Please Marten the Gap:

A Spatial Prioritization approach for Red Squirrel Conservation in Cumbria, Under the Recovery of a Native Predator

Undergraduate Dissertation for Geography BSc

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Abstract:

Invasive grey squirrels (Sciurus carolinensis) have driven the red squirrel (Sciurus vulgaris) into decline across the UK. In northern England, protected areas reliant on unpopular and poorly funded lethal control are failing to secure long-term red squirrel persistence. The return of the native pine marten (Martes martes), a selective predator of grey squirrels, presents a novel biocontrol opportunity for red squirrel conservation. Full re-colonisation of Cumbria is expected within 25 years, and likely sooner following recent translocations in 2024.

This study presents a bespoke spatial prioritisation algorithm to identify priority areas for red squirrel management under the recovery of a native predator. Three plausible scenarios of predation efficiency, or suppression, are statically modelled on which a cluster-based multi-criteria decision analysis (MCDA) is applied to prioritise management efforts in Cumbria, and evaluate the future efficacy of the Lake District Stronghold Complex. Significant landscape-scale suppression shifts prioritised strongholds from conifer toward broadleaf and mixed woodlands, presenting a paradigm shift in red squirrel protected area strategy. Whinlatter consistently outperforms all possible strongholds, whereas half the stronghold complex score significantly poorly in comparison to generated alternatives.

Full pine marten recovery is expected to benefit all existing strongholds through significant grey squirrel extirpation; however, highly resistant refugia were identified in the north of Cumbria; a total extirpation of grey squirrels from the landscape is not plausible. This is the first study to apply a spatial prioritisation methodology to suppression modelling, it lays the groundwork for red squirrel conservation to move ecological theory to actionable management.

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Chapter 1: Introduction

Invasive species are the leading driver of vertebrate extinctions globally, and protected areas (PAs) are a key strategy for safeguarding threatened species (Bellard et al., 2016; Pacifici et al., 2020). In the UK, red squirrel (Sciurus vulgaris) populations have experienced severe decline due to disease-mediated competition from invasive grey squirrels (Sciurus carolinensis), which asymptomatically carry SquirrelPox virus (SQPV), a disease fatal to reds (Gurnell et al., 2004; Rushton et al., 2000).

Red squirrel strongholds, or PA's designated to preserve remaining populations, are primarily defended through lethal grey squirrel control (Shuttleworth et al., 2015). These interventions are necessary because the two species cannot coexist long-term, even under resource partitioning (Bryce et al., 2005).

Despite these efforts, current stronghold management is insufficient to deliver long-term conservation outcomes. The 2024 RSNE Spring Report recorded rising grey squirrel encroachment and declining red squirrel occupancy across Cumbria. In the Lake District Stronghold Complex (LDSC) (Figure 1), greys were present in 84.4% of monitored reserves, while red occupancy fell to 60.0%, its lowest since 2018. “Hold the line” strategies are not widely securing red squirrel recovery across North England (McQueen, 2024).

Landscape-scale control is needed (Gurnell et al., 2006; Parrott et al., 2009), but conservation agencies in northern England face substantial barriers. In Cumbria, 80% of grey squirrel control is volunteer-led, funding is limited, and public opposition to lethal methods is significant, with more indifferent to grey management as grey squirrels become increasingly culturally embedded (Dunn et al., 2018). Public ambivalence coupled with increasingly unappealing grant systems have led to declines in landowner engagement, which fragments and constrains grey squirrel management (Parrott et al., 2009; Shuttleworth et al., 2021).

The recovery of the native European pine marten (Martes martes) may offer a viable solution. Extirpated from the UK landscape due to intense persecution from game bird owners and the fur trade two centuries ago, its return has been associated with grey squirrel decline and red squirrel resurgence, even in broadleaf woodland where reds are especially vulnerable to competition (Sheehy et al., 2018; Joshua P. Twining et al., 2020).

Unlike classical biological control, which introduces non-native predators and risks disrupting ecosystems where native species lack evolved defences, pine marten reintroduction offers a native alternative where risks may be less uncertain (Pearson et al., 2022; Twining et al., 2022a). This is the 'marten-squirrel model system', where a native predator selectively suppresses an naive invasive prey species, with co-evolved species exhibiting reliable predator avoidance behaviour (Twining et al., 2020; 22).

Now a Schedule 5 protected species under the Wildlife and Countryside Act 1981, the pine marten has become a focal point for reintroduction efforts, recognised for both its cultural significance and its demonstrated conservation benefits (Twining et al., 2022; MacPherson and Wright, 2021). In 2024, thirteen individuals were translocated to the Grizedale Forest (Figure 1) under the Back on Our Map (BOOM) project, following extensive suitability assessments (Macpherson et al., 2024; Macpherson and Wright, 2021; Mayhew et al., 2022).

A full recovery of pine martens in Cumbria is expected within 25 years, based on conservative estimates from modelling prior to BOOM-led reintroductions (MacPherson et al., 2024). This is likely to reshape red squirrel conservation strategies, which have predominantly focused on habitat composition, selecting conifer woodland networks where reds have a natural competitive advantage (Gurnell, 2004). Since selective predation is consistent across all woodland types (Twining et al., 2022b), management focus could instead focus on landscape structure, prioritising areas that support higher pine marten densities regardless of habitat type. With broadleaf woodland comprising 64% of woodland in the Lake District National Park (LDNP, n.d), previously overlooked areas may now support larger, more effective, and resource-efficient strongholds. Although not assessed in relation to pine marten predation, Slade et al. (2021) referred to these areas of long term red squirrel persistence with minimal intervention as “natural strongholds".

Suppression is unlikely to occur evenly across the landscape, with grey squirrels likely to persist in structurally resistant or urban refugia where pine marten densities are low (Slade et al., 2022; Twining et al., 2021). As grey squirrel distribution becomes increasingly shaped by landscape features, targeted control may become more feasible and effective. This shift weakens the value of current stronghold strategies, and highlights the need for spatial prioritisation at a landscape scale to reallocate effort where it can deliver the greatest conservation gain. To date, no model of pine marten suppression has directly informed future management using decision-making frameworks for spatial prioritisation to enable the conservation triage required to conserve red squirrels within a landscape-wide invasion pressure.

This study integrates a linear suppression model derived from (Slade et al., 2023) with a bespoke spatial optimisation algorithm, using a multi-criteria decision analysis framework to test how full pine marten recovery could reshape the optimal allocation of limited conservation resources. In response to the continued pressures on red squirrels in the Lake District Stronghold Complex (LDSC) (Figure 1), it aims to generate evidence led landscape-scale policy recommendations aligned with recent calls from the rewilding literature and Red Squirrels United (RSU) (O'Connell and Prudhomme, 2024; Shuttleworth et al., 2021a). More broadly, it advances the marten-squirrel model as a transferable framework that can be integrated with priority area selection for invasive species management globally, and contributes to bridging the divide between ecological modelling and practical conservation implementation (Zurell et al., 2022).

[1.1] Research Questions:

1. What is the spatial extent and variability of grey squirrel populations across Cumbria under different levels of suppression, when pine martens are at carrying capacity?

2. How does the optimal conservation strategy change in response to scenarios of high, moderate and low suppression?

3. How can spatial prioritisation identify novel conservation opportunities, and appraise existing stronghold management under different levels of suppression?

[1.2] Study Area: Cumbria, UK

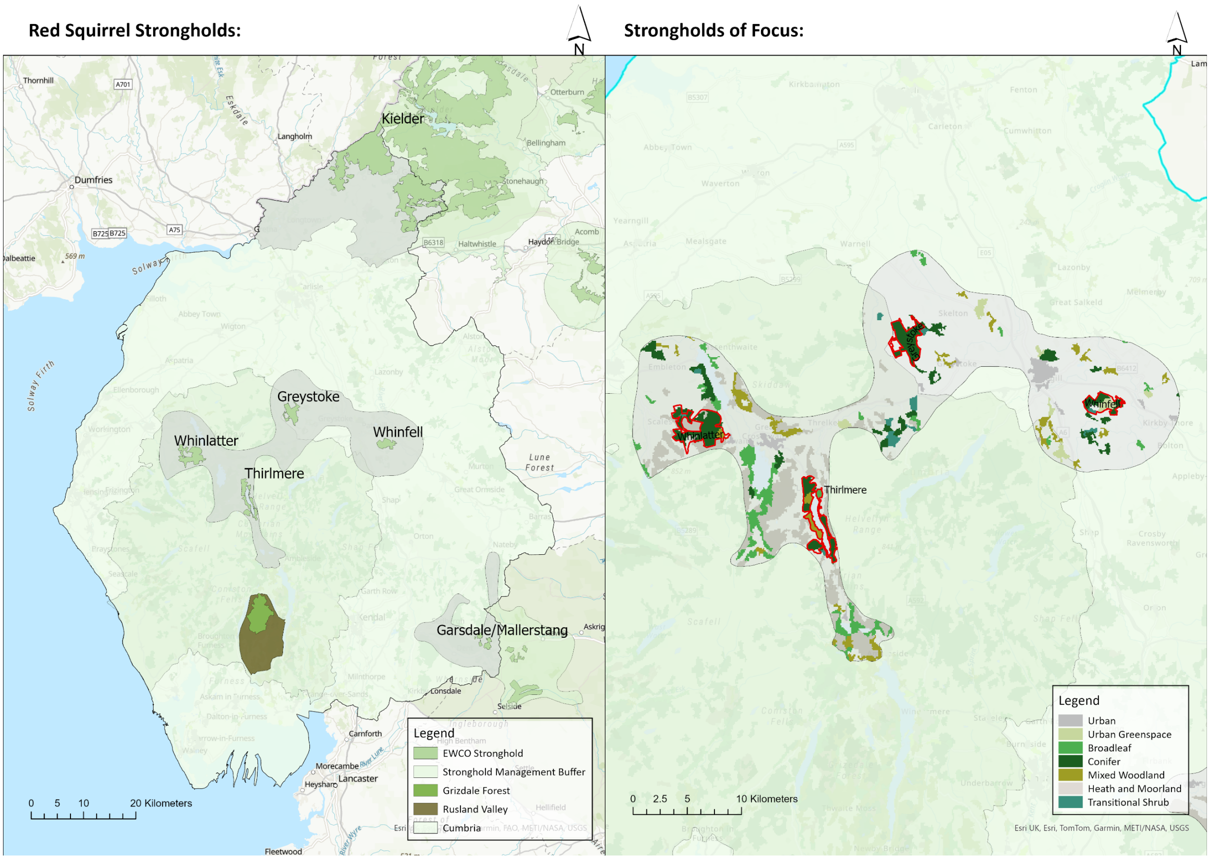

Figure 1: Study Area - Cumbria (Left) and the Lake District Stronghold Complex (Right)

Figure 1 Shows the Lake District Stronghold Complex, and the primarily conifer habitat composition of the strongholds within it for context throughout this dissertation. Additionally, on the Left, Grizedale Forest and the surrounding Rusland Valley are identified to present where BOOM translocated the 13 pine martens in 2024.

Chapter 2: Academic Context

[2.1] Limits to Landscape Scale Management

In the face of a UK-wide invasion, Rushton et al. (2006) reported that effective grey squirrel control would need to operate at a landscape scale. Between 2016 and 2020, the Red Squirrels United (RSU) project trialled this approach through a multi-partner collaboration, with each site reporting success locally (Shuttleworth et al., 2021). However, O'Connell and Prudhomme (2024), in a national review of rewilding projects, found that these kinds of volunteer-led initiatives often lacked formal spatial prioritisation or trade-off analysis, directing resources toward opportunistically selected areas, or sites already receiving management due to the feasibility constraints of working with landholders to pursue management at new sites (Shuttleworth et al., 2021).

Since the replacement of the English Woodland Grant Scheme (EWGS) with Countryside Stewardship Higher Tier (CSHT), landholder uptake of grants for grey squirrel control has decreased due to the burdensome requirement for Woodland Management Plans, or ineligibility due to the CSHT excluding woodlands under 3 hectares. This side lines small but important land parcels utilised for grey dispersal (White et al., 2014).

While the England Woodland Creation Offer (EWCO) provides grant support to landowners in stronghold buffers, NGOs are required to fill critical gaps (Parrot et al., 2009; Shuttleworth et al., 2009; McQueen et al., 2024). Technically eligible sites are often bypassed when incentives are weak or perceived burdens outweigh benefits — particularly where game management conflicts with control methods.

In contrast to common invasive species rhetoric, particularly pest narratives, a significant portion of the public holds positive perceptions of grey squirrels. This presents a barrier to landscape-scale management by conservation organisations that rely heavily on public funding (Dunn et al., 2018; Warren, 2023). Grey squirrels have been present in the UK for over

200 years, initially introduced for ornamental purposes, and are now familiar and highly visible in daily life. As a result of becoming embedded in the cultural landscape, they are subject to greater animal welfare concern (Dunn et al., 2018; Littin, 2010; Wauters et al., 2023).

Outside of stakeholders involved in woodland management or attentive landowners familiar with bark stripping behaviour, understanding of the ecological and economic damage grey squirrels cause is limited, and most people report generally positive wildlife interactions (Dunn et al., 2018). Lethal control methods raise serious welfare concerns when directed at culturally embedded species, even when those species are invasive and around half the UK public oppose lethal control of grey squirrels if it considered inhumane, like Warfarin poison (Dunn et al. 2018) Non-lethal strategies such as immunocontraception are more publicly acceptable, but they are the least practical and least effective when not used in conjunction with lethal control (Croft et al., 2021; Dunn et al., 2018; Shuttleworth et al., 2021) fragmented pattern of management feasibility and funding at the landscape scale. There is little evidence that eradication at scales beyond protected areas is feasible, except on Anglesey, where strong local support and isolation from mainland with limited dispersal routes enabled success (Schuchert et al., 2014).

