The effect of forest establishment on biodiversity and ecosystem function

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Contents

List of Figures & Tables p. 6

Thesis Abstract p. 11

Chapter 1: ***General Introduction*** p. 13

Chapter 2: ***The response of plants, carabid beetles and birds to 30 years of native reforestation in the Scottish Highlands*** p. 28

Chapter 3: ***Does restoring native forest restore ecosystem functioning? Evidence from a large-scale reforestation project in the Scottish Highlands*** p. 52

Chapter 4: ***Integrating research into rewilding from outset to outcome*** p. 75

Chapter 5: ***Aboveground carbon stocks are higher in mixed-species plantation forests than monocultures – a meta-analysis*** p. 92

Chapter 6 ***General Discussion*** p. 118

Appendix A: ***Supplementary information for Chapter 2*** p. 133

Appendix B: ***Supplementary figures & tables for Chapter 3*** p. 154

Appendix C: ***Supplementary methods for Chapter 3*** p. 162

Appendix D: ***Supplementary figures & tables for Chapter 5*** p. 164

Appendix E: ***Supplementary methods for Chapter 5*** p. 184

Appendix F: ***A Rewilding Diary by Emily Warner*** p. 208

References p. 235

List of Figures & Tables

Figures

Figure 2.1 Comparisons of species richness among forest × grazing treatments for plants, carabids and birds. p. 43

Figure 2.2 Species assemblage comparisons for plants, carabids and birds. p. 44

Figure 2.3 Relationship between site age and species richness for all birds and bird woodland specialists. p. 45

Figure 3.1 The response of each ecosystem function to the forest × grazing treatments. p. 66

Figure 3.2 Changes in aboveground tree carbon and topsoil carbon with time-since-reforestation p. 67

Figure 4.1 The relationship between rewilding goals and ecological concepts. p. 78

Figure 4.2 A summary of the connections between opportunities for experimental manipulation, rewilding interventions, rewilding principles and response variables. p. 80

Figure 5.1 The effect of plantation diversification on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 108

Figure 5.2 The effect of diversification at different levels of species richness on aboveground carbon stocks relative to the average of associated monocultures. p. 108

Figure 5.3 The effect of diversification with/without a nitrogen-fixing species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 109

Figure 5.4 The effect of diversification with all native or non-native/mixed origin species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 110

Figure 5.5 The effect of study design on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 111

Figure A1 The location of the fenced and reforested sites used in Chapter 2. p. 133

Figure A2 Close up of the site Am Meallan, showing the locations of the plant & carabid beetle and bird survey plots. p. 136

Figure A3 Venn diagram showing the number of plant species in each forest treatment category. p. 142

Figure A4 Mean species accumulation curves ± 95% confidence interval for plant species in the three categories of the forest treatment. p. 143

Figure A5 Relationship between site age and plant species richness. p. 144

Figure A6 Relationship between site age and species richness for plant specialist richness and Trees for Life plant priority richness. p. 145

Figure A7 The percentage of plots in each forest category that each carabid species was recorded in. p. 146

Figure A8 Venn diagram showing the number of carabid species in each forest treatment category. p. 147

Figure A9 Mean species accumulation curves ± 95% confidence interval for carabid species in the three categories of the forest treatment. p. 148

Figure A10 Relationship between site age and carabid species richness. p. 149

Figure A11 Venn diagram showing the number of bird species in each forest treatment category. p. 150

Figure A12 The percentage of plots in each forest category that each bird species was recorded in. p. 151

Figure A13 Mean species accumulation curves ± 95% confidence interval for bird species in the three categories of the forest treatment. p. 152

Figure A14 The percentage of plots in each forest category that each plant species was recorded in. p. 153

Figure B1 The location of the fenced reforestation sites used in Chapter 3. p. 154

Figure B2 Close up of the site Am Meallan, showing the locations of the survey plots. p. 157

Figure B3 (a) The response of soil carbon to plot type and (b) change over time in the difference in topsoil carbon between the paired reforestation, ungrazed plots and the unforested, grazed plots. p. 160

Figure B4 Frequency of seedlings per plot for each tree species, by seedling height category. p. 161

Figure D1 Number of mixed to monoculture comparisons at each level of species richness for mixed plantations compared to the average of relevant monocultures, best monoculture, and commercial monocultures. p. 166

Figure D2 The geographic distribution of study sites. p. 166

Figure D3 Data representation for each moderator. p. 167

Figure D4 The effect of diversification at different levels of species richness on aboveground carbon stocks relative to the best associated monoculture. p. 175

Figure D5 The effect of diversification at a species richness of two on aboveground carbon stocks relative to commercial monocultures. p. 175

Figure D6 The effect of diversification at different levels of species richness on aboveground carbon stocks relative to the average of associated monocultures and best associated monoculture. p. 179

Figure D7 The effect of diversification with/without a nitrogen-fixing species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 180

Figure D8 The effect of diversification with all native vs. non-native/mixed species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 181

Figure D9 The effect of study design on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. p. 182

Figure D10 The relationship between stand age and the standardised mean difference in aboveground carbon stocks relative to the average of relevant monocultures, the best associated monoculture, and commercial monocultures. p. 183

Tables

Table 2.1 Sample sizes for plant, carabid beetle and bird surveys. p. 36

Table 3.1 Sample sizes in each forest × grazing category for the ecosystem functions measured. p. 59

Table 3.2 The model structures used in the analysis of each ecosystem property. p. 63

Table A1 Information on the fenced and reforested sites surveyed in Chapter 2. p. 134

Table A2 Plant species lists for the unforested, reforested and mature forest treatment categories. p. 137

Table A3 Carabid beetle species lists for the unforested, reforested and mature forest treatment categories. p. 140

Table A4 Bird species lists for the unforested, reforested and mature forest treatment categories. p. 141

Table B1 Information on the focal fenced and reforestation sites in Chapter 3. p. 155

Table B2 Allometric equations used to calculate tree biomass in each plot. p. 158

Table B3 Response variables and units for each ecosystem function measured. p. 159

Table D1 Information on the studies used in the meta-analysis. p. 164

Table D2 Carbon accumulation in each mixed plantation, the average of monoculture plantations, and the most productive monoculture for each comparison. p. 168

Table D3 Species classified as commercial species. p. 174

Table D4 Carbon accumulation in mixed plantations compared to commercial species monocultures. p. 176

Thesis Abstract

Forest expansion is increasingly proposed as a mechanism to tackle the biodiversity and climate crises. It is therefore crucial we understand the impacts of forest establishment on biodiversity and ecosystem functions, so that we can optimise future forest creation.

In this thesis I use a long-term, large-scale native forest creation project in the Scottish Highlands to assess the impact of forest expansion on biodiversity and ecosystem functions in an upland context in the UK. Within the UK, the uplands are an area where forest expansion is likely to conflict less with other land-uses, so understanding the impact of forest expansion in these locations is important. I show that the newly created forest provides habitat for some plant and bird woodland specialists, but specialists are more abundant in mature forest. Plant, carabid beetle and bird communities are transitioning away from those found in unforested areas, towards the composition in mature forest. Ecosystem functions (including aboveground carbon, topsoil carbon, topsoil nitrogen, decomposition rates, soil invertebrate feeding, vegetation structure, tree regeneration) respond variably to the forest creation. Notably, topsoil carbon is lower in the forest creation sites relative to unforested and mature forest areas. Together these results highlight the biodiversity conservation value of forest creation in the Scottish Highlands, but the impact on carbon sequestration is less clear. This emphasises that forest creation targets must consider trade-offs with unforested habitats that may contain high soil carbon stocks and support different aspects of biodiversity.

I also consider the need for the integration of ecological research into rewilding projects from their outset. I provide a framework for understanding the links between ecological concepts and goals of rewilding projects, and highlight the need for baseline data collection, long-term monitoring and integration of experimental manipulation in future rewilding projects. A coherent framework for

monitoring rewilding and addressing uncertainties experimentally could inform future rewilding projects and allow their biodiversity conservation and carbon sequestration potential to be assessed.

Finally, I assess the effect of tree diversity on carbon storage in planted forests. I use a meta-analysis to compare carbon stocks in mixed forests to monocultures, using data from the literature and Tree Diversity Network. I show that carbon stocks in mixed forests outperform the average of associated monoculture plantations and monocultures of commercial species, with no clear difference between carbon stocks in mixed plantations and their best associated monoculture. These results provide further support for the diversification of future planted forests.

Overall, my thesis provides data that will inform future forest expansion at a range of scales. Where forest expansion is deployed due to its perceived benefits for biodiversity and carbon sequestration, it is important we understand the extent to which it will achieve this. My research highlights that carbon and biodiversity responses are not always congruent, and that approaches such as the diversification of planted forests could optimise carbon storage. Taking opportunities to incorporate data collection into future forest expansion projects from their outset will play an important role in filling research gaps and monitoring progress towards targets.

Chapter 1 General Introduction

Over the last 5,000 years we have lost 30% of the world's forests, with consequences for humans and biodiversity (Paquette et al., 2018). The remaining forests cover just under one third of the world's land area, but support 80% of its terrestrial biodiversity and provide a livelihood for roughly 1.6 billion people (Aerts & Honnay, 2011). Benefits to humans from forests include timber, carbon sequestration, climate regulation and cultural services (Felipe-Lucia et al., 2018). From 1990 to 2020 the rate of forest loss has slowed, due to decreased deforestation rates in some countries and an increase in forest expansion (FAO, 2020a). Of the world's forests, 7% are planted, of which just under half are plantation forests (intensively managed, even-aged stands of one or two species) (FAO, 2020a). Intact forest that has not suffered intensive anthropogenic degradation is of exceptional value for climate change mitigation, biodiversity and humans (Watson et al., 2018). As the area of newly created forest increases, it is important we understand how to maximise benefits from these forests and the extent to which they contribute to biodiversity conservation, climate change mitigation and other goals (Chazdon & Brancalion, 2019; Dave et al., 2017).

Future land-use and forests

Forest expansion and reforestation are among nature-based solutions to tackle the 21st Century challenges of biodiversity loss, climate change and improving human wellbeing (Seddon et al., 2020). Changes to land-use and management have the potential to make an important contribution to global carbon sequestration goals. However, current Nationally Determined Contributions fall short of the goal to restrict global heating to 1.5^{o}C (Griscom et al., 2017; Roe et al., 2019). Forest expansion often occurs within a mosaic of other land-uses (Chazdon, 2017) and decisions at the landscape scale aim to optimise ecosystem goods and services (Chazdon et al., 2017). Doing this effectively requires an understanding of the links between restored ecosystems, biodiversity, ecosystem functions, and ecosystem services (Bullock, Aronson, Newton, Pywell, & Rey-Benayas, 2011).

Newly created forest can be defined based on the method of establishment and prior land-use. Forest restoration is the assisted recovery of degraded, damaged, or destroyed forest. Reforestation is the re-establishment of forest cover in an area that was previously forested (Di Sacco et al., 2021). A distinction between reforestation, which is the reestablishment of trees on land that was previously forested within the last 50 years, and afforestation, which is the reestablishment of trees on land that has been unforested for more than 50 years, is sometimes made (Lamb, 2014). But as land-use histories are often unknown, reforestation is often used as a more inclusive definition, to provide a distinction from cases where trees are established in naturally treeless ecosystems, which is considered true afforestation (Lamb, 2014). Forest restoration or reforestation can occur through tree planting or natural regeneration, where trees naturally establish from surrounding seed sources, sometimes with human-assistance such as the removal of grazing pressure (Di Sacco et al., 2021). Planted forests can vary in composition and structure, from intensively manged even-aged plantation forest with one or two species, to semi-natural forest, with a composition and community structure similar to nearby naturally occurring forest (FAO, 2020a; Lamb, 2014; Lewis, Wheeler, Mitchard, & Koch, 2019). Here I also refer to forest expansion, as an inclusive term for reforestation or restoration, by planting, natural regeneration, or a mixture of both approaches.

Forests are among the slowest ecosystems to restore and the approach taken will depend on the level of prior degradation, with active approaches often necessary in more degraded ecosystems (Chazdon, 2008; H. P. Jones et al., 2018). After restoration efforts, sites are often compared to baseline and reference conditions to assess the extent of recovery in terms of biodiversity and ecosystem services (Meli et al., 2017; Rey Benayas, Newton, Diaz, & Bullock, 2009); this allows us to measure progress in restoring a degraded ecosystem. Restoration projects can have a range of objectives, for example maximisation of a specific ecosystem service, improving the connectivity of a habitat, or restoration of a certain species (Ockendon et al., 2018). Previously, restoration projects often had static targets

based on historical baselines, but functional targets are becoming more common (Perring et al., 2015). Restoration interventions can increase biodiversity and ecosystem service supply, but restoration will rarely achieve full recovery (H. P. Jones et al., 2018; Rey Benayas et al., 2009). The abundance of individuals increases more quickly than species richness, and populations will recover more quickly than interspecific interactions and ecosystem services (Meli et al., 2017; Montoya, Rogers, & Memmott, 2012). Restoration practices do not always integrate underlying ecological theory. Biodiversity is often a target of the restoration intervention, rather than a factor that will explain restoration success. However, restoration drawing on the principles of the biodiversity-ecosystem functioning field is becoming more common (Aerts & Honnay, 2011; Hughes, Grabowski, Leslie, Scyphers, & Williams, 2018). As community composition responds less predictably to restoration than species richness, revised targets that aim to restore functional groups are more likely to restore specific ecosystem functions and derived services (Laughlin et al., 2017; Montoya et al., 2012).

Biodiversity is a key driver of the processes that underpin ecosystem function (Cardinale et al., 2012; van der Plas, 2019). Ecosystem function depends on interactions among organisms and with their environment, driving processes such as carbon cycling, energy transfer between trophic levels and regulation of invertebrate pest species (Cardinale et al., 2012). Across ecosystems, the value of biodiversity for ecosystem function has been demonstrated by decades of biodiversity-ecosystem function experiments (Tilman, Isbell, & Cowles, 2014; Xu et al., 2020). Tree diversity within forests underpins the delivery of ecosystem services (Gamfeldt et al., 2013; Hertzog et al., 2019; Jonsson, Bengtsson, Gamfeldt, Moen, & Snäll, 2019) and enhances forest productivity (Liang et al., 2016), contributing to carbon storage. Multiple species are required to maintain stability of function over time, resistance to external perturbations and to simultaneously support multiple ecosystem functions (Gamfeldt et al., 2013; Hutchison, Gravel, Guichard, & Potvin, 2018; Tilman et al., 2014). Consequently there is a call for greater tree diversity within future forest establishment (Messier et al., 2021).

Benefits from forests – biodiversity, carbon, other ecosystem services

The motivation for forest expansion or reforestation rests on the assumption that forest creation will enhance ecosystem service provision and restore lost biodiversity. Despite an increase in research into different methods of, and outputs from, reforestation, there are still knowledge gaps and barriers between science and policy that hinder effective forest restoration (Chazdon et al., 2017b). It is often desirable for restoration to meet multiple objectives simultaneously; however, unless projects are designed to maximise synergy between different objectives from the outset, optimal outcomes may not be achieved (Ferreira et al., 2018; Strassburg et al., 2020).

Different forest types maximise different ecosystem services, for example natural forests provide more effective long-term carbon drawdown than plantation forests (Lewis et al., 2019). Within plantations, different types optimise different combinations of ecosystem services. For example, in southern China, Chinese fir and pine forests provide higher timber yields but lower overall ecosystem service benefits compared to economic forests planted for forest products other than timber (Dai, Wang, Zhu, & Xi, 2017). Forest type also influences cultural ecosystem services, with mixtures supplying a greater number of cultural ecosystem services than monocultures (Tew, Simmons, & Sutherland, 2019). The desired outputs at the landscape-scale will determine the relative quantities and types of forest creation, but this requires understanding the impact of any given forest type in different contexts. Where production is a key objective, large-scale plantations of productive (often non-native) species are likely to be prioritised in a landscape, whereas where biodiversity is a priority, the emphasis will be on native forests governed by natural processes (Burton, Metzger, Brown, & Moseley, 2019).

Restoration or creation of natural forest often aims to enhance biodiversity, conserving forest species and replacing forest that has been lost (Di Sacco et al., 2021). Specialist species, that are the ultimate target of forest creation, may take longer to respond to the creation of new habitat, whereas

generalist species may colonise new forest habitat more quickly (Watts et al., 2020). Therefore, the lower value of newly created habitat for biodiversity may reflect the early stage in its development and its value will increase over time (Meli et al., 2017; Watts et al., 2020). This is emphasised by the greater benefits to species with lower habitat specificity in the early stages of forest development, before the forests have developed all of the characteristics of mature forest (Fuentes-Montemayor et al., 2020; Fuentes-Montemayor, Peredo-Alvarez, Watts, & Park, 2015; Whytock et al., 2018). When forest is created on land that was previously open, species reliant on the open ground will be disadvantaged and the overall impacts of forest creation in this context should be considered at the landscape scale (Douglas, Groom, & Scridel, 2020; Silveira et al., 2021). Intensive plantation forests are not typically associated with high biodiversity, but they can buffer intact forest or provide habitat corridors in more intensive agricultural land-uses (Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008) and their impact on biodiversity depends on the intensity of management (Sing, Metzger, Paterson, & Ray, 2018).

As functional targets of restoration projects become more common, an understanding of how forest creation or restoration influences ecosystem function becomes more important (Perring et al., 2015). Monitoring of ecosystem functions within restoration projects has increased, although there are still certain functions that are underrepresented (Kollmann et al., 2016). Measuring functions alongside biodiversity gives the potential to explore links between biodiversity and ecosystem function in an applied context. Functions focussing on the flow of energy through a system and species interactions are a priority for investigation (Kollmann et al., 2016). Functions related to nutrient balances, productivity and carbon sequestration were among the most commonly studied in restored forest ecosystems (Kollmann et al., 2016). Functional targets of restoration range from soil stabilisation and protection, to carbon sequestration (Stanturf, Palik, & Dumroese, 2014).

A primary motivation for forest expansion is to sequester carbon (Bradfer-Lawrence et al., 2021; Cook-Patton et al., 2020). Monitoring carbon in developing forest ecosystems requires an assessment of carbon stocks across the whole system, including soil carbon, where gains or losses depend on the prior land-use and method of forest establishment (Guo & Gifford, 2002; Hong et al., 2020; K. B. Matthews et al., 2020). When land is converted from a land-use with semi-natural vegetation cover to forest, soil carbon is usually lost, with higher losses when the soil type has a high carbon content (Friggens et al., 2020; K. B. Matthews et al., 2020). The specifics of a forest expansion scenario (i.e. forest type, prior land-use and management regime) influence the potential for forest to contribute to climate change mitigation (K. B. Matthews et al., 2020). There is a clear positive effect of tree diversity on aboveground carbon accumulation (Liang et al., 2016; Xu et al., 2020; Zhang, Chen, & Reich, 2012). Diversification should be explicitly incorporated into future forest expansion strategies, to enhance forest productivity and increase resilience to future natural disturbances (Messier et al., 2021).

Forest creation in the UK, with a focus on Scotland

Forest cover in the UK is 13%, having risen from a low of 5% in the early 20th century (Forest Research, 2020) and is considerably lower than the EU average of 43% (European Union, 2018). There is increasing motivation to increase the country's forest cover, particularly for carbon sequestration, with a target of planting 30,000 hectares a year to increase tree cover to 17% by 2050 (Committee on Climate Change, 2020). Each of the UK nations has its own target for forest expansion, but historically most forest expansion has occurred in Scotland, with 80% of new planting occurring there in 2019-2020 (Forest Research, 2020). The Scottish Government aims to increase forest cover from 18% to 21%, by creating 10,000–15,000 hectares per year, of which 3,000–5,000 hectares will be native (Scottish Government, 2019).

The historical context of forest cover in Scotland gives an understanding of the potential for forest expansion. After the end of the last ice age 11,400 years ago, native forest recolonised Scotland, reaching a maximum of more than 60% forest cover c.5,000 years ago, with the Highlands dominated by a mixture of pine and birch (Oosthoek, 2013). A shift in the climate 5,000-4,000 years ago, with cooler temperatures and increased precipitation, is thought to have driven declines in forest extent (Oosthoek, 2013; Tipping, 1994; Tipping, Davies, & Tisdall, 2006). Humans are thought to have impacted forests concurrently however attributing a decline in forest cover to human activity is complicated. Human-driven deforestation has been suggested as occurring as early as 6,000 years ago and humans are known to have been present in the Scottish landscape at this time, but we lack unequivocal evidence of their impact on forest cover (Oosthoek, 2013; Tipping, 1994). These initial human impacts are likely to have been small in scale and occurred prior to and simultaneously with the Holocene climate changes. From 6,000 to 4,200 years ago more widespread declines in forest cover are evident, likely driven by a combination of agriculture and climate (Oosthoek, 2013; Tipping, 1994). More intense agriculture and forest clearance from c.4,000 years ago caused more persistent forest openings, with cover falling to 25% with the arrival of Romans in Scotland c.2000 years ago (Oosthoek, 2013). Most wildwood was lost by the end of the first millennium and deforestation continued throughout the Middle Ages, with demand intensifying from 1500 (Oosthoek, 2013). Forest cover reached a low of 6% in 1900, reflecting intensifying deforestation over the preceding centuries, and a transition in land-use from native forest to grazed uplands occurred in the mid-19th century as a decline in timber prices pushed landowners to pursue an income from sheep grazing and hunting (Oosthoek, 2013). During the late 20th Century Scotland experienced a large increase in forest cover, rising from 8.4% in 1965 to 16.7% in 1998, predominantly driven by the establishment of commercial conifer plantations (Forest Research, 2020; Wong, Urquhart, Feliciano, & Slee, 2015).

Historic patterns of forest loss and expansion provide context to targets for forest expansion in Scotland and have implications for future land-use decisions. In the UK, including in Scotland, the

uplands are likely to be a focus of future land-use changes, particularly as the agricultural subsidies system, that supports farming in these areas, changes with the UK's exit from the EU (Sandom et al., 2019). The uplands provide a number of important ecosystem services, including biodiversity conservation, recreation, water supply and carbon sequestration (Haines-Young & Potschin, 2009). There are several potential future land management strategies in these locations, with different implications for ecosystem supply (Tinch, Tinch, & Provins, 2009). These include forest creation, and increasing scrub and tree cover through rewilding, which aims to create dynamic self-sustaining ecosystems, governed by natural processes (Carver et al., 2021). Understanding how forest expansion in upland areas influences biodiversity and ecosystem function is important. There are anticipated large-scale opportunities for carbon sequestration through forest expansion in the uplands (Fletcher, Scott, Hall, & Spracklen, 2021; O'Neill, Lim, Edwards, & Osborne, 2020), but we require more data on the impact of different forest expansion scenarios on ecosystem functions and processes in these locations, particularly given the indication that in some cases it could have a negative impact on the carbon balance (Friggens et al., 2020). Much of the evidence for the consequences of forest expansion for biodiversity and ecosystem services in the UK comes from commercial conifer plantations and an evidence gap in native forest has been highlighted (Burton, Moseley, Brown, Metzger, & Bellamy, 2018).

In the Scottish Highlands the landscape is predominantly unforested, with remnants of native forest remaining in places (Patterson, Nelson, Robertson, & Tullis, 2014). High numbers of browsing herbivores prevent tree regeneration and have negative impacts on heathland and forest condition (Armstrong, Holl, & Halley, 2014; Patterson et al., 2014). Extensive reforestation with native forest has been proposed as a suitable future land-use in the Scottish Highlands, with expected benefits including carbon sequestration, increased forest products and conservation of biodiversity (Armstrong, 2015; K. Holl & Smith, 2007). The trade-offs and benefits with an increase in forest cover in Scotland require an understanding of how ecosystem service supply and biodiversity will respond (Burton et al., 2018).

Integration of ecological changes with economic and social considerations is also important. In Scotland there will potentially be short term economic losses with a reduction in sheep and deer grazing, but in the longer-term increased tourism and employment may balance these losses (Armstrong, Halley, & Holl, 2017). Additionally, Scotland has complex cultural associations with the current land-uses: deer stalking maintains open landscapes that some people see as characteristic of Scotland (Wilson, 2017). Visions for forest expansion in Scotland range from those focussed on production of forest products, through scenarios that balance productive forest with forest for recreation and biodiversity conservation, to a landscape governed by natural processes, generating wild biodiversity-rich woodland (Burton et al., 2019). Quantification of change in ecosystem function and biodiversity with forest creation will allow the potential benefits in the Scottish uplands to be assessed, allowing the consequences of different scenarios to be predicted (Burton et al., 2019).

In the UK much of our information on the response of biodiversity and ecosystem functions to native forest expansion comes from a lowland environment, where forest expansion often occurs on past agricultural land (Watts et al., 2016). This limits our understanding of how native forest expansion will influence biodiversity and ecosystem function in upland areas, where forest will replace existing semi-natural vegetation. Currently, much of the data from these environments has come from an experimental setting that may not reflect future native forest expansion projects (e.g. (Friggens et al., 2020; Mitchell et al., 2007). Given visions for an increase in native forest across the Scottish Highlands (Armstrong et al., 2014; Scottish Environment LINK, 2020), it is important we understand how biodiversity and ecosystem functions will respond, so that we can make more accurate predictions about the consequences of this forest expansion.

Monitoring the outputs of large-scale reforestation projects

The UN Decade of Ecosystem Restoration (2021-2030) has begun (FAO, IUCN CEM, & SER, 2021). Efforts to restore degraded ecosystems will therefore increase, in an attempt to restore the

biodiversity loss caused by human driven habitat destruction, degradation and fragmentation (Newbold et al., 2016, 2015). Emphasis has been put on restoration as a method to reverse human damage to ecosystems, but a cohesive monitoring framework for assessing restoration projects is needed, given the unpredictability of restoration projects (Brudvig, 2017; Stuble, Fick, & Young, 2017). Challenges to monitoring the outcomes of forest restoration projects include a lack of a clear monitoring framework, the difficulty of monitoring multiple diverse response variables, and differences in approaches to and expected outcomes of restoration (Mansourian & Vallauri, 2021).

As forest expansion increases, including via the harnessing of natural processes (Broughton et al., 2021), effective monitoring of the response of ecosystem functions and biodiversity is important (Svenning et al., 2016; Trogisch et al., 2017). We have specific knowledge gaps, such as on the response of biodiversity and ecosystem functions to upland reforestation in the UK, but it is also important that the contributions of restoration projects to tackling biodiversity loss and climate change are monitored as projects are implemented (Svenning, 2020). Carbon sequestration is strongly dependent on the method and location of forest expansion, highlighting that there is no guarantee that area-based targets for forest creation will meet countries' climate change mitigation goals (K. B. Matthews et al., 2020). Modelling of different forest expansion and other habitat scenarios, particularly those implemented to meet specific biodiversity conservation or carbon sequestration goals should be supported by on-the-ground monitoring. An assessment of tree planting initiatives over the last 50 years in northern India found no increase in forest canopy, suggesting that the initiatives have not contributed to climate mitigation, and there is also no evidence that the tree planting has provided benefits to local people (Coleman et al., 2021).

Rewilding is a restoration method that is receiving increasing support as a solution to global environmental problems such as climate change and biodiversity loss (Svenning, 2020). Rewilding aims to create dynamic self-sustaining ecosystems governed by natural processes and can be one approach

to increasing tree cover (Broughton et al., 2021; Carver et al., 2021). The dynamic nature of rewilding means that it is inherently unpredictable and the outcomes of projects that aim to establish tree cover can be stochastic, dependent on factors such as seed sources, local ground cover and the presence of grazing herbivores (Tanentzap, Zou, & Coomes, 2013). An assessment of the potential for natural forest regeneration to accumulate carbon found that the IPCC carbon accumulation rate is an underestimate; the new estimate uses a higher resolution spatial dataset integrating more on the ground measurements (Cook-Patton et al., 2020). But the study also highlights the high level of variation in carbon accumulation with natural forest regeneration within countries (Cook-Patton et al., 2020).

As new forest expansion projects begin, using approaches ranging from rewilding to tree planting, there is an important opportunity to implement monitoring within these projects, to better understand the underlying ecological mechanisms driving outcomes and to verify projects' contributions to biodiversity conservation and climate change mitigation (Brudvig, 2017; Svenning et al., 2016). Defining a simple and effective monitoring approach, targeting ecosystem functions and biodiversity will be important (Kittipalawattanapol, Jones, Barmuta, & Bain, 2021; Trogisch et al., 2017).

Carbon accumulation in planted forest

On the global scale, future land-use decisions have the potential to influence worldwide carbon stocks, influencing the supply of an ecosystem service to the entire human population (Griscom et al., 2017; Krause et al., 2018). Reforestation, avoided deforestation or degradation of forests, and afforestation have the potential to maintain and enhance the global forest carbon stock (Dixon et al., 1994; Hawes, 2018). Reforestation of previously deforested land, such as past agricultural land, can lead to increases in aboveground and soil carbon stocks. For example, reforestation of abandoned farmland in the

tropics leads to rapid carbon accumulation in the first 20 years and uptake continues for up to 80 years (Guo & Gifford, 2002; Post & Kwon, 2000; Silver, Ostertag, & Lugo, 2000).

Although the global area of forest is declining, the area of planted forest is increasing (Keenan et al., 2015). Plantation forest established as monoculture achieves a fraction of the carbon stocks gained through reforestation with natural forest (Lewis et al., 2019). Despite this, plantation forest will continue to be established to meet timber and other provisioning demands, therefore ecosystem services from plantations must be maximised. Currently most plantation forest is established as monoculture, despite evidence that diverse plantations can be more productive and can enhance the delivery of other ecosystem services (Bielak, Dudzińska, & Pretzsch, 2014; Nichols, Bristow, & Vanclay, 2006; Ruiz-Jaen & Potvin, 2011; Verheyen et al., 2016). There is therefore the potential for plantations to take up a greater amount of atmospheric CO_2 through diversification of the tree species planted (Pawson et al., 2013).

Evidence for enhanced productivity, and therefore carbon uptake, in diverse forests compared to monoculture forests comes predominantly from biodiversity-ecosystem function experiments (Verheyen et al., 2016). The gains in carbon storage with diversification can be large: an experiment in tropical forest in China found that 16-species mixtures stored twice the amount of carbon stored in monocultures (Huang et al., 2018). Environmental variation also influences overall carbon storage and alters the effect of tree diversity on carbon storage. However, even when environmental variation is accounted for, the effect of tree diversity is still significant (Healy, Gotelli, & Potvin, 2008; Li et al., 2019; Poorter et al., 2017). Species traits in mixtures can also be important in driving the positive diversity effect on biomass, for example nitrogen-fixing species in a mixed plot can increase tree growth throughout the plot (Piotto, 2008). There is evidence that diversity has the same positive effect on functioning in plantation forest outside of experiments: in mixed plantations complementarity between species leads to higher species level productivity and higher total carbon storage (Chamagne

et al., 2017; Erskine & Lamb, 2006). Furthermore studies have demonstrated economic advantages of mixed species compared to monoculture plantations (Piotto, Craven, Montagnini, & Alice, 2010).

Young forests sequester carbon at fast rates (Bongers, Chazdon, Poorter, & Peña-Claros, 2015), but plantation forests are generally not permanently established, and provide a less significant carbon stock than old-growth forests (Canadell & Raupach, 2008). Despite their impermanence, plantation forests still make a significant contribution to the global carbon balance; however, afforestation in certain locations e.g. boreal regions could lead to overall climate warming through changes in albedo (Betts, 2000; Nuñez et al., 2021). Current land-uses constrain country's abilities to meet nationally determined contributions to global carbon budgets, therefore the design of future land-uses, such as plantations, should integrate current theoretical knowledge of biodiversity-ecosystem function relationships to maximise effectiveness (Brown, Alexander, Arneth, Holman, & Rounsevell, 2019; Seddon, Turner, Berry, Chausson, & Girardin, 2019).

Diversifying plantations could enhance the contribution of plantations to global carbon stocks and bring additional associated benefits (Gamfeldt et al., 2013; Messier et al., 2021). Mixed plantations are also less susceptible to pests, pathogens, and abiotic disturbances, support more biodiversity and provide a greater level of ecosystems services beyond wood (Messier et al., 2021). As planted forests increase in area globally, a synthesis of existing data on the effect of tree diversity on carbon stocks in mixed forests is timely, helping to increase support for establishment of mixed forest.

Thesis research objectives & structure

Thesis aim

At a time when forest expansion is increasing at global and national scales, this thesis aims to contribute to the evidence base that informs decisions on forest expansion. There are still situations where our understanding of the response of ecosystem functions and biodiversity to a land-use change limits land-use planning. My research aims to explore the effect of native forest establishment on biodiversity and ecosystem function in the Scottish Highlands, where current evidence is limited but extensive forest expansion opportunities exist. As forest expansion projects increase, opportunities are often missed to integrate experimental manipulation and monitoring programmes from the outset of the project. I use the context of the increasing interest in rewilding in the UK, to provide a framework for integrating science into rewilding projects. On a global scale, the diversification of plantation forest has been slow, despite theoretical and experimental evidence that diversification could enhance carbon storage. I conduct a global synthesis of studies assessing the effect of tree diversity on carbon storage in planted forest, quantifying carbon storage in mixed vs. monoculture plantations to inform plantation establishment in the future.

Research objectives 1 & 2 – How does native forest expansion in the Scottish Highlands influence biodiversity (Chapter 2) and ecosystem functions (Chapter 3)?

I used a large-scale native reforestation project in the Scottish Highlands to assess the response of biodiversity (Chapter 2) and ecosystem functions (Chapter 3) to native forest expansion. Biodiversity (plants, carabid beetles and birds) and ecosystem functions (aboveground carbon, topsoil carbon, topsoil nitrogen, decomposition rates, soil invertebrate feeding activity, tree regeneration, and ground-layer and moss height) were measured in reforestation plots, and plots in unforested and mature forest areas, to allow comparison to the prior state and target habitat. Chapter 2 was

published in the *Journal of Applied Ecology* in July 2021 and Chapter 3 was published in *Restoration Ecology* in August 2021.

Research objective 3 – Developing a framework to integrate ecological research (experimental manipulation & monitoring) into rewilding projects (Chapter 4).

Using the context of the increasing interest in rewilding to tackle the climate and biodiversity crises in the UK, I provide a framework for integrating science into rewilding projects from their outset. I highlight the relationship between existing ecological concepts and goals of rewilding and the potential to investigate these experimentally within rewilding projects. Opportunities are often missed to integrate experimental manipulations and monitoring programmes in rewilding projects at their outset. I highlight the crucial features that should be included within monitoring programmes and experimental manipulations. Chapter 4 will be submitted to *Trends in Ecology & Evolution*.

Research objective 4 – Comparing carbon stocks in mixed vs. monoculture plantations (Chapter 5).

Using a global reforestation database, supplemented with data from the Tree Diversity Network of experiments, I conducted a meta-analysis assessing carbon stocks in mixed vs. monoculture plantations. I consider the effect of some potential underlying drivers on carbon storage in mixed vs. monoculture plantations. Chapter 5 will be submitted to *Global Change Biology*.

Statement of authorship

The chapters of this thesis are published or draft manuscripts. I led all of the work and the contributions of co-authors, alongside the details of publication or planned manuscript submission, are given at the start of each chapter.

Chapter 2: The response of plants, carabid beetles and birds to 30 years of native reforestation in the Scottish Highlands

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Authors' contributions: EW conceived the idea, analysed the data and led the writing of the manuscript. EW, OL, AH & NB designed the study. DG & AM helped to define the focus of the research and provided background information on the reforestation project. EW, RG & AS collected the data. All authors contributed to the drafts and gave approval of the final version for publication.

Data availability: Data available via the NERC Environmental Information Data Centre https://doi.org/10.5285/d31bcee5-736b-4aed-bda2-c11cacd5dfc7 (Warner, Lewis, Hector, Brown, Green, Savory, et al., 2021).

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 for 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 was higher in reforested (4.4 [95% CI: 3.2, 5.9]) than 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 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 native forest is scarce and fragmented in the Scottish Highlands and that the ultimate gain from native forest expansion may accrue over long timescales.

Keywords: Native reforestation, forest expansion, biodiversity, plants, carabid beetles, birds, Scottish Highlands

Introduction

Between 1990 and 2020 an estimated 420 million hectares (ha) of forest was lost worldwide, and there are global targets to restore 350 million ha of degraded and deforested land by 2050 (Dave et al., 2017; FAO, 2020b). 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, Towers, & Ellis, 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.2000 years ago (Oosthoek, 2013; 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, Hampson, & Edwards, 2004; Scottish Natural Heritage, 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., 2019). 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, Miles, & Gimingham, 1991a).

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, Good, & Williams, 1992). For all three species groups we aimed to (i) assess the effect of forest (unforested, reforested, mature) and grazing (grazed, ungrazed) treatments on species richness and the presence of woodland specialists; (ii) compare species assemblages in the ungrazed, reforested treatment with the grazed/ungrazed unforested and mature forest treatments; and (iii) assess trajectories of community recovery by investigating the effect of forest age on species richness and richness of specialist species across reforested sites.

Materials and Methods

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) (Fig. A1 in Appendix A). These landscapes contain a mosaic of habitat types, including mature Caledonian pinewood, productive conifer plantations, unforested heathland and regenerating native forest. We focused on fourteen 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 15-446 ha in area (Table A1 in Appendix A). 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 km^2 in Glen Moriston and c.8 per km^2 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 A1). 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.

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 × 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 centre 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 2.1, Fig. A2). 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 2.1, Fig. A1). 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 2.1).

Table 2.1 Sample sizes for plant, carabid beetle and bird surveys.

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

Plant surveys

Plants were surveyed from 22nd June to 5th July 2018. Three 1 × 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 *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 × 10 m plot was carried out to identify any species absent from the three quadrats.

Specialist plant species were defined based on two categorisations: (i) woodland specialists: using the Ancient Woodland Indicator list of species (Kirby, 2020b) and (ii) Trees for Life priority species: species characteristic of the Caledonian pinewood and noted as desirable by Trees for Life staff (Table A2).

Carabid beetle surveys

Carabid beetles were surveyed using pitfall traps from 7th June to 18th 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 A3).

Bird surveys

Bird survey plots were visited twice, during 23rd May – 1st June 2019 and again during 5th – 14th June 2019. All surveys were conducted between 06.00 & 11.30 am. If the first survey was conducted during the earlier part of this period the second was conducted later, and vice versa. After a 2-minute settling

period, birds were surveyed for 15 minutes. 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 A4).

Data analysis

All statistical analysis was carried out using R (R Core Team, 2020). Our analysis uses a fractional factorial combination of the two factors, forest (unforested, reforested, mature) and grazing (grazed, ungrazed), where the grazed × reforested combination is absent (Table 2.1).

Mixed-effect models were fitted using the package *lme4* (Bates, Machler, Bolker, & Walker, 2015), testing the effect of forest × 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 × 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 1000 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.

Results

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]) (Fig. 2.1a). 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 [0.2, 1.4]); there was no effect of grazing on woodland specialists (−0.05 [95% CI −0.8, 0.7]) (Fig. 2.1b). 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]) (Fig. 2.1c).

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 (Fig. 2.2a).

Eighteen species were unique to the unforested treatment, 17 to the reforested treatment and 3 to mature forest (Fig. A3, Table A2). Unforested, reforested and mature forest plots had a high degree of overlap in the species present (Fig. A3). Species richness accumulated most rapidly across plots in the reforested treatment and slowest in the mature forest treatment (Fig. A4).

Time since reforestation had no clear effect on overall plant richness (effect age 0.08 [95% CI −0.3, 0.4], Fig. A5), woodland specialist richness (effect age 0.02 [95% CI −0.2, 0.2], Fig. A6a) or richness of Trees for Life's desired species (effect age −0.01 [95% CI −0.1, 0.09], Fig. A6b).

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]) (Fig. 2.1d). Only one woodland specialist carabid was found (*Pterostichus oblongopunctatus*), which was restricted to mature forest (Fig. A7).

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 (Fig. 2.2b).

The unforested plots supported seven unique carabid species and the reforested and mature forest plots supported two unique species respectively (Fig. A8, Table A3). 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 (Fig. A9).

Time since reforestation had no clear effect on species richness for carabid beetles (effect age −0.08 [95% CI −0.2, 0.06], Fig. A10).

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]) (Fig. 2.1e). 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]) (Fig. 2.1f). 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 (Fig. 2.2c). 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 (Fig. A11, Table A4). Only five of the 21 bird species were recorded across the unforested plots, where Meadow Pipit (*Anthus pratensis*) was the most frequent species (Fig. A12). Species richness accumulated most rapidly across plots in the mature and reforested treatments, but quickly began to plateau in the unforested treatment (Fig. A13).

In the reforested plots bird species richness (sqrt-transformed effect Age 0.05 [95% CI 0.009, 0.08], Fig. 2.3a) and bird specialist richness (effect Age 0.08 [95% CI 0.02, 0.14], Fig. 2.3b) 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.

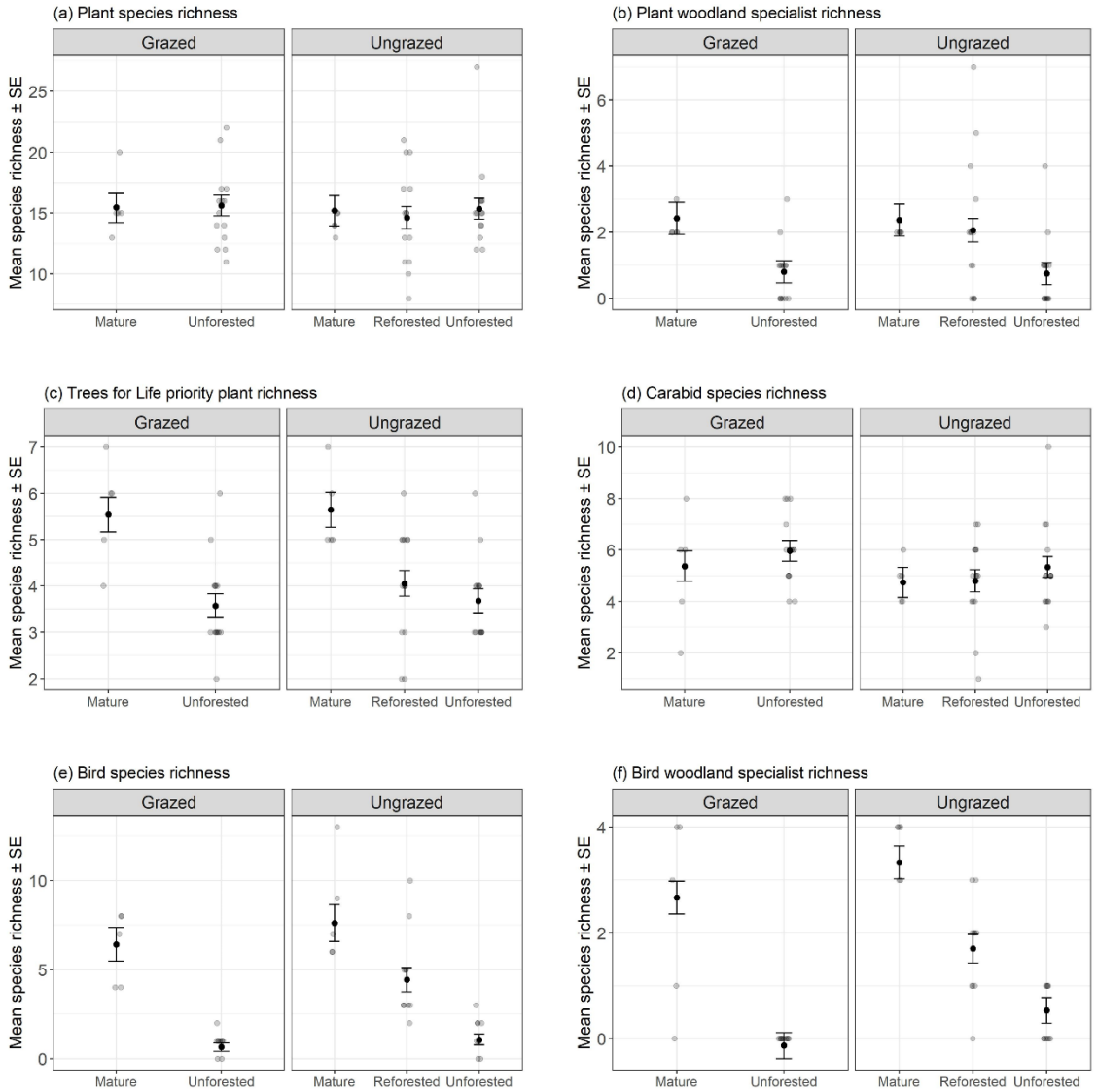


Figure 2.1 Comparisons of species richness among forest*grazing categories for plants, plant woodland specialists and Trees for Life priority plants (a, b, c), carabid beetles (d), and birds and bird woodland specialists (e, f). All estimates and standard errors were extracted from the models.

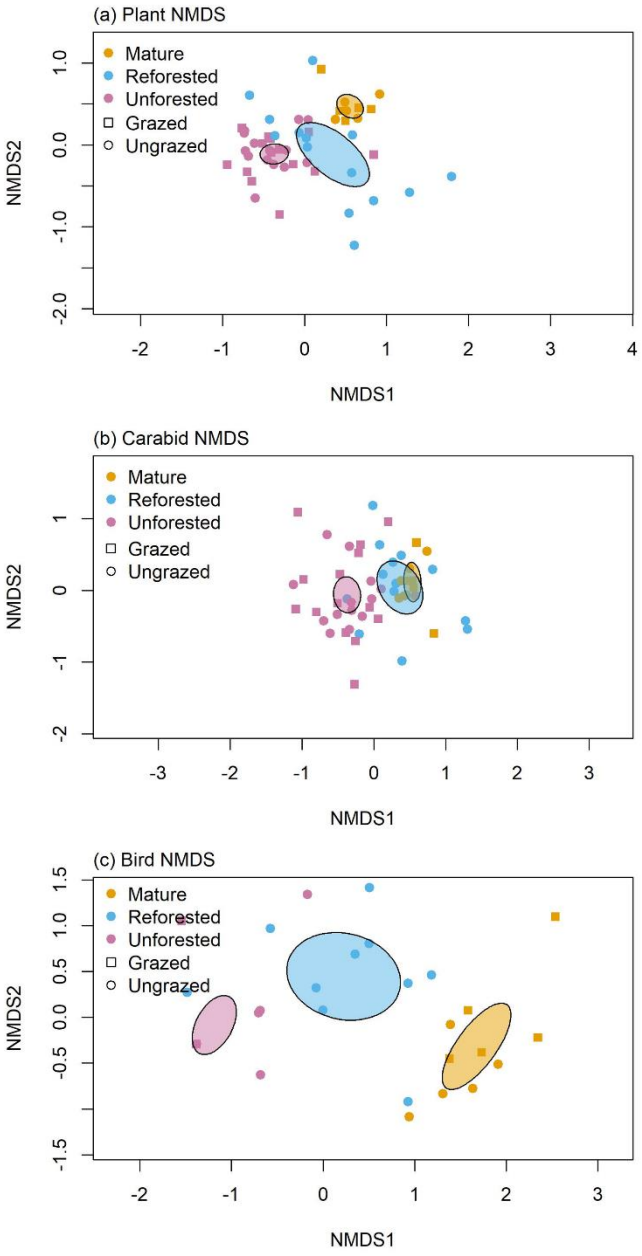


Figure 2.2 Species assemblage comparisons for (a) plants, (b) carabids and (c) birds, based on NMDS with the 95% confidence interval of the centroid plotted for each forest category.

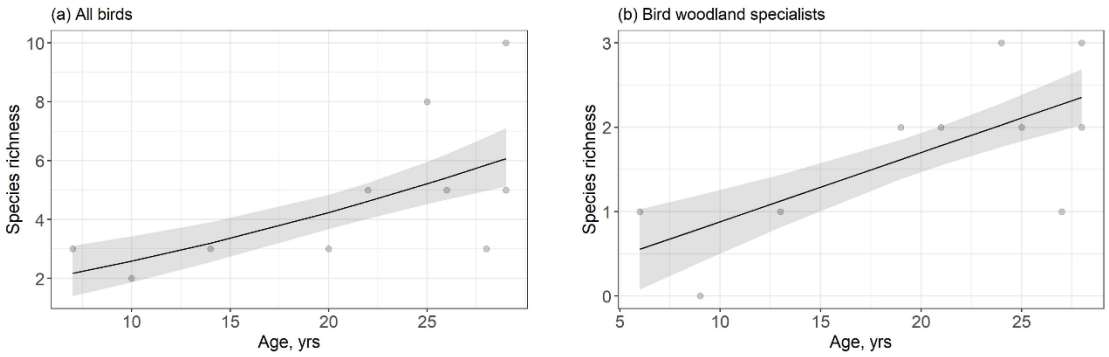


Figure 2.3 Relationship between site age and species richness for (a) all birds and (b) bird woodland specialists, reforested plots only (n = 10). Model fit ± SE extracted from the models.

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 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.

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 timescales, with realistic long-term targets to account for ecological lags (H. P. 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 timescale 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, Blackburn, Whyatt, Kirby, & Smart, 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 (R. . 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 (Fig. A12). 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 (Figs A7 & A14). 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 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.

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, Paterson, Metzger, & Sing, 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 allows 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 boggier heathland habitat (Figs A7 & A14) 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, Wilson, Browne, & Vickery, 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, Groom, & Douglas, 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, Wilson, & Beeley, 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 (Scottish Natural Heritage, 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 (Scottish Natural Heritage, 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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Chapter 3 Does restoring native forest restore ecosystem functioning? Evidence from a large-scale reforestation project in the Scottish Highlands.

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Authors' contributions

EW conceived the idea and led the analysis and writing; EW, OL, AH, NB designed the study and analysis; AM, DG helped to define the research focus and provided background information; EW, RG collected the data; all authors contributed to manuscript drafts and approved the final version.

Data availability: Data available via the NERC Environmental Information Data Centre https://doi.org/10.5285/b76223dd-28ae-4b0e-acd3-3b2104eaae0c (Warner et al., 2021).

