Report for Forestry and Land Scotland[1]

Part 2: Identification of Natural Red Squirrel Strongholds

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Executive Summary

This report uses mathematical modelling to identify regions of forest that are capable of maintaining a viable red squirrel population, under standard forest management practice, both with and without the grey squirrel trapping. In particular we identify regions of forest that are vulnerable to organic grey squirrel expansion beyond the grey squirrel control boundary as well as regions of forest that act as natural strongholds, which are forests that can maintain a red squirrel population under a worst case scenario where grey squirrels have successfully colonised the entirety of Scotland. The impact of pine marten on red and grey squirrel viability, and a comparison between predation and trapping, is also investigated. The key findings are:

- If the current red and grey squirrel distributions are maintained, potentially via the continuation of grey squirrel trapping along the grey squirrel control boundary, then there exist large expanses of forest north of the control line that support viable red squirrel populations.

- If grey squirrel control ends and grey squirrels are allowed to expand their range then the process of red replacement will be slow and consequently there would still remain large expanses of forest in north and north west Scotland that will support viable red squirrel populations.

- Grey squirrels are predicted to expand northwards, most notably along the north-east and northern coast, with their expansion directly north curtailed by the Cairngorm mountains. Expansion of grey squirrels into central or western Scotland is also impeded by the geography, with the Grampian mountains forcing grey squirrels to migrate along the west coast which provides poor habitat.

- An assumed worst case scenario where grey squirrels can expand to all regions in Scotland was simulated and highlighted regions which could act as natural strongholds for red squirrels. The report highlights a range of forest regions across Scotland that could support red squirrels under standard forest management practice (see Figure 12).

- An analysis of the available land-cover data provided for this assessment indicated that the forest composition of natural strongholds is comprised predominantly of Sitka spruce in southern Scotland and Sitka spruce, Scots and lodgepole pine in northern Scotland combined with an absence of broadleaf and urban habitat.

- Grey squirrel control applied in regions that are adjacent to natural strongholds indicated that this would allow the red squirrel distribution to expand and thereby enhance viability. Grey squirrel control could also be effective in connecting natural strongholds. Overall, simulated grey squirrel control at low and medium levels did not uncover new regions that would support red squirrels.

- The impact of pine marten that preferentially predate on grey squirrels compared to red squirrels had a similar impact as grey squirrel control in expanding the distribution of red squirrels.

Contents

1 Introduction

Red squirrel strongholds are defined by the Forestry Commission Scotland as 'large areas of coniferous and mixed forest identified as having the potential to sustain resilient and healthy populations of red squirrels...over the long-term' [1]. Currently there are 19 forest regions in Scotland that have been designated as red squirrel strongholds (Figure 1). In the first part of this report [2] the effectiveness of 6 of these strongholds was assessed under both the UK Forestry Standard [3] and the Stronghold Management [1] forest management strategies. In the presence of grey squirrels the report stated that the Stronghold Management (SM) policy provides an advantage to red squirrels over grey squirrels when compared to the UK Forestry Standard. However the SM policy, which alters to forest composition to favour red squirrels over greys, was not sufficient in and of itself to ensure that a stronghold was capable of maintaining a viable red squirrel population in the face of competitive pressure from grey squirrels. These findings therefore highlight the importance of the wider landscape that surrounds a stronghold. In particular the connectivity of the stronghold to the forest areas around it, and the suitability of the surrounding region for grey squirrels played a key role in determining the success of the stronghold. When strongholds were highly connected to surrounding regions of forest that were capable of maintaining a grey squirrel population the strongholds failed to protect red squirrel populations. When strongholds had fewer connections to the surrounding area which would support lower grey squirrel densities the strongholds were successful in protecting red squirrels. Additionally, the composition of the stronghold itself was important in determining its success at maintaining red squirrel populations, with a high proportion of Sitka spruce, which is unsuitable for grey squirrels, being of particular importance.

In this second report we investigated the red and grey squirrel population abundance within the current forest composition across Scotland in order to identify regions of forest that act as natural red squirrel strongholds. Here we define a natural stronghold as a region of forest that is able to maintain a viable red squirrel population, in the presence of grey squirrels, without the need for specific forest management or large-scale grey squirrel trapping. We will consider the following scenarios:

A: We assume that the current distribution of red and grey squirrels remains fixed and assess which regions are most suitable for red squirrels. This implicitly assumes that current levels of grey squirrel control are maintained to prevent any expansion of grey squirrels.

B: The model is initiated with the current distribution of red and grey squirrels and both species are allowed to disperse. This assumes that there is no grey squirrel control. This highlights the regions that are vulnerable to grey squirrel expansion as well as regions that are resilient in the face of grey squirrel expansion.

C: The model is initiated with the current distribution of red and grey squirrels and both species are allowed to disperse. Grey squirrel trapping is applied to all regions that contain grey squirrels (and we compare two levels of trap intensity). This identifies regions that can become resilient to grey squirrel invasion if grey squirrel control is applied.

D: Grey squirrels are added to every model 1km by 1km grid-square capable of maintaining a population of 5 or more individuals in order to simulate the situation where grey squirrels have fully colonised Scotland. This will allow the identification of 'natural strongholds' which are defined as regions that can support red squirrels, under standard forestry practice, when threatened with grey squirrel invasion.

E: The same scenario as (D) except with the addition of grey squirrel trapping in all regions that contain grey squirrels (and we compare two levels of trap intensity). This identifies whether a natural stronghold can be significantly enhanced by the addition of grey squirrel control.

F: Predation by pine marten is included in scenario (B), in areas where pine marten have been seen in the wild, to test whether the presence of pine marten can act as a natural grey squirrel control method. This allows the identification of regions of forest that can become viable or enhanced for red squirrel viability due to predation by pine marten (rather than by grey squirrel trapping and control).

2 Methods

Part 1 of this report [2] examined the effectiveness of changes in forest composition for the viability of red squirrels in designated stronghold regions. This report (part 2) uses the same modelling framework that was outlined in part 1 of this report [2, Section 2] but considers the whole of Scotland and assumes all regions follow the UK forest standard policy of management and so does not consider changes made to the composition of forests in Scotland, which includes potential compositional changes imposed by future climate change. However, the simulations still include age structure and seed crop dynamics of the forests. Forests that form part of the National Forest Estate include a detailed breakdown of forest composition using data from the 2017 dataset. Forests that are not in the National Forest Estate are quantified as being broadleaved or coniferous trees, with the data coming from the 2016 National Forest Inventory dataset. Initial red and grey squirrel locations are taken from the National Biodiversity Network (NBN) database and the model run for an initial 10 years to allow stable densities to be reached which act as the initial condition. Regions are classified as being occupied by either red or grey squirrels when two or more individuals are present. Note, this classification of occupancy assumes genetic and population size viability is automatically met. In practice, some regions may require active management in the form of red squirrel translocations. For more information on the methods, as well as the mathematical model, see Section 2 of *Part 1: Evaluation of Red Squirrel Stronghold Forest Management* [2].

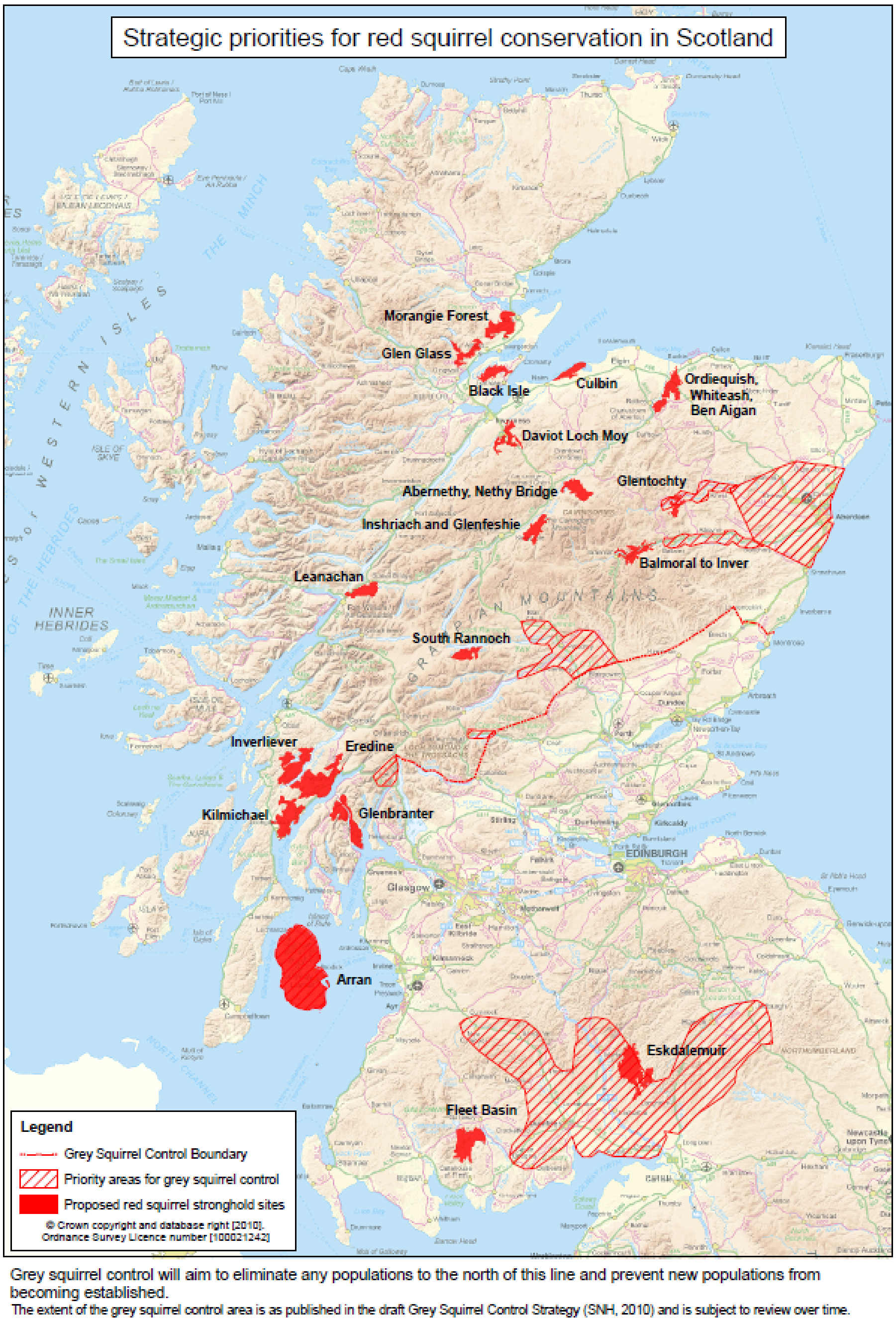

Figure 1: Map of Scotland with the 19 stronghold regions shown in solid red. The map also includes the grey squirrel control boundary which is the northern most extent (excluding Aberdeen) of the grey squirrels as well as regions that are the focus for grey squirrel control (hatched area). Image courtesy of Scottish Natural Heritage

3 Results

Scenario A: An Assessment of Red Squirrel Viability Assuming a Fixed Grey Squirrel Distribution

The grey squirrel control boundary (Figure 1) constitutes the northern-most extent of grey squirrels in Scotland, with the exception of the isolated grey squirrel populations in and around Aberdeen. This population is genetically distinct from grey squirrels south of the control boundary which suggests that they were introduced into Aberdeen independently of the population in the south of Scotland. The expansion of grey squirrels beyond these regions is prevented by grey squirrel trapping and control. In this model scenario we assume the current grey squirrel distribution is maintained, but cannot expand.

Figure 2 shows the average population density and distribution of grey squirrels in Scotland for year 10 to year 40 of the model simulation. The clear boundary between grey squirrel presence and absence represents the grey squirrel control boundary and the regions of high density mostly correspond to urban areas in the central belt of Scotland. Grey squirrel absence in the north of Scotland is due to the imposed restrictions on the distribution expansion in the model whilst their absence in the south of Scotland corresponds either to areas of poor grey squirrel habitat or to the absence of suitable grey squirrel habitat.

Figure 3 shows the corresponding average population density and distribution of red squirrels in Scotland. As expected, the regions where red squirrels are present corresponds closely to the regions where grey squirrels are absent, with the highest densities being found in the north of Scotland. There are also regions in the south of Scotland that support red squirrel populations.

Figure 4 shows the relative occupancy of each 1km grid-square and highlights a clear separation between the distribution of red and grey squirrels, with only limited regions where coexistence occurs (orange regions in Figure 4). Since the expansion of grey squirrels beyond their current distribution is prevented, the model predicts that the north of Scotland provides suitable habitat for red squirrels. In southern Scotland there are regions of forest that can support red squirrel populations, particularly in Dumfries and Galloway, above and close to the Fleet Basin stronghold as well as around the border between Dumfries and Galloway and the Scottish Borders, near the stronghold at Eskdalemuir.

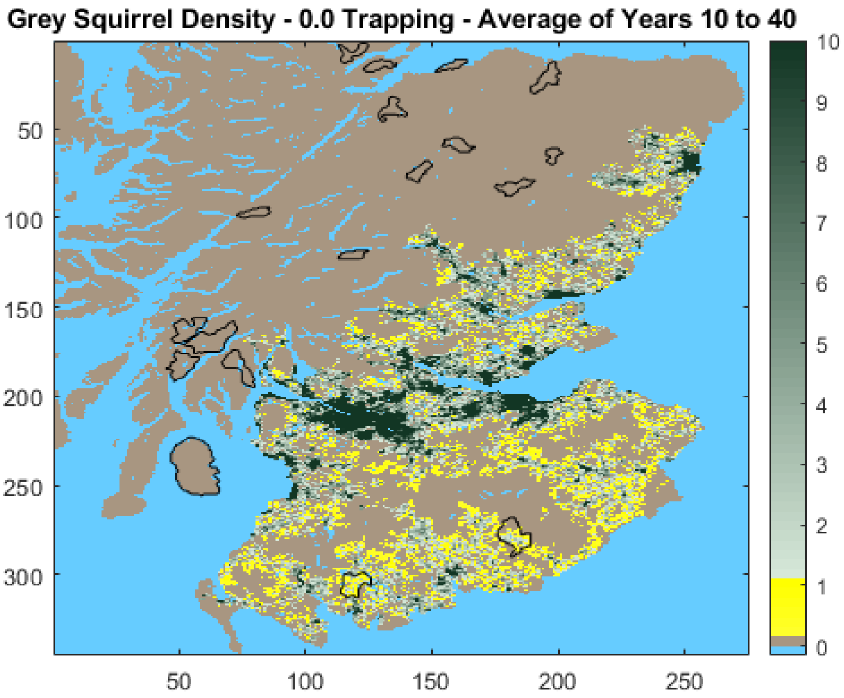

Figure 2: Average grey squirrel density when they have been limited to their initial range. Result is an average of the 10 simulations, with each simulation result being a 30 year average from year 10 to 40 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

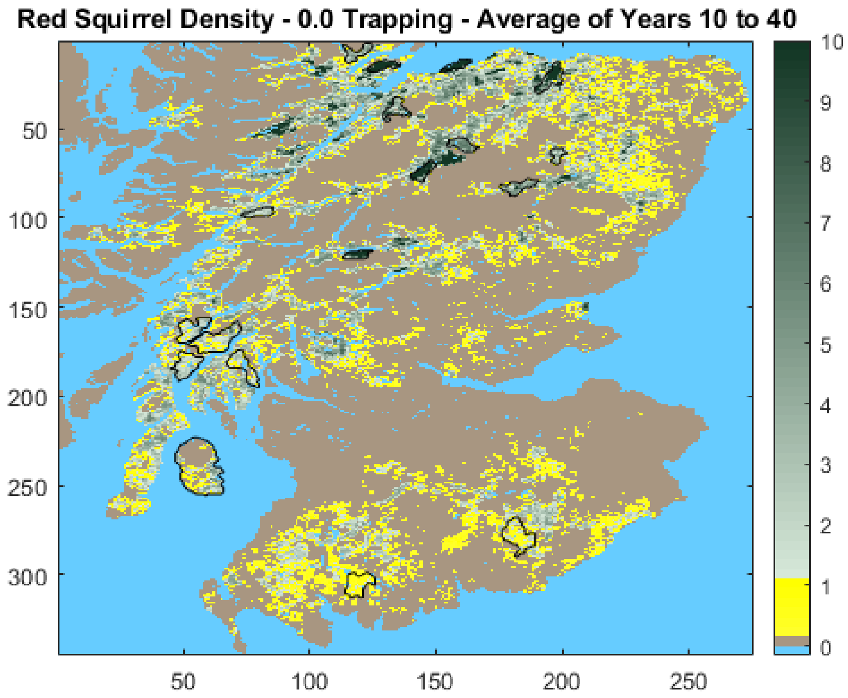

Figure 3: Average red squirrel density when grey squirrels have been limited to their initial range. Result is an average of the 10 simulations, with each simulation result being a 30 year average from year 10 to 40 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

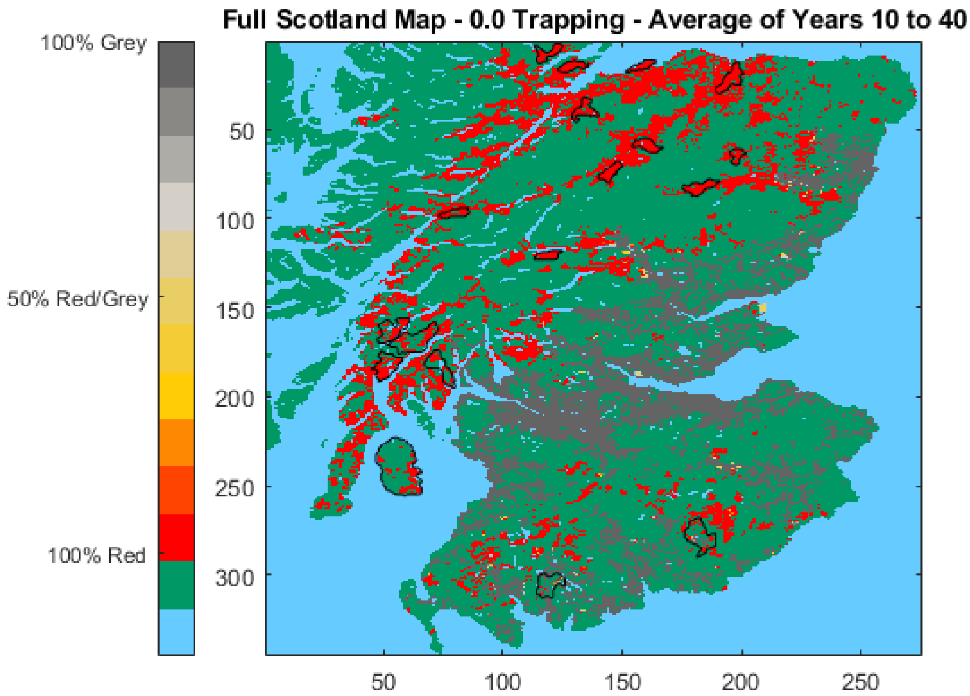

Figure 4: Map of red and grey squirrel occupancy. The colour scale denotes the relative proportion of model simulations that ended with 2 or more red or grey squirrels being present in each 1km grid-square. Grid-squares that are red denote that only red squirrels were present, dark grey means only grey squirrels were present whilst orange means that half of the simulations that met the criteria had red squirrels present and half had grey squirrels present. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

Scenario B: An Assessment of Red Squirrel Viability When Current Efforts to Prevent Grey Squirrel Expansion are Removed

The central aim of stronghold management policy is to identify and manage regions of forest that can maintain a viable red squirrel population in the event that grey squirrels encroach beyond the grey squirrel control boundary and become resident in the north of Scotland. Thus we will consider the scenario whereby the current trapping efforts that are used to limit the grey squirrel distribution expansion are removed.

