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Natural strongholds for red squirrel conservation in Scotland

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Abstract

The Eurasian Red Squirrel (*Sciurus vulgaris*) is under threat from the invasive North American eastern Grey Squirrel (*Sciurus carolinensis*) with 80% of the remaining red squirrel populations in the British Isles found in Scotland. In this study we develop a spatially explicit mathematical model of the red and grey squirrel system and use it to assess the population viability of red squirrels across Scotland. In particular, we aim to identify existing forests – natural strongholds for red squirrels – that can successfully support red squirrels under UK Forestry Standard management and protect them from potential disease-mediated competition from grey squirrels. Our model results indicate that if current levels of grey squirrel control, which restrict or reduce the distribution of grey squirrels, are continued then there will be large expanses of forests in northern Scotland that support viable red squirrel populations. Model results that represent (hypothetical) scenarios where grey squirrel control no longer occurred indicated that grey squirrel range expansion and the process of red squirrel replacement would be slow. Model results for an assumed worst-case scenario where grey squirrels have expanded to all regions in Scotland identified forest regions – denoted natural strongholds – that could currently support red squirrels under UK Forestry Standard management practice. The results will be used to inform forest management policy and support a strategic review of red squirrel management by land management agencies and other stakeholders.

Keywords

Ecological modelling, forest management, invasive species, policy

Introduction

The Eurasian red squirrel (*Sciurus vulgaris*) is under threat in the British Isles. Recent estimates (Mathews et al. 2018) indicate that just over 80% of the remaining British populations are now thought to live exclusively in Scotland. The decline of red squirrel populations has arisen due to the expansion of the North American eastern grey squirrel (*Sciurus carolinensis*) which was introduced into the British Isles in the 19th century (Middleton 1930). The replacement of red squirrels by greys has occurred due to the disease-mediated competition that occurs between the two species, with grey squirrels acting as a reservoir for squirrelpox virus that is lethal to red squirrels, but non-lethal and endemic in grey squirrels (Tompkins et al. 2003; Rushton et al. 2006).

Current efforts to protect red squirrels in Scotland are focused on defending priority populations of red squirrels (Scottish Natural Heritage 2015) across their Scottish range. This is achieved mainly through grey squirrel control, via trapping, that aims to prevent grey squirrel expansion northwards across a chosen boundary line (a line approximately between Helensburgh and Montrose (Scottish Natural Heritage 2015), henceforth called the grey squirrel control boundary). There are also efforts to protect red squirrels in priority regions that lie south of the grey squirrel control boundary. Grey squirrels typically dominate habitat south of the grey squirrel control boundary as well as habitat in Aberdeen and surrounding areas. The grey squirrel population at Aberdeen has persisted since a separate introduction in the 1970s (Saving Scotland's Red Squirrels 2020). At present, grey squirrel control, coordinated by Saving Scotland's Red Squirrels (Scottish Natural Heritage 2015) aims to prevent grey squirrels from expanding northwards beyond the grey squirrel control boundary, to reduce the distribution of greys in Aberdeen and the surrounding area and to defend the isolated red populations in southern and central Scotland. Red squirrel conservation policy also recommends conservation action through sympathetic forest management in selected forest sites (strongholds), which are meant to provide refuge for red squirrels against the incursion and competition from grey squirrels (Scottish Forestry 2020). The native habitat of the grey squirrel is the broadleaved forests of eastern North America, meaning grey squirrels are broadleaf specialists. Consequently, they enjoy a significant competitive advantage over native Eurasian red squirrels in deciduous but not coniferous woodland. Strongholds tend to therefore be large, conifer-dominated forests (Gurnell et al. 2004; Forestry Commission Scotland 2012).

There are currently 19 sites throughout Scotland that have been designated as strongholds (Forestry Commission Scotland 2012; Scottish Forestry 2020). Forest management guidance in these strongholds aims to "use woodland management to maintain healthy self-sustaining populations of red squirrels" (Forestry Commission Scotland 2012). The guidance is based on five key principles: (i) the maintenance of a dependable tree seed food supply, (ii) a resolution of conflicts with other management objectives, (iii) planning for red squirrels at the landscape scale, (iv) long-term planning to sustain resilience and (v) the establishment of a monitoring system. Whilst the guidance acknowledges that stronghold sites should have been chosen to minimise conflicts (e.g. sites with a low proportion of broadleaved trees that favour grey squirrels), it recognised the challenge for forest managers to integrate red squirrel conservation with other forest management objectives.

A recent study has examined red squirrel viability in designated strongholds under recommended stronghold forest management compared to UK Forestry Standard (UKFS) management for strongholds in Scotland (Slade et al. 2020). The findings showed that forest management policy specifically designed to reduce competition has little benefit in the absence of grey squirrels. Thus, the rationale for managed strongholds north of the grey squirrel control boundary could be reconsidered to account for the distribution of grey squirrels. However, when grey squirrels are present the strongholds perform as intended, with stronghold forest management benefiting red squirrels at the expense of grey squirrels. The study (Slade et al. 2020) also highlighted that some designated strongholds could not protect red squirrels from potential grey squirrel invasion regardless of forest management policy – largely due to the high connectivity of these strongholds to habitat that is favourable for grey squirrels. These designated strongholds are therefore unsuitable for red squirrel protection and reflect an unwise choice in stronghold site selection. Furthermore, the study also described the potential for natural strongholds, where red squirrel populations would persist under UKFS management (Forestry Commission 2017) despite the threat from grey expansion. Management of the designated strongholds requires resources and additional management time. Therefore, the identification of natural strongholds, both north and south of the grey squirrel control boundary, within which red squirrels can persist under UKFS management, even in the presence of grey squirrels, would free resources and management time that could be deployed elsewhere.