Abstract

Given the worldwide plans for extensive tree planting we urgently need to understand how and where implementation will contribute to goals such as those for carbon sequestration. We used a long-term, large-scale native reforestation project in the Scottish Highlands to assess the response of carbon storage and other ecosystem functions to reforestation and grazing exclusion. We measured aboveground carbon, topsoil carbon, topsoil nitrogen, decomposition rates, soil invertebrate feeding activity, tree regeneration, and ground-layer and moss height at 14 sites that are in the early stages of reforestation and fenced to exclude grazing. Reforestation areas were compared to unforested and mature forest areas that are both grazed and ungrazed, using 10 × 10 m plots. Aboveground carbon in the reforestation plots (1.4 kg/m^2 [95% CI: 0.6, 2.6], average age 20 years since reforestation) was c. 8% of the mature forest plots (17.1 kg/m^2 [13.1, 21.8]). Topsoil carbon was lower in the reforestation plots (18.78 kg/m^2 [11.79, 25.78]) than in the unforested (29.82 kg/m^2 [24.34, 35.29]) or mature forest (31.39 kg/m^2 [22.91, 39.88]) plots. Responses of other functions to the reforestation and grazing interventions varied. Our results suggest that reforestation may trigger carbon loss from areas with high initial soil carbon even with low disturbance establishment, at least in the short term. Our work emphasises where we lack knowledge: on the potential for long-term re-accumulation of soil carbon under semi-natural native reforestation, soil carbon sequestration in the deeper soil layers and the response of soil carbon to natural regeneration.

Key words

Reforestation, forest restoration, forest expansion, ecosystem functioning, soil carbon

Implications for practice

- Loss of soil carbon may occur even with low-density native reforestation, established with low disturbance techniques. This emphasises a need to understand routes of soil carbon loss during the early stages of reforestation, particularly the role of biotic processes.
- Changes in ecosystem functions documented in tree planting experiments may not be observed or may take longer to emerge under the less-controlled conditions of actual reforestation projects.
- In future reforestation projects, baseline soil carbon surveys and ongoing monitoring of carbon accumulation are recommended to ensure accurate carbon accounting and to provide a clearer understanding of the soil carbon trajectory after reforestation.

Introduction

There is a global pledge to restore 350 million hectares of degraded forest, with multiple anticipated benefits, including carbon storage, biodiversity conservation and livelihood enhancement (Dave et al., 2017). Forest expansion receives particular attention as a climate change mitigation strategy (Seddon et al. 2019). Given these initiatives we urgently need scientific research on how reforestation can best be done and where it is most effective (Di Sacco et al. 2021).

In the UK, the Committee on Climate Change recommends planting c. 30,000 hectares a year to increase tree cover to 17% by 2050 and contribute to the country's net-zero target (Committee on Climate Change 2020). Forest cover in the UK is currently c. 13%, rising from a minimum of c. 5% at the beginning of the 20th century, covering 19% of Scotland, 15% of Wales, 10% of England, and 9% of Northern Ireland (Forest Research 2020). The UK government has so far failed to meet annual planting targets; in 2019-2020 only 13,660 ha of new forest was planted, more than 80% of which was in Scotland, where historically forest expansion has occurred most rapidly in the UK (Forest Research 2020; HM Government 2020).

An analysis of global reforestation pledges suggests that restoring natural forest would store up to 42 times more carbon than plantation forest and provide greater co-benefits, such as habitat for associated native species (Lewis et al. 2019). A key portion of forest carbon is stored in the soil, c. 60% of total carbon in temperate forests, with forest soils storing close to half of global terrestrial organic carbon (Mayer et al. 2020). Forest restoration and expansion for climate change mitigation intends to enhance existing stores of carbon, but the outcome will depend on the location and type of forest establishment (Matthews et al. 2020). With forest growth carbon accumulation occurs aboveground, but the net outcome depends on the rate of tree growth and changes to soil carbon. Prior land-use influences this: afforestation of former cropland leads to the greatest carbon accumulation whereas forest establishment on peatland leads to carbon losses (Thomas et al. 2015). Soil disturbance during

forest establishment can drive net carbon losses, but can potentially be compensated for by carbon accumulation aboveground and inputs belowground with tree growth (Vanguelova et al. 2013; Mayer et al. 2020).

It is widely recognised that forest establishment on deep peat (depth more than 50 cm) leads to overall carbon losses through soil disturbance and drying (Morison et al., 2012; Vanguelova et al., 2018). The outcome on shallow peats is less well understood (Vanguelova et al. 2018). Semi-natural forest, which will not be disturbed by harvesting, might provide a more certain carbon stock on these soil types, but modelling suggests that due to slower growth it takes longer to re-accumulate carbon lost during initial disturbance (Matthews et al. 2020). Even with low disturbance planting, native reforestation on carbon-rich soils can result in no net carbon storage after 39 years, as a consequence of soil carbon losses (Friggens et al. 2020). In the UK, soil carbon stocks are 86 times greater than the vegetation carbon store and the most carbon-rich soils are disproportionately found in Scotland (Milne & Brown 1997; Vanguelova et al. 2018). The Scottish uplands provide opportunities for forest expansion; however carbon-rich soils occur in the uplands and there is mixed evidence on the impact of reforestation on net carbon balances in these areas (Friggens et al. 2020; Matthews et al. 2020; Vanguelova et al. 2018).

Assessing the impact of forest expansion requires more than quantification of aboveground and belowground carbon stocks. It is important to monitor how other ecosystem functions respond, giving a wider view of the value of the new habitat for humans and other organisms (Kollmann et al. 2016). Tree establishment on heather moorland has been shown to influence belowground properties and processes, altering soil structure and functions, for example by increasing nutrient availability, decomposition rates and the abundance of soil fauna (Kollmann et al. 2016; Mitchell et al. 2007). Aboveground, the structure and composition of the vegetation determines habitat provision and the future of a reforested ecosystem depends on tree regeneration (Mitchell et al. 2012; Patterson et al.

2014). To provide a more holistic understanding of the impact of forest establishment we measured soil nitrogen, decomposition rates, soil invertebrate feeding, tree regeneration and vegetation structure. Changes in decomposition rates provide additional background to understand any changes in soil carbon and soil nutrient availability, which will be indicated by soil nitrogen levels. Soil invertebrate feeding provides a proxy to assess the abundance and activity of the soil fauna community. Tree regeneration is crucial to the continued development of the reforestation sites. Finally, we measured vegetation structure to quantify habitat provision and responses to grazing exclusion; in the Scottish Highlands high deer numbers generally prevent tree regeneration, such that grazing exclusion is necessary to facilitate forest restoration (Tanentzap et al. 2013).

We used a long-term large-scale native reforestation project in the Scottish Highlands to assess the effect of grazing exclusion and native reforestation on carbon storage and a suite of other ecosystem functions. Given that existing data on native reforestation in this context is primarily from experimental studies (e.g. Mitchell et al. 2007; Friggens et al. 2020), we use a conservation-focussed reforestation project that reflects likely future native reforestation in the Scottish uplands. Comparisons were made between ungrazed, reforestation sites and unforested and mature forest areas that are both grazed and ungrazed. We assessed (i) the impact of forest status (unforested, reforestation, mature) and grazing (grazed, ungrazed) on aboveground and topsoil carbon storage; (ii) the impact of the forest and grazing treatments on topsoil nitrogen, decomposition rates, soil invertebrate feeding, tree regeneration and vegetation structure; and (iii) the effect of reforestation site age on aboveground and topsoil carbon storage.

Methods

Study area

The reforestation sites are located in 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), adjacent glens in the Scottish Highlands (Fig. B1 in Appendix B) (Warner et al. 2021). These landscapes contain multiple habitats, including mature Caledonian pinewood, productive conifer plantations, unforested heathland and regenerating native forest. The unforested parts of the wider landscape are thought to have experienced a decline in forest cover driven by human and climatic influences from c. 3,800 years ago (Tipping et al. 2006). The mature forest is part of one of the largest Caledonian pinewood remnants, with trees up to 260 years old (Mason et al. 2004). Our study used fourteen reforestation sites that were planted and fenced to exclude grazing, predominantly by Red, Roe and Sika deer (*Cervus elaphus*, *Capreolus capreolus*, *Cervus nipon*) and feral Wild boar (*Sus scrofa*). The sites were established between 1990 and 2012 by Trees for Life, Forestry Commission Scotland, and the National Trust for Scotland (Table B1 in Appendix B). We classified the fenced areas as "ungrazed", although as permeability to deer increases as the fences age, grazing is reduced rather than totally excluded at most "ungrazed" sites. Reforestation sites were replanted with native Caledonian pinewood species, cultivated from local provenance seed (Table B1). At each site, planting was predominantly targeted to well-drained areas, with some wet areas planted with *Alnus glutinosa* and *Salix* spp.. Tree cover at each site is heterogenous, as the success of tree establishment varied depending on drainage and topography. Further information on the study system including biodiversity data is reported by Warner et al. (2021).

Study design

Our study has a fractional factorial design in which combinations of two treatments are replicated across multiple locations. Sites are the 14 locations where reforestation has occurred, with nearby unforested reference habitat present at each site. All possible combinations of the treatments forest

status (unforested, reforestation, mature) and grazing status (grazed, ungrazed) are represented in our study, excluding reforestation × grazed, which does not exist because tree regeneration is suppressed by deer grazing in the wider landscape. 10 × 10 m plots were established within each treatment combination (Table 3.1, Fig. B2). In the study landscape, mature Caledonian pinewood is of limited extent. Mature forest was therefore only associated spatially with three reforestation sites. Grazed and ungrazed mature forest plots were established at these three sites and a further two pairs of grazed and ungrazed mature forest plots at two of the sites, at least 500 m from the other mature forest plots, in non-contiguous areas of mature forest (Fig. B1). This gave a total of five pairs of ungrazed and grazed mature forest plots (Table 3.1). This design allowed the effect of forest (unforested, reforestation, mature) and grazing (ungrazed, grazed) status on the ecosystem functions to be assessed.

Table 3.1 Sample sizes in each forest × grazing category for the ecosystem functions measured.

	Unforested	**Reforestation**	**Mature**
Ungrazed	14*	14	5
Grazed	14*		5

*At two sites it was not possible to extract soil cores, so for soil carbon and nitrogen the sample size is 12.

As reforestation success was heterogeneous, plots were placed to represent the best-case scenario of forest establishment at a site (reforestation, ungrazed). At each site, an unforested, grazed plot was established, at the nearest location to the reforestation, ungrazed plot, matched on topography, aspect and elevation. A plot in the nearest unforested, ungrazed area was also established at each site. Plots in the mature forest were matched to the reforestation and unforested plots at these sites. At each site, the plots were 30-400 m apart.

Aboveground tree carbon

The diameter at breast height (dbh) was recorded for every tree with dbh greater than 2.5 cm in each plot. For multi-stemmed species every stem greater than 2.5 cm dbh was recorded. Plot level estimates of aboveground biomass were calculated using species specific allometric equations (Table B2). *Betula* and *Salix* spp. were identified to genus level, and the allometric equations developed for *Betula pendula* and *Salix caprea* were used. For *Sorbus aucuparia* and *Salix caprea* equations for aboveground biomass were not available, so allometric equations for stem biomass were used. Where multiple allometric equations were available an equation developed in the UK or with the highest R^2 value was used (Muukkonen & Mäkipää 2006; Zianis et al. 2005). Biomass was converted to carbon (kg/m^2) based on carbon concentrations of 49% for broadleaves and 50% for conifers (Matthews 1993).

Topsoil carbon and nitrogen

Soil samples were taken using a 3 cm diameter soil corer from the top 10 cm of the soil, directly below any undecomposed litter. Soil was sampled at this depth as the surface layers were expected to be most sensitive to the change in land-use. At two unforested, ungrazed plots and two unforested, grazed plots it was not possible to extract intact soil cores due to the wet ground, so the sample sizes for these two categories are n = 12. Three cores per plot were homogenised to provide a sample for analysis of total carbon and nitrogen and three additional cores were used to calculate bulk density. The height of each bulk density core was measured to the nearest mm on sampling. The samples for carbon and nitrogen analysis were air dried to remove residual moisture and sieved using a 2 mm sieve. The air dried and sieved samples were sent to Forest Research, Alice Holt Lodge, Surrey, UK for analysis. Percentage soil carbon and nitrogen were estimated simultaneously by combustion using a Carlo Erba CN analyser (Flash1112 series), following the ISO 10694 protocol (International Organization for Standardization, 1995) and the ISO 13878 protocol (International Organization for Standardization 1998). Samples were ball milled for homogenisation at mg level. Approximately 30

mg of milled soil was weighed in a tin capsule using a 6 decimal balance and then pressed, before being analysed. The bulk density samples were dried at 105^{o}C for 24 hr and sieved through a 2 mm sieve, bulk density (g/cm^{3}) was calculated based on the dry weight of the sample and the volume of soil collected. Bulk density and percentage soil carbon and nitrogen were used to estimate soil carbon and nitrogen stocks (kg/m^{2}) in the top 10 cm of the soil in each grazing × forest category.

Decomposition rate

The decomposition rate constant, *k*, was calculated using the Tea Bag Index (Appendix C) (Keuskamp et al. 2013). In each plot six pairs of teabags (faster decomposing green tea and slower rooibos) were buried at 8 cm depth in random locations. Prior to burial the bags were weighed. The bags were left buried for a minimum of 54 and up to 67 days (mean ± SE, 61.6 ± 0.17 days). On collection the bags were dried at c. 70^{o}C for 2 hours and subsequently air dried for 48 hours to stop the decomposition process. Prior to weighing to estimate the final mass of the bags, the bags were dried at 70^{o}C for 24 hours.

Soil invertebrate feeding

Soil faunal feeding was measured in the top 12 cm of the soil using bait lamina (Terra Protecta GMbH, Berlin, Germany). Bait lamina are PVC strips (1 mm × 6 mm × 120 mm) with 16 1.5 mm perforations that are impregnated with a bait substrate composed of cellulose powder, wheat bran and activated charcoal (70:23:7) (Kratz 1998). In each plot six bait lamina were inserted into the soil in a 3 × 2 grid with 3 cm spacing. At 15 days two strips were removed to assess the appropriate exposure period. After 30 days the remaining bait lamina were removed. Feeding activity at each perforation was recorded if light penetrated the bait material. For analysis, feeding was assessed at the level of each bait lamina stick, generating a binary response variable: feeding or no feeding, using the four bait sticks assessed at day 30.

Tree regeneration

In each plot all young trees with dbh less than 2.5 cm were recorded in the height categories: less than 50 cm, 50 to less than 100 cm, 100 to less than 150 cm, and more than or equal to 150 cm, for each species.

Ground-layer & moss height

Three 1 × 1 m quadrats were placed randomly in each plot. The height of the ground vegetation and depth of the moss layer were measured at five points evenly distributed across the diagonal of the quadrat.

Data analysis

All statistical analysis was carried out using R (R Core Team, 2020). The study design is a fractional factorial combination of the two factors forest (unforested, reforestation, mature) and grazing (grazed, ungrazed), where the grazed × reforestation combination is absent (Table 3.1). Linear and generalized mixed-effect models were fitted using the package *lme4* (Bates et al. 2015), testing fixed effects for forest (unforested, reforestation, mature) and grazing (grazed, ungrazed) and the forest × grazing interactions on each ecosystem function (Table 3.2, Table B3), with a random effect for site (a factor with 16 levels). Where the forest × grazing status interaction was not significant it was removed from the model for simplicity, this was the case in all models except the tree regeneration model. As the unforested plots contained no trees with dbh greater than 2.5 cm, the analysis of aboveground tree carbon only included the reforestation and mature forest treatments. An extreme outlier (k = 0.091) was removed from the decomposition rate constant dataset; all other values fell in the range 0.0076 to 0.035 and this result is assumed to reflect a data processing error. To test the effect of time since reforestation on aboveground tree and topsoil carbon, linear models were fitted using the chronosequence of reforestation plots (Table 3.2). Additional analyses of the topsoil carbon data were carried out: linear models were used to test the effect of plot type (a factor with five levels

representing each forest × grazing combination) on topsoil carbon and the effect of site age on the difference in topsoil carbon between reforestation, ungrazed and unforested, grazed plots at each site. Where estimates and 95% confidence intervals are given for levels of the forest or grazing treatment alone, these were derived from models fitted with the forest or grazing term only.

Table 3.2 The model structures used in the analysis of each ecosystem property. Models to assess the effect of time since reforestation on tree carbon, topsoil carbon and the topsoil carbon difference were fitted using data from the reforestation sites only. Response variables are given to the left of the tilde (~), fixed-effects for explanatory variables on the right and random effects for (nested) design variables within parentheses.

Model	Units	Error structure
sqrt(Tree carbon) ~ Forest + Grazing + (1|Site)	kg/m^2	Normal
Topsoil carbon ~ Forest + Grazing + (1|Site)	kg/m^2	Normal
Topsoil nitrogen ~ Forest + Grazing + (1|Site)	kg/m^2	Normal
Decomposition rate constant (k) ~ Forest + Grazing + (1|Site)		Normal
Feeding versus no feeding ~ Forest + Grazing + (1|Site/Plot)		Binomial (logit link)
Seedlings per plot ~ Forest * Grazing + (1|Site)		Poisson (log link)
Ground layer height ~ Forest + Grazing + (1|Site)	cm	Normal
Moss depth ~ Forest + Grazing + (1|Site)	cm	Normal
ln(Tree carbon) ~ Site age	kg/m^2	Normal
ln(soil carbon) ~ Site age	kg/m^2	Normal
Topsoil carbon ~ Plot type + (1|Site)	kg/m^2	Normal
Topsoil carbon difference reforestation, ungrazed vs. unforested, grazed ~ Site age	kg/m^2	Normal

Results

Carbon storage

Aboveground tree carbon was an order of magnitude higher in mature forest plots (17.1 kg/m^2 [95% CI: 13.1, 21.8]) than in the reforestation plots (1.4 kg/m^2 [0.6, 2.6], average age 20 years since reforestation) (Fig. 3.1a). There was no effect of grazing on aboveground tree carbon (grazed, mature 16.5 kg/m^2 [11.1, 22.9] vs. ungrazed, mature 17.9 kg/m^2 [12.2, 24.6]). Aboveground tree carbon accumulated over the chronosequence of reforestation sites, with a clear relationship between aboveground tree carbon and time since reforestation (effect of age on ln(tree carbon) 0.13 [0.06, 0.2]) (Fig. 3.2a).

Topsoil carbon was lower in the reforestation plots (18.78 kg/m^2 [11.79, 25.78]) than in the mature forest (31.39 kg/m^2 [22.91, 39.88]) and unforested (29.82 kg/m^2 [24.34, 35.29]) plots (Fig. 3.1b). There was no effect of the grazing treatment on topsoil carbon (4.02 kg/m^2 [−4.69, 12.73]). When comparing topsoil carbon by plot type, the difference between reforestation, ungrazed and unforested, grazed plots was less clear (8.83 kg/m^2 [−1.37, 19.02]) (Fig. B3a). There was no clear effect of time since reforestation on topsoil carbon (effect on ln(topsoil carbon) −0.0049 [−0.056, 0.046]) (Fig. 3.2b) or on the difference in topsoil carbon between the reforestation, ungrazed and unforested, grazed plots (effect on topsoil carbon difference 0.38 [−1.13, 1.89]) (Fig. B3b), suggesting no accumulation of soil carbon over the chronosequence.

Soil properties and processes

Soil nitrogen was higher in the ungrazed plots than the grazed plots (mean difference 0.40 kg/m^2 [95% CI: 0.062, 0.74]) (Fig. 3.1c). Soil nitrogen was higher in the unforested plots than the reforestation plots (0.60 kg/m^2 [0.22, 0.97]).

The decomposition rate was higher in the unforested plots (0.0151 [0.0142, 0.0160]) than mature forest plots (0.0136 [0.0123, 0.0150]) (Fig. 3.1d). There was no clear difference in the decomposition rate in the reforestation plots (0.0146 [0.0135, 0.0157]) compared to mature and unforested plots.

Soil invertebrate feeding activity was lower in the reforestation plots (0.080 [0.021, 0.26]) than in the mature (0.42 [0.15, 0.75]) or unforested (0.53 [0.32, 0.73]) plots, and higher in ungrazed than grazed plots (Fig. 3.1e).

Tree regeneration and ground layer vegetation structure

Tree regeneration was higher in the mature forest (54 seedlings per plot [95% CI: 19, 89]) and reforestation plots (9 [3, 14]) than in the unforested plots (1 [0.5,2]) (Fig. 3.1f). There was an interaction between grazing and forest status, the grazed mature plots had more seedlings than the ungrazed mature plots (70 [24, 116] vs. 38 [13, 62]). No seedlings taller than 1 m were found in the grazed plots (Fig. B4).

The ground layer vegetation was taller in the mature (31.1 cm [24.2, 38.2]) than reforestation (27.0 cm [19.9, 34.1]) and unforested (19.7 cm [15.4, 23.9]) plots, and taller in the ungrazed (26.5 cm [21.9, 31.0]) than grazed (18.4 cm [13.3, 23.6]) plots (Fig. 3.1g). The depth of moss was thicker in the ungrazed (6.45 cm [5.1, 7.8]) than grazed (3.4 cm [1.8, 5.0]) plots, and thinner in the reforestation (4.5 cm [2.6, 6.4]) than mature (7.17 cm [4.96, 9.39]) plots (Fig. 3.1h).

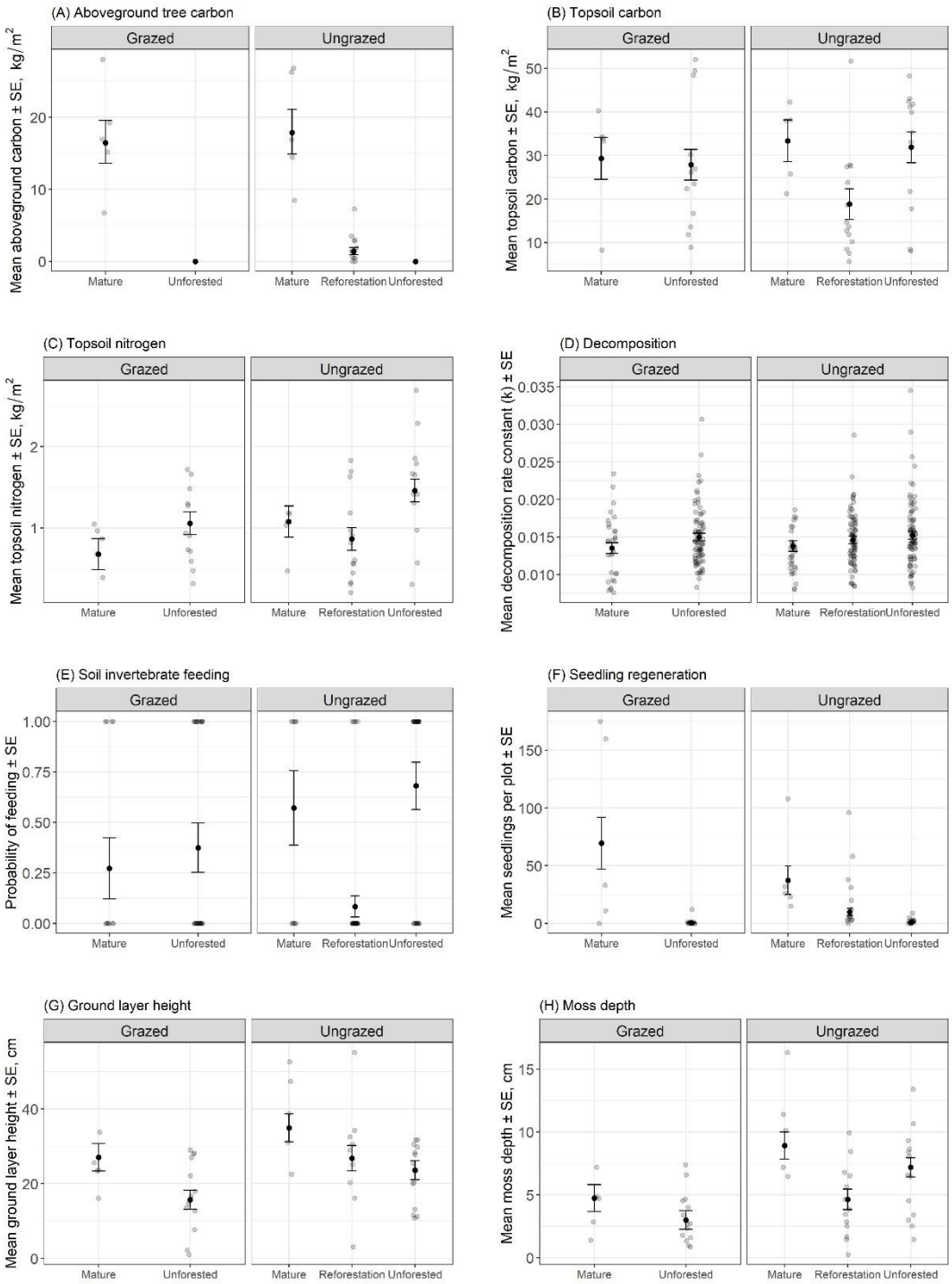


Figure 3.1 The response of each measured variable to the forest × grazing treatments. (a) Aboveground tree carbon, (b) topsoil carbon, (c) topsoil nitrogen, (d) decomposition rate, (e) soil invertebrate feeding, (f) seedling regeneration, (g) ground-layer height and (h) moss depth. Estimates and standard errors were extracted from the models.

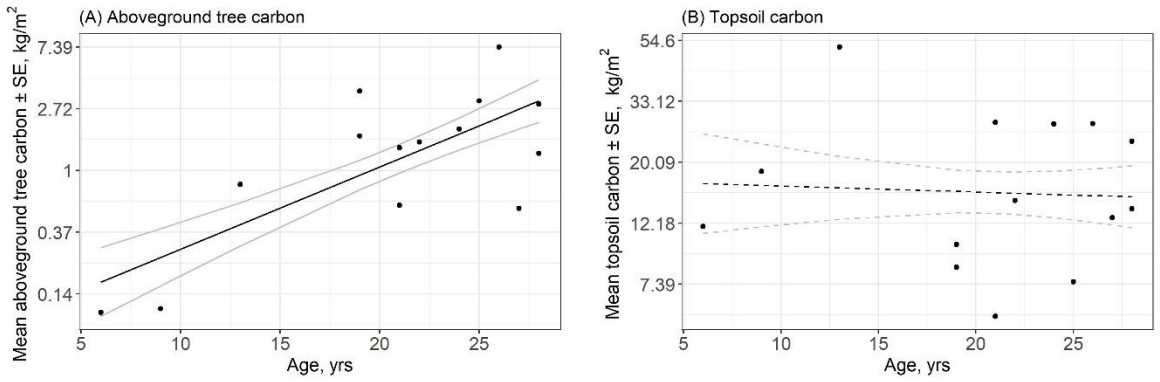


Figure 3.2 Changes with time-since-reforestation (a) aboveground tree carbon and (b) topsoil carbon across the chronosequence of reforestation plots (log-scales). Non-significant trends are shown with dashed lines.

Discussion

Carbon balance

A possible reason for the lower topsoil carbon in the reforestation plots relative to unforested plots is soil carbon loss following reforestation. No baseline measurements were taken prior to reforestation, so unforested areas represented the pre-reforestation state. With relatively slow tree growth aboveground and no trend in soil carbon accumulation over the chronosequence of sites, this suggests net loss of carbon in the early stages of reforestation.

Soil carbon losses following forest establishment are expected in locations with high initial soil carbon and semi-natural vegetation cover, often driven by soil disturbance (Mayer et al. 2020). Tree planting on deep peats is avoided to prevent release of carbon from the soil, and emerging evidence suggests negative impacts of planting on carbon-rich organic soils, such as those at our study sites (Friggens et al., 2020; K. B. Matthews et al., 2020; Morison et al., 2012; Vanguelova et al., 2018). An experimental study in Scotland, assessing the effect of planting native trees (*Betula* spp. or *Pinus sylvestris*) in single species plots on moorland with organic soils, found soil carbon loss 12 and 39 years after planting, resulting in no net increase in total ecosystem carbon at any sites and a decline at one site (Friggens et al. 2020). In Friggens et al. (2020) the planting density was 40,000 trees per hectare (39 year old sites) and 10,000 trees per hectare (12 year old site). Our study sites had initial densities of 119-1,549 trees per hectare, with the density in study plots 1,100-5,100 trees per hectare, reflecting the initial planting and subsequent natural regeneration; the signs of significant soil carbon loss at these lower planting densities are notable. Medium and high productivity production forests on peaty soils can achieve net soil carbon storage over multiple production cycles, c. 100 years after the first planting event, with losses from the peat horizon compensated for by inputs to the upper fermentation horizon (Mayer et al. 2020; Vanguelova et al. 2019). Variable, but in some cases significant, amounts of aboveground carbon were accumulated within the first 30 years of reforestation in our study; the highest aboveground carbon recorded was at the 26-year-old site (7.3 kg/m^2), while the oldest sites

(28 years old) had 1.2 and 2.8 kg/m^2 of aboveground carbon. With a trajectory of carbon accumulation aboveground in the reforestation sites, we would expect aboveground carbon to increase to the levels seen in the mature forest in our study.

Soil disturbance during forest establishment can cause soil carbon loss, driven by erosion, oxidation, decomposition and leaching (Vanguelova et al. 2018; Mayer et al. 2020). Extensive disturbance during establishment of production forest leads to large soil carbon losses, whereas hand planting disturbs c. 2% of the soil, causing smaller soil carbon losses (Vanguelova et al. 2018). Most of our study sites were hand planted, but the three youngest sites were prepared by machine mounding (a digger inverted small mounds of soil into which the trees were planted). There was no evidence for lower topsoil carbon at these three sites and one had the highest soil carbon recorded.

Biotic factors also determine the soil carbon balance and there is evidence that tree establishment can alter the soil microbial and mycorrhizal fungi communities, influencing the carbon balance, which may explain soil carbon losses at our study sites. Microbes play a key role in soil carbon storage, transforming labile carbon into more stable forms, while microbial respiration and breakdown of carbon by extracellular enzymes can contribute to carbon loss from the soil (Wiesmeier et al. 2019; Mayer et al. 2020). The experimental investigation of tree planting on organic soils found higher soil respiration at the sites planted with trees compared to heather moorland, potentially explaining the loss of soil carbon (Friggens et al. 2020). A hypothesis is that this was driven primarily by a shift in the mycorrhizal fungi community and stimulation of the soil microbial community by recent carbon inputs into the soil (Brzostek et al. 2013; Friggens et al. 2020). Further work suggests that nitrogen mining by ectomycorrhizal fungi can drive higher turnover of soil carbon stocks under forest soils (Clemmensen et al. 2021).

Our study is limited by a lack of baseline data. The literature supports the hypothesis that the lower topsoil carbon in the reforestation sites represents loss of soil carbon, particularly as the study sites have peaty soils and were previously vegetated (Friggens et al. 2020; Guo & Gifford 2002; Matthews et al. 2020). We matched the unforested plots representing the baseline condition to the reforestation plots, but we cannot rule out that the reforestation sites had lower soil carbon prior to reforestation. For example, drier areas of the reforestation sites were targeted for planting and the unforested, ungrazed plots may not represent the prior condition as well as the unforested, grazed plots, where we were less constrained in matching these to the reforestation plots. We found a less clear difference in topsoil carbon between the unforested, grazed plots and the reforestation plots, with the 95% confidence interval including zero, although extending to 19 kg/m^2 (−1.37, 19.02 kg/m^2). If the reforestation sites had lower initial soil carbon than the ungrazed areas, then the aboveground accumulation of biomass in the trees will lead to net carbon gain. These challenges in interpretation highlight the need to monitor soil carbon within reforestation projects.

Soil samples taken to greater depths and a larger number of samples from each site would provide a clearer picture of overall carbon changes and allow soil carbon to be quantified within each soil horizon (Vanguelova et al. 2016). This would also allow us to assess whether losses in the upper horizons were compensated for by inputs at greater depths (Vanguelova et al. 2018). Additionally, as reforestation at our study sites is heterogeneous, an overall assessment of the carbon balance would need to consider soil carbon and the variable tree establishment success and growth rates across the entirety of each site. More data are needed to understand the long-term response of soil carbon to reforestation, the management factors that influence soil carbon and how strategies such as natural forest regeneration might mitigate the risk of soil carbon loss.

The response of other ecosystem functions

Carbon storage is an important ecosystem service derived from reforestation and explicit target of many reforestation projects (Lewis et al. 2019), but it is important to understand how other functions linked to wider aspects of the ecosystem respond (Aerts & Honnay 2011). Reforestation has the potential to influence multiple belowground processes, with consequences for soil quality and the soil community (Amacher et al. 2007; Ashwood et al. 2019; Jackson et al. 2000). Aboveground, the future of the forest will depend on the regeneration of seedlings (Cook-Patton et al. 2020; García et al. 2020) and the structure of the understorey can be important in determining habitat availability (Fuller et al. 2018).

As planted *Betula pubescens* establishes on moorland in Scotland it can trigger changes to soil properties. For example, increasing fertility, decomposition rates and the availability of mineralizable nitrogen (Mitchell et al. 2007; Mitchell et al. 2010). We found that soil nitrogen was highest in the unforested areas and higher in the ungrazed than grazed areas, giving no indication that nitrogen availability has increased with forest establishment.

Decomposition rates in our study were highest in the unforested and lowest in the mature forest areas, with rates in the reforestation areas not clearly different from the other two habitats. There is evidence that tree-associated mycorrhizal fungi can increase decomposition of litter in the soil (Clemmensen et al. 2021). The trends in decomposition rates across habitat types do not correspond with this, however. But it would be valuable to confirm our decomposition rates over a longer time period.

Forest establishment on moorland in Scotland led to an increase in the abundance of soil predators such as nematodes and increased microarthropod abundance (Mitchell et al. 2007; Mitchell et al.

2010). This contrasts with the results of our bait lamina experiment, which found lower invertebrate feeding activity at the reforestation sites.

Seedling regeneration occurred at very low levels in the unforested plots, despite these plots being located within 400 m of reforestation sites. Grazing intensity by deer and ground cover favourability are more important than presence of a seed source for *Betula* spp. regeneration in the Scottish Highlands (Tanentzap et al. 2013). In our study, in the grazed, unforested areas deer grazing pressure negatively impacts seedling regeneration and in the ungrazed, unforested areas the higher ground vegetation due to grazing release may suppress seedling regeneration. In the grazed, mature plots high abundances of seedlings, particularly *Sorbus aucuparia* in one plot, were found despite the grazing pressure, potentially reflecting seed dispersal by birds, but were restricted to the smallest height categories, highlighting the threat that grazing presents in mature woodland (García et al. 2020).

The ground vegetation and moss layer were lower in the reforestation plots. This could reflect low light availability under the typically denser tree cover in these plots (Dormann et al. 2020). A tall ground layer dominated by ericaceous shrubs and a thick moss layer is characteristic of mature Caledonian pinewood, but the reforestation sites do not appear to have developed these, despite characteristic species being present (Mason et al. 2004; Warner et al. 2021). Development of the understorey will play a key role in forest functioning, as well as providing food, habitat and shelter for a range of organisms (Landuyt et al. 2019).

The less clear directional shift in belowground functions and processes in our study compared to the experimental investigation may reflect the contrast between a controlled experimental study with high-density single species planting (40,000 trees per hectare) and our study assessing lower density reforestation (1,100-5,100 trees per hectare in study plots) across a more heterogeneous landscape

(Mitchell et al. 2007; Mitchell et al. 2010). Despite this, the conservation project used in our study might better represent planned native reforestation in the Scottish Highlands. We suggest that the results from experimental studies must be upscaled with caution in predicting likely outcomes from real world reforestation projects.

Planning future reforestation

The reforestation project studied here began in 1990 with the objective of restoring areas of native Caledonian pinewood. During its lifetime, interest in forest expansion has grown globally, including in the UK, where expansion has occurred most quickly in Scotland (Forest Research 2020). Forest expansion usually aims to meet multiple objectives, but carbon storage is often a key priority. This study contributes evidence that reforestation on high carbon content soils can lead to net carbon losses in the early stages of reforestation. Soil carbon losses must be monitored in similar projects and losses accounted for, with new research needed to assess how losses can be minimised.

Area based forest expansion targets can provide a risk in meeting carbon sequestration targets if woodland that initially leads to net carbon release is not accounted for in estimates of carbon storage (Matthews et al. 2020). Carbon release from carbon-rich soils is typically attributed to the initial disturbance caused by site preparation. In our study either the minimal soil disturbance is driving soil carbon loss, or other pathways, for example changes to soil fungal and microbial communities, are driving the losses (Brzostek et al. 2013; Friggens et al. 2020). Forest expansion by natural regeneration could reduce impacts on soil carbon, by avoiding soil disturbance and limiting reforestation of peat soils, which are less favourable for seedling establishment (Limpens et al. 2014). However, carbon accumulation aboveground by natural regeneration can be less predictable and impacts on soil carbon are not well understood. To inform forest expansion ambitions in Scotland, future research should aim to understand aboveground carbon accumulation in naturally regenerating forest, the extent to which trees naturally colonise high carbon content soils, and the impact on soil carbon stocks.

Single-criterion objectives for restoration projects risk compromising gains related to other objectives (Strassburg et al. 2020). Caledonian pinewood is a priority habitat for conservation in the UK and its restoration is critical to the maintenance of associated specialist species (Mason et al. 2004). At our study sites the value of the reforestation areas for specialist species has been shown (Warner et al. 2021). Future reforestation with conservation objectives is important and carbon targets should not compromise targets for biodiversity. Nonetheless, these projects should be designed in a way to minimise soil carbon release and carbon accounting must be conducted accurately.

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Chapter 4 Integrating research into rewilding from outset to outcome

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Authors' contributions

EW conceived the idea, OL & AH helped to develop the manuscript. EW led the writing with feedback from OL & AH.

Abstract

Rewilding is receiving increasing attention as a conservation intervention to tackle the climate and biodiversity crises. But we frequently lack integration of ecological research into rewilding projects. As new rewilding projects begin, we must capitalise on the opportunity to integrate experimental interventions into projects, allowing us to test key unanswered questions. Here we discuss how existing ecological research methods could be integrated into rewilding projects. We highlight the need for development of study designs at the outset of a project and the collection of baseline data. This will help to assemble the evidence base necessary to improve implementation of future rewilding projects.

Keywords

Rewilding, experimental design, monitoring

Highlights

Rewilding can be linked to existing concepts within ecology. But despite having relevant ecological understanding and methods, ecological research is rarely integrated into rewilding projects and there is no cohesive approach to monitoring.

Considering the monitoring strategy at the outset of a rewilding project is critical, allowing important baseline data to be collected.

Identifying opportunities to integrate experimental manipulations to address research questions and uncertainties should be a key stage during the planning of rewilding projects.

A common framework for monitoring rewilding projects would provide a clearer understanding of how different interventions influence biodiversity, carbon, and ecosystem services.

An ecological research framework for rewilding

Having first arisen as the concept of restoring large interconnected areas of wilderness to support **keystone species** (see glossary, p 88), rewilding has been defined in numerous ways (Pettorelli et al., 2018). A unifying set of principles highlight that rewilding aims to create dynamic **self-sustaining ecosystems**, governed by **natural processes** and implemented at large scales (Carver et al., 2021). These principles link to existing ecological concepts (Fig. 4.1). Despite a clearer understanding of what rewilding is, we lack experimental data exploring the impact of rewilding interventions on the outcomes of rewilding projects (Garrido et al., 2021; Svenning et al., 2016). We need a cohesive framework for integration of experimental manipulation, long-term monitoring and measurement of the outputs in rewilding projects. Existing methods for assessing rewilding projects include remote-sensing and qualitative assessment of indicators of success (Mata, Buitenwerf, & Svenning, 2021; Segar et al., 2021; Torres et al., 2018). But a clearer evidence-base is critical given current proposals that rewilding be used to tackle the climate and biodiversity crises (Svenning, 2020). This could move rewilding up the policy agenda and would ensure its effective implementation (Pettorelli et al., 2018; Svenning et al., 2016). Here we consider the need and opportunities for integration of ecological research into rewilding. We draw on examples from the UK context, where rewilding is an increasingly accepted conservation method (Dempsey, 2021; Sandom et al., 2019).

How do rewilding interventions alter ecological processes?

Although we can define underlying principles that unify all rewilding projects, the interventions used in a specific project are influenced by local factors and the desired outcomes of the project (du Toit & Pettorelli, 2019; Perino et al., 2019). In the UK, rewilding projects are limited by existing patterns of land-use and ownership, with differences in opportunities between upland and lowland landscapes (Loth & Newton, 2018; Sandom et al., 2019; Sandom & Wynne-Jones, 2019). The UK lowlands are dominated by agricultural production, often on high-quality agricultural land; in this context **naturalistic grazing** has been identified as the most acceptable intervention (Loth & Newton, 2018).

In the uplands, agricultural production and forestry dominate, but poor soils and steep slopes mean farming is often marginal (Sandom et al., 2019). Again, in upland areas, naturalistic grazing regimes are a commonly used rewilding mechanism, and there is a particular preference to increase tree cover in these areas (Sandom et al., 2019; Sandom & Wynne-Jones, 2019).

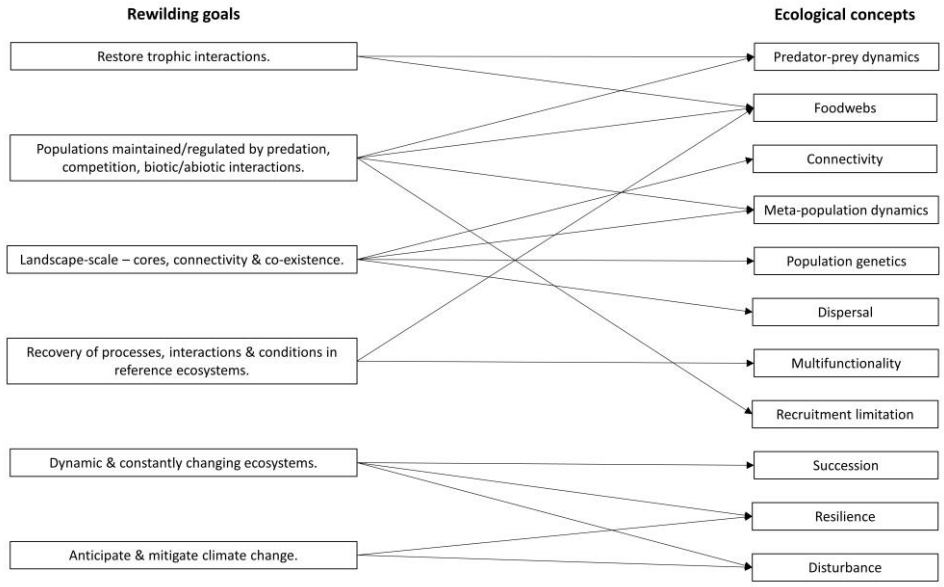


Figure 4.1 The relationship between rewilding goals (left; modified from (Carver et al., 2021)) and ecological concepts (right).

Using the project listings from the UK NGO Rewilding Britain we defined commonly used rewilding interventions in the UK setting (Fig. 4.2) (Rewilding Britain, 2021a). Despite the large number of projects across a range of locations, the variety of interventions is quite low. Manipulation of grazing regimes is a common approach, for example establishing extensive grazing regimes that replace more intensive agricultural grazing, as on the Knepp Estate (Knepp Wildland, 2021), or excluding grazing animals to facilitate **natural regeneration** of scrub and woodland, as in a project in the Scottish Highlands restoring Caledonian Pinewood (Trees for Life, 2021). Tree planting is an additional action that is commonly used in both lowland and upland projects, although the aims overlap with natural

regeneration and this method does not clearly align with some of the rewilding principles. Introducing or reintroducing species is often associated with rewilding. This can take two forms, either translocations of priority species (e.g. water voles) or introduction of keystone species (e.g. beavers) that have a disproportionate influence on an ecosystem or trigger **trophic cascades** (Svenning et al., 2016). In locations that incorporate river systems or have the potential to restore wetter habitats, hydrological restoration, such as removal of artificial drainage or restoration of natural river channels (e.g. naturalisation of Swindale Beck (Natural England, 2016)), and wetland restoration (e.g. Steart Marshes (Rewilding Britain, 2021b)) are also commonly used.

Rewilding interventions influence ecological processes linked to rewilding goals (Carver et al., 2021) (Fig. 4.2). Extensive grazing and grazing exclusion alter the structure and dynamics of the vegetation community, depending on the balance between grazing and natural regeneration (Smit, Ruifrok, van Klink, & Olff, 2015). Large herbivores and keystone species can cause natural disturbance, as can species that trigger trophic cascades (Foster, Barton, & Lindenmayer, 2014; Kuijper et al., 2016; Svenning et al., 2016). Reinstatement of natural processes can enhance abiotic disturbances, for example natural hydrological regimes that allow the influx of floodwater.

A key objective of rewilding projects is to achieve trophic complexity, with a diversity of species interacting at different trophic levels (Perino et al., 2019). Often large herbivores and species at higher trophic levels, such as predators, have been lost from a system, so their reintroduction can increase trophic complexity as well as reinstating natural processes (Foster et al., 2014; Kuijper et al., 2016). Species interactions are important for ecosystem functioning and governing the flows of energy through an ecosystem, but the presence of species in an ecosystem does not guarantee the reinstatement of interactions and their downstream effects (Valiente-Banuet et al., 2015).

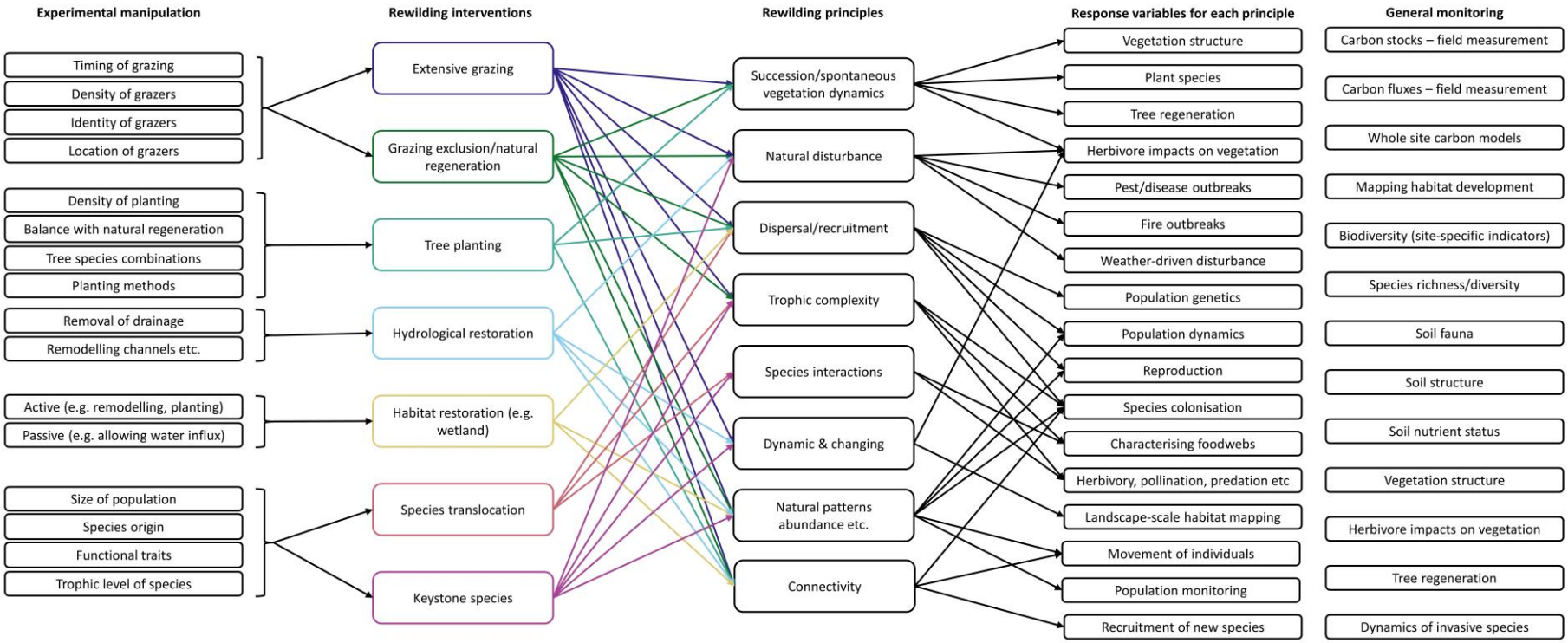


Figure 4.2 A summary of the connections between opportunities for experimental manipulation, rewilding interventions, rewilding principles and response variables to monitor changes linked to each of the principles. The final column suggests more general indicators that can be used for monitoring.

Rewilding can also influence landscape scale dynamics, creating new habitat that increases connectivity, and facilitating dispersal and recruitment (Carver et al., 2021; Perino et al., 2019). Rewilding projects rarely have targets to achieve a specific habitat type and instead aim to generate a dynamic and changing mosaic of habitats, supporting naturalistic communities of species native to the rewilded landscape (Carver et al., 2021).

Integrating science from the outset

Given the multi-faceted nature of rewilding, assessing whether interventions have achieved their objectives can be challenging. Opportunities to collect baseline data, set up a long-term monitoring strategy and integrate experimental manipulations are often missed at the outset of rewilding projects. For example, an assessment of the influence of trophic rewilding on arthropod communities found that experimental work and systematic monitoring was rare, and that where it was conducted there was little consistency between studies, which often lacked control groups (Van Klink & WallisDeVries, 2018). There are examples of observational data collection within established rewilding projects (e.g. Smit et al., 2015), but experimental manipulation addressing specific research questions related to rewilding is rarer (e.g. Garrido et al., 2021). A recently developed qualitative framework allows practitioners to use indicators to assess the extent of human forcing and ecological integrity in a site (Torres et al., 2018). This indicates whether rewilding projects are fulfilling core rewilding objectives and identifies barriers to implementation (Segar et al., 2021). Given the long timescales over which rewilding unfolds, the monitoring of actions rather than outcomes is often all that is tractable within a funding timeframe (Corlett, 2019).

Without baseline data the impact of subsequent monitoring efforts in rewilding projects is reduced. An ideal study design captures response variables before and after the rewilding intervention as well as simultaneously monitoring them in a control site (Before-After-Control-Impact) (De Palma et al., 2018). Our recent study of a rewilding project restoring Caledonian pinewood in the Scottish Highlands

emphasised the challenges of interpreting data on soil carbon without measurements taken before the woodland creation interventions (Warner, Lewis, Brown, et al., 2021). In Box 1 (p 89) we describe the process of fitting a study design onto a rewilding project post-hoc and the opportunities for research within an existing rewilding project, but emphasise the consequent limitations to interpretation. Without data on conditions prior to the rewilding intervention, estimating the impact of the project on the overall ecosystem becomes challenging.

There are three study design features that are crucial to maximising our understanding from long-term monitoring or experiments: controls, replication and randomisation. Controls, which do not receive the rewilding intervention, allow us to understand the extent to which changes recorded are driven by the intervention (Ockendon et al., 2021). The large-scale of rewilding may make the replication of whole studies impractical, but where smaller-scale interventions are applied, replication may be possible (e.g. grazing exclusion plots). Replication within one study site allows more accurate characterisation of response variables and their associated variance. However, experiments would ideally be replicated at multiple study sites to understand the repeatability of an outcome in different contexts (Ockendon et al., 2021). The level of replication should be guided by the expected effect size of the intervention; in some cases this can be calculated using a power analysis (Ockendon et al., 2021). Randomisation avoids human biases, such as inadvertent association of the treatment or control plots with confounding variables (Ockendon et al., 2021).