Given the infeasibility of landscape-scale eradication, red squirrel conservation is confined to protected areas. Stronghold policy in Northern England prioritises conifer woodland networks, based on the long-standing view that conifer habitats provide a competitive refuge for red squirrels (Figure 1). A minimum of 2000 ha of connected woodland, with commute distances between 300 and 600 m, is recommended to support viable populations. However, smaller core areas of 200–300 ha, buffered 100 m from edge habitat, can also support populations if habitat quality is high (Rodríguez and Andrén, 1999; Stevenson-Holt et al., 2014; Verbeylen et al., 2003). A managed buffer of 1 to 3 km is typically required to prevent grey squirrel incursion (Pepper and Patterson, 1998).

Red squirrels maintain a competitive advantage in conifer woodland, particularly plantations, where low-calorie small seed mast yields, and delicate canopy are unsuitable for sustaining the larger-bodied grey squirrel. However, grey squirrels exhibit a suite of advantages, such as enzymatic digestion of high-tannin acorns, superior ground foraging, and cache pilfering, that allow them to dominate in broadleaf and mixed woodlands. High fecundity and near-absence of natural predation enable greys to sustain populations at or near carrying capacity in nearly all woodland types, excluding red squirrels from resources, reducing juvenile recruitment, and asymptomatically spreading SQPV, causing fatal disease in reds and rendering long-term coexistence nearly impossible which highlights the significance of grey presence found in strongholds (Gurnell et al., 2004; Santicchia et al., 2018).

Red squirrels avoid habitat patches smaller than 3.5 ha, and 96% of patches under 10 ha remain unoccupied (Verbeylen et al., 2003), although use of patches 3.5 ha and above has been recorded in Cumbria Stevenson-Holt et al. (2014) modelled grey squirrel dispersal networks in Cumbria, observing a strong dispersal ability between habitat fragment patches up to 8km apart, and can colonise even structurally isolated habitat units. This recolonisation risk is particularly problematic for the long-term viability of red squirrels in Cumbria, where the landscape is heavily fragmented (Stevenson-Holt, 2008)

To reduce recolonisation risks, isolated habitat patches are often selected for stronghold designation. However, this introduces other vulnerabilities. Red squirrel populations in isolated reserves are more susceptible to stochastic collapse and show signs of reduced gene flow and inbreeding, threatening long-term viability (Chandler et al., 2025; Cox et al., 2020). Given these risks, and evidence of stronghold strategies failing (McQueen et al., 2024), pine martens as a biocontrol are increasingly called for investigation by conservation agencies (Shuttleworth et al., 2021).

[2.2] The European Pine Marten as a Biocontrol

Pine marten recovery is strongly associated with grey squirrel decline and red squirrel resurgence (Sheehy et al., 2018; Sheehy and Lawton, 2014). Grey squirrels show little predator avoidance behaviour toward martens, a naivety which contrasts red squirrels' co-evolution, leading to higher predation rates of grey squirrels where both species co-occur (Twining et al., 2020b). Scat analysis further supports selective predation, with grey squirrel remains appearing three times more frequently than red (Twining et al., 2019; 2020a; 2022).

This interaction reduces both competitive exclusion and disease transmission, although suppression does not eliminate SQPV risk, as even low-density grey populations can sustain reservoir dynamics. The exact threshold can be determined by complex, site contextual modelling, and a more appropriate approach is to consider any sustained grey populations as a disease risk (Roberts and Heesterbeek, 2021; Slade et al., 2023; Travaglia et al., 2020).

Pine martens are generalist predators with home ranges following translocation averaging 9.5 km^2 in the UK. They use landscape supplementation to persist in fragmented landscapes with as little as 20% woodland cover and while a woodland denning species, they exploit forest edges, recently felled areas, and disturbed shrubland for hunting, as they are rich in small mammals like field voles (Angoh et al., 2023; Caryl et al., 2012; McNicol et al., 2020). They avoid grassland, farmland, and anthropogenic structures (MacPherson and Wright, 2021). Habitat suitability peaks in broadleaf woodland, which offers natural denning and prey abundance. Mixed woodland offers intermediate suitability, while conifer plantations are prey-poor and den-limited (Brainerd and Rolstad, 2002; Caryl et al., 2012).

The extent to which pine martens reliably conserve red squirrels are subject to spatial and temporal concerns. As a prey-switching generalist, grey squirrel predation is sensitive to routine four-year cycles of increased field vole abundance. During these peaks, predation is significantly reduced as field voles are preferred prey (Twining et al., 2022). Though not under the context of landscape scale suppression, full population recovery has been observed in just a month following the cessation of high intensity trapping, due to high fecundity, and dispersal from nearby populations(Lawton and Rochford, 2007; Wauters et al., 1995). Slade et al. (2023) accounted for this uncertainty by modelling three predation rates. This study follows that approach, evaluating the robustness of spatial prioritisation and trade-off analysis across those scenarios.

Additionally, while pine martens can substantially reduce disease-mediated competition, the threshold at which grey squirrels are suppressed enough to eliminate SQPV reservoirs is highly contextual, dependent on local densities and habitat carrying capacity, creating uncertainty in effectiveness. Concurrently, dispersal from nearby sustained grey populations can act as an infection risk; though red squirrel populations will rarely sustain a reservoir of disease because of its near immediate lethality, it evidences that even low densities of grey squirrels can be significantly harmful under pine marten suppression (Travaglia et al., 2019; Roberts and Heesterbeek, 2021).

The re-introduction of the pine marten is contingent on public support. As a native species, their re-introduction has cultural legitimacy, perceived as both ecologically valuable and intrinsically worth restoring. Two of the top three public motivations for its return are "restoring a natural balance" and "bringing back a native species" (Ambrose-Oji et al., 2018). This contrasts sharply with the stoat (Mustela erminea) in New Zealand, another mustelid with near identical aesthetic and morphological introduced for biological control, now the target of nationwide eradication due to unintended predation on valued native birds (Morris, 2020). Framed as a morally corrupt outsider under the native-alien binary, the stoat has become a symbol of ecological invasion (Warren, 2023). It is the intrinsic value afforded to native species, and their predation of grey squirrels viewed as natural process, which has conservation value in overcoming the moral objections that limit the efficacy of lethal grey squirrel control.

However, pine martens are not immune to controversy, with concerns around their predation on birds, game species, and pets, particularly in rural areas where land-use conflict is more likely (MacPherson and Wright, 2021). They also predate red squirrels, contributing to population declines in conifer plantations lacking alternative prey, and primary conservation areas of competitive advantage (Twining et al., 2019; 2020). However, across most contexts, pine marten recovery benefits red squirrels, although at densities lower than in the absence of predation and competition (Twining et al., 2022).

[2.3] Modelling for conservation triage

Multi-Criteria Decision Analysis (MCDA) enables conservation triage by weighing trade-offs between conflicting criteria to achieve the greatest conservation value using the most effective balance between total amount target species conserved with the feasibility, and cost of management. It can be used in combination with spatial prioritisation to rank candidate protected areas to best allocate limited resources spatially (Esmail and Geneletti, 2018; Zurell et al., 2022). Under future uncertainty, these can be used in conjunction with modelling that improves decision making by systematically investigating invasive species management scenarios to achieve the greatest conservation benefits. For example Nishimoto et al. (2021) combined MCDA with a state-space model to evaluate the long-term impact of culling on invasive snapping turtles. Spatial prioritisation identified optimal intervention sites by scoring trade-offs between control effort, a product of density, and the value of locations to stakeholders.

However, frequently these detailed insights are not explicitly pursued to inform practical decision-making, and there is a significant disconnect between models built for ecological understanding, and the reality of applied conservation planning (Garcia-Diaz et al., 2019; Schuwirth et al., 2019). Trust and interpretability in model outputs are critical to facilitate confident decision making by conservation managers, but ecological modelling often involves complexity and abstractions that can be challenging to interpret, especially as these two disciplines are siloed (Garcia-Diaz et al., 2019; Schuwirth et al., 2019). Understanding ecosystem relationships is valuable for conservation managers, but if models fail to show how these changes inform the broader, multifaceted demands of decision-making, they rarely lead to policy change (Lecours, 2017; Weiskopf et al., 2022).

Slade et al. (2021) was the first peer-reviewed model to explore natural strongholds, defined as areas where red squirrels persist even under full invasion. Their model simulated competition dynamics under current and hypothetical woodland management scenarios, identifying 19 conifer-dominated natural strongholds resistant to competition. These natural strongholds shared no overlap with designated management zones, suggesting their design is inefficient in light of new evidence. The results were used in a formal review of Scottish stronghold policy, presenting the scope for current designations in the UK to be evaluated; however, while ecologically feasible, these sites were not evaluated with management constraints in mind, and used no criteria analysis to suggest management strategies. The natural extension of this literature is to evaluate existing strongholds against the opportunities presented by pine marten predation, for the purpose of policy review.

Croft et al. (2021) used an agent-based model to simulate grey squirrel suppression in North Cumbria via trapping and immunocontraception, incorporating functional connectivity through resistance surfaces and cost-distance metrics. Suppression efficiency varied spatially with landscape structure: isolated woodland fragments were easier to clear, while larger, connected sites resisted eradication due to meta-population recovery. At 0.125 traps/ha, culling halved grey populations in one year; complete eradication over 50 years required at least 0.25 traps/ha. Despite its labour demands, live trapping remains the most reliable method of grey squirrel control; however, recent evaluations suggest far lower efficacy than projections by Croft et al. signalling that despite the high relevance to management, its impact is limited by the absence of operational, site-specific recommendations (Shuttleworth et al., 2021; McQueen et al., 2024). Furthermore, Croft et al. assigned higher carrying capacities to mixed woodland than to broadleaf woodland based on field validation in mixed woodland sites only, which contradicts widely used empirical evidence of grey squirrel carrying capacities (Wauters et al., 2008).

Slade et al. (2023) modelled red-grey-pine marten dynamics in North Wales to assess red squirrel recovery under predator-mediated suppression. It estimated suppression using retrospective field data on pine marten density, applying fixed rates uniformly across the landscape. Designed to advocate for translocations, the study focused on demonstrating the viability of pine martens as a biological control rather than optimising post-reintroduction management. In Cumbria, where reintroductions have already occurred, the principles of Slade et al.'s model should be extended to inform management.

Although suppression dynamics are increasingly well parameterised, they remain disconnected from spatial optimisation frameworks. While red squirrel viability has been mapped (Slade et al., 2021) and suppression effects quantified (Slade et al., 2023), these insights are rarely integrated. Prioritisation logic is often absent, and trade-offs remain underexplored. No existing study provides an operational framework that translates suppression modelling into actionable strategies under real-world constraints. This dissertation addresses that gap directly.

Chapter 3: Methodology

[3.1] Investigative framework

To address the research questions, a three-part methodology is employed. First, the static density and distribution of grey squirrels and pine martens at full carrying capacity are modelled by assigning species-specific density estimates to relevant land cover types. Second, the suppressive effect of pine martens on grey squirrel density is simulated using three empirically plausible suppression coefficients, reflecting uncertainty in predation efficiency (Slade et al., 2023). Third, for each suppression scenario, a clustering algorithm is applied in conjunction with a multi-criteria decision analysis (MCDA) function to generate and evaluate candidate red squirrel strongholds.

The clustering algorithm produces hundreds of potential stronghold configurations by aggregating high-priority habitat patches and selects the top scoring five. Each candidate stronghold is then evaluated using a multiplicative MCDA based on three variables: grey cost, total core area, and management feasibility (see Section 3.2).

Subsequent analysis examines: (i) the habitat composition of the selected strongholds, (ii) the correlation between each MCDA variable and final scores under different suppression assumptions, (iii) spatial overlap between top strongholds across scenarios, and (iv) changes in stronghold size and location. This allows evaluation of how optimal stronghold strategy shifts with increased pine marten suppression, informing trap placement, revealing new more efficient candidate areas, and novel conservation tactics regarding landscape and habitat structure.

Finally, existing strongholds in the Lake District Stronghold Complex are evaluated using the same scoring criteria. Their performance is compared against all candidate strongholds identified under each scenario, allowing appraisal of their relative value under long-term pine marten recovery.

[3.2] Identifying Criteria and Data Collection

Correctly identifying relevant criteria is the first step of any Multi-Criteria Decision Analysis (Esmail and Geneletti, 2018; Zurell et al., 2022). The numerous constraints to conservation activity are abstracted to three components:

[3.2.1] Grey Cost

Post-suppression grey squirrel density, calculated as the mean grey squirrel density within the stronghold as well as within a 3 km buffer zone surrounding it. This buffer zone represents areas from which grey squirrels could disperse into the stronghold and therefore must also be managed. The combined internal and external densities reflect the total expected cost of grey squirrel control, incorporating both direct and adjacent management effort.

[3.2.2] Total Core Area

Total core habitat area, defined as the combined area of high-suitability patches within the stronghold. This serves as a proxy for conservation value, representing the potential carrying capacity for red squirrels.

[3.2.3] Management Feasibility

Feasibility of actively trapping an area, or undertaking other control methods, which reflects spatial variation in landowner willingness or capacity to participate in conservation actions. This is derived from a proxy layer capturing past landowner behaviour and current incentive.

These criteria reflect the dominant concerns repeatedly highlighted in the literature, including the cost of grey squirrel control, the availability of viable red squirrel habitat, and the social feasibility of conservation interventions (Parrott et al., 2009; Shuttleworth et al., 2020). Adopting an equal weighting reflects a practical compromise in the absence of published formalised stakeholder weightings. Adopting an initial equal weighting yields transparent and interpretable results that can be adjusted in future participatory settings, while highlighting emerging trade-offs as suppression increases.

