

The response of plants, carabid beetles and birds to 30 years of native reforestation in the Scottish Highlands

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Abstract

1. Globally, there is increasing interest in tree planting, leading to many country-level commitments to reforestation. In the UK, current commitments would achieve 17% forest cover by 2050, with the highest rates of forest expansion expected in Scotland. Forest expansion with native trees is expected to increase biodiversity, particularly woodland specialist species, and associated ecosystem services. Despite this, data on biodiversity changes over the early stages of reforestation are sparse, particularly for upland areas in Scotland where opportunities for forest expansion are greatest.
2. We collected data on the response of plants, carabid beetles and birds to native reforestation and grazing exclusion, using sites reforested over the last 30 years in the Scottish Highlands. Biodiversity in ungrazed, reforested sites was compared to unforested controls and mature native forest, both grazed and ungrazed.
3. Mean bird species richness in reforested plots (4.4 [95% CI: 3.2, 5.9]) was higher than in unforested plots (0.8 [0.5, 1.3]), but lower than in mature forest plots (7.0 [5.4, 8.3]). In contrast, there was no systematic difference in plant or carabid beetle species richness in reforested, unforested or mature forest plots, or between grazed and ungrazed plots for the species richness of any groups. Woodland specialist bird and plant species were found in the reforested plots, and richness of woodland specialist bird species was predicted to reach levels in mature forest c. 36 years after reforestation.
4. Species assemblages differed across habitat categories. For birds and plants, species assemblages in reforested sites were intermediate to unforested and mature sites. For carabid beetles, the assemblages in mature and reforested sites were comparable and differed from unforested sites. Grazing did not strongly influence species assemblages.
5. *Policy implications.* We show that woodland specialists colonise reforested sites and species assemblages transition towards those found in the target habitat within the first 30 years of reforestation with native species. Native forest should be prioritised in Scotland's future forest expansion targets, given that mature

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native forest is scarce and fragmented in the Scottish Highlands and that the ultimate gain from native forest expansion may accrue over long time-scales.

KEYWORDS

biodiversity, birds, carabid beetles, forest expansion, native reforestation, plants, Scottish Highlands

1 | INTRODUCTION

Between 1990 and 2020, an estimated 420 million hectares (ha) of forest was lost world-wide, and there are global targets to restore 350 million ha of degraded and deforested land by 2050 (Dave et al., 2017; FAO, 2020). The outcome of reforestation depends on an ecosystem's initial level of degradation and environmental constraints (Bullock et al., 2011). In the past, human-driven increases in tree cover were primarily as plantation forests for timber production. Increasingly, however, forest expansion aims to enhance forest-associated biodiversity and the supply of other ecosystem services (Lamb, 2014). Outputs depend on the method of forest establishment; for example, productive plantation forest can enhance aspects of ecosystem functioning but will not restore the biodiversity or community composition of natural forest (Chazdon, 2008).

The UK is one of the least-forested nations in Europe and has an overall target to increase tree cover from 13% to 17% by 2050 (Committee on Climate Change, 2020). Historically, more tree planting has occurred in Scotland than the other UK countries and this trend continues: 80% of planting in the UK in 2019–2020 occurred in Scotland (Forest Research, 2020). Less than a quarter of Scotland's forest is native (>50% of the canopy composed of native species), of which 62% is semi-natural in structure and composition (Patterson et al., 2014). To meet their forest expansion target of increasing forest cover from 18% to 21%, the Scottish Government plans to increase forest cover by 10,000–15,000 ha per year, of which 3,000–5,000 ha will be native (Scottish Government, 2019). The Scottish uplands present the greatest opportunities for forest expansion with fewer conflicts with other land uses (Sing et al., 2013).

Native forest covered >60% of Scotland until c. 5,000 years ago (Oosthoek, 2013). Climate change, increased grazing pressure and human-driven deforestation all contributed to the fall in forest cover to 25% c. 2,000 years ago (Oosthoek, 2013; Richard Tipping, 1994). Forest loss continued, and today much of the Scottish uplands is maintained in a treeless state by burning and grazing; although sheep grazing has declined in some areas, high deer numbers continue to prevent natural forest regeneration (Armstrong et al., 2014). Reforestation, rewilding and reducing grazing intensity are proposed to increase native forest cover and improve the health of other habitats across the Scottish uplands, which would enhance ecosystem service supply and biodiversity (Armstrong, 2015; Haines-Young & Potschin, 2009; Scottish Environment LINK, 2020). The Caledonian pinewood is a priority for restoration in Scotland; it occupies 1% of its former range in the Scottish Highlands and is a UK Biodiversity Action Plan (BAP) priority habitat, supporting nationally rare and

specialist species (Mason et al., 2004; NatureScot, 2008; Trees for Life, 2020).

