NOTTINGHAM TRENT UNIVERSITY

HABITAT CONNECTIVITY FOR RED SQUIRRELS (*SCIURUS VULGARIS*) AND GREY SQUIRRELS (*SCIURUS CAROLINENSIS*) FOR CONSERVATION EFFORTS FOR THE MID WALES RED SQUIRREL PROJECT

by

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Research project submitted in partial fulfilment of the MRes 'Endangered Species Recovery and Conservation' degree

2024

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to my supervisor, Kat Hamill, for her invaluable guidance, insight, and support throughout this project. I would also like to extend my heartfelt thanks to Ben Clutterbuck and Alex Dittrich for their advice and constructive feedback.

My sincere appreciation goes to The Wildlife Trust of South and West Wales, particularly the Mid Wales Red Squirrel Project partnership. I am especially grateful to Alice, who was always ready to provide additional information and advice, significantly aiding the progress of this research.

Finally, I wish to acknowledge Phaidon for his support and belief in me.

This work would not have been possible without the support and contributions of all these individuals, to whom I am deeply grateful.

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Paper 1

RED SQUIRREL CONSERVATION IN A CHANGING LANDSCAPE: A SYSTEMATIC REVIEW OF HABITAT CONNECTIVITY AND GREY SQUIRREL CONTROL MEASURES

By

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Abstract:

The Eurasian red squirrel (*Sciurus vulgaris*), a small arboreal mammal native to Europe and parts of Asia, faces severe population declines primarily due to competition with the invasive grey squirrel (*Sciurus carolinensis*), introduced from North America in the 19th century. The grey squirrel's rapid range expansion, combined with habitat loss and fragmentation, has significantly contributed to the red squirrel's decline. This study critically evaluates the importance of habitat connectivity in red squirrel conservation and grey squirrel control, synthesizing findings from 31 studies conducted between 1997 and 2024, including 14 from the UK. The research focuses on the ecology and habitat preferences of red squirrels, as well as the incursion patterns of grey squirrels and their impacts on red squirrel populations. Habitat connectivity is essential for red squirrel conservation, facilitating dispersal, gene flow, and resource access while helping to target grey squirrel control efforts. The review highlights that maintaining diverse and continuous coniferous seed supplies, creating habitat corridors, and managing forest compositions are crucial for red squirrel survival. Additionally, the use of predictive spatial models in tandem with systematic grey squirrel control is necessary to secure red squirrel populations against ongoing threats. The findings underscore the need for conservation strategies that prioritize habitat connectivity to support the resilience and long-term survival of the endangered red squirrel. This systematic review provides a comprehensive overview of the current literature and offers insights into effective management practices for red squirrel conservation amidst the challenges posed by grey squirrel competition and habitat fragmentation.

1.0 Introduction:

1.1 Red squirrels

The Eurasian red squirrel (*Sciurus vulgaris*) is a small arboreal mammal native to and widely distributed across Europe and parts of Asia, inhabiting a range of forest types including coniferous and mixed-deciduous forests (Olah et al., 2022; Trizio et al., 2005, de Raad et al., 2021a). Red squirrels weigh between 270 and 320 g, with sharp claws and strong limbs that they use to navigate through tree canopies where they forage primarily on seeds and nuts but also fungi, fruits, and occasionally insects (Shannon et al., 2023; Thorington & Ferrell, 2006). Red squirrels play a vital role in their ecosystems; as scatter-hoarders, they contribute to forest regeneration by burying seeds, some of which are forgotten and later germinate, leading to new tree growth (Bamber et al., 2020a). This behaviour not only helps maintain forest health but also promotes biodiversity. Moreover, red squirrels serve as prey for various predators such as foxes (*Vulpes vulpes*), martens (*Martes martes*), and owls (*Strigiformes*), forming an integral part of the forest food web (Lacher et al., 2019). Their presence is an indicator of healthy forest ecosystems, as they are sensitive to changes in habitat quality and availability (Shannon et al., 2023).

In terms of habitat, red squirrels prefer areas with a diverse structure, offering plenty of canopy cover and a mix of tree species that provide year-round food sources (Flaherty et al., 2012). They are particularly dependent on large, mature trees for nesting and foraging. In fragmented landscapes, red squirrels suffer from reduced genetic diversity due to isolated populations and low rates of immigration (Trizio et al., 2005). However, reforestation efforts and the creation of habitat corridors can help increase gene flow and restore genetic diversity within these populations. Studies in the Italian Alps have demonstrated that habitat connectivity can significantly enhance the genetic variability of red squirrels, which is crucial for their long-term survival (Trizio et al., 2005).

Historically, red squirrels were widespread across Great Britain, but their numbers have dramatically declined over the past century (Flaherty et al., 2012). Red squirrels are classified as endangered in the UK, with their extent of occurrence (EOO) having declined by over 60% in the last three generations in both England and Wales (Mathews & Harrower, 2020). The area of occupancy (AOO) has also decreased by 31% in England and 44% in Wales over the same period. While the EOO has remained stable in Scotland, the AOO has still seen a 4% decline over the past three generations (Mathews & Harrower, 2020).This decline is largely attributed to habitat loss and fragmentation (which will be discussed in more detail in section 1.3), the introduction of the invasive Eastern grey squirrel (*Sciurus carolinensis*) from North America, and squirrelpox virus (SQPV; Cox et al., 2020; Rushton et al., 2006). The grey squirrel outcompetes the red squirrel for food and habitat, and carries SQPV that is lethal to red squirrels (Cox et al., 2020; LaRose et al., 2010).

The public perception of red squirrels in the UK is overwhelmingly positive. They are considered charismatic and endearing animals, seen as a symbol of Britain's natural heritage, and their decline has spurred numerous conservation initiatives (Bamber et al., 2020a). Organizations, such as the Red Squirrel Survival Trust and local wildlife trusts, are dedicated to protecting and restoring red squirrel populations through habitat management, grey squirrel control, and public education (Shuttleworth & Halliwell, 2016; Denman, 2006).

In the UK, red squirrels are legally protected and listed in the UK Biodiversity Action Plan (Flaherty et al., 2012). Long-term habitat management is a key goal of the UK conservation strategy, with an emphasis on maintaining and enhancing suitable reserves or strongholds. Selection criteria for these reserves consider species composition, food availability, and forest structural factors, highlighting the importance of canopy closure and tree density in influencing red squirrel foraging behaviour (Flaherty et al., 2012). Conservation strategies also involve reforestation and the creation of natural corridors to promote genetic diversity and population connectivity (Trizio et al., 2005).

1.2 Threats for red squirrels

1.2.1 Grey squirrels and SQPV

Competition with grey squirrels is one of the most critical factors contributing to the decline of red squirrels. Grey squirrels, introduced to the UK from North America in the 19th century as well as parts of mainland Europe, have rapidly expanded their range and outcompeted the native red squirrels for resources (Rushton et al., 2006; Everest et al., 2021). Grey squirrels are more adaptable and efficient in exploiting available food sources, which puts red squirrels at a disadvantage, particularly in mixed deciduous woodlands where both species overlap (Olah et al., 2022). The grey squirrels' ability to consume a wider variety of foods and store fat more effectively enables them to survive harsher conditions, giving them a competitive edge over red squirrels (Blackett et al., 2018). Their distribution now covers much of England, Wales, Ireland, parts of Scotland, and northern Italy, where they have had a profound impact on local ecosystems, particularly on native red squirrel populations, and have become a significant ecological concern (Gurnell et al., 2004).

The introduction of grey squirrels to these regions has led to the decline of red squirrels through several mechanisms. One of the primary ways grey squirrels outcompete red squirrels is through more efficient resource utilization. Grey squirrels are better at exploiting certain food sources, such as acorns, because they can neutralize phytotoxins more effectively (Kenward & Holm, 1989). This gives them a nutritional advantage, allowing them to accumulate body mass more effectively in autumn, which enhances their winter survival and breeding success (Gurnell, 1996). In mixed woodlands where both species coexist, the presence of grey squirrels correlates with reduced body growth in juvenile and subadult red squirrels as they compete for tree seeds, leading to lower fecundity and recruitment rates for red squirrels (Gurnell et al., 2004).

Grey squirrels are asymptomatic carriers of the SQPV, which is lethal to red squirrels but does not affect grey squirrels (Rushton et al., 2006). In regions where grey squirrels are prevalent, the presence of SQPV has led to significant mortality rates in red squirrel populations, often exceeding 80% (Chantrey et al., 2014). When infected with SQPV, red squirrels exhibit typical poxvirus symptoms: the development of extensive ulcerative lesions around the mouth and eyelids (Darby et al., 2014; Fig. 1). They often suffer a rapid and painful death, leading to the decimation of local populations. The disease spreads quickly among red squirrels, exacerbating their decline wherever grey squirrels are present and contributing to local population extirpations (Shannon et al., 2023). Red squirrel populations decline 25 times faster in areas where SQPV is present in the grey squirrel population compared to areas where SQPV is absent from the grey squirrel population. (Rushton et al., 2006). Grey squirrel densities negatively impact the number of juvenile and subadult red squirrels that can settle in mixed-species sites, further reducing red squirrel recruitment rates as grey squirrel densities increase (Gurnell et al., 2004). The presence of grey squirrels significantly increases the risk of SQPV outbreaks, making grey squirrel management a critical component of red squirrel conservation efforts (Shannon et al., 2023; Chantrey et al., 2014).

Figure 1. Red squirrel infected with squirrelpox virus (SQPV). Image by Lancashire Wildlife Trust taken from Shuttleworth et al., 2019.

The need for effective grey squirrel control management is evident to mitigate the competitive and disease pressures they exert on red squirrel populations, ensuring the conservation of the native species. Current UK laws, such as the Grey Squirrels

(Prohibition of Importation and Keeping) Order of 1937 and the Wildlife and Countryside Act 1981, prohibit the keeping and release of grey squirrels without a license (Shuttleworth et al., 2019). However, these measures need to be harmonized across the UK to ensure a coordinated and effective approach to grey squirrel management.

Proposals for further management include culling programs and exploring biotechnological solutions, such as immunocontraceptives and gene editing, to control grey squirrel populations (Everest et al., 2021). Developing a red squirrel SQPV vaccine also holds promise but requires additional research to bring it into practical use (Everest et al., 2021). Citizen-led conservation actions and volunteer-based monitoring are increasingly vital for managing isolated red squirrel populations and responding to disease outbreaks effectively (Everest et al., 2021). Such integrated and well-supported efforts are crucial to reversing the decline of red squirrels and preserving biodiversity in affected regions.

1.2.2 Habitat loss and fragmentation

Habitat loss and fragmentation have also played a substantial role in the decline of red squirrels. Urbanization and agricultural expansion have led to the loss of suitable habitats for red squirrels, which require large, contiguous areas of mature woodland to thrive (Olah et al., 2022). Fragmented habitats lead to isolated populations, reducing genetic diversity and increasing vulnerability to disease and environmental changes (Everest et al., 2021). The destruction and alteration of forests disrupt the red squirrels' ability to find food, breed, and avoid predators, further endangering their survival.

Despite conservation efforts, red squirrels remain vulnerable to ongoing threats. The competition with grey squirrels and the diseases they carry continue to pose significant challenges to red squirrel conservation. Effective monitoring and management strategies are essential to address these threats and support the recovery of red squirrel populations. This includes developing cost-effective monitoring tools to assess the impact of conservation actions, engaging the public in conservation efforts (Shannon et al., 2023), and implementing multifaceted conservation strategies such as habitat restoration, disease management, and possibly captive breeding and release programs (Olah et al., 2022). Recent studies have shown that habitat connectivity can significantly enhance genetic variability, underscoring the importance of a well-connected and diverse habitat for the long-term conservation of red squirrels (Trizio et al., 2005).

1.3 Importance of habitat availability and connectivity

Red squirrels primarily inhabit coniferous forests, as these environments offer a competitive refuge from grey squirrels, which prefer broadleaved forests with abundant large-seed-producing trees such as oaks (*Quercus* spp.; Shuttleworth et al., 2012). In these coniferous habitats, red squirrels exhibit specific habitat preferences. They tend to select dense Sitka spruce (*Picea sitchensis*) plantations over areas dominated by Scots pine (*Pinus sylvestris*), likely due to the higher densities of grey squirrels in Scots pine areas (Wauters et al., 2000). This habitat selection underscores the importance of maintaining and enhancing coniferous habitats, particularly those that are less favourable to grey squirrels.

Effective habitat management strategies for red squirrels include creating and maintaining a mosaic of coniferous species to ensure a continuous and reliable seed supply. Recommendations suggest that Sitka spruce-dominated forests should include about 20% of other conifers, such as pine species, larch (*Larix* spp.), or Norway spruce (*Picea abies*), to provide a diverse and steady food source while limiting habitat suitability for grey squirrels (Shuttleworth et al., 2012). Such strategies help maintain red squirrel populations by ensuring that food resources are available year-round, thereby supporting their nutritional needs and reproductive success.

In addition to managing the composition of tree species, habitat connectivity is crucial for enabling red squirrels to move between different forest patches. Fragmented habitats can isolate populations, making them more vulnerable to local extinctions and reducing genetic diversity. Connected habitats allow for gene flow between populations, which is vital for maintaining genetic health and adaptability. Efforts to create corridors and mitigate the effects of fragmentation can significantly enhance the resilience of red squirrel populations. These corridors facilitate movement and dispersal, enabling squirrels to find new habitats and resources, especially in response to environmental changes or local disturbances (Lurz et al., 1997).

The role of spatially explicit models in predicting habitat suitability and potential spread of invasive species is also noteworthy. Such models can inform conservation strategies by identifying areas at risk of invasion and guiding management actions to enhance habitat connectivity for red squirrels (Bertolino et al., 2020). These models rely on ecological data about the target species and their habitat requirements, emphasizing the need for detailed ecological information to support effective conservation planning (Lohr et al., 2017).