There have been multiple calls for greater integration of ecological science into rewilding, particularly addressing questions experimentally (Jepson, 2016; Svenning et al., 2016). Inclusion of research objectives within rewilding projects is possible without compromising the project goals and provides an important opportunity to increase rewilding's evidence-base. Integration of research into conservation projects is optimal when the output will have a clear application, the necessary skills exist within the project team and research will integrate into the management plan (Ockendon et al.,

2021). Using a hypothetical example of a new rewilding project in the UK lowlands, we consider how monitoring could be implemented in the project and questions relating to typical rewilding interventions addressed experimentally (Box 2, p 90). For example, the use of grazing herbivores could be manipulated to understand the knock-on effects of different timings, locations, combinations, and densities of animals. Manipulation of this rewilding intervention would influence multiple rewilding principles, which could be monitored using a range of response variables (Fig. 4.2). We can also work backwards from the rewilding principles, for example trophic complexity, to see that more than one intervention would influence this principle: keystone species, species translocations/introductions and manipulation of grazing (Fig. 4.2). Carefully planned factorial experimental designs, combining different combinations of treatments, could help to isolate the key drivers of response variables. To truly understand whether trophic complexity has been achieved we would need to monitor the species present in a project and the reinstatement of species interactions (Valiente-Banuet et al., 2015).

We can also ask questions about how rewilding interventions will influence the outputs from a project. Biodiversity enhancement and carbon sequestration are common objectives of rewilding. In the UK uplands, particularly in locations with high carbon content soils, we need more information on the relative impact of **natural colonisation** vs. tree planting on ecosystem carbon stocks. Tree planting can release significant amounts of soil carbon, but to what extent would natural colonisation, which avoids disturbance, mitigate this (Friggens et al., 2020; Warner, Lewis, Brown, et al., 2021)? This would allow us to elucidate the extent to which soil carbon losses are a consequence of disturbance during planting or result from changes to the soil community and abiotic environment triggered by tree establishment.

The landscape and objectives of a project will guide the variables that are monitored, but there are some variables that are likely to be common to all projects. For example, monitoring biodiversity will usually include the vegetation community, aspects of the invertebrate community, and groups at

higher trophic levels (e.g. birds), dictated by the study site (e.g. (Hawkes et al., 2021; Warner, Hector, et al., 2021)). Sometimes specific functional groups will be monitored in response to specific research questions (Buse et al., 2021), or there may be species that are a key target of the rewilding project (Broome et al., 2021). Similarly, in a world where carbon sequestration is a critical outcome of land-use change, accurately monitoring changes in above and belowground carbon should be integral to any rewilding project (Roe et al., 2019; Seddon et al., 2020). Most rewilding projects aim to alter vegetation dynamics and development, and patterns of dispersal and recruitment connected to this should be assessed. The Knepp project is fairly unusual in having undertaken wide-ranging ecological surveys, which aimed to establish baseline data, however a number of these were conducted several years after the first interventions took place (Greenaway, 2006).

Ultimately, we want rewilding efforts to be effective at fulfilling the core principles of rewilding and at meeting societal and ecological needs. Collecting data to understand what works under different conditions, in different landscapes, and with different interventions will ensure successful implementation of rewilding elsewhere, as well as improving its policy acceptability (Pettorelli et al., 2018).

What should we be measuring – monitoring outcomes vs. understanding processes?

The complexities of monitoring rewilding projects, with their inherent uncertainties and lack of clear objectives, have been discussed (Corlett, 2019). Here we consider two overlapping but conceptually different approaches to monitoring rewilding projects. In the first scenario, the objective would be to assess changes in the rewilding principles, monitoring response variables clearly linked to the principles (Fig. 4.2). The second is a more general approach to monitoring outputs from rewilding, targeting variables that assess a project's contribution to climate change mitigation and biodiversity conservation, and indicators of change in key aspects of the ecosystem, without drawing causal links to rewilding principles.

The links between the rewilding principles and potential response variables are shown in Figure 4.2. It is unlikely to be feasible for every rewilding project to monitor the processes and variables underpinning every rewilding principle at once. There may be some projects better suited to assessing change in certain rewilding principles over others, particularly where experimental interventions aiming to test specific research questions have been included in a project. Drawing on existing paradigms and methods within ecology, the influence of rewilding on different aspects of the ecosystem can be assessed. For example, assessing distributions and abundances of species could draw on methods from population ecology, to monitor the demographics of populations (e.g. (Fuentes-Montemayor et al., 2020; Whytock et al., 2018)), and movement ecology (Allen & Singh, 2016) to monitor movement of individuals. These same parameters could also provide information on the connectivity between habitats within a project and to habitats outside the project.

Although some view the quantification of ecosystem services derived from rewilding projects as a risk to their inherent purpose of enhancing biodiversity and wildness (Genes, Svenning, Pires, & Fernandez, 2019), much of the interest in rewilding projects derives from their anticipated enhancement of ecosystem services (Hodder, Newton, Cantarello, & Perrella, 2014). Quantifying ecosystem services empirically is important, but existing assessments emphasise that the outcome depends on the service monitored (Zu Ermgassen, Mckenna, Gordon, Willcock, & Haslett, 2018). As a minimum, we suggest monitoring indicators of biodiversity and carbon. Mapping habitat development across a project landscape, supplemented by more detailed mapping of vegetation changes and patterns of dispersal from nearby areas of habitat would be valuable (Kirby, 2020a). Monitoring the response of soil structure, nutrient status and biotic communities after the transition to rewilding should also be a priority, particularly in ex-agricultural landscapes (Andriuzzi & Wall, 2018; Marrs et al., 2018).

Concluding remarks

Rewilding has always been subject to complex dialogue, as the longstanding debate surrounding how to define rewilding emphasises (Jørgensen, 2015; Schulte to Bühne, Pettorelli, & Hoffmann, 2021). There has also been resistance to the idea that rewilding should meet specific objectives, such as the provision of ecosystem services (Genes et al., 2019). Investigating rewilding more systematically, through the lens of ecological research will allow us to understand its potential contribution to current ecological and climate challenges at a time-critical stage where it is crucial our efforts are effective. Key research questions going forwards are highlighted in the *Outstanding questions*. Science can complement rewilding, and integrating baseline data collection, experimental manipulation and monitoring into projects could boost the impact of this unfolding field of conservation and ecology. Increased integration of ecological research should be conducted alongside social, cultural, and economic research within rewilding projects, giving us a wider understanding of its impacts.

Outstanding questions

Which rewilding interventions are most important for achieving the core principles of rewilding (i.e. establishing species interactions and ecosystem processes, and generating dynamic self-sustaining ecosystems)? Interventions at a site can range from an altered grazing regime (influencing the balance of succession and disturbance) to more conventional approaches to habitat restoration (e.g. tree planting or wetland creation).

In which landscape contexts and under which prior land-uses are different rewilding interventions likely to be effective in achieving the rewilding principles? The landscape context, prior land-use and level of degradation will determine the ecological outcome of a project, which will depend on recruitment and dispersal from surrounding habitat. Understanding where management interventions may be needed to overcome barriers on the project trajectory will be important.

How do we quantitatively monitor outputs (ecological processes, biodiversity, carbon sequestration) in response to rewilding interventions? We require a set of variables that can be easily monitored across projects, allowing the contribution of rewilding projects to the biodiversity and climate crises to be assessed.

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Glossary

Keystone species – a species with a disproportionate effect on an ecosystem: its introduction or loss from a system will influence the rest of the community. These species influence other organisms through direct interactions (e.g. predator-prey) or indirectly (e.g. through habitat modification).

Naturalistic grazing – grazing aiming to emulate systems where herbivore dynamics are influenced by natural processes rather than human management. Densities of grazing animals should be determined by resource availability within a site. The influence of herbivores on natural processes (e.g. vegetation dynamics) is the objective of this intervention.

Natural colonisation – the natural establishment of trees and shrubs from existing seed sources without human intervention, in areas that have not been forested in the recent past.

Natural regeneration – the natural establishment of trees and shrubs from existing seed sources without human intervention, in areas that were recently forested.

Self-sustaining ecosystem – a dynamic ecosystem regulated by natural processes, without the need for human management.

Trophic cascade – the propagation of impacts through trophic levels within a foodweb. For example, a predator can drive a top-down cascade (e.g. wolves may depress grazing herbivores, triggering tree regeneration) and primary producers may drive bottom-up cascades (e.g. reduction in food availability suppresses herbivores, leading to a decline in predators).

Box 1 – Caledonian pinewood restoration in the Scottish Highlands – applying a study design post-hoc & missing baseline data

Project overview

A large-scale rewilding project, aiming to restore Caledonian pinewood, in Glen Affric and Glen Moriston in the Scottish Highlands was the focus of our recent work to assess the response of biodiversity and ecosystem functions to the forest creation interventions (herbivore exclusion and tree planting) (Warner, Hector, et al., 2021; Warner, Lewis, Brown, et al., 2021). No systematic data collection or monitoring was established at the start of the project.

Study design

Our study design aimed to understand the transition from unforested habitat to newly created forest. The presence of multiple distinct forest creation sites in our study landscape allowed us to have a good level of replication (n = 14); survey plots were randomly allocated to an area of successful forest establishment within each site. These plots were matched to plots in unforested areas in the wider landscape accessible to grazing herbivores (mainly deer), providing a control, and to unforested areas within the fenced reforestation sites, allowing the effect of grazing exclusion to be separated from the effect of forest establishment. Further plots were established in mature Caledonian pinewood within the study landscape, providing a reference in the target habitat.

Challenges in interpretation

The study design makes a space-for-time substitution, assuming that the unforested, grazed plots reflect the habitat prior to the rewilding interventions and that differences between the two categories of plot are causally related to the interventions (De Palma et al., 2018). A key finding was significantly lower soil carbon in the reforested plots compared to the unforested and mature forest plots. Without baseline data or experimental manipulation, interpretation of this result is challenging. It could reflect differences in soil carbon among the sampling areas unrelated to the interventions or a decline in soil carbon resulting from the forest establishment (e.g. through soil disturbance during planting or changes in the soil environment triggered by tree establishment). It is important to know which of these is the case, as this determines whether the woodland creation has been a net source or sink of carbon. Understanding mechanisms behind soil carbon loss will require experimental investigation, to test whether the method of forest establishment and associated soil disturbance drives losses or whether the decline in carbon is driven by the influence of the trees on soil processes. A comparison between natural regeneration and tree planting could help reveal mechanisms.

Box 2 – baseline and ongoing monitoring and experiments in a lowland UK rewilding project

Integrating monitoring design from outset

Baseline monitoring should be undertaken, including in control plots (ideally in land continuing under the previous land-use and in habitats representing the target habitat).

Sampling design

- Replication – there should be enough replication to allow each response variable to be captured accurately. The level of replication will depend on the expected effect size of the intervention, where an estimate of natural variation in the response variable is known a power analysis could be used to estimate the level of replication needed (Ockendon et al., 2021). Where multiple variables are monitored simultaneously, they may require measurement at different scales/with different levels of replication.
- Randomisation – study plots should be randomly distributed, and control and intervention treatments randomly allocated to these.
- Stratification – if there is underlying heterogeneity (e.g. different prior land-uses, natural abiotic gradients) this should be incorporated into the experimental design, and randomisation stratified across categories or gradients (Figure I).

Baseline data

- Broad habitat categories – mapping.
- Carbon – stocks (above & belowground), fluxes.
- Biodiversity – specific taxa depending on site.
- Soil – soil organic matter, soil nutrient status, soil structure, soil communities.
- Ecosystem services.

Experimental manipulation

- Manipulation of extensive grazing: grazing densities, species combinations, timing of grazing, location of grazing.
- Natural tree regeneration vs. tree planting: planting densities, methods, species combinations.
- Active vs. passive restoration: areas of the site receiving traditional conservation management interventions vs. rewilding management, approaches to wetland restoration.
- Species introductions: introduced into some areas of the site only, introduction of species with specific traits/ecosystem roles.

Key ecological questions

- Dispersal limitation.
- Recruitment limitation.
- Loss/restoration of habitat heterogeneity.
- Loss/restoration of trophic structure (herbivores and predators, often large body size).
- Balance between disturbance and succession.

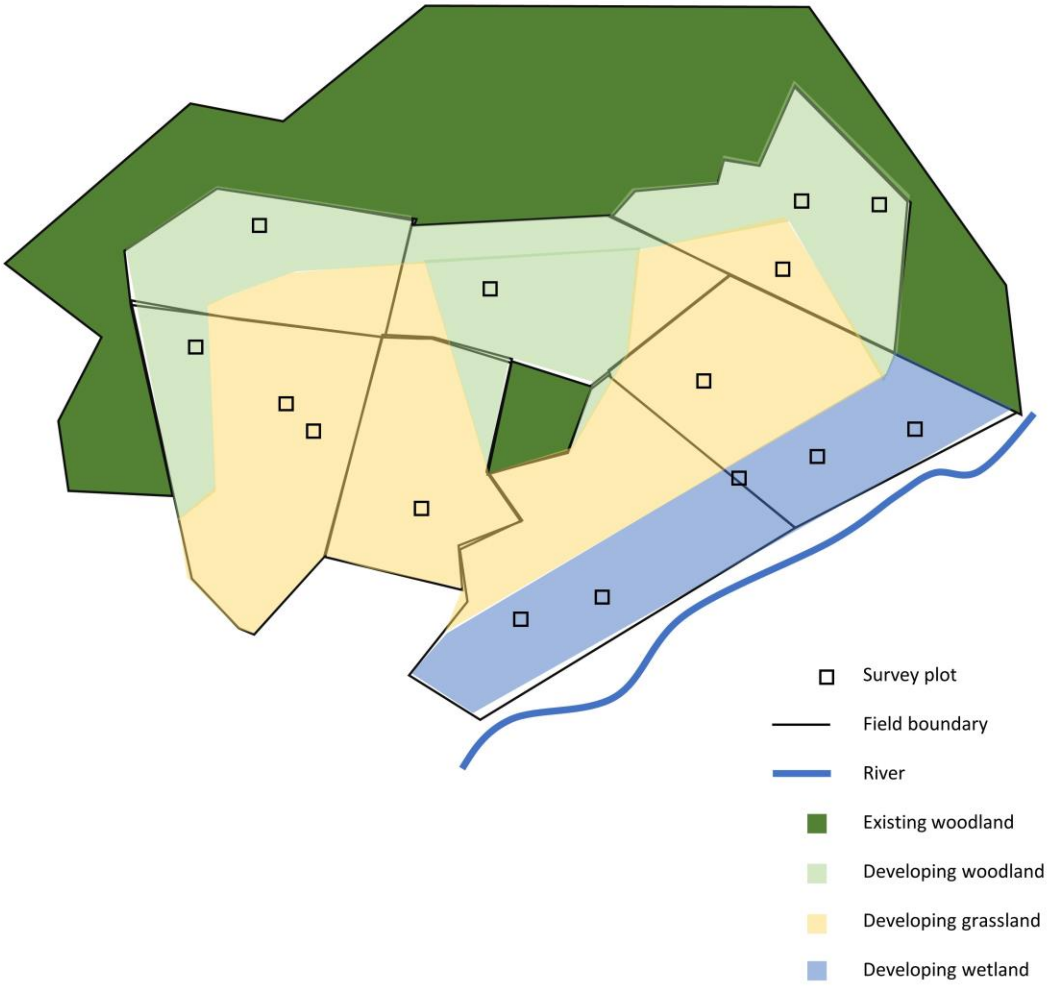


Figure I. Schematic of a hypothetical idealised lowland farm landscape, adjacent to existing woodland and bounded by a river. Theoretical areas of newly developing habitat after removal of the previous agricultural management are shown.

Chapter 5 Aboveground carbon stocks are higher in mixed-species plantation forests than monocultures – a meta-analysis

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This chapter has been written to the style requirements of *Global Change Biology* and will be submitted to this journal.

Authors' contributions

S.C.C-P. and A.H. conceived the study idea and E.W. shaped the research focus. E.W. conducted the data extraction and analysis. J.K. gave advice on the analysis. N.E., O.F., D.G., J.S.H., H.J., C.M., C.M., C.M., A.P., W.C.P, C.P., and P.B.R. contributed data to the analysis. E.W. led the writing, alongside A.H and S.C.C-P. All authors commented on and approved the manuscript.

Abstract

Natural forest cover is declining globally, but the area of plantation forest is increasing; this will likely continue given ongoing deforestation and increased tree planting. However, most plantations are monocultures, despite some evidence that higher species richness improves their functioning and stability. We performed a meta-analysis, using data from the literature and Tree Diversity Network, assessing 1) aboveground carbon stocks in mixed-species plantations vs. (a) the average of constituent species monocultures, (b) the best constituent species monoculture, and (c) commercial species monocultures; 2) whether any advantage of mixtures over monocultures was positively related to their diversity; and 3) mechanisms driving differences in carbon stocks between mixtures and monocultures. The final dataset included 79 comparisons from 21 sites. Carbon stocks in mixed plantations were on average 70% higher than the average of stocks in monocultures of their constituent species, and on average 77% higher than commercial monocultures. There was c.25% more carbon in mixed plantations relative to the best performing monocultures, although this increase was not statistically significant. Overyielding was highest in four-species mixtures (richness range 2-6 species). More data providing better coverage of richness and age gradients (study sites aged 3.5-28 years) is needed to increase confidence in these results. None of the moderators (nitrogen-fixer present vs. absent; native vs. non-native/mixed origin; tree diversity experiment vs. forestry plantation) assessing potential mechanisms behind diversity effects had a clear effect. This suggests that our findings are driven by combined small, statistically insignificant effects from several of the proposed mechanisms or unidentified mechanisms. We conclude that increasing tree species richness in plantations can increase carbon stocks, while bringing other benefits associated with diversification. However, implementation will depend on the balance of these potential benefits relative to the operational challenges and costs of diversification.

Key words

Tree diversity, aboveground carbon, carbon stocks, plantation, forest

Introduction

Globally, natural forest cover is declining, but the area of planted forests is increasing and currently comprises 7% of global forest cover (FAO, 2020a). Planted forests comprise both plantation forests, which usually contain one or two species and are managed intensively for production purposes, and other planted forests, containing one or more tree species and managed less intensively for multiple uses (Messier et al., 2021). There is growing momentum to restore forest cover for climate change mitigation, biodiversity conservation, and sustainable development goals (Di Sacco et al., 2021; Griscom et al., 2017; Seddon et al., 2020), but many national forest restoration commitments focus on monoculture plantations. Indeed, 45% of commitments from tropical countries to restore forest cover involve establishing monoculture plantations, despite diversification of plantations being a key policy recommendation in a recent IPBES-IPCC report (Lewis et al., 2019; Pörtner et al., 2021). Experimental and theoretical work demonstrates that diverse plant systems are more productive and stable through time compared to monocultures, as well as better able to support diverse animal assemblages and provide other critical ecosystem services (Cardinale et al., 2012; Messier et al., 2021; Tilman et al., 2014). With the increasing calls for diversification of planted forests and the increasing number of studies addressing the effect of planted tree diversity on productivity, it is timely to assess whether carbon stocks in mixed-species planted forests can equal or outperform monocultures (Messier et al., 2021). Without this evidence, forestry practitioners lack the certainty needed to deviate from the more commonly deployed and understood monoculture systems.

The global forest carbon stock is estimated at 662 Gt of carbon, with 295 Gt stored in living organic matter, 300 Gt in the soil and 68 Gt in dead wood and litter (FAO, 2020a). At their maximum pre-agricultural extent global forests are estimated to have contained 500 Gt of carbon in living biomass and 700 Gt of carbon the soil (Malhi, Meir, & Brown, 2002). Restoration of forest cover could therefore sequester large amounts of carbon, with global reforestation efforts capable of sequestering c.10 $GtCO_2e$ a year (Griscom et al., 2017). However, the method of reforestation used has a strong

influence on the level of carbon sequestration, with monoculture plantations limited in their potential to store carbon (Lewis et al., 2019). Future planted forests will contribute to climate change mitigation through terrestrial carbon storage and the substitution of wood products for fossil fuels and high-carbon products such as concrete (Forster, Healey, Dymond, & Styles, 2021). New planted forests must be optimised for carbon storage and to maximise other benefits; diversification could be one route to achieving this.

Many studies have demonstrated a positive relationship between diversity and productivity in natural (e.g. Liang et al., 2016; Xu et al., 2020) and planted forest systems (e.g. Ewel et al., 2015; Huang et al., 2018). Several meta-analyses have shown the existence of overyielding in mixed forests, with primary production exceeding the average productivity of component monocultures by about 15-20% (Jactel et al., 2018; Zhang et al., 2012). Forests established with higher numbers of tree species would therefore be expected to store more carbon in aboveground biomass than less diverse forests (Jucker, Bouriaud, Avacaritei, & Coomes, 2014). Moreover, although monoculture species are often selected for their high yield and ease of management (Nabuurs, Verkerk, Pieter Johannes Schelhaas, González Olabarria, José Ramón Trasobares, & Cienciala, 2018), they may lack resilience to perturbation (Jactel et al., 2017, 2021), which could compromise their long-term carbon storage potential (Hutchison et al., 2018; Messier et al., 2021; Osuri et al., 2020). For example, in a tree planting experiment over 15 years in Panama, growth in diverse stands was less sensitive to climatic extremes, and tree mortality was lower, compared to single-species stands (Hutchison et al., 2018). There is also evidence from India that carbon capture can be more stable through time and recover more rapidly after drought events in species-rich natural forests, compared to species-poor plantations (Osuri et al., 2020; Pardos et al., 2021). The simple act of mixing species with different functional traits can also result in more reliable levels of establishment, compared to a mosaic of monocultures of different species, where some may perform poorly (Tuck et al., 2016).

Alongside increased resilience to perturbation, there are other mechanisms that may lead to greater carbon accumulation in mixed-species planted forests compared to monocultures. For example, species mixtures may demonstrate “complementarity”, whereby niche differentiation or facilitation among individual species enhances overall performance (Loreau & Hector, 2001). Crown architecture complementarity is one mechanism that can achieve overyielding in mixed-species planted forests (Jucker, Bouriaud, & Coomes, 2015; Williams, Paquette, Cavender-Bares, Messier, & Reich, 2017). Complementarity may also be higher among native species that have coevolved (Cook-Patton & Agrawal, 2014; Zuppinger-Dingley et al., 2014). Species with particular traits can also enhance the overall productivity of a mixture. For example the presence of nitrogen-fixing species can enhance nitrogen availability for species unable to fix nitrogen, boosting carbon accumulation potential (Loreau & Hector, 2001; Mayoral, van Breugel, Cerezo, & Hall, 2017). However, species mixing could lead to lower productivity in diverse stands where a lower yielding species dilutes a monoculture of a fast-growing, commercially valuable species. Mixing lower yielding species with a very high yielding species could lead to lower stand-level carbon accumulation because the diverse stand would fail to demonstrate “transgressive overyielding”, where diverse systems outperform even the most productive monoculture. Finally, diversification of forests is expected to increase resistance to pests and disease (Gamfeldt et al., 2013; Jactel et al., 2021; Jactel & Brockerhoff, 2007; van der Plas et al., 2016), which could also improve carbon stability and storage.

Planted forests can provide timber and other forest products, support local communities and provide an economic income, while helping to alleviate pressure on primary and semi-natural forest (McEwan, Marchi, Spinelli, & Brink, 2020; Messier et al., 2021). Given the dominant practice of establishing plantations as monocultures and the anticipated benefits of mixed-species planting for carbon accumulation (Beugnon et al., accepted) and biodiversity (Ampoorter et al., 2020), we need a robust examination of how carbon stocks compare in mixed plantations relative to monocultures. Here, we present results of a meta-analysis, combining data from the Tree Diversity Network (TreeDivNet)

(Verheyen et al., 2016) with information from other relevant published data to assess the effect of diversification on carbon stocks in planted forests, addressing the following research questions:

1. Are carbon stocks in mixed-species plantations higher than in monocultures? We compared carbon stocks in mixed plantations to carbon stocks in (a) the average of monocultures within an experiment, (b) the most productive monoculture and (c) monocultures of commercial timber species.
2. Is any advantage of mixtures over monocultures positively related to their diversity?
3. What are potential mechanisms driving differences in carbon stocks between mixed species and monoculture plantations? Specifically, we compared how responses changed in stands with and without nitrogen fixers and in native versus non-native stands. We also compared tree diversity experiments to forestry plantations, to assess whether methodological differences explained variation in carbon stocks.

This work builds on previous meta-analyses assessing the effect of tree diversity on carbon accumulation in planted and naturally occurring forests (Zhang et al., 2012), biodiversity-productivity relationships in forests and their relation to climate (Jactel et al., 2018) and growth rates in mixed vs. monoculture plantations (Piotto, 2008). By focussing solely on planted forests and assessing carbon stocks, we address this question in the context of the increasing interest in tree planting for carbon sequestration.

Methods

Data collation

This meta-analysis used studies compiled in a previous systematic literature review. Cook-Patton et al. (2020) compiled 10,937 studies using a systematic keyword search in Web of Science (19 April 2017) for studies published since 1975: TOPIC: (biomass OR carbon OR agb OR recover* OR accumulat*) AND (forest) AND (restorat* OR reforest* OR afforest* OR plantation* OR agroforest* OR secondary*). This initial literature set was augmented to 11,360 studies by including additional papers referenced within the original studies and datasets from Oak Ridge National Laboratory, International Centre for Research in Agroforestry, and the Chinese Academy of Forestry. Abstracts were reviewed to identify studies describing reestablishment of forest cover; these were reduced to 1,400 studies which quantified carbon or biomass stocks. Of these, 62 studies compared carbon in mixed and monoculture plantations.

We selected the subset of studies that met our criteria for inclusion: mixed and monoculture plantations of the same age and containing a measure of aboveground carbon or biomass, monocultures composed of a constituent species of the mixed plantation, and studies provided a geographic location (to classify species as native or non-native and to classify commercial species). Studies also needed to contain necessary information to calculate the effect size for the meta-analysis (mean, standard deviation, sample size). A total of 9 of the 62 studies met these criteria (Table D1 in Appendix D). Common reasons for exclusion were confounding variables in the mixed and monoculture plantations (e.g. mixed and monoculture stands of different ages) or failure to provide the metrics needed to conduct a meta-analysis. We included two additional studies from a meta-analysis by Zhang et al. (2012). We then augmented this literature-based dataset with seven additional datasets from TreeDivNet (https://treedivnet.ugent.be/), made available by TreeDivNet projects in response to a call for data, bringing the total dataset to 18 studies. Some studies included multiple experiments, producing 21 independent experiments from 18 studies. The studies often included

multiple distinct mixed plantation treatments (multiple species combinations or ratios between species), yielding a total of 79 monoculture-to-mixed comparisons. Each unique species combination (based on species composition or species ratios) was defined as a treatment. We extracted from each experiment: (1) mean aboveground carbon or biomass for each treatment (calculated in the original studies using allometric equations); (2) standard deviation of the carbon or biomass measure (in some cases calculated from standard error and sample size); (3) sample size for each treatment; (4) species composition of each treatment; (5) stand age and (6) geographic location. When data were presented graphically in the papers, we extracted estimates using WebPlotDigitizer (https://apps.automeris.io/wpd/).

Within the 79 monoculture to mixed comparisons in our maximum dataset, there were 51 unique mixed-species combinations from a pool of 54 species (Table D2). Carbon stocks in mixed plantations were compared to carbon stocks in the average of constituent species monocultures, the best performing constituent monoculture (from a pool of 26 species) and, for a subset of comparisons, commercial species monocultures (from a pool of 11 species). Two species mixtures were the most well represented across the diversity range (species richness 2-6) (Fig. D1 in Appendix D). Geographically the study sites used were biased to the northern hemisphere, with no sites in Africa or South America (Fig. D2). The age of study sites ranged from 3.5 to 28 years, with most comparisons from sites less than 20 years old (Fig. D3d).

Data preparation

To calculate the standardised mean difference (SMD), Hedges' g (Hedges, 1981), we required the mean carbon stock, standard deviation and sample size for the mixed and monoculture plantation in each comparison.

For research question 1a, where we were comparing carbon stocks in mixed plantations to the average of carbon stocks in constituent species monocultures, this required us to calculate the mean and standard deviation across the monocultures relevant to each mixed plantation. In 9 of the 79 comparisons, only one of the mixed plantation constituent species was planted as a monoculture, so in these cases this monoculture was used in the comparison to the mixed plantation. Where two or more monocultures were available, we calculated the average carbon/biomass and standard deviation. For the TreeDivNet data we had access to the full raw data, which was used to calculate the mean and standard deviation. For the studies resulting from the literature search, we used the extracted means and standard deviations for each monoculture treatment, to calculate a mean, standard deviation and sample size across monoculture treatments. The standard deviation was calculated based on the formula $\sqrt{({sd_1}^2 + {sd_2}^2 \ldots + {sd_n}^2)}$ (Frey, Penman, Hanle, Monni, & Ogle, 2006). The sample size of the average carbon/biomass measure was the aggregate sample size of all contributing monoculture treatments. The resulting means, standard deviations and sample sizes were used to calculate the SMDs.

For research questions 1b and 1c, the calculated (TreeDivNet studies) or extracted (studies from literature search) means, standard deviations and sample sizes from the mixed and monoculture plantation within each comparison were used to calculate SMDs. Question 1b compared carbon stocks in mixtures to the associated monoculture with the highest carbon/biomass stocks (n = 79 comparisons), again including the 9 comparisons where only a single monoculture was available. For research question 1c, we compared carbon stocks in mixtures to monocultures composed of commonly used commercial plantation species (n = 38 comparisons). We classified commercial species monocultures when there was evidence that these species were commonly used as commercial production species in the study region (Table D3). We hypothesised that, as commercially grown tree species are often selected for their high yields, they may outperform mixed plantations. The calculated (TreeDivNet studies) or extracted (studies from literature search) means, standard deviations and

sample sizes were used to calculate SMDs for the comparison to the best or commercial species monocultures.

To assess some potential mechanisms behind differences in carbon stocks between mixed and monoculture treatments we classified each mixed treatment based on its species richness, presence of a nitrogen-fixing species in the mixture (yes/no), origin of the species (all native vs. some/all species non-native) and study design (designed experiment vs. existing forestry plantations). Plantations diversified with a nitrogen-fixing species might be expected to achieve higher carbon stocks due to higher nitrogen availability. Species origin could influence carbon stocks, as non-native species used in planted forest are often chosen for their higher yields. Conversely, native species may have higher complementarity and therefore higher carbon stocks in mixtures. Study design may influence the effect of diversification on carbon stocks. In experiments confounding factors are likely to be more tightly controlled, so any positive effect of diversity may be clearer.

To also present our results in real terms we calculated the percentage of monoculture carbon in the mixed plantation for each comparison, as SMD is on the scale of standard deviations. The carbon stocks in each treatment are presented in Tables D3 and D4. Where stocks were given as biomass in the original study, we converted these to carbon using the conversion factor of 0.47 (Aalde et al., 2006).

Meta-analysis

All data manipulation, calculations and analysis were carried out in R (R Core Team, 2020). We used the *escalc* function in the package *metafor* to calculate the SMD (Hedges' g) in carbon or biomass for each monoculture-to-mixed plantation comparison and the associated sampling variance (Viechtbauer, 2010). Although some studies reported biomass stocks and others carbon stocks, we assume that carbon is a constant proportion of biomass (Aalde et al., 2006). Given this assumption,

the calculation of the SMD therefore converts biomass and carbon onto the same scale. We hereafter refer solely to aboveground carbon stocks in the Results and Discussion. We calculated SMDs of the mixture treatment relative to the average of the monoculture treatments (overyielding), the monoculture treatment with the highest carbon stocks in a study (transgressive overyielding) and commercial monoculture treatments (when available).

Multi-level random-effects models with restricted maximum likelihood estimation were fitted using the function *rma.mv* in the metafor package (Viechtbauer, 2010). Many of our studies contained multiple mixed treatments which were compared to the same monoculture controls (71 out of 79 comparisons shared a monoculture with at least one other comparison). We included a random effect for study site to account for this. For the comparison to the best monoculture, we also included a random effect for monoculture plantation nested within study site. For the comparison to commercial monocultures, in some cases the same mixed plantation was compared to different monocultures and there were also cases where different mixed plantations were compared to the same monoculture; we included a random effect grouping by either shared mixed or monoculture plantation, nested within study site. All comparisons within a study site were between plantations of the same age, however study sites covered the age range 3.5 to 28 years, the random effect for study site therefore also accounts for this. A random effect for each comparison was also included, to allow heterogeneity within study sites. We assessed the significance of the SMDs by determining whether the 95% confidence intervals included zero.

To assess the effect of the level of diversity on SMD, we fitted a mixed-effects model with a moderator for species richness (2-6 species), as a discrete variable, and separately compared mixed vs. average of monoculture and mixed vs. best monoculture. For mixed vs. commercial species monoculture comparisons, there were insufficient data across the levels of species richness to fit it as a moderator. For the mixed vs. average of monocultures and mixed vs. best performing monoculture analyses we

fitted separate models for two, four, and six species mixtures, to estimate the effect size for each level of species richness; mixtures with three and five species only had one monoculture-to-mixed comparison each. We also fitted a model to estimate the effect size for two species mixtures compared to commercial monocultures.

To test potential predictors of differences in carbon stocks, we fitted separate mixed-effects models with moderators for presence vs. absence of nitrogen-fixer in the mixed treatment, native vs. some or all non-native species in the mixed treatment and designed experiments vs. existing plantations. For these models we only used data from two-species mixtures, as this was the only species richness level with good representation of both factor levels (Fig. D3). To estimate the overall effect size for each moderator level, we subset the data by each level of the moderator and fitted separate models for: nitrogen-fixer present, nitrogen-fixer absent, native species, non-native/mixed origin species, designed experiments, and existing plantations.

Age may mediate the effect of diversity on carbon stocks, to assess this we fitted a mixed-effects model with a continuous moderator for stand age for the mixed vs. average, best and commercial monoculture comparisons. These models were fitted using data from two-species mixtures, as this was the only species richness level with good representation across the age range (Fig. D3a). A linear and quadratic fit were compared using AIC; the quadratic relationship was fitted post-hoc, based on visual inspection of the data.

We checked for publication bias using funnel plots fitted for each analysis (Appendix E) and explored the removal of the most extreme positive and negative SMDs. The impact on the interpretation of our results is discussed in Appendix E.

Results

Our overall meta-analyses showed that aboveground carbon stocks in mixed plantations were higher than in the average of the monocultures (pooled SMD 1.41 [95% CI 0.75, 2.07], k = 79, Fig. 5.1) and higher than in commercial monocultures (pooled SMD 1.06 [0.47, 1.65], k = 38, Fig. 5.1). Carbon stocks in mixed plantations were on average higher than the most productive monoculture plantation, but the confidence interval overlapped zero slightly (pooled SMD 0.62 [−0.0095, 1.25], k = 79, Fig. 5.1). We noted that for the comparison to the best monoculture, removal of the most extreme outliers (SMD >6 and <−3) alters the confidence interval for this result (pooled SMD 0.75 [0.32, 1.17], k = 73) (Appendix E). Although the statistical tests are based on SMDs (in units of standard deviations), the underlying data suggest that mean carbon in mixed plantations was 171% [95% CI 144, 198] (Table D2) of the carbon in the average of monoculture plantations, 174% [121, 127] of the carbon in commercial monocultures (Table D4) and 127% [111, 142] of the carbon in the most productive monocultures (Table D2). The community with the greatest relative gain in aboveground carbon was a 3.5-year-old four-species mixture comprised of *Betula pendula*, *Fagus sylvatica*, *Quercus petraea* and *Tilia platyphyllos* in Saxony-Anhalt, Germany, which contained 43.9 Mg/ha of carbon compared to an average of 6.5 Mg/ha across the monocultures and 13.7 Mg/ha in the best monoculture (*Betula pendula*) (Table D2).

The greatest positive difference in carbon stocks was seen in mixed plantations with four species, which had greater aboveground carbon stocks than the average of monocultures (pooled SMD 8.76 [95% CI 4.82, 12.7], k = 11, Fig. 5.2) and most productive monocultures (pooled SMD 3.82 [1.69, 5.95], k = 11, Fig. D4). Using the raw data, we calculated that carbon in the four-species mixtures was 411% [95% CI 325, 497] of the carbon in the average of monocultures and 232% [218, 247] of the carbon in the best monoculture. Two-species mixtures also had greater aboveground carbon stocks than the average of monocultures (pooled SMD 0.90 [0.53, 1.27], k = 58, Fig. 5.2) and commercial monocultures (pooled SMD 0.97 [0.34, 1.61], k = 32, Fig. D5), but carbon stocks were not significantly greater than

the most productive monoculture plantations (pooled SMD 0.40 [−0.28, 1.08], k = 58, Fig. D4). Carbon in two-species mixtures was 135% [122, 149] of carbon in the average of monocultures and 113% [107, 120] of carbon in the most productive monoculture (Table D2). There was no clear difference in aboveground carbon stocks in six-species mixtures compared to the average of monocultures (pooled SMD 0.11 [−0.55, 0.77], k = 8, Fig. 5.2) and potential under-yielding relative to the most productive monoculture, although with a wide interval (pooled SMD −0.38 [−0.79, 0.042], k = 8, Fig. D4). A moderator for species richness was fitted for the comparison to the average of monocultures and the best monoculture. The moderator for species richness was significant for the comparison of mixtures to the average of monocultures (Q_M = 46.79, p < 0.01, k = 79, Fig. D6a), but not for the comparison to the best monoculture (Q_M 8.78, p = 0.067, k = 79, Fig. D6b).

Moderators for presence vs. absence of a nitrogen-fixer in mixtures (analyses possible for two-species mixtures only) were not significant for the comparison to the average of monocultures (Q_M = 0.37, p = 0.54, k = 58, Fig. D7), best monoculture (Q_M = 1.35, p = 0.25, k = 58, Fig. D7) or commercial species monoculture (Q_M = 1.33, p = 0.25, k = 32, Fig. D7). We used data subset by presence or absence of a nitrogen-fixing species in the mixture to estimate the pooled effect sizes for aboveground carbon stocks in each group (Fig. 5.3). In mixtures with a nitrogen-fixer present carbon was 145% [95% CI 136, 153] of the carbon in the average of monocultures and in mixtures without a nitrogen-fixer carbon was 128% [120, 136] of the carbon in the average of monocultures.

Species origins in the mixed plantation (analyses possible for two-species mixtures only) were not significant for any of the comparisons (average of monocultures, Q_M = 0.94, p = 0.16, k = 58; best performing monoculture Q_M = 0.75, p = 0.39, k = 58; commercial monoculture Q_M = 0.091, p = 0.76, k = 32; Fig. D8). Post-hoc, overall effect sizes estimated for each level of the moderator using subsets of the data confirmed that there was no clear effect of diversification based on the geographic origin of the species used (Fig. 5.4). In mixtures of non-native species or a mixture of non-native and native

species carbon was 156% [95% CI 148, 164] of the carbon in the average of monocultures and in mixtures with native species only carbon was 130% [122, 137] of the carbon in the average of monocultures.

The effect of study type (analyses possible for two-species mixtures only) was not significant for any of the mixed to monoculture plantation comparisons (average of monocultures $Q_M = 0.24$, $p = 0.62$, $k = 58$; best monoculture $Q_M = 0.63$, $p = 0.43$, $k = 58$; commercial species monoculture $Q_M = 0.46$, $p = 0.50$, $k = 32$; Fig. D9). Subsequently, overall effect sizes were estimated using subsets of the data, confirming that there were no clear differences in the effect of diversification based on study type (Fig. 5.5). In studies using forestry plantations, carbon in the mixed plantation was 128% [95% CI 120, 135] of the carbon in the average of monocultures and in experimental studies carbon in mixtures was 136% [129, 144] of the carbon in the average of monocultures.

Analyses of the effect of age were possible for two-species mixtures only. Age had a better fit as a quadratic predictor rather than linear predictor for the comparison of mixed to the average of monocultures (AIC 155.9 vs. 162.6), showing a peak in the positive effect of diversification at the middle of the age range (quadratic term −0.013 [95% CI −0.023, −0.003]) (Fig. D10a). For the relationship between age and SMD relative to the best monoculture, a post-hoc quadratic predictor provided a better fit than a linear predictor (AIC 149.3 vs. 158.7), showing a peak in the positive effect of diversification before a downturn after age 17 yrs (quadratic term −0.019 [−0.029, −0.008]) (Fig. D10c). For the relationship between age and the difference in aboveground carbon stocks for mixed plantations compared to commercial monocultures a linear relationship provided the best fit but was not statistically significant ($Q_M = 0.14$, $p = 0.71$, $k = 32$, Fig. D10b).

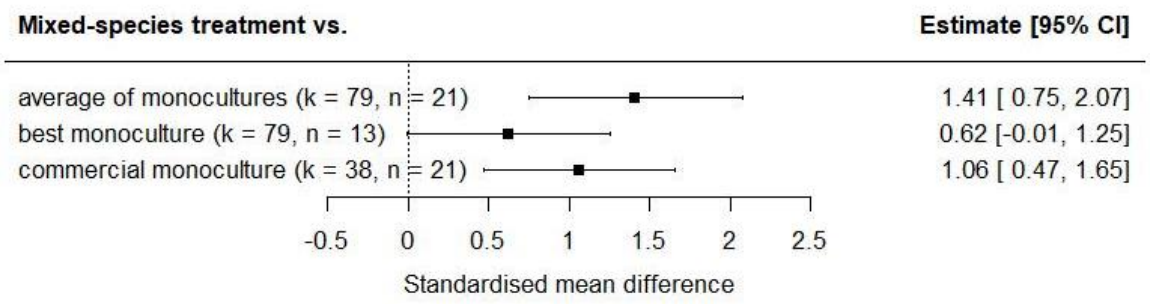


Figure 5.1 The effect of plantation diversification on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species. Effect sizes are standardised mean differences. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

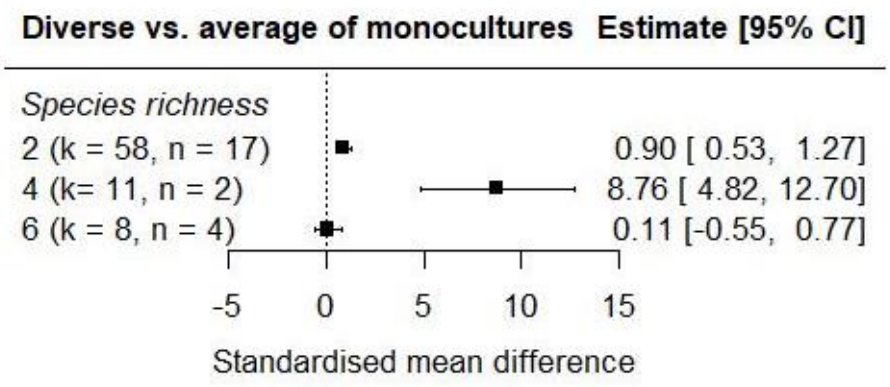


Figure 5.2 The effect of diversification at different levels of species richness on aboveground carbon stocks relative to the average of associated monocultures. Effect sizes are standardised mean differences, calculated using data subset by each level of species richness. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

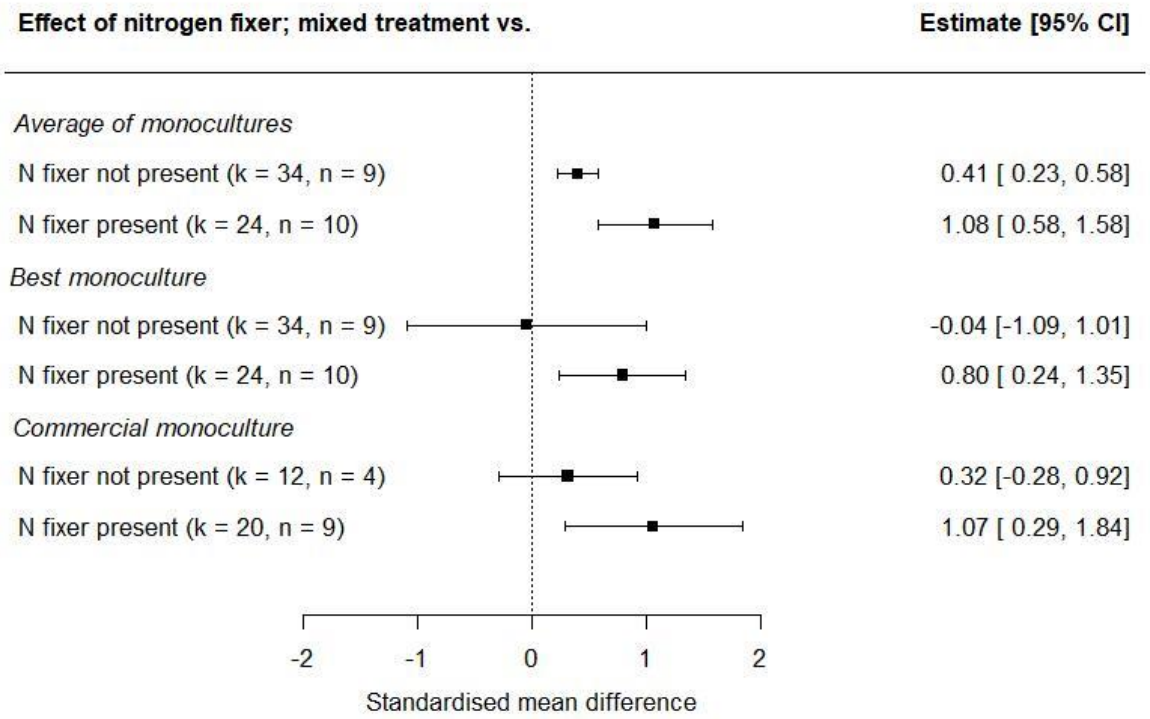


Figure 5.3 The effect of diversification with/without a nitrogen-fixing species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species (analysis limited to two-species mixtures). Effect sizes are standardised mean differences, calculated using data subset by presence or absence of a nitrogen-fixing species in the mixture. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

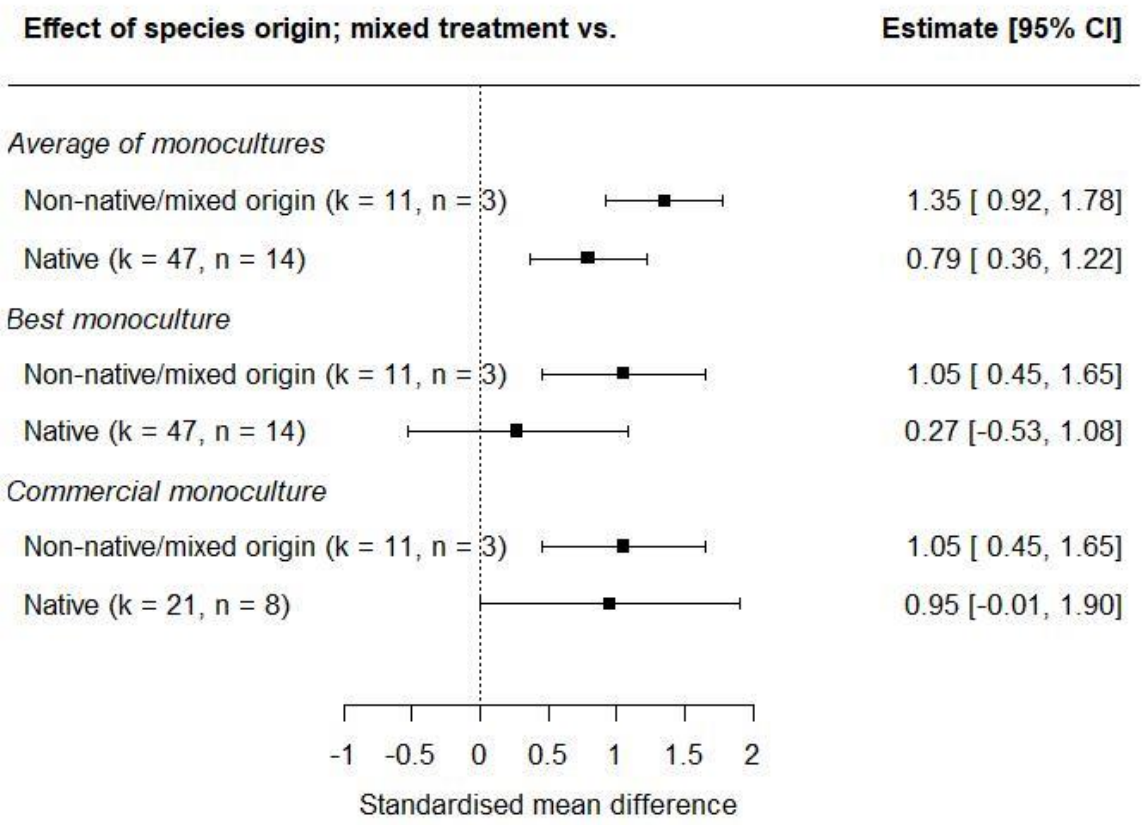


Figure 5.4 The effect of diversification with all native or non-native/mixed origin species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species (analysis limited to two-species mixtures). Effect sizes are standardised mean differences, calculated using data subset by species origin in the mixture. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

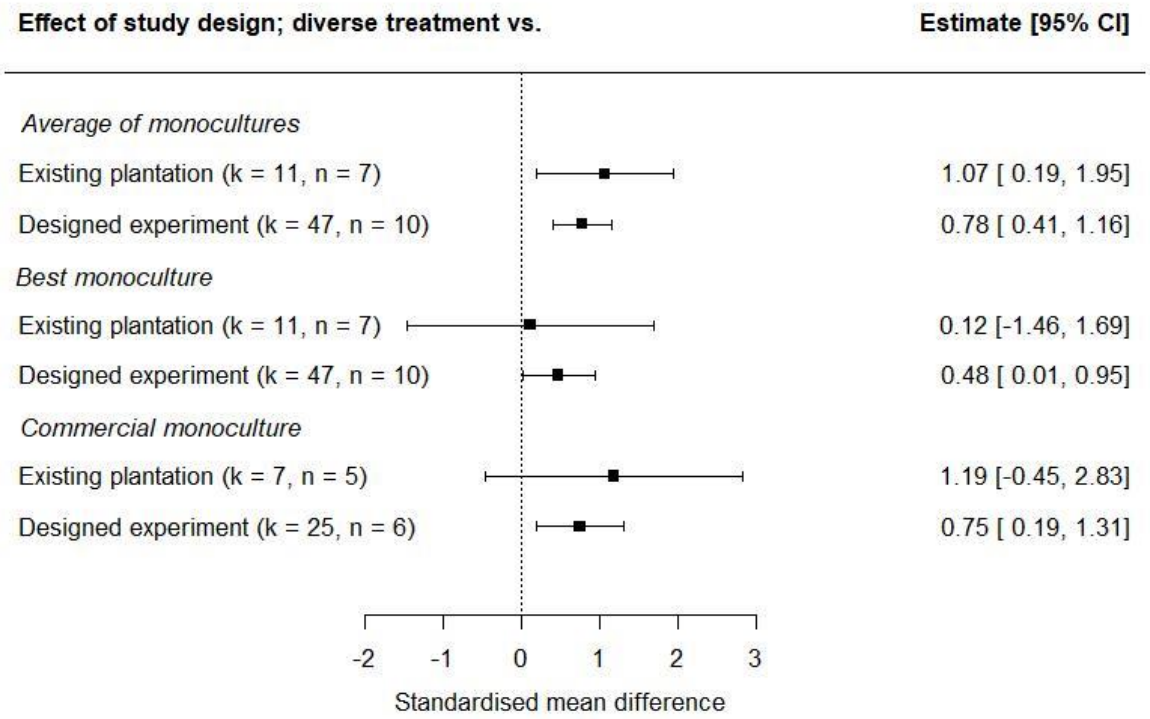


Figure 5.5 The effect of study design on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species (analysis limited to two-species mixtures). Effect sizes are standardised mean differences, calculated using data subset by study design. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

Discussion

Mixed plantations clearly outperformed the average of monocultures and commercial monocultures, with no carbon stock penalty even relative to the best performing monoculture. This highlights the opportunity to maximise carbon stocks through diversification of the increasing area of planted forests worldwide (FAO, 2020a). We found a peak in the diversity benefit in four-species mixtures. However, our meta-analysis also highlights the lack of data from planted forests at higher levels of tree diversity, and more data across the range of species richness is needed to better characterise this relationship. Given the young age of the plantations used in our meta-analysis (3.5-28 years), and the expectation that diversity relationships will strengthen over time, further analysis as these plantations age and from older plantations would be informative (Guerrero-Ramírez et al., 2017). Alongside the expected benefits of increased provision of other ecosystem services, enhanced resilience, and resistance to pests and disease, our results further support diversifying planted forests (Aerts & Honnay, 2011; Messier et al., 2021). This information will need to be integrated with information on the economics of diversifying plantations, but the focus on ecological rather than economic research within forestry is a barrier to our understanding of the economic impacts of diversification (Hildebrandt & Knoke, 2011).