Mathematical models that combine accurate habitat information, such as land-cover information provided by GIS data and data on a species' ecology from field studies, with dynamic modelling to capture the population dynamics and species interaction can be utilised to inform conservation policy (Broome et al. 2014; Carter et al. 2015; Heikkinen et al. 2015). Such model frameworks have been successfully employed to inform red squirrel conservation, with models being used to examine the potential spread of squirrelpox in Scotland (White et al. 2016), to assess the importance of grey squirrel control to protect red squirrel populations on Anglesey (Jones et al. 2017), to determine how forest management practice affects red squirrel viability in the absence of grey squirrels (Jones et al. 2016) and in designated red squirrel strongholds in Scotland (Slade et al. 2020). In collaboration with Forestry and Land Scotland (FLS), the Scottish Government agency responsible for managing Scotland's publicly-owned forests and land, we extend the established spatially explicit mathematical modelling framework for the red and grey squirrel system (White et al. 2016; Jones et al. 2016, 2017; Slade et al. 2020) and use it to assess the population viability of red squirrels across Scotland. In particular we aimed to identify existing forests, natural strongholds for red squirrels, that can successfully support red squirrels against potential disease-mediated competition from greys under UK Forestry Standard management. The results will be used to inform forest management policy and support a strategic review of red squirrel management by FLS and other stakeholders.

Methods

In this study we have developed a mathematical model to assess the long-term viability of red squirrels in Scotland. The model 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 (White and Lurz 2014; Jones et al. 2016; White et al. 2016; Slade et al. 2020). 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:

$$\frac{dS_G}{dt} = A_G(t) - bS_G - \beta S_G \left(I_G + I_R\right),$$

$$\frac{dI_G}{dt} = \beta S_G \left(I_G + I_R\right) - bI_G - \gamma I_G,$$

$$\frac{dR_G}{dt} = \gamma I_G - bR_G, \tag{1}$$

$$\frac{dS_R}{dt} = A_R(t) - bS_R - \beta S_R \left(I_G + I_R\right),$$

$$\frac{dI_R}{dt} = \beta S_R \left(I_G + I_R\right) - bI_R - \alpha I_R$$

where

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

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 $A_R(t)$, which represents the periodic birth rate of red squirrels, is equivalent to $A_G(t)$ with the subscripts for R and G interchanged. Note, $H_G = S_G + I_G + R_G$ and $H_R = S_R + I_R$ represent the total populations for grey and red 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 et al. 2016). 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 carrying capacities being habitat dependent (see Suppl. material 1: Section S1.1). All parameter values assume an annual timescale. To generate the stochastic model, the rates for birth, death, infection, recovery etc., in the deterministic model are converted into probabilities of events that account for changes in individual 1 km by 1 km patch level abundance (Renshaw 1993) – see Suppl. material 1: Section S1.2 for full description. The stochastic model also includes events that allows for dispersal of individuals between patches (see Suppl. material 1: Table S2 for details) as well as the possibility of control through the removal of grey squirrels (see Suppl. material 1: Section S1.4).

The stochastic model is used in conjunction with landscape information, primarily forest composition data and information on masting, which gives forest capacity dynamics. These data provides estimates for red and grey squirrel carrying capacity at the 1 km^2 level (see Suppl. material 1: Section S1 for further details).

In this paper we considered the following scenarios:

(i) The natural expansion of red and grey squirrel populations beyond the grey squirrel control boundary. This allows an examination of the threat to current red squirrel population from 'natural' grey squirrel expansion.

For this scenario 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). In regions where only one squirrel species was observed the model was initialised at the respective carrying capacity for that grid-square, based 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 simulated 10 times, with each simulation being run for 10 years and an average taken, in order to allow for changes in density in grid-squares with both squirrels present and for squirrels to expand into nearby available habitat. The average result of the 10-year spin-up serves as the initial conditions for this scenario.

(ii) The assumption that grey squirrels initially occupy all viable habitat in Scotland. This allows the model to predict the composition and location of current natural strongholds in Scotland in which viable red populations would persist when faced with the threat from grey squirrels.

For this scenario the model was initiated by assuming red squirrel occupancy is as in scenario i (see Fig. 1a) and that grey squirrels are present at their carrying capacity in all grid squares in which the grey carrying capacity is greater than, or equal to, 5 km^{-2} (and therefore this scenario assumes that grey squirrels have dispersed to all regions in Scotland).

To generate results each scenario was simulated 10 times, with each simulation of the model being run for 150 years each to ensure that the model is predicting the long-term population dynamics. The simulation results are then averaged. Regarding occupancy, a grid square is classed as being occupied if there are 2 or more individuals of either species present. Habitat, carrying capacity and occupancy maps were generated using MATLAB R2018b. Simulations were run using Fortran90.

Results

Fig. 1a shows the initial distribution of red and grey squirrels used in the model simulations and is indicative of the current distribution in Scotland. This highlights how red squirrels currently occupy suitable habitat in the north of Scotland (above the grey squirrel control boundary) as well as in isolated populations in southern and central Scotland. Grey squirrels dominate habitat south of the grey squirrel control boundary as well as habitat in Aberdeen and surrounding areas.

