The use of mathematical models in red squirrel conservation: Assessing the threat from grey invasion and disease to the Fleet basin stronghold.

Andy White[1], Peter W.W. Lurz[2], Hannah E. Jones[1], Mike Boots[3], Jenny Bryce[4], Mel Tonkin[5], Karen Ramoo[5], Lindsay Bamforth[5]and Andrew Jarrott[6].

[1]Department of Mathematics and the Maxwell Institute for Mathematical Sciences, Heriot-Watt University, Edinburgh, EH14 4AS.

[2]Lurzengasse 3, D-97236 Randersacker, Germany.

[3]Biosciences, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Treliever Road, Penryn, Cornwall, TR10 9EZ.

[4]Scottish Natural Heritage, Great Glen House, Leachkin Road, Inverness, IV3 8NW

[5]Scottish Wildlife Trust, Harbourside House, 110 Commercial Street, Edinburgh, EH6 6NF

[6]Forestry Commission Scotland, Galloway Forest District, Newton Stewart, DG8 6AJ

Corresponding Author: Andy White – a.r.white@hw.ac.uk

Summary

We present an overview of mathematical modelling techniques that have been used to represent the interaction of red and grey squirrels in the UK. These models simulate competition between red and grey squirrels and the impact of a shared disease - squirrelpox - that is carried by greys and lethal to red squirrels. The models indicate that both competition and disease have been responsible for the replacement of reds by greys. We also present a new model analysis that has been used to assess the conservation of red squirrels in the Fleet basin red squirrel stronghold, Dumfries and Galloway. The model suggests that the exclusion of greys from the stronghold via control is sufficient to protect reds from replacement in the stronghold. However, disease can spread from greys outside to reds inside the stronghold leading to periodic outbreaks of infection in the red population. These disease outbreaks lead to population reductions in red squirrels, followed by disease fade-out and the subsequent increase of reds population density to pre-infection levels.

Overview of models of the UK squirrel system

There is a long history of using mathematical models to help understand species interactions and the population dynamics of ecological systems. In 1926 Lotka and Volterra developed mathematical frameworks to understand dynamics of interacting species (see Murray 2002), highlighting, for example, that population cycles could be generated through predator-prey interactions. In parallel with this has been the development of models of infectious disease, where Kermack and McKendrick (1927) (later extended by Anderson and May, 1979) proposed a compartmental model that separated the host into Susceptible, Infected or Recovered classes (the SIR model) to describe the population dynamics of infectious disease (see Murray 2002). A key result outlined the concept of the basic reproductive ratio of the disease, R_0. When $R_0>1$ the disease can persist in the population. These frameworks are a greatly simplified representation of the real world and focus primarily on laying bare the key mechanisms that occur within ecological systems. Nevertheless these model structures underpin many of the more recent, sophisticated models that aim to include additional biological realism to answer current questions in ecology and conservation. In particular, they have been a crucial tool to understand the complex interactions of competition, disease and landscape features in the replacement of red by grey squirrels in the UK.

The earliest mathematical model of the red and grey squirrel system was developed by Okubo et al. (1989). They extended the Lotka-Volterra competition framework to include the spatial dispersal of squirrels by including a diffusion term to represent random movement. They parameterised the model from life history data and assumed that grey squirrels have a competitive advantage over reds. Their aim was to show how competitive pressure from greys could lead to the observed expansion in the distribution of greys and replacement of reds. Their work showed that a travelling (invasion) wave would spread from the point of grey squirrel introduction, transforming red squirrel populations in the absence of greys in front of the wave to grey squirrel only populations behind the wave. A detailed comparison with observed red replacement was not presented, due largely to lack of available data, but Okubo et al. (1989) concluded that a general form of competition was sufficient to account for the progressive replacement of red by grey squirrels in England and Wales.

Rushton et al. (1997) developed an alternative approach for modelling red and grey squirrel competition. They developed individual based models to represent reproduction, mortality, competition and dispersal of red and grey squirrels on a realistic habitat (obtained through Geographical Information Systems (GIS) analysis of satellite landcover data and forestry records). The population processes in this framework are modelled using rule-based algorithms. They compared the model findings with the observed replacement of reds by greys in Norfolk, East Anglia between 1960 and 1981 (Reynolds 1985). The model predicted the competitive replacement of reds, but the closest fit to the observed expansion of grey squirrels and decline in reds required that mortality was lower and fecundity higher in grey squirrels than that obtained from field estimates. This led to an extension of the rule-based modelling framework to additionally include the impact of squirrelpox virus (SQPV). SQPV is carried by but harmless to grey squirrels but leads to high levels of mortality in red squirrels. The model results were again compared to the findings of Reynolds (1985) and Rushton et al. (2000) concluded that SQPV like interspecific competition could have led to the replacement of reds in Norfolk. This modelling approach has also been used, successfully, to predict the expansion of grey squirrels in North Italy (Lurz et al. 2001), to assist in the development of landscape-scale conservation strategies in the North of England (Lurz et al. 2003, Gurnell et al. 2006) and has been extended to understand the population dynamics of a range of squirrel species (Rushton et al. 2006 and see Lurz et al. 2008 for a review).