With increasing interest in rewilding and reforestation as solutions to the ecological and climate crises, we must understand how biodiversity will respond to these interventions (Sandom et al., 2018). Management decisions in upland areas, such as the Scottish Highlands, will consider multiple priorities, for example, balancing biodiversity conservation with targets to maximise specific ecosystem services (Burton et al., 2019). A recent review (Burton et al., 2018) highlighted the lack of field-based evidence from native woodland on biodiversity responses to reforestation in the UK. Most studies focus on conifer plantations and those that consider native reforestation are largely from lowland landscapes dominated by agriculture (e.g. Watts et al., 2016), limiting our understanding of how biodiversity will respond to replacement of semi-natural vegetation in the uplands. The expectation that native forest expansion will enhance biodiversity in these locations requires an objective assessment of biodiversity relative to the prior land use; most current studies are limited to case studies, or address a single aspect of the ecological community (Armstrong et al., 2014; Bunce et al., 2014; Douglas et al., 2020; Hester et al., 1991).

In this study, we used a series of sites in the Scottish Highlands that have been fenced and reforested over the last 30 years to assess the effect of grazing removal and reforestation on plant, carabid beetle and bird assemblages, making comparisons to unforested and mature forest areas, which are both grazed and ungrazed. The three focal taxa represent phylogenetically and functionally diverse components of the ecosystem and are widely used in biodiversity assessments of forest habitat (Coll & Bolger, 2007; Graham et al., 2017; Wallace et al., 1992). For all three species groups we aimed to (a) assess the effect of forest (unforested, reforested, mature) and grazing (grazed, ungrazed) treatments on species richness and the presence of woodland specialists; (b) compare species assemblages in the ungrazed, reforested treatment with the grazed/ungrazed unforested and mature forest treatments and (c) assess trajectories of community recovery by investigating the effect of forest age on species richness and richness of specialist species across reforested sites.

2 | MATERIALS AND METHODS

2.1 | Study area

The reforested sites are located in adjacent glens in the central Scottish Highlands: Glen Affric (57°12'50"N, 05°13'48"W to

57°17'15"N, 004°56'04"W) and Glen Moriston (57°12'28"N, 004°50'54"W to 57°13'23"N, 004°43'32"W; Figure S1). These landscapes contain a mosaic of habitat types, including mature Caledonian pinewood, productive conifer plantations, unforested heathland and regenerating native forest. We focused on 14 reforested sites that were established between 1990 and 2012 by Trees for Life, Forestry and Land Scotland, and the National Trust for Scotland, creating a chronosequence. Sites range from 15 to 446 ha in area (Table S1). They were fenced to exclude deer *Cervus elaphus*, *Capreolus capreolus*, *Cervus nipon* and feral boar *Sus scrofa*, sheep are also present at very low numbers in parts of the landscape. Wild deer represent the main grazing pressure, numbers at our study sites are c. 6 per km² in Glen Moriston and c. 8 per km² in Glen Affric, although this varies across the landscape. We refer to fenced areas as 'ungrazed', although as permeability to deer increases as the fences age, grazing is reduced rather than totally excluded at most sites. Sites were replanted with native Caledonian pinewood species, cultivated from local provenance seed (Table S1). Planting was generally targeted to well-drained areas, with some wet areas planted with *Alnus glutinosa* and *Salix* spp. The success of tree establishment varied depending on drainage and topography, consequently tree cover is heterogeneous.

2.2 | Study design

The sampling design is hierarchical, units are defined as follows. Sites are the 14 focal reforested sites. In our study, the treatments forest status (unforested, reforested, mature) and grazing status (grazed, ungrazed) are represented in all possible combinations, excluding reforested × grazed, which does not exist due to deer grazing pressure in the landscape. Plots (10 m × 10 m for plants and carabids, 50-m radius for birds) were established in each treatment combination. To maintain a minimum 150 m between the centres of bird plots, the plots were in some cases located in different places within a site to the plant and carabid beetle plots. A reforested, ungrazed plot, an unforested, grazed plot and an unforested, ungrazed plot were established at each site (Table 1; Figure S2). Given the heterogeneous reforestation success at each
















site, the reforested plot was positioned to represent an example of best-case forest establishment in the site (reforested, ungrazed). Each reforested, ungrazed plot was matched (on topography, aspect and elevation) to a plot in the nearest unforested, grazed area and a plot in the nearest unforested, ungrazed area. The unforested, grazed areas reflect the prior land use of the reforested areas and the unforested, ungrazed areas allow the effect of grazing exclusion without tree establishment to be assessed. Unforested areas are thought to be the result of a decline in forest cover from c. 3,800 years ago, driven by climatic and human influences (Tipping et al., 2006). Only three reforested sites had associated mature Caledonian pinewood. Therefore, at two sites, two pairs of grazed and ungrazed mature forest plots were established with at least 500 m between them, in non-contiguous areas of mature forest, to give a total of five grazed and ungrazed mature forest plots (Table 1; Figure S1). These areas reflect the target habitat and are part of one of Scotland's largest Caledonian pinewood remnants, containing trees up to 260 years old (Mason et al., 2004). The plant and carabid beetle plots were 30–400 m and the bird plots 150–450 m apart. Bird surveys were conducted at a subset of 10 of the 14 reforested sites, due to logistical constraints in 2019 (Table 1).