Red squirrel viability when grey squirrels naturally expand their range of occupancy

Fig. 1a–d shows occupancy maps for 150 years of model simulation when squirrels can disperse beyond their current distribution. Findings show that grey squirrels swiftly expand their range into the north-east of Scotland, with consequent loss of red squirrel populations.

The range expansion of grey squirrels into the north-east beyond the initial expansion (through habitats in Moray and along the river Spey) is slow.

There is limited expansion in grey squirrel distribution across the grey squirrel control boundary and into red squirrel occupied regions in central and southern Scotland. In the model this range expansion occurs within the first 30 years and the grey distribution remains relatively fixed thereafter. The mathematical model has been fitted to qualitatively reproduce observed rates of red and grey squirrel expansion through suitable habitat (Jones et al. 2016). Therefore, the absence of grey squirrel expansion north of the grey squirrel control boundary is due to a lack of suitably connected habitat in relation to the assumed and validated grey squirrel dispersal ability.

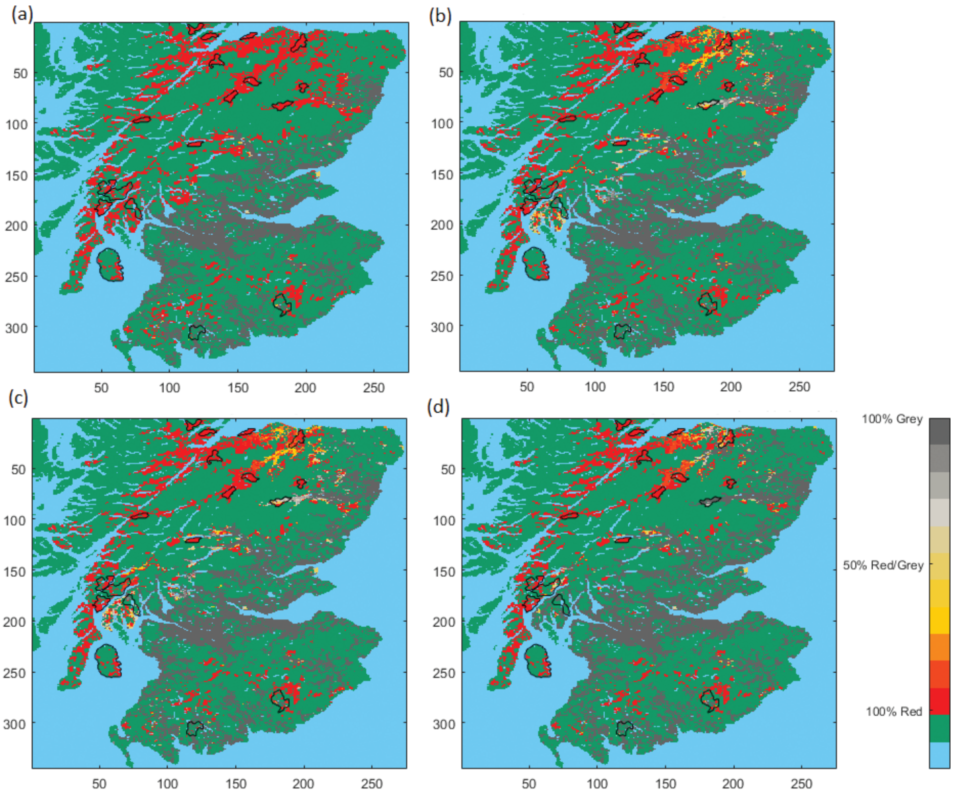

Figure 1. Results showing the relative occupancy of each 1 km grid square. Here (**a**) shows the initial occupancy, defined using the 10-year model spin-up based on observation data, as maintained by trapping at the grey squirrel control boundary, (**b**) shows an average occupancy of the first 30 years of the simulation after grey squirrels are allowed to disperse freely, (**c**) shows the average occupancy results for years 65 to 95 of the simulation where grey squirrels are allowed to disperse freely, and (**d**) shows the long-term occupancy (150 years after the simulation begins) of red and grey squirrels after greys have been allowed to disperse freely. A grid square is classed as being occupied if there are 2 or more individuals of any species present. The scale bar indicates the proportion of the 10 simulations that ended with either red or grey squirrel occupancy. For example, 70% red occupancy in a given grid square indicates that 7 of the 10 simulations that ended in occupancy were occupied by red squirrels. The 19 designated strongholds (Scottish Forestry 2020) are outlined in black.

Much of northern Scotland, above the grey squirrel control boundary, remains occupied by viable red squirrel populations (maps of average squirrel density for these simulations can be found in Suppl. material 1: Fig. S1). This is primarily due to the inability of grey squirrels to disperse to suitable habitat in northern Scotland. Isolated red squirrel populations persist in central and southern Scotland and indicate that these regions are natural strongholds for red squirrels. Here red squirrel populations persist in conifer-dominated regions even though grey squirrels occupy neighbouring habitat.

