

An assessment of long-term forest management policy options for red squirrel conservation in Scotland - Supplementary information

Map of Current Scottish Red Squirrel Strongholds

Currently there are 19 regions of forest, primarily in publicly-owned forests, that are designated as red squirrel strongholds which are coloured solid red in Figure S1. The three strongholds that are examined in the main paper are at Balmoral to Inver (Eastern Stronghold), Leanachan (Western Stronghold) and Eskdalemuir (Southern Stronghold). Three more strongholds will be examined in this document. They are at Daviot Loch Moy (East2 Stronghold) located south of Inverness, Glenbranter (West2 Stronghold) located in southern Argyll and Bute and Fleet Basin (South2 Stronghold) in western Dumfries and Galloway.

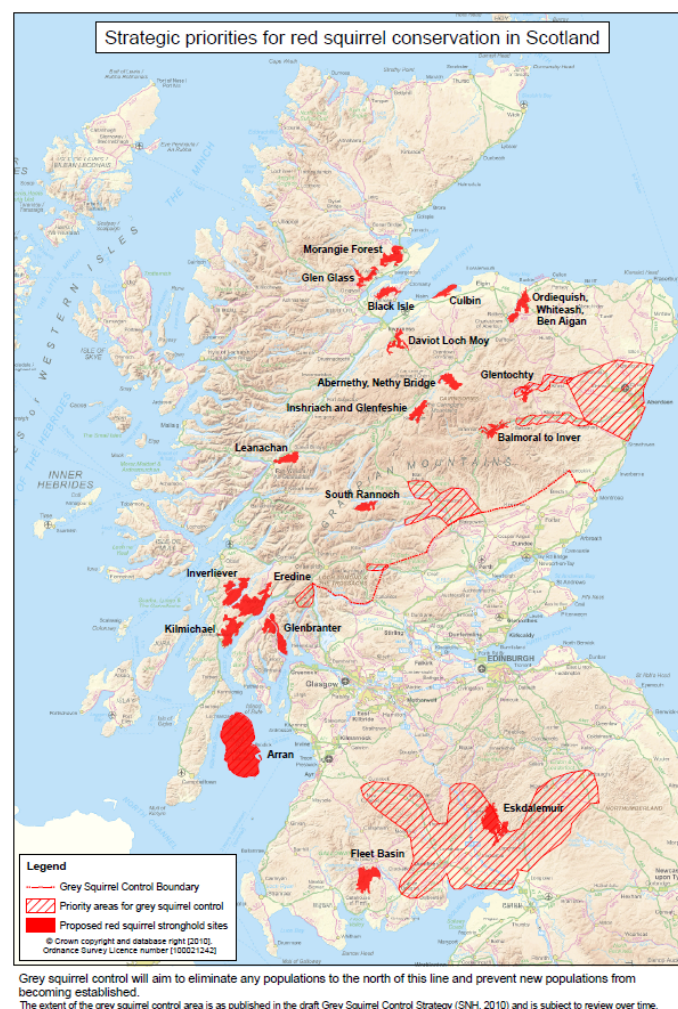


Figure S1: Map of Scotland with the 19 stronghold regions shown in solid red. The map also includes the grey squirrel control boundary which is the northern most extent (excluding Aberdeen) of the grey squirrels as well as regions that are the focus for grey squirrel control (hatched area). Image courtesy of Scottish Natural Heritage

Current Distribution of Red and Grey Squirrels

The following image outlines the current distribution of red and grey squirrel in Scotland.

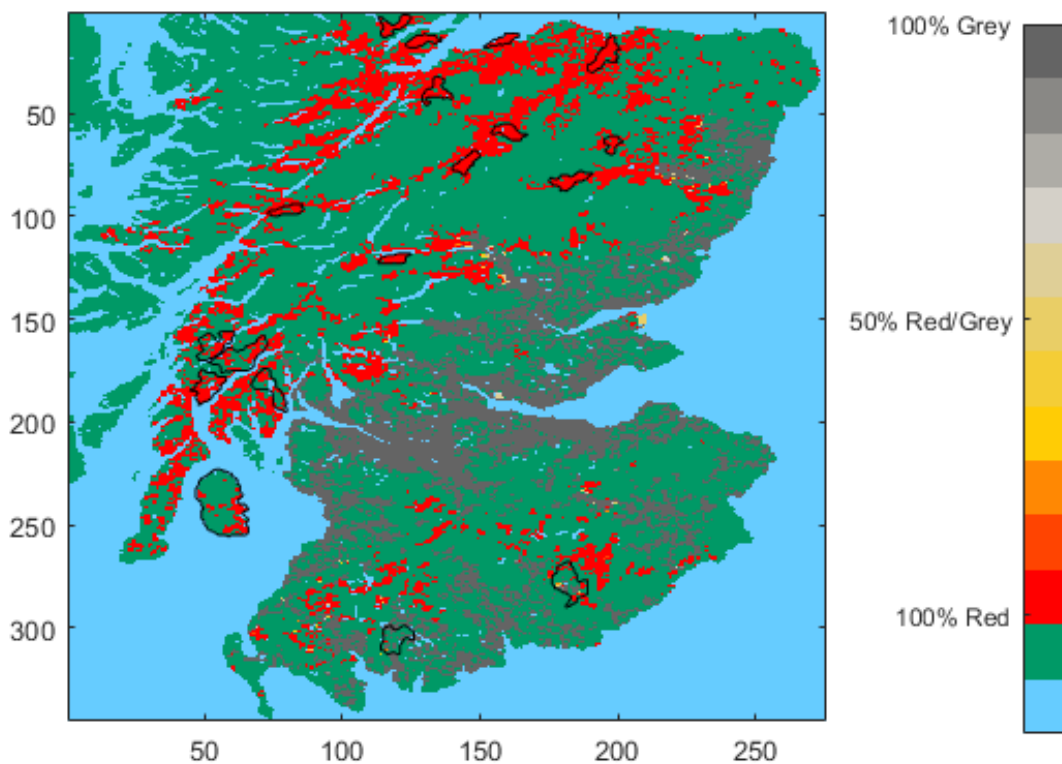


Figure S2: Current distribution of red and grey squirrels in Scotland. The northern extent of the grey squirrel distribution is defined by the Highland Protection Boundary (not including the population at Aberdeen). The 19 stronghold regions are outlined in black.

Map of Grey Squirrel Introductions at the Eastern & Western Strongholds

To test if the strongholds located north of the grey squirrel control boundary are capable of acting as strongholds in the event that grey squirrels colonise the surrounding region, grey squirrels were artificially introduced in grid squares with carrying capacity of 5 or more that were located in the area surrounding the Eastern Stronghold (Figure S3) and at the Western Stronghold (Figure S4).