The establishment of red squirrel strongholds in northern England exemplifies the importance of habitat connectivity in conservation planning. These strongholds are strategically located in coniferous forests where red squirrels can thrive, and grey squirrels are less competitive. For instance, 17 strongholds have been established in northern England (Fig. 2) and 18 more have been proposed in Scotland to secure habitat for red squirrels (Shuttleworth et al., 2012). These strongholds serve as refuges and population reservoirs, supporting red squirrel conservation on a regional scale.

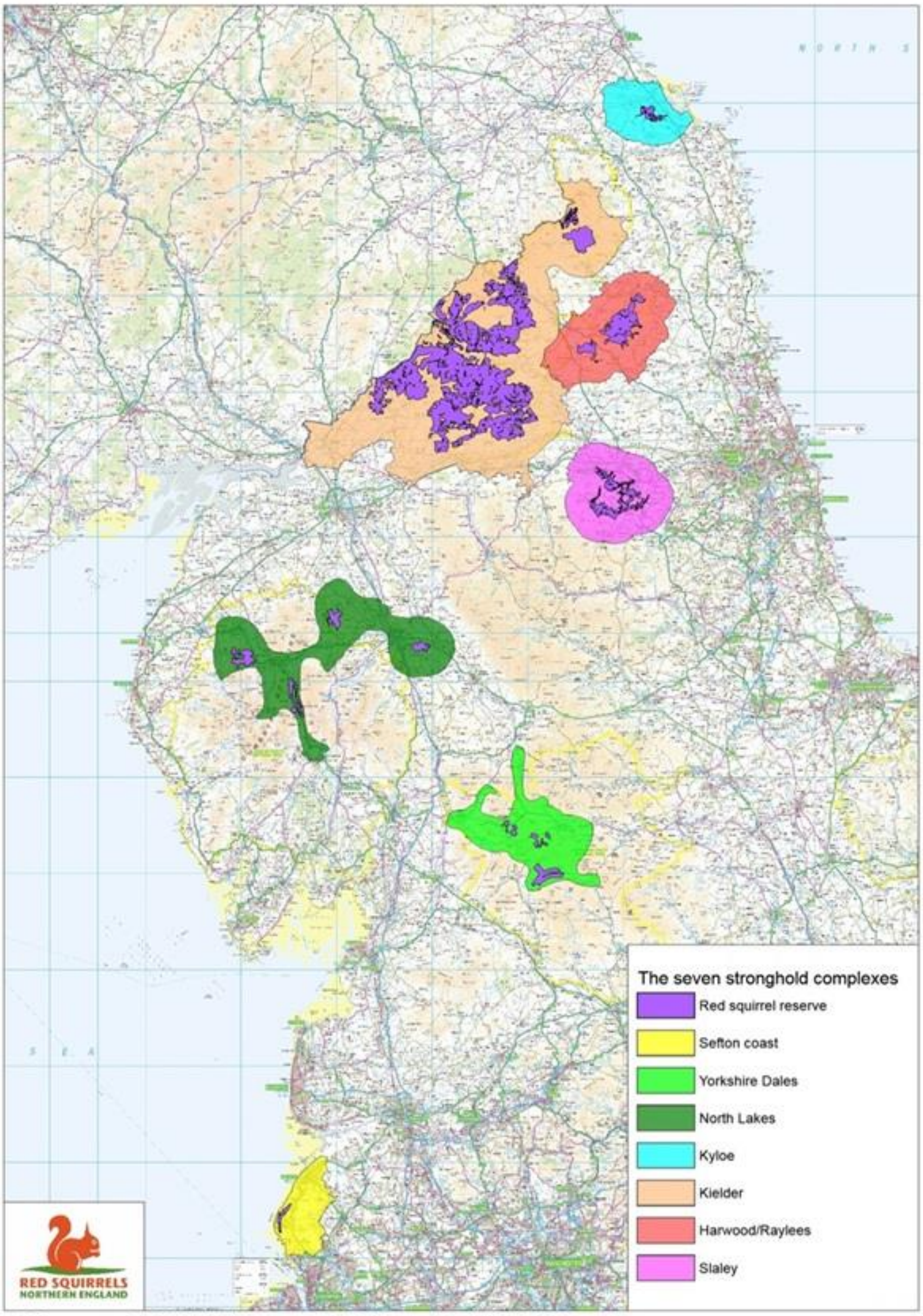

Figure 2. 17 strongholds for red squirrels established in northern England. Image taken from Red Squirrels Northern England (RSNE, 2015).

Moreover, proactive forest management practices are essential to enhance habitat quality, connectivity, and to mitigate the damage caused by both invasive species and forestry activities. This includes controlling invasive grey squirrels to reduce competition, disease transmission, and the bark stripping damage they cause to trees, which can significantly impact forest health. Systematic grey squirrel control programs have been implemented as part of regional conservation strategies to prevent the establishment of sympatric grey squirrel populations and reduce their competitive ability (Shuttleworth et al., 2012). Additionally, managing tree species composition to favour conifers over broadleaves not only creates less attractive environments for grey squirrels but also reduces the risk of bark stripping, thereby indirectly benefiting red squirrel populations and overall forest integrity.

Fragmented habitats not only limit the resources available to red squirrels but also restrict their ability to migrate and repopulate areas where populations have declined or disappeared (Rushton et al., 2006). Connectivity between habitats is crucial for maintaining healthy populations, as it allows for gene flow and reduces the risks associated with inbreeding and local extinctions (Everest et al., 2021). Conservation efforts must focus on creating wildlife corridors and restoring fragmented habitats to support red squirrel populations.

1.4 Research aims and objectives

The overall aim of this study is to critically evaluate the existing literature investigating the importance of habitat connectivity for red squirrel conservation and grey squirrel control. Understanding habitat connectivity is an important aspect of red squirrel conservation for allowing dispersal and gene flow, as well as identifying incursion routes for grey squirrels to target control efforts.

The research objectives are:

- To synthesize and appraise the existing research on the ecology of red squirrels, particularly focusing on their habitat preferences and population dynamics.
- To examine the existing literature on the behaviour and ecology of grey squirrels, particularly focusing on their incursion patterns into red squirrel habitats and their impact on red squirrel populations.

2.0 Methods:

2.1 Literature search

A systematic literature review was conducted in June 2024 following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocols (Page et al, 2021).

A literature search was conducted on Google Scholar with the following search terms:

(‘red squirrel*’ OR ‘Sciurus vulgaris’) AND (‘competition’) AND ('Grey squirrel*' OR 'Sciurus carolinensis') AND ('invasive species' OR 'non-native species' OR ‘alien species’) AND ('control' OR 'management') AND (‘habitat management’ OR ‘habitat use’ OR ‘forest management’) AND (‘conservation*’) AND (‘population dynamics’ OR ‘population demography’) AND (‘disturbance’ OR ‘fragmentation’).

The search terms returned 378 results. After 11 pages, the results became less relevant to the research topic, therefore only the first 110 articles were collected (Fingland et al., 2022). There was no specification regarding year of publication included in the search. Articles were excluded if they were not peer-reviewed, not available in English, or not accessible with university access.

2.2 Inclusion criteria

The remaining articles were screened using the following criteria: the title, abstract, or keywords must include 'red squirrel', 'Sciurus vulgaris', and either 'habitat', 'forest', or 'woodland’, but with a specific focus on the relationship between these environments and the red squirrel’s habitat preferences and population dynamics.

Articles that passed this initial screening were then assessed in full based on the following criteria: the study must have been conducted in Europe, ensuring the research is geographically relevant to European red squirrel populations. Additionally, the study may include discussions on the impact of grey squirrels on red squirrel populations, particularly focusing on aspects such as competition for resources, habitat displacement, or the transmission of diseases.

Only the key findings from the final collated dataset were reported in this review.

3.0 Results:

The initial literature search yielded 110 articles. During the screening process, 79 articles were excluded, leaving a final dataset of 31 articles (Fig. 2). These articles were published between 1997 and 2024 (Fig. 3). The majority were conducted in the UK (14), with additional studies from Italy (6), Ireland (3), Poland (2), Germany (2), Finland (1), Spain (1), Belgium (1), and one systematic review encompassing the UK, Ireland, and Italy.

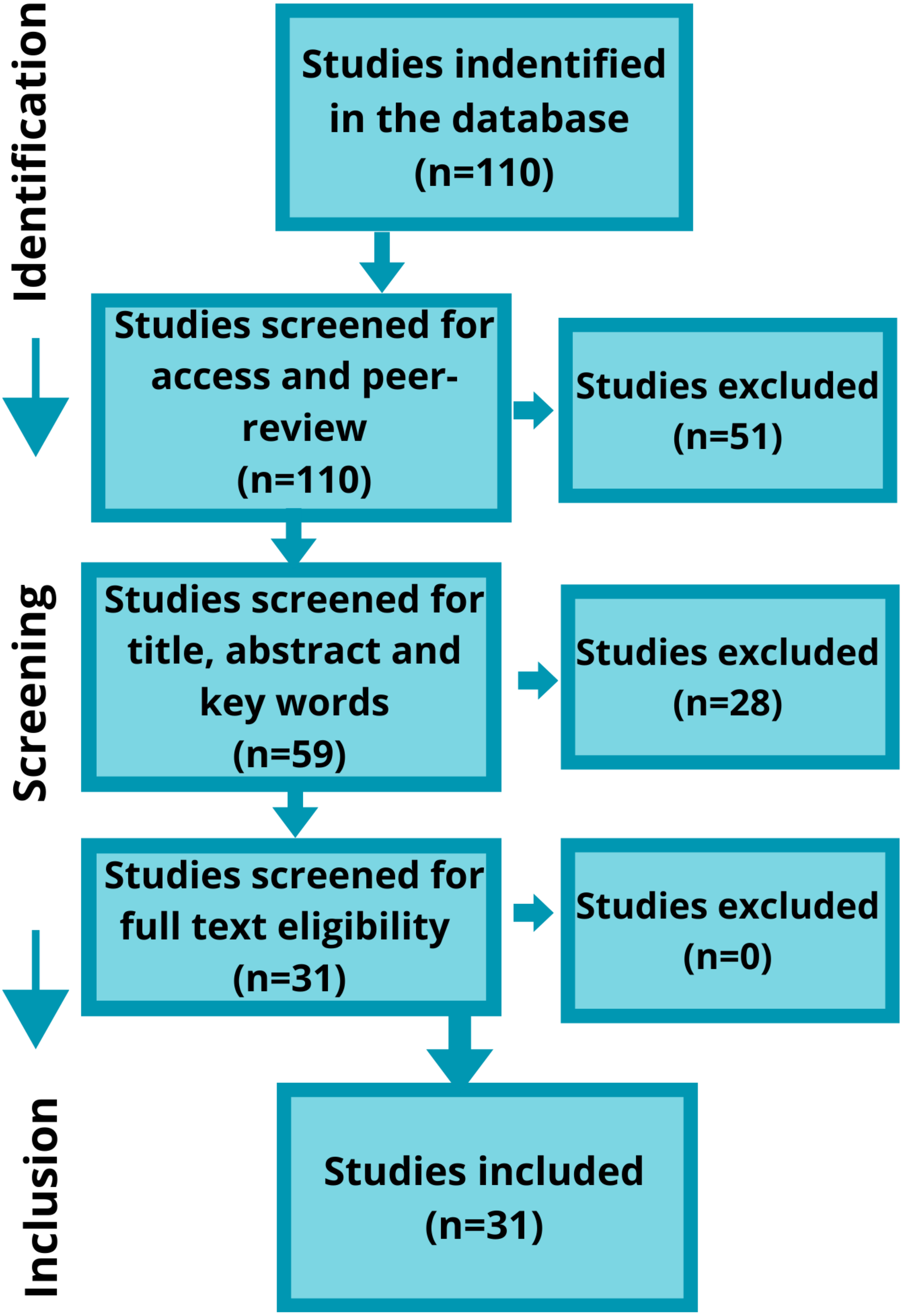

Figure 3. PRISMA flow diagram illustrating the literature search and screening process, including studies that were included and excluded from the analysis. Diagram adapted from: The Edanz team, 2023.

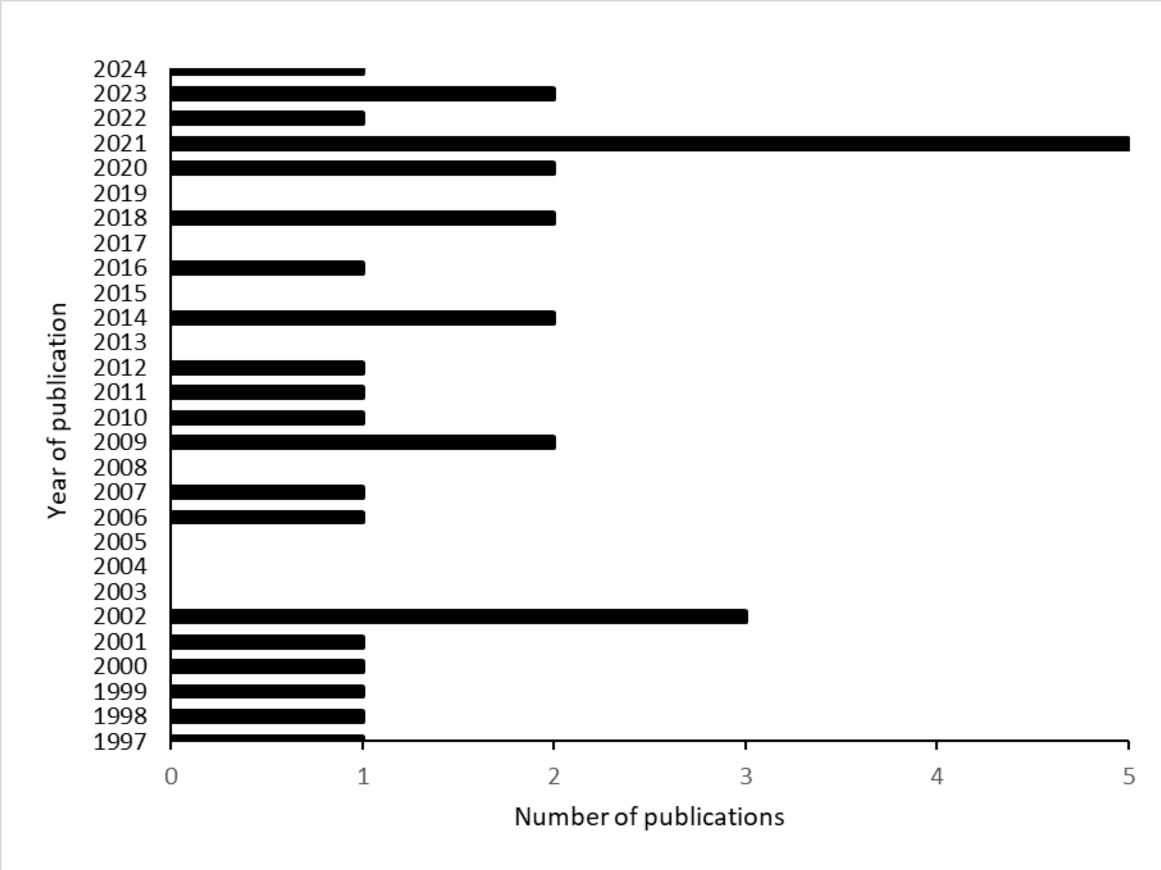

Figure 4. Number of studies included in final dataset (n = 31), published between 1997 to 2024.