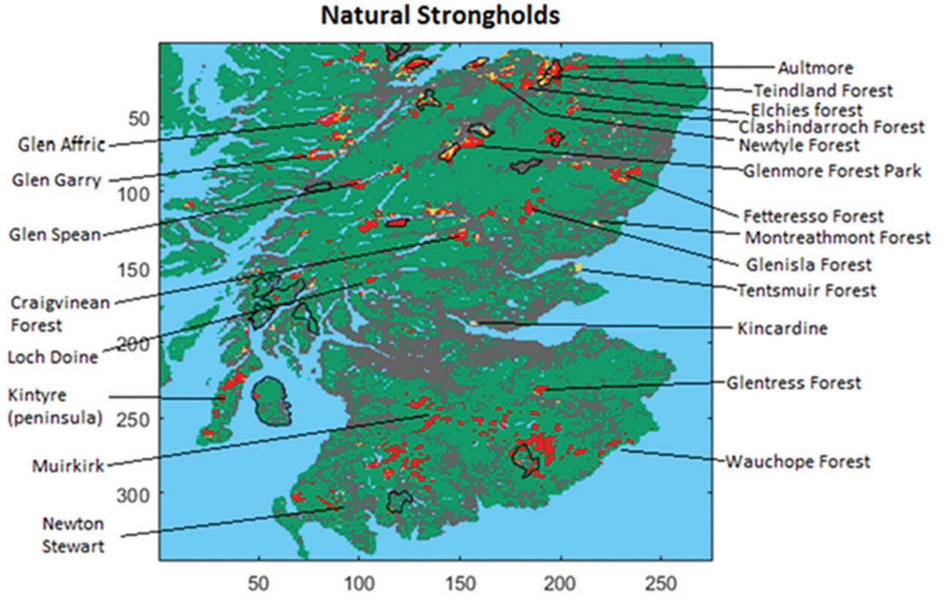

Figure 2. Relative occupancy of red and grey squirrels when grey squirrels are assumed to initially occupy all viable habitat. The names are of the forests that the model predicts can act as natural strongholds. Note, not all natural strongholds have been named due to overlap or close proximity to existing strongholds, which would enable their location to be determined. The 19 designated strongholds (Scottish Forestry 2020) are outlined in black.

Identifying natural red squirrel strongholds in Scotland

Results showing the occupancy of red and grey squirrels at the end of the model simulations, when grey squirrels are assumed to initially occupy all viable habitat, are shown in Fig. 2 (see also Suppl. material 1: Fig. S2). The regions where red squirrels persist in Fig. 2 can be defined as natural strongholds that would support red squirrel populations under a worst-case scenario of grey squirrel expansion across the whole of Scotland. The density of red and grey squirrels for this scenario is shown in Fig. 3a(i)–c(i). There are numerous natural strongholds, but they are often isolated and support low-density red squirrel populations. The qualitative nature of the simulations do not allow us to decide which strongholds would support viable red squirrel populations. The habitat composition for red-dominated regions (natural strongholds) and grey-dominated regions in Fig. 2 is shown in Fig. 4. Natural red squirrel strongholds are predicted for regions composed of conifer and pine species with a general absence of broadleaf and urban habitat. This is typical of large forest plantations in Scotland. Grey squirrel dominated regions contain broadleaf species and urban habitat and grey squirrels can occupy conifer and pine habitats where they are adjacent to broadleaf and urban habitats.

Fig. 3a(ii)–c(ii) shows red and grey squirrel densities, as well as squirrel occupancy, when grey squirrel trapping is applied in grid-squares that contain a grey squirrel population. The amount of trapping applied is equivalent to 18 trap-days per year in each

