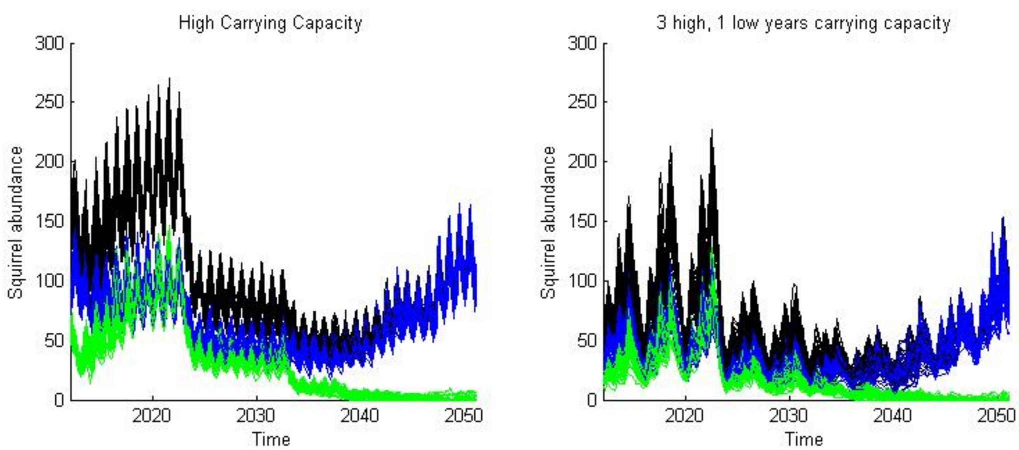

Figure 10: 50 model realisations for the high (left) and 3 high, 1 low (right) carrying capacity scenario driven by data derived by the original forest management plan (Scenario A) for 2012-2052 - Kidland (blue), Uswayford (green) and both (black).

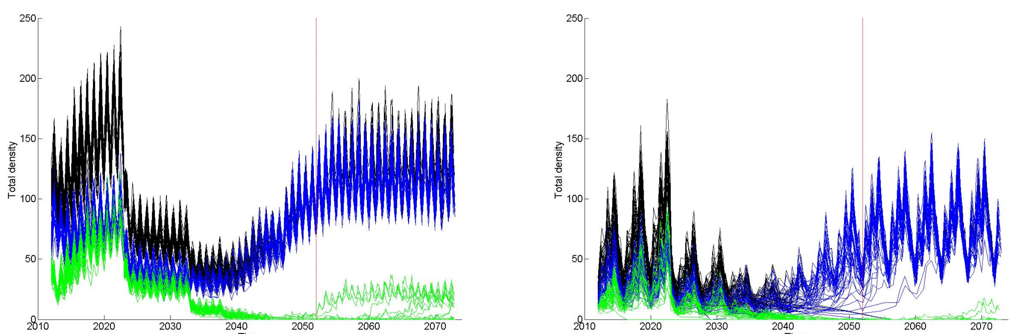

Figure 11: 50 model realisations with Scenario A's high carrying capacity (left) and 3 high, 1 low carrying capacity scenario (right) for 40 years with extrapolation of an additional 20 years beyond the red line in Kidland (blue), Uswayford (green) and both (black).

6.1 The importance of dispersal between Kidland and Uswayford

The model was used to simulate the current and predicted change in population abundance under the Scenario A forest design plans when Kidland and Uswayford were considered as unconnected forests. This provides information on the importance of squirrel dispersal between Kidland and Uswayford in sustaining viable red squirrel populations.

Model simulations using the high and 3 high, 1 low carrying capacity scenarios were undertaken in which dispersal was prevented between Kidland/Tilhill and Uswayford (Figures 12-13). There is little difference in the results when dispersal can occur (right panels of Figures 12-13) and when dispersal is prevented between Kidland/Tilhill and Uswayford (left panels of Figures 12-13) which indicates that dispersal is having little impact on the population dynamics and at the potential re-population of Uswayford.

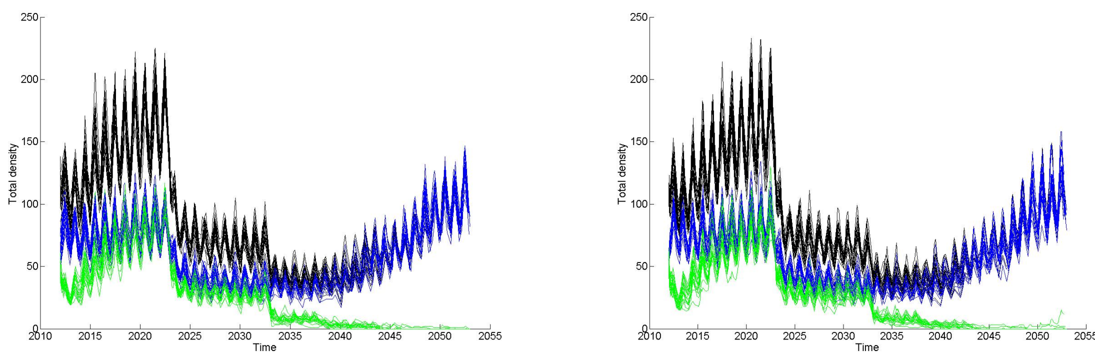

Figure 12: 50 model realisations when dispersal was prevented between Kidland/Tilhill and Uswayford (left) and when dispersal was allowed (right) in the high carrying capacity case for Scenario A for Kidland (blue), Uswayford (green) and both (black).