The data of Reynolds (1985) on the replacement of red squirrels in Norfolk was also the focus of a modelling study by Tompkins et al. (2003) who combined the classical deterministic techniques for modelling competition (as in Okubo et al. 1989) and infectious disease (Anderson & May 1979) to assess the impact of disease-mediated invasion. Tompkins et al. (2003) used a simplified representation of habitat where the carrying capacity was the same in each of an array of 5km by 5km grid squares. They showed how simulation with competition alone could not replicate the replacement of reds by greys observed in the field but that including SQPV in addition to competition was essential for the model results to match observations. The model provided an intuitive biological explanation for the enhanced replacement and showed that SQPV induces an epidemic in red squirrels that greatly reduces their density, and invading greys can therefore replace reds more rapidly. Furthermore, the model showed that although SQPV is a key driver of red replacement, the density of infected individuals at any time is low (due to the high virulence of SQPV in reds) and therefore would be difficult to observe in the field. Tompkins et al. (2003) emphasised that the role of pathogens must be considered when assessing the impact of species introductions and that mathematical models could be extended to understand specific questions in the ecology and conservation biology of the UK squirrels system.

The deterministic approach of Tompkins et al. (2003) provides a clear understanding of influential mechanisms that arise between interacting populations that share a disease, but cannot accurately assess the risk of invasion of grey squirrels or SQPV spread since they do not include the chance of extinction or disease fade-out at low density that may arise through stochasticity. The rule-based approaches of Rushton et al. (1997, 2000, 2006) include stochasticity, but here it is difficult to determine the key drivers of the population dynamics due to the complicated arrangement of rules and large number of model parameters. To answer specific issues regarding the conservation of UK red squirrels White et al. (2014) considered a framework that lay between the two previous approaches. They developed a stochastic version of the model of Tompkins et al. (2003) and used it to assess the importance of grey competition and SQPV in forests managed for red squirrel conservation (termed strongholds; see Parrott et al 2009 for a historical overview of red squirrel conservation). Strongholds are local forest regions that are large enough to sustain viable red squirrel populations over the long-term, and in which habitat composition and management offers native red squirrels a competitive advantage over greys. White et al. (2014) indicated that in regions where grey squirrels have a competitive advantage over reds, control was required to prevent grey invasion and protect red populations within the stronghold. A key result indicated that SQPV spread from adjacent grey populations could lead to epidemic outbreaks in reds in the stronghold even when the invading species is prevented from establishing. The model predicted that there would be periodic SQPV epidemics that lead to a population crash in reds in the stronghold, followed by disease fade-out and the subsequent increase of reds population density to pre-infection levels. The model predictions are supported by evidence from UK red squirrel strongholds in Formby and Whinfell, where reds are protected by trapping and removal of greys but have suffered repeated outbreaks of SQPV (Parrott et al. 2009).

The stochastic framework of White et al. (2014) provided a clear understanding of the role of disease in conservation strongholds, however, the spatial set-up was idealised. In the rest of this study we therefore show how the framework of White et al. (2014) can be extended to examine the red-grey-SQPV system on a realistic landscape that includes habitat information extracted from digitised landcover maps using GIS (see also White and Lurz 2013).

A mathematical model of the Fleet basin red squirrel stronghold

The modelling strategy developed in White et al. (2014) can be extended to examine specific stronghold systems. In consultation with Scottish Natural Heritage (SNH), the Scottish Wildlife Trust (SWT) and the Forestry Commission Scotland (FCS) we chose the Fleet basin red squirrel stronghold, Dumfries and Galloway to provide a case-study example.

The Fleet basin red squirrel stronghold is contained within the National Forest Estate and habitat composition was extracted using the Forestry Commission Scotland Database (Forestry Commission 2014). This provides species level information within Forestry Commission controlled regions and generic tree type classification (conifer, broadleaf, shrub) for all remaining regions. Habitat composition can be combined with estimates of red and grey squirrel abundance from trapping data in different forest types. We note that the density estimates are derived from studies across the UK and therefore provide potential population levels that these forest types can support. These are used to produce carrying capacity estimates at a 1 km grid square level (Figure 1). Therefore these do not represent current red and grey squirrel density but the potential density of each species in the absence of the other. The Fleet basin stronghold can be identified as the inner rectangle in Figure 1 (a 15km x 16km area), with model simulations being undertaken for the region within the outer rectangle (a 45km x 50km area).

