



Research Note

Modelling ecological networks and dispersal in grey squirrels

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Understanding the role of the landscape matrix in species dispersal is important when targeting conservation and management strategies. This Research Note shows how least-cost modelling was used to assess invasive grey squirrel *Sciurus carolinensis* dispersal movements within the UK, with a focus on the county of Cumbria. Two major networks were identified separated by the Cumbrian Mountain range. This indicated that there may be multiple colonisation routes into the county. These findings were supported by evidence from DNA sequencing of seven grey squirrel populations. Least-cost model predictions were further validated through data from five global positioning system (GPS) collared grey squirrels. Buffered least-cost path analysis and the development of a least-cost corridor model enabled the most likely grey squirrel dispersal routes to be identified and validated using GPS data. To provide information on movements and land cover use, the individual movements of each squirrel were assessed. A case study was then used to highlight how the validated least-cost model can be applied to areas where red squirrels *Sciurus vulgaris* are still threatened by the invasive grey squirrel to provide information to target management and conservation actions. The findings should influence management strategies for grey squirrel control and conservation of the native red squirrels.

Introduction

The eastern grey squirrel *Sciurus carolinensis* is a species of tree squirrel native to the broadleaved woodlands of North America. In Great Britain the species was initially introduced in the 1870s and has since been able to colonise the majority of England and Wales, with populations also established in Scotland and Ireland. The spatial expansion shows that the grey squirrel has adapted to the British landscape, dispersing to new habitat areas, and increasing in population size and distribution. Grey squirrels are now classed as an alien invasive species in Britain and are listed in the International Union for Conservation of Nature's (IUCN) 100 worst alien invasive species.

The colonisation has had a considerable negative impact on commercial forestry through damage associated with bark stripping (Mayle, Ferryman and Pepper, 2007) and has occurred simultaneously with the decline and replacement of the native red squirrel *Sciurus vulgaris* (Figure 1). Since the colonisation, there have been numerous localised extinctions of the red squirrel by direct competition and by infection with squirrelpox virus, which the grey squirrels carry (Sainsbury *et al.*, 2008). As the grey squirrel population continues to expand in northern England and Scotland, where the majority of remaining red squirrel populations are present, it is necessary to control the population through management. Knowledge and predictions of grey squirrel landscape use during inter-habitat patch movements are vital for management strategies to be successfully implemented.

Figure 1 The red squirrel *Sciurus vulgaris*.



Photograph: David Holt

Study aims

The aim of this study was to focus on grey squirrel dispersal and movements using a combination of least-cost modelling, genetic analysis and global positioning system (GPS) telemetry to provide information on landscape usage to aid grey squirrel management and red squirrel conservation.

The objectives of the study were to:

- Validate and refine grey squirrel ecological networks created by Forest Research's 'BEETLE' least-cost modelling tool.
- Assess diversity and dispersal direction of grey squirrels in England, Scotland and, in particular, Cumbria using genetic mitochondrial DNA sequencing.
- Improve knowledge of temporal and spatial movement rates of the grey squirrel.
- Provide much needed information on what may constitute conduits and barriers for grey squirrel dispersal in the landscape.
- Develop recommendations for grey squirrel management and red squirrel conservation.

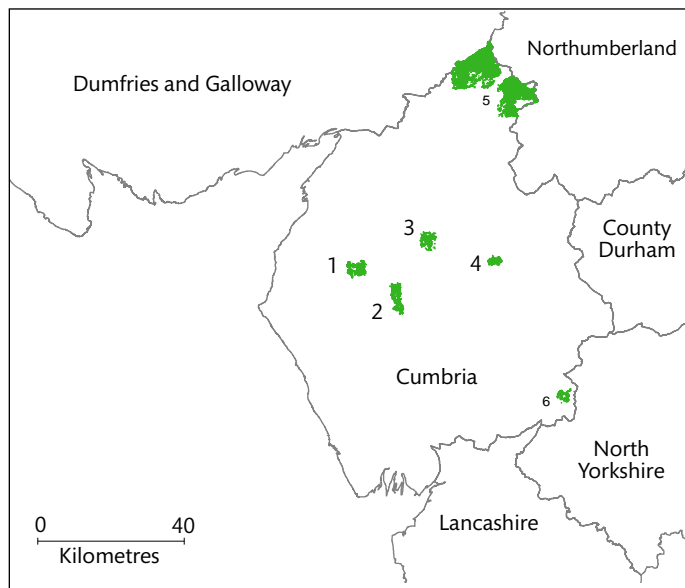
The study

Least-cost analysis

Least-cost analysis is a GIS modelling technique that combines detailed habitat and landscape matrix data with behavioural characteristics of a species. This produces measurements of the connectivity of habitat within the landscape and indicates possible movement areas or most probable movement paths. Such information is useful in species conservation and management. This type of analysis has been used previously to assess both red and grey squirrel movements in the landscape.