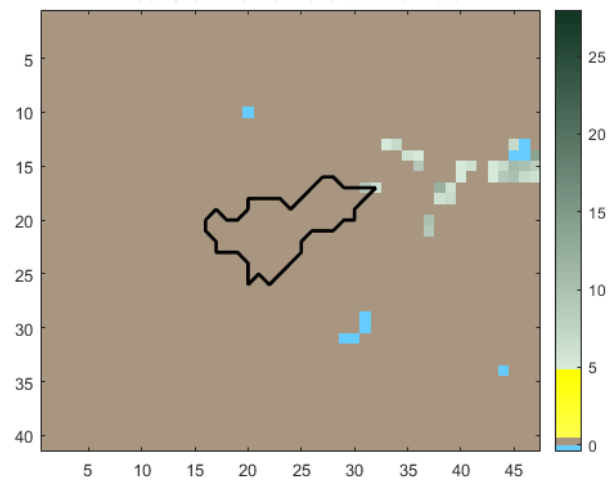


Figure S3: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the Eastern Stronghold. Colour scale to the right indicates the number of individuals per square kilometre.

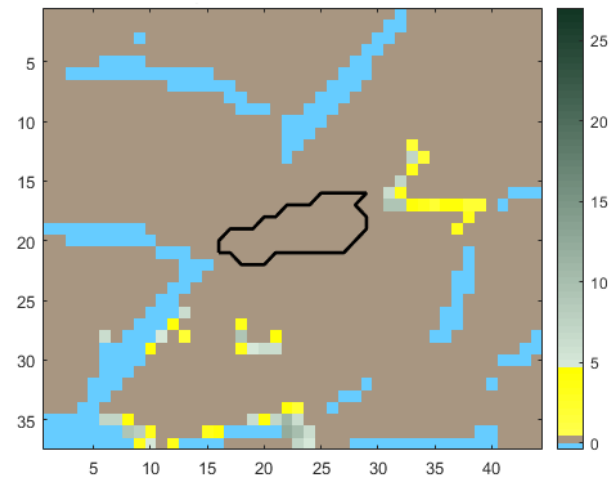


Figure S4: Population size and geographic spread of grey squirrels that are artificially introduced into the region surrounding the Western Stronghold.

Density Maps for the Eastern, Western & Southern Strongholds

The following are the maps showing the red and grey squirrel density at the Eastern, Western and Southern Strongholds under the UK Forestry Standard and the Stronghold Management strategy.

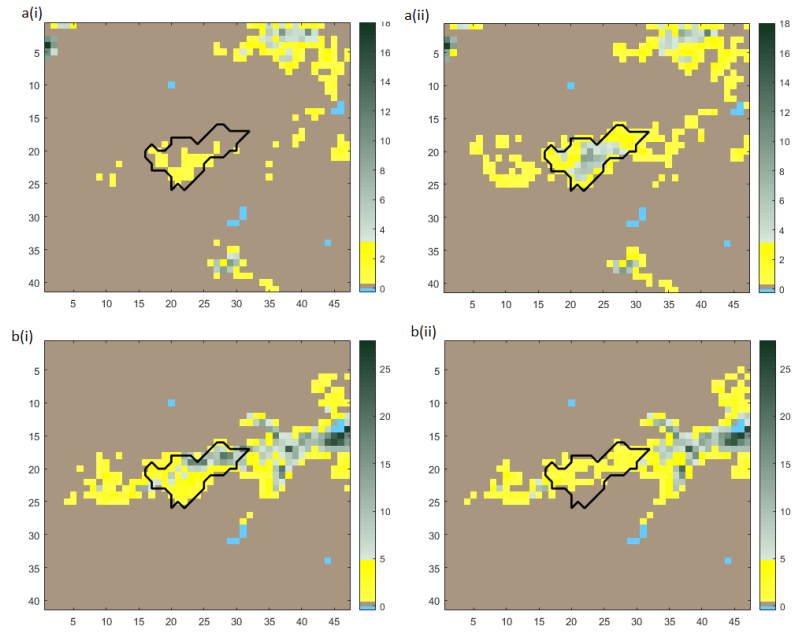


Figure S5: Population density (animals per gridsquare) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the Eastern Stronghold at the end of the 150 year model simulation.

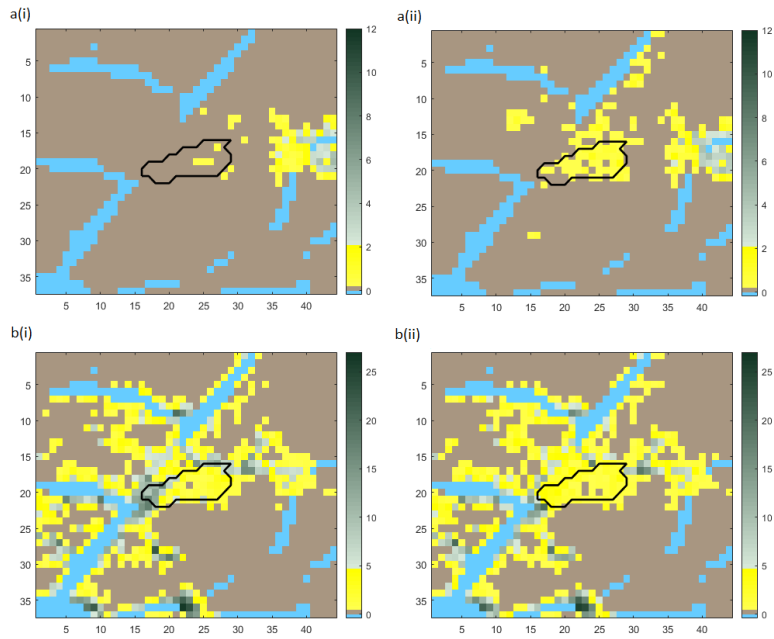


Figure S6: Population density (animals per gridsquare) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the Western Stronghold at the end of the 150 year model simulation.