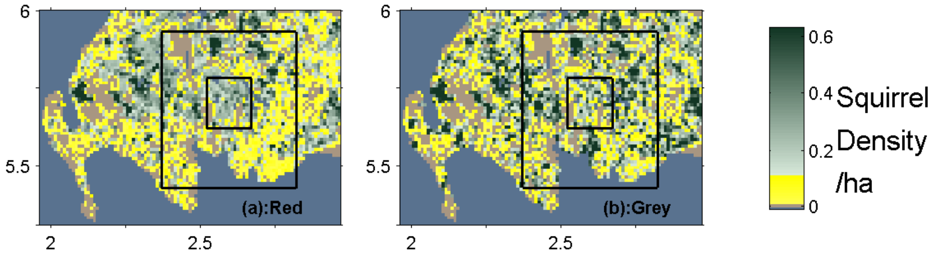

Figure 1: Carrying capacity estimates for (a) red and (b) grey squirrels for South West Scotland where the inner rectangle represents the Fleet basin stronghold and model simulations are undertaken for the region within the outer rectangle. The axes show easting and northing values (/10^6).

Within each grid patch the population dynamics of red and grey squirrels and SQPV infection are represented by the individual based, stochastic model outlined in White et al.

(2014). The dynamics of susceptible and infected red (S_R and I_R) and grey (S_G and I_G) squirrels and recovered (immune) greys (R_G) within each 1 km grid square are represented by the event probabilities shown in Table 1.

Birth of Grey to S_G	$P(S_G \to S_G + 1)$	$:\left[(a_G - q_G(H_G + c_R H_R))H_G\right]/R$
Natural Death of S_G	$P(S_G \to S_G - 1)$	$:\left[bS_G\right]/R$
Infection of Grey	$P(S_G \to S_G - 1, I_G \to I_G + 1)$	$:\left[\beta S_G\left((I_G + I_R) + \theta \sum_{Adjacent}(I_G + I_R) + \theta^2 \sum_{Corner}(I_G + I_R)\right)\right]/R$
Natural Death of I_G	$P(I_G \to I_G - 1)$	$:\left[bI_G\right]/R$
Recovery of Grey	$P(I_G \to I_G - 1, R_G \to R_G + 1)$	$:\left[\gamma_G I_G\right]/R$
Natural Death of R_G	$P(R_G \to R_G - 1)$	$:\left[bR_G\right]/R$
Birth of Red to S_R	$P(S_R \to S_R + 1)$	$:\left[(a_R - q_R(H_R + c_G H_G))H_R\right]/R$
Natural Death of S_R	$P(S_G \to S_G - 1)$	$:\left[bS_R\right]/R$
Infection of Red	$P(S_R \to S_R - 1, I_R \to I_R + 1)$	$:\left[\beta S_R\left((I_G + I_R) + \theta \sum_{Adjacent}(I_G + I_R) + \theta^2 \sum_{Corner}(I_G + I_R)\right)\right]/R$
Death of I_R	$P(I_R \to I_R - 1)$	$:\left[(b + \alpha)I_G\right]/R$
Dispersal of S_G	$P(S_G \to S_G - 1)$	$:\left[mS_G \exp\left(-\left(K_G - (H_G + c_R H_R)\right)\right)\right]/R$

Table 1: The stochastic individual based model that represents the red-grey-SQPV dynamics within each 1km grid square. Model parameters are taken from White et al. (2014) : $a_G = 1.2$, $a_R = 1.0$, $b = m = 0.4$, $\alpha = 26$, $\gamma_G = 13$; with the exception of $\beta = 0.55$ taken from White & Lurz (2013). The carrying capacities K_R and K_G are shown in Figure 1 for each grid patch and are used to derive the crowding parameters q_R, q_G respectively.

Here, $H_G = S_G + I_G + R_G$ and $H_R = S_R + I_R$ represent the total squirrel populations and $R = \sum[rates]$ (the sum of the terms in square brackets). We follow Tompkins et al. (2003) and assume the two species have the same rate of adult mortality, b, but different rates of maximum reproduction (a_R, a_G). Within each 1km x 1km grid square the two species have different carrying capacities (K_R, K_G) (as shown Figure 1) and these lead to grid square dependent susceptibilities to crowding (q_R, q_G) (since $q = (a - b)/K$). The competitive effect of grey squirrels on red squirrels is denoted by c_G, whilst that of red squirrels on grey squirrels is denoted by c_R. A key model assumption is that greys outcompete reds in most habitats, except those that are predominantly composed of Sitka Spruce (*Picea sitchensis*; see White and Lurz 2013).

