Measuring Biodiversity for Future Forests

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Declaration

I declare that this thesis has not been submitted as an exercise for a degree at this or any other university and is entirely my own work except where duly indicated and clearly acknowledged in the text.

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Kate Harrington

When we try to pick out anything by itself, we find it hitched to everything else in the universe.

My First Summer in the Sierra, John Muir

Summary

There are a growing number of policies and incentives in Ireland which are aimed at planting new forests to help meet national and international climate and biodiversity goals. While expanding woodland and forest areas is generally viewed positively across political and public spheres, there are important trade-offs to consider, particularly in relation to existing land uses and livelihoods, and the specific ecosystem services that we want these forests to deliver. Since different forests provide different ecosystem services, achieving afforestation goals requires carefully balancing priorities to establish forests that deliver a wide range of benefits for both people and nature, including timber production, climate regulation, and habitat restoration. As biodiversity underpins the benefits forests provide, its measurement has become a shared priority among scientists, policymakers, and investors, providing the evidence needed to track restoration success. In this thesis I use forest data derived from field studies, the Irish National Forest Inventory (NFI), and expert knowledge, to critically examine how we measure forest biodiversity in different contexts.

Expanding native woodland cover by planting mixed native species is widely considered beneficial for both biodiversity and climate objectives. However, evidence remains limited on whether these sites, often established on former agricultural land, are on track for long-term success. In newly established woodlands, traditional vegetative indicator metrics may offer insights into whether sites are progressing toward desired habitat types, however such early-stage habitats may also possess ecological value that these metrics fail to capture. Through the study of a chronosequence of woodland sites, I demonstrate the shift from non-woodland to woodland plant communities as sites progress toward canopy closure, with a high proportion of older plots achieving their target woodland habitat. I also find increased colonisation of trees, primarily by hedgerow species, and through incorporating plant trait data and landscape metrics into my analyses, reveal how site and landscape factors affect species assembly, suggesting woodland species may be favoured in low fertility contexts where sessile oak is more frequently planted. This research provides new insights into floral biodiversity changes in planted native woodlands, offering findings relevant to the monitoring and management of such plantations, as well as to broader land-use planning.

Increasingly, faunal metrics are being incorporated into a broader suite of measures to demonstrate positive biodiversity change. While most forest monitoring approaches focus on floral or structural metrics, fewer studies have looked at insect responses to developing woodland plantations, and their potential use as a monitoring group. Examining bee and hoverfly communities along a subset of sites associated with the above-referenced chronosequence, I find that the transition toward woodland specialists is less pronounced than for flora, yet compositional shifts are still detectable when beta-diversity metrics are applied. My findings suggest that the bee community may provide a more sensitive and stable metric for assessing woodland development. This research also highlighted the importance of woodland edges as key foraging resources for pollinators. The findings demonstrate how pollinator data can offer multiple insights depending on the metrics

applied. These metrics, whether used for ecosystem service assessment or conservation policy, could help set interim targets for tracking afforestation progress. This study emphasises the challenges of monitoring transitional habitats and the importance of selecting appropriate sampling methods, target taxa, and biodiversity metrics.

Expanding from a regional to a national scale, I analysed the NFI dataset, using a two-step modelling process, with two aims: first, to investigate the factors influencing floral biodiversity across the Irish forest estate, an area not previously explored using this rich resource, and second, to determine which commonly used proxies for biodiversity best align with direct measures. The findings highlight the structural or categorical metrics that may be of most use in reflecting floral biodiversity, with evidence that the number of tree species, deadwood logs, semi-natural establishment, bryophyte cover, and uneven aged forests are linked to higher overall floral diversity, or that of woodland species. My findings also support the use of floral diversity data from the NFI as a direct compositional biodiversity indicator, encoding both site and landscape influences, that can be derived from the current inventory with no additional survey effort and minimal data processing. I suggest that the identified indirect indicators, direct measurements of floral diversity, or a combination thereof, could inform the selection of metrics for reporting requirements under the Nature Restoration Regulation, devising condition criteria for ecosystem service accounts, or monitoring forest biodiversity in the context of offsetting proposals or sustainable forest management. My study shows how the NFI data can be harnessed to both provide more information on biodiversity across the forest estate, and help identify indicators of forest biodiversity for a wide range of potential uses.

Finally, I examined the limitations of NFI data for determining the biodiversity value of future planting scenarios and addressed knowledge gaps by drawing on expert knowledge. Using the Delphi technique, I surveyed a panel of ecologists and foresters, asking them to score the biodiversity value of three potential future planting scenarios across the production forest life cycle. The scores reflected the influence of light availability and stand structure changes associated with canopy closure and thinning. Unexpectedly, the two professional groups were closely aligned in their assessments, with only minor differences. Employing expert elicitation methods alongside available evidence allows us to harness the breadth of existing knowledge, facilitate integration with ecosystem service models, and can meaningfully contribute to quantifying the nature-related impacts of future afforestation policies.

This thesis advances our understanding of what constitutes successful native woodland establishment, identifies the components of biodiversity we should be measuring to meaningfully track biodiversity change, and outlines appropriate metrics and monitoring approaches for different conservation and policy contexts.

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List of main contributors to each chapter

Chapter	Name	Contributions
1	Kate Harrington	Concept, Structure, Writing
	Jane Stout	Comments on draft chapter
	Fraser Mitchell	Comments on draft chapter
2	Kate Harrington	Concept, Study Design, Field site selection, Field work and data collection, Statistical analysis, Results interpretation, Writing
	Jane Stout	Concept, Study Design, Comments on draft chapter
	Fraser Mitchell	Concept, Study Design, Field work assistance, Comments on draft chapter
	Hannah Devine	Field work assistance and data-entry assistance
	Eleni Kolinziki	Field work assistance and preliminary GIS analysis
3	Kate Harrington	Concept, Study Design, Field site selection, Field work and data collection, Statistical analysis, Results interpretation, Writing
	Jane Stout	Concept, Study Design, Comments on draft chapter
	Fraser Mitchell	Concept, Comments on draft chapter
	Owen Beckett	Identification verification for bee and hoverfly specimens
4	Kate Harrington	Concept, Study Design, Data acquisition, Statistical analysis, Results interpretation, Writing
	Jane Stout	Concept, Comments on draft chapter
	Fraser Mitchell	Concept, Comments on draft chapter
5	Kate Harrington	Concept, Study Design, Data collection, Statistical analysis, Results interpretation, Writing
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	Mary Ryan	Concept, Study Design, Comments on draft chapter
	Martha O'Hagan Luff	Concept, Study Design
	George Smith	Review of survey instructions
6	Kate Harrington	Concept, Structure, Writing
	Jane Stout	Comments on draft chapter
	Fraser Mitchell	Comments on draft chapter

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CHAPTER 1

General Introduction

1 General Introduction

The climate and biodiversity crises have brought increasing attention to afforestation in recent years prompting ambitious global targets and initiatives to cease deforestation and increase tree cover such as the Paris Agreement, Aichi targets, Sustainable Development Goals, Bonn challenge, Global Partnership on Forest and Landscape Restoration, Reducing Emissions from Deforestation and Forest Degradation (REDD+) mechanism, and the New York Declaration on Forests (Kleinschmit et al., 2024). Afforestation is seen as an important strategy for climate change mitigation, whilst also providing for timber production and a range of other ecosystem services (Bastin et al., 2019; Gamfeldt et al., 2013; García et al., 2020), however it is essential that the number of trees is not seen as the end goal (Brancalion & Holl, 2020) and that we create resilient and biodiverse forests.

Afforestation has become a key component of the European Union's (EU) climate, biodiversity, and land-use agenda, under the overarching policy framework of the European Green Deal (European Commission, 2019a). The EU Biodiversity Strategy (European Commission, 2020a), Forest Strategy (European Commission, 2021a) and Farm to Fork Strategy (European Commission, 2020b) all support objectives to mitigate climate change, halt biodiversity loss, and promote sustainable forestry and agriculture. As part of these efforts, the EU has pledged to plant at least three billion additional trees by 2030, an ambitious target that must be met amid competing land-use pressures from agriculture, housing, and energy.

In order to achieve these objectives, the EU's Forest Strategy provides nation states with a framework for creating, protecting and restoring forests. It sets out high level policies and objectives for sustainable forest management, enhancing forest biodiversity, and combatting climate change. Following the EU-level strategic objectives, forest policy in Ireland is guided by the Forest Strategy 2023-2030 (DAFM, 2024a), with goals focused on climate action, biodiversity, sustainable timber supply, community and wellbeing, and resilience and adaptation. Stemming from the strategy, the current forestry programme (2023-2027) aims to implement these goals, specifying a range of afforestation grants, with a strong emphasis on native woodland establishment and environmental protection, and support for agroforestry and continuous cover forestry (DAFM, 2024b). Despite attractive financial incentives, afforestation targets have not been met in recent years, a cause of concern in the context of climate goals, as current rates of tree planting cannot offset increasing sources of carbon emissions from ongoing harvesting and forestry on organic soils (EPA, 2025).

Aligning with and supporting the EU and Ireland's forestry, biodiversity and climate ambitions, Ireland is also developing a Nature Restoration Plan in order to implement the EU Nature Restoration Regulation (European Commission, 2025). This regulation is aimed at restoring at least

20% of EU's land and sea areas by 2030, in part by restoring native woodland and facilitating climate mitigation through increased tree cover.

Since different forests provide varying ecosystem services, many of which are positively linked to biodiversity (Balvanera et al., 2014; Gamfeldt et al., 2013; Paquette & Messier, 2011), achieving these afforestation goals requires carefully balancing priorities to establish forests that deliver a wide range of benefits for both people and nature, including timber production, climate regulation, and habitat restoration. As biodiversity underpins these benefits, its measurement has become a shared priority among scientists, policymakers, and investors, providing the evidence needed to track restoration success. Decisions about where to plant trees, and what types of forests to establish, depend on diverse data sources, including data on the relative biodiversity value of different types of forest habitats. This data can then be used by policy makers or forest managers, and potentially integrated into agri-environmental schemes, ecosystem accounting frameworks or novel decision tools. Innovative nature finance mechanisms are increasingly being explored to access funding for afforestation projects. These include public incentives such as payments for ecosystem services (PES) and the development of finance models that attract private sector investment in forest-based solutions, again demanding robust biodiversity data.

With strong drivers to expand the forest estate in ways that deliver benefits for nature, people, and the wider environment, it is important to assess whether current approaches are meeting their objectives. Furthermore, the need to manage forests sustainably amid increasing climate-change related volatility, and the level of monitoring required to track progress and support informed decision-making, demands a robust evidence base. This evidence must be fit for purpose and relevant to conditions in Ireland. This thesis identifies and addresses key knowledge gaps and explores the challenges involved in valuing biodiversity in a forestry setting.

I do not formally distinguish between the terms *woodland* and *forest*, as they are often used interchangeably in the literature. In this work, a *metric* refers to a quantifiable measure of biodiversity, while an *indicator* denotes a metric that can be interpreted in the context of a specific objective, such as assessing condition or tracking biodiversity change.

1.1 Forests in Ireland

Forest trees began recolonising Ireland approximately 10,000 years ago and are estimated to have once covered much of Ireland's landscape (Mitchell, 2006). Long-term palaeoecological and historical studies indicate that a gradual decline in woodland cover, beginning with early agricultural clearance and continuing through the Bronze Age, Iron Age, and early medieval periods, continued up to the fifteenth century (McCracken, 1971). Deforestation in Ireland accelerated from the fifteenth century driven by expanding agriculture, colonial land use changes, and growing timber demand, resulting in just 1% forest cover remaining at the beginning of the

twentieth century (McCracken, 1971). State afforestation was relatively low up until the 1950's, but thereafter increased up to the year 2000 (DAFM, 2023a), while private afforestation started developing in the mid-1980's. The area of forest in Ireland currently covers 11.6% of total land area, comprising 69.4% conifers and 30.6% broadleaves (DAFM, 2023a). The Irish Government aims to increase forest cover to 18% by 2050 (DAFM, 2024a), though planting rates have continued to decline in recent years (CSO, 2024), suggesting this target may be difficult to achieve. In terms of ownership, 49.1% of forests are in public ownership (mainly managed by the state forestry company Coillte), with 35.7% in grand-aided private ownership, and the remainder in non-grant-aided private ownership. Non-grant aided private forests tend to be older, with grant-aided private forest predominately less than 30 years old reflecting increased afforestation rates in this category arising from government policies. The average size of private grant-aided parcels of land afforested between 1980 and 2022 was 8.6 ha (DAFM, 2023a) indicating many of these forests are quite small relative to the older public-owned forests, typically planted on larger areas of unenclosed marginal lands. While Sitka spruce (*Picea sitchensis*) dominates the existing forest estate, and conifers accounted for 72% of afforestation between 2002 and 2022, broadleaf afforestation increased to 42% in 2022, and there has been a steady increase in area of new native woodlands established in recent years. Reforestation is also ongoing, particularly as the early spruce plantations have been felled. Forest owners are legally required to replant land after felling (or if trees are lost due to disease, fire or windthrow) under the 2014 Forestry Act, with this being one of the reasons frequently cited for the low uptake of the afforestation scheme by farmers.

1.2 Irish Native Woodlands

Only around 2% of the country is covered by native or semi-natural woodland, that is, woodland dominated by native tree species. Native woodland in Ireland can be subdivided into groups depending on age (Cross & Collins, 2017) as follows:

- Possible ancient woodland – stands that have been continuously wooded since 1660, even if subsequently disturbed or re-planted;
- Long established woodlands – stands that have been continuously wooded since the 1st edition OS maps of 1830/1840s but for which there is no evidence they had been wooded for longer, or for which there is evidence that the wood is not ancient;
- Recent woodland – woodland likely to have originated since the 1st edition OS maps; and
- New woodland - comprises broadleaf plantations dominated by native species and created in the last 20 years or so through the afforestation of farmlands, typically with support under various forestry programmes. These include sites afforested under the Native Woodland Establishment Scheme since its launch in 2001.

In general Ireland's native woodlands are highly fragmented in the landscape, have nearly all been subject to past silvicultural management or other human-mediated disturbances, and are frequently

altered by naturalised non-native species such as beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*), or invasive non-natives such as *Rhododendron ponticum* and *Prunus laurocerasus* (Perrin et al., 2008). While older studies focused on phytosociological classification and surveys of specific sites (Cross, 1998; Kelly, 2005; Kelly & Iremonger, 1997; Kelly & Kirby, 1982; Mitchell, 1990), in more recent decades national surveys have helped document the location, extent and condition of existing native woodlands (Daly et al., 2023; O'Neill & Barron, 2013; Perrin et al., 2008; Perrin & Daly, 2010). Of 1320 sites surveyed in the National Survey of Native Woodlands (Perrin et al., 2008), the majority of sites were less than 6ha despite larger woodlands being prioritised for survey.

Native woodlands in Ireland belong to a number of phytosociological categories, principally acidophilous oak woods (Blechno-Quercetum petrae) dominated by sessile oak (*Quercus petraea*) and ash-elm hazel woodland (Corylo-Fraxinetum) on more fertile soils (Braun-Blanquet & Tüxen, 1952; White & Doyle, 1982). The classification scheme of Fossitt (2000), developed based on these previous phytosociological approaches, is commonly used in habitat surveys to classify woodlands in Ireland. Fossitt (2000) describes seven native woodland categories and two modified non-native woodland categories. More refined classifications centred around the Fossitt categories were developed by Kelly (2005) and Cross (2006), and updated following the National Survey of Native Woodlands (Perrin et al., 2008) with some subsequent additions (Cross & Collins, 2017).

Many of our fragmented native woodlands also meet the requirements to be classed as Annex I habitat under the Habitats Directive (Council of the European Communities, 1992), with the best examples of these designated as part of Special Areas of Conservation (SAC's). Four Annex I woodland habitat types occur in Ireland (* indicates priority habitat):

- 91A0 Old sessile oak woods with *Ilex* and *Blechnum* in the British Isles
- 91D0 Bog woodland *
- 91E0 Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-padion, Alnion incanae, Salicion albae) *
- 91J0 *Taxus baccata* woods of the British Isles *

In order to classify all Irish habitats to a greater level of detail than the broad Fossitt habitat categories, the Irish Vegetation Classification (IVC) System (Perrin et al., 2018) has recently been developed. The IVC development captured the data generated from national native woodland surveys, and comprises the most up-to-date evolution of woodland classification schemes in Ireland. The IVC scheme also identifies affinities with Fossitt, Annex I, phytosociological alliances and the British National Vegetation Classification (NVC) system (Rodwell, 1991) for woodland categories. The IVC scheme comprises 5 broad native woodland community groups. Within these groupings woodlands are classified according to their vegetation community,

reflective of soil conditions and drainage, resulting in 24 community types, with some communities further refined with sub community types. The 5 broad groups are as follows:

- WL1 *Quercus petraea – Luzula sylvatica* group (aligned with Fossitt habitat WN1 and Annex I habitat 91A0)
- WL2 *Fraxinus excelsior – Hedera helix* group (aligned with Fossitt habitat WN3 and Annex I habitat 91J0)
- WL3 *Alnus glutinosa – Filipendula ulmaria* group (aligned Fossitt habitat WN4 and Annex I habitat 91E0)
- WL4 *Betula pubescens – Molinia caerulea* group (aligned with Fossitt habitat WN7 and Annex I habitat 91D0)
- WL5 *Picea sitchensis – Larix decidua* group

1.3 Native Woodland Afforestation

The Native Woodland Scheme was launched in 2001 to provide funding and technical support for the conservation of existing native woodlands (Native Woodland Conservation Scheme (NWCS)) and the creation of new native woodlands (Native Woodland Establishment Scheme (NWES)). The NWES has since been recategorised in the latest forestry programme (DAFM, 2024b) under four Forest Types (FT's):

- FT 1 – Native Forests;
- FT 2 – Forests for Water;
- FT 3 – Forest Creation on Public Lands; and
- FT 5 – Emergent Forest /Rewilding (enrichment planting in gaps).

Terminology has shifted to the use of 'forest' rather than 'woodland', and the NWCS is now referred to as the Native Forest Conservation Scheme. There is also a category linked to planting of native forests after clear-felling conifer stands associated with the Climate Resilience Scheme, and a Native tree Area (NTA) Scheme for small forests between 0.1 and 2ha in size, aligning with categories FT1 and FT2. Subject to certain criteria the NTA scheme does not require an afforestation license.

The Native Forest Framework (NFF) has been developed in order for a forester to determine the most appropriate native woodland type to prescribe based on soil, type, location and existing vegetation. An ecologist involvement is required for applications associated with the Native Forest Conservation Scheme (DAFM, 2024b) and in the case where environmental sensitivities are identified by the forester or DAFM e.g. High Nature Value farmland or the requirement for a Natura Impact Statement (DAFM, 2024b). Foresters and ecologists involved must have completed a Native Forest Scheme training course. The site must be capable of supporting vigorous growth and long term development of the chosen woodland type without the use of fertiliser and be at least

0.1ha in size. Sites over 10ha are required to allow for 'Areas for Biodiversity Enhancement' which can include setbacks from roads, aquatic zone buffers, open space and hedgerow, up to 15% of the total area (DAFM, 2024b). There are detailed guidelines around plant material, planting techniques, and protection from fire and grazing (DAFM, 2023b). The native woodland establishment scenarios with corresponding soil types and native woodland types are as follows:

- Scenario 1: Podzols / Oak-Birch-Holly Forest
- Scenario 2: Brown Podzolics / Oak-Birch-Holly with Hazel Forest
- Scenario 3: Brown Earths / Oak-Ash-Hazel Forest
- Scenario 4: Gleys / Alder-Oak-Ash Forest
- Scenario 5: Highly Modified Peat & Peaty Podzols /Pioneer Birch Woodland
- Scenario 6: Alluvial Floodplains/Alluvial Forest (FT 2)

At a high level, Scenarios 1 and 2 are targeting sessile oak forest habitats (Fossitt category WN1 and IVC category WL1), Scenario 3 is targeting pedunculate oak/ash woodlands (Fossitt category WN2 and IVC category WL2), Scenarios 4 and 6 are targeting wet woodlands (Fossitt categories WN4/5/6 and IVC category WL3), while Scenario 5 is targeting birch woodlands (Fossitt categories WN1/WN7 and IVC category WL4). In the case of Scenarios 3 and 4, alternatives to ash are now required due to ash dieback disease (Broome et al., 2019).

There is growing interest in irregular silviculture, also known as Close-to-Nature Forest Management, which promotes the use of complementary species and natural regeneration, mimicking natural succession in order to develop an irregular forest structure with greater ecological resilience (Spazzi et al., 2019). Sites planted under NFF may be suitable for growing timber and other wood products on an ongoing long-term basis using Continuous Cover Forestry (CCF) based on shelterwood, selection/thinning and coppicing systems that are consistent with natural woodland processes. Category FT5 is specifically aimed at implementing CCF in early stage naturally arising forests to support the establishment of 'rewilded' forest habitat

1.4 Measuring woodland biodiversity

Depending on the context, we may seek to understand and measure intrinsic, instrumental or relational values of nature (IPBES, 2019; Pascual et al., 2017). Intrinsic values, independent of any benefit to humans, recognise the values of nature and need for conservation regardless of their utility. Instrumental values are linked to the benefits nature provides to humans, e.g. flood protection, crop pollination. Relational values are linked to human-nature relations that are rooted in cultural identity, spiritual fulfilment and belonging. These values can be integrated to help understand 'Nature's Contribution to People', an evolution of the ecosystem services concept that embraces concepts associated with other worldviews on human-nature relations and knowledge systems (Pascual et al., 2023).

Understanding these values requires measuring attributes of biodiversity directly or indirectly. In a broad sense, biodiversity encompasses the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system (Díaz et al., 2006). Consequently the range of potential measurable attributes is extensive, and depending on the context may not sufficiently capture ecological change across space and time to serve as reliable indicators (Hill et al., 2016).

Based on biotic and abiotic characteristics, commonly used biodiversity metrics focus on structural, functional or compositional attributes of ecosystems, habitats, communities, or species (Noss, 1990), as well as measures of extent, connectivity and diversity at a landscape level (Bellamy et al., 2024). Some, or all, of these attributes may then be used as indicators to describe the ecological quality, condition, or 'potential' of the component of biodiversity under consideration. When interpreted collectively and in relation to a reference or natural state, these metrics can also serve as proxies for assessing ecological integrity - the extent to which an ecosystem retains its structure, functioning, and resilience over time (Parrish et al., 2003). Many condition metrics, such as those assessing habitat quality, species abundance, or ecosystem functioning, can then be integrated into conservation assessments, ecosystem service accounts, and pressure-response frameworks (Burgess et al., 2024; Pereira et al., 2013).

Surrogate measures, a subset of indicators often used when biodiversity data is lacking or challenging to acquire (Evans et al., 2017; Gao et al., 2015; Noss, 1999), potentially provide a short-cut in survey or monitoring programmes (Ferris & Humphrey, 1999). Typically, species-based or habitat-based surrogates are used, with their efficacy depending on their ability to describe the ecological needs of the target taxa or variable (Lindenmayer et al., 2014). Surrogates can be used as proxies for different ecosystem components such as ecological processes and functions, environmental conditions, and the abundance or diversity of particular groups of species (Lindenmayer et al., 2014). The selected surrogates are examined for correlative or causal relationships with patch, site or landscape level variables. For monitoring trends in forest conditions, Noss (1999) identifies that species that make good targets for use as surrogates or direct indicators are those that can be used to define different attributes that must be present in a landscape if it is to retain its biota e.g. area-limited species, resource-limited species, process-limited species, keystone species or narrow endemic species. Habitat-based surrogates are likely to be superior to species-based surrogates when the habitat requirements of a species are well known and there is measurable limiting resource that is part of those requirements e.g. old trees, deadwood, host plants for insects (Lindenmayer et al., 2014).

Indicators of forest and woodland condition have been developed for sustainable forest management (Forest Europe, 2015), biodiversity monitoring (Barsoum et al., 2025; Gao et al., 2015) and conservation status assessment (Cantarello & Newton, 2008; Daly et al., 2023), but inconsistent results have been achieved when attempting to find core indicators that work over

wide geographic ranges and for different use contexts. Not all studies of biodiversity indicators clearly identify the relationship between the indicator and their indicatum (i.e. the indicated aspect of biodiversity), and with the exception of deadwood, where correlations have been identified these have typically only been tested in one or few forest types (Gao et al., 2015). Structural indicators of habitats, such as heterogeneity and complexity, capture the complex of niches that enhance the diversity of associated plant, animal and microbial communities and can play a key role in the description of biodiversity in forests, with the advantage that they are easily discernible and can be undertaken rapidly and so are a valuable approach for biodiversity monitoring (Ferris & Humphrey, 1999; Jokela et al., 2018; Lindenmayer et al., 2014). In particular, the abundance of dead and dying wood is a key structural indicator for biodiversity in forest ecosystems, particularly when a range of deadwood is present (Ferris & Humphrey, 1999; Lindenmayer et al., 2014).

The vegetation communities of different mature native woodland communities and their indicator species have been well-described, and those of conservation value could be seen as the ultimate restoration target or reference condition from a botanical biodiversity perspective. However, new native woodlands may be established in various ways and subject to varying management measures and pressures. Coupled with the structural changes that occur within establishing woodland as it ages, high variability in the plant and animal communities can be expected across the forest life cycle.

1.5 Factors influencing the development of biodiversity in new woodlands

Much of this thesis considers the biodiversity value of young or immature woodlands and changes across the woodland development cycle. A new woodland goes through a series of successional or developmental stages before reaching maturity with the interplay of structure and light driving most change (Ferris & Humphrey, 1999; Guo, 2003; Kirby et al., 2005; Paquette & Messier, 2011). There are four general stages of stand development; stand initiation, stem exclusion, understory re-initiation, and old growth. Considering the scenario of a naturally arising woodland, new seedlings will emerge either by regeneration from seed sources within the site, or colonisation (vegetative spread, or spread via wind, gravity or animal means) from outside sources, while in contrast in a planted woodland scenario, the forester will densely plant saplings. Either way, a dense stand of young saplings may develop. Shrubs such as gorse *Ulex europaeus* and bramble *Rubus fruticosus* agg. may also form dense growths during these early and intermediate stages (Poole et al., 2003). In an unmanaged situation, this is then followed by a stem exclusion phase where no new individuals appear, some of the existing ones die, and remaining species grow larger, while in a planted woodland thinning and tending will be carried out. As a natural woodland matures there will be an understory re-initiation phase as gaps appear in the canopy and natural regeneration of trees and shrubs becomes possible, while in a planted woodland, unless being managed under CCF

principles, gaps created by thinning are designed to facilitate growth of the retained trees. Natural old growth forests are typified by gap disturbance dynamics, with overstory trees that die in an irregular fashion, promoting understory trees to grow upwards into the gaps created. CCF principles seek to recreate this process.

As the woodland develops there is a transition from ground flora dominated by species characteristic of open habitats to communities containing species with a high affinity for woodlands, with species richness typically declining in intermediate stages and rising again as the floral community shifts (French et al., 2008; Smith et al., 2008). Changes in the understorey vegetation are driven primarily by changes in light availability (Kirby et al., 2017), which may be linked to the age of the woodland and/or variability in the canopy structure (Fahy & Gormally, 1998; Ferris, 1999), and can arise from structural changes that occur after thinning operations in managed forests (Smith et al., 2008). A range of other site and landscape level factors play a role in determining the floral diversity and composition of a woodland including proximity to older woodland (Brunet et al., 2012; Coote et al., 2013; French et al., 2008; Kirby et al., 2017; Poole et al., 2003; Verheyen, Honnay, et al., 2003), fragmentation of forest in the landscape (Brunet et al., 2012), grazing (Corney et al., 2006; Kirby et al., 2005), as well as site-specific soil, slope, and wetness attributes (Corney et al., 2006; Ferris, 1999; Storch et al., 2023). While semi-natural forests and native broadleaf managed forests have been found to support greater floral diversity than non-native conifer plantations (Coote et al., 2013; French et al., 2008; Irwin et al., 2014), there are exceptions depending on the choice of comparison (Brockerhoff et al., 2008; Quine & Humphrey, 2010).

Poorly dispersing woodland plant species may take a very long time to colonise slowly developing ecosystems such as forests in fragmented landscapes (De Frenne et al., 2011; Fuentes-Montemayor et al., 2015). Most colonising shade species arrive due to an effective dispersal mechanism, proximity of seed sources, or capacity to thrive in marginal habitats such as hedges (Broughton et al., 2021; García et al., 2016; Tiebel et al., 2020). Ancient woodlands differ greatly from younger forests in regard to their floristic composition (Ferris & Humphrey, 1999; Hermy et al., 1999; Schmidt et al., 2014; Verheyen, Honnay, et al., 2003) with plants generally shade tolerant and with lower dispersal capacity.

A variety of other taxa also respond to developing woodland, and to both local and landscape factors, potentially serving as indicators of woodland quality and condition. Lower plants have received some attention, particularly due to their association with old growth features (Brosnan & Ellis, 2020; Coote et al., 2007; Ferris et al., 2000; Humphrey et al., 2002) and functional roles in forest ecosystems (Crowther et al., 2012; Seibold et al., 2021), but present challenges in terms of sampling and taxonomy. Forest dwelling mammals and birds, often quantified as part of red-listed or specialist faunal indicators, are generally favoured by habitat heterogeneity and/or larger sites (Fitzgibbon, 1997; Fuentes-Montemayor et al., 2017, 2020; Irwin et al., 2014) together with

landscape level attributes (Fitzgibbon, 1997; Fuentes-Montemayor et al., 2017; Fuller et al., 2001; Hinsley et al., 1995; Vanhinsbergh et al., 2002). As for plants, bird community assemblages shift through the successional stages, with generalist species colonising early developing woodlands, followed by woodland specialists in more mature woodlands (Baguette et al., 1994; Whytock et al., 2018), however Ireland lacks the same diversity of forest specialists found elsewhere in Europe (Wilson et al., 2006) and many woodland specialists such as tawny owl, marsh tit and nuthatch (Fuller et al., 2001) do not occur here.

Invertebrate studies in mature forest systems have tended to focus on forest-associated arthropods, particularly saprophytic beetles, which are strongly influenced by stand structural features such as deadwood, more typical of semi-natural forests or old stands (Gao et al., 2015; Grove, 2002; Jokela et al., 2018; Stenbacka et al., 2010; Storch et al., 2023). Butterflies, bees and hoverflies may be favoured by younger sites and the extent of edges and openings (Gittings et al., 2006; Proesmans et al., 2019a; Sparks et al., 1996; Taki et al., 2013). Moths have been associated with structurally diverse forests (Fuentes-Montemayor et al., 2012; Merckx et al., 2012), and similarly features of structural diversity such as wet areas, edge habitats and clear-fell areas would appear to support diverse carabid beetle populations (Butterfield, 1995; Jokela et al., 2018; Spake et al., 2016). Bees and hoverflies are important pollinators, and the presence of forest patches at a landscape scale can support diverse flower visiting insect communities on nearby agricultural land, with positive effects on crop yields (Kremen et al., 2004; Pfeiffer et al., 2019; Priess et al., 2007). Broadleaved woodland is one of the top habitats for nectar production per unit area in the UK (Baude et al., 2016) and has been found to support high abundances of key pollinator groups, potentially linked to the presence of bramble, ivy and flowering trees as sources of pollen and nectar (Alison et al., 2022; Allen & Davies, 2023; Baude et al., 2016; Jones et al., 2021).

1.6 Thesis structure and knowledge gaps addressed

The breadth of potential forest biodiversity metrics and applications for their use are extensive, yet reliable indicators appropriate to the Irish setting are needed for a range of purposes, including to inform emerging nature finance markets, reporting related to EU strategies and regulations, forest or conservation management, ecosystem accounting, and for land use decision tools and models. In this thesis I use forest data derived from field studies, the National Forest Inventory, and expert knowledge, to critically examine how we measure forest biodiversity in different contexts.

Woodland ecology has been the subject of thorough research, though many studies have focused on non-native plantation forests or established semi-natural woodlands. Those studies that have been carried out on planted farm woodlands, such as the WrEN study in UK (Fuentes-Montemayor et al., 2022), did not include the earliest establishment phases (<10 years), and did not frame the studies in the context of the woodland habitat targeted. Native woodlands are now being established for biodiversity and climate benefits, rather than solely for wood-product benefits, and

so it is essential we understand whether they are achieving this outcome. Currently, the extent to which new native woodland sites achieve the typical ecological features of their targeted habitats remains unclear. We are also unsure how long this process takes, whether there are benefits for nature realised in the interim development stages, and what the main drivers influencing biodiversity outcomes in these young sites may be.

To address these knowledge gaps, Chapters 2 and 3 focus in on questions related to native woodland afforestation on former agricultural lands. In **Chapter 2** I explore these biodiversity outcomes using field collected data on the structure and floral composition of these woodlands, examine the influence of local and landscape level variables, consider how species traits mediate the floral community response, and classify the emerging habitats.

Outside of a research context, faunal studies of woodland sites are rarely undertaken due to the time effort and skills involved, yet there is an increased need to establish faunal metrics for use in monitoring and management, particularly where woodlands are being planted for the nature finance sector requiring robust evidence that the promised benefits are being delivered. Specifically, there are a dearth of faunal studies spanning native woodland establishment phases, and few studies that examine pollinating insects, despite the potential for this community to serve as ecosystem service providers. In **Chapter 3** therefore I focus on the pollinator community, in order both to understand how the community changes as native woodlands develop, and to explore their value for monitoring and management.

A second theme in this thesis explores how we can harness existing biodiversity data and knowledge to inform decision making, monitoring and management of the Irish forest estate. Two different practical applications are considered with Chapter 4 focusing on national level biodiversity reporting, and Chapter 5 considering how expert knowledge can be utilised.

Forest inventory surveys have resulted in the availability of a large and detailed dataset representative of the Irish forest estate, yet the biodiversity data collected have not been examined in detail. In **Chapter 4** I use the National Forest Inventory to examine the key drivers influencing floral biodiversity across the forest estate in Ireland. Here I consider a range of forest types, including semi-natural, reforested and afforested plots, to understand how floral biodiversity varies between them. I describe the nature of those relationships, identify the best indicators for floral biodiversity, and consider which metrics are most suitable for monitoring the biodiversity of the forest estate.

There are significant data gaps in the NFI and literature with regard to certain planting scenarios that may be favoured into the future, particularly broadleaf plantations, yet policy-level decisions are being made around the future of the forestry estate and the relative trade-offs between the benefits related to carbon, timber and biodiversity. With the resource efforts required for field surveys presenting a challenge for data gathering, **Chapter 5** uses expert knowledge to devise

biodiversity scores for different forest types that can be incorporated into such models, and discusses the benefits and challenges of this approach.

I conclude in **Chapter 6** by reflecting on the key findings of the previous four chapters, and integrating these to discuss implications for forest policy, adaptive management and future research.

CHAPTER 2

Vegetation development and progress towards target habitats in newly established native woodlands in Ireland

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Target journal: Forest Ecology and Management

2 Vegetation development and progress towards target habitats in newly established native woodlands in Ireland

2.1 Abstract

In Ireland, only around 2% of the country is covered by native or semi-natural woodland, that is, woodland dominated by native tree species. The expansion of native woodlands is being primarily delivered through the government-funded Native Woodland Scheme (NWS), which targets several native woodland habitats, depending on the soil type and landscape setting, including sessile oak (*Quercus petraea*) woodland, pedunculate oak (*Quercus robur*) woodland, and wet woodlands. No systematic monitoring of recently afforested native woodlands, primarily established on private farmland, has yet been undertaken in Ireland, despite ongoing plans for expansion. Here we seek to understand some of the complex site and landscape scale interactions influencing establishing native woodland plantations by examining patterns of species assembly using a life-history trait-based approach, and also determine whether these new woodlands are reaching their target woodland type.

The study was conducted in the agricultural landscape of the east and midlands of Ireland across a 20 year chronosequence of new woodland sites. Field data on vegetation composition and structure were collected. The data were first analysed using exploratory methods followed by regression models to identify significant predictors of floral species richness metrics. RLQ and fourth-corner analyses were then used to identify significant relationships across matrices of species cover, environmental variables, and vegetation traits. Finally we used NFI data and a habitat classification tool (ERICA) to identify if sites were on track to meet their target woodland type.

The data revealed a clear transition from non-woodland to woodland plant species corresponding with a shift in habitat classification from grassland to woodland habitats over the woodland establishment timeframe. A high proportion of older plots achieved their target habitat grouping, indicating successful habitat development, and we also found an increase in natural colonisation of young trees with stand age. The findings also pointed to an imprint of past land use associated with a landscape gradient favouring specialist flora, as demonstrated through integration of plant traits into the analysis. Our research helps with understanding the changes in floral biodiversity in planted native woodlands and suggests NWS sites are on a positive trajectory towards meeting their target woodland habitat, with the potential to help expand biodiverse and resilient forest networks.

2.2 Introduction

In response to climate change and biodiversity loss, afforestation has received increased attention as part of wider international strategies aimed at halting deforestation and increasing global tree cover. In this context, native woodland afforestation, aimed at establishing diverse woodlands that provide multiple ecosystem services, is being promoted as a win-win solution for humans and biodiversity (Gamfeldt et al., 2013; García et al., 2020; Messier et al., 2022), though with the caveat that numbers of trees should not been seen as the end goal, and trade-offs for people and nature need to be carefully considered (Holl & Brancalion, 2020).

In Ireland, only around 2% of the country is covered by native or semi-natural woodland, that is, woodland dominated by native tree species. These sites are highly fragmented in the landscape, have nearly all been subject to past silvicultural management or other human-mediated disturbances, and are frequently altered by naturalised non-native species such as beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*), or invasive non-natives such as *Rhododendron ponticum* and *Prunus laurocerasus* (Perrin et al., 2008). The expansion of native woodlands has been primarily delivered through the government-funded Native Woodland Scheme (NWS), originally launched in 2001, and recently reorganised as a number of 'Forest Types' under the latest afforestation programme (DAFM, 2024b). Tree species mixes are chosen with reference to soil and landscape scenarios set out in the Native Forest Framework (NFF) (DAFM, 2024b), with most NWS woodlands planted in relatively small sites on privately-owned agricultural land. Several native woodland habitats are targeted depending on soil type and landscape factors, including sessile oak (*Quercus petraea*) woodland, pedunculate oak (*Quercus robur*) woodland, and wet woodlands.

The challenge of determining where to restore our native woodlands is complex especially in modified landscapes (Marshall et al., 2023). Until recently there has been a general lack of field-based evidence for the effects of native woodland creation on biodiversity over-time relative to non-native plantation woodlands (Burton et al., 2018), with chronosequence studies focused on highly modified forests (Brunet et al., 2021; Coote et al., 2012; French et al., 2008). The exception being the valuable outputs that have emerged from the long-term 'WrEN' study in the UK, which examined structural and biodiversity changes in post-agricultural woodlands compared to ancient woodlands in a lowland agricultural landscape (Fuentes-Montemayor et al., 2022; Fuentes-Montemayor et al., 2017; Waddell et al., 2024).

Through matching a target native woodland habitat to a particular site, and applying a structured forestry approach, the NWS aims to plant '*the right tree in the right place*'. Most sites are proposed for management under Continuous Cover Forestry (CCF) principles (European Commission, 2023) with the ultimate aim of providing benefits for biodiversity, carbon and timber. NWS woodlands have been established over the last 20 years during a period of increasing pressure

on all habitats due to unpredictable climatic conditions, intensification of agricultural practices, and declining biodiversity. Ongoing native woodland expansion is a key action under the Nature Restoration Law (Regulation (EU) 2024/1991), aligning with the broader objectives of the EU Biodiversity Strategy, which support the protection and restoration of natural ecosystems across the EU. As Member States develop national restoration plans to meet legally binding targets for the recovery of forest ecosystems, evidence is needed to inform realistic targets for monitoring success. We therefore wanted to investigate if these recent tree-planting interventions in highly modified agricultural landscapes resulted in the expected accumulation of woodland floral species, and a shift toward the target woodland type.

At a landscape level, the effects of woodland size and the degree of connectivity or fragmentation have been identified as essential factors in maintaining and restoring forest ecosystems (Humphrey et al., 2015; Lawton, 2010). Natural colonisation of trees tends to be most successful where sites are located near existing seed sources (Bauld et al., 2023; Morris & Davies, 2025), and woodlands created adjacent to existing woodland have been shown to grow faster, taller and have higher structural diversity than isolated sites (Hughes et al., 2023). Proximity to ancient forests facilitates forest herb immigration in post-agricultural woodlands (Brunet et al., 2021), while hedgerows have been identified as potential pathways of colonisation for certain woodland plants (McCollin et al., 2000; Wehling & Diekmann, 2009).

At a site level, factors such as substrate, past land use, successional development, site management and grazing all influence how biodiversity changes and develops (Broughton et al., 2021; Corney et al., 2006; Harmer et al., 2001; Waddell et al., 2024). Many of these factors influence aspects of structural diversity creating favourable habitats and conditions for woodland species (Humphrey et al., 2015; Smith et al., 2008; Waddell et al., 2024). The tree species planted also have differing future biodiversity potential (Kennedy & Southwood, 1984), with mature oaks in the UK shown to support 2,300 species including 326 obligate associates (Mitchell et al., 2019).

The assembly of the forest plant community, depending on this interplay of site, landscape and climate factors, is driven by their functional traits, explaining their affinities for certain abiotic conditions (Verheyen et al., 2003). Forest specialist and generalist species may respond differently to afforestation (Bremer & Farley, 2010; Brunet et al., 2011), with specialists potentially taking decades to colonise post-agricultural woodlands (Brunet et al., 2021; Honnay et al., 2002), if at all (De Frenne et al., 2011). Ellenberg indicator values (Hill, 1999) are frequently used to understand a plants preferred environmental conditions for light, nutrients, pH and moisture (Hermy et al., 1999; Honnay et al., 2002; Hughes et al., 2023; McCollin et al., 2000), while a plants strategy with regard to stress, disturbance and competition (Grime, 1979) can similarly help us determine the dominant environmental filters acting on a site's flora (Hermy et al., 1999; Timmermann et al., 2015).

We are not aware of studies that have taken a focused look at younger mixed native woodland plantations or considered a specific target woodland habitat as a reference point. Furthermore, no systematic monitoring of recently afforested native woodlands, primarily established on private farmland, has yet been undertaken in our study landscape, despite ongoing plans for expansion. We seek to understand some of the complex site and landscape scale interactions through examining patterns of species assembly using a life-history trait-based approach. Specifically, we ask the following questions:

1. How are woodlands changing in terms of structure and plant biodiversity across the chronosequence, and does this vary depending on the tree species planted, or other plot, site or landscape factors?
2. Are the new woodlands reaching their target woodland type?

Given the age profile of our sites, we expect to see a shift towards larger trees and associated changes in canopy cover and light. We anticipate that some differences between tree-species groupings will be apparent, due to the influence of soil and landscape factors, and expect a shift in community composition with age, but do not expect to find significant colonisation of woodland specialist species. We expect that some of our older sites will align with their target woodland type, as judged by the use of an available habitat classification tool, and comparison with National Forest Inventory Data.

2.3 Materials and Methods

2.3.1 Study region and site selection

The study was conducted in the agricultural landscape of the east and midlands of Ireland (Fig. 2.1). This region was chosen as it captures a landscape and edaphic gradient supporting a range of woodland habitats of relevance to our study. Study sites were primarily afforested under the NWS. While public funding provision and uptake has varied with the economic context over time, afforestation under this scheme has been increasing since 2015 (DAFM, 2023a). Following initial engagement with the Forest Service, and subject to securing permission from private landowners, we were able to access a chronosequence of 47 new woodland sites, planted between 2000 and 2021 (Appendix A, Table A1). Sites were grouped into three broad woodland development stages: 'Open' sites that were characterised by young trees in a post-planting phase and were 2-5 year's old at the time of survey; 'Thicket' sites where tree branches were touching but the understorey was still dominated by grasses, and which were 6-14 year's old at the time of survey; and 'Closed' sites, between 13 and 22 year's old, where the closing canopy of maturing trees had shaded out most of the ground flora. Overlap in age ranges between these stages is a result of differing growth rates between species, and differing planting densities.

We also grouped sites into three broad composition types, aligning with the NWS planting 'Scenarios' 1-4, depending on the dominant tree species planted at the site: Sessile Oak (SO) *Quercus petraea* (NWS Scenario 1 targeting oak-birch-holly woodland on podzols, and NWS 2 targeting oak-birch-holly with hazel woodland on brown podzolic soils), Pedunculate Oak (PO) *Quercus robur* (NWS Scenario 3 targeting oak-ash-hazel woodland on brown earth soils) and Alder (ALD) *Alnus glutinosa* (NWS Scenario 4 targeting alder-oak-ash woodland on gley soils). Our tree species groupings are therefore intended to capture environmental context in terms of soil characteristics together with the target woodland type. Due to lower planting rates of alder, overall the number of alder sites is lower than that for the oak categories (Appendix A, Table A2). There was also an absence of thicket-stage sessile oak from our dataset, due to lower rates of planting of sessile oak during a period of economic recession, combined with lack of access granted to sites that did exist.

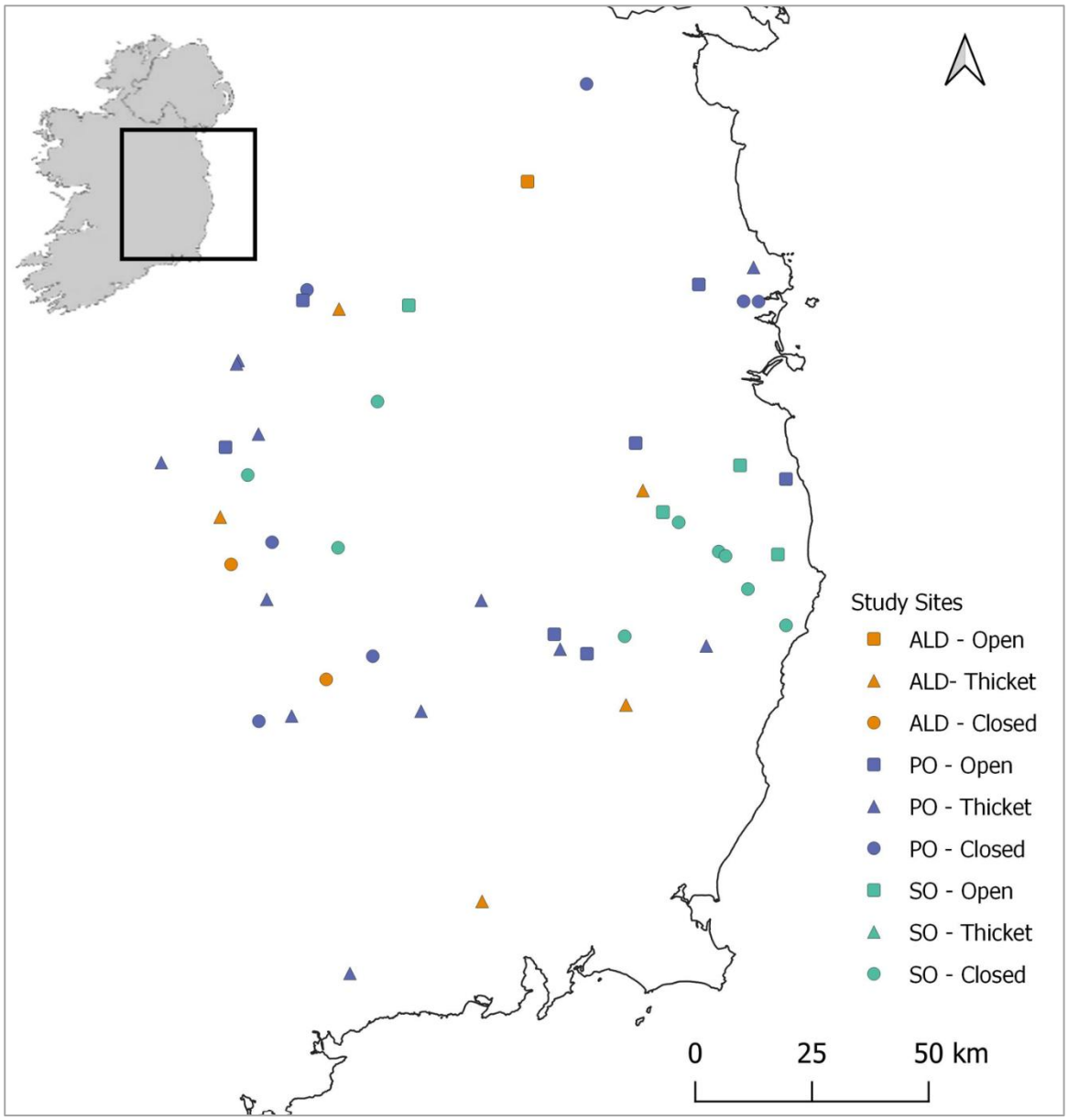

Figure 2.1 Study region in east and midlands of Ireland, with site locations colour-coded by dominant planted-species (ALD = Alder *Alnus glutinosa*, PO = Pedunculate oak *Quercus robur* and SO = Sessile oak *Quercus petraea*) with shape indicating development stage.

2.3.2 Field Survey Methods

The site surveys involved the collection of data on vegetation composition and structure. Vegetation surveys were carried out in 3-5 10x10m plots per site. Where possible, these were sited ca. 50m from woodland edges or paths, or at least 1 tree height length from these edges for narrow woodland plots, and 50m from other plots. These constraints limited the plot number to 3 at small sites, whereas 4 and 5 plots could be accommodated in larger sites. Surveys were carried out between May and August 2022, and in June 2023. The plot-level vegetation survey involved recording the species, height and DBH (Diameter at Breast Height) of trees with a DBH>2cm. Younger trees (saplings and seedlings) were categorised into 4 classes; S1 (Cotyledon stages), S2 (Seedling <25cm height), S3 (Sapling 25cm-2m height) and S4 (Sapling >2m height). It was also noted whether the tree was planted or naturally regenerated if this was possible to determine. We recorded the median height and percent cover of the following vegetation layers: canopy, large shrub/understorey, dwarf shrub, field and ground. A 'tree layer' was recorded where there was no canopy/understory understorey structure, and otherwise this tree layer was recorded as the pooled cover of the canopy and understorey layers to enable comparison of tree cover across sites. Other non-floristic variables recorded included cover of coarse woody debris (CWD), fine woody debris (FWD), leaf litter and bare ground cover. We also recorded the percentage cover of vascular plants and of bryophytes rooted on ground surfaces. Some basic soil measurements were taken (pH, moisture, temperature and conductivity), and indicators of grazing, invasive species and soil drainage recorded. The plot selection method and specific attributes measured are further described in further detail in Appendix A, Table A3.

2.3.3 Structural, environmental and landscape variables

Plot-level metrics derived from tree data collected during field surveys were basal area, mean DBH, the standard deviation of DBH (sd_DBH), mean tree height, number of trees, and number of stems (as some trees had multiple stems). As potential indicators of the extent of natural colonisation of non-planted trees, we calculated the total number of non-planted tree seedings and saplings and the number of distinct species of non-planted seedings and saplings.

Relevant environmental and landscape variables for each site were extracted from available datasets, where relevant the shorthand nomenclature used in later figures/text is provided in italics:

- Landscape classification based on Carlier et al., (2021) with categories comprising: Extensive Mountainous *ExtUp*, Semi-intensified Elevated *SemiElv*, Peatlands *Peat*, Intensified Lowlands *IntLow* and Semi-intensified Lowlands *SemiLow*.
- Soil type extracted from online datasets (Teagasc & EPA, 2018) and assigned to 5 broad groups: podzols *Podzol*, shallow mineral soils *ShallowMin*, alluvium/gleys *AlluvGley*, brown earths *Brown* and peat *Peat.*

- Using the buffer and intersection tools in QGIS, the extent of Fossitt Level 2 habitat (Fossitt, 2000) in a 2km matrix surrounding the site was calculated from the National Landcover Map (EPA & Tailte Éireann, 2024). We used the following habitat categories: All Woodland *All_Wood*, Conifer Forest, Broadleaf Forest, Transitional Forest, Mixed Forest, Scrub, Wet Grassland, Dry Grassland, All Semi-natural Grassland *All_SemiNat_Grass*, Improved Grassland, Cultivated Grassland, All Agricultural Grassland *All_Agri_Grass* and Hedgerow.

2.3.4 Traits

Trait data for vascular plant species were extracted from two published datasets. We used broad habitat categories and Ellenberg indicator values from the PLANTATT dataset (Hill et al., 2004) together with data on seed mass and life strategy from Henniges et al. (2022). The latter included data on seed mass devised by Westoby (1998), and data on life strategies derived from CSR categories (Grime, 1979) that classify each species as either a competitor (C), stress tolerator (S) or ruderal (R), or a combination of these (e.g. S, CS, CSR, SR/CSR). For analysis purposes, CSR categories were converted to numeric values by assigning each species a total of 12 points divided across the three strategies C, S, and R depending on the combination (Ejrnæs & Bruun, 2000). We used Ellenberg Indicator Values for light (L), moisture (F), reaction (preference for soil acidity) (R), and nitrogen (preference for soil fertility) (N). We calculated the community-weighted mean of trait values for each site based on mean percentage cover across all plots.

2.3.5 Habitat Classification

For each plot, the vegetation community (inclusive of the planted trees) was classified according to the Irish Vegetation Classification (IVC) system (National Biodiversity Data Centre, 2024) using the ERICA web application tool (Perrin, 2019). The ERICA tool uses a fuzzy clustering technique, following De Cáceres et al. (2010) and Wiser & De Cáceres (2013), to determine the degree of membership of each plot to a community within the IVC on a scale of 0–1. A noise class was also defined in the tool to capture outliers to the classification scheme. Plots with membership ≥ 0.5 for any vegetation community are considered to represent the core definition of that community and are classified as 'assigned'. Plots with a membership ≥ 0.5 for the noise class are viewed as poorly represented by the classification scheme and are marked as 'unassigned'. Plots with membership scores < 0.5 for all vegetation communities and the noise class fall within the scope of the classification scheme but do not correspond to the core definition of any community; these are classified as 'transitional' (Perrin, 2015).

2.3.6 National Forest Inventory Data

The National Forest Inventory (NFI) (DAFM, 2023c) collects structured data on a range of forest attributes, including floral biodiversity, across forest plots throughout the Republic of Ireland. Using the most recently-published data (Fourth cycle – 2022), comprising 2020 plots, we filtered

the dataset to identify data for our target semi-natural woodland habitats, excluding scrub and bog woodland, recently-felled woodland and forest open-areas. Plots for oak-birch-holly woodland and oak-ash-hazel woodland were extracted directly, however we combined riparian woodland, wet willow-alder-ash woodland, and wet pedunculate oak-ash woodland into a 'wet woodland' grouping. We further selected only plots from our study region and excluded 3 no. extreme outliers (for which there was no plant species cover data), resulting in 52 plots. To align with our young woodland dataset, we combined the species data for all floral attributes other than the planted trees i.e. ferns, grasses, herbs and shrubs. We also extracted data for bryophyte cover, shrub cover, age, soil type, and development stage to align with our scenarios. To account for differences in plot size between our study (100 m^2) and the National Forest Inventory (500 m^2 for shrubs; 153.9 m^2 for other vegetation), species data were converted to presence/absence for comparative analysis. Although the larger NFI plots may increase species detectability, this approach nonetheless facilitates an ecologically meaningful exploration of overall differences in species composition.

2.3.7 Data Analysis

All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2023). We computed species richness accumulation curves and sample coverage curves for each woodland stage using the *iNEXT* R package (Hsieh et al., 2016).

To understand the relationship between structural variables and site age, we carried out Spearman correlations and produced a correlation matrix using the R packages *corrplot* and *ggcorrplot*, with p-values adjusted using a Bonferroni correction to account for multiple comparisons. Where numeric variables were compared across categorical variables, we used Kruskal-Wallis (K-W) tests followed by Dunn's tests.

The species richness (S) and Shannon diversity index (H') of all taxa, other than the planted trees, was calculated. Based on the habitat categories of Hill et al. (2004) we extracted the richness of woodland specialist, woodland generalist, and non-woodland species from the dataset. Woodland specialists were those species that have a recognised affinity solely with woodland habitats, while woodland generalists were those associated with woodland habitats as well as other habitat types. We similarly assigned bryophytes to the same categories based on Atherton et al. (2010). We also extracted the richness of Ancient Woodland Indicator (AWI) species (a combination of woodland specialists and generalists) based on the list devised by Perrin & Daly (2010) for our study area.

In order to understand key drivers of species richness and diversity (response variables), generalised linear mixed models (GLMMs) and linear mixed models (LMMs) were used. Initial exploration of data showed that many plot, site and landscape variables we collected were naturally correlated e.g. site age and structural metrics, or species category, soil category and landscape classification. To avoid model over- parameterisation, and to enable comparison of different

diversity metrics, we chose age and species category as model variables based on exploratory analysis.

Site was set as a random factor in all models to account for multiple plots within sites and avoid pseudoreplication. GLMM's were used for richness metrics and were fitted using the glmmTMB R package (Brooks et al., 2017) specifying a Poisson error distribution using a log-link function, while LMM's were used for the diversity metric and were fitted using the lme4 R package (Bates et al., 2015). We inspected the distribution of residuals, dispersion and checked for zero-inflation, spatial autocorrelation and influential points using the DHARMa R package (Hartig, 2022). The variance inflation factor (VIF) of each predictor was calculated using the 'car' R package (Fox & Weisberg, 2019), and we checked that VIF was <4 (Zuur et al., 2013) indicating no high correlation among predictors. We confirmed that the best-fitting model differed from the null model using the ANOVA function in the in lme4 R package.

Using the same modelling structure, we also examined best-fitting models, simplifying the model using a backwards elimination process to remove variables/interactions with non-marginal p-values ($p>0.1$) and selecting the model with remaining significant p-values and/or the lowest AIC_c. We included variables for age, woodland size (correlated with no. plots/site), survey year and forest type (reforested/afforested) together with separately modelling variables for tree species grouping, soil type, landscape class and selected landscape cover metrics (conifer, broadleaf, semi-natural grasslands, agricultural grasslands and hedgerow).

To visualise vegetation community composition, we used non-metric multidimensional scaling (NMDS) ordination and fitted environmental vectors to the ordination plot using the *envfit* function (*vegan* R package) (Oksanen et al., 2022). We ordinated species cover values at the site level, averaged species cover across plots. For ordinations, to compare our dataset with NFI data, we excluded bryophytes as the NFI did not record this group to species-level, and based these ordinations on presence-absence data.

Finally, we completed an RLQ analysis to assess the relationship between vegetation traits and gradients in selected environmental variables using the ade4 R package (Dray & Dufour, 2007). Variables demonstrating relationships with species diversity, richness, or composition, based on preliminary exploratory analyses and NMDS ordination, were selected for further investigation. RLQ analysis produces a constrained ordination that incorporates information on the environmental variables at each sampled site (matrix R), species cover (as a proxy for abundance) (matrix L), and the trait data for each species (matrix Q). The analysis maximises the covariance between the traits and the environmental variables mediated by the species abundance (Dray et al., 2014), and is helpful in summarising correlated environmental datasets into few dimensions. It involves performing a Correspondence Analysis (CA) on species data, and using the column weights produced to undertake a multiple correspondence analysis (MCA) on the trait matrix, while the row

weights from the species CA are used in a Principle Component Analysis (PCA) on the environmental matrix. The RLQ analysis then compares the co-variance of the three separate analyses with co-inertia analysis. We then carried out a fourth-corner analysis, which complements RLQ analysis by directly testing and quantifying the link between all combinations of species traits and environmental attributes using permutation tests. Two combined permutation models (model 2 and 4) were applied with 49,999 repetitions following (Dray et al., 2016). To account for multiple testing of environmental variables and multiple traits, we adjusted P values to account for false discovery rates.

2.4 Results

We recorded a total of 232 vascular plant and bryophyte species across 184 plots within 47 sites. The sites spanned a chronosequence of 20 years, from 2 to 22 years post-planting, with 12 open stage sites, 17 thicket stage sites, and 18 closed stage sites. Species accumulation curves for floral species richness within each planting scenario plateau, suggesting sampling effort captured the majority of species present in the study area, while sample coverage curves approached saturation (all over 96%) indicating thorough sample coverage (Appendix A, Fig. A1 & A2).

2.4.1 How are woodlands changing in terms of structure and biodiversity?

2.4.1.1 Structure

As expected, site age was strongly positively correlated with metrics reflecting bigger trees, including basal area ($R = 0.91$, $p<0.001$), DBH ($R = 0.81$, $p<0.001$), standard deviation of DBH (sd_DBH) ($p = 0.88$, $p<0.001$), tree cover ($R = 0.77$, $p<0.001$), tree height ($R = 0.089$, $p<0.001$), FWD ($R = 0.87$, $p<0.001$) and litter ($R = 0.69$, $p<0.001$) (Appendix A, Fig. A3). Also, as expected, younger sites had a greater herb layer, represented by the strong negative correlation between site age and field cover ($R = -0.57$, $p<0.001$). Variables that were strongly associated with the age gradient were also cross correlated (Appendix A, Fig. A3). The structure of the woodland sites therefore changed across the chronosequence, with the increasing growth of trees, increasing diversity in structure, an associated change in the cover of forest layers (increasing ground, litter and tree layer cover), and decreasing field layer cover.

There was no significant difference when the structural metrics of basal area, DBH and sd_DBH were compared across the tree species groups, however the number of trees was significantly higher in the oak sites relative to alder (Kruskal-Wallis (KW) chi-squared = 13.368, p-value <0.002).

The cover of the field layer was significantly higher in the alder group (KW chi-squared = 6.407, p-value =0.041), as was the height of this layer (KW chi-squared = 7.806, p-value =0.020), while ground cover (bryophytes) was significantly higher in the sessile oak group (KW chi-squared = 13.888, p-value <0.001). Other cover/height variables did not significantly differ between tree species groups, and correlations between the percentage cover of the focus tree species and structural variables were weak (Appendix A, Fig. A3).

The number of naturally colonising tree saplings were most strongly correlated with the number of planted trees (No. Trees) ($R = 0.65$), litter ($R – 0.62$), tree cover ($R = 0.58$), and basal area ($R = 0.56$), while the number of distinct naturally colonising tree sapling taxa were most strongly correlated with litter ($R = 0.70$), the number of trees ($R = 0.65$), basal area ($R = 0.62$), tree cover ($R = 0.61$) and site age ($R = 0.60$) (all significant with $p<0.001$). Regression models (Appendix A, Table A4) confirm age and species category were key explanatory factors explaining 45% and 46%

respectively for the number of colonising tree species and total number of colonising trees. Colonisation was higher in older sites, and higher in both the oak categories relative to alder. No other environmental or landscape variables (of those uncorrelated with age) were significant in our models.

A total of 166 trees were recorded colonising open stage woodlands, 650 in thicket stage woodlands and 669 in closed stage woodlands (Appendix A, Table A5). Blackthorn (*Prunus spinosa)* and sycamore (*Acer pseudoplatanus)* were found in large numbers at single sites in open and thicket stage sites respectively (Appendix A, Table A5). As such, on average, open and thicket stage sites supported very few colonising saplings (Appendix A, Fig. A4). Otherwise, there was a greater variety of species, and a dominance of ash (*Fraxinus excelsior*), blackthorn and hawthorn (*Crataegus monogyna*), in older sites (Appendix A, Table A5).

2.4.1.2 Species Diversity & Composition

Examining the flora of the understorey layers (excluding the planted trees), we calculated metrics of overall species richness and diversity, as well as that of the non-woodland, woodland generalist and woodland specialist components. We also extracted a species richness metric for AWI's. Based on models with *a priori* selected variables for age and species category (Table 2.1, Fig. 2.2), floral diversity (Shannon Diversity Index) was significantly associated with the age of the site, however the model explained only 8% of the variance. In contrast, overall species richness was not explained by either variable.

The richness of woodland generalist species, bolstered by bryophytes that were mostly assigned to this group, was primarily explained by a significant association with site age and sessile oak plantations (relative to pedunculate oak and alder), with these factors explaining 51% of variance. When bryophytes were eliminated, the richness of woodland generalist species in sessile oak sites was no longer significantly higher than pedunculate oak sites, though both oak categories were significantly more species-rich than alder (Appendix A, Table A6).

Age was significantly and positively associated with the richness of woodland specialists, with the fixed terms explaining 41% of variance. In contrast, age was significantly and negatively associated with the richness of non-woodland species, with the fixed terms explaining 42% of variance. Ancient woodland indicators (vascular plants only) were positively associated with older sites and sessile oak plantations.

Best-fitting models (Appendix A, Table A6) indicated a significant association between overall diversity and the area of semi-natural grasslands in the landscape, though explaining just 5% the variance. The best-fitting model for richness indicates lower richness in peaty soils, and higher richness in podzols, explaining 17% of variance. The best-fitting models for woodland generalist and non-woodland species were those with the *a priori* chosen model variables. Age and the area

of conifer in the landscape matrix were positively associated with woodland specialists and ancient woodland indicators, and though the area of conifer was not significant for the woodland specialist model, including this variable improved model fit as judged by AICc.

Forest type (afforested or reforested) was not significant in any model, and as a check, models run on a smaller dataset without the four reforested sites were found not to differ from the models run on the full set of sites. The size of the woodland or survey year was not significant in any model.

Exploratory ordinations (Appendix A, Fig. A5-A7) indicated that the vegetation (excluding planted trees) community composition of the alder and sessile oak sites diverged, but that both these tree species groupings broadly overlapped with pedunculate oak sites aside from those sessile oak sites associated with more upland areas, and the wettest alder site. High stress levels, revealed when data was plotted in two dimensions, indicated that composition was best captured in three dimensions, suggestive of more than a single gradient of change influencing our data. Fitted vectors for landscape composition metrics illustrated the correlation between the extent of conifer plantation in the landscape, and the upland sessile oak sites. Conversely, vectors for area of agricultural land and length of hedgerow in the surrounding landscape matrix were fitted in the opposing direction to the woodland cover variables, indicating a negative relationship with woodland cover. Vectors for pH and field cover indicated an association with the vegetation composition in more intensive agricultural landscapes. Vector length for age suggested a strong relationship with community composition overall, with this vector positively aligning with structural metrics.

