Natural strongholds for red squirrel conservation in Scotland

Supplementary Information

Andrew Slade*, Andy White*,

Kenny Kortland†, Peter W.W. Lurz‡

S1 Mathematical model

In this section we outline how detailed habitat information is used to determine squirrel carrying capacities and we detail the stochastic model that is generated from the deterministic model in the main paper.

S1.1 *Carrying capacity*

The mathematical model uses forest habitat information obtained from the National Forest Estate 2017 (available at: https://data-forestry.opendata.arcgis.com/datasets/) and National Forest Inventory 2016 (available at: https://data.gov.uk/dataset/) land cover data sets and is supplemented by the Scottish National Heritage (available at: https://www.nature.scot/) dataset which contains information on the urban landscape of Scotland. Primary tree species information for each 25m by 25m area was extracted from these datasets using the GRASS GIS

*Maxwell Institute for Mathematical Sciences, Department of Mathematics, Heriot-Watt University, Edinburgh, UK, EH14 4AS

†Forestry and Land Scotland, 1 Highlander Way, Inverness Business Park, Inverness, IV2 7GB

‡Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Midlothian, UK

software package (https://grass.osgeo.org). This data was used in MATLAB to create a map consisting of a 1km^2 resolution grid with each grid square containing the proportion of land covered by each tree species as well as the proportion of urban environment.

The link between squirrel density, habitat and tree seed crops is well evidenced (Gurnell, 1983, 1987; Lurz et al., 2000). Thus, the gridded habitat data is combined with estimates of squirrel density in different habitat types. This produces a red and grey squirrel carrying capacity value for each 1 km grid square. These values signify the potential population density that the landscape can support. In the model the carrying capacity is not fixed but instead fluctuates due to seed crop dynamics which assumes that tree species undergo a mast year with a defined period, producing higher yield of seed crops that can support increased squirrel densities (Table S1) (Gurnell, 1987; Bosch and Lurz, 2012). These mast years are largely cyclical and occur simultaneously for the majority of trees within a single species that are present in a local, connected forest. During the non-mast years, the trees can either undergo 'intermediate' or 'poor' years in terms of cone or seed production which have been averaged in this modelling framework to produce a single non-mast value for each species. Each tree species undergoes a period of non-mast and mast years at regular intervals (with the period defined in Table S1). The starting point for this period was chosen at random for each tree species at the beginning of the simulation. Carrying capacity values for each tree species were updated every year, using the relevant values in Table S1, to account for seed crop dynamics, which allowed the forests carrying capacity dynamics to be incorporated into the model. Where data were available in the literature for specific tree species these have been used (Table S1); where they were not available they have been conservatively set at being one quarter of the mast values. The latter estimate is based on data from Spadeadam Forest, Northern England (Lurz et al., 1998), an analysis of 16 years of cone crop data for Sitka spruce and Scots pine at Kidland Forest, Northern England (Lurz, 2016) and an examination of a 25 year cone data set for Scots pine (Broome et al., 2016).

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

Table S1: Carrying capacities for red and grey squirrels, in individuals per hectare, for mast and non-mast years for each of the tree species considered in the model. Values for Other Broadleaf and Other Conifer are averages of the known broadleaf or conifer trees. The last column is the (average) interval between mast years. Mast interval data is based on Aldhous et al. (1972).

S1.2 *Model framework*

To generate the stochastic model, the different rates in the deterministic model are converted into probabilities of events that account for changes in individual patch level abundance (Renshaw, 1993). To do this, we calculate the relevant rate for each event by adding/multiplying the relevant parameter values together. For example, the rate associated with the natural death of a susceptible grey squirrel (S_G) is given by $b \times S_G$, where $b = 0.9$ and S_G is the susceptible grey squirrel density in the relevant grid square. When each event has an associated rate, these are added together to give the parameter R. By dividing each event rate by R we attain the probability of each event occurring. The relationship between the terms in the model equations, the different events (birth, death, infection, dispersal, etc.), the change in population abundance and the probability of each event in the stochastic model are given in Table S2. The time between events can be determined as $T_{event} = -ln(\sigma)/R$ where R is defined in Table S2 and σ is a random number drawn from a uniform distribution between 0 and 1 (which assumes that the time to the next event is an exponentially distributed random variable). The events are incremented at random with the associated probabilities updated due to changes in population density after each event. Individual simulations can be undertaken in FORTRAN90 using a Gillespie algorithm and provide information of the behaviour in a single realisation. Ten realisations are run for each scenario, and averages taken. For further information see (Renshaw, 1993).

