Biodiversity in Britain's Planted Forests

Results from the Forestry Commission's Biodiversity Assessment Project

Edited by Jonathan Humphrey, Richard Ferris and Chris Quine

Forestry Commission

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Contents

Section One: Introduction and context

Section Two: Plant, fungal and microbial communities

Section Three: Invertebrate and bird communities

Section Four: Conclusions

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Preface

Planted forests dominated by coniferous species such as Sitka spruce and Scots pine make up over half of the 2.8 million ha of woodland in the UK. These forests have been viewed by some as having little wildlife and even being inimical to nature conservation. However, others have suggested that such views are unduly influenced by the visual character and youthfulness of the forests.

As plantations have matured and been restructured to form diverse mosaics, so perceptions of their value for wildlife have shifted. Conservation and enhancement of biodiversity has become an important objective of much forest and rural land management, necessitating new research. In 1995 the Forestry Commission set up a project to assess biodiversity in planted forests. This publication brings together the findings of this project, demonstrates that many native species find the forest conditions to their liking, and challenges the notion that plantations are ecological deserts, or irrelevant for biodiversity. The scope for improvements in habitat quality, combined with their large area, means that planted woodland can make a significant contribution to UK biodiversity in the future as well as providing continued economic and social benefits.

The majority of papers in this publication were presented at the symposium 'Assessing Biodiversity in Britain's Forests', held in Harrogate in November 2000. The symposium brought together researchers, managers and policy-makers, with two main aims:

- To disseminate the results of the Biodiversity Assessment Project, undertaken by Forest Research; and
- To stimulate debate relating to the future management of planted forests and the identification of biodiversity indicators.

The publication is aimed at woodland managers, planners and policymakers concerned with the maintenance and enhancement of biodiversity within managed forests, particularly at the stand and habitat scales. Some of the chapters are based on more detailed papers in the scientific literature. Where this is the case, full references are given. Further valuable source material is also referenced. Participants in the symposium were encouraged to share their experiences, identify areas in which further work was required, and highlight key issues, within the framework of four separate workshops. The key points have been incorporated into the final chapter.

There are three main sections and a concluding section in these proceedings:

Section 1 **Introduction and context** reviews current international and UK forestry policies and incentives and how they relate to biodiversity conservation (Chapter 1). The origins of, and the rationale for the Forestry Commission's Biodiversity Research Programme are discussed in Chapter 2, with the Biodiversity Assessment Project itself described in more detail in Chapter 3. Chapter 4 gives an overview of the analytic methods used in the project.

Section 2 **Plant, fungal and microbial communities** comprises chapters on vascular plants (Chapter 5), the analysis of soil microbial communities (Chapter 6), deadwood volumes (Chapter 7), fungal assemblages (Chapter 8) and lichen and bryophyte communities (Chapter 9).

Section 3 **Invertebrate and bird communities** describes invertebrate assemblages recorded within and between the different forest stands in Chapter 10, while Chapter 11 gives a more general review of the effects of forest management and stand structure on forest bird communities.

Section 4 **Conclusions.** Based on the international literature, the results for the various species groups presented in Chapters 5–11 and the subsequent discussions in the four symposium workshops, Chapter 12 presents a number of options for the future management of planted forests, and for the development of biodiversity indicators. Further research needs are also highlighted.

Following on from the Biodiversity Assessment Project, Forest Research has established a **Biodiversity Evaluation and Indicators Development Project** which aims to update and synthesise the Biodiversity Assessment Project datasets, identify potential biodiversity indicators and disseminate findings to the forest industry. Further details of this project can be obtained from the editors.

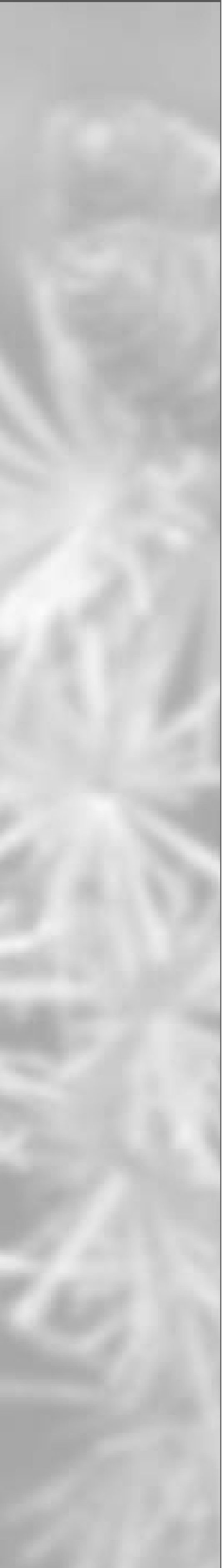
SECTION ONE

Introduction and context

CHAPTER 1

Introduction: the policy context for biodiversity

Tim Rollinson



Summary

Over many thousands of years, we in the UK cleared almost all of our natural woodland cover. Our forests helped to fuel our economic development and satisfy the demands of an increasing population for timber, fuel and farm land. But we paid a price; at the beginning of the 20th century woodlands in the UK covered just 5% of the land area, and little of this resembled the natural woodland cover. In the past century a million hectares of land were reforested, increasing our forest cover to over 10%. This was a substantial achievement. Throughout this period, we have had to address the challenges of rehabilitating and restoring our woodlands and forests. Our new forests are very different from what we know of our lost natural woodlands, but they have put woodland back on the map. We are improving them and, at the beginning of the 21st century, we can hand on a *bigger* woodland legacy to the next generation. A further challenge is to make sure that it is also a *better* and truly sustainable legacy.

The global background

In 1992 the world's leaders committed themselves to sustainable development at the United Nations Conference on Environment and Development (the Earth Summit) (UNCED, 1992). The Conference produced the world's first global agreement on how the world's forests should be managed in the *Statement of Forest Principles*. Since the Earth Summit, the UK and other European governments have built on the Rio Forest Principles and are committed to implementing:

- *The guidelines for the sustainable management of forests in Europe* – agreed at Helsinki in 1993 (Secretariat, 1993);
- *The guidelines for the conservation of the biodiversity of European forests* – also agreed at Helsinki (Secretariat, 1993);
- *The declaration and resolutions of the pan European ministerial conference on the protection of forests in Europe* – agreed at Lisbon in 1998 (Secretariat, 1998).

The Helsinki Guidelines interpreted the Rio Principles for European conditions and articulated the common concern of European countries to manage their forests sustainably. Through the Lisbon declaration, countries gave further recognition to the social and cultural importance of forestry in Europe. These international agreements are an expression of world-wide interest in sustainable forestry. Following their adoption, European countries, including the UK, have agreed a range of criteria for defining sustainable forest management and indicators for measuring progress towards it.

Sustainable forestry in the UK

Sustainable forestry is one component of the UK Government's wider commitment to sustainable development. In 1999, the UK Government published *A better quality of life: a strategy for sustainable development in the UK* (Anon., 1999). The strategy confirmed that the Government's approach to sustainable forestry is based on better management of existing forests; the continuing expansion of the woodland area; and conservation of natural capital: biodiversity, air, soil and water. Defining sustainable forest management is complex. It results from the interaction of the three functions of forests – economic, social and environmental, as represented in Figure 1.1.

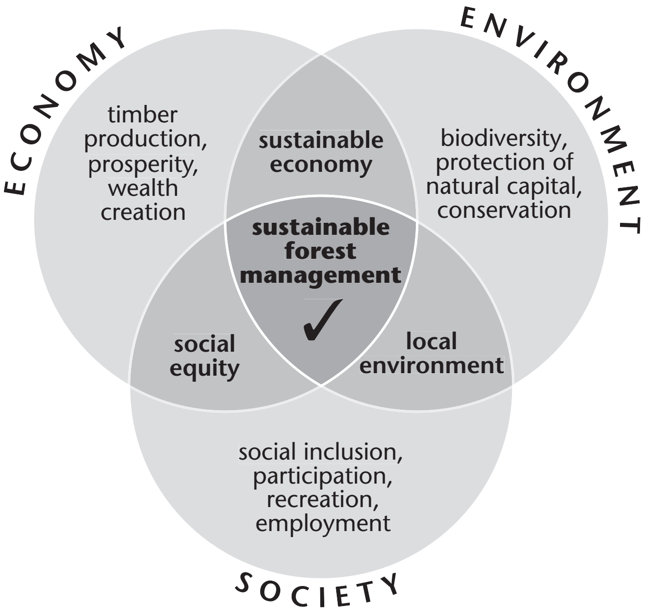


Figure 1.1

A conceptual model of sustainable forest management.

Biodiversity and the other environmental values of forests must be balanced with economic and social values in decisions about sustainable forestry. While the remnant ancient and semi-natural woodlands are the best overall for biodiversity, our maturing and restructured planted forests have an increasingly important role to play across the UK. Indeed, over the past 20 years, there has been unprecedented interest in the management of all types of woodlands and their biodiversity. Table 1.1 below gives examples of some of the policy and practice initiatives introduced in recent years which are relevant to the management of biodiversity within planted forests.

Table 1.1

Some policy and practice initiatives relating to woodlands.

Year of publication	Initiative
1990	Forest nature conservation guidelines
1996–8	Habitat and species action plans
1998	UK Forestry Standard
2000	Forests and water guidelines 3rd edition
2000	Forests and Peatlands guidelines
2000	UK Woodland Assurance Standard

The UK Forestry Standard

A cornerstone of the Government's commitment to sustainable forest management is the *UK forestry standard* (Forestry Commission, 1998). The standard provides a single, comprehensive statement of the Government's approach to sustainable forestry in the UK. It explains how the principles of sustainability will be delivered in practice and lists the criteria and indicators for the sustainable management of all forests in the UK. The standard includes guidance on a range of forest management practices including the felling and restocking of planted woodland, management of existing woodland, and the planting and management of new woods.

The UK Biodiversity Action Plan and forestry

The Government published *Biodiversity: the UK action plan* (UKBAP) in 1994 (Forestry Commission, 1994). The overall goal is to 'conserve and enhance biological diversity within the UK and to contribute to the conservation of global biodiversity through all appropriate mechanisms'. The emphasis is on partnership between public and private sector and NGOs at local, regional and national levels, and across sectors. The UKBAP lays emphasis on integrating biodiversity conservation measures into all sectors of economic activity so that it becomes part of sustainable development. In addition priority species and habitats have been defined and are subject to multi-agency and cross-sectoral action plans. The focus of attention has now shifted to implementation of the Biodiversity Action Plan targets throughout the UK (Anon., 1995).

Delivery

The development and publication of the *UK forestry standard*, *UK biodiversity action plan* and *UK woodland assurance standard*, together with the introduction of a range of schemes and incentives to encourage delivery on the ground has resulted in substantial changes in the way that plantations are designed and managed. In particular, the publicly owned forests managed by Forest Enterprise in England, Scotland and Wales, are currently undergoing a massive transformation. The large post-war forests, established as predominantly even-aged conifer plantations, are being redesigned. This involves diversifying age classes through planned, sequential felling followed by replanting and natural regeneration using a wider range of species, including a higher proportion of native broadleaves. Some stands of timber will be managed using silvicultural systems which avoid clear felling and encourage natural regeneration, for example through continuous cover systems of management. Areas of forest will be left unplanted as important open habitats to link key sites and encourage wildlife to move through the forest landscape. Forest Enterprise has recognised the importance of such landscape scale changes to forest structure, but increasingly managers are turning to the equally important ‘midi’ and ‘micro’ scale aspects of management which will enhance forest ecosystems and therefore biodiversity. Measures at these scales include diversifying stand structure, rehabilitating riparian zones and increasing the amount of deadwood.

In tandem with the diversification of the national forest estate has come a much greater awareness of the potentially damaging effects that some existing coniferous plantations can have on open-ground communities such as heathland and mires. Guidelines have been developed to help prevent further damage to valuable open habitats and to encourage restoration of areas previously planted with conifers. Native woodlands are being restored to semi-natural woodland on a large-scale across Britain. In addition, proposals for new plantations are subjected to rigorous environmental scrutiny and environmental assessments carried out when potential threats to biodiversity are identified.

Working together

Real progress has been made in recent years in delivering a range of policies for the enhancement of biodiversity in planted forests. We have learned that the greatest progress will be made where research, policy, regulation, incentives and published guidance are made to work together effectively. This requires: a shared understanding of the issues and barriers to progress; flexibility of approach to accommodate the needs of many stakeholders; resources to deliver desirable programmes; and a more ‘joined-up’ approach, with stakeholders working together and not solely to their own agendas.

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CHAPTER 2

An introduction to biodiversity research

Chris Quine

Summary

The origins of the Biodiversity Assessment Project, which is the topic for the remainder of the publication, are described and placed in context. The Biodiversity Research Programme (BRP), of which the Assessment Project was a major component, was part of the Forestry Commission's response to the UNCED Rio Summit. The BRP sought to bridge the gap between policy developments, and management by providing sound information based on research.

The Assessment Project has provided a baseline understanding of the biodiversity of representative planted forests. Increasingly, attention is being given to the impact of forest management activities, the needs of special habitats and species and the planning of biodiversity at the landscape-scale.

Introduction

In response to the UNCED Rio summit, the Forestry Commission introduced a Biodiversity Initiative (Ratcliffe, 1993) to develop a biodiversity policy for the management of forests supported by a multi-disciplinary biodiversity research programme. The particular objectives were to identify methods for improving biodiversity in managed forests, and to develop standards for managed forests.

The FC Biodiversity Policy has since been summarised (Forestry Commission,1998) as to:

- Conserve and where practical enhance the overall populations and natural ranges of native species, and the quality of wildlife habitats and ecosystems within woodlands.
- Contribute to the conservation and enhancement of internationally and nationally important and threatened species, habitats and ecosystems and of natural and managed habitats which are characteristic of local areas.
- Increase public awareness of and involvement with woodland biodiversity conservation.

Initial standards have also been summarised (Forestry Commission, 1998), elaborated in voluntary schemes (UKWAS, Anon., 2000), and a new suite of Biodiversity Guidelines are in preparation.

Biodiversity research

The Biodiversity Assessment Project was the major component of the initial Biodiversity Research Programme (BRP). The purpose of the project was to provide a baseline for biodiversity in planted forests, develop methods of measuring biodiversity, and inform standards and more general policy development. Research into biodiversity necessarily involves a range of skills and techniques. The project brought together scientists with diverse interests, including Forestry Commission staff, specialist contractors, and PhD students through collaboration with institutes in Britain and abroad.

As knowledge has increased, and managers have identified new aspects of biodiversity requiring research, other projects have developed; these will assume greater prominence in the future. Brief details of these research areas – developing methods of enhancing biodiversity, and catering for the needs of special species and habitats – are given below and summarised in Table 2.1.

So far it has rarely been possible to proceed by formal experimentation. Much of the initial work has relied upon review of existing literature, primary survey or monitoring. Only after this work has refined our understanding of the problems, is it possible to consider the application of demonstration projects or full experimentation. A variety of other outputs have been developed, including technical papers and seminars for practitioners, and scientific and conference papers to inform other scientists. There is increasing demand, where knowledge is well advanced, to integrate findings into decision support tools.

Management for special species and habitats

The conservation of special species and habitats is widely held to be desirable, and their protection is the target of domestic legislation and European Union directives (Chapter 1). Research is required to understand the specific requirements, identify the influence of forest management and identify beneficial activities.

There have been three strands to this research (Table 2.1):

- Genetic conservation, in particular the use of native tree species, and the benefits of locally-adapted trees.
- Special species, in particular species dependent upon woodland habitats, and the subject of UK Species Action Plans (Anon., 1995).
- Special habitats, in particular native woodland and important semi-natural open habitats found in close proximity (or within) forests, and the subject of UK Habitat Action Plans (Anon., 1995).

Management to conserve and enhance biodiversity

Managed forests can provide important habitats for a range of native species. Stand management, and the resultant structure, can have an important influence on this biodiversity. Some of the beneficial features of existing stands have been obtained accidentally, but there is an opportunity for planned provision to enhance their value – for example through tree species diversity, open space, stand retention, and incorporation of deadwood (Table 2.1). The control of effects of potentially damaging species (such as the grey squirrel and deer) is important, but some grazing may also have a beneficial effect.

An integrated approach at the landscape scale

Recently, there has been an acknowledgement that biodiversity conservation and enhancement requires planning at scales greater than the individual stand. In addition, the focus of forest planning has increased in scale, through development of strategic, long-term and forest design plans. The ability to conduct such work has benefited from the rapid developments in, and adoption of, geographic information systems (GIS). Landscape-scale solutions are required to meet the needs of special species, restore the best examples of native woodlands and gain benefits of biodiversity from the management of productive forests (Table 2.1). The Forestry Commission has developed an Ecological Site Classification to ensure that productive species and new native woodlands are placed on appropriate sites. The potential for ESC to be combined with knowledge of natural disturbance regimes to provide new processes of forest design has been explored. Most recently, the importance of the mosaic of habitat types, and the needs of special species has been combined in a landscape ecology research project.

Table 2.1 *Main strands of Forestry Commission biodiversity research, with example publications.*

General theme	Topics	Subjects
Needs of special species and habitats	Genetic conservation	*Conservation of genetic resource* (Ennos *et al.*, 2000)
		Use of local origins (Herbert *et al.*, 1999)
	Special habitats	*Restoration of native pinewoods and oakwoods* (Humphrey and Nixon, 1999)
		Peatland restoration (Patterson and Anderson, 2000; Anderson, 2001)
	Special species	*Red squirrel* (Pepper and Patterson, 1998)
		Raptors (McGrady *et al.*, 1997; Petty, 1998)
Habitat management and enhancement	Tree species diversity	*Inclusion of broadleaves* (Humphrey *et al.*, 1998a)
	Impacts of herbivores	*Grazing* (Humphrey *et al.*, 1998b; Mayle, 1999; Gill, 2000)
	Encouragement of structural diversity	*Deadwood* (Ferris-Kaan *et al.*, 1993; Hodge and Peterken, 1998; Humphrey *et al.*, 2002); *Silvicultural systems* (Kerr, 1999)
Integrated research at the landscape scale	Landscape and sites	*Selection of suitable sites for woodlands – Ecological Site Classification* (Ray, 2001; Pyatt *et al.*, 2001)
	Mimicking natural processes	*Natural disturbance regimes* (Quine *et al.*, 1999; Quine *et al.*, 2002)
	Landscape ecology	*Landscape ecology* (Ferris *et al.*, 2000; Bell, 2003; Humphrey *et al.*, 2003)

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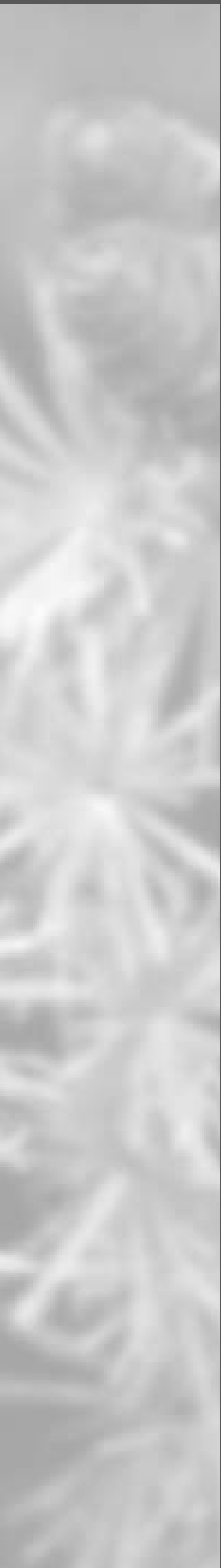

CHAPTER 3

The biodiversity assessment project: objectives, site selection and survey methods

Jonathan Humphrey, Richard Ferris and Andrew Peace

Summary

The background to, and the objectives of, the Biodiversity Assessment Project are presented, together with an overview of the project methodology. The rationale for selection of sites and the types of biodiversity assessed is described together with illustrations of crop types and plot design. Fifty-two permanently marked plots were surveyed in total, covering a range of different crop and site types in three contrasting bioclimatic zones (upland, foothills and lowlands). Assessments were carried out over a 2–4 year period at each site and covered: structural aspects of biodiversity (e.g. vertical foliage cover and deadwood); taxa important in ecosystem functioning (e.g. fungi); and a range of different groups which make up the 'compositional' aspect of biodiversity (e.g. higher and lower plants, invertebrates). A chronosequence of four different stand stages was replicated twice for each crop type in each climate zone. The stages were: pre-thicket (age 8–10 years); mid-rotation (20–30 years), mature (50–80 years) and over-mature (70–250 years), selected to encompass the normal range of stand structures generated by patch clearfelling. Additional plots were established in semi-natural woodland to allow comparisons between the biodiversity of plantations and native stands. Summary data for stand structure, soil and climate are presented as a reference source for subsequent chapters.

Introduction

The Biodiversity Assessment Project was established in 1995 in support of Forestry Commission policies relating to the conservation and enhancement of biodiversity in UK forests (Chapter 2). The primary focus of the assessment project was productive conifer forest, which at 1.54 million ha currently comprises 6.7% of the total UK land area (Anon., 1998). The majority of these forests have been established within the past 100–150 years, usually on previously unwooded ground (Hodge *et al.,* 1998), but occasionally through conversion of ancient semi-natural woodland (Spencer and Kirby, 1992). Opinions differ as to the potential value of these 'new forests' for biodiversity. Attention has often been drawn to deleterious effects on the flora and fauna of the habitats which forestry replaces or modifies (e.g. Ratcliffe and Thompson, 1989), but there have also been a number of studies which have highlighted the positive value of planted forests for wildlife (e.g. Petty *et al.*, 1995; Ratcliffe and Claridge, 1996). However, these studies have been mostly site specific, and there have been no comparative studies of plantations of different crop species in contrasting bioclimatic zones, or on a range of varied site types. Similarly, there have been few attempts to compare the biodiversity of planted forests with that of native or semi-natural woodlands. This base-line information is needed to provide a quantitative framework for understanding the levels/types of biodiversity currently found in plantations, and to offer a way of measuring future improvements, or otherwise, in biodiversity brought about by changes in management practices.

Assessing biodiversity is an extremely difficult task, as it is rarely cost-effective or practical to conduct a complete census of all taxa within a forest stand, let alone an entire catchment or forest landscape. Therefore, the identity of biodiversity 'indicators' or surrogate measures of biodiversity has become a research priority in recent years (Ferris and Humphrey, 1999). Indicators are species or features whose presence, magnitude or abundance are believed to reflect the occurrence and abundance of other species in the community (Simberloff, 1998). Ferris and Humphrey (1999) have proposed a number of easily measurable indicators which could be used by forest managers to assess biodiversity at the forest stand scale (1–50 ha). Examples include: deadwood, vertical stand structure and the occurrence of particular tree species such as birch (*Betula* spp.). However, the link between such indicators and wider biodiversity has not be substantiated in British forests to the same degree as in other countries.

The objectives of the Biodiversity Assessment Project were therefore to:

- Obtain base-line information on the types/levels of biodiversity in planted forests.
- Evaluate the contribution of planted forests to the conservation of native flora and fauna through comparisons with semi-natural woodlands.
- Identify potential biodiversity indicators by relating the diversity of range of measured taxa to soil, climate, vegetation and stand structure variables.

Site selection

Assessments were conducted within planted conifer forests managed by clearfelling (when stands are approximately 40–80 years old) and restocking, essentially the ‘normal’ silvicultural practice for commercial forests (Hibberd, 1991). Extensive ‘restructuring’ of these forests over the last 10–20 years in response to landscape considerations has created a patchwork of different stand ages/stages, including stands retained beyond normal economic felling age for amenity purposes or as ‘natural reserves’ (McIntosh, 1995; Anon., 2000). To encompass the structural variability generated by restructuring, a chronosequence approach was adopted, following Spies (1991) and Pollard (1993). This approach allows comparisons to be made between stands of different ages without the necessity for monitoring over long time periods within individual stands. However, a number of provisos must be adopted – stands should have similar soils, climate, altitude and site history and be located on comparable topographies.