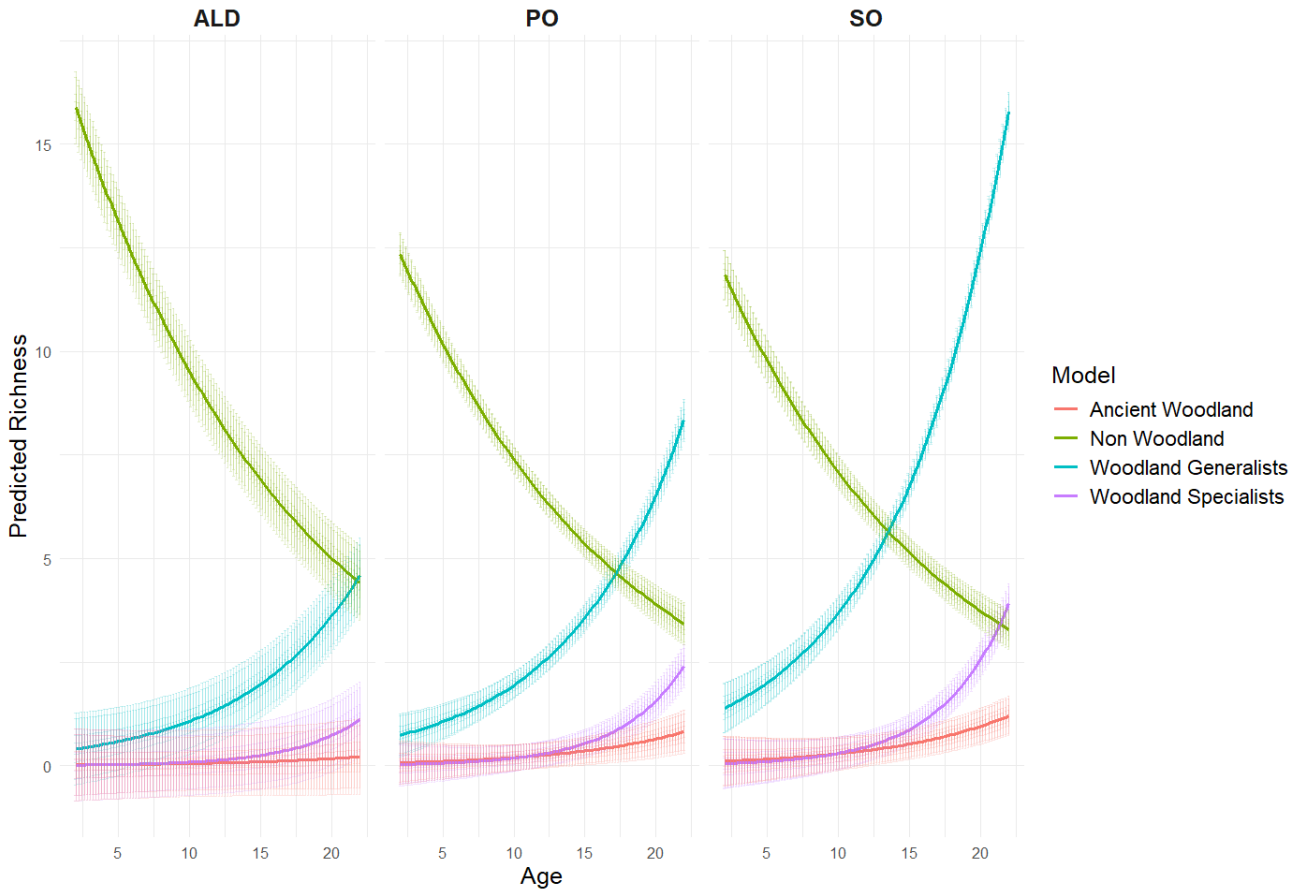

Figure 2.2 Relationships between predicted species richness (± SE) and woodland age for each tree species group (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak) for woodland specialists (purple), woodland generalists (blue), non-woodland species (green), and ancient woodland indicator species (red).

Table 2.1 Results of Mixed Models for Diversity and Richness explained by Age and Tree Species Group (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak). Positive estimates indicate higher values for diversity and richness, and vice versa for negative estimates. Incidence Rate Ratios (IRR's) for Poisson models describe how the rate of the outcome changes with a one-unit increase in the predictor variable, with values greater than 1 indicating an increased rate of the outcome, and below one indicating a decreased rate. p-values (to test the null hypothesis that the coefficient estimate is equal to zero, i.e. no effect) were calculated from z-values: the ratio between the estimated coefficient and the standard error of the estimate (estimate/SE). Large z-values show that the estimate is large (in relation to its SE) and significantly different from zero.

	Estimate	**IRR**	**Confidence Interval**	**Z**	**p value**	**Marginal R^2 / Conditional R^2**	**Moran's I (p value)**	**AICc**
Overall Diversity								
(Intercept)	1.891	-	1.60– 2.18	12.89	**<0.001**	0.081 / 0.410	-0.024 (0.958)	245.25
Age	-0.024	-	-0.04– -0.01	-2.71	**0.007**			
Sps [PO]	-0.094	-	-0.37– 0.18	-0.68	0.496			
Sps [SO]	0.0391	-	-0.27– 0.35	0.25	0.802			
Overall Richness								
(Intercept)	2.461	11.72	9.33– 14.71	21.21	**<0.001**	0.079 / 0.450	0.041 (0.147)	1041.74
Age	0.0008	1	0.99– 1.01	0.11	0.911			
Sps [PO]	-0.043	0.96	0.77– 1.19	-0.39	0.694			
Sps [SO]	0.196	1.22	0.96– 1.55	1.59	0.111			
Woodland Generalist Richness								
(Intercept)	-1.149	0.32	0.16– 0.62	-3.35	**0.001**	0.507 / 0.752	0.0291 (0.244)	708.35
Age	0.12	1.13	1.09– 1.17	6.52	**<0.001**			
Sps [PO]	0.597	1.82	0.98– 3.37	1.89	0.059			
Sps [SO]	1.236	3.44	1.76– 6.72	3.62	**<0.001**			
Woodland Specialist Richness								
(Intercept)	-4.626	0.01	0– 0.05	-5.52	**<0.001**	0.413 / 0.589	0.0185 (0.355)	285.97

	Estimate	IRR	Confidence Interval	Z	p value	Marginal R^2 / Conditional R^2	Moran's I (p value)	AICc
Age	0.215	1.24	1.14– 1.35	5.17	**<0.001**			
Sps [PO]	0.766	2.15	0.56– 8.20	1.12	0.262			
Sps [SO]	1.254	3.5	0.87– 14.05	1.77	0.077			
Non-Woodland-Species Richness								
(Intercept)	2.893	18.05	13.55– 24.06	19.76	**<0.001**	0.424 / 0.661	0.0005(0.0005)	928.53
Age	-0.064	0.94	0.92– 0.96	-6.88	**<0.001**			
Sps [PO]	-0.252	0.78	0.59– 1.02	-1.84	0.066			
Sps [SO]	-0.294	0.75	0.55– 1.01	-1.87	0.061			
Ancient Woodland Indicator Species								
(Intercept)	-4.148	0.02	0– 0.09	-4.55	**<0.001**	0.234 / 0.517	-0.022 (0.598)	265.76
Age	0.119	1.13	1.04– 1.22	2.97	**0.003**			
Sps [PO]	1.323	3.75	0.78– 18.18	1.64	0.1			
Sps [SO]	1.710	5.53	1.06– 28.85	2.03	**0.043**			

2.4.1.3 RLQ & Fourth Corner Analyses

Using the same dataset of understorey flora, though excluding bryophytes for which trait data were not available, an RLQ and Fourth Corner Analysis was undertaken. Incorporating species, environmental and trait datasets, the RLQ Analysis was used to analyse the main relationships between environmental gradients and trait syndromes mediated by species abundances (cover). The first two axes explained 92% of the total inertia of the three tables, with the first axis explaining 67% of the total variance, and the second explained 25%. The first and second axes showed moderate correlations (0.48 and 0.53 respectively) between traits and environment (Appendix A, Table A7). Axis associations with all factors are illustrated in Appendix A, Fig. A8.

We then explored the significance of the relationship between the RLQ axes and environmental variables and traits by combining RLQ and Fourth Corner analysis (Fig. 2.3, Table A8). The analysis of adjusted p values highlights the significant negative correlation between the first RLQ axis with Ellenberg scores for soil reactivity (pH) and nitrogen (fertility), together with a negative correlation with the pedunculate oak category, afforested sites and areas of agricultural land-use. On the positive side of this axis were the variables associated with upland sessile oak sites on podzols, with more woodland in the landscape, and supporting plants with a stress-adapted life strategy. Taken together, this axis primarily represented the landscape/fertility gradient and transition from sessile oak sites in the uplands, to more fertile pedunculate oak sites in the lowlands, the former characterised by heathland flora, and the latter by flora adapted to higher nutrient levels. The species scores associated with the positive end of axis 1 were those adapted to heath habitats, while the species scores associated with the negative end of axis 1 included those associated with improved soils (Appendix A, Table A9).

The second axis was significantly positively correlated with the Ellenberg light score and a ruderal life strategy, associated with afforested sites and a semi-intensive lowland landscape. This axis was negatively associated with site age and reforested sites. Overall, this axis appears to primarily reflect the age gradient, with many woodland species at the negative end of the gradient, while light-adapted species, and to a lesser extent some with a ruderal strategy, appeared at the opposite end. Species at the positive end of the axis included some weedy species and sedges, with species at the negative end of the axis including many of the colonising trees and woodland specialists (Appendix A, Table A9).

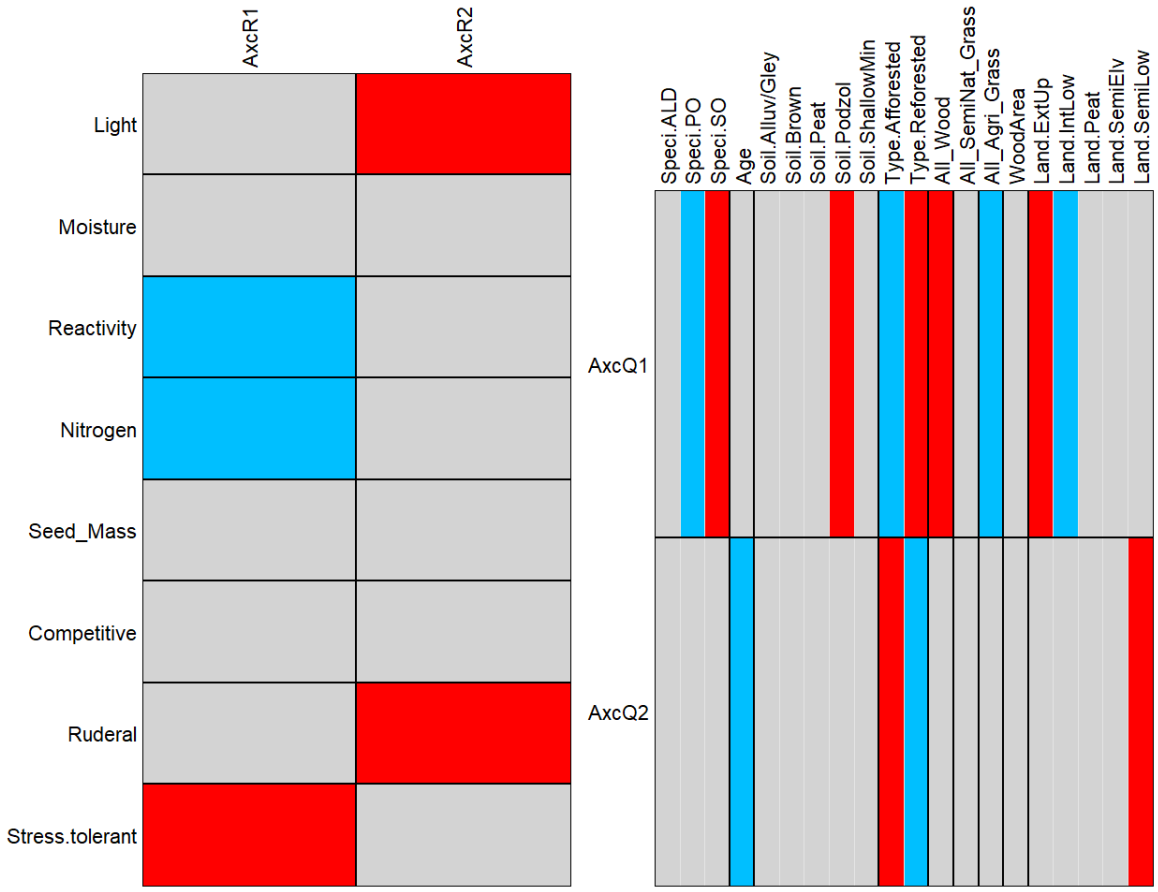

Figure 2.3 Fourth corner analysis results. The panel on the left illustrates associations between the RLQ axes and plant traits, while the panel on the right shows associations with environmental variables. Variables are as described in Section 2.3.3. Significant positive correlations are shown in red, while significant negative correlations are in blue.

2.4.2 Are the new woodlands reaching their target woodland type?

For sites classified as '*Assigned'* (greater than 50% membership of a habitat) and '*Transitional'* (less than 50% membership of a habitat) by the ERICA habitat classification tool, we see that most open-stage plots were matched to a grassland category, while most closed-stage plots were matched to a woodland category, with thicket-sites generally intermediate (Table 2.2). Examining the *Assigned* closed-stage sites only (Fig. 2.4), all but one plot was matched to woodland habitats, with the alder and pedunculate oak matched to their broad target woodland type (WL3 *Alnus glutinosa-Filipendula ulmaria* group, and WL2 *Fraxinus excelsior-Hedera helix* group, respectively). The sessile oak group plots were split between WL1 *Quercus petraea-Luzula sylvatica* group and WL4 *Betula pubescens – Molinia caerulea* group. The uneven number of plots listed for each species category reflect the uneven number of sites, with less closed-stage ALD and PO sites available for survey relative to SO (Appendix A, Table A2).

Of the 72 plots matched to a grassland category, 27 plots in 14 sites were associated with semi-natural grassland types noted to have affinities to Annex I habitats (Appendix A, Table A10). Reviewing the structural and compositional data for these plots with reference to Martin et al. (2018) and Perrin et al. (2014), single plots at 3 sites supported species-rich Annex I grasslands: 6410 *Molinia* meadows at two sites, and 6230 *Nardus* grassland at one site.

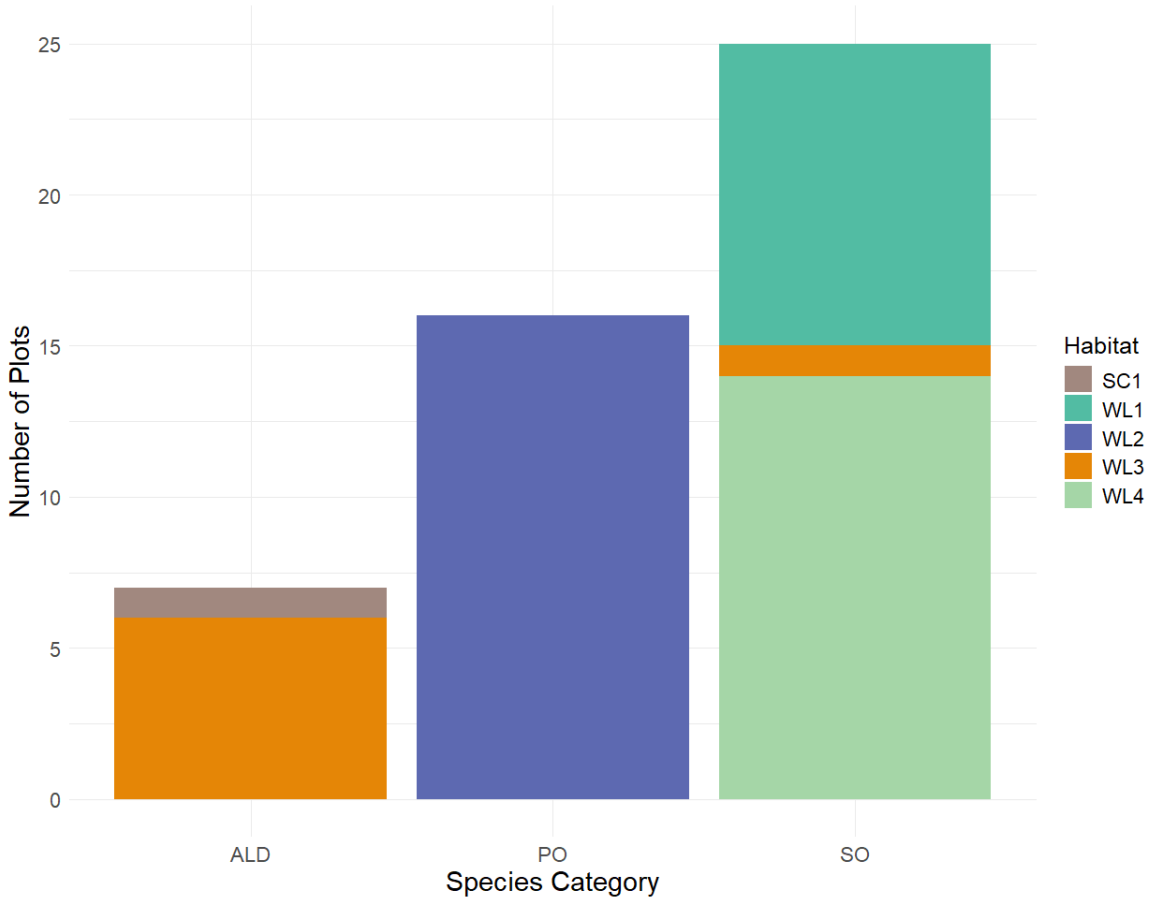

Figure 2.4 Output from the ERICA classification tool. - Number of plots per tree species category for closed-stage sites classified (assigned only) to Woodland habitats. Habitat codes correspond to: SC1 - *Rubus fruticosus* agg. – *Galium aparine* group; WL1 - *Quercus petraea-Luzula sylvatica group*; WL2 - *Fraxinus excelsior-Hedera helix* group; WL3 - *Alnus glutinosa-Filipendula ulmaria* group; and WL4 - *Betula pubescens – Molinia caerulea* group. Species Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak).

Table 2.2 Output from the ERICA classification tool. Number of plots per development stage and tree species category classified (assigned, transitional and the combined total) to Grassland, Woodland and Other habitats.

	Open			Thicket		Closed		
	ALD	**PO**	**SO**	**ALD**	**PO**	**ALD**	**PO**	**SO**
Grassland								
Assigned	2	10	9	3	7	0	0	0
Transitional	2	16	4	6	12	0	0	1
Total	4	26	13	9	19	0	0	1
Woodland								
Assigned	0	0	1	5	10	6	16	25
Transitional	0	1	1	4	13	1	7	10
Total	0	1	2	9	23	7	23	35
Other Habitat								
Assigned	0	0	1	1	1	1	0	0
Transitional	0	2	1	2	2	0	1	0
Total	0	2	2	3	3	1	1	0
Total No. Plots	**4**	**29**	**17**	**21**	**45**	**8**	**24**	**36**

Ordinating our data with the latest NFI data for semi-natural woodlands plots (n = 52) in our study area, we saw a merger of most of our older sites with the NFI sites (Fig. 2.5 & Appendix A, Fig. A9). The age/development stage gradient was clearly evident, aligning with shrub and bryophyte cover variables. Ordinating the semi-natural woodland habitat and NWS categories separately showed that the semi-natural woodlands compositionally overlap (Appendix A, Fig. A10 & Fig. A11).

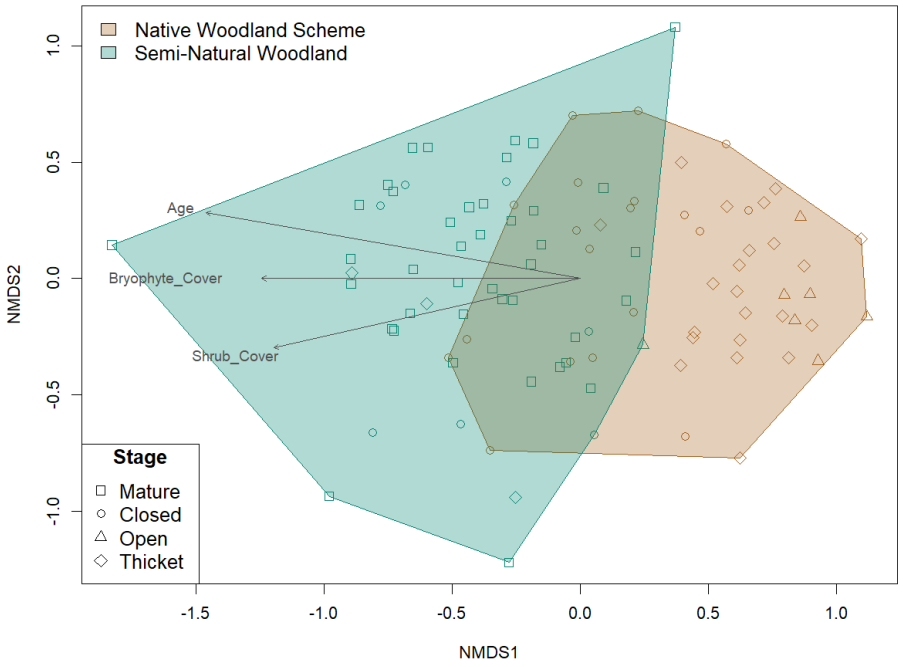

Figure 2.5 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites and semi-natural woodlands extracted from the NFI database for the same study area. Symbols illustrate development stage with arrows showing fitted variables for shrub cover, bryophyte cover and age. (Axes 1 & 2 plotted, k = 3, stress 0.148)

2.5 Discussion

The data revealed a clear transition in vegetation structure and composition across the woodland establishment timeframe with a gradual shift from non-woodland taxa to woodland taxa. Analyses of community composition and plant traits highlighted an imprint of past land use, reflected in a landscape/fertility gradient that appeared to favour the establishment of specialist flora. With the tree layer also factored-in, many older plots achieved their target habitat classification indicating successful habitat development. We also observed increased natural colonisation by young trees with stand age.

2.5.1 Woodland Structure

A new woodland goes through a series of successional stages before reaching maturity with the interplay of structure and light driving most change (Ferris, 1999; Guo, 2003; Kirby et al., 2017). In our planted sites, as they aged, there was an increase in the size of trees, tree cover and structural diversity, with an associated increase in litter and bryophyte cover and a decrease in cover of herbs and grasses. This reflected the expected change in woodland structure with age/development stage, with just minor differences between species groupings. These differences were explained by habitat-specific characteristics linked to physical and environmental factors, with the increased cover of ground flora (bryophytes) in sessile oak sites typical of this habitat (Cross, 2012), while taller herb cover in alder sites is likely explained by the presence of tall herbs such as nettle (*Urtica diocia*), common in wetter woodlands on more nutrient-rich soils (O'Neill & Barron, 2013). Variation in tree size has been proposed as a proxy for habitat quality, indicating healthy forest dynamics with natural regeneration/colonisation occurring (Fuentes-Montemayor et al., 2022), however we could not disentangle this factor from site age in our study given the strength of the age gradient, and it likely presents a more valuable indicator when comparing older woodlands.

The increase in the number and variety of naturally colonising trees with site age highlights that interventions such as tree-planting do not forgo opportunities for a degree of process-driven restoration. Of these naturally colonising trees, the predominance of hedgerow species could suggest the hedgerow network provides a source of colonists, and though their number/variety did not appear to be explained by metrics for hedgerow extent and composition in the surrounding landscape, it is possible that the explanation lies at a more granular level e.g. proximity of the surveyed plot to a nearby mature tree (Morris & Davies, 2025; Murphy et al., 2022). Trees, particularly those species with small or winged seeds (e.g. sycamore *Acer pseudoplatanus*, willows *Salix* spp., birches *Betula* spp.), are known to establish in greatest numbers close to a seed source (Bauld et al., 2023), declining with distance (Broughton et al., 2021). Aligning with our findings, higher tree colonisation rates were associated with age and structure in a recent study of young planted woodlands in England (Morris & Davies, 2025), however they found much higher frequency of occurrence and counts than in our study. The reasons for such a disparity are unclear

and require further exploration, but potentially relate to soil characteristics, grazing pressure, the presence/proximity of mature trees, survey-timing and site management factors. Uncontrolled deer populations in certain regions of Ireland present a significant challenge to the successful establishment and long-term viability of both planted and naturally arising woodlands (DAFM, 2023d). Conversely, our surveys likely underestimated the natural colonisation of birch and willow that occurred during stand initiation at a couple of sites and could not be distinguished from planted trees. Such sites would be appropriate candidates for a lower scale of initial planting intervention, such as planting clusters or islets of trees (Benayas et al., 2008; Holl & Brancalion, 2020), as tree-planting and natural colonisation need not be mutually exclusive approaches to woodland establishment (Bauld et al., 2023).

2.5.2 Community Assembly

The floral communities of pedunculate oak sites were compositionally similar to those of the sessile oak and alder woodlands, however sessile oak and alder diverged in their composition. Though we expected the pedunculate oak communities to also diverge, the tree species mix in sites dominated by pedunculate oak often included alder in wetter areas and sessile oak in drier areas, with the resultant heterogeneity in site flora creating a compositional spectrum of change, which may in part explain the extent of overlap in our crude species categories. Sessile oak and alder sites are more likely to be planted in more contrasting soil and moisture conditions, and coupled with the age distribution of the sites within these groups, this is likely to explain their compositional separation. Planting flexibility is inherent in the native woodland afforestation framework, acknowledging the potential spectrum of site conditions. Together with the structural changes driven by the age gradient, compositional changes in flora across these dual gradients will be influenced by the complex interplay of site-level environmental factors, and the resultant diversity in habitat niches, together with dispersal processes that may operate at both a local and landscape scale (Baeten & Verheyen, 2017; Honnay et al., 1999; Ozinga et al., 2009).

Overall species richness did not change significantly across our chronosequence, demonstrating that the loss of grassland species associated with the former land use is counterbalanced by the colonisation of new species. However, diversity significantly declined indicating that our community was becoming dominated by fewer species, likely those that are more shade-tolerant (Guo, 2003; Hermy et al., 1999). This was reflected in the positive trajectory for woodland generalist and specialist species across the age gradient, the clear signal for the latter being unexpected given all sites were relatively young.

Our results indicated that the richness of specialist species and ancient woodland indicators, though low, was greater where there was a greater proportion of conifer plantations in the landscape. Many forest plant species have low dispersal capacity, low diaspore production and low competitive ability with their occurrence strongly linked to forest continuity (Peterken & Game, 1984), and

hence colonisation of new forest sites can be very slow (Brunet et al., 2012; De Frenne et al., 2011; Hermy et al., 1999; Waddell et al., 2024). The assembly of a woodland plant community is known to be accelerated by targeting new native woodland adjacent to ancient woodland, which increases core habitat area and functional connectivity (Quine & Watts, 2009). The diversity of forest-associated plants (Coote et al., 2013; French et al., 2008; Kirby et al., 2017; Poole et al., 2003; Smith, 2003; Verheyen et al., 2003) consequently increases, though community composition may differ to adjacent mature sites (Broughton et al., 2021; De Frenne et al., 2011). Conversely, a combination of habitat fragmentation, and low proportions of core populations means forest species may remain absent entirely (Brunet et al., 2011), particularly with a concurrent loss of dispersal vectors (Ozinga et al., 2009).

The association of our specialist indicator species with conifer plantations needs to be interpreted with caution, as our exploratory analyses revealed conifer cover was associated with other variables such as landscape class, soil type and pH. We cannot fully disentangle these factors in our study, and it is likely some element of proximity to woodland, continuity associated with historic or refuge woodland habitats, and appropriate soil conditions combine to favour specialist species in these sites. For example, some slow colonisers may have found refuge in fringe relic habitats in our landscape i.e. small strips and patches of native woodland habitat (Honnay et al., 1999) located in proximity to sites. Additionally, our specialist group also includes a number of fern species, known to be faster colonists due to their minute wind-dispersed diapsores (Brunet et al., 2012), as well as wind-dispersed birch saplings, which could have colonised from more distant woodlands. The occurrence of ancient woodland indicator species in our younger plantations does not imply these sites were ancient in origin, nor does it suggest the ancient woodland indicator list lacks credibility, as these indicator species were recorded at low frequencies and did not approach thresholds specified for ancient woodland classification (Perrin and Daly, 2010).

While our results indicate woodland generalists may be colonising sessile oak sites significantly more than our other tree species categories, this effect appears to be explained mainly by the bryophyte component of this group. Bryophyte communities show associations with different forest types driven by substrate moisture, fertility and pH (Kutnar et al., 2023; Stefańska-Krzaczek et al., 2022) as well as canopy cover (Petersson et al., 2021), and the bryophyte community in sessile oak woodlands is known for its richness (Cross, 2012). With the exception of species with high substrate-specificity (Mölder et al., 2015), bryophytes are effective dispersers (Vanderpoorten et al., 2019) and may establish more readily in older sessile oak sites on lower fertility soils where there may be less competitive pressure from vascular plant species (Cornwell & Grubb, 2003; Müller et al., 2019) and greater substrate availability, conditions which are also likely to favour woodland specialists (Hermy et al., 1999). As we only surveyed forest floor bryophytes (i.e. epigeic and epixylic species), our surveys did not record many of the more specialist epiphytic species, and hence many of the generalist forest floor species we encountered could also occur in,

and have spread from, hedgerows and nearby areas of semi-natural or plantation woodland. Bryophyte mats on the woodland floor have also been found to enhance seedling establishment (Rehm et al., 2019) pointing to potential synergies between the expanding bryophyte community and colonisation of tree species in our older sites, and highlighting their potential as an interim indicator of woodland development in young plantations.

The legacy of former land use can also act as a strong environmental filter, with restoration on former woodland sites yielding more positive results in terms of the composition of the target habitat, potentially attributed to an ancient woodland seedbank (Kirby et al., 2017). As the reforested conifer plantations in our study were also older sessile oak sites, we expected forest type (afforested or reforested) might influence our woodland species richness models, however it was not significant in any model once the site age was accounted for. While the composition of the reforested community appears to be distinct, we caution that this was potentially influenced by a small sample size, and further research focusing on afforested versus reforested sessile oak sites would be warranted. The size of the woodland did not appear to be an important factor explaining the richness of any grouping, though may emerge as a more important driver over time (Pedersen et al., 2023), as has been identified in other studies (Waddell et al., 2024).

Looking at the whole vascular plant community, the RLQ /fourth corner analyses draw together the strong and interacting gradients of change driven by landscape, light and soil characteristics. The plant species characterising the sessile oak woodlands had a negative association with fertility and acidity and were generally stress-tolerant, with a contrasting trend for higher fertility soils and pedunculate oak. These mainly upland sites were associated with a floral community characteristic of semi-natural grasslands or heathlands, in contrast to ruderal species which dominated the pedunculate oak end of the axis, having readily colonised from disturbed fertile agricultural soils. Site specific soil chemistry has also been found to account for much of the variation in plant species composition (Ferris et al., 2000; Wilkins & Aherne, 2016) between forest sites. Higher levels of nutrients favour highly competitive and fast-dispersing species such as nettle and bramble (*Rubus fruticosus* agg.), limiting the ability for forest species to establish or persist (Baeten & Verheyen, 2017; Brunet et al., 2021; Hermy et al., 1999; Verheyen et al., 2003). Though these effects may decline as light levels lower (Baeten & Verheyen, 2017; Kirby et al., 2017), they can present again in scenarios such as ash dieback (Baeten & Verheyen, 2017).

Taken together, the dual gradients of age or light, and land use intensity or soil fertility, strongly influence the pattern of woodland species assembly with implications for setting biodiversity targets for native tree planting schemes. Our findings highlight the challenge of disentangling the various factors driving the establishment of planted woodlands but point to the greater potential for woodland indicator species to establish in less intensive landscape settings, where land use legacies may favourably interact with environmental gradients. Though this suggests expectations may need to be moderated in higher fertility contexts, afforestation decisions must be balanced with the

potential for native tree plantations on degraded lands to nonetheless deliver a long-term biodiversity gain in those landscape contexts (Bremer & Farley, 2010; Felton et al., 2010).

2.5.3 Meeting target woodland type

The survival and growth of key tree species coupled with establishing woodland flora means as a whole our closed-stage pedunculate oak and alder sites are meeting their target woodland type based on the output of the habitat classification tool. The lower level of alignment in the sessile oak category is due to a proportion of sites being assigned to birch habitat classes, inclusive of some communities known to represent seral stages in succession to sessile oak forest (Cross, 2012; National Biodiversity Data Centre, 2024). As birch is a fast-growing pioneer species (Hynynen et al., 2010), their dominance could be explained by natural colonisation from the wider landscape during the forest establishment phase, potentially combined with adverse impacts of birch growth on planted oak sapling development (Liziniewicz et al., 2016; Rock, 2004). Intervention in the form of tending and thinning is needed to ensure early successional species such as birches (*Betula* spp.) and willows (*Salix* spp.) do not limit the potential for successful oak growth (Liziniewicz et al., 2016) or regeneration (Mölder et al., 2019), while effects of browsing and competitive plant species need to be considered in a local context for optimal outcomes (Kelly, 2002).

We were also interested to see whether, excluding planted tree cover, comparison with NFI data indicated whether our older woodlands were compositionally aligned with semi-natural woodlands from the same study area. While our oldest sites were compositionally similar to semi-natural woodland in general, the specific semi-natural habitat categories identified in the NFI were not compositionally distinct, and so we cannot infer alignment with any particular target woodland category. The woodland floral communities in Ireland reflect the intersection of edaphic, hydrological and climatic gradients (Kelly, 2005), and therefore a continuum of change is exhibited. It is also possible that, aside from mature high-quality conservation sites, the ground flor and understorey in younger sites, or those in sub-optimal condition, is somewhat homogenous. Phytosociological classifications of semi-natural woodlands, as summarised by (Perrin et al., 2008), inherently include the tree cover. Conservation condition monitoring protocols (O'Neill & Barron, 2013; Perrin et al., 2008) additionally consider a range of structural and functional attributes that characterise particular woodland habitats. Hence relying on compositional similarities of lower forest layers alone for the purpose of habitat classification or condition-assessment will have its limitations.

At the other end of the age spectrum, habitat classification indicates that 30% of sites support grasslands that have the potential to develop into species-rich communities, with the RLQ analysis revealing an association with younger sessile oak sites and stress-tolerant grassland and heath species. This pattern implies that species-rich grasslands may represent a transitory state, emerging due to reduced grazing pressure following afforestation, but it also highlights that species-rich

grassland itself could represent an alternative restoration target for some sites, rather than a temporary phase on the path to woodland development.

2.6 Conclusions

The data revealed a clear transition in vegetation structure and composition from grassland to woodland habitats over the course of woodland establishment. A high proportion of older plots achieved their target habitat classification, indicating successful habitat development, and we also observed increased natural colonisation by young trees with stand age. While such structural and compositional changes were expected, the extent of colonisation by woodland specialist species, and the strong alignment of most older sites with their target woodland habitat, was less anticipated. Furthermore, the analysis of plant traits highlighted an imprint of past land use, reflected in a landscape gradient that may favour the establishment of specialist flora.

We need a diversity of habitats in our landscapes, as well as connectivity between them, in order to facilitate landscape level nature recovery (Lawton, 2010) as complex agricultural landscapes host more biodiversity than simple ones (Estrada-Carmona et al., 2022). Our research helps with understanding the changes in floral biodiversity in planted native woodlands and suggests NWS sites are on a positive trajectory towards meeting their target woodland habitat, with the potential to help expand biodiverse and resilient forest networks.

CHAPTER 3

The changing nature of biodiversity in transitioning habitats: a case study using pollinators as indicators

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3 The changing nature of biodiversity in transitioning habitats: a case study using pollinators as indicators

3.1 Abstract

The creation of native woodlands is playing an increasingly prominent role in international efforts to address biodiversity loss and climate change, driven not only by public policy and conservation goals but also by the growing influence of carbon and biodiversity offsetting projects. The monitoring of appropriate biodiversity metrics is essential for optimising and validating afforestation outcomes, however young plantations may hold ecological value that traditional forest monitoring metrics fail to capture. This study explores the potential of pollinating insects, specifically bees and hoverflies, as indicators of biodiversity change in newly planted native woodlands in Ireland. We surveyed 18 young native woodland plantations using a combination of pan trap and transect walk methodologies. The data revealed an initial decline of open-habitat specialists associated with the interior areas of the plantations. Beta diversity metrics and interaction networks uncovered more nuanced community dynamics, highlighting differences between bees and hoverflies and suggesting that off-site influences may have a stronger effect on hoverfly communities than on the bee community, likely due to differences in their foraging strategies. Our findings demonstrate how pollinator data can offer multiple insights depending on the metrics applied. These metrics, whether used for ecosystem service assessment or conservation policy, could help set interim targets for tracking afforestation progress. This study emphasises the challenges of monitoring transitional habitats and the importance of selecting appropriate sampling methods, target taxa, and biodiversity metrics.

3.2 Introduction

Afforestation plays a central role in global biodiversity and climate strategies, supported by both public policy and private initiatives. While robust methods exist to assess the carbon sequestration potential of new forests, evaluating their biodiversity value remains a significant challenge. Although a substantial body of research addresses forest biodiversity metrics, much of it focuses on intensively managed production forests or mature natural woodlands, often relying on assessing woodland indicator taxa that require specialist expertise (Ampoorter et al., 2020; Burrascano et al., 2023). In newly established woodlands, traditional vegetative indicator metrics may offer insights into whether sites are progressing toward desired habitat types. However, such early-stage habitats may possess ecological value that these metrics fail to capture. This highlights the need for more appropriate approaches to measuring biodiversity in young planted woodlands, in order to better reflect their emerging contributions to nature.

Habitat metrics based on vegetation structure and composition, such as the UK's Biodiversity Net Gain metric (DEFRA, 2024; McVittie & Faccioli, 2020), are widely used demonstrate the uplift or net gain associated with biodiversity-enhancing interventions like woodland creation or restoration. However, such habitat-focused metrics often fail to capture changes at the species level (Marshall et al., 2024). Emerging biodiversity credit methodologies, such as that developed by the Wallacea Trust (Wallacea Trust, 2023), are moving towards a 'basket of metrics' approach. These typically combine a habitat-based metric with at least one faunal indicator, commonly birds or invertebrates, to provide a more holistic assessment of biodiversity outcomes. It is anticipated that the selection of metrics will vary by region and intervention type, with appropriate indicators and survey methods tailored to local ecological contexts (BCA, 2024). Nevertheless, both the selection of component metrics and the methods used to combine them remain contested, raising ongoing debates around standardisation, transparency, and ecological validity (Duffus et al., 2025; Wauchope et al., 2024).

In this study, we examined the challenges of measuring and monitoring a faunal group as an ecological indicator (Noss, 1990) across the establishment phase of a newly planted woodland. We focused on pollinating bees and hoverflies, a diverse group comprising species adapted to both grassland and woodland habitats, as well as generalists, whose role in forest biodiversity is underrepresented in current research (Tinya et al., 2023). Trends in these taxa can reflect underlying patterns in the flowering plant community and habitat structure (Eckerter et al., 2022; Kennedy et al., 2013; Roberts et al., 2017). Bees and hoverflies also exhibit distinct life history traits: bees are central place foragers whose larvae consume pollen (Goulson, 2010), while hoverflies lay eggs independently of foraging sites, and their larvae display a variety of feeding strategies (Doyle et al., 2020). Many common species within both groups are key crop pollinators (Klein et al., 2007), with the larvae of aphidophagous hoverflies also acting as biocontrol agents for aphid crop pests (Stubbs & Falk, 2002). Consequently, monitoring these taxa offers potential not only as a biodiversity indicator but also for assessing ecosystem functioning and the provision of ecosystem services. In addition, pollinating insects are the focus of specific targets for restoration and conservation as part of the EU Biodiversity Strategy (European Commission, 2020a) and EU Nature Restoration Law (Regulation (EU) 2024/1991), and established monitoring protocols for these groups are already well developed (European Commission, 2021b).

Numerous studies have investigated how pollinator communities respond to both local and landscape-scale factors in forested environments, yielding varied outcomes depending on the taxa assessed, biodiversity metrics applied, successional stage, sampling location, timing of surveys, and broader landscape context (Proesmans et al., 2019a; Rivers-Moore et al., 2020; Roberts et al., 2017; Taki et al., 2007, 2011; Winfree et al., 2007). Additionally, commonly used survey methods have been shown to preferentially detect certain taxa over others, potentially biasing results (Boyer et al., 2020; O'Connor et al., 2019). The response of the pollinator community to establishment-phase native woodland plantations in agricultural landscapes has received little attention, and we are not

aware of any studies focusing solely on early development stages (<20 years) in this context, despite this being a period of rapid structural and compositional change in vegetation, during which management interventions can be especially impactful. In this context, we anticipate that pollinator community dynamics may reflect both an extinction debt (Tilman et al., 1994) due to the loss of open grassland habitat, and a colonisation credit (Jackson & Sax, 2010) reflecting delayed colonisation by woodland specialists, potentially clouded by the response of the generalist community. We also expect the pollinator community to respond to changes in floral resource availability, and for bees and hoverflies to exhibit differing responses, due to their contrasting life histories and resource requirements.

We used sites recently planted with native trees under the afforestation programme in the Republic of Ireland (DAFM, 2024b) as a case study to explore the use of pollinators as an indicator of biodiversity change. This government scheme, facilitating afforestation via the planting of native woodlands, is generally targeted at farmers and private landowners. Our study sites are located within an agricultural landscape, and were planted on fertile soils formerly used for livestock or arable farming.

Specifically, we tested the following hypotheses;

1. Pollinating insect communities change over the transition from an open to a closed-canopy habitat, in line with changes in floral resource availability, and with taxon specific patterns driven by phylogeny (i.e. differences between bees and hoverflies) and ecological traits (including habitat and floral preferences);
2. The sampling methods used, timing and location of sampling, and biodiversity metrics applied to samples, influence our interpretation of how the communities are changing with consequences for their use as indicators.

The implications of using pollinating insects as a biodiversity metric for the creation and enhancement of native woodland are explored, and practical recommendations for monitoring discussed.

3.3 Materials and Methods

3.3.1 Study region and site selection

The study was conducted in the agricultural landscape of the east and midlands of Ireland (Fig.3.1), corresponding to the study region previously explored in Chapter 2. Study sites were primarily afforested under a government scheme that funds the planting of native woodland and subsequent provision of subsidies to landowners. The scheme has been in operation since 2001, and while funding provision and uptake has varied with the economic context over time, afforestation under this scheme has been increasing since 2015 (DAFM, 2023a). We selected a chronosequence of 18

new woodland sites (a subset of sites used in Chapter 2), planted between 2002 and 2021 on lowland agricultural grassland, predominately with pedunculate oak (*Quercus robur*), and on mineral soils (Appendix B, Table B1). The subset was chosen on the basis of landowner permission and travel logistics that allowed for multiple site visits within the daily sampling window. Our sites were grouped into three woodland development stages (Fig. 3.2): 'Open' sites which were characterised by young trees in a post-planting phase and were 2-6 year's old at the time of survey; 'Thicket' sites where tree branches were touching but the understorey was still dominated by grasses, and which were 8-12 year's old at the time of survey; and 'Closed' sites, between 15 and 21 year's old, where the closing canopy of maturing tees had shaded out most of the ground flora. Locations were chosen to ensure that sites of each development stage were spread throughout the region. To ensure independence of pollinator communities, sites were all at least 2km apart from each other, with 2km considered the typical limit of the foraging range for pollinating species (Osborne et al., 2008; Zurbuchen et al., 2010), notwithstanding hoverfly migrations (Doyle et al., 2020).

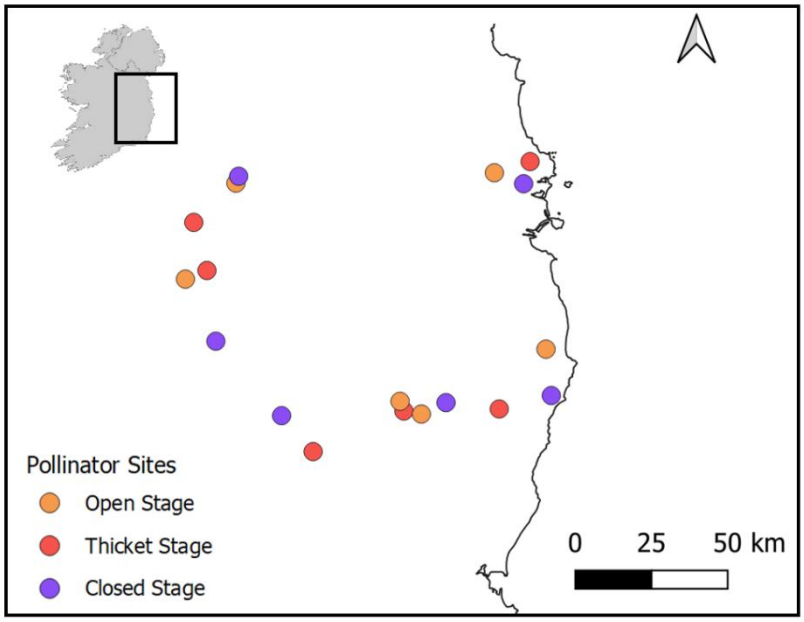

Figure 3.1 Study region in east and midlands of Ireland, with site locations colour-coded by woodland stage

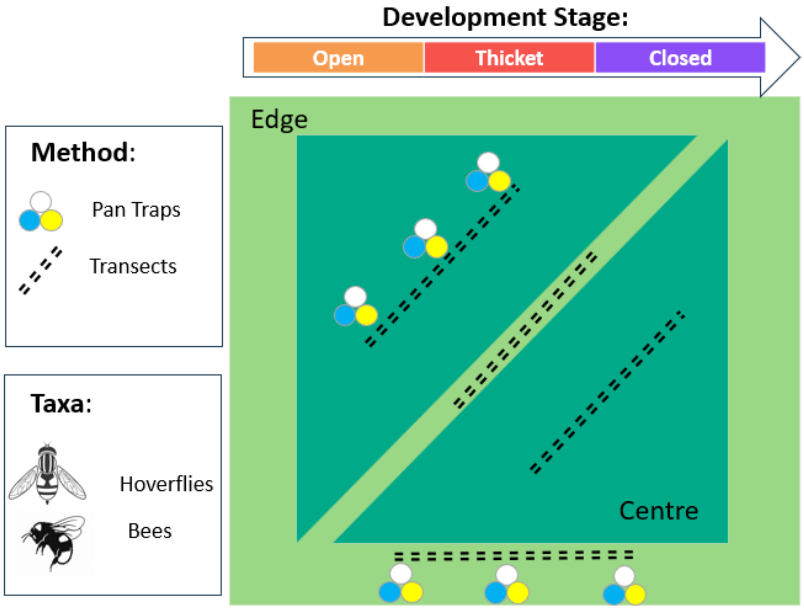

Figure 3.2 Study design. Pan traps (blue, white and yellow circles) and transect walks (dashed lines) were used to assess hoverflies and bees in each woodland site, both at woodland edges (peripheral or internal e.g. paths/wayleaves – shown in lighter green), and in the planted areas (darker green). The arrow indicates the three woodland development stages, with each site belonging to one stage: Open (young trees in a post-planting phase, 2-6 year's old), Thicket (tree branches touching but understorey dominated by grasses, 8-12 year's old), and Closed (closing canopy of maturing tees shading out most of the ground flora, 15 and 21 year's old).

3.3.2 Pollinator and floral resource sampling

Bumblebees, solitary bees and hoverflies were sampled using standardised transect walks and pan traps, both considered robust sampling methods for pollinating insects (European Commission, 2021b; Westphal et al., 2008). All sites were sampled within a 2 week period in each of three survey rounds between late-April to late-July 2023, representing the main period of pollinating insect activity in Ireland.

At each visit, two edge and two central 100m transects were walked (Fig. 3.2). Central transects were at least 10m from the edges of the planted area to minimise extreme edge effects. Transects were walked between 10:00 and 16:00 at a slow steady pace for 10-15 min in dry, bright conditions (temperature >13˚C, wind force 0-4 Beaufort scale). Typically, two sites were surveyed per day, one in the morning and one in the afternoon, and time of day each site was visited (am or pm), as well as the order in which transects were walked, were alternated across the sampling rounds to control for time-of-day bias in sampling effort. Individual insects and their behaviour were recorded up to 2 m on either side, above and in front of observer, with the plant species noted if the insect was foraging. Any individuals that could not be identified on the wing in the field were captured using a sweep net and frozen for later identification in the laboratory.

Pan trapping was undertaken along one edge, and one central transect, at each site visit. The plastic 12oz bowls used for the pan traps were painted with UV-bright fluorescent paint in white, blue and yellow colours to mimic attractive flowers (Moreira et al., 2016). At three points along each transect, a cluster of three painted plastic bowls (one of each colour) were attached to 1.8m high wooden stakes (9 bowls in total per transect) with an adjustable metal clamp (as per Stanley and Stout (2013)). Each set of pan traps were placed at the same height as the surrounding field/shrub layer of vegetation. Traps were filled with water and a drop of detergent to reduce surface tension, erected prior to 10am, and left for 7-9 hours. Collected specimens were stored in vials containing 70% IMS with 5% glycerol, before sorting and identification of wild bees and hoverflies in the laboratory following Stubbs & Falk (2002), Ball & Morris (2015) and Falk (2015).

During each sampling round, the abundance and species richness of flowering plants in bloom (excluding Order Poales) were recorded using ten 1 × 1 m quadrats were placed at regular intervals along each transect. Identification followed Stace (2019), and the floral unit abundance of each species was counted (Dicks et al., 2002). During the second round, other ground and vegetation cover variables (litter, bare ground, grassy hummocks, stems, holes, shrubs) were also recorded.

3.3.3 Data Analysis

Transect and pan trap data were initially analysed separately to examine patterns in species richness and abundance between bees and hoverflies, as these methods have been found to favour different taxa (Boyer et al., 2020; O'Connor et al., 2019). During the second sampling round, pan traps captured a notably low number of individuals (Appendix B, Fig. B1), likely due to the high availability of floral resources at the time, particularly flowering bramble (*Rubus fruticosus* agg.), which may have reduced trap attractiveness (Westerberg et al., 2021). Due to this sensitivity to the immediate floral environment and poor catch performance for certain taxa (Potts et al., 2021), pan trap data were excluded from species abundance analyses. For species richness analysis, transect data were aggregated within each location type (i.e. the two edge transects combined and the two centre transects combined) to allow comparison with pan trap data. Unless otherwise stated, data from the three survey rounds were pooled for analysis, with site as the level of replication of interest.

To describe floral resources, two metrics were used; floral richness, defined as the number of vascular plant species flowering at the time of survey, and floral area, calculated as the product of the number of floral units recorded and the average flower unit size. The latter was derived from an online database of Irish wildflowers (www.irishwildflowers.ie) and/or species descriptions from Stace (2019), and is intended to serve as a proxy for the overall floral reward available to pollinators (Ortiz et al., 2021).

Data on species traits and habitat affinities for bees and hoverflies were collated from published data sources (Appendix B, Table B2 and B3) including Falk (2015), Speight et al. (2020), Speight

& Castella (2020), and Webb et al. (2018). On the basis of these data, each species was assigned to a habitat preference category (open habitat specialists, generalist or woodland specialist).

Using the buffer and intersection QGIS tools, the extent (m^2) of 'Level 2' habitat in a 2km matrix surrounding the site was calculated from the National Landcover Map (EPA & Tailte Éireann, 2024). We used the following habitat categories: Conifer Forest, Broadleaf Forest, Transitional Forest, Mixed Forest, Scrub, Wet Grassland, Dry Grassland, Improved Grassland, Cultivated Grassland, Bare Ground, Lakes, Artificial Surfaces, Buildings, Amenity Lands, Treelines and Hedgerow. We also calculated the combined extent of habitats within the following broader groupings: all forest/woodland habitats, all semi-natural grassland habitats, all agricultural grasslands, and all linear boundary habitats.

All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2023). We computed species richness accumulation curves and sample coverage curves for each woodland stage using the *iNEXT* R package (Hsieh et al., 2016).

To test for differences in species richness/abundance metrics across categorical variables, non-parametric Kruskal-Wallis (K-W) tests were employed, assuming independent observations, rankable data, and similarly shaped group distributions. Where significant differences were found, Dunn's post-hoc tests with Bonferroni correction were applied to identify specific group differences.

To analyse relationships between developing woodland sites (site age or woodland stage), their floral resources (floral richness or area), woodland size, the location of the transect (edge or centre) and the abundance and richness of pollinators (response variables), generalised linear mixed models (GLMMs) were used. As there was a relationship between woodland stage and site age, and between floral richness and floral area, these fixed effects were analysed in separate models. Landscape variables that showed at least a moderate correlation with our response variables ($R>0.3$) were also added to models (Appendix B, Fig. B2). GLMM's included transect location as a fixed effect, with site as a random factor to account for two transects within each site and avoid pseudoreplication.. We scaled and centred all continuous variables to improve the performance and interpretability of the models. All GLMMs were fitted using the *glmmTMB* R package (Brooks et al., 2017).

Poisson error distribution using a log-link function was specified for count data and the negative binomial distribution was specified for abundance data. Initial models included 2-way interactions between fixed effects. The most parsimonious model was selected by sequentially removing the least significant interactions and terms, while at each step the corrected Akaike's information criterion (AICc) was used to compare candidate models. We then inspected the distribution of residuals, dispersion and checked for zero-inflation, spatial autocorrelation and influential points using the *DHARMa* R package (Hartig, 2022). To deal with multicollinearity issues, we calculated

the variance inflation factor (VIF) of each predictor using the 'car' R package (Fox & Weisberg, 2019), we checked that VIF <4 (Zuur et al., 2013) which indicated no strong correlation among predictors.

We confirmed that the best-fitting model differed from the null model using the *ANOVA* function in the in *lme4* R package. Taking the selected model we used the *emmeans* R package (Lenth, 2024) to obtain model predictions that were plotted with the *ggplot2* R package (Wickham, 2016).

To visualise pollinator community composition, we used non-metric multidimensional scaling (NMDS) ordination and fitted environmental vectors to the ordination plot using the *envfit* function (*vegan* R package) (Oksanen et al., 2022). Shortened taxa names used in plots are provided in Appendix B, Table B2 & B3. We confirmed homogeneity of variances using the *betadisper* function prior to using permutational analysis of variance (PERMANOVA) to test for differences in community composition across woodland stages (*adonis* function). The PERMANOVA tests were based on Bray–Curtis dissimilarity between sites for the abundance dataset, and Jaccard dissimilarity for the species richness dataset. We then used the R package *pairwiseAdonis* (Arbizu, 2017), which applies a Bonferroni correction for multiple comparisons, to test for difference between stages.

We further compared pollinator community composition across the woodland stages by computing beta diversity metrics. We used the *betapart* package (Baselga, 2010), with which it is possible to partition the Sørensen index of beta diversity, a measure of total dissimilarity, into its two components, species turnover and species nestedness. Only presence/absence data from the combined pan trap and transect dataset were used for these calculations. We calculated overall beta diversity (*beta.multi* function) and then pairwise dissimilarity (*beta.pair*). We used *adonis* tests to test for differences in the partitioned elements of community composition across woodland stages. We also used Mantel permutation tests (*mantel* function in *vegan*, n = 9999 permutations) to compute correlations between these partitioned matrices with a distance matrix for site age.

Finally, we built plant–pollinator interaction matrices, using the total number of visits by each pollinator species to each plant species grouping interactions across woodland stages, and also across sampling rounds, and used the *plotweb* function in the *bipartite* R package (Dormann, 2011) to illustrate the interactions. We then used the *networklevel* function to calculate Network specialization (H2), which measures the overall level of specialization of the interacting species in a network (Blüthgen et al., 2006) varying from 0 (fully generalised network) to 1 (fully specialised network).

3.4 Results

A total of 1,414 individuals were observed on transect walks, comprising 1,028 hoverflies (Diptera, Syrphidae, 37 taxa), 335 bumblebees (Hymenoptera, Apidae, *Bombus* spp, 8 taxa) and 51

solitary bees (Hymenoptera, Apoidea, 7 taxa). Additionally, a total of 494 individuals were collected in pan traps: 222 hoverflies (32 taxa) 88 bumblebees (8 taxa) and 184 solitary bees (23 taxa). A total of 12 bee and 22 hoverfly taxa were common to both the transect walk and pan trap sampling methods.

In total, 68 flowering plant taxa were recorded on the surveyed transects, of which insect foraging interactions were observed with 36 taxa. In terms of the overall number of floral units recorded, hawthorn (*Crataegous monogyna*) flowers were most abundant (20,247). Floral area, a metric taking account of the size of flowers, was highest for bramble (*Rubus fruticosus* agg.) (61,975). Most insect visits were recorded on bramble (197 of 551 total visits) followed by dandelion (*Taraxacum officinale* agg.) (116 of 551 total visits).

Richness-based species accumulation curves for bees and hoverflies in each woodland stage level-off, suggesting sampling effort captured the majority of species present in the study area in the year of sampling, while sample coverage curves approached saturation (all over 97%) indicating thorough sample coverage (Appendix B, Fig. B3a -d).

3.4.1 Abundance & Richness of Bees and Hoverflies

The overall (total) species richness of hoverflies and bees did not significantly change across the woodland development stages (Fig. 3.3 a-b), with abundance following a similar trend (Appendix B, Fig. B4). In contrast, there were significant declines in floral resources across the woodland stages (Fig. 3.4 a-b), mirrored by a negative correlation with site age with floral richness (Spearman rank correlation $R = -0.66$, $p = 0.003$) and floral area (Spearman rank correlation $R = -0.62$, $p = 0.006$)

The richness of hoverflies classed as open habitat specialists declined significantly between the open and thicket stages, and open and closed stages (Fig 3.3a and Appendix B, Table B4), with a similar trend observed for the abundance of hoverflies (Appendix B, Fig. B4). There was no significant change in the number of generalist or woodland specialist hoverflies, with numbers of the latter low across all stages.

As the woodlands develop, there was no significant change in the number of bee taxa that can be classed as open habitat specialist, generalist species, and woodland specialists (Fig 3.3b and Appendix B, Table B3). The bee community was dominated by ground-nesting (94% of total no. of taxa) primarily polylectic taxa, and is otherwise split between smaller bodied solitary bees, larger bodied social bees, with cleptoparasites of both groups recorded (Appendix B, Table B3). The mean number of cleptoparasite taxa in closed stage sites was significantly greater than open stage sites, though species richness was low in all cases (Appendix B, Fig. B5 and Table B4). Significantly more solitary bees were caught in the first sampling round, while significantly more bumblebees and hoverflies were caught in the last sampling round (Appendix B, Fig. B6 and Table B4).

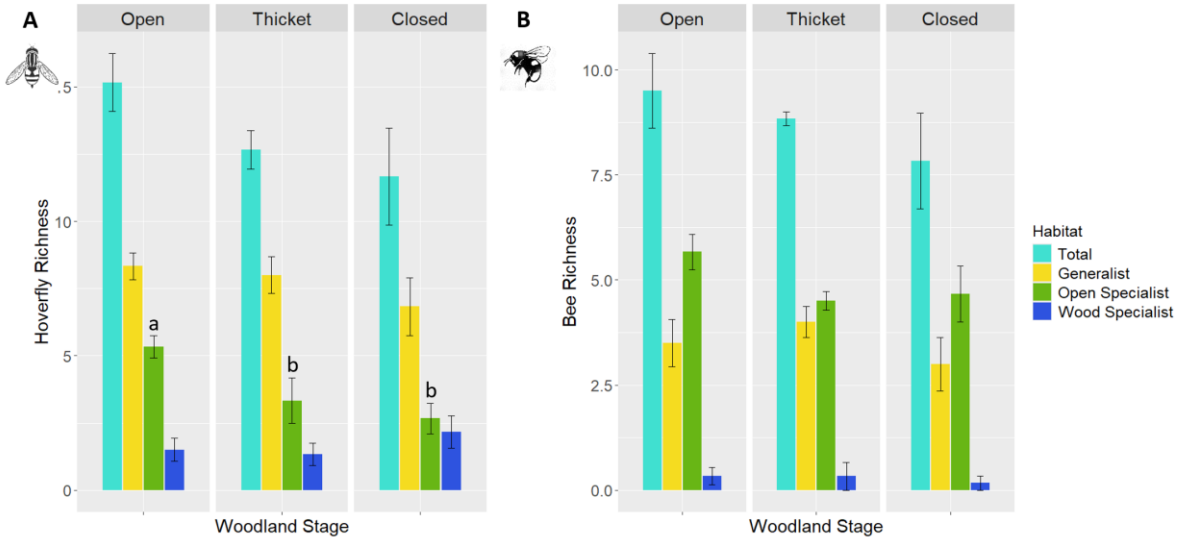

Figure 3.3 Mean (±SE) of (A) Hoverfly and (B) Bee (Solitary and Bumblebee) Richness across Woodland Stages (Open, Thicket and Closed). Letters over a bar indicate significant differences between stages for that attribute, tested with Kruskal-Wallis (K-W) tests followed by Dunn's tests (Table B4).

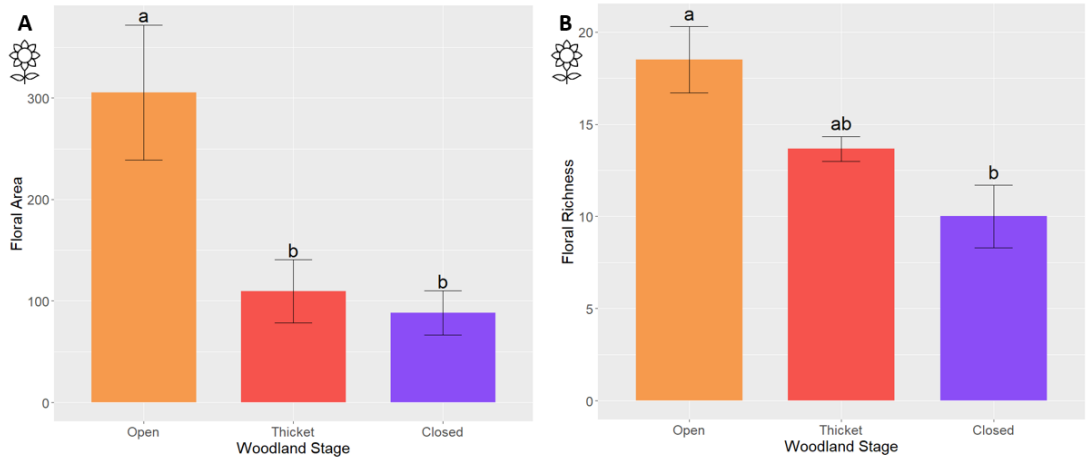

Figure 3.4 Mean (±SE) of (A) Floral Area and (B) Floral Richness, across Woodland Stages (Open, Thicket and Closed). Letters over a bar indicate significant differences between stages for that attribute, tested with Kruskal-Wallis (K-W) tests followed by Dunn's tests (Table B4).

Regression models indicated that abundance of both bees and hoverflies was positively associated with woodland edges and significantly associated with increasing floral area (Fig. 3.5a-b and Appendix B, Table B5), while the size of the woodland also explains bee abundance (Appendix B, Table B5). Hoverfly abundance was also significantly lower in areas with more improved

agricultural land in the surrounding matrix. Within the bee community, the abundance of bumblebees responded to floral richness, though this model needs to be interpreted with caution (Appendix B, Table B5). The abundance of solitary bees reflected an interaction between site age and transect location (Appendix B, Table B5).

Models for hoverflies and bee species richness suggested there was a significant interaction between age and transect location, with a lower number of species within central transects in older sites relative to younger sites (Fig. 3.5c-d and Appendix B, Table B5). Within the bee community, significant explanatory variables for bumblebees and solitary bees were similar to the abundance models, but only explained a small proportion of the variance (Appendix B, Table B5).

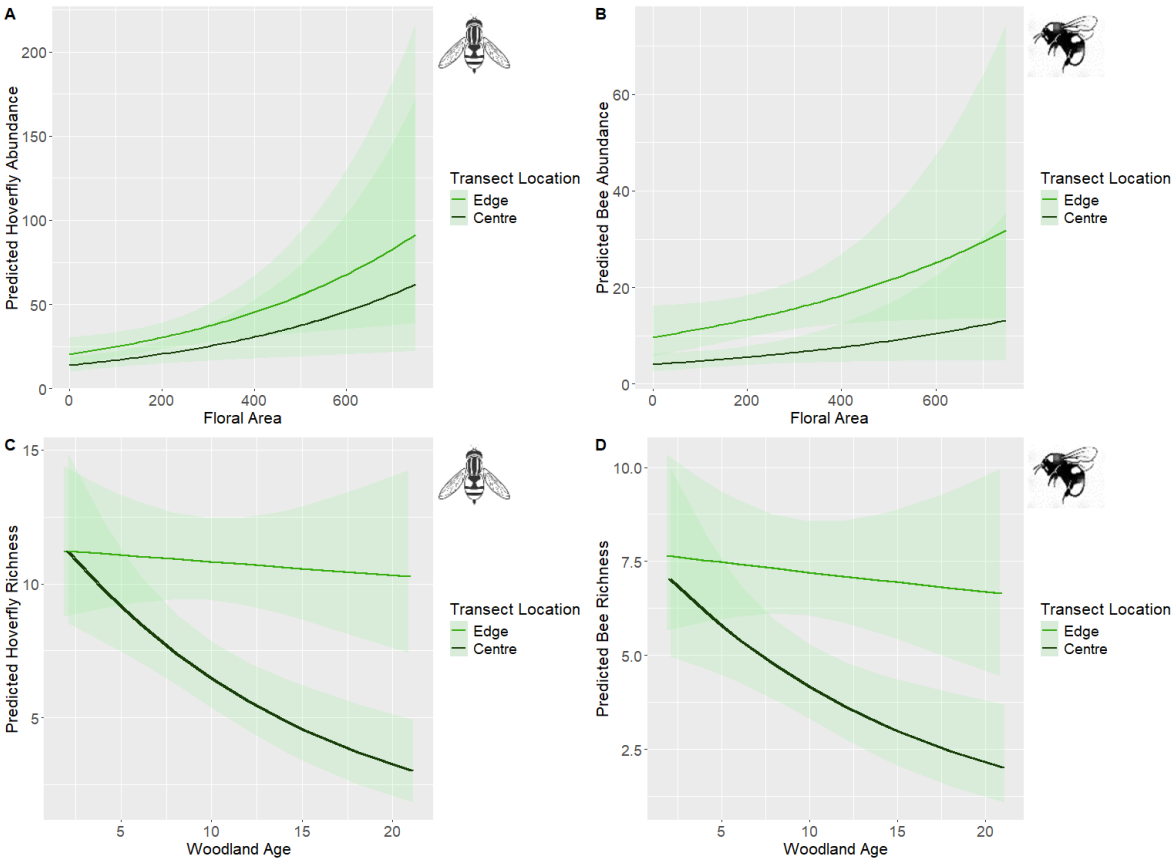

Figure 3.5 Predicted (A) Hoverfly Abundance (B) Bee Abundance, (C) Hoverfly Richness and (D) Bee Richness in Edge and Centre transects, versus predictor variables from best-fitting models. The first fixed factor is plotted on the y-axis and all other fixed effects terms held at their mean values, with random effects excluded. In each plot, the estimated relationship is shown as a solid line or point, with the 95% CI shown as a ribbon or bar

3.4.2 Community Composition

The hoverfly communities in open and closed habitats showed divergence (Fig. 3.6a and b) based the abundance dataset, but these stages generally overlapped in the presence/absence dataset. Plots for the bee community showed little difference between stages for the abundance dataset (Fig. 3.6c), but the open and closed communities diverged for the presence/absence dataset which benefited from the increased capture rates of solitary bees pan trap data (Fig. 3.6d). For both bees and hoverflies, the shift in community composition of closed sites aligned with increasing woodland age, while the shift in community composition of open sites was associated with increasing floral richness and area.