2.3 | Plant surveys

Plants were surveyed from 22 June to 5 July 2018. Three 1 m × 1 m quadrats were placed randomly in each plot. All vascular plants were identified to species level; non-vascular species were identified to genus or morphospecies level, apart from *Huperzia selago*, *Hylocomium splendens*, *Pleurozium schreberi* and *Pleurozia purpurea*. Percentage cover of each species, genus or morphospecies was recorded using the DOMIN scale (Rodwell, 2006). A survey of the 10 m × 10 m plot was carried out to identify any species absent from the three quadrats.

Specialist plant species were defined based on two categorisations: (a) woodland specialists: using the Ancient Woodland Indicator list of species (Kirby, 2020) and (b) Trees for Life priority species: species characteristic of the Caledonian pinewood and noted as desirable by Trees for Life staff (Table S2).

TABLE 1 Sample sizes for plant, carabid beetle and bird surveys

	Unforested	Reforested	Mature
Ungrazed	 14	 14	 5
	 14	 14	 5
	 10	 10	 5
Grazed	 14		 5
	 14		 5
	 10		 5

2.4 | Carabid beetle surveys

Carabid beetles were surveyed using pitfall traps from 7 June to 18 August 2018. Six traps were set per plot, with two traps associated with the location of each plant survey quadrat. 200 mL plastic cups were buried flush with the ground surface, one-third filled with 1:3 propylene glycol:water. A rain-cover was positioned over the top, leaving a 2-cm gap above the ground. The traps were emptied at 2-week intervals for the first 4 weeks and a final time after a 4-week interval. Beetles were stored in propylene glycol until identification to species level using (Luff, 2007). Voucher specimens have been deposited in the Oxford University Museum of Natural History (ENT-OUMNH-2021-001). Carabid woodland specialists were defined based on habitat associations given in Luff (2007) (Table S3).

2.5 | Bird surveys

Bird survey plots were visited twice, between 23 May and 1 June 2019 and again between 5 and 14 June 2019. All surveys were conducted between 06.00 and 11.30 hr. If the first survey was conducted during the earlier part of this period, the second was conducted later, and vice versa. After a 2-min settling period, birds were surveyed for 15 min. Birds were identified visually or by songs and calls. Each plot was surveyed by two people simultaneously, covering 50% of the plot each. Immediately after each survey, the surveyors compared the location and time of each record and collated a final list of observations to avoid double counting. Woodland specialist birds were defined as the Specialist Woodland Species in the UK Wild Bird Indicator (Eaton & Noble, 2020) (Table S4).

2.6 | Data analysis

All statistical analysis was carried out using R (R Core Team, 2019). Our analysis uses a fractional factorial combination of the two factors forest (unforested, reforested, mature) and grazing (grazed, ungrazed), where the grazed \times reforested combination is absent (Table 1).

Mixed-effect models were fitted using the package *lme4* (Bates et al., 2015), testing the effect of forest \times grazing on plant, carabid beetle and bird species richness, and plant woodland specialist, Trees for Life plant indicator and bird woodland specialist species richness. For plants, species richness is the number of vascular and non-vascular plant species (or number of specialist species) recorded per plot. For carabid beetles, species richness is the total number of species trapped per plot over the whole survey period. For birds, species richness is the number of species (or number of specialist species) observed in each plot across the two survey periods. In all cases, the forest \times grazing status interaction was not significant and was removed from the model, leaving the two main effects forest

and grazing. In all models, AIC decreased with removal of the interaction. All models contained a random effect for site. Models were assessed by plotting model residuals and qq-plots. Estimates and standard errors were extracted from the fitted models and used to determine differences between the levels of each treatment. The effect of time since reforestation on plant, carabid beetle and bird species richness or specialist richness was tested using linear models, with data from reforested plots only. In both bird species richness models, a square root-transformed response was used to improve normality of the model residuals and back-transformed responses are displayed.

Species assemblages for plants, carabid beetles and birds were assessed using non-metric multidimensional scaling (NMDS), with the package *VEGAN* (Oksanen et al., 2018). Bray–Curtis was used as the dissimilarity metric. For plants and carabid beetles, a Wisconsin double standardisation and square root transformation of percentage cover and abundance data was performed. For birds, a Wisconsin double standardisation of the abundance data was performed. Analysis of similarities (ANOSIM) was used to test for significant differences between the treatment levels, using the function *anosim* in the package *VEGAN* (Oksanen et al., 2018). The ANOSIM statistic, *R*, assesses whether compositional dissimilarities between groups are greater than within groups. *R* ranges from -1 to $+1$, with 0 indicating completely random grouping (Oksanen et al., 2018). 95% confidence intervals of the centroid for each forest category were plotted. If confidence intervals do not overlap, then groups are approximately different at the 95% level.