In total, 52 assessment plots were sampled over a 4-year period (Figure 3.1). These were stratified initially by bioclimatic zone following the Forestry Commission’s Ecological Site Classification (ESC – Pyatt *et al.*, 2001). The zones were uplands, foothills and lowlands, delineated by annual rainfall totals of: >1500 mm – uplands; 800–1500 mm – foothills; and <800 mm – lowlands. Study sites were established in the main commercial crop types found with each bioclimatic zone: Sitka spruce (*Picea sitchensis* (L.) Bong. Carr.) in the uplands; Sitka spruce and Scots pine (*Pinus sylvestris* L.) in the foothills; Scots pine, Corsican pine (*Pinus nigra* var. *maritima* L.), and Norway spruce (*Picea abies* (L.) Karst.) in the lowlands. Two replicate sites were selected for each species x bioclimatic zone combination. To minimise edge effects and the influence of non-forest habitats, sites were chosen from within large forest blocks.

At each site, a chronosequence of 1 ha (100 m x 100 m) sample plots (each with a 30 m buffer) was established in forest stands in different developmental stages (with one plot per stage):

- Pre-thicket – restock sites, crop height 2–4 m, age 8–10 years, incomplete canopy closure.
- Mid-rotation – crop height 10–20 m, age 20–30 years, canopy closure, no understorey.
- Mature – crop height 20–25 m, age 50–80 years, canopy closure, some development of understorey layers.
- Over-mature (beyond economic maturity and acquiring some of the ecological characteristics of natural old-growth forests *sensu* Oliver, 1981) – crop height >25 m, age 60–250 years, canopy break-up, well-developed understorey layers, accumulation of deadwood.

Stage 4 stands were not available in some of the lowland crop types and in the foothills Scots pine chronosequences. In the latter case, over-mature plots were set up in self-seeded ‘old-growth’ semi-natural pinewood areas. These represent modified remnants of the original natural boreal forest in Scotland (Worrell, 1996). In the uplands and lowlands, semi-natural oakwood plots were established for comparison with the conifer stands. Only stages 2 and 3 were available in the oakwoods owing to a lack of large areas of newly regenerating oak and lack of very old stands (as a consequence of past management). The full set of site details is recorded in Annexe 1.

Figure 3.1

Location of Biodiversity Assessment plots; 52 plots were sampled in total over a 4-year period.

Locating suitable assessment sites according to the chronosequence rules proved to be more difficult than anticipated. Few stands were homogeneous in terms of site and crop parameters; with over-mature stands of a suitable size (2.5 ha) being very rare. The search strategy adopted was to locate over-mature stands first and then search for the three younger stages on the same site types as nearby as possible. Inevitably, suitable stands were not always found within the immediate vicinity (e.g. Knapdale – site 5.3; Windsor – site 4.4, see Annexe 1). In addition, it was impossible to select sites with the same site history and rotational age. The majority of pre-thicket plots were located in second rotation stands, but all mature and over-mature stands were first rotation. The consequence of these compromises in the site selection criteria is discussed in relation to the analyses of individual species groups (see Chapters 5–11).

Assessment methods

Plots were selected to minimise internal heterogeneity in terms of stand structure, species composition, topography and hydrology. A standardised system of assessment stations was established to maximise potential comparisons between measured attributes and to minimise disturbance during sampling (Figure 3.2). The plots were permanently marked. Features and species groups were selected for assessment on the basis of:

- The ‘structure-function-composition’ model of biodiversity (Schulze and Mooney, 1994; Figure 3.3). This model rationalises biodiversity into compositional aspects (e.g. species), structure (e.g. physiognomy of forest stands and associated habitats) and function (processes such as natural regeneration, nutrient and carbon cycling).

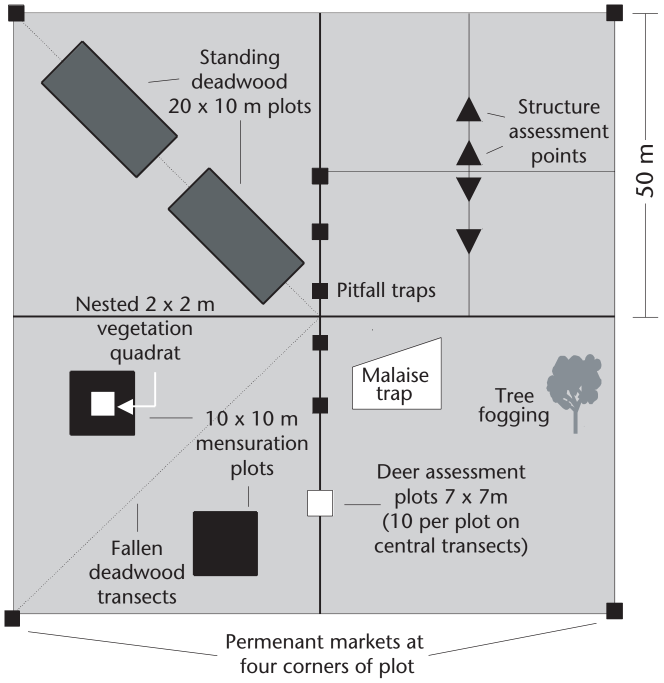

Figure 3.2

Basic layout of 1 ha assessment plot. The mensuration, vegetation, stand structure and deadwood quadrats and transects were replicated within teach 50 x 50 m quadrant.

- Practicality: the cost, and availability of taxonomic expertise were taken into consideration together with the need to identify features readily measurable by field staff.

- Ecology: species groups with wide ecological amplitude and where possible known habitat requirements were prioritised over more site-specific groups to allow comparisons between sites and stands.

A list of the main assessments stratified by the ‘structure-function-composition’ model is given in Figure 3.3. The full list of assessments is given in Table 3.1 with a quick overview of the assessment methodologies. Methodologies for the site and stand assessments are outlined in detail below. More details of the survey methods for individual taxonomic groups can be found in the relevant chapters. Pilot surveys of deer, songbirds and small mammals were conducted on an initial subset of plots to determine practicality of assessment methods. Deer densities were estimated from fecal pellet counts (following Mayle *et al.*, 1999). However, at the scale of 1 ha this method is not thought to provide

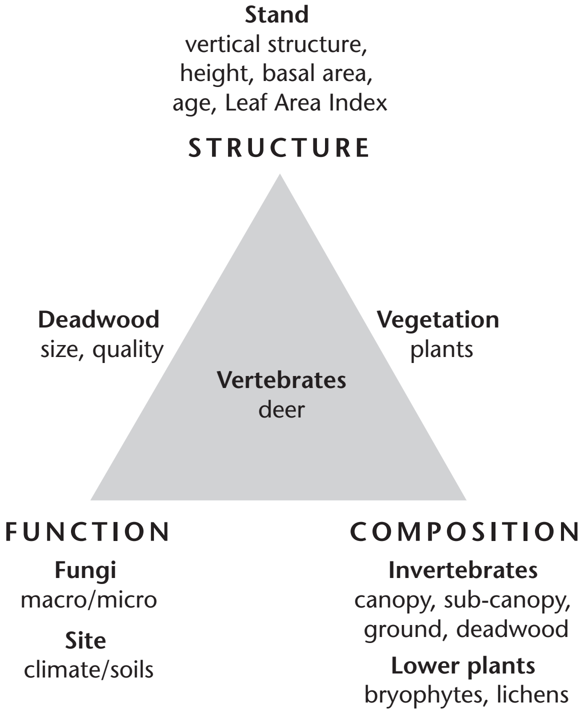

Figure 3.3

Theoretical model of biodiversity attributes used to stratify selection of features and taxa to assess.

Table 3.1 *Assessments and summary of assessment methodologies. Locations of sampling stations are given in Figure 3.1.*

Feature/taxonomic group	Assessment methodology
Climate variables	Output from ESC-DSS (see section below)
Soil chemistry and litter depth	One soil pit dug per 1 ha plot and described, chemical analysis of two strata – 32 bulked samples per strata per 1 ha sample plot (see section below). Mean litter depth/ha estimated from 32 random samples (four in each mensuration plot)
Vertical structure	Per cent cover of foliage estimated in four vertical strata – ground, shrub, lower and upper canopy layers – at 16 sampling points (see section below)
Leaf Area Index	Estimated from light measurements along transects with each 1 ha plot (see section below)
Mensuration	Diameter at breast height, height to live crown, height of all trees within the eight 10 m x 10 m plots (see section below)
Natural regeneration of seedlings (< 1.3 m in height)	Height of all seedlings recorded in 10 randomly located 40 cm x 40 cm plots within each mensuration plot (data not yet analysed)
Soil seed banks	One sample per plot bulked from collections in each mensuration plot (data not yet analysed)
Ground vegetation (bryophytes, lichens and vascular plants)	Per cent cover and frequency in 2 m x 2 m quadrats nested within the eight 10 m x 10 m mensuration plots (details in Chapter 5)
Soil microbial communities	Thirty-two soil samples taken from each 1 ha plot, four in each mensuration plot (details in Chapter 6)
Deadwood: fallen (logs), standing (snags) and stumps	Volume and length of logs recorded on two diagonal transects using the line intercept method (Warren and Olsen, 1964), volume of snags and stumps recorded in eight 20 m x 10 m plots (details in Chapter 7)
Macrofungi	Frequency and abundance of fruiting bodies recorded 3 times yearly over 4 years in each mensuration plot (details in Chapter 8)
Bryophytes and lichens growing on deadwood	Species frequency and abundance estimates on individual pieces of deadwood (details in Chapter 9)
Invertebrates: sampling stratified by ground, sub-canopy, canopy strata and deadwood	Five pitfall traps/ha, one malaise trap/ha, one tree fogged, deadwood emergence traps (details in Chapter 10)
Songbirds	Point counts within and adjacent to each 1 ha plot, plus territory mapping (details in Chapter 11)
Small mammals	Live capture/release using paired longworth traps (data not analysed)
Deer	Densities estimated from ten 7 m x 7 m fecal pellet group clearance plots per 1 ha (data not analysed)

reliable estimates of population densities (Gill, 2000), so no interpretation of these datasets has been undertaken within this publication. Scale is also a problem with interpretation of the songbird data, bird territories range to a much greater spatial scale than 1 ha, and the problems associated with the sampling method are discussed more fully in Chapter 11. Finally, small mammal sampling was abandoned after only one year owing to excessive costs and logistical difficulties.

Assessment of climatic variables

The climate data were obtained from datasets held within the ESC computer-based decision support system (ESC-DSS – Ray, 2001). For both accumulated temperature (AT) and soil moisture deficit (MD), 30-year means have been calculated for all 10 km squares throughout Great Britain using meteorological data collected over the 1961–1990 period (Barrow *et al.*, 1993).

AT expresses the degree of warmth or available heat energy (Bendelow and Hartnup, 1980) and is measured by the number of days-degree above 5°C. MD is expressed as the maximum accumulated amount that monthly potential evaporation exceeds precipitation (Bendelow and Hartnup, 1980), and is essentially a measure of climatic wetness/dryness. The 'Detailed Aspect Method of Scoring' (DAMS) wind score is an index developed by Quine and White (1993), which measures the physiologically constraining effect of wind on tree growth and mortality (and hence may link with deadwood accumulations). DAMS calculations involve a windiness map, elevation, topex and aspect. Continentality expresses the seasonal variation or range of climate. Oceanic areas tend to have cool summers and mild winters, whereas continental areas exhibit more extremes of warmth and cold. This factor helps shape the length of the growing season (although it was not included as an environmental parameter within any of the subsequent analyses).

The digitised climate data did not become available until after the plots had been assessed, and with hindsight it is clear that annual precipitation totals have not been a particularly good indicator of differences in climate between sites, as AT, MD and DAMS vary on a site by site basis rather than at the zonal scale (Annexe 1). The most pronounced differences in climate were between northern (foothills and uplands) and southern sites (lowlands) with few differences in mean values between foothills and upland sites. The analyses of the various taxonomic groups described in subsequent chapters were therefore interpreted in terms of this north-south division where appropriate.

Stand structure and mensuration assessments

Two 10 m x 10 m quadrats were arranged diagonally across the centre of each 50 m x 50 m quarter of the 1 ha plot, giving eight quadrats in total per plot. Within these quadrats, assessments of dbh, height to the base of the live crown (HTLC), and top height (TOPHT), were made by species, for all living trees ≥ 7 cm dbh. In those plots where stocking density was low (e.g. stage 4 stands), the quadrats were extended (proportionately from each corner) to 25 m x 25 m to obtain a sufficient sample of trees. Mean basal area (MBA) was calculated for each 1 ha plot following Hamilton (1975). Vertical stand structure was assessed using a visual cover method within each 50 m x 50 m quarter of the 1 ha assessment plot. Four measurements, each 10 m apart were made along a north-south transect, running through the centre point of each quarter, yielding 16 measures in total for each 1 ha plot (Figure 3.2). Four vegetation strata were defined: S1 (field) 10 cm –1.9 m in height; S2 (shrub) 2–5 m; S3 (lower canopy) 5.1–15 m; and S4 (upper canopy) 15.1–20 m. Percentage cover of vegetation within each vertical stratum was described to the nearest 5% and expressed as a mean of the 16 stand structure measures. To convert these cover values to a unified measure of stand structure, a cover index (CI) was calculated using the formula:

$$\mathrm{CI} = 1.9s_1 + 3s_2 + 10s_3 + 5s_4$$

where $s_1 - s_4$ are the values for field, shrub, lower canopy and upper canopy strata, and numbers refer to the depth of each stratum in metres. The C.I. therefore ranges in possible values from 0–1990 (assuming a maximum cover value of 100% in each layer). Summary statistics for stand structure and mensuration data are shown in Table 3.2.

Leaf area index

Measurements of photosynthetically active radiation (PAR) were taken under diffuse light conditions at 5 m intervals, along two diagonal transects across each assessment plot. For this purpose, a hand-held sunfleck ceptometer (Decagon Instruments, USA) with an 80 cm probe was used, held at a height of approximately 1.5 m above the ground. A second, calibrated probe was placed outside the assessment plot, in a clearing not obscured by trees. Sets of five readings were taken simultaneously at 30 second intervals with both probes, averaged and then recorded. The data were converted to Leaf area index (LAI) values using the canopy radiation model of Goudriaan (1988) for diffuse light conditions. Under these conditions of incident light (PAR_{inc}), only LAI and the light extinction coefficient (K) determine canopy light absorption (PAR_{abs}) i.e. ($PAR_{abs}=PAR_{inc}(1-e^{(-K*LAI)})$). Summary statistics for the LAI are shown in Table 3.2.

Soil and litter sampling

Soil samples were taken from the four corners of the eight 10 m x 10 m plots (i.e. 32 locations per 1 ha plot) at two depths: 0–5 cm and 5–10 cm in depth. The samples were bulked to give one sample

Table 3.2 *Summary of soil, climate, and stand data. SD: standard deviation.*

Variable	Description	Max.	Min.	Mean	SD
pH1	pH – layer 0–5 cm	5.3	3.3	4.1	0.5
P1	Soil phosphorus (mg l^{-1}) – layer 0–5 cm	45.5	0.6	12.9	11.5
K1	Soil potassium (mg l^{-1}) – layer 0–5 cm	704.0	19.6	161.5	140.7
Mg1	Soil magnesium (mg l^{-1}) – layer 0–5 cm	982.0	9.4	204.2	207.2
Ca1	Soil calcium (mg l^{-1}) – layer 0–5 cm	2 499.0	47.5	514.7	554.6
ORG1	Soil organic matter content (%) – layer 0–5 cm	95.1	2.9	46.8	31.3
$NH_4$1	Soil ammonium (mg kg^{-1}) – layer 0–5 cm	373.0	8.0	111.2	97.8
$NO_3$1	Soil nitrate (mg kg^{-1}) – layer 0–5 cm	164.0	0.0	17.3	36.0
pH2	As above – layer 5–10 cm	7.9	3.6	4.3	0.8
P2	As above – layer 5–10 cm	33.5	0.1	5.8	8.8
K2	As above – layer 5–10 cm	415.0	6.7	84.6	95.4
Mg2	As above – layer 5–10 cm	456.0	3.8	98.9	121.7
Ca2	As above – layer 5–10 cm	35 270.0	17.2	1 042.4	6 683.7
ORG2	As above – layer 5–10 cm	84.9	0.7	17.0	22.8
$NH_4$2	As above – layer 5–10 cm	346.0	2.5	42.8	81.4
$NO_3$2	As above – layer 5–10 cm	79.5	0.0	7.5	17.6
AT	Accumulated temperature (no. day-degrees > 5°C)	2 002.0	771.0	1 405.7	370.5
MD	Soil moisture deficit (mm)	225.0	24.0	128.7	63.5
DAMS	Windiness/exposure	18.0	10.0	13.4	2.1
S1	Vertical cover field layer (%)	72.6	0.0	17.3	21.0
S2	Vertical cover shrub layer (%)	40.9	0.0	4.7	8.2
S3	Vertical cover lower canopy layer (%)	52.5	0.0	12.9	14.4
S4	Vertical cover upper canopy layer (%)	31.6	0.0	7.2	9.6
CI	Cover Index	651.6	34.0	211.8	163.8
TOPHT	Top height (m)	32.9	2.1	15.4	7.5
HTLC	Height to live crown (m)	17.9	0.0	7.5	5.1
MBA	Mean basal area (m^2 ha^{-1})	60.0	0.0	27.7	15.7
LAI	Leaf area index	10.2	0.5	2.7	1.9
TREESP	No. of tree species per plot	9.0	1.0	3.5	2.2
AGE	Crop age (years)	238	6.0	59.6	49.8
LITTER	Litter depth (to nearest 0.5 cm)	8.0	0.0	2.9	2.0

for each depth per plot. Available P, K, Ca and Mg were obtained by extraction, using 0.5 M ammonium acetate/acetic acid solution at pH 4.5, following a modification of Morgan's method (Morgan, 1941). Mineralised N (in NH_4^+ and NO_3^- form) was determined before and after a 28 day incubation period at 30ºC following the ADAS/MAFF method (Anon., 1986); pH was determined in aqueous solution using the MLURI/SAC method (Anon., 1985). Organic matter content was determined by loss on ignition. Litter depth was recorded in each 10 m x 10 m vegetation assessment plot by taking a mean of four random measurements. Summary values for soil chemistry, and litter depths are in Table 3.2.

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CHAPTER 4

The use of multivariate statistics – a brief introduction

Andrew Peace

Summary

Community ecologists can explore the ways in which abiotic environmental variables influence biotic composition by way of multivariate statistical techniques. One commonly used set of multivariate techniques is called ordination where sample plots are arranged along environmental gradients on the basis of their species composition. A brief description is given of the ordination methods used to interpret the data collected as part of the Biodiversity Assessment Project. The outputs from the various ordination analyses are described in Chapters 5–10.

Introduction

The assessment phase of the Biodiversity Research Project has resulted in tens and often hundreds of species being recorded within individual components of the study. As a consequence, one key aim of the statistical analyses of these datasets has been to discover and summarise the main patterns of variation in the species community data, and relate these to sets of environmental variables recorded at each sample plot. Analyses of complex community datasets benefit from the use of specific multivariate statistical techniques. One such technique, that allows inferences to be made on the relationship between plant and animal communities and their environment, is known in general terms as ordination.

Ordination is simply the arrangement or ‘ordering’ of species and/or sample units along environmental gradients. Its purpose is to interpret patterns in species composition. Basically it summarises community data by reducing the high dimensionality of the original dataset (one dimension for each recorded species) to a lower dimensional ordination space in which ecologically similar species and samples are plotted close together, and dissimilar species and samples are placed far apart. The benefits of using ordination methods include:

- Relationships within datasets containing a large number of sites and species are virtually impossible to visualise or interpret before reduction to low-dimensional space.
- Axes of this low-dimensional space will, more often than not, represent important and interpretable environmental gradients.
- By focusing on a few important dimensions there is less risk of interpreting ‘noise’.
- Environmental gradients can be ordered in terms of importance.
- Graphical outputs from ordination analyses can greatly assist the interpretation of species-environment relationships.

Ordination methods are most often applied to matrices of community data. A matrix of this type normally has rows which are species names, columns which are quadrats, sites or transects and elements (values) that contain species abundance measures such as presence/absence, counts and percentage cover.

A community data matrix tends to share several common properties whatever taxa are being recorded:

- A large part of the data matrix will contain zeros as many species are found infrequently.
- There is much redundant information as species often share similar distributions. For example the abundance of *species y* may act as a predictor for the abundance of *species z*.

- The number of factors influencing species composition is potentially very large, although typically there are not many important factors. A few factors can explain the majority of the variation in species abundance.
- There will be ‘noise’ in the data. Replicates are often quite variable and observer differences can create additional variability.

Several different ordination techniques can be used on a community matrix to unravel its ecological patterns. Each method differs slightly in the mathematical approach used and can be placed into one of two groups: ‘direct methods’ or ‘indirect methods’, depending on whether environmental data have also been recorded at each sampling plot. Within either group, a suitable ordination technique should be able to filter out the ‘noise’ component of the community data matrix and identify the few important dimensions defining the inter-relationships between samples, species and the environment. A brief description of the most commonly used methods is given below. Further details can be found in the suggested further reading (see page 21).

Indirect ordination methods

Ordinations by indirect gradient analysis use only the species by sample community matrix. Gradients are formed from species associations and are unconstrained by any environmental data that may or may not have been collected. If there is any information about the environment it is used after the indirect gradient analysis, simply as an interpretative tool.

Principal Component Analysis (PCA)

PCA involves the transformation of a data matrix of *p* variables into a set of *p* principal components. Each principal component is a linear combination of the original variables, computed in such a way that the first principal component accounts for the largest amount of variation in the original data. Subsequent components are computed to be uncorrelated with previous components while accounting for the maximum amount of the remaining variation in the data. All of the original variance is accounted for after all the PCA axes have been computed.

PCA can be extremely useful in interpreting environmental data matrices which contain variables that are measured in different units such as mean basal area, top height, % litter and leaf area index. In PCA these variables are standardised to zero mean and unit variance before analysis. Resulting axes can be used as input variables in subsequent ordinations (see Chapter 5 for an example).

Correspondence Analysis (CA)

CA is based on the assumption that each species exhibits a **unimodal** response to the underlying environmental gradients. A unimodal model requires there to be a unique set of optimal conditions for a species to occur at maximal abundance and as conditions differ from this optimum, abundances in this species will decrease. Mathematically, CA maximises the correspondence between species scores and sample scores. For the first axis, species and sample scores are estimated such that the weighted correlation between the two is maximised, where weighting is the abundance of the species. Resulting axes species scores can be interpreted as estimates of the unimodal peaks for those species.

Direct ordination methods

In direct gradient analysis, species are directly related to a set of explanatory variables. These are usually environmental variables which were thought to influence the ordering of the observed species distributions. Direct analysis tells us if species composition is related to our measured environmental variables as axes are constrained to be linear combinations of the measured environmental variables.

Canonical Correspondence Analysis (CCA)

As with CA, CCA assumes that species responses are bell-shaped curves along environmental gradients. Sample scores are constrained to be linear combinations of the environmental variables. If a combination of environmental variables is strongly related to the species composition, CCA will use these environmental variables to create an axis in which the species response curves are separated. Further axes can be formed in a similar manner, each being orthogonal to all previous axes.

The usefulness of any CCA output is dependent on the quality of the chosen explanatory variables. One must have recorded important environmental variables. Even then, underlying gradients may be related to unmeasurable factors.

Interpretation of ordination scatter plots

As species and samples are ordinated simultaneously they can be represented in the same ordination diagram known as a biplot. In CCA the inclusion of environmental variables into the same space creates a triplot.

- The ordination diagram graphically represents the community structure.
- The direction of the axes (e.g. left vs. right; up vs. down) is arbitrary and has no influence on any interpretation.
- The numeric scale of the axes do not generally aid interpretation.
- Samples tend to be dominated by species that are located near to them in the ordination space.
- Species that occur close together in ordination space tend to prefer the same environmental conditions.
- Sample locations indicate their similarity to each other in terms of species composition.
- Environmental variables in CCA that make small angles (i.e. point in the same direction) with one another imply high positive correlations. Arrows pointing in opposite directions will be negatively correlated.
- Projections of species onto these environmental variable arrows gives an interpretation of which species are linked with high or low values of the environmental variables.