The PERMANOVA results indicated there were significant differences between the open and closed stages, and open and thicket stages, for hoverfly abundance (Appendix B, Table B6), reflecting the notable separation of these communities on the ordination plot (Fig. 3.6c). A similar significant difference between open and closed communities was observed for floral presence-absence (Fig. 3.6e), and floral area (Fig. 3.6f).

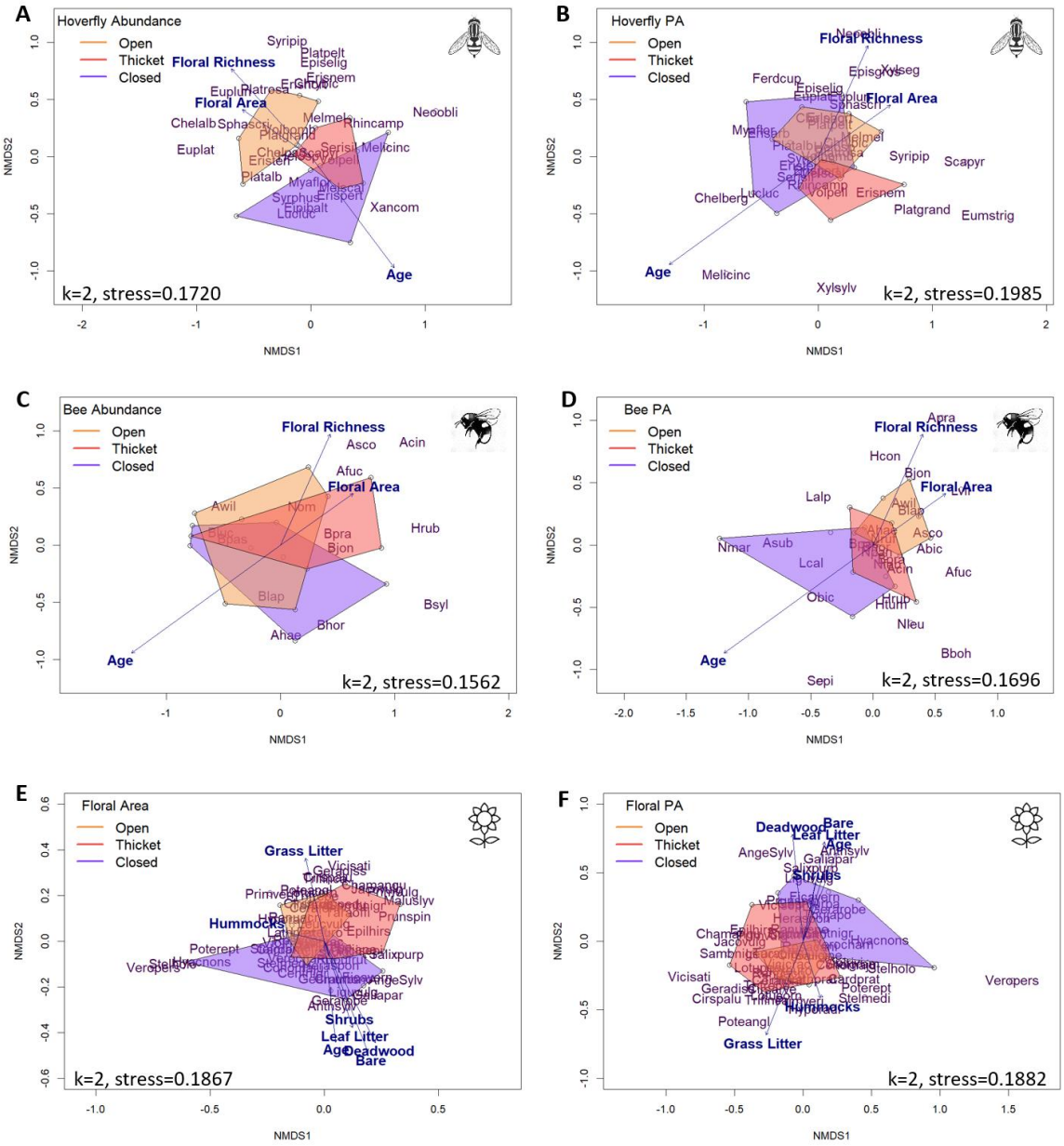

Figure 3.6 NMDS Ordinations for (A) Hoverfly abundance (transects only) and (B) hoverfly presence absence (PA) (Pans and transects), (C) Bee abundance and (D) bee presence absence, (E) Floral Area and (F) Floral Richness. Dimensions (k) and stress value given in bottom right of each plot. Floral and vegetation cover variables, described in Section 3.3.2, are shown as fitted vectors. Refer to Appendix B, Table B2 and B3 for bee and hoverfly name codes.

Beta diversity across sites was largely explained by species replacement (turnover) (Table 3.1).

Correlating overall beta diversity with increasing differences in pairwise site age (Fig. 3.7 and Appendix B, Table B7), revealed a positive relationship for both bees and hoverflies. Partitioning beta diversity showed that the correlation was explained by increasing site turnover for bees but not for hoverflies.

Applying PERMANOVA tests to the partitioned matrices (Appendix B, Table B8) similarly revealed significant differences in overall beta diversity, and in the turnover portion, between open and closed stages for bees. This analysis also suggested that there was a significant difference in overall beta diversity between open and thicket stages for hoverflies.

Table 3.1 Beta Diversity Partitioning for Bee and Hoverfly communities

Community	Overall Beta Diversity	Turnover	Nestedness
Bees	0.817917	0.7534517	0.06446529
Hoverflies	0.8210188	0.7556391	0.06537972

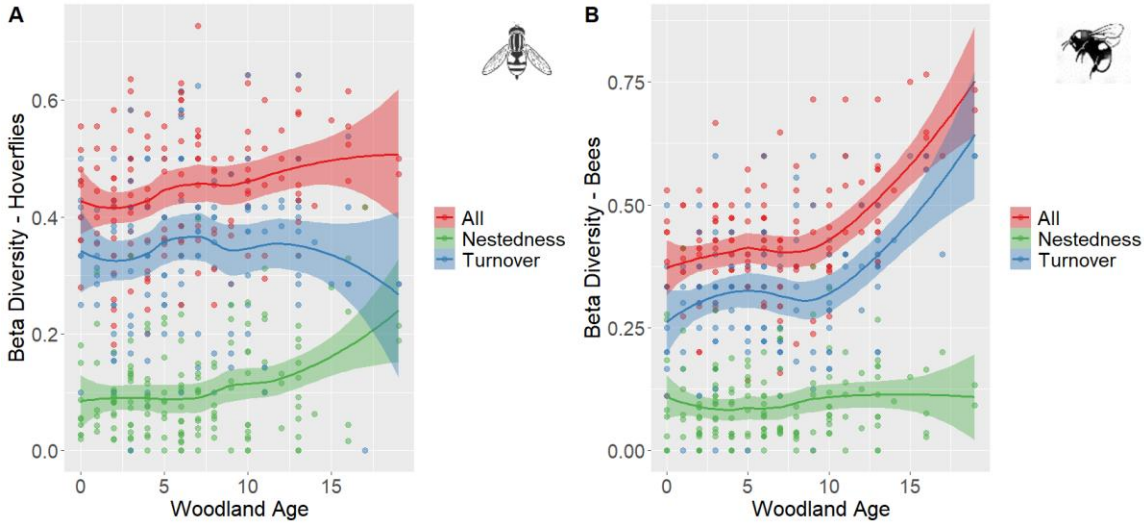

Figure 3.7 Pairwise beta diversity, and its turnover and nestedness components, plotted against pairwise age differences for our study sites for (A) hoverflies and (B) bees. A loess fitted line with associated estimate of variation has been applied.

3.4.3 Interaction Networks

All networks revealed the importance of bramble as a foraging resource (Fig. 3.8), particularly mid-season. The late season network highlighted that the abundance and diversity of common flora present at our study sites supported a wide range of pollinators (Fig. 3.8c). Splitting these networks across the growth stages (Appendix B, Fig. B7), illustrated how bramble dominated the thicket-stage site network, and also featured strongly in the closed-stage site network. The flowering trees and spring flowers appeared to be of greater relative importance in the closed-stage woodland sites. The network specialisation metric is low in all cases, ranging from 0.202 to 0.415, indicating networks were generalised.

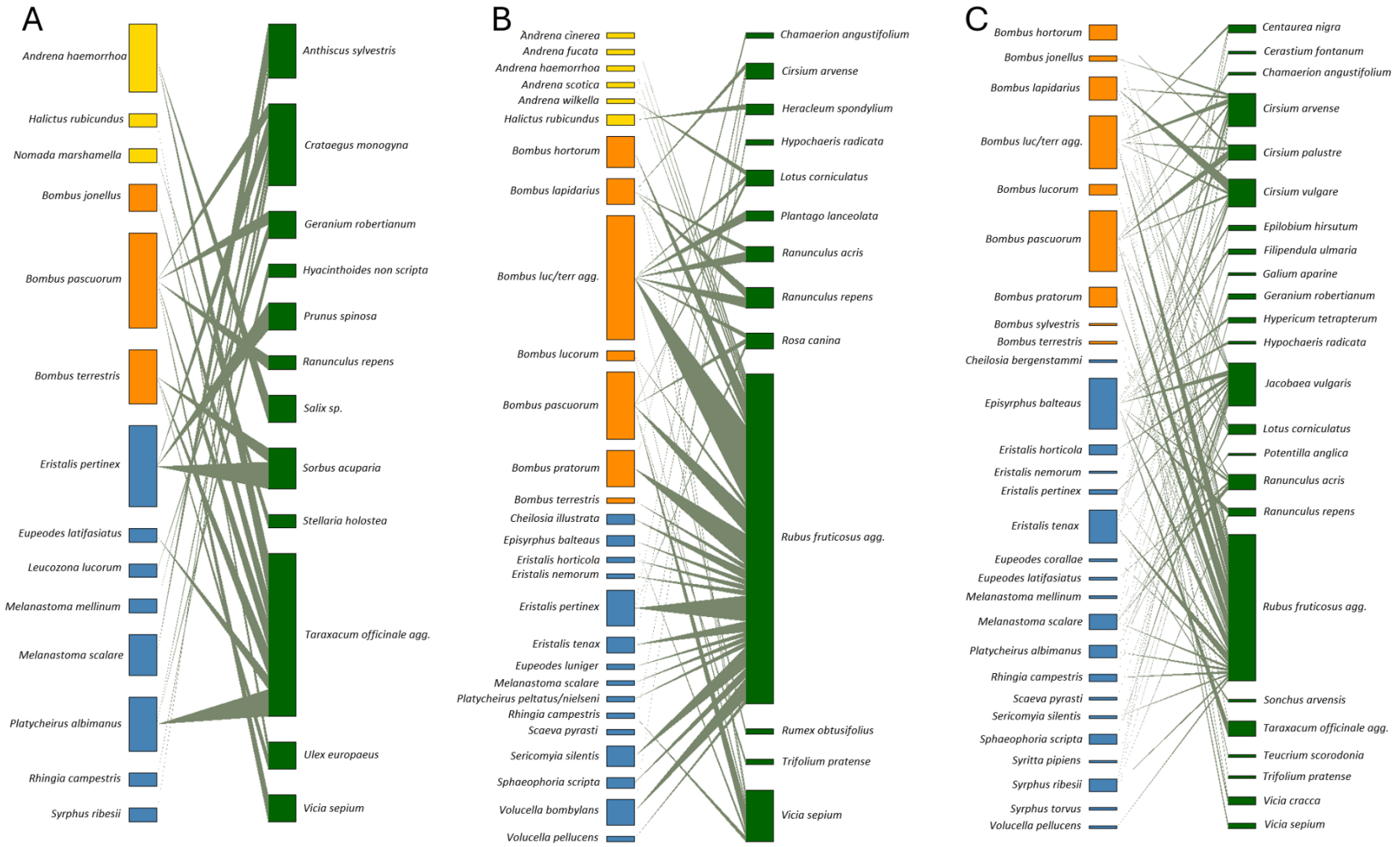

Figure 3.8 Pollinator networks for (A) early, (B) mid and (C) late season sampling rounds. Yellow = Solitary Bees, Orange = Bumblebees, Blue = Hoverflies. Network specialisation (H2) scores were (a) 0.415 , (b) 0.215 and (c) 0.242.

3.5 Discussion

3.5.1 Community change

3.5.1.1 Abundance and Richness

While overall species richness and abundance of our two pollinator groups did not significantly change across woodland development stages, models revealed a significant decline with age, associated with diminishing floral resources in the planted areas of our sites. When we look at habitat preferences, the decline in the hoverfly community appears to be primarily explained by the significant loss of common open-habitat specialists. 'Commonness' appears to be increasingly rare in other systems (Gaston & Fuller, 2008; van Klink et al., 2024), with consequences for ecosystem services provision (Cardinale et al., 2012), and could raise questions regarding the potential trade-offs of land-use change. However, caution is warranted in interpreting these results, as our study does not determine whether early-stage woodlands offer richer floral resources for pollinators compared to their pre-planting state. Studies in contrasting forest systems and landscapes have illustrated the importance of newly established or early-successional woodland for overall bee abundance and diversity due to an increase in ground flora emulating grassland habitats (Odanaka & Rehan, 2020; Roberts et al., 2017; Taki et al., 2013). Given that our sites were previously used for agriculture, it is plausible that the early years of woodland establishment provide a temporary floral boost for pollinators. This may result from the combined effects of reduced agricultural pressure and soil disturbance during tree planting, before floral resources decline as competitive grasses become dominant. Conversely, where woodlands replace species-rich grasslands, known to support more diverse pollinator communities (Kennedy et al., 2013; Larkin & Stanley, 2021), pollinator diversity may decline from the outset, reflecting the loss of high-quality habitat. In such cases, woodland establishment could result in a net reduction in pollinator communities during the early stages of succession.

We observed no significant change in the abundance or richness of woodland specialists which occurred in very low numbers. This is unsurprising given that our sites are still relatively young. Woodland specialist hoverflies, for example, have larval associations with deadwood and are known to respond to its availability at both the forest patch (Smith et al., 2008) and landscape scale (Proesmans et al, 2019a). Similarly, cavity-nesting bees were scarce across our sites, likely reflecting the limited availability of dead vegetation in these early successional woodlands. Woodland-associated pollinators will need to overcome an immigration/colonisation credit (Jackson & Sax, 2010) and may take a long time to colonise woodland creation sites, if at all (Fuentes-Montemayor et al., 2022). The extent to which this credit can be reduced depends on several factors, including the proximity to source populations, the size and shape of the site (Fuentes-Montemayor et al., 2012, 2022; Smith et al., 2021), structural complexity (Fuller et al.,

2018), and site-level pressures such as grazing or deadwood removal. Higher-quality hedgerows within agricultural landscapes, often the only other wooded habitat locally, may serve as a reservoir for wood-adapted species. They can also serve as movement corridors, facilitating landscape connectivity for pollinators (Cranmer et al., 2012) and have been proposed as a dispersal route for functionally important aphidophagous hoverflies between their hibernation sites in forests and the surrounding agricultural matrix (Haenke et al., 2014). Therefore, successful future colonisation of Irish woodland creation sites by specialist pollinators will likely depend on landscape-scale conservation of both remaining mature woodlands and the hedgerow network.

Interestingly, the number of cleptoparasitic bee taxa, though low, increased significantly between the open and closed stages. The presence of this guild, aside from reflecting the presence of their host species, has been proposed as a positive indicator implying a stable and healthy bee community (Sheffield et al., 2013).

3.5.1.2 Beta Diversity

At first glance, the loss of species richness and abundance in the planted areas of our sites, driven primarily by the decline of open-habitat species, suggests a reduction in biodiversity value as new woodlands develop. However, aggregate metrics such as overall abundance and richness can obscure important shifts within the pollinator community (Fleishman et al., 2006; Hillebrand et al., 2018; Smith et al., 2021). These shifts may reflect community responses to site-level and landscape-scale factors that are positive in the context of woodland development (Kirby et al., 2022).

Our ordinations and associated analyses revealed compositional changes in our communities with distinct bee assemblages in open and closed stage sites based on the larger species richness dataset, and differences in the hoverfly community across stages when abundance was considered. For both bees and hoverflies these changes were primarily driven by species replacement (turnover), a process common in insect groups with high dispersal ability and sensitivity to landscape-level or stochastic influences (Baselga, 2010). This dynamic presents a challenge when using these taxa as indicators of change at the forest patch scale.

Differences in how beta diversity components relate to woodland age suggest that landscape-scale influences may be stronger drivers of change for hoverflies than for bees. For bees, species turnover was associated with woodland age, indicating that successional development plays a role in shaping their communities. In contrast, hoverfly abundance was the only metric to show a significant response to landscape composition, specifically a negative association with the area of improved agricultural land. This finding is consistent with previous studies in grasslands, where bees responded to local-scale conservation measures and hoverflies to broader landscape-scale improvements (Larkin & Stanley, 2021; Power & Stout, 2011). Similarly, research in managed

conifer forests has shown that hoverfly diversity is shaped primarily at the landscape level (Straw et al., 2017).

These patterns likely reflect differences in foraging ecology. As central-place foragers, bees, particularly solitary species with limited foraging ranges, are more responsive to local patch characteristics. Hoverflies, lacking nesting constraints, exhibit lower site fidelity and are more influenced by the broader landscape matrix. Our findings also show that bee communities responded to woodland patch size, a relationship not observed for hoverflies. With turnover potentially linked to woodland development for bees, this community may serve as a robust indicator for tracking ecological change over time in these systems. While bees exhibit greater dispersal abilities than some traditional indicators (e.g., woodland plants), they still respond to local site conditions, making them suitable for monitoring habitat quality and successional progress.

In practical terms, descriptive tools such as ordination can support long-term monitoring, but more advanced approaches, including time-lag analysis and community trajectory analysis, offer valuable means for examining temporal community changes (Buckley et al., 2021).

3.5.1.3 Foraging & Nesting Resources

Our plant-pollinator interaction networks suggest that emerging woodlands offer valuable early-season foraging resources, with spring-foraging species utilising spring herbs and flowering trees in closed-stage sites. Notably, the majority of solitary bee records came from our spring sampling round, underscoring the critical importance of survey timing and aligning with findings from other studies that emphasize the role of woodlands in supporting pollinators early in the season (Proesmans et al, 2019b; Smith et al., 2019; Taki et al., 2007; Watson et al., 2011). Early-season floral resources are particularly important for queen bumblebees, which rely on them to establish colonies (Carvell et al., 2017; Mola et al., 2021). However, in temperate climates, optimal weather windows for spring surveys are limited. As a result, key shifts in pollinator responses to woodland creation could be overlooked if this critical period is excluded from monitoring protocols.

Our findings also highlight the relative importance of woodland edge habitats for pollinating insects, largely due to the sustained availability of floral resources throughout the woodland development cycle. Pollinator diversity and abundance are typically higher at woodland edges compared to interior areas (Hanula et al., 2015; Roberts et al., 2017; Sarthou et al., 2005). The structure and composition of these edge communities, depending on site context and the pollinator guild examined, are shaped by both local and landscape-scale factors (Carvell et al., 2022; Eckerter et al., 2022; Gittings et al., 2006; Rivers-Moore et al., 2020), including the availability of floral resources (Proesmans et al., 2019b), as supported by the patterns we observed in pollinator responses at site edges. In the Republic of Ireland, the current native woodland establishment framework (DAFM, 2024b) encourages the planting of flowering trees along woodland margins, while boundary hedgerows are left unmanaged. Consistent with this approach, both our ordinations

and plant–pollinator interaction networks highlighted the ecological role of woody shrubs such as bramble (*Rubus fruticosus* agg.), which may expand into the site from the surrounding hedgerow following the release of agricultural pressure. Hedgerows have been associated with increased social bee abundance in our study region (Maher et al., 2024), while bramble is a well-documented predictor of pollinator abundance (Alison et al., 2022; Bartual et al., 2019) and appears to play a key role in supporting pollinator communities at our sites.

The shift in the floral community observed in older sites, marked by a decline in grassland flora, coincides with increasing cover of litter, bare ground, and deadwood. As woodlands age, they begin to offer a broader suite of resources beyond floral provisions. These include flowering wind-pollinated and insect-pollinated trees (Allen & Davies, 2023; Bertrand et al., 2019; Persson et al., 2018; Urban-Mead et al., 2021), as well as overwintering sites, deadwood, and other non-floral resources (Requier & Leonhardt, 2020). Bare ground in grassland systems has been found to benefit ground-nesting bees (Lichtenberg et al., 2025). Together, these features may support a more functionally diverse pollinator community, offering habitat niches for species with varied life-history traits. Forests have been shown to provide favourable nesting conditions for bumblebees (Mola et al., 2021), with nest searching bumblebee queens frequently observed in woodland interiors and along edges (Kells & Goulson, 2003; Svensson et al., 2000). In our study, however, nest-searching queen bumblebees were infrequently recorded, particularly in open-stage sites, and nests were mostly found within grassy tussocks in thicket-stage areas (KH, pers. obs.). To better understand how woodland creation influences pollinator nesting opportunities over time, future research should incorporate targeted nest surveys across woodland development stages. Such work would provide important insights into the changing nesting value of these habitats for bumblebees and other pollinators.

3.5.2 Sampling, metrics and monitoring

3.5.2.1 Sampling methods

We recorded more solitary bee species in pan traps than transect walks, reinforcing the value of employing complementary sampling methods, which are known to record compositionally distinct subsets of pollinator communities (O'Connor et al., 2019). Transect walks are potentially biased towards larger and more conspicuous species (Dennis et al., 2006), while pan traps tend to sample more species of bees (Westphal et al., 2008) and may be more effective for capturing Dipterans (Hoffmann & Stoll, 2025). Previous studies have shown that pan trap effectiveness can be negatively influenced by floral resource availability (O'Connor et al., 2019; Westerberg et al., 2021), and this pattern was evident here (low pan trap catches during midsummer coincided with peak foraging activity on bramble). Both methods detected similarly low numbers of woodland specialist species. However, how these methods perform in older woodland sites, where

communities may comprise fewer but more specialised species, remains an open question and warrants further investigation.

3.5.2.2 Metrics and Monitoring

A challenge with selecting ecological indicators is that they need to be relatively easy to apply in terms of time, expertise and resources, but also accurately measure aspects of complex ecosystems (Dale & Beyeler, 2001). While broad measures of species abundance and richness are appealing for their simplicity, they are seldom recommended as indicators in applied research or conservation, where targeted subsets of species, those most responsive to disturbance or management, are generally preferred (Kremen et al., 1993; Noss, 1990, 1999). With the evolution of biodiversity metrics to facilitate offsetting, a preference for less complex habitat or species-based metrics has emerged (Marshall, 2020) yet these may not reflect changes in key faunal groups (Marshall, 2024).

Functional groups such as pollinators have been proposed as particularly valuable ecological indicators (Kremen et al., 1993). Our findings support this proposition, demonstrating how pollinator data can offer multiple insights depending on the metric applied. For example, while species abundance may serve as a proxy for pollination service capacity, shifts in community composition provide a clearer picture of biodiversity change during forest establishment. Plant–pollinator interaction networks can be useful tools for tracking the outcomes of management interventions, especially at woodland edges, while the presence of woodland specialists or cleptoparasitic bees may serve as focal points for monitoring and restoration targets in more mature woodlands. Such metrics can also underpin the development of milestones or interim targets to track restoration progress, similar to those proposed for bird communities by Watts et al. (2020).

Our results also suggest that bees and hoverflies, despite showing broadly similar responses to woodland development, may not serve as surrogates for one another. Changes in bee community composition appear to offer a robust, site-specific monitoring metric for native woodland development, particularly when woodland edge habitats are included, spring sampling is conducted, and both pan traps and transect surveys are employed. In contrast, hoverfly responses seem more strongly influenced by landscape-scale factors, limiting their utility as indicators of patch-level changes or site-specific management interventions unless such broader variables are accounted for.

3.6 Conclusions

On the basis of our findings we recommend land-use planners should aim to optimise the temporal and spatial distribution of woodland development stages to sustain pollinator diversity and abundance at the landscape scale, thereby supporting pollination services (Kremen et al., 2004). Early-stage woodlands may host a higher number of species and greater abundance of certain generalist taxa, but later successional native forests that support deadwood-associated species are

also essential components of a biodiverse landscape (Eckerter et al., 2022). In addition, maintaining a high-quality hedgerow network is likely critical for facilitating connectivity between sites and supporting dispersal across fragmented habitats.

We also highlight the challenges of monitoring transitional habitats and the importance of selecting appropriate sampling methods, target taxa, and biodiversity metrics. In the case of pollinators, compositional and functional metrics, derived from the same core datasets as simpler richness or abundance measures, offer more nuanced insights that are often more relevant to conservation practitioners and land managers. Crucially, these analyses are increasingly accessible through open-source statistical tools, offering an opportunity to improve monitoring frameworks without substantial additional resource requirements.

CHAPTER 4

Floral Diversity in Irish Forests: Exploring Biodiversity Indicators Using National Forest Inventory Data

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Target journal: Forest Ecology and Management

4 Floral Diversity in Irish Forests: Exploring Biodiversity Indicators Using National Forest Inventory Data

4.1 Abstract

National Forest Inventories (NFIs) hold extensive information relevant to forest structure, composition, and ecological functioning. However, despite their widespread use for forest resource assessment and the recording of biodiversity indicators, comparatively few studies have utilised NFI data to directly assess floristic biodiversity. Here we use NFI data to explore the key drivers explaining floral diversity across the forest estate in Ireland. We identify whether common structural attributes are amongst those key drivers, and discuss the merit of different compositional and structural biodiversity indicators.

A two-step modelling approach was employed, first narrowing down potential predictors using a Random Forest model, followed by generalised linear models to assess their significance. Our results indicate that tree species diversity was the strongest indicator across all floral richness metrics, but that deadwood, uneven-aged structure, bryophyte cover, and the classification of semi-natural habitat may also present meaningful indicators for overall species richness or that of forest species subsets.

As indicated by the link with hedgerow area in our study, a degree of landscape influence is embedded within our forest species richness metrics, meaning our floral metrics may capture information on biodiversity that cannot be derived from plot-level structural metrics alone. While our findings support the relationship between several structural or categorical indicators and floral richness, our data suggest that using vegetation data as a direct compositional indicator of biodiversity may be more meaningful, as it encompasses a broader range of plot, site and landscape level influences.

Our findings support the use of floral diversity data from the NFI as a compositional biodiversity indicator that can be derived from the current inventory with no additional survey effort and minimal data processing. Our findings also highlight the structural or categorical metrics that may be of most use in reflecting floral biodiversity. This study shows how the NFI data can be harnessed to both provide more information on biodiversity across the forest estate, and help identify indicators of forest biodiversity for a wide range of potential uses.

4.2 Introduction

National Forest Inventories (NFI's) are systematic, county-wide assessments of forest resources (Vidal et al., 2016). They serve to record and assess the extent of and nature of national forest estates, both in private and public ownership, and provide information to inform sustainable forest management and forest policy. In recent years forest inventories have been expanded to include biodiversity attributes not directly related to forest industry interests (Corona et al., 2011). Countries are also striving to improve methodological alignment, for example in Europe, the European National Forest Inventory Network (ENFIN) seeks to harmonise data collection through the agreement of common definitions and use of common methodologies, facilitating comparable EU forest-related reporting (e.g. Land Use, Land-use Change, and Forestry (LULUCF) reporting for the EU climate policy).

NFI's hold a vast array of information of relevance to the ecological structure, composition and function of forests. A limited range of studies have examined the use of NFI data for the monitoring and assessment of forest biodiversity via individual or composite metrics of value or naturalness. In most cases these are based on tree composition and structural indices (Bellamy et al., 2024; Borghi et al., 2024; Chirici et al., 2012; Heym et al., 2021; Pignatti et al., 2012; Storch et al., 2018; Winter et al., 2008), metrics which are readily derived from standard inventory data (Corona et al., 2011). These indices have been used to identify forests with a high level of naturalness (i.e. closer to a reference natural state), which are expected to provide a greater abundance and variety of habitat niches, and consequently support higher levels of biodiversity (Winter, 2012). The species and structural diversity of trees in a forest, together with deadwood, known to be an indicator of biodiversity of many forest species (Kovac et al., 2020; Larrieu et al., 2018), are key attributes of many composite indices (Bellamy et al., 2024; Hekkala et al., 2023; Larrieu et al., 2018; Linser, 2024). Similar variables have also been specified as part of woodland condition assessment criteria used for Biodiversity Net Gain assessments (Barsoum et al., 2025), ecosystem service assessments (European Commission, 2018; Maes et al., 2023), and as metrics for forest restoration under the paragraph 62 of the Nature Restoration Regulation (European Commission, 2025).

However, the need to integrate data on certain taxonomic or functional groups has been highlighted (Paillet et al., 2024), with research identifying that a forest may have a high degree of naturalness, yet not have conservation value in terms of the species and habitats it supports (Paillet et al., 2008). The influence of landscape factors on forest biodiversity are also crucial to understand, and important to disentangle from site and plot level factors (Corona et al., 2011), especially where decisions are being made around management interventions (Bradfer-Lawrence et al., 2025).

Forest Europe, an intergovernmental organisation aiming to promote sustainable forest management (SFM) has devised a set of ten indicators (Forest Europe, 2015), currently subject to

review (Linser, 2024). The current indicators include only two that are not based on structural or tree data: threatened (ICUN red-list) forest species and common forest bird species, the latter is also specified as a mandatory indicator under the Nature Restoration Regulation. While potentially helpful for comparison of European-wide forest biodiversity, such indicators may not facilitate the evaluation of the relative biodiversity of forests in our study region due to a depauperate forest specialist fauna (Sweeney et al., 2010; Wilson et al., 2006).

Aside from tree-related indicators, studies exploring compositional biodiversity data collected by NFI's are few. Using forest inventory data, Chiarucci and Bonini (2005) examined forest vegetation species richness at different spatial scales in six forest sites in Italy. Recently, adapting the framework of Winter et al. (2012), Ruas et al. (2023) used Irish NFI data in the classification of high nature value forests and, as a validation exercise, correlated their scores with plant data from the Irish NFI, finding moderate correlations with the diversity of different broad floristic groups. A limited number of studies have used biodiversity data collected from other sources spatially overlaid with NFI plots, for example Reise et al. (2019) used the structural attributes in the inventory in conjunction with available breeding bird data, to understand drivers of forest bird richness and diversity, while Zellweger et al. (2015) integrated biodiversity studies of plants, snails and bryophytes with overlapping NFI plots, compiling metrics of overall species richness and forest species richness, and examining the influence of structural forest metrics and climatic variables.

Information on the vegetation of forest understory layers is an integral part of conservation-level assessments of woodlands (Perrin et al., 2008), and has the same potential relevance as tree related indicators for biodiversity assessment (Corona et al., 2011), however there is still a need to test indicators and thresholds at a national level (Alberdi et al., 2018). In a recent literature review, Zeller et al. (2023) found most evidence for gaps, stand age, the share of oak and conifers, as well as old-growth elements, being positively correlated with vascular plant species richness. Evidence also exists for associations between forest plant species richness and larger sites (Petit et al., 2004; Waddell et al., 2024), and variation in tree size (Waddell et al., 2024).

The efficiency of collecting forest vegetation data alongside the standard forest attributes is attractive and is unlikely to be matched by surveys needed for most forest fauna, potentially requiring multiple visits to capture temporal and spatial variation exhibited by mobile species. Forest vegetation is also easier to identify than more specialist invertebrate groups such as saproxylic beetles, and identification can be carried out in the field. While the vegetation data collected in the NFI may not provide data to the level of refinement needed for conservation status assessment under the EU Habitats Directive (Alberdi et al., 2018; Kovac et al., 2020), the question remains whether it can nonetheless be a useful and efficient means of directly monitoring forest biodiversity across all forest habitats at a national scale.

Surveys for Ireland's fourth NFI were undertaken between 2020 and 2022 based on a systematic grid sample design, and recorded a wide range of attributes related to the structure and characteristics of the national forest estate, including a range of data that can be used for characterising aspects of biodiversity and pressures acting upon it. Findings show that the national forest estate, expanded relative to past inventories, has reached 11.6% of total land area, with approximately half of forests being in private ownership and half in public (DAFM, 2023d). Broadleaf tree species account for approximately 30% of stocked forest areas, with the remainder comprising conifer species (DAFM, 2023d). Published reports from the Irish NFI have provided high-level data and analyses of vegetation cover and species diversity across forest-ownership categories (DAFM, 2023d, 2023e). However, cross-country syntheses indicate that biodiversity-relevant data collected by National Forest Inventories are underutilised in many countries, and highlight substantial scope for expanded and harmonised biodiversity assessment (Chirici et al., 2012; Gillerot et al., 2021). These findings highlight a clear opportunity for the Irish NFI to build on its existing strengths and further enhance its contribution to biodiversity assessment and reporting.

In this study, we analyse the most recent NFI survey of the Irish forest estate and examine relationships between vascular plant biodiversity in the forest understorey layers, and a range of forest level and landscape level factors, including known structural indicators of biodiversity. Specifically, we ask what the key drivers of floral diversity are, what the nature of those relationships is, and whether proxies commonly proposed as condition indicators reflect floral diversity. We explore whether NFI survey efforts inventorying understorey plant species are providing additional insights about biodiversity, above and beyond those that might be derived from common structural indicators, and highlight which metrics are most suitable for monitoring the biodiversity of the forest estate as well as how the NFI may be optimised for the collection of biodiversity data.

4.3 Materials and Methods

4.3.1 Data Collation and Processing

The 4th NFI collected structured data on a range of forest attributes, including floral biodiversity, forest characteristics, tree measurements, deadwood, biotic/abiotic damage and other site and plot level metrics, across a total of 2020 plots (DAFM, 2023c). The distribution of NFI plots is based on a systematic grid sampling approach, where sample plots are laid out across the country on a 2 x 2km grid, with plots that fall within forested areas selected for sampling (DAFM, 2023c). As a result, NFI plots are evenly distributed geographically but only located in areas confirmed to be forested, ensuring statistically representative sampling of Ireland's forest resource. The NFI employs a concentric circular plot design with three nested radii (4 m, 7 m, and 12.62 m), where different forest attributes are measured within subplots of varying radii. Tree measurements are

collected within the nested plots according to different diameter breast height (DBH) inclusion thresholds. Trees with a DBH ≥ 200 mm are assessed within the full 500 m² plot (12.62 m radius), those with DBH 120–199 mm within a 154 m² subplot (7 m radius), and those with DBH 70–119 mm, as well as smaller trees (DBH < 70 mm, height > 20 cm), within a 50 m² subplot (4 m radius). Shrub species and cover are recorded on the entire 12.62 radius plot, and other vegetation recorded on the 7m radius subplot.

NFI data were provided on request from the Forest Service as an excel workbook with tabs for various attributes linked by a common plot identifier. In order to obtain data for analysis, we first processed the vegetation data to derive floral species richness metrics, and then extracted or calculated a range of potential explanatory variables (Table 4.1).

Vegetation sampling of each plot was undertaken by the Forest Service between the months of May and September (2020-2022) where vascular herbs, grasses, shrubs and ferns were recorded to species level in most instances. For the purposes of this study, we pooled species records for shrubs, herbs, grasses, and ferns and calculated species richness per plot. Though acknowledging potential scale-related biases with regard to shrubs and other flora, pooling was considered appropriate for estimating plot-level richness as richness is less sensitive to sampling area than abundance-based metrics, and combining layers helps capture overall diversity patterns relevant to ecological functioning and forest habitat assessment. Where certain taxa, e.g. *Carex*, were recorded at genus-level and species-level, depending on the number of different species and records, we either reduced all records to genus-level identification, or removed the genus-level records, selecting the approach that resulted in the loss of least information. We also added zero value species richness plots to our dataset (i.e. those where no vegetation cover was recorded, or where vegetation cover was limited to bryophytes). Based on the habitat categories of Hill et al. (2004) we extracted the richness of woodland specialist, woodland generalist, and non-woodland species from the dataset. Woodland specialists were those species that have a recognised affinity solely with woodland habitats, while woodland generalists were those associated with woodland habitats as well as other habitat types. We also extracted the richness of Ancient Woodland Indicator (AWI) species based on the list devised by Perrin and Daly (2010) for our study region.

For the tree measurement data, to account for the differing sampling areas across DBH classes, each tree was assigned a weighting factor based on the inverse of the area in which it was sampled, relative to the full plot area. These weights were applied when calculating plot-level means and totals for DBH, basal area, and number of trees, ensuring unbiased estimates representative of the entire 500 m² plot area.

Using GIS tools, the extent of Fossitt Level 2 habitat (Fossitt, 2000) in a 2km matrix surrounding each plot was calculated from the National Landcover Map (EPA & Tailte Éireann, 2024). Areas for ‘Amenity’, ‘Buildings’, ‘Ways’ and ‘Artificial‘ were combined to a composite 'Urban' habitat.

Prior to selecting the variables for analysis, a correlation matrix was created to check for those continuous variables which strongly correlated (Spearman $r_s \geq 7$) (Appendix C, Table C1). This resulted in the removal of the landscape matrix values for transitional forests and improved grassland as they strongly correlated with areas of conifer and hedgerow respectively. We also reviewed categorical variables for those that were nested or strongly associated and retained the most meaningful variable. The final list of selected variables is provided in full, with an explanation of any calculations undertaken, in Table 4.1. This table also highlights those variables aligned with commonly-used forest biodiversity indicators. We then combined the richness metrics, NFI variables and landscape variables into a single dataset for analysis.

Table 4.1 Potential explanatory variables extracted from the NFI. Groupings and variable names follow NFI (DAFM, 2023c). Numbers in brackets show metrics closely aligned with 1, Forest Europe Indicators (Linser, 2024); 2, Nature Restoration Regulation Indicators (European Commission, 2025); 3, Index of Biodiversity Potential (Larrieu et al., 2019); 4, Woodland Condition Assessment criteria (Barsoum et al., 2025); 5, Ecosystem condition metrics (European Commission, 2018).

Variable	Description
Plot	
Survey Date	Survey year used to calculate plot age (see below).
Land Use Category	Forest Open Area (non-stocked) or Forest. Used as a filter to select Forest plots for data analysis.
Land Use Class	Descriptive classification of land use. Used in analysis for Forest plots only. We pooled plots assigned to edge or gap classes into one 'EdgeGap' variable. Other plots were assigned to Forest or Natural Succession.
Altitude	Height of plot above sea level in metres.
Aspect	Orientation of the slope categorised by cardinal points of a compass.
Slope	Steepness of terrain in degrees.
Forest	
Planting Year	Not used directly in analysis. Calculated Forest Age based on Survey Year minus Planting Year.
Ownership	Freehold owner of the lands: Coillte; Private (grant aided); Private (non grand aided); National Parks and Wildlife Service; Farm partnership; Bord na Mona; Other.
Mixture Type	Individually Mixed, Uniform, Forest Open Area, Group Mixed
Establishment Type (1, 5)	Reforestation, Afforestation, Semi-natural
Even/Uneven Aged (2, 3, 5)	Even or Uneven Aged
Tree Origin (1)	Natural, planted <20%; Natural, planted 20-50%; planted, natural 20-50%, Planted, natural <20%; Forest Open Area
Nativeness (1, 2, 4)	Native (>80%); Non-native (>80%); Mixed (20-80%); Forest Open Area
Development Stage (4, 5)	Development of the forest canopy: Post establishment; Pre-thicket; Thicket; Small pole; Pole, High forest, Overmature, Multi-storied.
Thin Status	History and frequency of harvesting operations: Juvenile forest; Respacing/pre-commercial thinning; First thinning; Second thinning; Subsequent thinning; No thinning; Not application (not suitable for thinning).
Pruning or Shaping	History of pruning and shaping: Pruning, Shaping, Pruning and shaping, No pruning or shaping.
Trees	
Species (1, 2, 3, 4, 5)	Calculated dominant species per plot, and no. tree species per plot.

Tree Density	No. of trees per plot, (weighted for subplot measurements)
DBH	Calculated mean and standard deviation of diameter breast height (DBH) (weighted for subplot measurements)
Total Basal Area	Calculated sum of basal area of all trees measured in a plot (weighted for subplot measurements)
Large Trees (4)	Number of large trees (DBH >450mm) (Larrieu & Gonin, 2008)
Canopy Cover (3, 4, 5)	Total canopy cover (%) for each plot. Where a secondary later (to the main layer) was recorded, as it is not known whether these trees underlie or adjoins the main layer, we added 50% of that layer to the main layer.
Natural Regeneration (1, 4)	Number of naturally regenerating trees recorded (recorded on the 4m radius subplot only)
Biotic Damage	
Biotic Damage Type (4)	Extracted Yes/No variable for Damage (if any present) related to the following categories: Animal; Disease; Harvesting; Insect; Vegetation.
Deadwood	
Deadwood type	Lying, stumps, standing.
Deadwood volume (1, 2, 3, 4)	Volume of each category above. For Lying and Stumps - decay status data was available, and volumes were based on the summed classes 'sapwood soft', 'largely diminished' and 'advanced decay' only.
Site	
Woodland Habitat (5)	Semi-natural woodland; Scrub/transitional woodland; highly modified/non-native woodland.
Woodland Habitat Subtype	Woodland habitat following Fossitt Level 3 categories. We combined riparian woodland, wet willow-alder-ash woodland, and wet pedunculate oak-ash woodland into a 'wet woodland' grouping.
Peat Depth	Depth in cm
Soil Group	Brown earth, Brown podzolic, Luvisol, Podzol, Groundwater Gley, Surface Water Gley, Rendzina, Lithosol, Alluvial, Ombotrophic and Minerotrophic
Bryophyte Cover (5)	NFI Cover Classes were converted to a numeric variable (centrepoint of coverclass).
Drainage (5)	Very poor, Poor, Imperfect, Moderate, Good, Excessive

4.3.2 Data Analysis

All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2023). Where numeric variables were compared across categorical variables, we used Kruskal-Wallis (K-W) tests followed by Dunn's tests.

In the first stage of analysis, we summarised the whole NFI dataset (Table 4.2, Fig. 4.1), grouping plots by land use class (Forest or Forest Open Area). Forest plots were then further classified by habitat type and development stage. Forest Open Areas include roads, utility wayleaves and setback zones. Development stages were broadly grouped into 'mature' and 'immature' categories, acknowledging that the pole stage may represent maturity from a silvicultural perspective under certain conditions. The dataset was heavily skewed toward immature highly modified/non-native woodland (Table 4.2), the majority of which were conifer plantations (Appendix C, Table C2). Comparatively there were just 28 immature semi-natural woodland plots. Given that our research question sought to examine the potential influence of habitat type amongst the range of NFI and landscape variables, we filtered the dataset to retain only plots corresponding to mature

development stages (i.e. high forest, overmature and multistoried), excluding those associated with younger forests. This delivered a dataset of 685 plots.

Table 4.2 Summary of NFI plots by broad habitat grouping and development stage. Woodland habitats and development stages as per NFI (DAFM, 2023c).

Woodland Habitat	High Forest	Multi-storied	Over-mature	Mature Total	Post establish-ment	Pre-thicket	Thicket	Small Pole Stage	Pole Stage	Immature Total	Forest Open Area	Temporarily Unstocked	Habitat Total
Highly modified/ non-native woodland	385	77	37	**499**	187	161	185	224	290	**1047**	193	16	**1754**
Scrub/ transitional woodland	1	13	0	**14**	5	6	10	2	0	**23**	8	1	**46**
Semi-natural woodland	11	160	1	**172**	2	5	5	13	3	**28**	19	0	**219**
Development Stage Total	**397**	**250**	**38**	**685**	**194**	**172**	**200**	**239**	**293**	**1098**	**220**	**17**	**2020**

One challenge with a large database such as the NFI is deciding which potential explanatory variables to use, so rather than selecting a limited range of attributes *a priori*, we used a combination of machine learning and statistical models to first identify key predictors of importance and then evaluate their predictive power.

We chose to use a Random Forest model to extract variables that are most important in explaining patterns of species richness. Random Forest is a non-parametric ensemble learning method that, using bootstrapping (a random sample of the data with replacement), builds independent decision trees through training on random subsets of data, and then averages their results (Breiman, 2001). This bootstrapping process, along with random feature selection at each split (controlled by the mtry parameter), helps to reduce model overfitting and increase the robustness of the model. The method is suitable for complex non-linear ecological datasets with a mix of categorical and continuous data (Cutler et al., 2007). The method is also robust to multicollinearity, as random feature selection reduces the dominance of slightly correlated variables, and though stronger correlations could lead to diluted variable importance scores, predictive accuracy remains stable. Spatial coordinates (X and Y) which relate to longitude and latitude were included as predictors to account for geographical spatial structure in species richness.

We used the caret package (Kuhn, 2008) for model training and cross-validation. We carried out hyperparameter tuning by specifying a custom tuneGrid for the *mtry* hyperparameter to explore the number of trees considered at each split, and optimise model performance. Additionally, the number of trees (*ntree)* was set to 500 by default, providing enough trees to ensure stable, robust predictions, while cross-validation (5-fold) ensured that the model's performance was validated on multiple subsets of the data. To confirm that the model was capturing meaningful structure rather than spurious patterns, we also trained a model on a dummy dataset where the target variable was randomly shuffled.

Model performance was evaluated on a held-out test set (20% of the data), trained with 80% of data, using R^2 (proportion of variance explained), RMSE (average prediction error, sensitive to large errors), and MAE (average absolute error). Feature importance was computed from a final model trained on the full dataset, with importance values reflecting each feature's contribution to reducing variance (the total decrease in node impurity) across all trees in the forest. The pseudo R^2 value indicated the proportion of total variance in the target variable explained by the model.

To visualise the marginal effects of individual predictors, we trained an additional Random Forest model using the randomForest package (Liaw & Wiener, 2002) using the unscaled dataset for interpretability. This model was used specifically for generating partial dependence plots (PDPs) via the pdp package (Greenwell, 2017) due to incompatibility between caret-trained models and the PDP functions. To ensure consistency with the final caret model, we extracted the optimal *mtry*

value identified during cross-validation and applied it when fitting the PDP model, while also keeping *ntree* value the same as the caret model.

To analyse relationships between our forest species metrics and the most important variables emerging from the Random Forest model, we used generalised linear models (GLMs) and generalised linear mixed models (GLMMs) with a negative binomial distribution, with the latter used so that a zero-inflation term could be included. We selected the top ten predictors from the Random Forest model, as we had observed that across multiple runs without a fixed seed, the top 8 to 10 variables remained consistently among the most important, even when accounting for randomness in model initialization and sampling. We then scaled and centred all continuous variables to improve the performance and interpretability of the models. The model includes smooth, nonlinear effects of the spatial variables X and Y using B-splines with 5 degrees of freedom each. All GLMMs were fitted using the *glmmTMB* R package (Brooks et al., 2017), while GLM's were fitted with the *MASS* (Venables & Ripley, 2002) package. The most parsimonious model was selected by sequentially removing the least significant interactions and terms, while at each step the corrected Akaike's information criterion (AICc) was used to compare candidate models. We then inspected the distribution of residuals, dispersion and checked for zero-inflation, spatial autocorrelation and influential points using the *DHARMa* R package (Hartig, 2022). To deal with multicollinearity issues, we calculated the variance inflation factor (VIF) of each predictor using the 'car' R package (Fox & Weisberg, 2019), and we checked that VIF <4 (Zuur et al., 2013) which indicated no high correlation among predictors, otherwise removing the least ecologically-meaningful variable.

4.4 Results

4.4.1 Floral richness in modified vs unmodified forests

While the unbalanced nature of the dataset limited interpretability, as expected, pooling all data by the three broad habitat groupings showed that semi-natural woodland and scrub/transitional woodland supported significantly greater species richness than highly modified/non-native woodland (Kruskall-Wallis chi-squared = 109.15, $p<0.001$). Further dividing these three broad habitat groups into those within mature development stages, immature development stages and forest open areas (Fig. 4.1) revealed that there were significant differences across these maturity groupings for semi-natural woodland but not other groupings, though noting the higher average age of the semi-natural woodland sites.

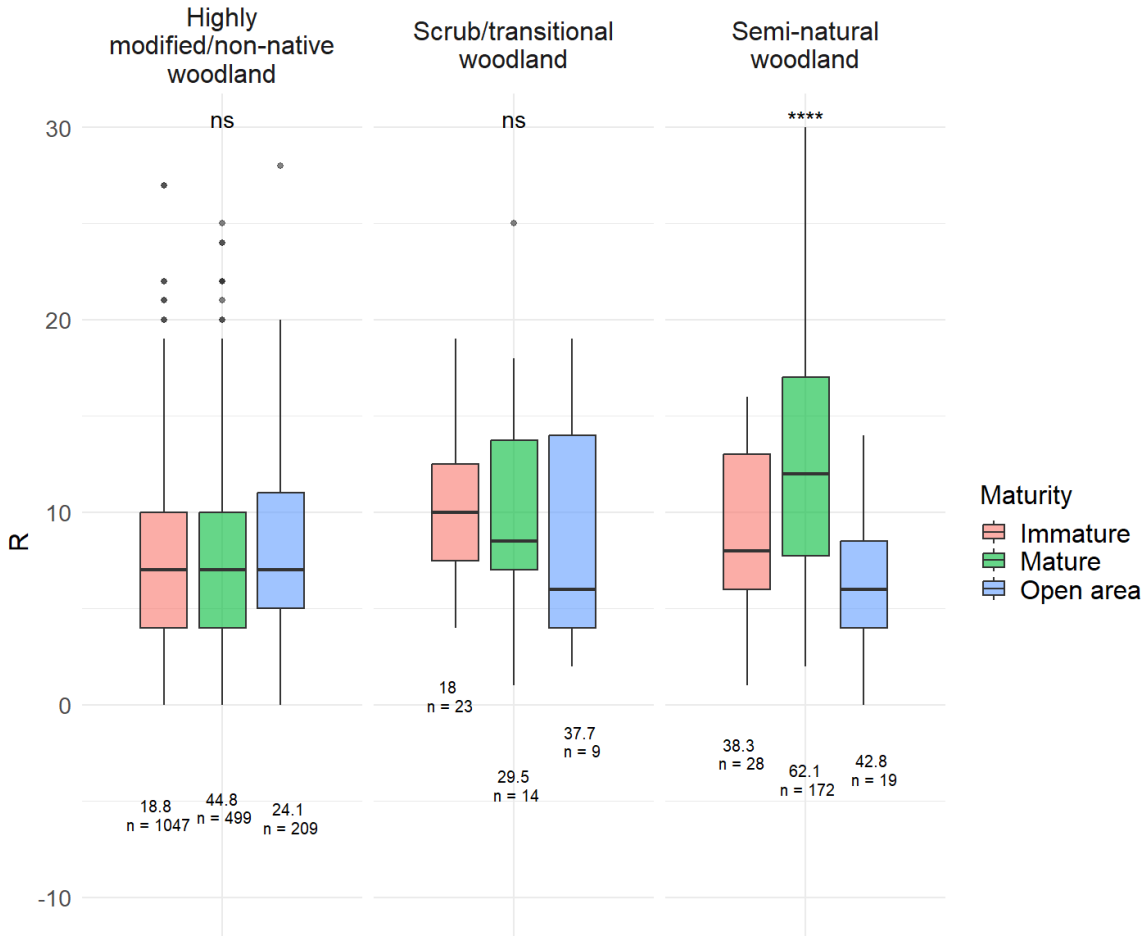

Figure 4.1 Floral Richness (R) compared across high-level habitat and maturity groupings (immature forest, mature forest and forest open area). At the base of each boxplot the average age of the plot is given, together with the number of plots (n). Significance indicators above each plot for within-habitat grouping refer to Kruskall- Wallis (KW) tests with the following results: Highly modified/non-native woodland - chi-squared = 1.56, p = 0.458; Scrub/transitional woodland = chi-squared = 1.83, p = 0.400; Semi-natural woodland - chi-squared = 26.3, $p < 0.001$.

4.4.2 Correlated variables

As described earlier, strongly correlated variables (Spearman $r_s \geq 0.7$) were removed from the dataset, however we highlight some moderately correlated variables ($r_s \geq 0.3, \leq 0.7$) that may still have relevance to interpreting the results (Appendix C, Table C1). Of note, the area of hedgerow and conifer habitat were moderately negatively correlated, as was hedgerow area and altitude ($r_s = -0.31$, $p \leq 0.001$), while altitude and conifer were positively correlated. Urban habitats showed moderate correlations with areas of hedgerow and improved grassland, and negative correlations with peat depth, altitude, and areas of conifer and heath habitats. Features indicative of compositional and structural diversity, such as the volume of deadwood, the standard deviation of DBH, age, and the number of tree species, were moderately correlated with each other.

4.4.3 Most important variables explaining Species Richness metrics

Focusing on mature woodlands, we used a Random Forest model to identify the contribution of a range of features to overall species richness, as well as the species richness of non-woodland species, woodland generalists and woodland specialists. Across all models, performance on the held-out test set was comparable or slightly better than in cross-validation. Test set RMSE and MAE values closely matched those from cross-validation, indicating stable predictive error, with values of these statistics between 9-18% of the range of the target variables, which was considered reasonable for ecological count data that tends to have natural variability. R^2 values increased across all test set models, suggesting the models generalised well and that the test set captured relationships similar to those seen during training. While R^2 values were modest (ranging from 0.20 to 0.56), they nonetheless provided consistent rankings of variable importance (Table 4.3), highlighting variables that have predictive signal, even if small.

Table 4.3 Results of Random Forest Models Showing R^2, Lowest RMSE (Root Mean Square Error), MAE (Mean Absolute Error), and Optimal mtry (Number of Variables Considered at Each Split) for Best (Training) and Test Sets

	Best Model				Test Set		
Variable	**mtry**	**RMSE**	**R^2**	**MAE**	**RMSE**	**R^2**	**MAE**
Overall Species Richness	60	4.449	0.427	3.556	4.445	0.470	3.403
Woodland Specialist Richness	65	1.235	0.203	0.932	1.249	0.336	0.924
Woodland Generalist Richness	50	1.874	0.510	1.464	1.882	0.559	1.489
Non-woodland Species Richness	22	2.837	0.218	2.203	2.465	0.312	1.946
Ancient Woodland Indicators	40	0.873	0.289	0.648	0.916	0.436	0.656

Here we discuss the top ten most important features highlighted by the model for each response variable under consideration (Fig. 4.2), though noting further variables contribute smaller proportions to explaining the model (see Appendix C, Table C3 for those that contribute 1% or more). The patterns observed in PDP plots (Appendix C, Fig. C1-C9), used to describe the nature of the relationship between the richness metrics and variables of importance, are described below.

Spatial coordinates were generally amongst the most important features, suggesting a strong spatial structure to the dataset. Spatial coordinate bi-plots demonstrate that overall richness of woodland species groupings was highest in the northwest of the country (Appendix C, Fig. C10). Examining richness across counties, grouped by semi-natural versus modified woodlands, indicated that the high species richness of semi-natural woodlands in Co. Donegal explained this trend (Appendix C, Fig. C11).

The number of tree species emerged the most important variable for woodland generalist and specialists richness, and it was also the second most important variable for overall richness and that of AWI's.

Overall richness was negatively associated with the number of trees, while non-woodland species declined with the number of trees, though increasing again in very dense plots. Overall richness and non-woodland species richness were also negatively associated with basal area, while woodland generalists richness rose to peak at low basal areas (Appendix C, Fig. C5C). Canopy cover was an important variable negatively associated with non-woodlands species, but not any other grouping.

The volume of decaying logs was an important variable positively associated with overall richness and that of woodland specialists. Across the pooled dataset, reforestation sites had significantly higher volumes of decaying logs relative to afforestation or semi-natural sites (Kruskall-Wallis chi-squared = 18.018, $p<0.001$).

The standard deviation of DBH, an indicator of structural diversity, was positively associated with woodland specialist richness, and showed a trough-shaped relationship with AWI's (Appendix C, Fig. C8F), with some high values at low structural diversities. Age also emerged as an important variable positively associated woodland specialist and AWI richness. The number of naturally regenerating trees only appeared amongst the top important variables for AWI's, while bryophyte cover only appeared amongst the top important variables for woodland specialists, both showing a positive association.

A negative association with peat depth was the most important feature in explaining overall richness and that of AWI's. Peat Depth was also an important feature in explaining the richness of woodland generalists and specialists, again with a negative association. Altitude was also negatively associated with woodland specialists.

Of the categorical variables that emerged as important, there was a negative relationship between a lack of thinning and overall richness, and a positive relationship with non-woodland species richness. Non-woodland species also showed a negative association with well-drained sites and plots classified as forest (as opposed to natural success or edge/gap features). In contrast, there was a positive association with overall richness and non-woodland species richness and plots dominated by native trees.

Semi-natural woodland establishment, as opposed to afforestation or reforestation, was positively associated with overall richness and the richness of non-woodland species and AWI's. Woodland generalists and AWI's were positively linked to habitats classed as oak-ash-hazel woodland. Woodland generalists were also positively associated with uneven aged plots.

Landscape variables were identified as important for woodland generalists, with this group exhibiting a positive relationship with the area of hedgerow, treelines and urban habitats in the landscape matrix. A positive association with hedgerow also emerged as an important feature for woodland specialists. The area of broadleaf woodland emerged as an important variable for non-woodland species and woodland specialists, with the association slightly trough-shaped (Appendix C, Fig. C3D, Fig. C7H) indicating some high values at low broadleaf cover, but generally increasing with higher cover.

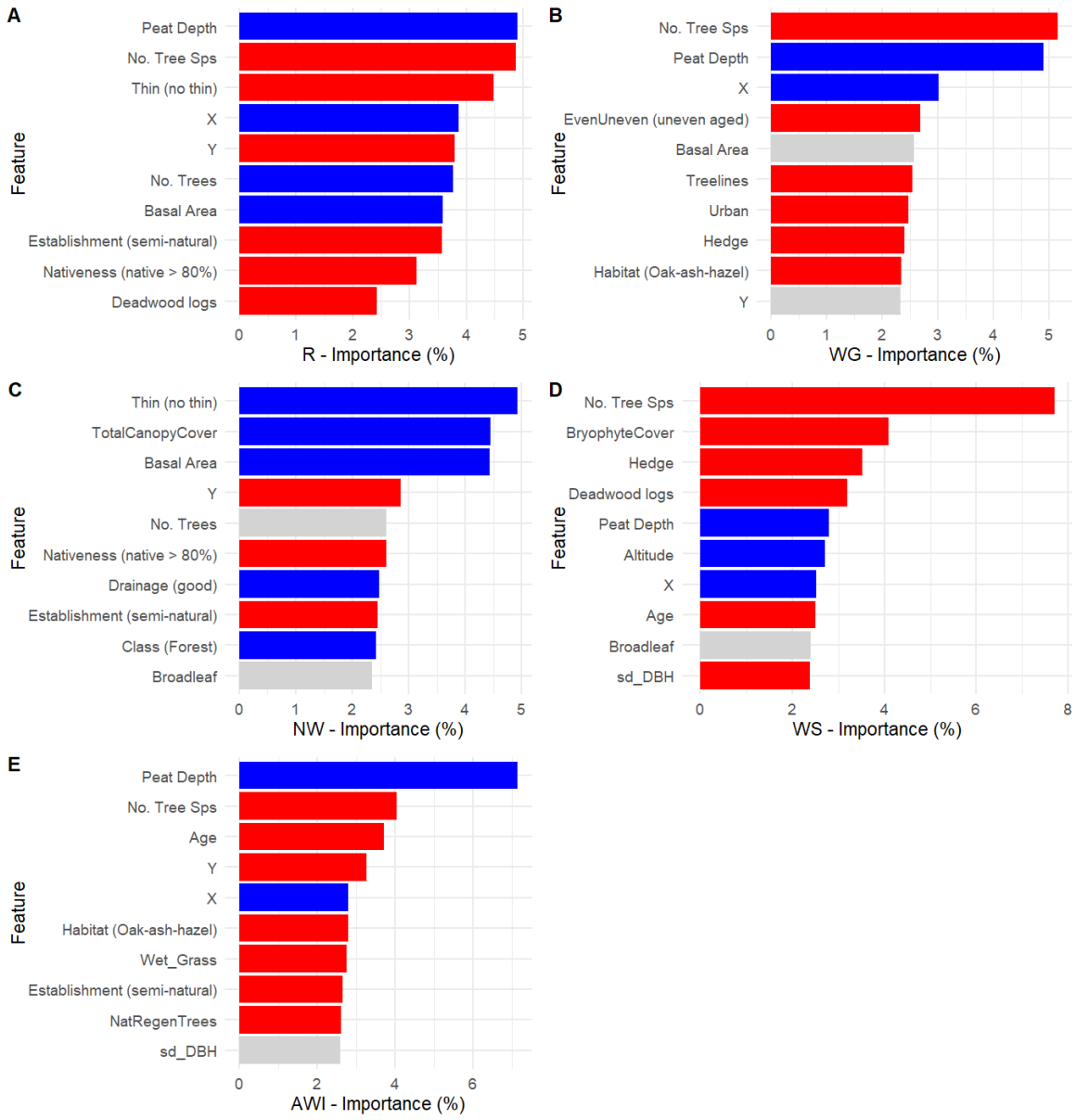

Figure 4.2 Percentage Importance for the top 10 most important variables from the Random Forest models for understory plant species richness (R), woodland generalist richness (WG), non-woodland species richness (NW), woodland specialist richness (WS) and AWI richness (AWI). X and Y refer to geographical spatial coordinates. Bars shown in blue are negative relationships, red are positive relationships, and grey are trough or hump-shaped.

4.4.4 Significant predictors of Species Richness metrics

While the Random Forest models showed how a wide range of variables may be contributing to explaining floral diversity, our statistical models refined those predictors, accounting for multicollinearity. We fitted zero-inflated mixed models for overall richness, woodland specialist and generalist species richness, and non-woodland species richness, and a generalised linear model for AWI's (Appendix C, Table C4). The incident rate ratio's of significant predictors, representing the multiplicative change in the rate of an event for a one-unit increase in a predictor variable while holding other variables constant, are shown in Fig. 4.3.

The best-fitting model for overall richness included the number of tree species, volume of decaying logs, and semi-natural establishment as positive predictors, and peat depth and basal area as negative predictors (Fig. 3A). This model explained 93% of the variance. Woodland specialist species richness was best explained by a model indicating they were positively associated with the number of tree species, area of hedgerow in the landscape, bryophyte cover and deadwood logs, and negatively associated with altitude and peat depth, with this model explaining 43% of the variance (Fig. 3B). The best-fitting model for woodland generalists (Fig. 3C) suggested species richness was positively associated with the number of tree species, area of hedgerow and treeline, and uneven-aged plots. In contrast the total basal area and depth of peat were negatively associated with this group. The model for woodland generalists explained 76% of the variance. The best-fitting model for AWI's (Fig. 3D) showed a positive association between species richness of this indicator and the number of tree species. In contrast, there was a negative association with modified woodland categories and peat depth. Thus AWI's were linked with woodlands characterised by larger trees in semi-natural settings, with a contrasting relationship with modified plantations on peat. The model for AWI's explained 52% of the variance. For non-woodland species (Fig. 3E), basal area, canopy cover, the area of broadleaf woodland in the matrix, and a lack of thinning, were all significant negative predictors, while dominance of either native or non-native species (with reference to a mixed situation) was a positive predictor. This model explained 73% of the variance.

