Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Online first – 2020
OPEN ACCESS
Available online at:
http://www.italian-journal-of-mammalogy.it
doi:10.4404/hystrix-00351-2020

Research Article

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

Andrew SLADE[1,*], Andy WHITE[1], Kenny KORTLAND[2], Peter W.W. LURZ[3]

[1] *Maxwell Institute for Mathematical Sciences, Department of Mathematics, Heriot-Watt University, Edinburgh, UK*
[2] *Forestry and Land Scotland, 1 Highlander Way, Inverness Business Park, Inverness, UK*
[3] *Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Midlothian, UK*

Keywords:
mathematical modelling
conservation
forest management
red squirrels

Article history:
Received: 19 June 2020
Accepted: 03 November 2020

Acknowledgements
This work was funded by Forestry and Land Scotland, an executive agency of the Scottish Government responsible for managing the national forest estate.
Andrew Slade was supported by The Maxwell Institute Graduate School in Analysis and its Applications, a Centre for Doctoral Training funded by the UK Engineering and Physical Sciences Research Council (grant EP/L016508/01), the Scottish Funding Council, Heriot-Watt University and the University of Edinburgh.
The authors would like to thank Colin Edwards for valuable discussion and advice.

Abstract

A spatially explicit mathematical model was developed to assess the population viability of red squirrels (*Sciurus vulgaris*) in designated forest strongholds in Scotland under the implementation of two forest management policies: a specific Stronghold Management for red squirrel conservation (SM) compared to the multi-purpose UK Forestry Standard (UKFS) for sustainable forest management. The study showed that, in the presence of grey squirrels (*Sciurus carolinensis*), the SM policy provides an advantage to red squirrels over grey squirrels when compared to the UKFS, and its implementation supports red squirrel conservation efforts. When grey squirrels are not present, there is no discernible benefit in the SM policy compared to the UKFS. The model results therefore indicate that species-specific forest management for red squirrel conservation in the absence of sympatric grey squirrels would not be required. This would allow less prescriptive forest management options that maintain viable red squirrel populations to be explored. The study also identified forest regions that, due to their composition, are capable of sustaining a viable red squirrel population, in the presence of grey squirrels, without the application of specific forest management policy. They can be considered 'natural strongholds'. Selecting such natural strongholds may afford more flexibility to conserve red squirrel populations whilst simultaneously delivering other multi-species conservation and forest management objectives. We review our findings in terms of criteria that were used in the original stronghold designation in Scotland and discuss how our work can be used to inform a forthcoming review of stronghold management policy by Scottish Forestry. Furthermore, the findings can inform red squirrel conservation strategies in other regions and the modelling techniques can be adapted to a wide range of conservation settings.

Introduction

Multi-objective forests are managed to meet a range of aims in addition to wood production. These include the long-term sustainability of the forest as well as the maintenance of species diversity (Dieler et al., 2017; Chaudhary et al., 2016). For this to be successful it will require the integration of wildlife conservation policy with other objectives of forest management (Reid, 2018; Bengtsson et al., 2000). Changes to forest composition once set in motion, can take decades to be completed. It is therefore critical to assess the potential impacts of forest compositional management plans on species viability prior to large-scale implementation.

Mathematical models can be used to explore the suitability of potential habitat-management strategies. Model results can help inform policies that combine commercial and conservation interests. Models can combine accurate habitat information, such as satellite-derived land-cover information and data on a species' ecology obtained from field studies, with dynamic modelling approaches to predict population change over time. They have successfully been used to assess the impact of habitat change in species conservation and applications consist of different modelling frameworks that cover a range of organisms and purposes. For example, Watkins et al. (2015) used an agent-based model to explore the interaction of jaguar (*Panthera onca*) and their landscape, Heikkinen et al. (2015) used a spatially-explicit population dynamics model to simulate the potential success of the translocation of specialist grassland butterfly (*Maniola jurtina*) and Broome et al. (2014) combined a statistical linear mixed effects model with forest yield models to evaluate the effect of forest thinning on capercaillie (*Tetrao urogallus*).

A group of species suited for mathematical modelling approaches are tree squirrels such as the Eurasian red squirrel (*Sciurus vulgaris*), since its forest habitat can easily be mapped and its ecology is well understood (Bertolino et al., 2020). Red Squirrels are under threat in the United Kingdom, Ireland and northern Italy and recent estimates for the UK (Mathews et al., 2018) indicate that just over 80% of the remaining populations are now thought to live exclusively in Scotland. The rest survive in isolated forests or offshore islands in England and Wales (Mathews et al., 2018). The decline of red squirrel populations has arisen due to the spread and competition with the North American grey squirrel. In the British Isles the grey squirrel was introduced in the 19th century and translocated from Britain to Ireland (Middleton, 1930); whereas the Italian populations stem from separate 20th century introductions (e.g. see overview by Martinoli et al., 2010). The competitive interactions between the two species can lead to stress in red squirrels, reduced body size and fecundity, as well as measurable reductions in local juvenile recruitment rates (Santicchia et al., 2018; Bertolino et al., 2014; Gurnell et al., 2004; Wauters et al., 2002).

In the UK, survival of red squirrel populations in the presence of grey squirrels has been longest in large, conifer-dominated forests and decline and their disappearance fastest in deciduous woodlands (e.g. Bosch and Lurz, 2012; Bryce et al., 2002). In their native range, grey squirrels inhabit the deciduous woodlands of eastern North America with highest densities in forests containing oak, hickory and walnut (Koprowsky, 1994). This specialisation on deciduous habitats and their

*Corresponding author
Email address: as316@hw.ac.uk (Andrew SLADE)

types of tree seeds is thought to be key in the ability of grey squirrels to cope with phytotoxic polyphenols in acorns. While red squirrels do feed on acorns, their digestive efficiency of acorns is only 59% compared to grey squirrels, giving the latter a food refuge and coupled with their high densities a decisive, competitive advantage in deciduous-dominated forest landscapes (Kenward and Holm, 1993).

But that is not the whole story. In contrast with Italy, the populations in the British Isles have also had to contend with the squirrelpox virus (SQPV). The virus is endemic but harmless in greys, yet lethal to red squirrels with observed mortality rates of >80% (Chantrey et al., 2014). This has resulted in disease-mediated competition between red and grey squirrels that significantly increases the speed of replacement of red by grey squirrels (Rushton et al., 2006; Tompkins et al., 2003).

Current UK efforts to aid the conservation of the red squirrel therefore encompass the different aspects of the competitive interactions. They include (i) targeted grey squirrel control (Gill, 2019) to reduce disease transmission and regional spread (e.g. see Highland Boundary Line, Saving Scotland's Red Squirrels, 2010), (ii) research on the development of contraceptives that would be applied to grey squirrels (e.g. Nichols and Gill, 2016; Yoder et al., 2011), as well as (iii) the designation and management of "stronghold" forests (see Figure S1) that are intended to provide refuge for red squirrels against the incursion of, and competition by grey squirrels (Forestry Commission Scotland, 2012).

The use of mathematical models to help inform conservation efforts for red squirrels has evolved and developed over time. The early model frameworks considered competitive interactions between red and grey squirrels (Okubo et al., 1989), but the model results could not match the rate of replacement of red squirrels observed in England and Wales. Rushton et al. (2000) and Tompkins et al. (2003) adapted the competition models to additionally focus on the role of squirrelpox (SQPV). Their model results highlighted the critical role of disease in the replacement of red squirrels, an aspect that up to then had been underestimated in its impact and scale (Rushton et al., 2006). The model frameworks were further developed to help inform evolving conservation priorities. White et al. (2016) showed that applied grey squirrel control methods in the Borders region of England and Scotland were insufficient to prevent the northward spread of squirrelpox due to multiple and complex dispersal routes for disease spread and insufficient available resources for disease management. This led to a shift in Scottish conservation policy from disease control at the landscape level in southern Scotland to protecting priority red squirrel populations in the region (Anonymous, 2015). Jones et al. (2017) used a 16-year field data set on grey squirrel control to parameterise and validate a model framework that was used to inform the best strategy to protect red squirrels on the Island of Anglesey from grey squirrel re-invasion. Jones et al. (2016) used a model of red squirrel dynamics to assess differing forest design plan scenarios at the local forest scale to ensure continued red squirrel population viability in the Kidland-Uswayford Forest System, Northern England. Following the research, a renewed monitoring programme based on feeding signs was set up in the forest in 2017 and red squirrel presence is monitored annually (Lurz and Gough, 2018). These studies highlight how mathematical modelling has had an impact on a range of red squirrel conservation initiatives. Our paper extends these previous model frameworks in order to inform national forest management policy options for red squirrel conservation areas (termed strongholds) in Scotland. We assess the potential impacts of two different forest management policies, namely, the stronghold management policy and the UK Forestry Standard policy, on red squirrel population viability both in the presence and the absence of grey squirrels.

The stronghold forest management policy (SM) provides species specific recommendations on forest management for red squirrels (Forestry Commission Scotland, 2012)). Based on research findings with respect to red-grey squirrel interactions, it makes recommendations on tree species composition and age structure to prevent or reduce grey squirrel competition. In contrast, the UK Forestry Standard policy (Forestry Commission, 2017a) has wider economic, environmental and social objectives. It provides recommendations for tree species composition and age structure to preserve and enhance biodiversity and sets guidelines for sustainable forest management.