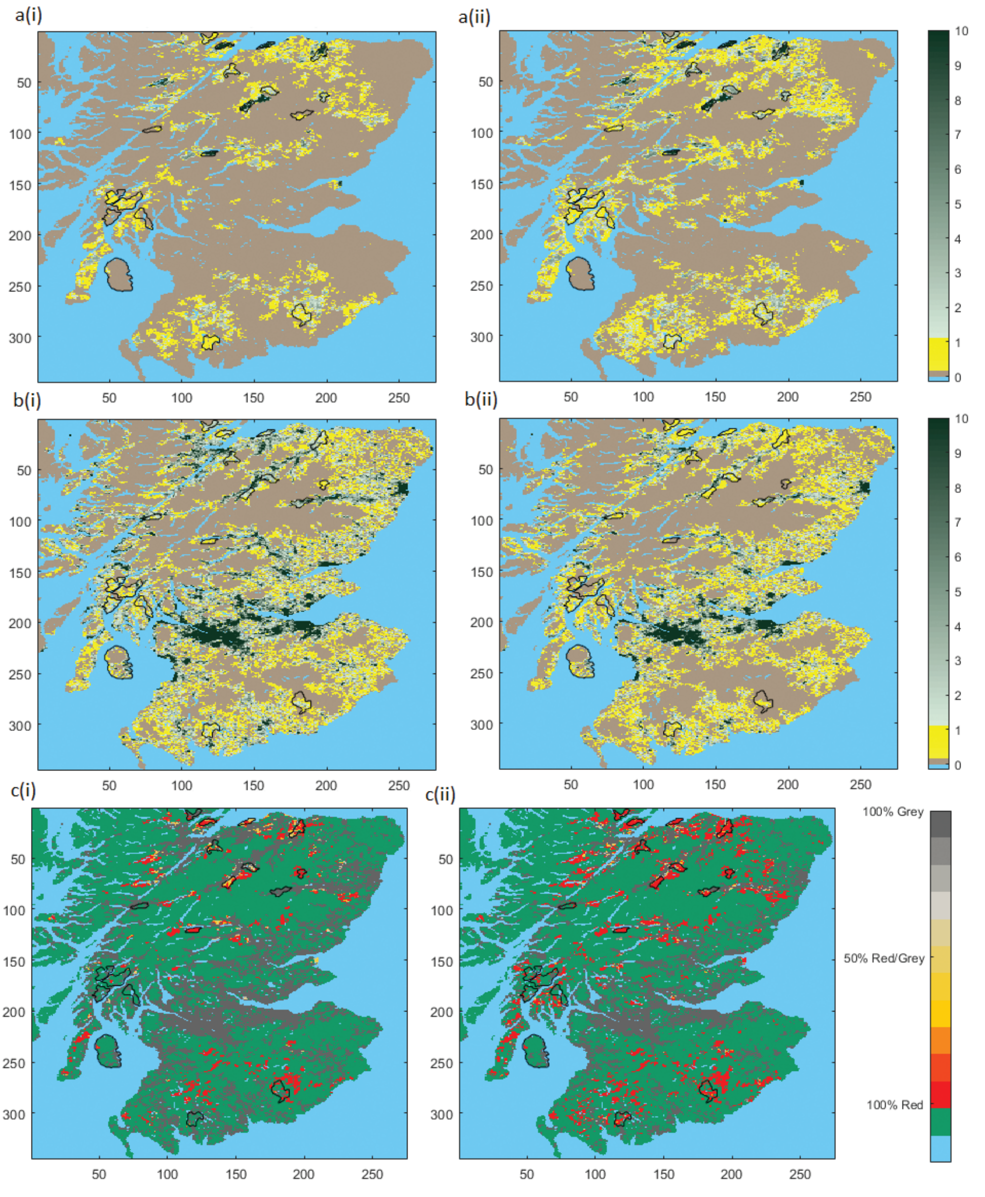

Figure 3. Density and occupancy results when grey squirrels have been introduced everywhere in Scotland. Here (**a**) shows the red squirrel density, (**b**) the grey squirrel density and (**c**) the occupancy results for (**i**) the simulation where no grey squirrel trapping was applied and (**ii**) the simulation where grey squirrel trapping (approx. 18 trap days per year) is applied to each grid square that contains grey squirrels. A grid square is classed as being occupied if there are 2 or more individuals of any species present. The 19 designated strongholds (Scottish Forestry 2020) are outlined in black.

grid cell. The results show that this level of grey squirrel trapping does not reveal new red squirrel strongholds, but does reinforce and enlarge existing natural strongholds. Increases in trapping effort further enhances this effect.

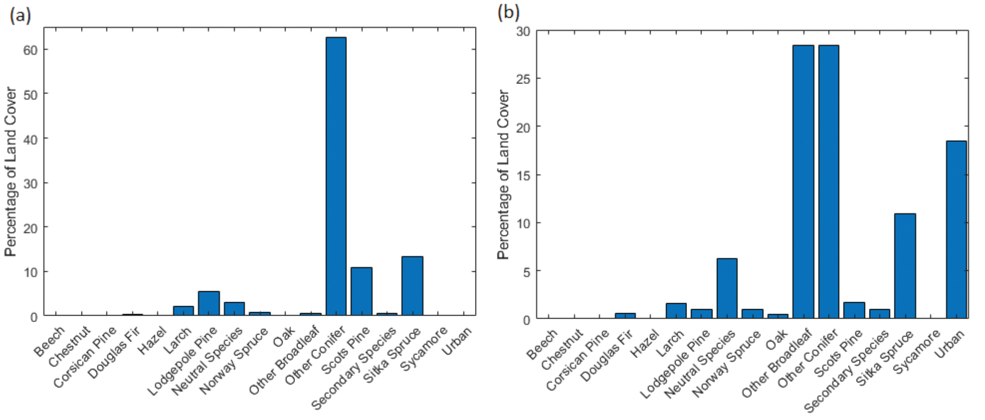

Figure 4. Habitat composition in regions where (**a**) red squirrels have greater than 80% occupancy and (**b**) grey squirrels have greater than 80% occupancy. Named species are from the National Forest Estate 2017 dataset whilst Other broadleaf and Other conifer data is from the National Forest Inventory 2016 dataset.

Discussion

In this study we have developed a spatial mathematical model that includes the competitive and disease interactions between red and grey squirrels in realistic habitats across Scotland to assess the viability of red squirrel populations under several scenarios of grey squirrel expansion. The current strategy for red squirrel conservation in Scotland aims to restrict or reduce the distribution of grey squirrels and to maintain viable red squirrel populations in priority areas for red squirrel conservation (Scottish Natural Heritage 2015). If this conservation strategy is successful (which observations suggest is currently the case (NBN Atlas Partnership 2017)) then the model predicts that there will be large expanses of forest north of the grey squirrel control boundary that support viable red squirrel populations.

The model allowed us to test 'what if' scenarios for red squirrel conservation and predicted that if current levels of grey squirrel control, which aim to restrict grey squirrels to their current distribution, were to end and grey squirrels were allowed to expand their range, then the process of red replacement would be slow. This would allow time for red squirrel conservation management policy to be implemented. Furthermore, during the period of grey expansion there would still remain large expanses of forest in north and north west Scotland that would support viable red squirrel populations. In the absence of control, grey squirrels are predicted to expand northwards, most notably along the north-east and northern coast, with their expansion directly north curtailed by geographical constraints (such as the Cairngorm mountains).

Our results support the current grey squirrel control efforts aimed at containing and removing grey squirrels from Aberdeen and the surrounding area (Scottish Natural Heritage 2015) as this will prevent grey squirrel expansion around the north-east and northern coast of Scotland. Expansion of grey squirrels into central or western Scotland is also impeded by the geography, with the Southern Highland mountains forcing grey squirrels to migrate along the west coast which provides poor habitat.