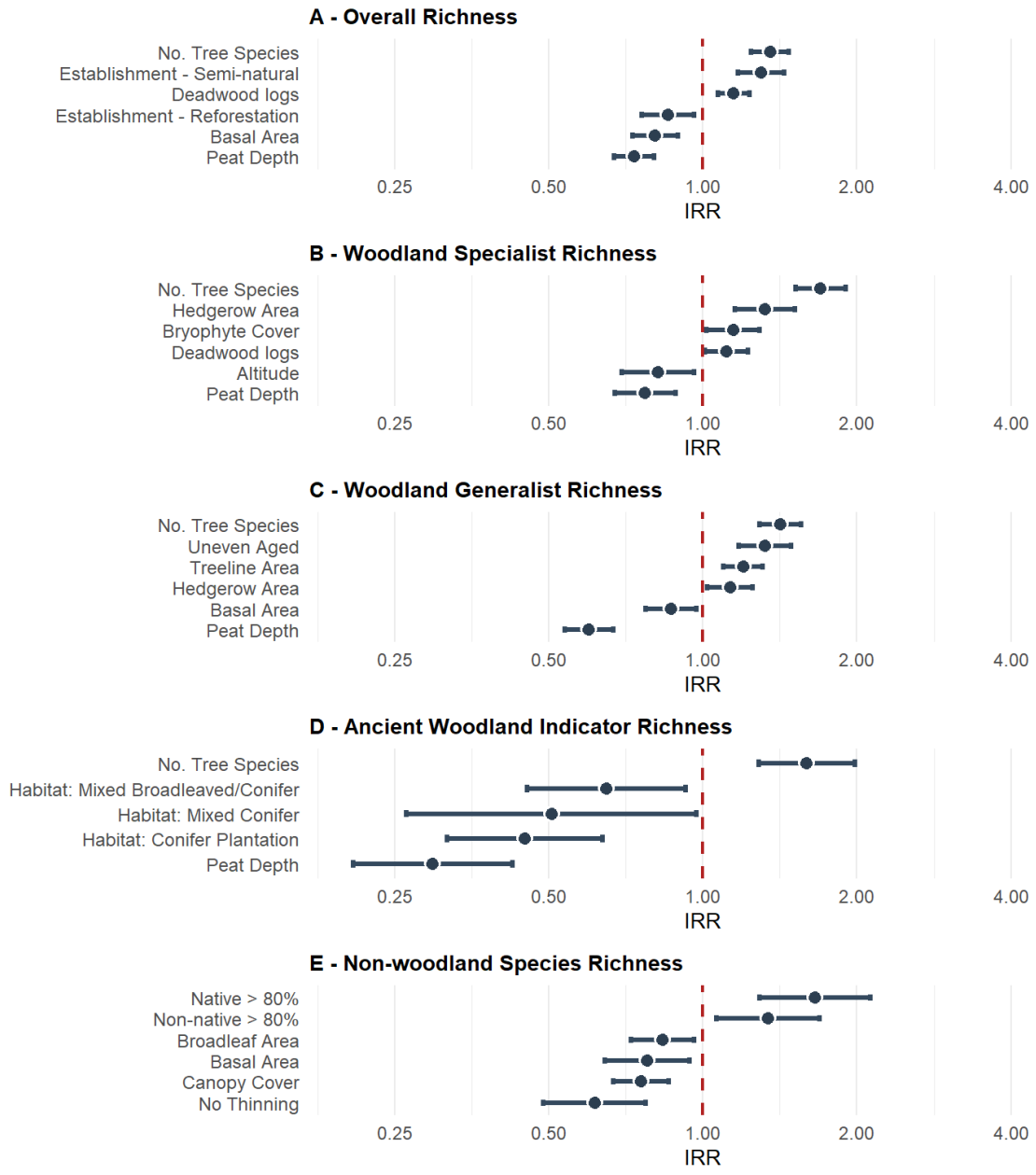

Figure 4.3 Incident Rate Ratio of Significant Predictors from Models. Values above 1 indicate positive relationships, and values below 1 indicate negative relationships

4.5 Discussion

The NFI provides a comprehensive picture of the Irish national forest estate across a proportional set of plots reflecting the age structure and habitats present. Using this data, we examine the key drivers influencing floral biodiversity, describe the nature of those relationships, identify the best indicators for floral biodiversity, and consider which metrics are most suitable for monitoring the biodiversity of the forest estate. Simply categorising the plots surveyed shows how the future mature forest estate is likely to remain skewed toward non-native conifer plantations given the lack of younger semi-natural forests. Thus, for the purposes of evaluating indicators, we focused our analysis on mature woodlands.

4.5.1 Plot and Site level influences on floral richness

A range of compositional, structural and functional biodiversity indicators can be used for monitoring trends in forest condition (Linser, 2024; Noss, 1990), and we have derived a range of these from NFI data collected in Ireland. We have also included a range of other variables, describing various forest attributes and landscape characteristics. While our modelling approach helps narrow down the most important predictors from the wide array of potential variables influencing vegetation diversity, the Random Forest model suggests that much of the remaining variance in our richness metrics was diffusely apportioned across a wide range of variables, with each contributing only a modest share, while a significant portion remained unexplained. Forest studies tend to be characterised by a shortage of uncorrelated variables (Kovac et al., 2020). This is apparent when we consider how naturalness is both explicitly and implicitly defined in the NFI - the former through definition of semi-natural establishment and classification of semi-natural habitats, and the latter through recording of a range of forest naturalness indicators e.g. forest structure, tree species, ground vegetation and deadwood. Thus all these variables may align to some degree. Therefore, though we checked for strong correlations, the range of variables revealed as contributing small portions to the variance could partly be due to non-linear or more nuanced relationships between variables. Capturing the entirety of factors influencing species diversity and richness in a woodland dataset is challenging, and though the NFI dataset is comprehensive, and we have additionally included metrics of landscape composition, there are also further variables that could be incorporated to potentially help understand unexplained variance and disentangle correlated variables. These include landscape composition metrics derived from broader-scale buffers and landscape configuration metrics.

The Random Forest model indicated a spatial gradient in our floral metrics, with a distinct trend towards higher richness in the northwest of the country. Analysis of species richness at a county level indicated that the spatial pattern may be particularly influenced by high values for semi-natural woodland in Donegal, as compared to modified woodlands. Higher rainfall and cooler temperatures in this part of Ireland may contribute to more stable soil moisture levels, reduced

drought stress, and slower rates of nutrient mineralisation, all of which can favour a wider range of plant species. Additionally, lower agricultural intensification and a greater extent of semi-natural habitats in the northwest may support more intact and diverse plant communities.

We note, however, that these conditions are not unique to the northwest, and comparable conditions occur across the extensive landscapes of many western and southern counties. Consequently, the possibility of surveyor-related bias cannot be entirely excluded, given that NFI field surveys are conducted on a county basis and surveyors botanical identification skills may differ. Additionally, the range of species richness values for semi-natural woodland in Donegal appeared consistently higher, rather than being skewed by a small number of high richness sites. That said, Perrin et al. (2008) similarly reported that 20 of the 27 highest-scoring native woodland sites, ranked by attributes including plant diversity and the presence of notable woodland species, were located in the west of the country, with the highest proportion in County Donegal. In contrast, French et al. (2008) found no significant east–west gradient in ground flora composition within conifer plantations, however they attributed this to the overriding influence of acidic soil conditions across their sampling sites. This interpretation is consistent with our finding that species richness in modified woodlands in Donegal did not significantly differ from that observed in other counties. Taken together, our results align with established climatic and edaphic gradients known to influence woodland flora in Ireland (Kelly, 2005).

Many variables drawn out by our analysis highlight known associations between plant species richness and more heterogenous woodland habitats, including positive associations with tree diversity (number of tree species), structural diversity (sd_DBH, uneven aged plots), semi-natural establishment type and habitats, and degree of nativeness. Tree species diversity emerged as one of the topmost important factors from our machine learning model, and as the strongest predictor for overall species richness, as well as for all the forest species richness metrics, in our statistical models. The presence of different tree species in the canopy results in a diversity of microclimate and light conditions facilitating different understory plant species (Barbier et al., 2008; Cavard et al., 2011) with benefits for multitaxon diversity (Ampoorter et al., 2020), and rates of ecosystem functioning, productivity and resilience (Gamfeldt et al., 2013; Jactel et al., 2021; Liang et al., 2016; Zhang et al., 2012). Patterns may vary depending on the spatial scale considered (Leidinger et al., 2021) and on the nature of ecological interactions (Devaney et al., 2020; Hooper et al., 2005; Loreau & Hector, 2001; Van Der Plas et al., 2016), though we need to take cognisance of the fact that some forests of conservation value naturally have few species (e.g. *Taxus baccata* woodlands). Though a recent review found significant positive effects of tree species richness on understorey plant diversity (Kremer et al., 2025), Zeller et al. (2023) highlighted that many studies have absorbed tree species into an overall metric of vascular plants rather than testing it as a separate indicator, and so by treating tree species richness as a distinct indicator, our study contributes to strengthening the evidence base.

In terms of structural diversity, the uneven aged variable, suggestive of a variety of age classes of trees being present, was a positive predictor for woodland specialist species richness, while the standard deviation of DBH emerged as an important variable in our Random Forest models for woodland specialists and AWI's, and the number of naturally regenerating trees was additionally drawn out for the latter group. The potential for increased plant diversity with greater structural diversity is not limited to semi-natural woodlands, with only two of our metrics (overall richness and AWI's) explicitly linked to semi-natural as opposed to modified woodlands in our statistical models. Although vascular plant richness in modified woodlands is often much reduced at low light levels associated with canopy closure, particularly in conifer monocultures, this may be mitigated by increasing the variability in canopy structure both in terms of vertical stratification and horizontal patchiness (Coote et al., 2012; Ferris et al., 2000; Smith et al., 2008). Current forest policy in Ireland (DAFM, 2024a) emphasises a move toward to CCF management in plantations, with the potential for NFI monitoring to be used to track future changes in biodiversity, including floral biodiversity, following such a shift in management strategy.

Age was one of the most important variables for woodland specialists and AWI's, though did not emerge as a predictor in models, likely due to the association with the structural metrics discussed above. AWI plants are present in the floral assemblage of forests that have been in existence for hundreds of years (Peterken & Game, 1984), and include both generalist and specialists as defined by (Hill et al., 2004). Such indicators exist as a consequence of habitat fragmentation and the resulting ecological isolation (Ferris & Humphrey, 1999). Woodland specialist species in particular disperse slowly (Verheyen, Guntenspergen, et al., 2003) and can take decades to colonise post-agricultural woodlands (Brunet et al., 2021; Honnay et al., 2002). Bryophyte cover was also a significant predictor in explaining woodland specialist richness. Forest floor bryophyte cover tends to be higher on less-fertile soils where there is less pressure from competitive plant species (Stefańska-Krzaczek et al., 2022), conditions which are also likely to favour woodland specialists (Hermy et al., 1999).

Deadwood is used as a key positive structural indicator of forest biodiversity (Ferris & Humphrey, 1999; Gao et al., 2015), with most supporting evidence derived from studies of various saproxylic taxa (Rotheray et al., 2001; Gao et al., 2015; Jokela et al., 2018; Mestre et al., 2018). One of the deadwood metrics, representing decaying logs, emerged as a significant predictor for overall species richness and that of woodland specialists. Recent reviews indicate there is little evidence for a direct association between deadwood and woodland flora (Gao et al., 2015; Paillet et al., 2024; Zeller et al., 2022), and its significance in our statistical model may partly reflect an association with reforested sites, which had greater volumes of deadwood, and/or associations with structural diversity or age.

No specific soil types were in the topmost important variables identified, however peat depth was an important factor exhibiting a negative association with overall richness and that of the woodland

species subsets, and was significant in those statistical models, reflecting a tendency for deeper and more fertile mineral soils to support higher richness of woodland species relative to deeper peat soils. In a region where much of the forest estate comprises conifer plantations on low-fertility peat soils (Renou-Wilson & Byrne, 2015), disentangling the effect of forest type and soil characteristics from each other becomes challenging in the absence of long-term field experiments. Foresters will choose to plant the more limited range of species that can tolerate poorer soil conditions (French et al., 2008), and higher quality soils tend to remain in agricultural use rather than be subject to afforestation, and so we lack sufficient numbers of comparable forests planted with different species across a variety of soil types, a challenge addressed in Chapter 5

4.5.2 Landscape level influences on floral richness

Our findings suggest linear woody habitats are important for the richness of woodland specialists and generalists, with hedgerow emerging as a significant predictor in both cases, and treelines also significant for woodland generalists. There is strong evidence for the corridor function of hedgerows, as supported by studies showing a decline in forest species with increasing distance from forested areas (Corbit et al., 1999; Sitzia, 2007; Verheyen, Guntenspergen, et al., 2003; Wehling & Diekmann, 2009). A subset of forest species with broader ecological requirements appear to be able to capitalise on the hedgerow network and so hedgerow networks may particularly facilitate the spread of woodland generalist species able to tolerate higher soil fertility and light levels, or spread via wind or animal seed dispersal (McCollin et al., 2000; Wehling & Diekmann, 2009). This suggests that, at least in agricultural landscapes, forest flora establishment may be more successful in sites which are connected by a hedgerow network. However, given that the area of agricultural grassland was strongly positively correlated with the area of hedgerow, we cannot confirm whether the association of woodland species and hedgerow relates to the functional connectivity provided by the hedgerow network, or an association with the more species-rich forests that may occur on more fertile soils, thus reflecting a landscape intensity gradient. Our regional field study of younger native woodland sites (Chapter 2) revealed a contrasting relationship, with greater woodland species richness in lower fertility upland areas with more conifer plantations. Although we cannot directly compare species richness metrics across the two datasets, while woodland species may initially establish more readily in lower fertility young sessile oak woodlands, ultimately a mature woodland on more fertile soils may support more woodland species in the long-term. As noted earlier, incorporating configurational landscape metrics could help disentangle the confounding effects of correlated landscape composition variables, offering clearer insight into the relative importance of hedgerow connectivity versus underlying soil fertility.

4.5.3 Selecting indicators for floral biodiversity

Of the indicators listed that we have investigated, our findings suggest tree species diversity was the most appropriate overall indicator for floral richness across all groupings, but that deadwood,

uneven-aged structure, bryophyte cover, and the classification of semi-natural habitat may also present meaningful indicators for overall richness and for the forest species subsets. This raises the question of whether these structural/categorical indicators could be used to represent floral biodiversity, whether a composite metric combining these indicators should be devised, or whether direct floral richness metrics could be used in lieu.

Studies seeking to validate composite indices find they correlate well with some species groups and not others, with little evidence of a strong link with floral diversity (Hekkala et al., 2023; Larrieu et al., 2018; Storch et al., 2023; Zeller et al., 2022). Evidence appears stronger when individual structural proxies are tested, but results must be interpreted in the context of whether the entire plant community, or a subset, is being considered. As a metric, overall richness or diversity may mask compositional changes (Hillebrand et al., 2018) and may not best reflect the value or condition of the habitat for woodland species, with functional or ecological guilds potentially revealing more meaningful patterns (Rota et al., 2025). Studies using vascular plant richness to test forest indicators often do not distinguish between compositional groups of plant species as we have here, which may explain the heterogeneous pattern of correlations found in different studies (Zeller et al., 2023).

Canopy cover, as an indicator, is particularly vulnerable to how species richness is measured. Reduced canopy cover typically results in increased overall flora richness (Smith et al., 2008; Zellweger et al., 2015) but may not favour forest species (Rota et al., 2025; Zellweger et al., 2015). Supporting this, our study demonstrated that canopy cover and basal area were negatively associated with non-woodland species richness, implying more open canopies favour these species. The outcome also likely depends on whether the reduced cover is associated with gaps in older structurally diverse forests, or is associated with open canopies in younger or disturbed sites. For example, in a large-scale study of European forest biodiversity data testing Forest Europe indicators, Paillet et al., (2024) found higher richness of vascular plants in plantation woodland compared with semi-natural woodlands, which they suggested may relate to a higher share of disturbance tolerant herbs. Nonetheless, aligning with the forest species guilds, our findings suggest that overall species richness also remains linked to more structurally diverse forests despite incorporating non-woodland species, which we expect is due to the maturity of the forests analysed in this study.

The richness of forest specialist species has been linked to landscape-level forest cover in many studies (Brunet et al., 2021; Hughes et al., 2023; Petit et al., 2004; Smith et al., 2008). The area of broadleaf woodland in our study explained lower non-woodland species richness, but it did not conversely positively predict forest species groups, though the Random Forest output indicated a generally positive relationship for woodland specialists. The lack of a strong signal aligns with findings of similar work in the UK (Waddell et al., 2024), who suggested this may potentially reflect the isolation of many sites in a predominately agricultural landscape.

However, as indicated by the link with hedgerow area in our study, a degree of landscape influence is embedded within our forest species richness metrics, meaning our floral metrics may capture information on biodiversity that cannot be derived from plot-level structural metrics alone. While our findings support the relationship between structural indicators and floral richness, our data suggest that using vegetation data as a direct compositional indicator of biodiversity may therefore be more meaningful, as it encompasses a broader range of plot, site and landscape level influences.

4.5.4 Optimising NFI Surveys for Biodiversity Data Collection

The NFI methodology could be optimised to capture floral data most relevant to forest biodiversity evaluation. As studies suggest that overall floral species richness might have limited value, we recommend that consideration is given to more targeted NFI surveys focusing on lists of forest indicator species, with surveyor efforts redirected to the inclusion of bryophyte indicator species, as an alternative to investing time in capturing the whole floristic inventory.

Our study was based on the existing NFI data and did not consider non-floral taxa. There have been many multi-taxon forest biodiversity studies, with variable results in terms of the congruence of different species indicators (Burrascano et al., 2023; Da Silva et al., 2019; Jokela et al., 2018; Paillet et al., 2010; Smith et al., 2008; Storch et al., 2023). Nonetheless most fauna have been linked directly or indirectly to structural diversity attributes due to the creation of habitats and food resources (Fuentes-Montemayor et al., 2017; Gao et al., 2015; Merckx et al., 2012; Spake et al., 2016; Storch et al., 2023; Sweeney et al., 2010). Despite the common structural drivers, the value of a forest site for other taxa may not follow floral values, as different taxa may be influenced by site, ecological or landscape-level factors to a greater or lesser degree (Humphrey et al., 2015). The analysis in Chapter 3 highlighted that bees and hoverflies respond differently to new woodland development, with the latter more exposed to landscape level influences. However, while multi-taxa metrics may therefore be preferable to facilitate a robust assessment of forest biodiversity, they are difficult to scale, particularly at a national level. One feature that could be readily integrated into NFI surveys is the identification and classification of tree-related microhabitats (TreMs). With proven linkages to bird and bat (Paillet et al., 2008) or saproxylic beetle (Larrieu et al., 2018) diversity, these features could be incorporated into NFI surveys following the Larrieu et al. (2018) typology. It could also be worthwhile incorporating accessible passive monitoring techniques while fieldworkers are already on-site to collect data on faunal indicators (Gibb et al., 2019).

4.6 Conclusions

The NFI provides a valuable resource of data for tracking biodiversity change in the forest estate. Our findings highlight the structural or categorical metrics that may be of most use in reflecting floral biodiversity, with evidence that the number of tree species, deadwood logs, semi-natural

establishment, bryophyte cover, and uneven aged forests are linked to higher overall floral diversity, or that of woodland species. Our findings also support the use of floral diversity data from the NFI as a direct compositional biodiversity indicator, encoding both site and landscape influences, which can be derived from the current inventory with no additional survey effort and minimal data processing. Therefore, we suggest that the identified indirect indicators, direct measurements of floral diversity, or a combination thereof, could inform the selection of metrics for reporting requirements under the Nature Restoration Regulation, devising condition criteria for ecosystem service accounts, or monitoring forest biodiversity in the context of offsetting proposals or sustainable forest management. This study shows how the NFI data can be harnessed to both provide more information on biodiversity across the forest estate, and help identify indicators of forest biodiversity for a wide range of potential uses.

CHAPTER 5

Using expert elicitation to determine the biodiversity value of managed forests

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5 Using expert elicitation to determine the biodiversity value of managed forests

5.1 Abstract

Biodiversity underpins the ecosystem services provided by forests, yet data on the relative biodiversity value of different managed forest types remain limited, despite needing it to inform future afforestation policy. To address this we used expert elicitation in the form of a Delphi survey to assess biodiversity values across selected afforestation scenarios in Ireland, with the aim of helping to address critical data gaps and support decision-making. An expert panel of both foresters and ecologists assigned numeric biodiversity scores to three managed monoculture plantation forests, representing a fast-growing conifer, fast-growing broadleaf and a slow-growing broadleaf taxon. Specifically, the experts scored sixteen different afforestation scenarios, across different development stages and environmental contexts, for three broad biodiversity indicators: flora, above-ground invertebrate fauna and vertebrate fauna. In doing so, experts synthesised a wide range of knowledge, both across biodiversity indicators and the multiple factors influencing forest structure and function. While the resulting indicators are relatively coarse and levels of consensus varied, the overall pattern of scores across the forest lifecycle were broadly supported by existing literature and available data. These patterns reflect known relationships between biodiversity and forest structure, and the general tendency for non-native plantations to support fewer species than native woodlands. This study highlights a key challenge in predicting the impact of afforestation decisions on both nature and its contributions to people, particularly where forest policy is shifting towards new planting scenarios for which biodiversity-related evidence may be limited or lacking. Yet, with altering climates and ongoing threats from both new and native pathogens, decisions will increasingly need to be made within shorter timeframes and often in the absence of comprehensive empirical data. Employing expert elicitation methods alongside available evidence allows us to harness the breadth of existing knowledge, facilitate integration with ecosystem service models, and can meaningfully contribute to quantifying the nature-related impacts of future afforestation policies.

5.2 Introduction

Afforestation has become a key component of the European Union's (EU) climate, biodiversity, and land-use agenda, under the overarching policy framework of the European Green Deal. The EU Biodiversity Strategy, Forest Strategy, Farm to Fork Strategy, and Nature Restoration Law all support objectives to mitigate climate change, halt biodiversity loss, and promote sustainable forestry and agriculture. As part of these efforts, the EU has pledged to plant at least 3 billion

additional trees by 2030, an ambitious target that must be met amid competing land-use pressures from agriculture, housing, and energy.

Since different forests provide varying ecosystem services, many of which are positively linked to biodiversity (Balvanera et al., 2006; Gamfeldt et al., 2013; Paquette & Messier, 2011), achieving these afforestation goals requires carefully balancing priorities to establish forests that deliver a wide range of benefits for both people and nature, including timber production, climate regulation, and habitat restoration. Therefore, to inform future afforestation plans, data on the relative biodiversity value of different types of managed forest habitats are required. Capturing such biodiversity values in decision tools and economic models can provide an understanding of the environmental trade-offs and synergies between future afforestation scenarios that involve different tree species, and aid the development of forestry policies and management approaches.

Biodiversity is typically valued using a suite of compositional, structural and functional indicators (Noss, 1999), which in a forest ecosystem often include metrics related to floral and faunal communities, or proxies such as canopy cover, deadwood and structural diversity metrics. Research has highlighted that different taxonomic groups respond variably to forest changes and consequently multiple indicators should be used, as cross-taxon congruence is often low and these groups do not reliably serve as surrogates for each other (Burrascano et al., 2023; Da Silva et al., 2019; Irwin et al., 2014; Jokela et al., 2018; Paillet et al., 2010; Smith et al., 2008; Storch et al., 2023).

At the landscape scale, afforestation can lead to the expansion of some populations and the contraction of others, due to the significant habitat changes it introduces (Horst & Gimona, 2005). As such, while the indicators typically used in forest systems are valuable for comparing different forest habitats and management interventions, they may not fully capture the compositional changes that occur over time in response to shifts in canopy cover, light availability and structural complexity (Fuentes-Montemayor et al., 2022; Kirby et al., 2017). Newly established forests or woodlands often support species associated with more open habitats (French et al., 2008; Oxbrough et al., 2006; Taki et al., 2007). Although these young stands may lack the structural features of older forests and may not yet support woodland specialist species, their biodiversity value can still be considerable. Furthermore, variable growth rates among different tree species, and interactions with soil type, introduce additional axes of ecological change, as forest structure and composition evolve over time (Bončina et al., 2023; Pretzsch, 2010).

Studies of biodiversity in managed forests are often conceived with the aim of comparing them with native or unmanaged forests (Albert et al., 2021; Bremer & Farley, 2010; Brockerhoff et al., 2008). Where the aim is to compare biodiversity in different production-focused afforestation scenarios, sourcing adequate and comparable data on different tree species plantations across their production life cycle is challenging, as current data are patchy and collected using differing

methodologies in varying landscapes. Additionally, as an outcome of shifting policies, often pivoting in response to pest/pathogen outbreaks, available data tend to include legacy planting scenarios rather than those that may be favoured in future afforestation programmes.

Though there have been recent advancements in capturing biodiversity with other ecosystem services indicators in Forest Management Decision Support Systems (Lundholm et al., 2020), a lack of comparable biodiversity data across the forest life cycle representing forests prior to canopy closure, after canopy closure, and before or after thinning operations, combined with a lack of data on tree species likely to be favoured into the future, presents a challenge for modelling and decision-making. While the trade offs between timber production and carbon sequestration/storage have been investigated in detail (Forster et al., 2021; Triviño et al., 2015), biodiversity has rarely been factored into whole production-cycle models, often due to the complexity of measurement and breadth of available metrics. Collection of new data is also hampered by costs, time, and a lack of ecologists with specialist skills. While field-based data collection remains the most appropriate method for addressing current information gaps, alternative approaches can help inform immediate decision-making at both forest and policy levels and support the development of decision-support tools. Using Ireland as a case study, where there is an ambitious afforestation programme aimed at increasing forest cover nationally (DAFM, 2024b), we explore the feasibility of filling such data gaps by surveying those with expertise in forestry and forest biodiversity.

Historically, Ireland's native woodlands were depleted to very low levels, and though the forestry programme in the last century increased forest cover from 1 to 11%, it was focused on afforesting marginal agricultural lands with non-native conifer monocultures, primarily dominated by Sitka spruce (*Picea sitchensis*) (Iremonger, 2007). It is in this context that many forest biodiversity studies have been undertaken here. Most notably, comprehensive surveys of flora and faunal groups across the production forest life cycle have been carried out in pure Sitka spruce, mixed Sitka spruce/ash (*Fraxinus excelsior*), pure ash, and Japanese larch (*Larix kaempferi*) plantations (French et al., 2008; Smith et al., 2008) to compare the relative values of these planting scenarios, and further studies have incorporated comparisons with semi-natural woodlands (Coote et al., 2012; Irwin et al., 2014; Oxbrough et al., 2016; Sweeney et al., 2010) or former land-uses (Oxbrough et al., 2006; Wilson et al., 2006). Ireland's remaining mature semi-natural woodlands have also been surveyed for compositional, structural and functional attributes on the basis of botanical surveys undertaken as part of conservation assessments for EU Habitats Directive (92/43/EEC) reporting (O'Neill & Barron, 2013; Perrin et al., 2008). Data on certain afforestation scenarios potentially favoured into the future (e.g. oak *Quercus* spp. and birch *Betula* spp.) are lacking and given the fragmented nature of forest cover in Ireland, and depauperate flora and fauna, it may not be appropriate to refer to data collected in similar forest types from other jurisdictions to fill knowledge gaps.

To generate interim data, we applied the Delphi technique (Mukherjee et al., 2015) to synthesise expert judgments on the relative biodiversity value of different forest types. The Delphi technique is a flexible, structured expert elicitation method involving two or more survey rounds. Its iterative process is designed to encourage convergence or stabilisation of opinion among participants (Jacobs et al., 2015). Although traditionally used to build consensus around contentious issues, the Delphi method is also employed to formulate or evaluate policies, explore areas of disagreement, or fill data gaps (Mukherjee et al., 2015). It is particularly useful in contexts where empirical data are lacking or where the complexity of measurement is high and associated costs are prohibitive. In such cases, the collective opinion of a panel of experts is considered more reliable than that of any individual, and the method has been widely applied in conservation and natural resource management (Crance, 1987; Geneletti, 2007; Hess & King, 2002; MacMillan & Marshall, 2006; Oliver, 2002; O'Neill et al., 2008). While other expert elicitation methods such as traditional surveys, focus groups, or expert panels may be used in similar contexts, the Delphi method offers distinct advantages by combining anonymity, iteration, and feedback, which together help to minimise bias and support more considered expert judgments.

In considering potential forest types for future afforestation scenarios that could provide multiple benefits, the research team consulted with 12 different stakeholders/actors across the forest innovation sector. These included policy makers and regulators, silvicultural researchers, ecologists, forest managers and forest owners. Based on this consultation, three afforestation scenarios were selected, each representing a distinct functional and ecological profile: 1. A fast-growing conifer (Sitka spruce), 2. A fast-growing broadleaf tree (Birch - *Betula pubescens* or *Betula pendula*) and 3. A slow growing broadleaf tree (Oak - *Quercus petraea* or *Quercus robur*). These tree taxa were considered most likely to form part of future afforestation efforts under government-led forestry programmes in Ireland.

The chosen species are the dominant fast-growing conifer, fast-growing broadleaf and slow-growing broadleaf species recorded in the National Forest Inventory (NFI) both in terms of overall stocked forest area, and for the youngest age class (DAFM, 2023e), though there are few NFI oak and birch afforested plots. While variability in biodiversity attributes at different life cycle stages has been demonstrated for fast-growing conifer plantations in Ireland (French et al., 2008; Smith et al., 2008), and floral data are available from the NFI, similar data are lacking for oak and birch plantations. The oak and birch species were also favoured for the purposes of our study due to the broader range of soils in which they can be planted (DAFM, 2023b) relative to other species options, their nativeness in our study region, and the genetic breeding programme in place for birch in Ireland which additionally indicates this species may be a sustainable long-term planting option. Broad soil categories were used in order to capture the associated environmental gradients in pH, fertility and moisture that influence forest biodiversity in our study region (Coote et al., 2013; Kelly, 2005).

The judgments of experienced foresters and ecologists were sought due to their combined expertise in afforestation programmes, practical field-level knowledge across diverse site types, and ecological training. Their professional backgrounds allowed them to provide informed assessments of the relative biodiversity value of each scenario at different forest life cycle stages within specific environmental contexts. Specifically, we hypothesised that 1.Scores for biodiversity indicators would be highest in our oldest (thinned) forest scenario; 2. Scores for Sitka spruce forests would be lower than oak and birch forests; and 3. Scores for foresters and ecologists would significantly diverge. We discuss the survey results in the context of available literature and NFI data, evaluate the benefits and challenges of this method, and provide recommendations regarding further biodiversity monitoring and research.

5.3 Methods

5.3.1 Afforestation scenarios

Our survey involved asking experts to score different afforestation scenarios for biodiversity value considering three broad biodiversity indicators: flora, invertebrate fauna (above-ground) and vertebrate fauna. The afforestation scenarios were developed based on three managed forest-types, to be planted for the purpose of timber-production, and representing a fast-growing conifer, fast-growing broadleaf and a slow-growing broadleaf taxa. Four life cycle stages relevant to production forests were prescribed based on merged categories from the development stage classification used in the NFI (see Appendix D, Table D1): open stage, canopy-closure stage, mature even-aged unthinned, and mature even-aged thinned. To provide environmental context, four broad soil groupings were considered which amalgamate dominant soil types present in our study area (Teagasc & EPA, 2018): podzols and brown podzolics, brown earths, gleys, and highly modified peat and peaty podzols. This resulted in sixteen forest scenarios for each tree taxon and biodiversity attribute (Fig. 5.1).

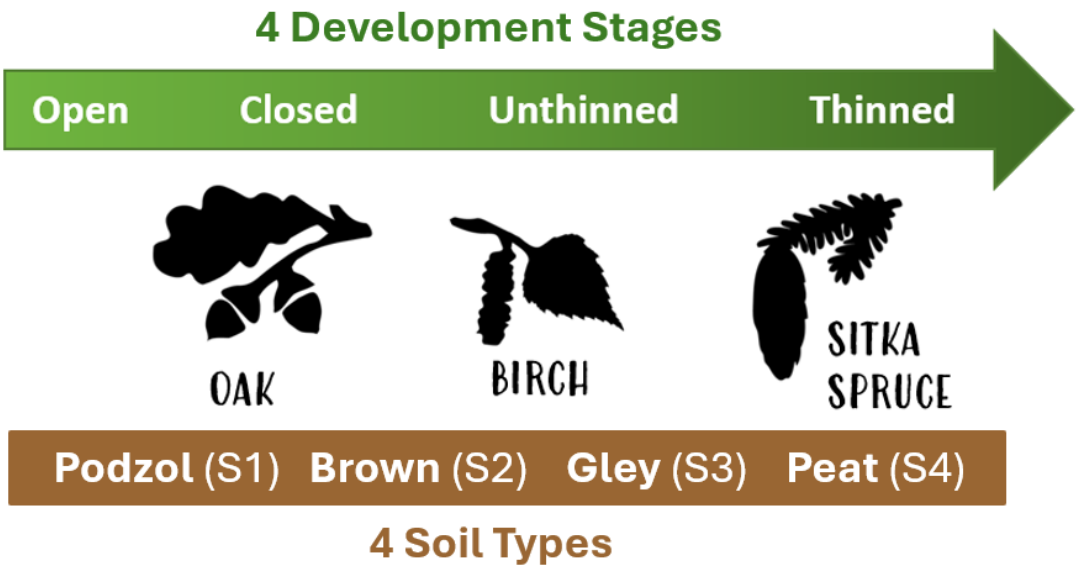

Figure 5.1 Afforestation Scenarios Scored by the Delphi Panel for each of three tree taxa planted on four soil types across four development stages. All scenarios were scored for each biodiversity indicator (flora, invertebrates, vertebrates)

5.3.2 Expert Survey

The Delphi method requires at least two survey rounds, with feedback to participants on scores from all participants, as well as their own scores, between each round. An initial list of 70 potential survey participants based in the Republic of Ireland was established. Potential experts were identified through registers of ecologists and foresters who were trained as part of the governments Native Woodland Scheme, personal knowledge of the authors, engagement with members of professional networks, and recommendations from recruited experts. This initial panel therefore included ecologists engaged in surveys and assessments of forestry ecosystems, or foresters with experience of working to achieve biodiversity objectives in afforestation sites. Both groups were considered experts due to their knowledge and experience, grounded in field science and practice (Krueger et al., 2012).

Two survey rounds were completed. The survey was initially issued to all potential experts together with an information leaflet and explanatory notes, with 23 experts completing the first survey round. A review by Mukherjee et al. (2015) found the number of participants in Delphi surveys ranged from two to 184, though most had fewer than 20 respondents. They further highlighted that the respondent panel size is not required to be a statistically representative sample in these surveys since the panel representativeness is judged based on the respondents attributes. As such, our panel of 20 experts was considered be a robust sample size of those with the relevant specialist technical knowledge. The panel comprised 12 ecologists and 11 foresters. In round one, participants were

asked to score the sixteen forest scenarios for the three tree species and three biodiversity attributes, assigning a score between 0 and 100 to each scenario in a spreadsheet provided. All experts provided scores for flora (n=23), while one ecologist and one forester did not complete the scoring sheets for invertebrates and vertebrates (n = 21). Participants were asked to apply a score of 0 to the scenario considered to support the lowest biodiversity, and a score of 100 to the highest. While 5-point scales are common to many similar scoring surveys in the natural resource management sector (e.g. Verbrugge et al. (2013)), similar to (Alejandre et al., 2023), a broader scale was used to give experts greater flexibility. Experts were requested to base their scores on a judgement of species richness as a proxy for biodiversity, and that in the context of their own experience they were to consider the typical planting and management interventions for the scenario in question e.g. while oak comprises two planted species, they would be aware that the planting choice would differ based on the soil category under consideration. After the first round, responses were collated and summary statistics generated.

In round two, the expert panel were provided with the summary of results, which included the mean, median, min and max scores from all participants for each scenario, together with a summary of anonymised comments received and their own first round scores. They then had an opportunity to revise their contributions, by adjusting their scores given the information provided, or otherwise retain their original scores. Only four participants adjusted their scores in the second round and given the low revision-rate the survey was closed at this point. Participants were also asked to provide an indication of their confidence in the estimated score on a scale of 1 (not very confident) to 5 (very confident), though this was used to aid interpretation rather than for computing weighted-scores (Alejandre et al., 2023; Campagne et al., 2017). Participants were provided with space to provide an explanation, justification or caveat for their score. Explanatory notes with instructions and assumptions were provided with the scoring sheet (Appendix D, Table D1). Participants returned the scoring sheets via email.

There is no standardised method for consensus measurement in Delphi studies (Von Der Gracht, 2012). Furthermore thresholds for consensus amongst experts in Delphi panel studies are not always defined, and depend on the structure of the survey and the nature of the data collected (Diamond et al., 2014; Hsu & Sandford, 2007). Commonly, surveys provide statements or attributes to select or rank, and then set a threshold for percentage agreement in selections/rankings (Gafo Gómez-Zamalloa et al., 2011; Maini et al., 2023) to describe the degree of convergence. Where experts are asked to score certain attributes, measures of range or variance are often used to describe levels of agreement, or lack thereof (Alejandre et al., 2023; Filyushkina et al., 2018; Scolozzi et al., 2012). On the basis of the final scores, median scores were calculated for each category and the median of absolute deviation (MAD) was used, which is robust to outliers (Leys et al., 2013), to describe the level of agreement between experts for that category. Given a

potential maximum MAD value of 50 for our data range, the following thresholds were defined: 0-10 (low variability), 10-30 (moderate variability), over 30 (high variability).

5.3.3 Comparison with NFI Data

The NFI collects structured data on a range of forest attributes, including floral biodiversity, across a wide range of sampling sites. Using the most recently-published data (Fourth cycle – 2022), the dataset of 2,020 plots was filtered to identify plots that met the following criteria: even-aged; pure (forest subtype); afforestation (establishment type); planted, natural <20% (tree origin). Plots assigned to the 'overmature' development stage were removed, as the focus of the study was on the production cycle. Aggregating plot data with tree measurement data, plots were selected where the dominant tree species was either Sitka spruce, pedunculate/sessile oak, or silver/downy birch. This resulted in 436 plots, predominantly Sitka spruce, with only 14 plots of oak and 3 of birch (as much of the existing stocked estate of these species is within mixed or semi-natural forests). For each plot, the species richness data were combined for all floral attributes other than the trees i.e. ferns, grasses, herbs and shrubs. Data were then pooled based on soil type, development stage and thinning status to align with the afforestation scenarios.

5.3.4 Data Analysis

As not all participants adhered to the instructions regarding setting the minimum score to 0 and maximum to 100, in these cases data were normalised between 0 and 100 in advance of preparing data summaries after round one, and in the collation of the final dataset after round two (where individuals had adjusted their non-normalised scores). In order to visually represent the relative mean scores for each afforestation scenario heatmaps were generated using the *pheatmap* R package (Kolde, 2018). To test for differences between the final scores for each biodiversity attribute and scenario across development stages, soil types and professions, non-parametric Kruskal-Wallis (K-W) tests were employed, which use the chi-squared distribution to assess statistical significance. Where significant differences were found, Dunn's post-hoc tests with Bonferroni correction were applied to identify specific group differences.

5.4 Results

5.4.1 Expert Scores

Fig. 5.2 presents a heatmap of median floral biodiversity scores across forest development stages, soil types, and tree planting scenarios, aggregated for all experts, and separately for ecologists and foresters. As illustrated by darker shading for higher values, and absent or lighter shading for lower values, experts judged that Sitka spruce forests had lower floral diversity than oak or birch forests, particularly in the closed and unthinned stages. There was some variation between soil types, with lower scores for the S4 soil category (modified peats and peaty podzols). While median scores from ecologists and foresters were broadly similar, ecologists tended to assign lower scores to Sitka spruce in the open and thinned stages compared to foresters. Similar patterns were observed for invertebrate and vertebrate biodiversity, as shown in Appendix D, Fig.'s D1 and D2.

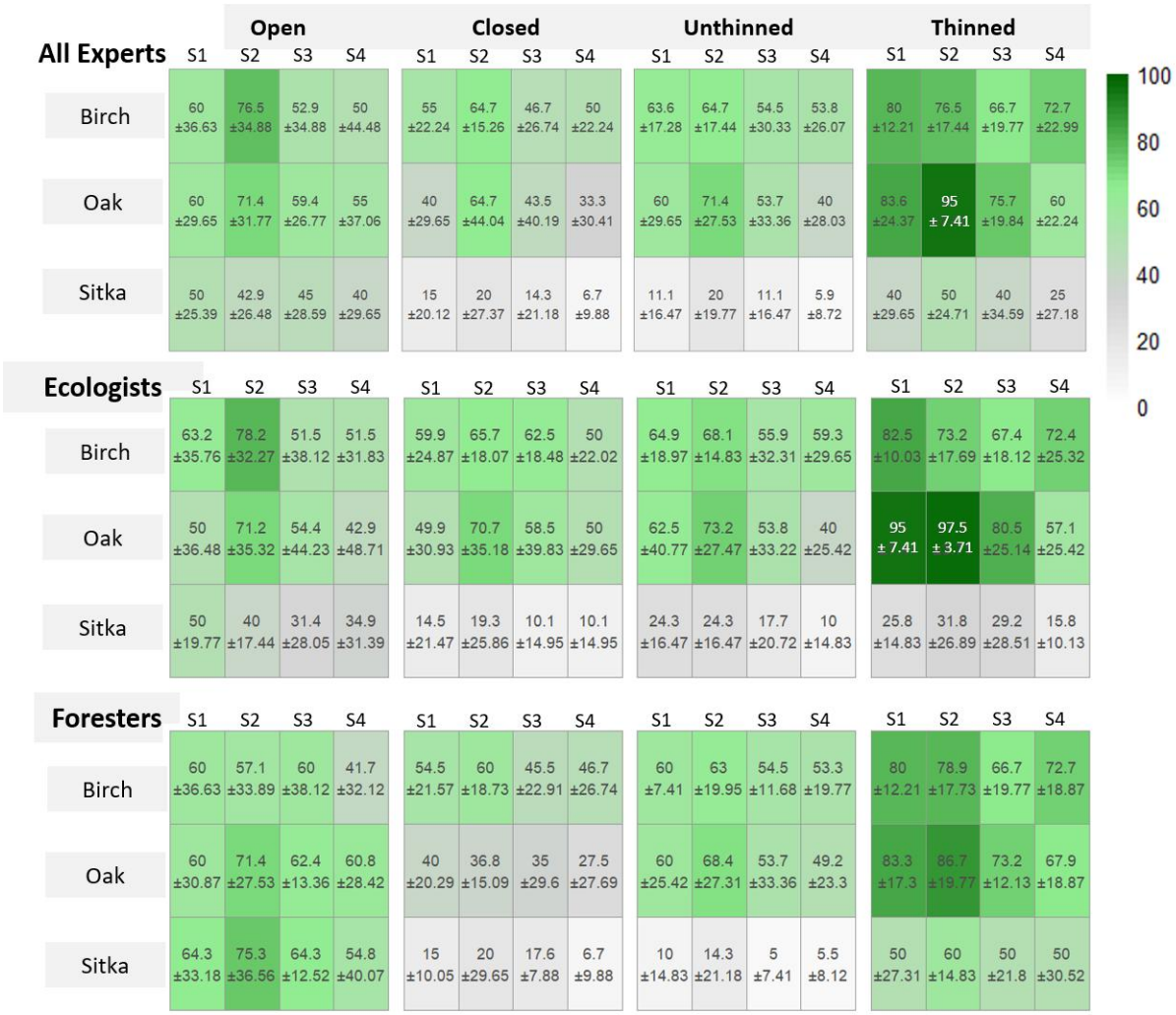

Figure 5.2 Median (±MAD) Flora Scores (with 0 representing low and 100 high biodiversity) for entire panel (n = 23), ecologists only (n = 12), and foresters only (n = 11). Scores are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned) and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Scale (0-100) colouring runs from white to grey to green, with darkest green being the highest values.

5.4.2 Variation in Biodiversity Scores Across Planting Scenarios

Pooling data across soil types, and examining scores for all experts combined, we tested for differences in perceived biodiversity among the tree planting scenarios (Table 5.1). The results indicate that Sitka spruce forests were judged to provide significantly lower flora diversity than oak or birch forests across all biodiversity indicators.

Table 5.1 Results of Kruskall-Wallis (KW) and Dunn's Post-Hoc Tests for comparisons of flora, invertebrate (Inverts) and vertebrate (Verts) scores across three tree planting scenarios (birch, oak and Sitka spruce)

		Flora	**Inverts**	**Verts**
Tree Taxa	chi-squared	29.983	28.426	25.674
	p value	**≤0.001**	**≤0.001**	**≤0.001**
Birch v Oak	Z	0.290	-0.994	-0.462
	p value	1.000	0.961	1.000
Birch v Sitka	Z	4.881	4.039	4.160
	p value	**≤0.001**	**≤0.001**	**≤0.001**
Oak v Sitka	Z	4.590	5.033	4.570
	p value	**≤0.001**	**≤0.001**	**≤0.001**

5.4.3 Variation in Biodiversity Scores Across Development Stages

Again pooling data across soil types, and examining scores for all experts combined, we tested for differences in expert scores between the development stages for each planting scenario. Richness for all biodiversity indicators was significantly higher for the thinned stage oak relative to all other stages (Table 5.2). For birch, scores for floral richness were significantly higher in thinned stages compared to closed stages, while invertebrates and vertebrate richness scores were significantly greater in thinned stages compared to open and closed stages (Table 5.2). For Sitka spruce, open and thinned stages were significantly higher in floral richness scores than closed and unthinned stages (Table 5.2). These differences, aligning with the patterns observed in the heatmaps, are summarised in Fig. 5.3.

Table 5.2 Results of Kruskall-Wallis and Dunn's Post-Hoc Tests for comparisons of flora, invertebrate (Inverts) and vertebrate (Verts) scores for three tree planting scenarios (birch, oak and Sitka spruce) across four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned)

		Sitka			Birch			Oak		
		Flora	**Inverts**	**Verts**	**Flora**	**Inverts**	**Verts**	**Flora**	**Inverts**	**Verts**
Stage	chi-squared	21.708	12.411	12.828	10.110	13.977	13.981	14.605	20.377	20.557
	p value	**≤0.001**	**0.006**	**0.005**	**0.018**	**0.003**	**0.003**	**0.002**	**≤0.001**	**≤0.001**
Open v	Z	3.335	2.627	2.840	0.765	-0.231	0.259	0.599	-0.665	-0.609
Closed	p value	**0.005**	0.052	**0.027**	1.000	1.000	1.000	1.000	1.000	1.000
Open v	Z	3.727	2.646	2.574	-0.080	-1.434	-0.345	-0.149	-1.937	-1.321
Unthinned	p value	**≤0.001**	**0.049**	0.060	1.000	0.909	1.000	1.000	0.317	1.000
Thinned v	Z	0.392	0.019	-0.266	-0.845	-1.203	-0.604	-0.748	-1.272	-0.712
Unthinned	p value	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Open v	Z	0.542	0.310	0.393	-2.254	-3.337	-3.041	-2.903	-4.184	-4.185
Thinned	p value	1.000	1.000	1.000	0.145	**0.005**	**0.014**	**0.022**	**≤0.001**	**≤0.001**
Closed v	Z	-2.793	-2.317	-2.447	-3.019	-3.106	-3.301	-3.502	-3.519	-3.575
Thinned	p value	**0.031**	0.123	0.086	**0.015**	**0.011**	**0.006**	**0.003**	**0.003**	**0.002**
Unthinned v	Z	-3.186	-2.336	-2.181	-2.174	-1.903	-2.696	-2.753	-2.247	-2.863
Thinned	p value	**0.009**	0.117	0.175	0.178	0.343	**0.042**	**0.035**	0.148	**0.025**

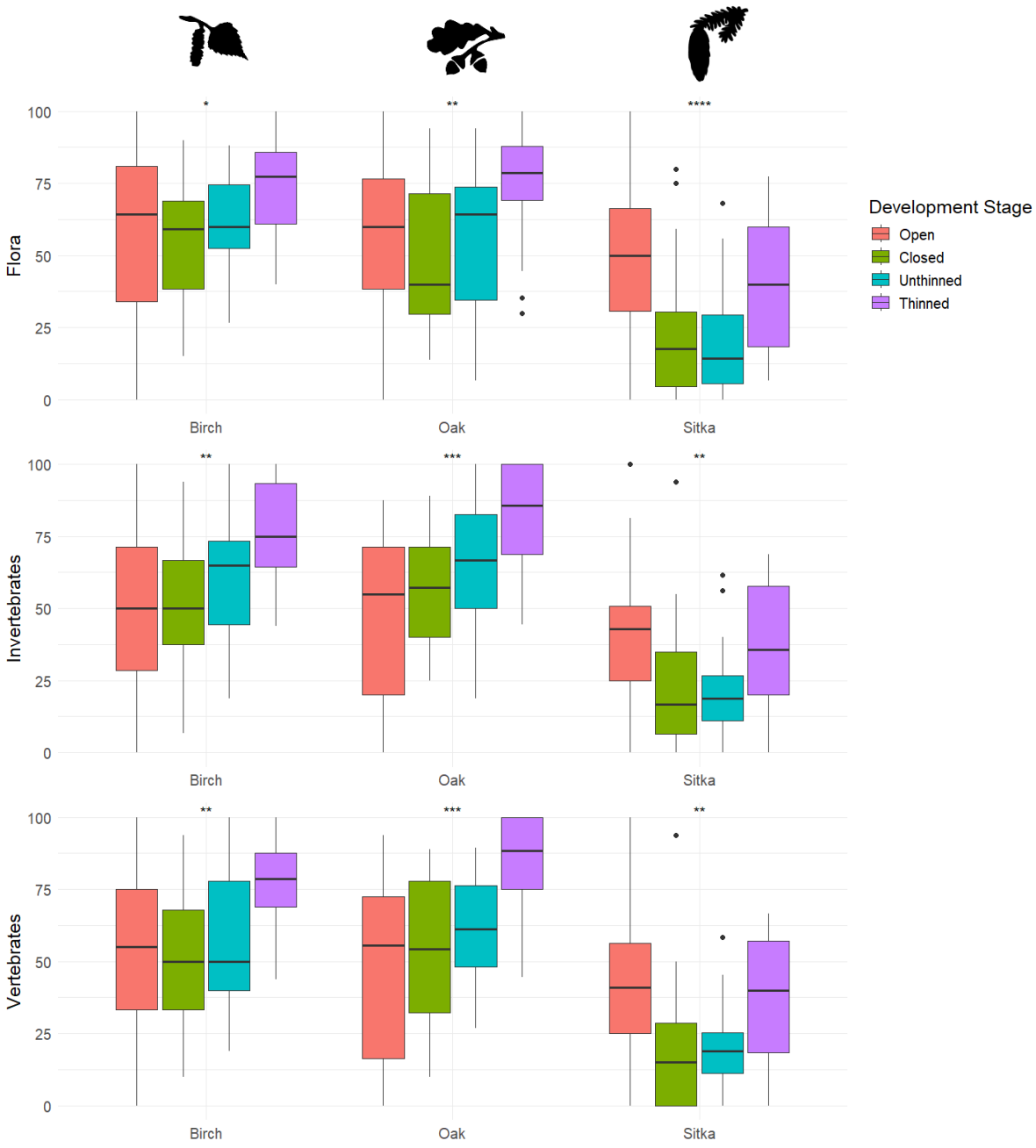

Figure 5.3 Scores for Flora, Invertebrates and Vertebrates for the expert panel (n = 23) grouped by the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned). Stars above plots indicate significance levels between stages as per Kruskall-wallis tests in Table 5.2

5.4.4 Variation in Biodiversity Scores Across Soil Types

Pooling data across development stages, no significant differences across soil categories were revealed, with the exception of flora in oak sites, which experts considered to be richer on brown

earth soils relative to peat soils (Dunn's test: z = 2.960, p = 0.018, Appendix D, Table D2), aligning with the patterns observed in the flora heatmap (Fig. 5.2).

5.4.5 Variation in Biodiversity Scores Across Professions

Fig.5.4 shows the median biodiversity scores assigned by ecologists and foresters across forest development stages. While no significant differences were found between the two expert groups for any biodiversity indicator or afforestation scenario overall, some differences emerged in their relative evaluations of Sitka spruce. As also shown in the heatmaps (see Fig. 5.2 and Appendix D, Fig.'s D1 and D2) and supported by statistical analysis (Appendix D, Table D3), foresters judged floral and vertebrate biodiversity to be significantly higher in the open and thinned stages of Sitka spruce compared to the closed and unthinned stages. In contrast, ecologists did not assign significantly different scores for these indicators across the development stages for Sitka spruce.

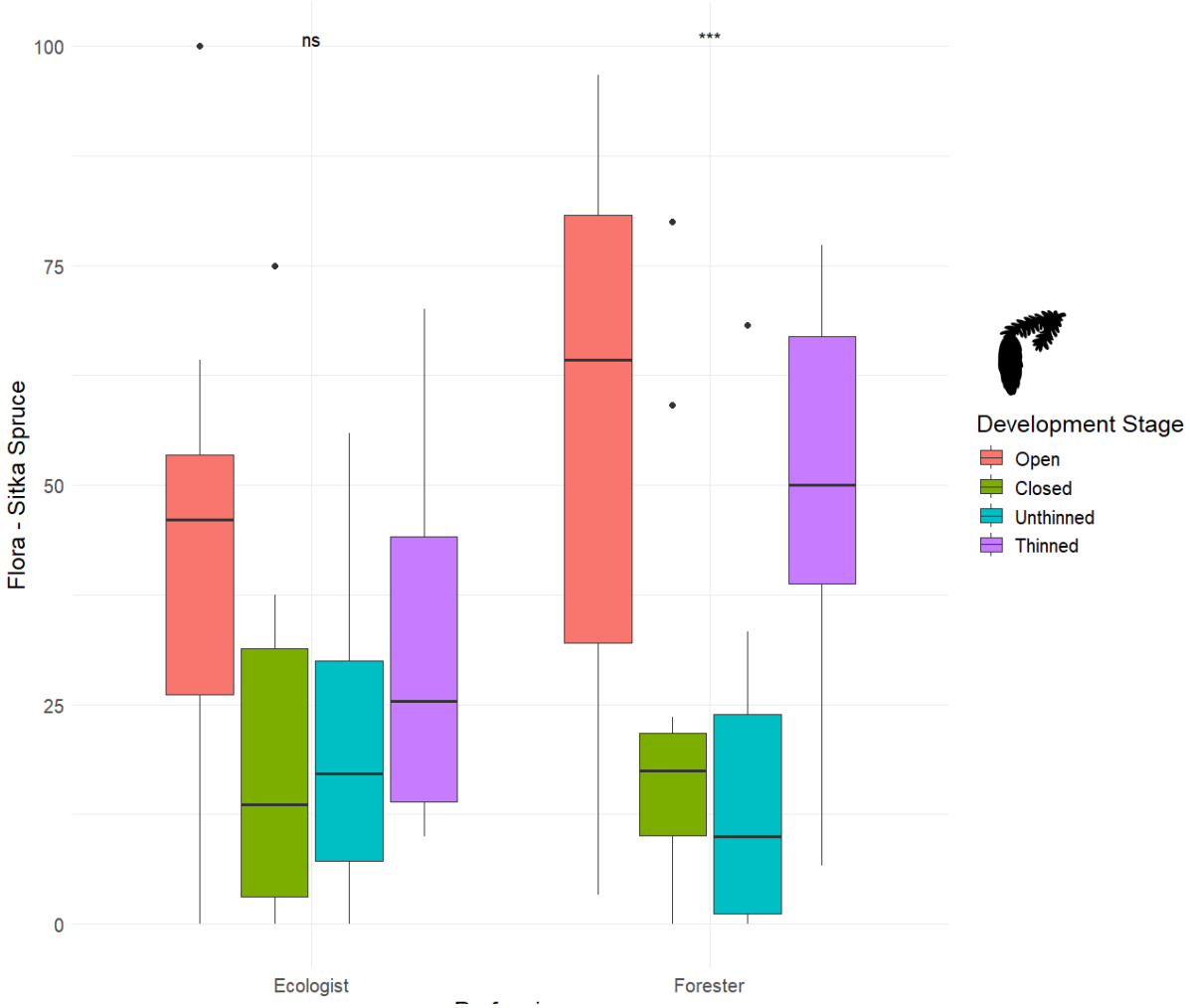

Figure 5.4 Scores for Flora under the Sitka spruce scenario for Ecologists (n = 12) and Foresters (n = 11) grouped by the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned). Stars above plots indicate significance levels between stages as per Kruskall-wallis tests in Table D3.

5.4.6 Consensus between experts

The percentage low, moderate and high consensus for each development stage and biodiversity attribute, based on the Median of Absolute Deviation (MAD), is presented in Fig. 5.5. The lowest levels of agreement between participants, as judged by comparing the MAD of scores within each scored category with our pre-defined consensus thresholds, were for the open stage scenarios across all tree taxa and all biodiversity indicators (Fig. 5.5). Highest levels of consensus for flora were for thinned-stage oak on brown earths, and closed/unthinned Sitka spruce on peat soils, which were also associated with the highest and lowest scores respectively. There was perfect consensus for invertebrates and vertebrates on thinned oak plantations on brown earth soils, which also represent the highest scores of these biodiversity indicators. Confidence ratings were highest for flora relative to invertebrates and vertebrates (Appendix D, Fig.'s D3-D5); however, this difference was not significant, and there was no significant difference between confidence ratings for foresters and ecologists across any biodiversity indicator group (Appendix D, Table D4).

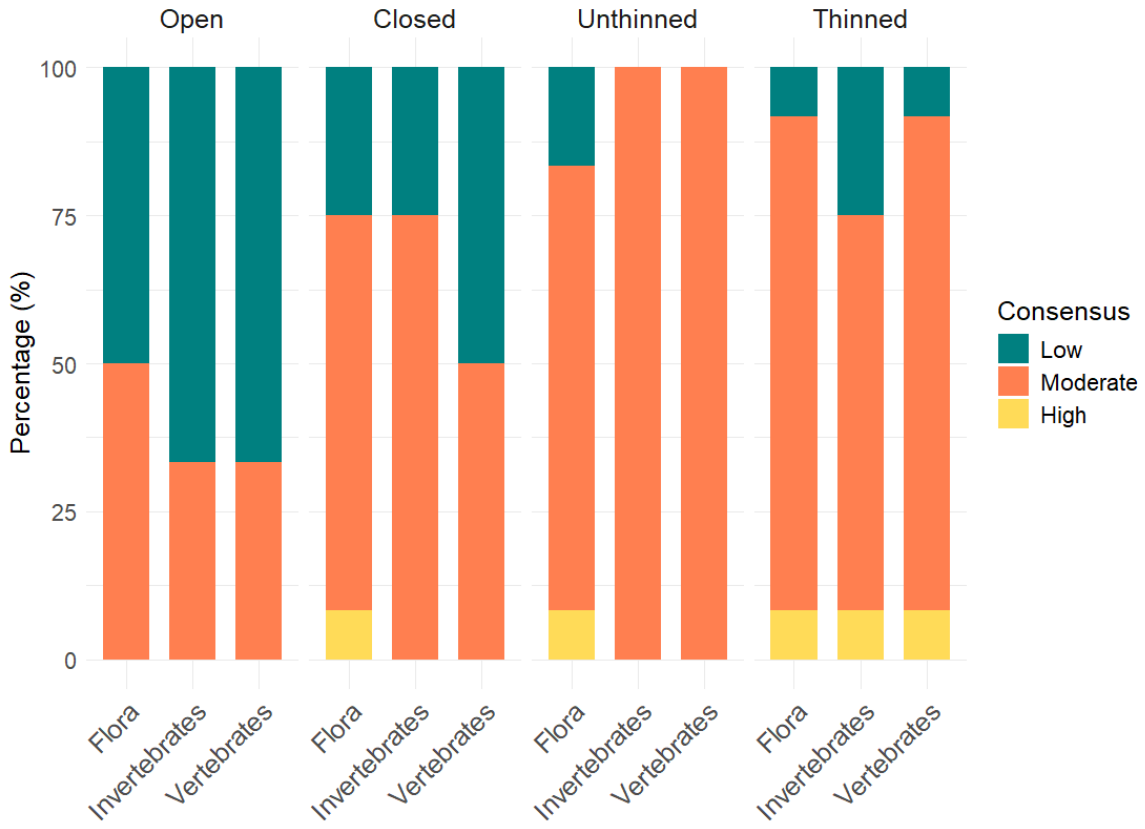

Figure 5.5 Percentage consensus based on the Median of Absolute Deviation (MAD) for the combined scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned). Consensus is as per pre-defined thresholds for MAD as follows: 0-10 (Low, 10-30 (Moderate) and over 30 (High).

5.4.7 Comparison with NFI Data for Sika Spruce

A heatmap of the median flora scores for the available NFI data of relevance to our planting scenarios is shown in Fig. 5.6. Scores for Sitka spruce drop at canopy closure and increase after thinning. Median scores for Sitka spruce were compared across development stages (pooling soil types), showing that there were significant differences between open and closed, open and unthinned, closed and thinned, and unthinned and thinned scores (Appendix D, Table D5). There were significant gaps in information in the NFI dataset with respect to pure birch or oak woodlands, with low numbers of plots and many missing values (NA) (Fig. 5.6). This likely reflects a combination of the absence of these woodland types in our landscape, together with an absence of data on those that do exist.

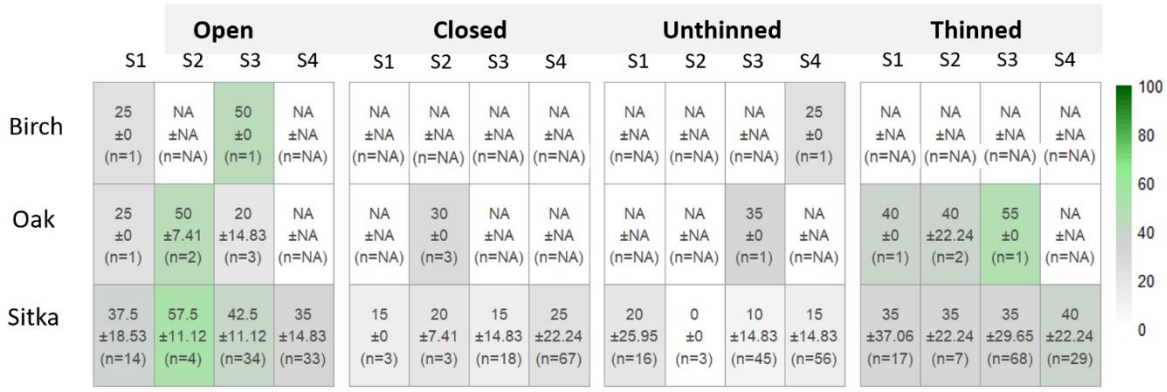

Figure 5.6 Median (±MAD) Species Richness of Herbs, Grasses, Ferns and Shrubs extracted from the NFI dataset. Richness values are converted to the same 0-100 scale as expert scores. The number of NFI plots (n) is given for each category. Values are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned) and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Scale (0-100) colouring runs from white to grey to green, with darkest green representing the highest values.

5.5 Discussion

Evidence bases can be improved by combining available evidence with the use of a structured process for eliciting expert opinion (MacLeod et al., 2022). Such survey methods rely on harnessing the participants scientific or experiential understanding of a complex system, as opposed to collating the subjective perceptions of non-experts (Bennett, 2016; Fazey et al., 2006; Jacobs et al., 2015). Expert surveys, including Delphi surveys, are commonly used to score or rate ecosystem services (Campagne et al., 2017; Scolozzi et al., 2012; Uhde et al., 2017; Walters et al., 2021), and the Delphi method has been applied in the forestry context to estimate biodiversity (Filyushkina et al., 2018), landscape (Geneletti, 2007) or recreational (Edwards et al., 2011) values, as well as identify forest restoration priorities (Orsi et al., 2011) and sustainable management indicators (Khadka & Vacik, 2012).

Adopting a similar approach, though allowing a greater degree of flexibility in the scoring range, scores were elicited for biodiversity value under different forestry planting scenarios from a panel of ecologists and foresters. Although levels of consensus varied, the scores provided were broadly supported by available field data and literature. This suggests that expert opinion can serve as a valuable tool for ranking the biodiversity potential of various planting scenarios across different environmental contexts. Such rankings can meaningfully contribute to understanding the nature-related impacts of future afforestation policies.

5.5.1 Woodland development & environmental factors

In line with our first hypothesis that experts would score thinned scenarios highest, participants judged that species richness for all indicators under birch and oak planting scenarios would be highest in thinned-stage forests, and lowest in canopy closure and unthinned stages, reflecting the dominance of the light gradient in structuring forest communities (Kirby et al., 2017), and the ultimate shift with age from a modified grassland community to one characterised by a greater diversity of forest species (Brunet et al., 2011; Peterken & Game, 1984). The strongest agreement between experts was found for the most polarised scenarios - thinned oak as compared to unthinned Sitka spruce. Scores for Sitka spruce indicated that experts anticipated a decline in biodiversity as the canopy closed, with an increase during the thinned stage, though not returning to the levels observed during the open stage. This trend, supported by studies of vegetation in Sitka spruce plantations in our region (Ferris et al., 2000; Smith et al., 2008), is also reflected in the NFI data for Sikta spruce. Compared to peat soils, our participants judged that floral richness would be significantly higher in thinned oak forests on brown earth soils, likely informed by the diversity observed in semi-natural oak woodlands in these settings (Cross & Collins, 2017). This judgment also reflects the recognised unsuitability of planting oak on peat soils, as outlined in forestry planting standards (DAFM, 2023b), a point emphasised by several experts in their comments.

Floral and faunal communities in afforested sites are influenced by a combination of site-level and landscape-level factors, which interact with stand age to shape species richness (Bremer & Farley, 2010; French et al., 2008; Fuentes-Montemayor et al., 2017). In our survey, defining soil and tree categories helped to capture some of this landscape-level variation, as soil type is often inherently linked to landscape context (Carlier et al., 2021) and is used to guide appropriate tree species selection in planting prescriptions (DAFM, 2023b). However, disentangling the relative influence of stand-scale versus landscape-scale drivers is challenging, may vary depending on the biodiversity indicator used, and likely contributes to the variation observed in expert scores. These factors could include proximity to older woodland (Brunet et al., 2012; Coote et al., 2013), woodland size (Waddell et al., 2024), grazing (Corney et al., 2006; Perrin et al., 2011), landscape-level influences (Humphrey et al., 2015), the nature of edges and openings (Gittings et al., 2006; Proesmans et al., 2019b; Spake et al., 2016), as well as site-specific soil, slope and wetness attributes (Corney et al., 2006; Ferris, 1999; Honnay 199, Storch et al., 2023). Comments suggested that participants may also have been observing differences in planting densities, management approaches, ground preparation and drainage.