Mean species accumulation curves (SAC) were calculated for the three groups using the function *specaccum* in the package *VEGAN*. The mean SAC and 95% confidence intervals were found based on 1,000 random permutations of the data (Oksanen et al., 2018).

Where estimates and 95% confidence intervals are given for levels of the forest or grazing treatment, these were derived from models fitted with the forest or grazing term only.

3 | RESULTS

3.1 | Plants

Plant species richness did not differ between reforested and unforested plots (effect unforested 0.7 [95% CI -1.6 , 3.1]), or reforested and mature plots (effect mature 0.6 [95% CI -2.4 , 3.6]). There was no clear difference between the categories grazed and ungrazed (effect ungrazed -0.3 [95% CI -2.3 , 1.8]) (Figure 1a). Richness of woodland specialist plants was no different between mature (2.4 [95% CI 1.5, 3.3]) and reforested (2.1 [95% CI 1.4, 2.8]) plots, but was lower in unforested plots (0.8 [95% CI 0.2, 1.4]); there was no effect of grazing on woodland specialists (-0.05 [95% CI -0.8 , 0.7]) (Figure 1b). Richness of Trees for Life priority species was higher in the mature plots (5.5 [95% CI 4.8, 6.2]) than reforested (4.0 [95% CI 3.4, 4.5]) and unforested (3.6 [95% CI 3.2, 4.0]) plots, with no effect of grazing (0.1 [95% CI -0.5 , 0.7]; Figure 1c).