Squirrelpox virus is transmitted at the rate β both within and between each squirrel species with infected reds dying due to the disease at rate α and infected greys recovering at rate γ. Due to daily squirrel movement within a core range of radius, $\theta = 0.15$ km, transmission can occur from infected squirrels within the focal grid square and also from the 8 neighbouring grid cells (with adjacent and corner cells weighted appropriately). Dispersal can occur from the focal cell to neighbouring cells at rate m. Here we set $m = b$ to reflect that on average there is one long distance dispersal event in a squirrels lifetime. The exponential function represents saturation dispersal (Rushton et al. 2000) which reflects the situation in which squirrels are less likely to disperse when the absolute density in the grid patch is below the carrying capacity and more likely to disperse when above it. In other words, when resources are plentiful in a patch and numbers are below what can be supported, squirrels will not disperse. In equation (1) the dispersal probability is shown for S_G but similar terms are used to represent dispersal in other classes. The time between events is an exponentially distributed random variable and can be determined as $T_{event} = -\ln(\sigma)/R$ where σ is a random number drawn from a uniform distribution between 0 and 1 (see Renshaw 1991). The events are incremented at random with the associated probabilities updated due to changes in population density after each event. Individual simulations can be undertaken using a Gillespie algorithm and provide information of the behaviour in a single realisation. Monte Carlo methods can be used to generate multiple simulations to assess the average behaviour and variability across realisations (see White et al. 2014 for further details of the model set-up).

Initial conditions were broadly based on current red and grey squirrel distribution data from Saving Scotland's Red Squirrels (SSRS). Hence we assumed red and grey squirrels are at 50% of their respective carrying capacities for regions north and east of the Fleet basin stronghold. Within the stronghold and to the south and west of the stronghold we assume reds are at 95% and greys at 5% of their carrying capacity. This assumption allows an investigation of the potential replacement of reds by greys. The disease is introduced into two areas - to the North East and South East representing New Galloway and Kirkcudbright respectively - at the beginning of each year to represent the threat of SQPV infection from populations outwith, but near the stronghold. This approximates regions where seropositive greys have been reported to the Saving Scotland's Red Squirrels project.

The population and disease dynamics in the Fleet Stronghold without control

Ten replicate simulations were undertaken and the results for a single realisation are shown in Figure 2. The single realisation presented is representative of the other model runs that were undertaken. The results indicate that greys can increase and replace reds in much of the region. This occurs as parameter values assume that greys outcompete reds in most habitats except regions predominantly dominated by Sitka Spruce. Note, however that in model simulations greys were initialised with low density within and to the south and west of the Fleet stronghold. In reality greys may not currently be present in some of these regions and would therefore need to disperse into these regions before replacement could occur – and so the model results highlight the potential for red replacement. Reds are not replaced in some parts of the Fleet Stronghold and to the North West of this region where the habitat is Sitka dominated. This emphasises how red squirrel densities can be sustained in habitats in which red squirrels have a competitive advantage over greys and calls for a better understanding of the potential densities and competitive ability of reds and greys across conifer dominated forest and their species mixtures in the field. There is still a knowledge gap in our ecological understanding of grey squirrels in conifer dominated landscapes!

The disease dynamics indicating the occurrence of infection each year in red and grey squirrels in a single model realisation is shown in Figure 2c. The disease spreads rapidly through populations where grey squirrels are at a sufficiently high density and results in infection in both reds and greys (indicated by the orange regions in Figure 2c to the north and east of the Fleet stronghold). This results in population crashes in red populations and their rapid replacement by greys. This is followed by epidemic outbreaks in red and grey populations in the Fleet stronghold, which occur periodically and will result in population crashes in red squirrel density. Red squirrel density can recover following these epidemics as there are areas where red squirrels persist for the 30 year duration of the simulation (see White and Lurz (2013) for further details).