Consensus was lowest for open stage scores, with comments provided by experts indicating that some participants considered the pre-planting scenario on certain soils may have comprised a species-poor grassland, while others suggested these soils may support grasslands associated with high nature value farming, highlighting the potential influence of past land use (Honnay et al., 1999). Participants also potentially envisaged different specific soil subtypes within the broad soil categories provided. Additionally, depending on the planting approach they were envisaging, some may have anticipated a flush of ruderal species following planting. All of these factors likely contributed to the variation in scores for the earliest development stages.

5.5.2 Native broadleaves vs non-native conifers

Supporting our second hypothesis that scores for Sitka spruce would be lower than for birch or oak, the judgement that the species richness for all biodiversity indicators would be higher in the native broadleaf plantations relative to non-native conifer plantations is broadly, but not universally, supported by the literature. The outcome largely depends on the afforestation scenarios being compared and the specific indicators selected (Brockerhoff et al., 2008; Quine & Humphrey, 2010; Smith et al., 2008; Wilson et al., 2006). Reviewing the NFI data and literature highlights the lack of reliable evidence for biodiversity in planted pure stands of oak and birch. The expert panel may have drawn on their knowledge of semi-natural woodlands, which generally support higher species richness than non-native conifer plantations (Albert et al., 2021; Coote et al., 2013; Pedley et al., 2014; Quine & Humphrey, 2010), although some invertebrate assemblages are comparable between these forest types (Humphrey et al., 1999; Irwin et al., 2014). There was no significant difference in scores between birch and oak for any biodiversity group. While the higher biodiversity value of mature oak forests has been documented (Cross & Collins, 2017; Kennedy &

Southwood, 1984; Mitchell et al., 2019), experts scores likely reflect the judgement that the managed even-aged nature of these stands may limit the realisation of this potential.

Since our focus was on the production life cycle within our study area, this survey did not aim to compare age-controlled species richness of the selected taxa, which is potentially similarly diverse in old-growth spruce as some broadleaf taxa (Humphrey, 2005). In the context of even-aged production forestry with current harvesting cycles, the biodiversity values associated with old-growth Sitka spruce are unlikely to be realised. Conversely, older existing conifer plantations, often established on marginal lands and densely planted (Renou-Wilson & Byrne, 2015), may not reflect the biodiversity potential of future planting approaches if planned and managed more sensitively (Iremonger, 2007) or under CCF principles (European Commission, 2023). Therefore, it is important to consider that our experts' judgements for Sitka spruce, largely based on experience with legacy plantations, could represent a conservative estimate of species richness.

5.5.3 Cross-congruence of Indicators

The general pattern of expert-scoring across forestry scenarios, soils and development stages was similar for plants and animals and suggests that participants considered that forests with a greater diversity of flora also support a wider diversity of associated fauna. Several participants noted in their comments that they expected invertebrate diversity to increase as the forest establishes, due to the creation of new niches, food sources, and structural complexity, judgments supported by numerous studies e.g. Gao et al., (2015), Jokela et al., (2018), Merckx et al., (2012), Spake et al., (2016), Storch et al., (2023).

The perceived biodiversity of vertebrates largely aligns with that of the other groups, as experts likely reasoned that forests supporting greater floral and invertebrate diversity, arising from increased structural complexity, would support a more diverse vertebrate community by providing foraging resources for groups such as birds and bats (Burton et al., 2018; Fuentes-Montemayor et al., 2017; Storch et al., 2023; Sweeney et al., 2010). Participants further observed that a greater vertebrate fauna may be facilitated by the creation of a generally undisturbed environment relative to nearby farmland, as well as by the presence of open spaces and access paths within the woodland. This highlights the importance of both landscape context and management practices. Confidence scores were marginally, but not significantly, lower for invertebrates and vertebrates than for flora, likely reflecting awareness of challenges such as taxonomic difficulty, detection bias, and temporal-sampling bias (Didham et al., 2020; Luke et al., 2023).

Given the aim of our study to derive comparable biodiversity scores for different afforestation scenarios, our broad biodiversity indicators required experts to amalgamate a variety of floral and faunal groups that may respond differently to a range of site characteristics that vary depending on age, plantation type and management (Fuentes-Montemayor et al., 2012; Gittings et al., 2006; Jokela et al., 2018; Oxbrough et al., 2006; Spake et al., 2016). While the use of specific taxonomic

and functional groups as indicators is appropriate in relevant contexts (Gao et al., 2015; Noss, 1999), studies of forest ecosystems generally recommend multi-taxon approaches (Burrascano et al., 2023; Paillet et al., 2024; Tinya et al., 2023), since no single taxon reliably serves as a proxy for all others. Forest structural attributes have also been proposed as a surrogate for biodiversity (Larrieu et al., 2018; Storch et al., 2023; Zeller et al., 2022). For the older development stages, experts likely combined judgments across multiple forest taxa to derive their scores, whereas for younger forests, they likely considered non-forest taxa and features more characteristic of scrub and grassland habitats, supporting fauna such as pollinating insects (Taki et al., 2013) and small mammals (Gasperini et al., 2016; Moro & Gadal, 2007).

There are limitations to using species richness as an indicator, as it does not necessarily capture compositional changes that may better reflect biodiversity value (Hillebrand et al., 2018). Combined with the reductionist nature of this survey, the results need to be interpreted with caution and used only to infer broad trends. Nonetheless, the cross-congruence between flora, invertebrates and vertebrates, suggests floral richness could serve as a useful proxy for overall biodiversity.

5.5.4 Influence of profession on judgements

Contrary to our predictions that the biodiversity value may be judged differently by foresters and ecologists, the views of foresters and ecologists broadly aligned. Our panel of experts included foresters with ecological training gained through experience with the government-funded native woodland scheme, as well as ecologists with forest ecology expertise. This may point to the effectiveness of training programmes, such as the government-funded Native Woodland Scheme training programme in Ireland, where both foresters and ecologists are trained together, and have opportunities to learn from each others' experiences.

Among the minor differences observed, our heatmaps suggest a tendency for ecologists to assign lower floral biodiversity values to open and thinned stage Sitka spruce forests, and higher values to closed-stage oak. In contrast, foresters' scores varied significantly across Sitka spruce development stages. While one might conclude that ecologists, with their deeper ecological knowledge, provided more reliable scores, foresters may have more direct experience with plantation forests and their lower scores for closed-canopy oak could reflect an understanding of silvicultural practices such as dense planting aimed at triggering self-thinning. (Saha et al., 2017). MacLeod et al., (2022) found experts were more certain but more conservative in scoring benefits when evaluating their specialty biodiversity groups; and highlighted the challenge of determining whether such a trend reflected their more in-depth knowledge and/or an unconscious bias. While judgements of both professions are rooted in knowledge and experience, the influence of unconscious biases cannot be completely excluded in our study context, particularly given negative perceptions of non-native conifers in Ireland (Ní Dhubháin et al., 2009). Interestingly, the NFI data for Sikta Spruce mostly closely reflects the median scores for the whole panel, suggesting

capturing those with technical ecological expertise, and practical forestry expertise, may help control for any biased judgements.

Greater differences between foresters and ecologists might have been expected if the survey had sought a broader view rather than an expert view, as greater tensions between different professional groups (Donfrancesco et al., 2023), or between specialists and the general public (Probst et al., 2024) are not uncommon. Similar Delphi studies have also found diverging views amongst experts within professions, particularly where views are sought on solutions to complex challenges (Maini et al., 2023; Orsi et al., 2011)

5.5.5 Benefits & Challenges of the Delphi Approach

As evidenced by our review of NFI data and relevant literature, systematic surveys of even-aged oak and birch plantations are rare in our study region. Since much of the forest estate is privately owned (DAFM, 2023a), conducting comprehensive quantitative surveys across key climate, soil and moisture gradients, would be valuable but would require significant time and financial investment. Such delays can lead to actions that are too little, too late (Bennett, 2016), which is especially problematic when swift decisions are needed in response to major losses or threats to established and preferred tree crops. In contrast, a desk-based expert survey can be completed quickly and at low cost.

Although biodiversity values for oak and birch plantations relative to Sitka spruce could have been inferred from the literature, this would provide a weak evidence base due to the limited data available for the specific forestry scenarios of interest. The Delphi approach enables us to pool expertise from individuals with practical experience of forest habitats, increasing our confidence in adapting global research evidence to the local context (MacLeod et al., 2022). It also allows for the aggregation of expert judgment into numeric scores, while capturing participants' observations and justifications, thereby providing valuable additional insights.

Only adequate Sitka spruce floral data could be extracted from the NFI, as faunal taxa are not monitored, and sufficient data were unavailable for birch and oak production forests. While the NFI site selection methods are designed to present a random and representative snapshot of the existing forest estate, they may not capture enough data on less-common forest types that could become more prominent under future climate conditions (Stanturf et al., 2024). We recommend adapting the NFI methodology for a targeted sampling programme focused on afforestation scenarios likely to feature in future forestry initiatives. Addressing this data gap would support more accurate comparisons of afforestation options and enable comparisons with NFI plots of semi-natural woodlands supporting these species. Additionally, both the existing NFI methodology and any supplementary surveys could be enhanced to include faunal indicators, as discussed in Chapter 4.

The variability among individual experts highlights the risk that would have arisen had a reliance been placed on a smaller subset of our panel (MacLeod et al., 2022; Sutherland & Burgman, 2015). Conversely, variability, particularly in scores for open-stage forests, may have been reduced if more experts had engaged with the second round of the survey. A narrower scoring range might also have led to lower variability. Overall, our consensus levels were generally moderate. Given the broad scoring range and the alignment of expert judgments with the research literature, we consider these scores to be suitable as interim biodiversity indicators until sufficient field-based data can be collected.

The scenarios and categories used were developed in collaboration with a smaller group of experts. The Delphi approach is highly flexible, and the panel could have been engaged earlier to reduce the complexity of the scoring sheet though a ranking process or open-ended questions e.g. Maini et al., (2023) and Orsi et al., (2011), prior to the scoring exercise. This approach could have fostered a shared understanding of the survey's scope and challenges at an early stage and may have improved engagement in the second round, as the volume of scores requested likely deterred some participants from reviewing their responses. Given that early-stage scores showed greater variability, future expert elicitation studies using this method might also consider presenting participants with representative background scenarios, including data on floral composition and prior agricultural intensity, as more refined reference points. Alternatively, the Nominal Group Technique (NGT) has been used in similar studies (Hugé & Mukherjee, 2018). Unlike the Delphi technique, NGT incorporates a facilitated group discussion following individual contributions, though it can also be applied after a Delphi survey.

5.6 Conclusions

This study aimed to generate a comparable value for three biodiversity indicators across three different afforestation scenarios, capturing the changes that occur over the development of the forest, as well as those related to the environmental setting.

The surveyed experts attempted to synthesise a broad range of information, both in terms of the biodiversity indicators and the various factors that can influence forest structure and function, when determining their scores. While the resulting indicators are relatively coarse, the overall pattern of scores across the forest lifecycle is broadly supported by existing literature and available data. These patterns reflect known associations between biodiversity and forest structure, as well as the general tendency for non-native plantations to support fewer species than native plantations.

EU proposals driving increased afforestation rates presents a challenge for decision-makers and landowners, as land deemed suitable for tree-planting is primarily in agricultural use. Modelling the potential trade-offs is necessary to ensure that nations achieve '*the right tree in the right place'*, thus facilitating a balance between benefits for nature and people. It is therefore essential to

capture biodiversity values within land use decision tools and models. For example, while biodiversity scores are lower for Sitka spruce, fast-growing species like this may deliver multiple production cycles of other ecosystem services, such as biomass, economic return, and carbon storage, within the time it takes slower-growing species like oak to complete a single cycle (Castro-Díez et al., 2019; Luyssaert et al., 2018). However in contrast, it is important to have oak forests in the landscape for long-term biodiversity benefit. In the absence of sufficient comparable field-derived data, our expert-derived scores could support the development and testing of models that assess trade-offs between biodiversity and other forest values across the production life cycle. The variables used (soil, growth/forest development stage), being derived from NFI data, facilitate easy integration within various model formats allowing the approach to be replicated for other counties.

This study highlights that a particular challenge exists, in terms of predicting impacts on both nature and its contributions to people, where forest policy is shifting towards new planting scenarios for which biodiversity-related evidence may be limited or lacking. Yet, with altering climates and ongoing threats from both new and native pathogens, decisions will increasingly need to be made within shorter timeframes and often in the absence of detailed empirical data. Employing expert elicitation methods alongside available evidence allows us to harness the breadth of existing knowledge, supporting more informed and transparent decision making, and offering a practical tool to help policymakers more confidently incorporate biodiversity considerations into afforestation strategies and land-use policy.

CHAPTER 6

General Discussion

6 General Discussion

6.1 The Right Metric for the Right Context

The measurement and evaluation of biodiversity are highly context-dependent (Pascual et al., 2023) and shaped by whether the emphasis is on intrinsic, instrumental (extrinsic), or relational values (IPBES, 2019; Pascual et al., 2017). We may be seeking to assess the state of biodiversity in order to detect changes, or guide conservation efforts, or we may be looking to assess the value of biodiversity through the benefits it provides to humans, ecosystems or economies. Consequently, no single approach or metric can fully capture the multifaceted state or value of biodiversity (Mace et al., 2012), and attempts to abstract it into a single unit are contentious (Wauchope et al., 2024). In the absence of evidence indicating which metrics are best suited to specific contexts, achieving the credibility and transparency desired by ecologists and policymakers will remain a challenge (Crawford et al., 2021).

The metrics used to assess biodiversity can vary widely, depending on the component or level of biodiversity being measured, as well as the geographic scale, scope, and objectives of the use case. In synthesising the findings of my chapters, I found no existing framework or conceptual model that maps the selection of metrics across different contexts, scales, and intended applications. Therefore, I have developed and presented my own interpretation in Fig. 6.1, as a foundation for this part of the general discussion. More complex and refined field data are often required for conservation status assessment, sustainable forest management, and to measure the effectiveness of habitat creation or enhancement projects associated with planned development and/or the biodiversity credit market. In such cases metrics need to support long-term tracking and monitoring, and align with legislative drivers that exist around protected species and habitats. A suite of metrics may be required (Burrascano et al., 2023; Oettel & Lapin, 2021; Wallacea Trust, 2023), though field data typically remain an essential component (Czúcz et al., 2025), with any conservation or restoration goals or targets tailored to the specific site (Baker et al., 2019; European Commission, 2019b).

By contrast, high level indicators tend to be used for international comparisons between countries (Burgess et al., 2024; Geijzendorffer et al., 2016), though these may stem from broad datasets (e.g. extent of protected habitats or native woodland), or from more refined scalable metrics (e.g. Forest Birds Index). Higher level metrics may also be more appropriate where agri-environmental interventions are being tracked and monitored for payment schemes (Kavanagh et al., 2023), in this case simple condition indicators or proxies that are sensitive to management actions, distinguish between higher and lower quality outcomes, and can be used by non-specialists in the field, are essential for practical implementation (Moran et al., 2021).

Spanning various scales, biodiversity condition metrics are also an integral part of ecosystem accounts (Costanza et al., 1998; Dasgupta, 2024; Farrell et al., 2022; United Nations, 2021), including site level accounts (Gorman et al., 2024). Within the core accounting system, biophysical condition metrics must be clearly and consistently linked to the flows of benefits they support (Smith et al., 2017), so that ecological integrity is meaningfully reflected in economic and policy evaluations. Specific themed accounts focusing on biodiversity are also supported by the methodology (Gorman et al., 2024).

Using afforestation in Ireland as a model, each chapter in this thesis explored a distinct aspect and context for biodiversity measurement. Biodiversity outcomes are increasingly recognised as core objectives of afforestation initiatives in Ireland (DAFM, 2024a), particularly those implemented under the Native Forest Framework (NFF). To support these objectives, the monitoring of appropriate biodiversity metrics is essential for optimising and validating afforestation outcomes. These metrics can inform transparent reporting on forest biodiversity at both national and EU levels, guide timely management interventions, and be integrated into models for ecosystem services, land-use decision-making, or agri-environmental scheme scorecards.

My research examined aspects of the vegetation and fauna communities of Irish woodlands across the forest life cycle, focusing on identifying attributes that function as reliable indicators of biodiversity and/or its value i.e. those that are sensitive to ecological change and respond directionally to it (Czúcz et al., 2021; Santini et al., 2017). The first two chapters are based on field surveys which examined the vegetation and pollinating insect communities across a chronosequence of woodlands of different ages. These selected communities are relatively accessible in terms of field data collection with the availability of standardised sampling methodologies and taxonomic resources. In practical terms therefore, they have the potential to generate usable and repeatable metrics. In the context of Fig. 6.1, Chapter 2 and 3 considered potential compositional metrics derived from woodland flora and faunal communities at a regional-scale, which may be applied for the evaluation of ecosystem services, for use in a state/pressure/response framework, for forest biodiversity monitoring and management, or for the assessment of ecological integrity.

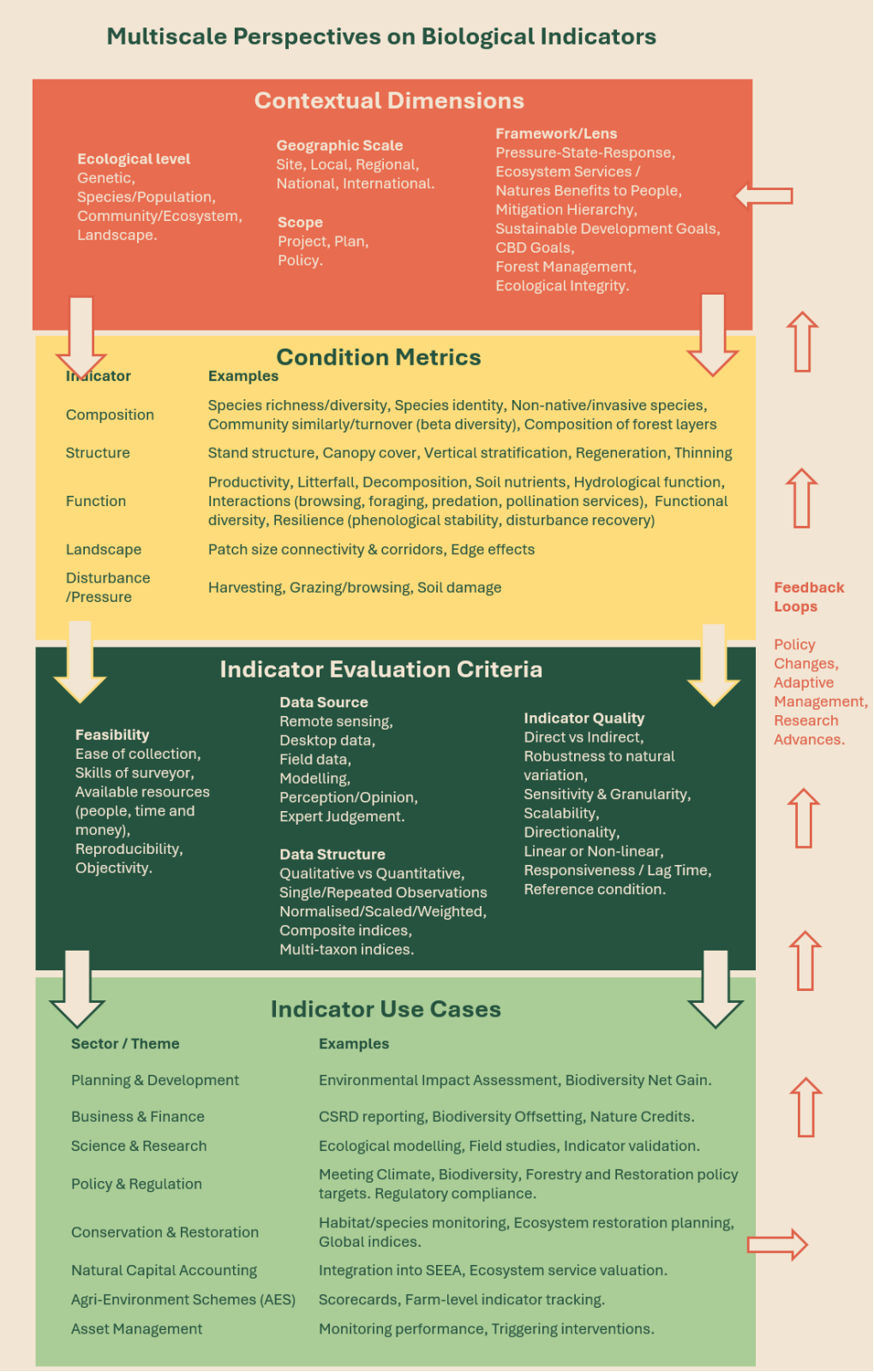

Figure 6.1 A multiscale framework for biological indicators. The first panel describes the conceptual framing for indicator selection, the second panel gives examples of the ecological properties that need to be measured, the third frame lists factors that assess how well different metrics can function as indicators based on technical and practical criteria, and the fourth panel connects the selected indicators to their real world applications ensuring they are fit for purpose. Feedback arrows are shown to illustrate flexibility and iteration in the chosen metrics which may need to adapt to changes in policy, research and management.

In Chapter 2, the data revealed a clear transition from non-woodland to woodland species corresponding with a shift in habitat classification from grassland to woodland habitats over the woodland establishment timeframe. A high proportion of older plots achieved their target IVC habitat grouping, indicating successful habitat development. These findings provide encouraging evidence that the native woodland afforestation scheme is meeting its objectives, and has the potential to make a meaningful contribution to native woodland restoration targets under Ireland's Nature Restoration Plan. The results further indicate that the bryophyte community, measured by cover or species richness, may serve as a sensitive indicator for sessile oak woodlands relative to other scenarios, as reflected in the Annex I indicator species list for this habitat type (Daly et al., 2023). The observed increase in natural colonisation of young trees with stand age also suggests that this metric could indicate a site's capacity to respond positively to close-to-nature management practices (European Commission, 2023; Spazzi et al., 2019; Zhang et al., 2025). As these indicators show measurable changes even in young woodland sites, they offer potential as effective interim measures of woodland development and should be considered for integration into long-term monitoring programmes.

This research also highlights metrics that may not be appropriate for monitoring developing woodlands, such as overall species richness, the limitations of which have been noted by other authors (Fleishman et al., 2006; Hill et al., 2016; Hillebrand et al., 2018). Additionally, although we measured structural indicators, which are often used as proxies for biodiversity, these were strongly correlated with the woodland age gradient. While this confirms their usefulness in tracking physical woodland development over time, it also limits their ability to independently explain variation in our floral metrics. Consequently, structural indicators are unlikely to serve as robust, standalone predictors of floral diversity in young or developing woodland sites, and would be most effective in comparing mature woodland sites.

Exploring the potential applications of a faunal metric, I used data on the pollinator community (Chapter 3), and demonstrated its potential application in a number of contexts. As with the floral metrics, species richness data revealed an initial loss of grassland species, however the transition to woodland species wasn't strongly evident, potentially reflecting a greater colonisation or immigration credit i.e., a temporal lag between habitat creation and species response (Hughes et al., 2023; Jackson & Sax, 2010). In contrast to species richness alone, beta diversity metrics and interaction networks revealed more nuanced community dynamics, highlighting distinctions between bees and hoverflies. Although the pollinator study controlled for landscape context and habitat type, the results suggest that off-site influences may have a stronger effect on hoverfly communities than on bees, likely due to differences in their foraging strategies (Doyle et al., 2020; Goulson, 2010). For bee communities, tracking compositional shifts may therefore provide a more sensitive and stable metric for assessing woodland development, particularly in its early stages, when woodland specialist species have yet to fully establish.

As shown in other studies (Alison et al., 2022; Dicks et al., 2015; Proesmans et al., 2019b), I found pollinator species richness and abundance responded strongly to floral resource availability, indicating monitoring pollinators could also be used to infer changes in pollination service capacity. Most pollinator conservation initiatives focus on enhancing the quality and quantity foraging resources (Dicks et al, 2015). In woodland settings , this typically involves managing the sequence and abundance of spring-flowering shrubs, as well as widening and scalloping woodland rides to create diverse flower-rich edge habitats (Falk, 2021). My data further highlights the potential of interaction networks, in particular, to assess the functional response of pollinator communities to such habitat interventions.

Faunal metrics present additional challenges due to detection biases and temporal variability (Didham et al., 2020; Luke et al., 2023). As shown in Chapter 3, and supported by other studies (Boyer et al., 2020; O'Connor et al., 2019), survey methods often favour certain taxonomic groups, potentially skewing assessments. To address this, a combination of methods should be employed. While more comprehensive monitoring programmes can accommodate this complexity, simpler indicators such as bumblebee abundance on transects may still provide practical value in agri-environmental schemes, especially when integrated with data on floral resources and habitat features.

Expanding from a regional to a national scale, in Chapter 4 we utilised the National Forest Inventory (NFI) dataset to investigate the factors influencing floral biodiversity across the Irish forest estate. Using the framework set out in Fig. 6.1, this chapter addresses compositional floral community metrics that can be derived from available data, of direct relevance to national-scale forest biodiversity monitoring, and plan and policy formation, but with learnings for other potential use cases. Structural and carbon metrics are already employed in European and international reporting frameworks (Chirici et al., 2012; Linser, 2024), with structural indicators often used as proxies for biodiversity value. However, the value of more direct biodiversity metrics that can be derived from the NFI, and their relationships with these proxies, has received limited attention. Adopting a similar approach to the analysis of young woodlands in Chapter 2, I examined compositional changes between woodland and non-woodland species, accounting for both site-level and landscape-scale influences. In this case, the focus on mature woodlands enabled an assessment of commonly used structural indicators, as these were not strongly confounded by site age.

Among the variables tested, tree species diversity emerged as the strongest predictor of floral biodiversity metrics. This finding supports its inclusion in EU-level reporting, and demonstrates that the evidence linking tree species diversity and floral richness (Kremer et al., 2025) is relevant to an Irish context. Tree species diversity is also associated with enhanced productivity (Liang et al., 2016), ecosystem service provision (Gamfeldt et al., 2013) and greater resilience (Jactel et al., 2021). Given its ease of extraction from field data and accessibility to non-specialists, this variable

holds promise for use as a condition indicator in agri-environmental scheme scorecards or Natural Capital Accounting frameworks.

Integrating the findings of Chapters 2 and 4, analyses of both my regional field surveys and the national-scale NFI reveal that the floral community responds to known geographic, climatic, and edaphic gradients (French et al., 2008; Kelly, 2005). In semi-natural contexts, these interacting gradients give rise to distinct plant communities and habitat types (Ellenberg, 1988; Whittaker, 1967). In contrast, for afforested native woodlands and other afforestation scenarios, the NFF and Forestry Standards Manual address these gradients to some extent by recommending species mixes or imposing planting constraints tailored to specific soil types (DAFM, 2023b, 2024b). The RLQ analysis in Chapter 2 highlights how habitat, age, soil, and landscape factors interactively influence floral composition. Chapter 4 builds on this, demonstrating how these and additional variables may each contribute modestly to floral diversity, while also revealing the complex, non-linear relationships that often emerge. Given that other taxa may be subject to different ecological drivers, these findings underscore the complexity of forest ecosystem dynamics and the potential need for a multifaceted suite of ecological indicators.

A range of habitat-specific indicators have been developed for assessing the conservation status of Annex I habitats, aimed at determining whether they meet favourable conservation condition (Daly et al., 2023; Perrin et al., 2008), however, in an Irish context, biodiversity condition indicators and associated targets are still lacking for many other forest types. Moreover, the targets and criteria set under the Habitats Directive may not always be appropriate or realistic as restoration reference points, particularly in modified or afforested landscapes. Recent developments in Biodiversity Net Gain (BNG) metrics have introduced condition criteria for broad habitat categories, such as grasslands or woodlands as a whole, rather than tailoring them to specific habitat types (Barsoum et al., 2025; DEFRA, 2024). While pragmatic, this broad-brush approach risks oversimplifying ecological variation and may undermine meaningful biodiversity outcomes (Duffus et al., 2025). This raises the question of whether more tailored habitat-specific targets, based on optimal species richness, could be developed for woodland flora using metrics explored in this study. In Chapter 2, woodland generalist species alone did not effectively differentiate between planting scenarios unless bryophytes were included. Similarly, woodland specialist richness showed no significant variation across planting scenarios. However, ancient woodland indicators (AWIs) were positively associated with sessile oak woodlands. The NFI analysis further suggested that, aside from AWIs, the richness of woodland specialists and generalists (vascular plants only) in mature woodlands was largely independent of specific habitat type. This implies that setting habitat-specific numeric targets for species richness may only be relevant for AWIs. Even in that case, the explanatory variables identified in Chapters 2 and 4, such as age, soil type, and landscape context, demonstrate that species richness metrics are context-dependent. Ultimately, the complex and interacting influences captured by natural-world datasets make it difficult to isolate single drivers. As such,

without accounting for these contextual factors, any fixed numeric target for richness-based indicators is likely to lack ecological validity.

Finally, I highlighted the limitations of NFI data for future planting scenarios, and sought to address knowledge gaps through use of expert knowledge. Referencing Fig. 6.1, this chapter addressed three broad compositional indicator groups at a national scale, with data derived from a survey, and of potential use for incorporation into ecosystem service frameworks and informing afforestation plans and polices. Applying a Delphi panel survey, Chapter 5 looked at forest biodiversity through an ecosystem service lens at a national scale with a view to informing policy. While critical of the use of overall species richness as a metric in the contexts considered in Chapters 2 and 3, here it was used as I was attempting to capture the contribution of biodiversity across all development stages and not specifically with reference to a target woodland ecosystem. The experts scores aligned well with existing data and the literature reviewed. The survey findings for flora and invertebrates covered a much more expanded age range than that addressed in Chapters 2 and 3, but nonetheless similarly pointed to the loss of diversity associated with a loss of grassland species in establishing woodlands. Though not appropriate for all applications of biodiversity metrics, scores derived based on embedded expert knowledge could be more simply integrated into ecosystem service models and accounts (Czúcz et al., 2021; Martini et al., 2024), as well as helping guide afforestation policy.

6.2 The right tree in the right place

The Irish government has set out a national vision for trees and forests in Ireland: "*the right trees in the right places for the right reasons with the right management – supporting a sustainable and thriving economy and society and a healthy environment*" (DAFM, 2022). This vision underpins recent forestry policy developments in Ireland, informing the most recent forestry strategy (DAFM, 2024a), and acknowledges that successful and sustainable afforestation must go beyond simple tree planting targets and calls for careful consideration of ecological compatibility, climate and carbon goals, socio-economic and cultural factors, and sustainable forestry management practices. However, the decision of where to plant trees can put afforestation goals in conflict with other land use proposals (Ryan et al., 2022). Early afforestation initiatives focused on marginal lands and uplands which were otherwise unproductive in terms of agricultural use. Advancements in understanding the carbon impacts of planting on peat soils have excluded many of these areas from current afforestation schemes (Renou-Wilson & Byrne, 2015). The result is that the 'right place' for trees now usually has alternative agriculture uses, including options such as high nature value farming, and so we need to determine the optimal use(s) of lands in any particular area or region to guide decision making. Overarching land use policy is currently being reviewed, with the ambition of reducing conflicting policies (Government of Ireland, 2023). Phase 1 of the land use review was completed in 2023, setting the relevant evidence base, with phase 2 currently pending in 2025

aimed at providing policies, measures and actions for optimal land use. Land can be framed or valued in different ways by different stakeholders, and a national land use strategy has the potential to manage these competing values and deliver more sustainable outcomes (Scott & Faulkner, 2023). Enabling factors for managing the interplay between different values include spatial plans, biodiversity action plans, agri-environmental changes as well as leadership, innovation, collaboration and participation (Scott & Faulkner, 2023). Notwithstanding the outcome of phase 2 of the land use review, there are ongoing challenges in the integration of forestry policy and broader land use policy, and with trees being planted to offset the impact of infrastructure development, the integration with the national planning framework is also necessary.

The findings of Chapters 2 and 3 provide insights into potential trade-offs between native woodland establishment and alternative land uses. The shifting patterns of generalist and specialist species over the transition from a newly planted forest to one with a closed canopy, highlights the need to provide a diversity of transitional forest in our landscapes supporting all these species. Where grasslands are initially released from intensive agriculture use, this may facilitate a pulse of floral-rich grassland habitat supporting abundant common pollinators in the early stages of establishment. As woodlands age, the release from agricultural pressure continues to manifest through the expansion of the hedgerow. In abandoned agricultural sites with low woodland cover in the landscape, these shrubs may dominate the site even after decades of 'passive rewilding' (Broughton et al., 2021). The expanding hedgerows can represent some of the only unmanaged habitats in otherwise intensive agricultural landscapes, providing crucial floral resources as well as nest-sites and overwintering habitat for a range of pollinating insects (Alison et al., 2022; Kells & Goulson, 2003; Requier & Leonhardt, 2020). Though our findings would indicate such transitional habitats may be dominated by generalist species, these species are nonetheless important ecosystem service providers (Klein et al., 2007; van Klink et al., 2024).

As identified in Chapter 2, my findings suggest that the hedgerow network may serve as an important source of colonising tree species, while birch colonisation appears more likely in upland areas. These naturally establishing trees have the potential to enhance both the species and structural diversity of plantation woodlands. While public discourse often presents tree planting and rewilding as opposing strategies, afforestation need not follow a strictly interventionist or process-led model. Instead, approaches can be blended and tailored to the specific ecological and land-use context of each site (Broughton et al., 2021; Hughes et al., 2023; Murphy et al., 2022). Regardless of the strategy adopted, effective outcomes are likely to depend on appropriate fencing and ongoing monitoring, particularly in areas under high browsing pressure.

The findings of Chapter 2 also pointed to an imprint of past land use associated with a landscape gradient favouring specialist flora, as demonstrated through the integration of plant traits into the analysis. Such temporal legacy effects, their interaction with current local and landscape drivers, and variations among taxa, are challenging to decipher (Bradfer-Lawrence et al., 2025; Watts et al.,

2020). Habitat classification indicated that many woodlands may have been planted in sites which also have the potential to restored to species-rich semi-natural grasslands. In all landscape contexts, farmers typically select the lowest yielding agricultural fields to afforest, and as these areas of the farm have been less-intensity managed, their potential to support a variety of semi-natural habitats is higher. Talking to landowners during field surveys, many commented that the plantation was put into the 'bad field' from an agricultural perspective, i.e. rocky, sloping, wet, or prone to flooding, with land use incentives facilitating or encouraging this approach. My analysis suggested that these sites may also have greater potential to develop a richer woodland flora due to lower nutrient conditions and proximity to other wooded areas. However, with appropriate management and depending on the soils, these fields could equally support diverse grasslands, heath, willow scrub or floodplain meadows, supporting the associated faunal communities, habitats also under threat from land use intensification (Seibold et al., 2019; Wagner et al., 2021). We currently lack incentives similar to those provided for afforestation to support the retention and restoration of many of these habitats, yet without these we will fail to achieve optimal benefits for nature.

With recent calls in government to plant in upland areas currently largely excluded from the afforestation programme, the need for robust site-level assessments in advance of planting is brought into sharp focus. Of the sites we surveyed with notable semi-natural grassland potential, a few sites clearly supported a diverse grassland flora of conservation significance. Though forestry environmental guidance (DAFM, 2024c) likely excludes many species-rich grasslands from the afforestation schemes, sites are screened at a desktop level or through input from the forester. As a consequence, depending on the quality of available data and the ecological skills of the forester, some biodiverse grasslands may be missed, particularly where their potential condition is masked by current agricultural practices. This demonstrates the need for a skilled ecologist, with vegetative identification skills, to survey sites prior to afforestation to determine their ecological potential.

While selecting the optimal restoration outcome for a given site is important, it is equally crucial to consider how best to maximise habitat diversity at the landscape scale. Complex agricultural landscapes tend to support more biodiversity than simplified ones (Estrada-Carmona et al., 2022). The spatial targeting of agri-environmental interventions can promote nature recovery at a broader scale (Lawton, 2010), but this requires systematic conservation planning (Baker et al., 2025; Margules & Pressey, 2000; Smith et al., 2022). In a landscape dominated by agriculture and food production, and constrained by finite land resources, realising the benefits of woodlands, grasslands, and other semi-natural habitats necessitates such spatial optimisation. One promising model is the 'TRIAD' functional zoning approach, which designates land for strict protection, intensive use, and extensive (multi-functional) use (Himes et al., 2022; Messier et al., 2009; Seymour & Hunter, 1999). This integrated approach moves beyond the traditional 'land-sharing versus land-sparing' debate (Green et al., 2005), which has often polarised land-use discussions by highlighting trade-offs such as the loss of farmland bird habitat (Finch et al., 2023), potential

impacts on food production, and the biodiversity costs of offshoring environmental burdens associated with land-sharing (Collas et al., 2023). Systematic conservation planning also addresses the 'single large or several small' (SLOSS) debate by considering the size, number, placement, and connectivity of habitat patches to enhance species colonisation and persistence (Fahrig et al., 2022). It further emphasises the importance of buffer zones around protected areas, linked via ecological corridors and stepping stones (Cranmer et al., 2012; Crick et al., 2020; Saura et al., 2014), though the effectiveness of these features can vary among taxa (Pedley & Dolman, 2020).

In addition, analysis of the broader NFI dataset (Chapter 4) highlights the potential role of hedgerow networks in supporting woodland floral diversity. National land cover maps can be used not only to identify potential afforestation zones near existing woodlands or locations where new woodlands might serve as stepping stones, but also to assess the structure and connectivity of hedgerow networks. This spatial information can inform the design of more effective, locally tailored nature recovery networks (Smith et al., 2022).

As part of a broader multidisciplinary project, where social considerations around afforestation in Ireland were also being explored, it is evident that while we can optimise for diverse habitats in strategic locations, the ultimate decision on whether to use an afforestation scheme, agri-environmental scheme, neither, or a combination, rests with the landowner. They are likely to be considering afforestation or habitat restoration initiatives with other land use demands, and need to be supported in selecting the optimal restoration use of their lands using participatory approaches (Baker et al., 2025; Hölting et al., 2022), bolstered by a strong and integrated financial and knowledge supports.

6.3 Metrics in Practice: Adapting to the context

Beyond considering what metrics are appropriate for different applications, our study also has implications for the mechanisms and approaches used for monitoring native woodland establishment sites, and any associated management interventions.

With increasing threats from pests, storms, drought and fire in our study region, intervention on a regular basis may be needed to secure optimal woodland restoration, requiring intermittent monitoring surveys. While few of our field sites had been actively managed to date, future trajectories will inevitably be shaped by management actions (Fuentes-Montemayor et al., 2022). Monitoring approaches must be adapted based on the policy or use context, who is proposed to undertake the monitoring, how often it needs to be done, what ‘level’ of indicator should be monitored, and whether actions or results are being rewarded.

Our field methods were designed to be repeatable, offering a framework for tracking long-term changes in afforestation sites. While they could be adapted for certain ‘high accountability’

contexts such as biodiversity offsetting or nature-based finance applications, such monitoring is unlikely to be scalable to the full network of native woodlands predominately on private farms.

At the most basic level, monitoring on private farms needs to be able to capture critical pressures and threats to the woodland. Though farm advisors may play a role, grant-aided afforestation schemes primarily rely on the landowner remaining the primary custodian of the woodland once the 5 year establishment phase is complete. Owners are expected to observe threats and pressures, and decide when a forester needs to be engaged for tending, thinning, or harvesting, however I found during my field visits that many sites were not frequently visited even by their owners, some of whom live remote from the site. Hence threats and pressures may go undetected where a landowner is not present or interested in woodland management. It was also evident from site surveys that deer damage is likely to be a challenge in the longer term for many sites, though did not merge as a significant variable in any analysis herein. Frequently tree guards had been left in-situ, damaging growing trees, while other landowners had not availed or been aware of reconstitution grants for ash dieback. These observations suggest that relying solely on landowner initiative is insufficient. To support better biodiversity outcomes, formal knowledge transfer mechanisms are needed, including improved forestry training for farm advisors and stronger support for landowners. The grant scheme could also be adapted to mandate periodic checks by a registered forester, enabling early detection and response. Additionally, landowners who do proactively monitor their sites could be rewarded, as early intervention would reduce reparation costs and enhance co-benefits such as carbon sequestration (Felipe-Lucia et al., 2018).

Where landowners choose to re-engage with forestry services after the 5 year establishment period has elapsed, Irish schemes offer payment options for thinning, tending, and conversion to Continuous Cover Forestry (CCF) or coppice-with-standards systems. Top-up payments are also available for certain ecosystem service-related actions under CCF, where native woodland is established in nutrient risk zones, or through corporate partnerships. However, these payments are typically tied to specific actions rather than ecological outcomes. Results-based scorecards have been successfully used in agri-environmental schemes in our study region (Moran et al., 2021), and incorporating some of the metrics highlighted earlier, could offer a practical solution. By providing a structured way to assess progress and management interventions, and support adaptive decision-making, they could help link payments to more meaningful outcomes for nature (Elmiger et al., 2023; Herzon et al., 2018; Moran et al., 2021).

For other applications, rigorous and professionally implemented monitoring will be required to track biodiversity change. This may involve the development of habitat/species management and monitoring plans that typically involve formal reporting to a competent authority (DEFRA, 2024), or may be subject to third party verification (Moilanen et al., 2024). However, the default condition criteria used in the DEFRA BNG metric are devised with reference to a mature woodland (Barsoum et al., 2025) and may not adequately reflect the value of early transitional habitats or

ecotones that develop during woodland establishment. Therefore, regardless of how refined the context-specific monitoring programme is, reporting on milestones or interim targets will be crucial for evaluating restoration success over time (Watts et al., 2020). In this thesis I have shown both how we can measure biodiversity with regard to a specific reference point of mature woodland, but also how interim targets could recognise the value of young and transitional woodlands for floral diversity and pollinators.

The monitoring timeframe may need to be devised on a case-by-case basis. DEFRA's BNG framework, for example, specifies a 30-year monitoring horizon for woodland sites. Based on my findings, this duration appears sufficient for the emergence of key woodland indicators. Even longer-term monitoring may be necessary to ensure optimal condition is maintained, particularly if outcomes continue to be linked to payments or credit systems.

6.4 Future Directions for Research

The assessment of forest biodiversity serves multiple purposes and relies on a diverse array of metrics. As afforestation targets in Ireland and across Europe continue to increase, amid escalating threats to forest habitats and a potential shift toward climate-resilient tree species, there is an urgent need for comparable, consistent, and accurate biodiversity data. Such data are essential to inform adaptive management strategies and support evidence-based policy adjustments.

While work to develop frameworks and standards for biodiversity assessment has progressed, the landscape is becoming increasingly fragmented, particularly with the rapid proliferation of metrics, tied to emerging biodiversity finance mechanisms. Although a unified and globally harmonised framework would be valuable for high-level reporting and comparability, it risks becoming unwieldy or ecologically irrelevant if applied uniformly across all ecosystems. Forests, with their transitional dynamics and diverse management regimes, require a more flexible and context-sensitive approach. I suggest this highlights the need for a forest-specific biodiversity assessment framework, one that is robust yet flexible, captures the entire development life cycle of forest ecosystems, and is capable of serving a range of ecological, policy, and management needs as identified in Fig 6.1. Such a framework can still be nested within global assessment systems by aligning a core set of forest biodiversity metrics with overarching standards like the UN System of Environmental-Economic Accounting - Ecosystem Accounting (Czúcz et al., 2025; United Nations, 2021), while also accommodating a range of context-specific applications. It would also facilitate the independent verification and auditing of afforestation outcomes through the use of common and appropriate metrics.

In the Irish context, woodlands are often the only patches of semi-natural habitat within intensively managed agricultural landscapes. As such, they may serve as vital refuges for a wide range of taxa, including invertebrates, birds, and small mammals. Any comprehensive biodiversity assessment

framework must therefore consider how to integrate multiple taxonomic groups, which, as noted in previous studies (Larrieu et al., 2019; Paillet et al., 2024; Zeller et al., 2022) respond differently to ecosystem change. While our current study focuses on vegetation and pollinating insects, other faunal groups also comprise both specialist and generalist species, and could similarly support the tracking of woodland development and ecological condition. We therefore recommend that future research investigates the suitability of additional faunal indicators for monitoring native woodland establishment and condition. Importantly, there is a pressing need to better understand the potential negative consequences for biodiversity of native woodland afforestation in agricultural landscapes, such as increased predation pressure on ground-nesting birds (Bertholdt et al., 2017; McGrory et al., 2024; Wilson et al., 2014), and to evaluate these risks alongside the associated biodiversity benefits at different spatial scales. Finally, emerging technologies, including passive monitoring approaches, offer significant promise for biodiversity assessment in afforestation sites (Bell & Malerba, 2025), with recent advancements even extending to invertebrate monitoring (Rodríguez Ballesteros et al., 2024), though the capacity of such tools to generate meaningful indicators of habitat quality and woodland condition across developmental stages remains to be critically assessed.

Both Chapters 4 and 5 highlight that there is a lack of data in the NFI regarding native woodland afforestation sites, including native monocultures, due to its reflection of the existing forestry estate. This currently limits our understanding of the relative biodiversity values of planting scenarios linked to future afforestation proposals. Aligning targeted surveys of any future planting scenarios with the NFI methodology would allow for comparison with other woodland types, including benchmarking against semi-natural woodlands, and hence provide a more robust evidence base for afforestation decision-making, while maximising the utility of this large dataset. This may be especially relevant in the case of planting scenarios linked to the contentious proposal of assisted migration (Park & Talbot, 2018; Williams & Dumroese, 2013), where in an effort to keep pace with climate change (Sittaro et al., 2017), planting efforts involve expanding tree species beyond their historical ranges.

6.5 Concluding Remarks

Amid a rapidly evolving policy and regulatory landscape, woodlands are increasingly being established to provide a wide range of benefits for both nature and people, however forest systems are dynamic and complex, governed by multiple ecological processes that may follow non-linear patterns or stochastic patterns (Messier et al., 2019). This inherent complexity contributes to ecological heterogeneity, which in turn sustains resilience in terms of biodiversity and ecosystem services at a local and landscape scale (Messier et al., 2019). Consequently, the way in which we measure biodiversity must reflect these dynamics, and acknowledge the range of benefits being delivered across the forest life cycle.

This thesis advances our understanding of what constitutes successful native woodland afforestation, identifies the components of biodiversity we should be measuring to meaningfully track biodiversity change, and outlines appropriate metrics and monitoring approaches for different conservation and policy contexts.

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8 Appendices

Appendix A – Supplementary Data for Chapter 2

Table A1 Study Sites – Summary of key characteristics. Table is ordered by Species Category, Stage and Code. Notes explaining certain column contents in more detail are provided below the table.

Code[1]	County	Area (ha)	Trees Planted[2] (%)	Species Category	NWS Scen-ario[3]	Year Planted (Age at Survey)	Stage
FG	Kilkenny	4.2	ALD (100)	ALD	4	2008 (14)	Closed
KG	Offaly	4.8	ALD (100)	ALD	4	2006 (16)	Closed
MG	Meath	3.7	PO (34.9), BI (14.9), ADB (10.1), ALD (40)	ALD	3	2018 (4)	Open
BI	Offaly	5.8	ADB (33.3), ALD (33.3), WIL (33.3)	ALD	4	2010 (12)	Thicket
DW*	Carlow	2.9	ALD (100)	ALD	4	2015 (7)	Thicket
FL*	Kilkenny	0.7	ALD (100)	ALD	4	2014 (8)	Thicket
HL	Westmeath	10.4	PO (10), ADB (20), SBI (10), ALD (60)	ALD	4	2014 (8)	Thicket
RS	Wicklow	4.6	PO (9.8). BI (19.9), ADB (10), ALD (60.2)	ALD	4	2016 (6)	Thicket
DH*	Dublin	3.1	PO (95), ADB (5)	PO	3	2002 (20)	Closed
DN*	Monaghan	0.7	PO, SP (% unknown)	PO	3	2002 (20)	Closed
FD	Laois	3.7	PO (68.6), ASH (18.3), HAW (10.3), HAZ (2.5)	PO	3	2008 (14)	Closed
JH*	Westmeath	2.3	PO (44), ALD (33), SP (22)	PO	3	2005 (18)	Closed
RM	Offaly	0.9	PO (86), ADB (14)	PO	3	2009 (14)	Closed
ST	Tipperary	3.5	SO (56.5). ALD (7.6). DB (7.6). ASH (28.2)	PO	3	2008 (14)	Closed
TV*	Dublin	1.0	PO, HZ, WIL (% unknown)	PO	3	2002 (20)	Closed
CL	Offaly	4.7	PO (40), DBI (20), ADB (40)	PO	3	2021 (2)	Open
DG	Dublin	3.4	PO (39.7), ADB (40.2), DB (20.1)	PO	3	2017 (5)	Open
FN	Carlow	2.0	PO (40), BI (22), HZ (22), ADB (16)	PO	3	2021 (2)	Open
MN	Wicklow	11.6	PO (60), BI (15), SP (15), ADB (10)	PO	3	2020 (2)	Open
MO	Kildare	6.8	PO (47), BI (24), ADB (22), RWN (7)	PO	3	2020 (2)	Open
NF	Westmeath	2.3	PO (50), BI (17.8), ADB (22.2), SO (10)	PO	3	2019 (3)	Open
TW	Carlow	4.6	PO (50), BI (10), HZ (12), ADB (20), SP (10)	PO	3	2018 (5)	Open
CA	Laois	2.6	PO (52.3), SBI (7), RWN (13.6), ALD (27.1)	PO	3	2013 (9)	Thicket
CM*	Carlow	0.9	PO (70.5), BI (7.6), SP (2.2), ADB (19.7)	PO	3	2015 (7)	Thicket
DE	Offaly	4.7	PO (60.3), SP (20.2), ABD (19.5)	PO	3	2015 (7)	Thicket
DY	Tipperary	5.2	PO (60), ADB (14.9), ASH (25)	PO	3	2008 (14)	Thicket

Code[1]	County	Area (ha)	Trees Planted[2] (%)	Species Category	NWS Scen-ario[3]	Year Planted (Age at Survey)	Stage
HS	Galway	9.4	PO (59.5). SP (20.7). ADB (19.3)	PO	3	2015 (7)	Thicket
JCE	Westmeath	2.0	PO (58), SP (21.7), ADB (20.3)	PO	3	2013 (9)	Thicket
JCS	Westmeath	1.5	PO (61.2), SP (20.4), ADB (18.4)	PO	3	2013 (9)	Thicket
NL	Kilkenny	1.0	PO (43), BI (21), RWN (6), HZ (21), WT (9)	PO	3	2015 (8)	Thicket
PB	Tipperary	14.3	PO (42.5), SP (5), SBI (42.5), RWN (10)	PO	2	2010 (12)	Thicket
RY	Tipperary	8.5	PO (65.0), SP (17.1), ADB (17.9)	PO	3	2015 (7)	Thicket
SM	Dublin	13.3	PO (42.5). ADB (20). SO (37.5)	PO	3	2011 (11)	Thicket
SW	Wicklow	5.2	PO (70.5). SBI (14.8). RWN (14.8)	PO	3	2013 (9)	Thicket
BG*	Wicklow	19.0	SO, BI (% unknown)	SO	1	2000 (22)	Closed
BK	Wicklow	2.2	BI (26.9), ABD (17.9), SO (55.2)	SO	1	2008 (14)	Closed
BR	Wicklow	2.7	SO (34), ASH (34), ALD (7), ADB (25)	SO	3	2008 (15)	Closed
BT	Carlow	9.6	SP (14), SO (82.9), SBI (3.1)	SO	2	2008 (14)	Closed
GK	Wicklow	5.0	BI (39), RWN (16), SO (17), SP (9), ADB (19)	SO	1	2009 (14)	Closed
LC*	Laois	10	SO, BI, RWN, WIL (% unknown)	SO	2	2000 (22)	Closed
PW	Offaly	5.2	SP (1.5), ADB (74), SO (2.3), ALD (22.1)	SO	2	2009 (13)	Closed
QN	Offaly	5.3	SP (25), SP (75)	SO	2	2007 (15)	Closed
SS	Wicklow	3.4	SO, BI, RWN, WIL (% unknown)	SO	2	2003 (19)	Closed
BC	Wicklow	6.5	BI (21.6), SP (9), ADB (42.8), SO (26.6)	SO	1	2017 (5)	Open
CO	Westmeath	10.1	SP (10), ADB (40), SO (50)	SO	3	2020 (2)	Open
RN	Wicklow	2.3	BI (33.2), SP (16.6), ADB (8.3), SO (41.9)	SO	2	2018 (4)	Open
VM	Wicklow	5.5	BI (20.2), SP (18.1), ADB (26.4), SO (35.4)	SO	2	2018 (4)	Open

Notes:

1: Sites marked with an asterix were planted under a mixed woodland afforestation grant category in similar way to the Native Woodland Scheme (NWS) i.e. mix of native species appropriate to the soil type.

2: Tree Species Codes – SO = Sessile Oak *Quercus petraea*, PO = Pedunculate Oak *Quercus robur*, ALD = Alder *Alnus glutinosa*, SP = Scots Pine *Pinus sylvestris*, SBI = Silver Birch *Betula pendula*, HZ = Hazel *Corylus avellana*, DB = Downy Birch *Betula pubescens*, WIL = Willow *Salix* spp., RWN = Rowan *Sorbus acuparia*, BI = Birch *Betula* spp., ASH = Ash *Fraxinus excelsior*, ADB = Additional Broadleaves (species unspecified).

3: NWS Scenario was inferred from species mix and soil

Table A2 Number of Sites and Plots in each Species Group and Development Stage (SO = Sessile Oak *Quercus petraea*, PO = Pedunculate Oak *Quercus robur*, ALD = Alder *Alnus glutinosa)*

	Development Stage							
	Open		**Thicket**		**Closed**		**Total**	
Species Group	SITES	PLOTS	SITES	PLOTS	SITES	PLOTS	SITES	PLOTS
ALD	1	4	5	21	2	8	8	33
PO	7	29	12	45	7	24	26	98
SO	4	17	-	-	9	36	13	53
TOTAL	**12**	**50**	**17**	**66**	**18**	**68**	**47**	**184**

Table A3 Field Survey Methods

Plot Selection	Plot locations were randomly selected on GIS prior to the site visit, with the edge-constraints accounted for. A corner tree was identified and marked with biodegradable tape, while a square plot was temporarily marked out with tape measures and metal flag markers. The GPS coordinates of the corner tree, and compass bearings of 2 perpendicular sides were recorded to aid re-finding should it be required, and a photograph of the marked tree and the diagonal view of the plot were taken.
Plot-level variables	The plot-level vegetation survey involved recording the species, height and DBH (Diameter at Breast Height) of trees with a DBH>2cm, although in the case of multi-stemmed shrubs (e.g., hazel or willow) the DBH of all stems was measured. Younger trees (saplings and seedlings) were categorised into 4 classes; S1 (Cotyledon stages), S2 (Seedling <25cm height), S3 (Sapling 25cm-2m height) and S4 (Sapling >2m height). It was noted whether the tree was planted or naturally regenerated if this was possible to determine. Where oak species were less morphologically distinct, which is a known taxonomic challenge for younger trees (Boratynski et al., 2008), they were assigned to the species given in the forest service database, though the possibility of the hybrid (*Quercus x rosacea*) being present is likely. The median height and percent cover of the vegetation layers were recorded as follows: ● Canopy layer - The uppermost tree stratum defined by relative height. ● Large shrub/understorey layer - Woody vegetation below the upper tree stratum and ≥2m tall. ● Tree layer - recorded in lieu of above categories where there was no Canopy/Understory structure, and otherwise recorded as the pooled cover of the canopy and understorey layer to enable comparison across sites. ● Dwarf shrub layer - Woody vegetation <2m tall (excluding planted trees). ● Field layer - Vascular herbs, including graminoids (grasses, rushes and sedges) and ferns; and ● Ground layer - Mosses, liverworts and lichens. Other non-floristic cover variables: ● Cover of coarse woody debris (CWD) - logs, branches, stump & snag diameter ≥10cm at widest point. ● Cover of fine woody debris (FWD) - twigs and branches <10cm diameter. ● Leaf litter; and ● Cover of exposed mineral or organic soil, rock and standing water. A list of vascular plants and bryophytes rooted in soil or established on soil substrates was taken with percentage cover estimated to the nearest 1%, with

	0.5% assigned to cover <1%. Epiphytes were not recorded except for bryophytes growing on tree bases at an angle of <45°. All vascular plant species were recorded. For bryophytes and lichens, species forming patches more than 5cm^2 (2.2x2.2cm) were recorded. Overall cover values of >100% were typical due to overlapping layers. Within some layers species also overlapped in cover e.g. straggling herbs in grassland. Grazing/browsing, drainage and invasive species were scored at the site level, and at the plot-level. ● Grazing score - Grazing intensity ranked on a four-point scale: 1- little or none, 2- light, 3- moderate, 4- heavy (judged by amount of dung in quadrat; topiary effect on woody vegetation; bark-stripping; browse line; trampling or damage to ground vegetation and shrub layer). ● Invasives score - The level of infestation was ranked on a five-point scale: 1 – none present; 2 - Plants scattered, not dominating any area; 3 – Plants dominating small areas <20% of site; 4 - Plants dominating larger areas, 20-50% of site, 5 – Plants forming dense thickets over more than half the site area. ● Soil drainage - At each 10x10m plot soil drainage wase ranked on a five-point scale on the basis of surface observation: 1- poor (waterlogged), 2- poor to moderate (Drainage significantly restricted), 3- moderate (Drainage partially restricted), 4- moderate to good (no signs of significant water impedance), 5- good (dry & no signs of water impedance). Soil parameters were measured in-situ. pH was measured on field-fresh samples, taken from the top 5cm of soil below the litter layer, using a glass electrode and a 1:1 soil / water paste. A WET-2 Sensor (Delta-T Devices), inserted to the depth of the probes, was used to measure soil moisture, temp and conductivity in 30 of the sites surveyed (the equipment was not available at the remaining 17 sites).
Site-level variables	A structured walk was undertaken around the woodland parcel to record the presence of any additional species in the wider site. Other site-specific information and variables recorded were; adjacent land use; slope; presence of woodland drains or drainage ditches; presence of paths, utility wayleaves or other open areas; extent of internal hedgerows; extent of perimeter hedgerows, and any other unusual features or information from the landowner or forester.
References	Boratyński, Adam & Marcysiak, Katarzyna & Lewandowska, Amelia & Jasińska, Anna & Iszkuło, Grzegorz. (2008). Differences in Leaf Morphology between Quercus petraea and Q. robur Adult and Young Individuals. Silva Fennica. 42. 115-124. 10.14214/sf.268.

Table A4 Results of Mixed Models for Total Number and Richness of Naturally Colonising tree seedings/saplings explained by Age and Tree Species Group (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak). Positive estimates indicate higher values for counts and richness, and vice versa for negative estimates. Incidence Rate Ratios (IRR's) for Poisson models describe how the rate of the outcome changes with a one-unit increase in the predictor variable, with values greater than 1 indicating an increased rate of the outcome, and below one indicating a decreased rate. p-values (to test the null hypothesis that the coefficient estimate is equal to zero, i.e. no effect) were calculated from z-values: the ratio between the estimated coefficient and the standard error of the estimate (estimate/SE). Large z-values show that the estimate is large (in relation to its SE) and significantly different from zero.

Predictors	**Model Estimate**	**IRR**	**Conf Interval**	**Z**	**p value**	**Marginal R^2 / Conditional R^2**	**Moran's I (p value)**	**AIC_c**
No. Colonising Tree Seedling/Sapling Species								
(Intercept)	-6.066	0	0.00–0.03	-4.76	**<0.001**	0.454 / 0.668	0.008	333.24
Age	0.196	1.22	1.12–1.33	4.45	**<0.001**		(0.496)	
Sps [PO]	2.910	18.34	1.88-178.52	2.51	**0.012**			
Sps [SO]	2.760	15.79	1.52–163.74	2.31	**0.021**			
No. Colonising Tree Seedlings/Saplings								
(Intercept)	-9.376	0	0.00 – 0.01	-4.04	**<0.001**	0.456 / 0.872	0.005	566.54
Age	0.370	1.45	1.18 – 1.77	3.62	**<0.001**		(0.536)	
Sps [PO]	4.887	132.58	3.05 – 5765.58	2.54	**0.011**			
Sps [SO]	4.474	87.75	1.65 – 4667.67	2.21	**0.027**			

Table A5 Naturally Colonising Seeding & Sapling Data from Open stage (12 Sites, 50 Plots), Thicket stage (17 Sites, 66 Plots) and Closed stage (18 Sites, 68 Plots) sites. Showing no. sites and no. plots where each species present, with min, max and total counts. Combined counts for all seeding/sapling stages (S1-S4) are presented.

Stage & Metric	***Fraxinux excelsior***	***Betula pubescens /pendula***	***Prunus spinos***	***Crataegus monogyna***	***Quercus robur***	***Quercus petraea***	***Acer pesudopat-anus***	**Other Species***	**All Species**
Open									
Sites Present	1	1	0	0	0	1	0	1	2
Plots Present	3	2	0	0	0	2	0	2	5
Min Count	1	52	0	0	0	1	0	1	-
Max Count	2	105	0	0	0	2	0	1	-
Total Count	4	157	0	0	0	3	0	2	166
Thicket									
Sites Present	2	0	0	3	2	1	1	3	6
Plots Present	2	0	0	3	5	1	2	3	10
Min Count	18	0	0	1	1	3	1	1	-
Max Count	27	0	0	1	1	3	590	1	-
Total Count	45	0	0	3	5	3	591	3	650
Closed									
Sites Present	7	5	4	6	8	4	3	11	14
Plots Present	16	10	7	13	13	8	3	24	38
Min Count	1	1	1	1	1	1	1	1	-
Max Count	123	15	69	36	9	5	13	17	-
Total Count	303	63	78	62	38	21	18	86	669

* *Alnus glutinosa, Malus spp., Fagus sylvatica, Sambucus nigra, Corylus avellana, Ilex aquifolium, Quercus rubra, Sorbus acuparia, Pinus sylvestris, Salix spp.*

Table A6 Results of Supplementary Mixed Models for Diversity and Richness explained by best-fitting fixed effects. Species Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak). Landscape variables refer to Area of named habitat in the 2km matrix surrounding the site. Positive estimates indicate higher values for diversity and richness, and vice versa for negative estimates. Incidence Rate Ratios (IRR's) for Poisson models describe how the rate of the outcome changes with a one-unit increase in the predictor variable, with values greater than 1 indicating an increased rate of the outcome, and below one indicating a decreased rate. p-values (to test the null hypothesis that the coefficient estimate is equal to zero, i.e. no effect) were calculated from z-values: the ratio between the estimated coefficient and the standard error of the estimate (estimate/SE). Large z-values show that the estimate is large (in relation to its SE) and significantly different from zero.

Predictors	Model Estimate	IRR	Conf Interval	Z	p value	Marginal R^2 / Condition -al R^2	Moran's I (p value)	AICc
Woodland Generalist Richness – original model excluding bryophytes								
(Intercept)	-1.393	0.25	0.12 – 0.50	-3.92	<0.001			
Age	0.089	1.09	1.05 – 1.13	4.85	**<0.001**	0.351 / 0.588	0.0159 (0.388)	576.90
Species (PO)	0.848	2.33	1.21 – 4.49	2.54	**0.011**			
Species (SO)	1.160	3.19	1.58 – 6.45	3.23	**0.001**			
Woodland Specialist Richness – Best fitting model								
(Intercept)	-3.513	0.03	0.01 – 0.08	-6.59	<0.001			
Age	0.190	1.21	1.13 – 1.29	5.73	**<0.001**	0.384 / 0.496	-0.0245 (0.950)	281.52*
Landscape – Conifer Forest	0.381	1.46	0.80 – 2.68	1.23	0.217			
AWI – Best fitting model								
(Intercept)	-2.86	0.06	0.02 – 0.17	-5.06	**<0.001**			
Age	0.118	1.12	1.04 – 1.21	3.09	**0.002**	0.216 / 0.484	-0.036 (0.741)	262.71
Landscape – Conifer Forest	0.885	2.42	1.19 – 4.94	2.44	**0.015**			
R – Best fitting model								
(Intercept)	2.529	12.54	10.99 – 14.31	37.56	**<0.001**			
Soil [Brown]	-0.070	0.93	0.78 - 1.11	-0.77	0.44	0.168 / 0.451	0.008 (0.489)	1035.20
Soil [Peat]	-0.294	0.75	0.59 - 0.94	-2.48	**0.013**			
Soil [Podzol]	0.279	1.32	1.01 – 1.73	2.04	**0.041**			

Predictors	Model Estimate	IRR	Conf Interval	Z	p value	Marginal R^2 / Condition -al R^2	Moran's I (p value)	AICc
Soil [ShallowMin]	0.170	1.19	0.92 – 1.52	1.34	0.179			
H – Best fitting model								
(Intercept)	1.61		1.50 – 1.71	31.47	**<0.001**			
Landscape – Semi-Natural Grassland	0.22		0.02 – 0.41	2.13	**0.035**	0.048 / 0.400	-0.051 (0.501)	234.74

*AICc for model excluding Conifer was 284.96

Table A7 RLQ Analysis Results

	Axis 1	**Axis 2**
Eigenvalues	1.97194	0.72844
Proj. inertia %	67.3006	24.8609
Cumulative Proj. inertia %	67.3	92.16
Total inertia: 3.349		
Eigenvalues decomposition	***Axis 1***	***Axis 2***
Covar	1.40426	0.853486
Sd. R	1.952439	1.338072
Sd. Q	1.509977	1.196118
corrr	0.476321	0.533265
Inertia & Coinertia R (PCA)	***Axis 1***	***Axis 1 & 2***
inertia	3.812017	5.602452
Max	3.965543	5.940618
Ratio	0.961285	0.943076
Inertia & Coinertia Q (PCA)	***Axis 1***	***Axis 1 & 2***
inertia	2.28003	3.710729
Max	2.537896	3.976063
Ratio	0.898394	0.933267
Correlation L (CA)	***Axis 1***	***Axis 1 & 2***
corr	0.476321	0.533265
Max	0.947693	0.792243
Ratio	0.502611	0.673108

Table A8 Fourth Corner Analysis Results showing associations between individual environmental variables or species traits and the RLQ axes. Adjusted p values for multiple comparisons provided. Species Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak). Refer to Section 2.3.3 for variable explanations.