Under this scenario the grey squirrel population density (Figures 5.b(i-iii)) south of the grey squirrel control boundary remains largely unchanged. This is expected given that grey squirrels are already resident in this region. There is grey squirrel expansion across the length of the grey squirrel control boundary with the main area of grey squirrel expansion being in the north-east where grey squirrels successfully migrate northwards along the coast from Aberdeen, stopping short of Inverness. The grey squirrel expansion across the centre and west of the grey squirrel control boundary is limited due to the lack of suitable connected habitat (which in turn is due to geographic factors) that prevent the large scale movement of individuals. The spread of grey squirrels occurs quickly in the model and thereafter the distribution of grey squirrels remains fairly fixed (there is little difference in the distribution of grey squirrels after 30 years and after 150 years). The density of grey squirrels in newly colonised areas increases slowly or remains low, since many of the newly colonised regions can support low density grey population only.

The red squirrel population density (Figures 5.a(i-iii)) does not significantly change due to the increased geographic spread of grey squirrels. South of the grey squirrel control boundary this is to be expected, given the long term residence of grey squirrels in this area, however in the north-east, where grey squirrels have expanded, the low density of grey squirrels is not sufficient to eradicate the resident red squirrel population for the majority of the simulation. At the end of the simulation there is a region to the north of Aberdeen that does see red squirrel extinction which could give some indication as to the time-scale necessary for extinction to occur. This suggests that the north-east of Scotland may be vulnerable to red squirrel extinction in the long term. Conversely, the north-west of Scotland remains a safe haven for red squirrels as it appears that, under the model assumptions regarding the squirrel densities for each tree species, grey squirrels struggle to colonise and/or establish at high density in the area.

Using the occupancy maps (Figures 5.c(i-iii)) we can see that grey squirrel expansion into the region directly north of the grey squirrel control boundary, as well as to the north of Aberdeen, occurs quickly and becomes fixed across the majority of the control boundary. Comparing this scenario with the previous one, where grey squirrels were not allowed to disperse north of the grey squirrel control boundary (Figure 6), it can be seen that red squirrels are excluded from the forest to the south of Aberdeen, except for Fetteresso forest which retains red squirrel occupancy despite the wider region being grey only territory. It can also be seen that red squirrels are almost entirely excluded from the Dee river valley, with only a small residual region of coexistence remaining at the end of the simulation, as well as from the southern part of Argyll and Bute, near the base of the Kintyre peninsula in the west. Grey squirrels also advance northwards towards Pitlochry, though they are unable to expand further north or west from there. The region directly north of Aberdeen is also vulnerable to grey squirrel expansion, and red squirrel exclusion, however despite grey squirrel expansion further along the northern coast, with grey squirrels nearly reaching Inverness, the north of Scotland remains a region of red squirrel occupancy due to the habitat being unable to support a sufficiently high grey squirrel density. Only the Spey river valley sees coexistence during the simulation, which begins to change into sole grey squirrel occupancy at the end of the simulation. In the south of Scotland there is little change to the regions of occupancy because red and grey squirrels were already present in the south before the simulations began.

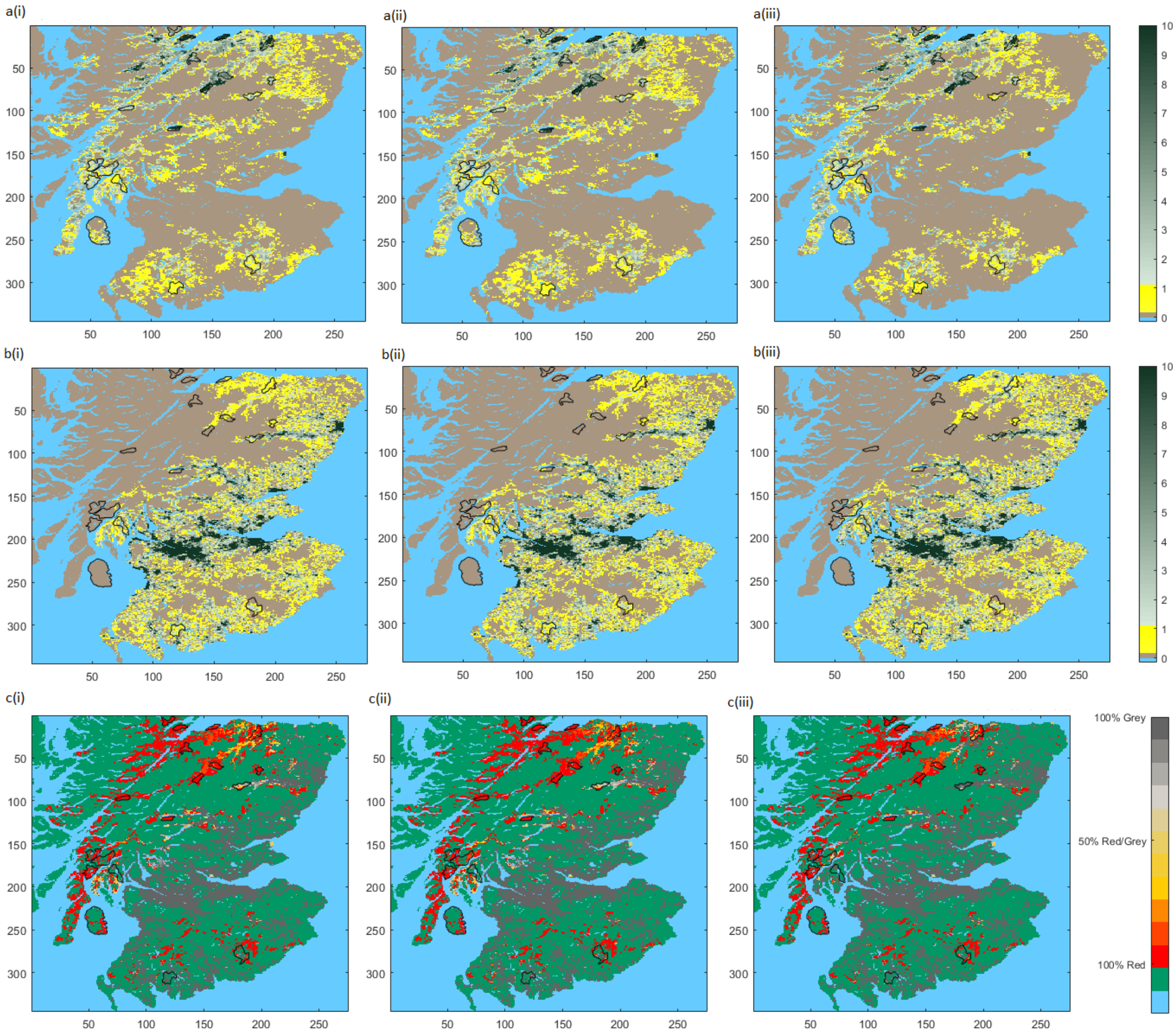

Figure 5: Results for the scenario where red and grey squirrels are allowed to disperse and compete freely, without any grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

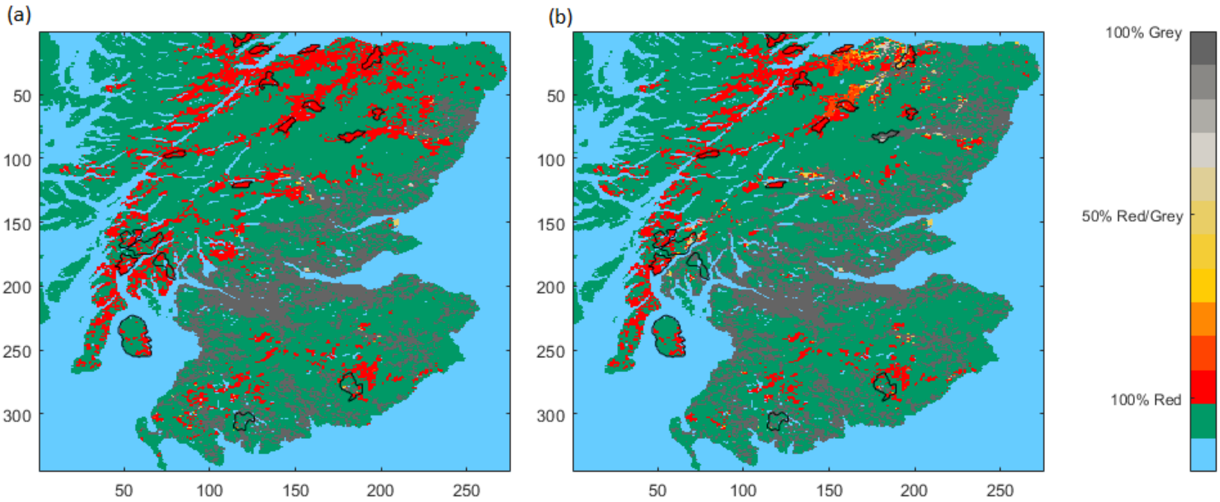

Figure 6: Results showing relative occupancy of each 1km grid-square. Here (a) shows the occupancy when grey squirrels are not allowed to disperse whilst (b) shows the results when grey squirrels are allowed to disperse freely. Both results have no extra trapping applied.

Given that the main area of grey squirrel expansion occurs to the north of Aberdeen it would be useful to assess the importance of Aberdeen as a gateway to the north of Scotland. There are currently ongoing efforts by Saving Scotland's Red Squirrels to remove grey squirrels from the city of Aberdeen as well as the surrounding rural area. Thus the results from a scenario where grey squirrels are removed from Aberdeen before the start of the simulation are of interest and are presented below. Two sub-scenarios were considered, one where grey squirrels were allowed to expand back into Aberdeen and a second where grey squirrels were prevented from re-colonising the area from which they were removed, thus simulating a continuing trapping regime that successfully excludes grey squirrels. Figure 7.a shows the final occupancy result when grey squirrels are allowed to recolonise and shows that grey squirrels will successfully recolonise Aberdeen if allowed, however their expansion north will be limited, potentially due to a lack of population density at Aberdeen which results in a lower rate of invasion into the north. Figure 7.b shows the results when grey squirrels are prevented from recolonising the area around Aberdeen and, as can be seen, this ensures that grey squirrels cannot invade the north of Scotland which means that Aberdeen does act as a gateway for grey squirrels into northern Scotland, primarily due to the physical barrier that is the Cairngorms, and so trapping efforts to the south of Aberdeen could safeguard the north of Scotland for red squirrel habitation. For full results see appendix A.

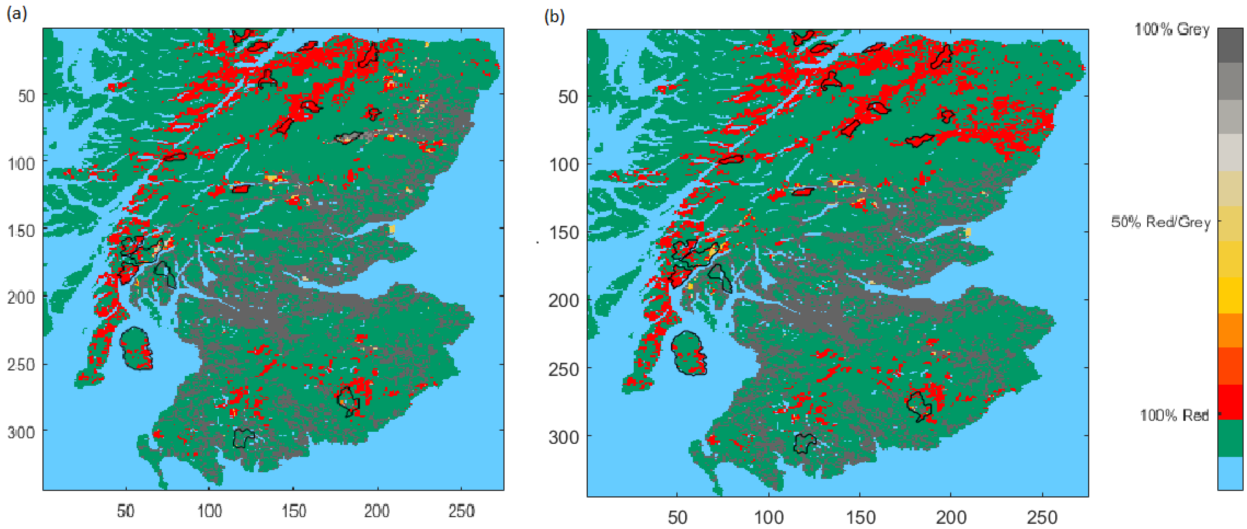

Figure 7: Results for when grey squirrels have been pre-emptively removed from Aberdeen and the surrounding environs. Here (a) shows the results when grey squirrels have been allowed to recolonise Aberdeen unimpeded whilst (b) shows the results when grey squirrels are prevented from recolonising Aberdeen.

Scenario C: An Assessment of Red Squirrel Viability when Current Efforts to Prevent Grey Squirrel Expansion are Removed and Grey Squirrel Trapping is Applied

In this scenario we investigate whether some regions of forest will support viable red squirrel populations with the application of grey squirrel trapping.

Two levels of grey squirrel trapping were implemented and are denoted as a low trapping level which corresponds to an average of 18 trap-days per year per kilometre grid-square ($T_D = 0.1$ in the model, see Table 5 in [2]), and a medium trapping level which corresponds to an average of 36 trap-days per year per kilometre grid-square ($T_D = 0.2$). Trapping levels above these led to near extinction of grey squirrels in Scotland, with residual populations residing in and around Edinburgh and Glasgow only. Trapping was applied between March and September to model grid squares that contained grey squirrels. The model assumes that any red squirrels that are inadvertently caught in the traps are released. For further details on how trapping is applied in the model see [4, 5].

Figure 8 shows the results when a low level of trapping is applied. The most noticeable impact of the trapping is that the grey squirrels (Figures 8.b(i-iii)) are unable to establish themselves along the north-east coast, with the expansion north being limited to the region directly north of Aberdeen. Thus the northern coast of Scotland, including the Spey valley, remains sole red occupancy areas. The Dee river valley, to the west of Aberdeen, initially sees coexistence. However, red squirrels are excluded from the majority of the valley near the end of the simulation, with a small region of red occupancy remaining at the western edge of the valley. This is despite the regions around the valley, to the west and south of Aberdeen, being regions of red occupancy which nearly isolates Aberdeen.

In the west of Scotland grey squirrels are unable to replace red squirrels in the south of Argyll and Bute, though there is still some regions of coexistence as well as red occupancy. The forests around Pitlochry also predominantly favour red squirrels with this level of trapping. In the south of Scotland the regions that previously allowed red squirrel occupation expand. However new regions, independent of the existing red occupancy areas, do not emerge.

Figure 9 shows the results when a medium level of trapping is applied. This level of trapping ensures that the grey squirrels (Figures 9.b(i-iii)) are unable to advance beyond the grey squirrel control boundary. Furthermore, the region of grey squirrel absence in the south of Scotland encompasses almost the entirety of the south of Scotland, meaning that the grey squirrels are confined to the central belt with a smaller population around Aberdeen which is at risk of becoming isolated by the end of the simulation. The density of grey squirrels in the central belt is also reduced when compared to Figure 2 with this level of trapping so that there exist high density areas that correspond to urban centres that are surrounded by low density grey squirrel regions which connect them. Consequently, the red squirrel density is higher in Figure 9 than it is in Figure 3 with red squirrels successfully re-colonising the majority of the south of Scotland.