The county of Cumbria, located in the northwest of England bordering Scotland, was chosen as the study site (Figure 2); it contains six designated red squirrel reserves and many other vulnerable populations, some of which are genetically unique. Grey squirrel management is currently undertaken within the county. Although there have been local successes of grey squirrel management, a review on red squirrel conservation in the north of England concluded that there is little evidence to suggest the current control efforts have had an effect upon the regional distribution of grey squirrels (Parrott *et al.*, 2009).

Figure 2 Red squirrel reserves in Cumbria: (1) Whinlatter; (2) Thirlmere; (3) Greystoke; (4) Whinfell; (5) Cumbrian section of Kielder; and (6) Garsdale/Mallerstang.



The BEETLE least-cost tool (Watts *et al.*, 2010) was applied to create least-cost networks for the grey squirrel in Cumbria. Networks indicate potential movement areas within the landscape matrix and show potential connectivity. To use least-cost modelling, land cover types were assigned a resistance score that was based upon the facilitating or impeding effects upon species movements. In this study, scores were derived using a combination of resistance sets from previous studies, expert opinion on the ecology of the grey squirrel and distribution data. Resistance scores derived from literature review and expert opinion are seen as subjective. Therefore, further empirical investigation through genetic analysis and GPS telemetry were used to validate the model outputs.

Genetic sequencing validation

Genetic analysis has enabled the identification of land cover types that either facilitate dispersal or provide barriers to red squirrels over large geographic scales. By combining least-cost analysis with genetic analysis, least-cost predictive movement areas can be validated. This study examined genetic sequence variation within grey squirrel DNA (Stevenson *et al.*, 2012). This was done to determine:

- (1) Whether there are any sequence differences between selected grey squirrel populations within the UK, which could identify different populations and where they are located.
- (2) Whether there are differences between populations within different least-cost habitat networks within Cumbria, which would identify whether or not the networks are truly separated or whether movement occurs between them.

Global positioning system telemetry validation

This study also used the least-cost analysis to indicate the most probable movement paths in the landscape. The fine-scale movements identified in a least-cost corridor analysis need detailed movement data for validation. Radio telemetry data are useful in validating least-cost analysis. GPS can also be used to record smaller mammal and bird dispersal movements by providing accurate and regular locations of an animal. Such data on land cover and feature use can also aid species management by identifying highly used areas in the landscape for management and control.

Squirrel movements were recorded using GPS travel trackers which were modified to make them durable and waterproof. Initial tests indicated fully charged devices would operate for around 5 days when location data were set to record every 3 minutes. A VHF radio transmitter was also fitted to the collars to enable tracking of individuals (Figure 3). A total of nine grey squirrels were captured, collared and released under a Natural England licence at an independent study site in Lancashire.

Figure 3 VHF radio and GPS collar.



Photograph: Mark Ferryman

Results

Identification of separate populations

The least-cost analysis identified two major grey squirrel networks within Cumbria, one in the north of the county and one in the south (Figure 4). These highlight the potential movement areas in the landscape for grey squirrels. The separation of the two networks occurs due to the combination of land cover types within the Cumbrian Mountain range, which runs through the middle of the county. The separation of the two networks also suggests that the grey squirrel populations within Cumbria have been derived from dispersing individuals from multiple infiltration directions in the north and south of the county.

Figure 4 Functionally-connected grey squirrel habitat networks identified from resistance sets.