	Test	Obs	Std.Obs	Alter	P value	P value.adj
Speci.ALD	AxcQ1	-0.093	-1.029	two-sided	0.308	0.397
Speci.PO	AxcQ1	-0.242	-2.643	two-sided	0.006	**0.013**
Speci.SO	AxcQ1	0.364	3.985	two-sided	<0.001	**<0.001**
Age	AxcQ1	-0.071	-0.525	two-sided	0.620	0.689
SoilC.Alluv/Gley	AxcQ1	-0.078	-0.915	two-sided	0.381	0.492
SoilC.Brown	AxcQ1	-0.117	-1.152	two-sided	0.268	0.397
SoilC.Peat	AxcQ1	-0.116	-1.290	two-sided	0.201	0.292
SoilC.Podzol	AxcQ1	0.357	3.954	two-sided	<0.001	**<0.001**
SoilC.ShallowMin	AxcQ1	0.109	1.214	two-sided	0.226	0.312
Fores.Afforested	AxcQ1	-0.281	-2.987	two-sided	0.001	**0.006**
Fores.Reforested	AxcQ1	0.281	2.987	two-sided	0.001	**0.006**
All_Wood	AxcQ1	0.345	3.787	two-sided	<0.001	**<0.001**
All_SemiNat_Grass	AxcQ1	0.172	1.910	two-sided	0.056	0.098
All_Agri_Grass	AxcQ1	-0.317	-3.482	two-sided	<0.001	**0.001**
WoodArea	AxcQ1	0.184	2.037	two-sided	0.041	0.083
Lands.ExtUp	AxcQ1	0.410	4.526	two-sided	<0.001	**<0.001**
Lands.IntLow	AxcQ1	-0.269	-2.954	two-sided	0.002	**0.004**
Lands.Peat	AxcQ1	-0.074	-0.896	two-sided	0.412	0.516
Lands.SemiElv	AxcQ1	0.123	1.358	two-sided	0.176	0.271
Lands.SemiLow	AxcQ1	-0.071	-0.778	two-sided	0.441	0.496
Speci.ALD	AxcQ2	0.084	1.794	two-sided	0.071	0.136
Speci.PO	AxcQ2	0.002	0.007	two-sided	0.995	0.995
Speci.SO	AxcQ2	-0.078	-0.969	two-sided	0.345	0.475
Age	AxcQ2	-0.569	-14.046	two-sided	<0.001	**<0.001**
SoilC.Alluv/Gley	AxcQ2	-0.155	-1.791	two-sided	0.070	0.136
SoilC.Brown	AxcQ2	0.171	1.731	two-sided	0.081	0.147
SoilC.Peat	AxcQ2	-0.064	-1.068	two-sided	0.300	0.429
SoilC.Podzol	AxcQ2	0.078	1.127	two-sided	0.262	0.397
SoilC.ShallowMin	AxcQ2	-0.044	-0.578	two-sided	0.575	0.676
Fores.Afforested	AxcQ2	0.218	2.311	two-sided	0.018	0.051
Fores.Reforested	AxcQ2	-0.218	-2.311	two-sided	0.018	0.051
All_Wood	AxcQ2	-0.072	-0.793	two-sided	0.447	0.541
All_SemiNat_Grass	AxcQ2	0.160	2.165	two-sided	0.024	0.064
All_Agri_Grass	AxcQ2	-0.014	-0.182	two-sided	0.862	0.884
WoodArea	AxcQ2	-0.018	-0.195	two-sided	0.850	0.884
Lands.ExtUp	AxcQ2	0.017	0.214	two-sided	0.837	0.884

	Test	Obs	Std.Obs	Alter	P value	P value.adj
Lands.IntLow	AxcQ2	-0.115	-1.523	two-sided	0.130	0.216
Lands.Peat	AxcQ2	-0.131	-1.668	two-sided	0.088	0.153
Lands.SemiElv	AxcQ2	-0.035	-0.523	two-sided	0.610	0.689
Lands.SemiLow	AxcQ2	0.188	2.574	two-sided	0.006	**0.021**
AxcR1	Ell_L	-0.180	-1.928	two-sided	0.052	0.103
AxcR2	Ell_L	0.490	5.314	two-sided	<0.001	**<0.001**
AxcR1	Ell_F	-0.084	-0.960	two-sided	0.358	0.521
AxcR2	Ell_F	-0.015	-0.162	two-sided	0.878	0.969
AxcR1	Ell_R	-0.492	-5.607	two-sided	<0.001	**<0.001**
AxcR2	Ell_R	0.000	-0.006	two-sided	0.996	0.996
AxcR1	Ell_N	-0.422	-4.808	two-sided	<0.001	**<0.001**
AxcR2	Ell_N	-0.186	-1.829	two-sided	0.065	0.116
AxcR1	seed_mass	-0.012	-0.202	two-sided	0.808	0.969
AxcR2	seed_mass	-0.132	-1.824	two-sided	0.086	0.153
AxcR1	C	-0.050	-0.575	two-sided	0.582	0.776
AxcR2	C	-0.011	-0.121	two-sided	0.908	0.969
AxcR1	R	-0.107	-1.228	two-sided	0.231	0.370
AxcR2	R	0.290	3.148	two-sided	<0.001	**0.001**
AxcR1	S	0.209	2.395	two-sided	0.012	**0.037**
AxcR2	S	0.176	1.904	two-sided	0.052	0.103

Table A9 Highest and Lowest Species Scores on the RLQ Axes

Axis 1	Axis 2
Highest 10	
Erica cinerea	*Carex flava*
Blechnum spicant	*Veronica arvensis*
Carex pilulifera	*Carex echinata*
Polygala serpyllifolia	*Carex panicea*
Vaccinium myrtillus	*Narthecium ossifragum*
Juncus squarrosus	*Polygala serpyllifolia*
Galium saxatile	*Scorzoneroides autumnalis*
Erica tetralix	*Erica tetralix*
Nardus stricta	*Eriophorum angustifolium*
Calluna vulgaris	*Hypochaeris radicata*
Lowest 10	
Rumex obtusifolius	*Quercus robur*
Crepis versicaria	*Fagus sylvatica*
Phalaris arundinacea	*Corylus avellana*
Galium aparine	*Quercus petraea*
Epilobium hirsutum	*Bromopsis ramosa*
Heracleum sphondylium	*Polystichum setiferum*
Carex riparia	*Acer psuedoplatanus*
Equisetum telmateia	*Hedera helix*
Urtica dioica	*Fraxinus excelsior*
Veronica persica	*Asplenium scolopendrium*

Table A10 ERICA tool output. SpsCat = Species Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak).. IVC = Irish Vegetation Classification. Plot codes derive from Site Codes listed in Table A1.

Habitat	Stage	SpsCat	Age	Plot	IVC Group	IVC Sub-group	Score	Type
Grasslands	Open	ALD	4	MG1	GL2	GL2D	52.64384	Assigned
Grasslands	Open	ALD	4	MG2	GL3	GL3C	34.44274	Transitional
Grasslands	Open	ALD	4	MG3	GL4	GL4A	90.95774	Assigned
Grasslands	Open	ALD	4	MG4	GL3	GL3C	30.09462	Transitional
Grasslands	Open	PO	2	CL1	GL3	GL3C	31.61387	Transitional
Grasslands	Open	PO	2	CL2	GL3	GL3C	16.18605	Transitional
Grasslands	Open	PO	2	CL3	GL4	GL4A	97.47515	Assigned
Grasslands	Open	PO	2	CL4	GL4	GL4A	81.03923	Assigned
Grasslands	Open	PO	5	DG3	GL2	GL2C	62.32485	Assigned
Grasslands	Open	PO	5	DG4	GL2	GL2C	37.51269	Transitional
Grasslands	Open	PO	2	FN1	GL4	GL4A	36.33353	Transitional
Grasslands	Open	PO	2	FN2	GL4	GL4A	15.29302	Transitional
Grasslands	Open	PO	2	FN3	GL4	GL4A	32.02736	Transitional
Grasslands	Open	PO	2	FN4	GL4	GL4A	30.78565	Transitional
Grasslands	Open	PO	2	MN1	GL2	GL2C	82.20701	Assigned
Grasslands	Open	PO	2	MN2	GL3	GL3C	37.99855	Transitional
Grasslands	Open	PO	2	MN3	GL2	GL2C	84.09169	Assigned
Grasslands	Open	PO	2	MN4	GL2	GL2C	38.95557	Transitional
Grasslands	Open	PO	2	MN5	GL2	GL2C	89.31477	Assigned
Grasslands	Open	PO	2	MO1	GL2	GL2C	39.50696	Transitional
Grasslands	Open	PO	2	MO2	GL4	GL4A	32.465	Transitional
Grasslands	Open	PO	2	MO3	GL4	GL4A	84.90233	Assigned
Grasslands	Open	PO	2	MO4	GL4	GL4A	86.85165	Assigned
Grasslands	Open	PO	2	MO5	GL4	GL4A	48.11355	Transitional
Grasslands	Open	PO	3	NF1	GL4	GL4A	86.13804	Assigned
Grasslands	Open	PO	3	NF2	GL2	GL2B	49.14499	Transitional
Grasslands	Open	PO	3	NF3	GL4	GL4A	79.16565	Assigned
Grasslands	Open	PO	5	TW2	GL3	GL3F	36.52326	Transitional
Grasslands	Open	PO	5	TW3	GL3	GL3E	23.55369	Transitional
Grasslands	Open	PO	5	TW4	GL3	GL3F	29.84203	Transitional
Grasslands	Open	SO	5	BC3	GL4	GL4A	36.99106	Transitional
Grasslands	Open	SO	2	CO1	GL4	GL4A	80.3248	Assigned
Grasslands	Open	SO	2	CO2	GL4	GL4A	57.20949	Assigned
Grasslands	Open	SO	2	CO3	GL4	GL4A	33.54057	Transitional
Grasslands	Open	SO	2	CO4	GL1	GL1C	26.997	Transitional

Habitat	Stage	SpsCat	Age	Plot	IVC Group	IVC Sub-group	Score	Type
Grasslands	Open	SO	2	CO5	GL3	GL3C	53.37385	Assigned
Grasslands	Open	SO	4	RN1	GL4	GL4A	95.50518	Assigned
Grasslands	Open	SO	4	RN2	GL4	GL4A	98.11824	Assigned
Grasslands	Open	SO	4	RN3	GL4	GL4A	89.45087	Assigned
Grasslands	Open	SO	4	RN4	GL4	GL4A	82.28158	Assigned
Grasslands	Open	SO	4	VM1	GL4	GL4A	96.64012	Assigned
Grasslands	Open	SO	4	VM2	GL4	GL4C	30.41179	Transitional
Grasslands	Open	SO	4	VM4	GL4	GL4A	94.25497	Assigned
Grasslands	Thicket	ALD	12	BI3	GL2	GL2A	26.78224	Transitional
Grasslands	Thicket	ALD	7	DW1	GL4	GL4A	34.92121	Transitional
Grasslands	Thicket	ALD	7	DW2	GL3	GL3C	18.4954	Transitional
Grasslands	Thicket	ALD	8	HL1	GL1	GL1D	66.7324	Assigned
Grasslands	Thicket	ALD	8	HL2	GL1	GL1D	77.35009	Assigned
Grasslands	Thicket	ALD	8	HL4	GL2	GL2C	40.26598	Transitional
Grasslands	Thicket	ALD	8	HL5	GL1	GL1D	92.84968	Assigned
Grasslands	Thicket	ALD	6	RS2	GL3	GL3C	29.21154	Transitional
Grasslands	Thicket	ALD	6	RS4	GL3	GL3C	26.08904	Transitional
Grasslands	Thicket	PO	9	CA1	GL2	GL2D	59.87373	Assigned
Grasslands	Thicket	PO	7	DE1	GL3	GL3C	14.49308	Transitional
Grasslands	Thicket	PO	7	DE3	GL4	GL4A	51.90682	Assigned
Grasslands	Thicket	PO	7	DE4	GL4	GL4A	66.81455	Assigned
Grasslands	Thicket	PO	7	HS2	GL3	GL3C	42.84016	Transitional
Grasslands	Thicket	PO	7	HS3	GL3	GL3C	23.13861	Transitional
Grasslands	Thicket	PO	9	JCE1	GL3	GL3C	53.40138	Assigned
Grasslands	Thicket	PO	9	JCE2	GL3	GL3C	14.63471	Transitional
Grasslands	Thicket	PO	9	JCE3	GL3	GL3C	60.86889	Assigned
Grasslands	Thicket	PO	9	JCE4	GL3	GL3C	69.19287	Assigned
Grasslands	Thicket	PO	9	JCS1	GL3	GL3C	55.22898	Assigned
Grasslands	Thicket	PO	9	JCS2	GL3	GL3C	30.69166	Transitional
Grasslands	Thicket	PO	9	JCS3	GL3	GL3C	29.02639	Transitional
Grasslands	Thicket	PO	11	SM2	GL2	GL2B	18.17406	Transitional
Grasslands	Thicket	PO	11	SM3	GL2	GL2C	13.33763	Transitional
Grasslands	Thicket	PO	11	SM4	GL2	GL2C	16.51168	Transitional
Grasslands	Thicket	PO	9	SW1	GL4	GL4A	16.65085	Transitional
Grasslands	Thicket	PO	9	SW3	GL2	GL2C	23.18494	Transitional
Grasslands	Thicket	PO	9	SW4	GL2	GL2B	48.67291	Transitional
Other	Open	PO	5	DG1	SM6	SM6B	40.85441	Transitional
Other	Open	PO	5	TW1	SC1	SC1E	41.38553	Transitional

Habitat	Stage	SpsCat	Age	Plot	IVC Group	IVC Sub-group	Score	Type
Other	Open	SO	5	BC1	SC1	SC1C	54.60266	Assigned
Other	Open	SO	4	VM3	HE4	HE4E	49.97908	Transitional
Other	Thicket	ALD	12	BI1	FW3	FW3F	36.33077	Transitional
Other	Thicket	ALD	6	RS1	SC1	SC1E	56.18384	Assigned
Other	Thicket	ALD	6	RS3	SC1	SC1E	32.01763	Transitional
Other	Thicket	PO	7	CM2	SM6	SM6B	64.02569	Assigned
Other	Thicket	PO	7	HS1	SC1	SC1F	30.87603	Transitional
Other	Thicket	PO	7	HS4	SM4	SM4A	16.00862	Transitional
Grasslands	Closed	SO	15	QN3	GL2	GL2C	38.86076	Transitional
Other	Closed	ALD	14	FG1	SC1	SC1F	53.03065	Assigned
Other	Closed	PO	18	JH2	SC1	SC1F	31.55027	Transitional
Woodland	Open	PO	5	DG2	WL3	WL3B	18.6641	Transitional
Woodland	Open	SO	5	BC2	WL3	WL3B	18.56607	Transitional
Woodland	Open	SO	5	BC4	WL4	WL4B	56.4925	Assigned
Woodland	Thicket	ALD	12	BI2	WL3	WL3F	23.45334	Transitional
Woodland	Thicket	ALD	12	BI4	WL3	WL3B	56.5445	Assigned
Woodland	Thicket	ALD	12	BI5	WL3	WL3F	49.54598	Transitional
Woodland	Thicket	ALD	7	DW3	WL3	WL3B	76.98328	Assigned
Woodland	Thicket	ALD	7	DW4	WL3	WL3B	68.86946	Assigned
Woodland	Thicket	ALD	8	FL1	WL3	WL3B	92.54791	Assigned
Woodland	Thicket	ALD	8	FL2	WL3	WL3B	40.82196	Transitional
Woodland	Thicket	ALD	8	FL3	WL3	WL3B	82.77277	Assigned
Woodland	Thicket	ALD	8	HL3	WL3	WL3B	33.63634	Transitional
Woodland	Thicket	PO	9	CA2	WL3	WL3B	88.35904	Assigned
Woodland	Thicket	PO	9	CA3	WL2	WL2A	40.11704	Transitional
Woodland	Thicket	PO	7	CM1	WL2	WL2A	45.40082	Transitional
Woodland	Thicket	PO	7	CM3	WL2	WL2A	31.22294	Transitional
Woodland	Thicket	PO	7	DE2	WL3	WL3B	34.86085	Transitional
Woodland	Thicket	PO	14	DY1	WL2	WL2A	48.43789	Transitional
Woodland	Thicket	PO	14	DY2	WL2	WL2A	66.79147	Assigned
Woodland	Thicket	PO	14	DY3	WL2	WL2A	35.83117	Transitional
Woodland	Thicket	PO	14	DY4	WL2	WL2A	77.90231	Assigned
Woodland	Thicket	PO	8	NL1	WL2	WL2A	36.30518	Transitional
Woodland	Thicket	PO	8	NL2	WL2	WL2A	26.14589	Transitional
Woodland	Thicket	PO	8	NL3	WL2	WL2A	46.12094	Transitional
Woodland	Thicket	PO	12	PB1	WL4	WL4B	74.76013	Assigned
Woodland	Thicket	PO	12	PB2	WL4	WL4B	35.58223	Transitional
Woodland	Thicket	PO	12	PB3	WL4	WL4F	60.58861	Assigned

Habitat	Stage	SpsCat	Age	Plot	IVC Group	IVC Sub-group	Score	Type
Woodland	Thicket	PO	12	PB4	WL4	WL4F	50.53055	Assigned
Woodland	Thicket	PO	7	RY1	WL2	WL2A	53.28614	Assigned
Woodland	Thicket	PO	7	RY2	WL2	WL2A	90.80403	Assigned
Woodland	Thicket	PO	7	RY3	WL2	WL2A	61.08994	Assigned
Woodland	Thicket	PO	7	RY4	WL2	WL2A	90.60831	Assigned
Woodland	Thicket	PO	11	SM1	WL1	WL1D	43.00849	Transitional
Woodland	Thicket	PO	11	SM5	WL4	WL4B	23.23482	Transitional
Woodland	Thicket	PO	9	SW2	WL4	WL4F	21.60419	Transitional
Woodland	Closed	ALD	14	FG2	WL3	WL3B	53.44401	Assigned
Woodland	Closed	ALD	14	FG3	WL3	WL3B	62.88051	Assigned
Woodland	Closed	ALD	16	KG1	WL3	WL3B	64.10907	Assigned
Woodland	Closed	ALD	16	KG2	WL3	WL3B	74.07545	Assigned
Woodland	Closed	ALD	16	KG3	WL3	WL3B	41.89605	Transitional
Woodland	Closed	ALD	16	KG4	WL3	WL3B	98.71489	Assigned
Woodland	Closed	ALD	16	KG5	WL3	WL3B	75.03323	Assigned
Woodland	Closed	PO	20	DH1	WL2	WL2A	99.27459	Assigned
Woodland	Closed	PO	20	DH2	WL2	WL2A	99.72511	Assigned
Woodland	Closed	PO	20	DH3	WL2	WL2A	99.98012	Assigned
Woodland	Closed	PO	20	DN1	WL2	WL2A	90.56582	Assigned
Woodland	Closed	PO	20	DN2	WL2	WL2A	95.43655	Assigned
Woodland	Closed	PO	20	DN3	WL2	WL2A	99.02948	Assigned
Woodland	Closed	PO	14	FD1	WL3	WL3C	25.04204	Transitional
Woodland	Closed	PO	14	FD2	WL3	WL3B	20.07411	Transitional
Woodland	Closed	PO	14	FD3	WL3	WL3B	46.52931	Transitional
Woodland	Closed	PO	18	JH1	WL2	WL2A	97.40088	Assigned
Woodland	Closed	PO	18	JH3	WL2	WL2A	93.59909	Assigned
Woodland	Closed	PO	18	JH4	WL2	WL2A	99.11732	Assigned
Woodland	Closed	PO	14	RM1	WL2	WL2A	70.49412	Assigned
Woodland	Closed	PO	14	RM2	WL2	WL2A	98.01844	Assigned
Woodland	Closed	PO	14	RM3	WL2	WL2A	98.77707	Assigned
Woodland	Closed	PO	14	ST1	WL3	WL3C	28.37649	Transitional
Woodland	Closed	PO	14	ST2	WL3	WL3C	23.23349	Transitional
Woodland	Closed	PO	14	ST3	WL2	WL2A	73.53367	Assigned
Woodland	Closed	PO	14	ST4	WL2	WL2A	86.71073	Assigned
Woodland	Closed	PO	14	ST5	WL2	WL2A	93.31474	Assigned
Woodland	Closed	PO	20	TV1	WL4	WL4E	21.79445	Transitional
Woodland	Closed	PO	20	TV2	WL2	WL2A	23.23229	Transitional
Woodland	Closed	PO	20	TV3	WL2	WL2A	59.41548	Assigned

Habitat	Stage	SpsCat	Age	Plot	IVC Group	IVC Sub-group	Score	Type
Woodland	Closed	SO	22	BG1	WL1	WL1B	54.93919	Assigned
Woodland	Closed	SO	22	BG2	WL1	WL1B	90.57479	Assigned
Woodland	Closed	SO	22	BG3	WL1	WL1B	99.57483	Assigned
Woodland	Closed	SO	22	BG4	WL1	WL1B	88.03583	Assigned
Woodland	Closed	SO	14	BK1	WL4	WL4A	99.56612	Assigned
Woodland	Closed	SO	14	BK2	WL4	WL4A	57.36167	Assigned
Woodland	Closed	SO	14	BK3	WL4	WL4E	46.56814	Transitional
Woodland	Closed	SO	15	BR1	WL3	WL3C	48.06397	Transitional
Woodland	Closed	SO	15	BR2	WL3	WL3B	92.62	Assigned
Woodland	Closed	SO	15	BR3	WL1	WL1B	40.26537	Transitional
Woodland	Closed	SO	15	BR4	WL4	WL4D	26.92408	Transitional
Woodland	Closed	SO	14	BT1	WL1	WL1B	51.18713	Assigned
Woodland	Closed	SO	14	BT2	WL1	WL1B	44.4694	Transitional
Woodland	Closed	SO	14	BT3	WL1	WL1B	93.79297	Assigned
Woodland	Closed	SO	14	BT4	WL1	WL1B	62.25579	Assigned
Woodland	Closed	SO	14	BT5	WL1	WL1B	29.14059	Transitional
Woodland	Closed	SO	14	GK1	WL4	WL4B	68.76251	Assigned
Woodland	Closed	SO	14	GK2	WL4	WL4B	48.29129	Transitional
Woodland	Closed	SO	14	GK3	WL4	WL4E	36.19377	Transitional
Woodland	Closed	SO	14	GK4	WL4	WL4B	38.23925	Transitional
Woodland	Closed	SO	22	LC1	WL4	WL4D	64.20424	Assigned
Woodland	Closed	SO	22	LC2	WL4	WL4A	50.62226	Assigned
Woodland	Closed	SO	22	LC3	WL4	WL4D	57.81013	Assigned
Woodland	Closed	SO	22	LC4	WL4	WL4A	78.54862	Assigned
Woodland	Closed	SO	13	PW1	WL4	WL4F	96.11064	Assigned
Woodland	Closed	SO	13	PW2	WL4	WL4F	59.73694	Assigned
Woodland	Closed	SO	13	PW3	WL4	WL4F	98.9543	Assigned
Woodland	Closed	SO	13	PW4	WL4	WL4F	61.1573	Assigned
Woodland	Closed	SO	15	QN1	WL1	WL1B	62.85076	Assigned
Woodland	Closed	SO	15	QN2	WL1	WL1B	78.29736	Assigned
Woodland	Closed	SO	15	QN4	WL1	WL1B	83.46617	Assigned
Woodland	Closed	SO	19	SS1	WL4	WL4B	93.80402	Assigned
Woodland	Closed	SO	19	SS2	WL4	WL4B	80.86492	Assigned
Woodland	Closed	SO	19	SS3	WL4	WL4F	43.8565	Transitional
Woodland	Closed	SO	19	SS4	WL4	WL4B	80.46797	Assigned

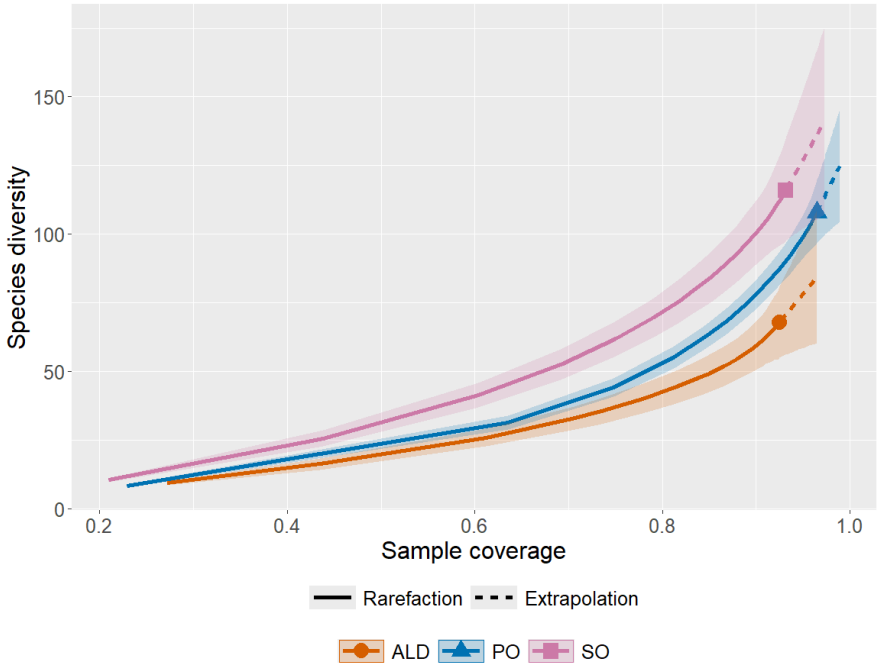

Figure A1 Comparison of species diversity at standardized sample coverage across woodland groups. Species Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak).

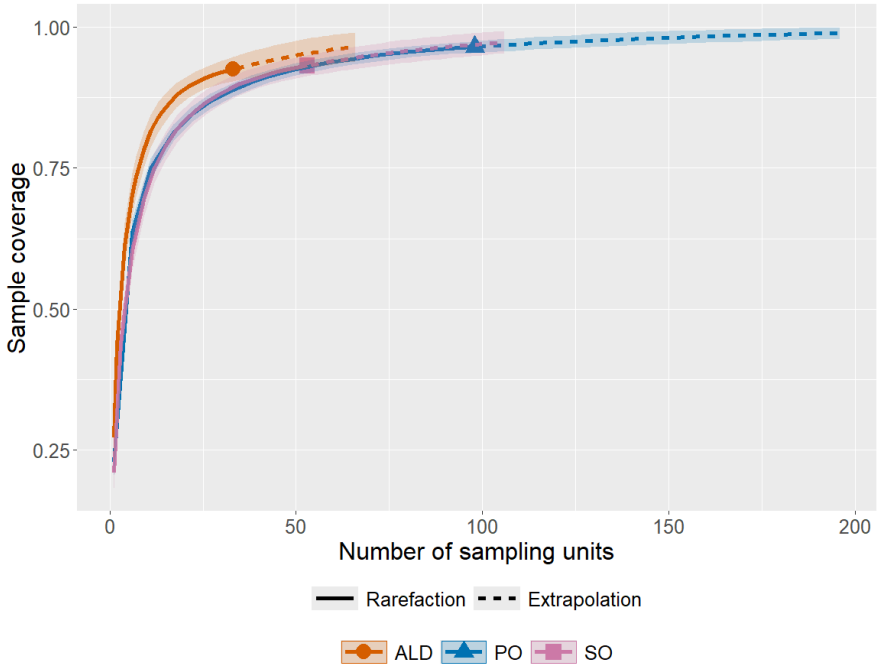

Figure A2 Sample coverage as a function of sampling effort across woodland groups. Species Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak).

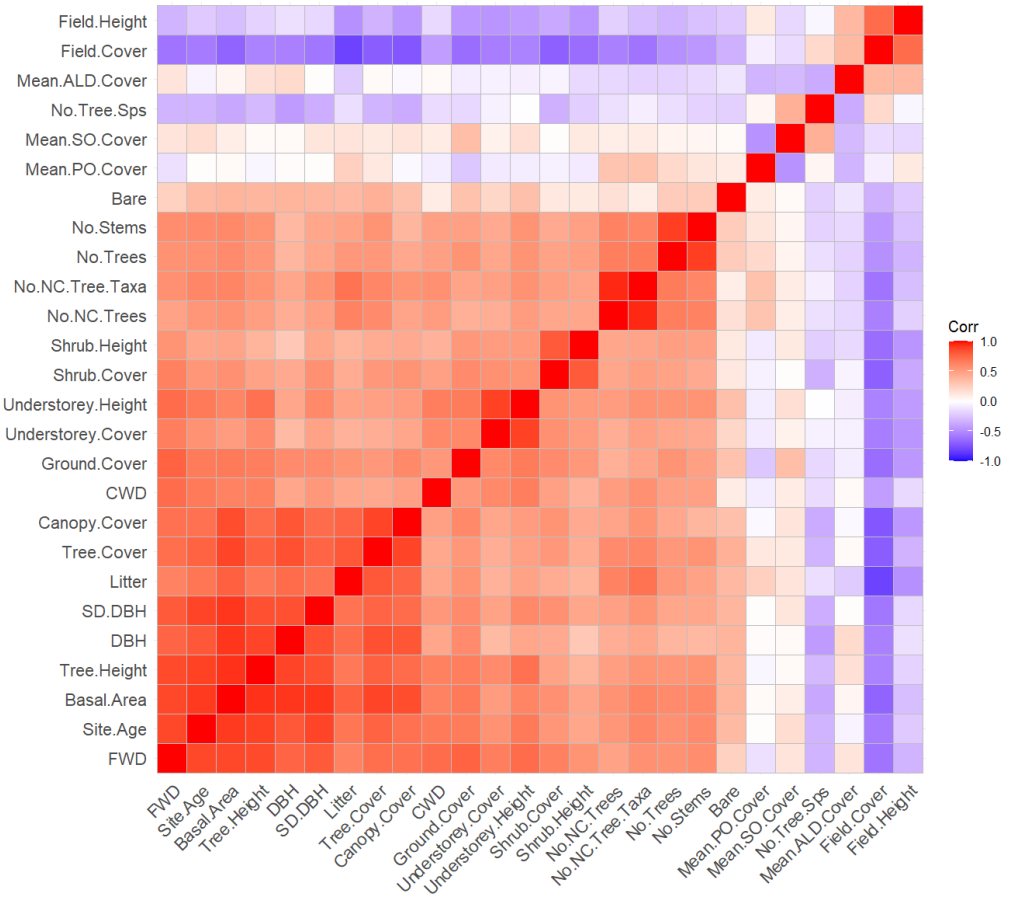

Figure A3 Correlation Matrix for all measured Structural Variables. Positive correlations are in red and negative in purple with the depth of shade indicating the strength of the relationship. Species Cover Categories reflect tree species group planted (ALD = Alder, PO = Pedunculate Oak, SO = Sessile Oak). NC = Natural Colonisation, CWD = Coarse Woody Debris, FWD = Fine Woody Debris, DBH = Diameter at Breast Height, SD_DBH = Standard Deviation of DBH, No. Trees = Number of planted trees. No. Stem = Number of stems associated with planted trees.

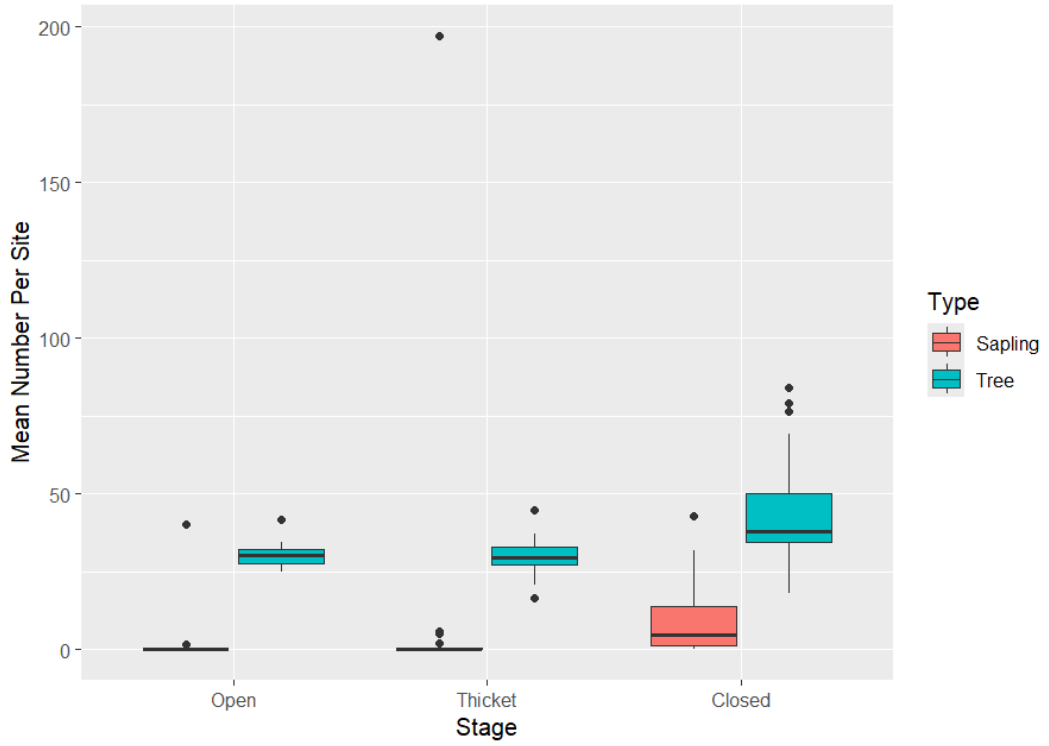

Figure A4 Mean number of naturally colonising saplings vs planted trees across stages.

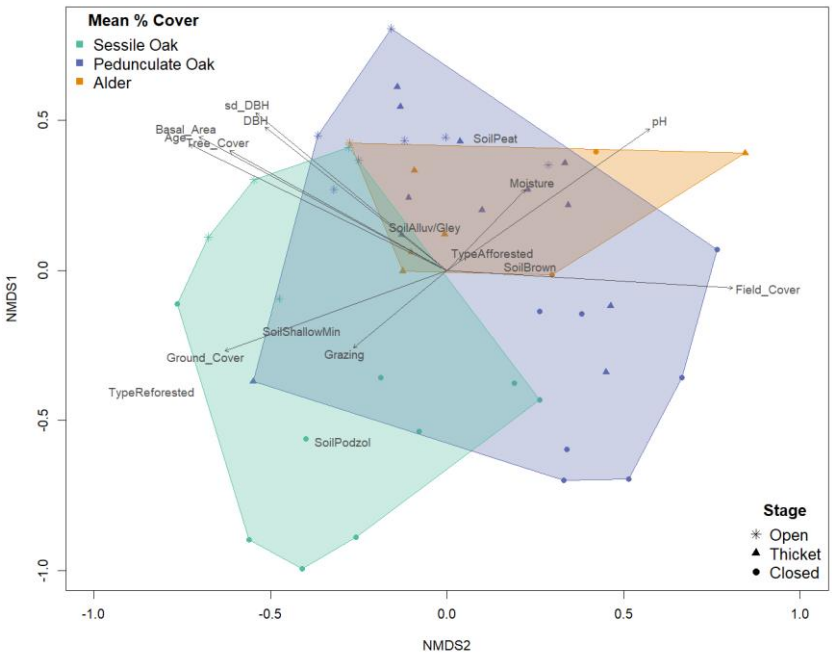

Figure A5 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites. Grouped by tree species group with symbols illustrating development stages and arrows showing fitted environmental variables for structural metrics, soil metrics, grazing and afforestation type. Axes 1 vs 2 plotted (k = 3, stress = 0.173).

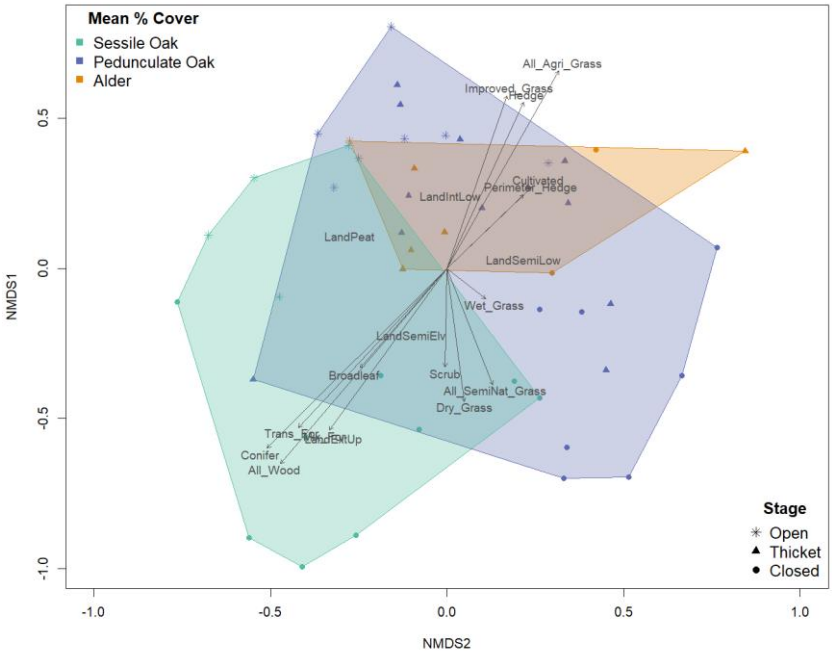

Figure A6 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites. Grouped by tree species group with symbols illustrating development stages and arrows showing fitted environmental variables for age, landscape class, perimeter hedgerow length and landscape composition. Axes 1 vs 2 plotted (k = 3, stress = 0.173).

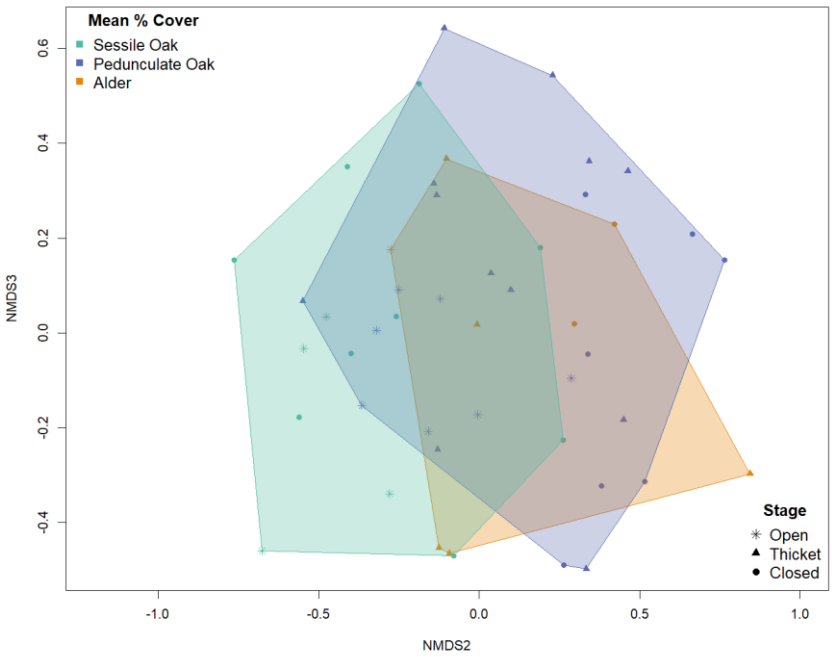

Figure A7 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites. Grouped by tree species group with symbols illustrating development stages. Axes 2 vs 3 plotted (k = 3, stress = 0.173).

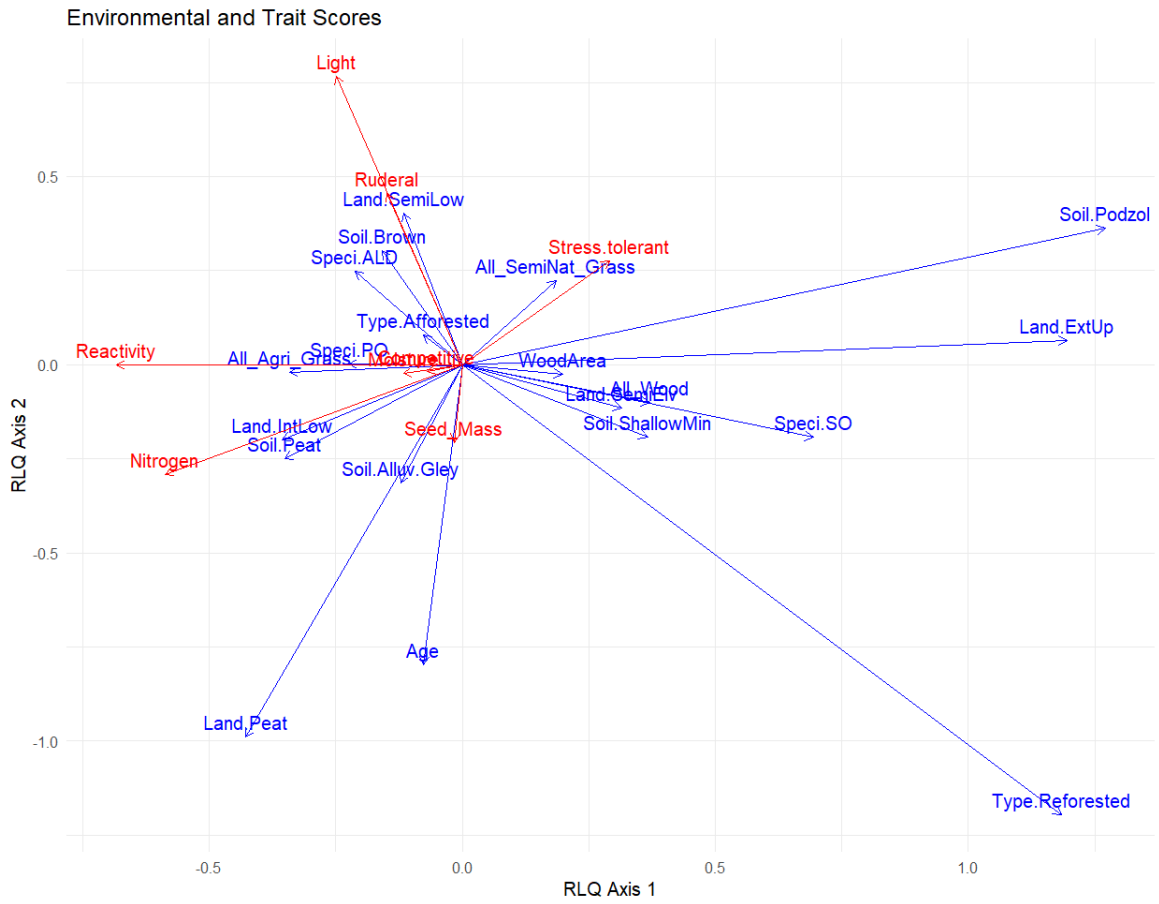

Figure A8 RLQ axes showing traits (red) and environmental variables (blue) with arrow indicating strength of relationship

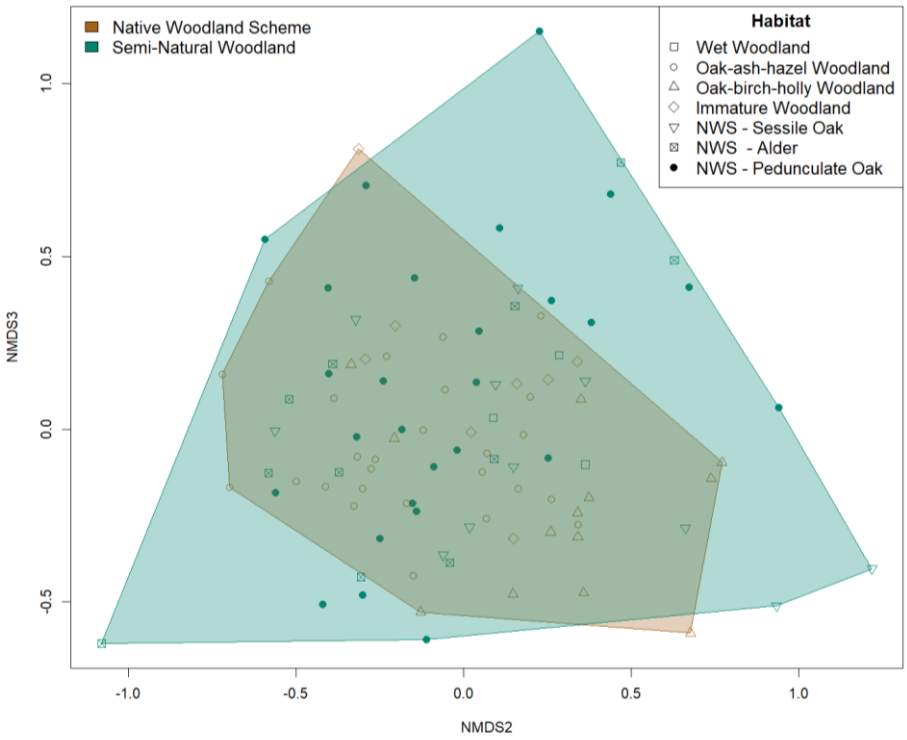

Figure A9 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites and semi-natural woodlands extracted from the NFI database for the same study area.
Symbols illustrate habitat type. (Axes 2 & 3 plotted, k = 3, stress 0.148)

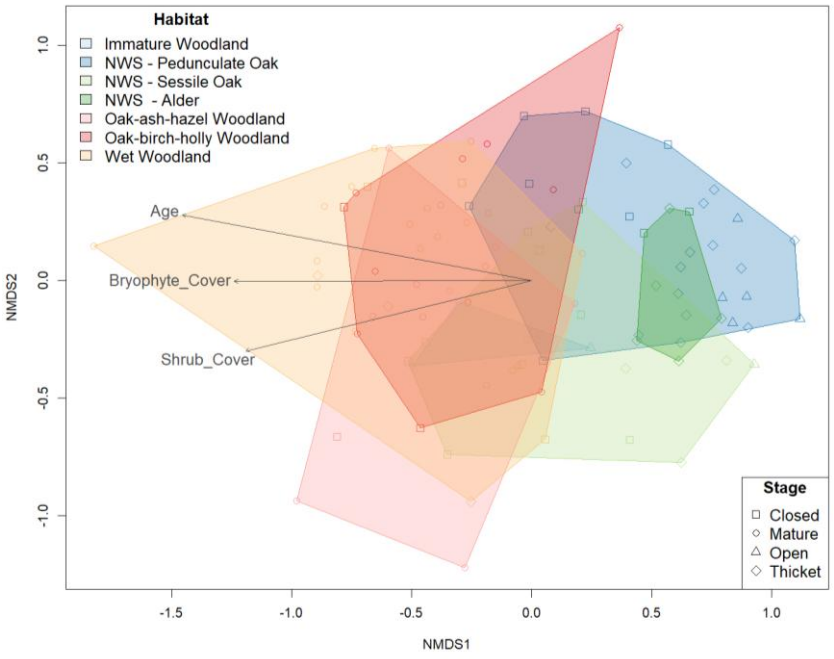

Figure A10 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites and semi-natural woodlands extracted from the NFI database for the same study area.
Grouped by habitat type with symbols showing development stage and arrows showing fitted variables for shrub cover, bryophyte cover and age. (Axes 1 & 2 plotted, k = 3, stress 0.148)

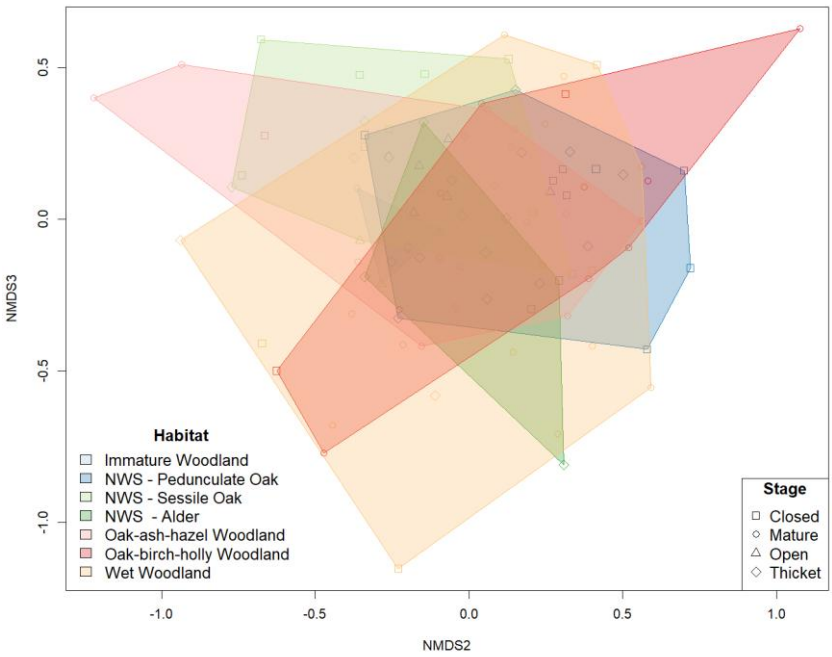

Figure A11 NMDS Biplot of floral composition of the surveyed Native Woodland Scheme sites and semi-natural woodland habitats extracted from the NFI database for the same study area. Grouped by habitat type with symbols showing development stage. (Axes 2 & 3 plotted, k = 3, stress 0.148)

Appendix B – Supplementary Data for Chapter 3

Table B1 Site information

Ref	County	Wood Area (ha)	Past Land Use[Note1]	Year Planted	Stage	Trees Planted[Note2] (%)
1	Carlow	9.65	GA1/GS4	2008	Closed	SP (14), SO (82.9), SBI (3.1)
2	Westmeath	2.76	GA1	2013	Thicket	PO (58) SP (21.7) ADB (20.3)
3	Carlow	0.922	GA1	2015	Thicket	PO(70.5) BI (7.6) SP (2.2) ADB (19.7)
4	Offaly	4.71	GA1/GS1/ GS4	2015	Thicket	PO (60.3), SP (20.2) ABD 19.5)
5	Westmeath	2.33	GA1	2019	Open	PO (50), BI (17.8) ADB (22.2) SO (10)
6	Laois	4.36	GA1/GS4	2008	Closed	PO (68.6) ASH (18.3) HAW (10.3) HZ (2.5)
7	Dublin	3.43	BC1	2017	Open	PO (39.7) ADB (40.2) DB (20.1)
8	Dublin	3.12	BC2	2002	Closed	PO (95) ADB (5)
9	Dublin	13.35	BC1	2011	Thicket	PO (42.5) ADB (20) SO (37.5)
10	Wicklow	2.35	GA1/GS1	2018	Open	BI (33.2), SP (16.6), ADB (8.3), SO (41.9)
11	Wicklow	5.22	GA1	2013	Thicket	PO(70.5) SBI (14.8) RWN (14.8)
12	Wicklow	2.67	GA1	2008	Closed	SO (34) ASH (34), ALD (7), ADB (25)
13	Westmeath	2.3	GA1	2005	Closed	PO (44) ALD (33) SP (22)
14	Offaly	1.04	GA1/GS1	2009	Closed	PO (86), ADB (14)
15	Carlow	2.03	GA1	2021	Open	PO (40), BI (22), HZ (22), ADB (16)
16	Carlow	5.4	GA1/WS1	2018	Open	PO (50), BI (10), HZ (12), ADB (20), SP (10),
17	Kilkenny	1.05	GA1	2015	Thicket	PO(43), BI (21), RWN (6), HZ (21), HAW (9)
18	Offaly	4.72	GA1	2021	Open	PO (40), DBI (20), ADB (40)

Note 1: Habitats listed in order of dominance following Fossitt (2000) categories & estimated based on historical aerial photography; GA1 = Improved Agricultural grassland, GS1 = Neutral grassland, GS4 = Wet grassland, BC1 = Arable Crops, BC2 = Horticultural land, WS1 = Scrub.
Note 2: Species as follows SP = Scot's Pine, SO = Sessile Oak, SBI = Silver Birch, PO = Pedunculate Oak, BI = Birch, ASH = Ash, HAW = Hawthorn, HZ = Hazel, DB = Downy Birch, RWN = Rowan; ALD = Alder, ADB = Additional Broadleaves (Native).

Table B2 Hoverfly Trait and Habitat Data Collated based on the information in Speight et al. (2020) and Speight and Castella (2020) with the exception of the adult habitat description which is from Stubbs and Falk (2002) and the Pantheon category which is from Webb et al.(2018). For categorical preferences/associations coded 1 (weak preference/association) to 3 (maximally-preferred) in Speight et al. (2020), the maximally-preferred category is used. Species length is based on the median of the range of lengths provided. As some *Syrphus* spp. and *Helophilus* spp. recorded on transects were identified on the wing but not collected for further identification, we used the median/dominant traits for all *Syrphus* spp. and 2 no. *Helophilus* spp in our analysis.

Name	Short name	Larval Activity Zone	Hibernation/ Overwinter-ing zone	Larval Food	Body length (median)	Adult Habitat Description	Pantheon Category	Habitat Category
Cheilosia albitarsis	Chelalb	Herbs	Roots	Plant	9	Damp meadows, marshes, woodland clearings	n/a	Gen
Cheilosia antiqua	Chelant	Herbs	Roots	Plan	7	Woodland	Shaded woodland floor	Wood
Cheilosia bergenstammi	Chelberg	Herbs	Roots	Plant	10.5	Rough grassland	short sward & bare; tall sward & scrub	Open
Cheilosia illustrata	ChelIll	Herbs	Various	Plant	10.5	Hedgerows & Woodland Edge	tall sward & scrub	Gen
Cheilosia pagana	Chelpag	Herbs	Various	unknown	7.5	Wooded & Open	Shaded woodland floor	Gen
Chrysotoxum bicinctum	Chrybic	Herbs	Roots	Animal	11	Grassy sites, near shrubs and trees	tall sward & scrub	Gen
Epistrophe eligans	Episelig	Trees	Ground Surface	Animal	11	Trees, Woodland edges	Arboreal	Wood
Epistrophe grossulariae	Episgros	Trees	Above Ground	Animal	12	Woodland edges, meadows	Arboreal	Wood
Episyrphus balteatus	Eipibalt	Trees	Above Ground	Animal	10	Woodland sun spots	tall sward & scrub	Gen
Eristalis arbursorum	Erisarb	Wet/ Organic	Water	Micro	10.5	Gardens, Urban Waste Ground, Open Habitats	acid & sedge peats	Open
Eristalis horticola	Erishort	Wet/ Organic	Water	Micro	12.5	Woody (Bushes & Trees)	acid & sedge peats	Gen

Name	Short name	Larval Activity Zone	Hibernation/ Overwinter-ing zone	Larval Food	Body length (median)	Adult Habitat Description	Pantheon Category	Habitat Category
Eristalis nemorum	Erisnem	Wet/ Organic	Water	Micro	12	Open - meadow & wasteland	acid & sedge peats	Gen
Eristalis pertinex	Erispert	Wet/ Organic	Water	Micro	13.5	Woodland rides	acid & sedge peats	Gen
Eristalis tenax	Eristen	Wet/ Organic	Water	Micro	15	Various	Rich flower resource	Open
Eumerus strigatus	Eumstrig	Herbs	Roots	Various	7	Wetlands, wider countryside	tall sward & scrub	Open
Eupeodes corollae	Eupcor	Various	Ground Surface	Animal	8	Fields, meadows, verges, hedges, heaths, gardens, waste ground	tall sward & scrub	Open
Eupeodes latifasiatus	Euplat	Litter/ Roots	Various	Animal	8	Wet meadows, rushes	tall sward & scrub	Gen
Eupeodes luniger	Euplun	Herbs	Ground Surface	Animal	9.5	Fields, meadows, verges, hedges, heaths, gardens, waste ground	short sward & bare ground, tall sward & scrub	Open
Ferdinandea cuprea	Ferdcup	Trees	Roots	Micro	9.5	Woodland	Decaying Wood	Wood
Helophilus spp.	Helosp	Wet/ Organic	Water	Micro	12	Near pond/ditch margins	acid & sedge peats	Open
Leucozona lucorum	Lucluc	Herbs	Ground Surface	Animal	11	Damp woodland rides and margins	Shaded woodland floor	Wood
Melanostoma mellinum	Melmel	Herbs	Ground Surface	Various	6	Grassland	tall sward & scrub	Open
Melanostoma scalare	Melscal	Litter/ Roots (forest)	Ground Surface	Various	8	Herbs beside scrub or woodland	tall sward & scrub	Gen
Meliscaeva cinctella	Melicinc	Trees	Ground Surface	Animal	10	Trees and bushes	Arboreal	Wood
Myathropa florea	Myaflor	Various	Various	Micro	12	Woodland	Decaying Wood	Wood

Name	Short name	Larval Activity Zone	Hibernation/ Overwinter-ing zone	Larval Food	Body length (median)	Adult Habitat Description	Pantheon Category	Habitat Category
Neoascia obliqua	Neoobli	Various	Water	Micro	5.5	Stands of butterbur	acid & sedge peats	Open
Neoascia podogaria	Neopoda	Various	Various	Micro	5.5	Hedgerows, Woodland Edge, Gardens		Gen
Platycheirus albimanus	Platalb	Various	Ground Surface	Animal	8.5	Woodland margins, hedgerows, gardens	acid & sedge peats; marshland	Gen
Platycheirus granditarsus	Platgrand	Litter/ Roots	Ground Surface	Animal	9	Marshy meadows by ditches and lakes	acid & sedge peats; marshland	Open
Platycheirus peltatus.nielseni	Platpelt	Herbs	Various	Animal	9.5	Lowland grasslands	tall sward & scrub	Gen
Platycheirus rosarum	Platrosa	Litter/ Roots	Ground Surface	Animal	9	Marshy meadows by ditches and lakes	acid & sedge peats; marshland; shaded woodland floor; wet woodland	Open
Rhingia campestris	Rhincamp	Wet/ Organic	Various	Micro	9.5	Open woodland/woodland edges/hedgerows	tall sward & scrub	Gen
Scaeva pyrasti	Scapyr	Various	Above Ground	Animal	12.5	Gardens, waste ground, meadows	tall sward & scrub	Open
Sericomyia silentis	Serisil	Wet/ Organic	Water	Micro	16	Heaths, wet grassland, Woodland clearings	acid & sedge peats	Gen
Sphaerophoria spp.	Sphascri	Herbs	Ground Surface	Animal	10	Grasslands and waste ground	tall sward & scrub	Open
Syritta pipiens	Syripip	Various	Various	Micro	8	Urban areas, rough meadows, hedgerows and marshy areas	tall sward & scrub	Open
Syrphus spp.	Syrphus	Trees	Ground Surface	Animal	11.5	Various	Arboreal (S. vitripennis)	Gen
Volucella bombylans	Volbomb	Nests	Various	Animal	14.5	Wooded areas, scrubby grassland	tall sward & scrub	Gen

Name	Short name	Larval Activity Zone	Hibernation/ Overwinter-ing zone	Larval Food	Body length (median)	Adult Habitat Description	Pantheon Category	Habitat Category
Volucella pellucens	Volpell	Nests	Various	Various	16.5	Woodland glades/near trees	Shaded woodland floor	Wood
Xanthandrus comtus	Xancom	Trees	Various	Animal	10.5	Meadows and scrub/woodland edges	Arboreal	Wood
Xylota segenis	Xylseg	Trees	Various	Micro	11	Woods & Hedgerows	Decaying Wood	Wood
Xylota sylvarum	Xylsylv	Trees	Various	Micro	14	Woods/Woodland edges	Decaying Wood	Wood

Table B3 Bee Trait and Habitat Data Collated based on the information in references cited below. As *Bombus terrestris* and *Bombus lucorum* workers cannot be reliably distinguished morphologically we used the average ITD and the earliest flight month in our analysis, with other traits being the same.

Name	Short Name	ITD (mm)	Nesting Location	Diet Breadth	Sociality	Tongue Length	Pantheon Wood/Woodland Category	Habitat preference	Habitat Category
Andrena bicolor	Abic	2.13	Soil	Polylectic	Solitary	short	Short sward & bare ground	Open habitats, excl. woodland interior	Open
Andrena cineraria	Acin	2.83	Soil	Polylectic	Solitary	short	Short sward & bare ground	Open habitats incl. open woodland	Gen
Andrena clarkella	Aclar	3.1	Soil	Oligolectic	Solitary	short	Short sward & bare ground	Willow scrub	Gen
Andrena fucata	Afuc	2.45	Soil	Polylectic	Solitary	short	Shaded woodland Floor	Woodland clearings & scrub	Wood
Andrena haemorrhoa	Ahae	2.65	Soil	Polylectic	Solitary	short	Short sward & bare ground	Wide variety	Gen
Andrena minutula	Amin	1.43	Soil	Polylectic	Solitary	short	Short sward & bare ground	Open habitats & wooded	Gen
Andrena praecox	Apra	2.26	Soil	Oligolectic	Solitary	short	Short sward & bare ground	Willow scrub	Gen
Andrena scotica	Asco	2.73	Soil	Polylectic	Solitary	short	Short sward & bare ground	Open habitats & wooded	Gen
Andrena subopaca	Asub	1.49	Soil	Polylectic	Solitary	short	Short sward & bare ground	Woodland openings & uplands	Gen
Andrena wilkella	Awil	2.32	Soil	Oligolectic	Solitary	short	Short sward & bare ground	Open habitats, grasslands, open woodland	Gen
Bombus bohemicus	Bboh	NA	Parasite	Polylectic	Social Parasite	long	Shaded woodland Floor	More frequent in upland acid habitats	Wood

Name	Short Name	ITD (mm)	Nesting Location	Diet Breadth	Sociality	Tongue Length	Pantheon Wood/Woodland Category	Habitat preference	Habitat Category
Bombus hortorum	Bhor	5.31	Soil	Polylectic	Social	Long	tall sward and scrub	Open habitats	Open
Bombus jonellus	Bjon	4.62	Soil	Polylectic	Social	Long	n/a	Open habitats, heath	Open
Bombus lapidarius	Blap	4.9	Soil	Polylectic	Social	Long	tall sward and scrub	Open habitats	Open
Bombus lucorum agg	Bluc	5.075	Soil	Polylectic	Social	Long	tall sward and scrub	Open habitats	Open
Bombus pascuorum	Bpas	4.45	Soil	Polylectic	Social	Long	tall sward and scrub	Open habitats	Open
Bombus pratorum	Bpra	4.61	Soil	Polylectic	Social	Long	Shaded woodland floor/ tall sward and scrub	Common in woods & wherever bramble	Gen
Bombus sylvestris	Bsyl	4.27	Parasite	Polylectic	Social Parasite	Long	Shaded woodland Floor	More common in woods	Wood
Halictus rubicundus	Hrub	2.18	Soil	Polylectic	Solitary*	short	Short sward & bare ground	Open habitats	Open
Halictus tumulorum	Htum	1.49	Soil	Polylectic	Solitary*	short	Short sward & bare ground	Open habitats	Open
Hylaeus confusus	Hcon	1.39	Cavity	Polylectic	Solitary	short	Decaying Wood	More frequent in woods	Wood
Lasioglossum albipes	Lalp	1.64	Soil	Polylectic	Solitary*	short	Short sward & bare ground	Open habitats	Open
Lasioglossum calceatum	Lcal	1.82	Soil	Polylectic	Solitary*	short	Short sward & bare ground	Open habitats	Open
Lasioglossum fratellum	Lfrit	1.51	Soil	Polylectic	Solitary*	short	Short sward & bare ground	Heath, acid woods	Gen
Lasioglossum villosulum	Lvil	1.33	Soil	Polylectic	Solitary*	short	Short sward & bare ground	Open habitats	Open

Name	Short Name	ITD (mm)	Nesting Location	Diet Breadth	Sociality	Tongue Length	Pantheon Wood/Woodland Category	Habitat preference	Habitat Category
Nomada fabriciana	Nfab	1.58	Parasite	Polylectic	Cleptoparasite	long	Short sward & bare ground	Open & wooded habitats	Gen
Nomada leucophthalma	Nleu	2	Parasite	Polylectic	Cleptoparasite	long	Short sward & bare ground	Open habitats	Open
Nomada marshamella	Nmar	2	Parasite	Polylectic	Cleptoparasite	long	Short sward & bare ground	Open habitats, more frequent in woods	Gen
Nomada panzeri	Npan	1.64	Parasite	Polylectic	Cleptoparasite	long	Short sward & bare ground	Thrives in coppice	Gen
Nomada ruficornis	Nruf	1.81	Parasite	Polylectic	Cleptoparasite	long	Short sward & bare ground	Open habitats incl. open woodland	Gen
Osmia bicornis	Obic	3.14	Cavity	Polylectic	Solitary	long	Shaded woodland floor/ tall sward and scrub	Wide variety	Gen
Sphecodes epihippus	Sepi	1.45	Parasite	Polylectic	Cleptoparasite	short	Short sward & bare ground	Open habitats	Open

*A number of sources refer to these as social bees as they exhibit social polymorphism and may be primitively eusocial or communal, however this tends to be associated with more southerly distributed populations.

Sources:

Bommarco et al.(2010) – ITD, Diet Breath, Sociality; Fortel et al. (2014) – ITD, Sociality, Tongue Length; Greenop et al. (2021) -Tongue Length; Steinert et al.(2020) – ITD, Nesting Preference; Falk (2015) – ITD, Nesting Preference, Diet Breath, Habitat Preference; Redhead et al. (2020) – Diet Breath, Sociality; Carrié et al. (2017) – Tongue Length.

Table B4 Kruskal Wallis (KW) Tests and Dunn Tests (DT) comparing species abundance and richness for pollinator groups and flora across woodland stages and survey rounds. Est = Estimate. DT's carried out where KW test had p values <0.1 (bold font). Shorthand as follows: HF = Hoverflies, B = Bees, BB = Bumblebees, SB = Solitary Bees, Clep = Cleptoparasites; Open = Open habitat specialist, Gen = Generalists, Wood = Woodland habitat specialists, T = Transects, P = Pan Traps.