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Web link: www.okstate.edu/artsci/botany/ordinate

SECTION TWO

Plant, fungal and microbial communities

Chapter 5 Relationships between site type, stand structure and plant communities
Jonathan Humphrey, Richard Ferris and Andrew Peace

Chapter 6 Soil microbial communities
Mike Morris, Jim Harris and Tom Hill

Chapter 7 Deadwood
Jonathan Humphrey and Andrew Peace

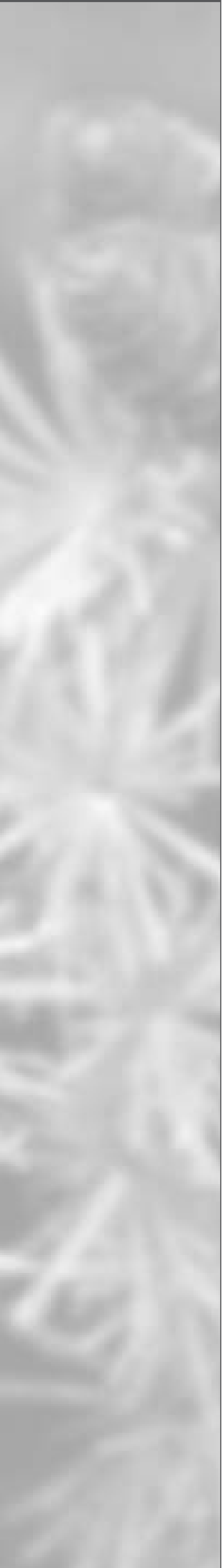
Chapter 8 The value of conifer plantations as a habitat for macrofungi
Jonathan Humphrey, Richard Ferris, Adrian Newton and Andrew Peace

Chapter 9 Lichen and bryophyte communities: the influence of site type, stand structure and deadwood
Jonathan Humphrey, Simon Davey, Andrew Peace, Richard Ferris and Kim Harding

CHAPTER 5

Relationships between site type, stand structure and plant communities

Jonathan Humphrey, Richard Ferris and Andrew Peace



Summary

Ground vegetation communities within the Biodiversity Assessment Project stands were classified using the National Vegetation Classification, and community composition and diversity related to stand structure and site characteristics. Mature and over-mature pine and spruce stands in the uplands and foothills climatic zones showed the greatest similarity with semi-natural pine and oak woodland communities respectively. Vegetation communities in lowland sites were less well correlated with semi-natural woodland analogues. Variation in community composition was related principally to a soil fertility gradient (increasing pH, exchangeable Ca, and available NO_3^-, coupled with decreases in soil organic matter and NH_4^+). Vascular plant and bryophyte species diversity was inversely related to available N. Uplands and foothills Scots pine and Sitka spruce sites had plant communities typical of acid, infertile soils, whereas lowland Norway spruce sites had communities associated with high soil fertility. Plant community composition and diversity was also significantly related to measures of vertical stand structure. Pre-thicket plots, with high values for field layer vertical cover had distinctive communities and were more diverse than mid-rotation and mature plots which had high canopy cover values, and low shrub and field layer cover. This influence of stand structure suggests that plant community diversity can be enhanced in commercial conifer forests by extending rotation lengths, and introducing alternative silvicultural systems such as shelterwood.

Introduction

Field and ground layer vegetation communities are key components of biodiversity within temperate and boreal forests (Hannerz and Hånell, 1997) as they provide habitat for dependent fauna, and influence the development of shrub layers and the natural regeneration of canopy trees. Vegetation succession through all, or part, of a managed rotation have been studied in a variety of different plantations (e.g. Hill, 1979). In general, where first rotation stands are established on non-wooded ground such as grassland or heath, there is an initial increase in the biomass of non-woodland vegetation, normally associated with a reduction in grazing pressure (Hill, 1979). After 30 or 40 years, when full canopy closure is attained, there is almost complete eradication of vascular plants under crops of densely shading spruce or fir, but greater survival under lighter shading canopies of pine or larch (Hill, 1979). After clear-felling, there is often a rapid increase in ruderal (weed) species such as rosebay willowherb *Chamerion angustifolium*[1] and tufted hair-grass *Deschampsia cespitosa* (Abdy and Mayhead, 1992) which then decrease rapidly in abundance during the second rotation.

Retention of some stands beyond normal economic felling age (40–100 years depending on site factors and crop species) allows development of some of the characteristics of 'old-growth' such as fallen and standing deadwood, and veteran trees. Some species typical of native or semi-natural woodlands may begin to colonise these stands, e.g. woodland bryophytes such as *Rhytidiadelphus loreus* or herbs such as wood sorrel *Oxalis acetosella*. Such colonisation is most likely where stands have been well thinned in the past, and there are sources of propagules nearby (Williams *et al.*, 1998). The vegetation communities of these older stands (and indeed their younger counterparts) have not been properly characterised using the National Vegetation Classification system (Rodwell,

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[1] Nomenclature follows Stace, C. (1997). *New flora of the British Isles*, 2nd edn. Cambridge University Press, Cambridge.

1991a, b), and it is not clear if their vegetation differs markedly from that of native woodlands on similar site types. In addition, few studies of ground vegetation in conifer plantations have attempted to relate vegetation community composition and diversity to stand characteristics and site types across a geographical range. This is important as forest managers need to know the potential benefits for plant diversity which could result from modifications to stand structure.

The objectives of the work described in this chapter were: 1) to characterise the plant communities (ground and field layer species) of planted conifer stands in terms of the National Vegetation Classification system; 2) to quantify the degree to which soil, stand structure and crop-species variables were related to variability in ground vegetation composition and diversity; and 3) to identify suitable stand management options for conserving and enhancing plant communities within plantations.

Methods

In addition to the soil, stand structure and mensuration assessments described in Chapter 3, field and ground layer vegetation composition was assessed visually, using the DOMIN cover-abundance scale, within eight 2 m x 2 m quadrats nested in the 10 m x 10 m mensuration plots (Figure 3.2, Chapter 3). These data were compared to the National Vegetation Classification (NVC) national datasets for woodland, heathland and upland grassland communities (Rodwell, 1991a,b; 1992) using the MATCH programme (Malloch, 1995). This programme calculates similarity coefficients between the vegetation sample and the national datasets for the different NVC sub-communities. The NVC sub-community that most closely resembled the vegetation of each 1 ha plot was identified.

In addition a Woodland Vegetation Similarity Coefficient (WVSC) was calculated for each stand using the formula:

$$\text{WVSC (\%)} = (M_{WC}/M_{NWC}) \times M_{WC}$$

where M_{WC} is the highest MATCH coefficient recorded against a woodland sub-community and MN_{WC} is the highest coefficient recorded for a match against a non-woodland sub-community. The WVSC gives some indication of the relative similarity of the vegetation samples to woodland communities as opposed to non-woodland communities (Humphrey *et al.,* 2001).

Canonical Correspondence Analysis (see Chapter 4) was used to identify the relationships between soil and habitat variables and the species-composition of the floristic data. These soil and habitat variables (Table 5.1) are summative measures derived by Principal Components Analysis of the wide range of soil and habitat factors listed in Chapter 3, Table 3.2 (see Ferris *et al.,* 2000 for details of the analysis). Plant species-richness and diversity were also related to the summative soil and habitat variables using Pearson correlations.

Results and Discussion

Development of woodland vegetation communities

With the exception of the lowland Scots pine and Norway spruce stands, the vegetation in the over-mature stand stage was more ‘woodland like’ in character than the vegetation in the mid-rotation and mature stages (Table 5.2). The highest WVSC coefficients (>60%) were for the older stages of the foothills Scots pine chronosequences at Glen Affric and Strathspey, which were matched with W18 communities (*Pinus sylvestris-Hylocomium splendens* woodland; Rodwell, 1991a; Ferris *et al.*, 2000). These stands are considered to be good examples of semi-natural Scots pine woodland.

The pattern of community development in the foothills Scots pine plots was repeated in the Sitka spruce foothills and upland plots with the mature and over-mature stands more closely resembling semi-natural woodland communities than the pre-thicket and mid-rotation stands (Table 5.2). The best fits for these older stands were W17 oakwood communities (*Quercus petraea-Betula pubescens-Dicranum majus* woodland; Ferris *et al.*, 2000). This pattern of community change has been recorded

Table 5.1 *Description of principal components of soil (SOIL 1–4) and habitat (HAB 1–4) variables related to plant community composition (CCA in Figure 5.1), species-richness and diversity (Table 5.3). Reproduced from Ferris* et al. *(2000).*

Principal Component	Description
SOIL 1	High P, K, Mg, organic matter and NH_4^+
SOIL 2	High pH, Ca and NO_3^-, low organic matter and NH_4^+
SOIL 3	High Mg, low NH_4^+ and NO_3^-
SOIL 4	Low pH, high NO_3^-
HAB 1	High values for field layer vertical cover (S1), low values for lower (S3) and upper (S4) canopy vertical cover, vertical cover index (CI), top height (TOPHT), height to live crown (HTLC), mean basal area (MBA) and rotten deadwood volume (DEADR)
HAB 2	High values for shrub layer vertical cover (S2), S3, C.I. and DEADR, low values for HTLC
HAB 3	High values for S1, DEADR and fresh deadwood volume (DEADF)
HAB 4	High litter depth values

in a number of similar studies (e.g. Hill and Jones, 1978) and could be a function of stand age where enough time has elapsed to allow slow-colonising woodland plants to become established in the stand. Site history may also be important, i.e. whether the stand was established on a site previously occupied by ancient semi-natural woodland (Humphrey *et al.,* 2001). The over-mature upland Sitka spruce stands (established on ancient woodland sites) had WVSC values approaching those of the semi-natural oakwoods (Table 5.2) and had a number of characteristic woodland herbs such as wood sorrel.

Table 5.2 *Changes in the Woodland Vegetation Similarity Coefficient (WVSC) in relation to stand stage and crop type (– stand stage not available). The WVSC gives a measure of how closely the sampled vegetation is matched to a National Vegetation Classification (NVC – Rodwell, 1991a,b; 1992) semi-natural woodland community type relative to a non-woodland vegetation community. Each value is the mean of two stands.*

Woodland vegetation similarity coefficient (%)	Pre-thicket	Mid-rotation	Mature	Over-mature
Lowland Corsican pine	43.2	32.8	27.4	58.2
Lowland Scots pine	21.9	34.6	34.9	32.0
Foothills Scots pine	41.3	58.2	69.1	70.8
Lowland Norway spruce	56.6	41.9	51.0	–
Foothills Sitka spruce	33.3	17.5	25.5	36.8
Upland Sitka spruce	44.7	33.9	49.9	58.6
Lowland oak	–	88.9	60.7	–
Upland oak	–	75.4	79.2	–

The pre-thicket stages in the foothills and upland sites were more closely matched with heathland or upland grassland communities, and had species associated with open conditions such as heather *Calluna vulgaris* (Ferris *et al.,* 2000). Although most lowland plots were matched with woodland communities (W10 *Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland and W16 *Quercus* spp.-*Betula* spp – *Deschampsia flexuosa* woodland; Ferris *et al.,* 2000), some of the lowland Scots pine plots were matched more closely with underscrub communities dominated by one or two species, often bracken *Pteridium aquilinum* (Ferris *et al.,* 2000). The lack of development of woodland vegetation within these stands may be due to the fact that they were established on previously unwooded areas and the process of colonisation by woodland species has been restricted by the distance to sources of colonising species.

Relationship between vegetation communities, habitat and soil variables

Species-environment correlations were high (r>0.87) for the first two axes of the Canonical Correspondence Analysis (CCA) of the plant community data, with 29% of the variation in the species data explained by the set of environmental variables (Figure 5.1). Axis 1 separated lowland sites from those in the foothills and uplands, and was strongly correlated (r>0.51) with SOIL2 suggesting that differences in plant community composition between these site groupings were related to a gradient of increasing litter depth, pH, exchangeable Ca, and mineralised N in NO_3^- form, and decreasing organic matter and N in NH_4^+ form. Lowland sites (such as 8.3) were dominated by species requiring high pH conditions such as slender false-brome *Brachypodium sylvaticum* and small nettle *Urtica urens* (Grime *et al.*, 1988). Northern sites (upland and foothills) had a more calcifuge flora (Grime *et al.*, 1988), with species such as blaeberry *Vaccinium myrtillus* and heather common. However, increasing pH and Ca (key factors in SOIL2) were not significantly correlated with plant species diversity (Table 5.3). In fact the only significant correlation recorded here was a positive correlation between SOIL 3 (high Mg and low N in both NH_4^+ and NO_3^- form) and vascular plant and bryophyte species diversity. The only habitat principal component which was correlated with the first axis of the CCA was HAB4 (litter depth; Figure 5.1). Litter depth was also negatively related to total species diversity, and bryophyte cover (Table 5.3). Plots with high litter depth values were dominated by bracken (lowland Scots pine, Thetford, sites 3.2 and 3.3) which is noted for its ability to accumulate considerable quantities of litter over time if undisturbed (Marrs and Hicks, 1986).

Figure 5.1 *Canonical correspondence biplot of assessment plots and environmental variables. Data labels for plots as in Annexe 1. The principal components of soil (SOIL 1–4) and habitat (HAB 1–4) variables are plotted as euclidean vectors (arrows); the direction and relative length of the arrows reflects the degree of correlation with the CCA axes; longer arrows are more strongly correlated.*

Table 5.3 *Pearson correlations relating vegetation community variables to the first four principal components of soil and habitat data. Significant correlations (P<0.01) indicated by **.*

	SOIL 1	SOIL 2	SOIL 3	SOIL 4	HAB 1	HAB 2	HAB 3	HAB 4
Total species diversity	0.02	-0.09	0.68**	0.03	-0.14	0.23	0.35	-0.53**
Total species % cover	-0.18	-0.33	0.31	-0.07	0.41**	0.01	0.42**	-0.27
Vascular species diversity	-0.10	-0.06	0.70**	-0.15	-0.07	0.22	0.35	-0.37
Vascular species % cover	-0.36	-0.24	0.24	-0.11	0.54**	-0.10	0.37	-0.02
Bryophyte species diversity	0.07	-0.09	0.39**	0.21	-0.13	0.27	0.40**	-0.35
Bryophyte species % cover	0.17	-0.32	0.28	0.03	0.02	0.18	0.31	-0.52**

Axis 2 of the CCA separated pre-thicket stands from the other stand stages, and was correlated with habitat parameters summarising differences in the vertical structure variables (HAB1 and HAB2). HAB1 describes changes in vertical stand structure through the chronosequence from older to younger plots (increasing field layer cover coupled with decreasing shrub and canopy layer cover). HAB2 describes a contrasting gradient of increasing vertical cover in the shrub and canopy layers. Pre-thicket plots had high vertical cover in the field layer, dominated by heathland and grassland species which are taller than typical woodland species growing under a canopy. Axis 2 also separated foothills spruce plots from pine plots. The pine plots tended to have a higher cover of more light demanding ericoid shrubs, grasses, rushes and sedges (Grime *et al.*, 1988) than spruce plots, reflecting the positive benefits from the lighter shading pine canopy (Hill, 1979).

HAB1 was positively correlated with the percent cover of vascular plants in the ground and field layer. Where canopy layer values were high (in mid-rotation plots) the cover of vascular plants in the field and ground layer vegetation was reduced through shading. This effect has been well documented for conifer stands on a range of different site types (e.g. Hill, 1986). Under densely shading crops such as Sitka spruce and western hemlock *Tsuga heterophylla*, vascular plants can be completely eradicated leaving only bryophytes (Hill, 1986). However, in pine forests, open old-growth stands frequently have lower plant diversity than closed canopy stands (Tonteri, 1994). The positive relationship recorded between deadwood volume (HAB 3) and bryophyte species diversity is in fact coincidental since bryophytes growing on deadwood were not recorded as part of this particular study. A separate survey of lower plants on deadwood was undertaken within the biodiversity plots and the results from this are discussed in Chapter 9.

Management implications

Ferris *et al.* (2000) suggest that even though soil fertility is important in determining the composition and diversity of the understorey plant communities there is still scope for considering the manipulation of forest structure as a means of increasing diversity within planted conifer stands (Kerr, 1999). Peterken *et al.* (1992) have proposed that the promotion of enhanced structural diversity through retention of a greater proportion of stands beyond financial maturity would help improve the biodiversity of upland conifer forests. This is supported by the evidence from our study where the over-mature stands in the uplands had greater structural complexity than their younger counterparts, both in terms of vertical stratification and horizontal patchiness. These stands also had a more diverse flora with a greater complement of woodland herbs and bryophytes.

Lowland plantations, many of which have been established on former heathland, are typically species-poor, a feature of such stands elsewhere in NW Europe (e.g. Scots pine stands in Belgium, Lust *et al.*, 1998). They have poor and uniform structural development, with very limited cover in the shrub and lower-canopy layers. In order to transform these stands into well-structured mixtures with higher vertical and horizontal structural diversity, conversion methods should be used over a sufficiently long time period to minimise the rate of change. Rotation lengths of more than 100 years are proposed, but structural diversity comparable to that found in established selection forests could arise in less than 30 years (Lust *et al.*, 1998).

Thinning in both upland and lowland forests can promote greater understorey development as a result of improved light, moisture and temperature conditions, but a review of studies overseas (Ferris *et al.*, 2000) concluded that early thinnings without subsequent treatments were unlikely to maintain stable herb and shrub populations. A shelterwood approach may be more beneficial to the development of a woodland flora in the long-term. For example, Hannerz and Hånell (1997) found that in Norway spruce forests in Scandinavia, shelterwood regimes benefited plants preferring shaded and moist conditions, whereas these species declined after clearcutting. As a result of the development of country-based forestry strategies within the UK (e.g. Anon., 2001), much more emphasis is being placed on evaluating alternatives to clearfelling in British forests both in terms of economic benefits, as well as in respect of biodiversity and recreation values (Mason *et al.*, 1999). However, more research is needed to establish the benefits of alternative silvicultural systems such as shelterwood or group selection, for enhancing ground flora diversity.

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CHAPTER 6

Soil microbial communities

Mike Morris, Jim Harris and Tom Hill

Summary

Soil microbial communities in a sample of the pine and spruce stands were characterised using a biochemical analysis of lipid and fatty acid composition. Significant differences in the composition and diversity of soil microbial communities were recorded between different stand stages and tree crop types reflecting differences in ground flora composition, tree and shrub species composition, soil organic matter content and soil nitrogen content. The importance of soil microbial diversity for maintaining ecological functions within forest ecosystems is stressed and the need for more research to characterise soil microbial communities is emphasised.

Introduction

The soil microbial community plays a vital role in the functioning of the forest ecosystems. As Jenkinson (1977) said *'The microbial biomass accounts for only 1–3% of soil organic C, but it is the eye of the needle through which all organic material that enters the soil must pass'*. As such, the microbial community lies at an interesting interface between the biotic and abiotic components of the ecosystem. Through the microbial community's activities, organic matter can be: incorporated into new microbial biomass; transformed to produce compounds which stabilise soil aggregate structures (Edgerton *et al.*, 1995); provide long-term nutrient reserves (and therefore buffers to supply); or respired to rejoin the pool of carbon dioxide in the atmosphere.

The soil microbial community may be characterised in a number of ways, but one schema involves three characteristics:

- **Size:** the total standing crop of microbial cells, expressed as numbers or, more usefully, as amount of living carbon.
- **Composition:** the relative abundance of different populations within the microbial community (e.g. bacteria vs fungi, or individual species).
- **Activity:** the rate at which the microbial community transforms or incorporates raw materials from simple sugars to complex polymers from the soil system.

This approach has been used most effectively in a number of studies not only to discriminate between different successional stages, but to gauge the effects of disturbance, such as opencast coal mining operations, on systems and the reclamation efforts made to restore them (Bentham *et al.*, 1992). In Bentham's study the microbial indices alone were demonstrated to be far better than traditional soil physico-chemical characteristics in discriminating between site history and management practices. Further to this, microbial community indices have been used specifically to address how ecosystem changes during succession from meadow to woodland affect both microbial community structure and functional characteristics related to the transition (Harris and Hill, 1995).

The study of soil microbial communities will also provide insights central to the current debate on the relationship between species diversity and ecosystem function. Because of the speed at which the whole diversity of a particular microbial system can be estimated, sometimes simultaneously with its functional measures, we can begin to construct a response model of the link between the two.

So how do we measure biodiversity in the soil? The main approaches currently employed are:

- **Traditional**
- **Genetic**
- **Biochemical**

Traditional methods rely on either culturing or direct observation. The extraction and culturing of soil fungi and bacteria, by means of dilution and plating onto agar media containing nutrients, leads to serious underestimates of the numbers of micro-organisms in a sample of soil. This is because of a number of factors – the most important being the need for widely different nutrients and growth conditions for different species to grow. Ideal conditions for the majority of micro-organisms known to be inhabiting the soil remain undiscovered. Underestimation is also caused by cells clumping together or by their destruction during sample homogenisation. Direct observation relies on highly skilled operators and as such is prone to operator bias. It also requires the use of universal staining procedures, i.e. stains specific for proteins, polysaccharides or nucleic acids, but staining, especially in forest soils, tends to be incomplete and success varies with the soil horizon and degree of humification.

The structure of microbial communities can also be described using **genetic** methods. Typically, the DNA sequence of the small sub-unit ribosomal RNA gene is used to define species or taxonomic groups. Numerous techniques, ranging in their resolution, are used to measure the diversity of rRNA genes. While this approach has the precision to provide a complete inventory of the microbial community in a soil sample (time and expense permitting) it also possesses several sources of error, some of which are unquantifiable. These undermine its accuracy and reliability as a tool to measure changes in relative abundances of species or broader groups in response to changes in soil conditions. Most bias occurs in the first steps of the method, the extraction of DNA from the soil sample and the many-million-fold replication of the rRNA genes using the polymerase chain reaction (PCR) needed to generate enough material to measure. Other complicating factors include the variation in copy number of rRNA genes between species and, for fungi, the frequency of occurrence of nuclei in the mycelium. The prodigious spore production by some fungi would also lead to an overestimation of their levels of vegetative growth.

Biochemical techniques, particularly using the analysis of lipids and fatty acids, have been the subject of rapid development in recent years as a consequence of their utility in characterising microbial community composition and diversity. Lipids are ubiquitous in their distribution and perform a vast range of structural and metabolic functions in both prokaryotes and eukaryotes (Ratledge and Wilkinson, 1988). It has long been known that various lipid classes can be powerful tools in the classification and taxonomy of microbial flora (Lechevalier, 1977). Fatty acids are long-chain carboxylic acids. Within bacterial cells they may occur free or esterified to an alcohol group. Most are component parts of large molecules such as phospholipids, glycolipids, lipoproteins, lipopolysaccharides and lipoteichoic acids. Although the fatty acids of eukaryotic organisms tend to be limited to straight chain saturated and unsaturated forms, bacteria possess a more heterogeneous selection. More than 300 different fatty acids have been found in bacteria, including soil bacteria (Sasser, 1990).

White *et al.* (1979) suggested that fatty acid composition might be useful in defining microbial community structure. Several studies have now demonstrated the usefulness of this technique in the study of terrestrial soils, especially with regard to the effects of environmental perturbations on microbial communities (Bååth *et al.*, 1995). Other workers have studied phospholipid fatty acid (PLFA) profiles in natural soils from different origins, in order to gain insight into the relative diversity of the microbial communities present (Zelles *et al.*, 1995; Bardgett *et al.*, 1997).

Although a variety of lipid classes can be used, the work presented here examines the utility of ester-linked PLFA determination to provide an indirect assessment of the diversity of microbial communities present within the Biodiversity Assessment Project sites, and to relate this diversity to factors of soil and stand structure.