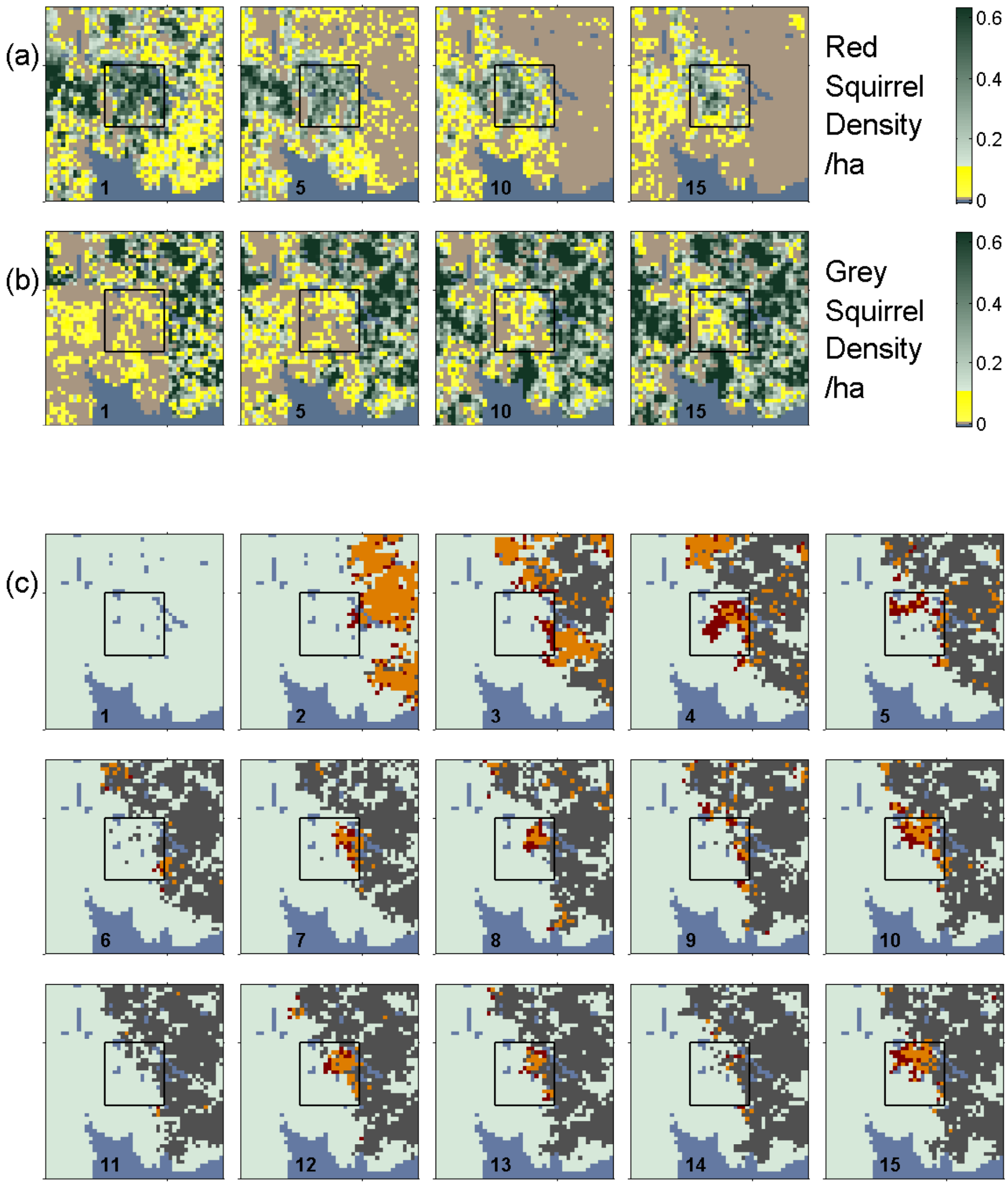

Figure 2: Population and disease dynamics for the model with no grey squirrel control for the region in the south west of Scotland represented by the large rectangle in Figure 1, with the inner rectangle representing the Fleet basin stronghold. (a) shows red squirrel density and (b) grey squirrel density for the years indicated in the figure for a representative model simulation. (c) indicates where SPQV infectious outbreaks occur in red populations (red), grey populations (grey) or both red and grey populations (orange) for the first 15 year of the model simulation. See the main text for initial conditions and recall that infected greys are introduced at the eastern boundary.

The population and disease dynamics in the Fleet Stronghold with control

In the field the Fleet basin stronghold and neighbouring areas are monitored, with trapping and removal applied in areas where grey squirrels are observed. To represent this in the model we set grey squirrel numbers within the Fleet stronghold region to zero every 3 months. The effort required in the model to exclude greys from the Fleet stronghold is the removal of approximately 100 squirrels per year (Figure 3).

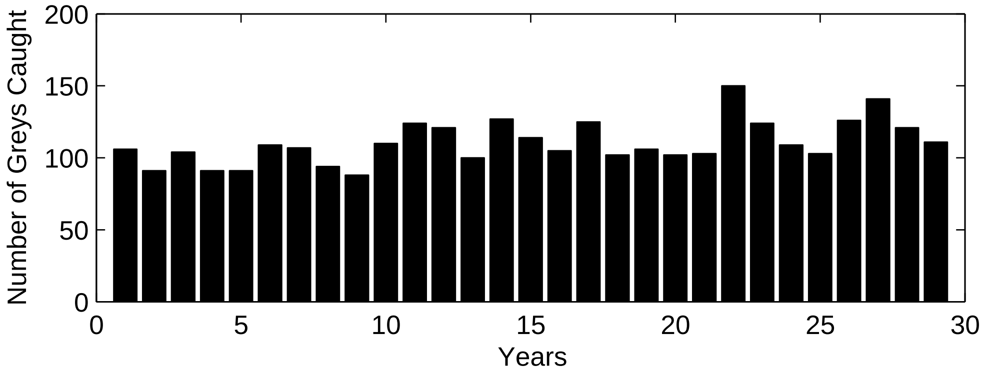

Figure 3: The number of greys removed each year to maintain the Fleet basin stronghold as a grey-free zone for a representative model realisation.