In collaboration with Forestry and Land Scotland, the government agency managing national forests, our principal aim was to assess red squirrel population viability, here defined as 125 individuals in a connected forest (Scottish Natural Heritage, *pers. comm.*), in designated strongholds under the SM policy (Forestry Commission Scotland, 2012) compared to the UK Forestry Standard. A further aim was to outline general guidance on what determines a suitable stronghold (protected area) for red squirrels. Forestry and Land Scotland (who advise on national policy for forest management) are about to embark on a review of red squirrel strongholds and the presented findings are intended to underpin this review. The methods and findings presented here are not specific to the Scottish system. They compare two different forest management policies that stipulate general rules for tree species composition which we apply to our mathematical model. Hence, they can be used to inform red squirrel conservation strategies for other regions where red squirrel are under threat. Hence, this paper provides an important case study of how mathematical models can assist forest-management practice and future planning to help protect endangered species, with the techniques being adaptable to a wide range of conservation settings.

Materials and methods

In this study we will use mathematical modelling to assess the viability of red squirrels under two forest management policies: UK Forestry Standard policy (UKFS) (Forestry Commission, 2017a) and Stronghold Management policy (SM) (Forestry Commission Scotland, 2012).

UK Forestry Standard

The UK Forestry Standard (Forestry Commission, 2017a), the UK standard guidance on sustainable forest management, stipulates that there should be a maximum of 75% of a single tree species present in a forest, there should be a minimum of 10% of other tree species along with a minimum 5% broadleaved trees and shrub. The remaining land should constitute either open ground or ground managed for conservation and enhancement of biodiversity. Alongside this, diversification should be pursued if possible. Note that the UKFS is defined as sustainable forest management in the Forestry and Land Management (Scotland) Act 2018.

Stronghold Management Policy

When the stronghold policy was developed it was assumed that grey squirrel expansion would continue into northern Scotland and eventually threaten the existence of red squirrels in Scotland. Consequently, 19 stronghold areas were proposed, based on the work by Poulsom (2005) and other stakeholders, with the intention of creating red squirrel safe havens in order to safeguard the population against incursion by grey squirrels. The main recommendations were that potential stronghold areas should be large (>20 km^2), defendable, not under immediate threat from grey squirrels, geographically representative of the then red squirrel distribution, and that the area of semi-natural or ancient woodland within the stronghold and in the area around it should be compatible with red squirrel management objectives (e.g. see Forestry Commission Scotland, 2012).

The Scottish Stronghold Management policy (Forestry Commission Scotland, 2012)) outlines forest management guidelines and stipulates that (if necessary) the forest composition inside strongholds should be altered incrementally over a period of roughly 30 years. It suggests that (i) a maximum of 5% of tree density is comprised of large-seeded broadleaved trees (discouraged trees, Tab. 1), and (ii) that the trees that are removed during normal forest operations should be replaced by coniferous trees (favoured trees, Tab. 1) that ideally provide a habitat advantage to red squirrels.

Whilst coniferous tree species support lower densities of both squirrel species, they can provide a competitive advantage to red squirrels due to low grey densities. Large-seeded broadleaved trees do provide a plentiful food supply that can maintain higher population densities of both squirrel species compared to coniferous trees, but they give a selective advantage to grey squirrels (Kenward and Holm, 1993; Wauters et al., 2002).

Seed mast intervals with good and bad seed years differ between conifer species, thus conifer species diversity reduces the likelihood of cone crop failures. The SM policy therefore also encourages the diversification of coniferous tree species to ensure a dependable tree seed supply, with no single non-native species constituting more than 80% of the forest. Local, native deciduous woodland should be diversified using native small-seeded tree species that do not provide grey squirrels with a competitive advantage over red squirrels. Forestry management should also aim to create an age structure that has ideally less than one third of trees be classed as young (not of seed bearing age) and the other two-thirds or more consisting of thicket and mature trees, as this would ensure that there is always some forest habitat that can support red squirrels since, on average, it takes more than 25 years for trees to regularly seed (Hibberd, 1991).

In this study, we do not consider the impact of SM policy on wider forest biodiversity, though we accept that the SM policy will have a negative impact that would need to be assessed if the SM policy were to be taken forward and implemented across Scotland. The results presented therefore provide a comparative assessment of the two management policies and allow us to test scenarios that would not be possible in field studies (such as the impact of introducing grey squirrels where they are currently absent). This study also does not consider the impact of climate change on forest composition. Climate driven compositional changes could distort the impact of the forest management policy which would render any comparison unreliable. Hence, the results should not be viewed as predictive with regards to exact squirrel densities and competitive outcomes in a specific location (which would require detailed information on the forest management techniques such the silviculture system or felling practice).

Study Area

Strongholds are defined by Scottish Forestry as "large areas of coniferous and mixed forest identified as having the potential to sustain resilient and healthy populations of red squirrels … over the long-term" (Forestry Commission Scotland, 2012). There are currently 19 stronghold regions throughout Scotland (Figure S1).

We consider three strongholds in this study (results for a further three are presented in the supplementary information), one in north-east Scotland, one in north-west Scotland and one in south Scotland. These strongholds are chosen as they encompass the different geographic regions, habitat structure and threats from grey squirrel invasion found in Scotland. Habitat in the west of Scotland is predominantly comprised of Sitka Spruce, whereas eastern habitats tend to be drier and more predominated by pine trees. The north of Scotland is currently free of grey squirrels whilst the south of Scotland has had a resident grey squirrel population for several decades.

The Eastern Stronghold is approximately 89 km^2, is located on the Balmoral Estate in the Cairngorms National Park and is mainly threatened by grey squirrels migrating west from Aberdeen. The Western Stronghold encompasses approximately 63 km^{2}in the FLS West Region to the east of Fort William on the western coast of Scotland. Neither of these strongholds currently have resident grey squirrels. Habitat in the south of Scotland (south of the Central Belt of Edinburgh and Glasgow) does have grey squirrels present. The Southern Stronghold encompasses approximately 180 km^{2}of the western section of the Eskdalemuir forest, which is located in south east Dumfries and Galloway. All three strongholds are predominated by conifers, primarily Sitka spruce in the west along with Scots pine, Larch, Lodgepole pine and Norway spruce but also contain broadleaved trees at levels that exceed those recommended under the current Stronghold Management policy. All three stronghold have a resident red squirrel population. Note, the strongholds considered in this study all comply with UKFS but do not comply with SM policy.

Determining Habitat Composition

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. The data was used to create a map consisting of a 1 km^{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 age structure of a forest cannot be accurately included in a 1 km^2 scale model. Instead, it is assumed that a proportion of each tree species is not mature and so does not provide resources for squirrels (given by the age of maturity divided by the expected lifetime of the species, Tab. 1). The proportion of each tree species in a given grid square can be altered incrementally to simulate the felling and replanting needed to allow the region to comply with SM policy. In this case study we impose the condition that all transitions to SM forest management occur incrementally over 30 years. In particular, the proportion of each tree species that needs to be replaced in order for a stronghold to comply with SM policy is calculated and 1/30$^{\text{th}}$ of this amount is removed every year.

The removed trees are replaced by favoured coniferous tree species, with the specific species of conifer being chosen to increase tree diversity in the stronghold. Trees that are replanted do not provide a resource for squirrels until they have matured (Tab. 1).

Determining the Carrying Capacity for Red and Grey Squirrels

The link between squirrel density, habitat and tree seed crops is well evidenced (e.g. Lurz et al., 2000; Gurnell, 1987, 1983 See also Table S1). 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 forest compositional changes and 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 (Tab. 1) (Bosch and Lurz, 2012; Gurnell, 1987). 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 Tab. 1). 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 Tab. 1, to account for tree felling, replanting and maturity changes as well as seed crop dynamics, which allowed the forests carrying capacity dynamics to be incorporated into the model. The seed crop dynamics lead to large temporal changes in carrying capacity (see Fig. 2).

Mathematical Model

The mathematical model used here is based on previous models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches (Tompkins et al., 2003) to develop a spatial, stochastic model (Jones et al., 2016; White et al., 2016, 2014). The deterministic approach underpinning the model (see equations 1 and 2) allows the key population processes to be defined and understood. However, deterministic models do not include the randomness and variability that is exhibited by real systems. We develop a stochastic version of the deterministic model, in which the probability of birth, death, infection, recovery and dispersal of individuals is used to determine the population dynamics. Hence, the stochastic model includes the variability seen in real systems and provides essential realism when squirrel numbers become low which gives a better representation of population extinction and the fade-out of infection. The underlying deterministic system, which assumes the existence of a shared disease, represents the dynamics of red squirrels who are susceptible (S_R) to the disease and those that are already infected (I_R) by the disease. The model also includes susceptible (S_G) and infected (I_G) grey squirrels as well as grey squirrels that have recovered (R_G) from the disease. The model we use is:

$$\begin{aligned}
\frac{dS_G}{dt} &= A_G(t) - bS_G - \beta S_G\,(I_R + I_G)\\
\frac{dI_G}{dt} &= \beta S_G\,(I_R + I_G) - bI_G - \gamma I_G\\
\frac{dR_G}{dt} &= \gamma I_G - bR_G\\
\frac{dS_R}{dt} &= A_R\,(t) - bS_R - \beta S_R\,(I_R + I_G)\\
\frac{dI_R}{dt} &= \beta S_R\,(I_R + I_G) - bI_R - \alpha I_R
\end{aligned} \tag{1}$$

where

$$A_G(t) = \begin{cases} (a_G - q_G(H_G + c_R H_R))H_G & 0 \leqslant t < 0.5 \\ 0 & 0.5 \leqslant t < 1 \end{cases} \tag{2}$$