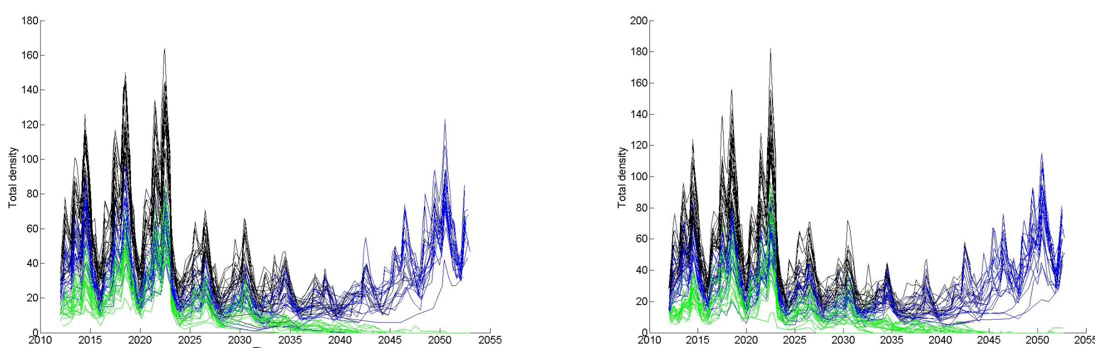

Figure 13: 50 model realisations when dispersal was prevented between Kidland/Tilhill and Uswayford (left) and when dispersal was allowed (right) in the 3 high, 1 low carrying capacity case for Scenario A for Kidland (blue), Uswayford (green) and both (black).

To investigate why dispersal from the red populations in Kidland and Tilhill does not aid the repopulation of Uswayford, we examine the distribution of suitable habitat for red squirrels under the forest design plans of Scenario A. Figure 14 shows that there is no suitable habitat at the closest borders of NW Kidland and SE Uswayford. Furthermore, under the Scenario A felling and restocking plan, there is no suitable habitat in Uswayford between 2038 and 2048 (since most regions contain immature trees). Therefore, while the forest boundaries are within the dispersal range for squirrels, the lack of suitable habitat makes dispersal highly unlikely.

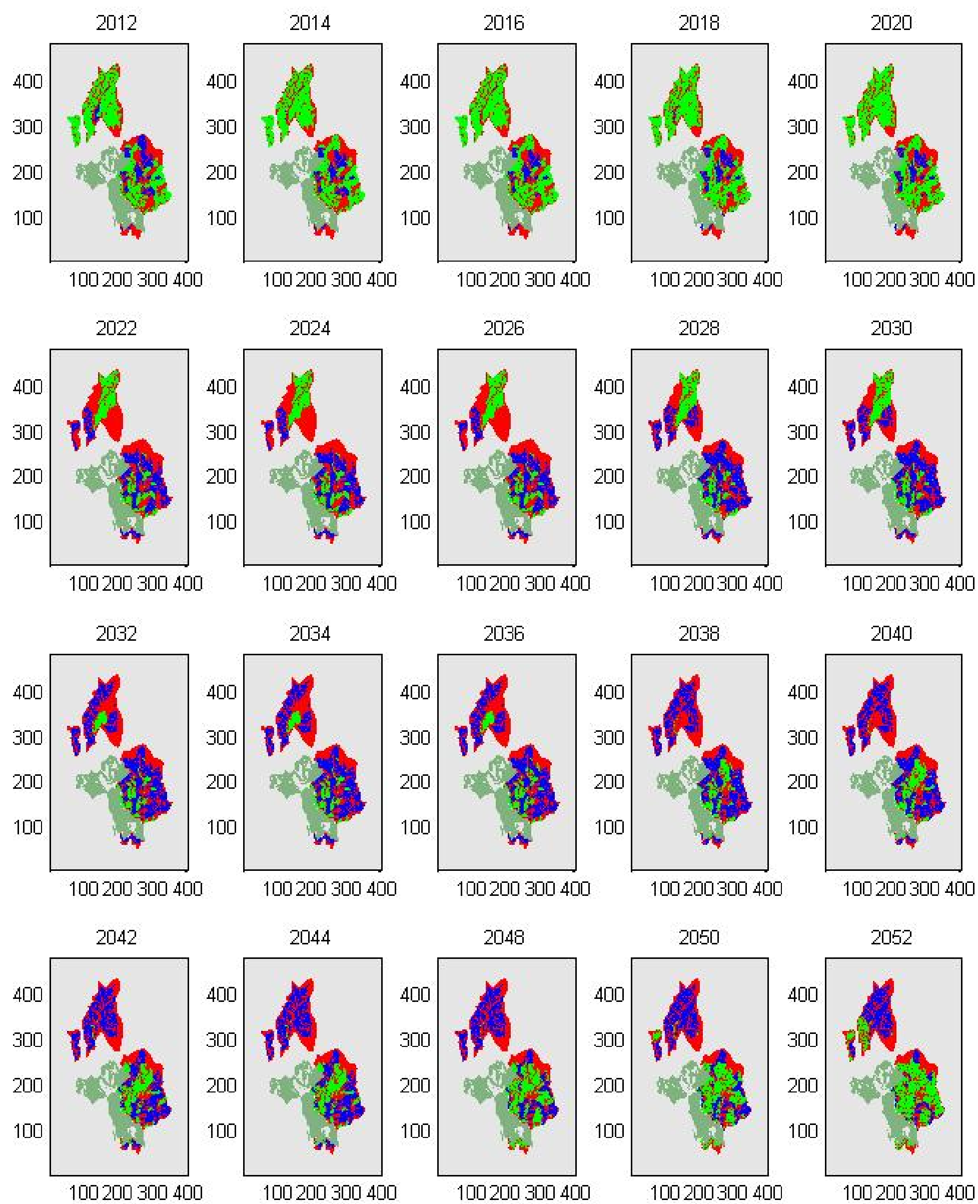

Figure 14: Maps showing the distribution of mature forest, > 30 years old, (green), immature forest (blue), no trees (red), Tilhill (dark green) based on the forest design plans of Scenario A.