S1.3 *Initial conditions*

The model was initialled with observed data for the presence of red and grey squirrels between 2014-2017 (using the National Biodiversity Network's (NBN) Gateway, `http://data.nbn.org.uk`). The observation data was used as the initial condition for a model spin-up, consisting of 10 simulations, to allow red and grey squirrels to expand into available habitat. The average result of the 10 spin-up simulations are then used as the initial condition for the main, 150 year, simulations. In regions where only one squirrel species was predicted the spin-up was initialised at the respective potential density based on available habitat types. In regions where both squirrel species were predicted the spin-up was initialised by assuming that reds and greys had access to half the habitable area in each grid cell.

S1.4 *Grey squirrel trapping*

Grey squirrel trapping is included in every square that has a grey squirrel population. Geographically, this level of trapping is unrealistic and much more comprehensive than what is currently applied. However, given that the location of natural strongholds is unknown a priori, trapping cannot be targeted. Hence, occupancy results that include trapping should be viewed according to local effects. Of particular interest is whether the use of trapping can either expand existing regions, or create new regions, where red squirrels persist compared to scenarios where trapping is absent. Grey squirrel trapping is only included during the squirrel breeding

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

Table S2: Stochastic model events that govern the dynamics that occur within each 1km grid square. The parameters representing control and dispersal were fitted with observed data on the Island of Anglesey (Jones et al., 2017). Here $R = \sum[rates]$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (6 months from the start of April to the end of September) and are set to zero otherwise. Transmission can occur from infected squirrels within the focal grid square and also from the 8 neighbouring grid cells due to daily movement within a core range of radius, $\theta = 0.15$km. The dispersal term is shown for the class S_G only but is similar for all other classes. The model assumes density dependent dispersal such that squirrel dispersal increases as density increases and the dispersal rate is $m = 2b$ when the patch density is equal to the potential density. Therefore, individuals undergo long distance dispersal on average twice in their lifetime and relocate to a different patch up to a distance of 2 km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). The control of squirrels is shown for class S_G only but is similar for all other classes (although when a red squirrel is caught there is no change in red squirrel abundance to reflect the fact that it is released unharmed). Here, $c = 3.5$, represents the rate of successfully trapping a squirrel and T_D is the trap intensity (trap effort per gridcell per day). Further details of the model framework and the calculation of parameter values can be found in Jones et al. (2017).

season (1 April - 30 September), which is 183 days. A trapping coefficient $T_D = 0.1$ (White and Lurz, 2018) is used and this is equivalent to 18 trapdays per year per 1km gridsquare.

S2 Results when grey squirrels naturally expand their range

Figure S1 shows the results for squirrel density and occupancy when grey squirrels are allowed to expand their range.

S3 Results when grey squirrels occupy the entirety of Scotland

S3.1 *Results without grey squirrel trapping*

Figure S2 shows results for squirrel density and occupancy for the scenario where grey squirrels have been introduced everywhere and grey squirrel trapping has not been included.

In central Scotland the regions of forest at Rannoch, which includes the forest of South Rannoch as well as the forest that lies directly west, would constitute good red squirrel strongholds. Furthermore, given the lack of grey squirrel occupancy in this region, these two forests could potentially be connected, using appropriate planting that give an advantage to red squirrels over greys, to create a single, larger, connected natural stronghold which would aid population viability. The forest to the east of Rannoch, just north of Loch Tummel, is contested between red and grey squirrels, with some simulations ending with grey squirrels present and some ending without grey squirrels, despite being connected to an area of grey squirrel occupancy. The forest of Craigvinean, to the south of Rannoch near Dunkeld, also acts as a natural red squirrel stronghold which suggests that trapping around Dunkeld could isolate the natural red squirrel strongholds at Rannoch due to geographic factors that prevent grey squirrel incursion via other routes. To the east of this region lies Glenisla forest which also acts as a natural red squirrel stronghold due to its relative isolation and lack of connectivity.

In the east of Scotland the region that includes the forest at Glentochty, which lies to the west of Aberdeen, is a natural stronghold. Directly south of Aberdeen is Fetteresso forest which also makes a good natural stronghold, especially given its proximity to Aberdeen.