Here, $A_G(t)$ represents the periodic birth rate of grey squirrels which assumes births occur for only half of the year (between March and September each year, representing observed peak litter periods and periods with no breeding activity). The term for $A_R(t)$ is equivalent to $A_G(t)$ with the subscripts for R and G interchanged. Note, $H_R = S_R + I_R$ and $H_G = S_G + I_G + R_G$ represent the total populations for red and grey squirrels respectively. The natural rate of adult mortality $b = 0.9$ (Barkalow et al., 1970) is the same for both red and grey squirrels but the rates of maximum reproduction differ with red squirrel birth rate $a_R = 3$ and grey squirrel birth rate $a_G = 3.4$ (Tompkins et al., 2003). The competitive effect of grey squirrels on red squirrels is denoted by $c_G = 1.65$, whilst that of red squirrels on grey squirrels is denoted by $c_R = 0.61$ (Bryce et al., 2002). Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient $\beta = 1.1$ (White and Lurz, 2018). Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ (Tompkins et al., 2003). The susceptibilities to crowding (q_R, q_G) are set to ensure the average density over one year is equal to the carrying capacity in each grid square for that year, with the carrying capacity being taken from the values derived in the section above. All parameter values assume an annual timescale. We provide a description of the model in terms of birth, death, infection, recovery and dispersal rates in the supplementary information (see Table S2). To generate the stochastic model (Tab. 2), the rates in the deterministic model are converted into probabilities of events that account for changes in individual patch level abundance (Renshaw, 1993).

Model Initialisation

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), see Figure S2. In regions where only one squirrel species was observed the model was initialised at the respective carrying capacity for that grid-square, based

Table 1 – Red and grey squirrel carrying capacity (CC) per km^2 for mast and non-mast years, the mast interval (Mast Int, years), seed bearing age (SBA, years), age at felling or average age (AF, years) and seed-bearing proportion (SBP). Favourable trees are those deemed to provide red squirrels with a competitive advantage over grey squirrels. Discouraged trees are large-seeded broadleaved trees that are favourable to grey squirrels. Other Broadleaf and Other Conifer refer to National Forest Inventory data which does not specify individual tree species. The values for these species are calculated as the average of the other broadleaf or conifer trees respectively. The Seed Bearing Age (SBA) is the age at which the trees start producing seeds, AF denotes either the age at which the trees are felled commercially or their average age whilst SBP refers to the Seed Bearing Proportion which is the proportion of a trees life that is seed bearing, which is found using the equation SBP=(AF-SBA)/AF with AF and SBA defined as above. Given the lack of information regarding the age structure of the forest, we use SBP as a proxy for the proportion of trees of a given species that are seed bearing. Neutral species do not contribute to the carrying capacity for red or grey squirrels, hence the data is not included. Secondary species are trees and bushes that provide no benefit to one squirrel species over the other and have thus been grouped together. SBA and Mast Int. data is from (Aldhous, 1972) and AF data comes from (Savill, 2013). References for species CC can be found in the supp. info. Where data for non-mast year carrying capacities was available in the literature for specific tree species these have been used; where they were not available, they have been conservatively set at being one quarter of the mast values (denoted by *). 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 CC		**Grey Squirrel CC**					
	Mast	**Non-Mast**	**Mast**	**Non-Mast**	**Mast Int**	**SBA**	**AF**	**SBP**
Favoured								
Larch	38	21	38	10*	4	15	47	0.68
Lodgepole Pine	21	5*	8	2*	2	15	50	0.7
Scots Pine	83	33	31	8*	2	15	55	0.73
Corsican Pine	110	28*	110	28*	3	25	50	0.5
Douglas-Fir	21	5*	8	2*	5	30	60	0.5
Norway Spruce	58	25	33	8*	4	30	65	0.54
Sitka Spruce	20	2	0	0	4	30	50	0.4
Discouraged								
Beech	110	28*	149	37*	7	50	100	0.5
Chestnut	100	25*	340	85*	4	40	100	0.6
Hazel	85	85	200	200	1	1	N/A	1
Sycamore	0	0	149	10	2	25	70	0.65
Oak	100	25*	340	85*	4	40	100	0.6
Other								
Other Broadleaf	78	19	245	61	5	30	80	0.63
Other Conifer	40	15	20	5	3	25	50	0.5
Neutral Species	0	0	0	0	N/A	N/A	N/A	N/A
Secondary Species	10	2	10	2	1	1	N/A	1
Urban	19	8	40	11	N/A	N/A	N/A	N/A

* non-mast carrying capacity data not available, used $\frac{1}{4}$ mast value.

Table 2 – Stochastic model events that govern the dynamics that occur within each 1 km grid square. The parameters representing control and dispersal were fitted with observed data on the Island of Anglesey (Jones et al., 2017). The events are assumed to be exponentially distributed with the time between events given by $dt = -ln(z)/R$ where z is a uniform random number between 0 and 1 and $R = \Sigma$[rates] (the sum of all thenumerators in the probability of events column). 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 as well as from the 8 neighbouring grid cells due to daily movement within a core range of radius, θ=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 2 km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). Further details of the model framework and the calculation of parameter values can be found in (Jones et al., 2017).

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

on available habitat types. In regions where both squirrel species were observed the model was initialised with red and grey squirrel densities at half their respective potential carrying capacities. Once initialised, the model was run for 10 years in order to allow for changes in density in grid-squares and for squirrels to expand into nearby available habitat.

In total we present results for four different scenarios for each stronghold. The first two scenarios outline the red squirrel dynamics, in the absence of grey squirrels, under UKFS and then SM policy. The remaining two scenarios detail both red and grey squirrel population dynamics under UKFS and SM policy, with both squirrel species being present at the start of the simulations. This stipulation will later be relaxed and we will consider scenarios where grey squirrels are introduced after 50 years in the model simulation in order to simulate the scenario where grey squirrels colonise during the transition from UKFS to SM policy. To generate results each scenario was simulated 10 times, with each simulation of the model being run for 150 years to ensure that enough time was allowed for forest management plans to be implemented and their effects to be fully realised. The UKFS results were gained by maintaining the initial forest composition for the 150-year simulations. SM policy simulations actively altered forest composition, as described in the previous sections, for each simulation. For each scenario we show results for each of the 10 simulations and this gives an indication of the variability between each model realisation. We also show the average of the 10 simulations in order to give a representative trend in population density for each scenario.

Note, in the stronghold regions we examine in this paper grey squirrel densities were not large enough to support an endemic infected population. Consequently, squirrelpox does not play a role in determining red and grey squirrel population dynamics in our study regions and so is not a factor in the results presented below. Evidence supporting this choice is presented at the end of the results section (and see S10).

Results

Eastern Stronghold

The tree species distribution at the Eastern Stronghold (Figure S1) complies with the UKFS but not with SM policy (Fig. 1.a(i)). The application of the SM policy would reduce the proportion of broadleaved trees present from around 18% to less than 5% (Fig. 1.b(i)) and replaces them with favoured species, primarily larch, lodgepole pine and Sitka spruce. The changes to the forest composition do not significantly alter the red squirrel carrying capacity (Fig. 2.a(i)) whereas the grey squirrel carrying capacity (Fig. 2.a(ii)) is noticeably reduced.

Currently, there are no grey squirrels in the region of the Eastern Stronghold (see Figure S2). In the absence of grey squirrels, the red squirrel population in the Eastern Stronghold is stable when the forest complies with UKFS, with an average size of 315 individuals (Fig. 1.a(ii)), which equates to approximately 3.5 red squirrels per km^2. Under the SM policy the red squirrel population initially falls to an average of 290 individuals (3.3 individuals per km^2) during the transition from the UKFS to the SM, which takes 30 years to complete. The reduction occurs as a result of the forest restructuring to comply with the SM policy and the concomitant lag in carrying capacity until planted trees reach coning age. Consequently, red squirrel density begins to recover once the replanted trees start to reach maturity (after 15 years in this study). The population size recovers in the long term to an average of 315 individuals (Fig. 1.b(ii)).

Although grey squirrels are not currently a threat to red squirrels at this stronghold, the rationale of the SM policy is to provide a safe haven for red squirrels should they be threatened by greys. We therefore examine the viability of red squirrels when grey squirrels are introduced to locations adjacent to the stronghold (Figure S3). Under UKFS the red squirrel population abundance collapses from its initial value (315) to an average of 20 individuals (Fig. 1.a(iii)), which is an average of 0.2 individuals per km^2. This population level is likely to be too small to be viable and long-term population extinction would be expected (and occurs in some model realisations). The grey squirrel population under the UKFS grows to a stable average of 340 individuals (3.8 ind. per km^2) (Fig. 1.a(iv)). When the SM policy is implemented the red squirrel population initially falls to an average of 160 individuals (1.8 ind. per km^2) during the transition from UKFS to SM policy but recovers in the long term to an average of 215 individuals (2.4 ind. per km^2) which we assume is large enough to be viable (Fig. 1.b(iii)). The grey squirrel population under SM (Fig. 1.b(iv)) initially grows to an average of 135 (1.5 ind. per km^2) but is reduced to an average of 70 individuals (0.8 ind. per km^2) once the SM policy changes have been fully implemented. The population density and geographic spread of red and grey squirrels in the Eastern Stronghold and the surrounding area under UK Forestry Standard and Stronghold Management policy can be found in Figure S5. Thus, the introduction of the SM policy and the linked changes to the forestry that this entails serves to reduce the grey squirrel population in the stronghold and allow the red squirrel population to survive and be more viable.