[3.3] Data Collection and Pre-Processing

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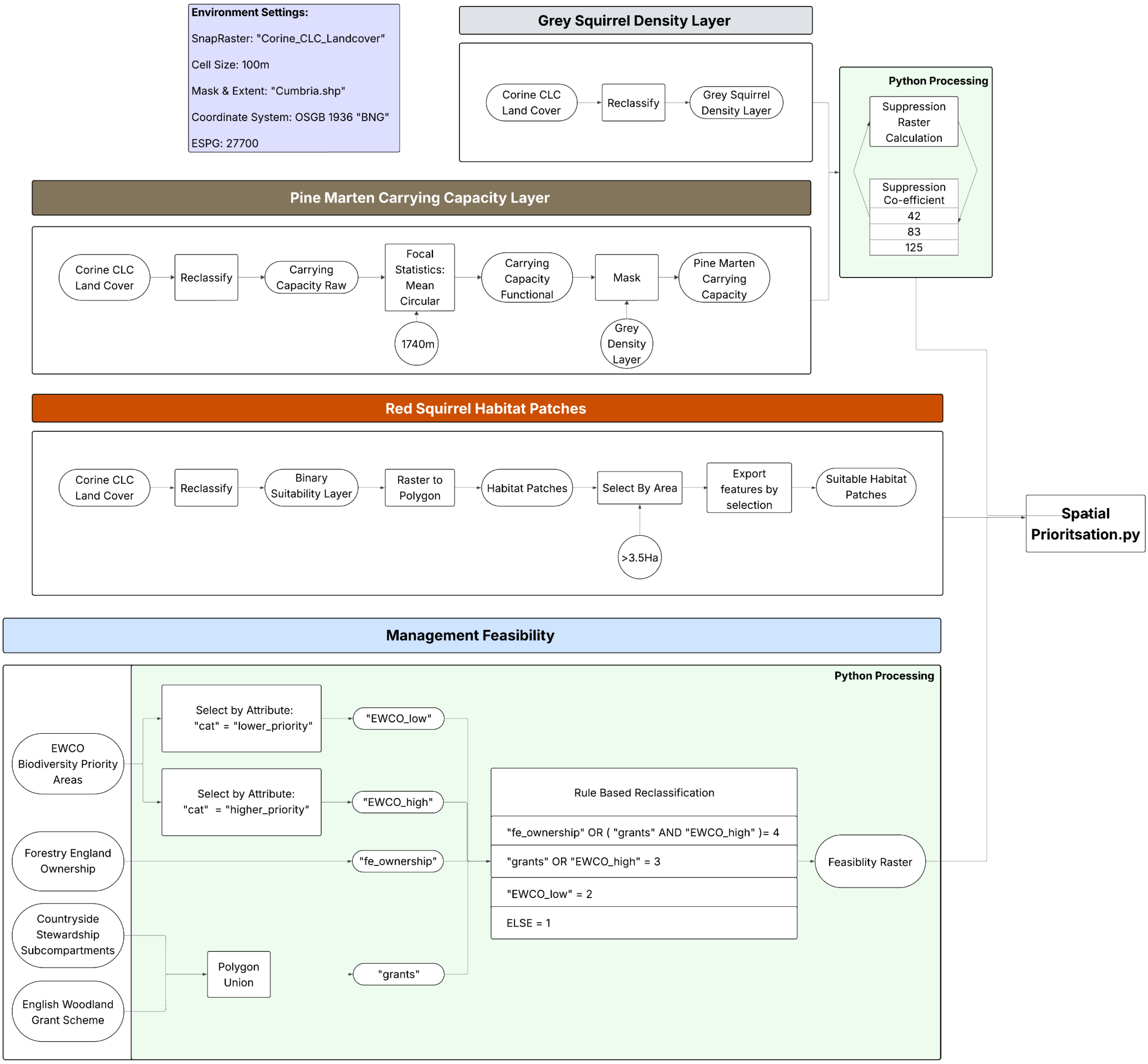

Figure 2: Pre-processing workflow of layers for the Spatial Prioritisation Algorithm

Figure 2 outlines the pre-processing steps required for the spatial prioritisation algorithm. Each Criterion is its own raster layer which feeds into the MDCA.

[3.4] Pine Marten Carrying Capacity Layer

Land-cover classes from the 2018 CORINE Land Cover (CLC) dataset were reclassified to pine marten carrying capacity (ind ha^{-1}) using habitat-specific values from Slade et al. (2023) where possible, though some classes were difficult to translate directly to CLC classes and omit explicit edge habitat estimates. To compensate, density estimates from the Gloucestershire Wildlife Trust pine marten feasibility study were used for scrub-like and transitional habitats omitted from Slade et al. (2023), as pine martens regularly exploit such habitats (Caryl et al., 2012; MacPherson and Wright, 2021). Lower-bound values were assigned to natural grasslands (CLC 324) used for hunting field voles and landscape connectivity. Upper-bound values were applied to Agricultural Mosaic with Significant Natural Vegetation (CLC 243), where vegetation structure is sufficient to support higher prey densities (GWT, 2022). All remaining classes, including agricultural and grassland categories unlikely to be used for landscape, were assigned a low placeholder density of 0.0001 ind ha^{-1} to prevent null divisions in downstream focal statistics.

Table 1: Pine Marten Carrying Capacity

CORINE code	Class Description	Density per ha	Citation
243	Ag/Natural Mix	0.0075	Slade et al., 2023
311	Broadleaf Forest	0.35	Slade et al., 2023
312	Coniferous Forest	0.0115	Slade et al., 2023
313	Mixed Forest	0.023	Slade et al., 2023
321	Natural Grasslands	0.075	Stringer et al., 2018
324	Transitional Woodland	0.0115	Stringer et al., 2018

Although outdated, the 2018 CLC was selected over more recent datasets due to its comparability with the land cover categories used in source studies (Slade et al., 2023; Croft et al., 2021). The influence of dataset choice is partially mitigated by the model's focus on strongholds between 200 and 2500 ha, results are less sensitive to finer-scale land cover change expected in Cumbria, where 35 percent of the county lies within an actively managed national park (LDNP, n.d.).

The resulting 100m resolution density layer is focally averaged using a moving window with a radius of 1740m (Figure 2) assuming a home range of 9.5 km^2 to account for habitat fragmentation and edge effects, and a landscape supplementation strategy that determines carrying capacity as a product of its spatial context (Dennis et al., 2024; McNicol et al., 2020).

The resulting model is validated against the published Habitat Suitability Model (HSM) by MacPherson et al. (2024), interpreted with the awareness that this layer is reflective of a recovering marten population, as the MaxEnt was trained on current species records in the UK (Macpherson et al., 2024).

[3.5] Red Squirrel Habitat Patches

The red squirrel habitat patches layer is a binary suitability map. All woodland patches larger than 3.5 ha are considered suitable habitat (Lurz et al., 2003); smaller patches are excluded. The layer represents the fundamental niche, assuming all woodland types are suitable, including transitional scrub which can be enhanced with woodland restoration in the moderate to long term to form viable conservation habitats (Shuttleworth et al., 2021). Grey squirrel competition is not explicitly modelled in this habitat suitability raster to avoid bias toward conifer woodland. Urban green space and Rural urban fabric is also modelled as suitable habitat, though is not expected to form viable strongholds due to high grey densities (Fingland et al., 2022).

[3.6] Grey Squirrel Density and Distribution Layer

Grey squirrel density is set to land cover-specific carrying capacity, reflecting the literature-standard assumption that populations reach maximum density without control (Slade et al., 2021). Cumbrian specific estimates were used for coniferous and mixed forest; however, the broadleaf estimate was replaced with a higher value that better aligns with broader literature consensus between the ratios of density between different habitat types, following earlier critique of Croft et al. (2021) (Wauters et al., 2023). Grey squirrels can achieve extremely high densities in urban fabrics due to improved foraging efficiency (Merrick et al., 2016; Wist and Dausmann, 2024); though urban fabric is not in consideration for stronghold sites, these densities are modelled for consideration in buffer cost calculations, representing re-invasion risk from urban refugia (Twining et al., 2022). These values are listed in Table 2.

Table 2: Grey Squirrel Densities for CLC Reclassification

CORINE Code	Class Description	Density per ha	Citation
111	Continuous	8.2	Merrick et al., 2016
112	Discontinuous Urban Fabric	8.2	Merrick et al., 2016
141	Green Urban Areas	8.2	Merrick et al., 2016
243	Ag/Natural Mix	0.3	Fitzgibbon, 1993
311	Broadleaf Forest	2.5	Slade et al., 2023
312	Coniferous Forest	0.31	Croft et al., 2021
313	Mixed Forest	2.2	Croft et al., 2021
324	Transitional Woodland	1.7	Fitzgibbon, 1993

[3.7] Modelling Suppression

Slade et al. (2023) model suppression using stochastic dynamics and time-dependent predation rates. In contrast, this study adopts a static, linear approach, representing the expected long-term equilibrium following full pine marten recolonisation assumed to occur within 25 years (MacPherson et al., 2024). While dynamic methods more accurately capture the Holling type III response typical of prey-switching predators (Malard et al., 2020; White et al., 2015), a static model was chosen due to insufficient empirical data to parameterise a species-specific suppression curve (Zurell et al., 2022)

Low, Moderate and High suppression coefficients were derived from Slade et al. (2023), where a pine marten density of 0.36/km² corresponds to a 30% reduction in grey squirrel abundance (See Appendix 1.1). To account for uncertainty in the suppressive efficiency in the pine marten, suppression coefficients were varied by ±50% in line with Slade et al. The co-efficient are used in a cell-wise linear regression formular in python, to modulate the grey squirrel density to an equilibrium expected at a full stable re-colonisation (Equation 1).

$$\text{Grey}_{\text{suppressed}} = \text{Grey}_{\text{current}} \times \left(1 - \left(\text{PM}_{\text{density}} \times \text{Suppresion Scalar}\right)\right)$$

Equation 1: Linear Regression to Model Pine Marten Suppression

Where $\text{Grey}_{\text{current}}$ is baseline grey-squirrel density (ind ha^{-1}), $\text{PM}_{\text{density}}$ is pine-marten density (ind ha^{-1}), and Suppression Scaler is the scenario-specific suppression coefficient. The remaining density value of each cell is later transformed into a grey cost criterion for use in the MDCA.

[3.8] Feasibility Layer

As data on landholder willingness to participate or allow culling cannot be feasibly collected across Cumbria in this study, following Kim et al. (2024) a land cover based economic and behavioural proxy was used to assess management feasibility (Table 3; 4). Each 100m pixel receives a feasibility score from 1 (Low) to 4 (High); where layers overlap, the highest score is retained. Reclassification was done using python (Figure 2), and the resulting layer is shown in Appendix 1.2.

Table 3 Grant Proxy Layers

LAYER	DESCRIPTION	PROXY FOR	CITATION
EWCO Priority Areas	England Woodland Creation Offer targeting – High or Low economic incentive for biodiversity related management	Likelihood that new woodland-creation grants will be approved	Forestry England (2024a)
Countryside Stewardship Sub-Compartments (2015)	Previously Approved CS management units	Past uptake of woodland-improvement funding	Forestry England (2024b)
EWGS English woodland grant scheme approvals (2005–2016)	Sites previously under English Woodland Grant Scheme agreements	Historical management activity and legacy obligations	Forestry England (2024c)
Forestry England Ownership	Public woodland managed by Forestry England	High feasibility owing to centralised authority and active management	Forestry England (2024b)

Table 4 Management Feasibility Layer

RULE	RATIONALE	SCORE
EWCO High ***AND*** **Past Grant Recipient**	Landowner has previously engaged with woodland funding, and will receive additional biodiversity incentives.	4
Forestry England Ownership	Management can proceed under a single sympathetic authority without further negotiation.	4
EWCO High ***OR*** **Past Grant Recipient**	Previous engagement or strong incentives suggest reasonable potential for management uptake, though anecdotal evidence indicates that reapplications have declined since past grant schemes ended (Parrott et al., 2009).	3
EWCO Low	Funding exists but incentives are weaker; first-time applicants may find compliance burdensome (Parrot et al., 2009)	2
None of the Above	Intervention is possible, but comparatively most impermissible.	1

[3.9] Spatial prioritisation Frameworks

Algorithmic spatial prioritisation methods check a large number of possible conservation interventions, and score them against predefined criteria to select the best approach. Several software packages formalise this workflow, most notably Marxan, Zonation, and the Locate Regions toolbox (Ball et al., 2009; Moilanen et al., 2014; ESRI, 2024). These tools optimise on continuous value surfaces, and are benchmarks in the literature for computational efficiency and replicability (Lehtomäki and Moilanen, 2013; Schröter and Remme, 2016). Their cell-based, edge-subtractive logic removes cells until the score stabilises or declines, producing a continuous raster surface rather than discrete habitat units (Ball et al., 2009; Moilanen et al., 2014). As a result, they do not explicitly identify or score clusters of habitat patches. In contrast, purpose-built clustering algorithms delineate management units from fragmented habitats and are better suited to identifying strongholds, which in Cumbria, often depend on collections of habitat patches (Nagkoulis et al., 2025).

These programs are also limited by their 'black box' nature, offering little insight into why specific areas are prioritised (Brunel et al., 2022). Combining multiple factors into a single static cost surface obscures trade-offs and provides limited scope for quantitative analysis of the results (Brunel et al., 2022). In Cumbria, the management trade-offs that emerge under different levels of pine marten suppression are not understood. A transparent, bespoke clustering algorithm allows for correlation analysis between MCDA criteria and final cluster scores, helping to identify the optimal balance of priorities for future management.

This algorithm uses greedy addition from a seed logic, utilised by prioritisation algorithms like Locate Region (ESRI, 2024) but has two crucial extensions; each cluster is scored under every suppression scenario using the same, equally weighted MCDA; and the full score matrix is analysed using correlation analysis to identify shifts in the trade-off relationships between decision criteria (Wieckowski and Sałabun, 2023). As weights stay constant and suppression increases, the relationships between the values of these weights change, functioning as an implicit value modification analysis to reveal how a fall in grey density leads to optimal management emphasis shifting from one criterion to another (Więckowski & Sałabun, 2023).