Along the northern coast of Scotland there is a significant region of forest that either has sole red occupancy or is contested. In the centre of this region is the forest of Ordiequish, to the east lies the forest of Aultmore whilst Teindland forest lies directly to the west, all of which either have sole red squirrel occupancy or contested occupancy, despite the wider region being grey dominated, which suggests that trapping could safeguard these forests for red squirrels. Sole red squirrel occupancy occurs at Elchies forest which lies to the south-west of Ordiequish. To the west of Elchies forest is the forests of Newtyle, Dallas and Monaughty, all of which can be found further west along the north coast, to the south-east of the forest at Culbin, and all of which see some grey squirrel incursion, but not dominance, during the simulations. The forest at Culbin is also contested between red and grey squirrels but is separated from the other three forests by a region of grey squirrel occupancy at Darnaway forest and the city of Elgin. However, trapping at Elgin could prevent grey squirrel expansion further west along the northern coast, which would isolate the region south of Culbin allowing red squirrel occupancy, due to the limited number of migration routes available to grey squirrels.

The river Spey is also in this region and includes the forests of Inshriach and Glenfeshie, which is a region that sees grey squirrel incursions, and Abernethy which only allows red squirrel occupation in part of the forest. However, the forest in between these two regions, Glenmore Forest Park, makes a good natural stronghold which suggests that this and the two adjacent forests could potentially be combined to create a single natural stronghold. Furthermore, given limited grey squirrel access routes imposed by the geography, trapping further along the Spey river, to the south of Ordiequish for example, could isolate the region and prevent grey squirrels entering from the north-east.

Further north the forest of Black Isle, which lies to the north of Inverness, makes for a good natural stronghold. The forests around Glen Affric and Glen Garry, which lie on the opposite side of Inverness from Black Isle, also act as natural strongholds. To the south of Glen Garry there is a region of red squirrel occupancy around Glen Spean, which lies to the east of Fort William, which makes a good natural stronghold.

The peninsula of Kintyre in west Scotland allows both red and grey squirrel occupation, with segregation occurring naturally and red squirrels occupying the west and grey squirrels the east of the peninsula. There is also a small region that could act as a natural stronghold at the western edge of Loch Doine, however the west of Scotland appears to offer little in the way of natural red squirrel stronghold.

In the south of Scotland the regions of red squirrel occupancy are the same as the current observational data, due to the current existence of grey squirrels in the region. Thus in the Scottish Borders the eastern section of the forest at Eskdalemuir allows sole red occupancy. The forest to the north of Eskdalemuir, at Glentress forest, as well as Wauchope forest at the border with England, which is connected to the stronghold at Kielder forest which is approx. 5000km^2 in area and is dominated by Sitka spruce, also act as natural red squirrel strongholds.

In Dumfries and Galloway the urban area at Gatehouse of Fleet as well as deciduous regions along the river valley to the north provide good grey squirrel habitat. The forests to the north of the Gatehouse of Fleet, east of the Waters of Ken, are better suited to be natural strongholds. Further north, near the town of Muirkirk, there are a number of small regions of forest that can act as red squirrel strongholds. There is also a region of forest, near the town of Newton Stewart, that can act as a natural stronghold.

Beyond this there are a few small regions, such as Tentsmuir forest, Kincardine and Montreathmont forest, that see both red and grey squirrel occupancy during the simulations, which suggests that trapping could exclude grey squirrels, despite these regions being surrounded by sole grey occupancy regions.

S3.2 *Results with grey squirrel trapping*

Figure S3 shows results for squirrel density and occupancy for the scenario where grey squirrels have been introduced everywhere and grey squirrel trapping is included. Grey squirrel trapping is applied to all grid squares in which greys are present with approximately 18 trap-days per year per grid square. The inclusion of grey squirrel trapping does not reveal new natural strongholds, though some regions that allow both red and grey squirrels to compete at low densities, such as the area on the north coast, only allow red squirrel occupancy when trapping is introduced. Existing natural strongholds are reinforced by the trapping, with some expanding slightly, but the results are not dramatic. Regions where red squirrels can survive despite grey squirrel competition are regions where grey squirrels cannot reside in large numbers. Thus the poorness of the habitat that allows red squirrels to survive also hinders their potential expansion when grey squirrel abundance is reduced via trapping.