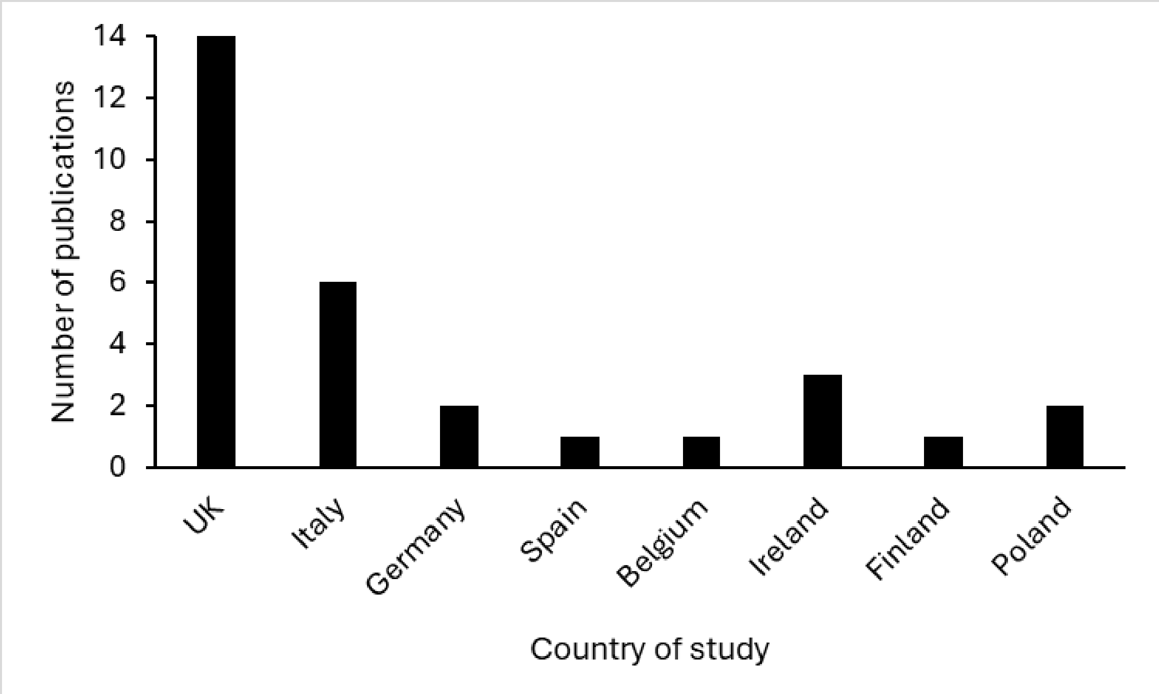

Figure 5. Number of publications (n=30, excluding the multi-country systematic review) in different European countries.

4.0 Discussion:

The overall aim of this study was to critically evaluate the existing literature on the importance of habitat connectivity for red squirrel conservation and grey squirrel control. This review synthesized research on red squirrel ecology, focusing on habitat preferences and population dynamics, to understand how connectivity supports their dispersal and gene flow. Additionally, it examined grey squirrel behaviour and ecology, particularly their incursion into red squirrel habitats, to assess the impact on red squirrel populations and identify potential control strategies. The findings underscore the critical role of habitat connectivity in balancing conservation efforts and invasive species management.

The studies included in this systematic review span from 1997 to 2024, indicating that red squirrel conservation has been an area of significant concern for many years. Of the 31 studies reviewed, 14 were conducted in the UK, underscoring the critical nature of red squirrel conservation in the region. This geographical concentration suggests that red squirrel conservation is more pressing in the UK compared to other parts of Europe, likely due to the intense competition from the invasive grey squirrel and habitat fragmentation challenges that are particularly pronounced in the UK.

4.1 Main findings

Habitat fragmentation has emerged as a significant issue for red squirrel populations. Several studies highlight the complex impacts of fragmentation on the spatial organization and behaviour of red squirrels. For instance, one study focusing on a red squirrel metapopulation in woodland fragments revealed that habitat fragmentation had varying effects on the space use and social organization of male and female squirrels. Male squirrels exhibited a fission response, expanding their home ranges in larger patches, whereas females' space use was more resistant to fragmentation, with their core area sizes decreasing in higher-quality habitats (Verbeylen et al., 2009). This suggests that male red squirrels may be more vulnerable to the effects of fragmentation, as they require larger territories that are difficult to maintain in fragmented landscapes.

Another study investigated the habitat use of red squirrels in a coastal region, demonstrating that red squirrels adapted to fragmented habitats by using the best available feeding areas, such as mature pine forests near cliffs and freshwater channels. These areas, despite being close to the sea and thus subject to saline stress, provided the necessary resources for feeding, although the squirrels avoided nesting in these locations, preferring more humid areas away from the cliffs (Duarte, 2023). This study underscores the importance of considering both feeding and nesting habitats in conservation strategies, as squirrels may use different areas for these activities depending on the habitat’s characteristics.

Moreover, the role of urban environments in red squirrel conservation has been explored, revealing that urbanization leads to significant changes in red squirrel behaviour and morphology. Urban squirrels were found to have smaller home ranges and exhibited changes in their activity patterns, likely due to the dense and reliable food sources available in urban areas, which reduce the need for extensive foraging (Thomas et al., 2018). However, urban environments might not be ideal refuges for red squirrels, as seen in a study that showed urban squirrels consuming a wider range of non-natural food items, potentially leading to nutritional mismatches and negative health effects (Wist et al., 2022). This indicates that while urban areas can provide some level of habitat for red squirrels, they are not without risks, particularly related to diet and health.

Finally, habitat management practices such as forest thinning have been shown to influence red squirrel populations. A study conducted in the Scottish Highlands revealed that standard thinning operations, which reduced the basal area of forests, did not adversely affect red squirrel survival or breeding activity. In fact, squirrel population density increased after thinning, and squirrels adapted their nesting behaviour by increasing their use of dreys (de Raad et al., 2021b). This suggests that while forest management practices like thinning can alter the habitat, they do not necessarily harm red squirrel populations and may even have some benefits if managed correctly.

The distribution of red squirrels has been extensively studied, with various factors influencing their presence and abundance across different landscapes. One study on the Isle of Wight highlighted the importance of maintaining large interconnected woodlands to ensure the future conservation of red squirrels (Rushton et al., 1999). The fragmentation of these woodlands could lead to isolated populations that are more vulnerable to extinction due to reduced genetic diversity and increased susceptibility to environmental changes.

In Finland, a long-term study using snow-track data over 29 years revealed that red squirrel populations are synchronized over large distances, driven by the availability of spruce cones, which are a crucial food resource (Turkia et al., 2020). This finding emphasizes the importance of food availability in determining red squirrel distribution and suggests that changes in cone production due to climate change or forest management practices could have significant impacts on red squirrel populations across large areas.

The presence of red squirrels in urban environments has also been documented, with some studies showing that red squirrels are capable of adapting to urban areas. For instance, red squirrels were found to use nest boxes more frequently in urban parks than in continuous forests, likely due to higher population densities and increased competition for shelter in urban environments (Gryz et al., 2021.). However, the suitability of urban areas as long-term habitats for red squirrels remains questionable, given the potential health risks associated with urban diets, as discussed earlier.

The spread of grey squirrels has had a profound impact on the distribution of red squirrels, particularly in regions like Norfolk, UK. A study modelling the spread of grey squirrels and its impact on red squirrels in Norfolk demonstrated that grey squirrels' expansion led to a significant decline in red squirrel populations, primarily due to interference competition (Rushton et al., 1997). This study aligns with broader patterns observed across the UK, where grey squirrel invasions have led to the replacement of red squirrels over large areas.

The invasive grey squirrel is perhaps the most significant threat to red squirrel populations in the UK and other parts of Europe. The competitive advantage of grey squirrels over red squirrels has been well-documented, with studies showing that grey squirrels outcompete red squirrels for food and habitat, leading to the decline and local extinction of red squirrels in many areas.

One study that employed a spatially explicit population dynamics model suggested that grey squirrel control measures, such as trapping and immunocontraception, could be effective in maintaining viable red squirrel populations in areas like Scotland. However, the effectiveness of these measures depends on their scale and the extent of grey squirrel populations (Rushton et al., 2002). Another study highlighted the importance of maintaining natural strongholds for red squirrels, which can support viable populations even in the presence of grey squirrels, provided that grey squirrel control is maintained (Slade et al., 2021).

The role of disease in the red-grey squirrel dynamic has also been explored, particularly the threat posed by SQPV, which grey squirrels can carry without being affected, but which is deadly to red squirrels. A study focused on managing the SQPV threat in the Kielder Forest in England emphasized the need to minimize contact between red and grey squirrels by monitoring and controlling grey squirrel populations in buffer zones around red squirrel refuges (Gurnell et al., 2006). This approach is critical in preventing disease transmission and ensuring the survival of red squirrel populations in areas where grey squirrels are present.

In some cases, the introduction of predators such as pine martens has been proposed as a natural control method for grey squirrels. A study on Anglesey, Wales, found that the introduction of pine martens led to a significant decline in grey squirrel numbers, which in turn allowed red squirrel populations to recover (Bamber et al., 2020b). This predator-prey management approach highlights the potential for using native predators to control invasive species and support red squirrel conservation.

Furthermore, the adaptability of grey squirrels to different environments, including urban areas, has been a major factor in their successful invasion. A study comparing the body size and mass of red and grey squirrels across rural, suburban, and urban gradients found that grey squirrels were larger in urban areas, likely due to better access to food and shelter, which could give them a competitive edge over red squirrels in these environments (Tranquillo et al., 2024). This phenotypic plasticity and adaptability make grey squirrels particularly difficult to control and further exacerbate the challenges faced by red squirrel conservation efforts.

4.2 Strengths and limitations of the study

One of the key strengths of this systematic review lies in its comprehensive approach to the literature search. By including studies spanning over two decades (1997-2024), this review captures a broad spectrum of research and insights into red squirrel conservation, allowing for a robust analysis of the trends and challenges that have emerged over time. The inclusion of diverse study types, from field studies to modelling approaches, enhances the depth of this review. Field studies provide valuable empirical data on red squirrel behaviour, habitat use, and interactions with grey squirrels, while modelling approaches offer predictive insights into the potential impacts of habitat management and grey squirrel control strategies on red squirrel populations.

Another significant strength is the focus on the ecological needs of both red and grey squirrels. By examining how these species interact with their environments and each other, this review provides a nuanced understanding of the conservation challenges at hand. This dual focus ensures that the review not only addresses the direct threats to red squirrels, such as competition from grey squirrels and habitat fragmentation, but also considers the broader ecological dynamics that influence these threats.

Moreover, the geographical coverage of the studies included in this review, though concentrated in the UK, extends to various regions in Europe, providing a diverse set of ecological contexts. This diversity helps in identifying common patterns and unique challenges in red squirrel conservation across different landscapes, thereby offering valuable insights for conservation strategies that can be adapted to specific regional needs.

Despite these strengths, this systematic review is not without limitations. One of the primary limitations is the variability in the quality of the studies included. While efforts were made to include only peer-reviewed studies, the methodologies, sample sizes, and analytical approaches varied significantly across the studies, which could introduce biases or inconsistencies in the findings. For instance, some studies may have used less rigorous methods for data collection or analysis, which might affect the reliability of their conclusions. This variability could influence the overall conclusions drawn from the review, as studies with lower methodological rigor might skew the understanding of red squirrel conservation challenges and the effectiveness of certain strategies.

Another notable limitation is the geographic bias present in the literature. A significant proportion of the studies focus on the UK, where red squirrel conservation is a particularly urgent issue due to the pervasive presence of grey squirrels. While this concentration is understandable given the context, it does limit the generalizability of the findings to other regions where the dynamics between red and grey squirrels might differ, or where other threats, such as habitat loss due to agriculture or urban expansion, might play a more significant role. This geographic bias could lead to an overemphasis on certain conservation strategies that are particularly relevant to the UK, potentially overlooking alternative approaches that might be more suitable in different regions.