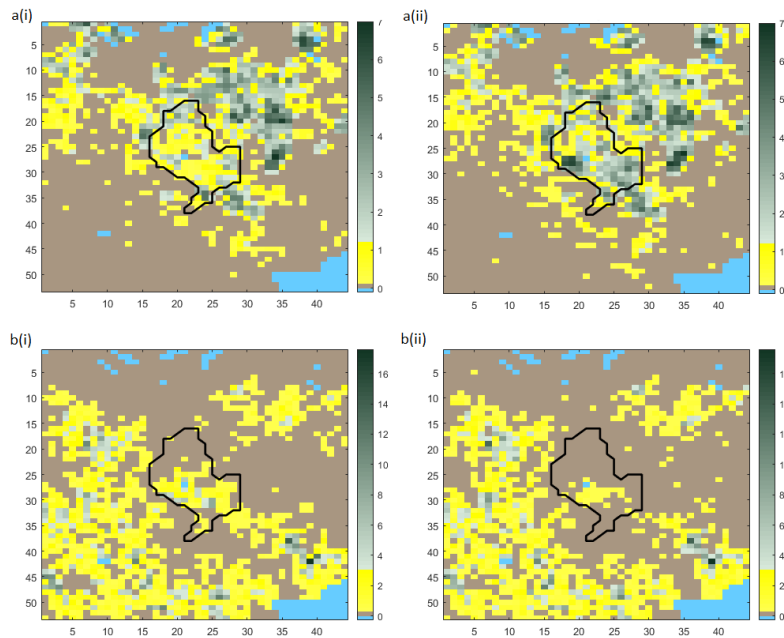


Figure S7: Population density (animals per gridsquare) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the Southern Stronghold at the end of the 150 year model simulation.

Results for Grey Squirrel Introduction at Year 50 of the Simulation

All of the results in the main paper assume that the transition in the stronghold from UK Forestry Standard to the Stronghold Management policy occurs simultaneously with the arrival of grey squirrels into the area surrounding the stronghold. This need not be the case as grey squirrel expansion could be predicted based on grey squirrel monitoring and the Stronghold Management policy be implemented in a stronghold before the arrival of the grey squirrels. This ensures that the reduction in the red squirrel abundance that occurs due to the transition between forest management polices is not compounded by competition from grey squirrels. Figure S8 shows the results with greys introduced at year 50 in the Eastern Stronghold whilst Figure S9 shows the same results for the Western Stronghold.

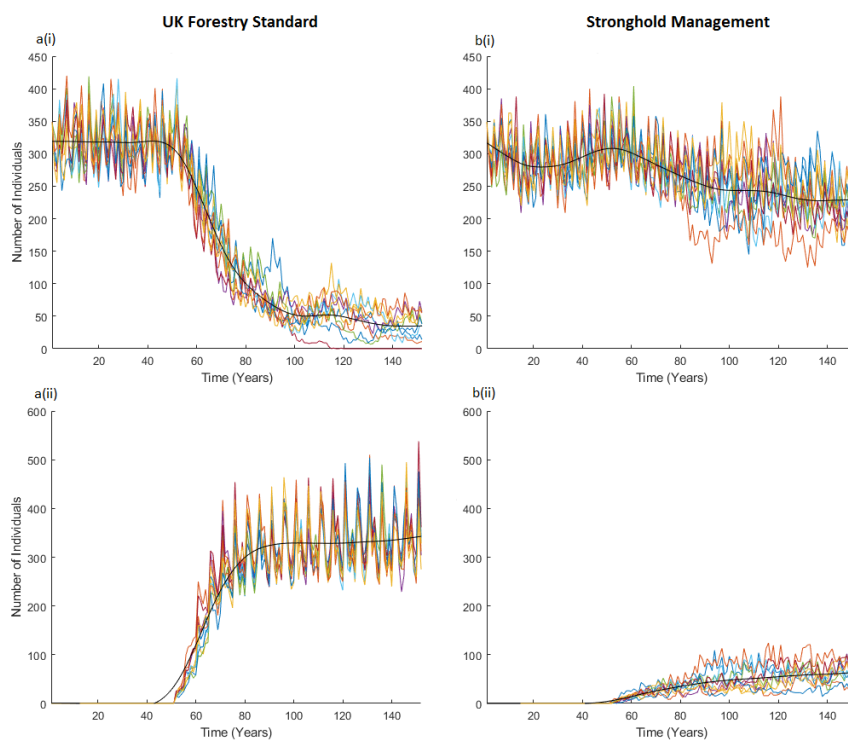


Figure S8: Timeseries data for the Eastern Stronghold when grey squirrels were introduced at year 50 of the simulation under (a) UK Forestry Standard and (b) Stronghold Management policy. Here (i) shows the red squirrel populations and (ii) shows the grey squirrel populations. The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

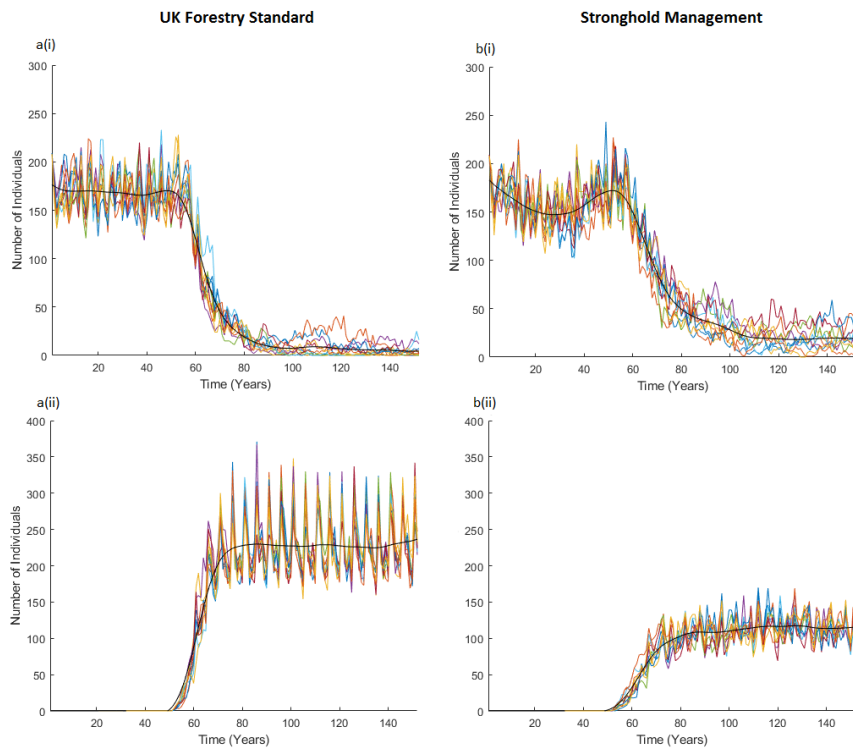


Figure S9: Timeseries data for the Western Stronghold when grey squirrels were introduced at year 50 of the simulation under (a) UK Forestry Standard and (b) Stronghold Management policy. Here (i) shows the red squirrel populations and (ii) shows the grey squirrel populations. The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

Results for the Introduction of Squirrelpox Virus

Squirrelpox can remain endemic in a resident grey squirrel population if the population density is high enough to ensure its survival. In this study we introduced infected grey squirrels in regions surrounding the strongholds in years 10, 15 and 20. Within the strongholds this led to short-lived outbreaks of squirrelpox but the disease did not persist within either grey or red squirrels in the long-term (Figure S10). Hence, squirrelpox did not play a significant role in the population dynamics within the stronghold at any of the 6 stronghold locations considered in this study.