Western Stronghold

The forest at the Western Stronghold (Figure S1) complies with the UKFS but not with SM policy (Fig. 3.a(i)). The application of the SM policy reduces the proportion of broadleaved trees present from around 14% to less than 5% (Fig. 3.b(i)) and replaces them with favoured species, primarily Norway spruce and Scots pine. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Fig. 2.b(i)) whereas the grey squirrel carrying capacity (Fig. 2.b(ii)) is noticeably reduced.

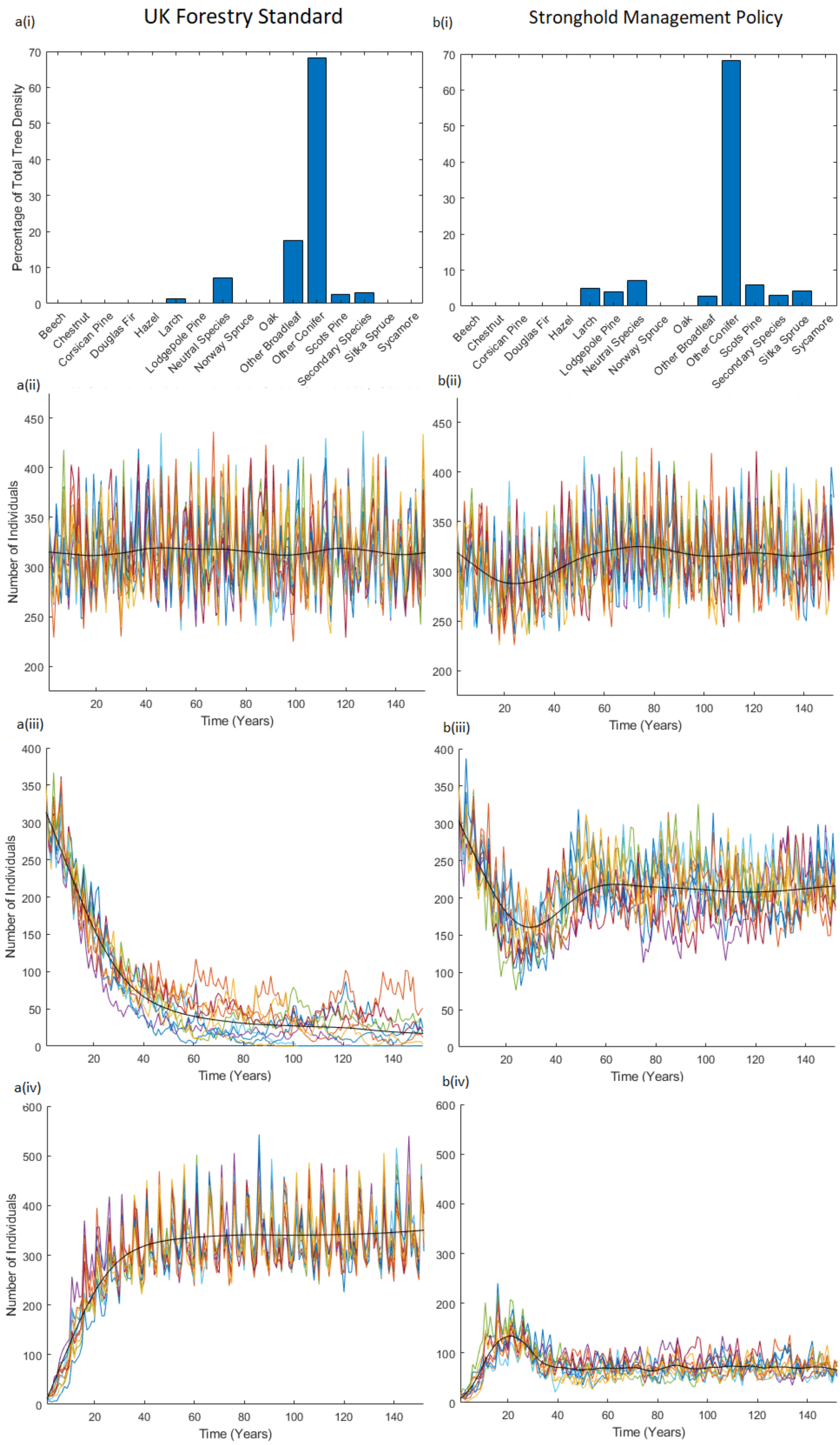

Figure 1 – Results for the Eastern Stronghold. Images a(i-iv) illustrate the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition (after SM policy has been implemented in (b)), (ii) shows the red squirrel population 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 realisations are shown and the darker lines indicate the average population trend for the 10 realisations.

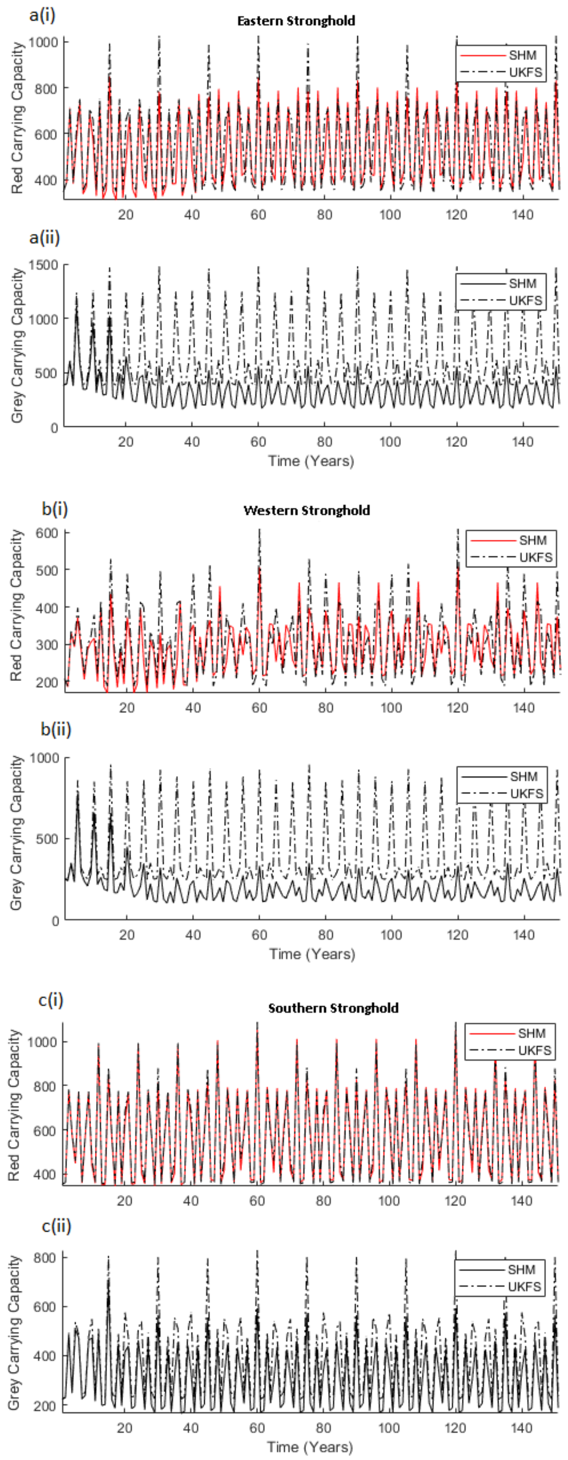

Figure 2 – Changes in carrying capacity over the 150-year simulation for (i) red and (ii) grey squirrels at (a) the Eastern Stronghold, (b) the Western Stronghold and (c) the Southern Stronghold. Each image shows the capacity under the UK Forestry Standard (dashed line) and the Stronghold Management (solid line).

Currently, there are no grey squirrels in the region of the Western Stronghold (see Figure S2). In the absence of grey squirrels the red squirrel population under UKFS is stable with an average size of 170 individuals (2.7 ind. per km^2) (Fig. 3.a(ii)), whereas under the SM policy the red squirrel population initially falls to an average of 150 individuals (2.4 ind. per km^2) during the transition from the UKFS to the SM but the population size recovers in the long term to an average of 175 individuals (2.8 ind. per km^2) (Figure 3.b(ii)). It is interesting to note that, even in the absence of grey squirrels, the red squirrel population is relatively small, due to the small stronghold area, and potentially vulnerable to extinction even after the SM policy is implemented.

Grey squirrels are not currently a threat to red squirrels at this stronghold — but as with the Eastern Stronghold we examine impact on red squirrel viability of grey squirrels. When grey squirrels are introduced into regions adjacent to the stronghold (Figure S4) the red squirrel population under UKFS collapses to an average of 5 individuals (>0.1 ind. per km^2) (Fig. 3.a(iii)) with population extinction in some model simulations. The grey squirrel population under the UKFS grows to a stable average of 230 individuals (3.7 ind. per km^2) (Fig. 3.a(iv)). When the SM policy is implemented the red squirrel population undergoes a similar dynamic as under UKFS, with the population collapsing during the first 20 years of simulation. The average population size under SM policy is 20 individuals (0.3 ind. per km^2) (Fig. 3.b(iii)), and again extinction occurs in some model simulations. The long-term grey squirrel population abundance under SM is 120 individuals (1.9 ind. per km^2) (Fig. 3.b(iv)). The population density and geographic spread of red and grey squirrels in the Western Stronghold and the surrounding area under UK Forestry Standard and Stronghold Management policy can be found in Figure S6. Thus, the introduction of the SM policy and the changes to the forestry that this entails would serve to reduce the resident grey squirrel population to just over half of its size under UKFS. However, despite red squirrel abundance being four times as large under SM policy than UKFS, the implementation of SM policy is insufficient to allow the red squirrel population to become viable. This suggests that the forest composition at the Western Stronghold is unsuitable as a red squirrel stronghold.