Overall, the application of grey squirrel trapping (at either level of simulated effort) does not allow new regions of red squirrel occupancy to emerge. Instead trapping allows pre-existing regions of red squirrel viability to expand which increases viability. In particular, the regions around Aberdeen, the Dee river valley, north-east Loch Lomond, southern parts of Argyll and Bute as well as highland Perthshire would benefit most from grey squirrel trapping. Whilst the medium level of trapping ensured that grey squirrels could not expand beyond the current grey squirrel control boundary, such a level of trapping is likely not viable, in terms of financial cost as well as energy expenditure, except in focused regions, with the regions stated above being ideal candidates.

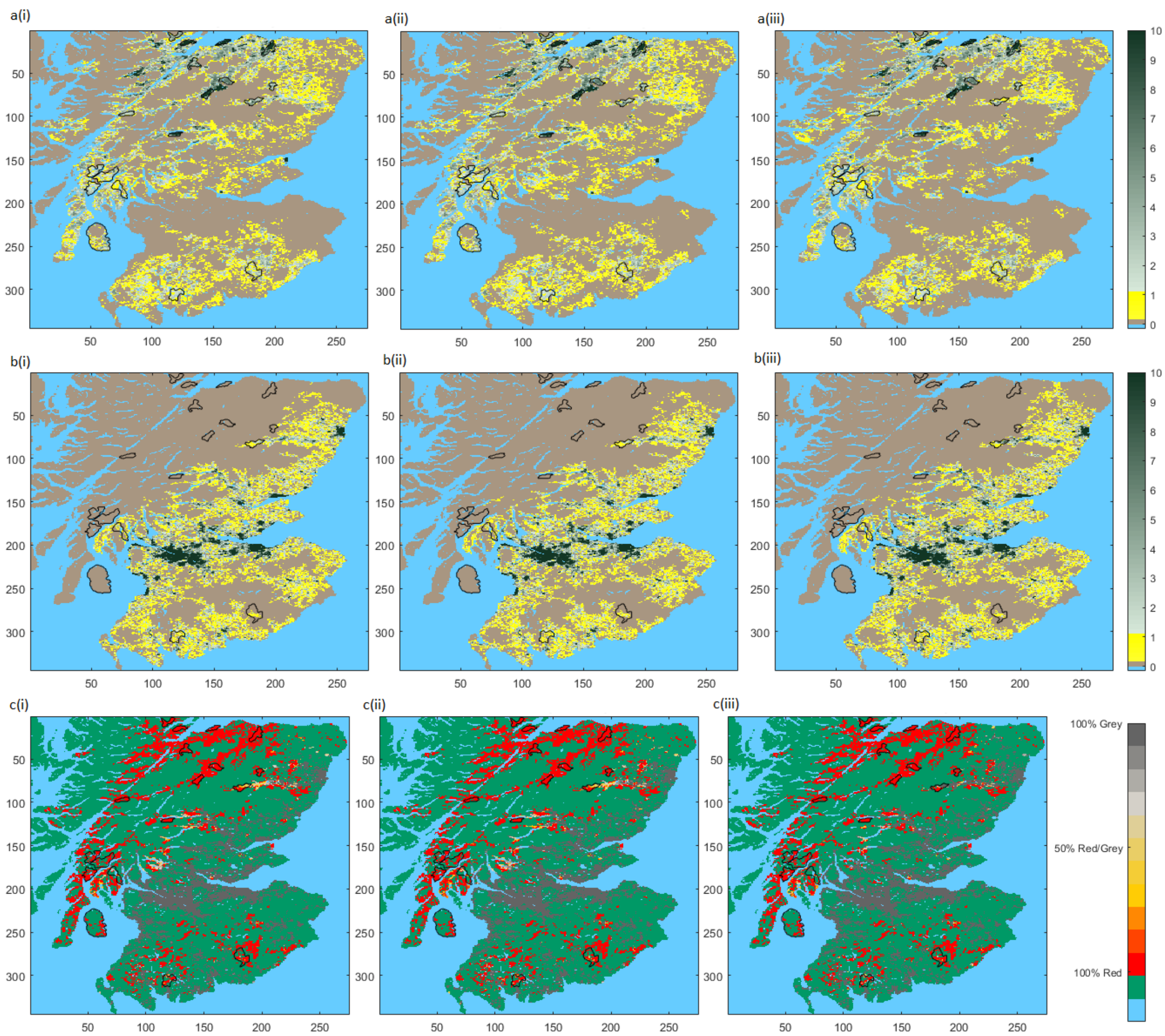

Figure 8: Results for the scenario where red and grey squirrels are allowed to disperse and compete freely, with 0.1 grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

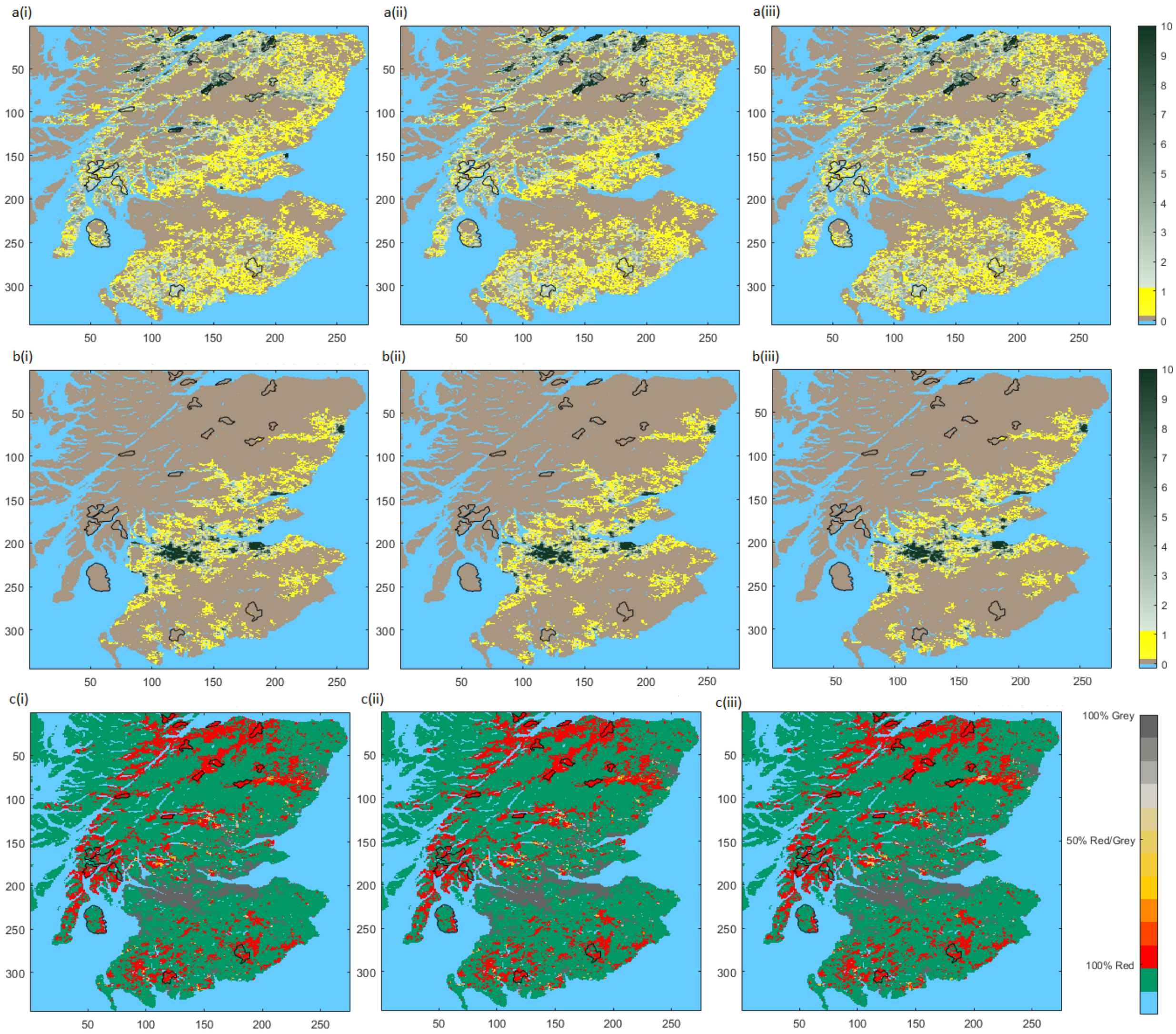

Figure 9: Results for the scenario where red and grey squirrels are allowed to disperse and compete freely, with 0.2 grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

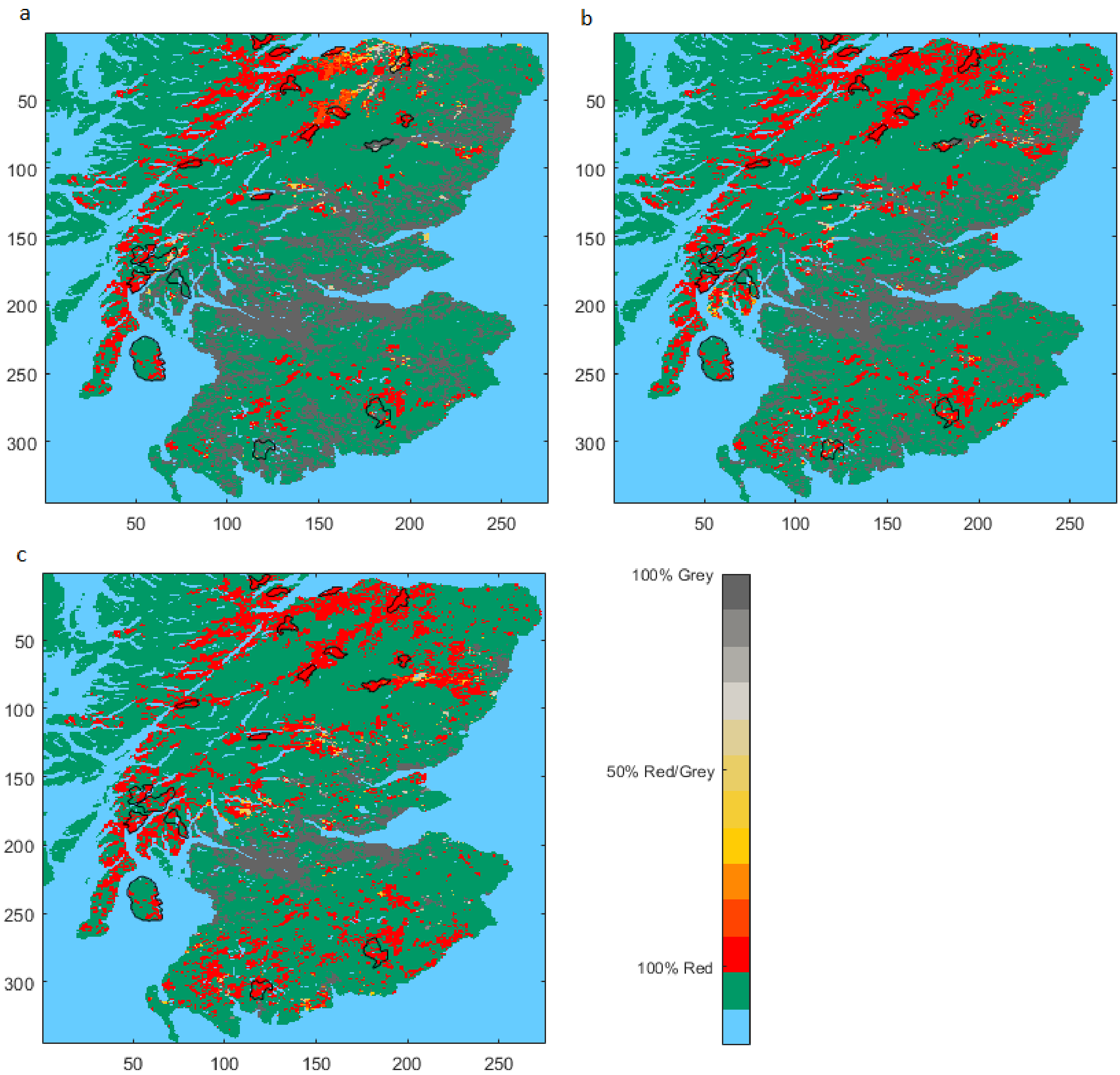

Figure 10: Final red and grey squirrel occupancy for (a) no grey squirrel trapping, (b) 0.1 grey squirrel trapping and (c) 0.2 grey squirrel trapping when grey squirrels were allowed to disperse and compete freely.

Scenario D: Identification of Natural Red Squirrel Strongholds

Natural red squirrel strongholds are regions of forest that can maintain a viable red squirrel population, here defined as a population that can survive despite competitive pressure from grey squirrels, under a worst case scenario where grey squirrels have successfully expanded their range across the entirety of Scotland. In order to identify these natural strongholds grey squirrels were included and placed at the beginning of the simulation, at their carrying capacity, in every grid-square that could maintain a population size of 5 or more grey squirrels. The results of the simulations, where no grey squirrel trapping was included, can be seen in Figure 11 whilst figure 12 shows the red and grey squirrel occupancy for this scenario, with the inclusion of names for forest regions that the model results indicate are currently natural strongholds.

In central Scotland the regions of forest at Rannoch, which includes the existing stronghold of South Rannoch as well as the region of forest that lies directly west, are best suited as red squirrel strongholds. Furthermore, given the lack of grey squirrel occupancy in this region, these two forests could potentially be connected, using appropriate planting that give an advantage to red squirrels over greys, to create a single, larger, and connected natural stronghold. This would further aid population viability. The forest to the east of the forests at Rannoch, just north of Loch Tummel, allows red and grey squirrel coexistence despite being connected to an area of grey squirrel occupancy. The forest of Craigvinean, to the south of Rannoch near Dunkeld, also acts as a natural red squirrel stronghold which suggests that trapping around Dunkeld could isolate the natural red squirrel strongholds at Rannoch due to geographic factors that prevent grey squirrel incursion via other routes. To the east of this region lies Glenisla forest which also acts as a natural red squirrel stronghold due to its relative isolation and lack of connectivity.

In the east of Scotland the forest that includes the stronghold at Glentochty, which lies to the west of Aberdeen, is a natural stronghold which suggests that the existing stronghold could be expanded to include the rest of the forest to which it is connected. Directly south of Aberdeen is Fetteresso forest which also makes a good natural stronghold, especially given its proximity to Aberdeen.

Along the northern coast of Scotland there is a significant region of forest that either has sole red occupancy or coexistence. In the centre of this region is the existing stronghold of Ordiequish, to the east lies the forest of Aultmore whilst Teindland forest lies directly to the west, all of which allow red and grey squirrel coexistence. Sole red squirrel occupancy occurs at Elchies forest which lies to the south-west of Ordiequish. To the west of Elchies forest is the forests of Newtyle, Dallas and Monaughty, all of which can be found further west along the north coast, to the south-east of the stronghold at Culbin, and all of which allow coexistence. The existing stronghold at Culbin also allows coexistence between red and grey squirrels but is separated from the other three forests by a region of grey squirrel occupancy at Darnaway forest and the city of Elgin. However, trapping at Elgin could prevent grey squirrel expansion further west along the northern coast due to the limited number of migration routes available to grey squirrels.

The Spey river valley is also in this region and includes the existing strongholds of Inshriach and Glenfeshie, which is a region of red and grey squirrel coexistence, and Abernethy which only allows red squirrel occupation in part of the stronghold. However, the forest in between these two strongholds, Glenmore Forest Park, makes a good natural stronghold which suggests that this forest and the two adjacent strongholds could potentially be combined to create a single stronghold. Furthermore, given limited grey squirrel access routes imposed by the geography, trapping further along the Spey river, to the south of Ordiequish for example, could isolate the region and prevent grey squirrels entering from the north-east.

Further north the stronghold of Black Isle, which encompasses the entire connected forest, makes for a good natural stronghold, as well as forests around Glen Affric and Glen Garry which lie on the opposite side of Inverness from Black Isle. To the south of Glen Garry there is a region of red squirrel occupancy around Glen Spean, which lies to the east of Fort William, which makes a good natural stronghold and which could replace the existing stronghold at Leanachan which currently appears to have no red squirrel presence.

The peninsula of Kintyre in west Scotland allows both red and grey squirrel occupation, with segregation occurring naturally and red squirrels occupying the west and grey squirrels the east of the peninsula. There is also a small region that could act as a natural stronghold at the western edge of Loch Doine, however the west of Scotland appears to offer little in the way of natural red squirrel stronghold.

In the south of Scotland the regions of red squirrel occupancy are the same as in Section B, due to the current existence of grey squirrels in the region. Thus in the Scottish Borders the forest at Eskdalemuir allows sole red occupancy in the eastern part of the forest whereas the western section, which is the current stronghold, does not fare well as a natural stronghold. However, as suggested in part one of this report [2], the western section of Eskdalemuir forest could act as a good stronghold with small alterations in the forest composition. The forest to the north of Eskdalemuir, at Glentress forest, as well as Wauchope forest at the border with England, which is connected to the stronghold at Kielder forest which is approx. 5000km^2 in area and is dominated by Sitka spruce, also act as natural red squirrel strongholds.