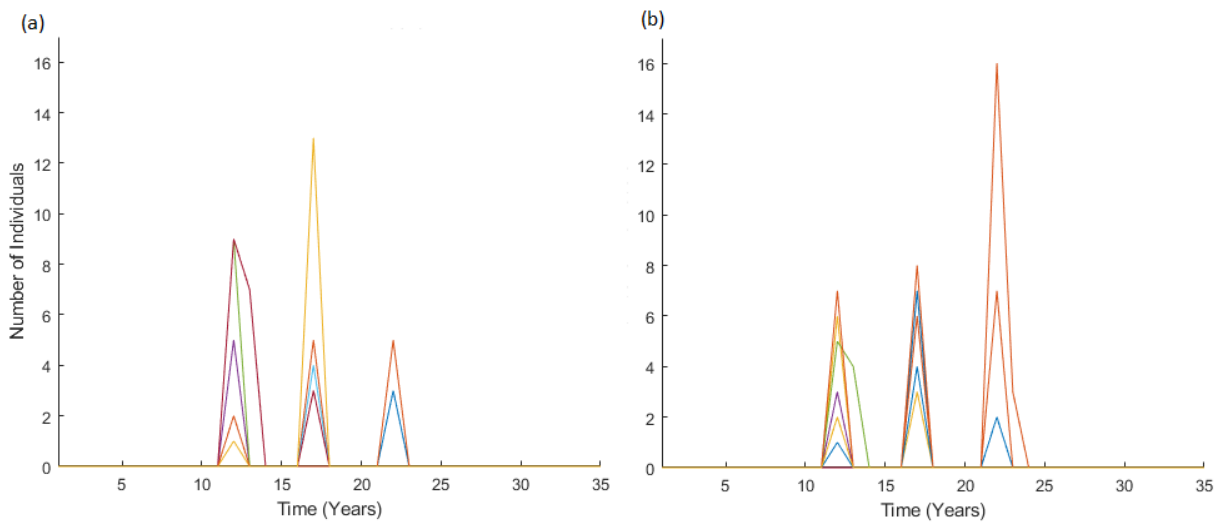


Figure S10: The abundance of infected grey squirrels in the Eastern Stronghold under (a) UK Forestry Standard and (b) Stronghold Management policy. The results for the 10 model simulations are shown.

Results for the Three Remaining Strongholds

East2 Stronghold

The forest at the East2 Stronghold, located at Daviot Loch Moy which is just south of Inverness (Figure S1), complies with the UK Forestry Standard (UKFS) but not with Stronghold Management (SM) policy (Figure S11.a(i)). The application of the SM policy reduces the amount of broadleaved trees present from around 13% to less than 5% (Figure S11.b(i)) and replaces them with favoured species: Norway spruce, Larch, Lodgepole pine, Sitka spruce and Scots pine. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure S12.a(i)) whereas the grey squirrel carrying capacity (Figure S12.a(ii)) is noticeably reduced.

Currently there are no grey squirrels resident in this stronghold. In the absence of grey squirrels the red squirrel population under UKFS is stable with an average size of 305 individuals (Figure S11.a(ii)), whereas under the SM policy the red squirrel population initially falls to an average of 290 individuals during the transition from the UKFS to the SM, which takes 30 years, but the population size recovers in the long term to an average of 305 individuals (Figure S11.b(ii)). This reduction is smaller than that at Eastern or Western Strongholds primarily due to the increased diversity of tree species present at the East2 Stronghold.

Grey squirrels are not currently a threat to red squirrels at this stronghold - but as with the Eastern and Western Strongholds we examine the impact grey squirrels have on red squirrel viability. When grey squirrels are introduced into regions adjacent to the stronghold the red squirrel population under UKFS collapses from its initial value (300) to an average of 120 individuals (Figure S11.a(iii)) which is close to being a large enough population to ensure viability of the stronghold (we assume a viable population needs to be larger than 125 individuals). The grey squirrel population under the UKFS grows to a stable average of 190 individuals (Figure S11.a(iv)). When the SM policy is implemented the reduction in red squirrel population abundance is reduced, with the average population size under SM policy being 175 individuals (Figure S11.b(iii)). The long term grey squirrel population abundance under SM is 85 individuals (Figure S11.b(iv)). The population density and geographic spread of red and grey squirrels in the East2 Stronghold and the surrounding area under UK Forest Standard and Stronghold Management policy can be found in Figure S13. Thus the introduction of the SM policy and the changes to the forestry that this entails serves to reduce the resident grey squirrel population to just over half of its size under UKFS which allows the red squirrel population to increase to a level that has the potential to be viable.