Southern Stronghold

The forest at the Southern Stronghold (Figure S1) complies with the UKFS but not with SM policy (Fig. 4.a(i)). The SM policy reduces the proportion of broadleaved trees from just over 5% to less than 5% (Fig. 4.b(i)) and replaces them with favoured species, primarily Scots pine, larch and Lodgepole pine. The changes to the forest composition do not appear to significantly alter the red squirrel carrying capacity (Fig. 2.c(i)) and leads to a minor reduction in grey squirrel carrying capacity (Fig. 2.c(ii)).

There are currently grey squirrels present in the Southern Stronghold (see Figure S2). In order to allow a better comparison between the three strongholds outlined in this paper the Southern Stronghold was initially simulated without grey squirrels being present. In the absence of grey squirrels, the red squirrel population in the Southern Stronghold has an average population size of 280 individuals (1.6 ind. per km^2) under UKFS and SM policy (Figure 4.a(ii) & b(ii)). The reduction in population size during the transition from UKFS to SM policy shown in the Eastern and Western Strongholds is not seen here since the transition removes only a small amount of broadleaved trees.

As previously mentioned, 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 160 red squirrels and 110 greys squirrels (0.9 and 0.6 ind. per km^2 respectively) (Fig. 4.a(iii) & b(iii)). Under SM policy the red squirrel population increases to a stable average population size of 250 individuals (1.4 ind. per km^2) (Fig. 4.a(iv)) and the grey squirrel population is reduced to an average of around 15 individuals (>0.1 ind. per km^2) (Fig. 4.b(iv)). The population density and geographic spread of red and grey squirrels in the Southern Stronghold and the surrounding area under the UK Forestry Standard and Stronghold Management policy can be found in Figure S7. Thus, the introduction of the SM policy would reduce the resident grey squirrel population and be sufficient to allow the red squirrel population to increase in number and improve viability.

Implementing SM Policy Before Grey Squirrel Arrival

The above results for the Eastern and Western Strongholds assume that the transition from UKFS to SM policy and the introduction of grey squirrels occurs simultaneously. We consider the introduction of grey squirrels at year 50 of the simulation (Figures S8 & S9), which corresponds to the forest management being implemented in advance of grey squirrel arrival. During the transition from UKFS to SM grey

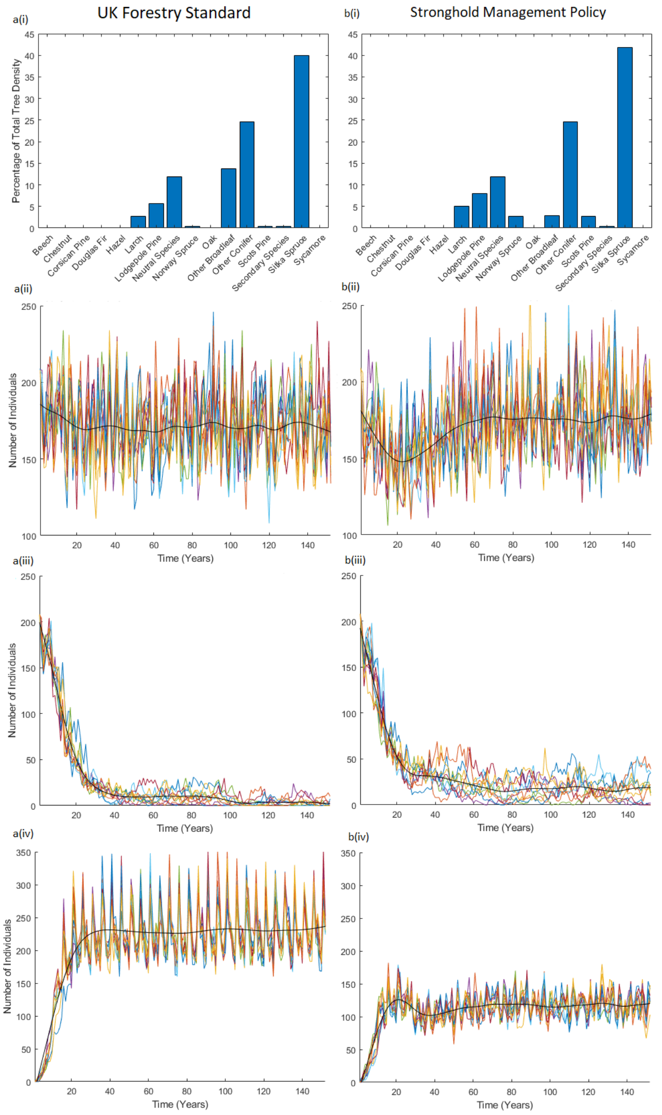

Figure 3 – Results for the Western Stronghold. Images a(i-iv) illustrate the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition (after SM policy has been implemented in (b)), (ii) shows the red squirrel population 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 realisations are shown and the darker lines indicate the average population trend for the 10 realisations.

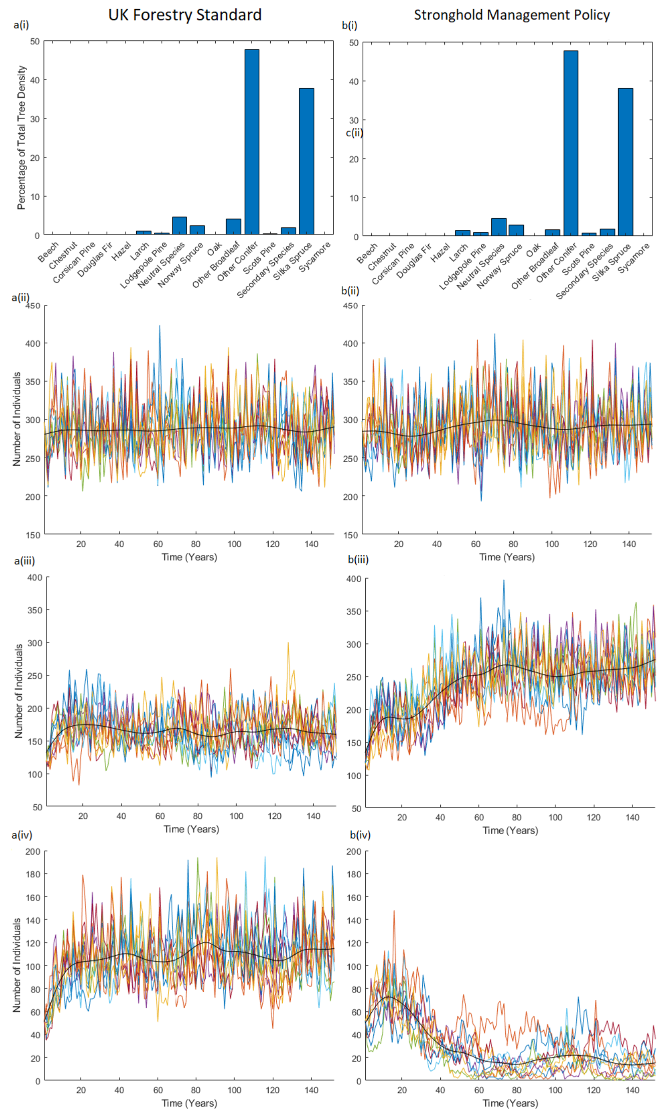

Figure 4 – Results for the Southern Stronghold. Images a(i-iv) illustrate the results under the UK Forestry Standard and b(i-iv) are the results under the Stronghold Management policy. Here (i) shows the forest composition (after SM policy has been implemented in (b)), (ii) shows the red squirrel population 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 realisations are shown and the darker lines indicate the average population trend for the 10 realisations.

squirrels are not present and the results are similar to those above when grey squirrels were not introduced (Fig. 1.b(ii) & Fig. 3.b(ii)) whereas the long-term results are similar to those above when grey squirrels are present (Fig. 1.b(iii) & Fig. 3.b(iii)). This implies that, for strongholds in the north of Scotland where grey squirrels do not currently reside and SM policy allows a stable red squirrel population to exist, the implementation of SM policy can be delayed until grey squirrels are a more pressing threat. Since grey squirrels are already present in the region surrounding the Southern Stronghold this scenario does not apply there.

Impact of the Squirrelpox Virus

Squirrelpox can be supported in grey squirrel populations and from there transmitted to adjacent red squirrels in which it causes a high level of mortality (Chantrey et al., 2014; Sainsbury et al., 2008). It is therefore important to assess the potential impact of squirrelpox on the viability of red squirrel strongholds. To do this we simulated the introduction of infected grey squirrels in regions around the strongholds that could support grey squirrels. In many of these regions the density of grey squirrels was insufficient to maintain squirrelpox which led to it dying out before it could become established in the wider population. Moreover, within the strongholds squirrelpox could not be supported, due to low squirrel density, and so had no impact on the ability of a stronghold to maintain a viable red squirrel population.