The greatest positive effect of diversification was in mixtures with four species. Other studies have identified a hump-shaped (Xu et al., 2020), positive (Huang et al., 2018), and positive plateauing relationship (Liang et al., 2016; Zhang et al., 2012) between tree species richness and productivity in forest systems. However, in all these studies the relationship remained positive beyond a species richness of 20, except in Zhang et al. 2012, where the relationship plateaued at six species. Our data indicates an apparent peak in the positive effect of diversification in four species mixtures, however, all but one effect size for this species richness level is from one study, where the experimental plots were aged 3.5 yrs. Our dataset limited exploration of the diversity gradient, and the paucity of studies

with higher levels of species richness could also explain the less clear effect of diversification in mixtures with >4 species.

Under intensive management where single tree growth is optimised, as in commercial plantations, the effects of diversification might be reduced (Liang, Zhou, Tobin, McGuire, & Reich, 2015), presumably due to decreased competition that could reduce the complementarity normally found in mixtures. The benefits of diversification may become more apparent over the longer term, when mixed plantations will be more likely to maintain productivity even under perturbation (Osuri et al., 2020). As the plantations used in our analysis age, diversity effects may become more pronounced, and the relationship between diversity and function has been shown to become increasingly non-saturating over time (Guerrero-Ramírez et al., 2017; Reich et al., 2012). A review found strong support for biodiversity effects resulting from both complementarity and selection effects (Cardinale et al., 2011). The selection effect may explain the lack of transgressive overyielding found in our analysis, as when the monoculture species is particularly high yielding, it is harder for the mixture to outperform this. This can often be the case in commercial plantations, where species are usually selected for their fast growth rates, as well as attributes such as wood quality (C. L. C. Liu, Kuchma, & Krutovsky, 2018).

Presence or absence of species with particularly influential functional traits are expected to have a large effect on productivity (Tilman et al., 1997). Addition of a nitrogen-fixing tree species is a reasonably common method of forest diversification, aiming to reduce the need for fertiliser inputs (Marron & Epron, 2019; Richards, Forrester, Bauhus, & Scherer-Lorenzen, 2010; Temperton, Mwangi, Scherer-Lorenzen, Schmid, & Buchmann, 2007). When we included nitrogen-fixer as a moderator in our models, which was only possible for two-species mixtures, there was no clear effect. Other studies have also found that the presence of nitrogen-fixers in a mixture does not explain overyielding (Jactel et al., 2018). It has been shown that different species of nitrogen-fixers fix nitrogen at different rates and that their contribution of nitrogen fixation to a forest stand can change as forests age (Batterman

et al., 2018, 2013). This may complicate the mechanism by which nitrogen-fixers contribute to overall forest productivity and accumulation of carbon stocks, which may not be captured in an analysis of presence vs. absence of a nitrogen-fixer in the mixture.

We expected that mixtures of native species could lead to lower aboveground carbon stocks than mixtures including non-native species, which are often selected for their fast growth rates (Heryati et al., 2011). Fast-growing species such as *Eucalyptus* and *Pinus* make up a large proportion of planted forests, collectively comprising c.75% of the world's commercial plantations, often in locations where these species are not native (Marron & Epron, 2019). But our analyses suggested that non-native/mixed origin plantations did not clearly outperform native plantations. This may reflect that in many of the studies used, the fast growing species selected for plantations were native to the study location, for example *Eucalyptus globulus* in Australia (Bauhus, Van Winden, & Nicotra, 2004).

It has often been questioned whether the influence of biodiversity on ecosystem function observed in controlled experiments is expressed in natural and managed ecosystems, where abiotic forcing and complex interactions occur (Duffy, Godwin, & Cardinale, 2017; Manning et al., 2019). Both operational forestry plantations and scientific tree diversity experiments are subject to some level of control relative to naturally established forests, with biodiversity experiments often being more tightly controlled than forestry plantations. However, we found no clear influence of the study context on the effect of diversification on carbon stocks.

There are some limitations to our study. We have already highlighted the lack of representation across the diversity gradient and lack of higher diversity studies. The plantations contributing to our meta-analysis are also relatively young, aged between 3.5 and 28 years. We accounted for the differing ages of the plantations in our analysis by including a random effect for study site; however, we also assessed the relationship between plantation age and the carbon accumulation relative to

monocultures for two-species mixtures. Previous meta-analyses have found that diversity effects increase over time (Cardinale et al., 2011), which has also been observed in forest systems (Guerrero-Ramírez et al., 2017; Huang et al., 2018). We found a peak in effect of diversity at 17 years old; however, our a-priori expectation was for a linear or saturating relationship (e.g. Reich et al., 2012; Thakur et al., 2015) and these quadratic models were fitted post-hoc following visual inspection of the data. The apparent downturn after age 17 is driven by the three comparisons at age 28, from two study sites. Given that the effects of complementarity between species are expected to strengthen over time (Fargione et al., 2007; Reich et al., 2012), the lack of data from older forests limits our potential to explore the consequences of diversification on timescales relevant to the forestry industry (Huang et al., 2018). Longer term data from the TreeDivNet experiments used here will be an important resource for further investigation of the effects of diversification on productivity in the future (Verheyen et al., 2016).

Data limitations also restricted our ability to assess the mechanisms behind differences in carbon accumulation. We were only able to assess moderators individually and for two-species mixtures only. We therefore cannot rule out collinearity between our moderators, although none of them were significant. Furthermore, there are other potential drivers of carbon accumulation that we did not explore. For example, mixtures of tree species with complementary light interception strategies have been found to show overyielding (Williams et al., 2021). Establishment of future experiments using species selected because they are expected to be functionally complementary will be more informative than some earlier biodiversity experiments where species were selected entirely at random (Ebeling et al., 2014; X. Liu et al., 2018). Finally, differences in the establishment of each plantation in our analysis (e.g. densities or spacings) may influence carbon stocks.

Our study focuses on aboveground carbon stocks only, which is typically the most easily measured forest carbon pool. However, belowground carbon stocks, in tree biomass and in the soil, can be

important, with soil carbon stocks ranging from up to 90% of the total carbon stock in boreal forests to c.50% in tropical forests (Malhi et al., 2002). Previous studies have found a neutral or negative influence of diversity on belowground biomass. A recent study showed that, while mixtures showed overyielding aboveground, the belowground response was neutral, although the overall impact on carbon stocks remained significantly positive (Martin-Guay, Paquette, Reich, & Messier, 2020). If this result is replicated in other tree diversity studies, this emphasises that, by focussing on aboveground biomass, we may overestimate the impact of tree diversification on forest carbon accumulation (Martin-Guay et al., 2020). Further data on the impact of tree diversity on total ecosystem carbon stocks and an assessment of the responses of different carbon pools would therefore be valuable.

Diversification of plantations is one of the key actions recommended in Messier et al. 2021 and in a recent IPBES-IPCCC report on biodiversity and climate change, which aims to identify synergies and trade-offs between biodiversity protection and climate change mitigation and adaptation (Pörtner et al., 2021). The justification for use of mixed species plantations is that they will store more carbon, be more resilient to perturbation and provide greater support for associated biodiversity (Messier et al., 2021; Pörtner et al., 2021). Our study further supports the use of mixed species plantations as a method to increase carbon stocks and hence contribute to climate change mitigation (Beugnon et al., accepted). Accumulating evidence that diversification can increase carbon storage, resistance to perturbation (Hutchison et al., 2018), resilience to pests and disease (Jactel & Brockerhoff, 2007) and delivery of other ecosystem services (Gamfeldt et al., 2013), provides a strong justification for wider implementation of diversification in plantations (Messier et al., 2021). Even where mixtures do not provide substantial increases in carbon storage over monocultures (and we re-emphasise that we find no clear yield losses in mixtures relative to the best monoculture), they may nevertheless be desirable to increase levels of diversity of both the trees and associated organisms (Schuldt et al., 2018, 2019), as well as providing other potential benefits.

There are different mechanisms that could be used to establish mixed plantations. On the larger scales at which plantations are typically established, diversification could be achieved through intermixing of species at the individual tree level or through compartments/zones comprising different species. The preferred option will depend on the scale at which diversity influences carbon accumulation, resilience and delivery of ecosystem services, and trade-offs with the practical constraints of planting, management and harvesting practices. If increased productivity depends on complementarity between individuals of different species then intermixing of species will be important, whereas resilience to extreme climatic events or delivery of certain services may occur at the landscape scale (Aquilué et al., 2020). These uncertainties call for studies exploring the potential scale-dependence of biodiversity effects on critical ecosystem services (Gonzalez et al., 2020).

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Chapter 6 General Discussion

In this thesis I have addressed the influence of forest expansion on biodiversity and ecosystem function at a range of scales. I provide new evidence to support decisions on forest expansion in upland areas of the UK. I show that newly created native forest in the Scottish Highlands supports woodland specialists, with increasing suitability for specialist birds with woodland age. The response of ecosystem functions to the same native reforestation project highlights the risk of large-scale releases of soil carbon during forest establishment in areas with high soil carbon. The results of these chapters provide important information that should be integrated into landscape scale land-use plans in the Scottish Highlands. I outline a framework for integration of scientific research into rewilding, highlighting opportunities to fill knowledge gaps and collect new data within future projects. Finally, my assessment of carbon storage in mixed vs. monoculture plantations shows that mixed forests equal or improve on carbon storage in monocultures, further supporting the call for diversification of plantation forests.

Integrating information on native forest creation into land-use decisions in the Scottish Highlands

Forest expansion in Scotland will increase over the coming decades, if the Scottish government is to meet its target of reaching 21% woodland cover by 2050 (Scottish Government, 2019). All visions of forest expansion in Scotland include some native forest (Burton et al., 2019). In Chapter 2, I show that new native forest in the Scottish Highlands supports forest specialist species in the early stages of reforestation, emphasising the potential for forest expansion in the uplands to contribute to biodiversity conservation. Chapter 3 considers the response of ecosystem functions to the same native forest expansion project. I show that the different functions respond variably to the reforestation, with a key result of lower topsoil carbon in the reforestation sites than in unforested areas, suggesting loss of soil carbon with reforestation. This information should inform future land-use strategies in

Scotland, allowing assessment of the potential for native forest to meet biodiversity conservation and climate change mitigation goals.

My results in Chapter 2 show that, while the newly created forest supports some specialist birds and plants, the plant community is compositionally distinct from mature forest, although the richness of specialist species does not appear to differ across the differently aged sites. In Chapter 3 I show that the understorey vegetation responds to the lower grazing pressure in the fenced reforestation sites, leading to growth of the plant community that is already present in the sites. The ongoing development of the plant community will depend either on the germination of propagules from the soil seedbank or arrival of seeds from elsewhere (Hester, Gimingham, & Miles, 1991). Native forest remnants are sparsely distributed in the Scottish Highlands and heavily impacted by high levels of grazing by deer, so the arrival of plant species into the new forest will be limited by their presence in the landscape (Hester, Gimingham, et al., 1991; Mason et al., 2004; Patterson et al., 2014). Seed inputs influence the composition of the vegetation, but the establishment of some species is influenced by their differential germination requirements. For example, *Vaccinium myrtillus* (Blaeberry), a key component of the Caledonian pinewood understorey, only becomes dominant if it is already present in forest creation sites (Hester, Gimingham, et al., 1991; Hester, Miles, & Gimingham, 1991b).

Caledonian pinewoods also support specialist species in groups that were not addressed in my research, these include taxonomically more challenging groups such as lichens, fungi and bryophytes (Mason et al., 2004). At least 18 lichen species of the British Isles are limited to native pinewoods and there are c.77 species of lichen that can be used to assess the ecological continuity and quality of pinewood habitat (Coppins & Coppins, 2006). The niche-rich habitat for lichens associated with mature pinewood develops over time and younger secondary pinewoods score poorly for presence of characteristic lichens (Coppins & Coppins, 2006). The value of newly created forest may have an upper

limit that is lower than mature pinewood, emphasising the need for protection of the remaining remnants.

As Chapter 2 shows, the creation of forest in the unforested landscape of the Scottish Highlands will lead to the replacement of open ground species associated with the prior land-use. Previous research shows that native woodland creation in the Scottish uplands favours woodland associated bird species and leads to corresponding declines in open-ground nesting species such as *Anthus pratensis* (Meadow Pipit) (Douglas et al., 2020). A modelling exercise aiming to find the optimum open-ground to woodland distribution in Glen Affric, balancing the needs of species with woodland vs. open-ground specialisms, found that responses of each species' population to changes in forest cover were complex and contrasting (Hope, Humphrey, & Stone, 2006). But forest habitat networks in the Scottish Highlands will generally provide greater benefits to heathland species than heathland networks to forest species (Moseley, Sing, & Ray, 2005). Recommendations for forest expansion in the Highlands prioritise buffering of and expansion from existing forest, with greater connectivity between forest patches to allow dispersal of associated species (Moseley et al., 2005).

The results from Chapter 3 further contribute to consideration of the balance between open ground and forest expansion in the Highlands. My results show that native forest establishment can cause topsoil carbon losses that could outweigh gains in carbon accumulation aboveground in the early stages of forest establishment. These findings are corroborated by other studies that show loss of soil carbon with the transition from existing semi-natural vegetation cover to forest in areas with high carbon content soils (Friggens et al., 2020; Guo & Gifford, 2002; K. B. Matthews et al., 2020). Restriction of forest expansion in areas with high carbon soils, including shallow peats or high peat content soils, could be key to maintaining important carbon stocks in the Scottish Highlands. This aligns with the results of Chapter 2, which indicate that overall species richness would be highest with maintenance of some open-ground at the landscape scale. Caledonian pinewood typically exists

within a mosaic of other semi-natural habitats, including open heath and bog, with a naturally patchy and dynamic distribution which benefits woodland and open-ground specialists (Hope et al., 2006). Aiming to recreate this mosaic, while maintaining and enhancing connectivity between forest patches but protecting soil carbon stocks, should be an important target of land management in the Scottish Highlands.

The apparent significant soil carbon loss, despite a combination of relatively low-density planting and natural regeneration, at my study sites brings into question the validity of anticipated carbon sequestration from native forest expansion in the Scottish Highlands. An estimate that the maximum extent of native forest expansion in the Scottish Highlands could sequester 6.96 Mt CO_2 per year doesn't account for soil carbon losses, despite acknowledging that they could be substantial (Fletcher et al., 2021). Other modelled estimates of carbon sequestration from native forest expansion are more conservative, accounting for net carbon losses driven by soil carbon loss during the early stages of establishment (K. B. Matthews et al., 2020). In Scotland, there are c.1,358,122 ha of organo-mineral soils available for forest expansion, but with a higher risk of soil carbon release, and c.549,595 ha of mineral soils available, with net carbon accumulation expected (Bradfer-Lawrence et al., 2021). Across the UK there are 2 million ha of mineral soils available for forest expansion, which could sequester 600 Mt CO_2e by 2100 (Bradfer-Lawrence et al., 2021). Where carbon sequestration is the objective of forest expansion, it should be restricted to mineral soils where there are guaranteed returns.

The results of Chapters 2 and 3 contribute to the debate on how we set targets for forest expansion and other habitat restoration methods. Targets for habitat restoration based solely on area can fail to optimise biodiversity conservation and carbon sequestration goals. Whereas target-oriented approaches, such as to sequester a certain amount of carbon or provide habitat for specific aspects of biodiversity are more likely to be successful (K. B. Matthews et al., 2020; Strassburg et al., 2020). Evidence from tropical forest conservation has shown that adjusting restoration actions to consider

outcomes for biodiversity alongside carbon sequestration can lead to large benefits for biodiversity with just a small shortfall in maximum carbon sequestration (Ferreira et al., 2018). Although I provide further evidence that native forest expansion in the uplands may not contribute to carbon sequestration goals on short timescales, this should not compromise the expansion of native forest to conserve the biodiversity associated with the Scottish Highland's limited native forest. The overall maximum contribution of nature-based solutions, such as forest expansion, to climate change mitigation in the UK is modest relative to bigger changes such as large-scale fossil fuel reductions (Bradfer-Lawrence et al., 2021). It is also key that emphasis is placed on the nature in nature-based solutions, to ensure that actions for climate change mitigation also have a positive effect on biodiversity (Bradfer-Lawrence et al., 2021).

A future landscape in the Scottish Highlands

Multiple stakeholders aspire to a landscape in the Scottish Highlands that is richer in nature and has greater forest cover (Armstrong et al., 2014; Scottish Environment LINK, 2020). Given the evidence in Chapter 2 that native forest expansion can support forest-associated biodiversity, but that in areas with carbon-rich soils there is the potential for carbon release (Chapter 3), how does this inform future forest cover in these areas?

Natural regeneration of forest could be a mechanism for achieving optimum outcomes for biodiversity and carbon in the Scottish Highlands. In Chapter 3 I show that deer grazing presents a barrier to tree establishment in my study sites, this is a problem throughout the Highlands (Scottish Environment LINK, 2020; Tanentzap et al., 2013). Reduced grazing would facilitate forest expansion and could potentially provide protection to higher carbon content soils by avoiding soil disturbance, while wetter peat-rich soils will naturally limit tree regeneration (Mayer et al., 2020; Mchaffie, Legg, Worrell, Cowie, & Amphlett, 2002; Ohlson, ØKland, Nordbakken, & Dahlberg, 2001). Natural regeneration has other benefits, such as development of a more natural species composition and structure, and

establishment of locally adapted individuals (Di Sacco et al., 2021; Fleischman et al., 2020). Aspiring for a habitat mosaic of forest alongside more open habitats, as is characteristic of Caledonian pinewood, is a good target for the Scottish Highlands (Hope et al., 2006). Achieving this through reduced deer grazing pressure would simultaneously benefit other habitats, such as peat bogs, which are degraded by high levels of grazing (Scottish Environment LINK, 2020).

How could future rewilding projects contribute to filling evidence gaps?

Chapter 4 provides a framework for integrating scientific evidence and ecological paradigms into rewilding projects from their outset. I established the links between ecological paradigms and the principles of rewilding projects, demonstrating how existing ecological techniques could be used to explore rewilding projects. If experimental manipulations, a monitoring design, and collection of baseline data had been implemented at the outset of the project I studied in Chapters 2 and 3, some of the research gaps in understanding the consequences of forest expansion in the Scottish Highlands could have been addressed. Given the explicit deployment of rewilding and reforestation projects to tackle biodiversity loss and climate change, understanding how key variables respond is crucial (Jepson, 2016; Pettorelli et al., 2018; Svenning et al., 2016).

Long-term experiments are valuable in understanding the processes involved in forest establishment; a study combining experimental manipulation with a long-term assisted natural regeneration project emphasised the complex interacting factors that dictate seedling establishment and survival (Martínez-Baroja, Rey-Benayas, Pérez-Camacho, & Villar-Salvador, 2021). This study emphasises that prior assumptions are often not met, for example seedling recruitment did not occur in closest proximity to tree islets. Additionally it shows that integrated research can result in important management recommendations, such as the recommendation to include species with fleshy fruits in forest islets to attract dispersers (Martínez-Baroja et al., 2021).

Taking the opportunity to integrate ecological monitoring protocols and experimental manipulations into rewilding projects from their outset will not compromise their overall objectives but could provide important contributions to the evidence-base for rewilding, alongside verification of projects' efficacies. Monitoring of tree planting programs is rare. In a study of pantropical tree planting projects, only 18% undertook any monitoring and only 5% monitored tree survival (Martin et al., 2021). This is particularly worrying given the rise in tree planting organisations, which are often aiming to tackle biodiversity loss and climate change (Martin et al., 2021). Given the risks and complexities in predicting the contribution of forest expansion to tackling global challenges, monitoring is needed (Veldman et al., 2019).

Will further evidence that mixed forests accumulate more carbon contribute to diversification of planted forests?

In Chapter 5, I show that mixed species plantations accumulate more carbon than the average of relevant monoculture plantations. I also show that carbon stocks are similar in mixed plantations and the most productive associated monoculture. These results emphasise that diversification of planted forests can increase carbon accumulation, alongside the other benefits expected of mixed plantations, it is therefore important to understand why establishment of mixed plantations is still uncommon (Lewis et al., 2019; Messier et al., 2021).

Monoculture plantations are typically easily managed and densely planted, with species selected for their fast growth rates and for attributes such as wood quality (C. L. C. Liu et al., 2018). Monocultures are efficiently harvested and the resulting product has a high uniformity, giving high economic returns (C. L. C. Liu et al., 2018). Forestry is dominated by ecological rather than economic research, making it difficult to assess the perceived higher economic cost of mixed plantations (Hildebrandt & Knoke, 2011). An assessment of the economic impacts of mixing species found that only small increases in yield or savings in inputs such as fertiliser would be needed to offset any increased harvesting costs

(Nichols et al., 2006). Economic models to assess mixed species stands typically fail to include risk in their assessments, meaning that the increased stability and resistance to disturbance seen in mixed stands is rarely valued (Knoke, Ammer, Stimm, & Mosandl, 2008). Forestry grants that explicitly reward diversification could help to increase establishment of mixed stands (Nichols et al., 2006). For practitioners, operational scale demonstrations of mixed plantations could help to remove barriers to their establishment (Nichols et al., 2006; Verheyen et al., 2016).

Looking to the future, plantations should be designed to meet multiple ecological, social and economic objectives (Paquette & Messier, 2010). Using mixed species in plantations can contribute to these goals and well-designed plantations can play an important role in protecting natural forests, while simultaneously meeting societal demands for timber and other services (Paquette & Messier, 2010).

Setting forest expansion within a wider context – social factors and avoiding unintended outcomes

The focus of my thesis has been ecological, but forest expansion projects occur within complex social settings (Barnaud et al., 2021). This is pertinent to all aspects of my thesis: native reforestation of the Scottish Highlands is just one land-use change that could occur in a culturally complex and highly valued landscape (Wilson, 2017), improving the evidence-base for rewilding projects could be an important step in increasing their political acceptability (Pettorelli et al., 2018), and plantation diversification may be limited most by practitioners' acceptance of proposals (Nichols et al., 2006).

Delivering social benefits to local people is another important objective of forest expansion and a lack of alignment between forest managers and local stakeholders can lead to the failure of projects (Höhl et al., 2020). However, ecological and social outcomes of forest expansion projects are rarely measured simultaneously, and going forwards joint assessment of these areas should be used to define success (Pritchard, 2021). A recent assessment of forest expansion efforts in northern India

found that, despite several decades of investments, there was no evidence of increased tree cover or livelihood benefits (Coleman et al., 2021).

One of the risks of the increasing interest in forest expansion, particularly in the form of tree planting, is that projects that are ecologically or socially damaging could go ahead, driven by high level global pledges (Pritchard, 2021). A solution to this problem is to consider forest expansion within the context of whole ecosystems (Brancalion & Holl, 2020; Fleischman et al., 2020), and to reframe nature-based solutions around restoration of native vegetation to draw the focus away from tree planting (Tölgyesi, Buisson, Helm, Temperton, & Török, 2021). As I have highlighted in Chapter 3, forest expansion is no guarantee of carbon storage, and tree planting can be damaging in naturally treeless ecosystems such as peatlands and savannas (Fleischman et al., 2020). Future nature-based solutions should firstly focus on protecting existing natural ecosystems, and secondly consider restoration of all ecosystems, rather than focusing primarily on forest establishment (Fleischman et al., 2020; Seddon et al., 2019; Tölgyesi et al., 2021).

Future forest expansion projects should always come second to the protection of existing forest (Brancalion & Holl, 2020; Di Sacco et al., 2021; K. D. Holl & Brancalion, 2020). Local people and all relevant stakeholders should be included in projects from the outset, which will also improve the likelihood of successful outcomes (Brancalion & Holl, 2020; Di Sacco et al., 2021). Projects should only occur in suitable locations, to mitigate any risks associated with inappropriate forest expansion, and where possible natural regeneration should be used (Di Sacco et al., 2021; K. D. Holl & Brancalion, 2020).

Forest expansion in a changing future world – mitigating future challenges or compromised by them?

Forests are increasingly proposed as a nature-based solution to mitigate climate change (Girardin et al., 2021; Lewis et al., 2019). However, the changing climate will also influence forests in the future and mediate their capacity to mitigate further climate change (Malhi et al., 2020).

Climate change will alter the suitability of past species' ranges. Under future climate change the species composition of many of Europe's forests will shift and future forest expansion or establishment should account for changing species ranges (Buras & Menzel, 2019). In the Caledonian pinewoods (Chapters 2 and 3), core Caledonian pinewood areas are anticipated to become less suitable for *Pinus sylvestris* (Scots Pine) and more suitable for *Quercus* spp. (Oak spp.) (Huntley et al., 2018). Future forest expansion projects should account for these findings.

Optimisation of Europe's forests for climate change mitigation should also consider their influence on radiative forcing and near-surface temperature and rainfall, alongside their carbon sequestration capacity (Luyssaert et al., 2018). In previously treeless areas forest establishment can influence albedo, particularly in high latitude areas where forest expansion could contribute to global heating (Nuñez et al., 2021).

Future forests will also be increasingly threatened by climate change. Forest establishment in some parts of Europe may increase the fire risk in these areas, which could cause large-scale releases of carbon (Hermoso, Regos, Morán-Ordóñez, Duane, & Brotons, 2021). On much longer timescales, the declining influence of CO_2 fertilisation on photosynthesis could reduce the capacity of terrestrial ecosystems to continue to absorb carbon, causing the strength of the terrestrial vegetation carbon sink to decrease (C. D. Jones et al., 2016; S. Wang et al., 2020). Overall, predicting the future contribution of forests to carbon sequestration is complicated, which is particularly pertinent in the

context of Chapter 3, where net carbon sequestration appears not to occur during the early stages of forest establishment.

A changing climate poses multiple challenges to forest expansion and increases the risk that projects may contribute less than expected to climate change mitigation. Yet, while foresters show awareness of the potential impacts of climate change on their practice, they are slow to implement changes in response, highlighting the gap between researchers and practitioners (Sousa-Silva et al., 2018).

Future work

The results of Chapters 2 and 3 complement large-scale forest expansion modelling in Scotland, which considers optimal conformations for connectivity (Gimona, Wright, Eastwood, Gallego, & Hester, 2021) and land suitability (Sing & Aitkenhead, 2020), and assesses maximisation of carbon storage (Bradfer-Lawrence et al., 2021; Fletcher et al., 2021; K. B. Matthews et al., 2020). However, we would still benefit from more on-the-ground data collection. The results of Chapter 2 provide important information on the biodiversity responses to forest expansion at three trophic levels. Additional information on how and if characteristic rare forest specialists colonise the new forest would be beneficial. It would also be valuable to explore management interventions to accelerate the transition of the plant community towards the composition found in the mature forest.

We particularly lack data to understand how naturally regenerating forest could contribute to forest expansion goals and how it would influence biodiversity and carbon sequestration. We need research to understand grazing thresholds that allow natural forest establishment and how this influences the tree composition and vegetation community in naturally regenerated forest. Research to understand the response of soil carbon to natural forest regeneration should also be a priority. New experiments comparing the response of multiple biodiversity and ecosystem function variables under natural regeneration vs. tree planting would provide valuable information. However, it would be informative

to investigate these variables in existing naturally established forest, with comparisons to matched areas of other habitats (e.g. planted forest, mature forest, heathland), given the need for data to inform the implementation of current forest expansion targets.

The results showing topsoil carbon losses in Chapter 3 have potentially some of the greatest implications from my thesis. However, interpretation of this was limited by the lack of baseline data in my study sites and the poor understanding of the drivers of soil carbon change with tree establishment. Recent experimental work corroborates my results (Friggens et al., 2020), but the planting density was higher in the experimental study, which complicates the comparison. To predict whether soil carbon losses will occur even under natural regeneration or much lower density planting, we need to understand the extent to which soil carbon losses are driven by disturbance, planting methods and tree densities vs. changes in the biotic community or soil conditions driven by tree establishment. Additionally, there is research suggesting that tree establishment can lead to carbon inputs in the deeper soil layers, potentially compensating for losses in the surface soil layers (Vanguelova et al., 2019). Assessing whether this has occurred in my study sites would be an important next step in understanding the impact of this forest expansion project on the whole ecosystem carbon balance. The limitations in interpreting the topsoil carbon results from Chapter 3 link to Chapter 4, where I emphasise the need for better integration of ecological research into rewilding projects. Integrating longitudinal studies into future forest expansion and rewilding projects could improve our understanding of issues such as the response of soil carbon.

Building on Chapter 4, the implementation of baseline and ongoing monitoring in rewilding projects, alongside integration of experimental manipulation, will allow evidence gaps to be addressed. Characterisation of the outcomes of rewilding projects will enhance their integration into future land-use plans, as current uncertainties limit their ability to contribute to biodiversity conservation and carbon sequestration goals. An improved understanding of the impact of rewilding interventions on

key ecological principles (e.g. recruitment limitation, dispersal limitation, restoration of habitat heterogeneity, restoration of trophic structure), could lead to a new generation of ecologically informed rewilding projects, that are optimised to maximise conservation, carbon sequestration and ecosystem service supply.

My meta-analysis in Chapter 5 demonstrates the potential for increased carbon storage in mixed plantations relative to monocultures. The studies contributing to my analysis highlighted the literature gaps in this area. Studies were heavily weighted towards two-species mixtures, with four-species mixtures the next most represented, and a paucity of studies at other levels of tree diversity. There was a particular lack of studies with a tree diversity higher than four species. Natural tree diversity in the study region may determine the upper level of species richness in diversity experiments, however, several of the studies included were tropical, where natural levels of tree diversity are higher than four species. It is anticipated that the Tree Diversity Network will contribute to filling this research gap as their experiments mature. I assessed some of the mechanisms that influence carbon storage in the mixed plantations. However, the studies available determined the mechanisms that could be assessed. For example, studies assessing the inclusion a nitrogen-fixing tree species in a mixture were particularly well represented. Studies which mix tree species with complementary traits, for example contrasting growth habitats, nutrient acquisition strategies, or water demands, would help to explore further mechanisms behind the benefits of diversification and could contribute to refining the establishment of mixed plantations in the future. Implementation of mixed plantations is limited partly by operational challenges and a lack of evidence of their economic benefits. Upscaling from experiments to applied forestry research in large-scale mixed plantations would help to bridge the gap between research and practice.

Conclusions

In this thesis I have used ecological research techniques to answer applied questions on the influence of forest establishment on biodiversity and ecosystem function. As we enter an uncertain future, with declining biodiversity and the increasing impacts of climate change, it is important to understand how proposed solutions, such as forest expansion, can contribute to solving these problems (Seddon et al., 2020; Steffen et al., 2015).

In the Scottish Highlands, where forest cover has been progressively lost over thousands of years and currently remains in scattered remnants, understanding the impact of re-establishing native forest cover is important. I have shown that native forest expansion in these areas benefits woodland specialist biodiversity, with the clearest benefits for birds. My assessment of the influence on native forest expansion on ecosystem functions provides a more mixed picture. Markers of the regeneration capacity of the new forest are positive, with seedling regeneration and growth, as well as growth of the ground vegetation. However, the loss of topsoil carbon in the reforestation sites suggests that these sites are not net accumulators of carbon in the early stages of reforestation. Future land-use decisions in the Scottish Highlands should consider these results, but a lack of carbon sequestration with native forest expansion in upland areas should not compromise targets to expand Scotland's fragmented native forest. More research assessing soil carbon under native reforestation and the potential for natural regeneration to prevent soil carbon losses is needed.

A framework for the integration of ecological research into future rewilding projects will help to inform future land-use decisions, and some of the knowledge gaps highlighted in Chapters 2 and 3 could be addressed by better integration of research into existing rewilding projects. There is an emphasis on rewilding as a solution to tackle the biodiversity and climate crises, but we are unable to fully understand its contributions to these problems without an improved evidence-base and monitoring of outcomes.

My assessment of carbon storage in mixed plantations relative to monocultures provides further support for diversification of plantations. My results suggest gains in carbon storage with diversification, and at the least no loss of carbon. However, I highlight the lack of studies assessing higher diversity plantations and a need for more data from older plantations. Upscaling of mixed plantations to demonstrate their potential to forestry practitioners will be an important next step, as the barriers to implementation may be linked to perceived operational challenges and economic shortfalls.

From a national to global scale, the optimisation of future forest expansion efforts is important. This requires an understanding of ecological responses to forest expansion. My thesis contributes to this by providing an assessment of local ecological responses to native reforestation in the Scottish Highlands, developing a framework for better integration of ecological research into rewilding projects, and analysing the available data on carbon storage in mixed plantations at a global scale. To provide the maximum benefits for local communities, biodiversity, and climate change mitigation, future forest expansion must be evidence based and integrated into existing land-uses.

Appendix A: Supplementary information for Chapter 2

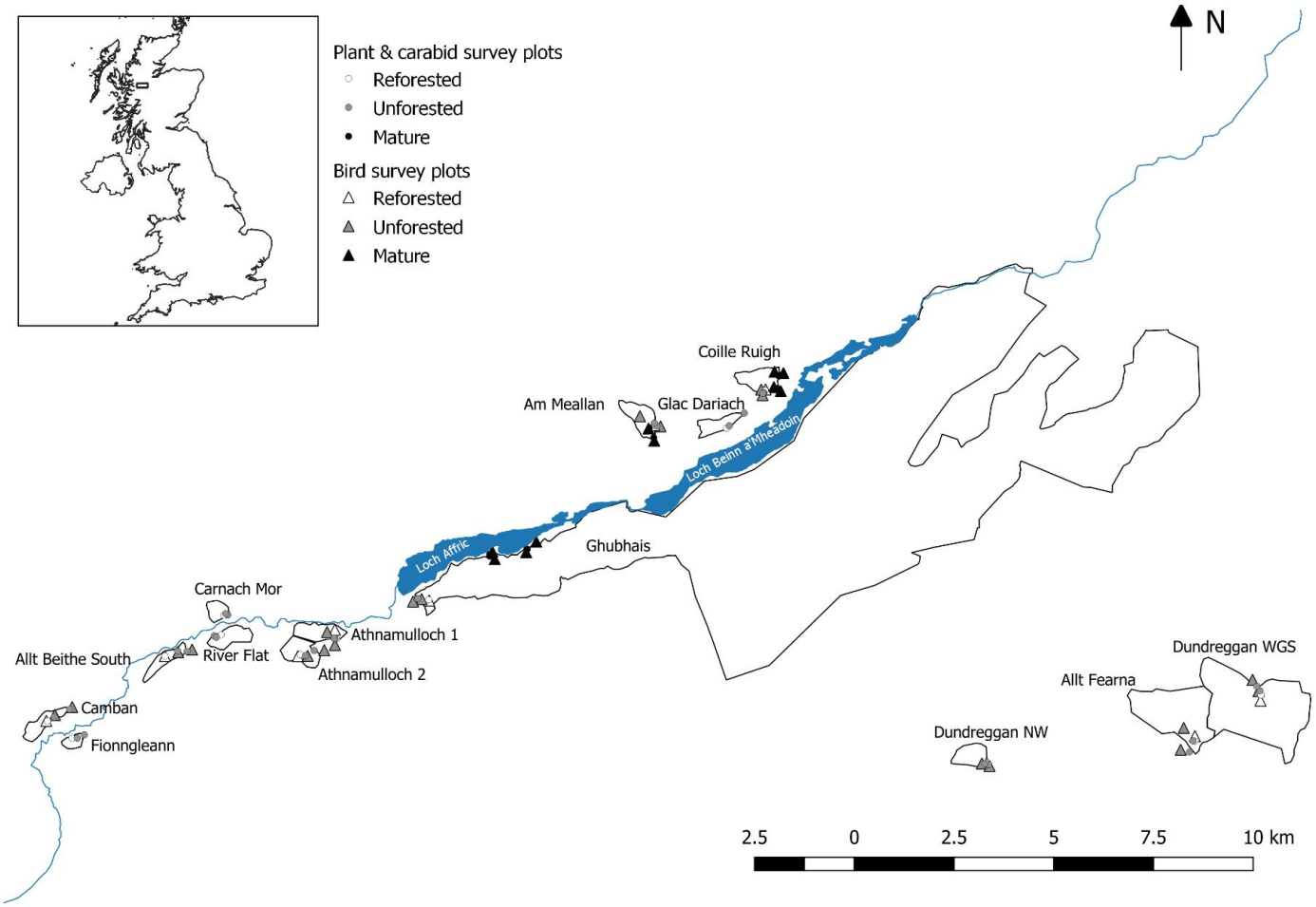


Figure A1 The location of the fenced and reforested sites used in this study. Circles and triangles indicate the plant & carabid beetle and bird survey plots, categorised by forest treatment. Inset: the rectangle indicates the location of the study area within the UK.

Table A1 Information on the fenced and reforested sites surveyed in this study. At both Coille Ruigh and Ghubhais two grazed and ungrazed mature forest plots were established in two discontinuous areas of mature forest at each site. The year of establishment is defined as the year in which the site was fenced. The age of the sites in 2018, the year of the first surveys, is calculated as the number of years from the first planting event. Planting was either by hand screefing, where a spade was used to clear vegetation before slit planting the trees, or by machine mounding, where a digger was used to create mounds into which trees were planted. The presence of mature forest at each site is indicated (N = not present, Y = present). The latitude and longitude of each site is given.

Site name	Size (ha)	Year site established	Number of trees planted	Age in 2018	Trees per ha	Type of trees planted[1]	Planting method	Mature forest	Latitude, longitude
Athnamulloch One	63	1990	20,994	28	333	SP, A, BL	Hand screefing	N	57.235622, -5.117791
Athnamulloch Two	57	1994	22,177	24	389	SP, B, A, BL	Hand screefing	N	57.230217, -5.128606
River Flat	52	1997	9,250	21	178	SP, BL	Hand screefing	N	57.235401, -5.155535
Carnach Mor	25	1996	15,500	22	620	BL, SP	Hand screefing	N	57.240799, -5.159719
Allt Beithe (South)	28	1997	4,150	21	148	SP, W, H	Hand screefing	N	57.228645, -5.180406
Fionngleann	15	1999	16,500	19	1,100	BL	Hand screefing	N	57.211372, -5.215899
Camban	29.45	1999	32,400	19	1,100	BL	Hand screefing	N	57.216728, -5.228811
Coille Ruigh	50	1990	Natural regeneration[2]	28	2,000	SP,BL	Hand screefing	Y	57.291874, -4.931883
Ghubhais	155	1993	18,380	25	119	A, SP, BL	Hand screefing	Y	57.246426, -5.039163
Dundreggan WGS	446	2005	8,000[3]	13	18[3]	BL	Machine mounding	N	57.218655, -4.731901
Allt Fearna	150	2012	144,000	6	960	BL, SP	Machine mounding	N	57.213062, -4.756109
Dundreggan NW	45.2	2010	70,000	8	1,549	SP, BL	Machine mounding	N	57.206726, -4.847144
Meallan	55	1991	27,085	27	492	SP, A, BL	Hand screefing	Y	57.285549, -4.984157

Glac Dariach	35	1992	26,551	26	759	SP, B, A, BL	Hand screefing	N	57.281532, -4.952896

[1] A = Aspen *Populus tremula*, B = Birch spp. *Betula* spp., BL = broadleaf trees (includes Silver Birch *Betula pendula*, Downy Birch *Betula pubescens*, Rowan *Sorbus aucuparia*, Goat Willow *Salix caprea*, Eared Willow *Salix aurita*, Alder *Alnus glutinosa*, Aspen *Populus tremula*, Holly *Ilex aquifolium*, Hazel *Corylus avellana*), H = Hazel *Corylus avellana*, SP = Scots Pine *Pinus sylvestris*, W = Willow *Salix spp.*.

[2] The site was fenced in 1990 and natural regeneration was subsequently successful. Trees for Life estimate that 100,000 young trees established as a result.

[3] This planting event supplemented a previous Woodland Grant Scheme planting prior to Trees for Life's ownership of the Dundreggan Estate from 2008.



Figure A2 Close up of the site Am Meallan, showing the locations of the plant & carabid beetle and bird survey plots. At this site all three forest categories (unforested, reforested, mature) were present.

Table A2 Plant species lists for the unforested, reforested and mature forest treatment categories, showing common and scientific names (Stace, 2010). [A] Denotes species defined as Ancient Woodland Indicators (Kirby, 2020b). [T] Denotes species defined as priority species by Trees for Life staff.

Unforested		Reforested		Mature	
Common name	**Scientific name**	**Common name**	**Scientific name**	**Common name**	**Scientific name**
Bell Heather[T]	*Erica cinerea*	Aspen	*Populus tremula*	Bell Heather[T]	*Erica cinerea*
Birch spp.	*Betula* spp.	Bell Heather[T]	*Erica cinerea*	Birch spp.	*Betula* spp.
Blaeberry[A,T]	*Vaccinium myrtillus*	Birch spp.	*Betula* spp.	Blaeberry[A,T]	*Vaccinium myrtillus*
Bog Asphodel	*Narthecium ossifragum*	Blaeberry[A,T]	*Vaccinium myrtillus*	Bog Asphodel	*Narthecium ossifragum*
Bog-moss spp.	*Sphagnum* spp.	Bluebell[A]	*Hyacinthoides non-scripta*	Bog-moss spp.	*Sphagnum* spp.
Bog-myrtle	*Myrica gale*	Bog Asphodel	*Narthecium ossifragum*	Bracken	*Pteridium aquilinum*
Bracken	*Pteridium aquilinum*	Bog-moss spp.	*Sphagnum* spp.	Brown Bent	*Agrostis canina*
Brown Bent	*Agrostis canina*	Bog-myrtle	*Myrica gale*	Common Cow-wheat[A]	*Melampyrum pratense*
Carnation Sedge	*Carex panicea*	Bracken	*Pteridium aquilinum*	Cowberry[T]	*Vaccinium vitis-idaea*
Cat's-ear	*Hypochaeris radicata*	Brown Bent	*Agrostis canina*	Cross-leaved Heath[T]	*Erica tetralix*
Chickweed-wintergreen[T]	*Trientalis europaea*	Common Sedge	*Carex nigra*	Deergrass	*Scirpus cespitosus*
Common Butterwort	*Pinguicula vulgaris*	Common Sorrel	*Rumex acetosa*	Field Wood-rush	*Luzula campestris*
Common Cow-wheat[A]	*Melampyrum pratense*	Cotton-grass spp. .	*Eriophorum* spp	Fringe-moss spp.	*Racomitrium* spp.
Common Sedge	*Carex nigra*	Creeping Soft grass[A]	*Holcus mollis*	Glittering Wood-moss[T]	*Hylocomium splendens*
Cotton-grass spp.	*Eriophorum* spp.	Cross-leaved Heath[T]	*Erica tetralix*	Haircap spp.	*Polytrichum* spp.
Cowberry[T]	*Vaccinium vitis-idaea*	Deergrass	*Scirpus cespitosus*	Hard Fern[A]	*Blechnum spicant*
Cross-leaved Heath[T]	*Erica tetralix*	Devil's-bit Scabious	*Succisa pratensis*	Intermediate Wintergreen[T]	*Pyrola media*
Deergrass	*Scirpus cespitosus*	Fairy Flax	*Linum catharticum*	Juniper[A,T]	*Juniperus communis*
Devil's-bit Scabious	*Succisa pratensis*	Field Wood-rush	*Luzula campestris*	Ling Heather[T]	*Calluna vulgaris*
Field Wood-rush	*Luzula campestris*	Fringe-moss sp.	*Racomitrium* sp.	Moss spp.	
Fir Clubmoss	*Huperzia selago*	Glittering Wood-moss[T]	*Hylocomium splendens*	Ostrich-plume Feather-moss	*Ptillium crista-castrensis*
Fringe-moss spp.	*Racomitrium* spp.	Great Wood-rush[A,T]	*Luzula sylvatica*	Purple Moor-grass	*Molinia caerulea*

Glittering Wood-moss[T]	*Hylocomium splendens*	Haircap spp.	*Polytrichum* spp.	Red-stemmed Feather-moss	*Pleurozium schreberi*
Haircap spp.	*Polytrichum* spp.	Hard Fern[A]	*Blechnum spicant*	Rowan	*Sorbus aucuparia*
Hard Fern[A]	*Blechnum spicant*	Heath Bedstraw[T]	*Galium saxatile*	Scots Pine	*Pinus sylvestris*
Heath Bedstraw[T]	*Galium saxatile*	Heath Spotted-orchid	*Dactylorhiza maculata*	Tormentil	*Potentilla erecta*
Heath Milkwort	*Polygala serpyllifolia*	Lesser Celandine	*Ranunculus ficaria*	Turf-moss spp.	*Rhytidiadelphus* spp.
Heath Rush	*Juncus squarrosus*	Ling Heather[T]	*Calluna vulgaris*		
Heath Spotted-orchid	*Dactylorhiza maculata*	Liverwort spp.			
Horsetail spp. .	*Equisetum* spp.	Male Fern[T]	*Dryopteris filix-mas*		
Lesser Butterfly-orchid	*Platanthera bifolia*	Marsh Thistle	*Cirsium palustre*		
Ling Heather[T]	*Calluna vulgaris*	Marsh Violet[A]	*Viola palustris*		
Liverwort spp.		Moss spp.			
Male Fern[T]	*Dryopteris filix-mas*	Pill Sedge	*Carex pilulifera*		
Marsh Fragrant-orchid	*Gymnadenia conopesa*	Purple Moor-grass	*Molinia caerulea*		
Marsh Lousewort	*Pedicularis palustris*	Purple Spoonwort	*Pleurozia purpurea*		
Marsh Violet[A]	*Viola palustris*	Red Fescue	*Festuca rubra*		
Mat-grass	*Nardus stricta*	Red-stemmed Feather-moss	*Pleurozium schreberi*		
Moss spp.		Rough Meadow-grass	*Poa trivialis*		
Oblong-leaved Sundew	*Drosera intermedia*	Rowan	*Sorbus aucuparia*		
Pill Sedge	*Carex pilulifera*	Scots Pine	*Pinus sylvestris*		
Purple Moor-grass	*Molinia caerulea*	Smooth Meadow-grass	*Poa pratensis*		
Purple Spoonwort	*Pleurozia purpurea*	Soft Rush	*Juncus effusus*		
Red-stemmed Feather-moss	*Pleurozium schreberi*	Sweet Vernal-grass	*Anthoxanthum odoratum*		
Ribwort Plantain	*Plantago lanceolata*	Tall Fescue	*Festuca arundinacea*		
Rough Meadow-grass	*Poa trivialis*	Tawny Sedge	*Carex hostiana*		
Round-leaved Sundew	*Drosera rotundifolia*	Tormentil	*Potentilla erecta*		
Rowan	*Sorbus aucuparia*	Tufted Hair-grass	*Deschampsia cespitosa*		
Slender St John's-wort[A]	*Hypericum pulchrum*	Turf-moss spp.	*Rhytidiadelphus* spp.		

Star Sedge	*Carex echinata*	Wood Anemone[A,T]	*Anemone nemorosa*		
Tawny Sedge	*Carex hostiana*	Wood Meadow-grass[A]	*Poa nemoralis*		
Tormentil	*Potentilla erecta*	Wood Speedwell[A]	*Veronica montana*		
Turf-moss spp.	*Rhytidiadelphus* spp.	Wood-sorrel[A]	*Oxalis acetosella*		
Wild Angelica	*Angelica sylvestris*	Yorkshire Fog	*Holcus lanatus*		
Wood Anemone[A,T]	*Anemone nemorosa*				
Yorkshire Fog	*Holcus lanatus*				

Table A3 Carabid beetle species lists for the unforested, reforested and mature forest treatment categories, showing common and scientific names (Luff, 2007). [S] Denotes woodland specialist species, defined based on habitat associations in Luff (2007).