The results of the model with grey control for a single realisation showing the density of red and grey squirrels are illustrated in Figure 4. The control of greys allows red squirrels to persist in suitable habitat in the Fleet stronghold. The control of greys does not appear to enhance red density or survival beyond the stronghold (the change in the density of reds and greys are similar with or without control in regions outside the Fleet stronghold). These results highlight that grey control can be an effective local measure to protect red populations in strongholds. The level of control required will depend on the density of grey squirrels in neighbouring habitats and the connectedness of these habitats to the stronghold. The more isolated the stronghold, the less control is required (see White et al. 2014).

The disease dynamics indicating the occurrence of infection in reds and greys in a single model realisation with control is shown in Figure 4c. The exclusion of greys from the Fleet stronghold reduces the occurrence of SQPV outbreaks in the stronghold. Disease still spreads rapidly through grey populations to the north and east of the stronghold and connections between these populations and the stronghold leads to periodic outbreaks of infection in red populations within the stronghold. The outbreaks are often localised to the boundary of the Fleet stronghold. However more wide spread outbreaks can occur in the stronghold, which can cause population crashes in red populations (see year 15 in Figure 4c). In Figure 5 we show the red squirrel density over time in a 1 km x 1 km grid square in which there is an SQPV outbreak. It can be seen that the red squirrel density drops rapidly to around 40% of its potential density due to the SQPV outbreak between years 14 and 16. This is followed by disease fade-out and the increase of red squirrel population abundance to pre-infection levels.

A key message therefore is that while control can protect red squirrel populations from exclusion by greys in strongholds, it cannot prevent periodic outbreaks of

disease within the stronghold (which is transmitted through red only populations). The outbreak of infection in strongholds should therefore not be considered a failure in the conservation strategy and prevention of disease spread is difficult to achieve. The model also predicts that red squirrel numbers will recover following the epidemic outbreak provided control measures are continued. The results here for the model on a realistic landscape support those of White et al. (2014) in which a simplified spatial structure is used. (Further analysis of these results can be found in White and Lurz (2013).)