[3.10] Clustering Algorithm

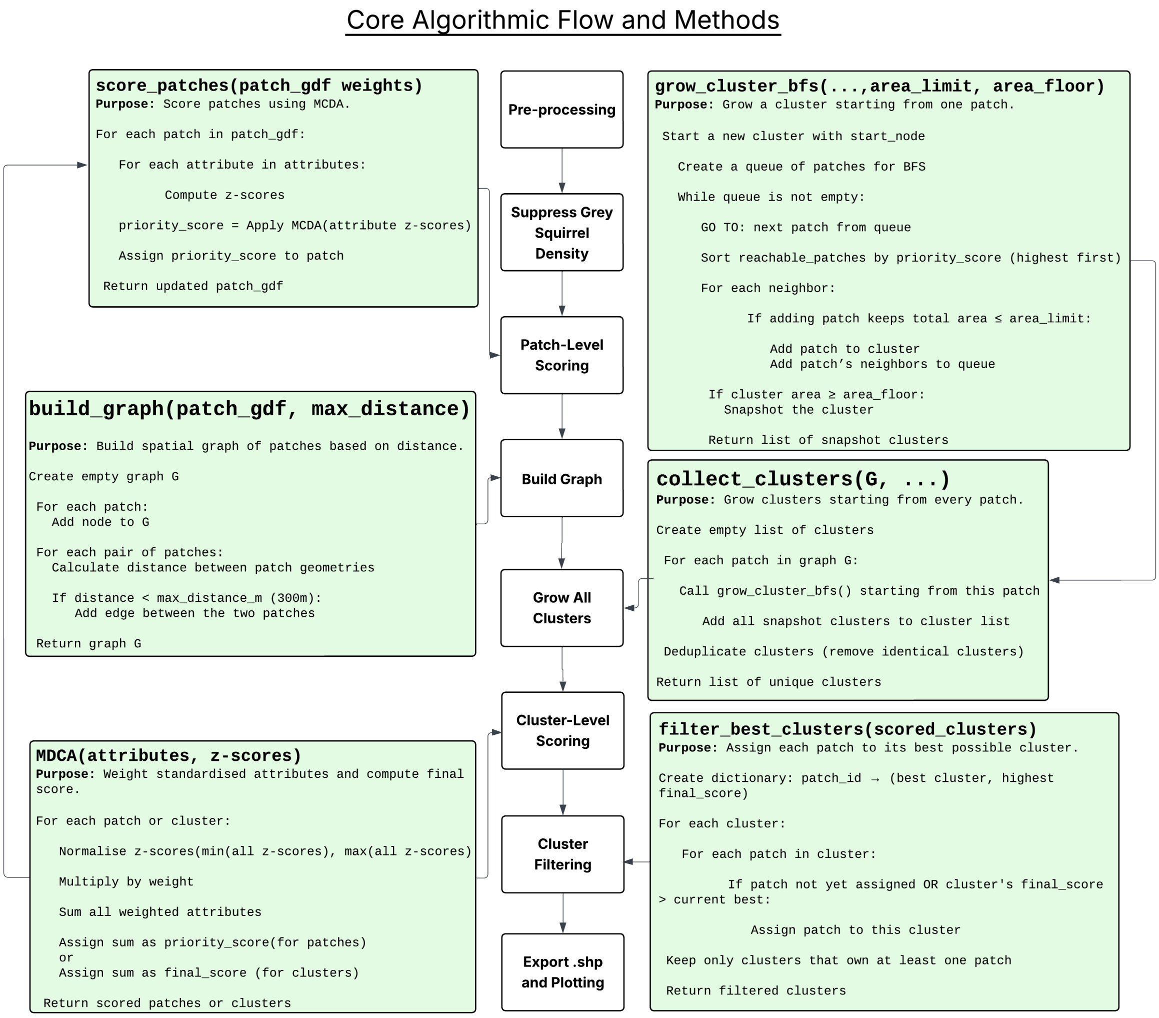

Figure 3: Cluster and MDCA Algorithm - Core Functions and Workflow

Figure 3 presents the workflow and core functions of the algorithm. Following pine marten suppression, each habitat patch in Cumbria is scored under the MDCA criteria. Scored patches are treated as discrete nodes, and added to a single graph of Cumbria. A tree of neighbouring nodes is created for each habitat patch, where a patch was immediately considered a neighbour and added if it was within 300 metres of the seed, or it is later added during cluster growth if within 300m of a patch at the cluster boundary. Cluster growth used a greedy breadth first search from a habitat patch, where patches with the greatest score was selected first.

Clusters were required to meet two area-based constraints, a minimum total area of 200 hectares to meet red squirrel population viability thresholds (Lurz et al., 2003), and a maximum limit of 2500 hectares, above the recommended minimum stronghold size. This cap was chosen, as strongholds in the LDSC are under 1200Ha, and this is a reasonable reflection of the management constraints that are involved with managing large strongholds in Central Cumbria. No additional connectivity weighting was applied, and dispersal connectivity beyond Euclidean distance was not modelled. Cluster growth from a seed terminates when either no adjacent patches remained within the distance threshold, or when adding new patches would breach the maximum area constraint. Clusters are generated using a snapshotting approach, meaning that every time an additional habitat patch is added, and the current version of that cluster is above 200Ha, that unique version of the cluster is saved. This means that in some cases, smaller versions of the cluster from the same seed may score greater than its larger counterparts. It is this logic which allows for trade-offs in core area, additional grey cost and management feasibility to be examined.

The full 2000+ lines of code is published to an anonymous GitHub repository following Zurell et al. (2022), available in Appendix 1.3.

[3.11] MDCA scoring

Both patch and cluster level scoring relies on MCDA to combine multiple attributes into a single prioritisation score. Each attribute x is standardised using a Z-score transformation, an essential requirement to ensure that each criterion is in a comparable scale for MDCA (Kim et al., 2020).

$$Z(x) = \frac{x - \mu_x}{\sigma_x}$$

Equation 2: Z-score transformation of criterion:

Where μ_x and σ_x are the mean and standard deviation of attribute x across all patches or clusters, meaning scores are relative to the range of attributes in that specific suppression scenario. Z-scores were then normalised using the minimum and maximum scores for each criterion in Cumbria, relative to the scenario. They are rescaled to a 0.1-1 scale, for intuitive positive scoring and to avoid multiplication by zero in later MDCA.

$$S(x) = 0.1 + 0.9 \times \frac{Z(x) - \min(Z)}{\max(Z) - \min(Z)}$$

Equation 3: Min-Max normalisation of criterion

Grey squirrel cost is inverted after scaling to reflect the conservation goal of minimising grey squirrel presence. As urban fabric density estimates significantly skewed standardisation of grey cost, they were hardcoded to 0.1.

$$S_{\text{inverted}}(x) = 1.1 - S(x)$$

Equation 4: Inverse grey squirrel density criterion

The final MCDA priority score p for a patch or cluster was computed as:

$$P = \sum_k w_k \times S(x_k)$$

Equation 5: Priority score calculation (MDCA)

Where w_k is the weight assigned to attribute x_k. Equal weights were used across all attributes; however, weighting was included in the parameterisation in anticipation of future tailoring to stakeholder needs.

Final cluster selection used a patch-level filtering algorithm, assigning each patch to the highest-scoring cluster it appears in. Since cluster geometries are formed by merging their constituent patches, this enforces non-overlapping, spatially distinct clusters. The top 5 clusters were selected from each scenario for additional analysis.

[3.12] Interpreting MDCA Results

Sensitivity testing in MCDA typically involves systematic weight variation (Więckowski & Sałabun, 2023). This study adopts a scenario-based, exploratory design to examine shifts in trade-off logic. Scenario testing and correlation analysis are used as defensible, literature-backed proxies for early-stage investigation. This aligns with other exploratory MCDA studies that apply fixed weights and scenario contrasts to assess design sensitivity without formal sensitivity analysis, recognising that results must be interpreted within their decision logic (Marta-Pedroso et al., 2018).

Pearson's correlation coefficient was used to evaluate the linear association between each standardised criterion and the final MCDA priority score. As the output of the MCDA is a continuous composite score rather than ordinal rankings, a parametric test was appropriate. Correlation analysis was conducted separately for each suppression scenario to assess how the influence of individual criteria shifted under changing conditions. Strong, consistent correlations across scenarios indicate stable contributions to prioritisation, while variation in correlation strength suggests dynamic trade-offs between factors. These patterns provide insight into how the value of each criterion changes in response to pine marten recolonisation, informing adaptive conservation strategy.

Chapter 4: Results and Analysis

[4.1] Validating Distribution Layer

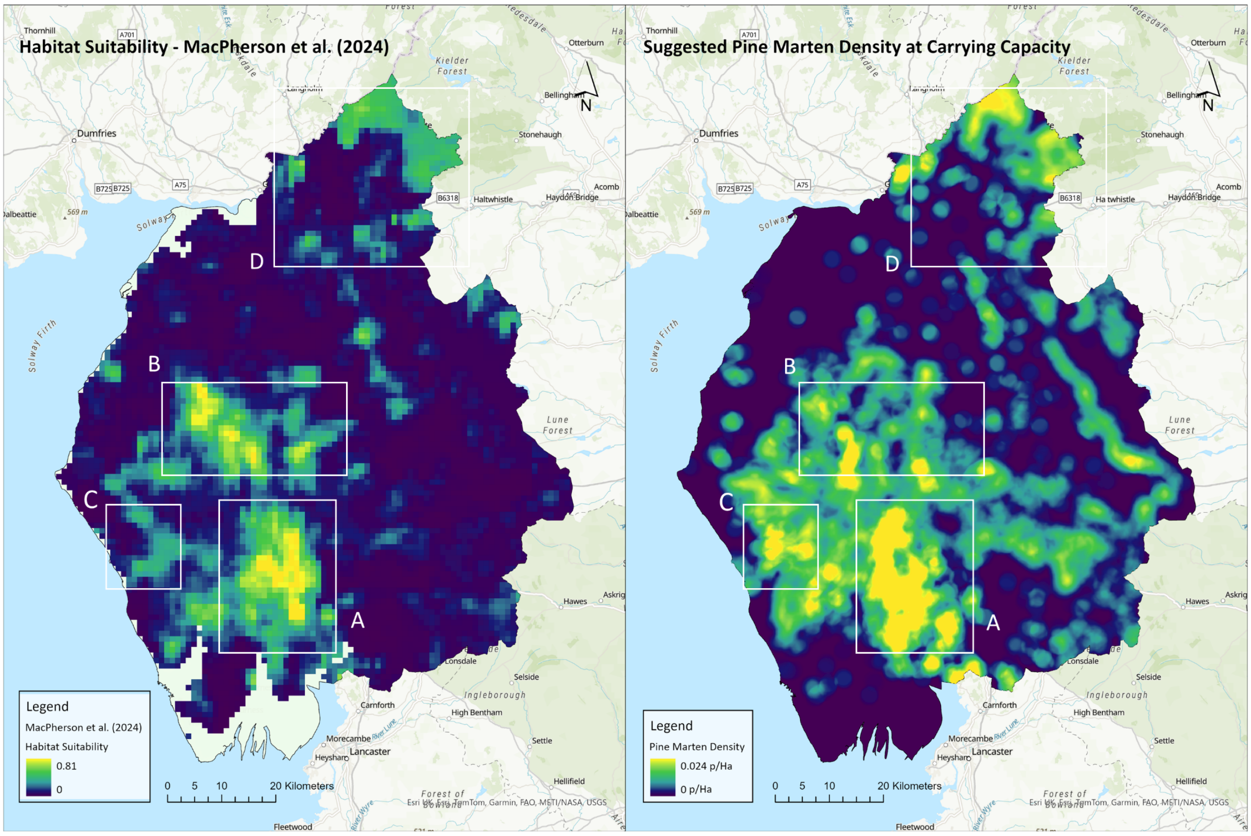

Figure 4: Validation of Pine Marten Layer Against HSM (MacPherson et al., 2024)

Figure 4 compares the results of the pine marten density distribution layer prior to masking to habitat, against Habitat Suitability Model results from MacPherson et al. (2024). Strong spatial congruence is observed at sites A, B, and C, where highly suitable areas in the HSM coincide with high-density zones in the carrying capacity model. Moderate density is observed in areas of lower habitat suitability, likely reflective of finer-grain landscape supplementation estimation; however, the HSM still considers these areas feasible and doesn't misalign with the distribution of density.

Focal mean analysis of the carrying capacity model reduced maximum predicted densities from 0.039 to 0.024 p/Ha, reflecting Cumbria's fragmented spatial context. Although higher than UK mean estimates for recovering populations, 0.05-0.01 p/ha depending on woodland type (MacPherson and Wright, 2021), these values are more conservative than previous suppressive models (Slade et al., 2023) and are plausible estimates considering ongoing reintroductions and data limitations. Supported by spatial alignment with published suitability prediction, this layer provides a strong foundation for analysis.

[4.2] Species Distributions

Figure 5 shows the species density and distributions for grey squirrels and pine martens, and the binary habitat suitability layer for red squirrel habitat. There is substantial spatial overlap between red and grey squirrel habitats, as well as significant overlap in pine marten habitats, excluding urban areas. Broadly, high pine marten density coincides with high grey density due to similar relationships in carrying capacity and woodland type; however, three sites (A, B, and C) illustrate notable divergence. At site B, pine marten and grey squirrel densities are inversely correlated, likely in response to habitat fragmentation and a matrix of low functional utility, such as farmland or grassland, which post focal statistics has resulted in a lower carrying capacity, an effect visible across the study area. In contrast, grey squirrels are modelled to persist in small woodland patches without restriction, suggesting that fragmented landscapes act as refuges, enabling their survival where pine marten carrying capacity is typically low.

In contrast, site A features strong functional connectivity between conifer and mixed broadleaved woodlands, facilitating high pine marten densities while serving as a local sink for grey squirrel density. Despite its isolation, Greystoke at site C encompasses a large contiguous coniferous patch capable of sustaining a high pine marten carrying capacity, but unsuitable for high grey carrying capacity.