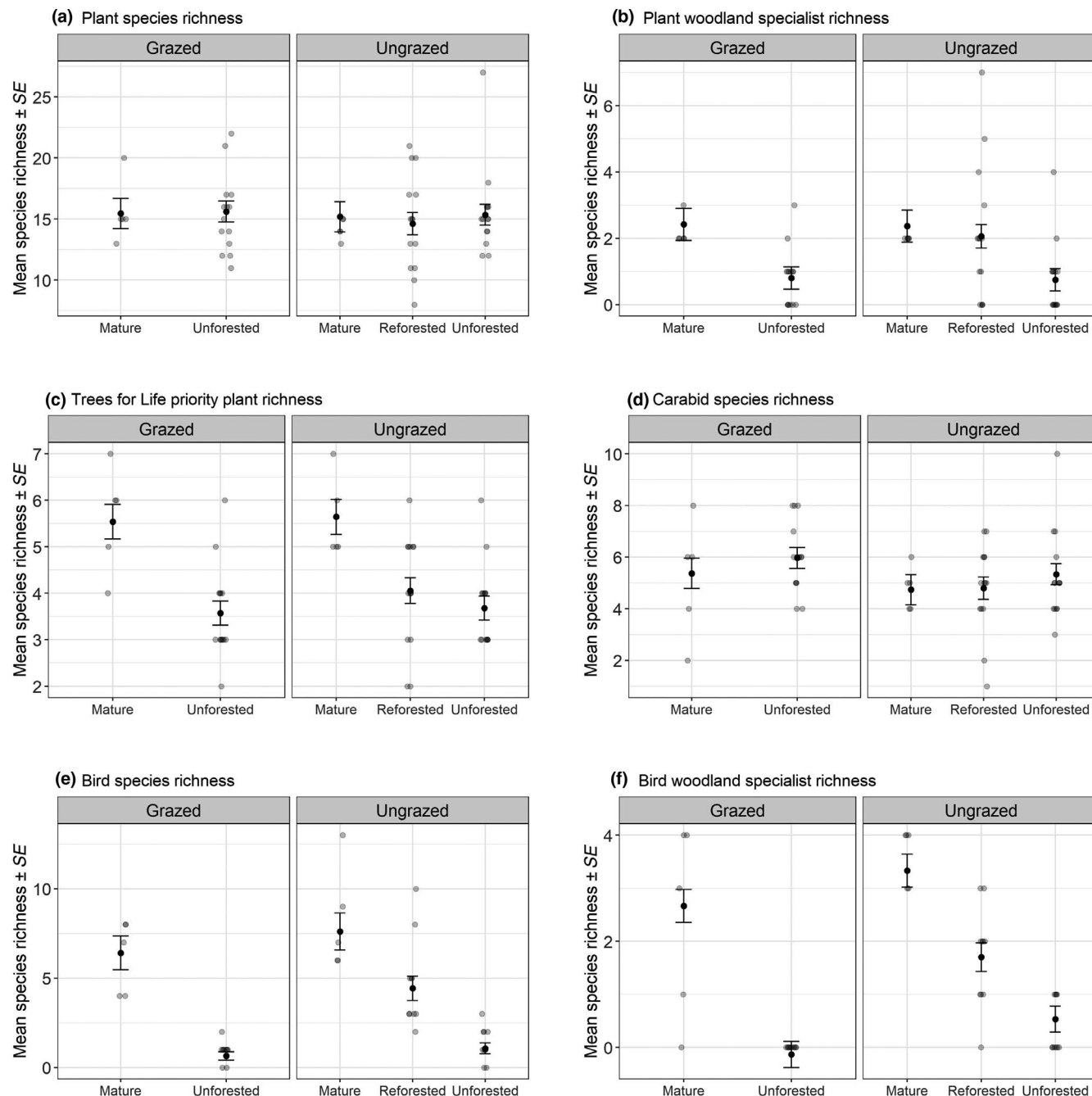


FIGURE 1 Comparisons of species richness among forest \times grazing categories for plants, plant woodland specialists and Trees for Life priority plants (a, b, c), carabid beetles (d), and birds and bird woodland specialists (e, f). All estimates and standard errors were extracted from the models

There was greater dissimilarity in species assemblages among levels of the forest treatment than within levels (ANOSIM: $R = 0.53$, $p < 0.001$) whereas the grazing treatment did not structure plant species assemblages (ANOSIM: $R = -0.034$, $p = 0.74$). Unforested, reforested and mature plots formed distinct clusters based on species assemblage, with reforested plots intermediate to unforested and mature forest (Figure 2a).

Eighteen species were unique to the unforested treatment, 17 to the reforested treatment and 3 to mature forest (Figure S3;

Table S2). Unforested, reforested and mature forest plots had a high degree of overlap in the species present (Figure S3). Species richness accumulated most rapidly across plots in the reforested treatment and slowest in the mature forest treatment (Figure S4).

Time since reforestation had no clear effect on overall plant richness (effect age 0.08 [95% CI -0.3 , 0.4]; Figure S5), woodland specialist richness (effect age 0.02 [95% CI -0.2 , 0.2]; Figure S6a) or richness of Trees for Life's desired species (effect age -0.01 [95% CI -0.1 , 0.09]; Figure S6b).

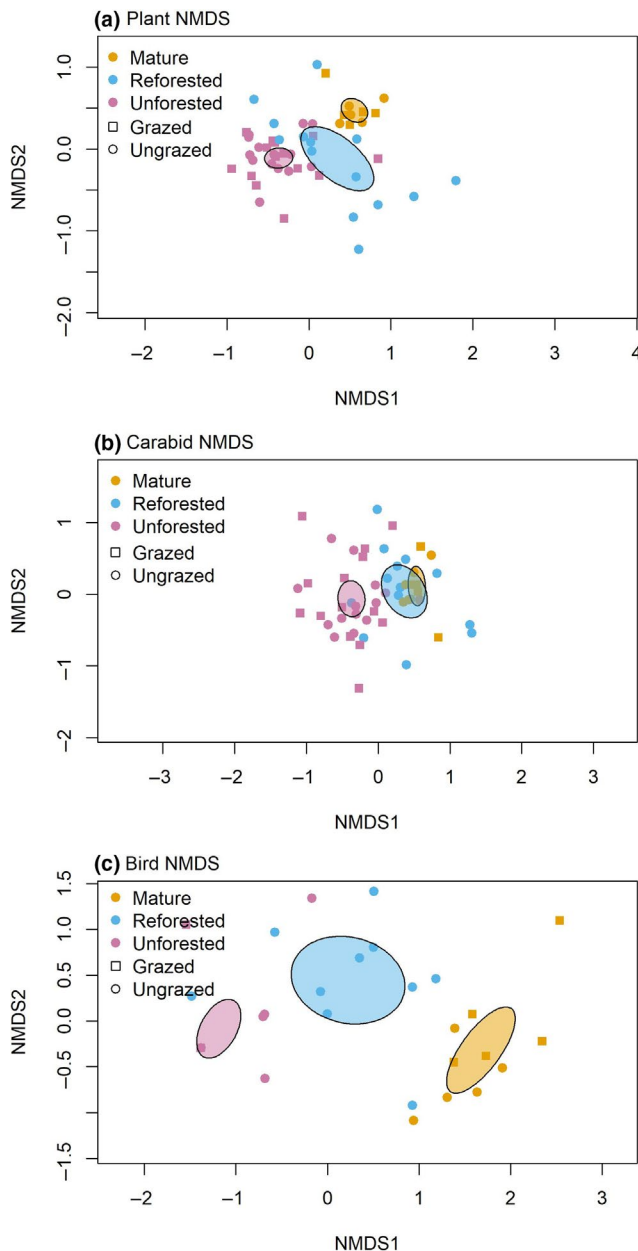


FIGURE 2 Species assemblage comparisons for (a) plants, (b) carabids and (c) birds, based on NMDS with the 95% confidence interval of the centroid plotted for each forest category

3.2 | Carabid beetles

There was no detectable difference in carabid species richness between the reforested and mature plots (effect mature -0.06 [95% CI $-1.5, 1.4$]), reforested and unforested plots (effect unforested 0.5 [95% CI $-0.6, 1.7$]), and grazed and ungrazed plots (effect ungrazed 0.6 [95% CI $-1.7, 0.4$]; Figure 1d). Only one woodland specialist carabid was found (*Pterostichus oblongopunctatus*), which was restricted to mature forest (Figure S7).