In Dumfries and Galloway the current stronghold at Fleet Basin does not act as a natural stronghold, primarily because this stronghold does not provide good red squirrel habitat (see [2]). Alongside this, the urban area at Gatehouse of Fleet as well as deciduous regions along the river valley to the north provide good grey squirrel habitat. The forests to the north of the stronghold, east of the Waters of Ken, are better suited to be a natural strongholds. Further north, near the town of Muirkirk, there are a number of small regions of forest that can act as red squirrel strongholds. There is also a region of forest, near the town of Newton Stewart, that can act as a natural stronghold.

Beyond this there are a few small regions, such as Tentsmuir forest, Kincardine and Montreathmont forest, that allow coexistence between red and grey squirrels despite these regions being surrounded by sole grey occupancy regions.

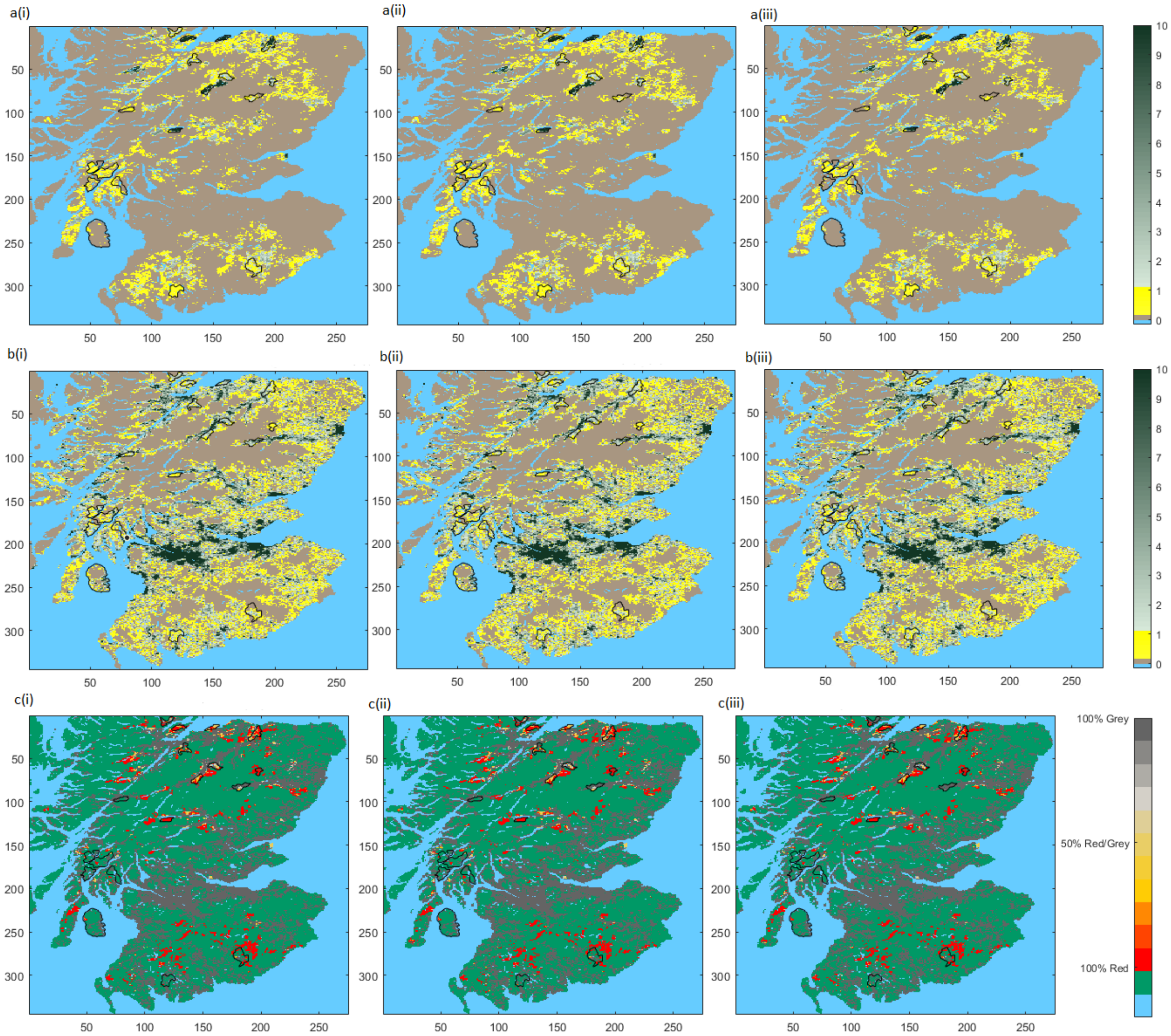

Figure 11: Results for the scenario where grey squirrels have been introduced everywhere, in order to simulate a situation where grey squirrels have successfully colonised the entirety of Scotland. These results have no grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

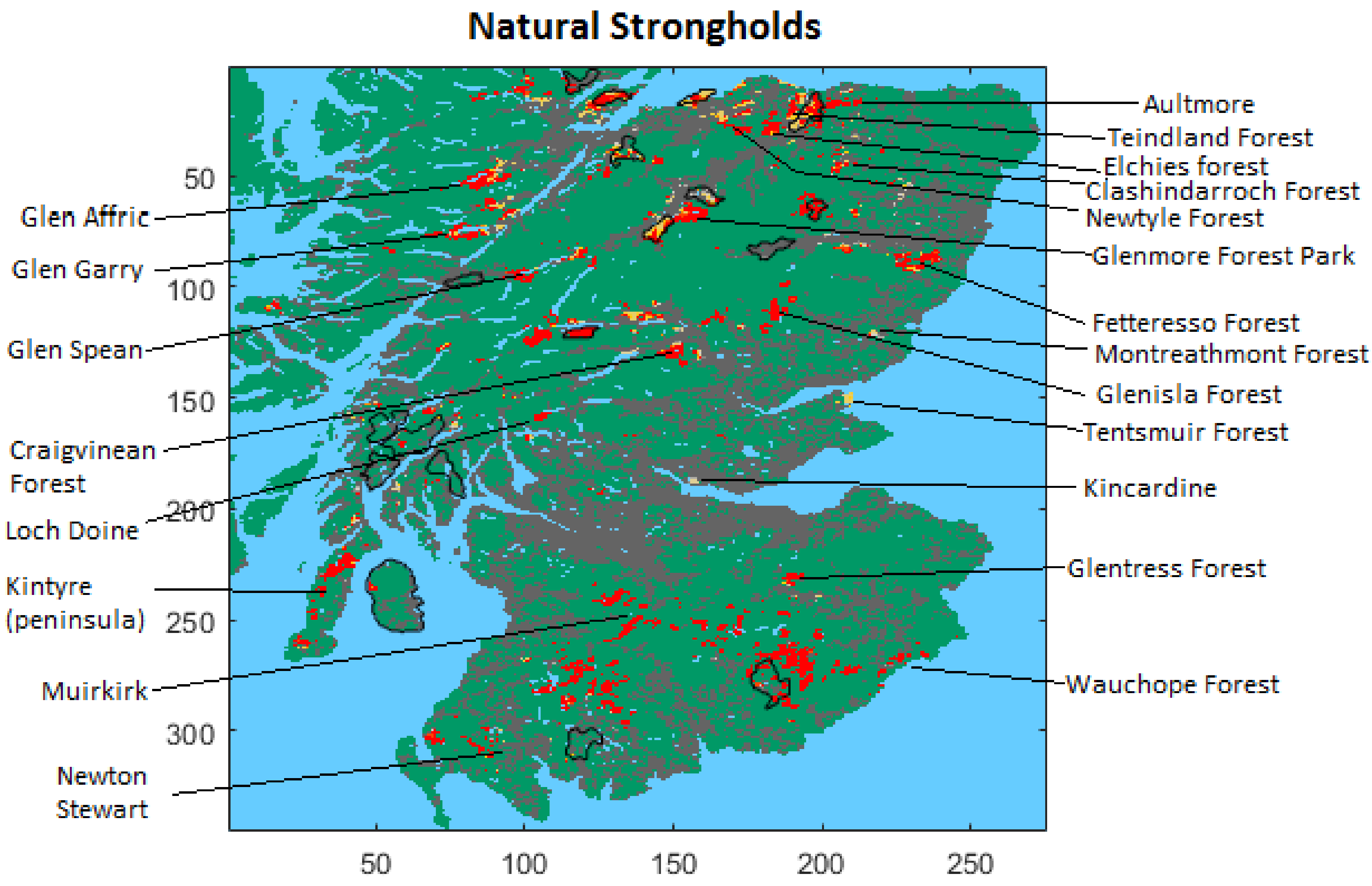

Figure 12: Relative occupancy of red and grey squirrels when grey squirrels have been introduced everywhere, with no grey squirrel trapping. Names are of natural strongholds. Existing strongholds are outlined in black.

Forest Composition of Red and Grey Squirrel Stronghold Regions

Based on the compositional information that is available, with the National Forest Inventory providing only basic land-cover data, we can see the composition of the landscape that had either 80% red squirrel occupancy or 80% grey squirrel occupancy (Figure 13), where the percentage occupancy details the proportion of the 10 simulations that ended with 2 or more red or grey squirrels present in the grid square. When all of the tree species, including other conifer and other broadleaf, are included (Figures 13 a(i) and b(i)) it can be seen that the primary difference in preferred habitat is that grey squirrels thrive when their is either a high proportion of broadleaf or a high proportion of urban environment present whereas red squirrels exist in conifer dominated regions (when greys are present), which is expected given the competitive advantage that broadleaved trees give to grey squirrels over reds. However, when only the National Forest Estate species are included (Figure 13 a(ii) and b(ii)) the primary habitat that grey squirrels exist in is the urban environment, with Sitka spruce and neutral species also providing a significant proportion of the habitat. The dominance of grey squirrels in regions with a significant proportion of neutral species is expected, given the competitive advantage greys have over reds regardless of habitat, however the predominance of Sitka spruce is unexpected and may suggest that the presence of adjacent broadleaved trees may provide a source of grey squirrels that is sufficient to overcome the disadvantages presented to grey squirrels by Sitka spruce. Conversely, red squirrels appear to survive well in regions that are dominated by either Sitka spruce or Scots pine, with Lodgepole pine also contributing a significant proportion of the habitat.

Figure 15 details the forest composition of red and grey squirrel occupancy for northern Scotland, where the dividing line between north and south Scotland that was used is shown in Figure 14. In this instance the composition results closely match those for the whole of Scotland. The primary difference for red squirrels is that, when all tree species are included, there is less 'Other Conifer' present (50% vs. 60%) and when only the National Forest Estate is considered there is more Scots pine (35% vs 30 %) and less Sitka spruce (30% vs 35%) in the composition. For grey squirrels the full forest composition for northern Scotland shows a slightly higher dependence on 'Other Conifer' (approx. 35% vs 30%) which is most likely due to the natural reduction in broadleaf trees that occurs further north because of climactic reasons. When only the National Forest Estate trees are considered the primary change is that there is a reduced dependence on the urban environment (40% vs 30-35%) which is most likely due to the exclusion of the central belt from our definition of northern Scotland. This reduced urban proportion is replaced by neutral species which do not offer a competitive advantage to either red or grey squirrels, and so the dominance of grey squirrels in this habitat is due to the inbuilt competitive advantage grey squirrels have over reds, regardless of habitat.

Figure 16 shows the forest composition of red and grey squirrel occupancy for southern Scotland. For red squirrels there is an overwhelming dependence in southern Scotland on 'Other Conifer'. This primarily indicates the lower proportion of National Forest Estate land in southern Scotland that can maintain a red squirrel population. When only National Forest Estate land is considered the main differences is the large reduction in Scots pine (approx. 5% vs 30%) and the much greater reliance on Sitka spruce (60% vs. 35%). There is also a smaller proportion of Lodgepole pine (15% vs 10%) and a larger proportion of neutral species (approx.

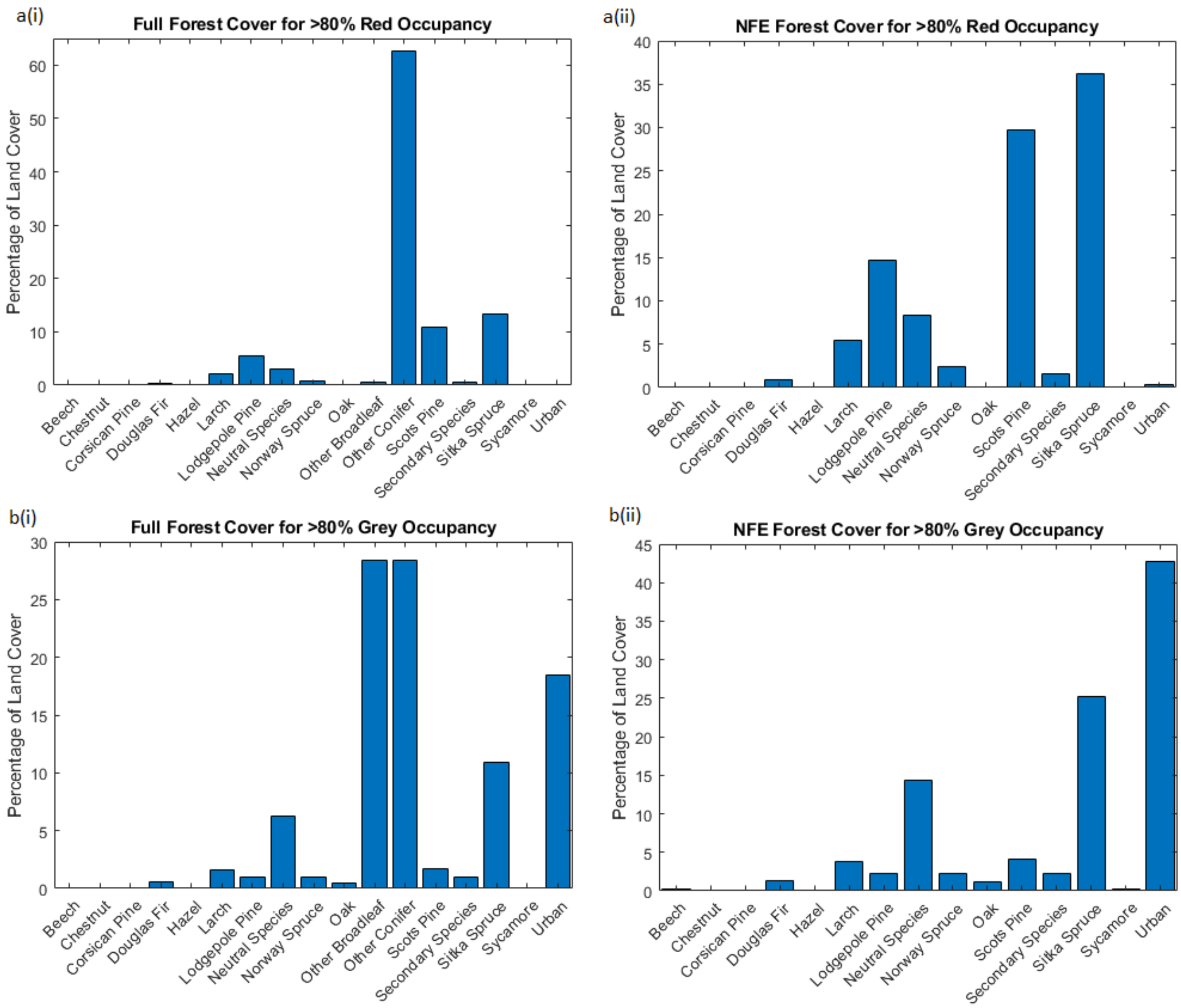

Figure 13: Composition of the landscape where either (a) red or (b) squirrels enjoy at least 80% occupancy. Here (i) details the full landscape composition whilst (ii) only details the National Forest Estate and urban composition.