To see whether dispersal is an important factor in the survival or recovery of squirrel populations in Uswayford, we therefore considered an 'idealised' scenario in which dispersal was allowed to any compartment, independent of its location. Figures 15-16 show that while extinction may still occur between 2040-2052 due to the low carrying capacity in Uswayford, the improved connectivity allows the population to recover in all model realisations. Therefore, a better connection between Uswayford and Kidland/Tilhill is likely to improve recovery in Uswayford following a population collapse.

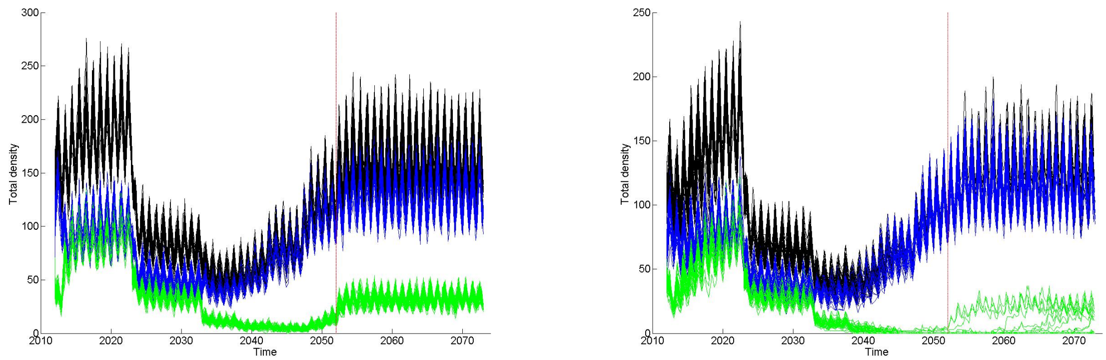

Figure 15: 50 runs with the high carrying capacities determined from Scenario A and global dispersal (left), 1km dispersal with connection (right) where the simulation are extrapolated for a further 20 year.

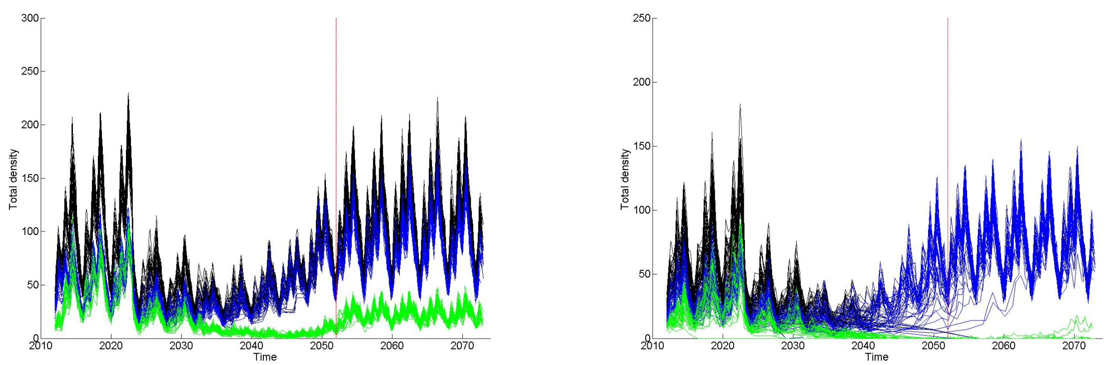

Figure 16: 50 runs with the 3 high, 1 low year carrying capacities determined from Scenario A and global dispersal (left), 1km dispersal with connection (right) where the simulation are extrapolated for a further 20 year.

7 Model predictions based on forest design plan Scenario A

Model simulations that use the Forestry Commission's Scenario A felling/restocking plans indicate that in the high carrying capacity scenario, red squirrel populations in Kidland never go extinct, while in Uswayford they may become extinct as the carrying capacity becomes very small between 2040 and 2052. In the 3 high, 1 low carrying capacity scenario, red extinctions occur in Kidland in some model realisations, leading to total population extinction in 2% of the realisations. In Uswayford 84% of the realisations predict that red squirrels will become extinct by 2052.

We assessed whether the connection between Kidland/Tilhill and Uswayford would aid population recovery from low levels. While the distance between compartments appears to be short enough for dispersal to occur, there is no suitable habitat to provide resources for squirrels near the borders of the forests. Therefore, dispersal between Kidland/Tilhill and Uswayford is currently ineffective. An idealised scenario in which dispersal between regions was improved indicated that dispersal could be an effective mechanism to drive population recovery.

Our interim findings were presented to the Forestry Commission in May 2014. The planned felling and restocking under Scenario A caused a large drop in the carrying capacities in both Kidland and Uswayford at the same time, so squirrel populations are simultaneously low in both forests. Adjusting the forest management plans so that low carrying capacities are out of phase in each forest would limit the likelihood of total population extinction. Furthermore, adjusting the tree mixtures to improve overall carrying capacity would also reduce the chance of extinction. Based on the model findings, it was agreed that the Forestry Commission would produce a new forest design plans (Scenarios B, C and D) that would attempt to improve red squirrel population viability while taking into account local planting and felling constraints (e.g. restrictions due to tree diseases and wind throw risks).

Discussions with the Forestry Commission concluded that considering the forests as one entity or system was desirable and would increase the overall viability of red squirrels. Therefore, if the connection between Kidland/Tilhill and Uswayford was improved, this would allow either forest to act as a source of squirrels if temporary extinctions were to occur in one of the forests. One possibility to improve connections between the two forests is to increase tree cover between the regions. While a road to connect Kidland and Uswayford is planned to transport timber from Uswayford, this proposed route is high, exposed and so not suitable for tree cover. It was proposed that the best option for improved connectivity was to increase tree cover along a river valley that runs from the north of Tilhill to Uswayford. This could provide a permanent corridor or a series of stepping stones between the forests. This is contingent on gaining compliance from the landowners and on the forest management plan for Tilhill. The model was used to assess whether an improved connection between Tilhill and Uswayford would improve population viability in Uswayford by allowing (artificially) enhanced dispersal between Tilhill and Uswayford. Improvements in the connectivity reduced the chance of red squirrel extinction in Uswayford and increased the likelihood of Uswayford being repopulated should population extinction occur (see Appendix A for details). It was agreed that future Forest Commission design plans should therefore also include the possibility of a dispersal corridor between Tilhill and Uswayford.