Species assemblages differed between levels of the forest treatment (ANOSIM: $R = 0.22$, $p < 0.001$), but not between levels of the grazing treatment ($R = 0.079$, $p = 0.063$). The species assemblages

of unforested plots formed a distinct grouping from the overlapping assemblages of mature and reforested plots (Figure 2b).

The unforested plots supported seven unique carabid species and the reforested and mature forest plots supported two unique species respectively (Figure S8; Table S3). Species accumulation increased fastest with sampling effort for the reforested treatment and slowest for the mature forest treatment; pooling plots irrespective of forest treatment achieved the fastest rate of species discovery (Figure S9).

Time since reforestation had no clear effect on species richness for carabid beetles (effect age -0.08 [95% CI $-0.2, 0.06$]; Figure S10).

3.3 | Birds

Bird species richness in the reforested plots (4.4 [95% CI $3.2, 5.9$]) was higher than in the unforested plots (0.8 [95% CI $0.5, 1.3$]) but lower than in the mature forest plots (7.0 [95% CI $5.4, 8.3$]). There was no clear difference in bird species richness between the grazed and ungrazed plots (effect ungrazed 0.2 [95% CI $-0.15, 0.6$]; Figure 1e). Richness of woodland specialists was higher in the mature plots (3.0 [95% CI $2.4, 3.6$]) than reforested plots (1.7 [95% CI $1.1, 2.3$]), which had a higher richness than the unforested plots (0.2 [95% CI $-0.2, 0.6$]; Figure 1f). Woodland specialist richness was also higher in ungrazed plots than grazed plots (effect ungrazed 0.7 [95% CI $0.05, 1.3$]).

Forest type influenced bird species assemblage (ANOSIM: $R = 0.76$, $p = 1e-4$), assemblages in the reforested plots were intermediate to those in the mature and unforested plots (Figure 2c). The grazing treatment had no clear effect on bird species assemblages (ANOSIM: $R = 0.079$, $p = 0.074$).

No bird species were unique to the unforested plots, whereas five species were unique to mature plots and two species to reforested plots (Figure S11; Table S4). Only five of the 21 bird species were recorded across the unforested plots, where Meadow Pipit *Anthus pratensis* was the most frequent species (Figure S12). Species richness accumulated most rapidly across plots in the mature and reforested treatments, but quickly began to plateau in the unforested treatment (Figure S13).

In the reforested plots, bird species richness (sqrt-transformed effect Age 0.05 [95% CI $0.009, 0.08$]; Figure 3a) and bird specialist richness (effect Age 0.08 [95% CI $0.02, 0.14$]; Figure 3b) increased with time since reforestation. Extrapolating the rate of species accumulation, equivalent specialist richness to mature forest plots would be expected approximately 36 years after reforestation.

4 | DISCUSSION

Our results show that reforestation can generate a species composition that is closer to mature forest than unforested habitat and supports some woodland specialist plants and birds. Bird species richness was higher in reforested areas relative to the unforested

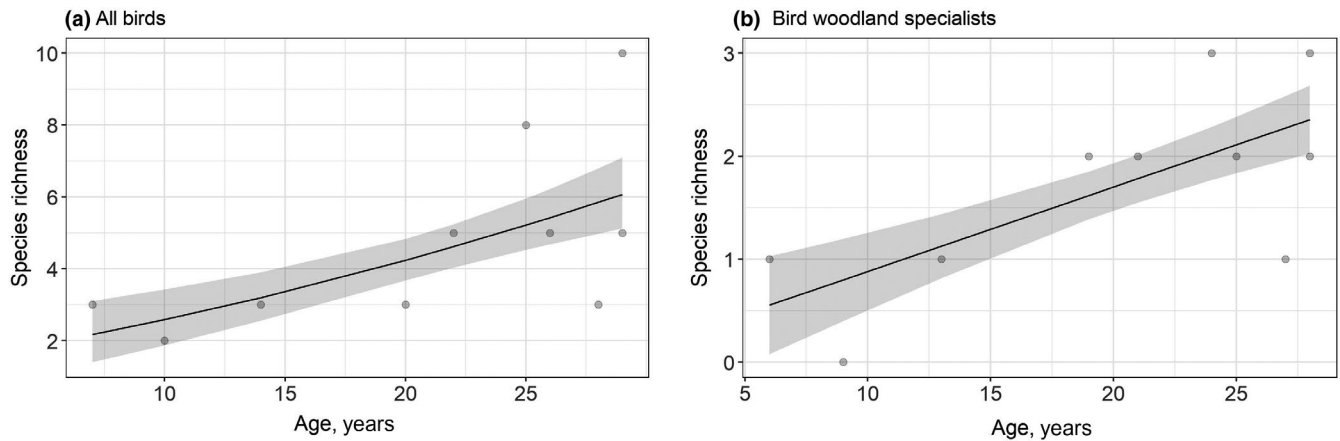


FIGURE 3 Relationship between site age and species richness for (a) all birds and (b) bird woodland specialists, reforested plots only ($n = 10$). Model fit \pm SE extracted from the models