Furthermore, there are potential gaps in the data concerning lesser-studied aspects of habitat connectivity, particularly in terms of its impact on long-term red squirrel survival and genetic diversity. While some studies have explored the effects of habitat fragmentation on red squirrel populations, there is still limited understanding of how different types of habitat corridors and connectivity measures influence red squirrel movement, gene flow, and resilience against environmental changes. These gaps in knowledge make it challenging to draw definitive conclusions about the most effective habitat connectivity strategies for red squirrel conservation.

These limitations may affect the robustness of the conclusions drawn about the effectiveness of habitat connectivity and other conservation strategies. For instance, the reliance on data from specific regions or studies with variable quality could result in an incomplete or biased understanding of what works best in different contexts. It also highlights the need for further research to address these gaps, particularly in regions outside the UK and in areas of habitat connectivity that have been less studied. Future research should aim to standardize methodologies where possible, expand the geographic scope of studies, and explore the long-term impacts of habitat management practices to provide more comprehensive guidance for red squirrel conservation efforts.

5.0 Conclusion:

In summary, the conservation of red squirrels is a complex issue that has been studied extensively over the past few decades. Habitat fragmentation, urbanization, and the spread of grey squirrels are the primary threats to red squirrel populations. While some red squirrel populations have shown adaptability to fragmented and urban environments, these habitats may not provide the necessary conditions for long-term survival. The invasion of grey squirrels poses a significant challenge, as they outcompete red squirrels for resources and are vectors for diseases like SQPV. Effective conservation strategies will need to focus on habitat management, grey squirrel control, and possibly the use of native predators to support red squirrel populations. Given the long history and ongoing challenges of red squirrel conservation, continued research and adaptive management practices will be essential to ensure the survival of this iconic species.

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Paper 2

Habitat Connectivity and MaxEnt Modelling of Red and Grey Squirrel Distribution, and The Impacts of a Proposed Windfarm

By

KORNELIA P. TWARDOWSKA

Abstract:

This study aims to investigate habitat connectivity and its implications for red squirrel (*Sciurus vulgaris*) conservation and grey squirrel (*Sciurus carolinensis*) control within the mid Wales project area. Specifically, it focuses on identifying habitat corridors, developing species distribution models (SDMs) for both red and grey squirrels using MaxEnt, and assessing the potential impact of a proposed windfarm on red squirrel conservation. Our findings indicate no significant differences in sightings of red and grey squirrels between the years, although an increase was observed in 2020. Similarly, no significant seasonal differences were noted for red squirrel sightings, with a notable increase during the summer of 2020. These trends highlight the importance of continuous monitoring and adaptive management strategies. Using MaxEnt, we developed SDMs to identify areas of high probability of occurrence for both red and grey squirrels. These models provide critical insights into habitat preferences and potential dispersal routes, which are essential for targeted conservation efforts and grey squirrel control measures. Additionally, the study assesses the potential direct and indirect effects of the proposed windfarm project on red squirrel populations and their habitat. The findings underscore the need for careful planning and mitigation measures to minimize negative impacts on red squirrel conservation. This research contributes to a better understanding of habitat connectivity and its role in the conservation of red squirrels and management of grey squirrels, providing valuable information for future conservation strategies and land-use planning in mid Wales.

1.0 Introduction:

Once abundant across Great Britain, the red squirrel (*Sciurus vulgaris*) has experienced a significant decline over the past century, resulting in its endangered status in the UK (Flaherty et al., 2012). The primary causes of this decline include habitat loss and fragmentation, the introduction of the invasive Eastern grey squirrel (*Sciurus carolinensis*) from North America, and the spread of squirrelpox virus (SQPV) (Cox et al., 2020; Rushton et al., 2006). Grey squirrels not only outcompete red squirrels for food and habitat but also carry SQPV, which is deadly to red squirrels (Cox et al., 2020). In the UK, red squirrels are legally protected under the UK Biodiversity Action Plan (Flaherty et al., 2012). The UK conservation strategy prioritizes long-term habitat management, focusing on maintaining and enhancing suitable reserves or strongholds.

1.1 Legal protection

The red squirrel (*Scurius vulgaris*) is protected under Schedules 5 and 6 of the Wildlife & Countryside Act 1981, with amendments from the Countryside & Rights of Way Act 2000. This protection makes it illegal to: intentionally kill, injure, or capture a red squirrel; damage or destroy their shelter or disturb them while they occupy it; possess or sell a red squirrel, alive or dead, or any part of it, without proof of legal acquisition; and additionally, it is illegal to set traps or use devices and substances aimed at harming red squirrels (Shuttleworth & Halliwell, 2016; Wildlife Trust of South & West Wales, n.d.).

Grey squirrel (*Scurius carolinensis*) control is legal without a license, but it is illegal to release or keep them in captivity, as specified by the Wildlife & Countryside Act 1981, the Wild Mammals (Protection) Act 1996, and the Destructive Imported Animals Act 1932. Any trapped grey squirrel must be humanely destroyed. Traps must be checked every 24 hours and twice daily if there is a risk of capturing non-target species like red squirrels (Shuttleworth & Halliwell, 2016; Wildlife Trust of South & West Wales, n.d.).

In Wales, grey squirrels can be managed using several legal methods. These methods include: (1) dispatching squirrels caught in live capture traps, (2) killing them with spring traps approved under the Spring Trap Approval Order (only permitted in areas where red squirrels are absent), (3) shooting them with an appropriate firearm or air weapon, and (4) for pre-weaned juveniles, removing and dispatching them from their dreys when the opportunity arises. Operators must comply with legislation regarding the placement, setting, and operation of traps, as well as animal welfare laws, which prohibit intentionally causing unnecessary suffering (Shuttleworth & Halliwell, 2016).

1.2 Importance of habitat and habitat resources for red squirrels

Habitat and the associated resources play a critical role in the survival and population dynamics of red squirrels. The competition between native red squirrels and the invasive grey squirrels has significantly impacted red squirrel populations, particularly in the UK. The interspecific competition, especially in mixed conifer plantations, highlights the importance of habitat selection and resource availability for red squirrels. For instance, Wauters et al. (2000) investigated this competition by comparing red squirrel populations in conifer plantations where only red squirrels were present to those where both red and grey squirrels coexisted. They found that red squirrels preferred dense Sitka spruce plantations over areas with high grey squirrel densities, indicating habitat avoidance as a strategy to reduce competition (Wauters et al., 2000).

A study by Shannon et al. (2023) on red squirrels' habitat preferences revealed several key findings. Red squirrels were more frequently live-trapped in areas with less canopy openness, suggesting a preference for denser forest canopies. The data collected on Anglesey (Wales, UK), also showed that certain locations, particularly Pentraeth, had higher squirrel abundance compared to others like Newborough, indicating site-specific differences in habitat suitability. Additionally, the presence of Scots pine was positively associated with higher squirrel captures, highlighting the importance of tree species composition in determining habitat quality. These findings suggest that red squirrels prefer habitats with denser canopies and specific tree species, such as Scots pine (*Pinus sylvestris*), which may provide better shelter and food resources.

Invasive species like grey squirrels are major drivers of global change, severely impacting biodiversity and ecosystem dynamics (Bertolino et al., 2020). To mitigate these impacts, regional conservation strategies focus on grey squirrel control (which will be discussed in more detail in section 1.3), and the management of conifer-dominated forests, which are less favourable to grey squirrels due to their inefficient utilization of conifer seeds compared to the larger seeds of broadleaved trees (Shuttleworth et al., 2012).

The management of forest habitats is crucial for maintaining viable red squirrel populations. The establishment of conifer forest reserves in northern England and Scotland aims to create strongholds for red squirrels by providing habitats that are less suitable for grey squirrels (Shuttleworth et al., 2012). These management strategies include the proactive planting of conifers such as Sitka spruce, which produce small seeds that grey squirrels cannot efficiently exploit. Additionally, maintaining a mix of conifer species can ensure a consistent annual seed supply, essential for sustaining red squirrel populations (Shuttleworth et al., 2012). Forest management strategies, such as thinning operations, also impact red squirrel nesting behaviour. Thinning can lead to increased use of dreys and nest boxes, indicating a shift in nesting strategies to adapt to changes in habitat structure (de Raad et al., 2021). The provision of nest boxes post-thinning has proven beneficial, with red squirrels showing a preference for lower-placed nest boxes and increased use over time (de Raad et al., 2021). Forest management practices must also consider the impact of pathogenic tree diseases like Red Band Needle Blight (RBNB) and *Phytophthora ramorum*, which threaten the quality of red squirrel habitats by affecting key conifer species (Shuttleworth et al., 2012). The loss or decline of these tree species can reduce habitat suitability and food availability for red squirrels, further complicating conservation efforts.

The spatial use of habitats by red squirrels is influenced by factors such as habitat fragmentation and forest management practices. In fragmented woodlands, red squirrels adjust their home ranges and social organization in response to patch size and habitat quality (Verbeylen et al., 2009). Males tend to have larger home ranges and higher overlap levels in larger patches, while females defend core areas based on food availability. This spatial behaviour highlights the resilience of red squirrels to habitat fragmentation, provided that the habitat quality is maintained (Verbeylen et al., 2009).

Habitat fragmentation significantly impacts red squirrel distribution, with fragment size and distance to the nearest habitat source being crucial factors. Study by Rodríguez & Andrén, (1999) showed that red squirrels are more likely to occupy forest fragments larger than 10 hectares and within 600 meters of another habitat source, especially when these fragments contain a substantial portion of coniferous trees, which provide year-round food and materials for dreys (Rodríguez & Andrén, 1999). According to Verboom & Van Apeldoorn (1990), the presence of conifers is an indirect measure of habitat quality and is crucial for supporting higher squirrel densities. Small woodlots, often less than 2 hectares, are more likely to be uninhabited due to insufficient size to support viable populations, leading to local extinctions and recolonizations that form a dynamic metapopulation system. Consequently, while models can predict squirrel distribution in larger, connected, and high-quality habitats, they struggle with smaller, more isolated fragments. This underscores the importance of maintaining sufficient habitat size, connectivity, and quality for red squirrel conservation.

The conservation of red squirrels is fundamentally linked to the management of their habitats and the resources available within them. Effective management strategies that consider the impacts of invasive species, urbanization, forest composition, and disease are essential for ensuring the long-term survival of red squirrels in their native ranges. The integration of habitat requirements with proactive conservation measures can help mitigate the threats posed by environmental changes and competitive pressures, thereby supporting sustainable red squirrel populations.

1.3 Grey squirrels control management success story

In 1998, grey squirrel control efforts began on Anglesey to restore red squirrels to their historical range (Shuttleworth et al., 2020; Shuttleworth & Halliwell, 2016). These efforts, combined with phased red squirrel reintroductions, led to the successful eradication of grey squirrels on the island and the restoration of the red squirrel population. By 2009, natural dispersal of red squirrels into mainland woodlands was recorded, establishing a small mainland population with occasional dispersal up to 15 km inland (Shuttleworth & Halliwell, 2016). Anglesey, a 720 km² island in north Wales, is separated from the mainland by the Menai Strait, which is spanned by two bridges (Bamber et al., 2020). The Menai Strait, a natural feature within the red squirrel range, does not act as a barrier to dispersal, as both red and grey squirrels can cross it, likely by swimming or using the bridges. Modelling indicates that without continued intervention, grey squirrels from the mainland could reinvade the island. Additionally, there is a risk of disease transmission as red squirrels move between the island and mainland populations (Shuttleworth & Halliwell, 2016). In 2013, grey squirrels were eradicated from Anglesey up to the sea channel boundary, enabling the red squirrel population to expand naturally and benefit from reinforcement translocations (Shuttleworth et al., 2020). Since 2009, red squirrels have been re-colonizing adjacent mainland woodlands in Gwynedd, demonstrating the landscape's permeability and complicating grey squirrel control and the risk of inter-species interactions (Bamber et al., 2020).

Typically, successful island eradications occur in areas that are geographically isolated or where strong preventative measures can be enforced. Anglesey's connectivity to the mainland through low tides and bridges challenges these measures. On the mainland, grey squirrel control may involve lethal traps with less frequent inspections, but the re-colonization of red squirrels has led to bans on such traps and stricter inspection requirements, reducing control efficiency (Bamber et al., 2020).

Between 2015 and 2020, seven grey squirrels were detected and removed from Anglesey, indicating both the risk of reinvasion and increased conservation costs. Additionally, interactions between mainland red and grey squirrels pose a risk of disease transmission, such as SQPV, which could affect the island's red squirrel population. These issues highlight the ongoing need for vigilant and adaptive management strategies (Bamber et al., 2020).

1.4 Mid Wales Red Squirrel Project

The Mid Wales Red Squirrel Partnership (MWRSP) is a large-scale initiative centred in the Tywi Forest area around the Llyn Brianne reservoir in central Wales (Figure 1). Established in 2002, this collaborative project includes Carmarthenshire, Powys, and Ceredigion County Councils, the National Lottery Heritage Fund, Natural Resources Wales, the Wildlife Trust of South and West Wales (WTSWW), the National Trust, private forest managers, and interested individuals (Wildlife Trust of South & West Wales, n.d.). The project area is a designated area specifically managed for red squirrel conservation, divided into two distinct parts: the focal zone and the buffer zone. The focal zone is the central region where the majority of red squirrels in mid Wales are concentrated. It primarily consists of non-native coniferous forestry plantations surrounded by livestock farms, with the Llyn Brianne reservoir and the village of

Abergwesyn located within it. The buffer zone encircles the core, serving as a transitional area that includes a mix of conifer woodland and privately-owned broadleaved woodlands, interspersed with livestock farms. It also contains several villages and small towns, providing a protective barrier that supports the core's ecological integrity (Mid Wales Red Squirrel Partnership, 2017).