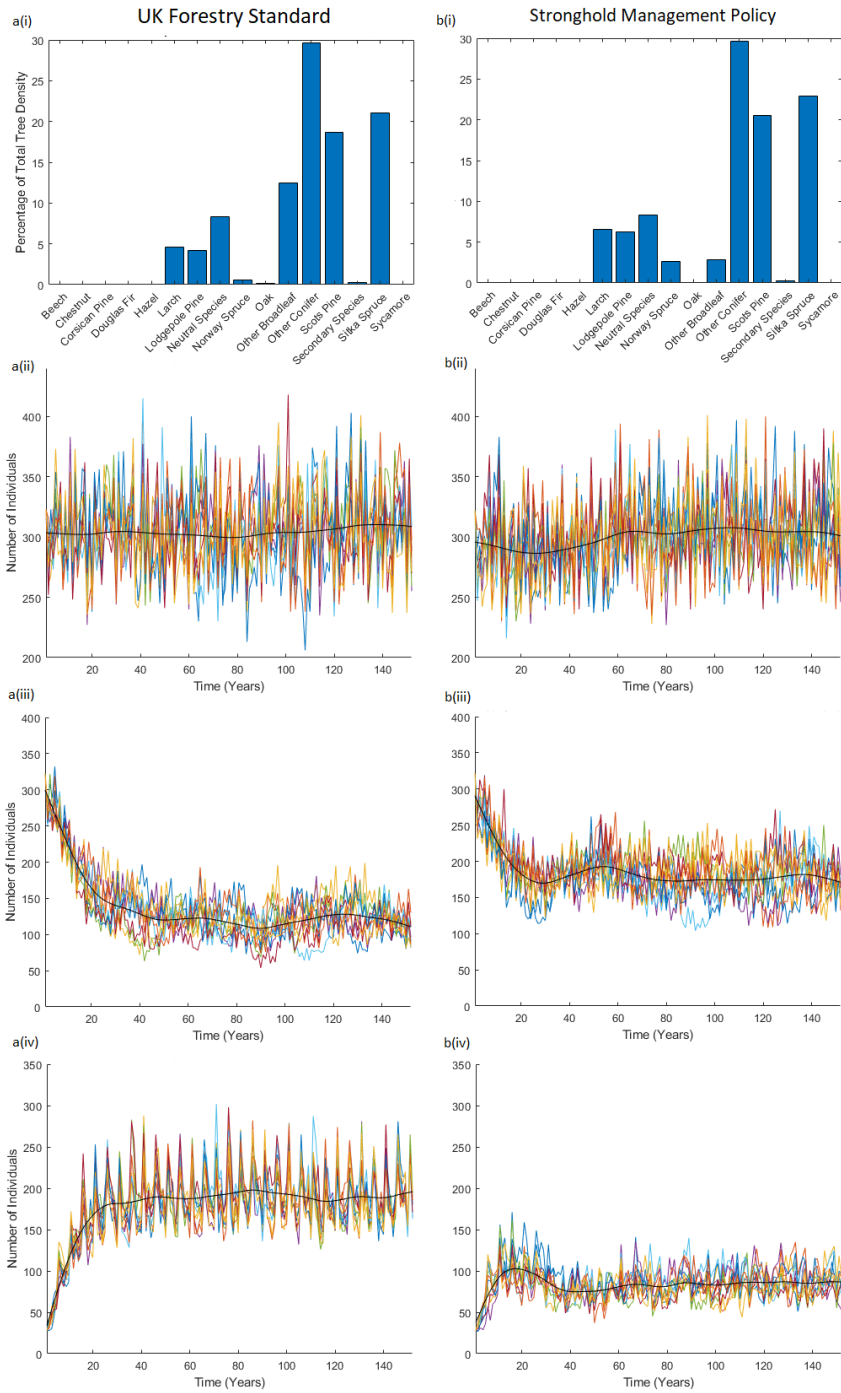


Figure S11: Results for the stronghold at East2 Stronghold. Images a(i-iv) are the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition, (ii) shows the red squirrel population timeseries when no grey squirrels are present, (iii) shows the red squirrel population timeseries when grey squirrels are present and (iv) shows the grey squirrel population timeseries (when red squirrels are present). The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

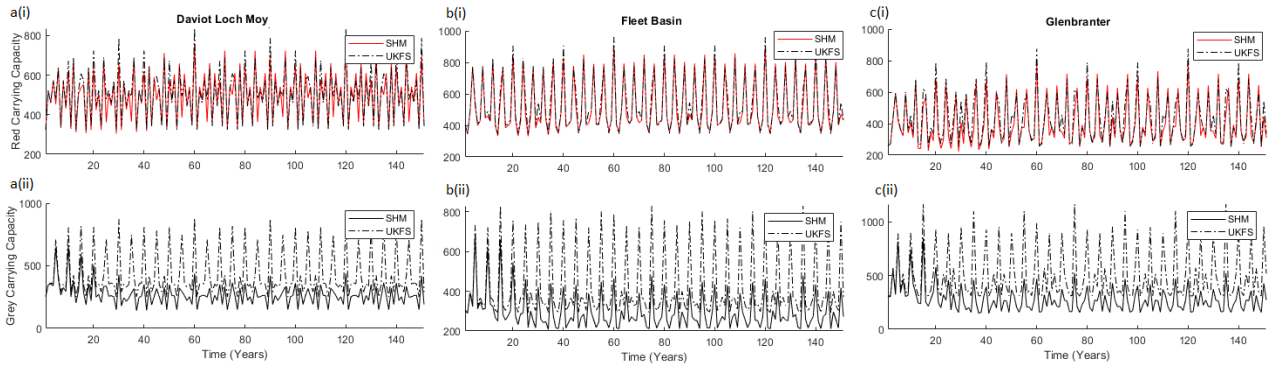


Figure S12: Changes in carrying capacity over the 150 year simulation for (i) red and (ii) grey squirrels at the (a) East2 Stronghold, (b) South2 Stronghold and (c) West2 Stronghold. Each image shows the capacity under the UK Forestry Standard (dashed line) and the Stronghold Management (solid line).

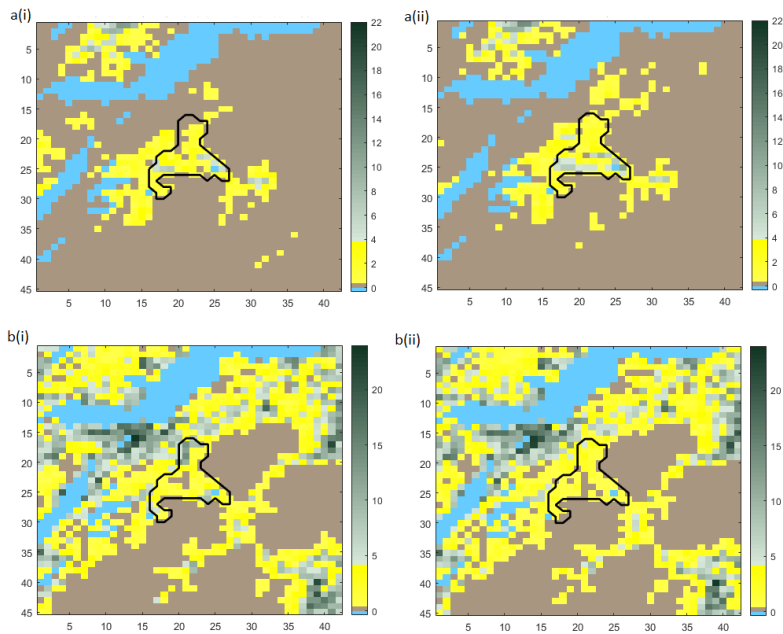


Figure S13: Population density (animals per gridsquare) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the East2 Stronghold at the end of the 150 year model simulation.

South2 Stronghold

The forest at the South2 Stronghold, located at Fleet Basin in south-west Dumfries and Galloway (Figure S1), complies with the UKFS but not with SM policy (Figure S14.a(i)). The SM policy reduces the amount of broadleaved trees from just over 5% to less than 5% (Figure S14.b(i)) and replaces them with favoured species. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure S12.b(i)) whereas the grey squirrel carrying capacity (Figure S12.b(ii)) is noticeably reduced.

There are currently grey squirrels resident in the landscape surrounding the South2 Stronghold. However, we initially examine a scenario where grey squirrels are absent. In the absence of grey squirrels the red squirrel population in the South2 Stronghold has an average population size of 280 individuals under UKFS and SM policy (Figure S14.a(ii) & b(ii)). The reduction in population size during the transition from UKFS to SM policy is small, with the population falling from 280 individuals to 260 individuals, due to only a small amount of broadleaved trees being removed.