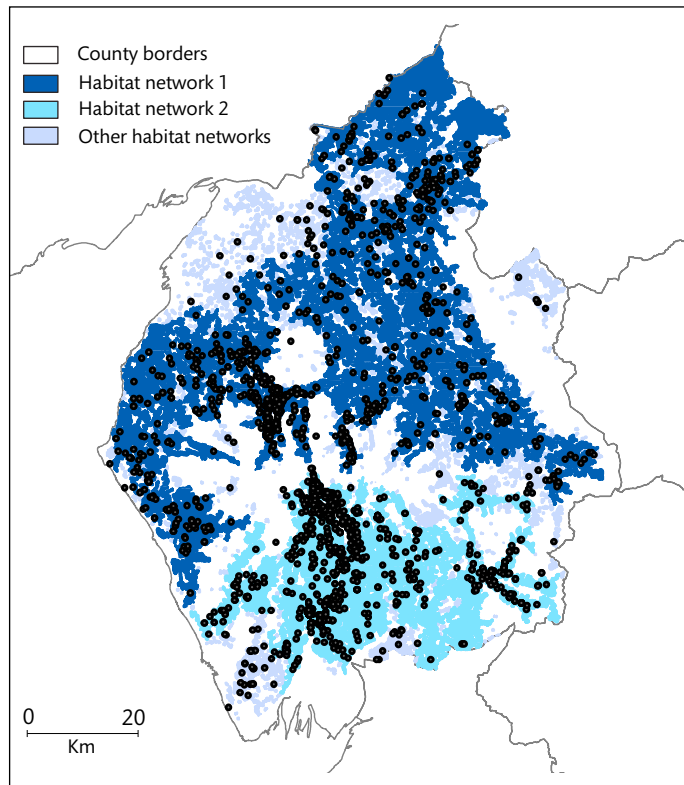


Figure 5 Grey squirrel sample locations for genetic analysis within Great Britain showing Cumbria (Stevenson *et al.*, 2012).



Validation using genetic sequencing

To test whether the grey squirrels in the northern network are separated from the ones in the southern network, genetic analysis was used. Fragments of genes were assessed by Stevenson *et al.* (2012) for seven grey squirrel populations in the UK (Figure 5). Although a small-scale study, it provided the first evidence of D-loop sequence variation within UK grey squirrel populations. The construction of a phylogenetic tree revealed that the samples taken from grey squirrel populations in the southern network in Cumbria were genetically different from the ones taken from the northern network.

The group separation would probably not have occurred if the land cover types within the Cumbrian Mountain range were not acting as a barrier to dispersal. Genetic analysis is therefore providing evidence for the validation of the two habitat networks identified by least-cost network modelling. The land cover types of the Cumbrian Mountains are providing a barrier to grey squirrel dispersal and lead us to surmise that there are northerly and southerly infiltration directions.

Least-cost corridors and landscape usage

Five of the nine grey squirrels collared and released in the Lancashire field site were recaptured. A total of nine instances where squirrels moved between habitat patches were selected. The least-cost corridor included 95% of the GPS movement points, thus validating the most probable movement paths identified with the least-cost analysis (Figure 6).

The squirrels did not take the most direct route between habitat patches; instead movements were longer and followed landscape features including field edges, habitat edges, paths, rivers/streams, roads, road verges and tracks (Figure 7). The GPS points were recorded close to landscape features and were not recorded in open areas, showing the importance of landscape features to grey squirrel movements.

The numbers of GPS points were not distributed proportionally among land cover types or features. This suggests that certain land cover types and features are preferred; for instance, woodland and river corridors were highly used during

Figure 6 Least-cost corridors and GPS movement data indicating the most probable movement areas for the squirrels at the Lancashire field site.