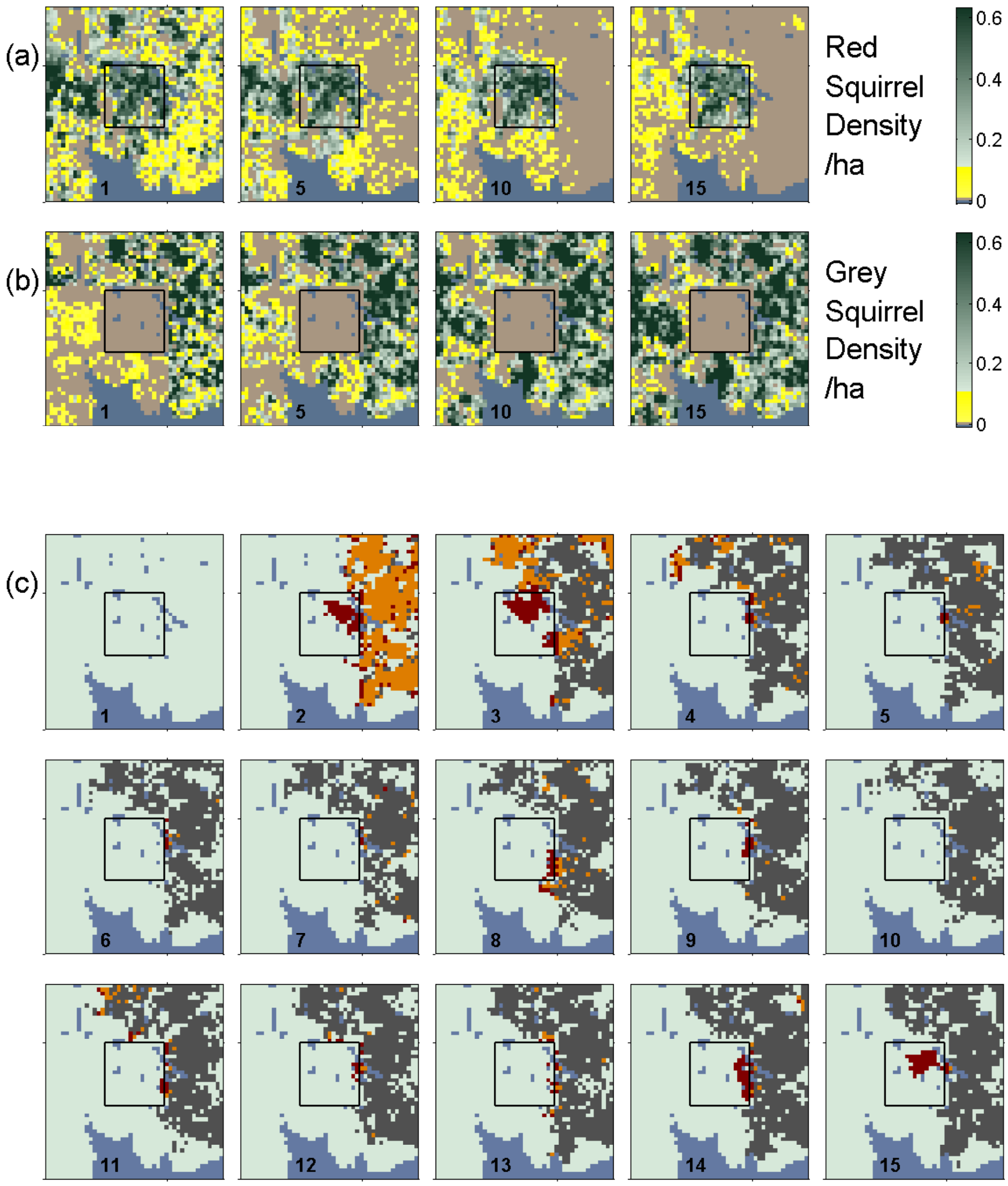

Figure 4: Population and disease dynamics for the model with grey squirrel control for the region in the south-west of Scotland represented by the large rectangle in Figure 1, with the inner rectangle representing the Fleet basin stronghold. (a) shows red squirrel density and (b) grey squirrel density for the years indicated in the figure for a representative model simulation. (c) indicates where SPQV infectious outbreaks occur in red populations (red), grey populations (grey) or both red and grey populations (orange) for the first 15 year of the model simulation. See the main text for initial conditions and recall that infected greys are introduced at the eastern boundary.

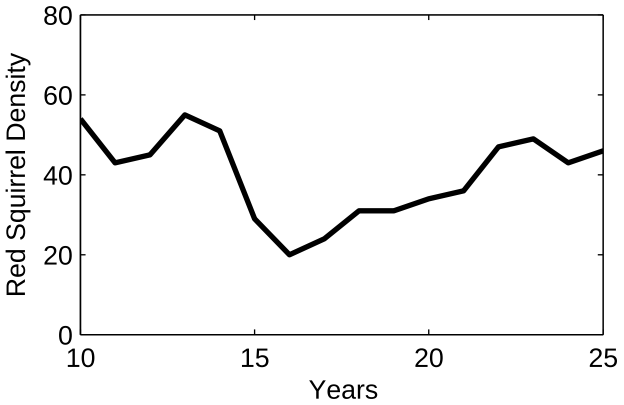

Figure 5: The density of red squirrels in an example 1km x 1km grid patch in the stronghold over time with grey squirrel control. The grid patch is located in the region in which a squirrelpox outbreak occurs within the Fleet basin stronghold in years 14-15 in Figure 4 and leads to the observed population reduction.

Discussion

In this study we have presented a historical overview of the way in which mathematical models have been used to understand the red-grey-SQPV system. Theoretical results played a key role in highlighting the importance of SQPV in the replacement of red squirrels in the UK and emphasised that low visibility of infection does not equate to low importance of the disease (Tompkins et al. 2003). This led to a fundamental shift in our understanding of red-grey squirrel interactions and a change in the strategy of how best to conserve red squirrels over the last 10-15 years. It illustrates the role mathematical models can play and how they can be used to develop conservation management strategies in the face of disease-mediated invasion by introduced alien species.

In the case of the Fleet basin stronghold, model predictions indicate the following key results.

- Red squirrel populations survive in the absence of grey control in habitat regions in which they have a sufficient competitive advantage only (Sitka Spruce dominated forests). This emphasises the need for a better understanding of red and grey squirrel potential densities and competitive interactions in specific conifer tree species mixtures. Much of the data for red and grey abundance, with the exception of Bryce (2000), is derived from mixed forest populations in England and Wales (e.g. Smith 1999, Cartmel 2000, Kenward et al. 1998) and there is still an acute lack of knowledge of grey squirrel ecology in spruce dominated forest landscapes.

- Squirrelpox spreads rapidly through well-connected grey squirrel communities once grey populations are established and at sufficiently high density. This has potential consequences for the spread of SQPV through squirrel populations in Southern Scotland and indicates that it may be very difficult to prevent disease spread to the high density grey populations in Central Scotland.