Species Distributions

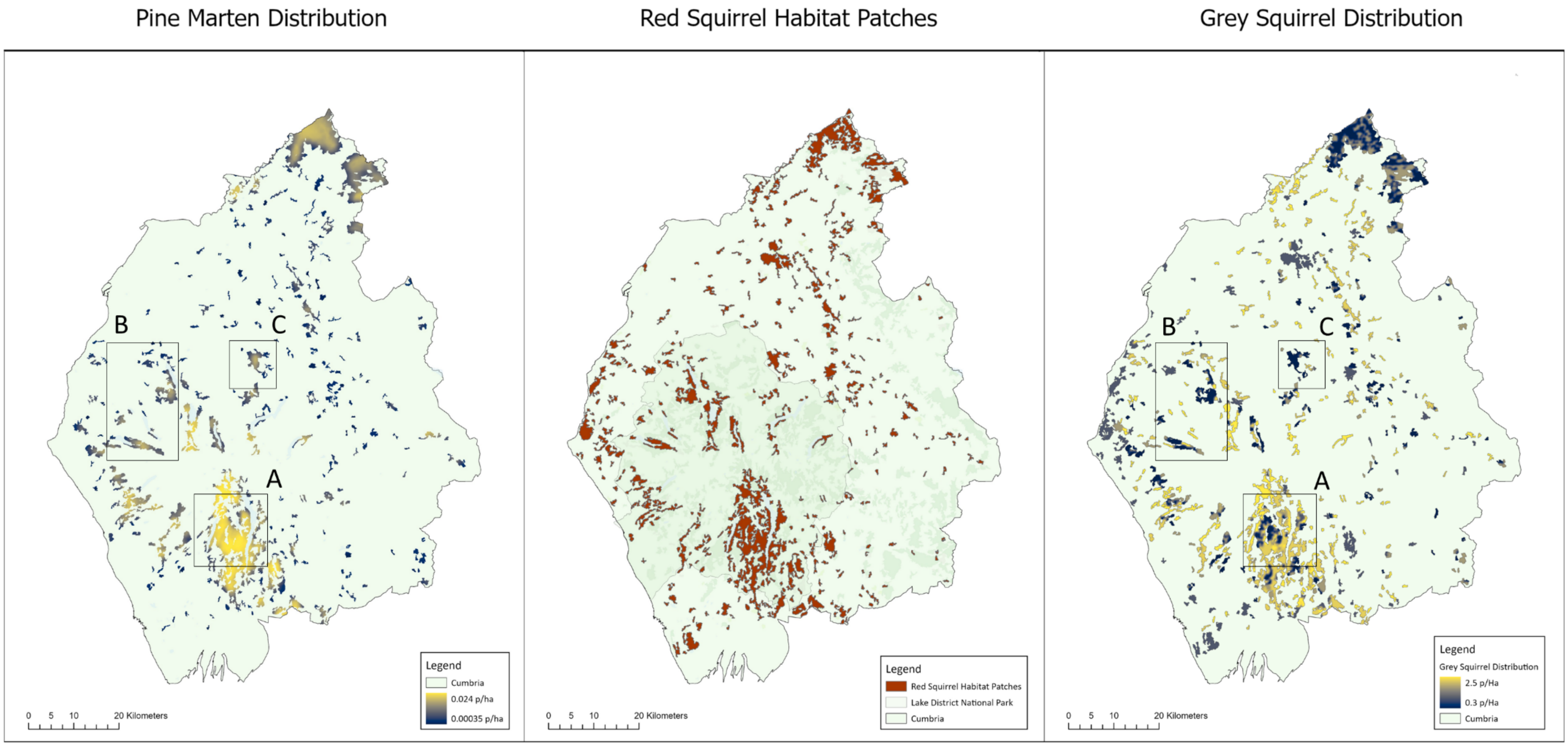

Figure 5: Distributions and Densities, or habitat of All focal Species

Grey Squirrel Density Post Suppression

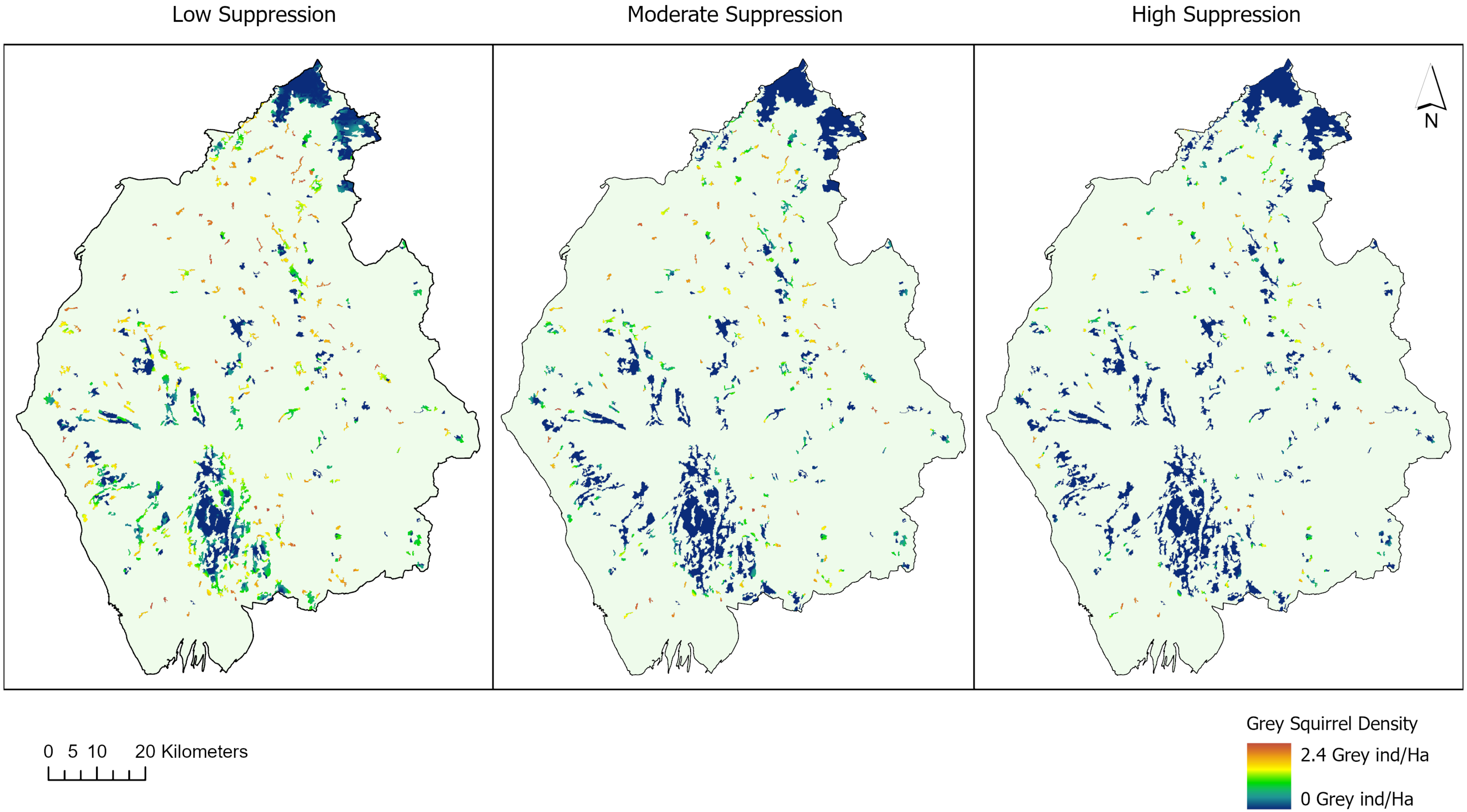

Figure 6: Grey Squirrel Density Post Suppression

[4.3] Grey Squirrel Suppression:

Figure 6 shows the grey squirrel density in Cumbria under three levels of suppression. As suppression intensifies, grey squirrel density declines across Cumbria. Under low suppression, grey squirrel density falls to near-zero only in the large, continuous woodlands of South Cumbria. At moderate suppression, significantly more of the landscape is completely extirpated of grey squirrels, particularly the east. A clear south–north gradient is visible, as grey squirrels are increasingly excluded from less fragmented southern woodlands, while persisting in patchy northern areas, particularly broadleaved woodland where grey density was initially high. Predation is widespread but not yet sufficient to suppress resistant populations. Under high suppression, grey squirrel density is reduced to near-zero across nearly the entire Cumbrian landscape. Only small, fragmented patches in the north and northeast maintain higher densities, where pine marten carrying capacity is low, forming a pattern of highly localised, but highly resistant and high-density grey squirrel refugia.

Figure 7 shows a close up of suppression in the LDSC. Whinlatter and Greystoke achieve nearly complete extirpation of grey squirrels even at low suppression; however, grey density within the managed boundary remains significant in habitat fragments of equal size within a kilometre of all strongholds in the complex, particularly Whinlatter and Thirlmere, which have a greater proportion of surrounding area not totally suppressed until a moderate level of suppression. Overall, from moderate to high suppression, grey squirrel density is completely suppressed to zero within all strongholds, with only small fragments within the management buffer less than a kilometre in length remaining resistant to suppression. Under moderate and high suppression, Whinlatter and Thirlmere are well isolated from these remnant populations, either topographically by a lake in Whinlatter's case, or because the fragments are completely suppressed of density; however, Greystoke, and to a greater extent, Whinfell are consistently surrounded by grey squirrel populations. In these fragments, grey squirrel density is initially moderate at around 1.8 ind/Ha; however, comparison to Figure 5 shows that pine marten carrying capacity is close to zero, explaining low suppression.

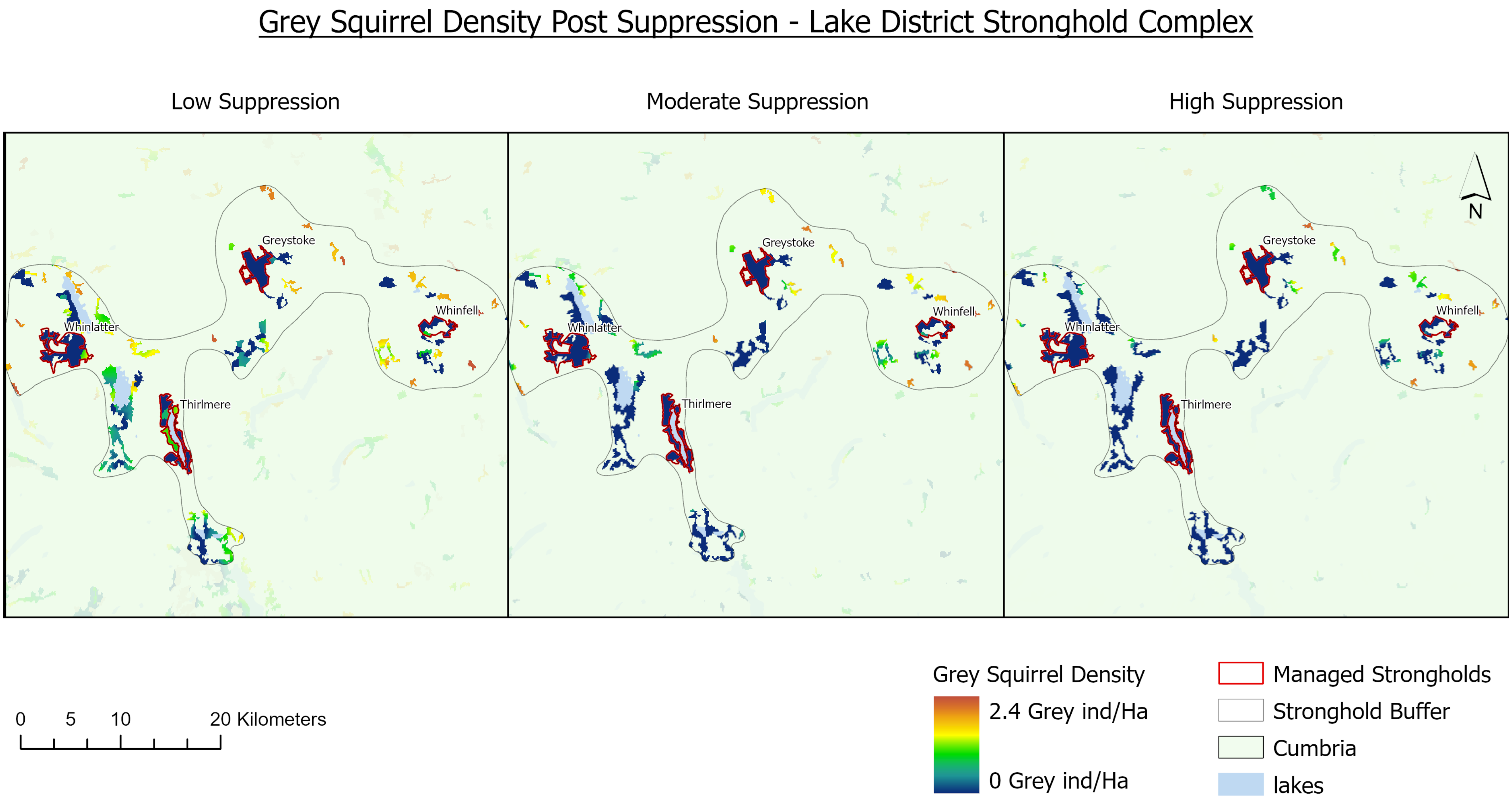

Figure 7: Suppression within the LDSC

[4.4] MDCA Scoring Analysis

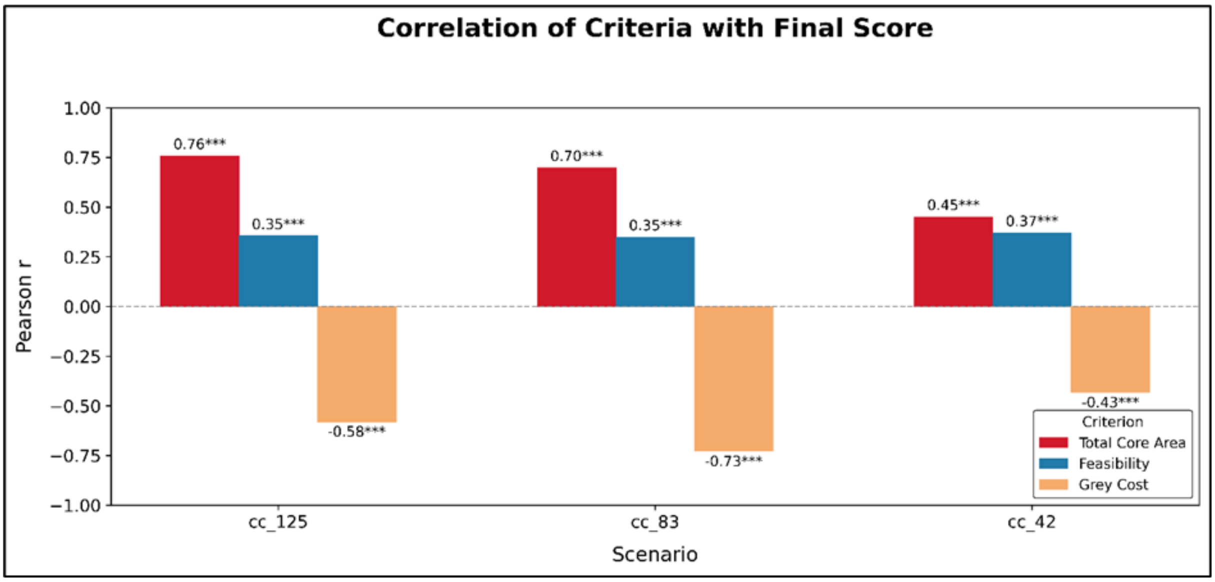

Figure 8: Correlation Analysis of Criteria with Stronghold Scores

As shown in Figure 8, the influence of scoring criteria shifts substantially across suppression scenarios. Core area becomes increasingly correlated to the final score, rising from r = 0.45 at low suppression to r = 0.76 at high suppression. Feasibility remains relatively stable across scenarios (r ≈ 0.35), while grey cost follows a non-linear trend: moderate at low suppression (r = –0.43), peaking in influence at intermediate suppression (r = –0.73), and diminishing at high suppression (r = –0.58).