Methods

Assessments were carried out on sites 1, 2, 9, 10, 11 and 12 (see Annexe 1 for details).

Sampling and preliminary lipid extraction

All samples were taken from the F_H horizon (humus layer) since this should provide the best indicators for the microbial communities present, and particularly those responsible for the decomposition of litter and sequestration of available nutrients (Kjøller and Struwe, 1982).

Five 0.2 m x 0.2 m areas were selected at random from each of the eight 10 m x 10 m mensuration quadrats within each 1 ha plot (Chapter 3, Figure 3.2). The F_H horizons of these five sub-areas were removed and bulked together. After preliminary mixing and removal of coarse debris the sample was riffled (sub-divided to obtain a representative sample), a sample placed in a plastic bag for complementary analyses, then riffled again until a representative sample of about 8 g was obtained and this placed in a 30 cm^3 glass vial for lipid analysis. To this sample 15 cm^3 of initial extraction solvent trichloromethane:methanol (1:2, v:v) was added both to fix the organisms present and begin lipid extraction. Vials were stored in the dark at ambient temperature until they were returned to the laboratory where the extraction was completed. Bagged samples were stored at 4°C until required.

Extraction and analysis of soil microbial PLFAs

Extraction and analysis of PLFAs from soil consists of 5 distinct stages: crude lipid extraction, liquid:liquid partition (initial clean-up), fractionation, derivatisation and chromatographic separation and analysis. These stages are summarised in Annexe 2. Comprehensive methodology is given in Morris (2000). Figure 6.1 shows a typical chromatogram obtained for phospholipid derived FAMEs of the assessment site soil samples.

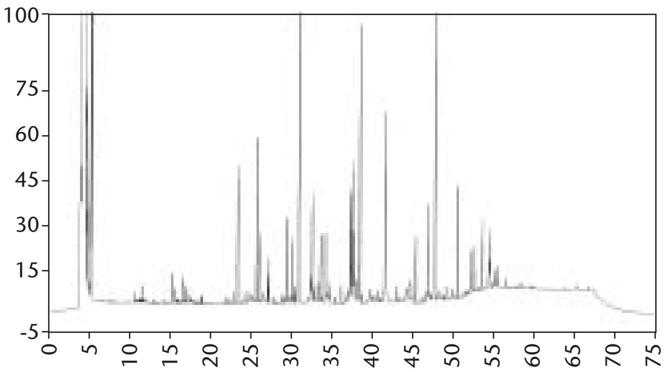


Figure 6.1

Typical example of a capillary GC chromatogram of fatty acid methyl esters of the phospholipid fraction of lipids extracted from the forest soil samples.

A total of 92 individual fatty acid peaks, selected on the basis of their occurrence in the phospholipid fractions of forest soil extracts, were chosen as a composite comparison profile for the soil PLFA extracts. The areas of identified peaks in each PLFA profile were recorded and normalised by dividing by the total profile peak area. Although eight replicate samples (one from each of the quadrats within each chronosequence) were taken, not all extracted profiles were appropriate for inclusion in the dataset due to low intensity profiles (see Morris, 2000). As a result, profile replicates from the chronosequences ranged from four to eight.

Data analysis

Statistical analyses were carried out using the Statistica version 5.1 (Statsoft, Inc., Tulsa, OK) and Statgraphics Plus version 7.0 (Manugistics Inc., Rockville, MD). The normalised PLFA profiles were transformed to their $\log_{10}$ values prior to principal components analysis (PCA; ter Braak, 1995) as performed by Bååth *et al.* (1995). The Shannon indices were determined using the EstimateS version 5 *Statistical estimation of species-richness and shared species from samples* programme (copyright Robert K. Colwell, 1994–97). Pearson product-moment correlations were calculated to investigate the statistical relationships between soil microbial community PLFA diversity and vegetation composition and diversity, soil chemistry variables, deadwood and stand structure (see Chapters 3, 5 and 7 for descriptions of these latter datasets). The ground vegetation data were divided into separate groups:

ericoid shrubs, ferns and herbs, forbs (grasses, sedges and rushes), bryophytes, lichens, trees and shrubs and bracken. The variation in PLFA composition of the assessment sites was also assessed using PCA (see Chapter 4 for a description of this technique).

Results

Diversity of PLFA profile data

The simplest indication of richness in traditional community studies is the total number of species present. Analogous to this in the present dataset is the total number of PLFAs (*S*) identified in each soil extract chromatogram. The maximum possible value of *S* is 92, but no individual site profile presented with this many. Although *S* is relatively limited in its information content, Table 6.1 shows that the pre-thicket stands consistently exhibit the fewest peaks in each chronosequence. Similarly, with the exception of Site 2, the over-mature stands present fewer peaks than those of the intermediate chronosequences.

The Shannon index (H^1) is a measure of the amount of information in the system and is positively correlated with both PLFA richness and evenness. This universally applied index of diversity is surprisingly well adapted to these data since it assumes that each data set comprises a random sample from an effectively infinite population in which the total number of peaks is known (i.e. 92 with these data; Krebs, 1985). While H^1 is weighted by the evenness of peak abundance, a more specific measure of evenness (*E*), based on H^1, can be determined by calculating the ratio of the observed H^1 to its maximum possible value. Maximum H^1 occurs when there is complete equitability (an equal abundance of all PLFAs). *E* is limited to a value between 0 and 1.0 with 1.0 representing maximum evenness. The calculated values for H^1 and *E* for the plots are given in Table 6.1. In contrast to *S*, the pre-thicket or post-mature stands tended to have the highest values for both H^1 and *E*, although the trends were generally less clear.

Table 6.1

Diversity indices calculated for normalised mean PLFA profile data from the BRP assessment sites. Key to site labels in Annexe 1; SP = Scots Pine; SS = Sitka spruce; CP = Corsican pine.

Site label	PLFA diversity index		
	Richness (max. value 92) (S)	Shannon index (H^1)	Shannon evenness (range 0–1) (E)
SP1.1 (*n* = 4)	68	3.12	0.83
SP1.2 (*n* = 7)	78	3.28	0.80
SP1.3 (*n* = 6)	77	3.23	0.79
SP1.4 (*n* = 4)	76	3.19	0.78
SP2.1 (*n* = 8)	79	3.32	0.80
SP2.2 (*n* = 8)	81	3.18	0.78
SP2.3 (*n* = 7)	79	3.22	0.79
SP2.4 (*n* = 8)	82	3.19	0.78
SS9.1 (*n* = 4)	67	3.33	0.83
SS9.2 (*n* = 7)	80	3.19	0.81
SS9.3 (*n* = 5)	86	3.23	0.80
SS9.4 (*n* = 5)	74	3.30	0.85
SS10.1 (*n* = 5)	79	3.41	0.81
SS10.2 (*n* = 5)	83	3.41	0.82
SS10.3 (*n* = 5)	85	3.50	0.82
SS10.4 (*n* = 5)	81	3.70	0.87
CP11.1 (*n* = 5)	82	3.54	0.84
CP11.2 (*n* = 5)	85	3.53	0.82
CP11.3 (*n* = 5)	87	3.53	0.81
CP11.4 (*n* = 8)	85	3.40	0.80
CP12.1 (*n* = 6)	79	3.32	0.79
CP12.2 (*n* = 6)	82	3.34	0.81
CP12.3 (*n* = 5)	78	3.36	0.81

Correlation of PLFA diversity with stand structure, soil and vegetation data

Significant correlations between PLFA diversity and stand, vegetation and soil variables are given in Tables 6.2 and 6.3. The percent cover of both the ericoid and the trees and shrubs groups showed significant negative correlations ($p < 0.01$) with PLFA richness. Percent cover of the ericoids also showed a significant negative correlation ($p < 0.05$) with H'. Further, ericoid richness was significantly negatively correlated with both H' and E ($p < 0.01$). By contrast, species-richness and percent cover of the ferns and herbs group was positively correlated ($p < 0.05$) with PLFA diversity and evenness (H' and E).

Table 6.2 *Pearson product-moment correlations relating the PLFA derived diversity measures to vegetation and stand structure variables. Analyses methods for stand structure and vegetation variables are described in Chapters 3 and 5 respectively. Marked correlations: * p < 0.05 ; ** p < 0.01; ns: not significant (n = 23, with casewise deletion of missing data).*

		PLFA diversity index		
Vegetation category/ vertical stand structure	**Measure**	**Richness (S)**	**Shannon index (H')**	**Shannon evenness (E)**
Ericoid	No. species	-0.26^{ns}	-0.60**	-0.63**
	% cover	-0.59**	-0.47*	-0.34^{ns}
Trees & shrubs	No. species	-0.32^{ns}	-0.34^{ns}	-0.32^{ns}
	% cover	-0.62**	-0.03^{ns}	0.19^{ns}
Ferns & herbs	No. species	0.09^{ns}	0.50*	0.50*
	% cover	0.16^{ns}	0.49*	0.48*
Field layer vertical cover	**cover**	**-0.46***	**0.22^{ns}**	**0.39^{ns}**

Table 6.3 *Pearson product-moment correlations relating the PLFA derived diversity measures to vegetation and stand structure variables. Analyses methods for stand structure and vegetation variables are described in Chapters 3 and 5 respectively. Marked correlations: * p < 0.05; ** p < 0.01; ns: not significant (n = 23, with casewise deletion of missing data).*

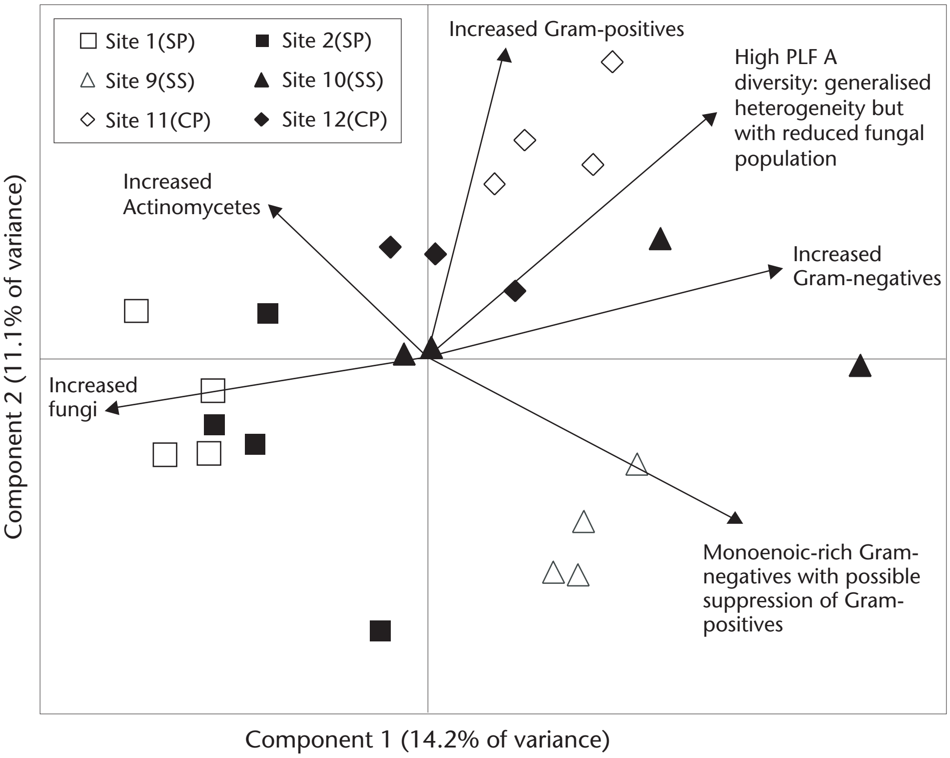
Chemical variable	PLFA diversity index		
	Richness (S)	**Shannon index (H')**	**Shannon evenness (E)**
Organic content	-0.48*	-0.80**	-0.74**
Moisture content	-0.47*	-0.69**	-0.60**
C	-0.15^{ns}	-0.71**	-0.75**
C:N ratio	-0.58**	-0.57**	-0.44*
P	-0.25^{ns}	-0.53**	-0.52*

Significant correlations between the PLFA diversity indices and soil chemical variables of the F_H horizon were always negative (Table 6.3). H' and E tended to be more strongly correlated than S, especially with the interrelated measures of amount of organic material present, percent moisture content and carbon content. Of the extractable metals, only phosphorus showed significant correlations. Although pH of the F_H horizon was not correlated with PLFA diversity, the pH of the lower soil horizon was positively correlated with both H' ($r = 0.51$, $p < 0.05$) and E ($r = 0.54$, $p < 0.01$; Morris, 2000).

Ordination

The PCA site ordination diagram is presented in Figure 6.2. Using all the individual PLFA profiles the first three axes of the PCA ordination accounted for 35% of the total variability in the dataset.

Figure 6.2 *PCA ordination of the Biodiversity Assessment Project sites with summary vectors indicating some of the general conclusions suggested in the text.*



However, when the analysis was carried out using the mean site profiles the first three axes explained 49% of the variance. Component 1 of the PCA separated the Scots pine sites from both the Corsican pine and Sitka spruce sites. It also had a major influence on separating the older two Glentress (Site 10) stands from the 'pre-thicket' and 'mid-rotation' stages. Component 2 separated the Corsican pine sites from the Sitka spruce stands at both Kielder (Site 9) and, to a lesser extent, at Glentress (Site 10). Component 2 also showed a negative gradient with age separating the Strathspey (Site 2) stands from the rest.

Discussion

Correlation of PLFA diversity with vegetation diversity

A possible explanation for the strong negative correlations between PLFA richness and percent cover of trees and shrubs and of ericoids is that both these vegetation classes are known to have strong mycorrhizal associations. Ericoid ectendomycorrhizas are a ubiquitous feature of the tribes Ericoideae (*Erica*, *Calluna*) and Vaccinoideae (*Vaccinium* spp). The vegetation assessment data showed that, while the Scots pine sites tend to be dominated by *Calluna vulgaris* and possess larger populations of *Vaccinium myrtillus* (bilberry) and *V. vitis-idaea* (crowberry) with age, *Calluna* is absent from all but the 'pre-thicket' stages of Sitka spruce stands and is an even rarer inhabitant of the Corsican pine stands. Similarly, while *V. myrtillus* is found occasionally on the Sitka stands, neither this species nor *V. vitis-idaea* were present in the Corsican pine stands.

It is not particularly surprising, given the known preference of these types of plants for heathland type areas and acidic or peaty soils (Richards, 1987) and considering the extent of canopy closure seen in the mid-rotation Sitka sites, to find such a divergence in distribution of PFLA-richness between stand types. However, the suppression of PLFA richness associated with dominant ericoid cover may well be attributable, to some extent, to their ectendomycorrhizal associations. These plants are typically woody shrubs with an extensive system of fine roots, the greater part of which is mycorrhizal. The dense nature of their root systems, together with the fact that soil within the mycorrhizosphere generally has lower microbial population densities than the rhizosphere adjacent to non-mycorrhizal roots (Killham, 1994), is a plausible explanation for the decrease in PLFA richness.

It would therefore be expected that, along with a generalised decrease in PLFA richness caused by a reduced population density of the microbial (bacterial) community, we should see a concomitant increase in the recovery of fatty acids associated with polar lipids of the mycorrhizal fungi (see the following section on PCA for the examination of individual fatty acid/site associations).

Correlation of PLFA diversity with soil variables and stand structure

Of the correlations displayed in Table 6.3, the fact that the organic matter content, elemental carbon and percent moisture all showed similar patterns of significant negative correlations is not surprising. Soil moisture content is partially dependent on organic matter content, and the proportion of organic material has been used in allied studies as a surrogate for the available water capacity when determining habitat preferences of indigenous species (Jukes *et al.,* 2001). Similarly, the bulk of the organic material tends to be composed of cellulose, lignin and other recalcitrant large molecule classes that, while containing relatively large amounts of other elements in functional groups, are primarily polymeric carbon chains. Thus organic material content will generally be proportional to elemental carbon content. A high C:N ratio is generally an indication of low quality, woody humus (usually dominated by fungi) and is characteristic of forest soils (Harris and Hill, 1995). The Scots pine stands show closest correlation to this generalisation demonstrating high organic matter and moisture contents along with high levels of fungal specific fatty acids and concomitant low fatty acid diversity.

A significant negative correlation ($r = -0.46$, $p < 0.05$) was also observed between the field layer vertical cover assessment (S1 = 10 cm to 2 m in height – see Chapter 3) and PLFA richness (not shown). This is probably due, primarily, to the association recorded between high field layer vertical cover values and the occurrence of heathy vegetation (as reported in Chapter 5). As the ericoids tend to be low growing, high-density shrubs it would be expected that sites with a high cover of ericoids would score highly in the S1 vegetation strata cover assessment.

Ordination

The fatty acids having the greatest influence in separating the Scots pine sites from the other sites (i.e. those fatty acids that correlate well with component 1) were proportionally high levels of C16:1w5, C16:1w7, C18:1w9*tr*+C18:1w7*cis*, C18:2w6 and C18:1w9*cis*. Following on from the tentative conclusions made with regard to the correlations between ericoid richness and low PLFA diversity, it would be expected that those fatty acids positively aiding the separation of the Scots pine sites from the other sites (i.e. those negatively correlated with component 1 of the PCA) would be associated with fungi and particularly ectendomycorrhizal species. Of those peaks which satisfy that criteria, C16:1w5, C18:2w6 and C18:1w9*cis* have been used in previous studies as markers for eukaryotic (fungal) presence. Stahl and Klug (1996) demonstrated that the latter two fatty acids comprise two of the four most abundant fatty acids (up to 95% of the total fatty acid content) found in whole cell extracts of 100 cultured filamentous fungi (72 of which were isolated from experimental soil samples). Though one should be circumspect about transposing whole cell, culture derived, profile data to *in situ* derived consortia data, Stahl and Klug (1996) showed that, in the species of Ascomycetes studied, C18:2w6 and C18:1w9*cis* comprised around 70% of the total fatty acid content. Ascomycetes are commonly implicated in ericoid type mycorrhizal infections.

The separation of the chronosequences within the Glentress site is also explained essentially by component 1 of the PCA and hence is also affected by the relative proportions of those fatty acids discussed above. The fatty acids demonstrating greatest effect on separating the Kielder stands from the other sites (vectors in the lower right quadrant of the ordination diagram) consist mainly of monoenoic forms, usually associated with Gram-negative bacteria. This area of the ordination showed virtually no methyl branched fatty acids, suggesting a possible suppression of Gram-positive bacteria. While not exclusive to Gram-positive bacteria (Lechevalier, 1977) branched chain fatty acids are invariably found as major lipid components of most Gram-positive bacteria (Zelles, 1997). A large number of fatty acids (42% of the total) showed positive correlations with both component 1 and component 2 of the PCA (upper right quadrant). It is an increase in the proportion of these fatty acids that helps to separate the Corsican pine sites from the other sites. The fatty acids comprising this group are a heterogeneous mix of methyl branched, unsaturated, cyclopropyl and hydroxy fatty acids. As no particular class of fatty acid is dominant it is not possible to claim that any specific group or groups of microorganism are particularly dominant at these sites. Such a heterogeneous mix of fatty acid classes necessarily suggests the presence of a similarly heterogeneous mix of microorganism classes. As far as one can make sweeping judgements with regard to the Corsican pine sites, it is possible only to state that (on the evidence of their PLFA profiles) their microbial communities contain a much lower fungal proportion than the Scots pine sites and a much higher proportion of Gram-positive bacteria than the Kielder Sitka spruce sites.

Because some aspect of equitability is included in the calculation of Shannon H^1 it would be reasonable to assume that those sites scoring highly for diversity (H^1) would be placed near to where the majority of peaks lie on the ordination. Thus it is no surprise that the three sites scoring highest for diversity (10, 11 and 12) are all represented in the upper right quadrant of the PCA.

Conclusions

The results of this investigation demonstrate that: there are clear links between vegetation type, rotational stage and microbial community composition and diversity; the diversity of the microbial community tends to be greatest at the mid-rotational stage; and the microbial community is a clear indicator of successional status. Management of conifer forests to maximise diversity while maintaining their function needs to address all parts of the ecosystem – the producer, the consumer and the decomposer subsystems – since all are interconnected and co-dependent. The plants impose top-down control over the soil community via the quantity and quality of their organic inputs, while, simultaneously and reciprocally, the decomposers exert bottom-up control. The soil microbial community is extremely diverse – every handful of forest soil may contain more than 10 000 bacterial ‘species’ alone – but is essentially unknown. There is also evidence of endemism among microbes, which, due to their small size and their rapid rate of evolution, may occur over distances of tens of metres. Until methods advance and we are able to make even partial inventories of microbial diversity in natural environments, and we start to understand their functional role in the ecosystem, it would be wise to be conservative and manage forests to encourage diversity of all groups, not just the things we can see. After all, size isn’t everything.

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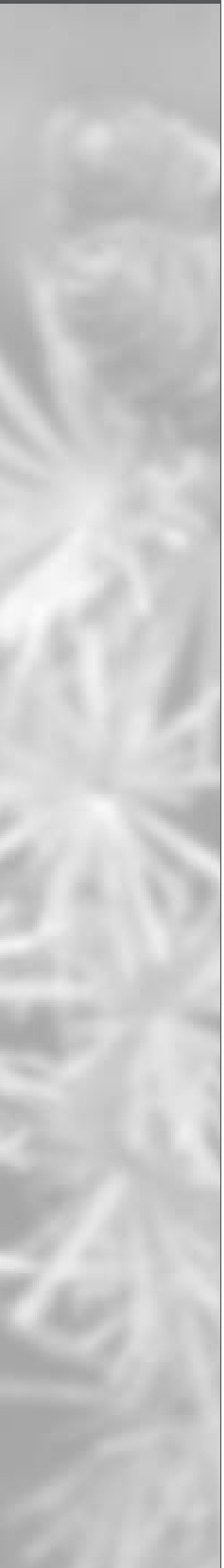


CHAPTER 7

Deadwood

Jonathan Humphrey and Andrew Peace

Summary

The frequency and volume of fallen deadwood (logs), standing deadwood (snags) and stumps were recorded in each of the biodiversity assessment plots. Volumes ranged from zero in newly planted stands to over 300 m^3 ha^{-1} in the over-mature upland Sitka spruce stands. Upland stands had significantly higher deadwood volumes, particularly of snags, than the lowland and foothills plots. This relates to the increased occurrence of windthrow in upland stands and to a past policy of no thinning. Deadwood volumes were significantly higher in the mature and over-mature stands than in the younger stand stages. Mean decay score for logs was the same through the chronosequence for all forest types, whereas mean decay score for snags tended to increase in the older stand stages, especially in pine stands. The foothills Scots pine plots and upland Sitka spruce plots had significantly higher volumes of large diameter (> 15 cm) and well-decayed (decay classes 4 and 5) deadwood compared to the other forest types. Deadwood volumes are considered to meet or exceed current guidelines over most of the sites surveyed, but volumes were very low in some of the lowland plots. Large diameter, well-decayed deadwood is generally considered to have the most value for wildlife, but occurs at a very low frequency and volume in most of the forest and stand types.

Introduction

The importance of deadwood in forest ecosystems is widely recognised (Samuelsson *et al.,* 1994). Standing (snags) and lying (logs or coarse woody debris) dead trees play a key role in the functioning and productivity of forest ecosystems through effects on carbon storage, soil nutrient cycling, energy flows and hydrological processes, natural regeneration of trees and biodiversity (Ratcliffe, 1993). In temperate and boreal forests, decaying wood provides important habitat for small vertebrates, cavity-nesting birds, and a host of lichens and bryophytes, polypores and other saproxylic fungi and invertebrates (Esseen *et al*., 1997). Different species require different types and quality of deadwood. Important factors include: tree species, stage of decay, size and whether standing or fallen (Ferris-Kaan *et al.,* 1993). A number of systems for estimating decay state have been developed and currently variants of the five point scale of Hunter (1990) are the most widely used.