- Grey squirrel control is an effective measure to protect red populations in strongholds. Evidence for the effectiveness of strongholds is, for example, provided by the long-term persistence of reds in the English strongholds at Formby, and Whinfell and the repopulation of reds in Anglesey (see Shuttleworth et al., this volume Chapter X; Seeward and O'Hara, this volume Chapter X).

- Outbreaks of SQPV may occur periodically within the stronghold and result in red squirrel populations crashes. The extent of SQPV epidemics within the stronghold is variable and often confined to localised areas at the boundary of the stronghold. A key message therefore is that while control can protect red squirrel populations from exclusion in strongholds it cannot prevent periodic outbreaks of disease within the stronghold. Therefore disease outbreaks in protected red populations should not be seen as a failure in the conservation strategy as red population density is predicted to recover if control is maintained.

The work here indicates that modelling frameworks that represent complex, realistic habitat and the stochastic nature of invasion and disease spread can be an important conservation management tool and help optimise conservation strategy and policy.

Acknowledgements
AW and PL were partly supported through a partnership project with SNH. AW, PL and MB were partly supported by a University of Exeter, NERC Impact Acceleration Award (NE/L012782/1).

References

Anderson RM, May RM (1979) Population biology of infectious diseases: Part I. *Nature* 280: 361-367.

Bryce J (2000) *Habitat use by sympatric populations of red and grey squirrels: the implications for conservation management*. PhD Thesis, Oxford University, UK.

Cartmel S (2000) *Squirrel ecology in a conifer forest in North Wales*. PhD thesis, Queen Mary & Westfield College, University of London.

Forestry Commission (2014) http://www.forestry.gov.uk/datadownload.

Gurnell J, Rushton SP, Lurz PWW, Sainsbury AW, Nettleton P (2006) Squirrel poxvirus: Landscape scale strategies for managing disease threat. *Biological Conservation* 131: 287-295.

Kenward RE, Hodder KH, Rose RJ, Walls CA, Parish T, Holm JL, Morris PA, Walls SS, Doyle FI (1998) Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. *Journal of Zoology* 244: 7-21.

Kermack WO, McKendrick AG (1927) A contribution to mathematical thoery of epidemics. *Proceedings of the Royal Society of London* A 115: 700-721.

Lurz PWW, Rushton SP, Wauters LA, Bertolino S, Currado I, Mazzoglio P. (2001) Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. *Landscape Ecology* 16: 407-420.

Lurz PWW, Geddes N, Lloyd AJ, Shirley MDF, Rushton SP, Burlton B (2003) Planning red squirrel conservation areas: using spatially explicit population dynamics models to predict the impact of felling and forest design plans. *Forestry* 76: 95-108.

Lurz PWW, Koprowski JL, Wood DJA (2008) The use of GIS and modelling approaches in squirrel population management and conservation: a review. *Current Science* 95: 7.

Murray JD (2002) *Mathematical Biology (Third Edition)*. Springer-Verlag, New York.

Okubo A, Maini PK, Williamson MH, Murray JD (1989) On the spatial spread of the grey squirrel in Britain. *Proceedings of the Royal Society of London* B 238: 113-125.

Parrott D, Quy R, van Driel K, Lurz PWW, Rushton S, *et al.* (2009) *Review of red squirrel conservation activity in northern England*. Natural England Contract No. 08/09/N/004.

Renshaw E (1991) *Modelling biological populations in space and time*. Cambridge University Press, Cambridge.

Reynolds JC (1985) Details of the geographic replacement of the red squirrel (Sciurus vulgaris) by the grey squirrel in eastern England. *Journal of Animal Ecology* 54: 149-162.

Rushton SP, Lurz PWW, Fuller R, Garson PJ (1997) Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology* 34: 1137–1154.

Rushton SP, Lurz PWW, Gurnell J, Fuller R. (2000) Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology* 37: 997–1012.

Rushton SP, Wood DJA, Lurz PWW, Koprowski JL (2006) Modelling the population dynamics of the Mt. Graham red squirrel: can we predict its future in a changing environment with multiple threats? *Biological Conservation* 131: 121-131.

Smith DFE (1999) *Grey squirrel, Sciurus carolinensis, population dynamics and feeding in a conifer forest*. Ph. D. Thesis, University of London.

Tompkins DM White AR, Boots M (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters* 6: 189-196.

White A, Lurz PWW (2013) *A modelling assessment of control strategies to prevent/reduce Squirrelpox spread*. Scottish Natural Heritage Commissioned Report No. 627.

White A, Bell SS, Lurz PWW, Boots M (2014) Conservation management within strongholds in the face of disease-mediated invasions: red and grey squirrels as a case study. *Journal of Applied Ecology DOI: 10.1111/1365-2664.12274.*