8 Changes in red squirrel abundance under the modified forest design plans (Scenario B, C and D)

The model system was used to assess red squirrel population levels under new forest management plans (Scenarios B, C and D) provided by the Forestry Commission in an attempt to increase population viability in Kidland and Uswayford.

Details of the new forest design plans

Recall that under Scenario A, population supported in Kidland remains at reasonable levels and can generally maintain squirrel populations continuously, while in 2032, the population supported in Uswayford falls to low levels, with only a few squirrels being supported until a slight increase by 2052. Therefore, the chance of population extinction in Uswayford is high (84% in the 3 high, 1 low carrying capacity scenario). Scenario B considers an alternative felling plan with extended coupes in Uswayford aiming to prevent such sustained low densities (see Figure 17). The densities in Uswayford remain higher, with very low densities between 2046 to 2051 only. However, the densities supported in Kidland are marginally lower in Scenario B compared to Scenario A. Scenario C has a similar felling trend to Scenario B in Uswayford, but with a reduced rate of felling in Kidland and the tree species chosen for restocking support a higher number of squirrels (see Figure 17). This leads to higher populations in Kidland (compared to Scenario B) and subsequently, a much higher total population at the end of the scenario in 2066. Scenario D has a reduced rate of felling in Kidland with delayed felling of coupes as in Scenario C, but has more economical restocking of the forests, with Sitka spruce being the dominant species planted.

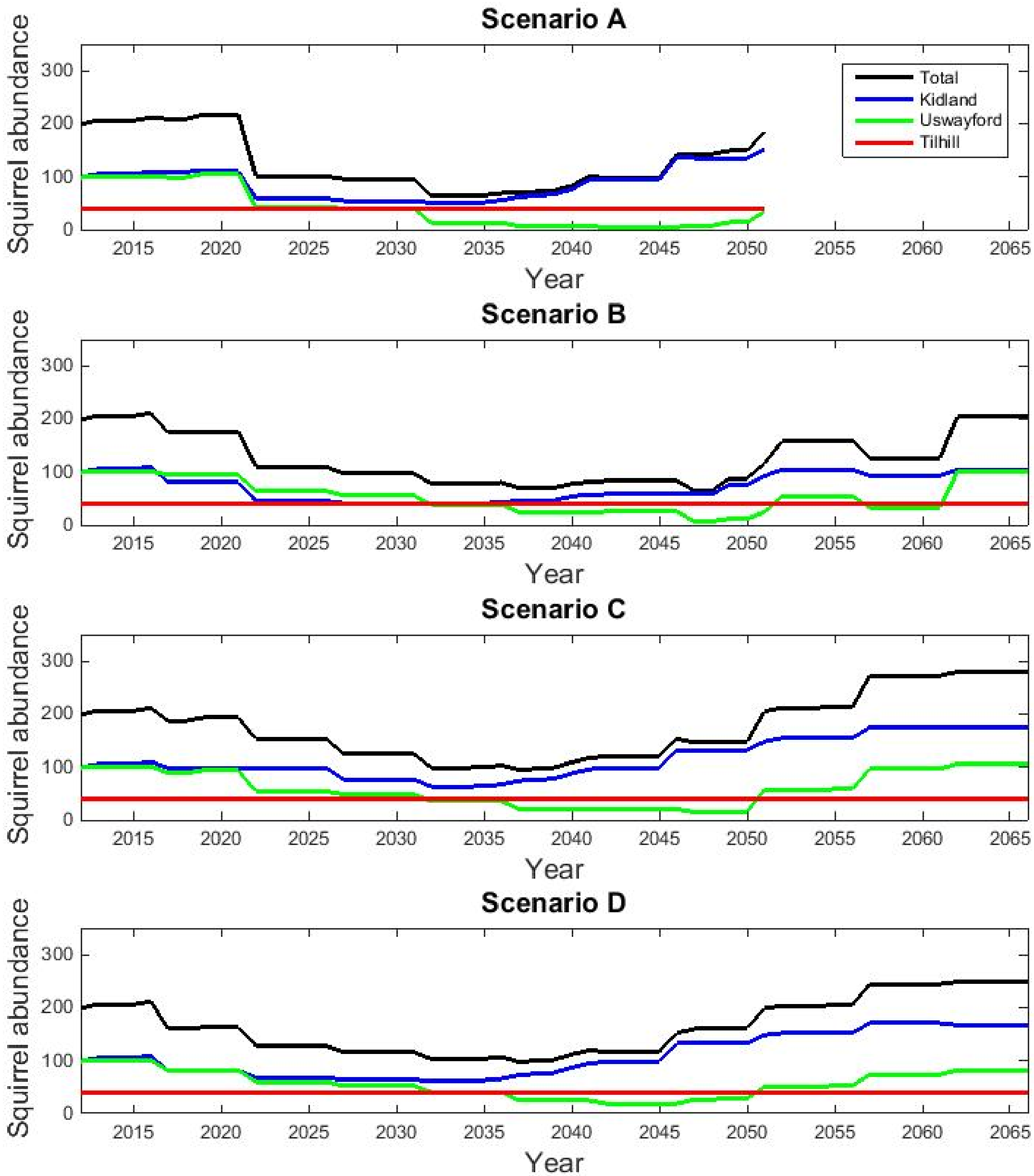

Figure 17: Changes in red squirrel carrying capacity using the high density estimates between 2012-2052 for Scenario A and 2012-2066 for Scenarios B, C and D.