WOODLAND STAGES								
Variable	**KW**		**DT: Open v Thicket**		**DT: Open v Closed**		**DT: Thicket v Closed**	
	Est	**p value**	**Est**	**p value**	**Est**	**p value**	**Est**	**p value**
Abundance								
HF	4.538	0.1	-	-	-	-	-	-
B	2.781	0.25	-	-	-	-	-	-
BB	3.956	0.14	-	-	-	-	-	-
SB	0.589	0.74	-	-	-	-	-	-
HF Gen	0.504	0.777	-	-	-	-	-	-
HF Open	13.398	**≤0.001**	2.301	**0.032**	3.616	**≤0.001**	-1.315	0.283
HF Wood	0.657	0.72	-	-	-	-	-	-
B Gen	0.738	0.691	-	-	-	-	-	-
B Open	4.616	**0.099**	0.732	0.696	-2.115	0.0516	-1.38	0.249
B Wood	1.062	0.588	-	-	-	-	-	-
Richness								
HF	3.664	0.16	-	-	-	-	-	-
B	2.049	0.36	-	-	-	-	-	-
BB	4.619	0.1	-	-	-	-	-	-
SB	0.719	0.7	-	-	-	-	-	-
BB excl. Clep	3.494	0.174	-	-	-	-	-	-
SB excl. Clep	2.493	0.287	-	-	-	-	-	-
Clep	4.911	**0.086**	-0.929	0.529	2.207	**0.041**	1.278	0.302
HF Gen	1.92	0.38	-	-	-	-	-	-
HF Open	8.218	**0.016**	2.214	**0.040**	-2.684	**0.011**	-0.470	0.957
HF Wood	1.423	0.491	-	-	-	-	-	-
B Gen	1.450	0.473	-	-	-	-	-	-
B Open	3.423	0.181	-	-	-	-	-	-
B Wood	0.439	0.803	-	-	-	-	-	-
Flora								
Floral Richness	9.050	**0.01**	1.585	0.169	-3.007	**0.004**	-1.421	0.233
Floral Area	8.456	**0.01**	2.433	**0.022**	-2.595	**0.014**	-0.162	1
SURVEY ROUNDS								
Variable	**KW**		**DT: Round 1v2**		**DT: Round 1v3**		**DT: Round 2v3**	
	Est	**p value**	**Est**	**p value**	**Est**	**p value**	**Est**	**p value**
SB	24.807	**≤0.001**	3.947	**≤0.001**	4.604	**≤0.001**	0.657	0.767
BB	19.776	**≤0.001**	-1.408	0.239	-4.357	**≤0.001**	-2.949	**0.005**
HF	9.007	**0.011**	-0.464	0.964	-2.800	**0.007**	-2.336	0.029
T-Richness	2.846	0.241		-	-	-	-	-
P-Richness	19.845	**≤0.001**	2.979	**0.004**	-1.380	0.251	-4.358	**≤0.001**
T-Abundance	4.287	0.117	-	-	-	-	-	-
P-Abundance	21.964	**≤0.001**	4.163	**≤0.001**	0.218	1	-3.945	**≤0.001**

Table B5 Model Estimates for best-fitting models. HF = Hoverfly, B = All Bees, BB = Bumblebees, SB = Solitary Bees. Positive estimates indicate higher numbers e.g. higher insect counts, and vice versa for negative estimates. Incidence Rate Ratios (IRR's) describe how the rate of the outcome changes with a one-unit increase in the predictor variable, with values greater than 1 indicating an increased rate of the outcome, and below one indicating a decreased rate. p-values (to test the null hypothesis that the coefficient estimate is equal to zero, i.e. no effect) were calculated from z-values, the ratio between the estimated coefficient and the standard error of the estimate (estimate/SE). Large z-values show that the estimate is large (in relation to its SE) and significantly different from zero. In some cases random effects variance was close to zero, however the random effect was retained in the model to ensure samples from the same site were not treated as independent in the model.

Model	Variable Name	Model Estimate	±SE	IRR	Confidence Interval	Z	p value	Moran's I (p value) Note 1	Random Effects Note 2	R^2 Note 3
					ABUNDANCE					
HF	(Intercept)	3.003	0.166	20.15	14.54 – 27.92	18.04	<0.001	-0.0588	σ^2 0.24	Marginal R^2 0.544
	Transect Location - Centre	-0.402	0.181	1	1.00 – 1.00	3.88	<0.001	(0.739)	$\tau_{00\ Code}$ 0	Conditional R^2 NA
	Floral Area	0.002	0.0005	0.67	0.47 – 0.95	-2.22	0.026		ICC NA	
	Improved Grassland (Landscape)	-0.465	0.184	0.63	0.44 – 0.90	-2.53	0.011		N_{Code} 18	
B	(Intercept)	1.8230	0.330	6.23	3.26 – 11.90	5.545	<0.001	-0.192	σ^2 0.24	Marginal R^2 0.537
	Transect Location - Centre	-0.881	0.200	0.41	0.28 – 0.61	-4.403	<0.001	(0.228)	$\tau_{00\ Code}$ 0.15	Conditional R^2
	Floral Area	0.002	0.001	1	1.00 – 1.00	2.147	0.032		ICC 0.29	0.718
	Wood Area	0.106	0.043	1.11	1.02 – 1.21	2.433	0.015		N_{Code} 18	
BB	(Intercept)	1.468	0.3598	4.34	2.15 – 8.78	4.08	<0.001	-0.059	σ^2 0.34	Marginal R^2 0.559
	Transect Location - Centre	-0.719	0.245	0.49	0.30 – 0.79	-2.94	0.003	(0.265)	$\tau_{00\ Code}$ 0.00	Conditional R^2 NA
	Floral Richness	0.065	0.027	1.07	1.01 – 1.13	2.39	0.017		ICC NA	
	Wood Area	0.088	0.036	1.09	1.02 – 1.17	2.47	0.013		N_{Code} 18	
SB	(Intercept)	0.283	0.792	1.33	0.28 – 6.26	0.36	0.721	-0.136	σ^2 1.16	Marginal R^2 0.693
	Age	0.034	0.095	1.03	0.86 – 1.25	0.35	0.724	(0.476)	$\tau_{00\ Code}$ 0.01	Conditional R^2
	Transect Location - Centre	0.872	1.298	2.39	0.19 – 30.49	0.67	0.502		ICC 0.01	0.696
	Age x Transect Location	-0.323	0.163	0.72	0.53 – 1.00	-1.98	0.048		N_{Code} 18	
	Age	-0.286	0.143	0.75	0.53 – 0.95	-2.006	0.045			
					RICHNESS					
HF	(Intercept)	2.429	0.149	11.34	8.48 – 15.18	16.34	<0.001	0.0047	σ^2 0.11	Marginal R^2 0.566

Model	Variable Name	Model Estimate	±SE	IRR	Confidence Interval	Z	p value	Moran's I (p value) Note 1	Random Effects Note 2	R^2 Note 3
	Age	-0.005	0.013	1	0.97 – 1.02	-0.35	0.726	(0.563)	$\tau_{00\ Code}$ 0	Conditional R^2 NA
	Transect Location - Centre	0.128	0.227	1.14	0.73 – 1.77	0.57	0.571		ICC NA	
	Age x Transect Location	-0.065	0.023	0.94	0.90 – 0.98	-2.87	0.004		N_{Code} 18	
B	(Intercept)	2.04	0.181	7.76	5.44 – 11.07	11.302	<0.001	-0.126,	σ^2 0.16	Marginal R^2 0.473
	Age	-0.007	0.016	0.99	0.96 – 1.03	-0.449	0.654	(0.532)	$\tau_{00\ Code}$ 0	Conditional R^2 NA
	Transect Location - Centre	0.035	0.281	1.04	0.60 – 1.80	0.124	0.902		ICC NA	
	Age x Transect Location	-0.059	0.028	0.94	0.89 – 1.00	-2.100	0.036		N_{Code} 18	
BB Note 4	(Intercept)	**0.547**	**0.220**	1.73	1.12 – 2.66	2.49	0.013	-0.145	σ^2 0.27	Marginal R^2 0.268
	Floral Richness	**0.067**	**0.019**	1.07	1.03 – 1.11	3.46	0.001	(0.420)	$\tau_{00\ Code}$ 0	Conditional R^2 NA
									ICC NA	
									N_{Code} 18	
SB	(Intercept)	1.153	0.133	3.17	2.44 – 4.11	8.703	<0.001	-0.115	σ^2 0.33	Marginal R^2 0.156
	Transect Location - Centre	-0.488	0.215	0.61	0.40 – 0.94	-2.271	0.023	(0.605)	$\tau_{00\ Code}$ 0	Conditional R^2 NA
	Age	-0.072	0.036	0.93	0.86 – 1.00	-1.986	0.047		ICC NA	
									N_{Code} 18	

Note 1: Moran's I. Moran's I measures spatial autocorrelation. Significant spatial autocorrelation in the residuals indicates that a spatial process might be influencing the outcome, which is not accounted for by the predictors. There was no significant spatial autocorrelation for any model scenario.

Note 2: Random Effects. σ^2 (Residual Variance) = unexplained variance after accounting for both fixed and random effects in the model. τ_{00} = variance of the random intercepts associated with the grouping factor *Site*. **ICC** = the proportion of the total variance explained by the grouping factor *Site*. **N** = number of unique levels in the grouping factor *Site*.

Note 3: R^2. Marginal R^2 = portion of variance explained by the fixed effects. Conditional R^2 = portion of variance explained by both fixed and random effects combined.

Note 4: Bumblebee Richness Model. The observed species richness of bumblebees exhibited a relatively flat distribution. A test for dispersion indicated significant underdispersion in the model (residual variance lower than expected under the Poisson assumption). This suggests that standard errors and p-values may be underestimated, potentially inflating the apparent significance of predictor variables. While the model fit was otherwise acceptable, results should be interpreted with caution due to this deviation from the Poisson assumptions. Other model distributions were explored but underdispersion remained.

Table B6 PERMANOVA results from Adonis and PairwiseAdonis tests. R^2 represents the proportion of variance explained by the grouping factor. The (pseudo) F value (with degrees of freedom in subscript) is the ratio of the between-group variance to the within-group variance with larger values corresponding to larger proportional importance of the grouping factor.

	Adonis	**Pairwise Adonis**		
Community	**Overall Difference**	**Open v Closed**	**Thicket V Closed**	**Open V Thicket**
Pans & Transects (Jaccard) – Presence/Absence				
Hoverflies	R^2 = 0.09897	R^2 = 0.09024	R^2 = 0.0459	R^2 = 0.08734
	F_2= 0.8238	F_1= 0.9919	F_1= 0.4887	F_1= 0.957
	p = 0.799	p = 0.448	p = 0.977	p = 0.52
Bees	R^2 = 0.14473	R^2 = 0.14125	R^2 = 0.09356	R^2 = 0.09809
	F_2= 1.2692	F_1= 1.6449	F_1= 1.0321	F_1= 1.0876
	p = 0.156	p = 0.064	p = 0.4	p = 0.393
Flora	R^2 = 0.15421	R^2 = 0.1634	R^2 = 0.10687	R^2 = 0.08786
	F_2= 1.3675	F_1= 1.9532	F_1= 1.1966	F_1= 0.9633
	p = 0.038	**p = 0.008**	p = 0.204	p = 0.492
Transects (Bray) – Abundance for insects and Area for Flora				
Hoverflies	R^2 = 0.23154	R^2 = 0.21486	R^2 = 0.10391	R^2 = 0.22479
	F_2= 2.2598	F_1= 2.7366	F_1= 1.1596	F_1= 2.8997
	p = 0.004	**p = 0.007**	p = 0.354	**p = 0.006**
Bees	R^2 = 0.11571	R^2 = 0.0968	R^2 = 0.11876	R^2 = 0.05464
	F_2= 0.9813	F_1= 1.0718	F_1= 1.3476	F_1= 0.578
	p = 0.429	p = 0.42	p = 0.273	p = 0.655
Flora	R^2 = 0.17224	R^2 = 0.19614	R^2 = 0.12056	R^2 = 0.07927
	F_2= 1.5606	F_1= 2.44	F_1= 1.3709	F_1= 0.861
	p = 0.06	**p = 0.008**	p = 0.198	p = 0.598

Table B7 Beta Diversity Mantel Correlations with Age

Community	**Overall Beta Diversity βsor**	**Turnover βsim**	**Nestedness βsne**	**Spatial Distance**
Hoverflies	r = 0.2355	r = 0.04864	r = 0.1613	r = -0.0904
	p = 0.0116	p = 0.3105	p = 0.0729	p = 0.839
Bees	r = 0.3483	r = 0.2916	r = 0.1404	r = -0.0149
	p = 0.0015	**p = 0.0041**	p = 0.0999	p = 0.596
Flora	r = 0.1513	r = -0.07406	r = 0.3009	r = 0.0636
	p = 0.0738	p = 0.761	**p = 0.0052**	p = 0.206

Table B8 Beta Diversity PERMANOVA. R^2 represents the proportion of variance explained by the grouping factor. The (pseudo) F value is the ratio of the between-group variance to the within-group variance with larger values corresponding to larger proportional importance of the grouping factor. Shorthand: O = Open, T = Thicket, C = Closed.

Community	Overall Beta Diversity	Adonis	Pairwise Adonis CvO	Pairwise Adonis CvT	Pairwise Adonis OvT
All Bees					
Overall Beta	0.817917	R^2 = 0.17012	R^2= 0.18163	R^2= 0.10043	R^2= 0.10424
Diversity		F = 1.5374	F = 2.2195	F = 1.1164	F = 1.1637
βsor		p = 0.072	**p = 0.026**	p = 0.375	p = 0.365
Turnover	0.7534517	R^2= 0.15983	R^2= 0.23946	R^2= 0.04327	R^2= 0.07979
βsim		F = 1.4267	F = 3.1485	F = 0.4523	F = 0.8671
		p = 0.195	**p = 0.016**	p = 0.796	p = 0.581
Nestedness	0.06446529	R^2= 0.04487	R^2= 0.02909	R^2= 0.04821	R^2= 0.02155
βsne		F = 0.3523	F = 0.2997	F = 0.5065	F = 0.2203
		p = 0.657	p = 0.594	p = 0.492	p = 0.665
All Hoverflies					
Overall Beta	0.8210188	R^2= 0.16301	R^2= 0.10796	R^2= 0.1057	R^2= 0.1749
Diversity		F = 1.4607	F = 1.2102	F = 1.1819	F = 2.1579
βsor		p = 0.101	p = 0.322	p = 0.308	**p = 0.03**
Turnover	0.7556391	R^2= 0.14459	R^2= 0.04943	R^2= 0.10407	R^2= 0.18338
βsim		F = 1.2677	F = 0.52	F = 1.1616	F = 2.2455
		p = 0.305	p = 0.725	p = 0.423	p = 0.06
Nestedness	0.06537972	R^2= 0.1908	R^2= 0.23001	R^2= -0.01137	R^2= 0.27343
βsne		F = 1.7684	F = 2.9872	F = -0.1124	F = 3.7633
		p = 0.252	p = 0.146	p = 0.749	p = 0.1
Flora					
Overall Beta	0.8874399	R^2= 0.12138	R^2= 0.13213	R^2= 0.08816	R^2= 0.05801
Diversity		F = 1.0361	F = 1.5224	F = 0.9669	F = 0.6159
βsor		p = 0.473	p = 0.113	p = 0.56	p = 0.821
Turnover	0. 8413926	R^2= 0.08595	R^2= 0.09351	R^2= 0.0719	R^2= 0.03133
βsim		F = 0.7053	F = 1.0316	F = 0.7747	F = 0.3234
		p = 0.754	p = 0.48	p = 0.682	p = 0.89
Nestedness	0.0460473	R^2= 0.26504	R^2= 0.23309	R^2= 0.09725	R^2= 0.36537
βsne		F = 2.7046	F = 3.0394	F = 1.0773	F = 5.7572
		p = 0.151	p = 0.153	p = 0.426	p = 0.096

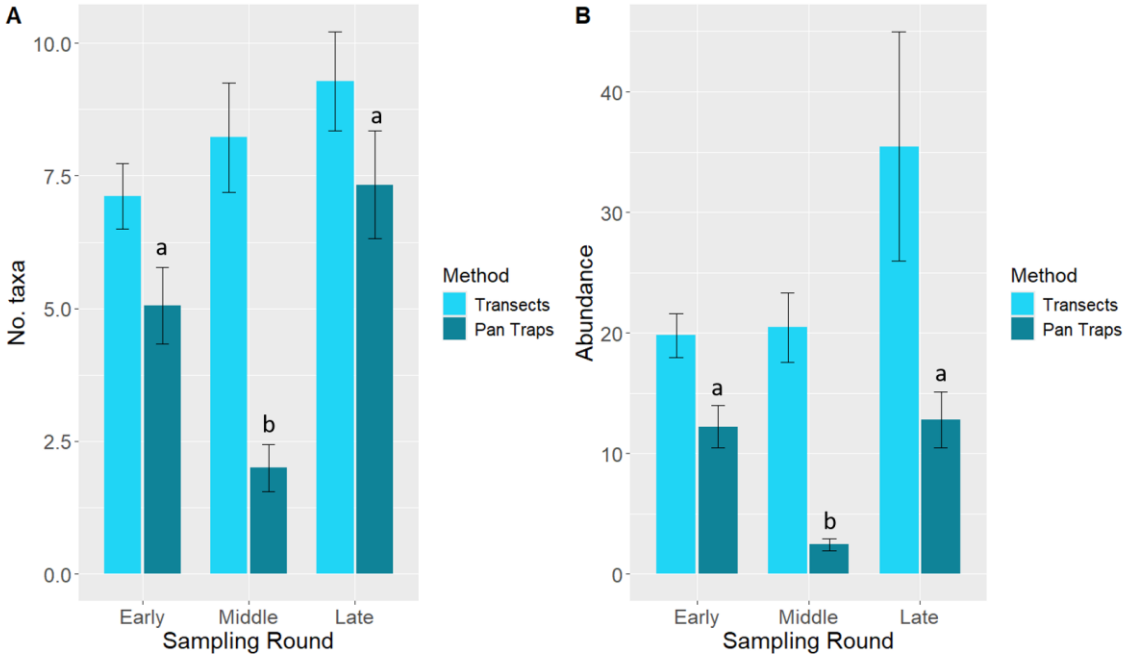

Figure B1 Mean (±SE) of overall Bee and Hoverfly (A) Richness and (B) Abundance from Pan Trap and Transect surveys. Letters indicate significant differences between stages tested with Kruskal-Wallis (K-W) tests followed by Dunn's tests (Table S4).

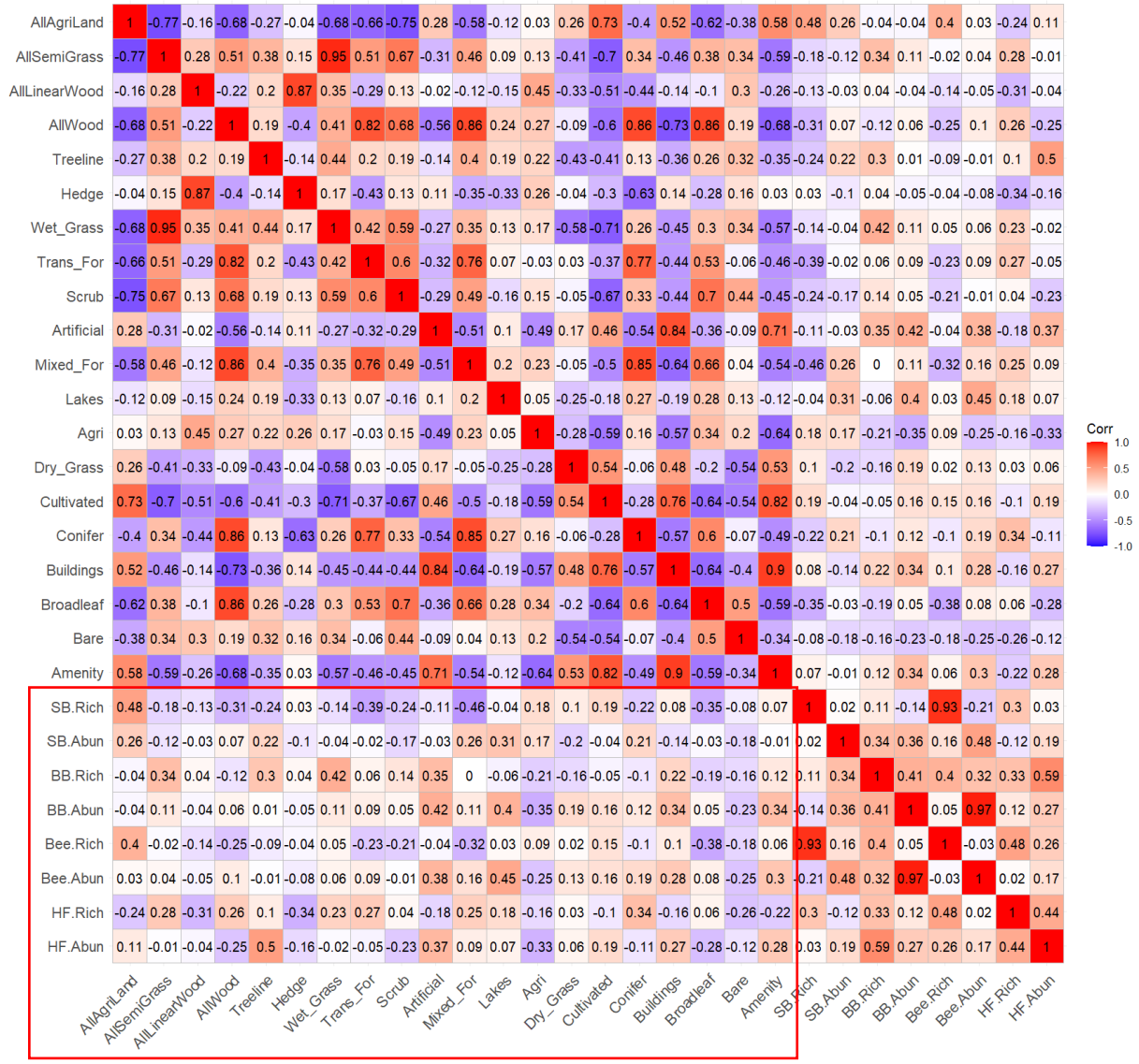

Figure B2 Correlation Matrix including Bee/Hoverfly Abundance and Richness together with Landscape Composition Metrics Spearman rank correlation (R) values shown. The red box highlights the pollinator group correlations with landscape variables. Correlations are shown for Richness (Rich) and Abundance (Abun) of All Bees (Bee), Solitary Bees (SB), Bumblebees (BB), and Hoverflies (HF). Landscape Composition (m^2 'Level 2' habitat in a 2km matrix surrounding the site was calculated from the National Landcover Map (EPA & Tailite Éireann, 2024)) metrics are shown for Conifer Forest (Conifer), Broadleaf Forest (Broadleaf), Transitional Forest (Trans_For), Mixed Forest (Mixed_For), Scrub, Wet Grassland (Wet_Grass), Dry Grassland (Dry_Grass), Improved Grassland (Agri), Cultivated Grassland (Cultivated), Bare Ground (Bare), Lakes, Artificial Surfaces (Artificial), Buildings, Amenity Lands (Amenity), Treelines and Hedgerow. We also calculated the combined extent of habitats within the following broader groupings: all forest/woodland habitats (AllWood), all semi-natural grassland habitats (AllSemiGrass), all agricultural grasslands (AllAgriLand) and all linear boundary habitats (AllLinearWood).

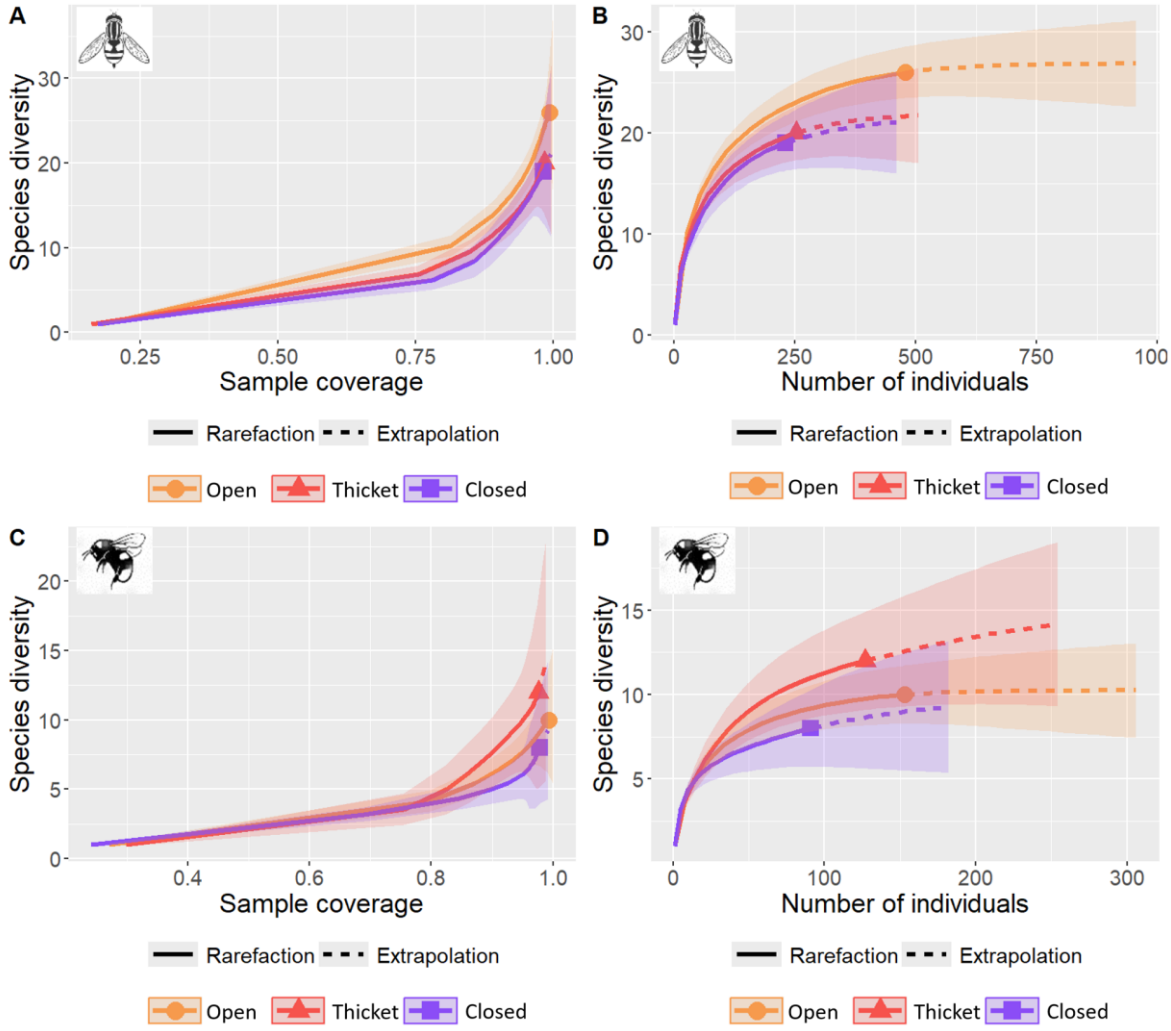

Figure B3 Richness-based sample coverage curves and species accumulation curves for hoverflies and bees

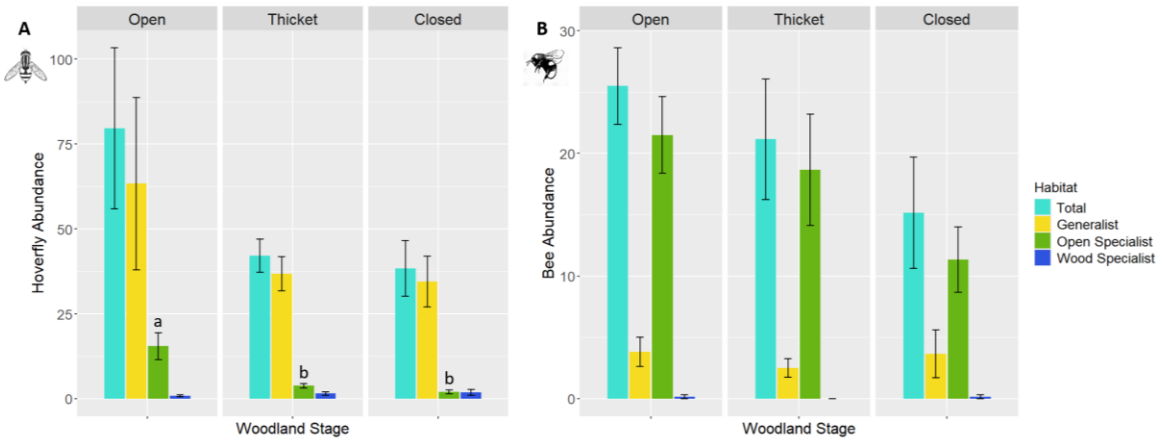

Figure B4 Mean (±SE) of (A) Hoverfly and (B) Bee (Solitary and Bumblebee) Abundance across Woodland Stages (Open, Thicket and Closed). Letters over a bar indicate significant differences between stages for that attribute tested with Kruskal-Wallis (K-W) tests followed by Dunn's tests (Table B4).

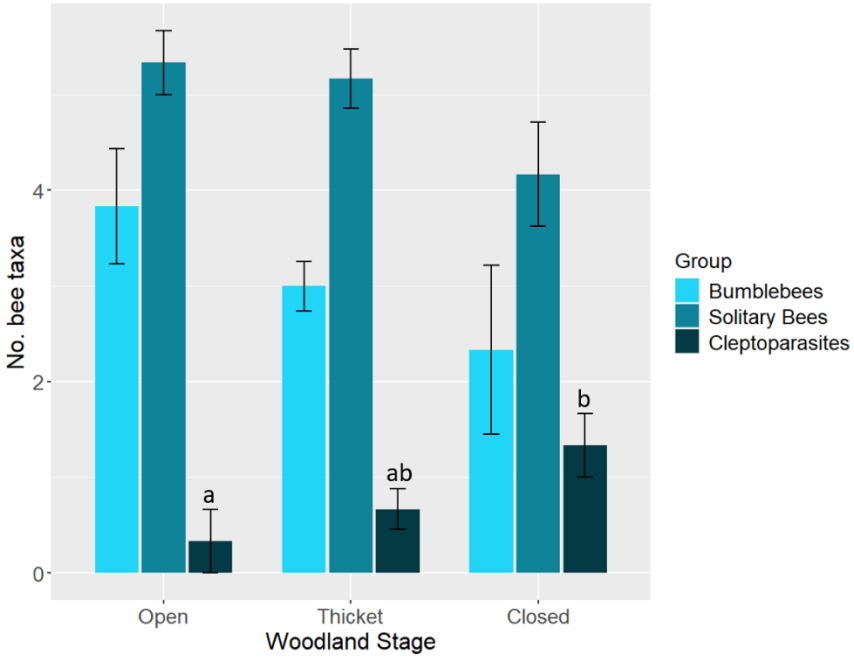

Figure B5 Mean (±SE) Bumblebee, Solitary Bee and Cleptoparasite Richness across Woodland Stages (Open, Thicket and Closed). Letters over a bar indicate significant differences between stages for that attribute tested with Kruskal-Wallis (K-W) tests followed by Dunn's tests (Table S4).

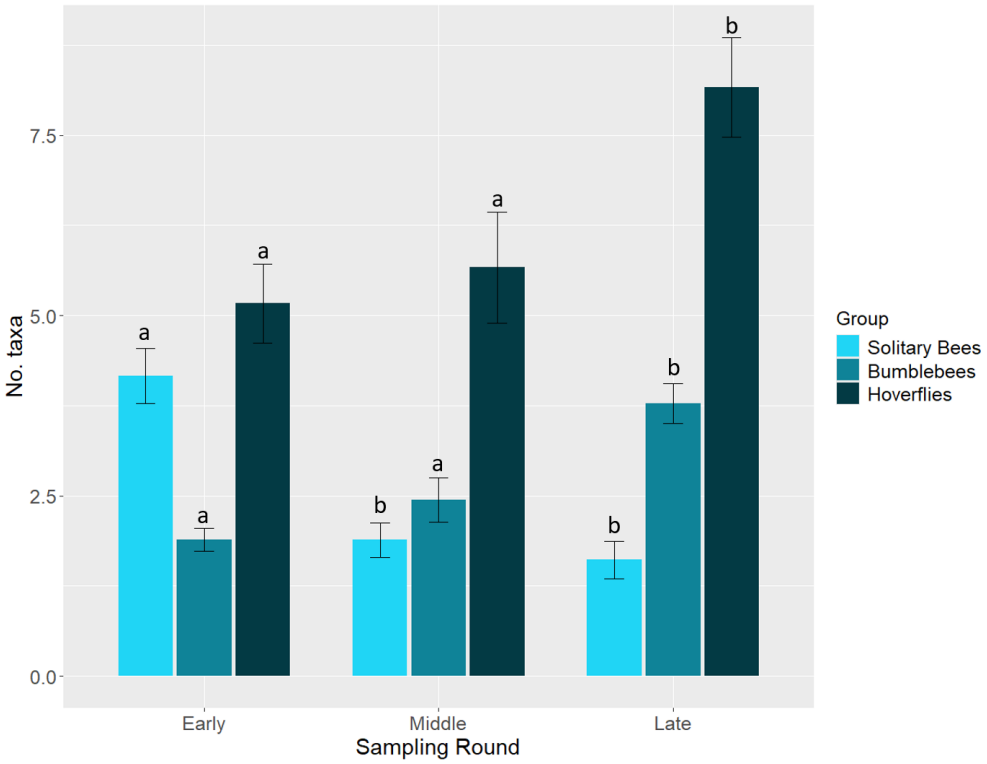

Figure B6 Mean (±SE) Hoverfly, Bumblebee and Solitary Richness recorded in each sampling round. Letters over a bar indicate significant differences between rounds for that attribute tested with Kruskal-Wallis (K-W) tests followed by Dunn's tests (Table S4).

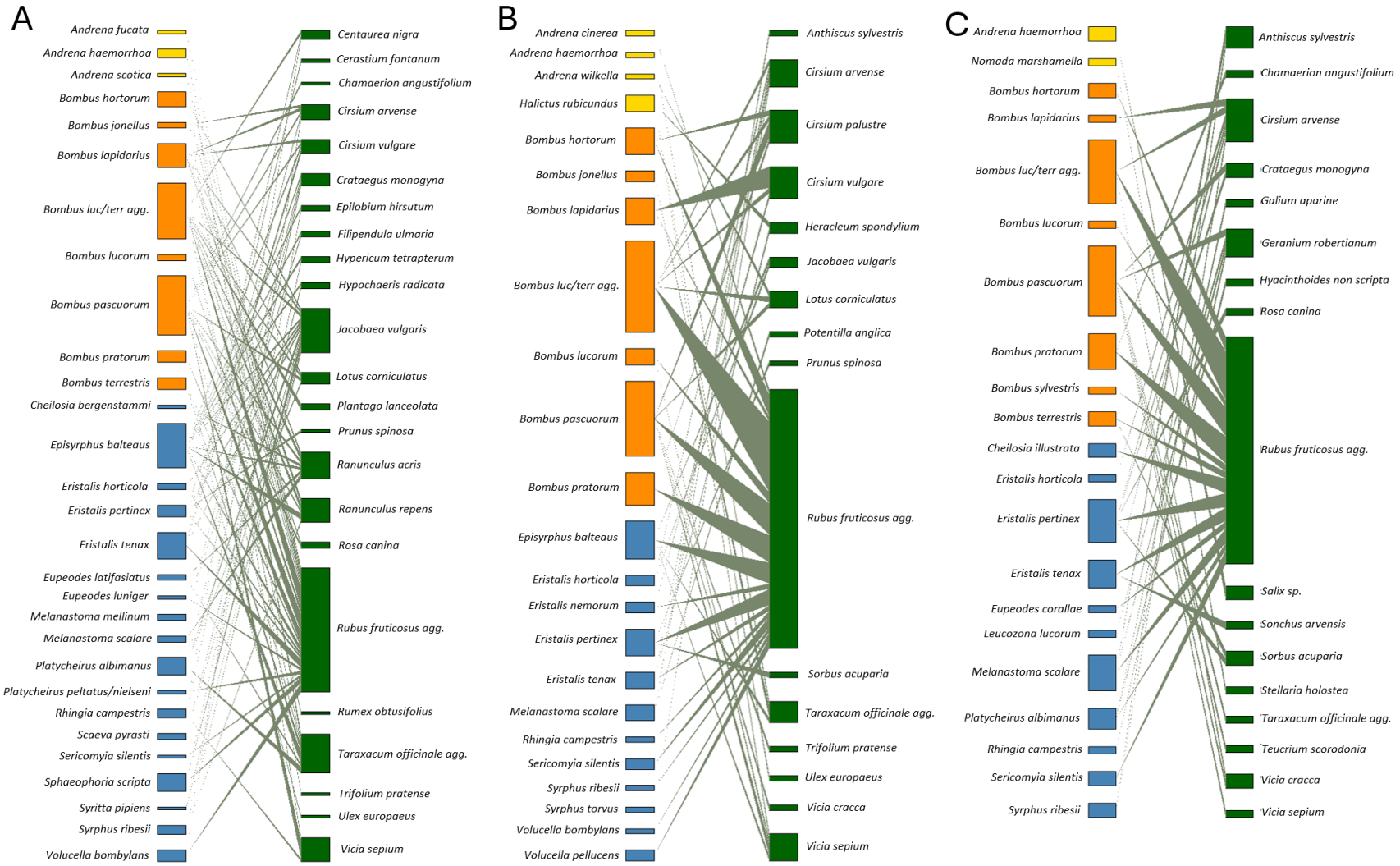

Figure B7 Pollinator networks for (A) open, (B) thicket and (C) closed stage woodland sites. Yellow = Solitary Bees, Orange = Bumblebees, Blue = Hoverflies. Network specialisation (H2) scores were (a) 0.202, (b) 0.321 and (c) 0.229

Appendix B References

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Appendix C - Supplementary Data for Chapter 4

Table C1 Spearman Correlations ($r_s \geq 0.3$) for NFI variables. Those with $r_s \geq 0.7$ were excluded from modelling analysis.

Positive Correlations			Negative Correlations		
Variable 1	**Variable 2**	**r_s**	**Variable 1**	**Variable 2**	**r_s**
Conifer	Trans_For	0.751	SoilDepth	PeatDepth	-0.736
Hedge	Imp_Grass	0.716	mean_dbh	No. Trees	-0.637
sd_dbh	large_tree_count	0.686	Cultivated	Blanket_Bog	-0.636
Dry_Heath	Wet_Heath	0.685	Imp_Grass	Blanket_Bog	-0.627
Cutover_Bog	Raised_Bog	0.622	Cultivated	Wet_Heath	-0.592
Hedge	Urban	0.621	Imp_Grass	Wet_Heath	-0.571
Imp_Grass	Urban	0.620	Dry_Heath	Imp_Grass	-0.558
Imp_Grass	Treelines	0.617	Trans_For	Urban	-0.554
Bare_Peat	Raised_Bog	0.601	Cultivated	Dry_Heath	-0.522
Dry_Heath	Blanket_Bog	0.596	Imp_Grass	Trans_For	-0.510
Cultivated	Imp_Grass	0.596	Wet_Heath	Urban	-0.502
Altitude	Conifer	0.592	Trans_For	Treelines	-0.496
Treelines	Urban	0.591	Blanket_Bog	Urban	-0.490
Age	sd_dbh	0.581	Treelines	Blanket_Bog	-0.474
Altitude	Trans_For	0.576	Dry_Heath	Urban	-0.469
Age	large_tree_count	0.576	Hedge	Blanket_Bog	-0.466
Hedge	Treelines	0.571	Dry_Heath	Hedge	-0.465
Broadleaf	Mixed_For	0.559	Hedge	Trans_For	-0.461
Cultivated	Urban	0.555	Conifer	Urban	-0.453
Bare_Peat	Cutover_Bog	0.553	Dry_Heath	Treelines	-0.453
Blanket_Bog	Wet_Heath	0.547	Cultivated	Wet_Grass	-0.447
Mean_dbh	Basal Area	0.527	Treelines	Wet_Heath	-0.446
Broadleaf	Treelines	0.522	Cultivated	Trans_For	-0.432
Deadwood Logs	Deadwood Stumps	0.491	Broadleaf	Trans_For	-0.425
No. Tree Species	Broadleaf	0.447	Altitude	Broadleaf	-0.409
PeatDepth	Bare_Peat	0.445	Hedge	Wet_Heath	-0.405
Cultivated	Treelines	0.436	Altitude	Rivers	-0.404
Bracken	Wet_Heath	0.432	Altitude	Urban	-0.398
Age	No. Tree Species	0.421	Broadleaf	Conifer	-0.393
Bracken	Dry_Heath	0.418	NatRegenTrees	mean_dbh	-0.388
Trans_For	Wet_Heath	0.411	No. Tree Species	Conifer	-0.378
Standing	Basal Area	0.409	Artificial_Water	Wet_Heath	-0.376
PeatDepth	Cutover_Bog	0.405	No. Tree Species	mean_dbh	-0.374
Broadleaf	Urban	0.404	SoilDepth	Bare_Peat	-0.371
TotalCanopyCover	Basal Area	0.403	Altitude	Lakes	-0.369
Mixed_For	Treelines	0.398	Conifer	Treelines	-0.365
Dry_Heath	Trans_For	0.381	Conifer	Imp_Grass	-0.361
Mixed_For	Urban	0.379	sd_dbh	No. Trees	-0.352
No. Tree Species	sd_dbh	0.371	Altitude	No. Tree Species	-0.349
Conifer	Basal Area	0.369	Conifer	Cultivated	-0.346
Cultivated	Hedge	0.366	Altitude	Treelines	-0.342
No. Tree Species	large_tree_count	0.363	Conifer	Hedge	-0.333
Bracken	Scrub	0.355	Bare	Blanket_Bog	-0.332
Trans_For	Blanket_Bog	0.353	PeatDepth	Urban	-0.330
Bare	Cultivated	0.351	Artificial_Water	Dry_Heath	-0.328
Deadwood Logs	sd_dbh	0.339	Artificial_Water	Blanket_Bog	-0.326
Artificial_Water	Cultivated	0.336	Age	Conifer	-0.326
No. Tree Species	NatRegenTrees	0.334	No. Tree Species	Trans_For	-0.320

Positive Correlations			Negative Correlations		
Variable 1	**Variable 2**	**r_s**	**Variable 1**	**Variable 2**	**r_s**
Altitude	Dry_Heath	0.334	Slope	Raised_Bog	-0.315
Altitude	mean_dbh	0.330	Altitude	Hedge	-0.315
Exposed_Rock	Wet_Heath	0.328	Broadleaf	Wet_Heath	-0.310
PeatDepth	LitterDepth	0.320	Mixed_For	Blanket_Bog	-0.307
Bracken	Blanket_Bog	0.319			
No. Tree Species	Urban	0.316			
Dry_Heath	Exposed_Rock	0.315			
Age	Deadwood Logs	0.308			
Altitude	Wet_Heath	0.306			
Exposed_Rock	Blanket_Bog	0.305			
No. Tree Species	Mixed_For	0.304			
SoilDepth	Cultivated	0.303			
Rivers	Treelines	0.301			
Trans_For	Basal Area	0.300			

Table C2 NFI Summary Table showing number of plots grouped by woodland habitat and development stage

	MATURE FOREST				IMMATURE FOREST						OTHER		
Woodland Habitat	**High Forest**	**Multi-storied**	**Over-mature**	**Mature Total**	**Post establish-ment**	**Pre-thicket**	**Thicket**	**Small Pole Stage**	**Pole Stage**	**Immature Total**	**Forest Open Area**	**Temporarily Unstocked**	**Habitat Total**
Highly modified/non-native woodland	**385**	**77**	**37**	**499**	**187**	**161**	**185**	**224**	**290**	**1047**	**193**	**16**	**1754**
(Mixed) broadleaved woodland	18	35	5	58	**12**	15	25	31	12	95	18		171
(Mixed) conifer woodland	20	2	5	27	**12**	10	21	21	32	96	6		129
Conifer plantation	301	8	21	330	**146**	115	117	135	212	725	147	16	1218
Mixed broadleaved/conifer woodland	46	32	6	84	**17**	21	22	37	34	131	22		237
Scrub/transitional woodland	**1**	**13**		**14**	**5**	**6**	**10**	**2**		**23**	**8**	**1**	**46**
Immature woodland	1	3		4	**3**		1	1		5			9
Recently-felled woodland					**1**	2				3		1	4
Scrub		10		10	**1**	4	9	1		15	8		33
Semi-natural woodland	**11**	**160**	**1**	**172**	**2**	**5**	**5**	**13**	**3**	**28**	**19**		**219**
Bog woodland	1	32		33	**2**	4	2	7		15	2		50
Oak-ash-hazel woodland	2	43		45			1	1		2	10		57
Oak-birch-holly woodland	7	39	1	47				1	1	2	5		54
Riparian woodland		13		13		1		1		2	1		16
Wet pedunculate oak-ash woodland		3		3			1			1			4
Wet willow-alder-ash woodland	1	30		31			1	3	2	6	1		38
Development Stage Total	**397**	**250**	**38**	***685***	**194**	**172**	**200**	**239**	**293**	***1098***	**220**	**17**	***2020***

Table C3 Random Forest Model Percentage Feature Importance. For all features >1% Importance. R = Species Richness, WG = Woodland Generalist Species Richness, NW = Non-Woodland Species Richness, WS = Woodland Specialist Species Richness, AWI = Ancient Woodland Indicator Species Richness.

R		WG		NW		WS		AWI	
Feature	**%**	**Feature**	**%**	**Feature**	**%**	**Feature**	**%**	**Feature**	**%**
Peat Depth	4.91	No. Tree Species	5.16	No Thinning	4.93	No. Tree Species	7.70	Peat Depth	7.16
No. Tree Species	4.88	Peat Depth	4.90	Canopy Cover	4.44	Bryophyte Cover	4.10	No. Tree Species	4.04
Thinning (no thin)	4.48	X	3.01	Basal Area	4.44	Hedge	3.53	Age	3.72
X	3.86	Uneven aged	2.69	Y	2.85	Deadwood Logs	3.19	Y	3.28
Y	3.80	Basal Area	2.57	No. Trees	2.61	Peat Depth	2.80	X	2.81
No. Trees	3.77	Treeline Area	2.54	Nativeness: native (>80%)	2.60	Altitude	2.71	Habitat: Oak-ash-hazel	2.79
Basal Area	3.59	Urban Area	2.47	Drainage - good	2.48	X	2.53	Wet Grassland Area	2.76
Establishment: semi-natural	3.58	Hedge Area	2.40	Establishment: semi-natural	2.45	Age	2.50	Establishment: Semi-natural	2.67
Nativeness native (>80%)	3.12	Habitat: Oak-ash-hazel	2.33	Class - Forest	2.41	Broadleaf	2.39	NatRegen Trees	2.61
Deadwood Logs	2.42	Y	2.33	Broadleaf Area	2.35	sd_DBH	2.38	sd_DBH	2.60
Canopy Cover	2.25	No. Trees	2.33	Damage (Yes)	2.32	Dry Heath Area	2.35	Dominant Tree Species: Hazel	2.60
Hedge Area	2.20	No Thinning	2.13	HabitatGroup: Semi-natural woodland	2.13	Wet Grassland Area	2.19	mean_DBH	2.46
Development Stage: multistoried	2.20	sd_DBH	2.12	sd_DBH	2.12	No. Trees	2.16	Slope	2.28
sd_DBH	2.19	Age	2.09	Habitat: Wet Woodland	2.06	Urban	2.12	No Thinning	2.00
Uneven aged	2.14	Nativeness non-native (>80%)	1.97	Bryophyte Cover	2.01	Treelines	2.12	Dominant Tree Species: Ash	1.98
Bryophyte Cover	1.95	No. Large Trees	1.94	Mixed Forest Area	1.78	Exposed Rock Area	2.10	Uneven Aged	1.83
Wet Grassland Area	1.91	Altitude	1.88	Harvesting (Yes)	1.63	Habitat: Conifer plantation	1.91	Deadwood Stumps	1.79
NatRegen Trees	1.71	Bryophyte Cover	1.66	X	1.56	HabitatGroup:	1.87	Disease (Yes)	1.76

R		WG		NW		WS		AWI	
Feature	**%**	**Feature**	**%**	**Feature**	**%**	**Feature**	**%**	**Feature**	**%**
						Scrub/transitional woodland			
Deadwood Stumps	1.68	Origin: planted, natural <20%	1.65	Development Stage: multistoried	1.55	Wet Heath Area	1.85	Cutover Bog Area	1.66
Bare Peat Area	1.67	Conifer Area	1.61	No. Tree Species	1.54	Basal Area	1.78	Cultivated Area	1.66
Treelines Area	1.59	Soil - Ombrotrophic	1.59	Wet Heath Area	1.51	Y	1.75	Basal Area	1.61
HabitatGroup: Semi-natural woodland	1.50	Habitat: Conifer plantation	1.57	Establishment: reforestation	1.42	NatRegen Trees	1.73	Deadwood Logs	1.55
Dry Grassland Area	1.43	Disease (Yes)	1.53	Wet Grassland Area	1.42	Soil - Brown Earth	1.61	No. Trees	1.53
Age	1.43	Deadwood Logs	1.53	Hedge Area	1.39	Dominant Tree Species: Hazel	1.57	Raised Bog Area	1.50
Urban Area	1.37	mean_DBH	1.52	Deadwood Stumps	1.37	Cultivated Area	1.55	Bare Peat Area	1.44
Wet Heath Area	1.23	Soil - Minerotrophic	1.48	Altitude	1.33	Soil - Surface Water Gley	1.40	Habitat: Conifer plantation	1.41
mean_DBH	1.16	Ownership: private (non grant aid)	1.46	Dry Heath Area	1.33	Uneven aged	1.39	Ownership: private (grant aid)	1.40
Slope	1.08	Development Stage: multistoried	1.42	Blanket Bog Area	1.31	Raised Bog Area	1.33	Habitat Group: Semi-natural woodland	1.37
Blanket Bog Area	1.08	Mixture - uniform	1.35	Age	1.30	Drainage - moderate	1.32	Blanket Bog Area	1.36
Ownership private (non grant aid)	1.04	Exposed_Rock	1.30	No. Large Trees	1.27	Dry Grassland Area	1.29	Soil - Rendzina	1.29
Drainage moderate	1.04	Establishment: semi-natural	1.27	Thinning - not applicable	1.26	Scrub Area	1.25	Ownership: private (non grant aid)	1.24
Dry Heath Area	1.04	Cultivated Area	1.27	Deadwood Logs	1.24	mean_DBH	1.23	Broadleaf Area	1.15
Cultivated Area	1.03	Dry_Heath Area	1.21	Cutover Bog Area	1.24	Soil - Groundwater Gley	1.21	Wet Heath Area	1.14

R		WG		NW		WS		AWI	
Feature	**%**	**Feature**	**%**	**Feature**	**%**	**Feature**	**%**	**Feature**	**%**
		NatRegen Trees	1.21	Standing Deadwood	1.16	Habitat: Scrub	1.20	Soil - Brown Earth	1.12
		Wet Grassland Area	1.21	Slope	1.14	Aspect - south	1.14	Origin: planted, natural < 20%	1.11
		Ownership: private (grant aid)	1.15	Dominant Tree Species: goat willow	1.13	Mixture - uniform	1.14	Development Stage: multistoried	1.07
		Scrub Area	1.09	Dominant Tree Species: Sitka spruce	1.13	Slope	1.11	Exposed Rock Area	1.07
		Litter Depth	1.09	Cultivated Area	1.12	Mixed Forest Area	1.10	Mixture - uniform	1.05
		Dominant Tree Species: Sitka spruce	1.07	Dominant Tree Species: Lodgepole pine	1.06	Dominant Tree Species: Japanese Larch	1.09	Dominant Tree Species: Sitka spruce	1.02
		Wet Heath Area	1.06	Bare Peat Area	1.05	Dominant Tree Species: Sitka spruce	1.02	No. Large Trees	1.02
				mean_DBH	1.04				

Table C4 Model Results for overall richness, woodland specialists, woodland generalists, ancient woodland indicators and non-woodland species. Positive z values indicate higher values richness, and vice versa for negative estimates. Incidence Rate Ratios describe how the rate of the outcome changes with a one-unit increase in the predictor variable, with values greater than 1 indicating an increased rate of the outcome, and below one indicating a decreased rate. p-values (to test the null hypothesis that the coefficient estimate is equal to zero, i.e. no effect) were calculated from z-values: the ratio between the estimated coefficient and the standard error of the estimate (estimate/SE). Large z-values show that the estimate is large (in relation to its SE) and significantly different from zero. The model flexibly captures nonlinear relationships between the response variable and spatial coordinates X and Y, using spline basis expansions. Each spline term does not have a direct standalone interpretation, but together they describe a smooth surface.

	Predictors	Incidence Rate Ratios	Confidence Interval	Z Stat	P value
R	**Count Model**				
	(Intercept)	8.47	4.97 – 14.45	7.84	**<0.001**
	X [1st degree]	0.77	0.40 – 1.49	-0.77	0.443
	X [2nd degree]	1.34	0.90 – 1.99	1.45	0.146
	X [3rd degree]	0.95	0.56 – 1.61	-0.18	0.859
	X [4th degree]	0.78	0.48 – 1.27	-1.01	0.312
	X [5th degree]	0.73	0.44 – 1.21	-1.23	0.218
	Y [1st degree]	0.94	0.52 – 1.69	-0.21	0.835
	Y [2nd degree]	0.99	0.68 – 1.44	-0.06	0.951
	Y [3rd degree]	0.87	0.52 – 1.44	-0.55	0.579
	Y [4th degree]	1.13	0.69 – 1.86	0.5	0.619
	Y [5th degree]	1.4	0.82 – 2.39	1.22	0.221
	No. Tree Species	1.35	1.24 – 1.47	7.06	**<0.001**
	Peat Depth	0.73	0.67 – 0.80	-6.78	**<0.001**
	Hedge Area	1.32	1.16 – 1.51	4.11	**<0.001**
	Establishment (reforestation)	0.86	0.76 – 0.96	-2.59	**0.01**
	Establishment (semi-natural)	1.3	1.17 – 1.44	4.89	**<0.001**
	Deadwood Logs	1.15	1.07 – 1.24	3.77	**<0.001**
	Basal Area	0.81	0.73 – 0.89	-4.14	**<0.001**
	Zero-Inflated Model				
	(Intercept)	0.02	0.01 – 0.04	-11.92	**<0.001**
	Basal Area	16	6.56 – 39.01	6.1	**<0.001**
	Observations	685			
	R^2 / R^2 adjusted	0.931 / 0.930			
	AICc	3947.92			
	Morans I (p value)	0.0053 (0.042)			
Woodland Generalists	**Count Model**				
	(Intercept)	4.97	2.96 – 8.37	6.05	**<0.001**

	Predictors	Incidence Rate Ratios	Confidence Interval	Z Stat	P value
	X [1st degree]	0.57	0.30 – 1.09	-1.7	0.088
	X [2nd degree]	1.09	0.73 – 1.63	0.41	0.684
	X [3rd degree]	0.57	0.34 – 0.96	-2.12	**0.034**
	X [4th degree]	0.55	0.33 – 0.92	-2.3	**0.022**
	X [5th degree]	0.64	0.39 – 1.07	-1.71	0.087
	Y [1st degree]	0.7	0.40 – 1.22	-1.27	0.206
	Y [2nd degree]	0.82	0.57 – 1.17	-1.11	0.265
	Y [3rd degree]	0.69	0.42 – 1.12	-1.51	0.131
	Y [4th degree]	1.15	0.70 – 1.89	0.57	0.569
	Y [5th degree]	1.14	0.68 – 1.90	0.49	0.626
	(Intercept)	4.97	2.96 – 8.37	6.05	**<0.001**
	No. Tree Species	1.42	1.29 – 1.55	7.36	**<0.001**
	Peat Depth	0.6	0.54 – 0.67	-9.22	**<0.001**
	Uneven Aged	1.32	1.17 – 1.49	4.62	**<0.001**
	Basal Area	0.87	0.77 – 0.97	-2.44	**0.015**
	Treelines Area	1.2	1.10 – 1.31	4.07	**<0.001**
	Hedge Area	1.13	1.02 – 1.25	2.36	**0.018**
	Zero-Inflated Model				
	(Intercept)	0.03	0.00 – 0.73	-2.15	**0.032**
	Thin [juvenille]	0	0.00 – Inf	-0.01	0.996
	Thin [no thin]	4.21	0.17 – 102.00	0.88	0.377
	Thin [not applicable]	0	0.00 – Inf	0	0.999
	Thin [second]	1	0.01 – 68.13	0	1
	Thin [subsequent]	0.03	0.00 – Inf	-0.16	0.871
	Observations	685			
	R^2 / R^2 adjusted	0.771 / 0.765			
	AICc	2739.64			
	Morans I (p value)	-0.00071 (0.821)			
Woodland Specialists	**Count Model**				
	(Intercept)	1.63	0.84 – 3.15	1.45	0.147
	X [1st degree]	0.95	0.39 – 2.32	-0.11	0.913
	X [2nd degree]	1.6	0.91 – 2.82	1.62	0.104
	X [3rd degree]	0.7	0.31 – 1.56	-0.88	0.382
	X [4th degree]	0.81	0.42 – 1.56	-0.62	0.534
	Y [1st degree]	0.95	0.46 – 1.96	-0.15	0.883
	Y [2nd degree]	1.1	0.68 – 1.80	0.4	0.691
	Y [3rd degree]	0.86	0.42 – 1.75	-0.41	0.682
	Y [4th degree]	1.35	0.75 – 2.44	1.01	0.314
	No. Tree Species	1.7	1.52 – 1.90	9.16	**<0.001**
	Bryophyte Cover	1.15	1.02 – 1.29	2.25	**0.024**
	Hedge Area	1.32	1.16 – 1.52	4.04	**<0.001**
	Peat Depth	0.77	0.67 – 0.88	-3.73	**<0.001**
	Deadwood Logs	1.11	1.01 – 1.23	2.13	**0.034**

	Predictors	Incidence Rate Ratios	Confidence Interval	Z Stat	P value
	Altitude	0.82	0.69 – 0.96	-2.44	**0.015**
	Zero-Inflated Model				
	(Intercept)	0	0.00 – Inf	-0.02	0.983
	Observations	685			
	R^2 / R^2 adjusted	0.446 / 0.433			
	AICc	2139.72			
	Morans I (p value)	0.00167 (0.346)			
Ancient Woodland Indicators	(Intercept)	0.69	0.18 – 2.21	-0.6	0.55
	X [1st degree]	1.09	0.24 – 6.12	0.1	0.92
	X [2nd degree]	1.67	0.65 – 4.77	1.01	0.312
	X [3rd degree]	1.54	0.45 – 6.21	0.65	0.515
	X [4th degree]	0.36	0.11 – 1.35	-1.56	0.118
	X [5th degree]	1.46	0.45 – 5.26	0.61	0.542
	Y [1st degree]	0.75	0.23 – 2.60	-0.47	0.636
	Y [2nd degree]	0.74	0.34 – 1.67	-0.73	0.463
	Y [3rd degree]	0.71	0.25 – 2.12	-0.62	0.533
	Y [4th degree]	1.99	0.69 – 5.89	1.26	0.209
	Y [5th degree]	1.06	0.37 – 3.07	0.12	0.907
	No. Tree Species	1.6	1.28 – 1.98	4.24	**<0.001**
	Peat Depth	0.3	0.20 – 0.42	-6.65	**<0.001**
	Habitat (Mixed conifer woodland)	0.51	0.25 – 0.93	-2.04	**0.041**
	Habitat (Bog woodland)	0.44	0.15 – 1.06	-1.67	0.095
	Habitat (Conifer plantation)	0.45	0.32 – 0.64	-4.48	**<0.001**
	Habitat (Immature Woodland)	1.35	0.32 – 3.82	0.5	0.617
	Habitat (Mixed broadleaved/conifer woodland)	0.65	0.45 – 0.92	-2.39	**0.017**
	Habitat (Oak-ash-hazel woodland)	1.32	0.94 – 1.85	1.59	0.112
	Habitat (Oak-birch-holly woodland)	1.15	0.79 – 1.66	0.73	0.467
	Habitat (Scrub)	0.89	0.26 – 2.22	-0.23	0.821
	Habitat (Wet Woodland)	1	0.66 – 1.49	-0.01	0.993
	Observations	685			
	R^2 Nagelkerke	0.521			
	AICc	1338.597			
	Morans I (p value)	-0.00480 (0.304)			
Non-woodland species	(Intercept)	2.13	0.78 – 5.82	1.47	0.142
	X [1st degree]	1.26	0.37 – 4.25	0.37	0.712
	X [2nd degree]	1.05	0.51 – 2.13	0.12	0.902
	X [3rd degree]	1.14	0.44 – 2.98	0.27	0.785
	X [4th degree]	0.71	0.29 – 1.72	-0.76	0.45
	X [5th degree]	0.65	0.26 – 1.63	-0.92	0.357
	Y [1st degree]	1.55	0.53 – 4.49	0.81	0.421
	Y [2nd degree]	1.55	0.78 – 3.10	1.25	0.213

Predictors	Incidence Rate Ratios	Confidence Interval	Z Stat	P value
Y [3rd degree]	1.06	0.43 – 2.61	0.13	0.898
Y [4th degree]	1.83	0.77 – 4.31	1.38	0.168
Y [5th degree]	2.87	1.15 – 7.17	2.26	**0.024**
Canopy Cover	0.76	0.67 – 0.86	-4.35	**<0.001**
Native >80%	1.66	1.29 – 2.12	3.97	**<0.001**
Non-native > 80%	1.34	1.06 – 1.69	2.47	**0.013**
Broadleaf Area	0.83	0.72 – 0.96	-2.51	**0.012**
Basal Area	0.78	0.64 – 0.94	-2.56	**0.01**
Thin [juvenille]	0.81	0.53 – 1.22	-1.01	0.311
Thin [no thin]	0.61	0.49 – 0.77	-4.13	**<0.001**
Thin [not applicable]	0.81	0.61 – 1.08	-1.44	0.149
Thin [second]	1.06	0.81 – 1.39	0.4	0.687
Thin [subsequent]	0.89	0.68 – 1.16	-0.86	0.39
Observations	685			
R^2 / R^2 adjusted	0.734 / 0.726			
AICc	3001.55			
Morans I (p value)	0.00325(0.157)			

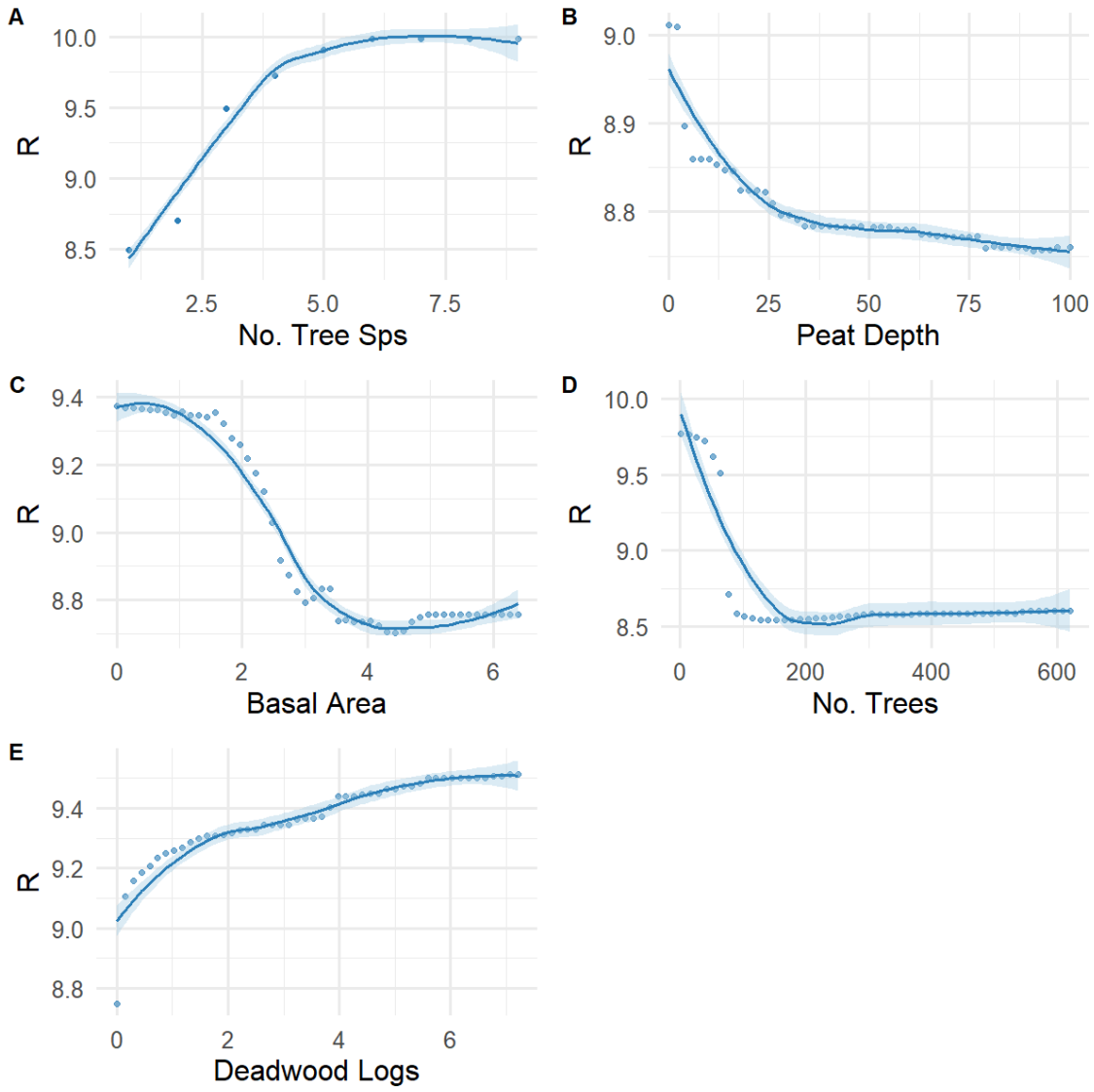

Figure C1 Effect of No. Tree Species (A), Peat Depth (B), Basal Area (C), No. Trees (D) and Volume of Deadwood logs (E) on Predicted Overall Species Richness R (Partial Dependence)