Under low suppression, grey densities remain high and relatively uniform, except in southern zones excluded due to the model's 2500 ha cap. This exclusion reduces the pool of low-grey clusters, resulting in a more balanced cost surface. Consequently, the cost associated with grey squirrels correlates modestly with the score (r = –0.43).

At moderate suppression, grey density becomes increasingly stretched across a range of values over the landscape. Some patches are near or completely extirpated of grey squirrels, while others are moderately suppressed, and resistant patches remain dense. This gradient creates stronger contrasts in grey cost, as there is a gradient of more competitive and higher-scoring stronghold options as unlike under low suppression, viable clusters under 2500 are completely suppressed, and there is no artificial exclusion of 0 values in the min-max normalisation. Hence, clusters with higher grey density are penalised more severely, driving the correlation to its most negative point (r = –0.73).

Grey presence is nearly eliminated at high suppression, except in small, fragmented woodlands. These areas tend not to be eligible strongholds due to minimum area size constraints, so grey cost becomes less important (r = –0.58). Core area becomes increasingly valuable. As grey cost flattens and feasibility becomes less limiting, the algorithm favours larger, contiguous patches that offer persistence value.

This behaviour reflects the changing value distribution of grey squirrel density, and spatial distribution across the landscape. Under low suppression, grey density spans a full, relatively uniform range, producing modest cost contrasts between patches. At intermediate suppression, density within stronghold clusters within the viable size range becomes bimodal, with some patches near-extirpated and others remaining dense, which amplifies normalised cost differences and maximises its negative weight in scoring. Under high suppression, densities collapse toward the lower bound with only a few high-cost outliers remaining, yet these outliers are too small to form viable clusters, reducing the importance of grey cost and re-weighting the correlations of criteria with final scores increasingly favouring core area and feasibility criteria.

Correlation analysis of dynamic prioritisation illustrates how optimal trade-offs among area, cost, and feasibility change in response to pine marten suppression. As grey cost flattens and feasibility becomes less limiting, the algorithm favours larger, contiguous patches that offer persistence value. This trend fits ecological logic and highlights how the scoring system prioritises differently depending on the suppression scenario. The behaviour of grey cost shows that under low and high suppression, avoiding management in areas with high grey squirrel densities is less important than feasibility and core area. Under low suppression, there are relatively few areas where the suppression of grey squirrel density is advantageous enough to disregard other constraints. Under high suppression, remnant grey squirrel population is of little concern across the landscape, and hence is not a limiting factor. These patterns have direct implications for how management should understand trade-offs in future planning.

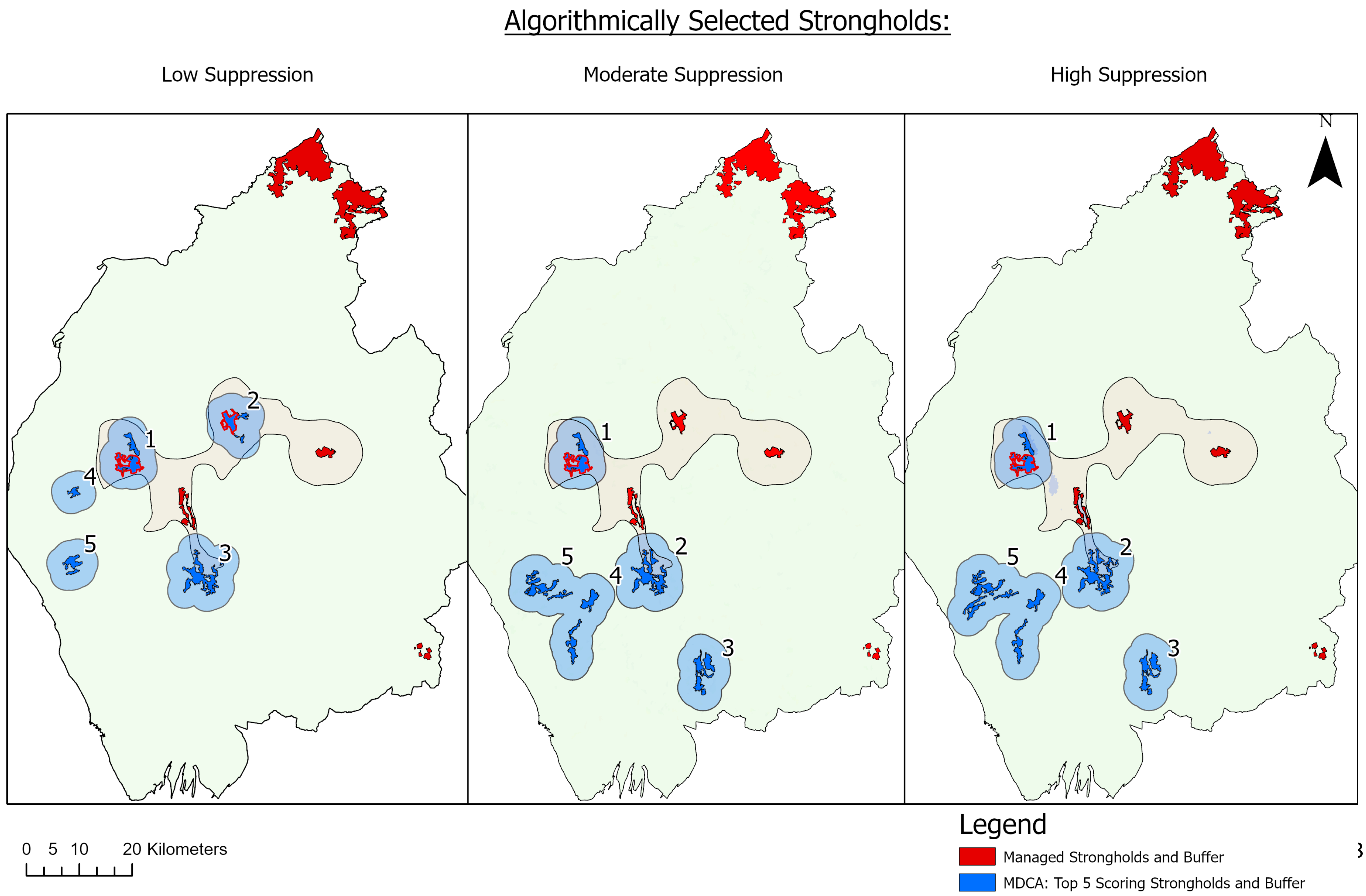

Figure 9: Strongholds Selected by the Algorithm, Against the LDSC:

[4.5] Algorithmically Selected Strongholds:

Figure 9 shows the 5 top scoring strongholds under each level of suppression. Consistently across all scenarios, the top rated stronghold is an extended version of Whinlatter. A slightly extended version of the Greystoke stronghold is rated as the second best use of resources under low suppression. Stronghold Low__3, hereby referred to as Elterwater, is the only other stronghold selected within the LDSC in all three scenarios. As the Greystoke extension stronghold, and Elterwater are selected within all three scenarios, these stronghold selections are the most robust to uncertainty in the level of suppression. Strongholds shift South from Low to Moderate suppression; however, the distribution of strongholds remains broadly the same between moderate and high. Instead, strongholds become larger, co-opting nearby habitats as extensions. The model's 2500 ha area cap prevents the selection of larger forest blocks in southern Cumbria.

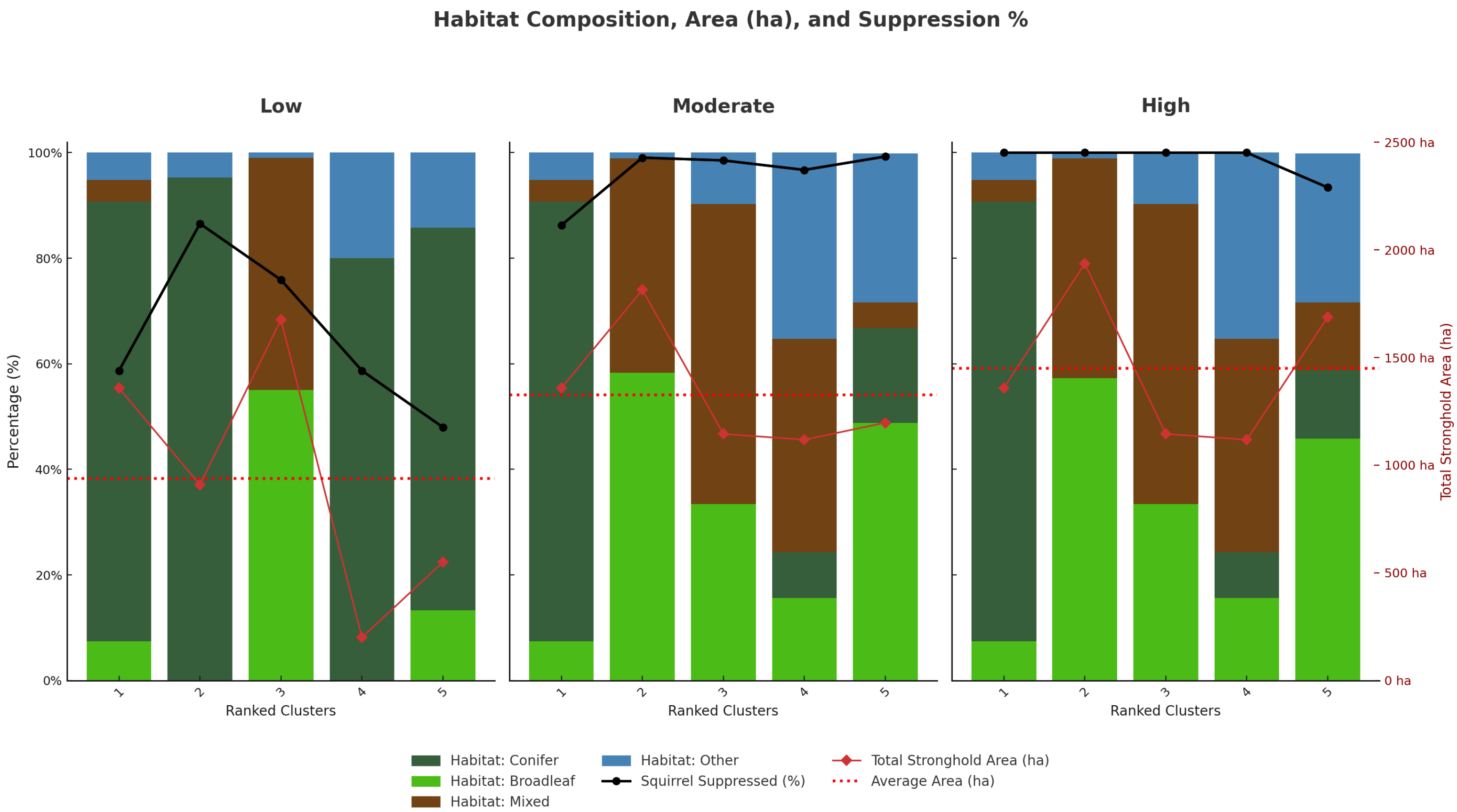

Figure 10: Habitat Composition, Size and total percentage grey suppression of Algorithmic strongholds in each scenario

Figure 10 shows that as suppression increases, the average size of the selected strongholds increase, though at a decreasing rate where greater suppression begins to dimmish in returns of total stronghold size from moderate to high.

Low_5 (550 ha) expands into Moderate_5 (1197 ha), which further grows into High_5 (1527 ha), representing the largest growth of any single stronghold. Elterwater also exhibits growth in size from low to moderate suppression, but does not increase beyond that.

As the suppression co-efficient increases, as does the percentage to which the strongholds exhibit a suppression of the total density of grey squirrels, most significantly between low and moderate scenarios, but also between moderate to high for the extended Whinlatter stronghold, which is most resistant to suppression of all the strongholds that appear across all three scenarios. The only exception is stronghold 5 (same across all scenarios), which falls from completely suppressed to 90% as the stronghold expands. Here, the trade-off of lower grey suppression is justified by the extension of core area for conservation. However, under moderate suppression, the cost of this extension without adequate suppression is not an unfavourable trade-off for additional core area, suggesting that the residual grey population within this extension is excessively high. Therefore, moderate suppression levels are inadequate to warrant the additional costs of extending this stronghold, ultimately resulting representing increased management expenses with minimal benefit.