The density of infected grey squirrels in the Eastern Stronghold is shown in Figure S10 when infected grey squirrels were introduced to the wider environment in years 10, 15 and 20 showing that the disease does not persist. This result holds for all strongholds considered in this study.

Discussion

Mathematical modelling is increasingly being applied to predict likely future distributions, density and population dynamics of native and introduced species. Model results can be used to assist with policy decisions, conservation and management - particularly in relation to non-native species (Bertolino et al., 2020). Recent successful applications of a spatial mathematical modelling approach (White and Lurz, 2018, 2014; White et al., 2017, 2016, 2015) has enabled a re-evaluation of existing red squirrel conservation policy. This has recommended new management guidelines in Scotland in relation to the current distribution of introduced North American grey squirrels. This paper outlines the model results which investigated the viability of red squirrels in three stronghold regions (with results for three more in the supplementary information), as designated by Scottish Forestry, both with and without the presence of grey squirrels. In particular, we assess red and grey squirrel abundance and thereby potential red squirrel viability under two forest management policies: The Stronghold Management policy (Forestry Commission Scotland, 2012)), and the UK Forestry Standard policy (Forestry Commission, 2017a).

Our model results indicate that grey squirrels could persist in the Eastern and Western Strongholds, and the surrounding regions (which we assume meet UKFS criteria), under both the SM and UKFS scenarios. However, the SM policy reduces grey squirrel abundance, and consequently increases red squirrel abundance and thus population viability inside the stronghold. This means that the SM policy provides an advantage to red squirrels over grey squirrels when compared to the UKFS (Tab. 3). Therefore, the SM policy does satisfy its intended objective of providing a forest habitat that is beneficial to red squirrels over greys. Hence, the SM policy would support red squirrel conservation in areas where grey squirrels have the potential to invade red habitat (such as below the grey squirrel control boundary (Figure S1)). At the time of publication, the SM policy has not been enacted in a stronghold and so there is no data to test the model results.

Our model findings also indicate that some of the currently designated strongholds (e.g. Western Stronghold) cannot support viable red squirrel populations in the presence of grey squirrels under either UKFS or SM practice (Tab. 3). These strongholds have neighbouring habitat that provides a source of grey squirrels that can disperse into the strongholds and prevent the maintenance of a viable red squirrel population. The model study therefore suggests that, despite SM policy improving these forests for red squirrels, they are unsuitable strongholds. This highlights the importance of considering red squirrel conservation management at the wider landscape scale compared to the local (stronghold) scale. It also highlights the potential need for a review of the existing stronghold sites that were originally selected over a decade ago (Forestry Commission Scotland, 2006). Landscapes are not static and forest cover is subject to change in terms of felling and replanting operations as well as in terms of longer-term climatic changes. The latter, for example, is predicted to affect suitability for the planting of certain tree species in parts of Scotland (e.g. Sitka spruce, *Picea sitchensis*; Ray, 2008) in the near future.

Furthermore, the model suggests that the Southern Stronghold can support red squirrels in the presence of greys under both UKFS and SM practice, with SM policy supporting a higher red population (Tab. 3). These regions are therefore capable of sustaining a viable red squirrel population, in the presence of grey squirrels, without the application of a specific forest composition management policy or grey squirrel control and can be considered ‘natural strongholds’. The reasons for this are two-fold. The Southern Stronghold is comprised primarily of

Table 3 – Red and grey squirrel average abundance at the end of the model simulations, rounded to nearest 5 individuals, under the UK Forestry Standard (UKFS) and Stronghold Management (SM) strategies.

		Red Squirrels				**Grey Squirrels**	
		No Grey		*With Greys*			
		UKFS	**SM**	**UKFS**	**SM**	**UKFS**	**SM**
Eastern	Avg	315	315	20	215	340	70
Stronghold	Min	225	225	0	75	225	25
(89 km^2)	Max	440	425	100	325	545	135
Western	Avg	170	175	5	20	230	120
Stronghold	Min	110	105	0	0	165	75
(63 km^2)	Max	245	270	30	60	355	180
Southern	Avg	280	280	160	260	110	15
Stronghold	Min	205	195	80	160	45	0
(180 km^2)	Max	425	410	260	365	195	75

Sitka spruce which, while a poor habitat for red squirrels, is generally unsuitable for grey squirrels. It therefore provides a red squirrel stronghold despite the stronghold being well connected with the surrounding area. Conversely, a stronghold that has a more diverse range of favoured conifer species (such as the East2 Stronghold in the supplementary information) as well as a limited number of access points into the stronghold (which reduces the potential dispersal of grey squirrels from neighbouring forests) can also maintain a viable red squirrel population in the presence of grey squirrels under both SM and UKFS. Hence, SM policy could be applied differentially and focus on strongholds, such as the Eastern Stronghold, which can only support a viable red squirrel population under SM policy. Our model study also found other potential natural strongholds such as regions east of the Western Stronghold (Figure S6) and north east of the Southern Stronghold (Figure S7). The current model study could thus be extended to examine the location and forest properties that promote natural strongholds that would require no or minimal additional management due to their tree species composition, size or geographic factors. These findings could then be utilised by forest managers to ensure that standard forestry practice either maintains these regions or that efforts to increase biodiversity and forest resilience do not undermine the ability of the forests to act as natural red squirrel strongholds.

Our model results also indicate that, in the absence of grey squirrels, sustainable red squirrel populations (defined as having above 125 individuals in a connected forest region, Scottish Natural Heritage, pers. comm.) are viable in all strongholds under the UKFS management practice. The transition from the UKFS to the SM policy reduces the red squirrel abundance in all strongholds during the transition period, with the size of the reduction being dependent on the scale of alteration required for transition. Thus, greater levels of alteration lead to larger reductions in population size. Conversely, a greater variety of tree species in a stronghold mitigates the population reduction. Following the transition between forest composition management strategies, red squirrel abundance is comparable under the UKFS and the SM scheme (Tab. 3). A key result therefore is that, in the absence of grey squirrels, there is no discernible benefit for red squirrels in the SM policy compared to the UKFS. It should be noted that other red squirrel conservation practice and mitigation, beyond the management of tree species composition, is applied during forest operations and therefore red squirrel viability may be enhanced above that predicted for the UKFS scenarios. Moreover, the focus of UKFS on enhancing biodiversity could lead to a more diverse forest ecosystem that may have been disrupted due to the implementation of the SM policy (Bellamy et al., 2018; Forestry Commission, 2017a; Rollinson, 2003; Bengtsson et al., 2000). Since the northern extent of grey squirrels in Scotland has been contained for the past 30 years (Bryce and Tonkin, 2019) this result suggests that species-specific management for red squirrels in the absence of sympatric grey squirrels would not be required. This would allow a more biodiversity-oriented management approach in currently designated strongholds that lie north of the grey squirrel control boundary (Figure S1).

Grey squirrels are not only a threat to red squirrels in the United Kingdom. Grey squirrels were first introduced into Piedmont in northern Italy in 1948 and in Genoa in the 1960s with further translocations to Lombardy in the late 1990s. They have since expanded their range south into Central Italy as well as north across the Po plain with a real risk of future expansion into France and Switzerland (Signorile et al., 2014; Martinoli et al., 2010; Lurz et al., 2001). This increase in range has led to a parallel and significant reduction in red squirrel density. In much of the UK red squirrel replacement is primarily driven by disease-mediated competition. However, the squirrelpox virus, carried by grey squirrels and lethal to native red squirrels in the UK, is not present in Italy (Romeo et al., 2019; Rushton et al., 2006; Tompkins et al., 2003). In Italy red replacement is due to food competition and increased red squirrel stress due to the presence of greys (Santicchia et al., 2018; Bertolino et al., 2014; Gurnell et al., 2004). Our findings for Scotland suggest that the virus does not play a critical role in red squirrel replacement inside strongholds since densities are too small to sustain the squirrelpox virus. This means our results and the situation in Scotland may be representative of the red and grey squirrel interactions in Italy. Furthermore, like Scotland, northern Italy has regions that favour grey squirrels in the deciduous forests at lower elevations and red squirrels in the more conifer dominated forests higher up in the mountains. We therefore think that our approach and findings hold lessons for the situation in Italy and could be used to inform management and conservation decisions. Notwithstanding, we recognise that the situation in Italy is much richer, complex and scientifically challenging, in that in addition to grey squirrels, there are also other introduced squirrel species present (see Mazzamuto et al., 2017) and the natural predator populations are not as depauperate as they are in the UK (Sheehy et al., 2018). This could form the basis of a new study.