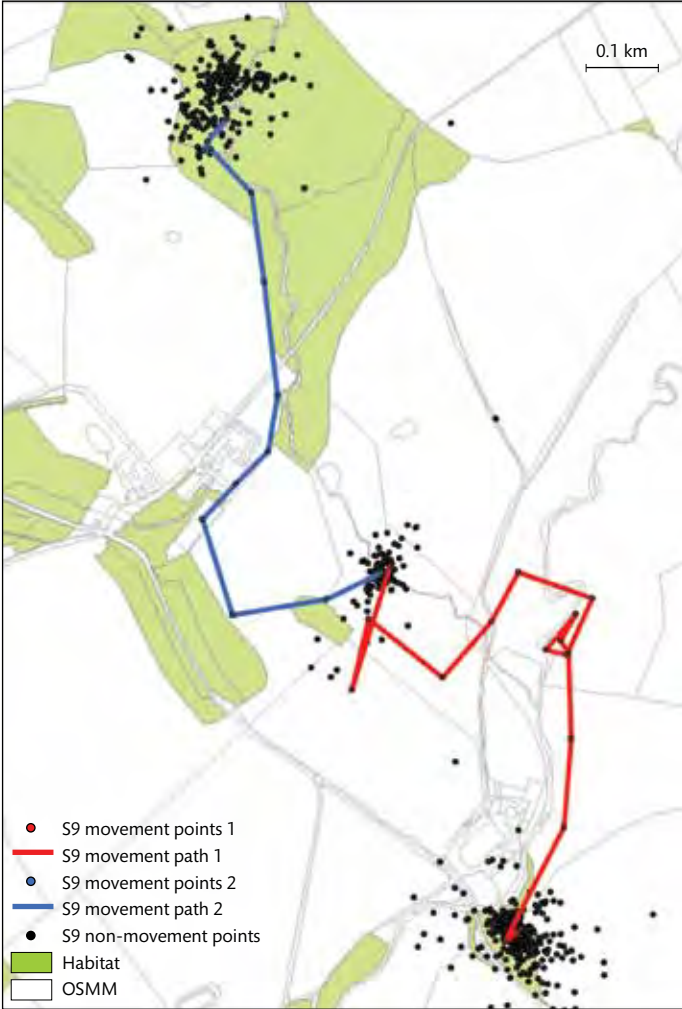


movements (Table 1). The availability of land cover types and landscape features is landscape specific and use and ranking will depend upon what is available.

Table 1 Ranked use (in order of most preferred first) of landscape features and land cover types by grey squirrels in the Lancashire field site study.

Rank	Feature type	Land cover type
1	River corridor	Woodland
2	Road/road verge	Road/path/road verge/track
3	Track/path	River/marsh
4	Field edge	Grassland/garden
5	Habitat edge	Urban/building
6	N/A	Heath/scrub
7	N/A	Improved/arable and amenity

Figure 7 GPS movement data for squirrel 9 in the Lancashire field site study showing the use of landscape features in movements.