At low suppression, selected strongholds are almost entirely coniferous with only Elterwater (Low_3) being made of a different woodland type, a near even split of Broadleaved and Mixed woodland at a higher ranking than two other conifer dominated woodlands. At a moderate and high suppressive co-efficient, four of the five selected strongholds are predominantly a mix of conifer, broadleaved, and to a lesser extent transitional woodland; however, these all rank below stronghold 1, which is the only site to remain significantly coniferous. Mixed and broadleaf woodlands are not only selected more frequently, but cover a higher proportion of core area

[4.6] Evaluation of LDSC strongholds

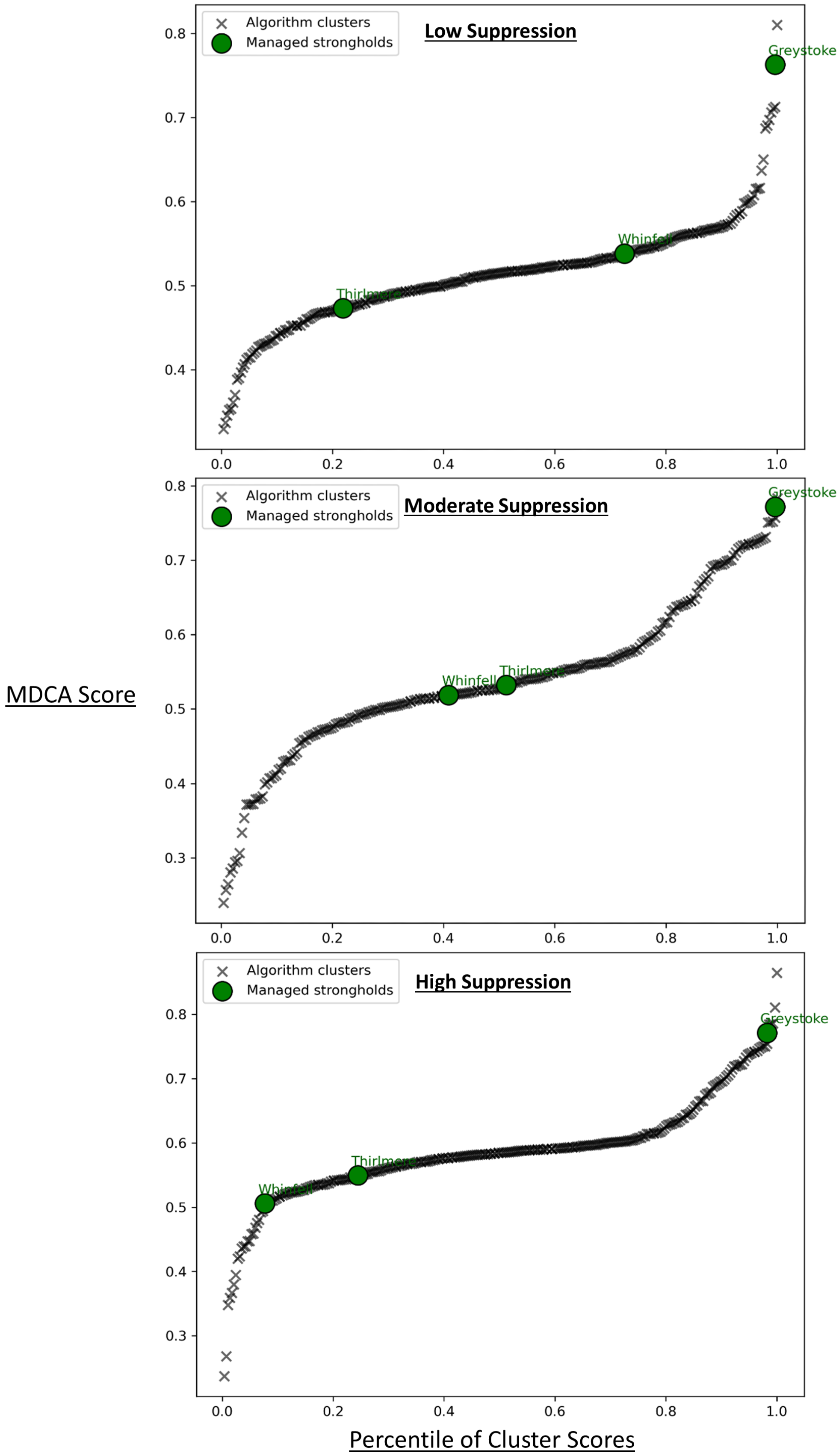

Figure 11: Comparison of LSDC strongholds to Every Algorithmic Stronghold

Figure 11 plots the MDCA score for each managed stronghold against all scored stronghold possibilities, except Whinlatter which is consistently selected within the top-rated strongholds in all three scenarios. This is likely due to its high core-area-to-total-area ratio and vulnerability to suppression. Additionally, Whinlatter's location in a high-priority England Woodland Creation Offer (EWCO) area contributes to its 'very high' feasibility score (Appendix 1.4).

Greystoke consistently scores in the top quarter of all tested clusters and ranks as the second-highest scoring stronghold under low suppression. Similar to Whinlatter, it benefits from a favourable disparity between grey and pine-marten carrying capacities. Importantly, it is spatially isolated from major grey-squirrel source patches within its 3 km buffer, contributing to a low grey cost score. As suppression increases, Greystoke remains high scoring, suggesting it's scores in other criteria are significant even when grey cost becomes less valued within the MDCA.

In contrast, Thirlmere and Whinfell consistently score poorly across all suppression scenarios. Despite some overlap with high-priority EWCO zones, both are partially within lower-priority areas, reducing average feasibility scores. Both face structural limitations, fragmented or elongated, leading to a limited total core area which is increasingly penalised as suppression increases. Although both strongholds achieve complete suppression at moderate or high suppression, these gains are largely insufficient to offset structural score constraints. An exception is Thirlmere's temporary promotion under moderate suppression when more value is placed on low grey cost; however, once suppression becomes widespread, this advantage collapses. Considering that the clustering algorithm will snapshot any cluster that is over 200Ha large, this performance is particularly poor, as at the lower percentile of performance the competition is very poor, consisting primarily of small and fragmented strongholds.

Chapter 5: Discussion

[5.1] Low Suppression Strategy

Under low suppression, grey squirrel density remains a key constraint on spatial prioritisation, with uniform correlations indicating that no single criterion dominates. As a result, conservation remains limited to defensible strongholds, particularly feasibly managed coniferous woodlands with naturally low grey presence and core-dominated structure.

Broadleaf woodlands remain largely unviable at this stage, as high grey squirrel pressure persists outside of core conifer strongholds. The only exception is in the large, continuous woodlands of South Cumbria, where high pine marten suitability has led to localised suppression even in habitat types typically associated with grey dominance. This highlights the importance of functional landscape structure in enabling suppression at low levels, suggesting that improving pine marten carrying capacity may offer wider conservation benefits for red squirrels.

Existing strongholds should be retained, as the conservation gains from relocating management are too small to justify the added administrative burden and stakeholder complexity. Continued management is important, as squirrel-resistant fragments remain within the management buffer, of particular note is the large grey dense source near Thirlmere and Whinlatter. To allocate resources efficiently, trapping should concentrate here over Whinfell and Greystoke where suppression is significant, re-invasion sources are smaller, and conservation value at these sites is lower (Figure x). Extending the Whinlatter stronghold to match stronghold Low.1 presents a feasible and actionable opportunity to secure likely conservation gains with minimal associated cost or burden. Although this approach resembles current strategy, greater success is likely possible due to ongoing suppression gains that have not been observed in current monitoring data (McQueen et al., 2024)

[5.2] Moderate suppression strategy:

Under moderate suppression, core area is highly valued and grey density is heavily penalised in the trade-off analysis. Management should therefore pursue greater conservation gains by investing in larger clusters and woodland fragments, while maintaining caution around remnant grey squirrel populations not yet sufficiently suppressed. Whinlatter and Greystoke remain strong candidates for investment. However, continued efforts at Thirlmere and Whinfell should be reassessed; both sites and buffer experience near-total suppression, but still score poorly for prioritisation. These locations may be appropriately left to operate under new found competitive advantage given near complete grey squirrel extirpation, freeing resources for investment into increasingly higher scoring stronghold sites.

Under low to moderate suppression, significant extirpation of grey squirrels across the landscape is unlikely. Remnant grey populations remain fragmented throughout the landscape, posing a continued risk of invasion and SQPV transmission. This is particularly concerning for conifer-dominated strongholds, where pine marten predation has already reduced grey squirrel presence, and where red squirrel densities are already lower to begin with. In the absence of greys, and in the context of conifer dominated habitat, pine martens may increasingly predate red squirrels, potentially reducing their densities even further (Twining et al., 2020). These depleted populations are especially vulnerable to infection if reinvasion occurs. At higher suppression levels, this risk is reduced, as grey squirrels are more effectively controlled across the landscape. However, under moderate and especially low suppression, reliance on conifer woodland is less viable. In this context, broadleaf and mixed-woodland habitats become more valuable conservation opportunities, as they support higher red squirrel densities, offering greater population resilience to stochastic effects, predation and disease (Jensen, 1985; Slade et al., 2023; Twining et al., 2019;20).

[5.3] High suppression strategy:

In high suppression conditions, trade-offs suggest management should maximise reserve size, leveraging low management costs. At this level of suppression, there may actually be no need for further culling and it may be plausible that protected areas may become redundant.

Resources could address broader issues, such as investing in translocations to resolve inbreeding, which is a significant issue for red squirrel recovery on a landscape scale (Cox et al., 2020)

However, grey squirrels are not eradicated completely by pine marten suppression. Resistant populations are still present in the fragmented habitats of north Cumbria, and may pose as disease reservoirs that still threaten red squirrel populations given the similar findings of Twining et al., (2022). Resources currently focused on 'holding the line' could be redirected toward a more ambitious goal of total grey exclusion from Cumbria. Croft et al. (2021) found that trapping in north Cumbria's fragmented habitats is highly efficient, suggesting strong returns on effort in these landscapes. This study shows that suppression is most effective in large, well-connected patches, areas that would otherwise support viable grey squirrel meta-populations. Together, these findings suggest that under moderate and high suppression scenarios where grey squirrel populations are largely constrained to highly fragmented refugia, trapping can be successfully prioritised within these fragmented patches, where it complements landscape suppression and enables more efficient resource allocation. However, a key limitation to this is that it is still restricted by management feasibility constraints, as woodland owned that is below 3.5Ha may still not be eligible for grants to employ this trapping under the CHST.

[5.4] Strategic Stronghold Expansion and Land Management Opportunities:

The model reveals a consistent spatial shift in stronghold distribution. With increased suppression, strongholds grow larger and shift south, following pine marten habitat suitability seen in the growth of Low_5 and Elterwater. As pine martens recover, stronghold boundaries do not be static; management can invest in core areas first, expanding them as suppression increases. This approach staggers investment, reduces early risk, and targets areas that gain value over time.

Given feasibility constraints and the potential benefits of pine marten recovery, the most viable course of action is to continue investing in Greystoke and Whinlatter, and to evaluate Elderwater as a candidate stronghold. Elderwater lies within the Lake District stronghold complex management buffer, aligning with the key criteria of presence of local volunteer support for site selection from scottish PARCs guidance and may already benefit from existing management (Scottish Wildlife Trust, 2020). Crucially, Elderwater is selected in all suppression scenarios, reducing risk under uncertainty, a core principle of conservation planning (Zurell et al., 2022). Its proximity and woodland corridor connectivity to Grizidale forest, the site of recent BOOM reintroductions (Appendix 1.3) further increases its value, as pine marten presence and suppression benefits are likely In the short to moderate term. It also provides an ideal location for monitoring whether suppression effects in broadleaf woodland align with model predictions.

Managers could begin enhancing pine marten carrying capacity in suppression-resistant fragments, as woodland regeneration will take years to influence future recolonisation. Targeted interventions, such as scrub enhancement, hedgerow planting, or increasing small mammal prey availability, could improve habitat quality without requiring extensive woodland creation. Even modest gains in foraging resources and connectivity may increase pine marten activity in structurally suboptimal landscapes, extending suppression networks (Hamston et al., 2023).

However, given the significant niche overlap between pine martens and grey squirrels, pre-emptive connectivity and regeneration must be applied cautiously. Enhancing landscape permeability in preparation for pine marten recovery could also facilitate grey squirrel reinvasion or disease transmission to red squirrel refugia, particularly in the absence of broader landscape-level suppression when pine martens are still recovering. Any high-risk connectivity measures near existing strongholds should therefore be guided by agent-based modelling to evaluate alternative strategies and suppression thresholds.

[5.5] Limitations of Modelling Approach:

The results of this model broadly align with those of Slade et al. (2023); however, this agreement may be influenced by methodological circularity, as the model is partially parameterised by Angelsey specific estimates from Slade et al. (2023). Wenger and Olden (2012) warn that cross-validating results with the original study area does not necessarily equate to validity, and naïve use of a model elsewhere can give overconfident predictions. (Sequeira et al., 2018) note that transfers typically assume species are at equilibrium and present in all suitable habitats, assumptions that may not hold in the new area. While this study has made these assumptions, methods were implemented to introduce spatial context into the model, and density distribution was validated against local secondary data from MacPherson et al. (2024).

The clustering algorithm used to delineate strongholds is a greedy method, selecting locally optimal patches based on priority heuristics, rather than all possible cluster permutations. This yields efficient, but non-exhaustive solutions to the prioritisation problem (Davis et al., 2003). Designed with Cumbria in mind, the number of candidate patches is computationally tractable; however, the viability of this algorithm implementation may be limited at larger spatial scales that incur greater combinatorial complexity (Davis et al., 2003). Furthermore, the spatial scale of this analysis introduces a Modifiable Areal Unit Problem. Spatial algorithms are sensitive to extent, and while Cumbria is ecologically and administratively appropriate for regional planning, optimising strongholds within this boundary may not reflect the best allocation of conservation resources at a national level (Dark and Bram, 2007; O'Connell and Prudhomme, 2024; Pohjanmies et al., 2017).

A static modelling approach obfuscates nuanced, yet important ecological processes that can affect conservation outcomes. Slade et al. (2023) note that landscape-level suppression and SQPV pathogen extinction may take up to 25 years, and management benefits are likely not immediate. Additionally, abstracting suppression as a linear process obscures phenomena such as temporal refuge for greys from predation, particularly when alternative prey is abundant, as seen during a 4-year cycle of high vole years (Twining et al., 2022). Furthermore, this model does not address the SQPV reservoir risk posed by remaining grey populations. Roberts and Heesterbeek (2021) emphasise the risk posed, even under pine marten suppression; however, the absence of a universal population density threshold for sustained SQPV introduces uncertainty regarding the exact risk faced.