habitat. We showed that plants, carabid beetles and birds responded to forest status rather than grazing. The plant and bird assemblages in reforested plots are intermediate to unforested and mature plots. For carabid beetles, the species assemblages in reforested plots converged with mature plots. Replanting native forest appears to have been successful as a habitat creation exercise.

4.1 | Does reforestation restore the communities associated with mature forest?

Aims of forest expansion differ, but the objective of restoring the mature forest community is common (Aerts & Honnay, 2011). Theory suggests that as species are restored, ecosystem functionality and processes will also recover (Montoya et al., 2012). In this study, species assemblages moved away from those found in unforested areas towards mature forest, and some woodland specialists were recorded in the reforested sites. We would expect this transition to continue in the reforested sites, as species associated with unforested areas are lost and mature forest species gained. The species assemblages of the reforested sites were more variable than in the unforested or mature forest sites, as were numbers of bird species and specialists in the oldest sites, emphasising that the outcome of reforestation is stochastic and may diverge over time depending on each site's history, reforestation method and local landscape influences.

Monitoring changes in species assemblage and numbers of specialist species can indicate progress towards recovery. Recovery slows over time, so restoration success should be assessed over long time-scales, with realistic long-term targets to account for ecological lags (Jones & Schmitz, 2009; Watts et al., 2020). Young forest is colonised first by generalists and its value will increase as the habitat develops and slower-dispersing specialists colonise (Watts et al., 2020; Whytock et al., 2018). Plants and carabid beetles are slower colonisers than birds, we expect these groups to continue to respond to the reforestation on a longer time-scale than is captured by our study.

The equivalent numbers of woodland specialist plant species in the reforested and mature plots may reflect recruitment from the soil seedbank rather than colonisation by these species, which typically have a limited dispersal ability (Kimberley et al., 2013). The similar number of Trees for Life priority plant species in reforested and unforested plots may reflect the reasonably slow turnover in the plant community. The priority plant species are characteristic of the Caledonian pinewood and their differing response to the woodland specialist plants emphasises that, while the reforested sites can support specialist species, they still have not converged on the species assemblage of the target habitat. Caledonian pinewood also supports specialist plants that are not included in the Ancient Woodland Indicator list. We recorded one of these species, *Pyrola media*, in a mature forest plot, but not in any of the reforested plots, suggesting that key rare plants are yet to colonise the reforested sites (Mason et al., 2004). The presence of woodland specialist birds in the reforested sites indicates that they provide suitable habitat at a young age and are on a trajectory to reach levels found in mature forest about 36 years after initiation of reforestation. Territory sizes of the woodland bird species are generally smaller than the areas of the reforested sites and surveys were conducted in the breeding season, so it is reasonable to assume that their presence at a reforested site reflects colonisation by these species (Fuller et al., 2014).

It is also relevant to consider the conservation status of species in each habitat category. A study comparing bird communities in regenerating native forest and moorland in the Scottish Highlands showed that Willow Warblers *Phylloscopus trochilus* would increase with reforestation and Meadow Pipits decline; both species are of conservation concern in the UK (Douglas et al., 2020; Eaton et al., 2015). Our results showed a similar pattern, although Meadow Pipits were recorded in the reforested and mature forest categories as well as unforested areas, potentially reflecting foraging activity. Overall, we found that mature and regenerating forest supported more Amber and Red listed birds than the unforested areas (Figure S12). Only two Vulnerable plant species and two Nationally Scarce carabid beetles were found, in both cases one in unforested and one in mature forest habitat (Figures S7 and S14). This partially fulfils the prediction that

restored sites will generally be colonised by more common generalist species which are typically good dispersers (Fuentes-Montemayor et al., 2015). Additionally, as our study plots only sample part of each site, they do not reflect the overall biodiversity value of the reforested areas; however, comparisons between habitat types allow an assessment of relative value.

All three species groups indicate that the development of the ecological community in the reforested sites is ongoing. Some specialist plant and bird species are present in the reforested sites, and for birds, we predict that on the current trajectory, the reforested sites would support numbers of species equivalent to mature forest at c.36 years post-reforestation. However, in all cases, mature forest species were missing from the reforested plots and species assemblages for reforested and mature plots only overlapped for carabid beetles.