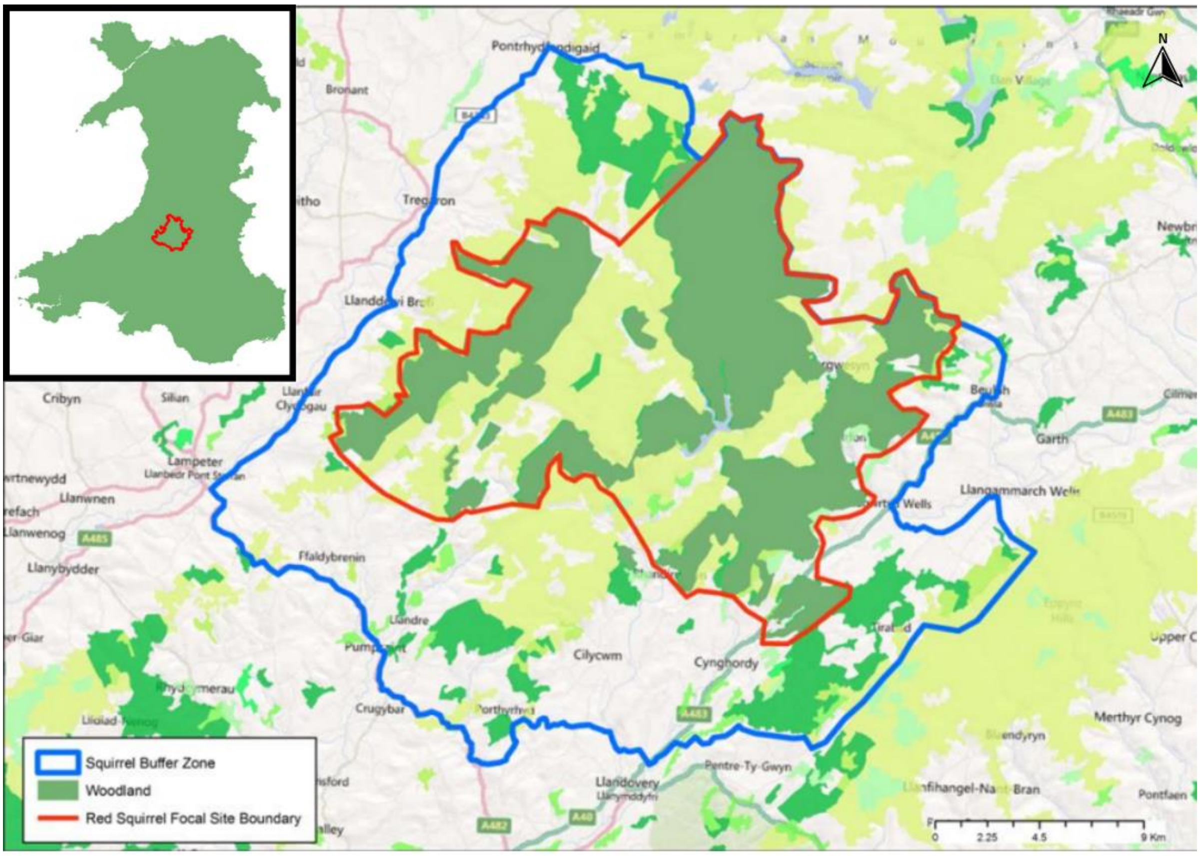

Figure 1. Study area of Mid Wales Red Squirrel Project with focal and buffer zones. Image modified from Mid Wales Red Squirrel Partnership (2017) by adding site location, Wales Boundary map taken from Blackwood (2017).

The project's goal is to protect and expand the genetically unique red squirrel population in the Tywi Forest, one of only three significant populations remaining in Wales and the only one in the southern half of the country (Figure 2). A targeted trapping program in mid Wales revealed significant genetic diversity within the local red squirrel population, with DNA analysis identifying five different mitochondrial DNA haplotypes (Wildlife Trust of South & West Wales, n.d.). Three of these haplotypes were previously unrecorded in Wales and unique to the Mid Wales population, while a fourth, newly identified in 2013, likely originated from historical British translocations and is now common in Ireland (Wildlife Trust of South & West Wales, n.d.). This discovery highlights the substantial genetic variation within the mid Wales red squirrel population, which is crucial for the success of conservation efforts, both locally and across Wales. The partnership initially focused on gathering comprehensive baseline information about the red squirrel population in mid Wales, leading to a solid understanding of the conservation efforts needed.

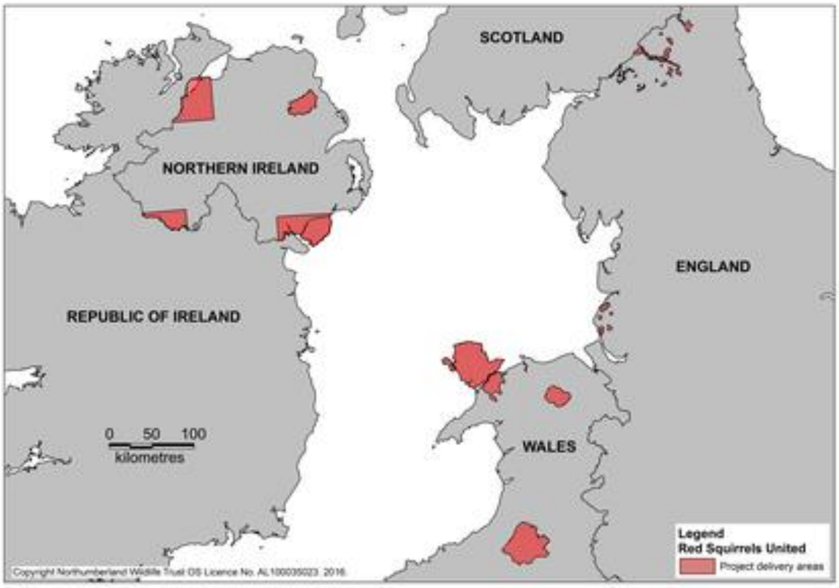

Figure 2. Project delivery areas for Red Squirrels United partnership, which was a four-year red squirrel conservation programme, uniting 9 areas across northern England, Northern Ireland and Wales, including Mid Wales. Image taken from Wildlife Trust of South & West Wales (n.d.).

The MWRSP's efforts have since included creating a buffer area with grey squirrel control, ongoing monitoring of the red squirrel population, advising landowners on habitat improvements, engaging local schools and communities, and enhancing forest planning to benefit red squirrels. In 2023, the Partnership expanded its focal site to include Cwm Rhaeadr and Upper Tywi, an important step in conserving this genetically unique population (Wildlife Trust of South & West Wales, n.d.).

Identifying grey squirrels as a major threat, the MWRSP emphasizes sustained local action for mitigation. Key success indicators for the project include the implementation of grey squirrel control across a significant area of the focal site, particularly in the buffer zone (Mid Wales Red Squirrel Partnership, 2017). The project aims to have at least eight active volunteer groups with a minimum of fifty volunteers actively controlling grey squirrels. Another crucial measure of success is a long-term trend of decreasing grey squirrel numbers relative to the effort expended. Additionally, success is indicated by forest managers producing and adhering to management plans that are sympathetic to red squirrel requirements, and by an increase in the size and extent of the red squirrel population in the focal area (Mid Wales Red Squirrel Partnership, 2017).

1.5 Windfarm project

The Bryn Cadwgan Energy Park, proposed by the renewable energy company Galileo, is planned to be situated on the Carmarthenshire-Ceredigion border, approximately 10 km east of Lampeter, 10 km south of Tregaron, and 16 km north of Llandovery (Figure 3). This project is presented as a contributing to the solution to the climate emergency, aiming to transition to more sustainable energy sources to reduce greenhouse gas emissions and mitigate the risks associated with dependence on imported fossil fuels, which have driven up energy bills (Bryn Cadwgan Energy Park, 2024).

While the Bryn Cadwgan Energy Park promises to contribute to Wales's renewable energy targets and support the Welsh Government's goal of 100% renewable electricity by 2035, it poses significant concerns for the MWRSP. The proposed wind farm is located within a critical conservation area for red squirrels, a species already facing challenges due to fragmented habitats and competition with grey squirrels. The development could potentially cause significant disruption to the red squirrel population and further fragment their critical habitats, posing a risk to ongoing conservation efforts and the delicate balance of their environment. It's essential to carefully assess the possible impact on the red squirrel population and their habitat, as this project may have the potential to undermine existing conservation achievements.

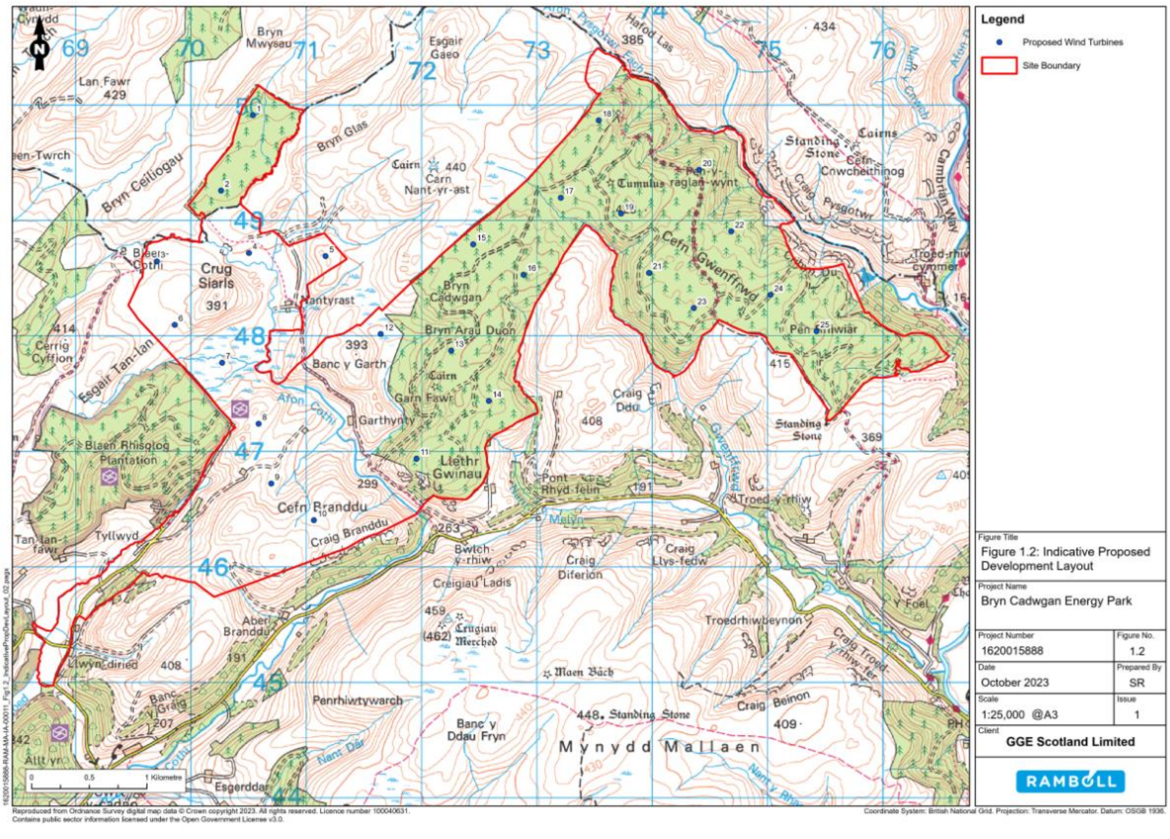

Figure 3. The proposed windfarm by the Bryn Cadwgan Energy Park in mid Wales. Image taken from Bryn Cadwgan Energy Park, 2024.

1.6 Species distribution modelling

Species distribution modelling (SDM) has emerged as a pivotal tool in predicting the spatial extent of biological invasions and identifying areas at risk of invasion by non-native species (Srivastava et al., 2019). These models integrate ecological and environmental data to forecast the potential distribution of species across various geographic landscapes (Miller, 2010). In the context of invasive alien mammals, SDMs are particularly valuable as they can help determine climatic and habitat suitability for species not yet present in an area but likely to arrive, thereby informing preventative management strategies (Srivastava et al., 2019).

While SDMs have been instrumental in climate matching and predicting species spread, their application in evaluating habitat connectivity and management options has been relatively limited (Bertolino et al., 2020). Understanding habitat connectivity is crucial, particularly when assessing the potential for invasive species to move between fragmented habitats and disrupt native species. Therefore, integrating habitat connectivity into SDMs could enhance our ability to predict invasion pathways and inform conservation efforts more effectively.

1.7 Research aims and objectives

The overall aim for this research is to investigate the habitat connectivity for dispersal of red squirrels and incursion of grey squirrels within the mid Wales project area. Understanding habitat connectivity is crucial for red squirrel conservation because it helps their dispersal and gene flow, as well as identifying incursion routes for grey squirrels to target control measures and prevent populations becoming established. Additionally, investigating the potential direct and indirect effects of the proposed windfarm project on the local red squirrel population and their habitat within the study area is essential for comprehensive conservation planning.

The research objectives are to:

- Identify potential habitat corridors facilitating squirrel movement, including for dispersal of red squirrels and for incursion routes of grey squirrels.
- Identify areas of high probability of occurrence for red and grey squirrels by developing species distribution models for each species.
- Assess the potential direct and indirect effects of the proposed windfarm project on the red squirrel population and their habitat within the study area.

2.0 Methods:

2.1 Data collection

The final dataset covers the twelve-year period from 2012 to 2023 for red squirrels and six-year period from 2018 to 2023 for grey squirrels.

2.1.1 Camera trapping

Camera trapping was conducted by WTSWW staff and volunteers. Camera locations were determined using local knowledge and scoping surveys by on-ground staff (e.g., identifying feeding signs). Various types of camera traps were used, resulting in both video footage and photographs. There was no standardized camera setup; it varied from case to case. Trapping was reactive and not systematic; camera traps were deployed randomly and opportunistically across the focal site and a random number of cameras were deployed at any one time. Camera trap footage was manually reviewed by WTSWW staff and volunteers without the aid of analysis software. Data were compiled into Microsoft Excel spreadsheets and returned to WTSWW staff, with no standardized reporting method in place.