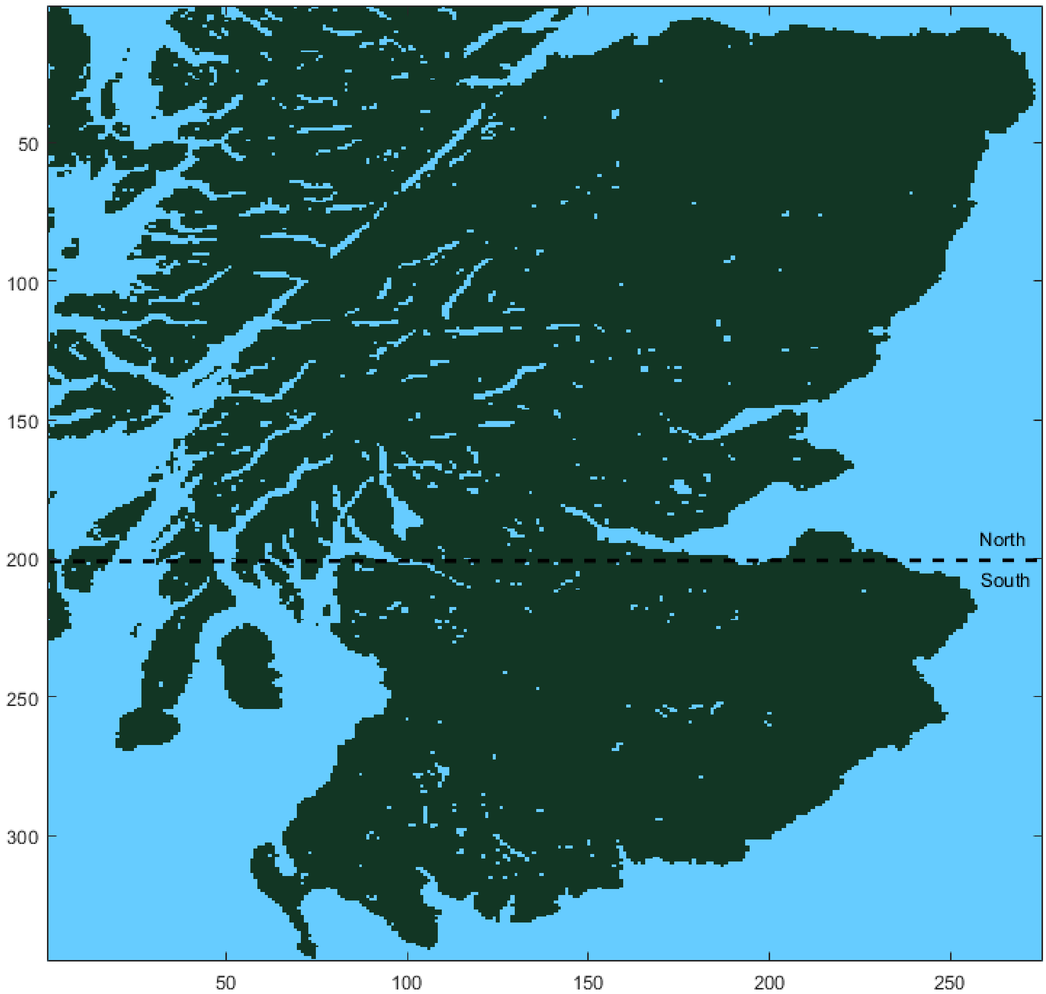

Figure 14: Map showing the line used to divide Scotland into northern and southern parts.

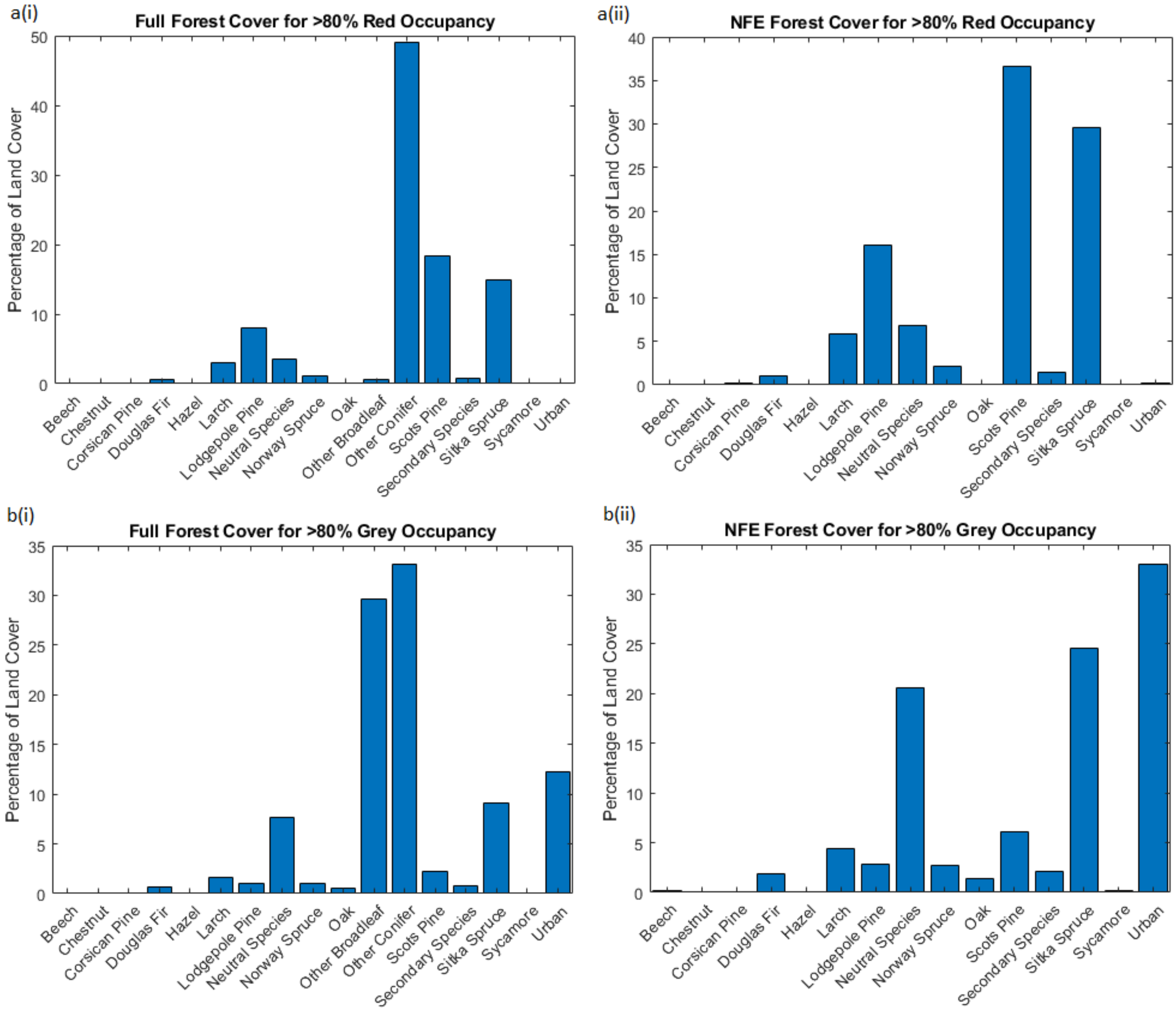

Figure 15: Composition of the landscape of northern Scotland where either (a) red or (b) squirrels enjoy at least 80% occupancy. Here (i) details the full landscape composition whilst (ii) only details the National Forest Estate and urban composition.

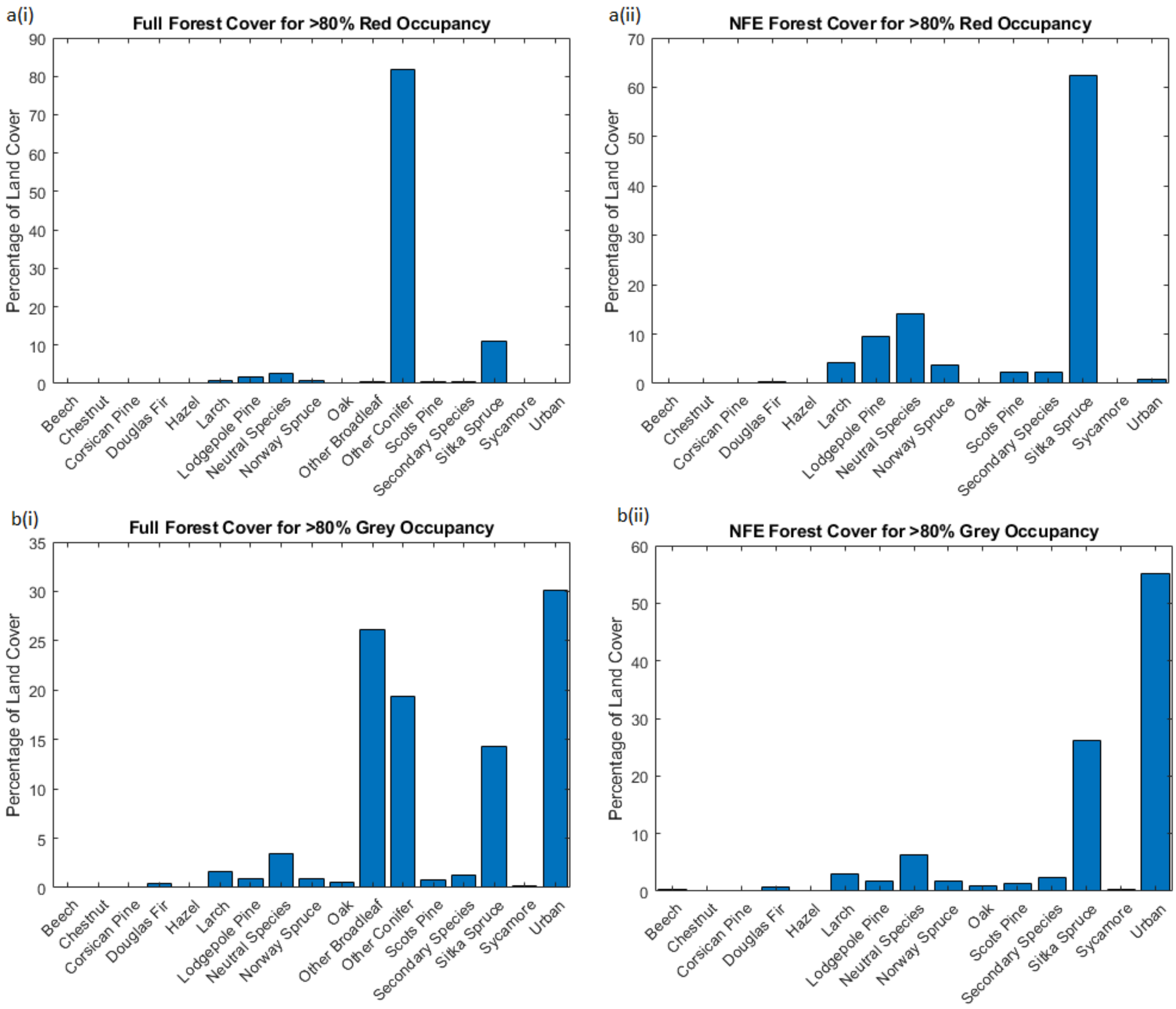

Figure 16: Composition of the landscape of southern Scotland where either (a) red or (b) squirrels enjoy at least 80% occupancy. Here (i) details the full landscape composition whilst (ii) only details the National Forest Estate and urban composition.

7% vs 15%). For grey squirrels there is a much greater reliance on the urban environment in south Scotland, due to the inclusion of the central belt. Other than this there is also a smaller proportion of 'Other Conifer' compared to 'Other Broadleaf' in south Scotland. When only the National Forest Estate is considered the reliance on neutral species that is present in north Scotland is no longer present, with the two main habitats being urban and Sitka spruce.

Scenario E: Identification of Natural Red Squirrel Strongholds when Grey Squirrel Trapping is Included

Figure 17.b shows the results when grey squirrels are introduced everywhere along with a low level of trapping. As expected, the areas that are capable of being red squirrel strongholds expand. Specifically, the forest area near Rannoch and the Craigvinean forest become viable as strongholds which suggests that trapping efforts around Pitlochry may yield useful results. Similarly, this level of trapping improves the ability of the forest regions along the north coast, which allow coexistence when no trapping is applied, to better exclude grey squirrels and become red occupancy areas (Note, occupancy is defined as having 2 or more individuals per $1km^2$. The region in question has at most 1 grey squirrel per km^2), although grey squirrels can still be found in Darnaway forest. Likewise, forest along the Spey valley which previously allowed red and grey coexistence can now act as red squirrel strongholds.

The regions to the north and west of Fetteresso forest, which lies to the south of Aberdeen, are now viable red squirrel strongholds and the stronghold at Balmoral to Inver, which lies along the Dee river valley, can maintain a red squirrel population in the west of the stronghold. Aberdeen itself remains a grey squirrel stronghold. In the west of Scotland there appears a number of regions that allow red squirrel occupancy as well as exclusion of grey squirrels from the Kintyre peninsula. The small isolated regions of coexistance at Tentsmuir, Kincardine and Montreathmont become red only occupied regions with this level of trapping. However, they do not expand in size.

In the south of Scotland there are new regions of red occupancy in the west of Dumfries and Galloway, which suggests that the whole region of Dumfries and Galloway could become a safe haven for red squirrels if enough resources were available to maintain the level of trapping required.

Figure 17.c shows the results when a medium level of trapping is applied. In this scenario the majority of the north of Scotland is suitable red squirrel stronghold territory with the only regions of grey squirrel occupation being Inverness and Aberdeen. There are a number of places where red and grey squirrels can coexist, such as along the Spey river valley near the current stronghold at Abernethy and along the Dee river valley near the Balmoral to Inver stronghold. In the south of Scotland the regions where red squirrels have sole occupancy has increased to encompass the majority of Dumfries and Galloway and the Scottish Borders, with only a small number of isolated regions where either grey squirrels have sole occupancy or coexistence is possible. The central belt of Scotland is still dominated by grey squirrels, although the region south of the Tay estuary can now support red squirrels. This could potentially isolate the populations at Aberdeen and Dundee making eradication easier.

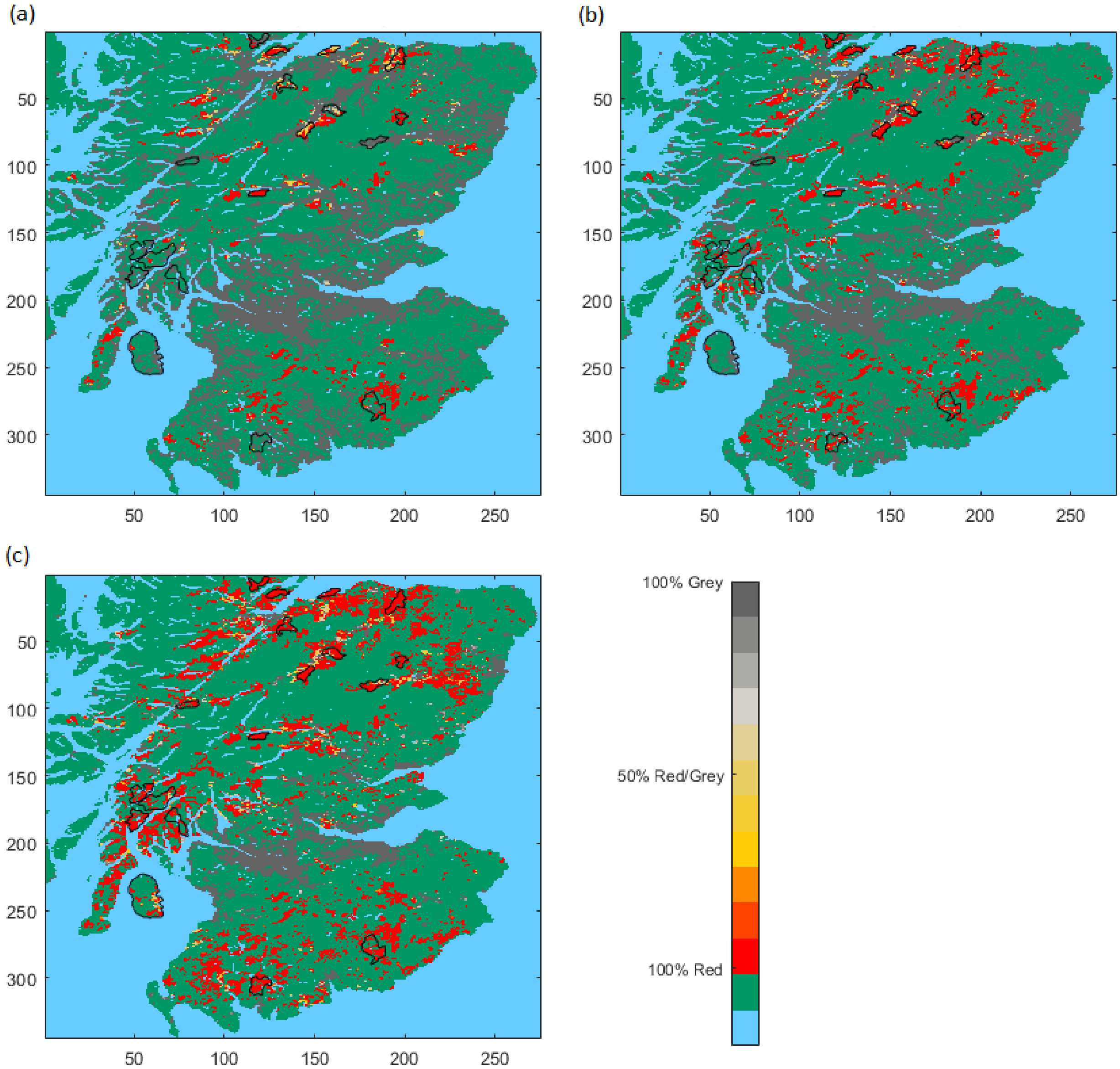

Figure 17: Final red and grey squirrel occupancy for (a) no grey squirrel trapping, (b) 0.1 grey squirrel trapping and (c) 0.2 grey squirrel trapping when grey squirrels were included everywhere in order to simulate successful grey squirrel colonisation of Scotland.

Scenario F: Investigation of Whether Pine Marten Can Act as A Natural Control Method

In 2014 Sheehy and Lawton [6] published their findings from an investigation into the decline of the grey squirrel population in the Irish Midlands. The grey squirrel population collapse, which occurred in a 9000 km^2 area, was correlated with a recovery in the pine marten population which has led some commentators [7] to see pine marten as a natural solution to the grey squirrel problem. Whilst the interaction between pine marten and red and grey squirrels are clearly complex [8] a follow up paper from Sheehy et. al. [9] demonstrated that grey squirrel occupancy is also negatively affected by pine marten presence in Scotland. Alongside predation it has been suggested that the presence of pine marten might create a "landscape of fear" [8] which could further reduce grey squirrel occupancy in regions where pine marten are resident. This negative correlation leads to a positive indirect effect on red squirrel occupancy, primarily due to lower competitive pressure, and reduced risk of disease transmission, via grey squirrel absence. Despite this positive correlation pine marten will predate on red squirrels and Halliwell [10] observed that in established pine marten areas in Scotland, red squirrel densities were lower than in equivalent habitats where they were absent. Here we adapt the model to represent the effect of predation by pine marten to assess the viability of pine marten natural grey squirrel control.