Unforested	Reforested	Mature
Abax parallelepipidus	*Agonum fuliginosum*	*Abax parallelepipidus*
Agonum ericeti	*Calathus micropterus*	*Calathus micropterus*
Agonum fuliginosum	*Carabus glabratus*	*Carabus glabratus*
Bradycellus ruficollis	*Carabus problematicus*	*Carabus problematicus*
Carabus arvensis	*Carabus violaceus*	*Carabus violaceus*
Carabus glabratus	*Cychrus caraboides*	*Cychrus caraboides*
Carabus problematicus	*Harpalus latus*	*Loricera pilicornis*
Carabus violaceus	*Leistus terminatus*	*Pterostichus oblongopunctatus*[S]
Cychrus caraboides	*Notiophilus germinyi*	*Trechus obtusus*
Harpalus latus	*Pterostichus diligens*	
Nebria salina	*Pterostichus madidus*	
Notiophilus biguttatus	*Pterostichus niger*	
Notiophilus palustris	*Pterostichus rhaeticus*	
Patrobus assimilis	*Trechus obtusus*	
Pterostichus diligens		
Pterostichus madidus		
Pterostichus niger		
Pterostichus rhaeticus		
Trechus obtusus		

Table A4 Bird species lists for the unforested, reforested and mature forest treatment categories, showing common and scientific names (McInerny, Musgrove, Stoddart, Harrop, & Dudley, 2018). [S] Denotes woodland specialist species as defined in (Eaton & Noble, 2020).

Unforested		**Reforested**		**Mature**	
Common name	**Scientific name**	**Common name**	**Scientific name**	**Common name**	**Scientific name**
Eurasian Stonechat	*Saxicola torquata*	Coal tit	*Periparus ater*	Coal Tit	*Periparus ater*
Meadow Pipit	*Anthus pratensis*	Common Chaffinch	*Fringilla coelebs*	Common Chaffinch	*Fringilla coelebs*
Skylark	*Alauda arvensis*	Common Cuckoo	*Cuculus canorus*	Common Cuckoo	*Cuculus canorus*
Tree pipit	*Anthus trivialis*	Common Redstart[S]	*Phoenicurus phoenicurus*	Eurasian Blue Tit	*Cyanistes caeruleus*
Willow Warbler[S]	*Phylloscopus trochilus*	Eurasian Bullfinch	*Pyrrhula pyrrhula*	Eurasian Siskin	*Carduelis spinis*
		Eurasian Stonechat	*Saxicola torquata*	European Crested Tit	*Lophophanes cristatus*
		European Crested tit	*Lophophanes cristatus*	European Robin	*Erithacus rubecula*
		European Robin	*Erithacus rubecula*	Goldcrest[S]	*Regulus regulus*
		Great Tit	*Parus major*	Great Tit	*Parus major*
		Lesser Redpoll[S]	*Carduelis cabaret*	Lesser Redpoll[S]	*Carduelis cabaret*
		Meadow Pipit	*Anthus pratensis*	Meadow pipit	*Anthus pratensis*
		Merlin	*Falco columbarius*	Merlin	*Falco columbarius*
		Skylark	*Alauda arvensis*	Mistle Thrush	*Turdus viscivorus*
		Tree pipit[S]	*Anthus trivialis*	Song Thrush	*Turdus philomelos*
		Willow Warbler[S]	*Phylloscopus trochilus*	Tree pipit[S]	*Anthus trivialis*
		Winter Wren	*Troglodytes troglodytes*	Willow Warbler[S]	*Phylloscopus trochilus*
				Winter Wren	*Troglodytes troglodytes*

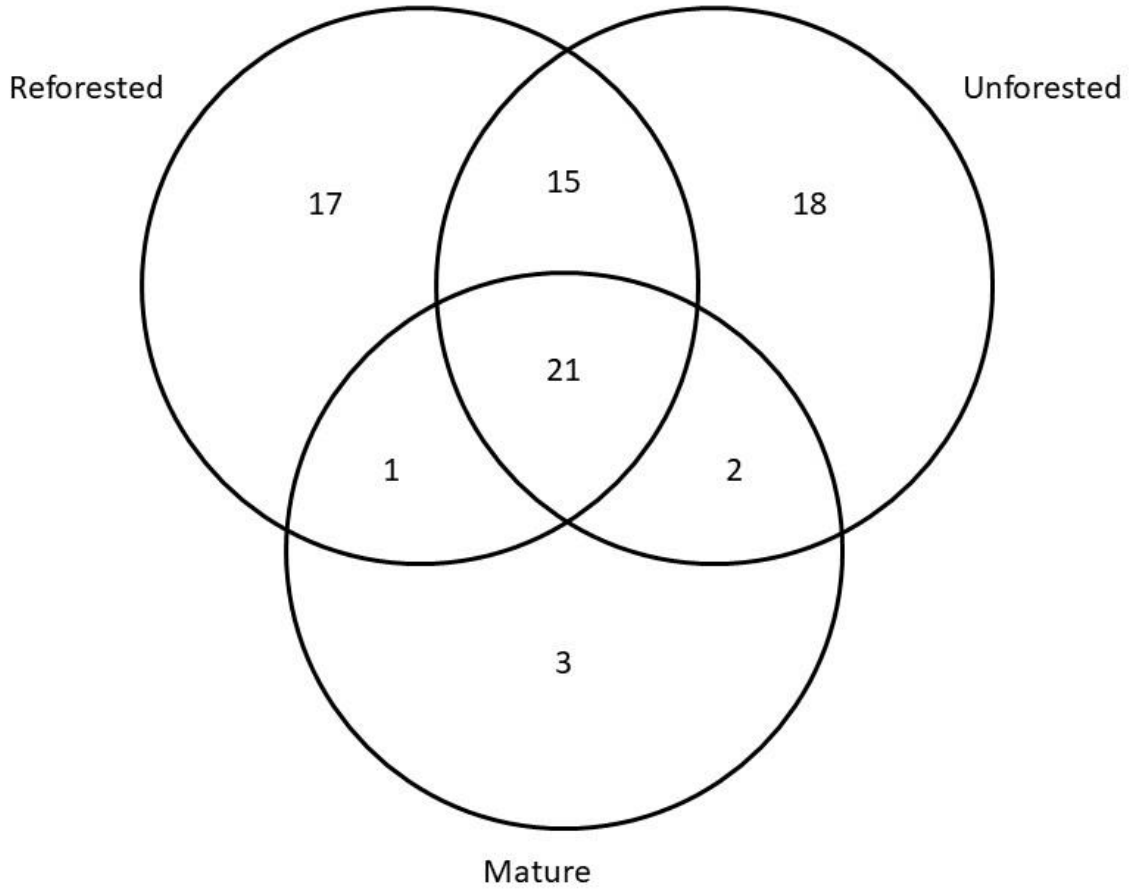


Figure A3 Venn diagram showing the number of plant species (total 77) in each forest treatment category (unforested, reforested, mature) and the numbers of shared species between categories.

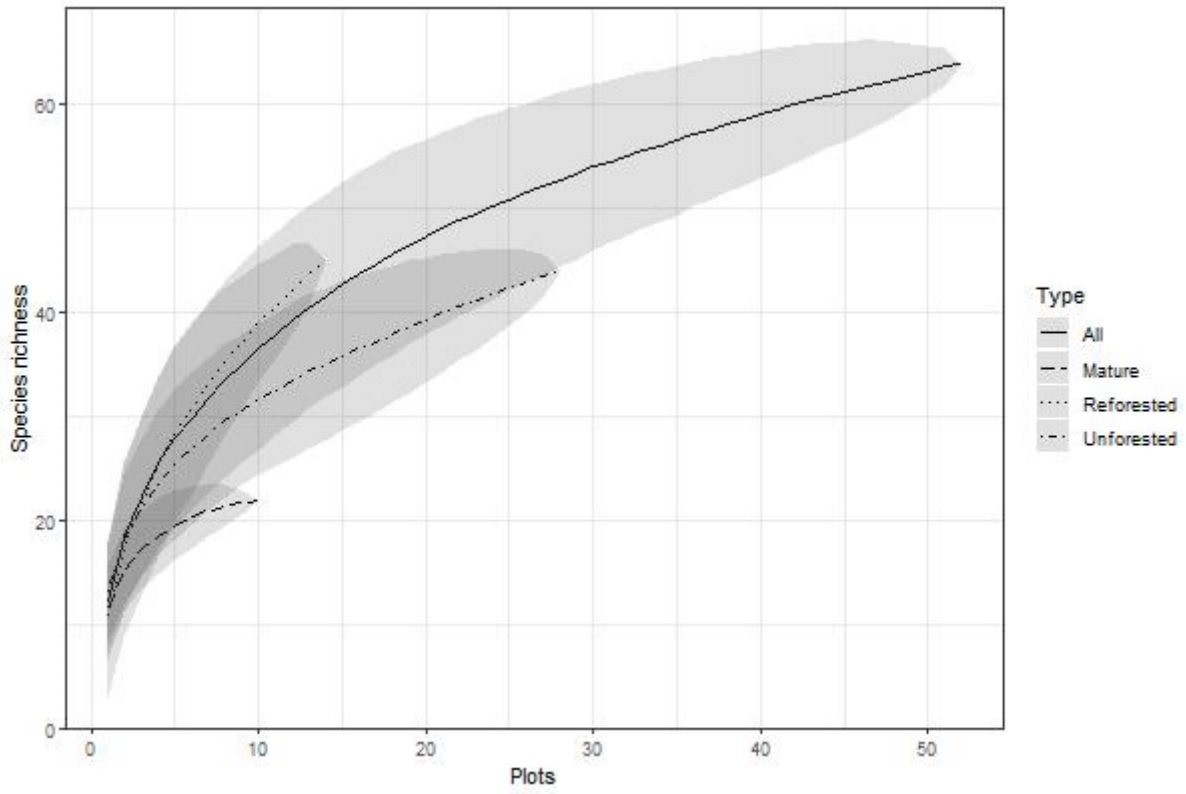


Figure A4 Mean species accumulation curves ± 95% confidence interval for plant species in the three categories of the forest treatment (unforested, n = 28; reforested, n = 14; mature, n = 10) and using all plots from the three forest categories (n = 52). The mean species accumulation curves and confidence intervals shown are based on 1000 random permutations of the data.

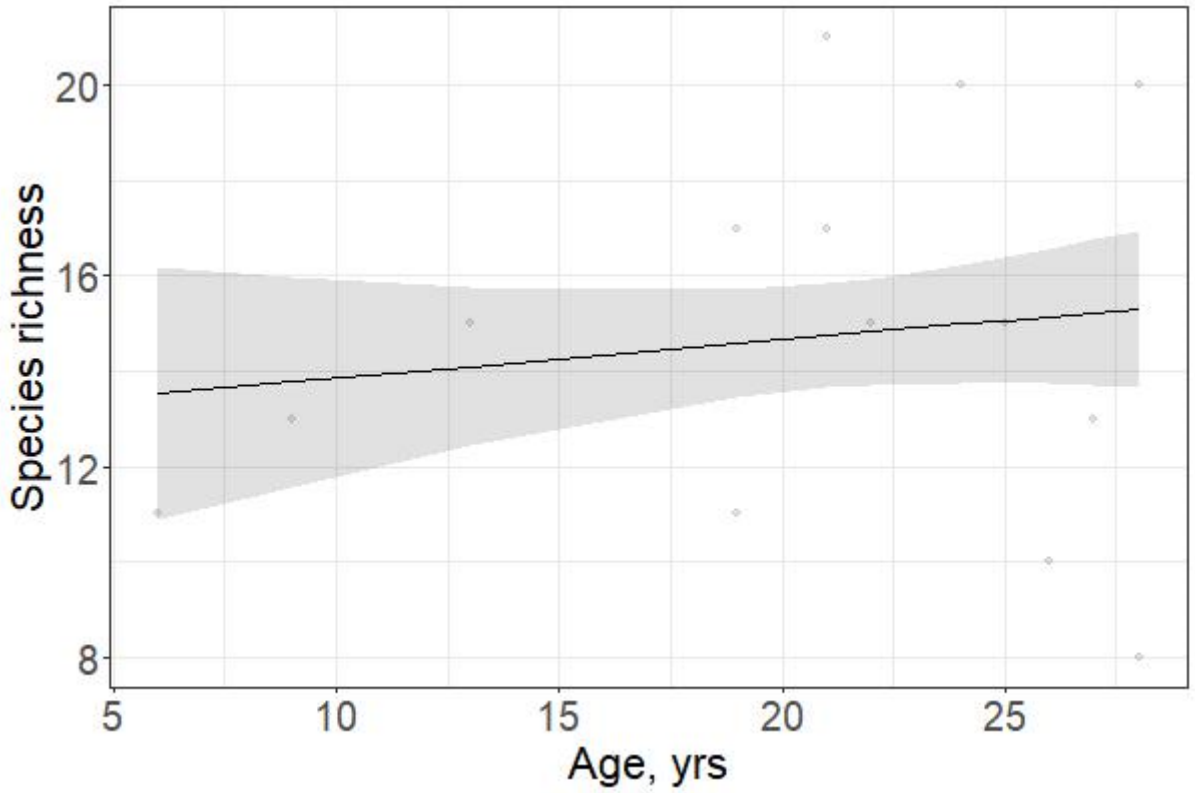


Figure A5 Relationship between site age and plant species richness (reforested plots only, n = 14). Model fit ± SE extracted from the model.

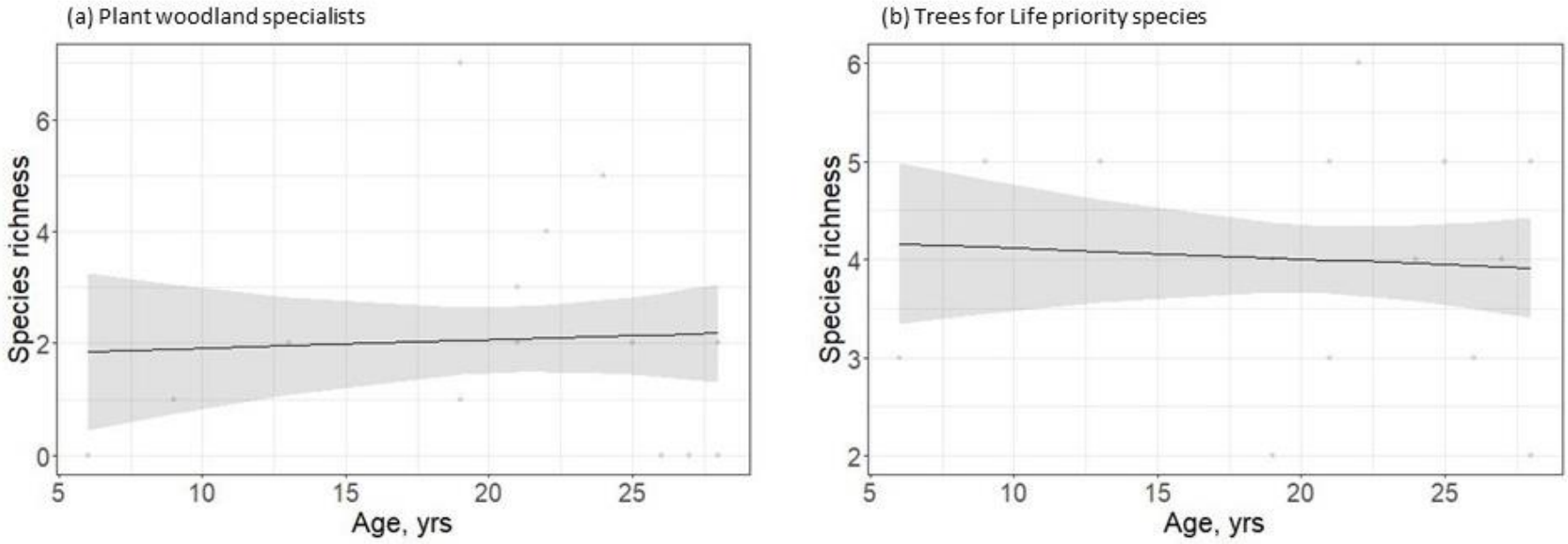


Figure A6 Relationship between site age and species richness for (a) plant specialist richness and (b) Trees for Life plant priority richness, reforested plots only (n = 14). Model fit ± SE extracted from the models.

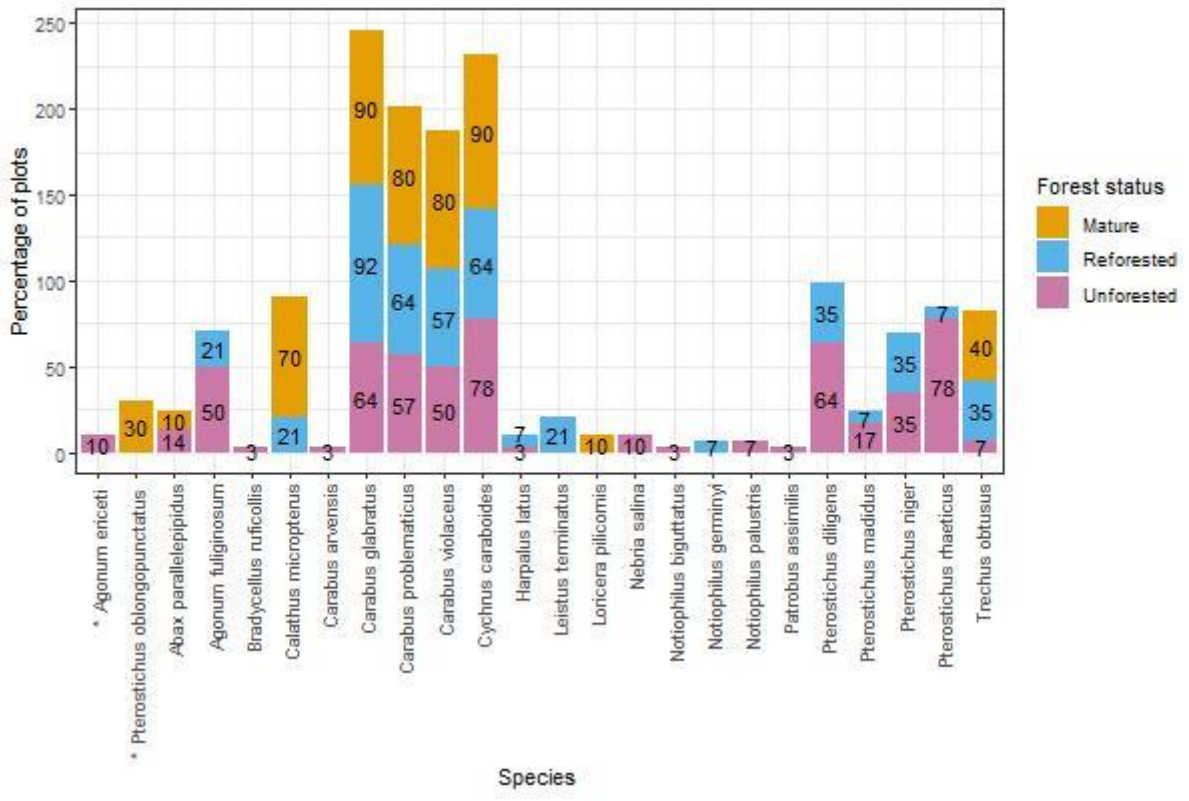


Figure A7 The percentage of plots in each forest category (unforested, n = 28; reforested, n = 14; mature, n = 10) that each carabid species was recorded in. Species classified as Nationally Scarce are denoted by *. All other species are not regarded as Nationally Scarce or Nationally Rare (Telfer, 2016).

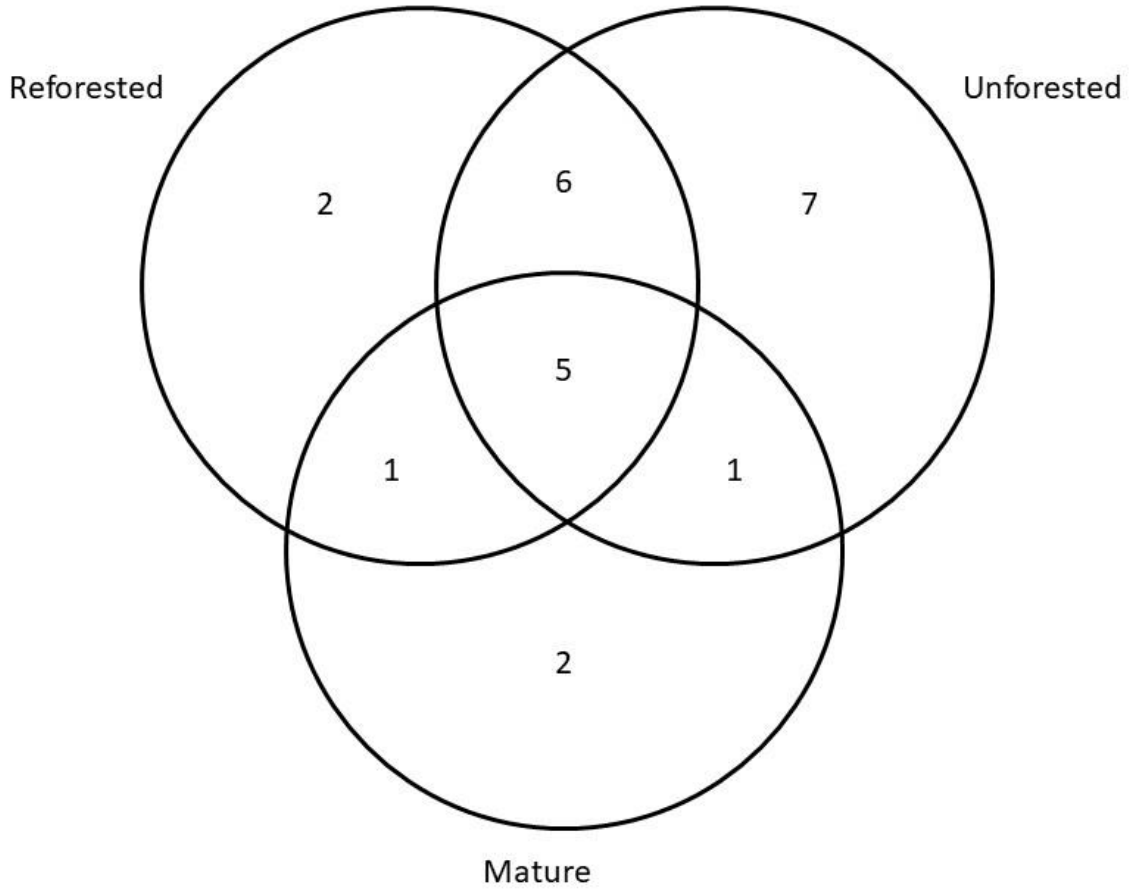


Figure A8 Venn diagram showing the number of carabid species (total 24) in each forest treatment category (unforested, reforested, mature) and the numbers of shared species between categories.

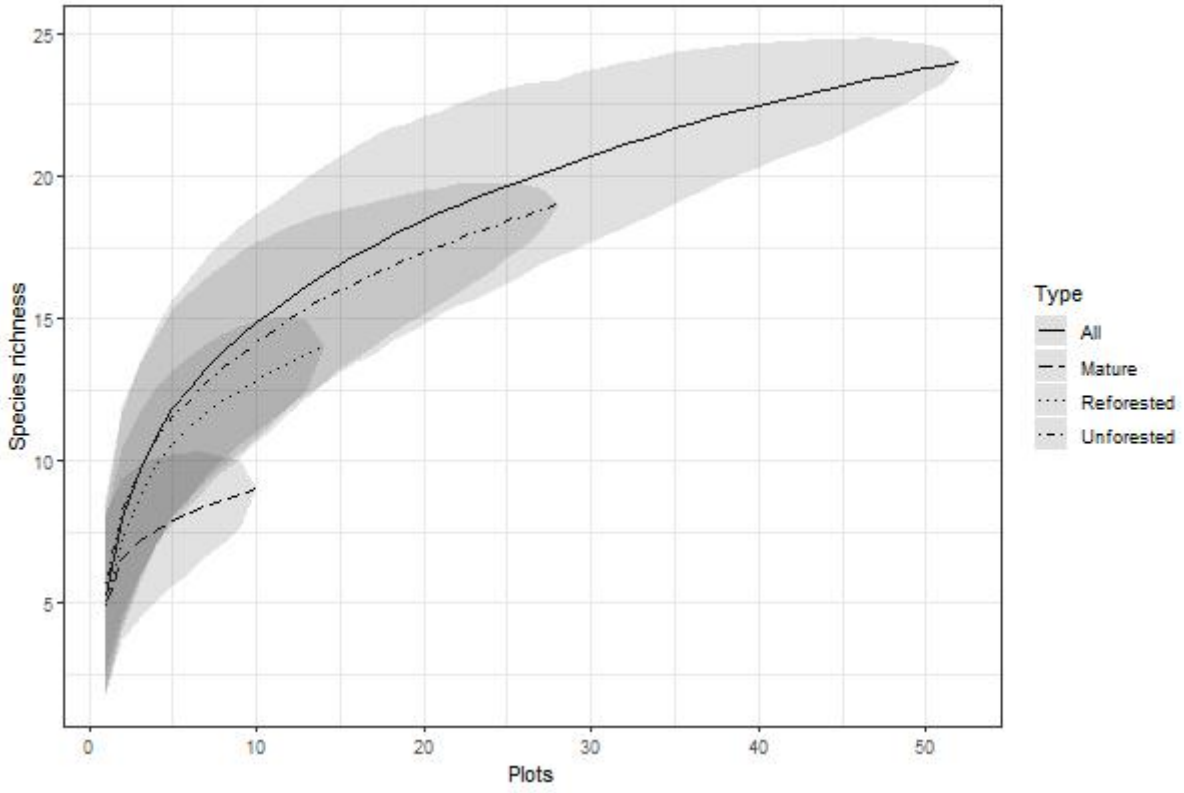


Figure A9 Mean species accumulation curves ± 95% confidence interval for carabid species in the three categories of the forest treatment (unforested, n = 28; reforested, n = 14; mature, n = 10) and using plots from the three forest categories (n = 52). The mean species accumulation curves and confidence intervals shown are based on 1000 random permutations of the data.

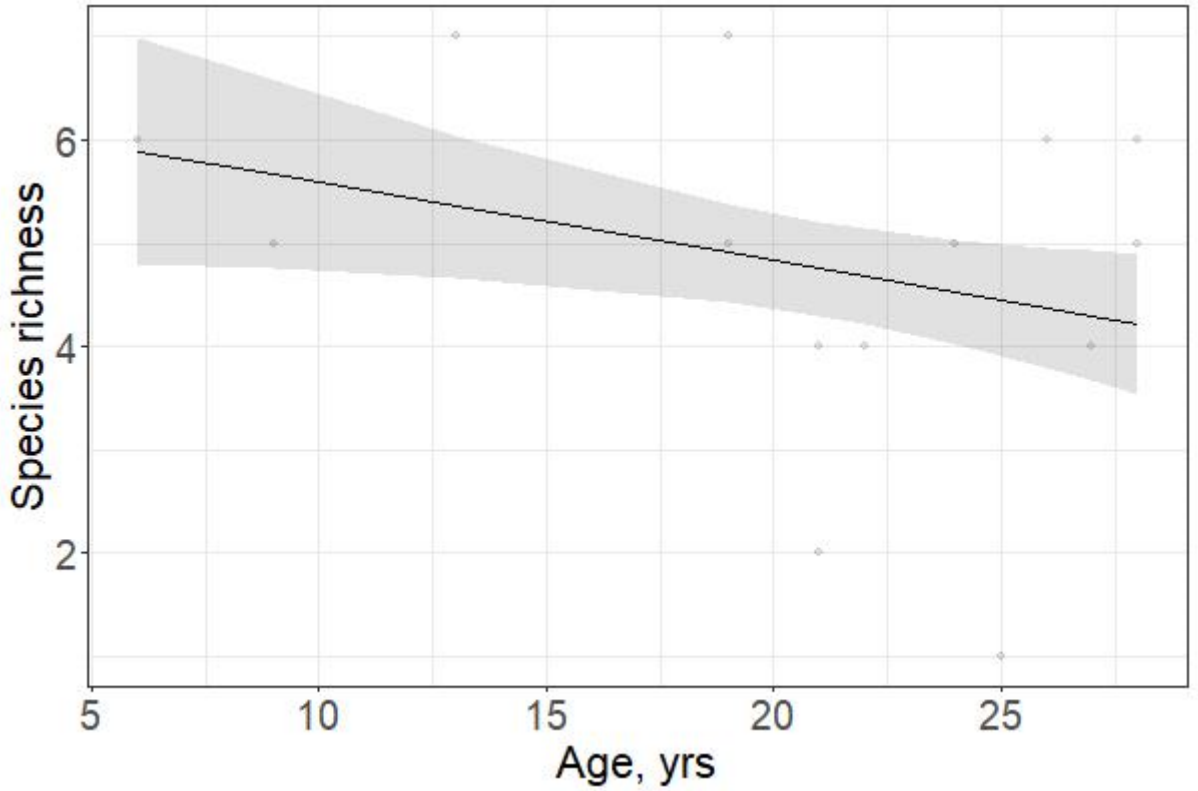


Figure A10 Relationship between site age and carabid species richness (reforested plots only, n = 14). Model fit ± SE extracted from the model.

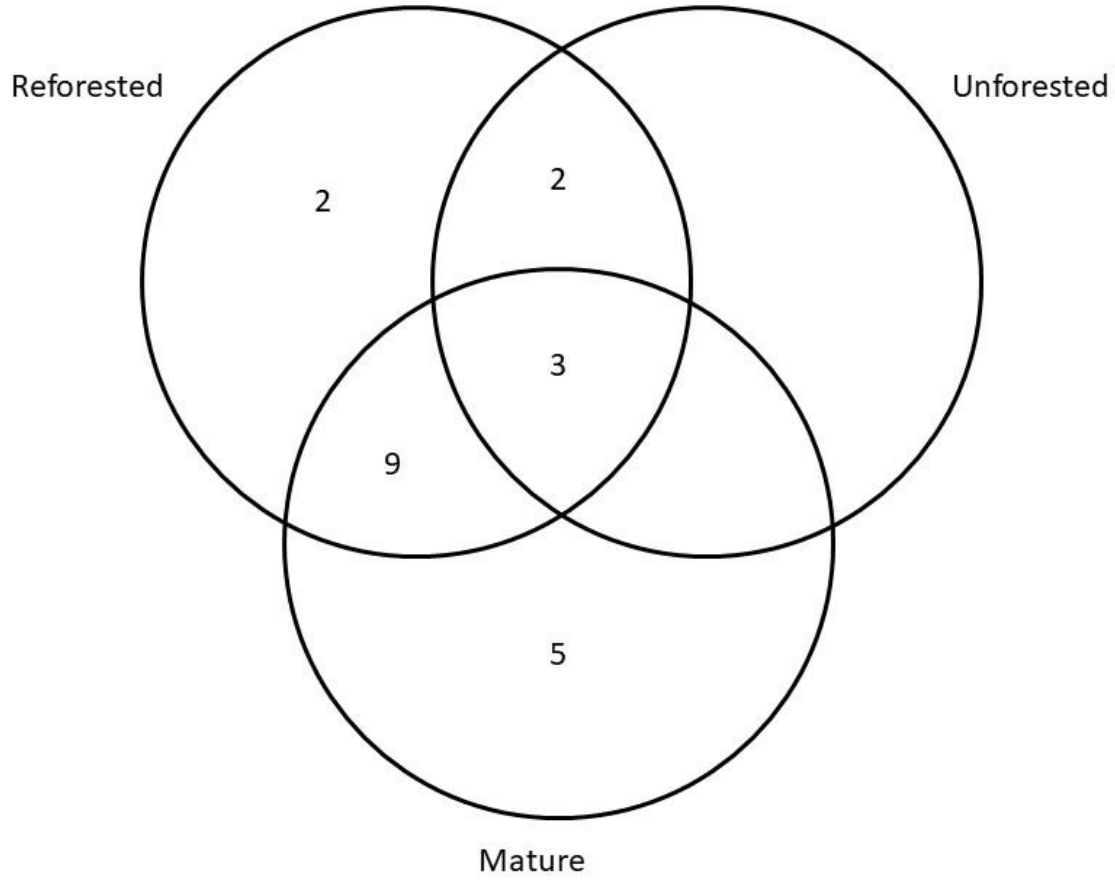


Figure A11 Venn diagram showing the number of bird species (total 21) in each forest treatment category (unforested, reforested, mature) and the numbers of shared species between categories.

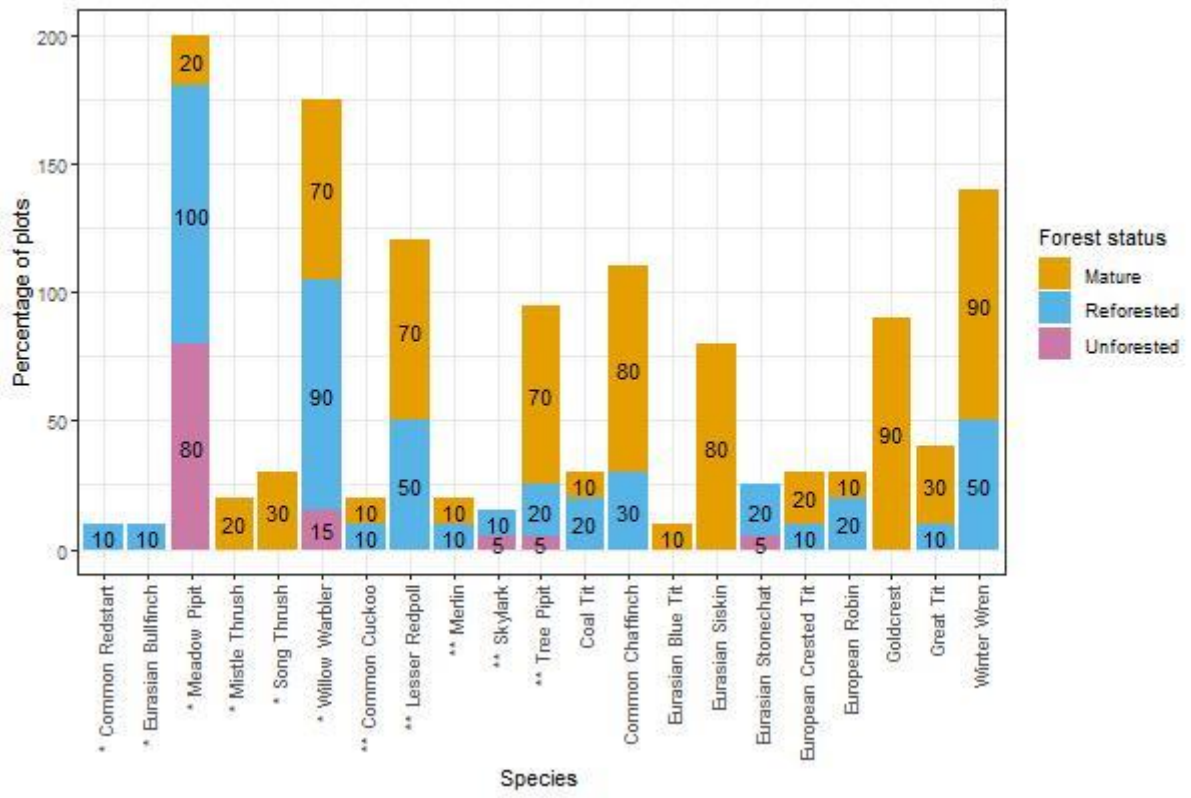


Figure A12 The percentage of plots in each forest category (unforested, n = 20; reforested, n = 10; mature, n = 10) that each bird species was recorded in. * indicates Amber listed species and ** indicates Red-listed species. All other species are Green-listed (Eaton et al., 2015).

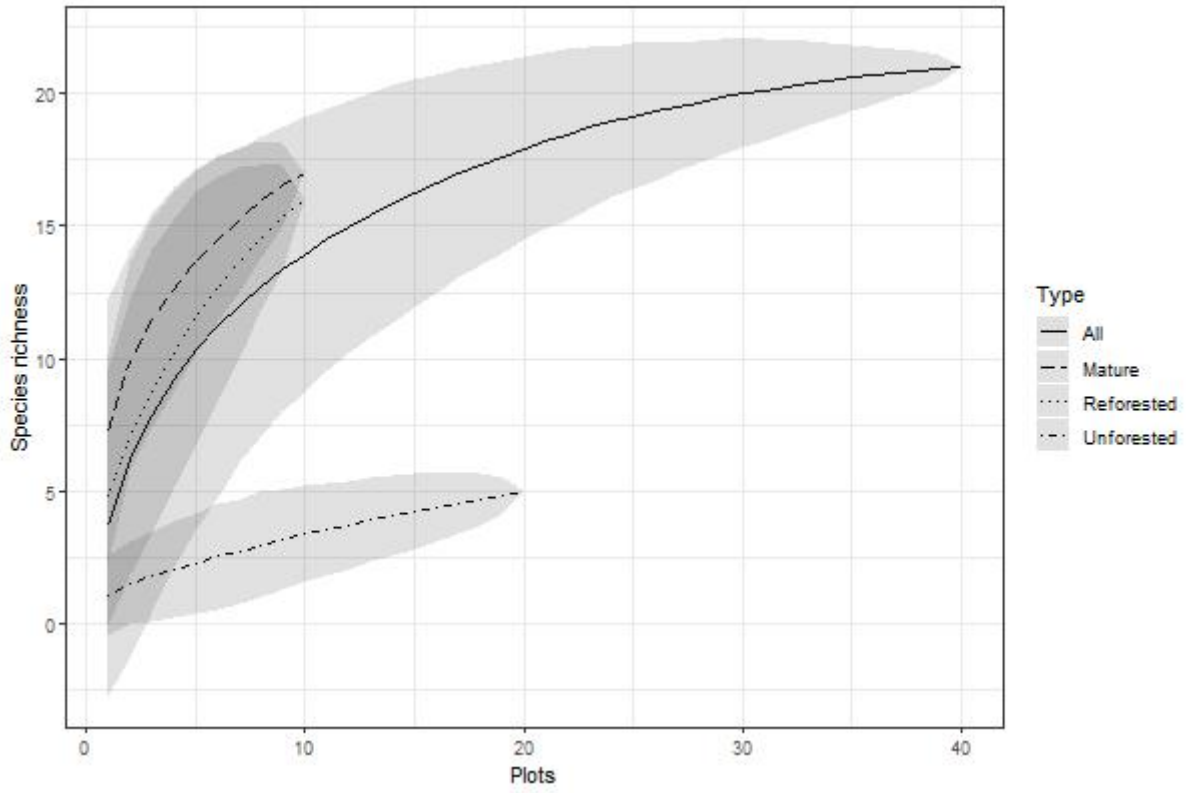


Figure A13 Mean species accumulation curves ± 95% confidence interval for bird species in the three categories of the forest treatment (unforested, n = 20; reforested, n = 10; mature, n = 10) and using all plots from the three forest categories (n = 40). The mean species accumulation curves and their confidence intervals shown are based on 1000 random permutations of the data.

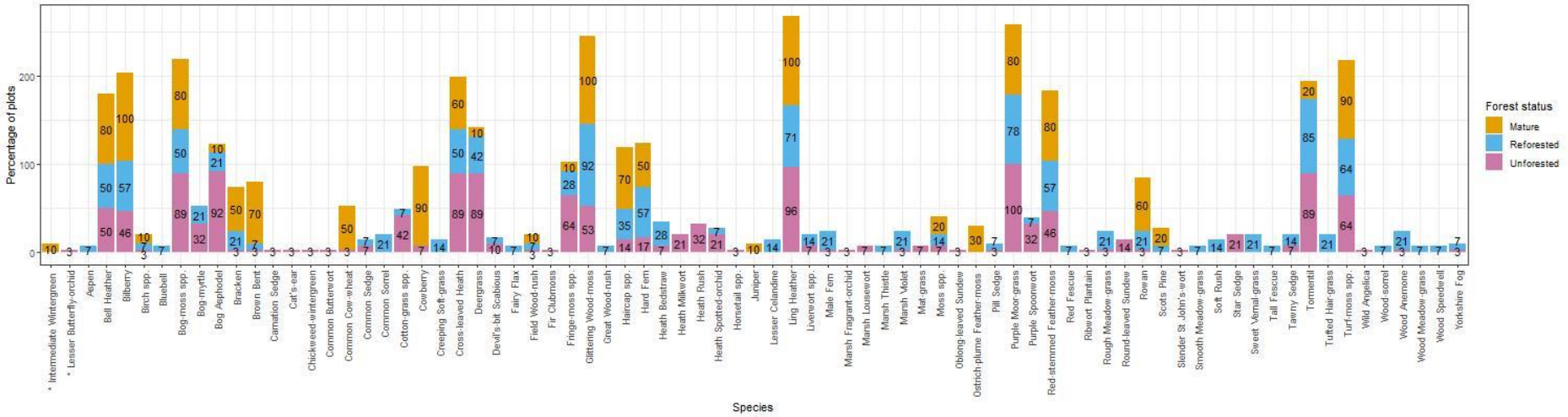


Figure A14 The percentage of plots in each forest category (unforested, n = 28; reforested, n = 14; mature, n = 10) that each plant species was recorded in. Species classified as Vulnerable are denoted by *, all other species are classified as of Least Concern (Cheffings et al., 2005).

Appendix B: Supplementary figures & tables for Chapter 3

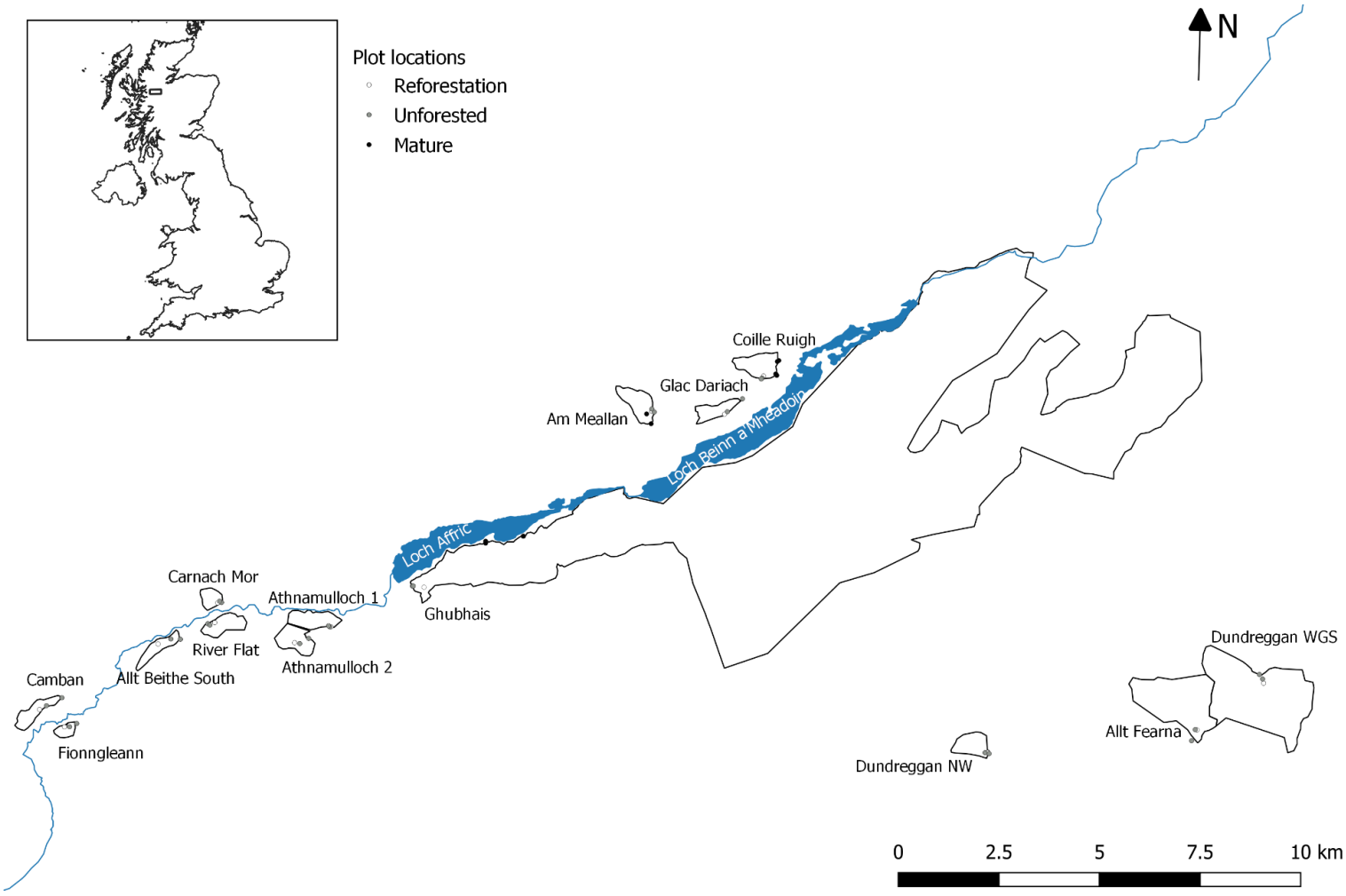


Figure B1 The location of the fenced reforestation sites used in this study. Circles indicate survey plots, categorised by forest treatment. Inset: the rectangle indicates the location of the study area within the UK.

Table B1 Information on the focal fenced and reforestation sites in this study. At both Coille Ruigh and Ghubhais two pairs of grazed and ungrazed mature forest plots were established in discontinuous areas of mature forest at each site. The year of establishment is defined as the year in which the site was fenced. The age of the sites in 2018, the year of the first surveys, is calculated as the number of years from the first planting event. Planting was either by hand screefing, where a spade was used to clear vegetation before slit planting the trees, or by machine mounding, where a digger was used to create mounds into which trees were planted. The presence of mature forest at each site is indicated (N = not present, Y = present). The latitude and longitude of each site is given.

Site name	Size (ha)	Year site established	Number of trees planted	Age in 2018	Trees per ha	Type of trees planted[1]	Planting method	Mature forest	Latitude, longitude
Athnamulloch One	63	1990	20,994	28	333	SP, A, BL	Hand screefing	N	57.235622, -5.117791
Athnamulloch Two	57	1994	22,177	24	389	SP, B, A, BL	Hand screefing	N	57.230217, -5.128606
River Flat	52	1997	9,250	21	178	SP, BL	Hand screefing	N	57.235401, -5.155535
Carnach Mor	25	1996	15,500	22	620	BL, SP	Hand screefing	N	57.240799, -5.159719
Allt Beithe (South)	28	1997	4,150	21	148	SP, W, H	Hand screefing	N	57.228645, -5.180406
Fionngleann	15	1999	16,500	19	1,100	BL	Hand screefing	N	57.211372, -5.215899
Camban	29	1999	32,400	19	1,100	BL	Hand screefing	N	57.216728, -5.228811
Coille Ruigh	50	1990	Natural regeneration[2]	28	2,000[2]	SP,BL	Hand screefing	Y	57.291874, -4.931883
Ghubhais	155	1993	18,380	25	119	A, SP, BL	Hand screefing	Y	57.246426, -5.039163
Dundreggan WGS	446	2005	8,000[3]	13	18[3]	BL	Machine mounding	N	57.218655, -4.731901
Allt Fearna	150	2012	144,000	6	960	BL, SP	Machine mounding	N	57.213062, -4.756109
Dundreggan NW	45	2010	70,000	8	1,549	SP, BL	Machine mounding	N	57.206726, -4.847144
Am Meallan	55	1991	27,085	27	492	SP, A, BL	Hand screefing	Y	57.285549, -4.984157

Glac Dariach	35	1992	26,551	26	759	SP, B, A, BL	Hand screefing	N	57.281532, -4.952896

[1] A = Aspen, B = Birch, BL = broadleaf trees (includes Silver Birch *Betula pendula*, Downy Birch *Betula pubescens*, Rowan *Sorbus aucuparia*, Goat Willow *Salix caprea*, Eared Willow *Salix aurita*, Alder *Alnus glutinosa*, Aspen *Populus tremula*, Holly *Ilex aquifolium*, Hazel *Corylus avellana*), H = Hazel, SP = Scots Pine *Pinus sylvestris*, W = Willow *Salix spp.*.

[2] The site was fenced in 1990 and natural regeneration was subsequently successful. Trees for Life estimate that 100,000 young trees established as a result.

[3] This planting event supplemented a previous Woodland Grant Scheme planting prior to Trees for Life's ownership of the Dundreggan Estate from 2008.

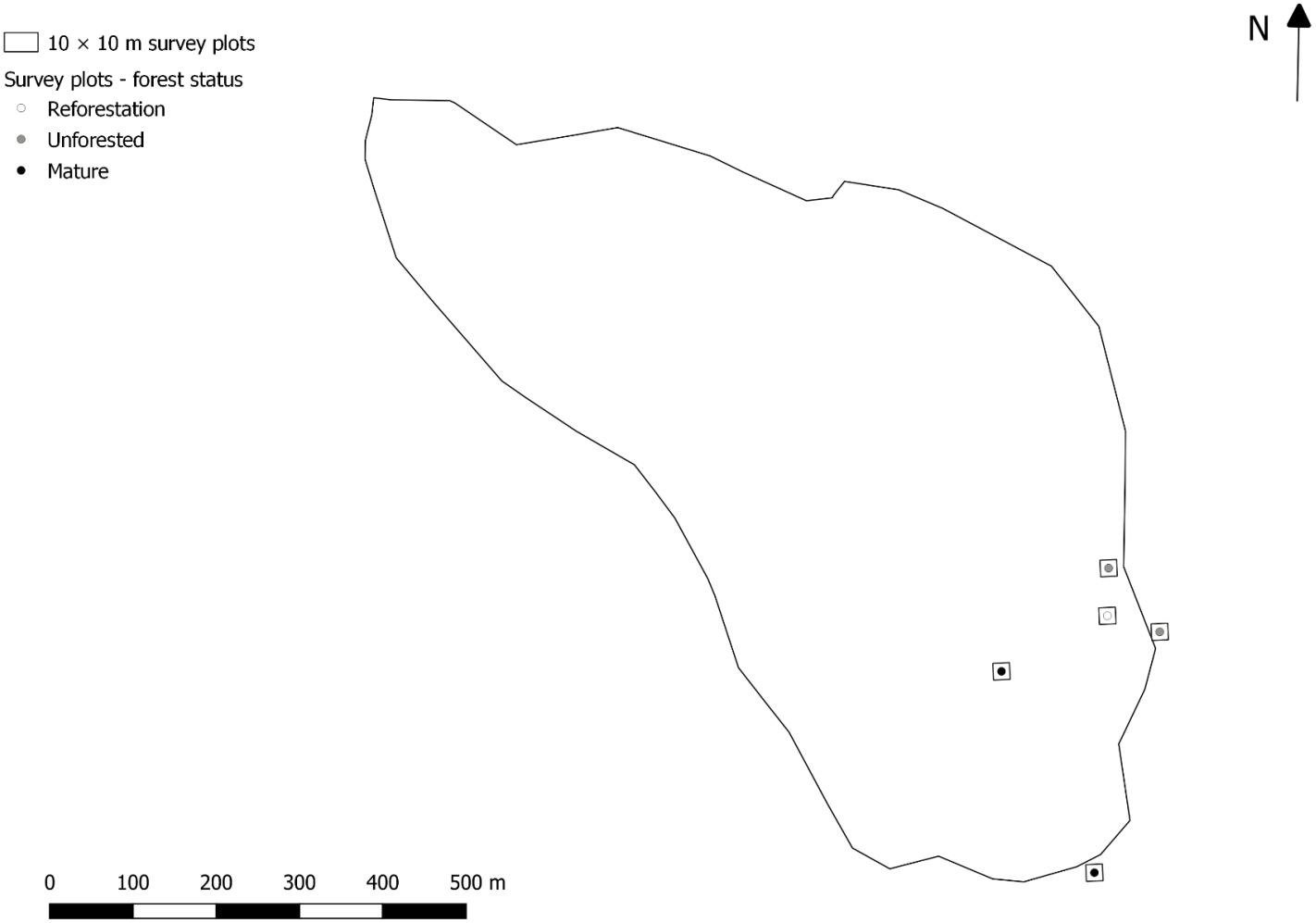


Figure B2 Close up of the site Am Meallan, showing the locations of the survey plots. At this site all three forest categories (unforested, reforestation, mature) were present.