In addition to the new forest design scenarios, the Forestry Commission also provided details of a potential habitat link between Tilhill and Uswayford. This dispersal link is shown in Figure 18 and in the model we assume this region represents a new compartment in which trees are planted in 2015. In the runs we consider two scenarios: (i) squirrels cannot utilise the dispersal compartment until 2045 (30 years after planting when tree are assumed to be mature) and (ii) squirrels can utilise the compartment in 2025. Here, while the trees may not be suitable habitat for red squirrels after 10 years, they can provide cover for squirrels moving between Tilhill and Uswayford.

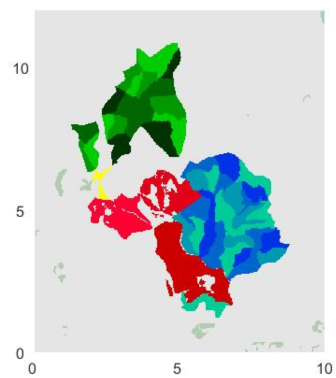

Figure 18: The yellow compartment indicates where the planting will produce a dispersal link between Tilhill (red) and Uswayford (green).

8.1 Results in the absence of the dispersal corridor

Model simulations for Scenario B (top panels in Figure 19) show that while red population abundance in Uswayford is predicted to fall around 2052, by 2066, populations are recovering to sustainable levels. In the high carrying capacity case, there is a 42% chance of extinction in Uswayford in 2052 which is an improvement on the 68% in Scenario A. Similarly in the 3 high, 1 low case, there is a 46% chance of extinction in 2052, while in Scenario A, it was 84%. Scenario B has therefore led to an improvement in red squirrel viability compared to Scenario A.

The Scenario C forest design plan further reduced the felling rate in Kidland (see Figure 17). Model realisations for this scenario (top panel in Figure 20) support a larger total population of squirrels throughout the period. While there is still a drop in the abundance of squirrels in Uswayford in 2052, only 14% of cases had extinctions in Uswayford in the high carrying capacity case and 30% in the 3 high, 1 low case. Scenario C has therefore reduced the probability of squirrel extinction compared to both Scenarios A and B.

The model realisations for Scenario D (top panels of Figure 21) are very similar to those in Scenario C. There is only extinction in Uswayford in 10% of cases in the high carrying capacity case, lower than in Scenario C and 30% in the 3 high, 1 low case, the same as in Scenario C. Therefore, the chance of survival is highest in this scenario. The total overall population is slightly lower in Scenario D than Scenario C as the tree species used in restocking cannot support as many squirrels. In Scenario D, Sitka spruce is the dominant species used for restocking, should this tree species suffer several poor seed years, squirrel abundance would suffer as there are few alternative food sources. Furthermore, Sitka spruce dominated habitat may lead to a lower future squirrel abundance than if a range of species types were planted.

The new scenarios improve population viability for red squirrels. However, even in the new scenarios, populations drop to low levels with a risk of extinction in Uswayford.