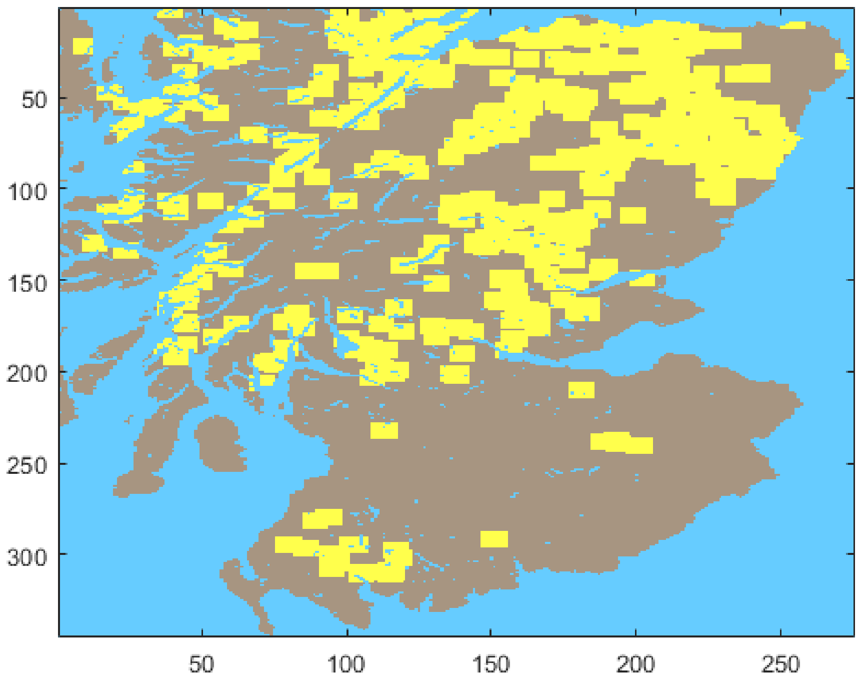

Figure 18: Initial pine marten occupancy. Data from the National Biodiversity Network was used to locate pine marten sightings which were then used as centre points for a 9x9 pine marten region of occupancy.

Exact data on pine marten occupancy and population density is not readily available so observation data from the National Biodiversity Network (NBN) database is used to locate pine marten in the landscape. It is known [11] that female pine marten can range over approximately 10km^2 of territory, with males ranging over approximately 25km^2. Given the lack of information regarding sex as well as limited knowledge of pine marten presence a conservative choice was made and each data point from the NBN database is used as the centre point for a 9x9km square of pine marten occupancy (Figure 18), where each occupied 1km grid square is assumed to have a fixed pine marten density. This choice allows for a higher pine marten density than is currently recorded and also makes allowances for overlapping ranges. A scenario where pine marten have expanded their range to include the entirety of Scotland is included as an appendix. The inclusion of pine marten predation follows the methods outlined in [5]. This considers two densities for pine marten, a low density of 0.08 pine marten per km^2, which is similar to the average density in the Scottish Borders, and a high density of 0.36 per km^2 which is similar to the average density in the region around Loch Lomond. It is assumed that red squirrel predation is 20% of the grey squirrel predation value which is based on red squirrels forming 2.5% and grey squirrels 15% of pine marten diet [6]. Given the lack of information regarding pine marten expansion, dispersion of pine marten is not included in this model.

Figure 19 shows the results when the pine marten density is set to its lower value of 0.08 individuals per km^2. The grey squirrel population (Figure 19.b(i-iii)) is restricted to the north-east of Scotland, to the north of Aberdeen, which means that the northern coast of Scotland remains free from grey squirrels for the entirety of the simulation. When comparing the occupancy result to that for the scenario when there is no trapping applied (Figure 20.a) it can be seen that the inclusion of pine marten means that, as well as the northern coast remaining free of grey squirrels, the Spey river valley also remains as red only regions. Alongside this the western edge of the Dee river valley becomes more viable as a stronghold, the regions of forest around Aberdeen, such as Pitfichie forest, can now act as natural red squirrel strongholds and the amount of Fetteresso forest that can maintain red squirrel occupancy increases. In the west of Scotland the Tay Forest Park, to the west of Pitlochrie, also fares better as a natural stronghold when pine marten are present whilst in the south the forest regions near Newton Stewart fare better at being red squirrel strongholds. Comparison with the result when a lower level of trapping is applied (Figure 20.b) shows that a pine marten density of 0.08 per km^2 is equivalent to the low trapping level in regions where pine marten are present, such as the north-east of Scotland.

Figure 21 shows the results when the pine marten density is set at the higher level of 0.36 pine marten per km^2. In this scenario grey squirrels (Figure 21.b(i-iii)) are restricted in the north of Scotland to the urban areas of the central belt and Aberdeen, although there are still grey squirrel populations in the south of Scotland. Comparing the result to that with a medium trapping level (Figure 22) it can be seen that the higher levels of pine marten density is similar to the higher trapping rate in regions where pine marten are present, with the sole difference being the smaller red squirrel density along the northern coast which is due to pine marten predation.

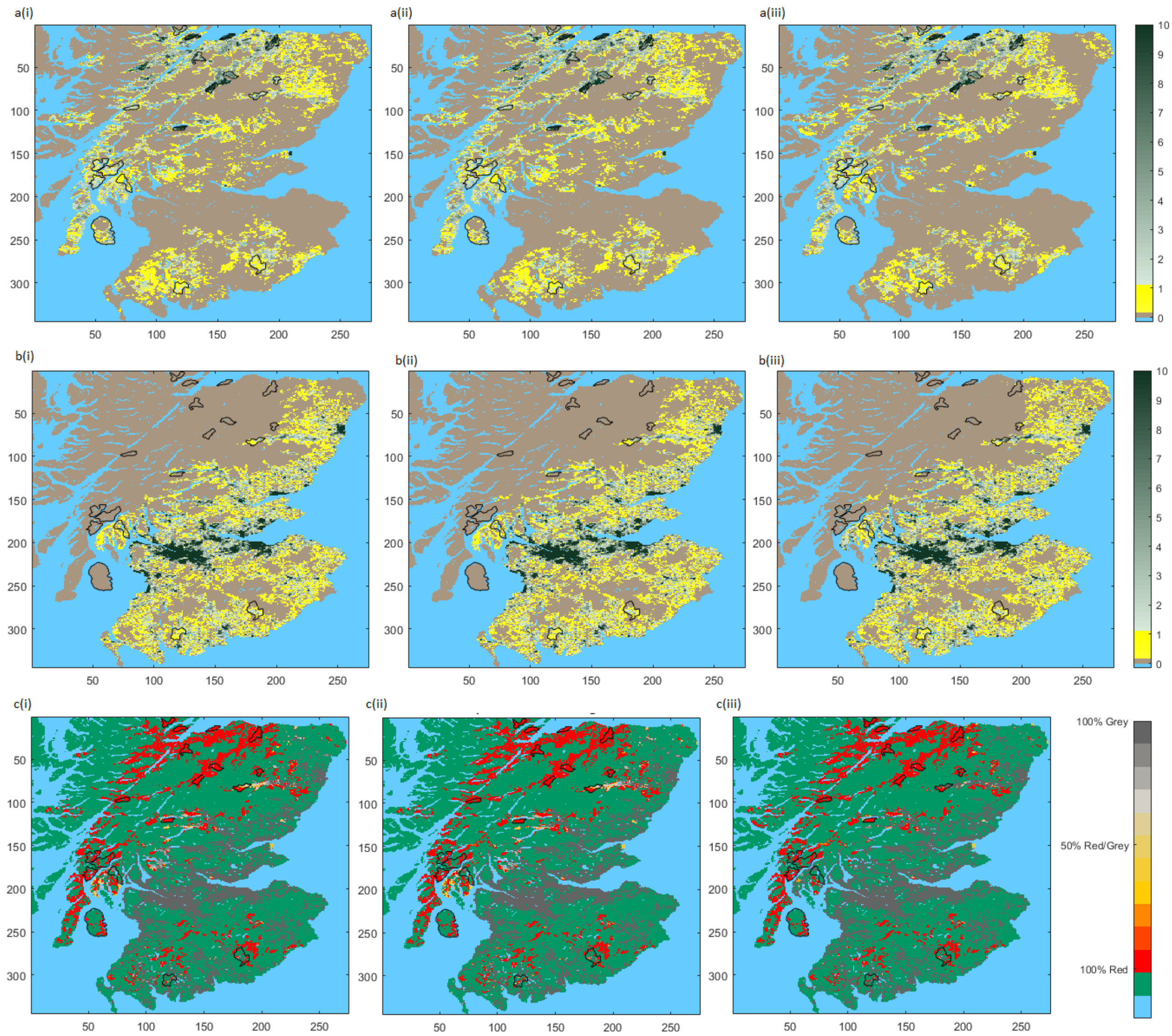

Figure 19: Red and grey squirrel population results when pine marten are included at the lower density of 0.08. Here (a) shows the red squirrel density, (b) grey squirrel density and (c) shows the relative occupancy of each grid square, with a squirrel species classed as occupying the square if 2 or more individuals are present.(i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

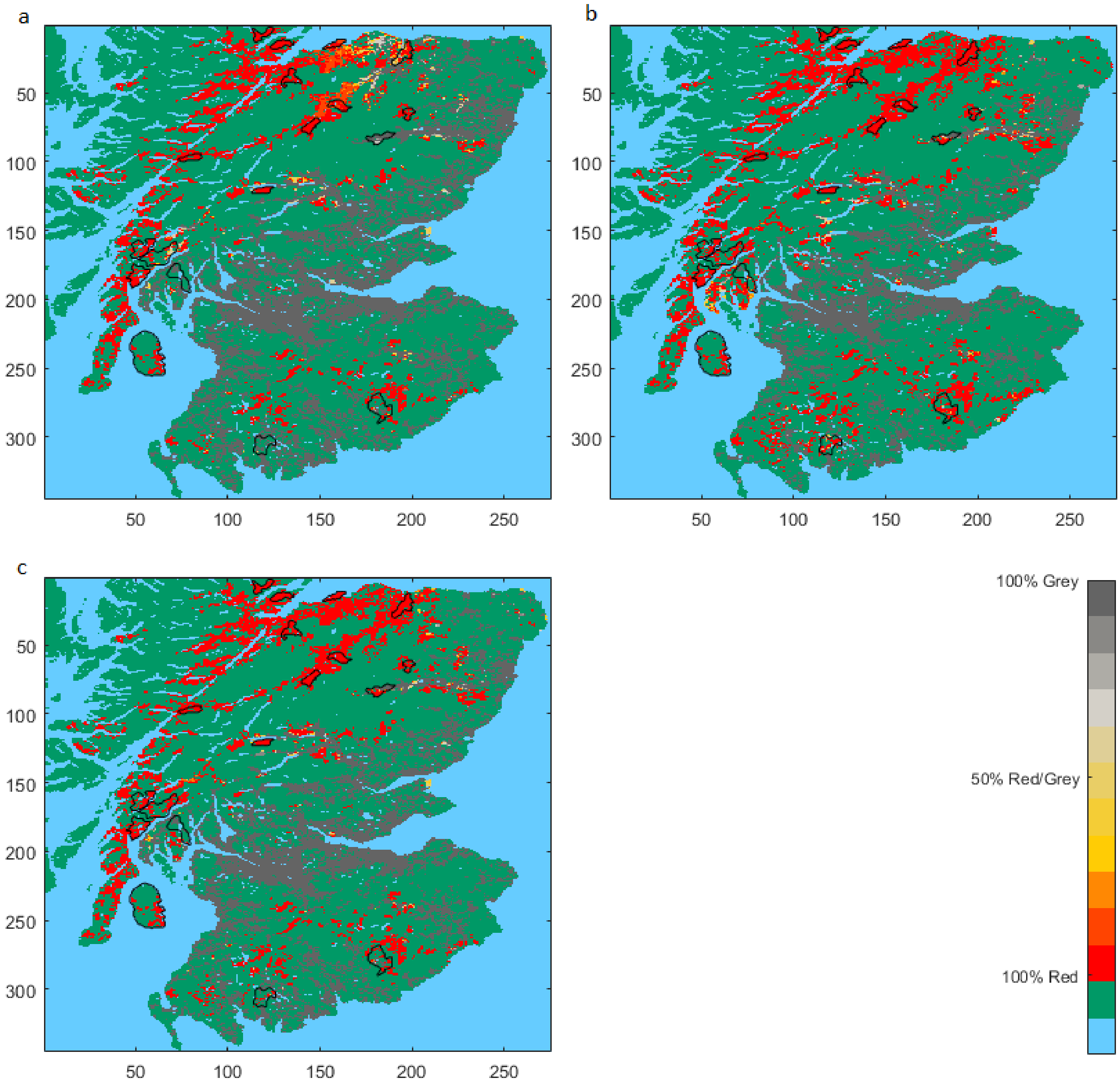

Figure 20: Comparison of 150 year occupancy under (a) zero trapping, (b) 0.1 trapping and (c) 0.08 pine marten density.

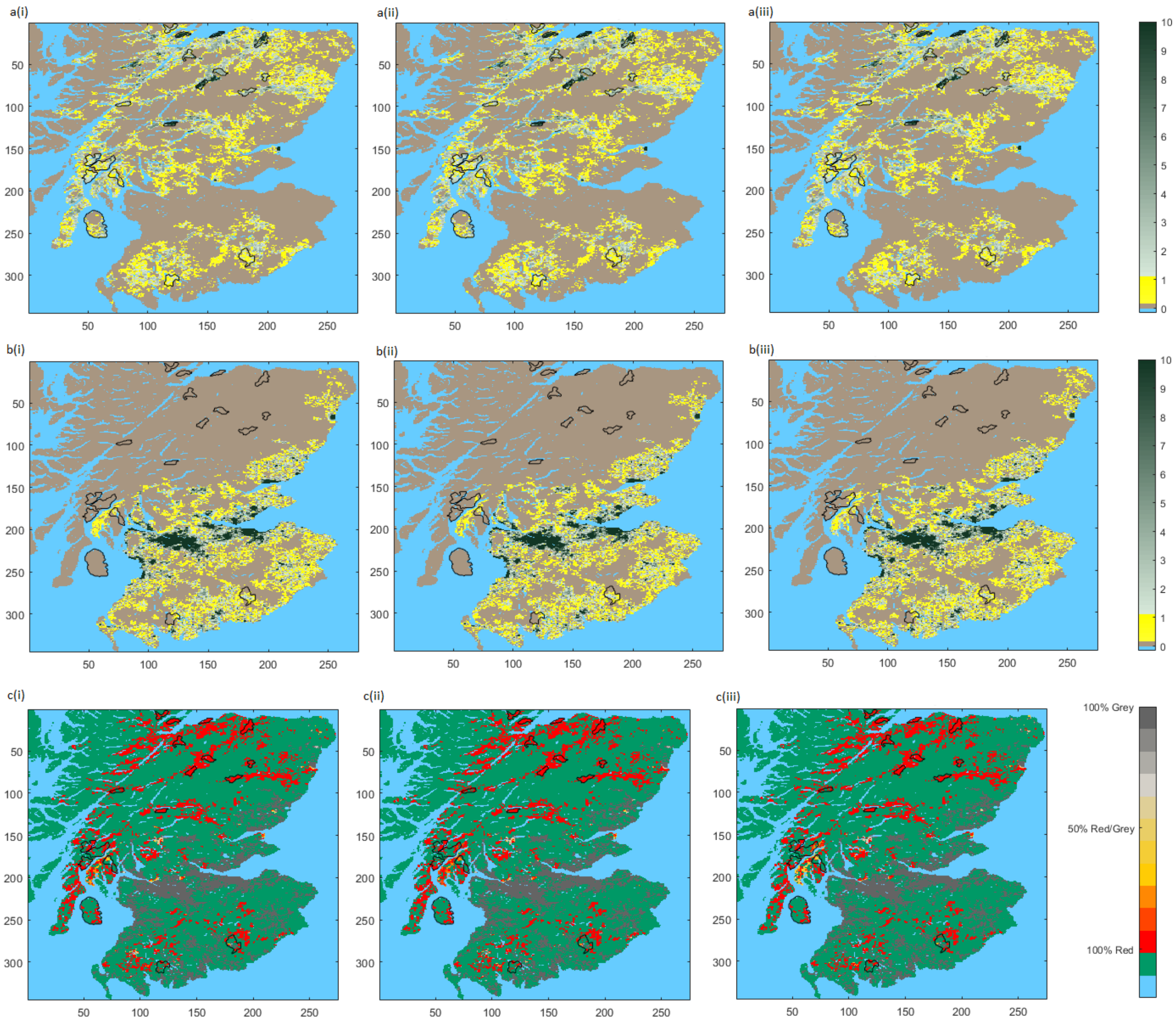

Figure 21: Red and grey squirrel population results when pine marten are included at the higher density of 0.36. Here (a) shows the red squirrel density, (b) grey squirrel density and (c) shows the relative occupancy of each grid square, with a squirrel species classed as occupying the square if 2 or more individuals are present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