Grey squirrels are present in the wider landscape in southern Scotland. To assess their impact on red squirrel viability we initialise the model with the observed distribution of red and grey squirrels. Under UKFS this leads to a long-term average of 45 red squirrels and 195 greys squirrels (Figure S14.a(iii) & b(iii)). Under SM policy the red squirrel population increases to a stable average population size of 105 individuals (Figure S14.a(iv)) and the grey squirrel population is reduced to an average of around 115 individuals (Figure S14.b(iv)). The population density and geographic spread of red and grey squirrels in the South2 Stronghold and the surrounding area under UK Forest Standard and Stronghold Management policy can be found in Figure S15. Thus the introduction of the SM policy would not significantly reduce the resident grey squirrel population due to the many access points into the stronghold for grey squirrels resident in the wider landscape. This means that the SM policy would be insufficient on its own to allow the red squirrel population to increase to a level that would be viable.

West2 Stronghold

The forest at the South2 Stronghold, located at Glenbranter in southern Argyll and Bute (Figure S1), complies with the UKFS but not with SM policy (Figure S16.a(i)). The SM policy reduces the amount of broadleaved trees from around 10% to less than 5% (Figure S16.b(i)) and replaces them with favoured species. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Figure S12.c(i)) whereas the grey squirrel carrying capacity (Figure S12.c(ii)) is noticeably reduced.

There are currently no grey squirrels in this stronghold, however they are resident in the wider landscape due to the strongholds proximity to the grey squirrel control boundary. In the absence of grey squirrels the red squirrel population in the West2 Stronghold has an average population size of 200 individuals under UKFS and SM policy (Figure S16.a(ii) & b(ii)). During the transition from UKFS to SM policy the red squirrel population falls to an average of 175 individuals, but recovers after the transition between forest management policies is completed.

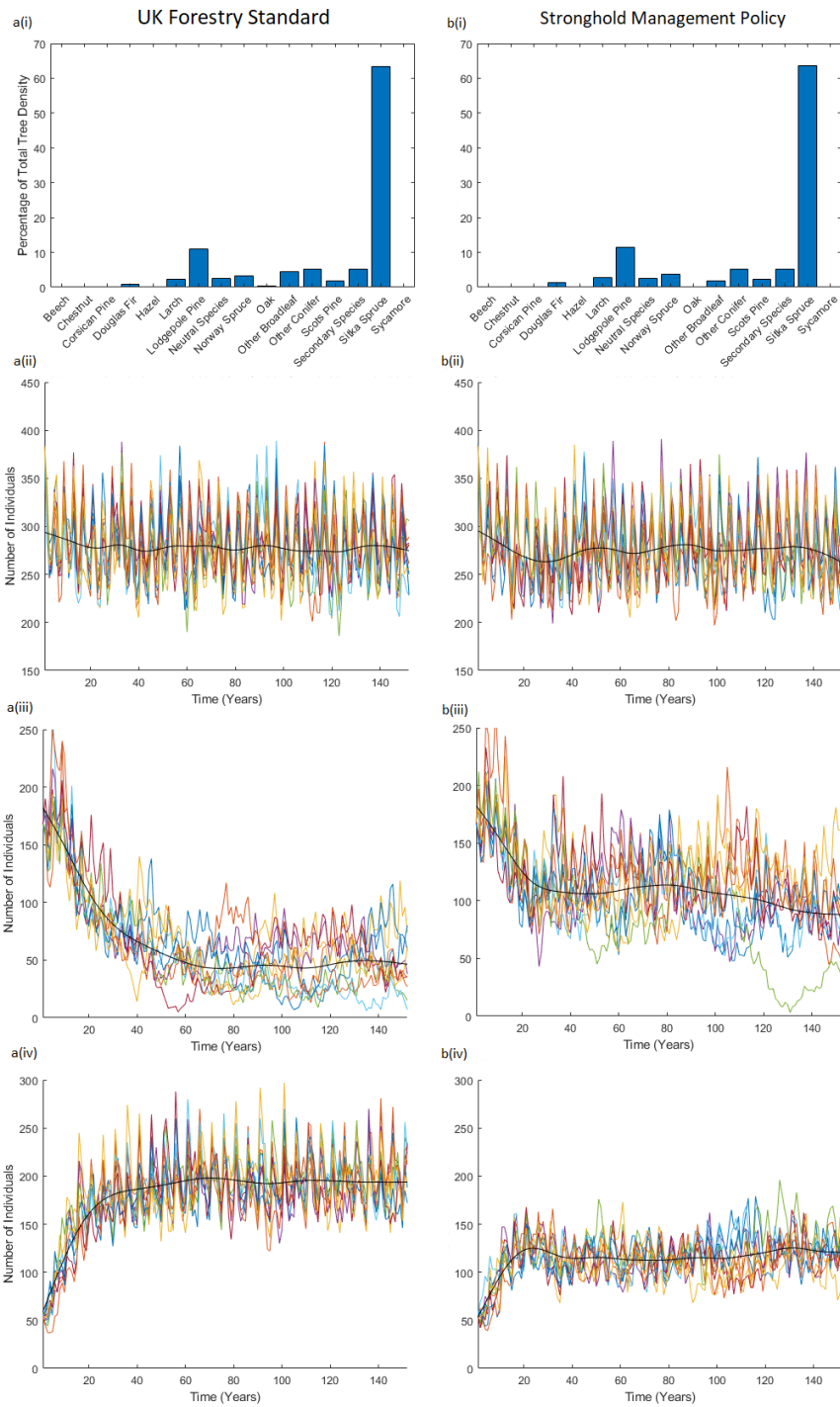


Figure S14: Results for the South2 Stronghold. Images a(i-iv) are the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition, (ii) shows the red squirrel population timeseries when no grey squirrels are present, (iii) shows the red squirrel population timeseries when grey squirrels are present and (iv) shows the grey squirrel population timeseries (when red squirrels are present). The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

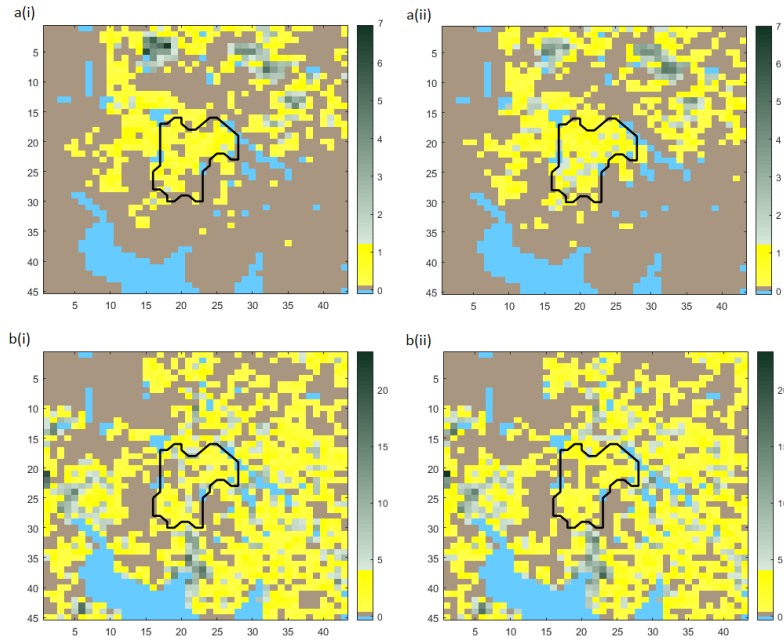


Figure S15: Population density (animals per gridsquare) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the South2 Stronghold at the end of the 150 year model simulation.