The amount of deadwood in British forests has decreased markedly over the last few hundred years due to timber harvesting and sanitation measures to reduce disease risk. Substantial accumulations of deadwood are now restricted to old-growth forest reserves, or to remnant habitat with old trees such as ancient parkland in the English lowlands (Harding and Rose, 1986). A large percentage of rare and endangered saproxylic species are often restricted to these relict habitats and the inputs of deadwood are governed largely by natural disturbance processes such as wind and fire (Kirby and Drake, 1993). Recognition of the value of deadwood for biodiversity has led to a plethora of guidance in different countries (see Hodge and Peterken, 1998 for a review) accompanied by surveys of the resource.

There have been few surveys of deadwood in British forests (Hodge and Peterken, 1998) with most studies covering individual woods or woodland types (e.g. Reid *et al*., 1996; Green and Peterken, 1997). Kirby *et al*. (1998) provide an overview and analysis of available datasets, but stress the necessity for more information from planted stands. Plantations have been overlooked in general with respect to deadwood and there is a need to relate deadwood accumulations and quality to successional stage and crop species type.

Here we present data on deadwood accumulations recorded within the assessment plots and relate the quality and quantity of snags, logs and stumps to stand stage and crop type. The results are discussed and compared with deadwood data from temperate and boreal forests in Britain and elsewhere. The role of management and natural disturbance in maintaining and enhancing the deadwood resource in planted forests is explored.

Methods

Accumulations of fallen deadwood (logs) were recorded along two transects bisecting the 1 ha plot diagonally from the plot corners (see Figure 3.2, Chapter 3) giving a total transect length of 180 m. Total length and volume of logs with a mean diameter ≥ 5 cm were estimated using the line intercept method (Warren and Olsen, 1964). The formula used to calculate length was taken from Kirby *et al.* (1998). Diameter classes were measured in 5 cm intervals and deadwood quality was described using a visual five-point decay class scale following Hunter (1990): 1 – bark intact, small branches present; 2 – bark loose or sloughing off, no sapwood degradation; 3 – no bark, some sapwood degradation; 4 – no bark, considerable sapwood degradation; 5 – sapwood and heartwood degradation. These categories were also used in the analysis of the lichen and bryophyte data (Chapter 9). However, for the analysis of the fungal data (Chapter 8), the 5 categories were simplified into two: 'fresh' (categories 1–3) and 'rotten' (categories 4 and 5). Volumes were calculated by assuming that the logs were cylindrical. In addition to carrying out estimates of total log volumes in all plots, specific measures of sizes and volumes of individual logs and stumps were made in all sites excluding the oak stands (sites 13, 14, 15 and 16).

The height and diameter at breast height (dbh ~1.3 m) of all individual snags ≥ 7 cm dbh were recorded within the eight 10 m x 20 m plots (Figure 3.2, Chapter 3). There were two of these plots placed diagonally and equidistant between the corners of each 50 m x 50 m quarter of the 1 ha plot. The total plot area was 1600 m^2. As with logs, volumes of snags were calculated by assuming that they were cylindrical.

Analysis

General linear models with log link functions were used to determine the effect of stand stage, location (uplands, foothills and lowlands) and crop species type on log, snag and total deadwood volumes including the frequency and volume of logs and snags in different diameter classes. The Kruskal-Wallis test was used to compare decay class distributions between crop species and locations, and to test the hypothesis that deadwood occurred in similar proportions across diameter classes. The classes used were 5–15 cm, 16–25 cm, 26–35 cm and > 35 cm. These classes were selected to encapsulate the spread of the diameter data, and ensure that there was enough replication within each class. This Kruskal-Wallis test on frequency distributions is used in preference to a standard chi-square test as it makes use of the fact that the decay classes have a natural ordering (1–5). There was insufficient stump volume data to carry out any statistical analyses.

Results

Total deadwood volumes ranged from zero to over 300 $m^3 ha^{-1}$ with a mean value per plot of 36 $m^3 ha^{-1}$ (Table 7.1). Log volumes were generally higher than snag volumes, with stump volumes extremely low (Table 7.1). Log and snag frequencies were higher in the upland and foothills spruce plots and the upland oak plots than in the foothills Scots pine plots and lowland plots (Figure 7.4a). Total deadwood volumes were significantly greater ($P < 0.001$) in the mature (stage 3) and over-mature stands (stage 4) than in the other stand stages (Figure 7.1). Upland stands had significantly ($P < 0.001$) more deadwood than stands in the foothills and lowlands. For snags, there was a strong positive correlation between stand stage and the amount of deadwood ($P < 0.01$), with mature and over-mature plots having the higher volumes. Upland and foothills plots had significantly higher snag volumes than the lowland plots ($P < 0.001$). Log volumes were highest in the over-mature stands and in the uplands ($P < 0.001$ in both cases; Figure 7.1).

Table 7.1 *Summary of deadwood data. Values are per 1 ha plot. SD = Standard Deviation. Volumes are in m^3 ha^{-1}. No stumps < 15 cm in diameter were recorded. Fresh deadwood category includes decay classes 1–3; rotten category includes decay classes 4–5. Deadwood variables are assigned codes referred to in Table 8.2. Minimum values were 0 in all cases.*

Variable	Description	Max.	Mean	SD
LOGL	Length of fallen deadwood (m)	6381.4	1132.8	1485.8
FLOG	Volume of fresh fallen deadwood	161.8	12.6	31.7
RLOG	Volume of rotten fallen deadwood	77.8	10.4	17.0
LOG < 15	Volume of fallen deadwood with mean diameter < 15 cm	38.9	5.9	9.6
LOG ≥ 15	Volume of fallen deadwood with mean diameter ≥ 15 cm	189.2	17.1	38.2
TLOG	Total fallen deadwood volume	194.0	22.9	39.9
FSNAG	Volume of fresh standing deadwood	123.7	8.8	27.5
RSNAG	Volume of rotten standing deadwood	66.1	3.3	13.2
SNAG < 15	Volume of standing deadwood with mean diameter < 15 cm	102.6	4.2	20.6
SNAG ≥ 15	Volume of standing deadwood with mean diameter ≥ 15 cm	136.7	8.3	29.3
TSNAG	Total standing deadwood volume	139.7	12.2	32.5
FSTUMP	Volume of fresh stumps	1.2	0.1	0.3
RSTUMP	Volume of rotten stumps	11.3	0.8	2.3
STUMP≥15	Volume of stumps with mean diameter ≥15 cm	11.3	0.9	2.3
TSTUMP	Total stump volume	11.3	0.9	2.3
TFRESH	Total fresh deadwood volume	285.5	21.5	55.0
TROTTEN	Total rotten deadwood volume	87.0	14.5	20.2
T < 15	Total volume of deadwood with mean diameter < 15 cm	106.5	9.7	21.7
T ≥ 15	Total volume of deadwood with mean diameter ≥ 15 cm	325.9	25.8	62.8
TVOL	Total volume of deadwood	333.7	36.0	65.2

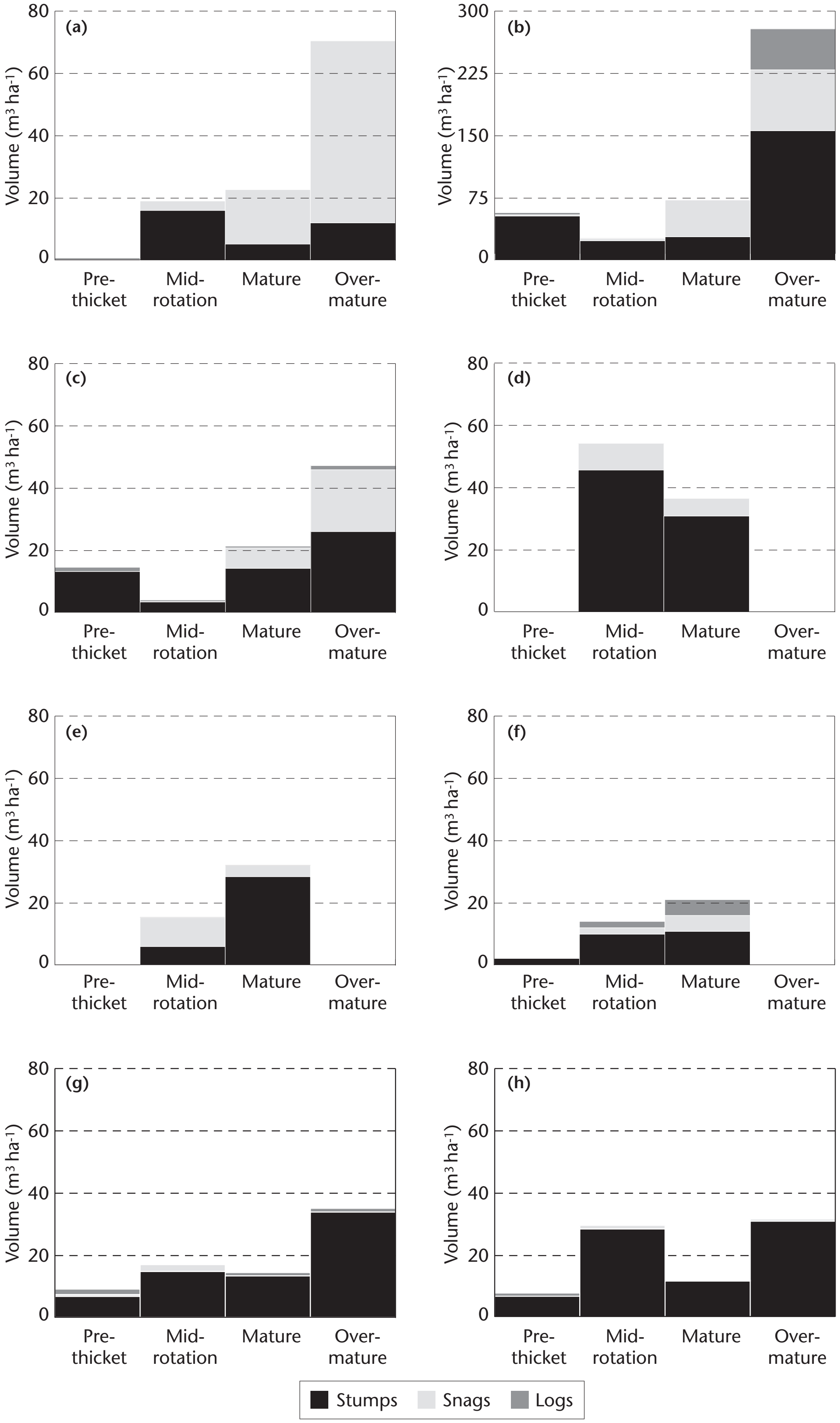
Mean decay scores for logs were constant throughout the chronosequence for pines, spruces and the upland oak sites (Figure 7.2), but mean snag decay score increased through the chronosequence ($P < 0.01$; Figure 7.2). There were no differences in log decay class distributions amongst the pines (foothills Scots pine, lowland Corsican pine, lowland Scots pine), the spruces (upland Sitka spruce; foothills Sitka spruce; lowland Norway spruce), between crop species within foothills and lowlands, or generally between pines and spruces (Figure 7.3a). There were significant differences between the lowland and upland oak sites ($P < 0.001$) with the upland oak sites having large numbers of decay class 5 deadwood items (Figure 7.3a).

Snag decay class distributions did not differ significantly amongst the pines (Figure 7.3a), but there were significant differences ($P < 0.01$) between the spruces, with upland Sitka spruce having a greater proportion of decay classes 4 and 5 snags in comparison to the other spruce stands. There were no differences between crop species within climate zones. The decay class distributions between logs and snags differed significantly for pines, spruces and upland oak (all $P < 0.001$). Across all sites there were proportionately more logs in the higher decay classes (3, 4 and 5) in comparison to snags (Figure 7.3a).

The relationship between the volume and number of pieces of deadwood was tested with respect to decay class. This tests the null hypothesis that there should be no differences in the relationship between volume and frequency between different decay classes. Similar results were obtained for both logs and snags. In the foothills Spruce plots, volumes by decay class were as expected, but for pines there were greater volumes of deadwood in decay classes 4 and 5 than expected relative to the number of pieces of deadwood within those classes (Figure 7.3b).

In the uplands and lowlands, greater volumes of spruce deadwood were recorded in decay classes 1, 2 and 3 relative to what could have been expected from the observed distribution of deadwood pieces of spruce amongst decay classes (Figure 7.3b). Pieces of deadwood in the oak stands were much smaller in volume terms than in the pines and spruces.

Figure 7.1 *Volume of stumps, logs and snags recorded in (a) Foothills Scots pine; (b) Upland Sitka spruce; (c) Foothills Sitka spruce; (d) Upland oak; (e); Lowland oak (f) Lowland Norway spruce; (g) Lowland Scots pine; (h) Lowland Corsican pine. Means of two crop type/stand stage replicates. Note change in abscissa scale on graph (B). For plot details see (Annex 1). All pre-thicket plots in pine and spruce stands are second rotation except Glen Affric plot 1.1.*



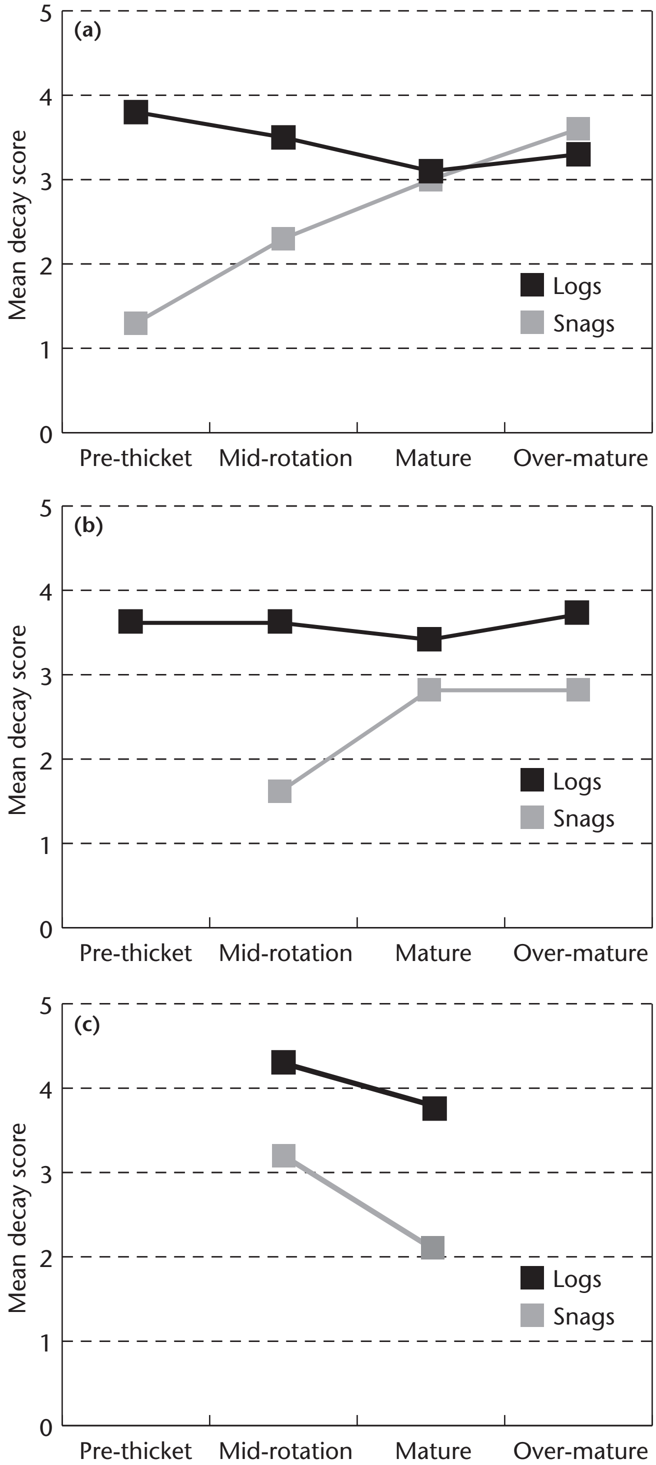


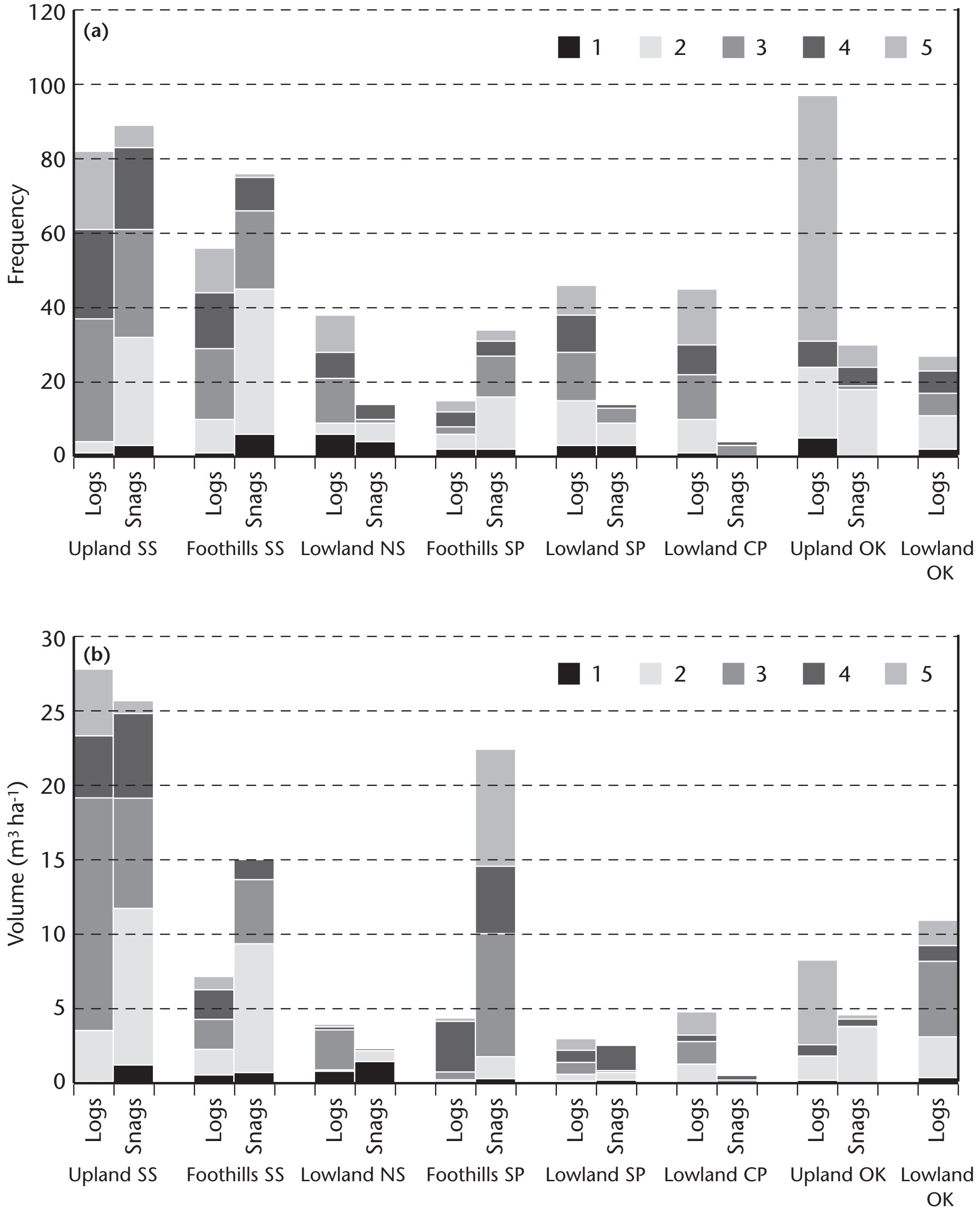
Figure 7.2

Mean decay score of logs and snags in relation to stand stage; (a) pine stands; (b) spruce stands; (c) upland oak stands.

There were no significant differences in the proportions of logs amongst diameter classes between foothills and lowland Scots pine plots, between Scots and Corsican pine or between upland and lowland oak plots (Figure 7.4a). Upland Sitka spruce plots contained proportionately more logs and snags in the larger diameter classes compared to the foothills Sitka spruce and lowland Norway spruce plots ($P < 0.001$ for both logs and snags). Upland oak plots had fewer large diameter logs than the upland spruce plots ($P < 0.01$), but similar snag distributions (Figure 7.4a). Foothills Scots pine plots had proportionately more snags in the larger diameter classes than the lowland Scots and Corsican pine plots ($P < 0.05$), but there was no difference between Scots and Corsican pine (Figure 7.4a).

Although there was much greater frequency of deadwood in the smaller compared to the larger diameter classes, the cumulative volume of the former was generally much lower than that of the latter (Figure 7.4b). Upland Sitka spruce and Foothills Scots pine had significantly higher volumes of large diameter logs and snags than the other crop types ($P < 0.01$).

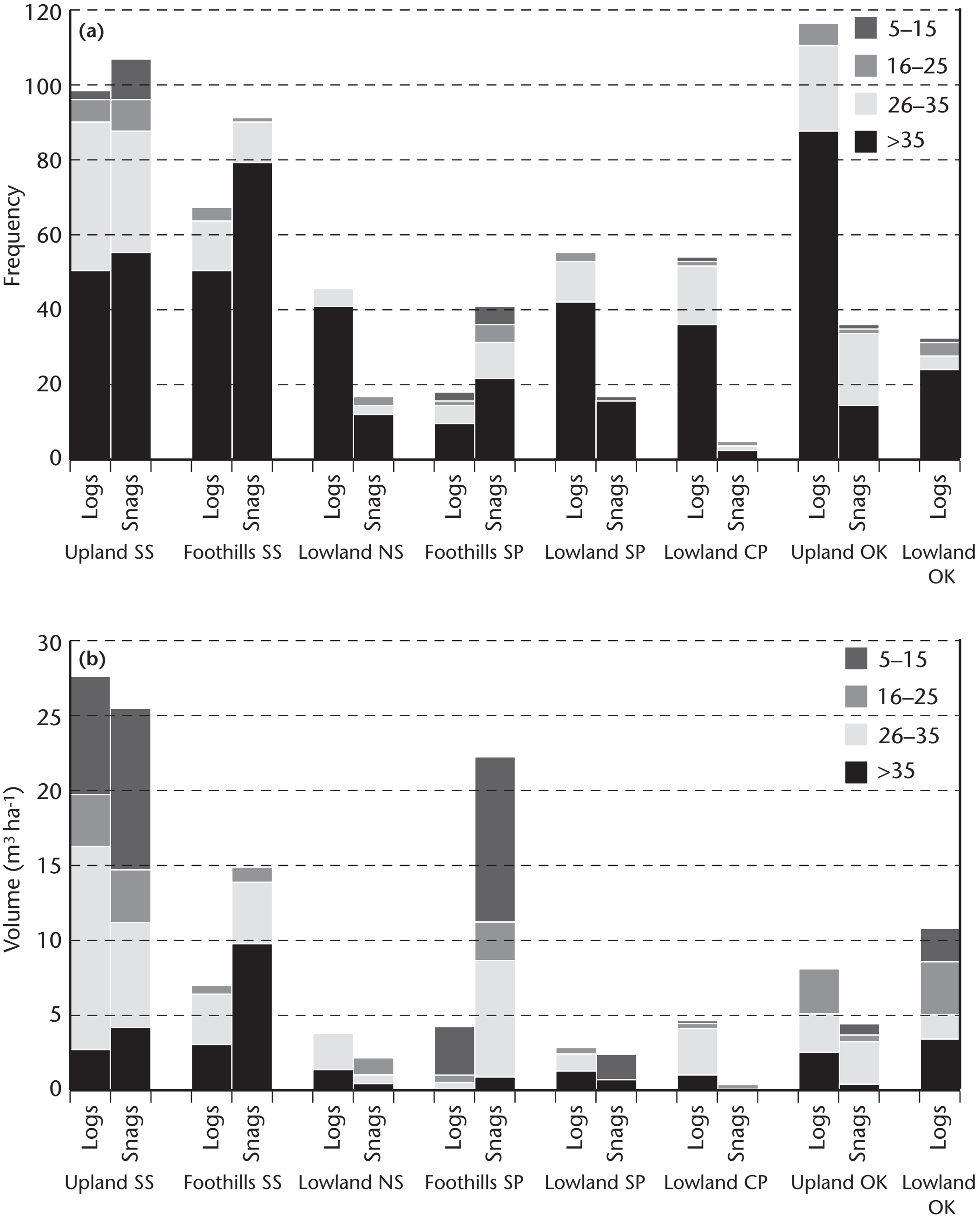
Figure 7.3 *Logs and snags in different decay classes (1–5 in key) and crop types; (a) frequency; (b) volume. Snag decay state was not recorded in the lowland oak stands. Number of plots given in Annexe 1.*



Discussion

Since deadwood is recognised as having an extensive range of ecological values in forest ecosystems, it is perhaps surprising that there have been few large-scale assessments of the resource in British forests before this current survey. The volume range (4–20 $m^3 ha^{-1}$) estimated by Hodge and Peterken (1998) for conifer plantations appears conservative as our survey found the average deadwood volume per hectare was more than 30 m^3, with a considerable number of stands having more than 40 m^3. This latter estimate falls within the 'high' deadwood benchmark proposed by Kirby *et al.* (1998) for British forests, and approaches the values normally associated with neglected coppice woodland, or unmanaged semi-natural broadleaved woodland (Green and Peterken, 1997; Kirby *et al*., 1998). These values for planted forests are also considerably in excess of average volumes of deadwood recorded in Swedish managed and old growth forests (6.1 $m^3 ha^{-1}$ and 12.8 $m^3 ha^{-1}$ respectively – Fridman and Walheim, 2000), but are between the values recorded for over-mature managed and old growth forests in southern Finland (Siitonen *et al*., 2000). Deadwood volumes in near-natural forests in the Pacific Northwest region range from 40 $m^3 ha^{-1}$ in middle-aged stands through to over

Figure 7.4 *Logs and snags in different diameter classes and crop types; (a) frequency; (b) volume. Snag diameter was not recorded in the lowland oak plots. Number of plots given in Annexe 1.*



500 m^3 ha^{-1} in old-growth stands (Spies *et al.*, 1988). Only deadwood volumes in the over-mature upland Sitka spruce stands at approximately 250–330 m^3 ha^{-1} approached these kinds of values.