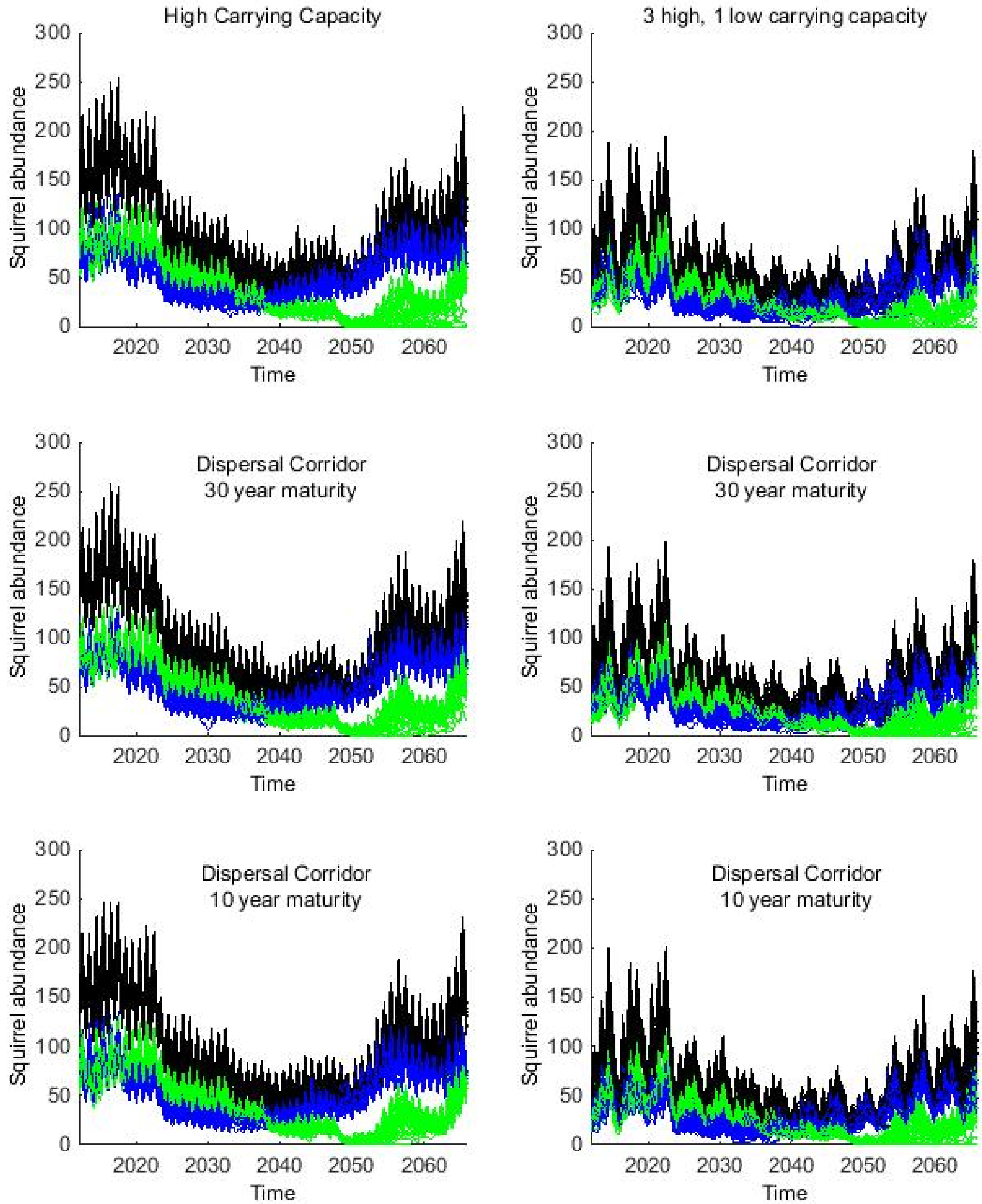

Figure 19: 50 model realisations for Scenario B from 2012 - 2066. These scenarios were run in the absence of the dispersal corridor between Tilhill and Uswayford (top), when the dispersal corridor is included but cannot be occupied till 2045 (middle) and when it is included and can be occupied in 2025 (bottom). The results for the high carrying capacity case are shown in the left panels and the 3 high, 1 low case shown in the right panels for Kidland (blue), Uswayford (green) and both (black).

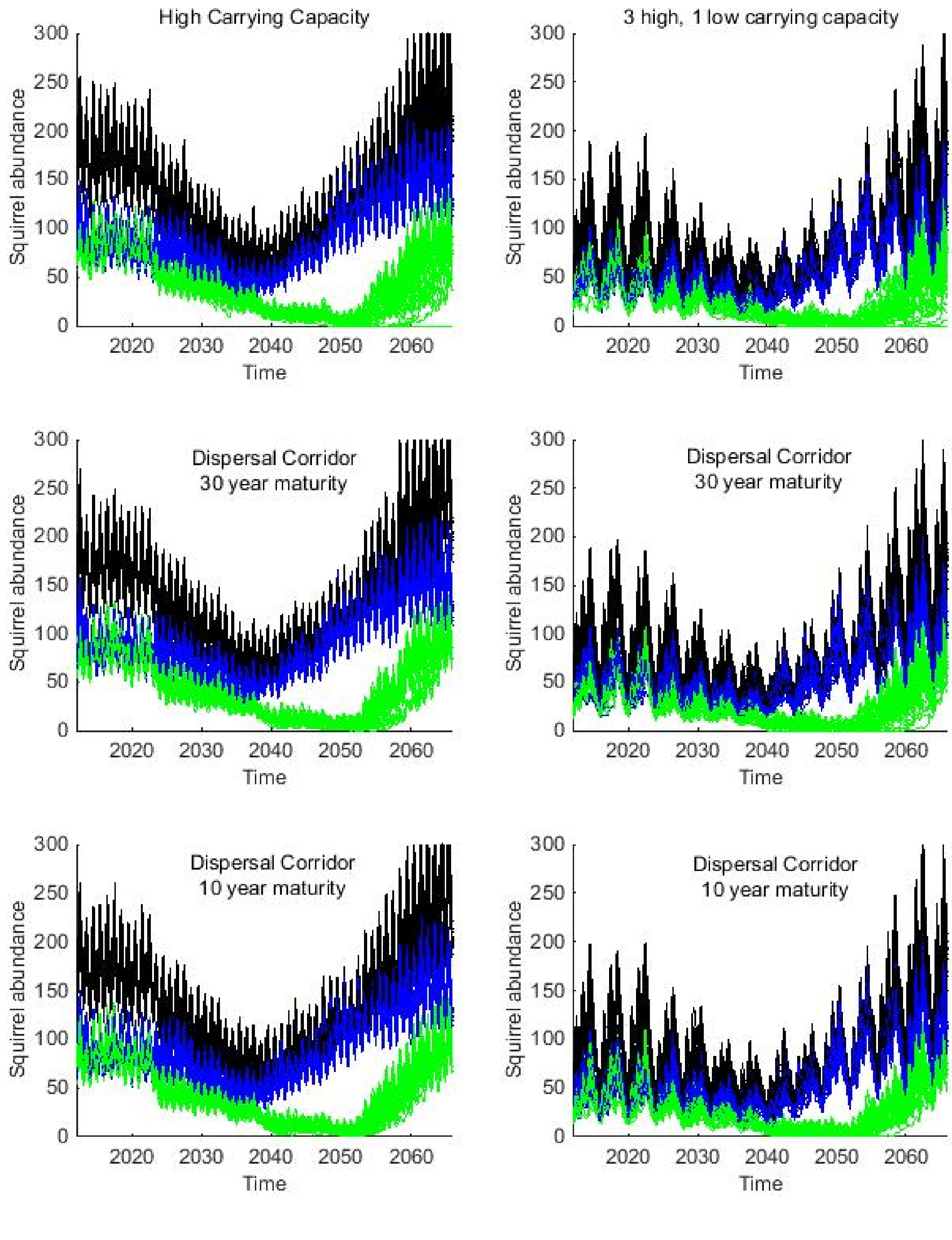

Figure 20: 50 model realisations for Scenario C from 2012 - 2066. These scenarios were run in the absence of the dispersal corridor between Tilhill and Uswayford (top), when the dispersal corridor is included but cannot be occupied till 2045 (middle) and when it is included and can be occupied in 2025 (bottom). The results for the high carrying capacity case are shown in the left panels and the 3 high, 1 low case shown in the right panels for Kidland (blue), Uswayford (green) and both (black).