Grey squirrels are present in the wider landscape in southern Scotland. To assess their impact on red squirrel viability we initialise the model with the observed distribution of red and grey squirrels. Under UKFS this leads to a long-term average of 20 red squirrels and 205 greys squirrels (Figure S16.a(iii) & b(iii)), with some simulations seeing red squirrel extinction. Under SM policy the red squirrel population does not stabilise and continues its downwards trajectory at the end of the 150 year simulation (Figure S16.a(iv)). The population size at the end of the simulation is approximately 30 individuals which indicates that the introduction of the SM policy does not significantly increase the population size and as such extinction is still a strong possibility. The grey squirrel population is reduced to an average of around 100 individuals (Figure S16.b(iv)). The population density and geographic spread of red and grey squirrels in the West2 Stronghold and the surrounding area under UK Forest Standard and Stronghold Management policy can be found in Figure S17. Thus, similar to the Western Stronghold, the introduction of the SM policy and the changes to the forestry that this entails serves to reduce the resident grey squirrel population to just over half of its size under UKFS however this is insufficient to allow the red squirrel population to become viable and suggests that the West2 Stronghold is unsuitable as a red squirrel stronghold.

Comparison

The East2 Stronghold, located at Daviot Loch Moy, is similar to the Southern Stronghold at Eskdalemuir in that red squirrels are supported under UKFS and the implementation of the SM policy increases the resident red squirrel abundance and improves viability (Figures S11 & S13). The South2 Stronghold at Fleet Basin is similar to the Eastern Stronghold at Balmoral to Inver since red squirrels are vulnerable under UKFS but are viable under SM policy (Figures

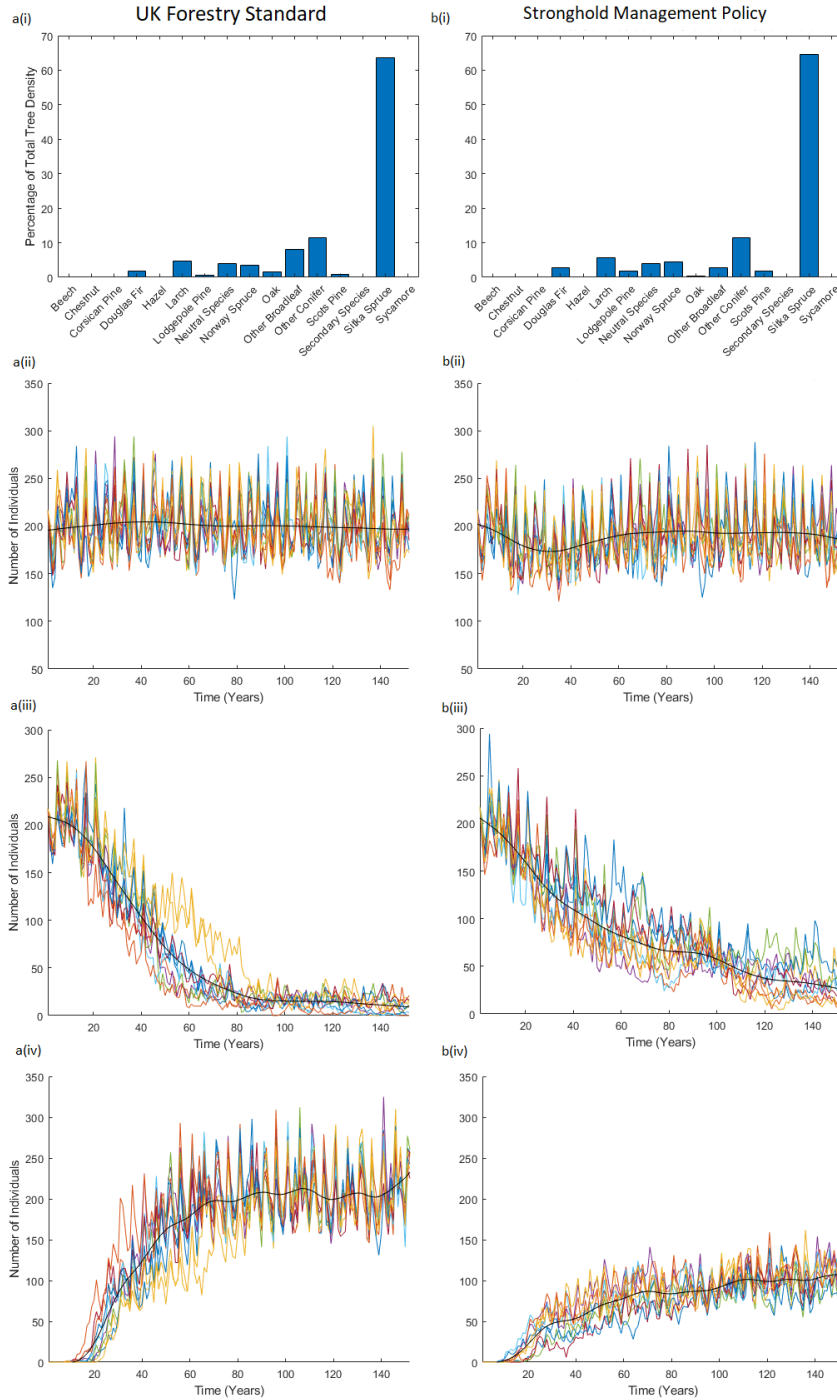


Figure S16: Results for the West2 Stronghold. Images a(i-iv) are the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition, (ii) shows the red squirrel population timeseries when no grey squirrels are present, (iii) shows the red squirrel population timeseries when grey squirrels are present and (iv) shows the grey squirrel population timeseries (when red squirrels are present). The results for the 10 model simulations are shown and the black lines indicate the average population trend for the 10 simulations.