Since large-scale grey squirrel range expansion beyond their current distribution is prevented by geographical constraints on natural migration, it will be important to provide public information regarding the threat of grey squirrels to prevent artificial dispersal, whether accidental or intentional, across geographical barriers by members of the public. History shows that grey squirrel range expansion was facilitated by humans (e.g. see Signorile et al. 2016). Grey squirrels were introduced into Aberdeen and its surroundings via separate introductions, and considerable resources and effort have been required to keep these populations under control, with the goal of eradication occurring in the future (Scottish Natural Heritage 2015). Further evidence of the risks inherent in the deliberate introduction of grey squirrels can be found in Italy. Grey squirrels were introduced into Piedmont in northern Italy in 1948. Subsequent introductions into Genoa in the 1960s and translocations into Lombardy in the late 1990s have led to further grey squirrel expansion southwards into central Italy as well as northwards across the Po plain, where future expansion into France and Switzerland is a real possibility (Lurz et al. 2001; Martinoli et al. 2010; Signorile et al. 2014). This increase in grey squirrel range in Italy has led to a corresponding reduction in red squirrel density and highlights the need for public information campaigns that detail the risks and consequences of translocations to native wildlife and forestry.

An assumed worst-case scenario where grey squirrels have expanded to all regions in Scotland identified a range of forest regions across Scotland that could support red squirrels under UKFS management practice. We define these forest sites as natural strongholds (see Fig. 2). Several forest sites in the north of Scotland are able to maintain a potentially viable red squirrel population, despite the presence of grey squirrels. However, these sites are relatively small and isolated, with densities of around 2 red squirrels km^{-2}, potentially placing the red squirrel populations resident in the natural strongholds at risk due to stochastic extinction and loss of genetic diversity (Wauters et al. 1994). To overcome this problem, the disparate forests could either be physically connected via forest management, or the genetic viability of the populations could be managed and enhanced by periodic translocations of red squirrels. It should be noted that the density of red squirrels in natural strongholds under UKFS management is in line with that predicted in model studies for the designated strongholds under stronghold forest management (Slade et al. 2020). The study by Slade et al. (2020) also showed that the additional forest management required (above that of UKFS) to satisfy the designated stronghold policy (Forestry Commission Scotland 2012; Scottish Forestry 2020) may have little benefit to red squirrel viability in the absence of grey squirrels. Moreover, it was predicted that some of the designated strongholds could not protect red squirrels from the threat of grey squirrel invasion even when their composition was modified to satisfy designated stronghold policy. The model results presented in this paper also show that the locations of the natural strongholds do not match the locations of the 19 designated forest strongholds in Scotland (the designated strongholds are outlined in black in Fig. 2). Our findings suggests that natural strongholds could offer similar or improved protection to red squirrels, if threatened by grey squirrel invasion, as offered by the designated strongholds.

A potential red squirrel conservation strategy could employ grey squirrel control to reinforce the ability of natural strongholds to sustain a red squirrel population.

Fig. 3 a–c(ii) shows results for squirrel density and occupancy when grey squirrel trapping is applied in all regions where greys are present (see also Suppl. material 1: Section S3). Grey squirrel trapping is applied to all grid squares in which greys are present with approximately 18 trap-days per year per grid square. Although it is unrealistic to apply grey squirrel control across all regions, the model results highlight whether grey squirrel trapping would improve red squirrel viability in natural strongholds. North of the grey squirrel control boundary, grey squirrel trapping leads to an expansion of the regions of red occupancy and an increase in red squirrel density. There is a small expansion of red squirrel occupied regions in southern Scotland. This indicates that grey squirrel control around natural strongholds can lead to red squirrel expansion and improved population viability.

An analysis of the available land-cover data indicated that the forest composition of natural strongholds is comprised predominantly of Sitka spruce in southern Scotland and Sitka spruce, Scots and Lodgepole pine in northern Scotland combined with an absence of broadleaf and urban habitat. This forest composition is already met by forest plantations in the north of Scotland, which consequently act as natural strongholds. Management would still be required to maintain a suitable tree species composition and age structure, in the face of normal timber and harvesting operations, to provide an advantage to red squirrels over greys and to maintain a viable population in the long term. Nevertheless, a review and potential change in management policy for some designated strongholds in northern Scotland may allow current efforts and resources to be reassigned to focus on vulnerable red squirrel populations that are threatened by incursions of grey squirrels. Note, whilst broadleaf and urban habitats are suitable to support viable (high-density) red squirrel populations these habitats favour grey squirrels who out-compete reds. This analysis is supported by a recent statistical occupancy model for red and grey squirrels in Northern Ireland. This study used data collected by citizen science to show that red squirrel occupancy was positively correlated with coniferous woodland and negatively correlated with urban habitat. Likewise, grey squirrels were positively correlated with broadleaved forests and urban habitat and negatively correlated with coniferous habitat (Twining et al. 2020). The study also found a negative correlation between grey squirrels and pine marten (*Martes martes*), a native mustelid whose numbers are increasing, and a positive correlation between pine marten and red squirrels. Theoretical studies using a two prey-one predator ecoepidemic model have also shown that the predator (pine marten) can destabilise the previous grey squirrel dominant equilibria, favouring the native red squirrel (Travaglia et al. 2020). Thus, the impact of a native predator could aid red squirrel survival in the United Kingdom and Ireland via a reduction in grey squirrel density and geographic spread (Twining et al. 2020).