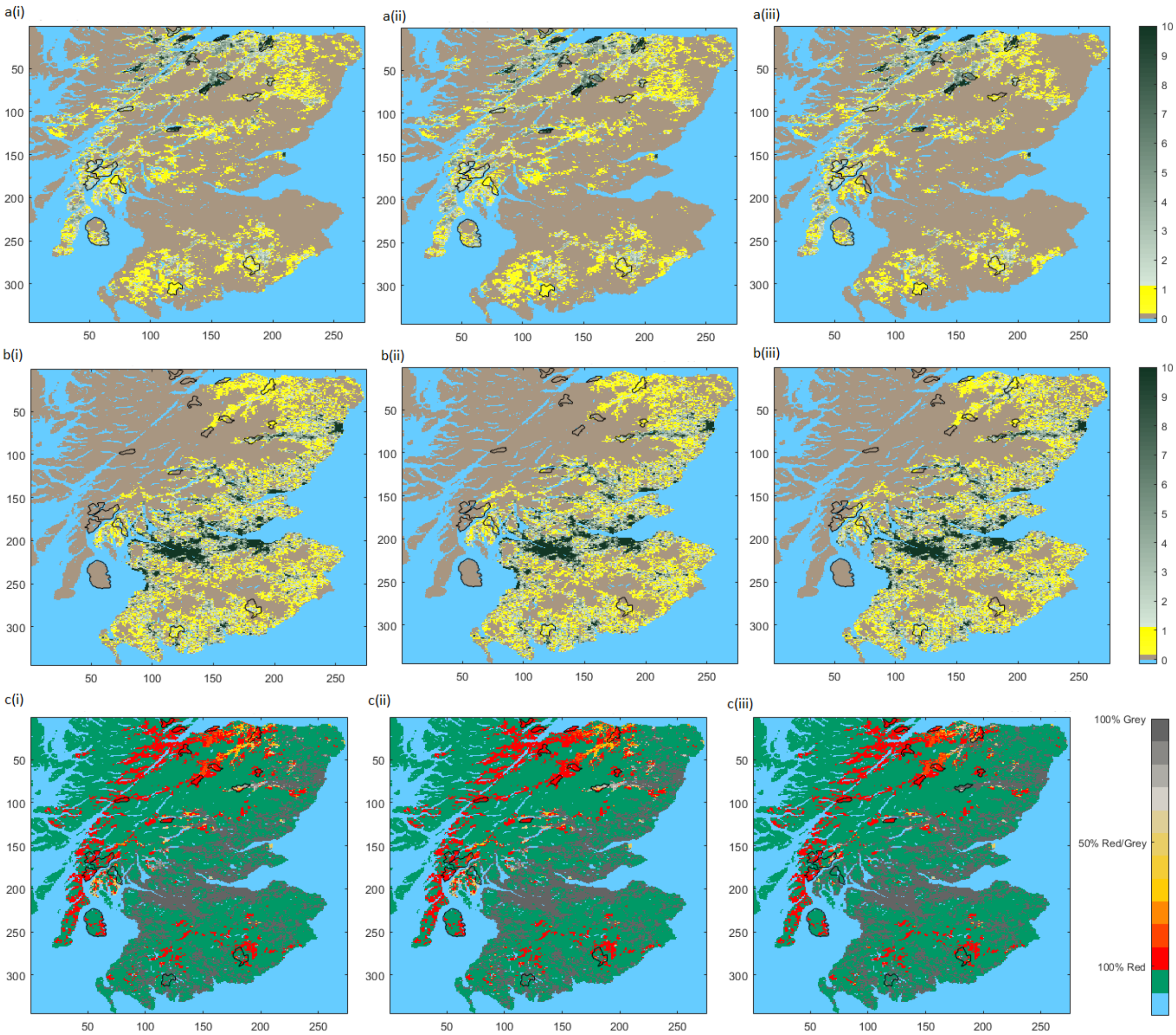

Figure S1: Results for the scenario where red and grey squirrels are allowed to disperse and compete freely. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The 19 designated strongholds are outlined in black.