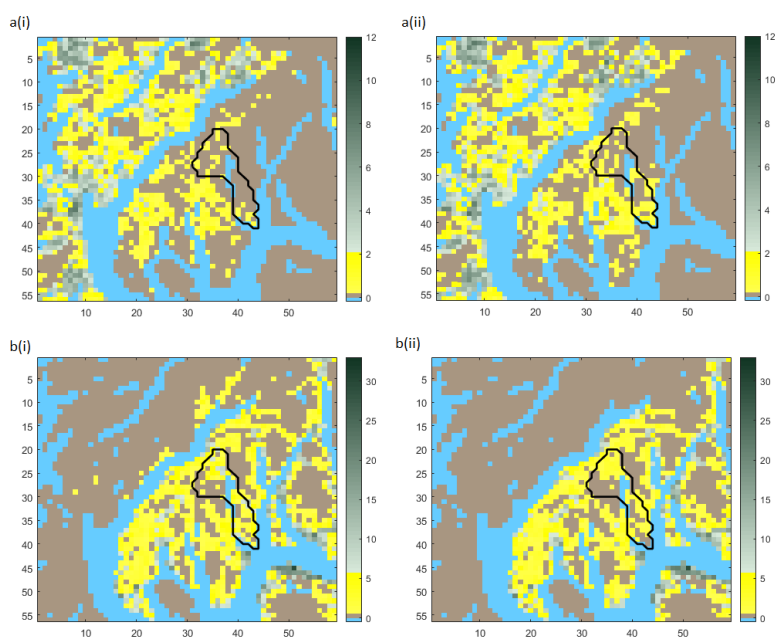


Figure S17: Population density (animals per gridsquare) for (a) red and (b) grey squirrels under (i) the UK Forestry Standard and (ii) the Stronghold Management strategies at the West2 Stronghold at the end of the 150 year model simulation.

S14 & S15). The West2 Stronghold at Glenbranter is similar to the Western Stronghold at Leanachan with the stronghold under both UKFS and SM policy being unable to support a viable red squirrel population, despite SM policy increasing red squirrel abundance compared to UKFS, and extinction being likely (Figures S16 & S17). From this we can state that access into the stronghold is a key feature of a successful red squirrel stronghold, with the Southern and East2 Strongholds having limited access points and a consequent ability to maintain a red squirrel population under UKFS. The western coast of Scotland appears to be unsuitable as red squirrel territory, as evidenced by the Western and West2 Strongholds both failing to support a red squirrel population under either UKFS or SM policy. The Eastern and South2 Strongholds are key candidates for the application of SM policy as red squirrels can reside in the strongholds under SM policy but not under UKFS.

References for Tree Species Carrying Capacities

The following outlines the references used for the carrying capacity associated with each tree species. Full references are to be found below the table.

Tree Species	References
Beech	Wauters et al. 2000, Münch 1998, Jones et al. 2017
Chestnut	Author's estimate
Hazel	Tonkin 1983, Holm 1990, Kenward et al. 1998, Magris 1998, Wauters et al. 1990
Sycamore	Authors' estimate
Oak	Tonkin 1983, Holm 1990, Kenward et al. 1998 Magris 1998, Wauters et al. 1990, Gurnell 1996
Other Broadleaf	Author's estimate based on combined data
Neutral Species	Not food plants for either species, do not support population in absence of other species
Secondary Species	Authors' estimate based on combined data
Larch	Halliwell 1997, Jones et al. 2016
Lodgepole Pine	Lurz et al. 1998, Lurz 2012
Scots Pine	Tittensor 1970, Moller 1986, Halliwell 1997, Cartmel 2000, Kenward et al. 1998, Smith 1999
Corsican Pine	Authors' estimate, Smith 1999
Douglas Fir	Jones et al. 2016
Norway Spruce	Halliwell 1997, Lurz et al. 1995, 1998, Cartmel 2000
Sitka Spruce	Lurz et al. 1995, 1998, Lurz 2012, Shuttleworth pers. comm.
Other Conifer	Authors' estimate based on combined data
Urban	Authors' estimate

Table S1: References for the link between tree species and squirrel carrying capacity.

- Cartmel, S. (2000). Squirrel ecology in a conifer forest in North Wales. PhD Thesis, Queen Mary and Westfield College, University of London
- Gurnell, J. (1996). The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology* 33: 325-338.
- Halliwell, E.C. (1997). The ecology of red squirrels in Scotland in relation to pine marten predation. PhD Thesis, University of Southampton.
- Holm, J. L. (1990). The ecology of Red Squirrels (*Sciurus vulgaris*), in deciduous woodland. PhD Thesis, Royal Holloway and Bedford New College, University of London.
- Jones, H.,A. White, P. Lurz, & C. Shuttleworth (2017). Mathematical models for invasive species management: Grey squirrel control on Anglesey. *Ecological Modelling* 359: 276-284.

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- Lurz, P. W. W., P. J. Garson & S. P. Rushton (1995). The ecology of squirrels in spruce dominated plantations: implications for forest management. *Forest Ecology & Management* 79: 79-90.
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- Magris, L. (1998). The ecology and conservation of the red squirrel (*Sciurus vulgaris*) on Jersey. PhD Thesis, Queen Mary and Westfield College, University of London.
- Münch, S. (1998). Eichhörnchen im Bergwald. PhD-Thesis Friedrich-Schiller University, Jena, Germany
- Smith, D. F. E. (1999). Grey squirrel, *Sciurus carolinensis*, population dynamics and feeding in a conifer forest. Ph. D. Thesis, University of London.
- Tittensor, A. M. (1970). The red squirrel (*Sciurus vulgaris*) in relation to its food resource. PhD Thesis, University of Edinburgh.
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- Wauters L. & Dhondt A. A. (1990) Red squirrel (*Sciurus vulgaris* Linnaeus, 1758) population dynamics in different habitats. *Zeitschrift für Säugetierkunde* 55:161-175
- Wauters, L.A., Lurz, P.W.W. & Gurnell, J. (2000). The interspecific effects of grey squirrels (*Sciurus carolinensis*) on the space use and population dynamics of red squirrels (*S. vulgaris*) in conifer plantations. *Ecological Research* 15: 271-284.

Description of Model Terms

The following is a written explanation of the model terms that appear in the manuscript.

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

Table S2: In addition to these terms it is assumed that the birth of squirrels occurs during the breeding season only (6 months, March-September) and that the maximum birth rate is reduced due to intra- and inter-specific competition between squirrels for resources. These equations underpin the stochastic model which represents changes to the abundance of the different classes of red and grey squirrels within 1km by 1km grid squares. In the stochastic model squirrels can undertake long distance dispersal to neighbouring grid squares within a 2km range.