Despite the variability in deadwood volumes between crop types and stand stages, plots in the north and west of Britain (uplands and foothills) had significantly higher volumes of both logs and snags than stands in the south and east (lowlands). The particularly high volumes recorded in the Sitka spruce stands are probably directly related to two factors: increased occurrence of windthrow and self-thinning in mature and over-mature stands. Wind speeds are generally higher in the north and west of Britain than in the south and east and damaging storms are more common (Quine *et al.*, 1995). Tree density and thus rates of self-thinning are much higher in Sitka spruce stands than in other crop types, owing to a policy of no commercial or pre-commercial thinning to reduce the risk of windthrow (Quine *et al.*, 1995). A typical characteristic of mature Sitka stands is a high frequency and volume of snags, mostly of small dimensions. Many of these snags remain undisturbed within the stand for a considerable length of time before felling, and this may explain why average decay class for snags tended to increase through the chronosequence.

In contrast, most of the mature and over-mature stands in the lowlands had been conventionally thinned and this, coupled with the lack of windthrow, are probably the main reasons why deadwood volumes were lower in these stands. However, catastrophic wind and other events such as drought are not unknown in the lowlands, and both Green and Peterken (1997) and Kirby *et al.* (1998) stress the general importance of individual events in determining the nature of the deadwood resource in British forests. The low deadwood values recorded in some of the stands may simply be due to the fact that no significant disturbance event has affected these particular stands.

Considerable volumes of deadwood are also left as harvesting residue, and some of the pre-thicket plots had quite significant log volumes (only one pre-thicket plot – Affric 1.1 – was a newly planted stand and this had no deadwood). This may in part explain the why decay scores for logs remained constant throughout the chronosequence for pines, spruces and the upland oak sites, whereas log volumes changed considerably. Some logs may have been present in a stand before felling and been left to decay further on site after harvesting, thus being more decayed than might be expected if felled when living.

Pine plots had a greater volume of deadwood in decay classes 4 and 5 than might be expected relative to the number of pieces of deadwood (when compared to spruce). It is possible that larger pieces of pine decay faster than large pieces of spruce (John Gibbs, personal communication). Decay rates in Norway spruce have been modelled by Kruys *et al*. (in press) for mid-northern Swedish conditions, but no comparisons have yet been made between different tree species, so it is not possible to confirm or refute this theory at the present time.

Deadwood volumes in the over-mature or semi-natural stands within the foothills Scots pine chronosequences were similar in magnitude to those within semi-natural pinewood stands recorded by Reid *et al.* (1996) at about 40–60 $m^3 ha^{-1}$. Large logs were much less common than large snags within the pinewoods and this observation tends to support the theory of Reid *et al.* (1996) that most old pine trees die *in situ*, rot gradually, and then shatter into smaller fragments when they are eventually blown over and become logs. A similar phenomenon may occur in the upland oak stands where large quantities of decay class 5 logs were recorded but with a small cumulative volume. These logs were mostly branches in the 5–15 cm diameter class. Large oak trees tend to lose branches during storms and snow rather than blow over entirely. In contrast, most of the high log and snag volumes in upland and foothill Sitka spruce plots were made up of a small number of large diameter pieces, in most circumstances whole trees which had been up rooted.

Conclusions

This preliminary analysis of the deadwood data has shown that both management and natural disturbance agents appear to have a considerable impact on both the quantity and quality of the deadwood resource. The fact that such high deadwood volumes were recorded across a considerable number of sites is encouraging, and many sites appear to meet or exceed current guideline volumes for plantations (Hodge and Peterken, 1998; Kirby *et al*., 1998). The log and snag frequencies recorded were also well in excess of current standards (frequencies of 3 logs and 3 snags per hectare) recommended in the UK Woodland Assurance Scheme (UKWAS – Anon., 2000).

None of the planted stands had been managed in any special way to encourage the accumulation of deadwood, so ‘normal’ plantation management seems to deliver acceptable volumes supplemented by windthrow. However, compared to near natural boreal and temperate forests there is a lack of large diameter, well-decayed snags and logs, particularly in the lowland stands. Chapters 8 and 9 will illustrate the value of large, well decayed material as a habitat for lower plants. The best option for encouraging the accumulation of this type of material is to retain stands beyond normal felling age, and this option is discussed further in subsequent chapters.

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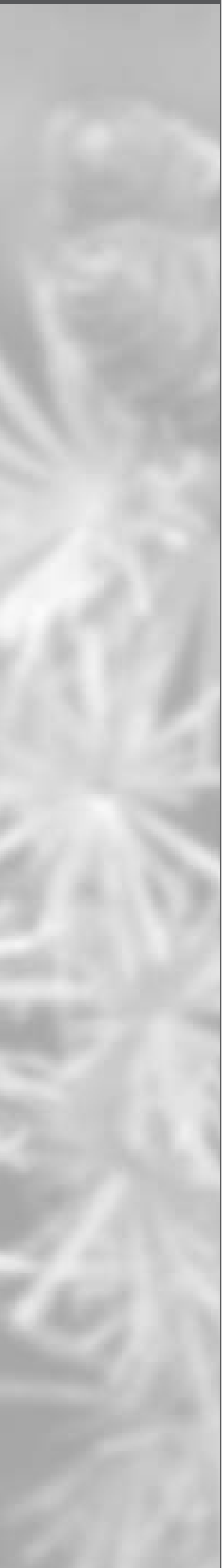

CHAPTER 8

The value of conifer plantations as a habitat for macrofungi

Jonathan Humphrey, Richard Ferris, Adrian Newton and Andrew Peace

Summary

Macrofungal communities were surveyed over a 4-year period in all the biodiversity plots, and species-richness and community composition were related to climate, soil, vegetation and stand variables. Six hundred and eighty species were recorded in total (223 mycorrhizal species, 262 litter saprotrophs, 180 wood saprotrophs, 15 parasites). Each crop species type had a distinctive mycota related to differences in climate, soil, stand structure, deadwood and site history. There were no significant differences in fungal species-richness between plantations and semi-natural woodlands. Mycorrhizal species-richness was highest in upland Sitka spruce stands and was positively correlated with shrub and lower canopy cover, soil magnesium and potassium. Host tree species diversity was positively correlated with mycorrhizal species-richness in lowland pine, spruce and oak plots. Wood saprotroph-richness was most closely correlated with fresh (bark intact) log volume in the southern plots, and log length per hectare in the northern plots, with older lowland Scots pine and oak stands having the highest species counts. Litter saprotoph richness was positively correlated with soil fertility. Twenty-nine Red Data list species of fungi were recorded; planted stands nearer to semi-natural pinewood areas in the Scottish Highlands, or on ancient woodland sites, had a higher number of records of threatened species. These results highlight the importance of planted forests as a habitat for native fungi. Habitat value could be further enhanced through increasing fallen log volumes (up to 20–40 $m^3\,ha^{-1}$), enhancing tree species diversity, and establishing more non-intervention 'natural' reserves preferably near to existing semi-natural woodland fragments.

Introduction

Fungi are a diverse taxonomic group with more than 16 000 species recorded in the UK (Usher, 1997). Macrofungi may be defined as those species of fungi which produce a relatively conspicuous sporocarp; this is an artificial and somewhat arbitrarily defined group which includes many Basidiomycetes (excluding rusts, smuts and yeasts) and some Ascomycetes (Pezizales; Watling, 1995). Woodland fungi play a key role in a number of ecosystem processes, such as the decomposition of cellulose and lignin, mediation of soil processes and the enhancement of tree growth through the development of mycorrhizal associations (Killham, 1994). Fungi also enhance habitat quality for other species. For example wood boring insects require wood infected by fungi before they can digest the lignin, and many other insect groups depend on fungi as a food source (Hodgetts, 1996).

Concern about the conservation of native woodland fungi has increased in recent years (Arnolds, 1991). Given the decline over the last 3000 years in the extent of native woodland habitat in the UK, it is likely that many native fungi must have declined substantially in abundance over the long-term (Newton and Humphrey, 1997). Whilst the recently published Habitat Action Plans for native woodlands (Anon., 1995) should (indirectly) go some way to redressing this decline in native fungi, there is a possibility that planted forests may offer potential habitat. Few mycological surveys have been undertaken in plantations to date (Newton and Haigh, 1998), although recent data suggests that they could have the potential to support a significant fungal diversity. For example, some 151 species of ectomycorrhizal fungi have been found associated with *Picea* spp. in the UK (Newton and Haigh, 1998). However, very little is known about the factors which influence the composition or diversity of fungal communities (Crites and Dale, 1998), as there has been little research concerned with clarifying the relative influences of factors such as site type, stand structure or climate (Humphrey *et al*., 2000). In this chapter, four questions are addressed.

- What types of fungal communities are there in planted forests?
- Which environmental/habitat parameters influence fungal diversity and community structure?
- Can plantations contribute to the conservation of rare and threatened taxa?
- What management, if any, is appropriate for enhancing fungal diversity?

The results presented update those published by Humphrey *et al*. (2000) for northern Britain and Ferris *et al*. (2000) for a subset of sites in southern Britain.

Methods

Fungal survey

Fungi were assessed in all plots except 8.1 (Fineshade – lowland Norway spruce). The presence/absence of macrofungal sporocarps (macroscopic ascomycetes and basidiomycetes) was recorded in the eight 10 m x 10 m mensuration quadrats (see Figure 3.2 – Chapter 3), giving an abundance score of between 1 and 8 for each species. Assessments were made over the August–October period to coincide with the main time of sporocarp production. Three visits were made to each plot at roughly monthly intervals over this period, and repeated over 3–4 years. This sampling period was designed to allow an estimated 80% of total species to be recorded for each plot (based on asymptotes for yearly species-accumulation curves). A total census would need a much longer time period and was beyond the scope of this study. Collections were identified by reference to standard texts, involving microscopic examination where necessary. Material of particularly critical taxa was dried for reference and deposited in national herbaria (Royal Botanic Gardens, Edinburgh and Kew). Species were placed into functional groups following Newton and Haigh (1998) and Ferris *et al*. (2000): M – mycorrhizal; P – parastic; L – saprotrophic species on litter and other fungi; W – deadwood saprotrophs.

Analysis

The effects of crop species type and stand stage on fungal species-richness were analysed using a generalised linear mixed model (see Humphrey *et al*., 2000). Fungal community composition was examined using correspondence analysis (CA; see Chapter 4 for details) to provide vectors (axes) summarising the main gradients of variability amongst the sample plots. The CA vectors (F1, F2 – all plots; FN1, FN2 – northern sites only; FS1, FS2 – southern sites only) together with values for species-richness (number of fungal species per hectare by functional group) were related to climate, soil, stand, and vegetation variables using correlation analysis. Separate analyses were carried out for the northern (1, 2, 5, 6, 9, 10, 15, 16) and southern (3, 4, 7, 8, 11, 12, 13, 14) groups of sites, and for all sites combined. Survey and analysis methods for stand structure, climate, soils, ground vegetation and deadwood, are described in Chapters 3, 5 and 7 respectively.

Results

The total number of fungal species recorded was 677. Of these, 29 were classed as threatened according to the provisional Red List for fungi in the UK (Ing, 1992). This total includes 22 species associated preferentially with native pinewood. There were two apparently new records for Britain: *Panellus violaceofulvus* (Glen Affric, Scots pine, pre-thicket stage plot 1.1) and *Cortinarius callisteus* (Clunes Sitka spruce plots 6.2 and 6.3). Over 50% of species were recorded only once and only 16 species were found in 50% or more of the plots (Table 8.1). The breakdown into functional groups was 223 mycorrhizals, 262 litter saprotrophs, 180 wood saprotrophs and 15 parasites. There were significant differences ($P < 0.01$) in species counts between different crop types for the four main functional groups (parasites are not considered further here) but no effect of stand stage.

Table 8.1 *Most common fungi recorded in the survey. Functional groups are: M – mycorrhizals, L – litter saprotrophs; W – wood saprotrophs. Habitat information was obtained from Philips (1981), Lange and Bayard-Hora (1985), Bon (1987), Jordan (1995), Buczacki (1992), Watling and Gregory (1993), Courtecuisse and Duhem (1994). Nomenclature follows these publications.*

Species	Functional group	Frequency (No. of plots)	Status and habitat in Britain
Mycena galopus	W	44	Very common, widespread in all kinds of woods
Mycena sanguinolenta	L	42	Very common, widespread in grass and litter in woods and heaths
Marasmius androsaceus	L	37	Very common, widespread on dead heather, pine needles and conifer litter
Mycena leptocephala	L	37	Very common, widespread in short grass, or woods
Calocera viscosa	W	36	Very common, widespread on conifer wood
Hypholoma fasciculare	W	35	Very common on wood of deciduous and coniferous trees
Mycena filopes	L	35	Uncommon, widespread on buried twigs in mixed wood
Mycena epipterygia	L	31	Common, widespread among moss and leaf litter in woods
Entoloma cetratum	L	30	Common, widespread in coniferous woodland
Mycena cinerella	L	28	Common, in birch and pinewood on broadleaf litter under mosses
Mycena galericulata	W	28	Very common, widespread on stumps and fallen branches of broadleaves
Hygrophoropsis aurantiaca	L	27	Very common, widespread in conifer woodland and heaths
Cystoderma amianthinum	L	26	Common, widespread on soil in woods and pastures
Hypholoma marginatum	W	26	Common, widespread on rotting conifer wood
Laccaria laccata	M	26	Very common, widespread on soil in woods, moorland and short grass
Russula ochroleuca	M	26	Very common, widespread on soil in conifer and broadleaved woods
Mycena rorida	L	25	Uncommon, widespread on plant debris in woods

Mycorrhizal species-richness

Upland Sitka spruce plots had the highest mycorrhizal species counts ($P < 0.01$) followed by the Scots pine and oak plots (Figure 8.1). Foothills Sitka spruce and lowland Corsican pine had the lowest counts. Species-richness was positively correlated with increasing lower canopy cover (S3), shrub layer cover (S2), cover index (CI) and soil phosphorus, potassium, magnesium and organic matter (Table 8.2) For the northern set of sites, there were positive correlations between species-richness and increasing magnesium, calcium and potassium, and a negative correlation with nitrate (Table 8.2). Similar relationships with soil factors were recorded for the southern sites, but here there were also positive correlations between species-richness, S2 cover, the number of tree species, increasing litter depth and accumulated temperature (AT). Negative correlations were recorded between species-richness, height to live crown and non-vascular plant species count (Table 8.2).

Litter saprotrophs species-richness

As with the mycorrhizals, litter saprotroph species counts were significantly lower ($P < 0.01$) in the foothills Sitka spruce and lowland Corsican pine stands than in the other crop types (Figure 8.1). Species counts were significantly correlated with increasing pH (Table 8.2). In the north, there was a positive correlation between litter saprotroph richness and species-richness of the ground flora; litter saprotroph richness was negatively correlated with increasing litter depth (Table 8.2). Nitrate and pH were the only variables that were significantly correlated with species-richness in the southern plots, with more nutrient-rich, high pH sites having more species.

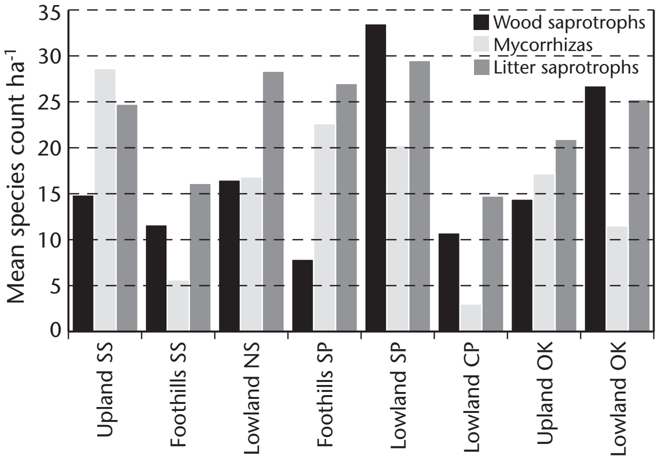

Figure 8.1

Number of fungal species recorded in the different stand growth stages of Scots pine (SP), Corsican pine (CP), oak (OK), Sitka spruce (SS) and Norway spruce (NS). Values are means for each stand/crop type within each climate zone.

Table 8.2

*Summary of significant correlations between fungal species counts and soil, climate, structure, vegetation and deadwood variables, based on Pearson correlation coefficients. Northern plots (sites 1, 2, 5, 6, 9, 10, and 15); southern plots (sites 3, 4, 7, 8, 11, 12, 13, and 14); (-) negative correlation; * P < 0.05; ** P < 0.01. For the key to soil, climate and stand structure variables see Table 3.3 (Chapter 3). For deadwood variables see Table 7.1 (Chapter 7). Vegetation variables: NVASC = number of vascular plant species; VASC = vascular plant diversity.*

		Species counts (number ha^{-1})		
		All plots	Northern plots	Southern plots
Mycorrhizals	Soil	P1* Mg1** ORG1* K**	Mg1** Ca1* K* (-)NO32*	pH1* P1* K*
	Climate			AT*
	Structure	S2** S3* CI*		S2** (-)HTCL*
	Vegetation			(-) NVASC* TREESP* LITTER**
Litter saprotrophs	Soil	pH1* pH2*		pH1* pH2* NH41* NO31*
	Vegetation		(-) LITTER* VASC*	
Wood saprotrophs	Soil	Ca1*		P1* Mg1**
	Climate	AT** MD**		
	Vegetation	VASC** LITTER**		
	Deadwood	FSTUMP*	LOGL**	RLOG**

Wood saprotrophs species-richness

There was a significant positive correlation between the quantity of deadwood and wood saprotroph species-richness (Table 8.2). Lowland Scots pine and oak plots had significantly higher ($P < 0.01$) species counts than the other plots (Figure 8.1 and Table 8.2), relating primarily to higher fresh stump volumes. There were also positive correlations between wood saprotroph richness and increasing litter depth, accumulated temperature (AT), moisture deficit (MD) and soil calcium (Table 8.2). Within the northern set of plots, there was a significant correlation between species-richness and log length per hectare; the relationship is illustrated in Figure 8.2a. No other significant correlations were recorded. In the south, rotten log volume was positively correlated with higher species counts as shown in Figure 8.2b. Positive corrrelations were also recorded between species-richness, increasing litter depth, phosphorus and magnesium. The only negative correlation was with non-vascular plant species count (Table 8.2).

Fungal community composition

The first two axes of the correspondence analysis (CA) of all plots combined (Figure 8.3a) accounted for 20.7% of the variability in the data; eigen values were 0.26 for axis 1 and 0.22 for axis 2. The

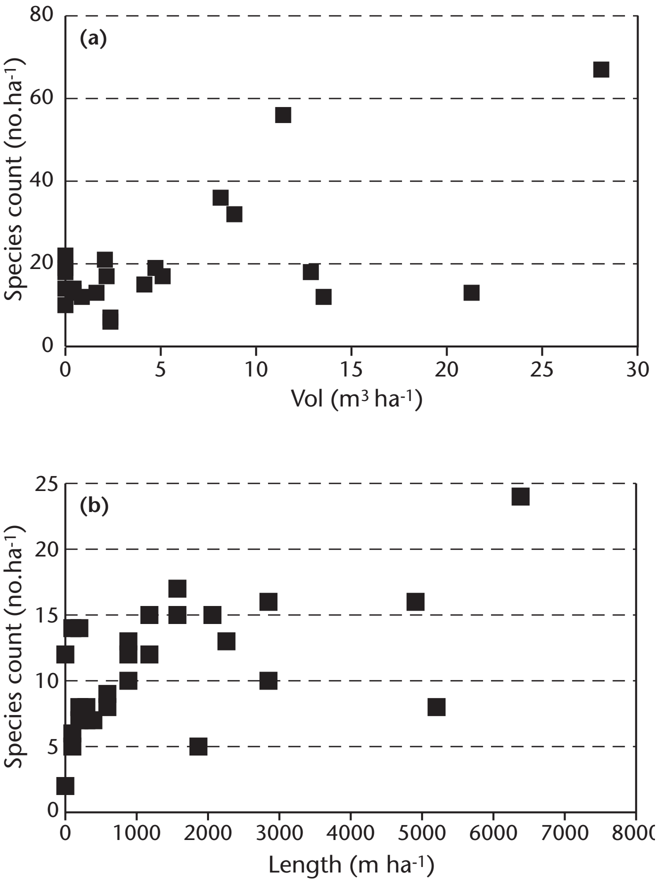

Figure 8.2

Relationships between wood saprotroph species counts (log transformed) and: (a) total fresh log volume per hectare in southern plots only; $y = 2.62 + 0.04x$; $R2 = 0.26$; $df = 21$; $F = 7.43$; $P < 0.05$; (b) total log length per hectare in northern plots only; $y = 2.09 + 0.0001x$; $R2 = 0.21$; $df = 26$; $F = 6.96$; $P < 0.05$.

Sitka spruce and foothills Scots pine plots were grouped separately from the other plots along axis 1 (F1). This axis was positively correlated with magnesium, organic matter and the number of non-vascular plant species. Axis 1 was negatively correlated with pH, nitrate, accumulated temperature (AT) and soil moisture deficit (MD), height to base of live crown (HTLC), and the number of tree and litter saprotroph species. Axis 2 (F2) which separated the oak and lowland Norway spruce plots from the other plots was positively correlated with ground vegetation (all species and vascular plants), tree and mycorrhizal species counts, stand age, pH and major soil nutrients. Negative correlations were recorded between axis 2 and ammonium, field layer cover (S1) and height to live crown (HTLC).