Our model study also considers the impact of squirrelpox virus on the potential of strongholds to support red squirrels. There is consensus that squirrelpox played a key role in the competition and disease mediated invasion of red squirrels when greys squirrels expanded through England and Wales (Bosch and Lurz, 2012; Tompkins et al., 2003) . Here the habitat consisted of broadleaved or mixed stands that could support high squirrel densities. Our modelling study showed that the impact of squirrelpox on red squirrel viability in strongholds was negligible. Viable strongholds under either UKFS or SM practice (or natural strongholds) contain predominately coniferous habitat that only supports low density red squirrel populations and minimises grey squirrel competition. Our study is in line with previous studies that show squirrelpox cannot be supported in red squirrel populations (Jones et al., 2017; White et al., 2014; Duff et al., 2010), that red squirrels can therefore 'live' with the threat from squirrelpox and that squirrelpox is unlikely to play a key role in grey squirrel invasion and replacement in low density populations in Scotland (Lurz et al., 2015). Outside of Scotland we expect squirrelpox to be a key factor in the red and grey squirrel competitive dynamics. Other factors could, however, impact on the ability of forest regions to act as strongholds for red squirrels. Coordinated grey squirrel control has acted to reduce grey squirrel density which in turn can reduce grey squirrel expansion (Forestry Commission Scotland, 2006). Furthermore, recent studies have suggested that a shared predator, the pine marten (*Martes martes*), may modify the competitive interaction between red and grey squirrels (Twining et al., 2020; Sheehy et al., 2018). The presence of pine marten has been shown to correlate with the absence of grey squirrels. This leads to an indirect positive affect on red squirrel presence. Pine martens are currently expanding their geographic range and population density in Scotland (Croose et al., 2014) and so may play a key role in determining the future distribution of red and grey squirrels and therefore affect the requirement for forest management to protect red squirrels.

While we recognise that it will become an increasingly important factor, we did not include the impact of climate change in our study. Including climate change impacts in population models is a complex process and we felt it could obscure the direct comparison of the two forest management policies that were the key focus of our study. We nevertheless discuss its potential impact here. Climate change would influence tree species composition (Neilson et al., 2005), the time to maturity as well as mast intervals (Bisi et al., 2016). All these effects would have as yet difficult to predict impacts on squirrel distribution, ecology and local population viability. A primary consequence of climate change is likely to be the increase in broadleaved trees, either through in situ expansion or species migration northwards ((Neilson et al., 2005). In Scotland, winters are likely to become milder and wetter, and summers warmer and drier with predicted benefits to some deciduous species such as beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*; e.g. see Ray, 2008). Given the competitive advantage grey squirrels have in broadleaved habitat, an expansion of deciduous tree species will lead to higher grey squirrel densities in Scotland. Higher grey squirrel densities may be able to sustain endemic squirrelpox that, when coupled with greater competitive pressure, could lead to a more rapid decline and local or regional red squirrel extinction (Rushton et al., 2006; Tompkins et al., 2003). Whilst some authors predicted an increase in woodland cover (Ray, 2008), climate change conversely could also increase the proportion of Scotland that is viable for agricultural use. An expansion in agricultural land could necessitate a reduction in the forested area, which in turn could reduce the connectivity of Scottish forests (Gimona et al., 2012). A more fragmented forest landscape could aid red squirrels by reducing the ability of grey squirrels to expand their range. However, a more fragmented landscape would also isolate red squirrel populations, reduce genetic diversity and increase the risk of local population extinction. Given the threat climate change poses to red squirrels, suitable forest management may need to be instituted in order to safeguard them in Scotland (Cameron, 2015).

Policy Implications

Our model study has examined the effectiveness of SM practice in protecting red squirrels from grey invasion. It has shown that, despite SM policy improving red squirrel abundance when compared to UKFS, some currently designated strongholds would not successfully achieve the objective of protecting red squirrels. This highlights the importance of careful site selection in terms of stronghold and landscape composition.

The study has also identified the potential of other regions to act as 'natural' strongholds. It is therefore worthwhile to review some of the criteria that were used in the stronghold designation, their current suitability and management plans. The original policy (outlined in the Materials and Methods section) assumed that grey squirrel expansion would continue into northern Scotland and eventually threaten the existence of red squirrels in the whole of Scotland. Consequently, the Red Squirrel Action Plan (Forestry Commission Scotland, 2006), which originally called for the establishment of stronghold areas, set out the provision of funds for grey squirrel control officers to prevent grey squirrel range expansion in strategic areas. This objective has since been successfully implemented by Saving Scotland's Red Squirrels and the strongholds established based on work by Poulsom (2005).

With hindsight, it is apparent that the final selection of strongholds (Figure S1) did not accomplish all these objectives (e.g. some strongholds have significant areas of deciduous woodland within and surrounding them). More importantly, the Action Plan, while building in a review process for Squirrel Conservation Officers, did not envisage a review of stronghold sites. This would be critical for several key reasons: i) there is a need to review if selected sites meet and can maintain the criteria set out in the Action Plan and ii) successful control operations would alter predicted expansion of grey squirrels in northern Scotland and potentially affect forest design plans in strongholds. This then highlights the need for rigorous scientific underpinning, combined with robust policy reviews, when embarking on conservation policy that has significant implications for a commercial sector.

Scottish Forestry intend to undertake a review of SM policy and the results presented here will form part of this review. For Forestry and Land Scotland (FLS), reconciling the SM policy with other management objectives, fluctuating timber markets and wind-blow events, requires significant additional management input and can affect income from timber sales. Furthermore, the single species focus of the SM policy has consequences for other environmental work. For example, restrictions on planting or regenerating oak (*Quercus* spp.) puts limits on FLS efforts to further the conservation of biodiversity. The results of this study are therefore important for FLS and will influence management across large parts of the national forest estate. A future focus on natural strongholds under the UKFS approach will afford more flexibility to conserve red squirrel populations whilst simultaneously delivering other forest management objectives.

References

Aldhous J.R., 1972. Nursery practice. Forestry Commission Bulletin (43).

Anonymous, 2015. Scottish Strategy for Red Squirrel Conservation . Report June 2015 produced on behalf of the Scottish Squirrel Group, Scottish Natural Heritage, Edinburgh, UK.

Barkalow F.S. Jr., Hamilton R.B., Soots R.F. Jr., 1970. The vital statistics of an unexploited gray squirrel population. J. Wildl. Manag. pp. 489–500.

Bellamy C., Barsoum N., Cottrell J., Watts K., 2018. Encouraging biodiversity at multiple scales in support of resilient woodlands. Forestry Commission Research Note (33).

Bengtsson J., Nilsson S.G., Franc A., Menozzi P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manag. 132(1):39–50.

Bertolino S., Di Montezemolo N.C., Preatoni D.G., Wauters L.A., Martinoli A., 2014. A grey future for Europe: Sciurus carolinensis is replacing native red squirrels in Italy. Biol. Invasions 16(1):53–62.

Bertolino S., Sciandra C., Bosso L., Russo D., Lurz P.W.W., Di Febbraro M., 2020. Spatially explicit models as tools for implementing effective management strategies for invasive alien mammals. Mamm. Rev. 50(2):187–199.

Bisi, F., von Hardenberg, J., Bertolino, S., Wauters, L.A., Imperio, S., Preatoni, D.G., Provenzale, A., Mazzamuto, M.V., Martinoli, A. 2016. Current and future conifer seed production in the Alps: testing weather factors as cues behind masting. European Journal of Forest Research 135(4):743-754

Bosch S., Lurz P.W.W., 2012. The Eurasian red squirrel: *Sciurus vulgaris*. Westarp Wissenschaften, NBB English Edition, 206 p.

Broome A.C., Connolly T., Quine C.P., 2014. An evaluation of thinning to improve habitat for capercaillie (Tetrao urogallus). For. Ecol. Manag. 314:94–103.

Broome A.C., Summers R.W., Vanhala T., 2016. Understanding the provision of conifer seed for woodland species. Forestry Commission.

Bryce J., Johnson P.J., Macdonald D.W., 2002. Can niche use in red and grey squirrels offer clues for their apparent coexistence? J. Appl. Ecol. 39(6):875–887.

Bryce J., Tonkin M., 2019. Containment of invasive grey squirrels in Scotland: meeting the challenge. In: Veitch C.R., Clout M.N., Martin A.R., Russel J.C., West C.J. (eds). Island invasives: scaling up to meet the challenge, pp.180-186. Gland, Switzerland: IUCN (62):180.

Cameron, A.D., 2015. Building resilience into Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forests in Scotland in response to the threat of climate change. Forests, 6(2), pp.398-415.

Chantrey J., Dale T.D., Read J.M., White S., Whitfield F., Jones D., McInnes C.J., Begon, M., 2014. European red squirrel population dynamics driven by squirrelpox at a gray squirrel invasion interface. Ecol. Evol. 4(19):3788–3799.

Chaudhary A., Burivalova Z., Koh L.P., Hellweg S., 2016. Impact of forest management on species richness: global meta-analysis and economic trade-offs. Sci. Rep. 6:23954.

Croose, E., Birks, J.D.S., Schofield, H.W., O'Reilly, C. 2014. Distribution of the pine marten (*Martes martes*) in southern Scotland in 2013. Scottish Natural Heritage Report No. 740

Dieler J., Uhl E., Biber P., Muller J., Rotzer T., Pretzsch H., 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. Eur. J. For. Res. 136(4):739–766.

Duff J.P., Holmes J.P., Barlow A.M., 2010. Surveillance turns to wildlife. Vet. Rec. 167:154–156.

Forestry Commission, 2017a. The UK Forestry Standard: The Government's approach to sustainable forestry. Forestry Commission, Edinburgh. ISBN: 978-0-85538-999-4

Forestry Commission, 2017b. Cheviots Forest Plan 2017. Forestry Commission – North England Report.

Forestry Commission Scotland, 2006. Scottish red squirrel action plan: 2006-2011.. Forestry Commission Scotland report.