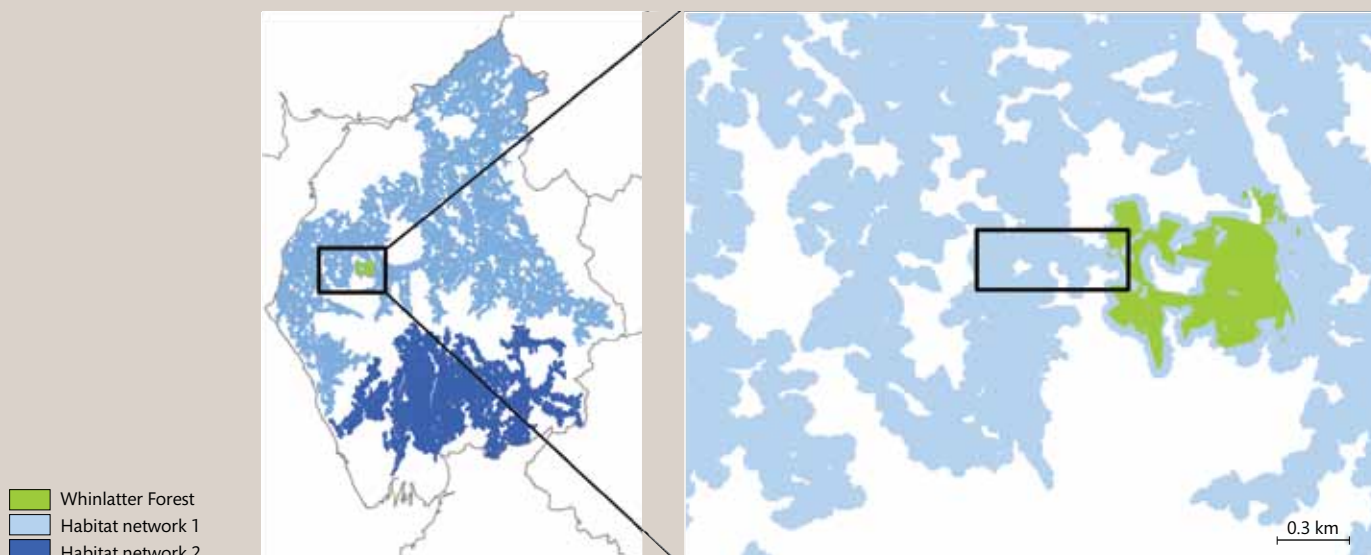
Implications for population management

Because of the negative impact of the grey squirrel population on the native red squirrel population and on forestry, it is critical to be able to manage species movements and expansion. In Cumbria there is increasing pressure to control the grey squirrel population to ensure the survival of the red squirrel within the county. The designation of red squirrel reserves is an important step in ensuring the survival of the red squirrel in England. It is critical to be able to protect these reserves and other vulnerable populations from grey squirrel colonisation. However, controlling grey squirrels at the county level is expensive and time-consuming, and funding for local voluntary organisations is often limited. Parrott *et al.* (2009) suggest that lack of available funding and disagreements over the conservation strategy by different organisations has caused control to be fragmented in the landscape and not targeted or co-ordinated. Since then a new project, Red Squirrels Northern England, has been established and is beginning to tackle grey

Case study: Protecting red squirrel reserves from incursion by grey squirrel – Whinlatter Forest red squirrel reserve

The validation of the least-cost corridor analysis identified a corridor for a section of the habitat network that connects Whinlatter Forest to other woodland patches within the buffer zone.

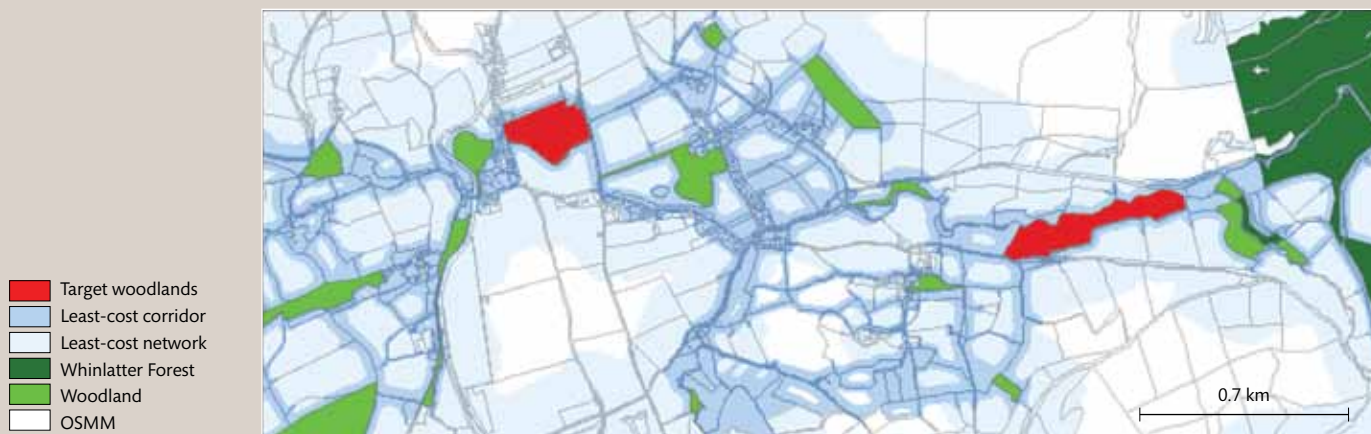
Location of the Whinlatter Forest red squirrel reserve in Cumbria and the area of least-cost corridor analysis (box in right part of figure).



Part of the suggested habitat management strategy for within red squirrel reserves and woodlands in the buffer zone is to use tree species composition, age and spatial structure to improve the carrying capacity of the red squirrels (Pepper and Patterson, 2001). Such management includes reducing or removing large-seeded broadleaf tree species (which are favoured by grey squirrels) within the reserves and buffer zones to try to discourage grey squirrel dispersal. Gurnell and Pepper (1993) also recommended that reserve buffer zones should contain at least 3 km of conifer forest or open land to reduce possible grey squirrel infiltration.