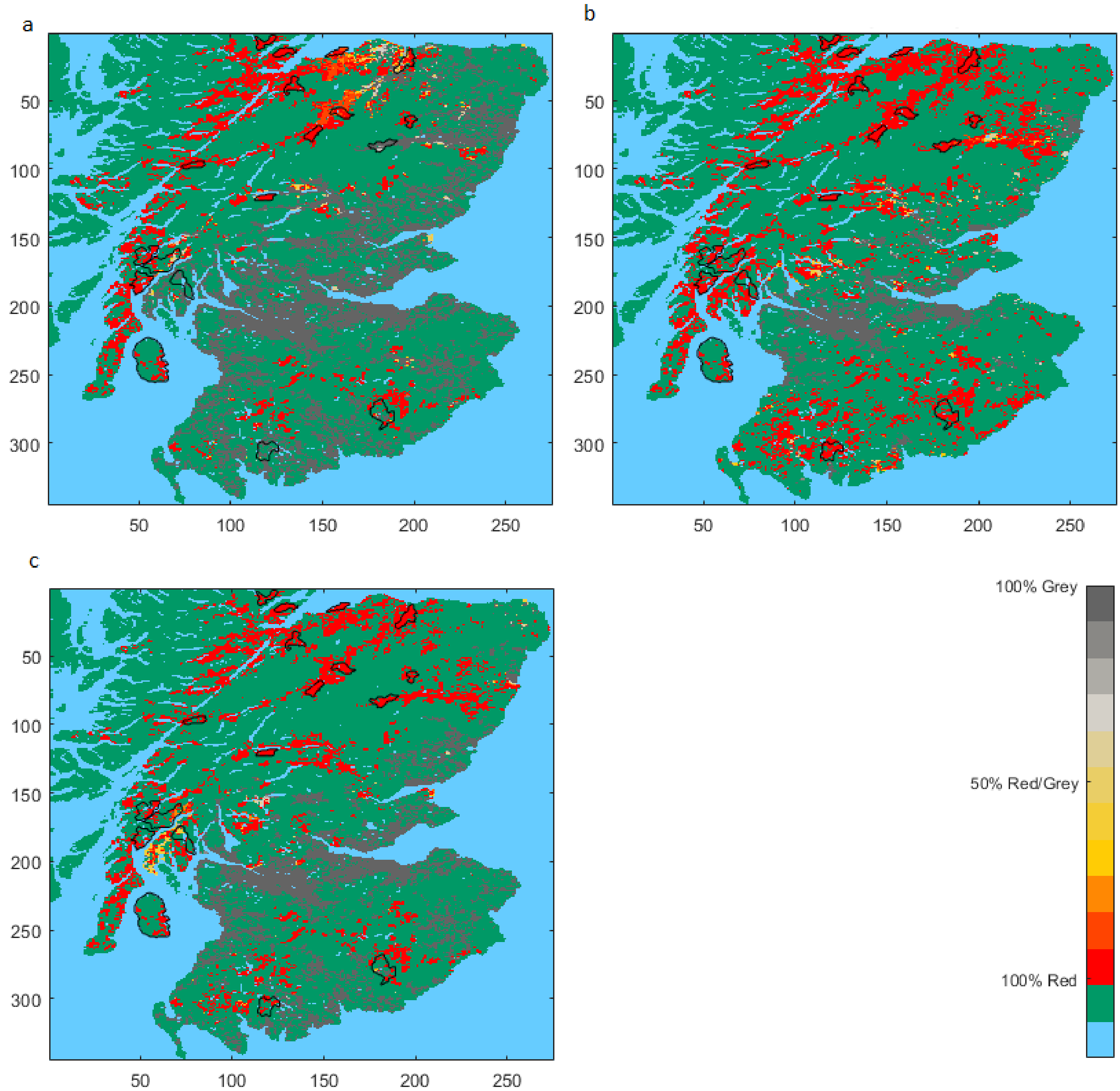

Figure 22: Comparison of 150 year occupancy under (a) zero trapping, (b) 0.2 trapping and (c) 0.36 pine marten density.

4 Conclusions

Our model findings lead to the following key points:

If the current red and grey squirrel distributions are maintained, potentially via the continuation of grey squirrel trapping along the grey squirrel control boundary, then there exist large expanses of forest north of the control line that support viable red squirrel populations.

If grey squirrel control ends and grey squirrels are allowed to expand their range then the process of red replacement will be slow and consequently there would still remain large expanses of forest in north and north west Scotland that will support viable red squirrel populations. Greys are predicted to expand northwards, most notably along the north-east and northern coast, with their expansion directly north curtailed by the Cairngorm mountains. Expansion of grey squirrels into central or western Scotland is also impeded by the geography, with the Grampian mountains forcing grey squirrels to migrate along the west coast which provides poor habitat.

An assumed worst case scenario where grey squirrels can expand to all regions in Scotland was simulated and highlighted regions which could act as natural strongholds for red squirrels. The report highlights a range of forest regions across Scotland that could support red squirrels under standard forest management practice (see Figure 12), however the report does not assess the ability of strongholds to ensure genetic viability.

An analysis of the available land-cover data provided for this assessment indicated that the forest composition of natural strongholds is comprised predominantly of Sitka spruce in southern Scotland and Sitka spruce, Scots and lodgepole pine in northern Scotland combined with an absence of broadleaf and urban habitat.

Grey squirrel control applied in regions that are adjacent to natural strongholds indicated that this would allow the red squirrel distribution to expand and thereby enhance viability. Grey squirrel control could also be effective in connecting natural strongholds. Overall, simulated grey squirrel control at low and medium levels did not uncover new regions that would support red squirrels.

The impact of pine marten that preferentially predate on grey squirrels compared to red squirrels had a similar impact as grey squirrel control in expanding the distribution of red squirrels.

In conclusion, the modelling clearly suggests that for current forest composition and management, there are areas in Scotland which could act as natural strongholds and support (isolated) red squirrel populations (see Figure 12) in the absence of grey squirrel management.

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A Appendices

A: Model Results when Grey Squirrels are Excluded from Aberdeen

The main area of grey squirrel expansion once distribution controls have been removed is in the north-east of Scotland, with the assumption being that grey squirrels migrate from an area of high density in and around Aberdeen, along the north coast until they nearly reach Inverness. Thus grey squirrels have been artificially removed from Aberdeen before grey squirrel expansion is allowed to occur in order to highlight the importance of Aberdeen as a gateway for grey squirrels into north Scotland. Initially, no grey squirrel trapping shall be applied once greys have been removed from Aberdeen. Secondly a low level of trapping is be applied and finally a high level of trapping shall be included only in the region surrounding Aberdeen in order to simulate continued deliberate exclusion of grey squirrels from the region.

Figure A1 shows the results when no grey squirrel trapping is applied. Despite the removal of grey squirrels from Aberdeen recolonisation occurs quickly. However, the grey squirrel density in the region surrounding Aberdeen is lower than is currently the case (see Figure 2). This lower density reduces the ability of the grey squirrels to expand their range into the north-east of Scotland, with grey squirrels only becoming established in the regions to the east of the current stronghold at Ordiequish. Grey squirrels do manage to quickly colonise the Dee river valley, near the Balmoral to Inver stronghold, with red squirrel exclusion occurring towards the end of the simulation. Thus the exclusion of grey squirrels from Aberdeen does not help the stronghold at Balmoral to Inver, nor the Dee river valley, maintain a viable red squirrel population. The exclusion from Aberdeen does prevent grey squirrel expansion across the northern coast of Scotland which suggests that non-continuous grey squirrel exclusion at Aberdeen may significantly delay grey squirrel expansion.

Figure A2 shows the results when a low level of trapping is applied to the entirety of Scotland. This level of trapping is insufficient to prevent grey squirrel expansion into the city of Aberdeen, however it does greatly reduce the rate of colonisation with the grey squirrel density remaining low in the city until the end of the simulation (Figure A2.b(iii)). This prevents grey squirrel expansion into the north-east of Scotland and limits expansion into the Dee river valley, with coexistence in the valley only occurring near the end of the simulation. Thus, the continued exclusion of grey squirrel from Aberdeen, via grey squirrel trapping to the south of Aberdeen (at Fetteresso forest for example), appears crucial in restricting the ability of grey squirrels to expand into the north of Scotland which in turn creates a natural red squirrel stronghold through grey squirrel exclusion.

In the above scenarios we assumed that once grey squirrels had been successfully removed form Aberdeen the trapping efforts were discontinued and grey squirrels allowed to recolonise. In reality, it is more likely that trapping officers would wish to continue their monitoring and trapping regime in order to ensure that their work is not swiftly undone and grey squirrels re-establish themselves. Thus to simulate this the grey squirrel carrying capacity in the region where grey squirrels are initially removed is set to zero (Figure A3), which assumes that the continued trapping is 100% effective, in order to assess the importance of Aberdeen for grey squirrel expansion into the north of Scotland.

Figure A4 shows the results when grey squirrels are permanently excluded from Aberdeen and its surrounding environs. Figures A4.b(i-iii) clearly show that Aberdeen acts as a gateway into the north of Scotland, due to the Cairngorms preventing grey squirrel expansion directly north, which allows the entirety of the north of Scotland to act as a red squirrel stronghold. The continued exclusion of grey squirrels from the region also safeguards the Dee river valley which also benefits from the fact that Glenisla forest, which lies to the south of the Dee river valley, is also a natural red squirrel stronghold which prevents grey squirrel incursion from the south. In the west of Scotland there is no discernible difference when grey squirrels are excluded from Aberdeen compared to when they are not, which suggests that their exclusion does not add extra population density to other areas of Scotland that would increase the rate of grey squirrel expansion.

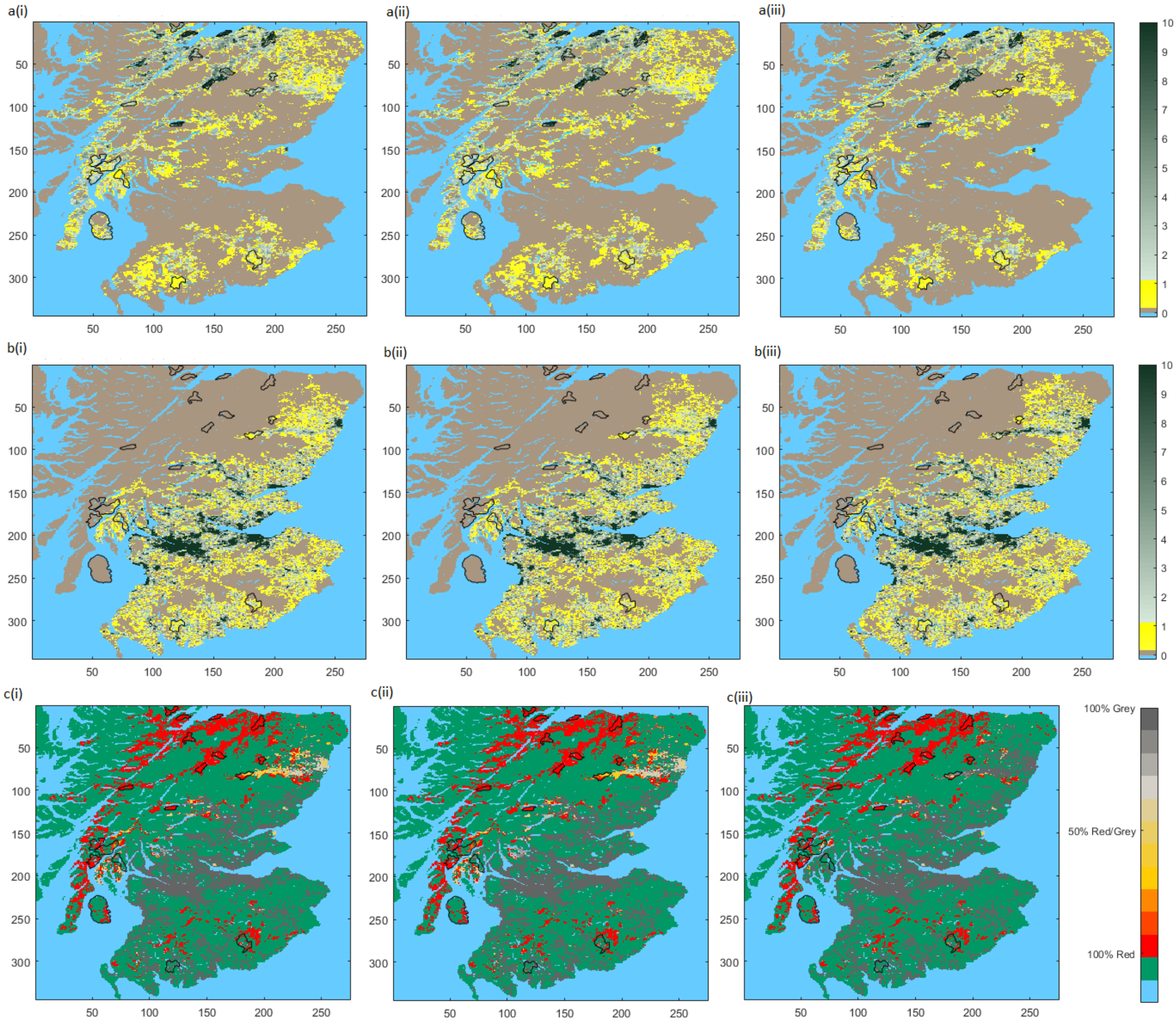

Figure A1: Results for the scenario where grey squirrels have been removed from Aberdeen and red and grey squirrels are allowed to disperse and compete freely, without any grey squirrel trapping. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

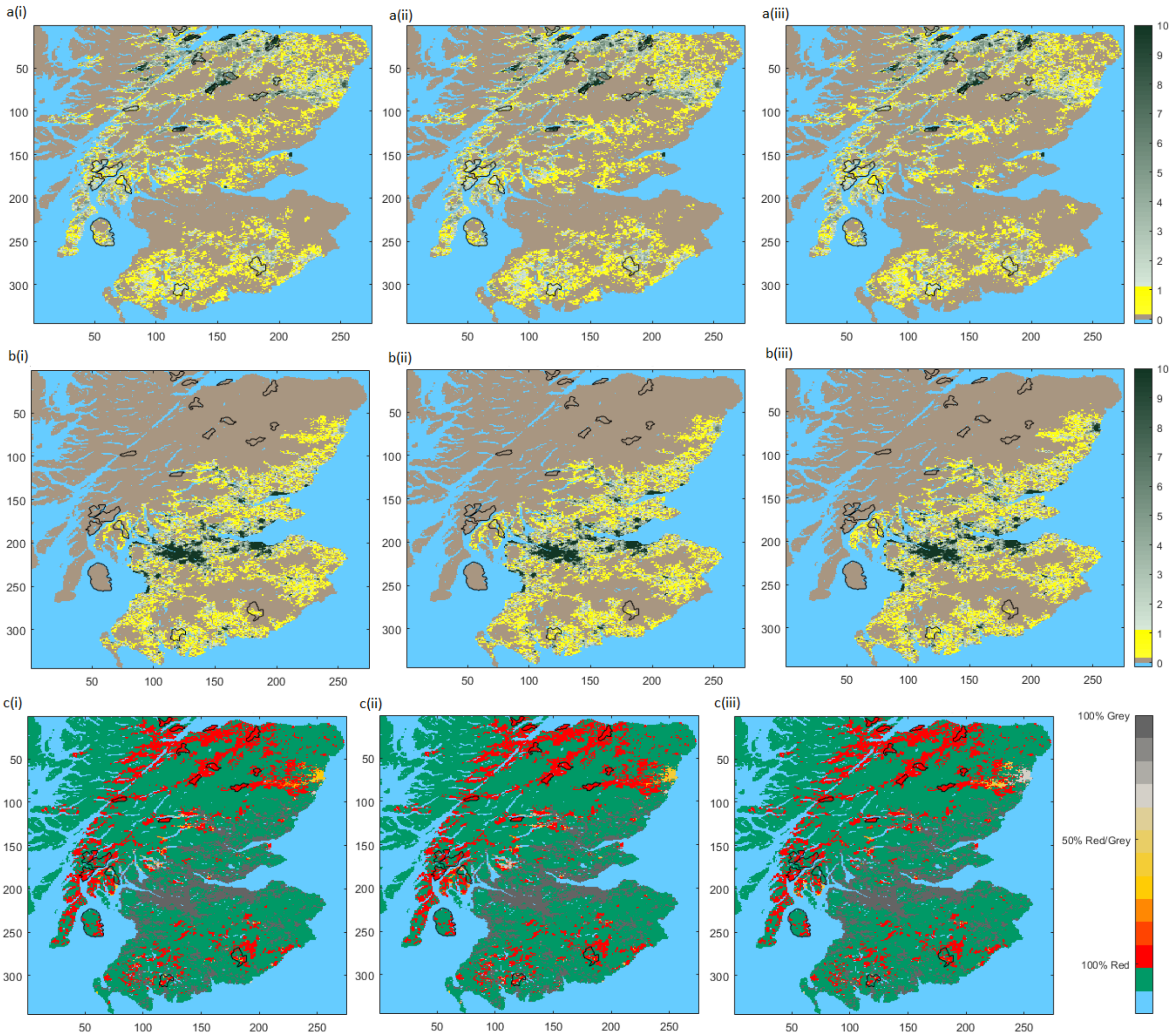

Figure A2: Results for the scenario where grey squirrels have been removed from Aberdeen and red and grey squirrels are allowed to disperse and compete freely, with a trapping level of 0.1 applied. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