2.1.2 Live trapping

Red squirrel live trapping was conducted by WTSWW staff in 2012,2013,2014,2019 and 2020 under the appropriate species licenses for various purposes, including genetic studies, health checks, and individual identification. Traps were baited with hazelnut and peanut mixture and left unset for around 10 days to habituate the squirrels before being set. Traps remained in a set position for 10 days. All trapping activities were recorded, with red squirrels and other bycatch being released, and grey squirrels dispatched.

Live trapping of grey squirrels was performed by WTSWW staff and trained volunteers in 2020,2021 and 2022 as part of a grey squirrel management plan, utilizing a trap loan scheme. All trapping activities by WTSWW staff were recorded, while volunteers provided intermittent reports. Traps were initially baited and left unset for 10 days to habituate the squirrels before being set. Any grey squirrels captured were humanely dispatched, while bycatch was released.

2.1.3 Verified sightings

In addition to the above methods, some data for red squirrels were provided from verified visual sightings. Sightings were verified by staff, trusted volunteers/individuals or those with photographic evidence. Verified sightings contributed additional data points for the target species, enhancing the extent of the dataset.

2.2 Collation of secondary data

Secondary data from WTSWW were provided in multiple Microsoft Excel spreadsheets. Due to the diversity of formats and reporting styles, a master spreadsheet was created to standardize the data. Some data were omitted due to improper recording, such as date ranges and clip counts instead of specific dates, times, and individual counts. Inconsistencies were also noted in age and sex records, with many entries lacking this information. The data included location details (either grid reference or latitude and longitude), date, species, and number of individuals.

2.3 Data analysis

2.3.1 Red squirrel sightings

The number of red sightings per year for the 2012-2023 dataset was counted using the `=COUNT` formula in Microsoft Excel. The data was subsequently entered into RStudio (version 2024.04.2+764, RStudio Team 2024) for further statistical analysis. The Shapiro-Wilk test was conducted to check for normality, and based on the results, the Kruskal-Wallis test was used to assess whether there were statistically significant differences in sightings across the years.

2.3.2 Grey squirrel sightings

The number of sightings per year for 2018-2023 for grey squirrels were counted using the `=COUNT` formula in Microsoft Excel. The data were subsequently entered into RStudio for further statistical analysis.

To examine whether there was a significant difference in the frequency of sightings across the years for grey squirrels, the Kruskal-Wallis test was performed (as the data were not normally distributed, as determined by a Shapiro-Wilk test, and it is well-suited for analysing repeated measures).

2.3.3 Seasonal changes in red squirrel sightings

For the 2012-2023 dataset, red sightings were categorized by season, with seasons defined as spring (March, April, May), summer (June, July, August), autumn (September, October, November), and winter (December, January, February). The seasonal data was then entered into RStudio for further analysis and visualization. A line plot was generated to display trends in sightings by season over time. The Shapiro-Wilk test was performed for each season to assess normality. Based on the results, the Kruskal-Wallis test was applied to determine if there were statistically significant differences in red sightings across the seasons, as this non-parametric test is suitable when the data does not meet normality assumptions.

2.3.4 Species distribution modelling

Sightings data from camera traps, live traps and verified sightings for both red and grey squirrels were provided by the MWRSP and was thoroughly compiled to ensure accurate geospatial references for each sighting. All coordinates were checked for errors to ensure accuracy

The sightings data for both species were uploaded into ArcGIS (version 10.8.1, ESRI 2020), along with focal zone and buffer zone (after the extension of buffer zone in 2023) shapefiles provided by Natural Resources Wales on behalf of the WTSWW. These shapefiles were utilized to contextualize the spatial distribution of the sightings within the relevant environmental zones.

The spreadsheets containing the sightings data were then imported into RStudio for further processing. Duplicate records of sightings were identified and removed to ensure that the analysis was based on unique occurrences. After removing the duplicates, there was 127 unique occurrences for red squirrels and 44 for grey squirrels.

An environmental layer in raster format was obtained to provide additional context for species distribution modelling. The layer of land use was downloaded from UK Centre for Ecology & Hydrology (Morton et al., 2024). The raster data was converted into an ASCII format (.asc file) to ensure compatibility with the MaxEnt software, which is used for species distribution modelling. A shapefile ‘’Wales Country Boundary’’ was downloaded from Edinburgh Data Share (Blackwood, 2017) and used to extract a specific area from the environmental layer, focusing on the area most relevant to this study.

MaxEnt offers an alternative method for evaluating habitat suitability, relying solely on presence data for the target species (Lishan et al., 2017). By comparing the environmental conditions at the site of interest with those at locations where the species is known to be present (“presence sites”), it estimates the likelihood that suitable habitat exists at sites lacking presence or absence data.

After removing duplicates, the cleaned sightings data for the red squirrels were saved as a CSV file. This CSV file, along with the environmental layer in .asc format, was inputted into MaxEnt (version 3.4.3, MaxEnt Team 2020) for species distribution modelling. The MaxEnt software was then run to generate the predicted distribution map for the red squirrels.

The same process was repeated for the grey squirrels, using their respective cleaned sightings data and the environmental layer.

The proposed windfarm project area was also added in later stages and the shapefile was created in ArcGIS based on the specified proposal site location (Bryn Cadwgan Energy Park, 2024).

3.0 Results:

The final dataset included 1288 sightings for red squirrels and 1366 sightings for grey squirrels. Sightings were then uploaded into ArcGIS (Figure 4).

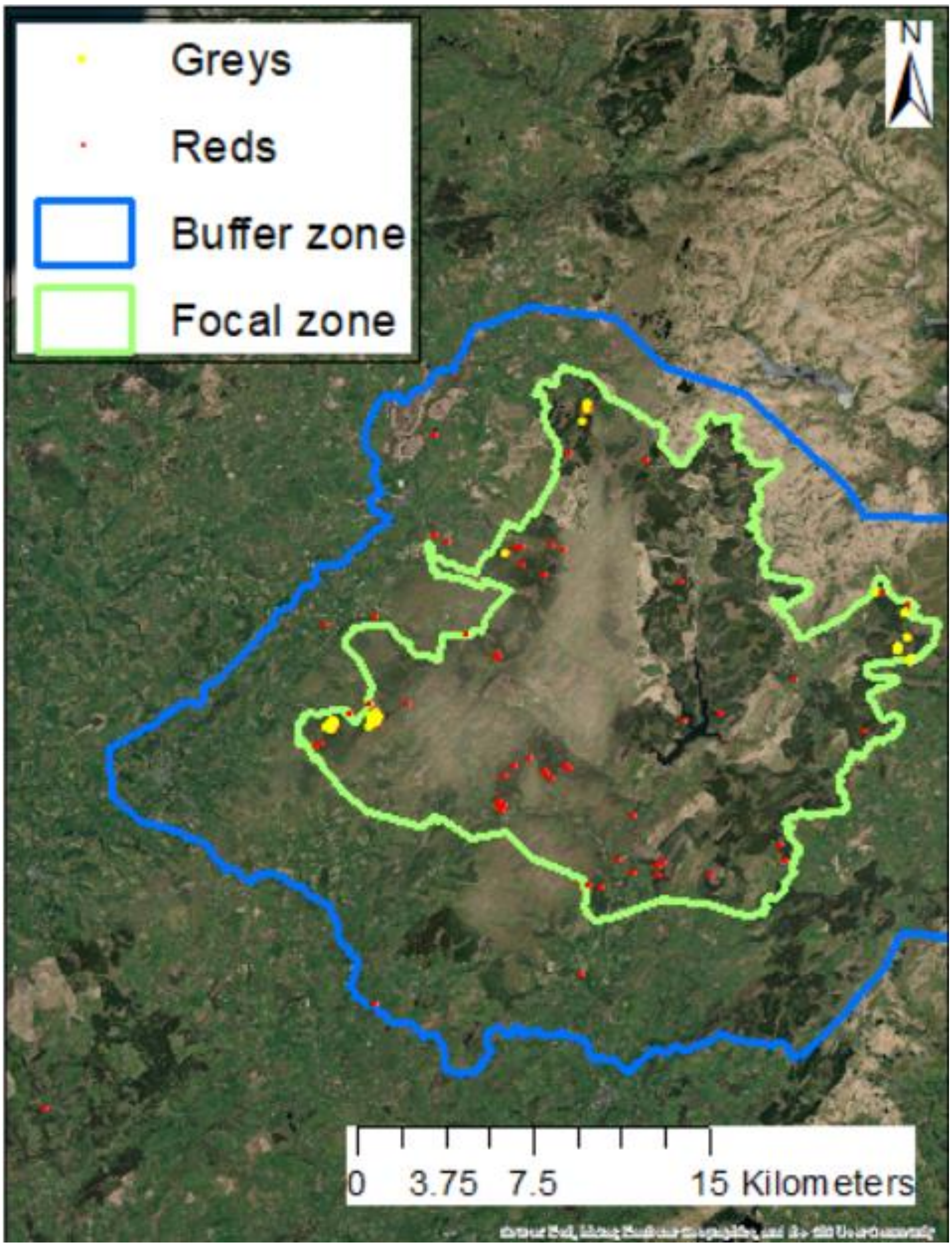

Figure 4. Sightings of red and grey squirrels recorded by the Mid Wales Red Squirrel Project, with boundaries of focal and buffer zones of the project area (created using ArcGIS (v10.8.1, ESRI 2020). Basemap World Imagery from ArcGIS.

3.1 Red squirrel sightings

The annual count of red sightings for the 2012-2023 period showed varying numbers across the years. In 2012, there were only two sightings, and the numbers rose moderately to 12 in 2013, six in 2014, and three in 2015. Sightings varied in the following years, with six in 2016 and a notable increase to 29 in 2017. The count continued to grow, reaching 23 in 2018 and 46 in 2019. The most significant rise occurred in 2020, with sightings increasing to 769. This peak was followed by a decrease in 2021 to 218, and a further drop to 125 in 2022. The decline persisted into 2023, with sightings falling to 49 (Figure 5).

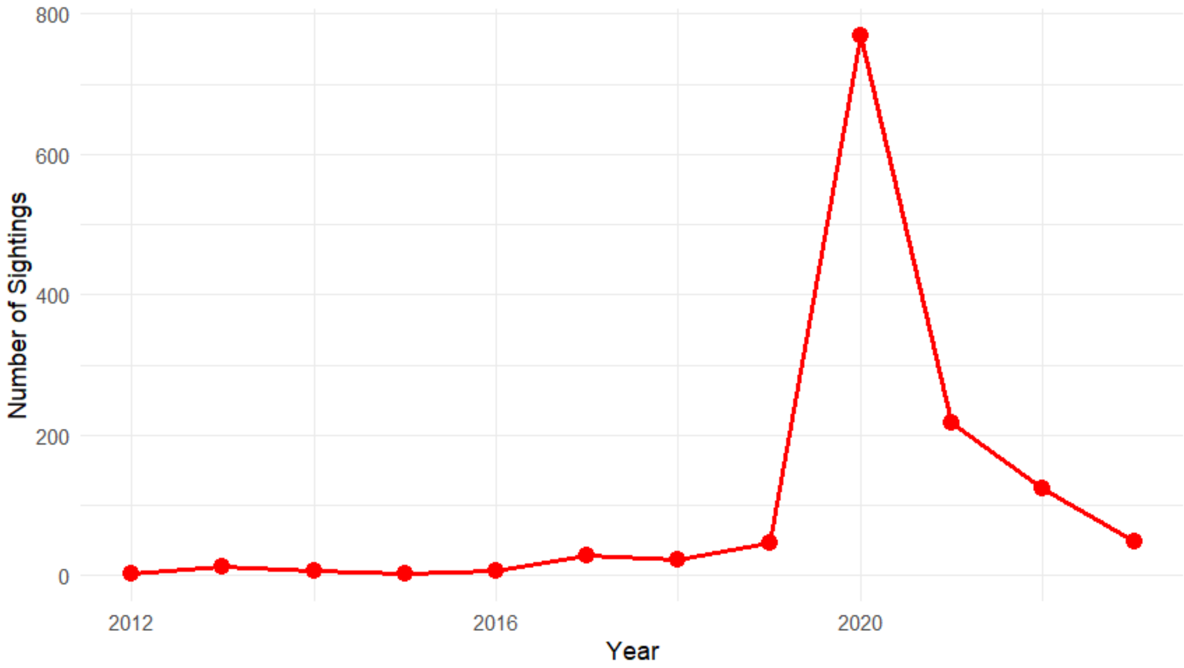

Figure 5. Number of sightings of red squirrels between 2012 and 2023 recorded by the Mid Wales Red Squirrels Project.

The Kruskal-Wallis test was conducted to evaluate differences in red sightings across the years. The test results showed no statistically significant difference between the years (Kruskal-Wallis chi-squared = 11, df = 11, p-value = 0.4433).

3.2 Grey squirrel sightings

In 2018, there were relatively low numbers of sightings with seven grey squirrels. Sightings increased in 2019, reaching 43 greys. The numbers surged dramatically in 2020, peaking at 1020 greys. However, this was followed by a decline in 2021, with sightings dropping to 182. The downward trend continued in 2022, with 52 greys, and persisted into 2023, where sightings were 62.

The Kruskal-Wallis revealed a non-significant difference in the number of sightings across the years for both species, with a higher number of sightings in 2020 compared to the other years (Kruskal-Wallis chi-squared = 5, df = 5, p-value = 0.4159; Figure 6).