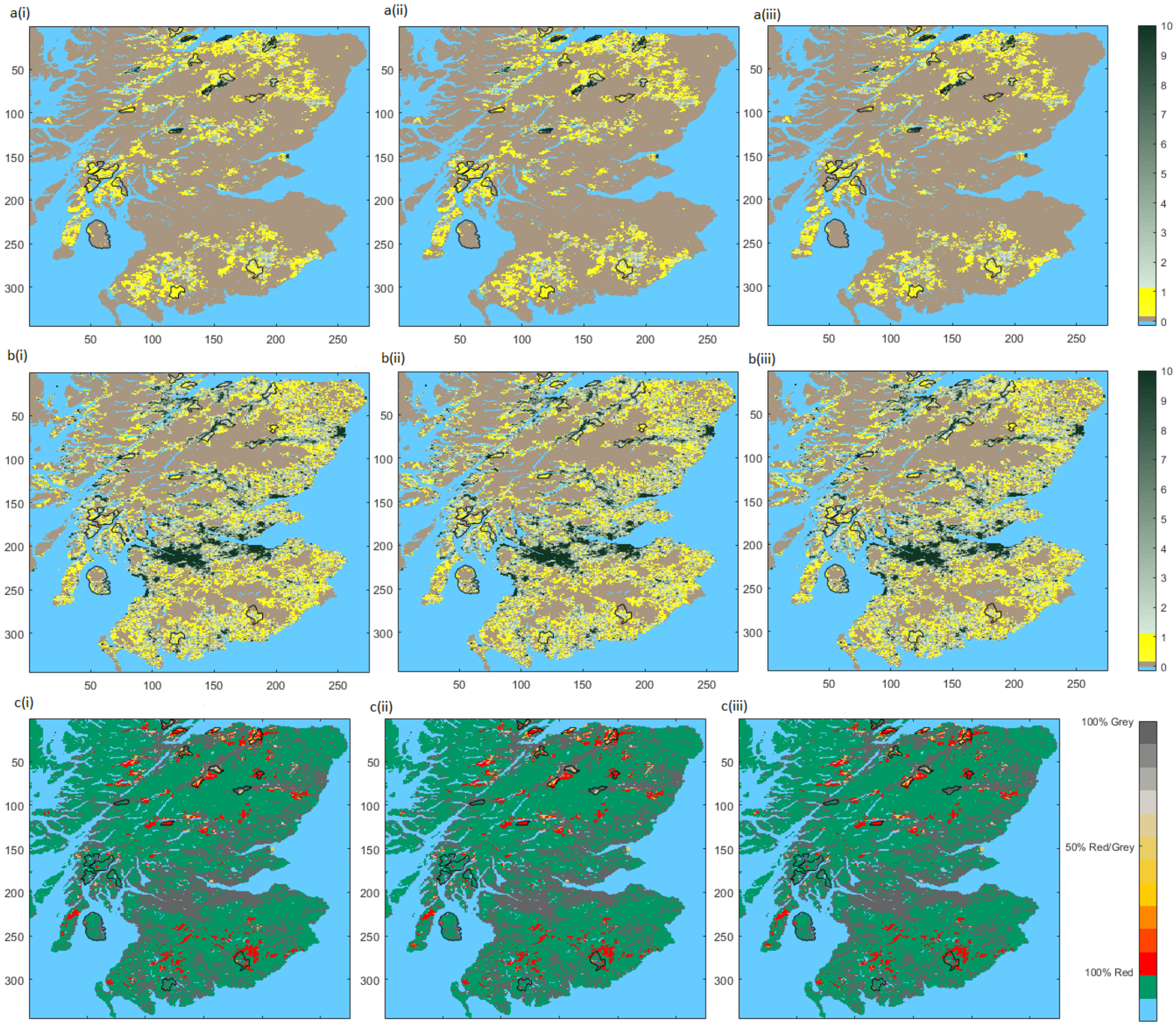

Figure S2: Results for the scenario where grey squirrels have been introduced everywhere, in order to simulate a situation where grey squirrels have successfully colonised the entirety of Scotland. These results have no grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The 19 designated strongholds are outlined in black.