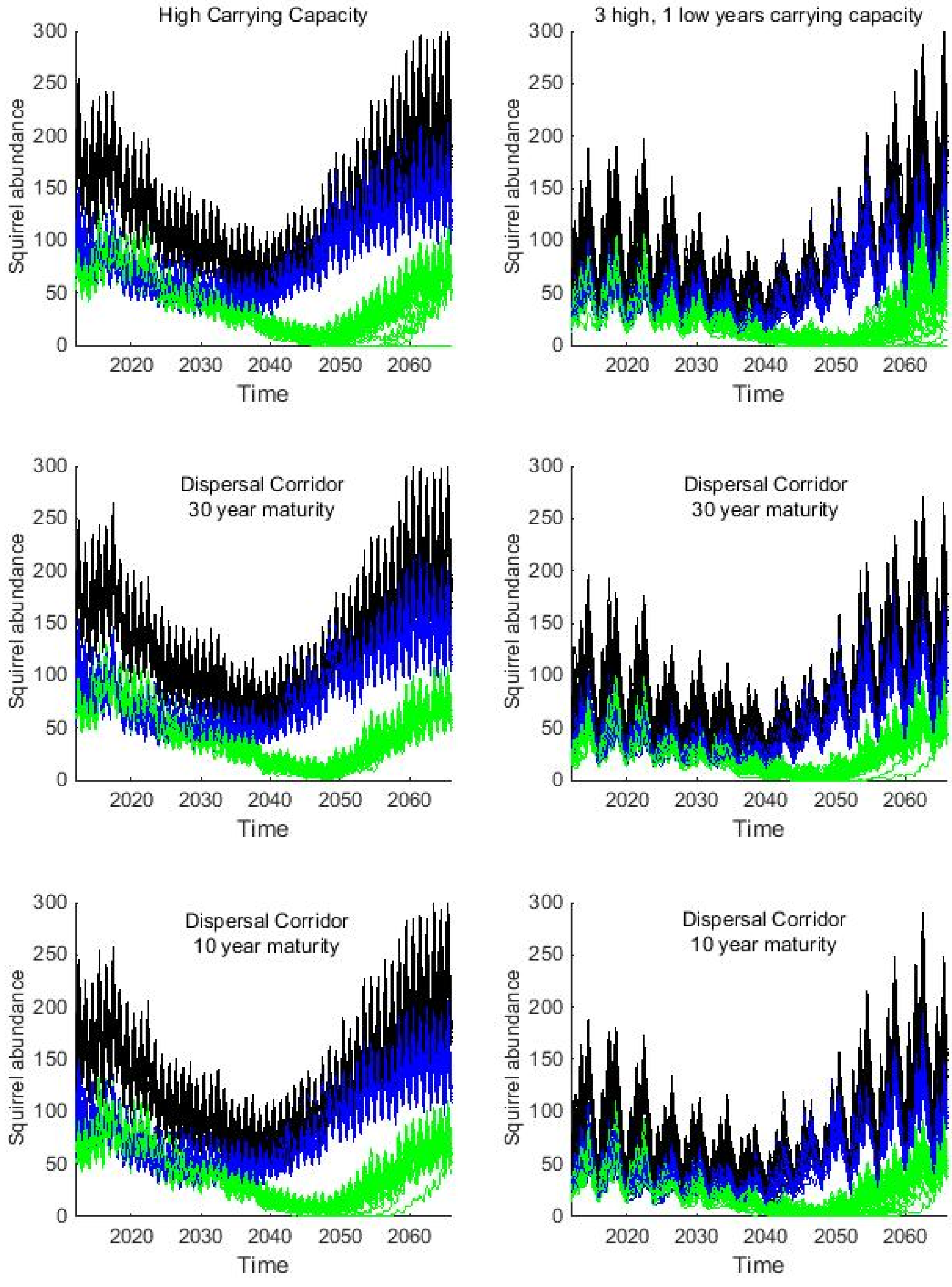

Figure 21: 50 model realisations for Scenario D from 2012 - 2066. These scenarios were run in the absence of the dispersal corridor between Tilhill and Uswayford (top), when the dispersal corridor is included but cannot be occupied till 2045 (middle) and when it is included and can be occupied in 2025 (bottom). The results for the high carrying capacity case are shown in the left panels and the 3 high, 1 low case shown in the right panels for Kidland (blue), Uswayford (green) and both (black).

8.2 Results when the dispersal corridor between Tilhill and Uswayford is included

The model results when the dispersal corridor is included between Tilhill and Uswayford for Scenarios B, C and D are shown in the middle and bottom panels of Figures 19-21. In all model runs squirrel population abundance drops to low levels in Uswayford by 2050 since there is little suitable habitat to support squirrel populations. However, recovery appears to be faster in the following 15 years in Uswayford when the link is included, and fastest when the dispersal corridor can be utilised 10 years after planting. Populations in Uswayford (and the total population) are highest by 2066 in Scenario C.

To compare the three forest design scenarios in more detail, we determined the chance of survival at 2052 under the four scenarios. The chance of total extinction in both Kidland and Uswayford was rare and only occurred in one realisation in the 3 high, 1 low carrying capacity case in Scenario A (and in no other model runs). We therefore focus on the chance of surivial in Uswayford (see Figure 22, Table 4). Without a dispersal corridor between Tilhill and Uswayford, the chance of survival is low in Scenario A (32% for high; 16% 3 high, 1 low)), increased in Scenario B (58%; 54%) and further increased in Scenarios C (86%, 70%) and D (90%, 70%). Scenarios B, C and D have projections up to 2066 and for the high carrying capacity case, in Scenario B, 33% of extinctions in Uswayford have not been re-populated, while in Scenario C, only 14% of previously extinct realisations remain extinct in 2066 and in Scenario D, 20% are still extinct in 2066. The same trend is observed in the 3 high, 1 low carrying capacity case. Therefore, the chance of extinction in Uswayford is least for Scenario D, and the chance of recovery is highest in Scenario C.