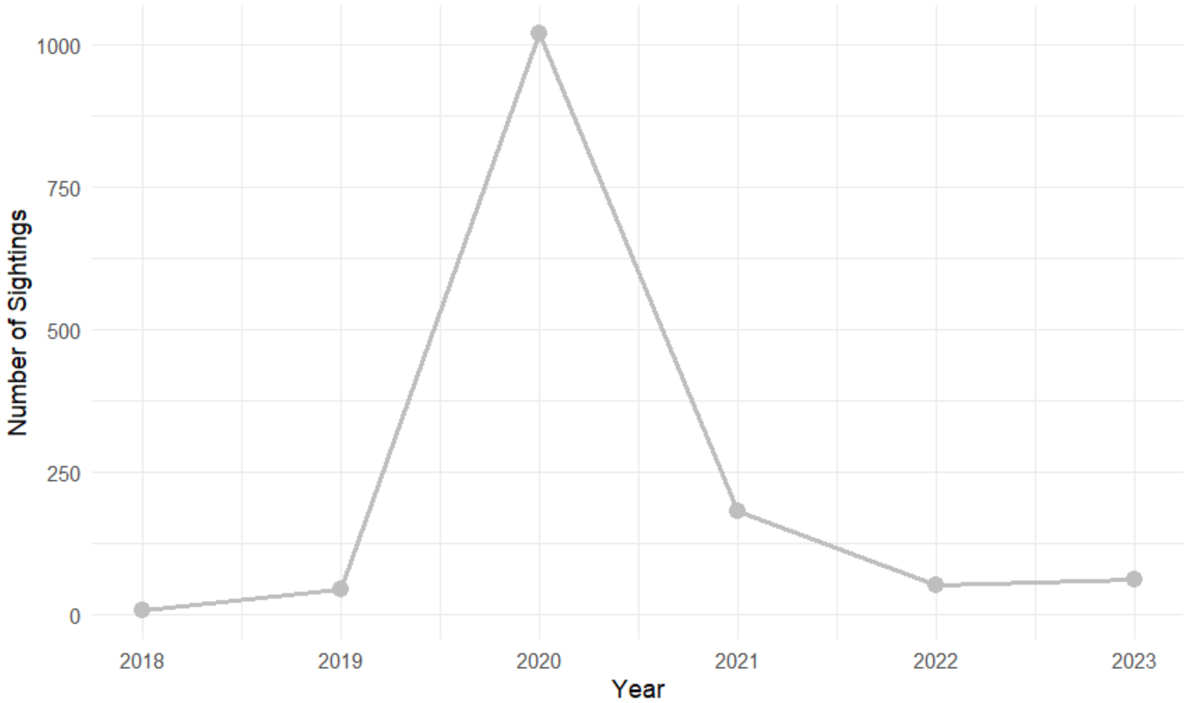

Figure 6. Number of sightings of grey squirrels between 2018 and 2023 recorded by the Mid Wales Red Squirrels Project.

3.3 Seasonal changes in red squirrel sightings

Between 2012 and 2023, red squirrel sightings exhibited a clear upward trend (Figure 7). From 2012 to 2016, sightings were scarce, with only a few recorded each season and some seasons without any sightings at all. This changed in 2017 when an increase in autumn sightings was observed, marking the beginning of a steady rise in red squirrel sightings.

The most significant surge occurred in 2020, with a dramatic spike in sightings across all seasons, particularly in summer (488 sightings) and spring (147 sightings), indicating a peak in red squirrel presence and activity. This high number of sightings continued into 2021, with substantial counts in autumn (137 sightings) and spring (34 sightings).

Although 2022 and 2023 saw a decline from the 2020 peak, sightings remained higher than in the initial years, with moderate counts across all seasons.

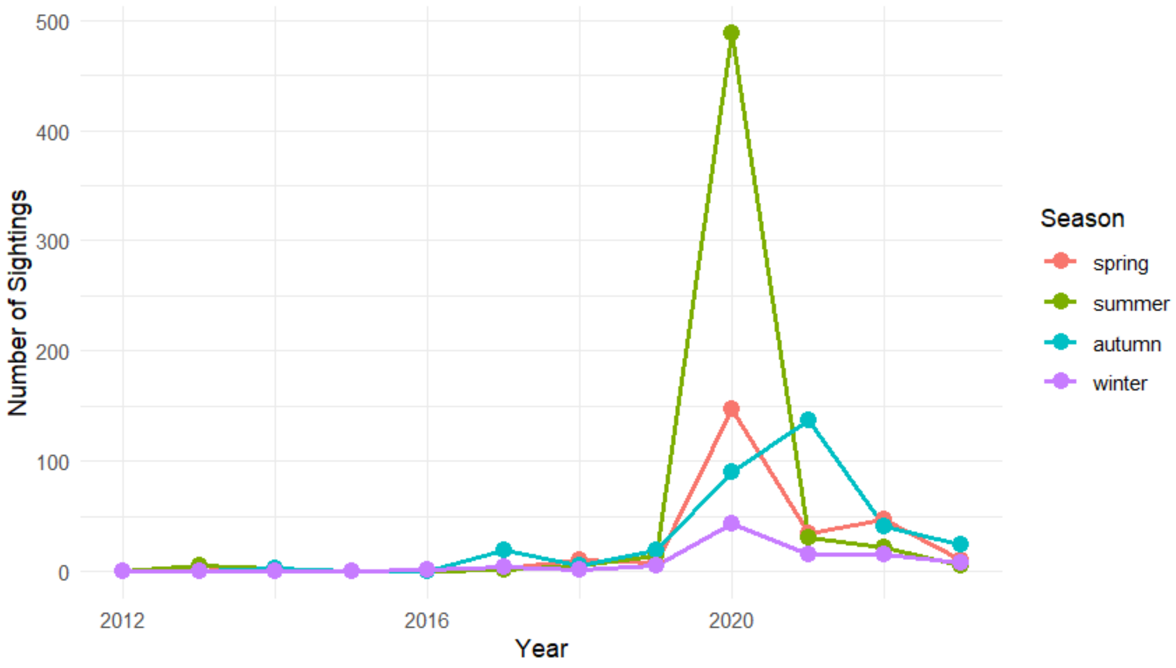

Figure 7. Number of sightings of red squirrels with seasonal distribution between 2012 and 2023.

The Kruskal-Wallis test was applied to determine if there were statistically significant differences in red sightings across the seasons. The test results revealed no statistically significant difference between the seasons (Kruskal-Wallis chi-squared = 2.0501, df = 3, p-value = 0.5621).

3.4 Species distribution modelling

3.4.1 Red squirrel distribution model

For the MaxEnt models, several thresholds were evaluated along with their corresponding omission rates. Binomial probabilities were calculated precisely when test samples were 25 or fewer, otherwise a normal approximation was used. These probabilities represent one-sided p-values testing the null hypothesis that the model predicts no better than random chance for the same fractional predicted area. The "Balance" threshold was determined by minimizing a function of the training omission rate, cumulative threshold, and fractional predicted area.

The analysis of different thresholds for the MaxEnt model revealed several noteworthy metrics:

- Perfect Prediction Thresholds:
  - Cumulative Threshold: 1.000

- Cloglog Threshold: 0.217
- Description: Minimum training presence and Balance training omission, predicted area and threshold value
- Training Omission Rate: 0.000

At these thresholds, the model achieved a perfect training omission rate, correctly predicting all training presences. This indicates highly effective prediction performance at these specific thresholds.

- Moderate Performance Threshold:
  - Cumulative Threshold: 48.430
  - Cloglog Threshold: 0.539
  - Description: Equal training sensitivity and specificity
  - Training Omission Rate: 0.442

This threshold balances sensitivity and specificity but shows a moderate omission rate, suggesting that while the model is balanced, it may not be as accurate as at other thresholds.

- Suboptimal Performance Threshold:
  - Cumulative Threshold: 100.000
  - Cloglog Threshold: 0.977
  - Description: Maximum training sensitivity plus specificity
  - Training Omission Rate: 0.500

This threshold demonstrates a higher omission rate, reflecting a less reliable prediction performance and indicating that this threshold is less optimal for the model.

The model's training data resulted in an AUC (area under curve) of 0.717, compared to a random prediction AUC of 0.5, suggesting that the model is at least 50 % accurate (Figure 8).

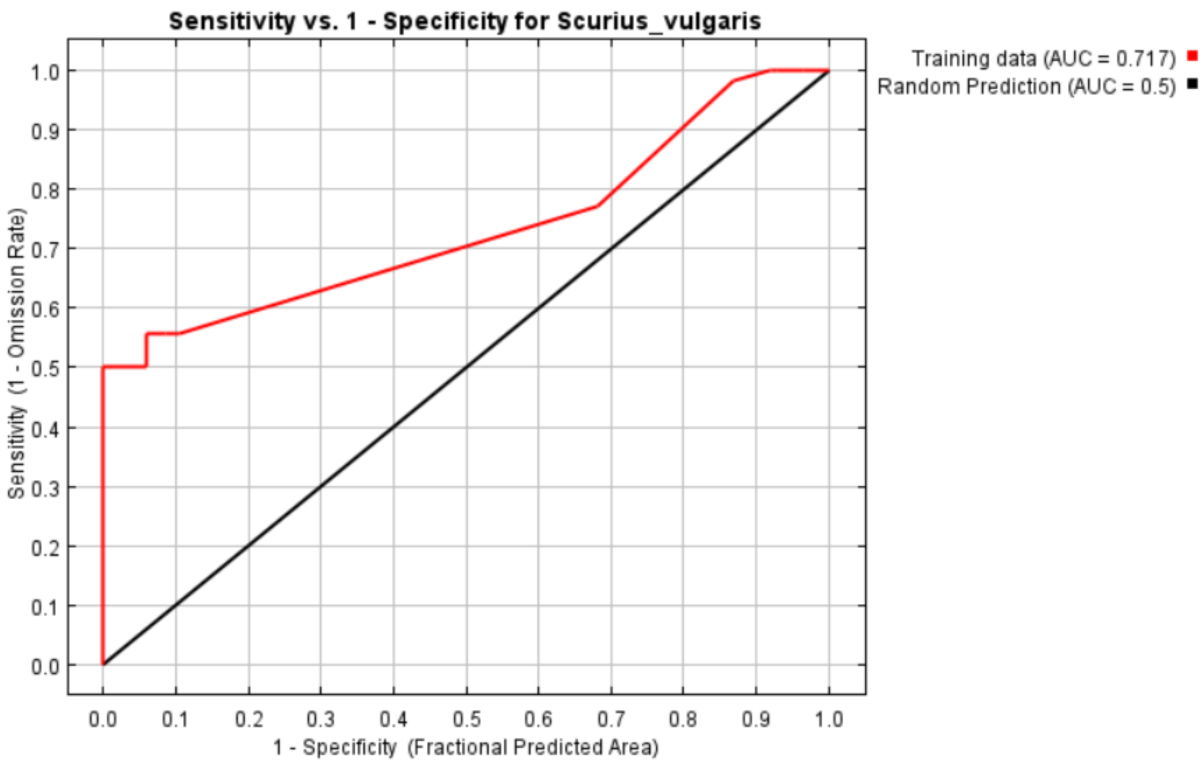

Figure 8. Model accuracy graph, the receiver operating characteristic (ROC) curve for the red squirrel data.

The MaxEnt model was assessed to determine its accuracy and reliability using the training data. The following metrics were calculated:

- Percent Correct Classification (PCC): 56%
  The model achieved a PCC of 56%, indicating that it correctly identified the presence or absence of the species 56% of the time. While this reflects moderate accuracy, it is worth noting that there were no false positives; the model did not incorrectly predict the species as present when it was not.
- Standard Deviation of Omission Rates: 0.223
  The standard deviation of the omission rates was calculated to be 0.223. This value reflects the variability in the model's prediction errors across different thresholds. A moderate standard deviation suggests that while the model performed consistently, there were some variations in its ability to correctly classify species presence or absence across different prediction scenarios.

These results indicate that the MaxEnt model provides reliable predictions with a high percentage of correct classifications and acceptable variability in omission rates. The absence of false positives and the moderate standard deviation suggest that the model is both precise and stable in its predictions.

The species distribution model generated by MaxEnt is shown in Figure 9. Areas with high probability (blue colour) visible in the focal area, but also going southeast into buffer zone and more south from the buffer zone. Proposed windfarm area is situated on the high probability patches as well as it is creating a barrier between potential suitable habitats.

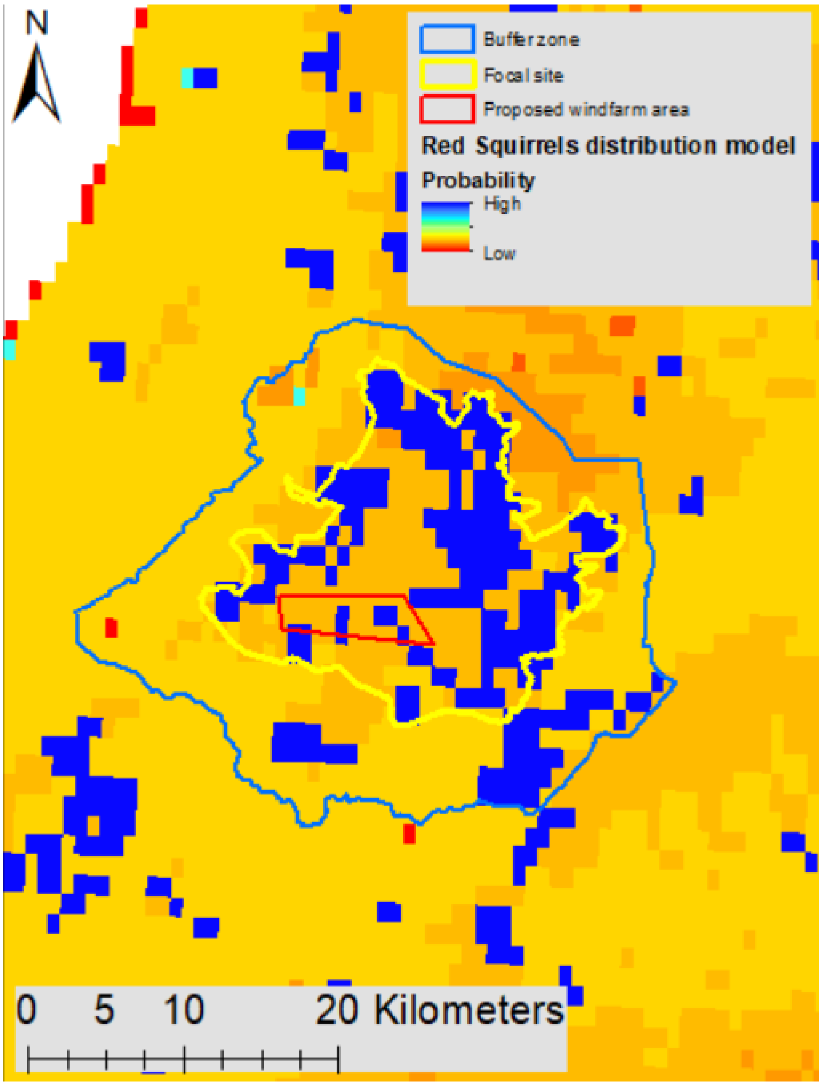

Figure 9. Red squirrel SDM developed in Maxent with focal and buffer zones of MWRSP and area of proposed windfarm. The model is showing areas with high and low probability of species distribution.