Table B2 Allometric equations used to calculate tree biomass in each plot. The biomass component calculated and country in which the equation was defined are given. The coefficient of determination (R^2) is given for each equation.

Tree species	Biomass component	Allometric equation	Country	R^2	Reference
Betula pendula	Aboveground	$0.00087 \times (dbh \times 10)^{2.28639}$	Sweden	0.985	Zianis et al. 2005
Pinus sylvestris	Aboveground	$10^{(0.981+2.289(\log_{10}(\pi \times dbh)))}/1000$	UK	0.996	Zianis et al. 2005
Alnus glutinosa	Aboveground	$0.00079 \times (dbh \times 10)^{2.28546}$	UK	0.987	Zianis et al. 2005
Sorbus aucuparia	Stem	$e^{(4.9569 + 1.5396 \times \ln(DBH) + 0.2613 \times (\ln(dbh))^2)}/1000$	Norway	0.991	Muukkonen & Mäkipää, 2006
Salix caprea	Stem	$e^{(4.5086 + 1.9234 \times \ln(DBH) + 0.2613 \times (\ln(dbh))^2)}/1000$	Norway	0.985	Muukkonen & Mäkipää, 2006

Table B3 Response variables and units for each ecosystem function measured

Ecosystem function	Response	Units
Aboveground carbon storage	Tree carbon	Mg/ha
Soil carbon storage	Soil carbon	Mg/ha
Soil nitrogen	Soil nitrogen	Mg/ha
Decomposition rate	Decomposition rate constant, k	
Soil invertebrate feeding	Feeding versus no feeding	
Tree regeneration	Seedlings per plot	
Ground layer height	Ground layer height	cm
Moss depth	Moss depth	cm

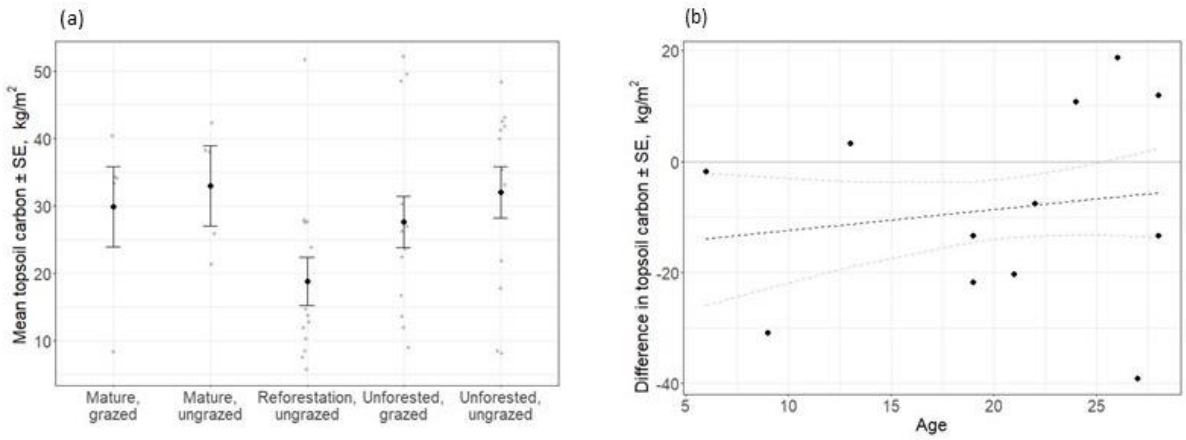


Figure B3 (a) The response of soil carbon to plot type (factor with 5 levels) and (b) change over time in the difference in topsoil carbon between the paired reforestation, ungrazed plots and the unforested, grazed plots (n = 12). Non-significant trends are shown with dashed lines and the solid grey line indicates no difference in topsoil carbon between the reforestation and unforested, grazed sites.

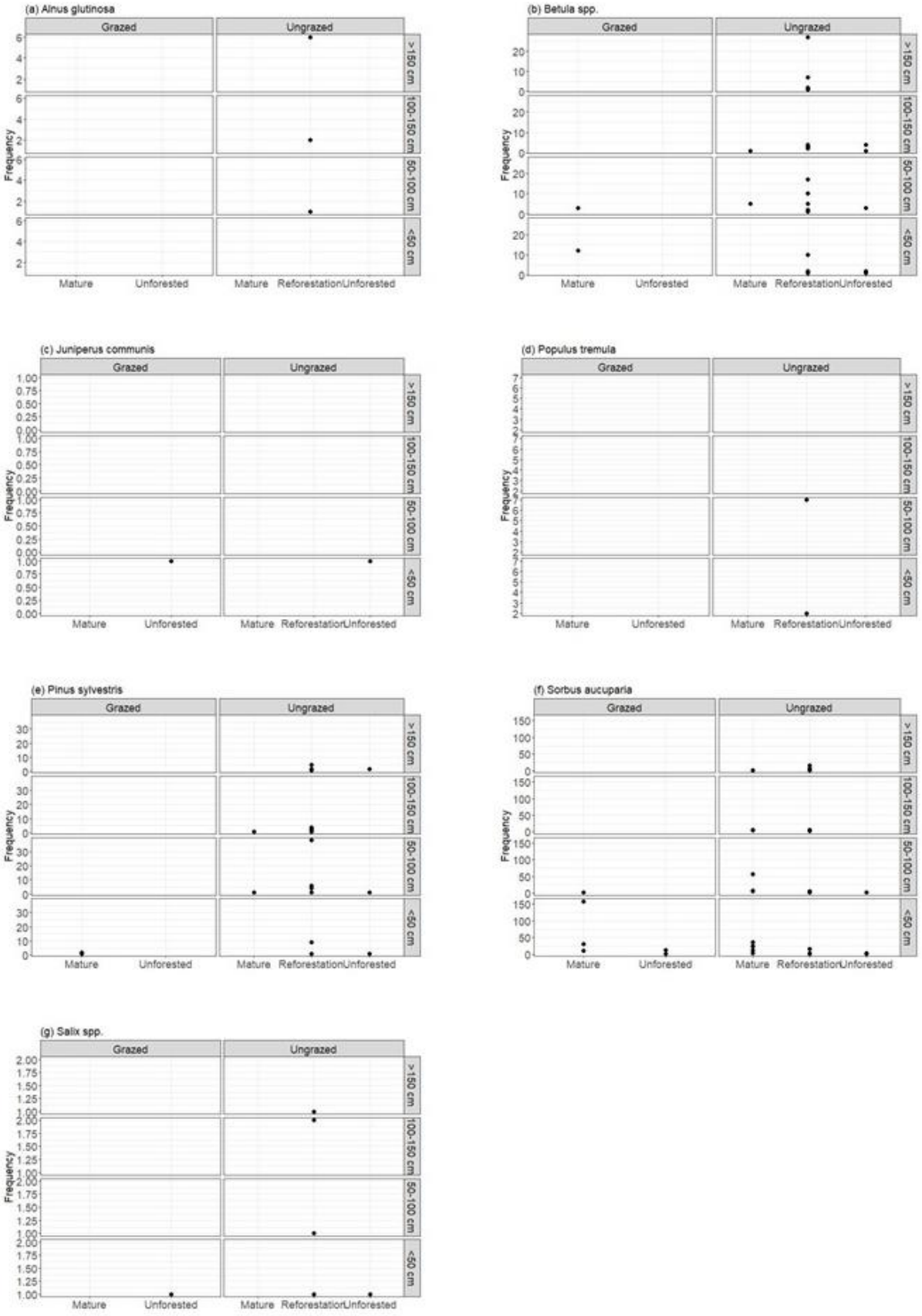


Figure B4 Frequency of seedlings per plot for each tree species, by seedling height category (<50 cm, 50-100 cm, 100-150 cm, >150 cm). (a) *Alnus glutinosa*, (b) *Betula* spp, (c) *Juniperus communis*, (d) *Populus tremula*, (e) *Pinus sylvestris*, (f) *Sorbus aucuparia*, (g) *Salix* spp.

Appendix C: Supplementary methods for Chapter 3

Calculation of decomposition rate constant, k

The decomposition rate constant, *k*, was calculated following Keuskamp *et al.* 2013. Weight loss at a given time, *t*, depends on the decomposition rate constant, *k*, and the decomposable fraction of litter present, *a* (eqn 1).

$$W(t) = ae^{-kt} + (1 - a) \quad \text{eqn 1}$$

Estimation of *k* requires a time-series, however, by using two types of tea with different decomposition rates, the Tea Bag Index allows calculation of the decomposition rate constant, *k*, from rooibos tea at a single time point (Keuskamp et al., 2013). The green tea represents more labile plant tissue, while rooibos represents less labile plant tissue which is expected to decompose more slowly.

The environmental conditions at a given location influence the properties of the litter, inhibiting decomposition and causing a portion of the labile material to become recalcitrant. This effect is calculated as the stabilisation factor, *S*, which can be calculated from the decomposable fraction of green tea a_g and the known hydrolysable fraction of green tea, H_g.

$$S = 1 - \frac{a_g}{H_g} \quad \text{eqn 2}$$

The expected decomposable fraction of the rooibos tea, a_r, can then be calculated based on *S* and the hydrolysable fraction of rooibos tea, H_r (eqn 3).

$$a_r = H_r(1 - S) \quad \text{eqn 3}$$

Given that the weight of rooibos tea remaining at time *t*, $W_r(t)$ is known, it is then possible to calculate *k* using eqn 1.

Appendix D: Supplementary figures & tables for Chapter 5

Table D1 Information on the studies used in the meta-analysis, including whether they were obtained from the original literature search, the Tree Diversity Network or a previous meta-analysis by Zhang *et al.* (2012).

	Study	Source	Site	Age	Country	Latitude	Longitude
1	(Debell et al., 1997)	Literature search	1	11	USA (Hawaii)	19.860	−155.150
2	(Bauhus et al., 2004)	Literature search	2	10	Australia	−37.600	149.162
3	(Forrester, Pares, O'Hara, Khanna, & Bauhus, 2013)	Literature search	3	11	Australia	−37.600	149.162
4	(He et al., 2013)	Literature search	5	28	China	22.0518	106.86854
5	(Piotto et al., 2010)	Literature search	6	17	Costa Rica	10.433333	−83.983333
6	(Piotto et al., 2010)	Literature search	7	17	Costa Rica	10.433333	−83.983333
7	(Piotto et al., 2010)	Literature search	8	16	Costa Rica	10.433333	−83.983333
8	(Nunes, Gower, Monteiro, Lopes, & Rego, 2014)	Literature search	9	28	Portugal	41.400000	−7.100000
9	(Q. Wang, Wang, & Zhang, 2009)	Literature search	10	15	China	26.826522	109.859850
10	(Mao et al., 2010)	Literature search	11	5	China	41.705729	119.454350
11	(Mao et al., 2010)	Literature search	11	15	China	41.705729	119.454350
12	(Nichols & Carpenter, 2006)	Literature search	12	11	Costa Rica	9.000000	−83.000000
13	(Kaye, Resh, Kaye, & Chimner, 2000)	Zhang *et al.* 2012	13	17	USA (Hawaii)	19.5	-155.25
14	(Son, Lee, Lee, & Yi, 2007)	Zhang *et al.* 2012	14	27	South Korea	37.783333	127.8

15	TreeDivNet – Orphee	TreeDivNet	15	9	France	44.740100	−0.796800
16	TreeDivNet – Ident SSM	TreeDivNet	16	6	Canada	46.546501	−84.455650
17	TreeDivNet – MyDiv	TreeDivNet	17	3.5	Germany	51.383000	11.883000
18	TreeDivNet – IDENT Auclair	TreeDivNet	18	8	Canada	47.696611	−68.656306
19	TreeDivNet – IDENT Cloquet	TreeDivNet	19	8	Canada	46.705083	−92.524972
20	TreeDivNet – Sardinilla	TreeDivNet	20	16	Panama	9.316667	−79.633333
21	TreeDivNet – Agua Salud	TreeDivNet	21	7	Panama	9.216667	−79.7833333

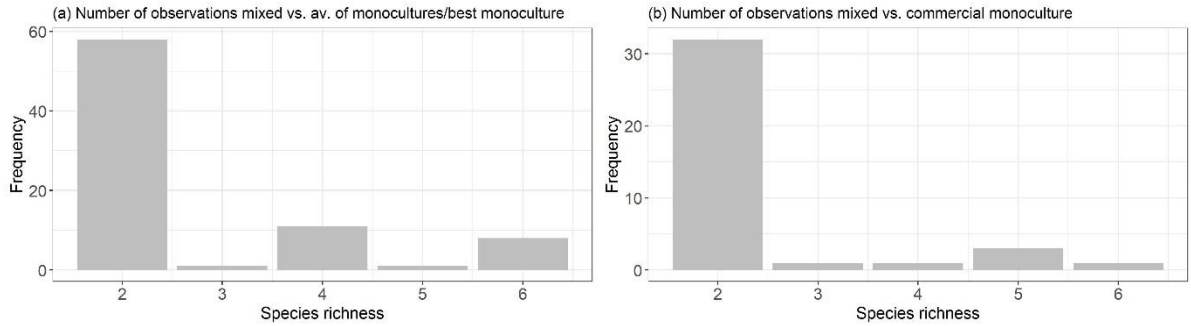


Figure D1 Number of mixed to monoculture comparisons at each level of species richness for (a) mixed plantations compared to the average of relevant monocultures/best monoculture and (b) mixed plantations compared to commercial monocultures.

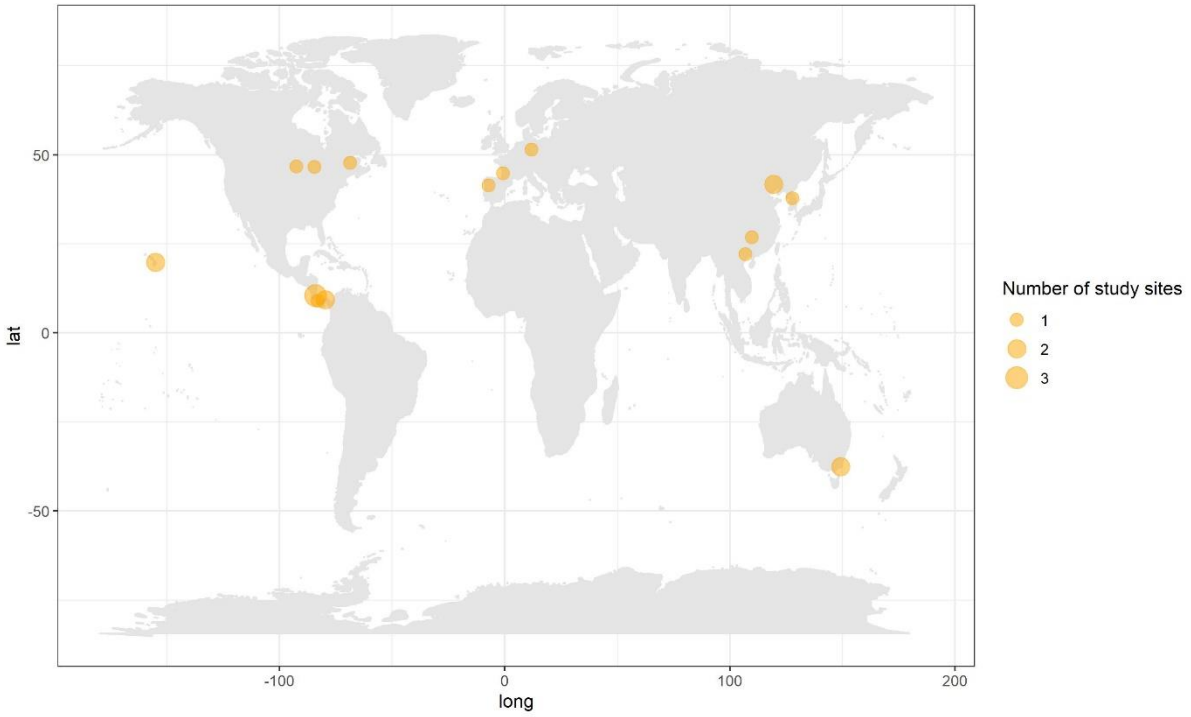


Figure D2 The geographic distribution of study sites. Points are proportional to the number of independent sites in that location (where sites are spatially separate at a distance that would not be discernible at this map scale).

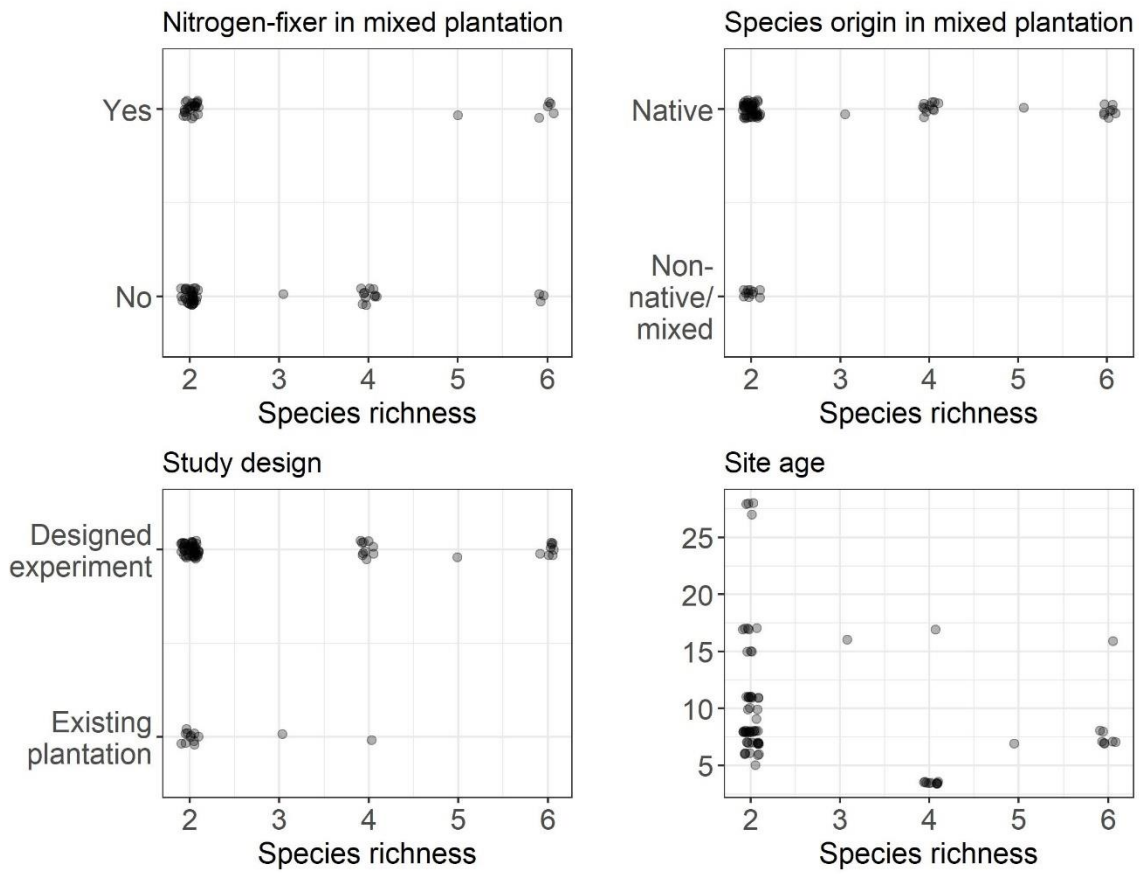


Figure D3 Data representation for each moderator, (a) presence of nitrogen-fixer in the mixed plantation, (b) species origin of the species in the mixed plantation, (c) study design, (d) age of plantations, used to assess differences in carbon accumulation in mixed plantations compared to the average of monocultures/best monoculture.

Table D2 Carbon accumulation in each mixed plantation, the average of monoculture plantations and the most productive monoculture for each comparison. The % carbon in the mixed plantation relative to the average of monocultures and best monoculture is also shown. The comparisons are ordered by species richness and the % of the average of monocultures carbon in the mixed plantation. The age and species in the mixed and most productive monoculture plantations are given.

SR	DP carbon (Mg/ha)	average of MPs carbon (Mg/ha)	most productive MP carbon (Mg/ha)	% of average of monocultures carbon in DP	% of most productive monoculture carbon in DP	Age	Mixed plantation species	Most productive monoculture species
2	4.9	10.2	16.9	48	29	8	*Larix laricina, Quercus rubra*	*Larix laricina*
2	8.2	11.7	12.9	70	63	8	*Acer saccharum, Picea glauca*	*Acer saccharum*
2	9.9	13.6	16.9	73	58	8	*Larix laricina, Pinus strobus*	*Larix laricina*
2	68.5	82.2	82.2	83	83	27	*Alnus hirsute, Pinus koraiensis*	*Pinus koraiensis*
2	3.5	4.2	6.7	84	53	7	*Anacardium excelsium, Tabebuia rosea*	*Anacardium excelsum*
2	9.9	11.8	12.2	84	82	8	*Betula papyrifera, Quercus rubra*	*Betula papyrifera*
2	4.8	5.4	6.6	89	73	8	*Acer saccharum, Picea glauca*	*Picea glauca*
2	13.1	14.0	16.2	93	81	6	*Pinus strobus, Quercus rubra*	*Pinus strobus*
2	8.1	8.5	10.3	96	79	8	*Picea glauca, Pinus strobus*	*Pinus strobus*
2	7.0	6.9	7.0	102	100	7	*Anacardium excelsium, Dalbergia retusa*	*Dalbergia retusa*
2	9.2	9.0	9.0	102	102	5	*Populus xiaozhuanica, Hippophae rhamnoides*	*Populus xiaozhuanica*
2	67.2	63.8	88.3	105	76	28	*Castanopsis hystrix, Pinus massoniana*	*Pinus massoniana*
2	24.7	23.1	49.2	107	107	15	*Cunninghamia lanceolata, Kalopanax septemlobus*	*Cunninghamia lanceolata*
2	11.0	10.1	10.6	109	104	8	*Picea glauca, Pinus strobus*	*Picea glauca*
2	4.8	4.4	7.0	110	68	7	*Dalbergia retusa, Tabebuia rosea*	*Dalbergia retusa*
2	16.6	15.1	17.6	110	94	6	*Larix larcinia, Picea glauca*	*Larix larcinia*

2	10.6	9.4	11.9	113	89	6	*Acer saccharum, Quercus rubra*	*Quercus rubra*
2	123.8	109.4	127.8	113	97	11	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	16.6	14.5	16.2	114	103	6	*Betula papyrifera, Pinus strobus*	*Pinus strobus*
2	12.3	10.6	10.8	117	114	8	*Betula papyrifera, Pinus strobus*	*Betula papyrifera*
2	5.2	4.4	6.7	118	78	7	*Anacardium excelsium, Pachira quinata*	*Anacardium excelsum*
2	12.9	10.8	12.2	119	106	8	*Betula papyrifera, Pinus strobus*	*Betula papyrifera*
2	43.0	36.0	36.0	119	119	11	*Eucalyptus globulus, Acacia mearnsii*	*Acacia mearnsii*
2	43.1	36.0	36.0	120	120	11	*Eucalyptus globulus, Acacia mearnsii*	*Acacia mearnsii*
2	131.9	109.4	127.8	120	103	11	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	60.0	49.2	49.2	122	122	15	*Cunninghamia lanceolata, Alnus cremastogyne*	*Cunninghamia lanceolata*
2	14.8	12.1	14.8	122	101	8	*Larix laricina, Pinus strobus*	*Larix laricina*
2	12.2	9.9	12.9	124	95	6	*Acer saccharum, Betula papyrifera*	*Betula papyrifera*
2	16.9	13.6	16.9	124	100	8	*Larix laricina, Pinus strobus*	*Larix laricina*
2	18.0	14.3	16.2	125	111	6	*Picea glauca, Pinus strobus*	*Pinus strobus*
2	10.8	8.5	10.3	128	105	8	*Picea glauca, Pinus strobus*	*Pinus strobus*
2	15.5	11.9	22.2	130	70	7	*Terminalia amazonia, Tabebuia rosea*	*Terminalia amazonia*
2	47.0	36.0	36.0	130	130	11	*Eucalyptus globulus, Acacia mearnsii*	*Acacia mearnsii*
2	19.1	14.6	22.2	131	86	7	*Dalbergia retusa, Terminalia amazonia*	*Terminalia amazonia*
2	144.8	109.4	127.8	132	113	11	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	17.4	13.1	14.8	133	118	8	*Larix laricina, Quercus rubra*	*Larix laricina*
2	31.4	23.5	30.6	134	103	10	*Eucalyptus globulus, Acacia mearnsii*	*Acacia mearnsii*
2	66.9	48.9	62.7	137	107	28	*Pseudotsuga menziesii, Castanea sativa*	*Pseudotsuga menziesii*

2	19.9	14.4	22.2	138	90	7	*Anacardium excelsium, Terminialia amazonia*	*Terminalia amazonia*
2	17.4	12.5	12.9	139	135	8	*Acer saccharum, Betula papyrifera*	*Acer saccharum*
2	170.3	120.5	120.5	141	141	15	*Populus xiaozhuanica, Hippophae rhamnoides*	*Populus xiaozhuanica*
2	162.1	109.4	127.8	148	127	11	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	35.0	23.5	30.6	149	115	10	*Eucalyptus globulus, Acacia mearnsii*	*Acacia mearnsii*
2	35.4	23.5	30.6	151	116	10	*Eucalyptus globulus, Acacia mearnsii*	*Acacia mearnsii*
2	156.1	101.1	100.7	154	155	17	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	19.2	12.1	22.2	158	86	7	*Pachira quinate, Terminalia amazonia*	*Terminalia amazonia*
2	180.6	109.4	127.8	165	141	11	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	46.7	27.5	40.6	170	115	17	*Vochysia guatemalensis, Jacaranda copaia*	*Vochysia guatemalensis*
2	83.7	48.9	62.7	171	133	28	*Pseudotsuga menziesii, Castanea sativa*	*Pseudotsuga menziesii*
2	12.9	7.5	10.8	172	119	8	*Acer saccharum, Betula papyrifera*	*Betula papyrifera*
2	177.5	101.1	100.7	176	176	17	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	8.1	4.6	7.0	177	115	7	*Dalbergia retusa, Pachira quinata*	*Dalbergia retusa*
2	3.5	1.9	2.1	185	166	7	*Pachira quinate, Tabebuia rosea*	*Pachira quinata*
2	191.1	101.1	100.7	189	190	17	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	209.9	101.1	100.7	208	208	17	*Eucalyptus saligna, Falcataria moluccana*	*Eucalyptus saligna*
2	17.9	7.2	10.8	250	165	8	*Betula papyrifera, Quercus rubra*	*Betula papyrifera*
2	31.2	11.0	12.5	285	250	9	*Betula pendula, Pinus pinaster*	*Pinus pinaster*

2	10.8	3.7	3.7	293	293	11	*Terminalia amazonia, Inga edulis*	*Terminalia amazonia*
3	26.5	18.5	22.1	144	120	16	*Hyeronima alchorneoides, Vochysia ferruginea, Balizia elegans*	*Hyeronima alchorneoides*
4	63.4	42.8	55.0	148	115	17	*Terminalia amazonia, Virola koschnyi, Dipteryx panamensis*	*Terminalia amazonia*
4	31.1	10.1	16.5	308	189	3.5	*Aesculus hippocastanum, Fraxinus excelsior, Prunus avium, Sorbus aucuparia*	*Sorbus aucuparia*
4	44.9	13.3	30.5	336	147	3.5	*Betula pendula, Carpinus betulus, Quercus petraea, Tilia platyphyllos*	*Carpinus betulus*
4	47.2	13.4	30.5	351	155	3.5	*Betula pendula, Carpinus betulus, Fagus sylvatica, Tilia platyphyllos*	*Carpinus betulus*
4	45.6	12.5	30.5	365	150	3.5	*Betula pendula, Carpinus betulus, Fagus sylvatica, Quercus petraea*	*Carpinus betulus*
4	51.6	14.1	16.9	367	304	3.5	*Acer pseudoplatanus, Fraxinus excelsior, Prunus avium, Sorbus aucuparia*	*Acer pseudoplatanus*
4	55.7	12.8	16.9	435	329	3.5	*Acer pseudoplatanus, Aesculus hippocastanum, Fraxinus excelsior, Sorbus aucuparia*	*Acer pseudoplatanus*
4	46.1	10.2	16.9	450	272	3.5	*Acer pseudoplatanus, Aesculus hippocastanum, Fraxinus excelsior, Prunus avium*	*Acer pseudoplatanus*
4	64.0	11.8	16.9	543	378	3.5	*Acer pseudoplatanus, Aesculus hippocastanum, Prunus avium, Sorbus aucuparia*	*Acer pseudoplatanus*
4	58.7	10.7	30.5	548	193	3.5	*Carpinus betulus, Fagus sylvatica, Quercus petraea, Tilia platyphyllos*	*Carpinus betulus*
4	43.9	6.5	13.7	674	321	3.5	*Betula pendula, Fagus sylvatica, Quercus petraea, Tilia platyphyllos*	*Betula pendula*

5	14.4	7.9	22.2	182	65	7	*Terminalia amazonia, Tabebuia rosea, Dalbergia retusa, Pachira quinate, Anacardium excelsium*	*Terminalia amazonia*
6	2.6	6.7	6.7	39	39	7	*Anacardium excelsium, Erythrina fusca, Gliricidia sepium, Inga punctata, Luehea speciose, Ochroma pyramidale*	*Anacardium excelsum*
6	5.1	7.0	7.0	72	72	7	*Dalbergia retusa, Erythrina fusca, Gliricidia sepium, Inga punctata, Luehea speciose, Ochroma pyramidale*	*Dalbergia retusa*
6	17.2	22.2	22.2	78	78	7	*Terminalia amazonia, Erythrina fusca, Gliricidia sepium, Inga punctata, Luehea speciose, Ochroma pyramidale*	*Terminalia amazonia*
6	7.9	8.7	16.9	91	47	8	*Acer saccharum, Betula papyrifera, Larix laricina, Picea glauca, Pinus strobus, Quercus rubra*	*Larix larici*
6	1.7	1.7	1.7	102	102	7	*Tabebuia rosea, Erythrina fusca, Gliricidia sepium, Inga punctata, Luehea speciose, Ochroma pyramidale*	*Tabebuia rosea*
6	13.5	11.9	14.8	113	91	8	*Acer saccharum, Betula papyrifera, Larix laricina, Picea glauca, Pinus strobus, Quercus rubra*	*Larix larici*
6	36.9	23.3	36.3	158	102	16	*Anacardium excelsum, Cedrela odorata, Hura crepitans, Luehea seemanii, Tabebuia rosea, Cordia alliodora*	*Luehea seemanii*

6	5.6	2.1	2.1	263	263	7	*Pachira quinate, Erythrina fusca, Gliricidia sepium, Inga punctata, Luehea speciose, Ochroma pyramidale*	*Pachira quinata*
Overall				**170.3 [95% CI 143.9, 196.8]**	**128.0 [95% CI 112.4, 143.5]**			

Table D3 Species classified as commercial species for the comparison of mixed plantation to monocultures of commercial species.

Study	Country	Commercial species
Debell et al., 1997	USA (Hawaii)	Eucalyptus saligna
Forrester et al., 2013	Australia	Eucalyptus globulus
Piotto et al., 2010	Costa Rica	Vochysia guatemalensis Terminalia amazonia Hyeronima alchorneoides
Nunes et al., 2014	Portugal	Pseudotsuga menziesii
Wang et al., 2009	China	Cunninghamia lanceolata
Mao et al., 2010	China	Populus xiaozhuanica
Nichols & Carpenter, 2006	Costa Rica	Terminalia amazonia
TreeDivNet – Agua Salud	Panama	Anacardium excelsum Tabebuia rosea Terminalia amazonia
Kaye et al., 2000	USA (Hawaii)	Eucalyptus saligna
Son et al., 2007	South Korea	Pinus koraiensis

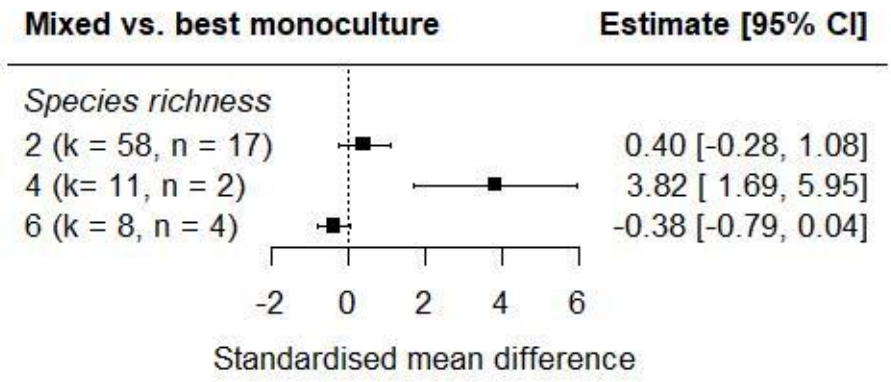


Figure D4 The effect of diversification at different levels of species richness on aboveground carbon stocks relative to the best associated monoculture. Effect sizes are standardised mean differences, calculated using data subset by each level of species richness. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

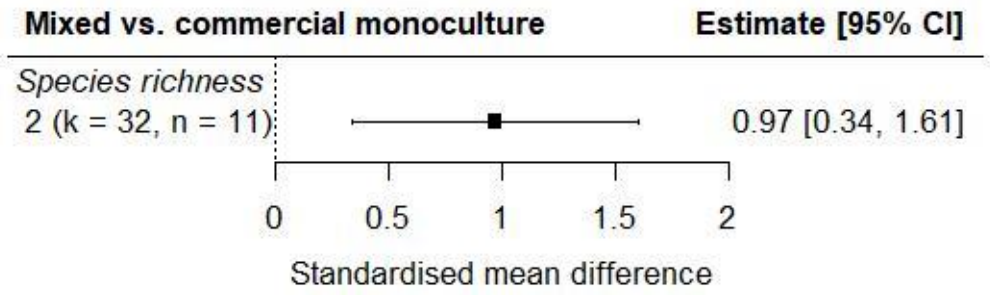


Figure D5 The effect of diversification at a species richness of two on aboveground carbon stocks relative to commercial monocultures. Effect sizes are standardised mean differences, calculated using data subset by species richness two. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

Table D4 Carbon accumulation in mixed plantations compared to commercial species monocultures. The % carbon in the mixed plantation relative to the commercial species monoculture is shown. The comparisons are ordered by species richness and the % of the commercial species monoculture carbon in the mixed plantation. The age and species in the mixed and commercial species monoculture plantations are given.

SR	DP carbon (Mg/ha)	commercial MP carbon (Mg/ha)	% of commercial monoculture carbon in DP	Age	Mixed plantation species	Commercial monoculture species
2	3.5	6.7	53	7	Anacardium excelsium Tabebuia rosea	Anacardium excelsum
2	15.5	22.2	70	7	Terminalia amazonia Tabebuia rosea	Terminalia amazonia
2	5.2	6.7	78	7	Anacardium excelsium Pachira quinata	Anacardium excelsum
2	68.5	82.2	83	27	Alnus hirsuta Pinus koraiensis	Pinus koraiensis
2	19.1	22.2	86	7	Dalbergia retusa Terminalia amazonia	Terminalia amazonia
2	19.2	22.2	86	7	Pachira quinata Terminalia amazonia	Terminalia amazonia
2	19.9	22.2	90	7	Anacardium excelsium Terminialia amazonia	Terminalia amazonia
2	123.8	127.8	97	11	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	9.2	9.0	102	5	Populus xiaozhuanica Hippophae rhamnoides	Populus xiaozhuanica
2	131.9	127.8	103	11	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	7.0	6.7	105	7	Anacardium excelsium Dalbergia retusa	Anacardium excelsum
2	66.9	62.7	107	28	Pseudotsuga menziesii Castanea sativa	Pseudotsuga menziesii
2	52.7	49.2	107	15	Cunninghamia lanceolata Kalopanax septemlobus	Cunninghamia lanceolata
2	144.8	127.8	113	11	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	46.7	40.6	115	17	Vochysia guatemalensis Jacaranda copaia	Vochysia guatemalensis
2	60.0	49.2	122	15	Cunninghamia lanceolata Alnus cremastogyne	Cunninghamia lanceolata

2	162.1	127.8	127	11	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	83.7	62.7	133	28	Pseudotsuga menziesii Castanea sativa	Pseudotsuga menziesii
2	180.6	127.8	141	11	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	170.3	120.5	141	15	Populus xiaozhuanica Hippophae rhamnoides	Populus xiaozhuanica
2	156.1	100.7	155	17	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	177.5	100.7	176	17	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	191.1	100.7	190	17	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	31.4	16.5	191	10	Eucalyptus globulus Acacia mearnsii	Eucalyptus globulus
2	209.9	100.7	208	17	Eucalyptus saligna Falcataria moluccana	Eucalyptus saligna
2	3.5	1.7	209	7	Pachira quinata Tabebuia rosea	Tabebuia rosea
2	35.0	16.5	213	10	Eucalyptus globulus Acacia mearnsii	Eucalyptus globulus
2	35.4	16.5	215	10	Eucalyptus globulus Acacia mearnsii	Eucalyptus globulus
2	4.8	1.7	282	7	Dalbergia retusa Tabebuia rosea	Tabebuia rosea
2	10.8	3.7	293	11	Terminalia amazonia Inga edulis	Terminalia amazonia
2	19.9	6.7	298	7	Anacardium excelsium Terminialia amazonia	Anacardium excelsum
2	15.5	1.7	913	7	Terminalia amazonia Tabebuia rosea	Tabebuia rosea
3	26.5	22.1	120	16	Hyeronima alchorneoides Vochysia ferruginea Balizia elegans	Hyeronima alchorneoides
4	63.4	55.0	115	17	Terminalia amazonia Virola koschnyi Dipteryx panamensis	Terminalia amazonia
5	14.4	6.7	216	7	Terminalia amazonia Tabebuia rosea Dalbergia retusa Pachira quinata Anacardium excelsium	Anacardium excelsum
5	14.4	22.2	65	7	Terminalia amazonia Tabebuia rosea Dalbergia retusa Pachira quinata Anacardium excelsium	Terminalia amazonia

5	14.4	1.7	851	7	Terminalia amazonia Tabebuia rosea Dalbergia retusa Pachira quinata Anacardium excelsium	Tabebuia rosea
6	17.2	22.2	78	7	Terminalia amazonia Erythrina fusca Gliricidia sepium Inga punctata Luehea speciose Ochroma pyramidale	Terminalia amazonia
Overall			**176.6 [95% CI 119.4, 233.8]**			

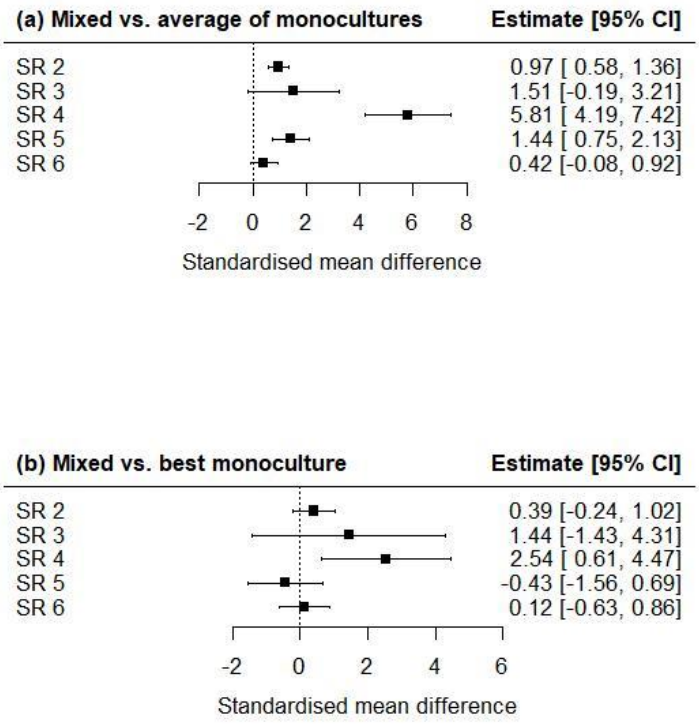


Figure D6 The effect of diversification at different levels of species richness on aboveground carbon stocks relative to (a) the average of associated monocultures and (b) the best associated monocultures. Effect sizes are standardised mean differences, predicted from models with species richness fitted as a discrete moderator. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures.

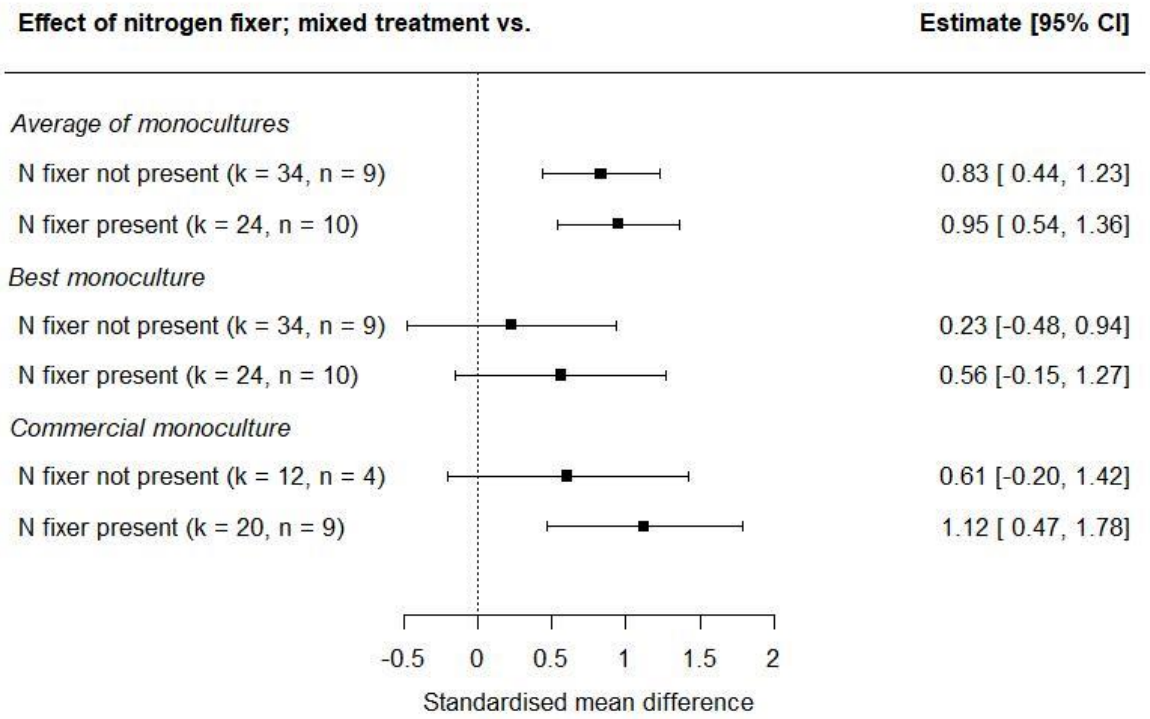


Figure D7 The effect of diversification with/without a nitrogen-fixing species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species (analysis limited to two-species mixtures). Effect sizes are standardised mean differences, predicted from models with presence/absence of a nitrogen-fixer fitted as a discrete moderator. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

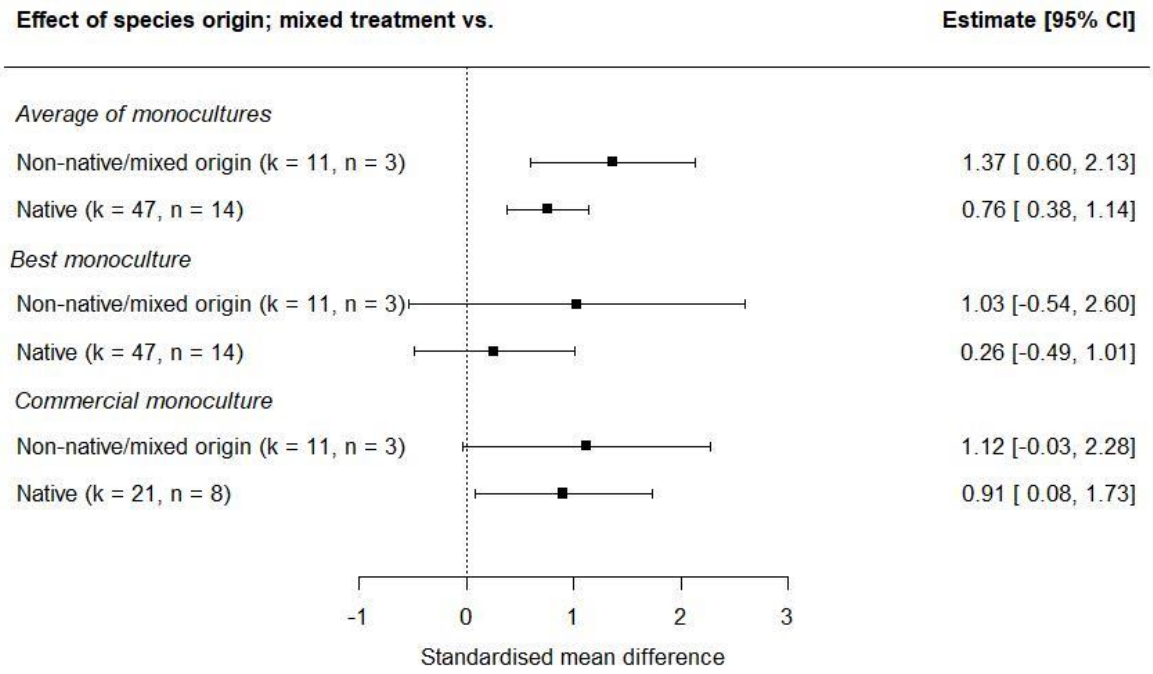


Figure D8 The effect of diversification with all native vs. non-native/mixed species on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species (analysis limited to two-species mixtures). Effect sizes are standardised mean differences, predicted from models with species origin fitted as a discrete moderator. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

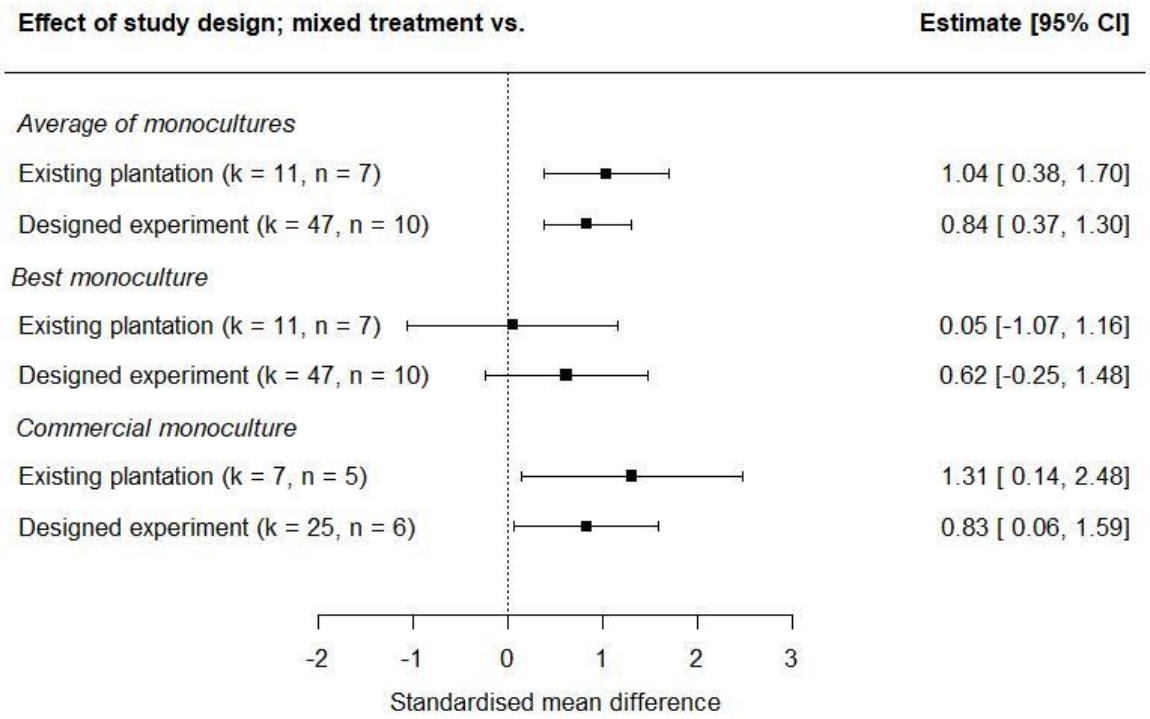


Figure D9 The effect of study design on aboveground carbon stocks relative to the average of associated monocultures, the best associated monoculture, and monocultures of commercial species (analysis limited to two-species mixtures). Effect sizes are standardised mean differences, predicted from models with study design fitted as a discrete moderator. Confidence intervals overlapping zero suggest no statistically detectible effect of diversification. Positive values indicate higher carbon stocks in mixtures than in monocultures. Number of comparisons (k) and number of study sites (n) are shown.