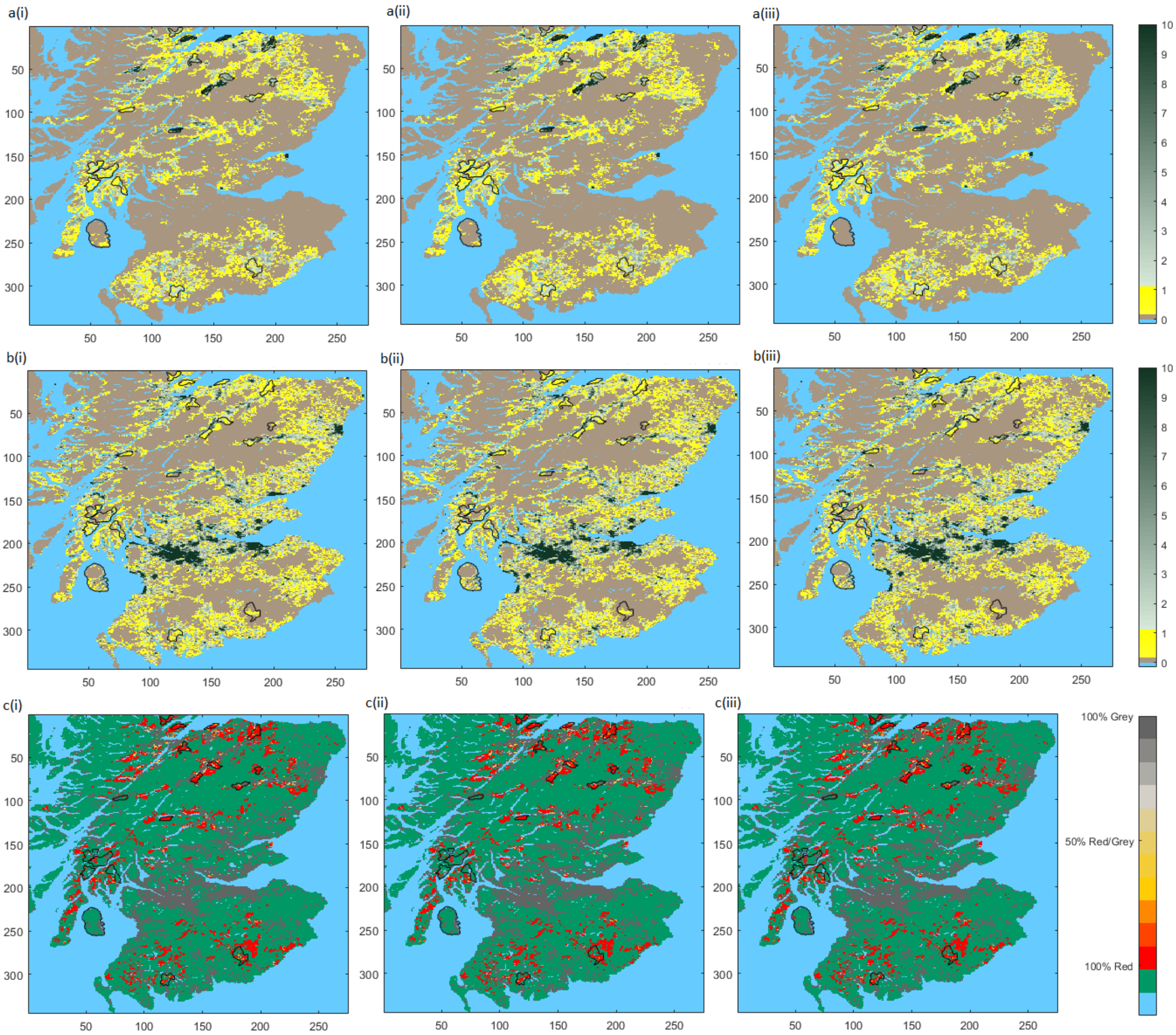

Figure S3: Results for the scenario where grey squirrels have been introduced everywhere, in order to simulate a situation where grey squirrels have successfully colonised the entirety of Scotland. These results include grey squirrel trapping (approx. 18 trap-days per year per grid-square in which greys are present). Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The 19 designated strongholds are outlined in black.

References

Aldhous, J. et al. (1972), ‘Nursery practice.’, *Forestry Commission Bulletin* (43).

Bosch, S. and Lurz, P. (2012), *The Eurasian red squirrel: Sciurus vulgaris*, Westarp Wissenschaften-Verlagagsgesellschaft.

Broome, A., Summers, R. and Vanhala, T. (2016), *Understanding the provision of conifer seed for woodland species*, Forestry Commission.

Gurnell, J. (1983), ‘Squirrel numbers and the abundance of tree seeds’, *Mammal Review* **13**(2-4), 133–148.

Gurnell, J. (1987), *Natural history of squirrels*, Christopher Helm.

Jones, H., White, A., Lurz, P. and Shuttleworth, C. (2017), ‘Mathematical models for invasive species management: Grey squirrel control on anglesey’, *Ecological modelling* **359**, 276–284.

Lurz, P. (2016), *Kidland forest monitoring*, Forestry Commission, Kielder Forest District.

Lurz, P., Garson, P. and Ogilvie, J. (1998), ‘Conifer species mixtures, cone crops and red squirrel conservation’, *Forestry: An International Journal of Forest Research* **71**(1), 67–71.

Lurz, P., Garson, P. and Wauters, L. (2000), ‘Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (sciurus vulgaris l.)’, *Journal of Zoology* **251**(2), 167–178.

Renshaw, E. (1993), *Modelling biological populations in space and time*, Vol. 11, Cambridge University Press.

White, A. and Lurz, P. (2018), *Grey squirrel control in southern Scotland: A model analysis*, Forest Enterprise Scotland.