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 (Tompkins et al. 2003; Bosch and Lurz 2012), where the habitat consisted of broadleaved or mixed stands that could support high squirrel densities. The natural strongholds predicted in this study are dominated by coniferous habitats that generally support low-density red squirrel populations. The impact of squirrelpox on the location of, and red squirrel density in, natural strongholds was negligible. This is in line with previous studies that show squirrelpox cannot be supported in low-density red squirrel populations (White and Lurz 2014; Jones et al. 2017) and that red squirrels can therefore 'live' with the threat from squirrelpox. Hence, squirrelpox is unlikely to play a key role in grey squirrel invasion in low-density populations in Scotland (Lurz et al. 2015).

In this study we did not consider the impact of climate change on forest composition as it went beyond the scope of this project. However, we recognise that it will be an increasingly important factor in the red/grey squirrel dynamics and therefore red squirrel conservation in the future. Natural strongholds in Scotland largely coincide with managed forest plantations, due to their tree species composition. Thus, incorporating climate change into the model to identify natural strongholds would require knowledge of detailed future forest management plans. Climate change will influence the tree species composition in forests, maturation time and seed mast cycles (Neilson et al. 2005; Bisi et al. 2016) and will likely favour an increase in broadleaf trees through range expansion and species migration (Neilson et al. 2005). Grey squirrels have a competitive advantage in broadleaved habitat and can reach higher densities which may be able to support endemic squirrelpox virus (Tompkins et al. 2003; Rushton et al. 2006). This could make natural strongholds vulnerable to grey squirrel invasion and threaten red squirrel viability. Studies also suggest that climate change may lead to an increase in woodland cover (Ray 2008). This could increase the avenues northwards, above the grey squirrel control boundary, which would facilitate and increase the rate at which grey squirrels can colonise the remainder of Scotland. Conversely, the mountainous habitat that lies directly north of the control boundary could remain resistant to reforestation by climate change. Alternatively, climate change could increase the proportion of land in Scotland that is viable for agricultural use, which in turn could reduce the connectivity of Scottish forests (Gimona et al. 2012). This could aid red squirrels by reducing the ability of grey squirrels to expand their range, but such isolation may reduce genetic diversity and increase the risk of local population extinction. The impact of climate change on red squirrel conservation should therefore be the focus of future research efforts to help sustain viable populations in the long term.

Conclusion

Our findings highlight the existence of forest areas (natural strongholds) north of the grey squirrel control boundary that would currently support viable red squirrel populations without the need for species specific management. Natural strongholds, which often correspond to large commercial forest plantations, are managed according to UKFS policy and are typically composed of Sitka spruce and other conifer and pine species. Our predictions suggest grey squirrel dispersal and expansion will likely be slow even in the absence of grey squirrel control, due to geography in northern Scotland forming a barrier between the current distribution of red and grey squirrels. Together with recently published results (Slade et al. 2020) our findings here support a policy review to better target effort and resources for red squirrel conservation in Scotland.

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References

Barkalow F, Hamilton R, Soots R (1970) The vital statistics of an unexploited gray squirrel population. The Journal of Wildlife Management 34(3): 489–500. https://doi.org/10.2307/3798852

Bisi F, von Hardenberg J, Bertolino S, Wauters L, Imperio S, Preatoni D, Provenzale A, Mazzamuto M, 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. https://doi.org/10.1007/s10342-016-0969-4

Bosch S, Lurz PWW (2012) The Eurasian red squirrel: *Sciurus vulgaris*. Westarp Wissenschaften-Verlagagsgesellschaft, 206 pp.

Broome A, Connolly T, Quine C (2014) An evaluation of thinning to improve habitat for capercaillie (*Tetrao urogallus*). Forest Ecology and Management 314: 94–103. https://doi.org/10.1016/j.foreco.2013.11.038

Bryce J, Johnson P, Macdonald D (2002) Can niche use in red and grey squirrels offer clues for their apparent coexistence? Journal of Applied Ecology 39(6): 875–887. https://doi.org/10.1046/j.1365-2664.2002.00765.x

Carter N, Levin S, Barlow A, Grimm V (2015) Modeling tiger population and territory dynamics using an agent-based approach. Ecological Modelling 312: 347–362. https://doi.org/10.1016/j.ecolmodel.2015.06.008

Forestry Commission (2017) The UK Forestry Standard: The Government's approach to sustainable forestry. Forestry Commission. https://www.gov.uk/government/publications/the-uk-forestry-standard

Forestry Commission Scotland (2012) Managing forests as red squirrel strongholds. Forestry Commission Practice Note 102. https://forestry.gov.scot/publications/22-managing-forests-as-red-squirrelstrongholds/viewdocument

Gimona A, Poggio L, Brown I, Castellazzi M (2012) Woodland networks in a changing climate: Threats from land use change. Biological Conservation 149(1): 93–102. https://doi.org/10.1016/j.biocon.2012.01.060

Gurnell J, Wauters L, Lurz PWW, Tosi G (2004) Alien species and interspecific competition: Effects of introduced eastern grey squirrels on red squirrel population dynamics. Journal of Animal Ecology 73(1): 26–35. https://doi.org/10.1111/j.1365-2656.2004.00791.x

Heikkinen R, Poyry J, Virkkala R, Bocedi G, Kuussaari M, Schweiger O, Settele J, Travis J (2015) Modelling potential success of conservation translocations of a specialist grassland butterfly. Biological Conservation 192: 200–206. https://doi.org/10.1016/j.biocon.2015.09.028

Jones H, White A, Geddes N, Clavey P, Farries J, Dearnley T, Boots M, Lurz PWW (2016) Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel. Hystrix, the Italian Journal of Mammology 27(1): e11673. [6 pp.]