For the CA of northern plots only (Figure 8.3b), eigen values were 0.26 and 0.21 for axes 1 and 2 respectively, with these two axes accounting for 26.9% of the variability in the data. Axis 1 (FN1) separated the foothills Scots pine plots from the other plots and was positively correlated with litter depth, ammonium, accumulated temperature (AT) moisture deficit (MD), upper canopy cover (S4), and wood saprotroph richness (Table 8.3). Negative correlations were recorded between this axis mycorrhizal and litter saprotroph species-richness, and soil organic matter (Table 8.3). The oak, upland and foothills Sitka spruce plots were grouped separately from the pine plots along axis 2 (FN2) relating to a gradient of increasing pH, calcium, potassium, magnesium, vascular plant, tree and mycorrhizal species-richness. Organic matter and ammonium were negatively correlated with axis 2 (Table 8.3).

Axes 1 and 2 (FS1 and 2) of the CA of southern plots accounted for 28.9% of the variability in the data (eigen values of 0.32 and 0.19 respectively). Axis 1 separating lowland oak and Norway spruce from lowland Corsican and Scots pine (Figure 8.3c) was positively correlated with pH and major soil nutrients, leaf area index (LAI), stand age and species-richness of vascular plants, trees, and mycorrhizals (Table 8.3). Moisture deficit (MD) and field layer vertical cover (S1) were negatively correlated with Axis 1. Axis 2 separated Corsican pine plots from the other crop types and was negatively correlated with accumulated temperature (AT), litter depth, litter saprotroph and mycorrhizal species-richness (Table 8.3).

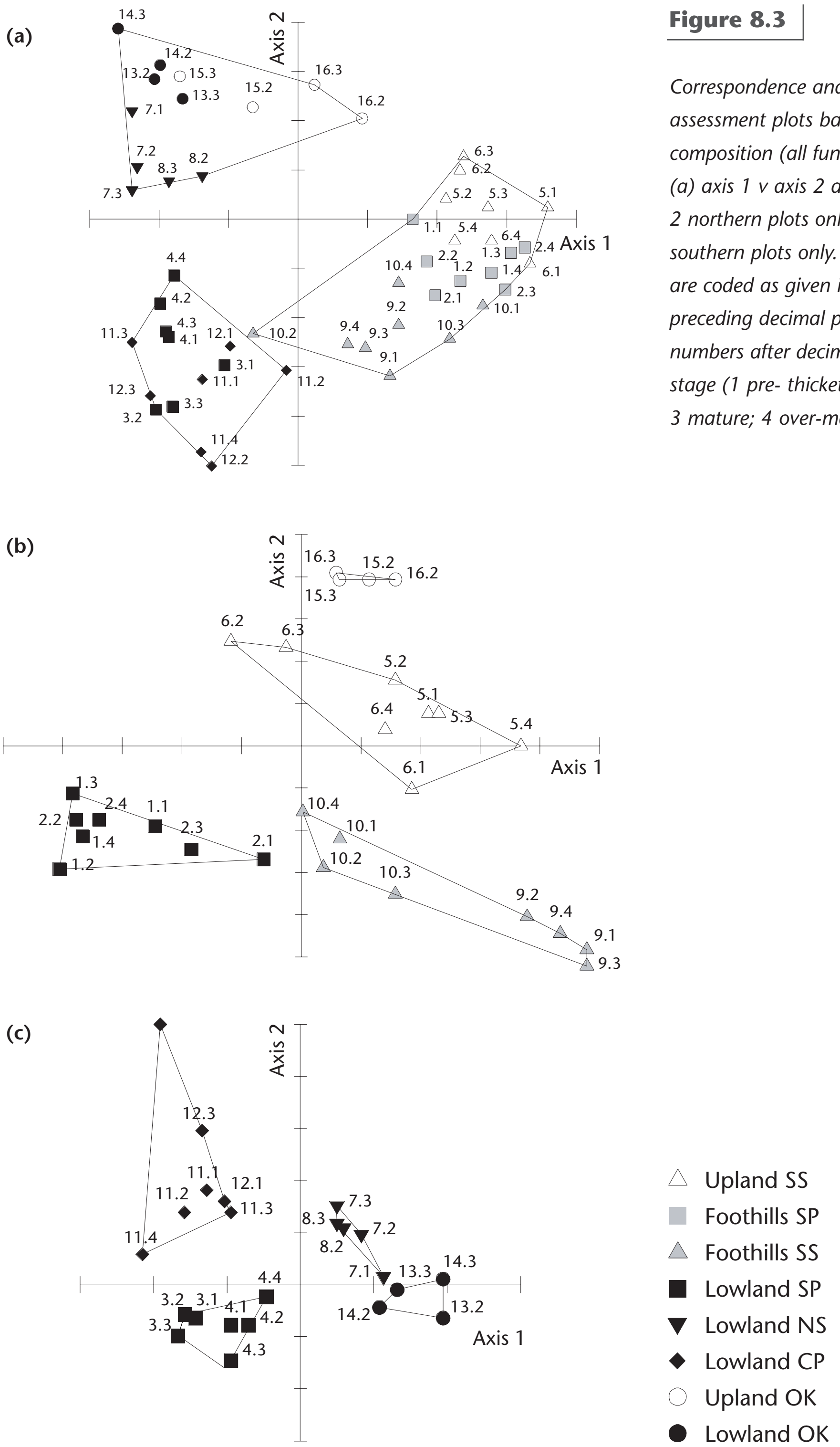

Figure 8.3

Correspondence analysis ordination of assessment plots based on fungal species composition (all functional groups); (a) axis 1 v axis 2 all plots (b) axis 1 v axis 2 northern plots only. (c) axis 1 v axis 2 southern plots only. Data labels for plots are coded as given in Annexe 1. Numbers preceding decimal point refer to sites, numbers after decimal point refer to stand stage (1 pre- thicket; 2 mid-rotation; 3 mature; 4 over-mature).

Species of conservation importance

Of the 29 threatened species recorded, 11 were specific to foothills Scots pine, five to Sitka spruce, four to lowland Scots pine, one to lowland oak, one to upland oak and one to lowland Norway spruce (Table 8.3). Norway spruce and lowland oak shared one species; foothills Scots pine and Sitka spruce had 5 species in common. Most species were recorded as being associated with conifer woodland, acid soil and mosses or conifer deadwood. Three species were associates of broadleaved or coppice woodland (Table 8.3). A negative correlation (Figure 8.4) was recorded between the distance to an extant native pinewood and the number of records of threatened pinewood species (all species in Table 8.3 excluding those found in the lowland plots and the oak plots). No other significant correlations were recorded between the number of threatened species records and any other habitat measure or site variable.

Table 8.3 *Threatened fungal species recorded during the survey. 'Status' refers to the IUCN categories of threat, as employed in Red Data Lists (see Mace and Lande, 1991 for Scotland). Abbreviations (following Ing, 1992): E – endangered; V – vulnerable; R – rare. W – wood saprotrophs; M – mycorrhizal species; L – litter saprotrophs; P – parasites. n/a – no habitat information available.*

Species	Functional group	Status	Plots where recorded	Habitat
Collybia acervata	L	V	2.4	Conifer stumps
Collybia racemosa	L	R	4.2	Decayed mushrooms or conifer litter
Cortinarius camphoratus	M	V	6.2, 6.3	Conifer woods, notably pine
Cortinarius laniger	M	V	6.2	n/a
Cortinarius limonius	M	V	1.2, 2.4, 6.2, 6.3, 6.4,	Soil – conifer woods
Cortinarius purpurascens	M	-	1.3	Acid soils in conifer/deciduous woods
Cortinarius scaurus	M	V	6.2	Conifer woods, especially spruce
Cortinarius violaceus	M	E	5.2	Deciduous woods, birch/beech
Craterellus cinereus	M	V	13.3	n/a
Fayodia gracilipes	L	R	5.2, 6.2, 6.3	Mosses especially under conifers
Galerina stylifera	L	V	3.1, 3.2, 3.3	Wet rotten wood/conifer debris
Hydnellum peckii	M	E[1]	2.2	Plant debris – conifer woods
Lactarius musteus	M	V	1.2, 2.1, 2.2	*Sphagnum*/moss – conifer woods
Leucoagaricus georginae	L	V	3.3	Mixed coppice especially disturbed
Lycoperdon lambinonii	L	V	7.2	n/a
Mycena purpureofusca	W	V	2.1, 6.3, 10.2	Pine cones and woody debris
Mycena rosella	L	V	1.1, 1.3, 1.4, 2.4, 6.2	Fallen conifer needles
Mycena rubromarginata	L	V	1.4, 2.1, 2.2, 2.3, 3.1, 5.1, 5.2, 5.3, 5.4, 6.1, 6.3, 6.4, 8.3, 10.1, 10.4, 11.3	Twigs/ litter – conifer woods
Mycena urania	L	E	2.3	n/a
Pholiota astragalina	W	R	4.1	Rotten conifer wood
Pseudocraterellus sinuosus	M	V	16.3	Leaf litter – deciduous woods
Ripartitis metrodii	L	R	8.2, 8.3, 13.3	Conifer woods, especially spruce
Rozites caperata	M	V	1.3, 1.4, 2.4	Acid soil – conifer woods/heather
Russula declorans	M	V	1.3, 1.4	Soil – conifer woods
Russula obscura	M	V	1.3	Soil – conifer woods
Sarcodon imbricatus	M	V[1]	2.2	Soil – conifer woods
Suillus flavidus	M	V	1.4	Wet soil/*Sphagnum*-Scots pine
Tricholoma sejunctum	M	V	1.4, 6.2	Soil – mixed/conifers especially birch
Xeromphalina campanella	W	V	2.1	Rotting conifer wood

[1] Species with Action Plans (SAPs – Anon., 1995)

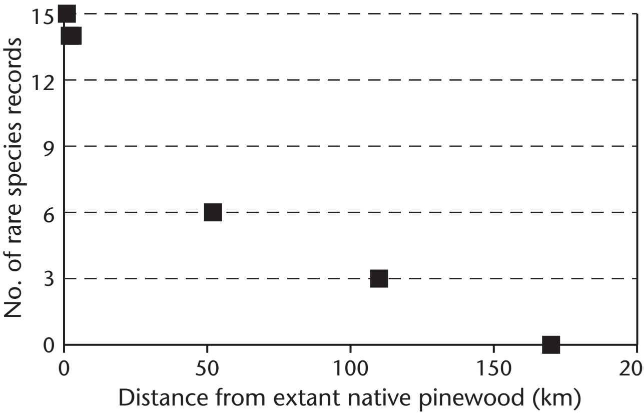

Figure 8.4

Records of threatened native pinewood fungi in relation to distance of recording site from extant native pinewood area; $y = -0.0154x + 2.785$; $R2 = 0.9799$; $df = 4$; $F = 194.8$; $P < 0.001$ (log transformation of count data).

Discussion

Limitations of the data

Fungal communities are notoriously difficult to assess comprehensively in the field. Surveys depend upon the presence of sporocarps to denote species occurrence, rather than the vegetative mycelia that generally form the greater part of fungal biomass. Sporocarp production is strongly influenced by weather conditions with sporadic and sometimes shortlived fruiting varying between different months and years (Watling, 1995). Orton (1987) considered that at least 10 years of survey data were required to define the species of macromycete present in an area with any precision, and there have been numerous studies where new species were still being recorded after 20 years (Watling, 1995). In this current survey, plots were only surveyed on three occasions and given this limitation the current data must therefore be viewed with caution. However, the fact that the plots were surveyed over the same period should increase the validity of comparisons drawn between them.

Relationships between environmental variables, fungal species-richness and community composition

Altogether, 679 fungal species were recorded during this survey. This figure compares favourably with those obtained from mycological surveys of temperate and boreal forests in Scandinavia and North America (e.g. Lindblad, 1998). Of the 16 most common species, over half were litter saprotrophs comprising widespread and abundant species found in both wooded and non-wooded habitats (e.g *Mycena sanguinolenta* and *Marasmius androsaceus*). As with the lichen and bryophyte data (see Chapter 9), a large proportion of the species were recorded only once. Consequently, fungal community composition differed markedly between sites, and even between plots within a site. Despite this variability three clear groupings were evident in the CA of all plots: a northern spruce/pine group, an oak/Norway spruce group and a lowland Corsican/Scots pine group. Part of the variability between these groups was related to large differences in the species-richness of wood saprotrophs and mycorrhizals. Mycorrhizal species-richness was significantly higher in the upland Sitka spruce plots (towards the right-hand end of axis 1 – Figure 8.4a) than in the other plots including oak. This finding contrasts with those of other studies that have suggested that the fungal flora of conifer stands is often less diverse than that of broadleaved stands. For example, Villeneuve *et al*. (1989) found that the diversity of both ectomycorrhizal and saprotroph species in Quebec forests was significantly lower in conifer stands than in deciduous stands, owing mainly to the scarcity of saprotrophs in conifer mor humus. In addition, Newton and Haigh (1998) in their study of ectomycorrhizal fungi in the UK, found that exotic conifer species displayed a lower mycorrhizal diversity than would be expected from their distributional areas (151 mycorrhizal associates of *Picea*, 201 for *Pinus* and 233 for *Quercus*).

The trend in mycorrhizal species-richness is driven mainly by plots 6.2 and 6.3 (Clunes, mid-rotation and mature stands). These plots, characterised by large numbers of *Cortinarius* and *Inocybe* spp., form a distinct grouping along axis 2 of the CA of northern plots, associated with increases in soil magnesium and potassium, shrub and lower canopy cover, and the number of tree species. It is possible that the denser stand conditions associated with the mid-rotation and mature spruce stands are conducive to the development of mycorrhizal communities by affording freedom from competing ground vegetation and providing a higher tree root density for mycorrhizal associations. The significant correlation recorded between mycorrhizal species-richness and the number of host tree species present confirms recent analyses indicating that many tree species in Britain are associated with distinctive assemblages of ectomycorrhizal fungi (Newton and Haigh, 1998).

These results therefore suggest that the diversity of host tree species could be used potentially as a simple indicator to infer patterns of diversity in this group of fungi. This finding also lends support to the inclusion of hardwood species in conifer plantations as a means of increasing biodiversity. For example, the addition of birch in spruce stands was found to increase numbers of vascular plant, bryophyte and lichen species (Humphrey *et al.,* 1998), and the same may be expected for mycorrhizals on the basis of the current study.

Paradoxically the foothills Sitka spruce stands, although comparable in terms of stand age and structure to the upland Sitka spruce plots were not nearly as rich in fungal species. Annexe 1 indicates that the upland and foothills Sitka stands differ markedly in their site histories; the upland plantations in Clunes and Knapdale having been established on ground previously occupied by ancient semi-natural woodland (Hamilton, 1995), whereas the foothills Kielder and Glentress stands were established on grass and heathland. Site history also appears to be a significant factor in the south. Low species counts were recorded in Corsican pine stands (sites 11 and 12) established on heath and grassland land, whereas the Norway spruce stands (sites 7 and 8), established on old oakwood sites, shared a number of species with the oak stands which were either absent, or much less common in the other plots (e.g. species such as the litter saprotrophs *Clitocybe fragrans*, *Collybia butyracea*, *Lycoperdon perlatum*, *Megacollybia platyphylla*, *Mycena polygramma* and *Ripartitis metrodii*, and the wood saprotroph *Xylaria hypoxylon)*.

The abundance and decay state of deadwood is a key factor influencing the diversity of wood saprotrophs in semi-natural temperate and boreal forests (Crites and Dale, 1998; Kruys *et al*., 1999; Hodgetts, 1996). In this current study, a number of positive relationships were recorded between log and stump volumes and the number of wood saprotroph species. Wood saprotroph richness was negatively correlated with axis 1 of the CA of all plots (Figure 7.3a), with plots 4.4 (Windsor, over-mature Scots pine) and 13.3 (Alice Holt mid-rotation oak) having significantly higher numbers of species than the other plot types and lying well to the left on this axis. Plot 4.4 was characterised by a high abundance of *Hypochnicium*, *Phlebia* and *Phlebiella* spp.; plot 13.3 had species which were not recorded in any other plots such as *Bulbillomyes farinosus, Peniophora quercina* and *Tomentella bryophila*.

Whilst this trend in species-richness was also correlated with factors such as accumulated temperature and soil moisture deficit, the strongest correlation was with fresh stump volume, plots 4.4 and 13.2 having very high values for this variable compared to the other plots. The importance of these two plots tends to mask other trends in the deadwood data that become apparent when the northern and southern plots are considered separately. In the north, log length (all decay categories) was the best predictor of species-richness, whereas rotten log volume was more important in the south. Unfortunately, the value of stumps as a predictor of wood saprotroph-richness appears to be limited as a high proportion of plots had no stumps.

In a number of studies in boreal forests, correlations have been recorded between wood saprotroph diversity and deadwood with both initial and advanced bark loss (e.g. Crites and Dale, 1998; Lindblad, 1998; Kruys *et al*., 1999). In Swedish Norway spruce forests, a number of Red Listed fungi showed strong preference for fallen deadwood with well-rotted bark (Kruys *et al*., 1999). Deadwood in more advanced states of decay, where the wood itself starts to rot, does not appear to support such diverse saprotroph communities (Kruys *et al*., 1999; Crites and Dale, 1998), although some specific fungi show a preference for this stage (Lindblad, 1998). This stage-specific factor may explain to some extent why higher species numbers were strongly correlated with rotten log volume in the south. However, no direct measurements of fungal species growing on different types of deadwood were undertaken in this study, so this assumption is difficult to verify.

Lowland Scots Pine and Norway spruce plots had the highest numbers of litter saprotroph species, but the differences between the crop types was less marked than for the other functional groups. Soil fertility appears to be the underlying factor influencing species-richness. The negative correlation recorded between litter depth and saprotroph richness is possibly a consequence of increased rates of decomposition.

Fungi of conservation importance

A striking feature of the survey results was the extensive new records for rare and threatened fungi, including one species not previously recorded the UK (*Panellus violaceofulvus*) and one not previously confirmed as being native (*Cortinarius callisteus*: Orton, 1987). In addition, a further 29 species are considered to be threatened with extinction, in that they have been listed on the provisional Red Data List for British fungi. The recording of 10 Red Data List species in spruce-dominated plots in Clunes and Knapdale was unexpected and suggests a possible ability of these fungi to 'host-shift' (Watling, 1995), as all are generally associated with native pine forests. Information on the distribution of native pinewoods taken from the Forestry Commission's Pinewood Inventory (Tuley, 1995) indicates that the spruce plots in Clunes forests are, on average, 5 km from existing pinewoods in the Loch Arkaig area. However, as noted earlier, the Clunes stands were planted on sites previously occupied by ancient semi-natural woodland. Thus temporal continuity as well as spatial proximity of pinewood habitat within the locality could help explain the relatively large number of rare species records from Clunes forest. In contrast, the Knapdale spruce plots are over 50 km from native pinewoods, the nearest group being in Glen Orchy and Glen Strae. It is possible that these plots could have acquired pinewood fungi in the short time since planting (in the 1920s and 1930s) and suggests that long-distance dispersal is possible in such species. There were few pinewood fungi recorded in Glentress and none in Kielder, reflecting perhaps the increasing distance of these sites from the nearest native pinewood fragment in Glen Falloch (Argyll). However, the ecological characteristics of these threatened pinewood fungi are poorly understood, particularly with respect to their ability to disperse and colonise new habitats. It is conceivable that some species may have been translocated during forestry operations, for example mycorrhizal species could have been transported via the root systems of planting stock (see Humphrey *et al.*, 2000).

Conclusions and management recommendations

Although the observed relationships between environmental parameters and fungal community composition and diversity are obviously very complex and little understood, some general conclusions can be drawn which have important implications for management. Firstly, it is clear that planted forests provide a range of environmental conditions suitable for the development of diverse native fungal communities that include a number of rare and threatened species. Different crop types support different species assemblages and it is therefore important to maintain a diversity of crop types at the landscape or whole forest scale. Mycorrhizal community development is influenced by stand structure, host tree species diversity and site history. The best sites for mycorrhizals, in terms of species-richness, appear to be relatively dense upland spruce plantations on ancient woodland sites, although pine and spruce plantations on ancient woodland sites in the lowlands are also valuable (for litter saprotrophs as well as mycorrhizals).

Wood saprotroph richness is strongly correlated with increases in fallen deadwood and stump volumes. A mix of fresh and well-decayed large diameter logs and stumps should provide a range of habitat types (Kruys *et al.*, 1999) with volumes in the range of 20–40 m^3 ha^{-1} providing for maximal diversity (based on the asymptotes of the regression curves of species-richness on deadwood volumes). This range falls close to the high (> 40 m^3 ha^{-1}) benchmark for deadwood in British broadleaved forests, as proposed by Kirby *et al.* (1998) and exceeds the 4–20 m^3 ha^{-1} range for fallen deadwood volume in conifer plantation forests reported by Hodge and Peterken (1998). Litter saprotroph community composition and diversity appears to be more closely related to soil variables than to any other environmental factors and is therefore less amenable to enhancement by management.

The high incidence of rare and threatened fungi in plantation stands of pine and spruce, was an unexpected finding of the survey. Temporal and spatial linkage with native woodland appears to be important for determining the occurrence and distribution of these species, particularly those associated with native pinewood. The Forest Habitat Network model of Peterken *et al.* (1995) provides an appropriate mechanism for the successful integration of plantations and native woodlands, and plans are in place to develop these principles further in a native pinewood area (Ratcliffe *et al.*, 1998). Such approaches could encourage the rapid colonisation of newly established pinewoods by native fungi.

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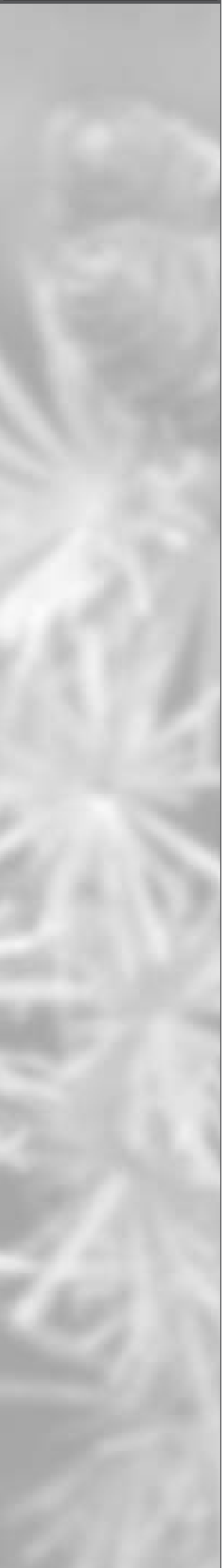
CHAPTER 9

Lichen and bryophyte communities: the influence of site type, stand structure and deadwood

Jonathan Humphrey, Simon Davey, Andrew Peace, Richard Ferris and Kim Harding



Summary

A survey of deadwood lichen and bryophyte communities was carried out over a 2-year period within all 52 biodiversity assessment plots. Community composition and diversity were related to measures of climate, site, stand structure and deadwood (snags, logs and stumps). Altogether, 106 lichen species and 77 bryophytes were recorded. The planted stands had a less species-rich lichen flora than the semi-natural stands. Bryophyte species counts were similar in plantations and semi-natural stands, and were positively correlated with large diameter (≥20 cm), well-decayed logs and stumps. Lichens species-richness was higher on well-decayed snags (especially in semi-natural Scots pine stands in the Scottish Highlands). Early successional stands were often the richest for lichens, stumps being important for Caliciales and Cladonia species. There is greater scope for enhancing the diversity of epixylic lichen and bryophyte communities within plantations in the north and west of Britain than in the south and east, as lower plant communities in the north and west have been less damaged by high pollution levels in the past and the cooler and wetter climate is more conducive to community development. Two management strategies are suggested: 1) introducing alternative silvicultural systems to clearfelling (e.g. single-tree selection) to foster continuity of woodland conditions and increase deadwood volumes; 2) modifying restocking practices on clearfells to avoid excessive shading of deadwood. The first strategy is most suited to spruce stands in areas of low wind risk, whilst the second is more appropriate for Scots pine forest in the Scottish Highlands.