The MCDA criteria were evenly weighted and drawn from peer-reviewed literature; however, this approach can be criticised, as due to project feasibility constraints, stakeholder perspectives of NGOs and landowners did not explicitly inform the selection or weighting process (Esmail and Geneletti, 2018). As a result, criteria may fail to reflect the nuance of the operational priorities of red squirrel management agencies, and landowner opinions. This gap is most evident in the management feasibility layer, which is inherently interpretive and guided by my positionality as a researcher. Scores were based on the assumption that economic incentive is the primary driver of landowner willingness, where areas with limited grant access were assigned lower feasibility scores. Yet, this risks overlooking complex landowner motivations, where regional identity or attachment to red squirrels may motivate landowner engagement even in underfunded areas, particularly where red squirrels are seen as part of local heritage (Dunn et al., 2018). While this economic framing is not unfounded, and secondary source interviews suggest landowners often disengage when administrative burden is high or support is lacking (Parrott et al., 2009; Kim et al., 2024), management feasibility as a product of landowner willingness remains unmeasured and represented spatially. More broadly, applying equal weights to all MCDA criteria may oversimplify the complex trade-offs of landscape-scale prioritisation, and a lack of formal sensitivity testing limits confidence in model robustness, leaving it vulnerable to hidden biases and design choices, for example, how criteria is normalised (Więckowski & Sałabun, 2023)

[5.6] From Modelling to Management

The BOOM reintroduction project presents a unique opportunity for coordinated field validation to address ongoing uncertainty surrounding pine marten suppression dynamics in Cumbria. Over the next five years, priority should be given to monitoring grey squirrel responses to pine marten presence, especially considering the synergies with Red Squirrels Northern England (RSNE), which already conducts landscape-scale monitoring through the Spring Monitoring Report (McQueen et al., 2024). Data collection through radio-tracking, home range analysis (McNicol et al., 2020), and modelling of SQPV suppression thresholds (Travaglia et al., 2020; Roberts and Heesterbeek, 2021) could parameterise dynamic, spatially explicit models to gain more robust management insights. Future research investigating how the efficacy of immunocontraceptives change under increased pine marten suppression remains a key research gap given its position as a more publicly supported grey squirrel control, and that the codebase for dynamic modelling of grey squirrel in fertilisation is available from Croft et al. (2021). As grey squirrel control is simply abstracted as cost per density regardless of method in this study, and management recommendations are made only in the context of static trapping placement, this further research would be valuable.

Future research should also seek to enhance the management feasibility layer by combining a deeper analysis of proxy indicators with direct stakeholder engagement (Esmail and Geneletti, 2018). Surveys or interviews with landowners, managers, and regional conservation groups would help ground MCDA criteria in real-world management contexts. These efforts would yield a more spatially accurate and socially realistic representation of feasibility.

Conclusion

The spatial distribution of grey squirrels in Cumbria is highly heterogeneous and shaped by both habitat structure and pine marten density. Under low suppression, grey squirrels persist across most of the landscape, with only large, contiguous woodland blocks in South Cumbria showing localised extirpation. Moderate suppression yields broader extirpation, especially in the east, while high suppression nearly eliminates grey squirrels, leaving small but highly resistant refugia in the fragmented north. These may be challenging to feasibly engage control with, as their small size may mean they are not eligible for woodland grants. However, given largescale suppression of grey squirrels, these resource constraints will likely lift.

Suppression intensity significantly reshapes the prioritisation logic for stronghold selection. Under low suppression, grey squirrel density is a dominant constraint, favouring existing, defensible conifer strongholds with low grey pressure. Moderate suppression shifts the balance toward larger woodland configurations where pine marten carrying capacity is greater, regardless of habitat composition. High suppression reduces the influence of grey cost entirely, with the algorithm favouring total core area and feasibility making large, well-connected mixed or broadleaf woodlands increasingly prioritised.

Spatial prioritisation reveals that several existing strongholds, notably Thirlmere and Whinfell, perform poorly across all scenarios, largely due to structural fragmentation that limits pine marten carrying capacity, and low core habitat area. In contrast, Whinlatter and Greystoke remain high-performing, particularly due to favourable suppression dynamics and feasibility. Crucially, the model identifies a new stronghold, Elterwater, as a novel but robust opportunity for experimentation, considering it is already within the boundaries of the Lake District Stronghold Complex. The opportunity of conservation in non-conifer woodland presents a complete paradigm shift to future management, particularly given uncertainty in predation pressure on already vulnerable red squirrel populations in small, conifer dominated woodland. This analysis highlights the potential for stronghold reallocation and expansion, particularly in areas historically overlooked due to grey dominance, but now viable under pine marten recovery.

Pine marten recovery offers a viable biocontrol for grey squirrel suppression, facilitating landscape scale conservation. Current stronghold designations will significantly benefit even under empirically low estimates of predation efficiency. In the short term, these results are in full support of pine marten reintroduction as a means of grey squirrel control, and offer a far more tenable solution to landscape scale recovery than current lethal trapping methods, in both public palatability, and feasibility. Future work should monitor species responses to recent reintroductions in Grizedale, generating empirical data to inform dynamic suppression models in the uniquely fragmented landscape of Cumbria.

Appendix

[1.1] Suppression co-efficient

Derived by Slade et al. (2023) from empirical evidence where a pine marten density of 0.36 individuals per km² is associated with a 30% reduction in grey squirrel abundance. As the spatial resolution of the analysis is 100m (i.e. 0.01 km²), the suppression coefficient scalar becomes:

$$\frac{30}{0.0036} = 83.33$$

Equation 6: Deriving the Suppression Co-efficients

Table 5 Suppression Co-efficients

Scenario	***Suppression co-efficient***
Low	42
Moderate	83
High	125

[1.2] Management Feasibility Laye

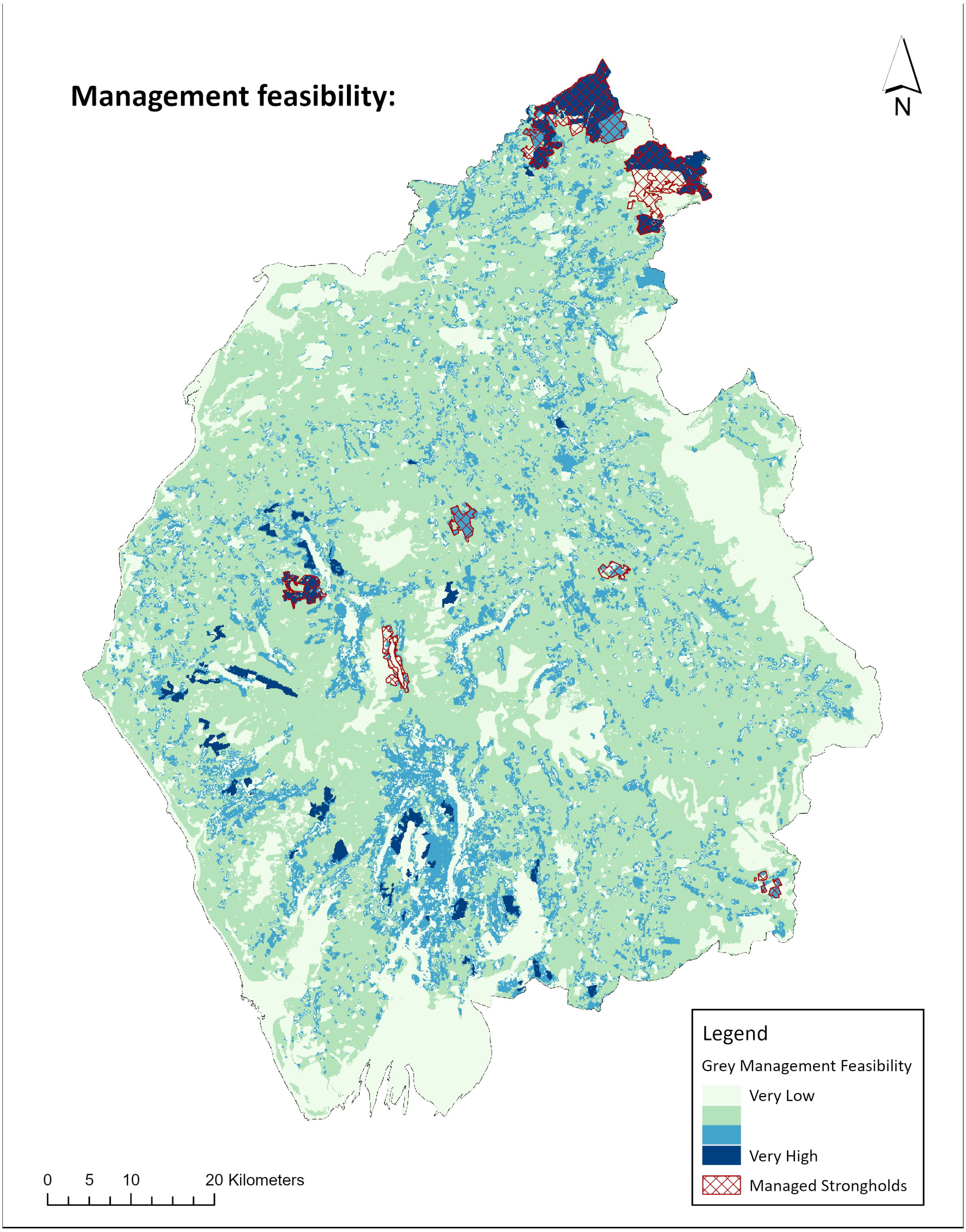

Figure 12: Management Feasibility Layer

[1.3] Anonymous GitHub Repository Link

This repository contains all Python code used to generate, evaluate, and prioritise red squirrel strongholds under varying pine marten suppression scenarios in Cumbria.

The repository has been created, and pushed to, with an anonymous email address and username under my student number: 10906064. There is no identifying information.

Available at: https://github.com/10906064/dissertation

[1.4] Proximity to Grizedale Forest

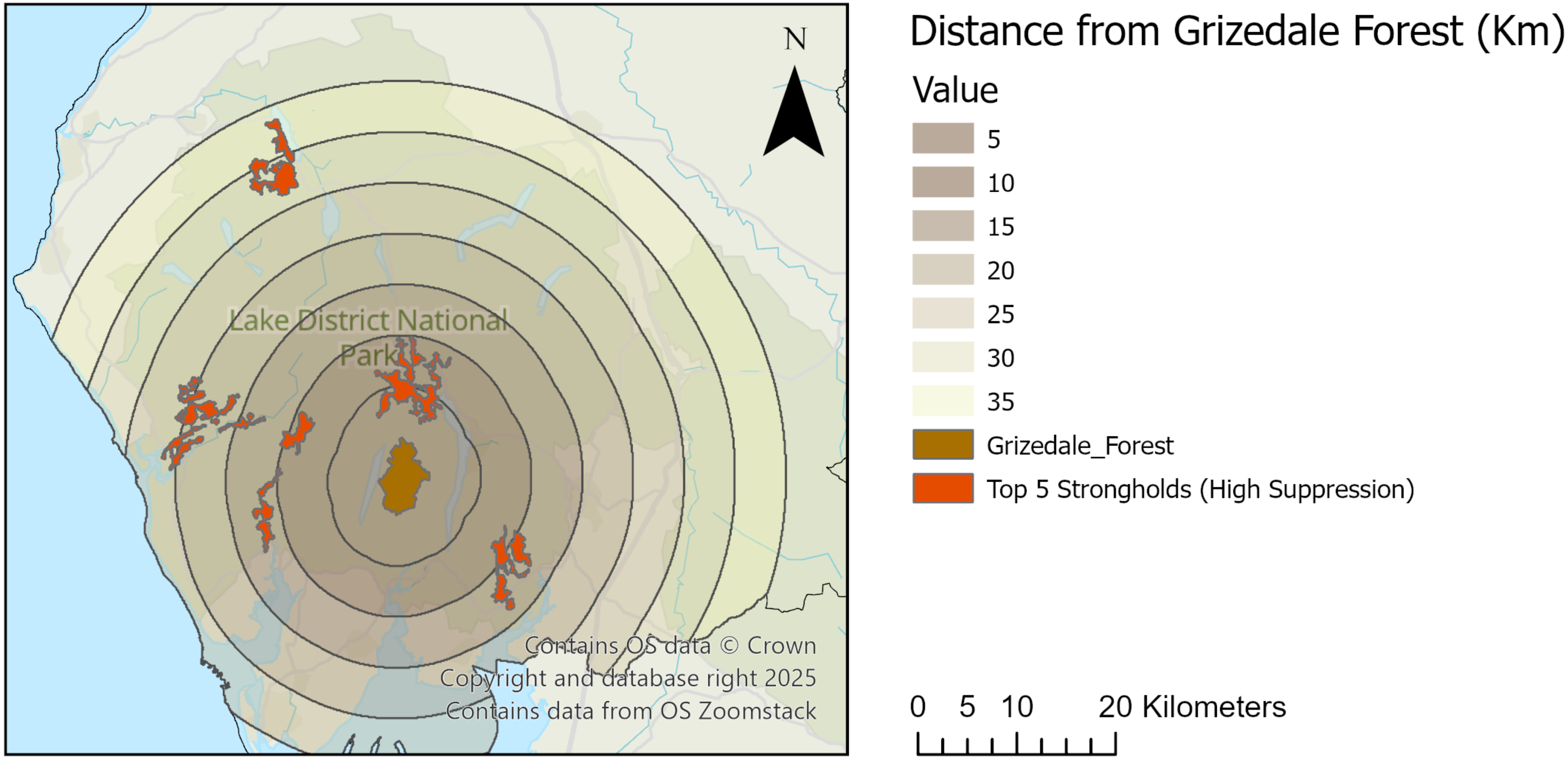

Figure 13: Distance of Top 5 strongholds (High Suppression) From Grizedale Forest

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