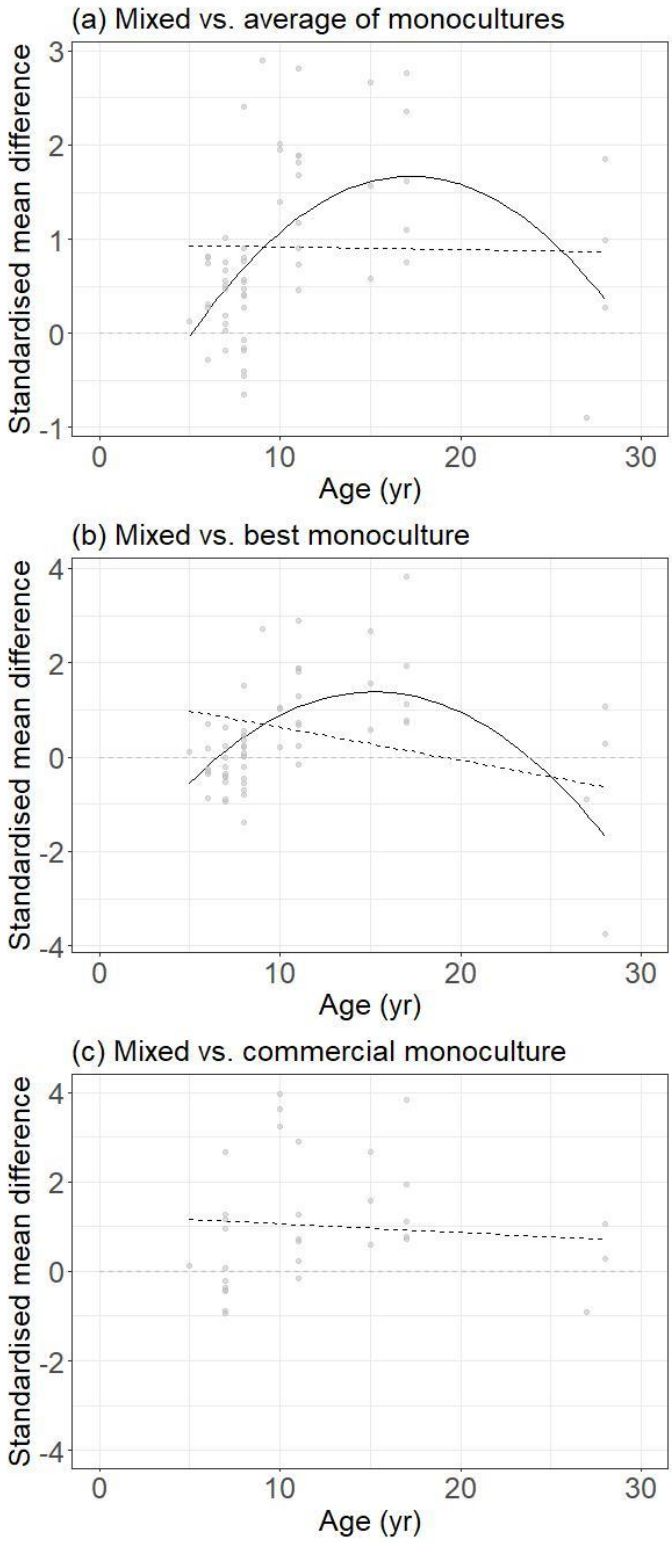


Figure D10 The relationship between stand age and the standardised mean difference in aboveground carbon stocks (analysis limited to two-species mixtures) relative to (a) the average of relevant monocultures, k = 58; (b) the best associated monoculture, k = 58; (c) commercial monocultures, k = 32. Non-significant trends shown as dashed lines.

Appendix E: Supplementary methods for Chapter 5

Publication bias and removal of outliers

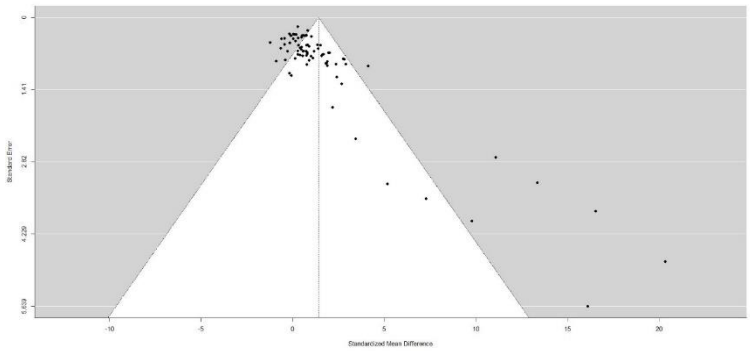
Methods

We used funnel plots (*funnel* function in the R package *metafor*) to assess the distribution of effect sizes in each of our models and considered the impact of removing the most extreme outliers on the results.

Results

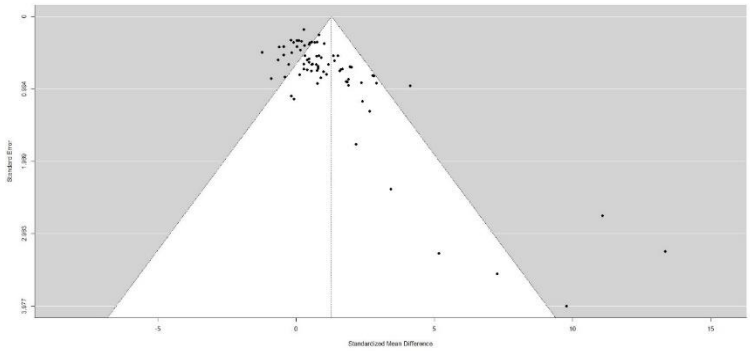
Research question 1a – mixed vs. average of monocultures

All comparisons included:



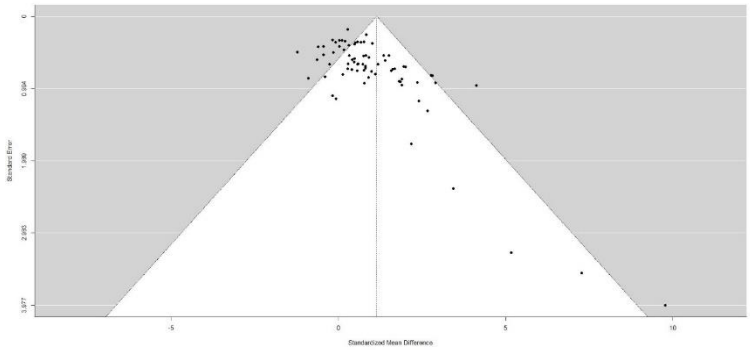
SMD 1.41 [95% CI 0.75, 2.07], k = 79

Removal of most extreme outliers, standardised mean difference > 15:



SMD 1.28 [95% CI 0.75, 1.82], k = 76

Removal of most extreme outliers, standardised mean difference > 10:

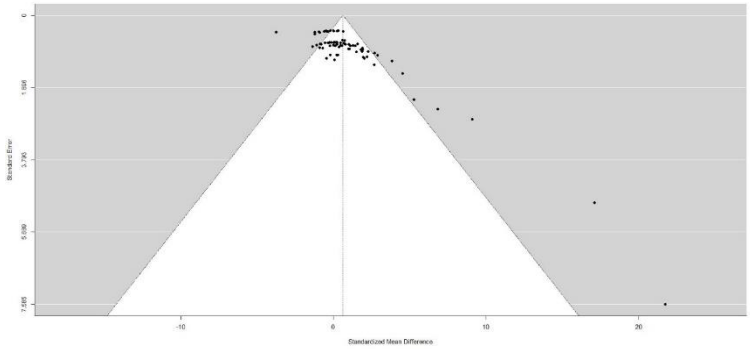


SMD 1.14 [95% CI 0.71, 1.56], k = 74

No qualitative change to results, carbon stocks in mixed plantation still clearly higher than the average of monocultures.

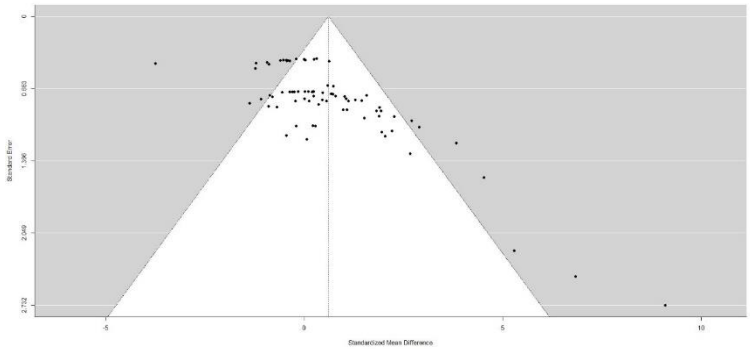
Research question 1b – mixed vs. best monoculture

All comparisons included:



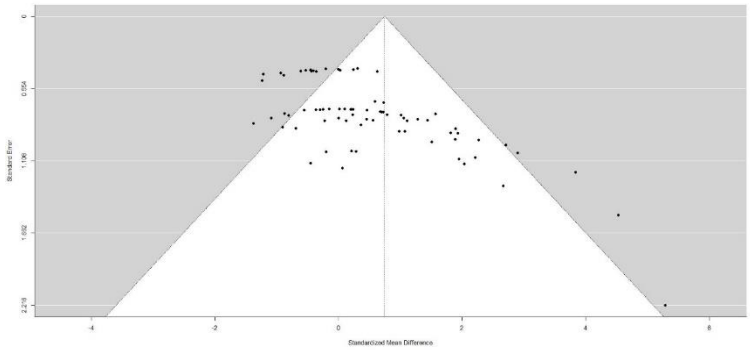
SMD 0.62 [95% CI −0.0095, 1.25], k = 79.

Removal of most extreme outliers, standardised mean difference > 10:



Pooled SMD 0.61 [95% CI −0.015, 1.23], k = 77.

Removal of additional outliers, standardised mean difference > 6 and < −3:

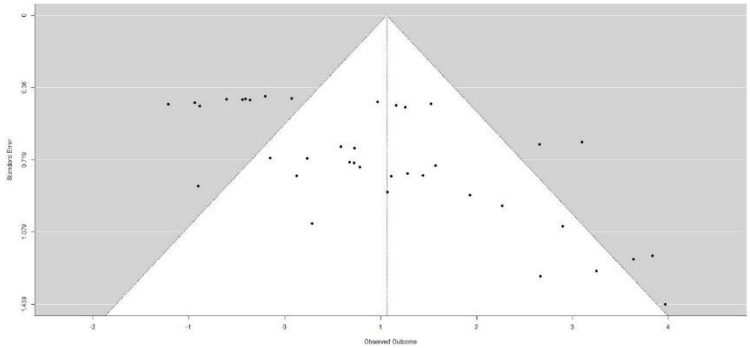


Pooled SMD 0.75 [95% CI 0.32, 1.17], k = 73.

Removal of these outliers alters the result to show higher carbon in the mixed plantation relative to best monoculture, with the confidence interval no longer overlapping zero. This contrasts to the result with the full dataset, which suggested no clear increase in carbon stocks in the mixed plantation relative to best monoculture.

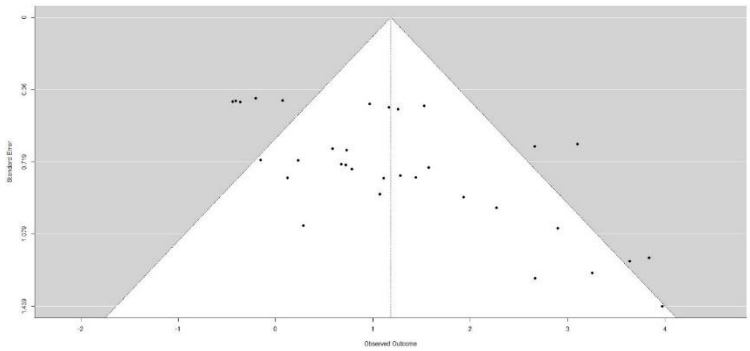
Research question 1c – mixed vs commercial monocultures

All comparisons included:



SMD 1.06 [0.47, 1.65], k = 38

Remove effect sizes < −0.5:



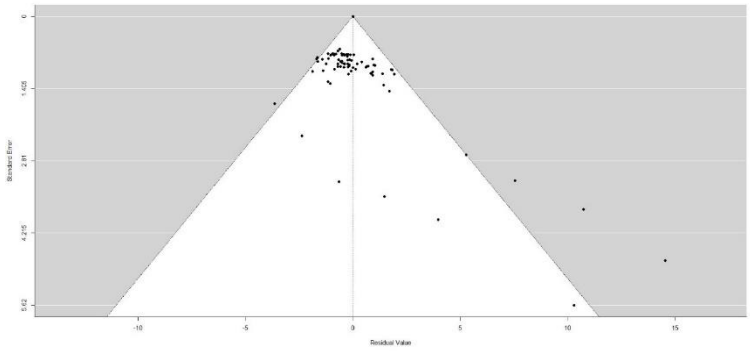
SMD 1.18 [95% CI 0.70, 1.67], k = 33

No qualitative change in results, still shows higher carbon stocks in mixed plantation relative to commercial monocultures.

Research question 2 – effect of richness in mixture on carbons stocks

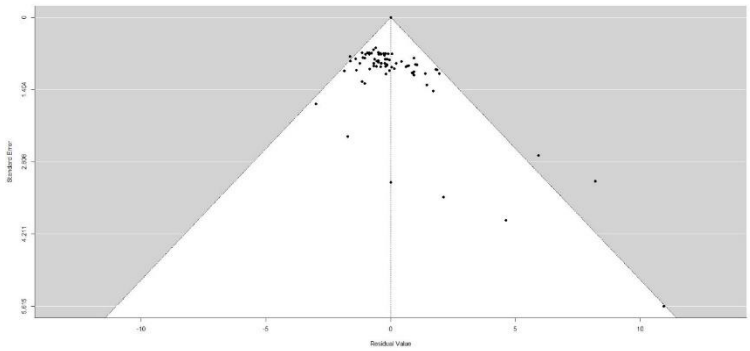
Effect of richness, mixed vs. average of monocultures

All comparisons included:



$Q_M = 46.79$, $p < 0.01$, $k = 79$

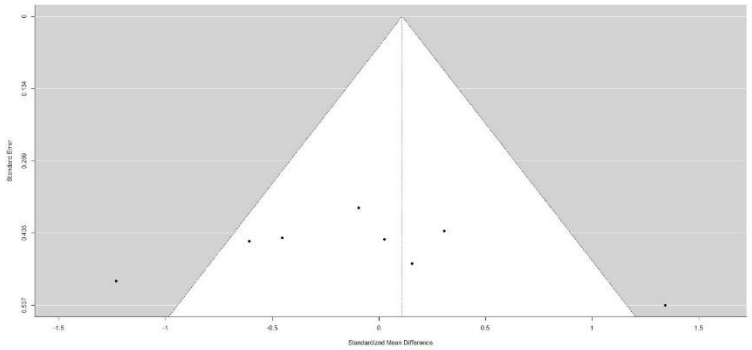
Remove effect sizes > 16.5



$Q_M = 39.22$, $p < 0.001$, $k = 77$

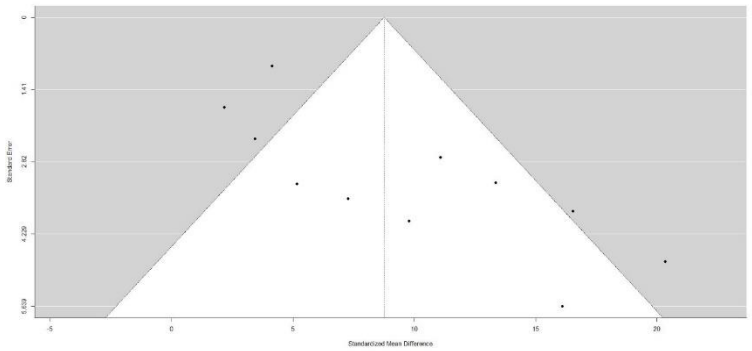
No qualitative change in results, still significant relationship between richness and carbon stocks in mixed vs. average of monocultures.

Species richness 6, mixed vs. average of monocultures



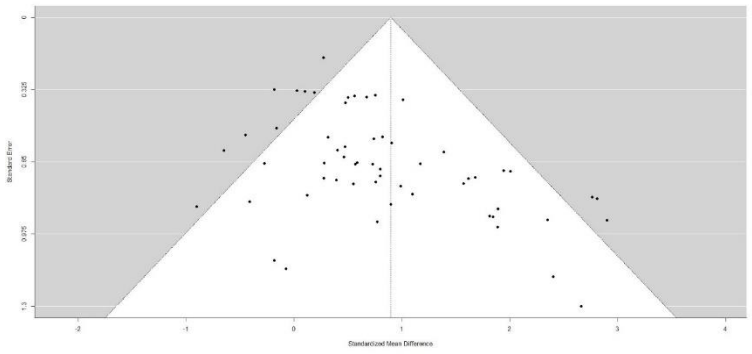
SMD 0.11 [95% CI −0.55, 0.77], k = 8

Species richness 4, mixed vs. average of monocultures



SMD 8.76 [95% CI 4.82, 12.7], k = 11

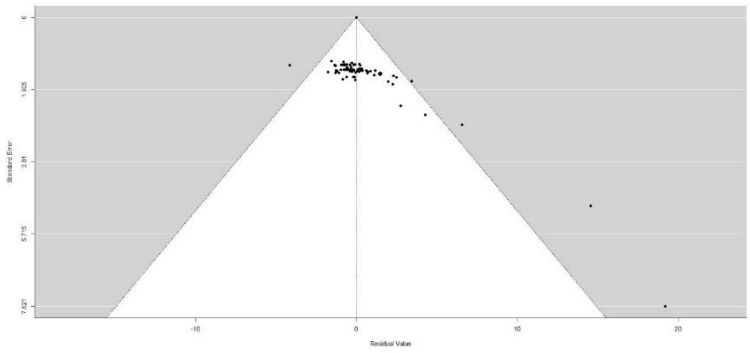
Species richness 2, mixed vs. average of monocultures



SMD 0.90 [0.53, 1.27], k = 58

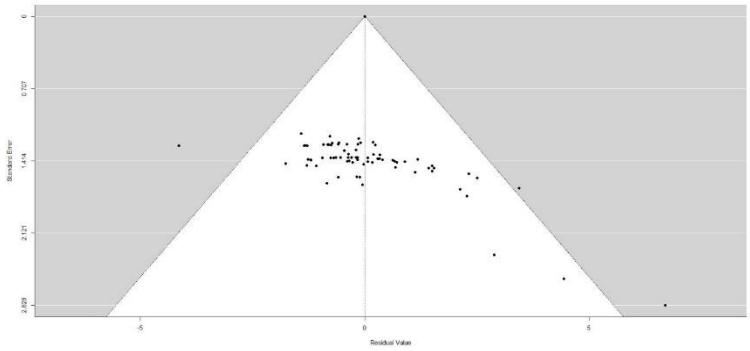
Effect of richness, mixed vs. best monoculture

All comparisons included:



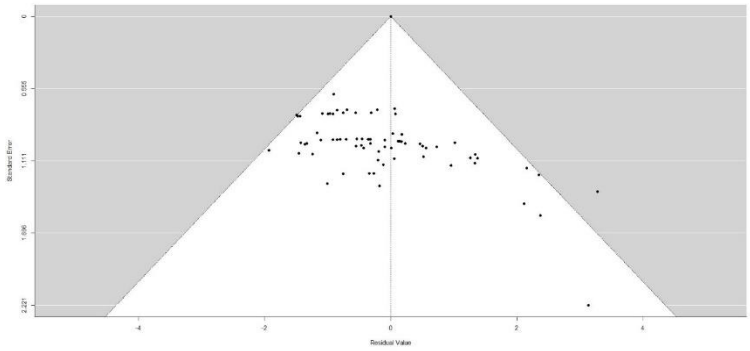
Q_M 8.78, p = 0.067, k = 79

Remove effect sizes > 10:



Q_M = 8.25, p = 0.083, k = 77

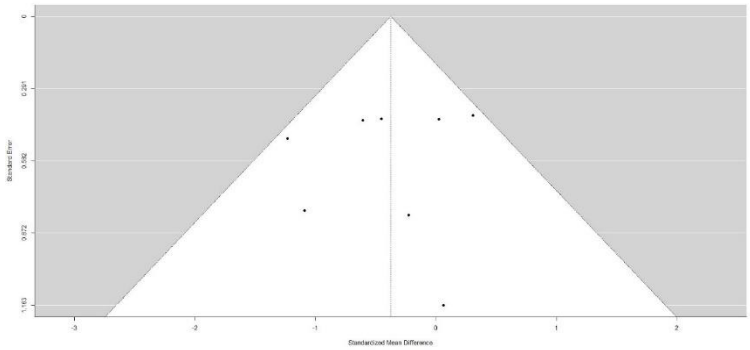
Remove effect sizes > 6 and < −3:



Q_M = 11.25, p = 0.024, k = 74

Removal of these most extreme outliers alters the result, showing a significant relationship between richness and carbon stocks in mixed vs. best monoculture.

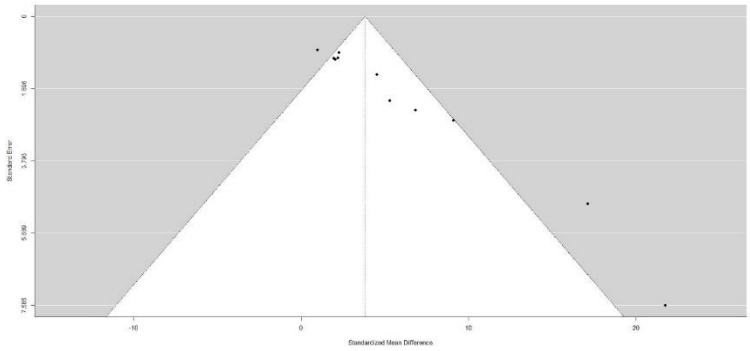
Species richness 6, mixed vs. best monoculture



SMD −0.38 [95% CI −0.79, 0.042], k = 8

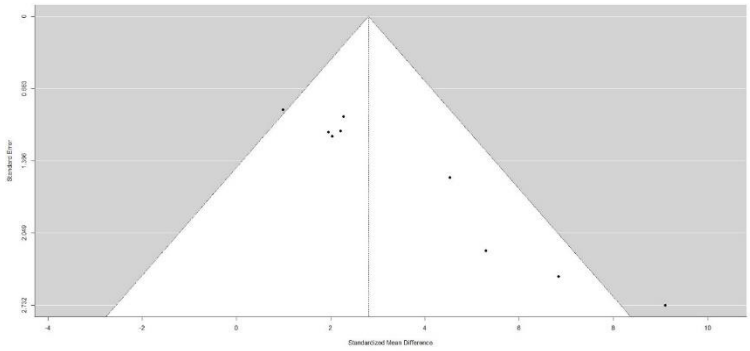
Species richness 4, mixed vs. best monoculture

All comparisons included



SMD 3.82 [95% CI 1.69, 5.95], k = 11

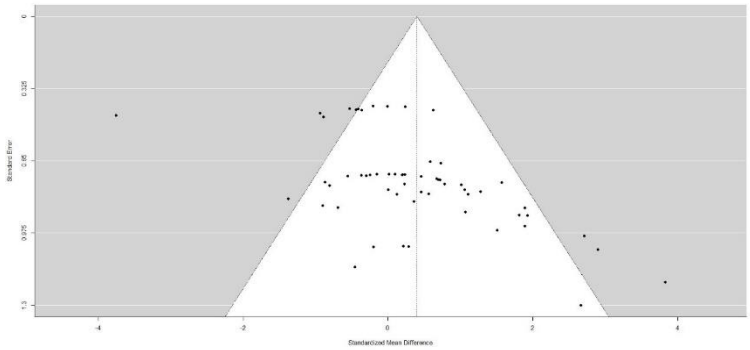
Remove effect sizes > 10:



SMD 2.80 [95% CI 1.69, 3.91], k = 9

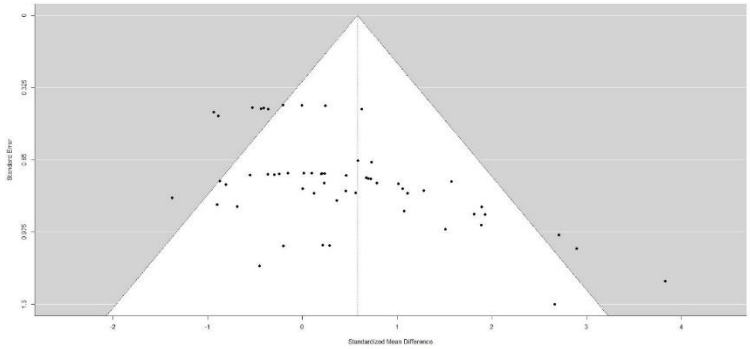
No qualitative change in results, still significantly higher carbon stocks in mixture relative to best monoculture for species richness 4.

Species richness 2, mixed vs. best monoculture



SMD 0.40 [95% CI −0.28, 1.08], k = 58

Remove effect sizes < −2:

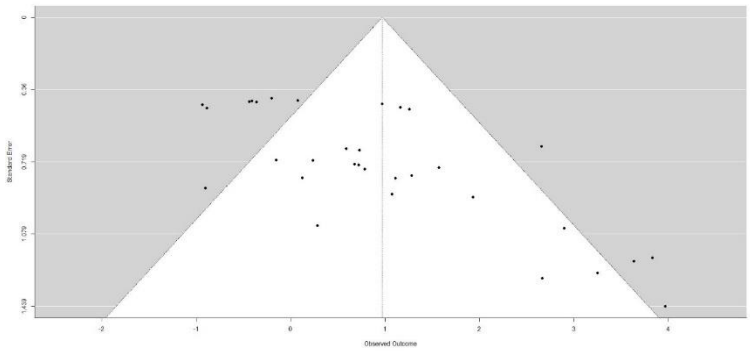


SMD 0.58 [95% CI 0.17, 0.99], k = 57

Removal of these most extreme outliers alters the result, showing greater carbon in mixed vs. best monoculture for species richness 2.

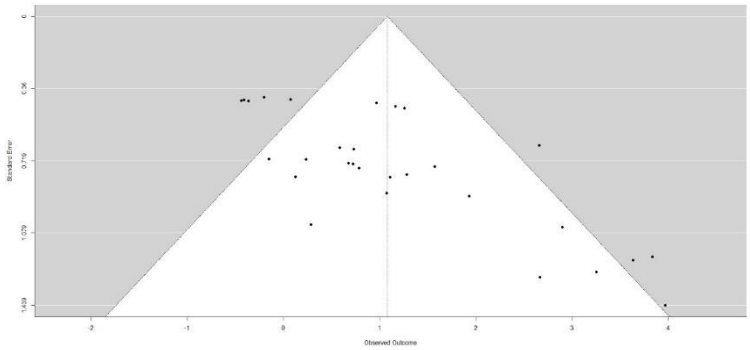
Species richness 2, mixed vs. commercial monoculture

All comparisons included:



SMD 0.97 [95% CI 0.34, 1.61], k = 32

Remove effect sizes < −0.5



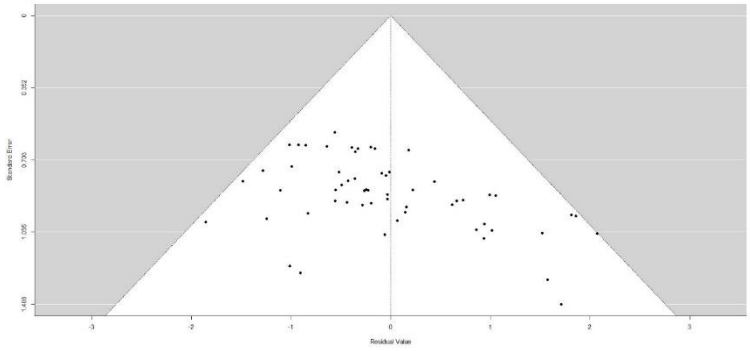
SMD 1.08 [95% CI 0.52, 1.64], k = 29

No qualitative change in results, still higher carbon stocks in mixed vs. commercial monocultures for species richness 2.

Research question 3 – potential mechanisms

Inclusion of N-fixer in mixture, mixed vs. average of monocultures

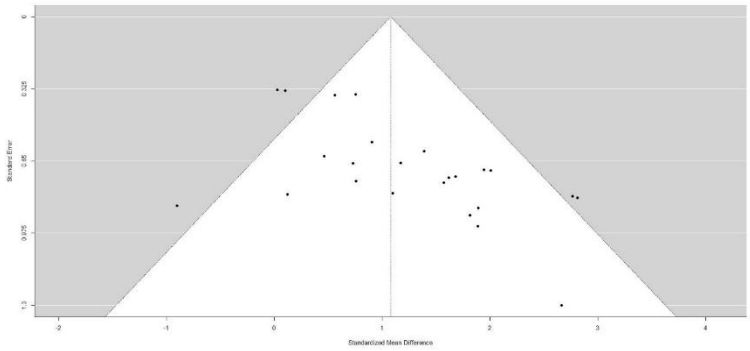
All comparisons included:



Q_M = 0.37, p = 0.54, k = 58

N-fixer present, mixed vs. average of monocultures

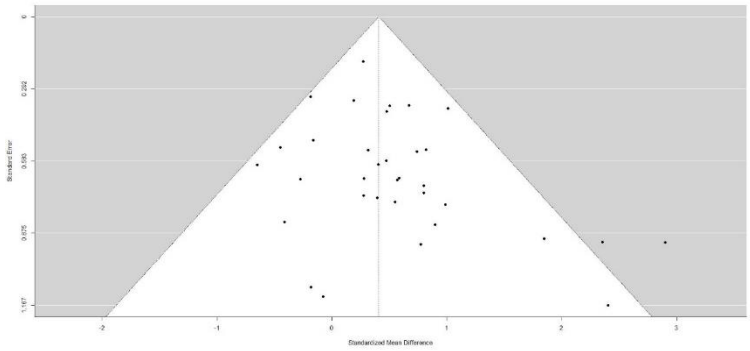
All comparisons included:



SMD 1.08 [95% CI 0.58, 1.58], k = 24

N-fixer not present, mixed vs. average of monocultures

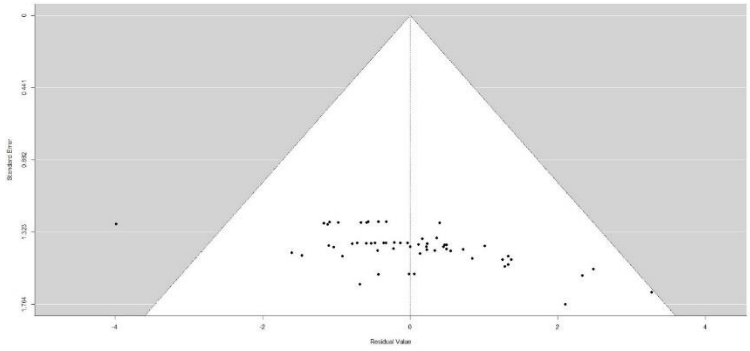
All comparisons included:



SMD 0.41 [95% CI 0.23, 0.58], k = 34

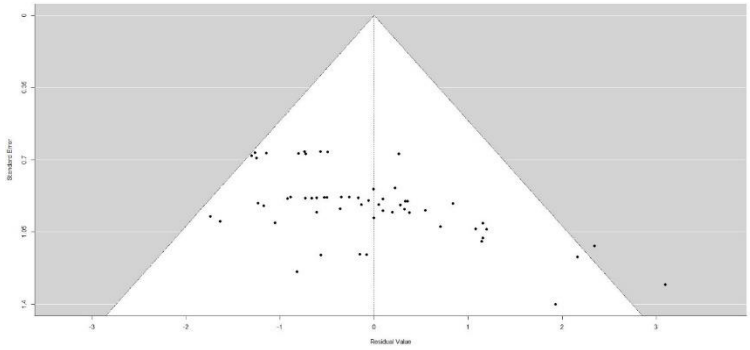
Inclusion of N-fixer in mixture, mixed vs. best monoculture

All comparisons included:



Q_M = 1.35, p = 0.25, k = 58

Remove effect size < −3:

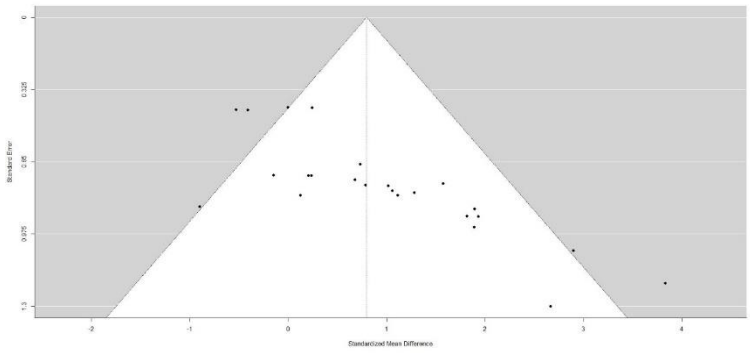


Q_M = 2.25, p = 0.13, k = 57

No qualitative change in results, moderator for nitrogen-fixer present vs. absent still not significant for comparison between mixed and best monocultures.

N-fixer present, mixed vs. best monoculture

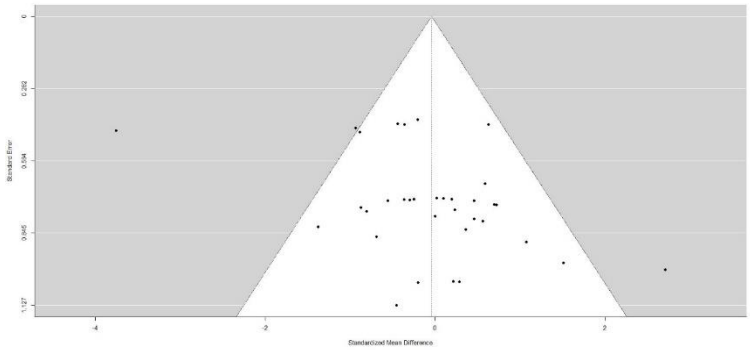
All comparisons included:



SMD 0.80 [95% CI 0.24, 1.36], k = 24

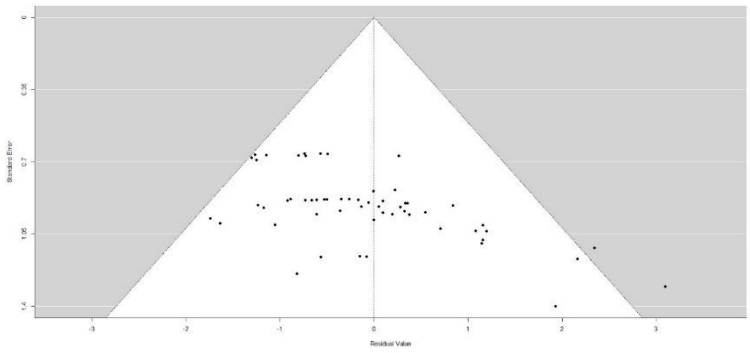
N-fixer not present, mixed vs. best monoculture

All comparisons included:



SMD −0.043 [95% CI −1.09, 1.00], k = 34

Remove effect size < −3:

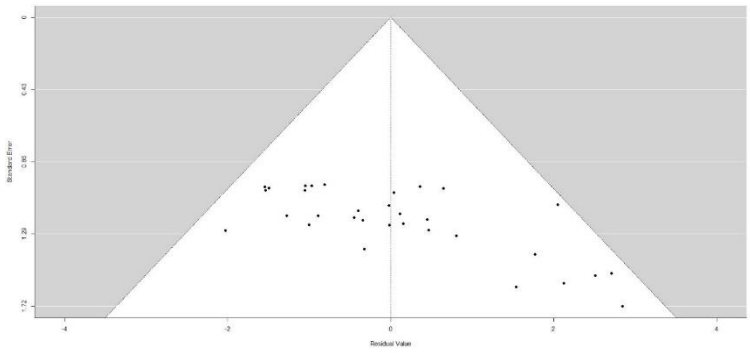


SMD 0.0098 [95% CI −0.28, 0.30], k = 33

No qualitative change in results, carbon stocks similar in mixed vs. best monoculture when N-fixer not present in the mixture.

Inclusion of N-fixer in mixture, mixed vs. commercial monoculture

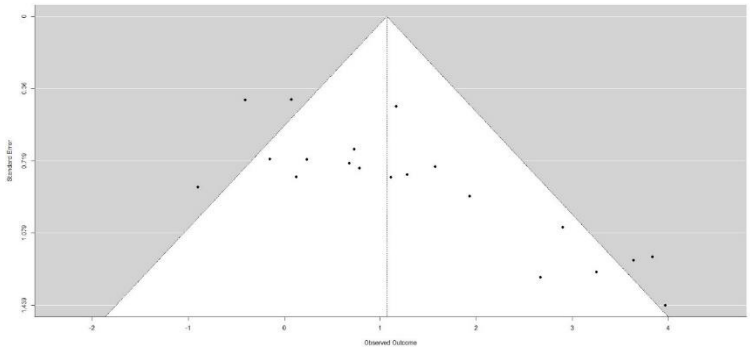
All comparisons included:



Q_M = 1.33, p = 0.25, k = 32

N-fixer present, mixed vs. commercial monoculture

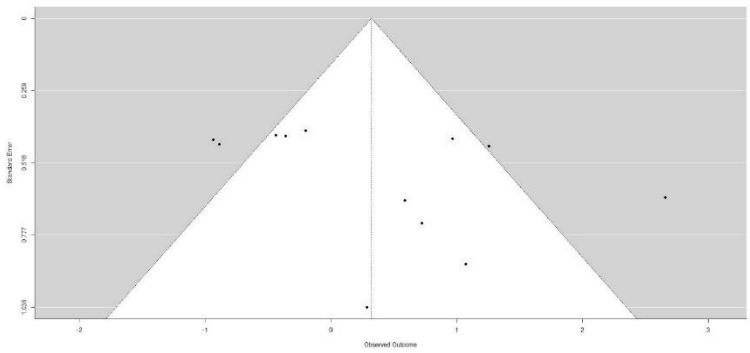
All comparisons included:



SMD 1.07 [95% CI 0.29, 1.84], k = 20

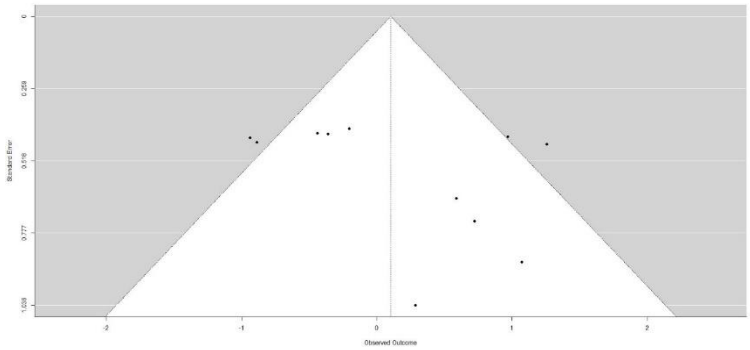
N-fixer not present, mixed vs. commercial monoculture

All comparisons included:



SMD 0.32 [95% CI −0.28, 0.92], k = 12

Remove effect size > 2:

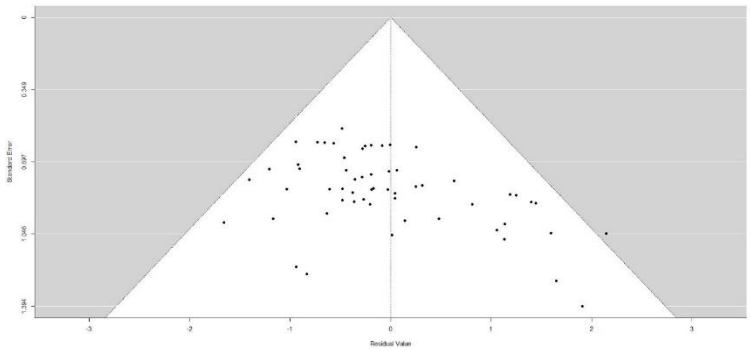


SMD 0.10 [95% CI −0.42, 0.63], k = 11

No qualitative change in results, carbon stocks similar in mixed vs. commercial monocultures when N-fixer not present in the mixture.

Effect of species origin in mixture, mixed vs. average of monocultures

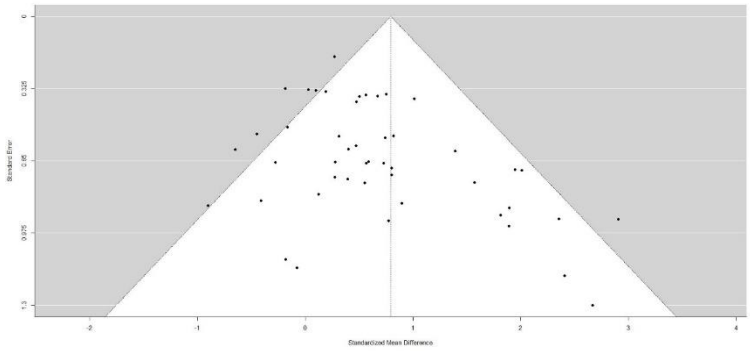
All comparisons included:



Q_M = 0.94, p = 0.16, k = 58

Native only in mixture vs. average of monocultures

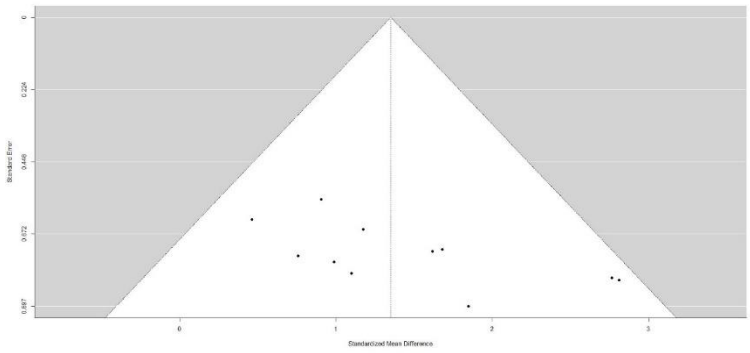
All comparisons included:



SMD 0.79 [95% CI 0.36, 1.22], k = 47

Non-native/mixed origin in mixture vs. average of monocultures

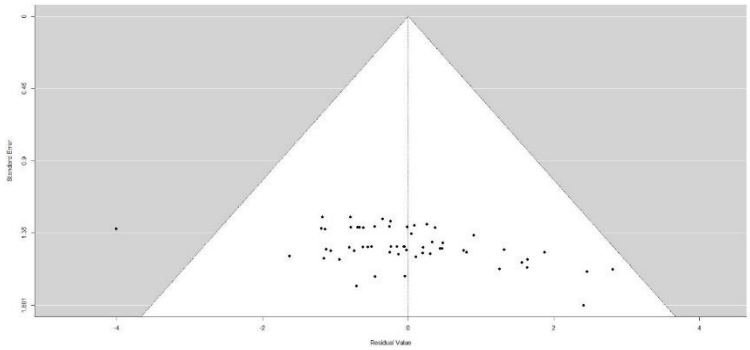
All comparisons included:



SMD 1.35 [95% CI 0.92, 1.78], k = 11

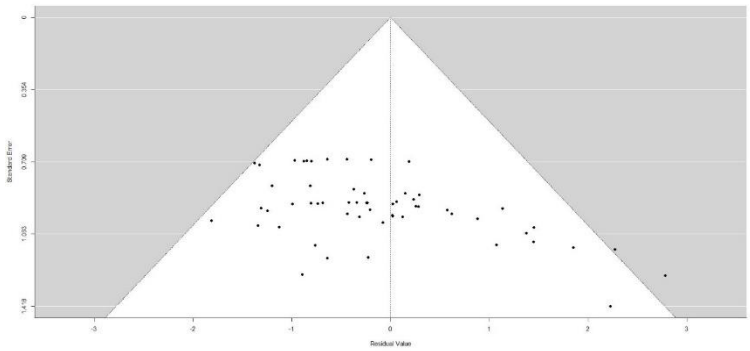
Species origin in mixture, mixed vs. best monoculture

All comparisons included:



Q_M = 0.75, p = 0.39, k = 58

Remove effect size < −3:

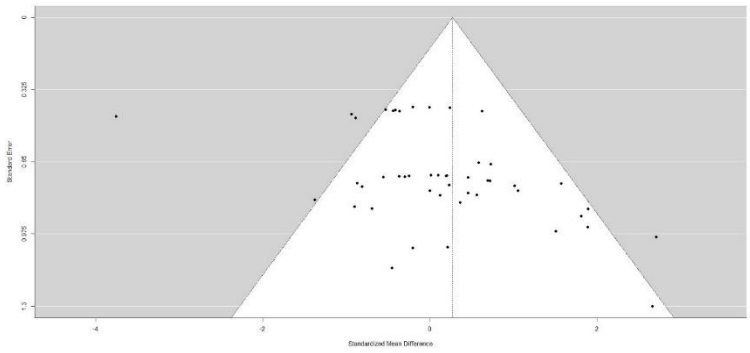


Q_M = 1.54, p = 0.21, k = 57

No qualitative change in results, moderator for species origin still not significant for comparison between mixed and best monocultures.

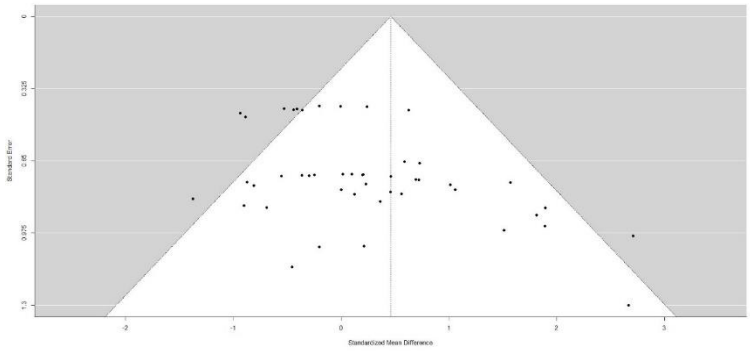
Native only in mixture vs. best monoculture

All comparisons:



SMD 0.27 [95% CI -0.53, 1.08], k = 47

Remove effect size < −3:

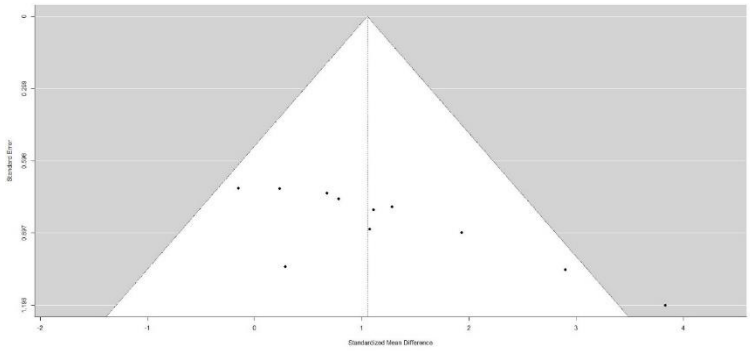


SMD 0.46 [95% CI 0.0008, 0.92], k = 46

No qualitative change in results, carbon stocks similar in mixed vs. best monoculture when all native species in mixture.

Non-native/mixed origin in mixture vs. best monoculture

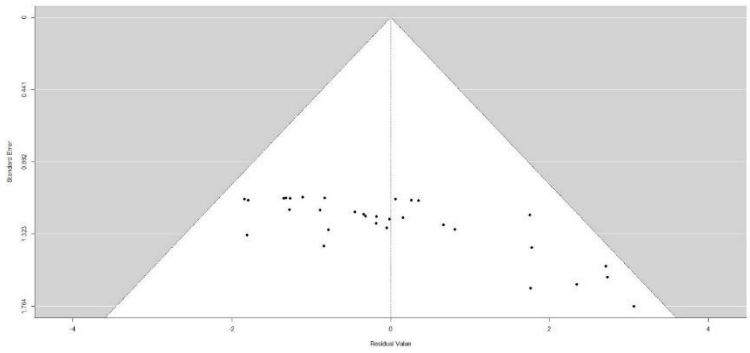
All comparisons included:



SMD 1.05 [95% CI 0.45, 1.65], k = 11

Species origin in mixture, mixed vs. commercial monocultures

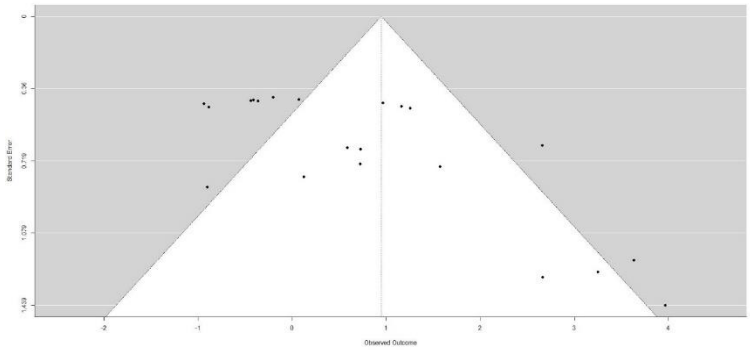
All comparisons included:



Q_M = 0.091, p = 0.76, k = 32

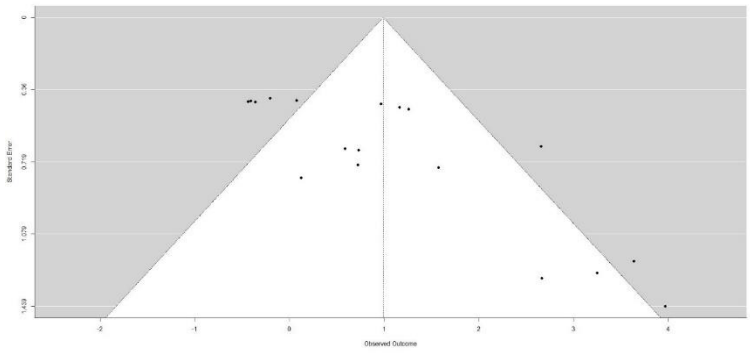
Native only in mixture, mixed vs. commercial monocultures

All comparisons included:



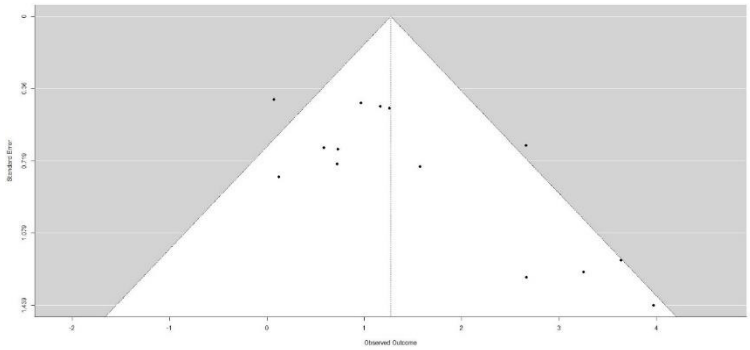
SMD 0.95 [95% CI −0.0072, 1.90], k = 21

Remove effect sizes < −0.5:



SMD 0.99 [95% CI 0.26, 1.71], k = 18

Remove effect sizes < 0:

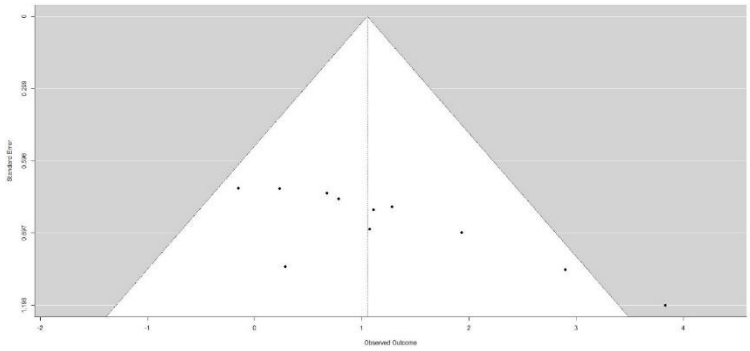


SMD 1.27 [95% CI 0.61, 1.94], k = 14

Removal of these outliers alters the result to show higher carbon in the mixed plantation relative to commercial monoculture when considering native species only in the mixture, with the confidence interval no longer overlapping zero. This contrasts to the result with the full dataset, which suggested no clear increase in carbon stocks in the mixed plantation relative to monoculture.