The least-cost corridor has identified the most probable movement paths through the landscape matrix into the reserve. Targeted management can be initiated by removing any large-seeded broadleaf tree species located within all woodland in the least-cost corridor and replacing it with conifer species. This is particularly important for woodlands that are located at 'pinch points' within the corridor. These are the narrowest areas of the corridor, which the grey squirrels will move through to get into the vulnerable woodland. Ideally, all woodland located at a pinch point should be removed to reduce movements.

Grey squirrel least-cost corridors leading into Whinlatter Forest reserve showing highlighted 'pinch points' within the corridors where targeted management can occur.



squirrel control in a much more targeted, systematic and rigorous way. It is too early to assess the efficacy of this approach but twice-yearly monitoring is being undertaken of red and grey squirrel presence/absence using fixed transects, so the effectiveness of this approach will be evident in a few years time.

Our study suggests that the Cumbrian Mountain range is acting as a barrier to dispersal, dividing populations into north and south Cumbria. Red squirrel reserves and other vulnerable populations are present within both habitat networks. At the county level the networks indicate all possible movements in the landscape and cover substantial areas across Cumbria. The data from the study aid understanding of the extent of potential dispersal and also indicate the importance of a co-ordinated management approach across the landscape, particularly within networks. Spreading limited resources across the entire landscape is costly and inefficient.

Assessing the grey squirrel movements at a small scale has enabled the creation of least-cost corridors. By using a combination of least-cost analysis and GPS this study was able to validate the least-cost corridor model outputs and also provide information on landscape use by grey squirrels. This information can be used to inform targeted grey squirrel control and landscape management in key areas within reserve buffer zones and the wider landscape. To highlight the applicability of the validated least-cost models one of the Cumbrian red squirrel reserves, Whinlatter Forest, and its buffer zone is used as a case study.

Assessment of landscape features

The GPS data have enabled the assessment of land cover type and feature use by grey squirrels. On a case-by-case basis the landscape features (such as river corridors, roads/road verges, tracks/paths and field edges) in the least-cost corridor can be assessed to see whether the feature type or management can be altered to make them less permeable for the grey squirrel. However, although this would create a less impermeable landscape matrix for grey squirrel movements, it should be borne in mind that it may also create a matrix unsuitable for other species, some of which will be native and possibly of conservation concern.

Targeted grey squirrel control

Although landscape management is useful, targeted grey squirrel control is also needed within the least-cost corridors, because of the immediate threat of grey squirrel incursion into many reserves. Instead of spreading grey squirrel control resources over the entire reserve buffer zone, resources can be targeted by controlling grey squirrel presence within the most probable movement areas within the least-cost networks and

least-cost corridors. Depending on resources available, grey squirrel control may be undertaken in all woodlands within the least-cost corridor and also along the landscape features used by grey squirrels (Table 1).

In areas where grey squirrel control resources are constrained and not co-ordinated, the least-cost corridor analysis used in this study can help identify pinch points where resources could be targeted to be most effective in protecting vulnerable populations of red squirrels. As grey squirrel control is a long-term management strategy, co-ordination of organisations working within the reserve buffer zones is vital to enable the most permeable areas of the landscape to be protected from incursions. By using least-cost analysis, a clear visual representation highlighting the most probable dispersal routes and areas to target resources can be distributed to all organisations involved in control. Note – these approaches have not been tested but they are based on expert opinion.

Conclusions and further research

The use of least-cost analysis has enabled the identification of habitat networks within Cumbria and has shown the extent of possible movements for the grey squirrel. Further least-cost analysis enabled the identification of least-cost corridors, which have the ability to aid targeted control and efficient use of resources by highlighting the most probable dispersal routes.

Once the incursion of reserves and vulnerable woodland areas is controlled, the extent of grey squirrel control can be increased to create grey squirrel-free areas such as in the northern habitat network in Cumbria.

Future work should use the least-cost modelling methods presented within this study to:

- assess areas at the forefront of the grey squirrel expansion and identify habitat networks;
- assess areas in the UK and abroad that are currently under pressure from grey squirrel incursions, using least-cost corridors to identify the most probable routes taken through the landscape and to select areas for targeted management.

A study could be undertaken to test the impact of the evidence-based landscape management and grey squirrel control recommendations presented in this study. Grey squirrel management is a long-term conservation strategy but one that is essential to ensure the survival of the native red squirrel.

Acknowledgements

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