3.4.2 Grey squirrel distribution model

The evaluation of various thresholds for the MaxEnt model yielded the following significant results:

- Perfect Prediction Thresholds:

- Cumulative Threshold: 0.542
- Cloglog Threshold: 0.200
- Description: Minimum training presence and Balance training omission, predicted area and threshold value
- Fractional Predicted Area: 0.904
- Training Omission Rate: 0.000

These thresholds achieved a perfect training omission rate, indicating that the model accurately predicted all training presences with no errors at these settings.

- Moderate Performance Thresholds:
  - Cumulative Thresholds: 1.000, 5.000
  - Cloglog Threshold: 0.431
  - Fractional Predicted Area: 0.716
  - Training Omission Rate: 0.200
  - Threshold: 10.000
  - Cloglog Threshold: 0.686
  - Fractional Predicted Area: 0.140
  - Training Omission Rate: 0.200

These thresholds show a moderate omission rate of 0.200, meaning the model was accurate 80% of the time. This is useful for understanding the model's performance where the omission rate is acceptable but not perfect.

- Suboptimal Performance Threshold:
  - Threshold: 57.555
  - Cloglog Threshold: 0.856
  - Fractional Predicted Area: 0.122
  - Training Omission Rate: 0.200

This threshold exhibits a smaller predicted area while maintaining the same omission rate of 0.200, suggesting that the model becomes less inclusive while still showing moderate performance.

The model's training data resulted in an AUC of 0.765, compared to a random prediction AUC of 0.5, suggesting that the model is at least 50 % accurate (Figure 10).

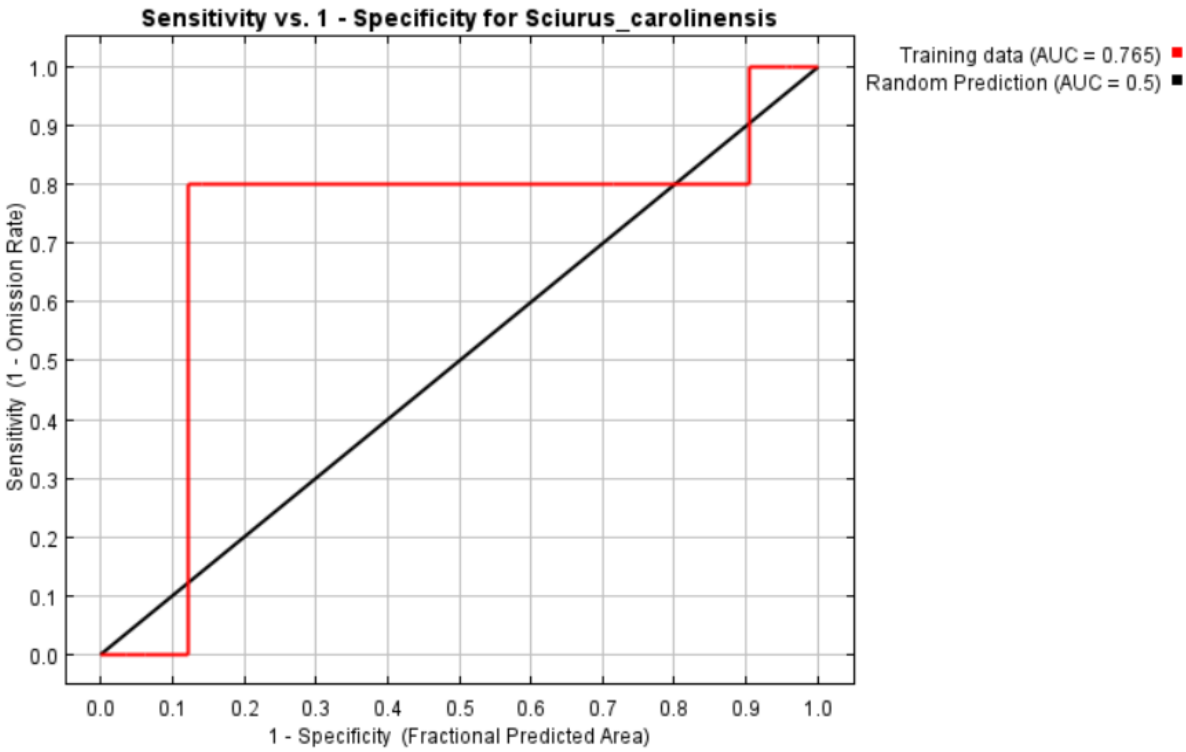

Figure 10. Model accuracy graph, the receiver operating characteristic (ROC) curve for the grey squirrel data.

The analysis of model performance yielded the following results:

- Percent Correct Classification (PCC): 80%
- Standard Deviation (Sample): 0.388

These metrics provide insights into the accuracy and variability of the model predictions. The PCC indicates that 80% of the classifications made by the model were correct, while the standard deviation reflects the variability in omission rates across different thresholds, giving a measure of dispersion around the mean omission rate.

The species distribution model generated by MaxEnt is shown in Figure 11. High probability patches similar to red squirrel SDM. High probability areas within focal site and in the southeast part of the buffer zone, which may indicate potential incursion route.

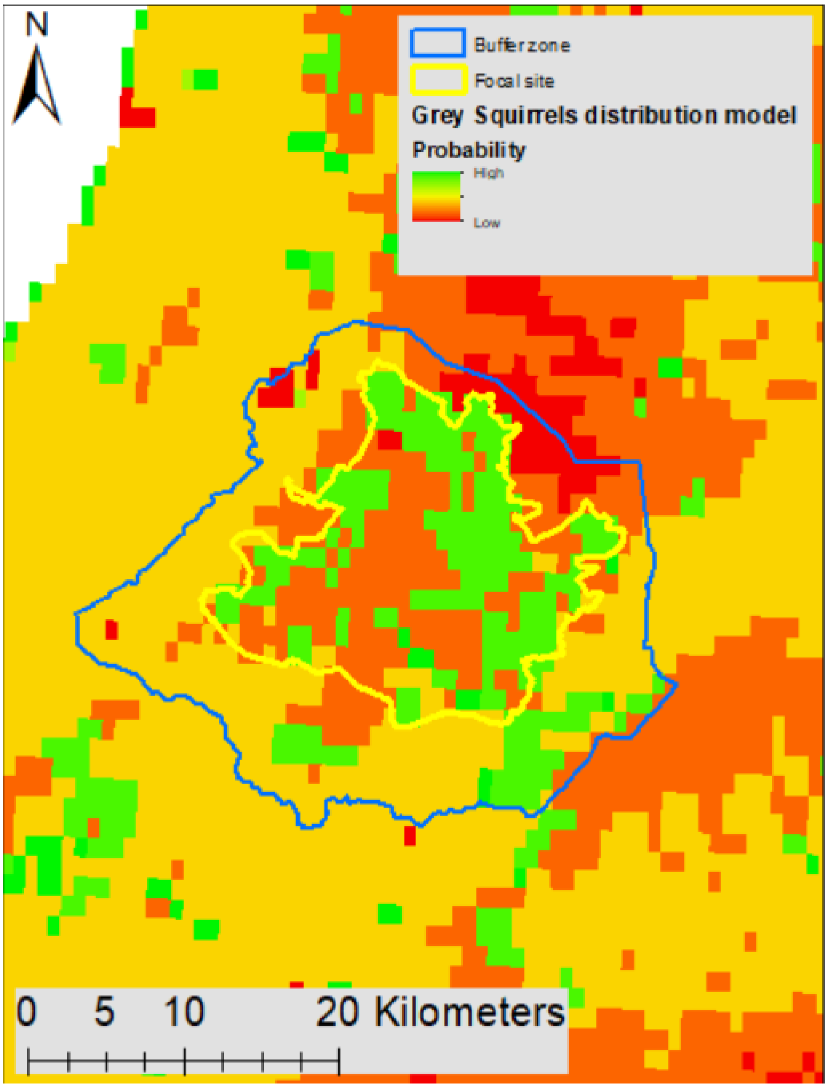

Figure 11. Grey squirrel SDM developed in Maxent with focal and buffer zones of MWRSP. The model is showing areas with high and low probability of species distribution.

4.0 Discussion:

4.1 Findings

The analysis showed no significant differences in the sightings between the years in both species and no significant difference in seasonal changes. However, the overall trend suggests a substantial increase in red squirrel sightings over the decade. This rise in sightings is particularly pronounced in the latter half of the study period. Annually, this indicates a positive trajectory in the red squirrel population, reflecting successful conservation efforts and possibly improved habitat conditions. Seasonally, the data reveals important fluctuations, with a notable increase in sightings during the summer of 2020. This seasonal peak suggests that red squirrels are more active or more easily observed during certain times of the year, which could be linked to their breeding cycles, food availability, or other ecological factors. Thus, while the annual data shows a general upward trend in population, the seasonal data highlights specific periods of heightened activity that are crucial for understanding the squirrels' behaviour and informing targeted conservation strategies.

The increase in red squirrel sightings in 2020 can also be explained by the possible influence of reduced human activity on wildlife behaviour. The year 2020 was marked by the global COVID-19 pandemic, which resulted in a significant reduction in human activities due to lockdowns and travel restrictions. This decrease in human presence likely led to less disruption for wildlife. With fewer vehicles on the roads, reduced noise levels, and minimized human-wildlife encounters, animals had the opportunity to venture into areas they might typically avoid.

Several studies support the idea that wildlife adjusts its behaviour in response to human disturbance. Lewis et al. (2021) found that animals tend to change their daily activity patterns to avoid times when humans are most active. Similarly, Cukor et al. (2021) observed that animals avoid locations visited by humans for a significant period, underscoring the direct negative impact of human activities on wildlife. In 2020 there were instances where animals that usually remain hidden started exploring human-dominated zones, for example, mountain goats roamed the streets of Llandudno, Wales, and fallow deer grazed near a housing estate in Harold Hill, London (Bar, 2021). These occurrences highlight how reduced human activity can lead to increased visibility and altered behaviour patterns in wildlife. Consequently, the increase in red squirrel sightings in 2020 can be partially attributed to these broader trends observed during the pandemic.

Species distribution model for red squirrel revealed majority of the high probability areas within the focal zone, which may indicate the success of the focal area. There are also some areas going southeast into buffer zone and more south from the buffer zone. These areas are also highlighted by the grey squirrel SDM, which indicates that these areas should become the focus for the next conservation and control management efforts as they seem to be connected with the focal zone, creating a potential habitat corridor for the red squirrels but also a potential grey squirrel incursion route. Proposed windfarm area is situated on the high probability patches, so if the proposed project takes place, red squirrels that are occupying that area will be forced to move. The proposed project is also creating a barrier between potential suitable habitat patches, potentially creating fragmentation for the habitat and separating the population, which will have a negative impact on the population genetics and reproduction success. Moreover, the creation of the windfarm will create further disturbance for the red squirrels. There are two distinguished low probability patches in the red squirrels SDM; one within the buffer zone on the west side and one just outside the buffer zone on the south side. These patches are situated in Lampeter and Llandovery, which may again indicate that red squirrels tend to avoid human interactions and disturbance.

4.2 Limitations

The limitations of the data reviewed in this study are significant and must be acknowledged. There are noticeable gaps in the records, likely due to underreporting from volunteers and the omission of data due to variable reporting quality. The absence data would be extremely valuable and would contribute significantly to a greater understanding of overall occupancy. Without detailed information on the number of cameras and traps set, as well as the monitoring start and end points, achieving accurate insights is challenging. Furthermore, the data is almost certainly skewed in terms of density distributions, as it is influenced by areas where staff surveying is more frequently undertaken. Given that the data is presence-only, with no standardized procedure for recording sightings, the limitations are further compounded. However, the WTSWW is actively working to improve these data collection methods. They are implementing more rigorous reporting standards and increasing efforts to collect absence data, aiming to provide a more comprehensive and accurate picture of red squirrel populations and their habitat use (Chapman, 2024).

5.0 Conclusion:

The findings emphasize the importance of enhancing habitat connectivity and managing grey squirrel incursions for effective red squirrel conservation. Key recommendations include focusing conservation and control efforts on areas identified by species distribution models as high probability zones for both red and grey squirrels. This includes monitoring potential habitat corridors and addressing grey squirrel incursion routes. Additionally, the potential negative impact of the proposed windfarm on red squirrel populations necessitates careful consideration and mitigation strategies to prevent habitat fragmentation and ensure population resilience. Continued improvements in data collection and monitoring by WTSWW will be crucial in refining and optimizing conservation strategies.

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