Jones H, White A, Lurz PWW, Shuttleworth C (2017) Mathematical models for invasive species management: Grey squirrel control on Anglesey. Ecological Modelling 359: 276–284. https://doi.org/10.1016/j.ecolmodel.2017.05.020

Lurz PWW, Rushton S, Wauters L, Bertolino S, Currado I, Mazzoglio P, Shirley M (2001) Predicting grey squirrel expansion in north Italy: A spatially explicit modelling approach. Landscape Ecology 16(5): 407–420. https://doi.org/10.1023/A:1017508711713

Lurz PWW, 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.

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

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

Middleton A (1930) 38. The ecology of the American grey squirrel (*Sciurus carolinensis gmelin*) in the British Isles. Proceedings of the Zoological Society of London 100(3): 809–843. https://doi.org/10.1111/j.1096-3642.1930.tb01000.x

NBN Atlas Partnership (2017) Scottish national biodiversity network atlas. https://scotland.nbnatlas.org

Neilson R, Pitelka L, Solomon A, Nathan R, Midgley G, Fragoso J, Lischke H, Thompson K (2005) Forecasting regional to global plant migration in response to climate change. Bioscience 55(9): 749–759. https://doi.org/10.1641/0006-3568(2005)055[0749:FRTGPM]2.0.CO;2

Ray D (2008) Impacts of climate change on forestry in Scotland – a synopsis of spatial modelling research. Forestry Commission Research Note 101(8): 1–8.

Renshaw E (1993) Modelling Biological Populations in Space and Time (Vol. 11). Cambridge University Press, 422 pp.

Rushton S, Lurz PWW, Gurnell J, Nettleton P, Bruemmer C, Shirley M, Sainsbury A (2006) Disease threats posed by alien species: The role of a poxvirus in the decline of the native red squirrel in Britain. Epidemiology and Infection 134(3): 521–533. https://doi.org/10.1017/S0950268805005303

Saving Scotland's Red Squirrels (2020) Saving Scotland's Red Squirrels, North-East Scotland. https://scottishsquirrels.org.uk/in-your-area/north-east-scotland/

Scottish Forestry (2020) Conserving Scotland's red squirrels. https://forestry.gov.scot/forests-environment/biodiversity/conserving-scotlands-red-squirrels

Scottish Natural Heritage (2015) Scottish Strategy for Red Squirrel Conservation. Technical report, Scottish Natural Heritage, 13 pp.

Signorile A, Paoloni D, Reuman D (2014) Grey squirrels in central Italy: A new threat for endemic red squirrel subspecies. Biological Invasions 16(11): 2339–2350. https://doi.org/10.1007/s10530-014-0668-3

Signorile A, Lurz PWW, Wang J, Reuman D, Carbone C (2016) Mixture or mosaic? genetic patterns in UK grey squirrels support a human-mediated 'long-jump' invasion mechanism. Diversity & Distributions 22(5): 566–577. https://doi.org/10.1111/ddi.12424

Slade A, White A, Kortland K, Lurz PWW (2020) An assessment of long-term forest management policy options for red squirrel conservation in Scotland. Hystrix, the Italian Journal of Mammology 31(2): 1–11.

Tompkins D, White A, Boots M (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. Ecology Letters 6(3): 189–196. https://doi.org/10.1046/j.1461-0248.2003.00417.x

Travaglia E, La Morgia V, Venturino E (2020) Poxvirus, red and grey squirrel dynamics: Is the recovery of a common predator affecting system equilibria? Insights from a predator-prey ecoepidemic model. Discrete & Continuous Dynamical Systems-B 25(6): 2023–2040. https://doi.org/10.3934/dcdsb.2019200

Twining J, Montgomery W, Tosh D (2020) Declining invasive grey squirrel populations may persist in refugia as native predator recovery reverses squirrel species replacement. Journal of Applied Ecology: 1–13. https://doi.org/10.1111/1365-2664.13660

Wauters L, Hutchinson Y, Parkin D, Dhondt A (1994) The effects of habitat fragmentation on demography and on the loss of genetic variation in the red squirrel. Proceedings of the Royal Society of London – Series B, Biological Sciences 255(1343): 107–111. https://doi.org/10.1098/rspb.1994.0015

White A, Lurz PWW (2014) A modelling assessment of control strategies to prevent/reduce squirrelpox spread. In Scottish Natural Heritage: Commissioned Report No. 627.

White A, Lurz PWW, Bryce J, Tonkin M, Ramoo K, Bamforth L, Jarrott A, Boots M (2016) Modelling disease spread in real landscapes: Squirrelpox spread in southern Scotland as a case study. Hystrix, the Italian Journal of Mammology 27(1): 1–8.

Supplementary material 1

Details on carrying capacity, habitat and grey squirrel trapping

Authors: Andrew Slade, Andy White, Kenny Kortland, Peter Lurz

Data type: Images, modelling details, extra results

Explanation note: The supplementary information also includes extra results that, whilst informative, were not deemed necessary in the main manuscript.

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