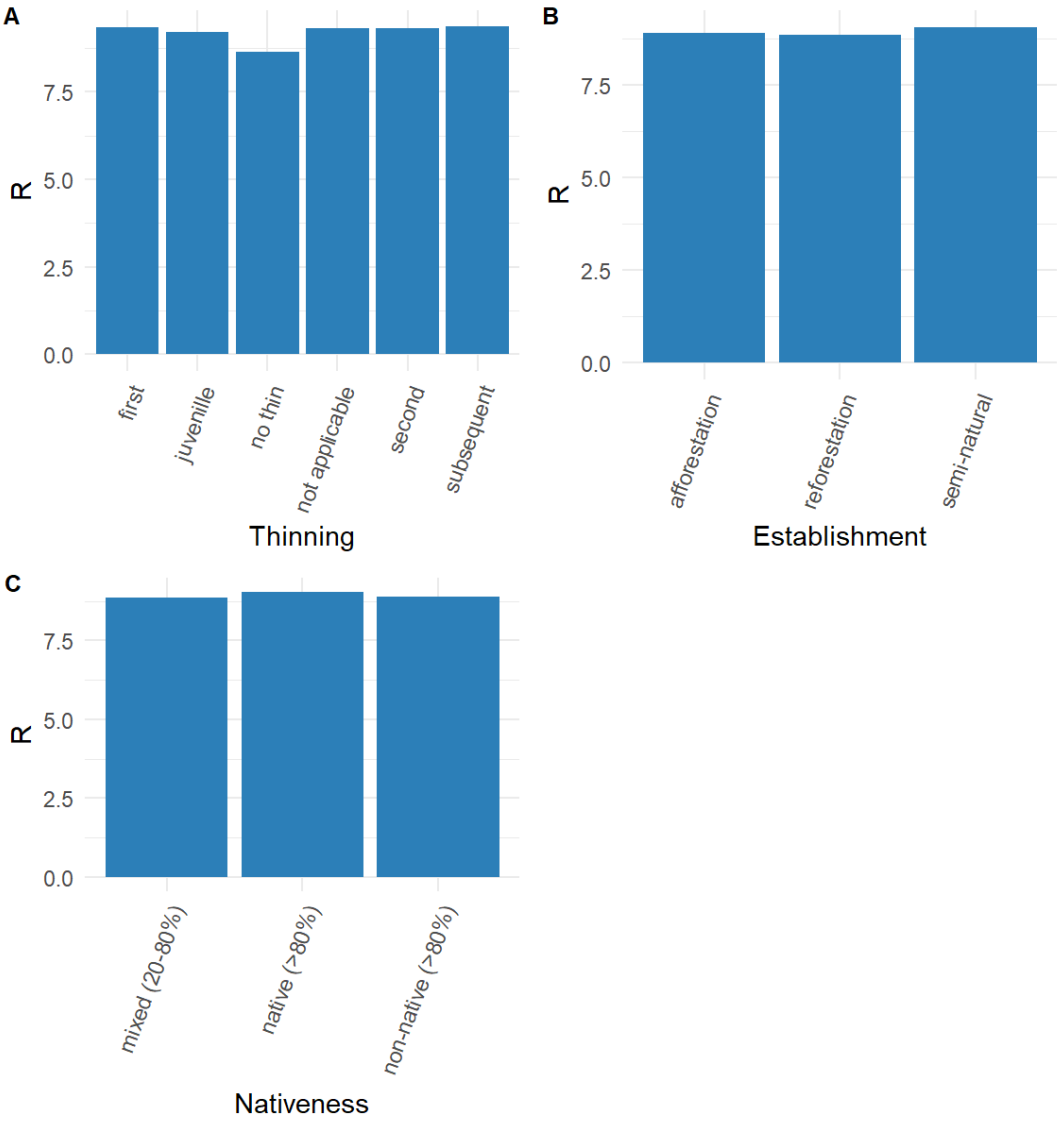

Figure C2 Effect of Thinning status (A), Establishment Type (B) and Nativeness class (C) on Predicted Overall Species Richness R (Partial Dependence)

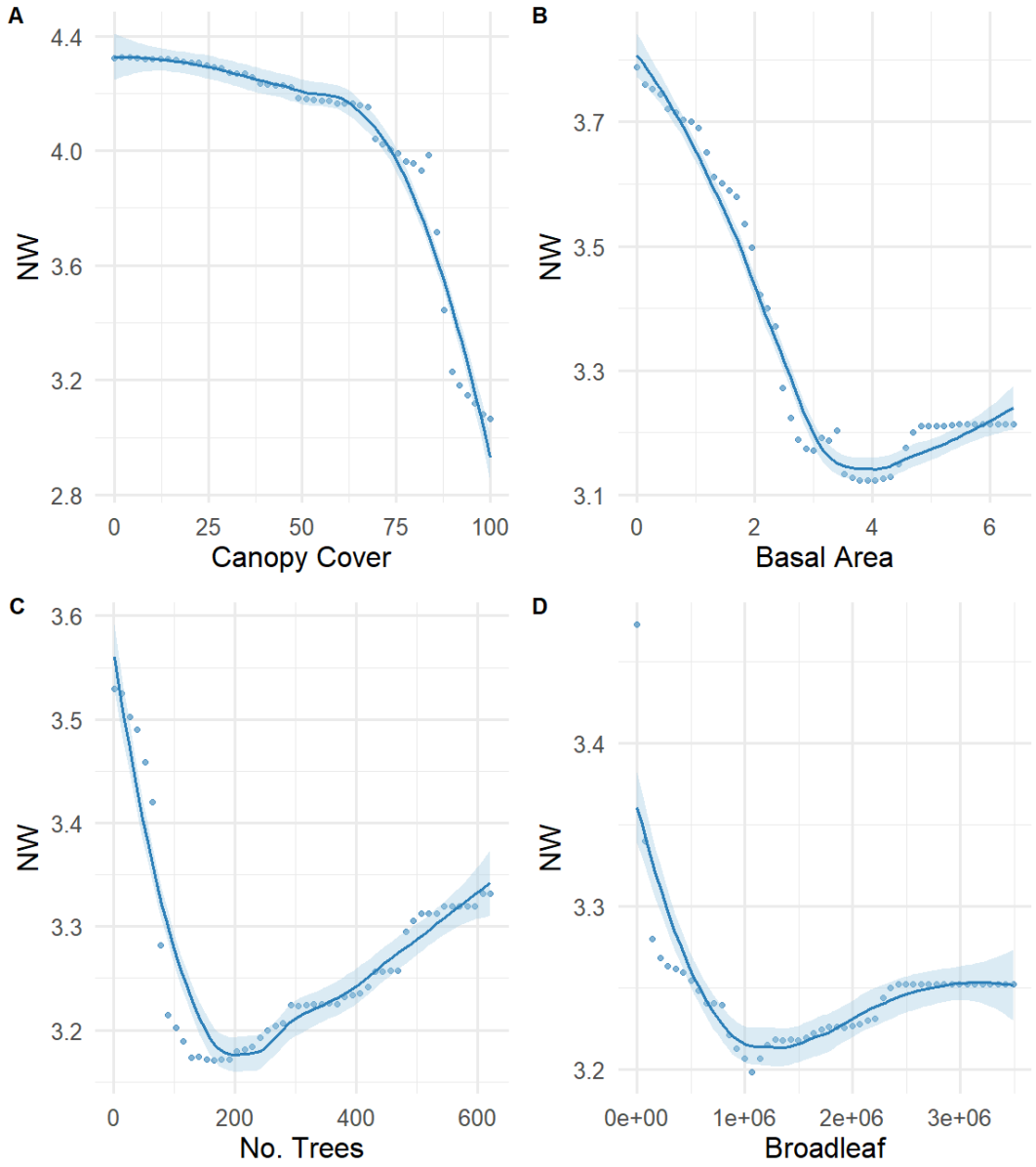

Figure C3 Effect of Canopy Cover (A), Basal Area (B), No. Trees (C), and Broadleaf Area in the landscape matrix (D) on Predicted Non-woodland Species Richness NW (Partial Dependence)

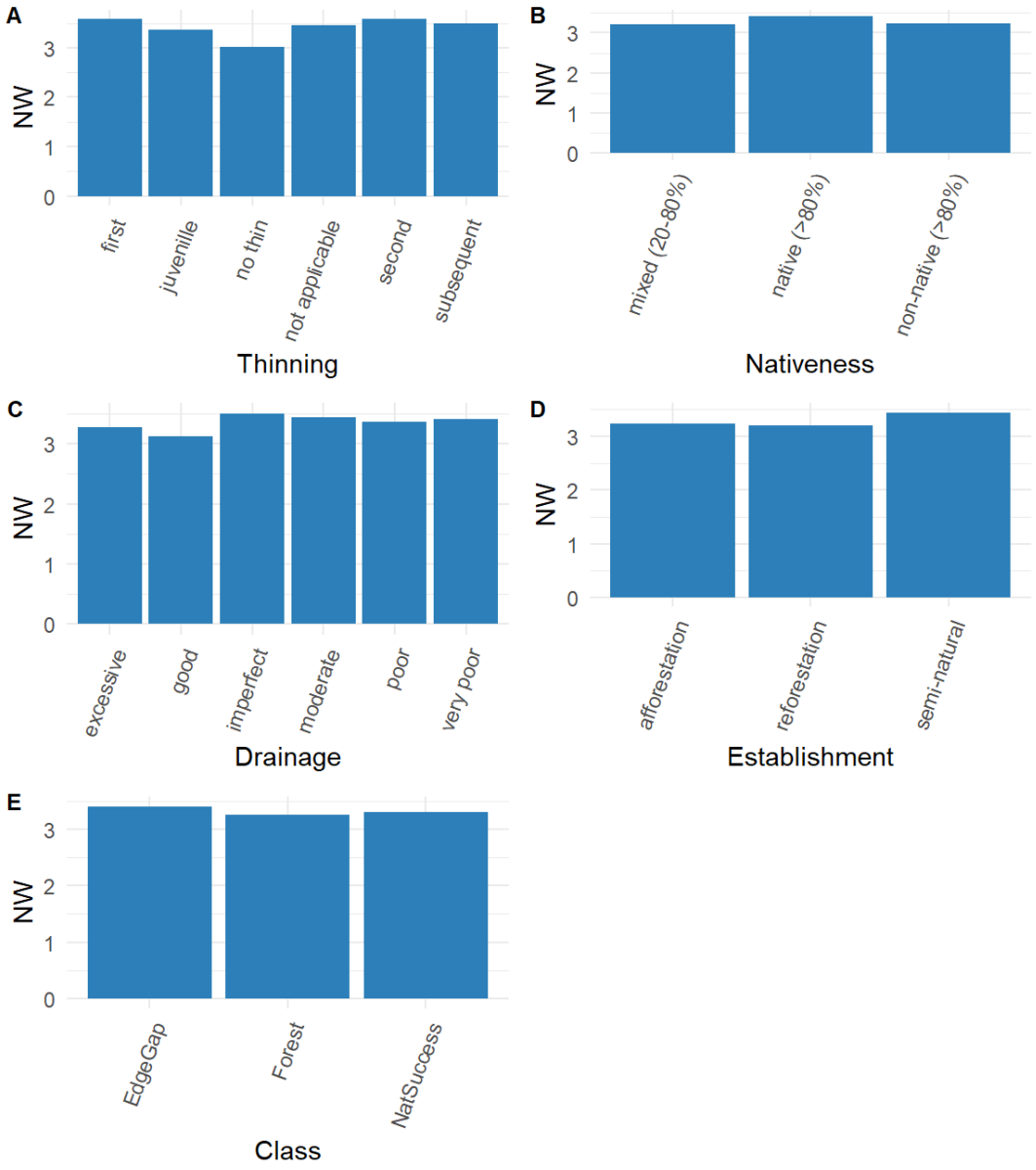

Figure C4 Effect of Thinning (A), Nativeness Class (B), Drainage (C), Establishment (D) and Forest Class (E) on Predicted Non-woodland Species Richness NW (Partial Dependence)

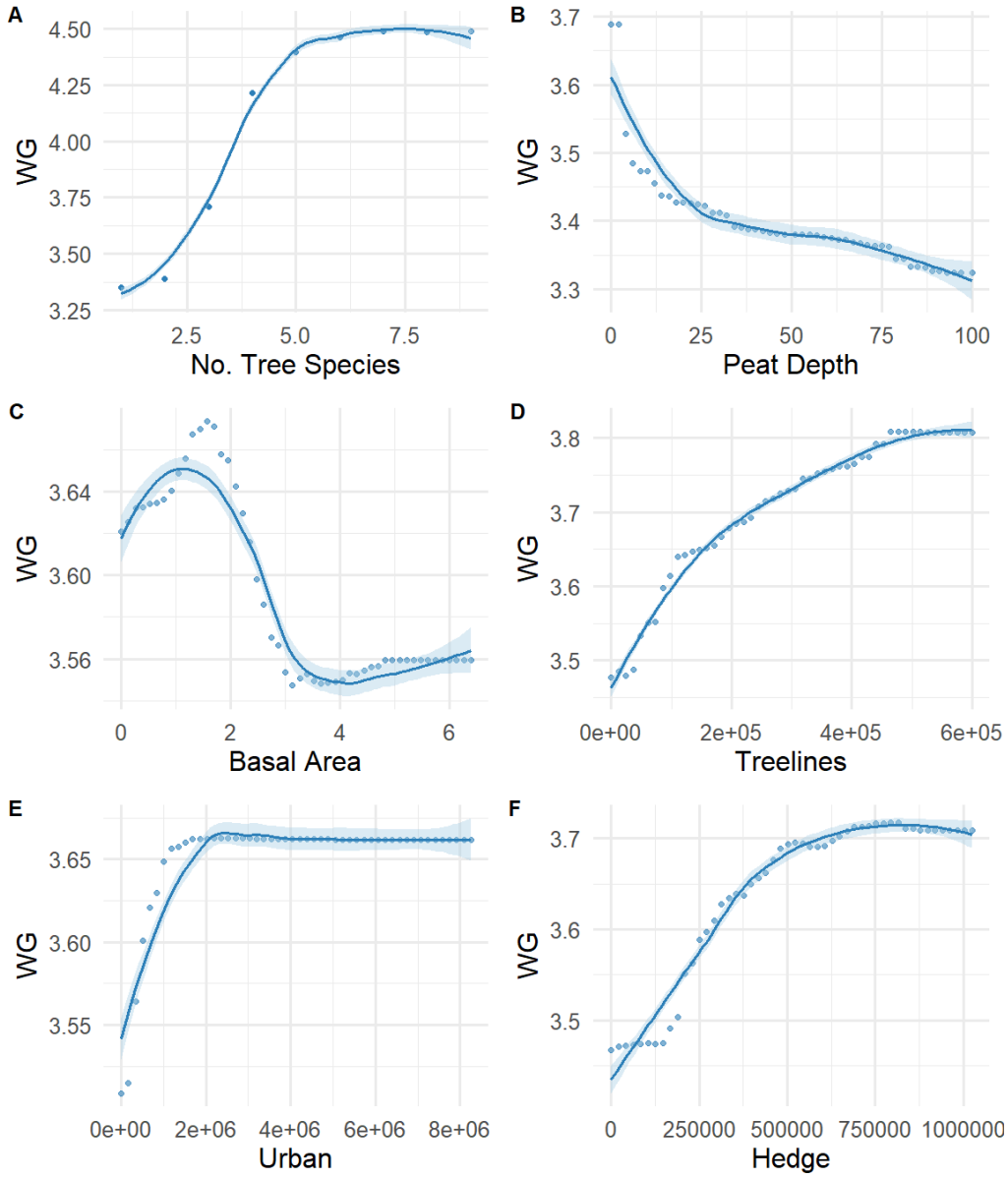

Figure C5 Effect of No. Tree Species (A), Peat Depth (B), Basal Area (C), Treelines Area in the landscape matrix (D), Urban Area in the landscape matrix (E), and Hedgerow in landscape matrix (F) on Predicted Woodland Generalist Species Richness WG (Partial Dependence)

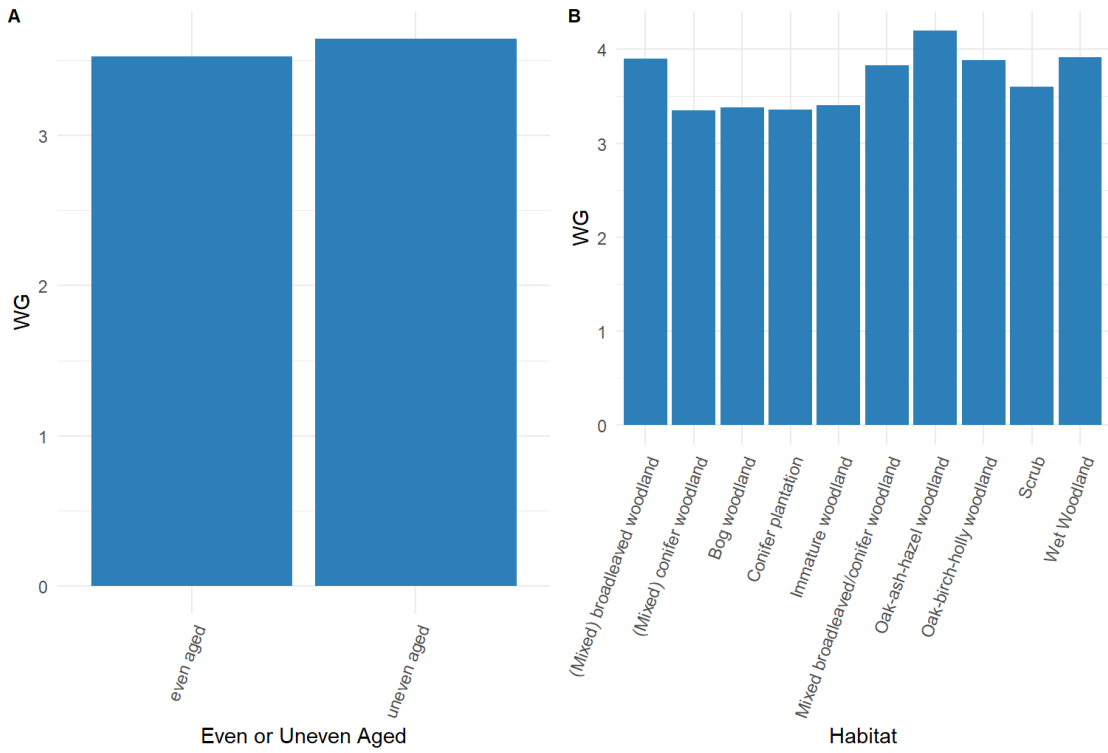

Figure C6 Effect of Even or Uneven Aged (A), and Habitat (B) on Predicted Woodland Generalist Species Richness WG (Partial Dependence)

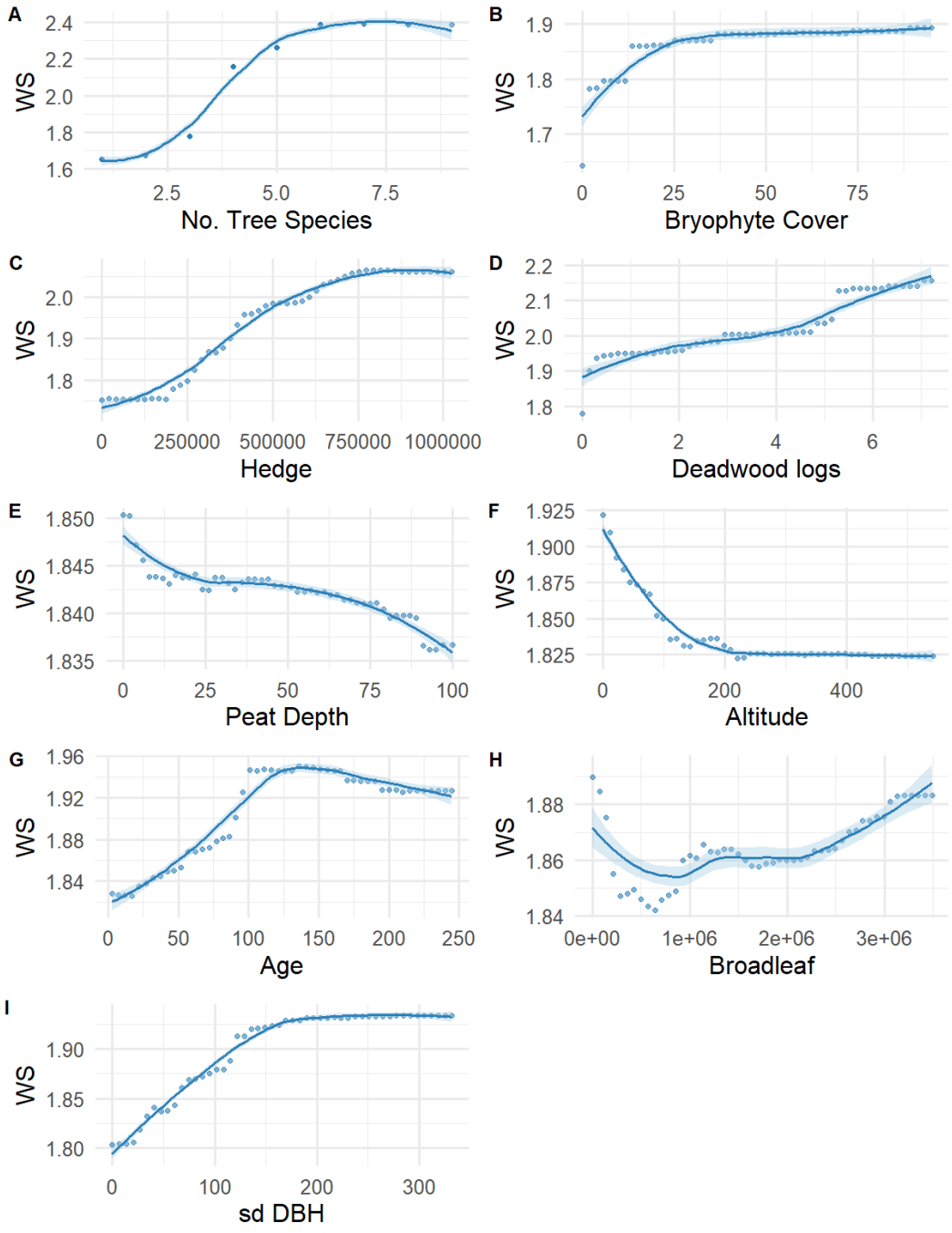

Figure C7 Effect of No. Tree Species (A), Bryophyte Cover (B), Hedgerow in the landscape matrix (C), Volume of Deadwood Logs (D), Peat Depth (E), Altitude (F), Age (G), Broadleaf woodland in the landscape matrix (H) and standard deviation of DBH (I) on Predicted Woodland Specialist Species Richness WS (Partial Dependence)

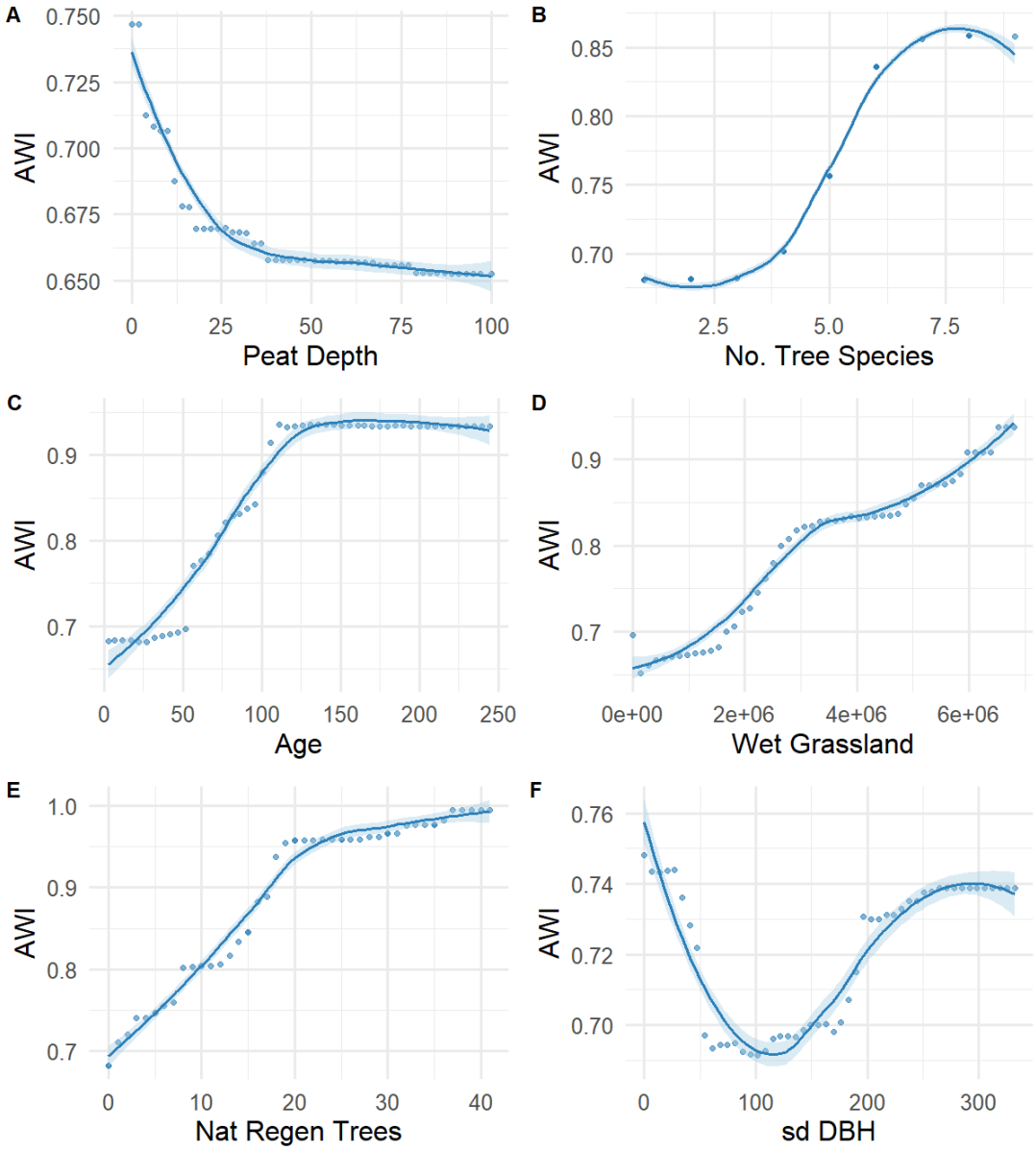

Figure C8 Effect of Peat Depth (A), No. Tree Species (B), Age (C), Wet Grassland in the landscape matrix (D), No. of Natural Regenerating Trees (E) and standard deviation of DBH (F) on Predicted Ancient Woodland Indicator Species Richness AWI (Partial Dependence)

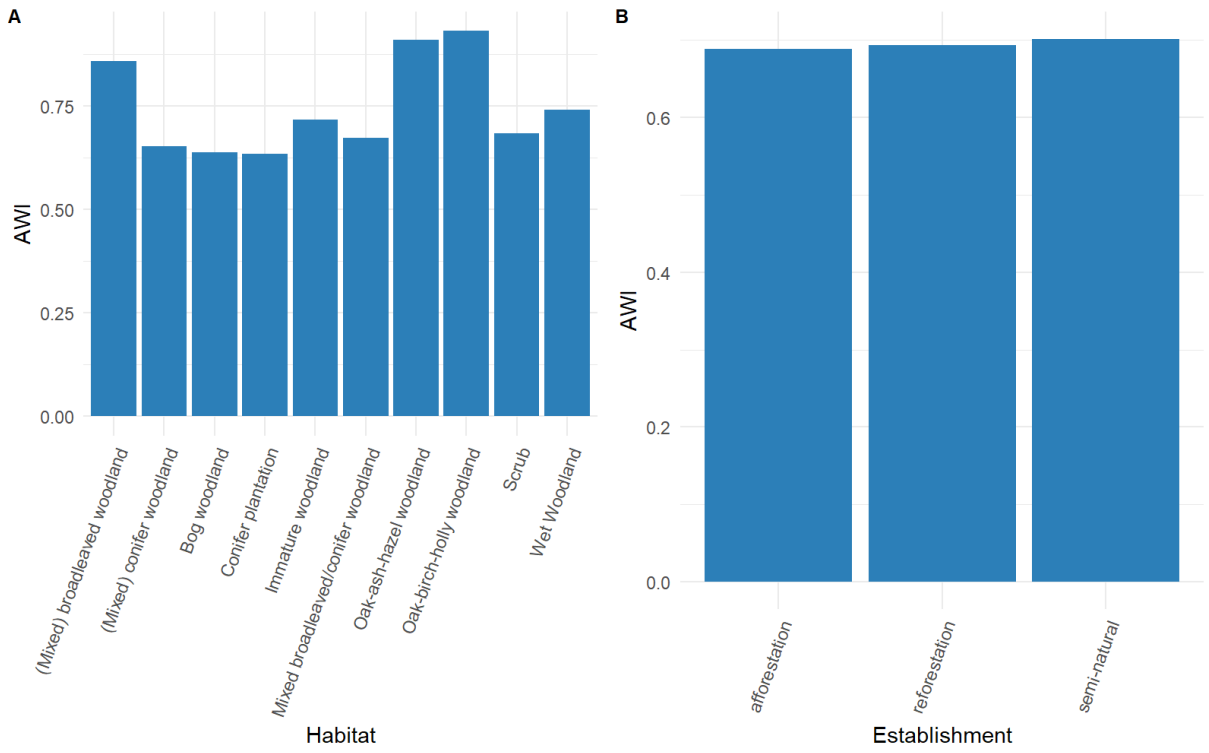

Figure C9 Effect of Ancient Woodland Indicator Species Richness with Habitat (A) and Establishment (B) on Predicted Ancient Woodland Indicator Species Richness AWI (Partial Dependence)

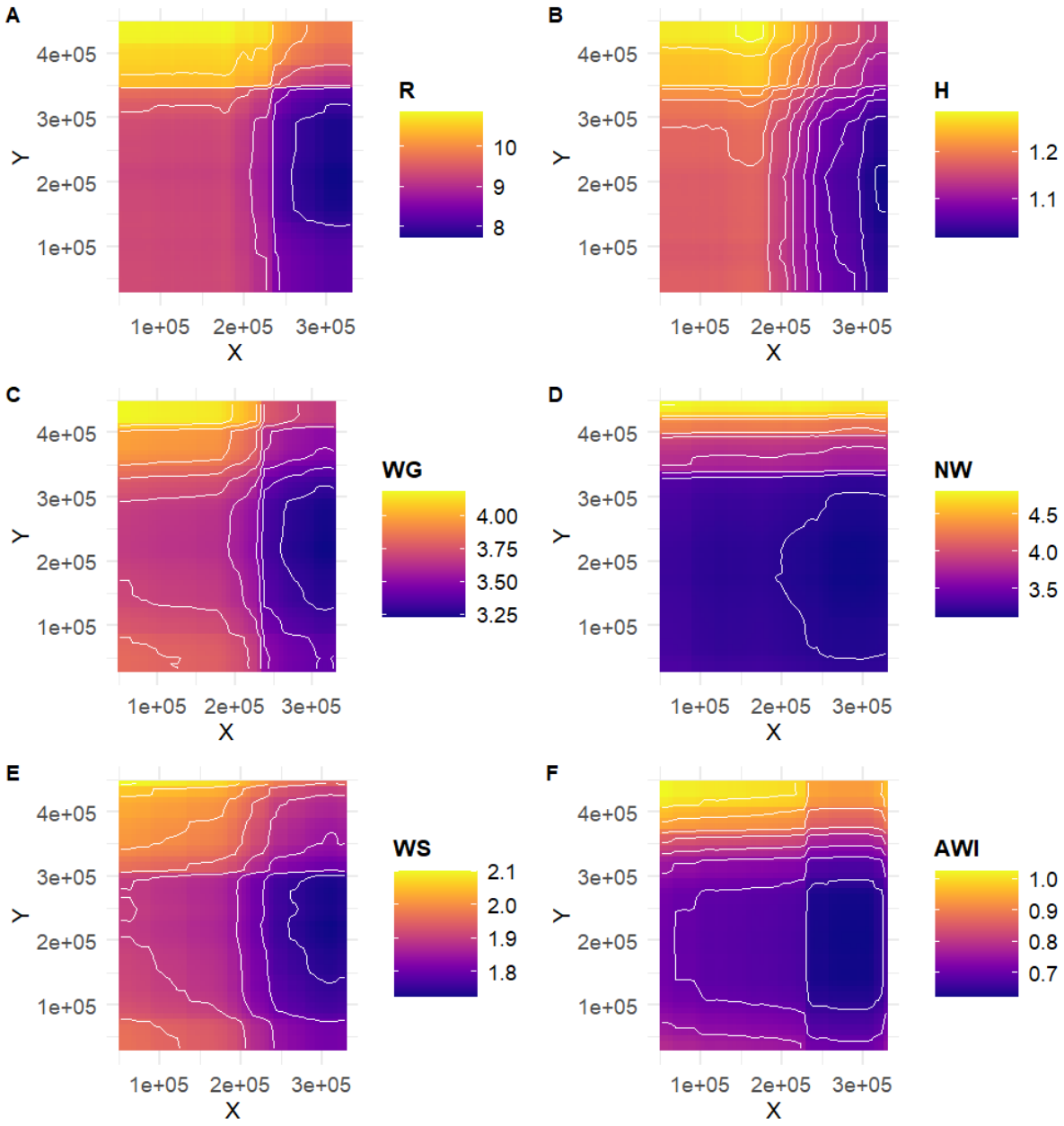

Figure C10 Partial Dependence of Spatial Coordinates (X, Y) on response variables: R - Species Richness (A), H – Shannon Diversity (B), WG - Woodland Generalists Species Richness (C), NW – Non-woodland Species Richness (D), WS – Woodland Specialist Species Richness (E) and AWI - Ancient Woodland Indicator Species Richness (F)

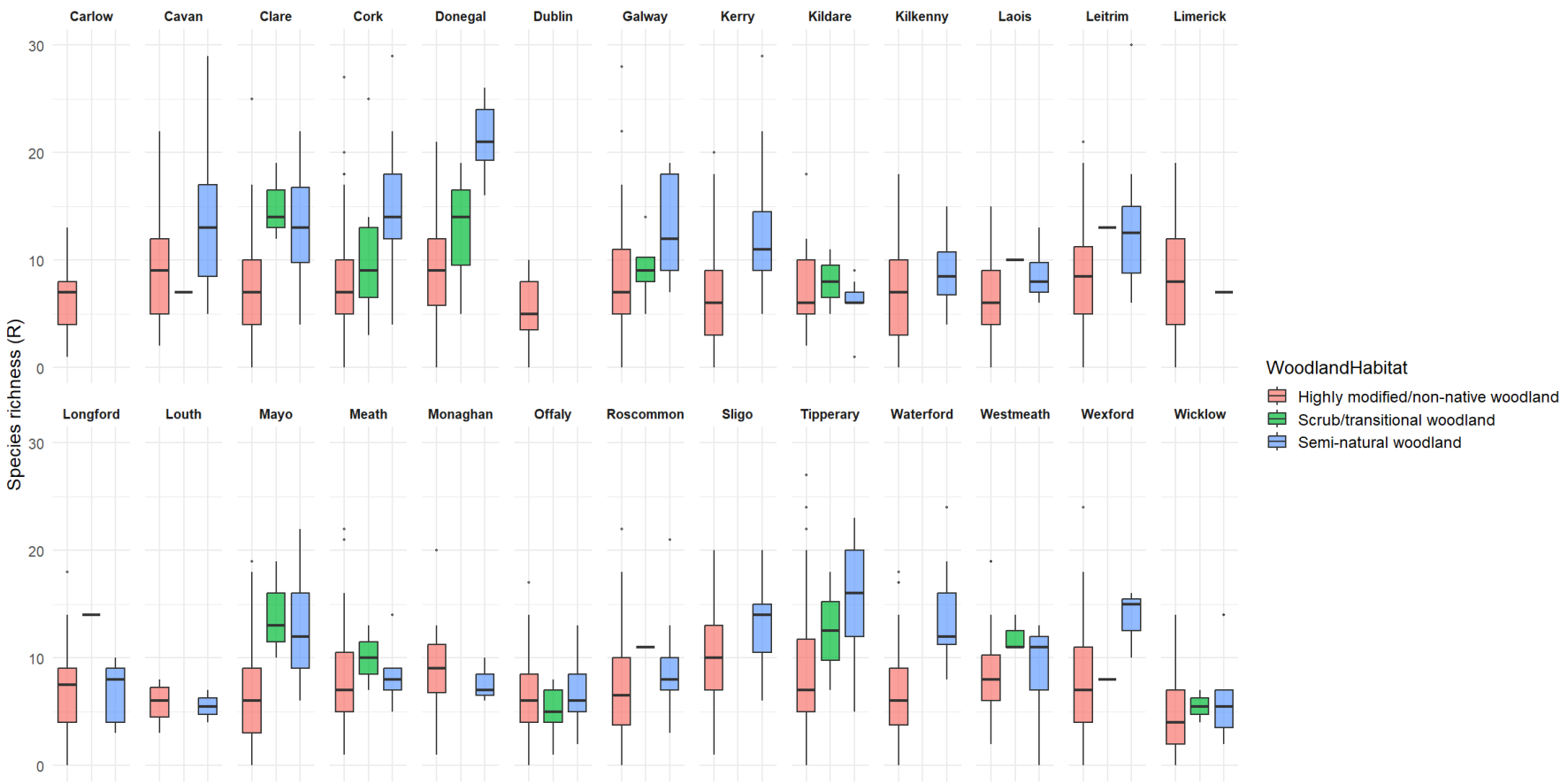

Figure C11 County level Species Richness (R) of flora recorded in National Forest Inventory (NFI) plots for three broad habitat groups (highly modified/non-native woodland, scrub/transitional woodland and semi-natural woodland). County labels sit above the relevant county boxplot.

Appendix D - Supplementary Data for Chapter 5

Table D1 Explanatory notes provided with scoring sheet

Overview
The purpose of this study is to estimate the typical biodiversity value of different types of forests planted for timber in Ireland, relative to each other, categorized by: * Species type * Life-cycle stage * Soil Type **Assumptions** The forests are planted primarily for timber. The forest is a first rotation plantation on former grassland. There is no landscape connectivity with semi-natural woodlands. The Forest Area comprises the planted trees inclusive of the broadleaf component planted with sitka, Areas of Biodiversity Enhancement (ABE's), internal roads and other open areas. The Forest Area excludes edge habitats outside of these areas. If you need to make any further assumptions, please include these in the comments column of the scoring sheet.
Estimating a Biodiversity Score
The biodiversity score should be estimated based on the perceived diversity of: * FLORA - All flora excluding the planted-trees i.e. shrubs, vascular plants and bryophytes * INVERTEBRATES - Above-ground invertebrates i.e. those living within or using the site associated with the litter, ground/field/shrub flora and planted trees. Including mobile species using the site as a foraging/hunting resource. For Example - Beetles, Butterflies, Bees, Hoverflies, Spiders * VERTEBRATES - Birds and mammals i.e. those living within or using the site associated with the litter, ground/field/shrub flora and planted trees. Including mobile species using the site as a foraging/hunting resource. The subset of species considered under each of the categories above will vary across life cycle stage and soil-types. **Do not limit score to woodland specialist species** - we also want to capture the biodiversity values of younger forest sites which may align more with those of open habitats. Apply a score in the range of 0-100, with 0 applied to the lowest forest type for each biodiversity group, and 100 for the highest. The score should be **relative to all other scores in the column** for each biodiversity group. For example, score flora in each forest/soil type relative to flora in all other forest/soil types using the full range of 0-100. Please assign the highest score of 100 to the forest type/soil combination(s) that you judge to support highest diversity (species richness/number of species) of each biodiversity group in your experience. Repeat for each of the three biodiversity groups. **When applying the score:** *** Imagine the 'typical' habitat for the species grouping, age and soil type, with its typical management, threats, former land-use, ABE's, open areas etc** *** "Typical" is defined as the most expected or representative value, equivalent to the mathematical term "mode"**
Confidence (optional)
Provide an indication of your confidence in the estimated score on a scale of 1 (not very confident) to 5 (very confident) We're aware that few people will have expertise across all biodiversity groups, however rather than omit these sections we ask you to complete all sections and give an indication of confidence in the relevant column.
Optional Comments (optional)
Use this section if you wish to provide a brief explanation, justification or caveat for your score.
Species Type
Sitka Spruce, Birch and Oak have been chosen to represent fast-growing conifer, fast-growing broadleaf and slow-growing broadleaf forests planted following the new forestry programme species composition requirements as follows: * Sitka Spruce - Planted following FT12, assume 20% broadleaf content * Birch - Planted following FT7

* Oak - Planted following FT6

Further Details here:
https://www.gov.ie/pdf/?file=https://assets.gov.ie/268169/c042cc66-08de-4818-b27a-409ce8c527f8.pdf#page=null

You can choose to add a comment to elaborate on any aspects of the woodland you have in mind when devising the score.

Oak refers to *Quercus robur* and/or *Quercus petraea*.

Birch refers to *Betula pubescens* and/or *Betula pendula*.

Mixed native forests are not considered in this survey, however an optional question is provided to help inform future research.

Life Cyle Stage

Broadly based on the 8-level Development Stage classification used in National Forest Inventory (NFI), we are examining the following categories considered likely to capture most future planted forest scenarios:

* Open (NFI 1 & 2)
* Canopy-Closure (NFI 3 & 4)
* Mature Even-Aged Unthinned (NFI 5-6)
* Mature Even-Aged Thinned (NFI 5-6)

NFI Development Stages:

1. Post establishment: A recently established forest that is not at free growing stage.

2. Pre-thicket: The forest is established, but the green branches are not yet touching.

3. Thicket: Forest where the canopy has closed but the lower branches are mainly green.

4. Small pole: Forest where the canopy has fully closed and the lower branches are dead.

5. Pole: A forest at a stage where it could be thinned or in the early stages of thinning.

6. High forest: A forest that has a high proportion of sawlog approaching or at normal rotation length.

7. Overmature: Forest retained beyond normal rotation length, resulting in the presence of large trees.

8. Multistoried: Forest with trees present at various stages of development.

Soils

These are broadly based on soil type groupings used in Native Woodland Scheme framework:

1. Podzols & Brown Podzolics - acid-infertile soils or moderately-fertile soils in upland hillside & valley settings
2. Brown Earths - Fertile, heavy/moist-light/dry, lowlands.
3. Gleys – mineral or peaty (wet/waterlogged soils, fertile).
4. Highly Modified Peat & Peaty Podzols – drained and grazed peat soils <50cm deep.

Assume a site with typical past land use and drainage on this soil type as per your own experience.

Insert 'not relevant' if some species are not planted on particular soil types.

Table D2 Results of Kruskall-Wallis and Dunn's Post-Hoc Tests for comparisons of flora, invertebrate and vertebrate scores across soil categories for three tree planting scenarios (birch, oak and Sitka spruce)

Variable		Flora	Inverts	Verts
Kruskall-Wallis Test:	**chi-squared**	5.360	1.995	0.844
Sitka	**p value**	0.147	0.574	0.839
Kruskall-Wallis Test:	**chi-squared**	4.287	1.896	2.097
Birch	**p value**	0.232	0.594	0.553
Kruskall-Wallis Test:	**chi-squared**	8.786	4.350	2.868
Oak	**p value**	**0.032**	0.226	0.412
Dunn's Test:	**Z**	2.960	-	-
Oak: Brown Earth Vs Peat	**p value**	**0.018**	-	-

Table D3 Results of Kruskall-Wallis Tests for comparisons of flora, invertebrate and vertebrate scores from foresters and ecologists for three tree planting scenarios (birch, oak and Sitka spruce)

		Forester		Ecologist	
		chi-squared	**p value**	**chi-squared**	**p value**
Kruskall-Wallis Test: Sitka	Flora	16.291	**0.001**	6.622	0.085
	Inverts	6.6793,	0.083	6.4682	0.091
	Verts	9.806	**0.020**	6.427	0.093
Kruskall-Wallis Test: Birch	Flora	4.8186,	0.186	4.583	0.205
	Inverts	6.314	0.097	10.344,	**0.016**
	Verts	6.3696,	0.095	8.8482,	**0.031**
Kruskall-Wallis Test: Oak	Flora	10.714	**0.013**	4.740	0.192
	Inverts	9.373	**0.025**	10.451	**0.015**
	Verts	10.601	**0.014**	11.52	**0.009**

Table D4 Results of Kruskall-Wallis Tests for Confidence Scores showing comparisons of median scores across biodiversity indicators, and comparisons of flora, invertebrate and vertebrate confidence scores between foresters and ecologists (pooled across all biodiversity indicators and tree taxa)

	chi-squared	p value
Biodiversity Indicator		
Median Score	9.182	0.327
Forester vs Ecologist		
Flora	7.146	0.210
Inverts	3.200	0.866
Verts	4.496	0.610

Table D5 Results of Kruskall-Wallis Tests and Dunn's Post-Hoc Tests for comparisons of NFI Flora Data for Sitka Spruce across Development Stages

Kruskall-Wallis Test	**chi-squared**	**p value**
Sitka Flora/Development Stages	85.954	**≤0.001**
Dunn's Tests	**Z**	**p value**
Closed - Open	-5.400	**≤0.001**
Closed - Thinned	-4.499	**≤0.001**
Open - Thinned	1.282	1
Closed - Unthinned	2.162	0.184
Open - Unthinned	7.893	**≤0.001**
Thinned - Unthinned	7.158	**≤0.001**

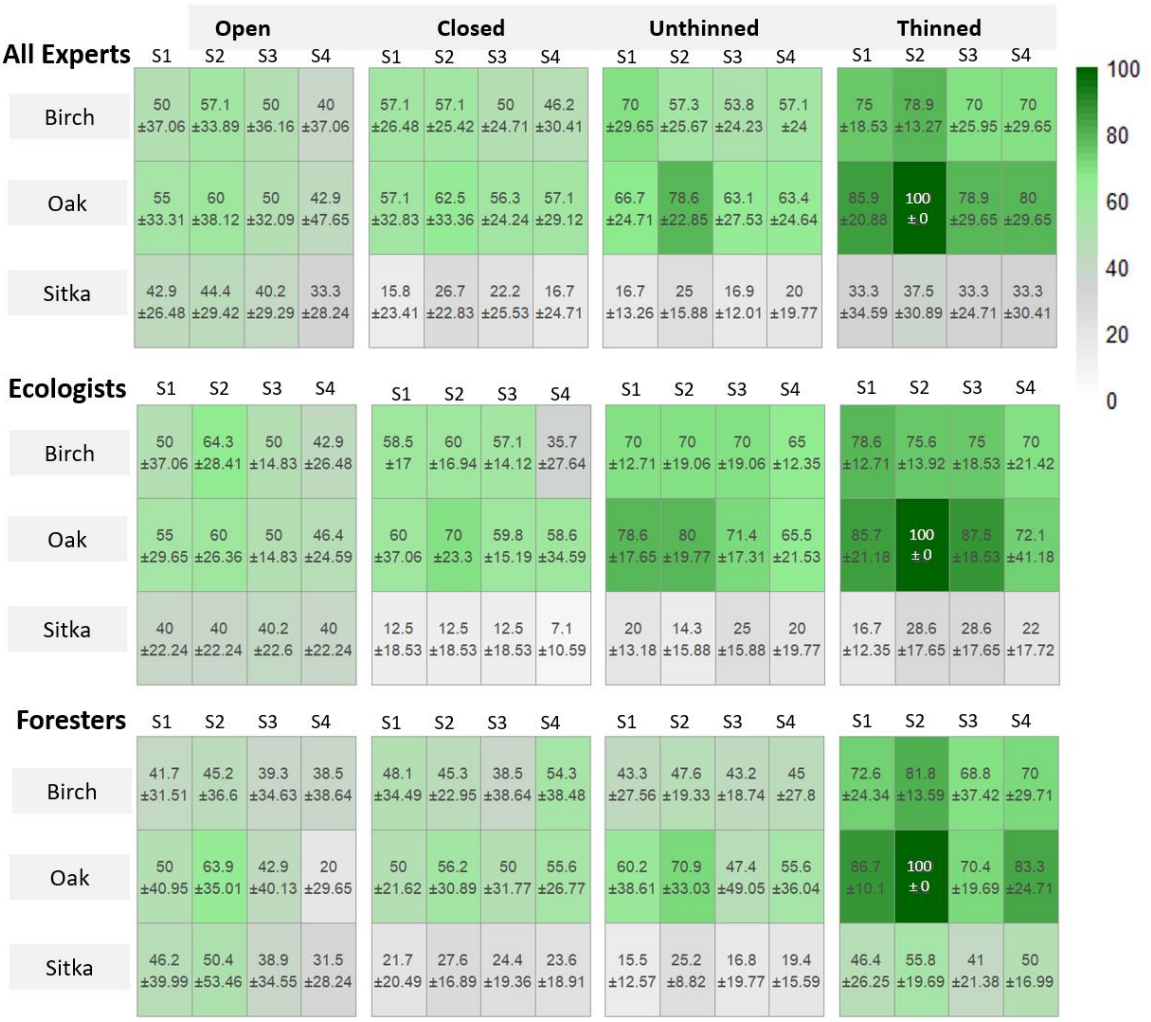

Figure D1 Median (±MAD) Invertebrate Scores (with 0 representing low and 100 high biodiversity) for entire panel (n = 21), ecologists only (n = 11), and foresters only (n = 10).

Scores are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Colours represent the scale (0-100) with colouring running from white to grey to green, with darkest green representing the highest values.

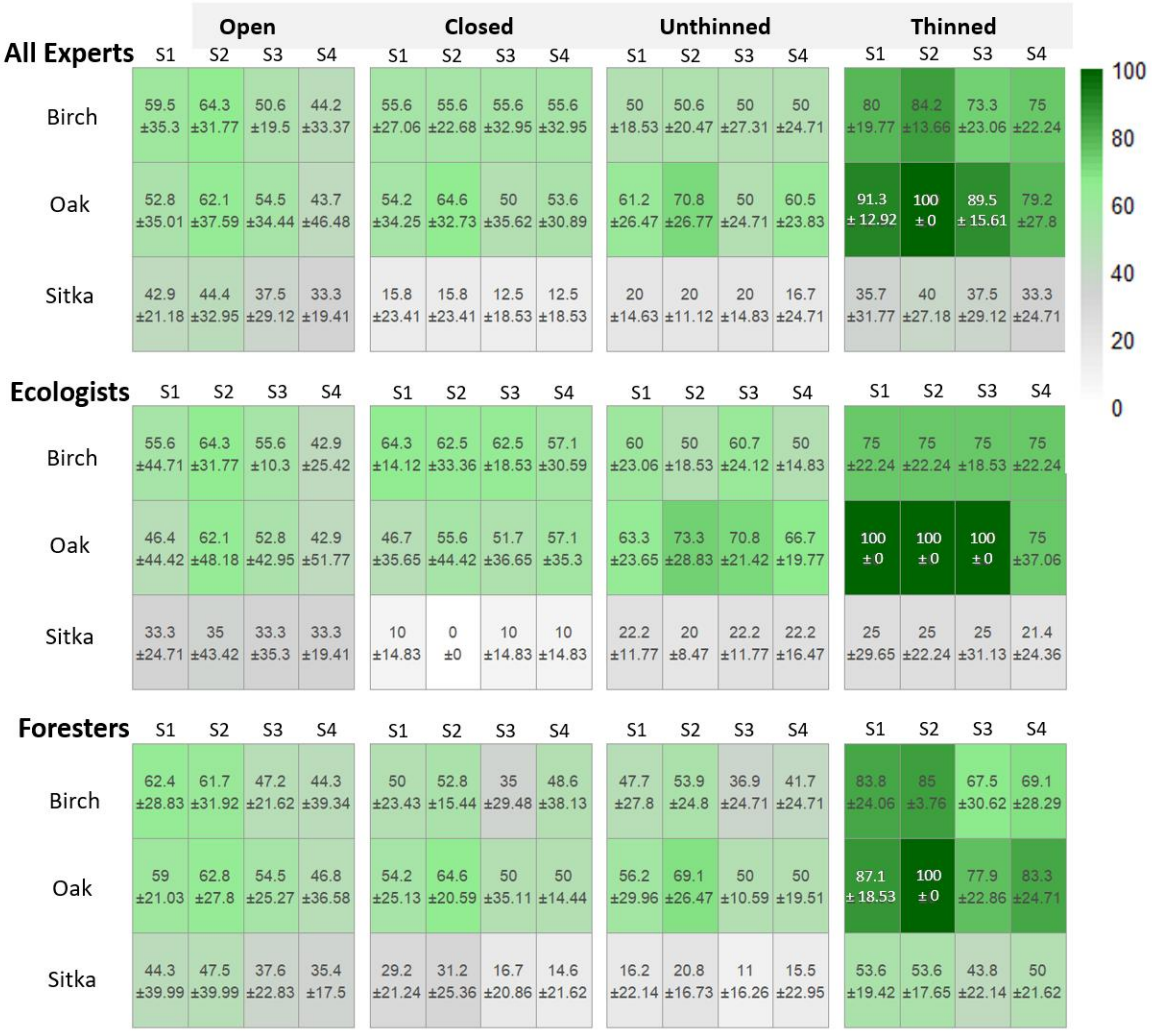

Figure D2 Median (±MAD) Vertebrate Scores (with 0 representing low and 100 high biodiversity) for entire panel (n = 21), ecologists only (n = 11), and foresters only (n = 10). Scores are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned) and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Colours represent the scale (0-100) with colouring running from white to grey to green, with darkest green representing the highest values.

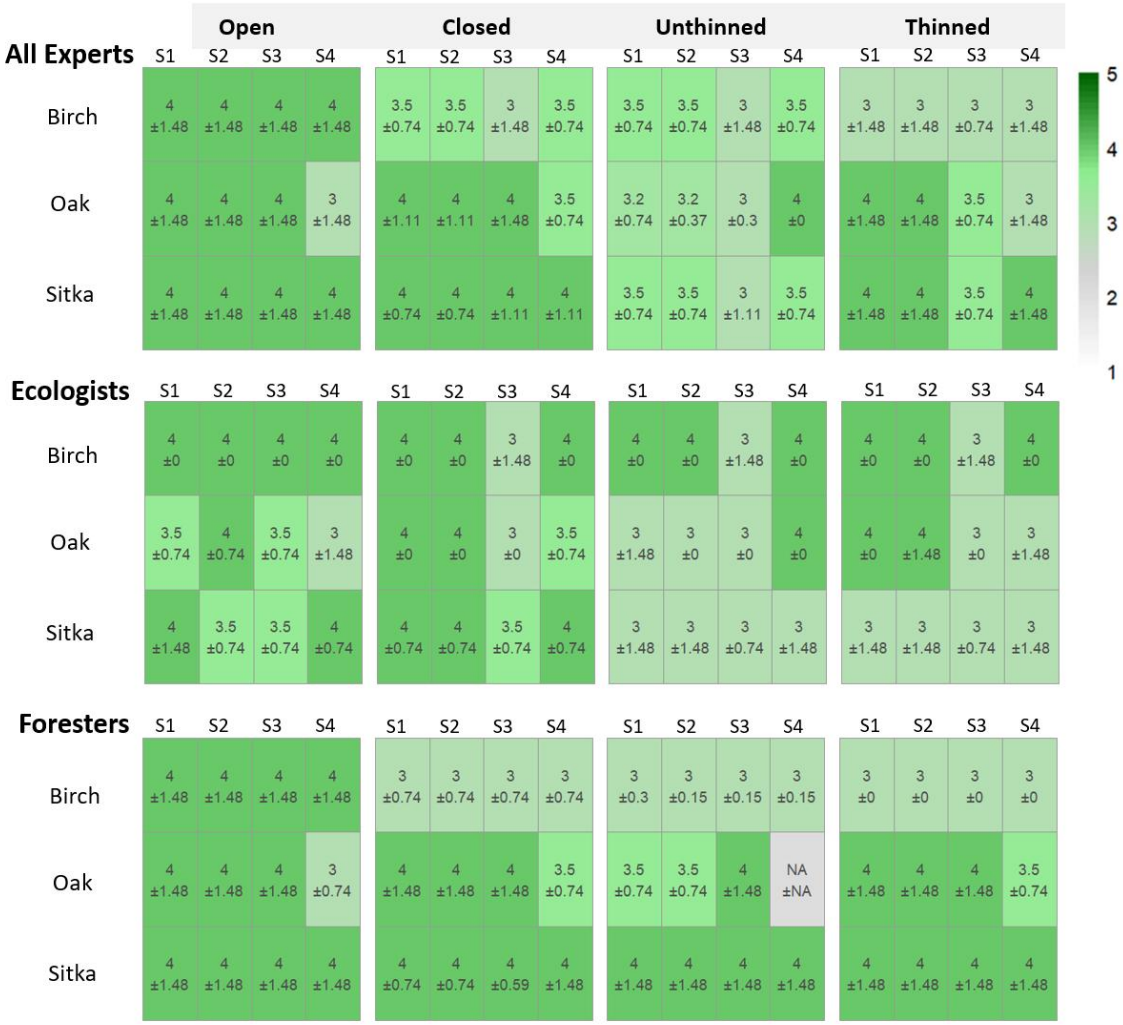

Figure D3 Median (±MAD) Flora Confidence Ratings (with 0 representing low and 5 high confidence) for entire panel (n = 23), ecologists only (n = 12), and foresters only (n = 11).

Scores are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned) and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Colours represent the scale (0-5) with colouring running from white to grey to green, with darkest green representing the highest values.

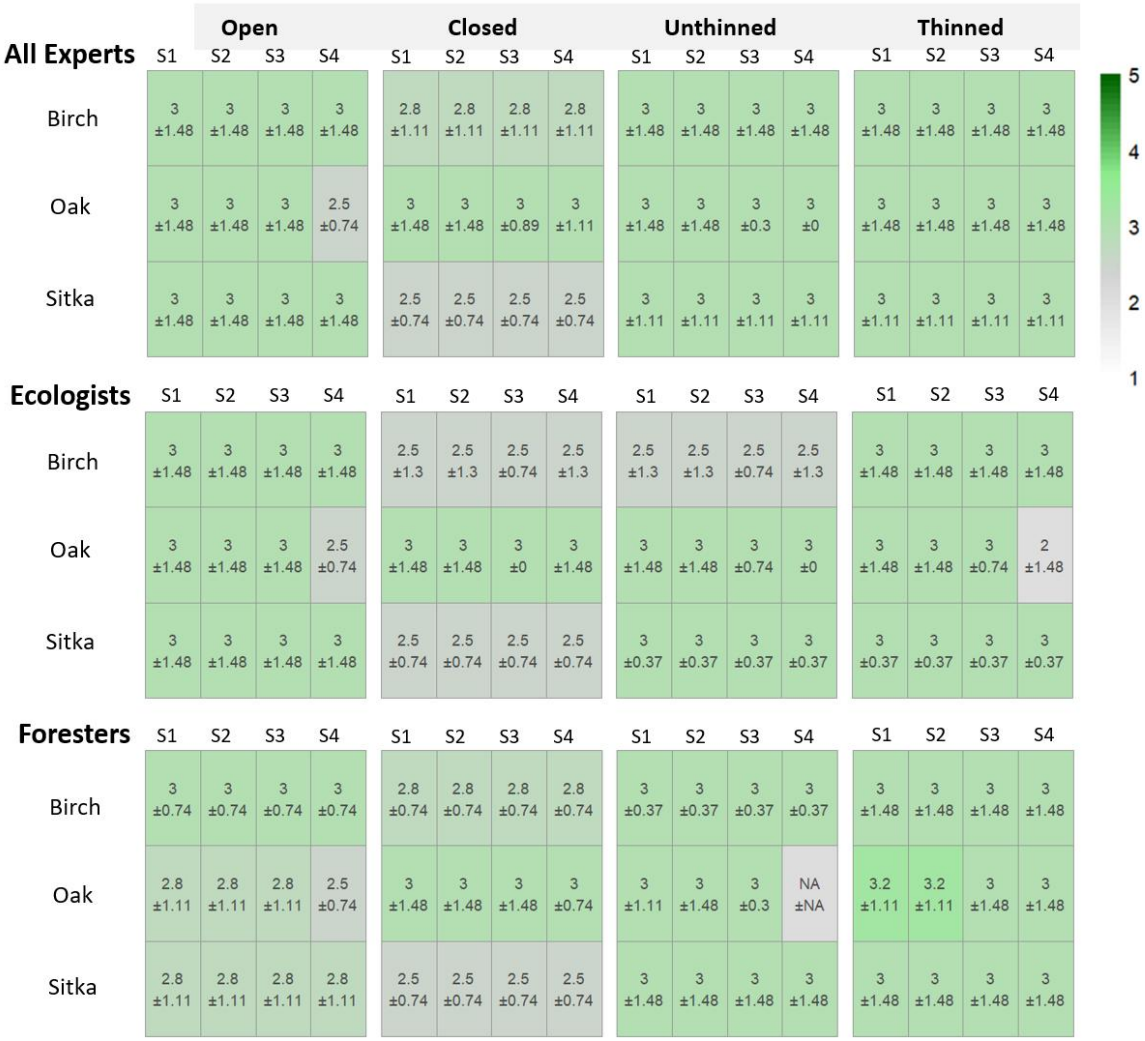

Figure D4 Median (±MAD) Invertebrate Confidence Ratings (with 0 representing low and 5 high confidence) for entire panel (n = 21), ecologists only (n = 11), and foresters only (n = 10). Scores are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned) and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Colours represent the scale (0-5) with colouring running from white to grey to green, with darkest green representing the highest values.

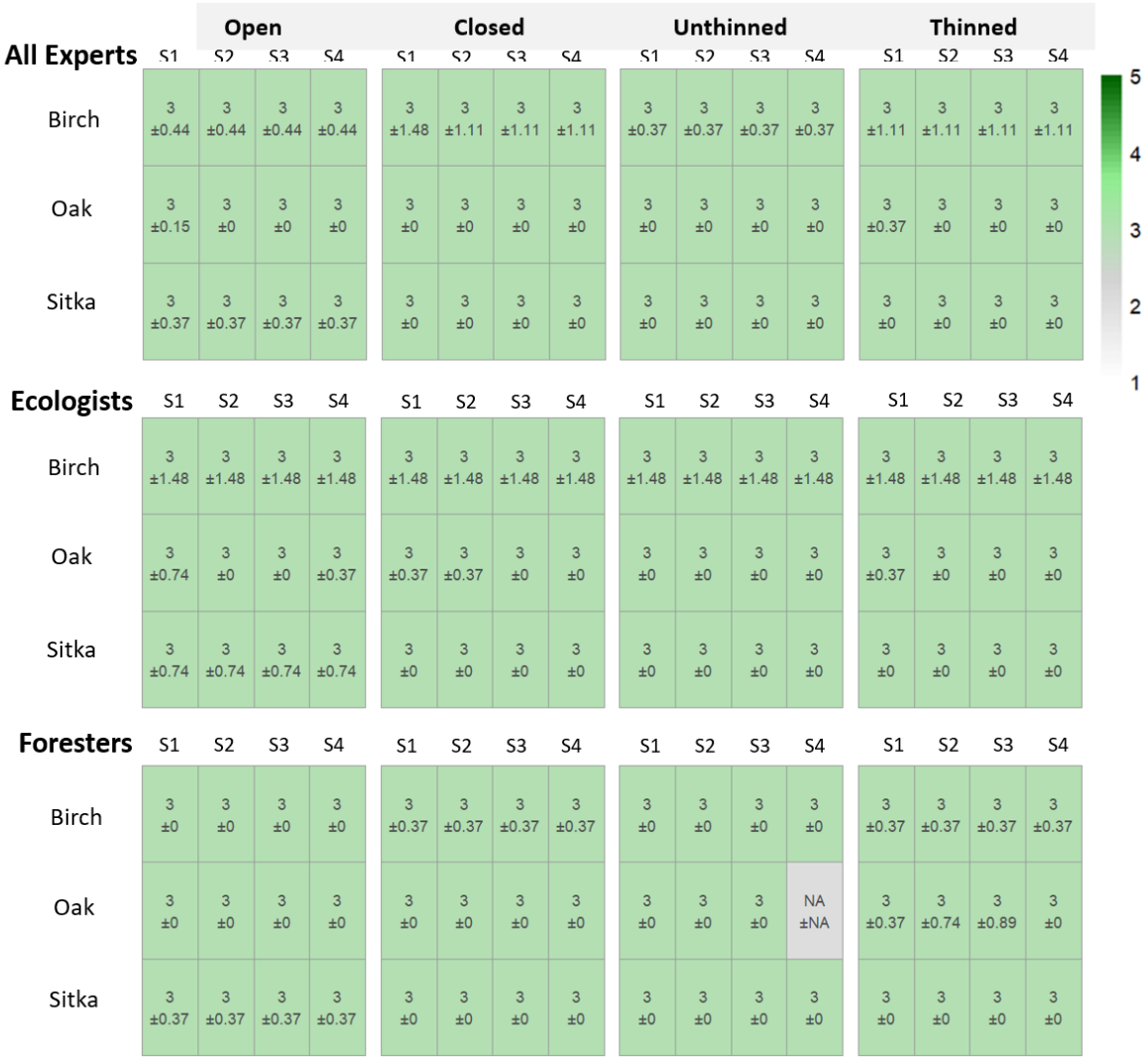

Figure D5 Median (±MAD) Vertebrate Confidence Ratings (with 0 representing low and 5 high confidence) for entire panel (n = 21), ecologists only (n = 11), and foresters only (n = 10). Scores are shown for the three scored taxa (Birch, Oak and Sitka Spruce), across the four development stages (Open = open stage, Closed = canopy-closure stage, Unthinned = mature even-aged unthinned, and Thinned = mature even-aged thinned) and for each soil type (S1 = podzols and brown podzolics, S2 = brown earth's, S3 = gleys; and S4 = highly modified peat and peaty podzols). Colours represent the scale (0-5) with colouring running from white to grey to green, with darkest green representing the highest values.