Forestry Commission Scotland, 2012. Managing Forests as Red Squirrel Strongholds. Forestry Commission Practice Note 102. Forestry Commission Scotland Report

Gill R., 2019. Controlling grey squirrels in forests and woodlands in the UK. UK Forestry Standard Technical Note (22). ISBN: 978-1-83915-004-3

Gimona, A., Poggio, L., Brown, I. and Castellazzi, M., 2012. Woodland networks in a changing climate: threats from land use change. Biological conservation, 149(1), pp.93-102.

Gurnell J., 1983. Squirrel numbers and the abundance of tree seeds. Mammal Review 13: 133-148.

Gurnell J., 1987. Natural history of squirrels. Christopher Helm.

Gurnell J., Wauters L.A., Lurz P.W.W., Tosi G., 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. J. Animal Ecol. 73(1):26–35.

Heikkinen R.K., Poyry J., Virkkala R., Bocedi G., Kuussaari M., Schweiger O., Settele J., Travis, J.M.J., 2015. Modelling potential success of conservation translocations of a specialist grassland butterfly. Biol. Conserv. 192:200–206.

Hibberd B.G., 1991. Forestry Practice. Forestry Commission Handbook No. 6. Forestry Commission Handbook (6). ISBN: 0-11-710281-4

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

Jones H.E., White A., Lurz P.W.W., Shuttleworth, C., 2017. Mathematical models for invasive species management: Grey squirrel control on Anglesey. Ecol. Model. 359:276–284.

Kenward R.E., Holm J.L., 1993. On the replacement of the red squirrel in Britain: a phytotoxic explanation. Proc. R. Soc. Lond. B 251: 187-194.

Koprowsky J.L., 1994. Sciurus carolinensis. Mammalian Species 480: 1-9.

Lurz P.W.W., 2016. Kidland forest monitoring. Report for Forestry Commission, Kielder Forest District.

Lurz P.W.W., Gough P., 2018. Kidland and Uswayford Forest squirrel monitoring . Report for Forestry Commission, Kielder Forest District.

Lurz P.W.W., Garson P.J., Ogilvie J.F., 1998. Conifer species mixtures, cone crops and red squirrel conservation. Forestry 71(1):67–71.

Lurz P.W.W., Garson P.J., Wauters L.A., 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrel (*Sciurus vulgaris* L.) . J. Zool., Lond. 251: 167-178.

Lurz P.W.W., White A., Meredith A., McInnes C., Boots M., 2015. Living with pox project: Forest management for areas affected by squirrelpox virus. Forestry Commission Scotland Report .

Lurz P.W.W., Rushton S.P., Wauters L.A., Bertolino S., Currado I., Mazzoglio P., Shirley M.D.F., 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. Landscape Ecol. 16(5): 407–420.

Martinoli A., Bertolino S., Preatoni D.G., Balduzzi A., Marsan A., Genovesi P., Tosi G., Wauters L.A., 2010. Headcount 2010: The multiplication of the grey squirrel introduced in Italy. Hystrix It. J. Mamm. 21(2):127–136.

Mathews F., Kubasiewicz L.M., Gurnell J., Harrower C.A., McDonald R.A., Shore R.F., 2018. A review of the population and conservation status of British mammals. Natural England.

Mazzamuto M.V., Morandini M., Panzeri M., Wauters L.A., Preatoni D.G., Martinoli A., 2017. Space invaders: effects of invasive alien Pallas's squirrel on home range and body mass of native red squirrel. Biol. Invasions 19(6):1863–1877.

Middleton A.D., 1930. 38. The Ecology of the American Grey Squirrel (Sciurus carolinensis Gmelin) in. the British Isles. In Proc. Zool. Soc. London. Vol. 100 Wiley Online Library pp. 809–843.

Neilson, R.P., Pitelka, L.F., Solomon, A.M., Nathan, R.A.N., Midgley, G.F., Fragoso, J.M., Lischke, H. and Thompson, K.E.N., 2005. Forecasting regional to global plant migration in response to climate change. Bioscience, 55(9), pp.749-759.

Nichols C.P., Gill R.M.A., 2016. Chapter 19. Bark stripping behaviour by the grey squirrel, *Sciurus carolinensis*. In: The Grey Squirrel: Ecology and Management of an Invasive Species in Europe (CM Shuttleworth, PWW Lurz & J Gurnell eds), pp. 369-392.

Okubo, A., Maini, P.K., Williamson, M.H. and Murray, J.D., 1989. On the spatial spread of the grey squirrel in Britain. Proceedings of the Royal Society of London. B. Biological Sciences, 238(1291), pp.113-125.

Poulsom L., 2005. Identification of priority woodlands for red squirrel conservation in North and Central Scotland: a preliminary analysis. Scottish Natural Heritage Report.

Ray D., 2008. Impacts of climate change on forestry in Scotland–a synopsis of spatial modelling research. Forestry Commission Research Note 101(8).

Reid C., 2018. Scotland's Forestry Strategy 2019-2029. Scottish Government.

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

Rollinson T., 2003. Introduction: the policy context for biodiversity. Biodivers. in Britain's Plant. For. 8:3.

Romeo C., McInnes C.J., Dale T.D., Shuttleworth C., Bertolino S., Wauters L.A., Ferrari N., 2019. Disease, invasions and conservation: no evidence of squirrelpox virus in grey squirrels introduced to Italy. Anim. Conserve. 22(1):14–23.

Rushton S.P., Lurz P.W.W., Gurnell J., Fuller R., 2000. Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline of the red squirrel in the UK? Journal of Applied Ecology 37: 997-1012.

Rushton S.P., Lurz P.W.W., Gurnell J., Nettleton P., Bruemmer C., Shirley M.D.F., Sainsbury A.W., 2006. Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. Epidemiol. Infect. 134(3):521–533.

Sainsbury A.W., Deaville R., Lawson B., Cooley W.A., Farelly S.S.J., Stack M.J., Duff P., McInnes C.J., Gurnell J., Russell P.H., 2008. Poxviral disease in red squirrels Sciurus vulgaris in the UK: spatial and temporal trends of an emerging threat. EcoHealth 5(3):305.

Santicchia F., Dantzer B., van Kesteren F., Palme R., Martinoli A., Ferrari N., Wauters L.A., 2018. Stress in biological invasions: Introduced invasive grey squirrels increase physiological stress in native Eurasian red squirrels. J. Anim. Ecol. 87(5):1342– 1352.

Savill P.S., 2013. The silviculture of trees used in British forestry. CABI.

Saving Scotland's Red Squirrels, 2010. Standard operating procedures for grey squirrel control. Saving Scotland's Red Squirrels Report.

Sheehy E., Sutherland C., O'Reilly C., Lambin X., 2018. The enemy of my enemy is my friend: native pine marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations. Proc. R. Soc. B: Biol. Sci. 285(1874):20172603.

Signorile A.L., Paoloni D., Reuman D.C., 2014. Grey squirrels in central Italy: a new threat for endemic red squirrel subspecies. Biol. Invasions 16(11):2339–2350.

Tompkins D.M., White A., and Boots M., 2003. Ecological replacement of native red squirrels by invasive greys driven by disease. Ecol. Lett. 6(3):189–196.

Twining J.P., Montgomery W.I., and Tosh D.G., 2020. Declining invasive grey squirrel populations may persist in refugia as native predator recovery reverses squirrel species replacement. J. Appl. Ecol. doi.org/10.1111/1365-2664.13660

Watkins A., Noble J., Foster R.J., Harmsen B.J., Doncaster C.P., 2015. A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecol. Model. 306:268–277.

Wauters L.A., Tosi G., Gurnell J., 2002. Interspecific competition in tree squirrels: do introduced grey squirrels (Sciurus carolinensis) deplete tree seeds hoarded by red squirrels (S. vulgaris)? Behav. Ecol. Sociobiol. 51(4):360–367.

White, A., Bell, S.S., Lurz, P.W.W., Boots, M., 2014. Conservation management within strongholds in the face of disease-mediated invasions: red and grey squirrels as a case study. J. Appl. Ecol. 51, 1631-1642.

White A., Lurz P.W.W., 2014. A modelling assessment of control strategies to prevent/reduce Squirrelpox spread. In Scottish Natural Heritage: Commissioned Report No. 627.

White A., Lurz P.W.W., 2018. Grey squirrel control in southern Scotland: A model analysis. Forest Enterprise Scotland.

White A., Lurz P.W.W., Boots M., 2017. Grey squirrel control along the highland line: A model analysis. Scottish Natural Heritage/ Scottish Wildlife Trust.

White A., Lurz P.W.W., Bryce J., Tonkin M., Ramoo K., Bamforth L., Jarrott A., Boots M., 2016. Modelling disease spread in real landscapes: Squirrelpox spread in Southern Scotland as a case study. Hystrix It. J. Mamm. 27(1).

White A., Lurz P.W.W., Jones H.E., Boots M., Bryce J., Tonkin M., Ramoo K., Bamforth L., Jarrott A., 2015. The use of mathematical models in red squirrel conservation: Assessing the threat from grey invasion and disease to the Fleet basin stronghold Red Squirrels: Ecology, Conservation & Management in Europe. European Squirrel Initiative, Woodbridge, Suffolk, England .

Yoder C.A, Mayle B.A., Furcolow C.A., Cowan D.P., Fagerstone K.A., 2011. Feeding of grey squirrels (Sciurus carolinensis) with the contraceptive agent DiazaConTM: effect on cholesterol, hematology, and blood chemistry. Integrative Zoology 6: 409-419.

Associate Editor: C. Tattoni

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Document S1 A document in pdf format reporting all the supplemental Figures and Tables cited in the text.