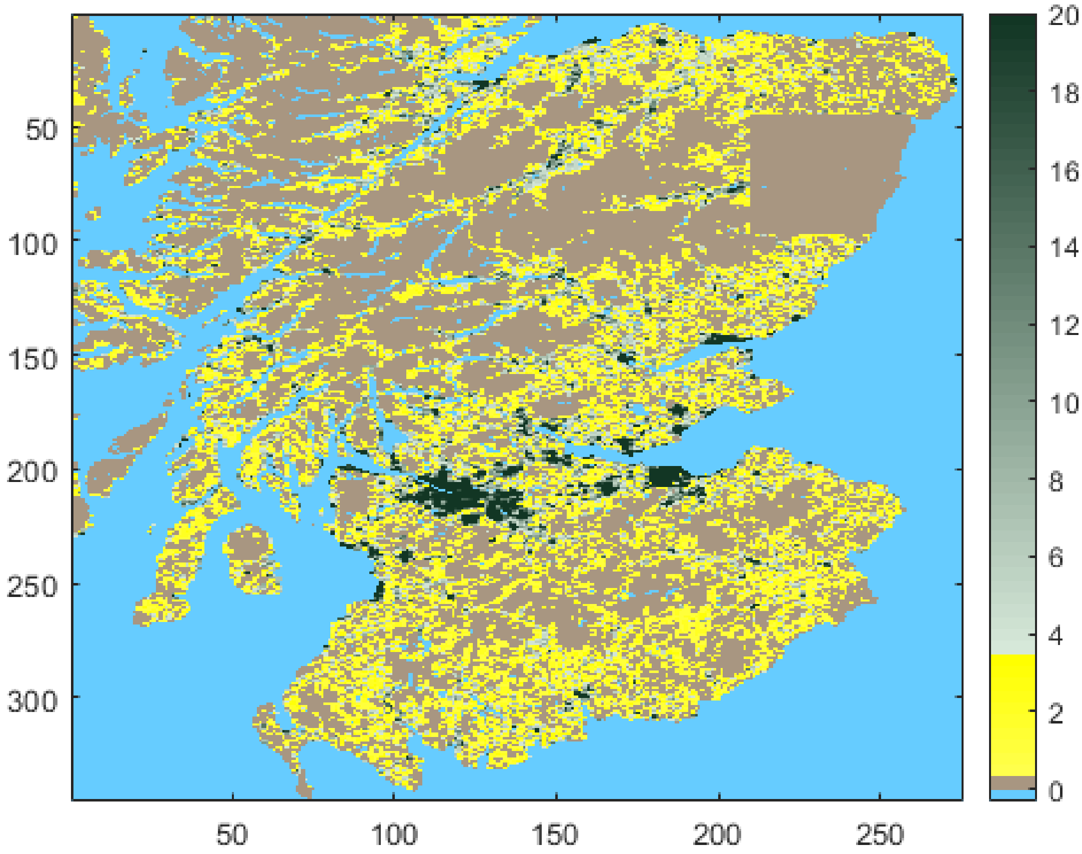

Figure A3: Grey squirrel carrying capacity in Scotland where the capacity in and around Aberdeen has been set to zero in order to simulate continued trapping efforts that eradicate grey squirrels from the region.

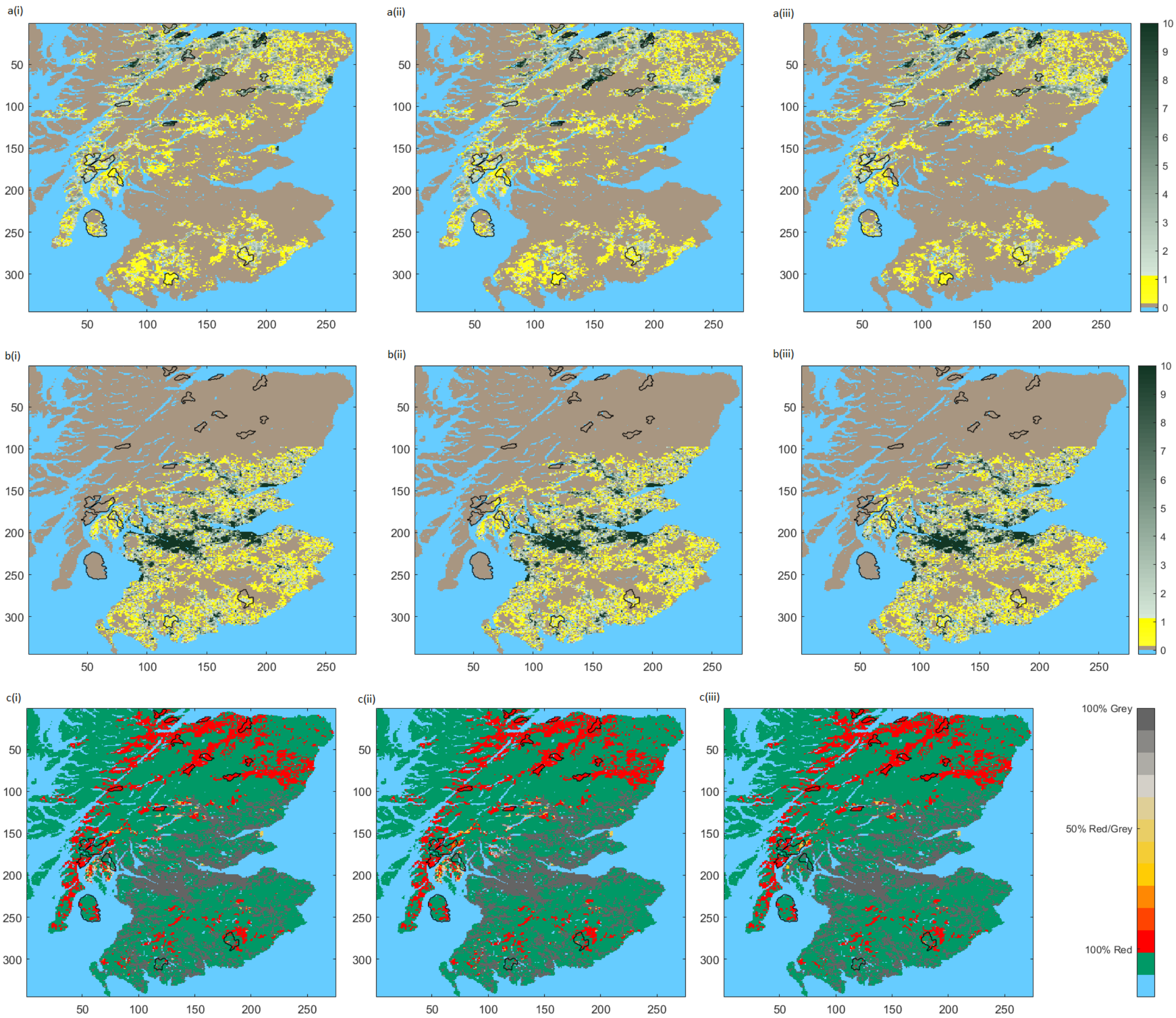

Figure A4: Results for the scenario where grey squirrels have been permanently removed from Aberdeen and red and grey squirrels are allowed to disperse and compete freely. Here (a) shows the red squirrel density, (b) the grey squirrel density and (c) the relative occupancy of each grid-square, which denotes the relative proportion of simulations that had 2 or more red or grey squirrels present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

B: Model Results when Pine Marten are Included Everywhere

It is a realistic expectation (Kortland, pers.comms.) that the increase in pine marten territorial range that has occurred over the last decade will continue and that pine marten presence will have expanded into suitable habitat across the majority of Scotland by the end of the next decade. To understand the potential effect of such pine marten expansion we run a model scenario where pine marten have been artificially introduced into every grid square that has less than 25% urban environment. For the red and grey squirrels we shall use the scenario outlined in section B - that grey squirrel control is removed and grey squirrels allowed to expand freely.

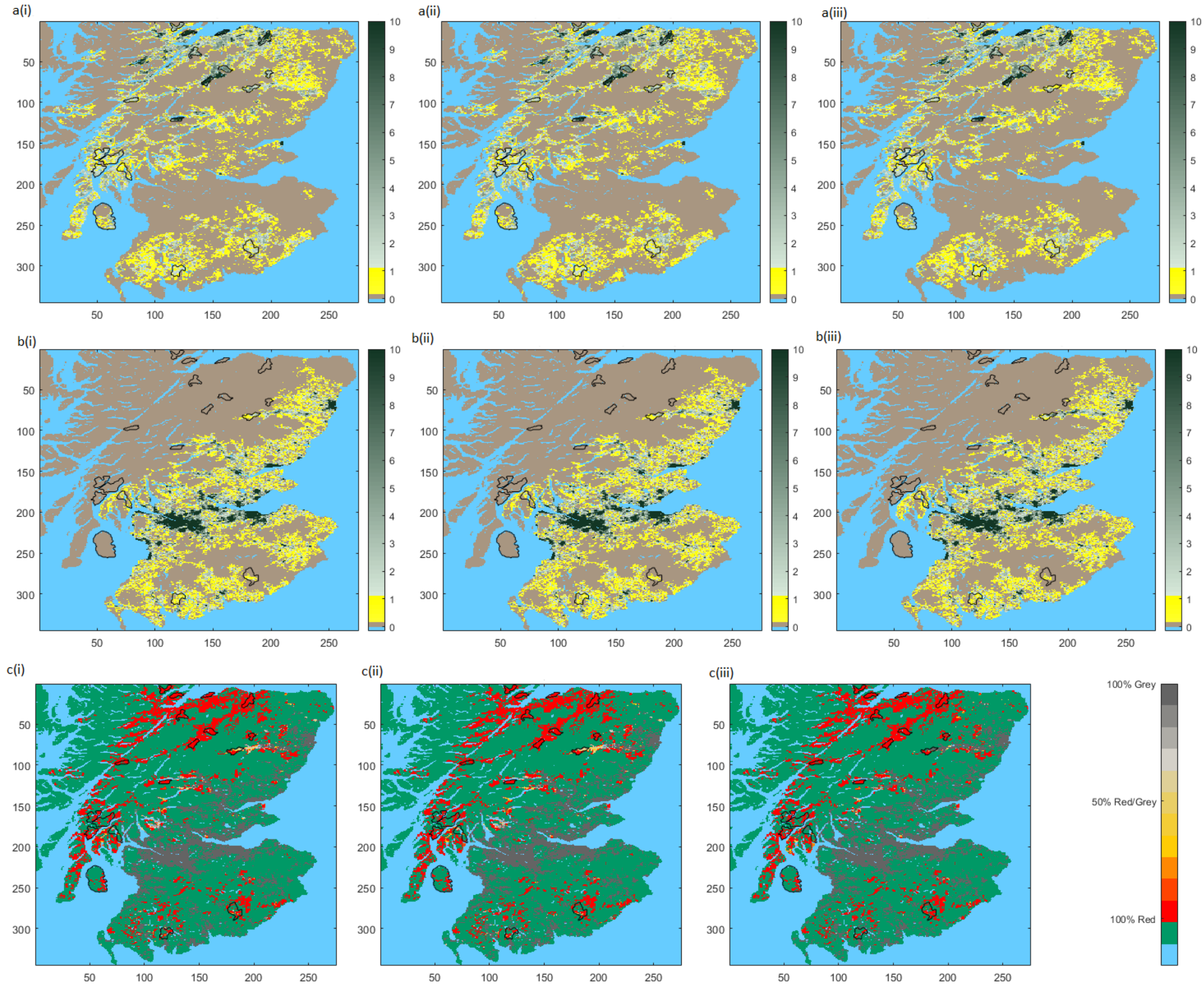

Figure B1: Red and grey squirrel population results when pine marten are included in all grid squares that have less than 25% urban environment at the lower density of 0.36. Here (a) shows the red squirrel density, (b) grey squirrel density and (c) shows the relative occupancy of each grid square, with a squirrel species classed as occupying the square if 2 or more individuals are present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.

Figure B1 shows the results when the pine marten density is set to its lower value of 0.08 individuals per km^2 in every grid square with less than 25% urban environment. The grey squirrel population (Figure B1.b(i-iii)) does not extend beyond the north-east of Scotland, to the north of Aberdeen, which means that the northern coast of Scotland remains free from grey squirrels for the entirety of the simulation. When comparing the occupancy result to that for the scenario when pine marten are included according to observation data (Figure 19.c(i-iii)) it can be seen that the inclusion of pine marten at all locations reinforces the regions of red squirrel occupancy in the south of Scotland and to the north of Aberdeen. Comparison with the result when a lower level of trapping applied (Figure 8.c(i-iii)) shows that a pine marten density of 0.08 per km^2 is equivalent to the lower trapping level.

Figure B2 shows the results when the pine marten density is set at the higher level of 0.36 pine marten per km^2 in every grid square with less than 25% urban environment. In this scenario grey squirrels (Figure B2.b(i-iii)) are restricted to high density urban areas only. Comparing the result to that with a medium trapping level (Figure 9) it can be seen that the higher levels of pine marten density is more effective at removing grey squirrels than the higher trapping rate except that this greater reduction does come at the cost of reduced red squirrel occupancy across Scotland, due to the effect of predation by pine marten on red squirrels. Thus a pine marten density that lies between the two that have been presented here could be a good compromise between increased grey squirrel removal and mitigating red squirrel predation.

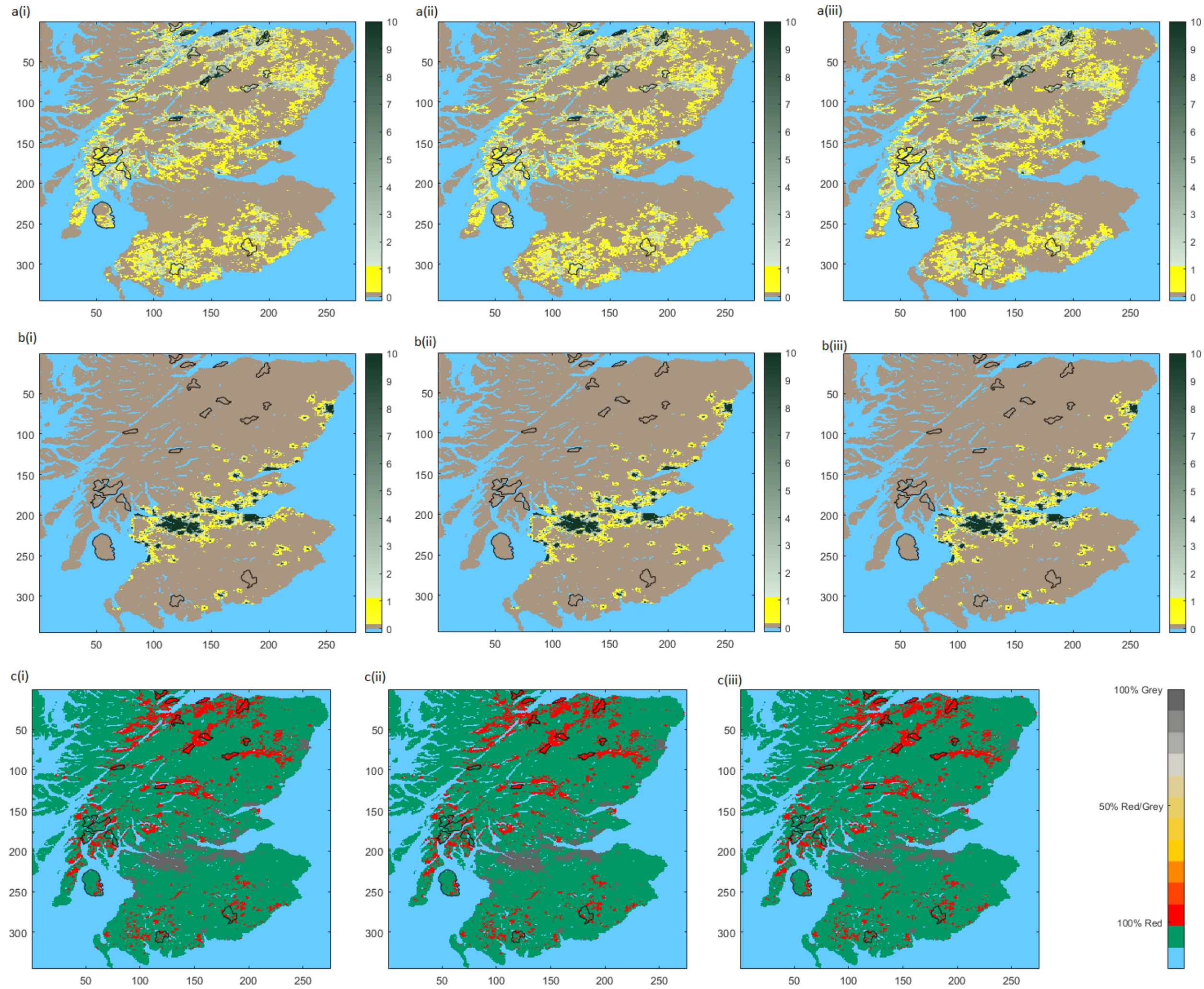

Figure B2: Red and grey squirrel population results when pine marten are included in all grid squares that have less than 25% urban environment at the higher density of 0.36. Here (a) shows the red squirrel density, (b) grey squirrel density and (c) shows the relative occupancy of each grid square, with a squirrel species classed as occupying the square if 2 or more individuals are present. (i) shows the average of years 10 to 40 of the simulation, (ii) the average of years 65 to 95 of the simulation and (iii) the average of years 120 to 150 of the simulation. The regions outlined in black denote the current locations of the 19 red squirrel strongholds.