4.2 | Integrating forest expansion into land use decisions

Decisions on future land use in the uplands must maximise multiple objectives, to produce heterogeneous multi-functional landscapes (Ockendon et al., 2018). Increasing native forest should increase associated biodiversity; however, this will depend on connectivity to existing forest (Thomas et al., 2015). We show that introducing native forest altered plant, carabid beetle and bird communities, supported woodland specialist plants and birds, and increased overall species richness for birds. Increasing native forest cover could increase the overall diversity within a landscape, particularly if native forest was not a dominant part of the prior landcover.

Understanding how species composition changes with different habitat types allow assessment of the value of increasing forest cover in the landscape. The plant and carabid species unique to unforested areas were generally characteristic of the boggy heathland habitat (Figures S7 and S14) and would benefit from maintenance of open ground habitat at the landscape scale. In contrast no bird species were unique to the unforested areas, although Skylark *Alauda arvensis* and Meadow Pipit nest in open habitats, so would be disadvantaged by a complete transition to forest cover at the landscape scale (Chamberlain et al., 1999; Vanhinsberg & Chamberlain, 2010). More broadly, forest expansion could negatively impact specific upland species, for example, the Red Listed Curlew *Numenius arquata*, but benefit others such as the Red Listed Black Grouse *Tetrao tetrix* (Douglas et al., 2014; Scridel et al., 2017). Reduced grazing pressure and increased vegetation height increases the availability of insect food in the Scottish uplands, improving the breeding success of birds of conservation concern (Baines et al., 1996; Dennis et al., 2008).

Although heathland is widespread in Scotland, covering 21%–31% of the country, it is a BAP priority habitat, representing a significant proportion of Europe's upland heathland (NatureScot, 2019). Caledonian pinewood, the target of restoration in this study, is another BAP priority habitat, and covers just 16,000 ha or c. 0.2% of Scotland (NatureScot, 2008). These current levels of heathland and

forest across Scotland suggest that Caledonian pinewood may be a greater priority for expansion. The species uniquely associated with the unforested treatment exist in a landscape where their habitat dominates. Since the unique species associated with forest rely on habitat that is more limited at the landscape scale, addition of forest would have a larger influence on landscape-level species richness. Forest expansion should also be targeted to areas close to mature forest to facilitate colonisation of the new forest.

Forest status was the primary driver of species assemblages and within the habitats studied grazing per se appears less important in structuring the communities. This may partly reflect the incomplete grazing exclusion at most of our sites. Reducing large herbivore grazing is critical to forest establishment. At our study sites, and across much of the Scottish Highlands, grazing prevents natural forest regeneration and threatens existing forest (Patterson et al., 2014). Reducing deer numbers is a key strategy for achieving natural forest regeneration and improving the health of other habitats in Scotland (Scottish Environment LINK, 2020). Grazing reduction would therefore provide the benefits of native forest expansion for biodiversity identified in this study; although grazing intensity was a less clear driver of species assemblages for the groups we studied, it is intrinsic to the health of many habitats in the Scottish Highlands.

Visions for the Scottish uplands emphasise a future with lower grazing pressures and increased forest regeneration (Armstrong, 2015; Armstrong & Forest Policy Group, 2015; Armstrong et al., 2014). Uptake of this requires evidence of the expected changes with altered management. The results of our study show that new native forest benefits forest-associated biodiversity in the Scottish Highlands. Biodiversity conservation priorities must be integrated with the wishes of local communities and other priorities, such as optimisation of ecosystem services such as carbon sequestration (Haines-Young & Potschin, 2009).

At the landscape scale, it can take longer to reach critical thresholds in functioning, even if communities are restored at the local scale (Lamb, 2014; Montoya et al., 2012). Future action in the Scottish uplands will be conducted on a larger scale than the sites in this study. Given that the unforested, reforested and mature forest habitats support unique species for all three species groups, a future landscape supporting a dynamic and heterogeneous mosaic of habitats would appear ideal. Low forest cover in the Scottish Highlands justifies expansion of native forest to increase habitat for the unique species it supports, but complete loss of open areas would compromise open habitat specialists. Altering grazing levels in the Scottish Highlands could be a route to achieving a more heterogeneous upland landscape, promoting natural forest regeneration while maintaining more open areas.

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AUTHORS' CONTRIBUTIONS

E.W. conceived the idea, analysed the data and led the writing of the manuscript; E.W., O.T.L., A.H. and N.B. designed the study; D.G. and A.M. helped to define the focus of the research and provided background information on the reforestation project; E.W., R.G. and A.S. collected the data. All authors contributed to the drafts and gave approval of the final version for publication.

DATA AVAILABILITY STATEMENT

Data available via the NERC Environmental Information Data Centre <https://doi.org/10.5285/d31bcee5-736b-4aed-bda2-c11cacd5dfc7> (Warner et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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