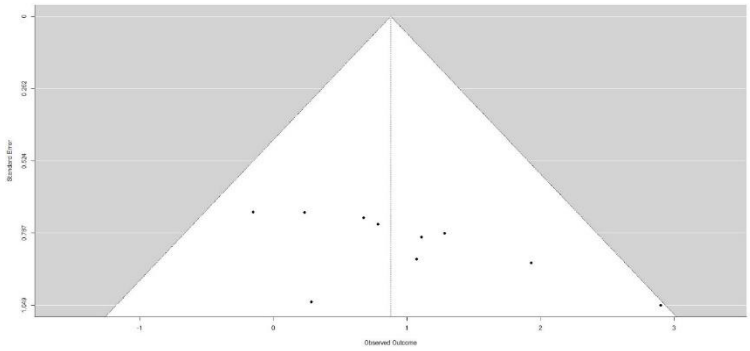
Non-native/mixed origin in mixture vs. commercial monocultures

All comparisons:



SMD 1.05 [95% CI 0.45, 1.65], k = 11

Remove effect size > 3:

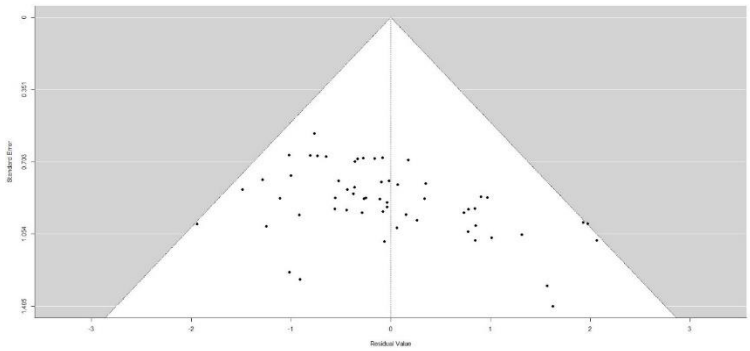


SMD 0.88 [95% CI 0.37, 1.38], k = 10

No qualitative change in results, carbon stocks similar in mixed vs. best monoculture when all non-native/mixed origin species in mixture.

Effect of study design, mixed vs. average of monocultures

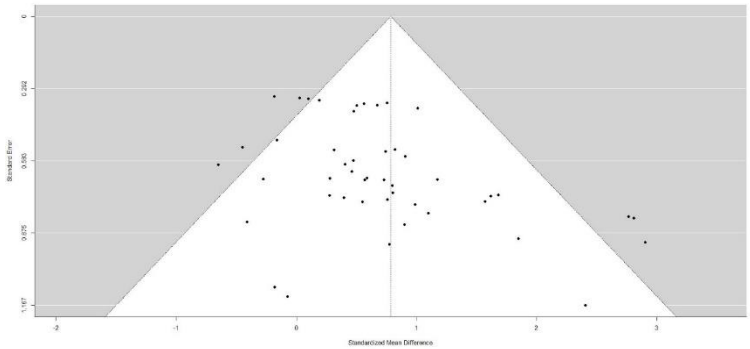
All comparisons included:



Q_M = 0.24, p = 0.62, k = 58

Designed experiment only, mixed vs. average of monocultures

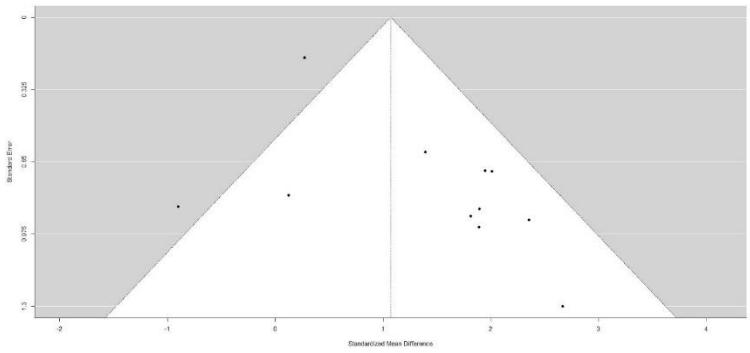
All comparisons included:



SMD 0.78 [95% CI 0.41, 1.16], k = 47

Existing plantation only, mixed vs. average of monocultures

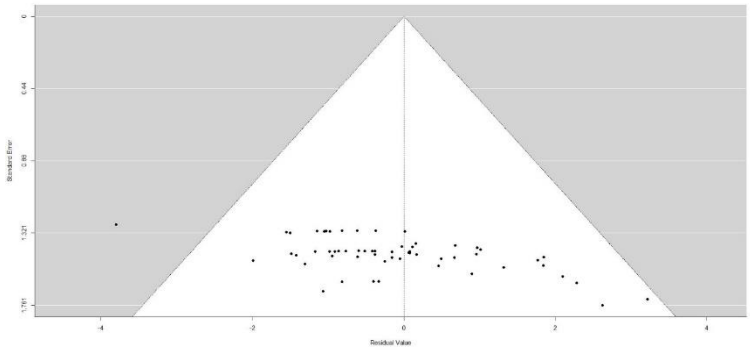
All comparisons included:



SMD 1.07 [95% CI 0.19, 1.95], k = 11

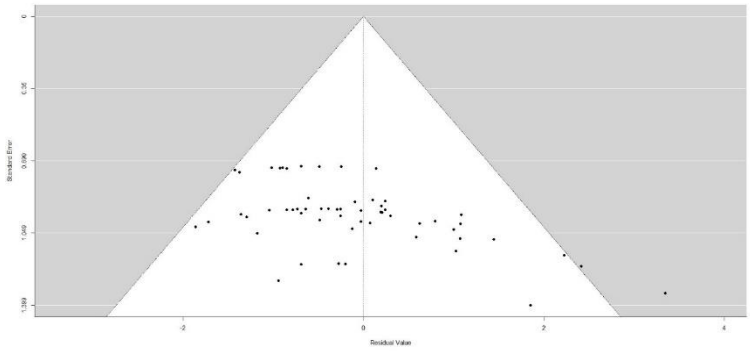
Effect of study design, mixed vs. best monoculture

All comparisons included:



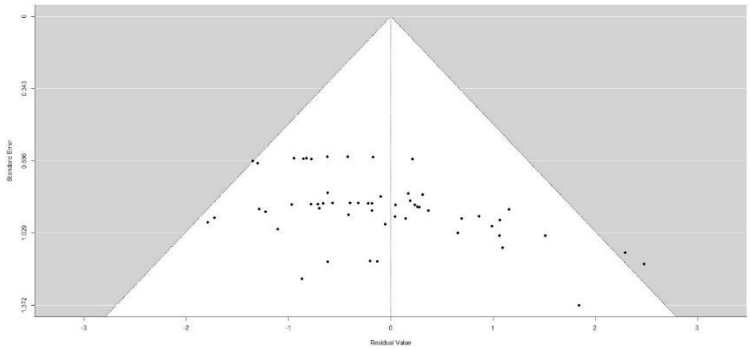
Q_M = 0.63, p = 0.43, k = 58

Remove effect sizes < −3:



Q_M = 0.51, p = 0.48, k = 57

Remove effect size > 3:

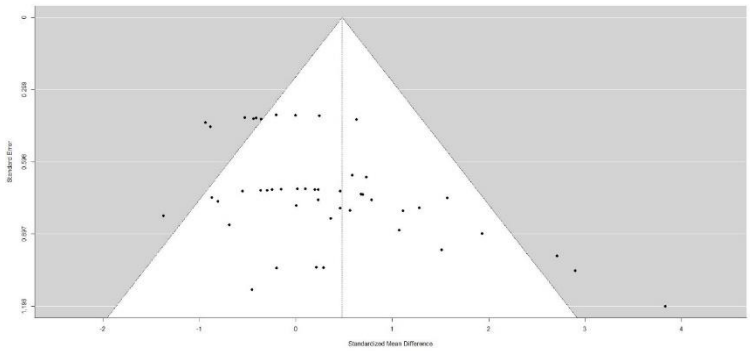


Q_M = 0.88, p = 0.35, k = 56

No qualitative change in results, moderator for study design still not significant for comparison between mixed and best monocultures.

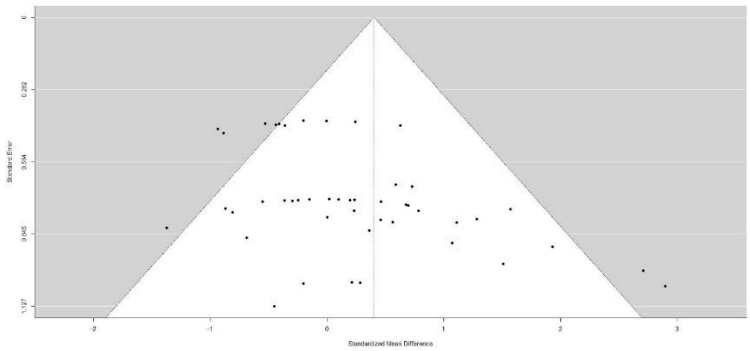
Designed experiment only, mixed vs. best monoculture

All comparisons included:



SMD 0.48 [95% CI 0.013, 0.95], k = 47

Remove effect size > 3:

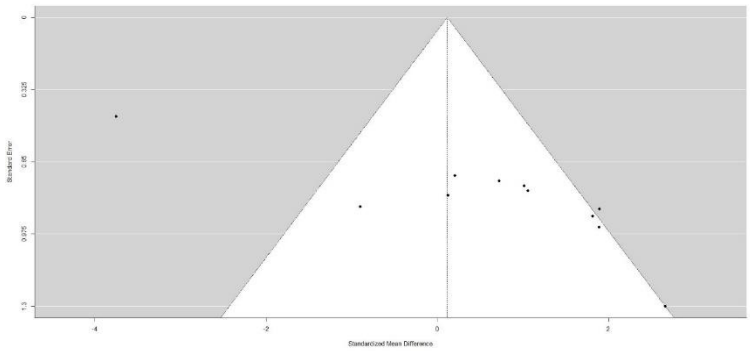


SMD 0.40 [95% CI −0.016, 0.82], k = 46

Removal of outlier alters the result to show no clear difference in carbon in the mixed plantation relative to best monoculture when considering designed experiments only, with the confidence interval overlapping zero. This contrasts to the result with the full dataset, which suggested higher carbon stocks in the mixed plantation relative to monoculture.

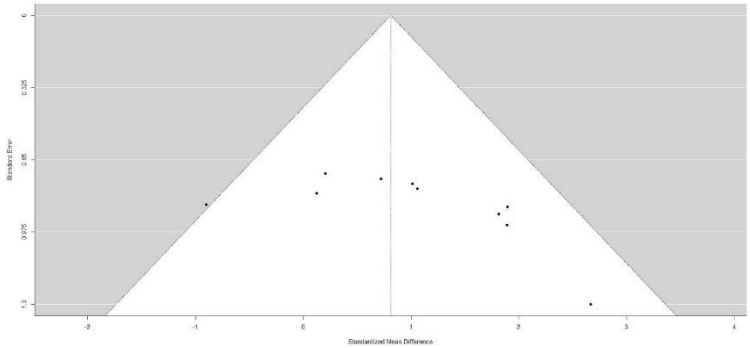
Existing plantation only, mixed vs. best monoculture

All comparisons included:



SMD 0.12 [95% CI −1.46, 1.69], k = 11

Remove effect size < −3:

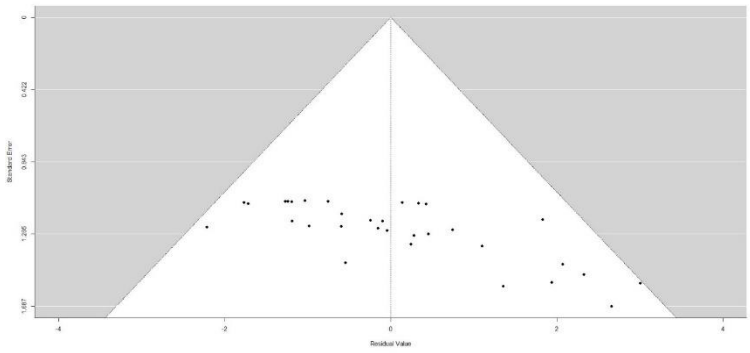


SMD 0.81 [95% CI −0.015, 1.64], k = 10

No qualitative change in results, carbon stocks similar in mixed vs. best monoculture for existing plantations.

Effect of study design, mixed vs. commercial monocultures

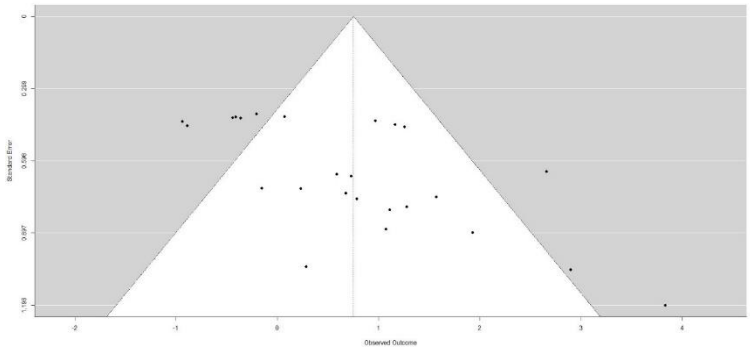
All comparisons included:



Q_M = 0.46, p = 0.50, k = 32

Designed experiment only, mixed vs. commercial monocultures

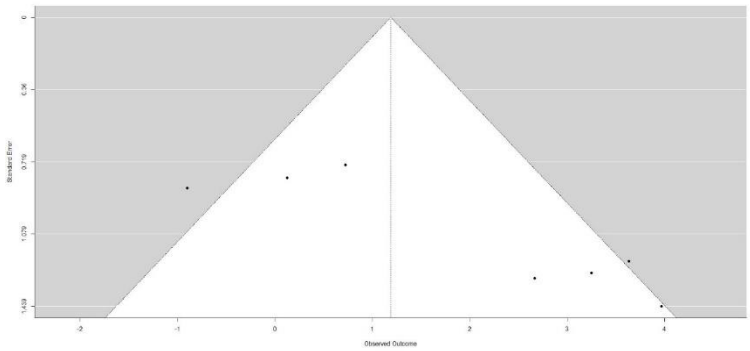
All comparisons included:



SMD 0.75 [95% CI 0.19, 1.31], k = 25

Existing plantation only, mixed vs. commercial monocultures

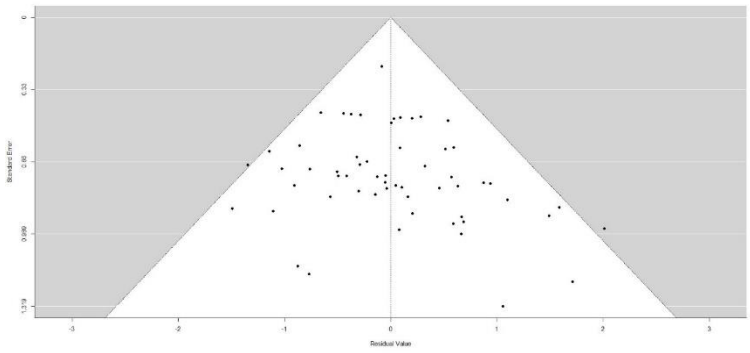
All comparisons included:



SMD 1.19 [95% CI −0.45, 2.83], k = 7#

Effect of age, mixed vs. average of monocultures

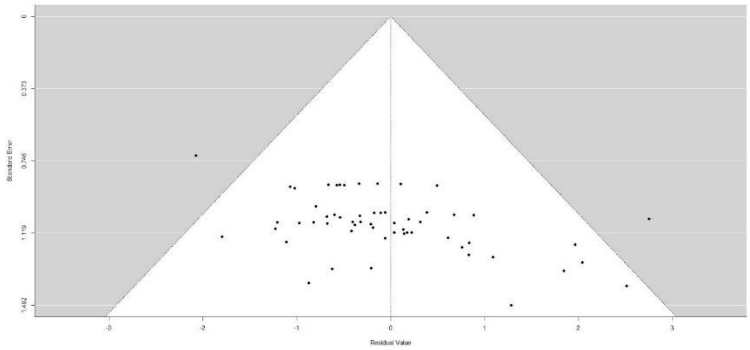
All comparisons included:



Q_M = 13.3, p = 0.001, k = 58, quadratic term −0.013 [−0.023, −0.003]

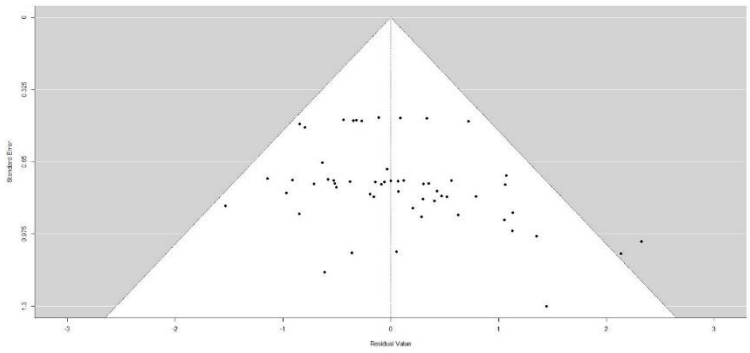
Effect of age, mixed vs. best monoculture

All comparisons included:



Q_M = 16.1, p < 0.001, k = 58, quadratic term −0.019 [95% CI −0.029, −0.008]

Remove effect sizes > 3 and < −3:

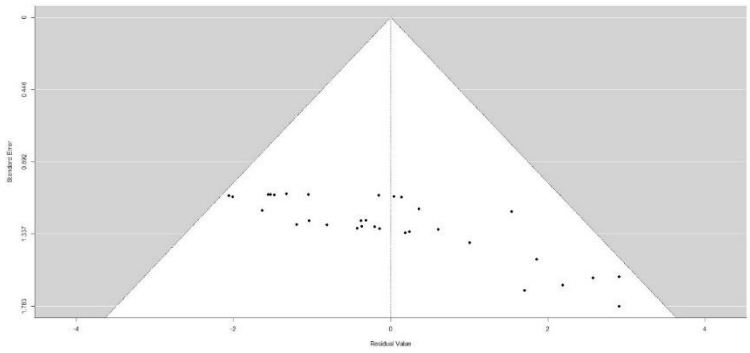


Q_M = 22.1, p < 0.001, k = 56, quadratic term −0.012 [95% CI −0.019, −0.006]

No qualitative change in results, moderator for age still significant for comparison between mixed and best monoculture.

Effect of age, mixed vs. commercial monocultures

All comparisons included:



Q_M = 0.14, p = 0.71, k = 32, effect Age −0.02 [95% CI −0.12, 0.082]

Appendix F: A Rewilding Diary by Emily Warner

During my PhD I was lucky enough to have the chance to write an occasional series for the nature-writing journal The Clearing, run by Little Toller Books, reflecting on my experiences conducting research in the Scottish Highlands. On a personal level, it gave me the chance to reflect on the more spiritual side of a wonderful experience. It also gave me a great opportunity to consider the implications of my results and to communicate my research to a different audience.



Diary introduction – published 13th November 2018

https://www.littletoller.co.uk/the-clearing/a-rewilding-diary-by-emily-warner-introduction/

My summer this year was spent living in a remote part of the Scottish Highlands, quantifying the benefits that restoration and regeneration of native forest can bring. My existence has been idyllic: combining purpose, productivity, rugged scenery, simple living and the chance to be a part of a positive conservation project.



Glen Affric, where I have been based for my research, contains one of the largest remnants of Caledonian forest. Now reduced by centuries of human exploitation to scattered pockets, this habitat is home to a host of the UK's wildest and rarest plants and animals. The deadwood habitats harbour

internationally important bryophyte and lichen communities, the structure of the understorey provides food and nest sites for birds, insects live throughout the forest matrix, rare plants grow amongst the ground layer, and red squirrels and pine martens spring through the branches. To visit these forest fragments is to see a type of habitat I wouldn't typically associate with the Highlands: huge contorted pines fringing the lochs and framing the sky. Yet these remnants of the forest are dying, the damage inflicted by an inflated grazing pressure from deer over recent decades is likely to show its true extent in the years to come. Deer are woodland animals, and with their high population levels, the remaining forest areas struggle to provide enough food for their herds. These beautiful ancient forests lack something therefore: the next generation of trees that should be pushing up through the shrub layer, filling the gap between their ancient ancestors and the understorey.

I first heard of Trees for Life, who work to protect and restore the Caledonian Forest, in 2014, when rewilding went from a subculture of ecology to a more mainstream concept. To many, the Scottish Highlands stand as one of the UK's true areas of wilderness: miles of predominantly uninhabited land, wild and untamed. To others, the influence of humans is clear, and the potential for the enhancement and expansion of a previously dominant forest ecosystem is stark. The Caledonian forest in Scotland once covered a huge swathe of the Highlands, supporting a rich and diverse ecosystem within the shelter and structure of the forest, in contrast to the bare and blasted heathland that dominates today.



It takes courage and inspiration to tackle a problem of such magnitude, and Trees for Life started their mission over 25 years ago to not only protect what remains, but also to expand these areas of forest. Thus, across the landscape in

Glen Affric lie a string of newly planted and fenced areas of regenerating forest, spanning from 6 to 28 years of age.

These areas of regeneration are the focus of my PhD. What can this new woodland provide? How does it alter the ecological quality of the landscape? And how do these patterns of change develop over time? The idea is that this could contribute to the endorsement of similar planting projects in other parts of the UK uplands, enhancing the diversity of plants and animals and resilience of ecosystem processes in these areas.

This summer my life has been driven by the push of fulfilling carefully planned fieldwork aims, and simultaneously synced with the rhythm of a raw and natural landscape, providing a level of fulfilment that I couldn't have predicted. It is hard to describe what it has been to live and work for two months in a remote and exceptionally beautiful part of the Scottish Highlands, conducting research that I am wholly invested in and working with an organisation whose vision I admire. I'm looking forward to sharing these experiences, both scientific and wild, in these occasional pieces for The Clearing.



Diary entry 1 – published 8th January 2019

https://www.littletoller.co.uk/the-clearing/a-rewilding-diary-by-emily-warner/

I visited Glen Affric during a mild week in April 2018. After a couple of months of planning, the realisation of my project rested on a scoping visit to the regenerating forest sites.



I had last been in Scotland in the autumn of 2015, and my only experiences of Glen Affric's forest had been autumnal ones. Returning on what had been the cusp of spring in Oxford, I found myself in a landscape still held in the tail end of winter. The birch, previously aflame with the colours of their autumn leaves, showed their exposed skeletons of deep chestnut branches, with the bright

green of the scots pine standing out against the deep oranges and browns of the landscape. Snow topped the surrounding mountains, turning to scattered patches on the lower slopes, which were periodically obscured by passing waves of fine mist.

Trees for Life's fenced and replanted enclosures fit neatly onto an A4 page: "25 years of tree planting." I had pored over this map: thirty-eight sites, established between 1990 and 2014, offering an amazing opportunity to look at the re-establishment of native woodland over almost thirty years. The difficulty lay in rationalising this to the scale of the landscape. The limit of my experiences in Glen Affric lay at the western end of Loch Beinn a'Mheadhoin (over nine miles of water represented by less than 10cm on the map), where the tarmac road ends at the final Forestry Commission car park. Most of the sites lie further west of this, beyond Loch Affric, forming a pathway of stepping stones for six miles down the valley, where Glen Affric then branches into Fionnglean and Gleann Gnomiadh.

I had identified a minimum number of sites that I would need to study to answer my questions robustly, and I now needed to work out whether a single summer would be enough. So, I found myself waiting with my supervisor, Owen, at the end of the road by Loch Beinn a'Mheadoinn for Doug and Alan from *Trees for Life* and our transport down to the western end of Loch Affric. Here we would be left to explore the sites for the next three days, using *Trees for Life's* Athnamulloch Bothy as a base.



Driving west along the track to the south of Loch Affric there is a transition in the form of the forest. The shores of Loch Beinn a'Mheadoinn are cloaked in a thick tangle of mature forest, gnarled pines and birches interspersed with rowans. But as you travel west the patches of mature forest become scarcer. There are patches of mature forest to the south of Loch Affric and a huge enclosure has allowed birch, willow and pines to establish in the treeless areas. A scattering of smaller seedlings has sprung up, forming dense patches of young forest in many places. Travelling slowly through this in the minibus, the branches of the young trees scraped against the windows, allowing only glimpses of the surrounding mountains. Finally emerging at the loch end, we were greeted by the channel of mountains that stretches away ahead and a narrower valley holding the River Affric. The series of fenced areas of regeneration along the valley stood out as dark patches on the flanks of the mountains, dwarfed by the surrounding Munros.

The next two days were filled with walking. Ten kilometres from Athnamulloch Bothy to the furthest site at Camban Waterfall, passing the UK's most remote youth hostel, still shut over winter. Dipping in and out of the sites and gaining an overview of the ones on the opposite side of the valley. The fences marking the perimeter of the sites were emphasised by a boundary of heather regeneration, the ground layer rebounding in direct response to deer exclusion.



Lady's mantle seedling.

Over three days in Glen Affric, an idea that had initially felt overwhelming slowly spawned into the possibility of an idyllic summer of fieldwork. I had had no idea of what to expect, and in reality the forest patches that barely filled a side of A4 covered a scale far more expansive than the limits of my imagination. Likewise, twenty-eight years of tree regrowth had generated

patches of forest that a person could vanish within. Possibilities for fieldwork and for the forest itself seemed alive with potential. If a forest could regenerate beyond the bounds of my optimistic imagination, what did that mean for biodiversity and the ecosystem processes generated by the developing ecosystem? A scientific quantification of the intuitive positive effects of forest regeneration became a very exciting prospect.

Looking back, this short trip feels like a gateway to my experiences of the summer. Stumbling upon the dried remains of last year's plants and the tiny seedlings destined for this summer; relative rarities in the wider heathland and indicators of ancient woodland habitat, such as lady's mantle, bluebells and wood cranesbill. The buds were bursting on the birches and willows and the woods were just beginning to fill with the songs of breeding birds establishing their territories.

On the final day, as we set out to walk back alongside Loch Affric to the road, light rain began to fall for the first time, amidst bursts of scattered sunshine. Walking away from Glen Affric is hard, and as the track rose away from the floodplain valley where Athnamulloch Bothy sits we turned to look back: ochre and yellow snow-capped mountains, dark patches of the enclosures in the distance, the bothy a tiny white dot in the valley bottom, sitting perfectly at the end of a rainbow arching over the River Affric to the valley side beyond.



Diary entry 2 – published 20th March 2019

https://www.littletoller.co.uk/the-clearing/a-rewilding-diary-by-emily-warner-2/

Having left Glen Affric at the end of April, full of anticipation for the prospects of my project, I then had a month to make plans for my fieldwork before the start of June. To me it seems that periods of intense intellectual activity, and I suppose stress, are condensed into short spans during a PhD. After a fairly meandering period of defining my research project over the winter, I suddenly found myself faced with the need to finalise my methods and gather all of my equipment in just four weeks. This was accompanied by a keen sense of personal responsibility for the success of my project: I have a real hope that my research will provide objective support for the expansion of native woodland in upland areas throughout the UK. It is therefore crucial that my research methods have the maximum possibility of capturing the ecological changes driven by woodland regeneration.

As the weeks passed the piles of equipment in my office grew: wooden stakes to mark the corners of my plots, plates and cups to make pitfall traps to sample ground dwelling beetles, tubes to collect specimens, quadrats, soil augers, a midge net. And in no time I was driving out of Oxford, heading northwards to put my plan into action.

Returning to Scotland was also in itself the fulfilment of some personal passions. A chance to engage with Trees for Life's work in a new way, and hopefully spread their message to a new audience. An opportunity to spend a prolonged period in a ruggedly inspiring landscape. All whilst reconnecting with the friends I made in Scotland three years ago whilst volunteering with Trees for Life.

For my first week in Glen Affric I was joined by my friend Tony, who had agreed to a week's retreat to the wilderness and volunteered to help me to set up my plots. Tony was my supervisor during the time I spent volunteering, and during two months working alongside this patient and practical character we became good friends. Arriving in Glen Affric in his company made a huge difference to my mindset, and the potential to enjoy my fieldwork as an adventure in itself was clear, whatever the scientific output.



Glen Affric in the throes of summer was a very different landscape to its April incarnation. Shades of orange and brown had been replaced by a spectrum of greens. The birds that had just been beginning to gather in spring had reached a climax, breeding willow warblers, robins and chaffinches had been joined by stonechats, cuckoos and siskins. The calls of the cuckoos echoed and re-echoed from woodland patches up and down the valley. Rowan trees were laden with huge umbels of white flowers. The grassland was filled with orchids and hundreds of bog asphodel spikes were just waiting to flower.

This first week felt like the moment of truth. I had produced idealised, cartoon-like diagrams of the proposed layout of a plot, and a map of these plots scattered across the landscape. Whether this would work in the physical reality of Glen Affric was less clear. My main research aim is to compare the regenerating forest to the surrounding deer-grazed heathland and demonstrate the positive effects that woodland regeneration can have. To do this I wanted to set up paired plots at 16 regenerating sites, with a plot in the young woodland and a matched plot outside the fence in the treeless heathland at each site.

Within each plot I would measure a number of response variables, each relating to an aspect of ecosystem function or component of biodiversity. These included tree and soil carbon stocks, tree regeneration, plant community composition and diversity, the height of the shrub layer, ground beetle community composition, decomposition rates, and rates of soil invertebrate feeding. Next year I plan to survey the bird community and soil microbial community during another round of fieldwork.



The scramble to set up my plots took me from one end of Glen Affric to the other, and up and down the surrounding hillsides, bringing me into unexpected contact with a range of its occupants. Golden eagles soaring above the surrounding peaks, an adder sunning itself at the side of the path, a freshly emerged northern eggar moth hanging in the heather, floodplain meadows dominated by orchids. Personal excitement came from sightings of four species of orchid that were new to me, early marsh orchids, the marsh fragrant orchid (worth bending down to catch the honeysuckle scent), a lesser butterfly orchid and a small white orchid.

By the end of the week I felt a sense of relief with the progress I had made in plot establishment. As an individual on foot a huge swathe of Glen Affric was surprisingly accessible. On Tony's last day, the glen opened itself to steady rainfall, the dried moss absorbed the water after weeks without significant rainfall, and the burns and waterfalls rose from a gentle trickle to a brimming rush of water.



Diary entry 3 – published 31st July 2019

https://www.littletoller.co.uk/the-clearing/a-rewilding-diary-by-emily-warner-3/

With my survey plots established, the transition from the physical work of hammering in marker posts to the methodical collection of data was mirrored by a transition in the weather. My expectations for a Scottish summer had been realistic, and a fortnight of heavy rainfall, a thunderstorm and glimpses of sunshine had conformed perfectly to my expectations. The beauty of our isolation was that the arrival of the heatwave was something we could only guess at. Subtle shifts in the ambience of the glen hinted of what was to come: the wind slipping round to blow from the east, clearing the sky and bringing with it a noticeable influx of campers, setting up tents at three or four points down the valley.

I swapped the assistance of Tony for that of an undergraduate, Ro. I had recruited Ro before leaving Oxford, offering him the opportunity to experience scientific research first-hand in exchange for his practical help with data collection. The extra help proved invaluable in getting the fieldwork done, but a shared enthusiasm for ecology and Scotland's remote wildness made the process a joy.



Phase one of the fieldwork focussed on the plant communities. Differences in the plant species present in each plot and the structure of their communities will allow me to document some of the effects of deer exclusion and tree regeneration. The plots established in regenerating woodland, ungrazed and grazed heathland, and grazed and ungrazed mature woodland, allowing me to make comparisons between the habitat types present in the glen. Strikingly, and intuitively, the height of the shrub layer responds dramatically to the reduced grazing pressure. The heather, bilberry and bog myrtle rising in a complex tangle, precisely marking the fenced boundaries of each site.

As the days progressed and we moved deeper into the heatwave, the unexpected warmth brought a euphoria to the everyday tasks of fieldwork, as we revelled in the simultaneous eruption of life around us. Stepping through the grassland, frogs would leap from our path, as dragonflies flickered past with clattering wings and bees thronged to the exuberantly flowering patches of bird's foot trefoil. The floodplain meadow surrounding the bothy, and at the river and loch shores, was not part of our surveys, instead offering a source of delight at the start and end of our commute. Combinations of wildflowers that I associate with the carefully managed and fragile meadows that are rare gems in lowland Britain lifted my heart. Fields of orchids, yellow rattle, eyebrights, bird's foot trefoil, red clover and a diversity of fine grasses.

The quadrats that we put down in each plot provided a focus for our surveys. But more sparsely distributed in the reforested sites were plants hinting at the past presence of woodlands in these locations: bluebells and wood cranesbill making an auspicious appearance in the westmost site. In the quadrats

themselves we found common cow-wheat, cowberry, bilberry, heath bedstraw, chickweed wintergreen and one cluster of intermediate wintergreen.



The heatwave brought us closer to the streams and rivers in the glen. The River Affric was our constant companion, a place to refresh and refocus at the end of the day, and our source of drinking water. Even becoming the object of our fantasies as we scrambled up and down the hillsides in 30°C heat. Despite this, it took some courage to enter the ice-cold water: we developed a trick of crouching in the shallows, before slithering incrementally down the slope of smooth pebbles to stand immersed on the peat riverbed. Gasping at the cold before gradually being released to the felt-like feel of the peat beneath our feet, the whisper of shoals of fish at our ankles and the tug of the water around our chests. And what a world to unlock: diving below the surface and detaching from the warm buzz of the sunlit landscape above, becoming isolated in the throb and rattle of the flowing water. Revealing to us perfect translucent vistas, tinged sepia by the peat, of tumbled stones, shelved banks and shoals of speckled fish sweeping past. For me these moments in the river perfectly captured the tranquillity and bliss that Glen Affric provided.

Two weeks of plant surveys later and part of me wondered if my quadrats perhaps provided an unfair constriction on the bursting life in the glen. But I am, and am learning to be, a scientist, applying objective methods to a landscape that up to now I had best understood by the influence it has on my mood and senses. The rush and breath of gazing at acres of regenerating trees, the simple elation of passing a canon of rowan trees, unbrowsed and proudly displaying their frothing white umbels, the joy of a stonechat clacking from the top of a young birch. But equally, my elating eye as I walk through a

regenerating enclosure is drawn to the successes that I hope and desire to see, so in many ways the more impartial focus of the quadrats is what I need. A key allowing me to explore the changes in plant communities with reforestation and the species that may be gained or lost.



Diary entry 4 – published 21st January 2020

https://www.littletoller.co.uk/the-clearing/seeking-the-trees-a-rewilding-diary-by-emily-warner/

Absent from this story so far, but their impact ever present in the forest and character of the landscape, are the deer. The fences exclude them from the regenerating forest, but more widely it is clear that they are abundant. The deer took on an almost mythical aura during the summer, we saw little of them, but their marks and impact provided a clue to their number. Then one evening, emerging from the bothy, we were confronted by a herd. Their heads turned towards us and we attempted to count the pairs of ears, pricked above wary and curious faces. We stopped when we got to fifty, struggling to pick apart each shadowy individual, until suddenly our threat became too much, and with a gathering trot they moved up the glen.

Of course, the deer and the trees are inextricably linked, the deer are the engineers of the forest, they hold the key to its destiny, yet themselves rely upon it: a delicate balance. Much as we humans have played a role in the landscape, erecting fences and planting trees in the present, clearing forest and farming land as we go deeper into the past, the deer also influence the trajectory of their habitat. Unconscious of their future, the deer rip and tear at the young saplings, gorging on the protein rich food source in the understorey of the forest. The forest is a key resource for a species that is a woodland animal, providing shelter during the harsh Scottish winters and a nutritious food source in the understorey shrubs and regenerating trees. The grazed hillsides that are almost

ubiquitous throughout the Scottish Highlands emphasise the deer's effectiveness at preventing natural forest regeneration.



To document the extent of the deer's impacts we conducted seedling surveys across the survey plots, comparing the grazed treeless heathland to the regenerating ungrazed forest, and comparing that to grazed and ungrazed areas of mature forest. Counting the seedlings within the boundaries of each plot was an absorbing task. Our search was meticulous, and hopefully exhaustive, but challenged by boulders, leggy heather, dense bracken and sprawling willows. Two things were marked: seedlings occur much less frequently in the grazed treeless areas and when they do occur outside the fence, they are maintained in a bonsai state by constant grazing. Hidden below the shrub layer are tiny stunted seedlings that have been grazed back repeatedly by deer, the evidence of repeated false starts described in their contorted form. In the grazed treeless plots not a single seedling taller than the protective ground layer of shrubs was found.

It became clear that the combination of the presence of trees and absence of grazing has a complex effect on the development of the next generation of trees, influencing both the species present and their potential to grow. In the mature forest plots, rowan seedlings were more prevalent than in any of the other plots we sampled. Hinting at the birds that must perch amongst the branches of the mature trees, releasing the rowan seeds in their droppings. As a result, even in the grazed plots, rowan seedlings were surprisingly abundant. Despite this, the effects of grazing were striking: of the 360 rowan seedlings that were found across the grazed mature forest plots only two had reached a height of more than 0.5 m. Rowan is one of the most palatable Caledonian forest species, and

where the deer have access to it they selectively remove it from the forest. In contrast, the ungrazed mature forest plots also harboured abundant rowan seedlings, but covering a healthy spectrum of heights from less than 0.5 m to taller than 1.5 m.

The relationship between the future of the forest in this landscape and the future of the deer is complicated further by a third dimension: people. For many, the bare and treeless hillsides of the Scottish Highlands represent an important cultural landscape, one maintained and managed for the sport of deer stalking. To a certain extent, the numbers of deer present in the landscape reflect the will of large sporting estates, which generate an income based around stalking deer. However, in a landscape with no natural predators and with the human desire to maintain the recreational opportunities that large deer populations provide, the deer population is booming. Growing numbers of deer act in direct opposition to the regeneration of the forest, and overall this scenario also compromises the health of the deer populations. The increasing population of deer has occurred in parallel with a decline in the condition of the animals, living in a landscape without the forest habitat that should support them.



The fences provide an impermanent solution to the deer problem. The smaller roe deer can often squeeze under or around the gates, plundering the young trees inside the enclosure. Whilst the fences themselves are subject to the unrelenting Scottish winters, and require constant checking and maintenance to ensure they continue to act as a defence against deer. In one enclosure, a 10 m strip of fencing had been crushed by a small landslide. Inside, the marks of the deer were everywhere. Paths had been worn through the undergrowth, and areas of trees that had been used for shelter were stripped of their bark. The

tastes of the deer were also clear: the palatable rowan trees had suffered particularly, and we encountered many torn and snapped saplings.

The deer are a direct barrier to forest restoration: they clearly prevent the regeneration of the forest and alter the composition of the tree community that does manage to regenerate. However, they do have a role to play in the ecosystem, and in lower numbers the level of disturbance that they would create could actually be positive. Add to this the conflicting human investment in different deer levels and you have a seemingly intractable problem. The fences are a way of allowing trees to regenerate and a diverse seedling community to grow up, but in the longer term we must aim for a more sustainable solution and a naturally regulated ecosystem where clumsy human interventions are no longer needed.



Diary conclusion – published 30th November 2020

https://www.littletoller.co.uk/the-clearing/a-rewilding-diary-by-emily-warner-4/

Over the last two years, I have been carrying out scientific research in regenerating native forest in the Scottish Highlands. This has been an experience that has mixed the spiritual and personal with the objective and universal. The scientific questions that I am pursuing are extremely relevant to the exploding interest in tree planting in the UK, and I hope will play a small role in sculpting the policy decisions surrounding this. My research also attempts to increase our ecological understanding of an ecosystem set within a web of complex cultural and social interactions in Scotland. But equally, gathering data in such a place, living in sublime balance, has been a privilege and a delight, a rare chance to step out of normal life and retune to the frequency of nature.

In the summers of 2018 and 2019 I spent time in Glen Affric and Glen Moriston, transplanted from periods of planning, data analysis and writing to the intensity of data collection. These fragments of time mirror the glimpses of enlightenment that my results give to our understanding of native forest expansion. Using methodical comparison, between the reforested areas, unforested prior state and mature Caledonian Pineforest, it is possible to see patterns emerging. As I begin the process of transforming my results into scientific papers, I return again and again in my mind to the rhythm of my summers and the time that I spent in the relative wild.

As a scientist I am called upon to present my research in the most objective light. But the experience of conducting research is so much more than that. It provides the chance to live with simplicity in proximity to nature, disconnected from the rest of the world and yet wholly aligned with the ecosystem that surrounds you. The methodical precision of data collection draws your entire focus to specific parts of the landscape. Entwining mindfulness with the discipline of science, to reach a state of complete immersion. Sitting in total concentration for 15 minutes at a time, listening and watching for each bird that visits a plot. Crouching over a quadrat, meticulously identifying each plant species that is present. Searching the understorey, recording every tree seedling. Repeating these ritualistic processes again and again, in different sites and habitats. Comparing mature forest to young forest, the young forest to the unforested landscape. The days of work build into weeks, and those into months, until finally you are rewarded with an accumulated set of data containing thousands of observations. Somehow the process and the purpose inform each other, the tranquil calm of repeated actions perfectly complimented by the overall aims of the research. The physical days of fieldwork transition to the analysis of data and identification of patterns and trends, which will eventually be woven into the narrative of a scientific paper. From there, that information enters the world, where each tiny fragment has the potential to shift norms and shape perceptions, altering our idea of how we should interact with the landscape in the future.

The backdrop to the repetition of everyday tasks was the ephemeral and shifting mood of the landscape, played out in an endless sequence of unique combinations of light and weather. For stretches of time days were demarcated only by their marginally differing depths of mist and weights of drizzle. Interspersed with evenings of golden sunlight, imparting a stillness over everything, or mornings where gathered mist would rise with the first rays of the sun to reveal the frosted tops of the mountains. There were days when rain poured down and the mountainside streams roared across the paths. Days where sites were inaccessible, out of reach beyond a deepened river. On some days we staggered across the landscape, plunging a leg hip deep into a bog, lurching over tussocks or crashing to our knees in a rocky streambed. On others we covered ground in bounds, springing off thick beds of heather and moss, propelling ourselves uphill from tree trunk to tree trunk, forging through streams, the ice cold water a welcome relief to bare feet on a hot day. On all days, we never felt anything less than insignificant on the scale of the landscape, our

data collection trivial, the results received with indifference by a glen that has harboured nature and humanity for thousands of years.



I have sought science as a method to achieve a more objective understanding of the potential benefits of reforestation, or rewilding if you prefer, compared to the unforested state that dominates in the Scottish Highlands. Three years into my PhD, my expectations of the outcomes or answers to these questions have shifted. Science rarely provides complete and conclusive answers to questions. You pitch a question, seek to answer it, often refining and shifting your focus in the process, and frequently find that your results illuminate further recesses of the unknown. To say that my research has highlighted how much we don't know would be going too far, but as much as it provides new information, it emphasises important things that we don't know much about. Failure to acknowledge and explore these uncertainties will make predictions of the consequences of large-scale native reforestation in similar scenarios uncertain. The two main spheres that my work has addressed are the influence of native reforestation on biodiversity and on ecosystem functioning.

Firstly, given that the original motivation for planting areas of native forest in this part of the Scottish Highlands was to extend an existing ancient remnant of Caledonian Pineforest, how do the organisms living there respond to restoration? The Caledonian Pineforest is thought to cover just 1% of its former extent, but in Glen Affric a large remnant remains. This habitat supports a specific community, including rare lichens, invertebrates, birds and mammals. My work shows that in the reforested areas plant, bird and carabid beetle communities begin to transition towards those found in the mature forest habitat, moving away from the unforested community. This emphasises that

reforestation drives the formation of a forest community. However, the particularly rare and characteristic species that specialise on the mature forest do not yet seem to appear in the reforested areas. This forest represents future potential, and intuitively we would expect the more specialist species to take longer to recolonise. So, the adage that the best time to plant a tree was 20 years ago holds. We create forests now, to become the forests of the future.



The second key finding relates to carbon storage, adding further evidence to our emerging understanding of the carbon balance with upland reforestation. My research shows that the soil carbon in the reforested sites is much lower than in the unforested and mature forest areas. This suggests that the process of tree planting may have led to a release of carbon from the soil, of a magnitude far greater than the carbon captured during tree growth, even after thirty years. During the short time that I have been working on my PhD, the interest in reforestation as a solution to climate change seems to have gathered pace exponentially. This ambition reflects the ability of trees to remove carbon from the atmosphere and store it in their biomass (trunk, branches, roots, leaves). Helping to erase some of the huge debt of carbon dioxide that has accumulated in the atmosphere. But this is not the whole picture, trees are not planted on a blank canvas or inert substrate, they are being introduced into existing ecosystems, with geological, ecological and human histories. In the Scottish Highlands a huge store of soil carbon, our most important terrestrial carbon stock, lies below the surface. Even outside the particularly carbon rich areas of peat bog, there can be high levels of carbon in the very organic soils. It is thought that tree planting alters the soil environment, aerating it and stimulating the microbial and fungal communities, which start to break down the carbon in the soil. In locations with carbon rich soils, tree planting could alter a delicate balance, stimulating the release of carbon that has been locked up for centuries.

As the trees grow relatively slowly, they will take decades to centuries to compensate for this loss. At the sites I have studied, even in the oldest areas of reforestation, the accumulated tree biomass is still much smaller than the amount of carbon that appears to have been lost from the soil.

This presents a conundrum: unintuitively and inadvertently tree planting in some locations could release carbon. Simultaneously as I have reached these results, experimental work and modelling similarly show soil carbon loss after reforestation in equivalent areas of high soil carbon. The interpretation is however complex. We tend to think of carbon targets on decadal timescales, with relation to our ambitions for net zero, and reforestation with these methods and in these contexts does not seem to be a potential contributor. However, on much longer timescales these forests might begin to tip the balance, reaccumulating the carbon that they have lost.

Additionally, one of the key themes of the reforestation debate in the Scottish Highlands is the influence of grazing. Reduced pressure from deer would see the spontaneous heterogeneous establishment of native woodland, mixed with less forested habitat across a wide area. My feeling is that, under natural regeneration, the trees would establish more effectively in the lower carbon soils, whilst the wetter and more carbon rich areas might remain treeless. The risk of releasing large amounts of carbon from the soil seems likely to be reduced, soil disturbance will be avoided and the clumsy human judgement of where trees are appropriate is removed. Reduced grazing would also benefit the existing forest, stimulating regeneration to maintain the carbon stored in this habitat, and areas of peat bog, which have also been degraded by overgrazing. So other carbon-rich habitats would benefit from lower deer grazing. This is an area that still needs unpicking, we have very little information on large scale natural regeneration and lack monitoring data over the longer term. In a country where high grazing pressure in the uplands prevents natural regeneration and maintains the treeless state this is hardly surprising.



With both the carbon and biodiversity questions we need to think beyond the small scale and consider a wider landscape. Diversity begets diversity, and different habitats, both forested and unforested existing alongside each other would likely lead to the overall richest habitats for wildlife and potentially help to optimise carbon sequestration. Additionally, we should not be making judgements on one metric alone, the high value of these future forests for biodiversity might outweigh the carbon sequestration priority. What is crucial is that we are accurate in our understanding of what the reforestation brings and don't assume that every forest expansion project equates with carbon storage.

My time conducting fieldwork has also had many human influences. The players in the social and cultural stories that are the context within which the landscape is set, but also personal relationships and bonds forged with like-minded people. On many days Glen Affric seemed to bustle with walkers, both groups and individuals, following the Affric-Kintail way or circumnavigating Loch Affric. Often, we had stepped sideways from the well-trodden path, and unobserved from the valley-side could chart the progress of other visitors to the glen. Occasionally we would cross paths, quadrats and bamboo canes drawing curious questions. My work in Glen Affric has also been a tale of collaboration: friends, field-assistants and family giving themselves wholly to my fieldwork for chunks of time; input from staff and volunteers at Trees for Life; the pick-me-up of a hot shower and fresh scones with Hanne at the youth hostel. The reforestation in the glen is also the result of much larger collaboration, driven forward by Trees for Life, Forestry and Land Scotland, and the National Trust over the last 30 years, the work of dedicated staff and countless volunteers who have felt compelled to do something to restore a dying ecosystem.

Even a year on from my last visit to Glen Affric I still catch a scent of heather and air and rock when I open my rucksack, an intangible essence of what it was to work in such an environment. It carries me straight to the view down the narrowing valley of the River Affric, Loch Affric at my back, and mist drifting across the gullies and slopes of the unfolding mountains. It reminds me of so many moments during fieldwork. An eagle gliding to meet us as we stepped out from the canopy of ancient pines on the shore of Loch Affric, the early morning sunshine burnishing the feathers on its back as it gyred upwards over the water. The gradual progression of the season marked in the unfurling and then fading of rowan flowers, followed by the appearance of bright red berries. The lifting of hours of drizzle to reveal brightness across the base of a deep mass of clouds.



My research has given me a chance to learn more about a landscape that I love, and to address questions that may help to drive decisions about its future. But it has been so much more than that. I have had a chance to be within something, observing and documenting, happy to better understand even a fraction of the perhaps unknowable whole. Human nature craves certainty, we seek simple messages and answers to our problems. The natural world is the opposite of that, it is inherently diverse, complex and contradictory. We can record emergent patterns, create experiments to answer specific questions and model expected future trajectories. But ultimately, in the real-world, things won't always happen as we expect, our understanding is crude. We yearn for simplicity, but nature is complex, and if we want to construct any kind of narrative for our future, we must begin by embracing that.

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