When the dispersal corridor is included (Scenarios B, C and D), the chance of survival is increased further (compared to when the corridor is absent), being highest when the link is considered to be mature enough to provide suitable cover for the squirrels 10 years after planting (Figure 22). Population extinction can still occur in Uswayford when the dispersal corridor is included but in all of these cases the model predicts Uswayford will be re-populated by 2066. Therefore, the dispersal corridor reduces the chance of extinction and significantly improves the re-population of Uswayford if extinction does occur. In the 3 high 1 low scenario the model predicts that the chance of survival for red squirrels in Uswayford is 96% in Scenario D.

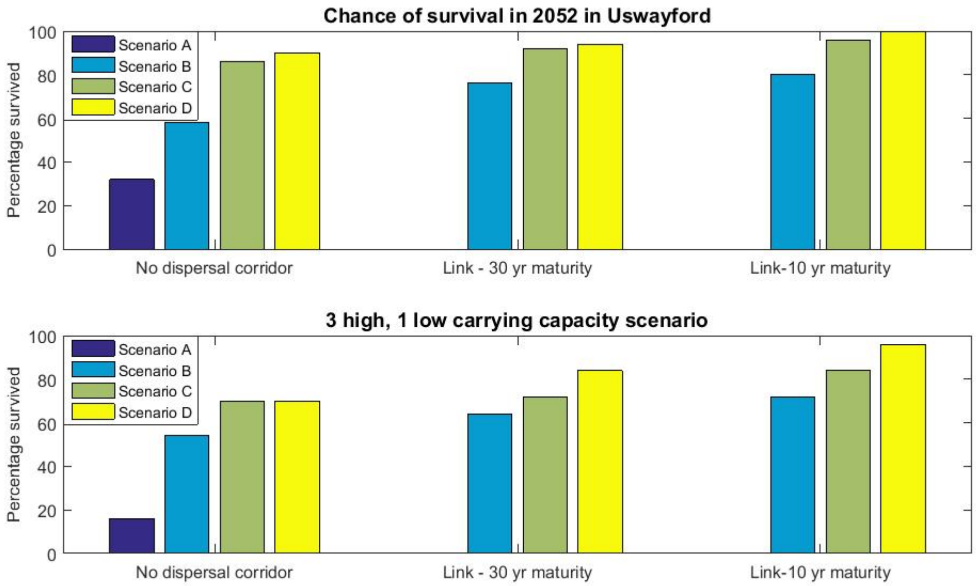

Figure 22: Percentage of survivals in Uswayford in 2052 for the four forest design scenarios where there is no dispersal corridor (left) and when the corridor is planted in the compartment shown in Figure 18 and has a 30 year growth time before it can be used (middle) or a 10 year growth time (right).

	% of cases of squirrel present in Uswayford in 2052							
	high CC				3 high 1 low CC			
Scenario	A	B	C	D	A	B	C	D
No dispersal corridor	32%	58%	86%	90%	16%	54%	70%	70%
Dispersal corridor-30 yrs maturity	NA	76%	92%	94%	NA	64%	72%	84%
Dispersal corridor-10 yrs maturity	NA	80%	96%	100%	NA	72%	84%	96%

Table 4: Chance of Uswayford being populated by red squirrels in 2052 based on 50 model realisations in Scenarios A-D.

9 Discussion

The process of iterative feedback between modellers and foresters and the resulting new scenarios (A-D) led to a continuous improvement of the future forest habitat at Kidland and Uswayford. The forest design plan represented by Scenario C and D provide the most viable habitat for red squirrels. Model results indicate that Scenario C supports the highest abundance of squirrels, while Scenario D has the least chance of population extinction in Uswayford, though the percentages are similar to those for Scenario C. Viability is further improved when the dispersal corridor between Tilhill and Uswayford is included as this reduces the chance of population extinction in Uswayford and enhances the re-population of Uswayford should an extinction occur. Based on the model findings, we would recommend that the Scenario C forest design plan be implemented in an ideal world. However, the more economical option of Scenario D produces a similar (in fact slightly higher) chance of surivival in Uswayford, but supports a slightly lower overall density of squirrels than Scenario C. In Scenario D, the tree species composition is dominated by Sitka spruce and therefore squirrel abundance would suffer if there were several consecutive poor seed years for this species as there would be few alternative food sources. The minimum viable population size for red squirrels has been estimated to be 200 [10] and therefore the enhanced population sizes predicted for Scenario C are closer to this estimate.

Model predictions clearly show that the early availability of the dispersal corridor (i.e. after 10 years) has marked and beneficial impacts on population viability and recolonisation. The key benefit of the corridor is less due to actual increased available habitat, more in terms of a link allowing animals to move more freely between the two forests. Species composition of the corridor should therefore include a significant component of fast growing shrub and tree species suitable for upland conditions, and their utility as a red squirrel food plant should only be a secondary consideration.

It is also worth noting that the significance of the dispersal corridor depends largely on the assumption that Tilhill provides continuous suitable habitat for squirrels since the connection from Uswayford to Kidland requires dispersal through the corridor and Tilhill. The forest design plans for Tilhill are unknown but would influence the effectiveness of the dispersal corridor. Given the lack of information with respect to the design plans for the plantations managed by Tilhill, we have modelled this part of Kidland forest so that it provided a constant proportion (33%) of mature habitat. This allowed a careful examination of Forestry Commission design plans in the absence of confounding impacts. However, the Tilhill area given its size, and linkage to Uswayford has the potential to make a significant contribution to red squirrel conservation at Kidland Forest.

Whilst it is an imperfect crystal ball, the developed modelling system does allow the exploration of different forest design plan options with respect to red squirrel population viability and abundance. It is worth stressing though, that its success critically depends on close collaboration, input and interaction with forest managers and planning staff.

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