Introduction

Lichens and bryophytes are now an increasingly valued component of woodland biodiversity, and this is reflected in the recent production of Species Action Plans targeted at maintaining and improving habitat for the most threatened and rarest species (Anon., 1995). However, lichens and bryophytes also fulfil a number of important ecological functions within woodland ecosystems such as: regulation of hydrological processes through interception and retention of precipitation (i.e. reducing peak flows in streams during floods), stabilising steep ground in western woodlands, contributing to nutrient cycling, and providing food and shelter for a range of dependent organisms (Hodgetts, 1996). Lichens and bryophytes are often described as being ‘epiphytic’ (using living trees or shrubs for anchorage, but not as a source of nutrients) and/or ‘epixylic’ (using dead woody material for anchorage).

Semi-natural woodlands in Britain are of international importance for lichens and bryophytes (Hodgetts, 1996). Key biotopes include lowland pasture woodland (e.g. the New Forest, Suffolk), Atlantic oak-birchwoods (*Quercus-Betula* spp.) in northern and western regions, and native Caledonian pinewoods (*Pinus sylvestris* L.) in the Scottish Highlands (Rose, 1993). The particular value of these woodland types as a habitat for lower plants is related to low pollution levels, continuity of woodland conditions over many hundreds of years, the survival of very old trees, and relatively open canopies ensuring adequate light levels for growth and development (Rose, 1993; Fletcher, 1999).

Deadwood is a key habitat for lower plants in boreal and temperate forests (Esseen *et al.*, 1997; Crites and Dale, 1998). A number of studies in Fenno scandian boreal forests have highlighted the value of large diameter, well-decayed fallen and standing deadwood for rare and threatened taxa (e.g.

Gustafsson and Hallingbäck, 1988; Kruys *et al*., 1999). Old, unmanaged stands usually have the highest diversity of deadwood habitats (including a high proportion of large, well-decayed material) and hence have a more diverse lower plant flora (Gustafsson and Hallingbäck, 1988; Kuusinen and Siitonen, 1998).

Currently, there is very little information on the potential value of conifer plantations for lower plants, or how they might be managed to improve habitat quality. Despite numerous calls for managers to increase deadwood volumes in managed forests, the value of deadwood as a substrate for lower plants remains to be investigated (e.g. Hodge and Peterken, 1998). In this chapter, we present the results of a survey carried out in all 52 biodiversity plots of lichen and bryophyte communities associated with deadwood. Community composition and diversity were related to climate, stand structure (successional stage and vertical foliage cover) and deadwood parameters. The potential of conifer plantations as a habitat for native lichens and bryophytes is discussed, and management strategies are proposed for enhancing habitat quality. For a more detailed analysis of the lower plant data, including species recorded on substrates other than deadwood, see Humphrey *et al*. (2002).

Methods

Lichen, bryophyte and deadwood assessments

Lichen and bryophyte species were recorded in four 10 cm x 20 cm quadrats on individual pieces of deadwood. The quadrats were spaced more or less evenly along the length of each piece, on the upper surface of logs and stumps (i.e. omitting the sides and lower portions), and up to 2 m in height on snags (aspect was selected randomly for snag sampling). The abundance of individual species was estimated using the DOMIN scale (see Chapter 4 for details of this approach). Volume and size measurements for individual items of deadwood were only carried out in sites 1–12 (the oak stands, sites 13, 14, 15 and 16 were excluded). Methods for calculating deadwood volumes are described in Chapter 6.

Analysis

Generalised linear models (see Humphrey *et al*., 2002 for details) were used to assess the relative importance of crop type (combining species and bioclimatic zone), stand stage, deadwood type, decay stage, size and volume in determining species-richness of lichens and bryophytes growing directly on deadwood. As no quantitative measures of deadwood were undertaken in the oak stands these were not included in the model. The species count data were then related to climate, soils and stand variables using correlation analysis. The assessment methods for these variables are described in Chapter 3. Variability in the species-composition of deadwood communities (all crop types, including oak) was examined using correspondence analysis (CA). This analysis provides vectors or axes summarising the main gradients of variability amongst the sample plots (see Chapter 4). The principal CA vectors (BRYO1 and 2; LICH1 and 2) were correlated with climate, soil and stand variables.

Results

Overview

Altogether, 106 lichen species and 77 bryophytes were recorded on deadwood. Over 40% of lichen and 27% of bryophyte species were recorded only once (Table 9.1) and no single species of either group was recorded in all plots. The most commonly recorded lichen genera were: *Cladonia* (25 species); *Parmelia* (14 species); *Pertusaria* (9 species) and *Lecanora* (8 species). The most common species were: *Cladonia coniocraea*, *Hypogymnia physodes*, *Cladonia chlorophaea*, *Cladonia squamosa* and *Lepraria incana*. Lichen species counts were generally higher in the semi-natural stands (oak and over-mature foothills Scots pine plots) than in the planted stands (Figure 9.1). The main bryophyte genera were: *Dicranum, Calypogeia, Plagiothecium* and *Polytrichum*, and the most common species were: *Hypnum cupressiforme*, *Dicranum scoparium*, *Eurhynchium praelongum*, *Polytrichum formosum* and *Plagiothecium undulatum*. Bryophyte species-richness was similar in planted and semi-natural stands (Figure 9.2).

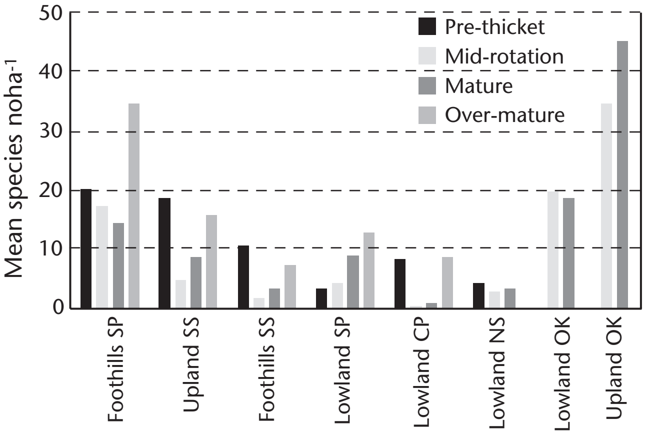


Figure 9.1

Number of lichen species recorded in different stand growth stages of Scots pine, Corsican pine, Sitka spruce, Norway spruce and oak. Values are means for each crop/stand type within each climate zone. Details of site history are given in Annexe 1.

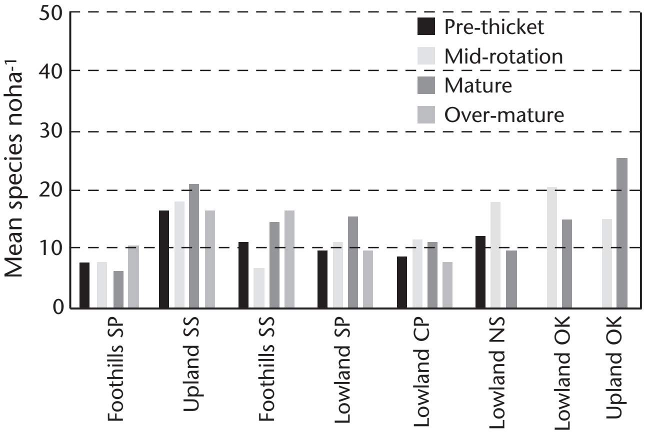


Figure 9.2

Number of bryophyte species (mosses and liverworts) recorded in different stand growth stages of Scots pine, Corsican pine, Sitka spruce, Norway spruce and oak. Values are means for each crop/stand type within each climate zone. Details of site history are given in Annexe 1.

One Red Data Book lichen species was recorded on deadwood: *Bryoria furcellata* (Glen Affric, over-mature Scots pine – plot 1.4). *B. furcellata* is classed as 'Vulnerable' in accordance with the revised IUCN categories of risk (World Conservation Union, 1994), and is a Wildlife and Countryside Act 1981, Schedule 8 species (Church *et al.*, 1996). The number of NIEC (New Index of Ecological Continuity – Rose, 1993) lichen species recorded was 18, and the number of RIEC (Revised Index of Ecological Continuity – Rose, 1976) species was 9 (Table 9.1). These indices give a measure of long-term continuity of woodland conditions at the stand level and of habitat quality for uncommon species (Rose, 1993). However, their relevance is restricted to lowland England and Wales (Rose, 1993). The only sites with NIEC or RIEC species falling into this zone were: Alice Holt oak (2 species); New Forest oak (10 species) and New Forest Scots pine (2 species).

Table 9.1

Lichen and bryophyte summary data. RDB – Red Data Book species (Church et al.*, 1996). NIEC – New Index of Ecological Continuity (Rose, 1993); RIEC – Revised Index of Ecological Continuity (Rose, 1976). Mosses and hepatics were combined for subsequent analyses. n/a – not applicable.*

	Lichens	Mosses	Hepatics	Total
Species count	106	49	28	183
RDB species	1	0	0	1
NIEC species	18	n/a	n/a	18
RIEC species	9	n/a	n/a	9
Mean species count/plot	9	8	3	18
Max. species count/plot	51	15	10	56
Min. species count/plot	0	0	0	0
Species recorded only once	43	12	8	63
Species recorded in >50% of plots	2	4	0	6

Conifer stands only: effects of crop type, stand structure and deadwood on lichen and bryophyte species-richness
Crop type (combining species and bioclimatic zone) was the most significant factor (P <0.01) influencing both lichen and bryophyte species counts on deadwood. For lichens the ranking was (Figure 9.1): foothills Scots pine > upland Sitka spruce > (foothills Sitka spruce and lowland Scots pine) > (lowland Corsican pine and lowland Norway spruce) (P < 0.01). This south to north gradient in increasing species-richness was positively correlated with decreasing accumulated temperature (AT) and soil moisture deficit (MD) (Table 9.2). A contrasting pattern was recorded for bryophytes, with the ranking being (Figure 9.2): (upland Sitka spruce, lowland Norway spruce and foothills Sitka spruce) > (lowland Corsican pine and lowland Scots pine) > foothills Scots pine (P <0.01).

Table 9.2 *Pearson correlations between climate and stand structure variables, lichen and bryophyte species-richness, and the first two ordination axes of the CA plots (Figure 9.5). Species counts exclude oak stands; ordinations include oak stands. Significance levels are *P < 0.05; **P < 0.01. The key to the soil, climate and stand structure variables is in Chapter 3, Table 3.2.*

	Species counts ha^{-1}		**Ordination axes**			
	Bryophytes	**Lichens**	**BRYO1**	**BRYO2**	**LICH1**	**LICH2**
AT	-0.01	-0.59**	0.48**	0.21	0.49**	0.33*
MD	-0.08	-0.59**	0.54**	0.22	0.61**	0.21
S1	0.16	0.24	0.03	-0.02	0.09	-0.43**
S4	0.51**	-0.25	0.06	-0.46**	0.36*	0.37*
CI	0.39**	-0.24	0.01	-0.32*	0.00	-0.04
HTLC	-0.05	-0.39**	0.35*	-0.27	0.47**	0.28
MBA	0.12	-0.34*	-0.06	-0.38**	0.13	0.22
LAI	0.05	-0.47**	0.16	-0.09	0.18	0.17
TREESP	-0.04	-0.34*	0.29	0.09	0.10	0.52**
AGE	-0.26	0.55**	-0.13	0.17	-0.33*	0.42**
Bryophytes (total species count.ha^{-1})	–	-0.18	–	–	–	–
Lichens (total species count.ha^{-1})	-0.18	–	–	–	–	–

Stand stage also had a significant effect on lichen species-richness, with pre-thicket plots having higher lichen counts than over-mature plots followed by mature then mid-rotation plots (P<0.01). Lichen species-richness was positively correlated with stand age (Table 9.2) and negatively correlated with height to live crown (HTLC), mean basal area (MBA) and leaf area index (LAI). High values for these latter three parameters indicate stands with dense, well-developed, tall canopy layers. The difference in bryophyte species-richness between stand stages was less marked, but there were positive correlations between richness, upper canopy cover (S4) and cover index (CI) (Table 9.2).

Stumps and logs had significantly lower lichen species counts than snags (P < 0.01, Figure 9.3), but higher bryophyte counts (P < 0.01). Bryophyte species-richness was positively related to increasing diameter of logs and to decay class (Figure 9.4a), with classes 4 and 5 having significantly higher species numbers than classes 1, 2 and 3 across all deadwood types. There was no significant effect of increasing snag diameter on lichen species-richness, but the relationship with decay class was highly significant (Figure 9.4b). Classes 3, 4 and 5 were more species-rich than classes 1 or 2 (P < 0.01).

All stand types: differences in the species-composition of lichen and bryophyte communities
Axis 1 (LICH1) of the lichen ordination separating foothills Scots pine, upland oak and upland Sitka spruce from lowland Scots pine, oak, Corsican pine, Norway spruce and foothills Sitka spruce (Figure 9.5a), was positively correlated (P < 0.01) with accumulated temperature (AT), moisture deficit (MD)

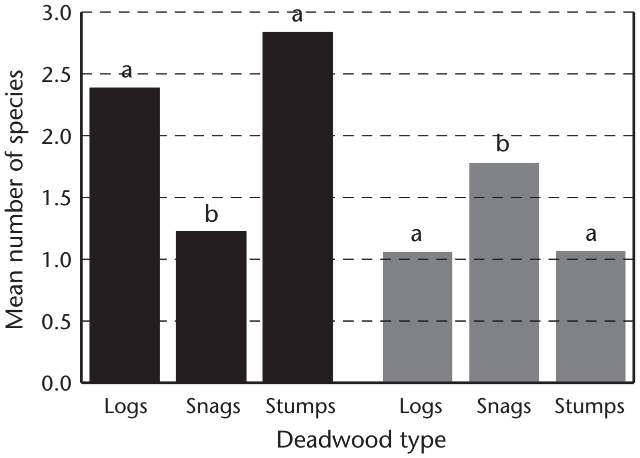


Figure 9.3

Mean number of bryophyte (black) and lichen (grey) species recorded on different types of deadwood. Bars annotated with different letters are significantly different at the P < 0.05 level (within each taxonomic group).

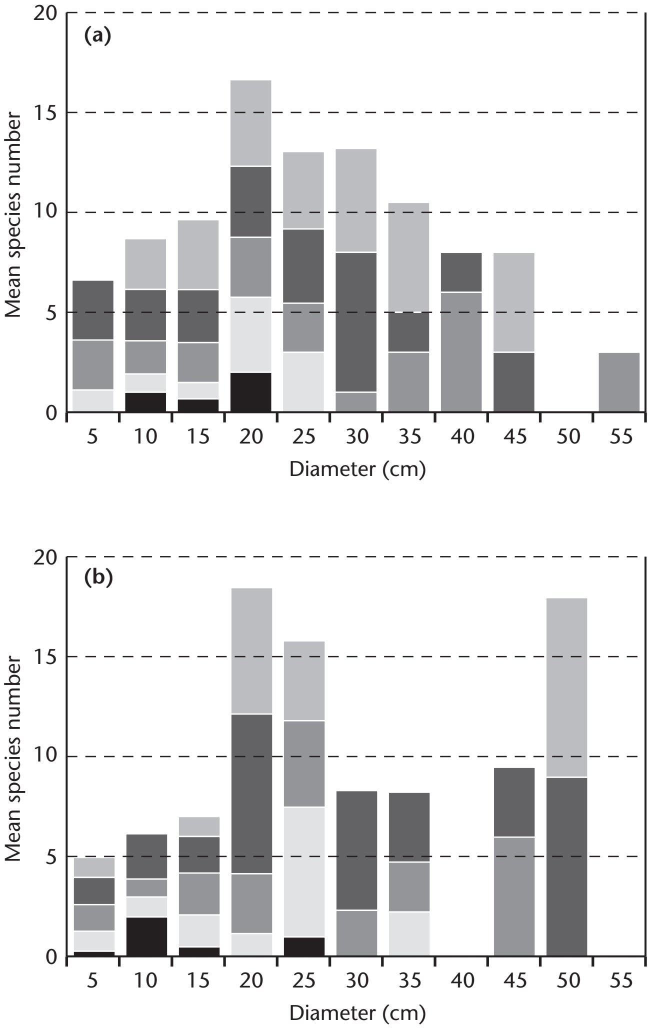


Figure 9.4

(a) Mean number of bryophyte species recorded on different sizes and decay stages of logs; (b) mean number of lichen species recorded on snags.

and height to live crown (HTLC) (Table 9.3). The oak plots (both lowland and upland) were grouped at the upper end of axis 2 (LICH2), with the pre-thicket spruce and pine plots grouped towards the lower end. LICH2 was positively correlated ($P < 0.01$) with tree age, the number of tree species in the canopy (TREESP), and upper canopy cover (S4). A negative correlation was recorded with field layer vertical cover (S1) (Table 9.2). In the bryophyte ordination (Figure 8.5b), most of the upland and foothills plots were grouped towards the lower end of axis 1 (BRYO1), with axis 2 (BRYO2) separating over-mature pine plots (1.4, 2.4, 4.4) at the upper end of the axis from some of the over-mature Sitka spruce plots (5.4, 9.4, 10.4) at the lower end. The Clunes Sitka spruce plots formed a distinctive grouping with the upland oak plots. BRYO1 was positively correlated with AT and MD; BRYO2 was negatively correlated with upper canopy cover (S4) and mean basal area (MBA), (Table 9.2).

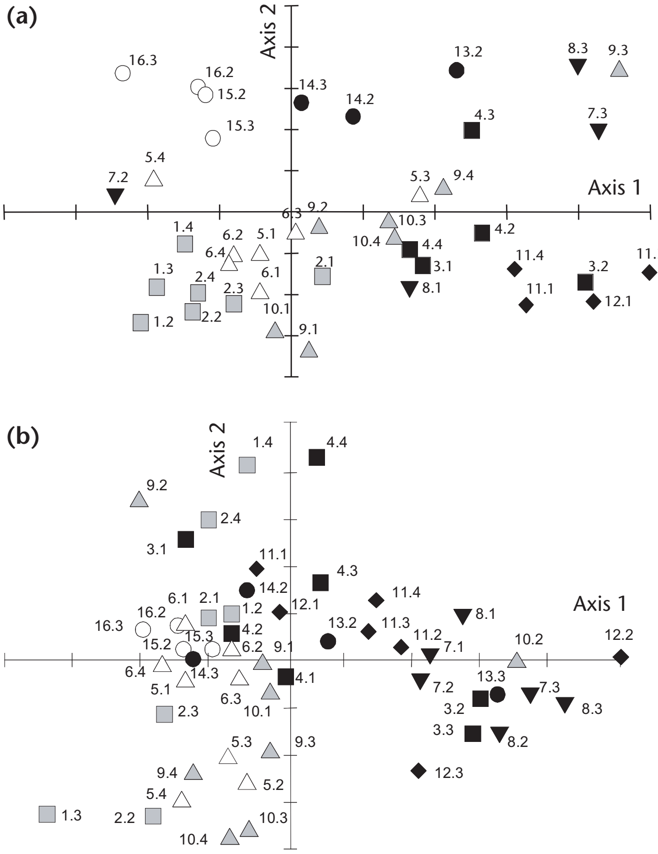


Figure 9.5

Correspondence analysis of assessment plots based on: (a) lichen species composition, (b) bryophyte species composition. Axes 1 and 2 of (a) accounted for 19.2% and 13.4% of the variability in the data respectively (eigen values 0.46 and 0.28). For (b) the corresponding values were 16.5% and 10%; 0.48 and 0.33. Data labels for plots are coded as given in Annexe 1. Numbers preceeding the decimal point refer to sites, numbers after the decimal point refer to stand stage (1: pre thicket; 2: mid-rotation; 3: mature; 4: over-mature).

△ Upland SS
■ Foothills SP
▲ Foothills SS
■ Lowland SP
▼ Lowland NS
◆ Lowland CP
○ Upland OK
● Lowland OK

Discussion

Effects of conifer crop type, stand structure and deadwood on the species-richness of lichen and bryophyte communities

Very few species were recorded in more than half the plots. The fungal data showed a similar pattern (Chapter 8) as have other studies (Vitt *et al.*, 1995). It is possible that the 1 ha sampling plot used is too small to capture a representative sample of lower plant diversity in forest stands, as a minimum sampling area of 1 km^2 is recommended (Rose, 1993). However, this may not always be practical in fine-grained heterogeneous landscapes where the aim is to relate diversity to different stand types, many of which will be less than 1 km^2 in size. The low frequency of rare species records (one species only) for lichens and bryophytes contrasts greatly with the results for the fungi (Chapter 8) where 29 rare and threatened species were recorded. The contrasting results are probably due, in part, to under-recording of fungi in the past, coupled with a long history of intensive recording of lower plants (e.g. Ratcliffe, 1968). However, the key semi-natural woodlands for lichens and bryophytes were under-sampled in this survey, so it is perhaps not surprising that the count of rare species was quite low.

The north-south effect on species richness was much more pronounced for lichens than bryophytes, substantiating existing views that oceanic conditions in the north and west of Britain provide much better conditions for lichen growth (Rose, 1993). The positive correlation between lichen species-richness and decreasing moisture deficit confirms this view. Bryophyte species-richness was more closely related to crop type than climate, with spruce stands being richer than pine stands regardless of climate zone. This observation has not previously been recorded in Britain, but is consistent with findings in Scandinavia, where spruce is generally considered a more notable habitat for bryophytes than pine (Esseen *et al.*, 1997).

Low light levels are considered to be highly detrimental to lichen growth (Rose, 1993; Fletcher, 1999) which explains why stand structure had such a significant effect on lichen species-richness; mid-rotation and mature stages having lower species counts than the pre-thicket and over-mature stands. Under denser stand conditions, only the most shade-tolerant of lichen species such as *Hypogymnia physodes* and *Cladonia coniocraea* were recorded. However, bryophytes were less affected by shading, and most spruce stands had a reasonable complement of deadwood species in all stand stages. The best stands appear to be those with high values for upper canopy cover (i.e. mature and over-mature stand stages). It is possible that these stands offer a more optimal combination of high humidity, adequate light levels and constancy of microclimate.

The finding that bryophyte species-richness was higher on logs and stumps, whilst snags were more important for lichens, supports observations from overseas (Andersson and Hytteborn, 1991; Esseen *et al.*, 1997; Kruys *et al.*, 1999). In Scandinavian old growth swamp forests dominated by Norway spruce, logs are not considered to be especially important as lichen habitat (Ohlsson *et al.*, 1997). Bryophytes (particularly hepatics) appear to dominate successional processes on spruce logs in these moist stands, whereas lichens are more common on standing dead trees (Kuusinen and Siitonen, 1998). In drier Scots pine-dominated boreal forest, both logs and snags are key habitats for crustose lichens (Esseen *et al.*, 1997). It is possible, therefore, that humidity and soil moisture status (together with size and decay state) are the most important determinants of the relative value of logs for bryophytes and lichens, rather than tree species in itself.

Well-decayed (decay class 3 and above) logs of 20 cm in diameter or more provide a more valuable habitat for mosses and liverworts than small and fresher material. Reasons for this include: greater potential surface available for colonisation; improved moisture retention and greater range of microhabitats; provision of niches from competing vascular plant species or dense leaf litter (Samuelsson *et al.*, 1994; Crites and Dale, 1998). Intermediate to late decay classes provide additional heterogeneity and hence more niches for different species (Kruys *et al.*, 1999). The results from our study support the view (Esseen *et al.*, 1997; Kruys *et al.*, 1999) that lichen species-richness tends to be highest in decay classes 3–5 , whereas bryophyte richness peaks in stages 4 and 5.

Differences in the species-composition of epixylic lichen and bryophyte communities

The main gradients of variability in the lichen community relate to differences between northern and southern crops and between mid-rotation and mature oak stands and pre-thicket spruce and pine stands. The negative correlation between axis 2 (LICH2) and field layer cover is relevant here, because it is known that the pre-thicket pine and spruce stands have a well-developed field layer vegetation characterised by tall ericoid vegetation (see Chapter 5) which supports a range of heathland lichens (e.g. *Cladonia glauca*, *C. gracilis* and *C. uncialis).*

The foothills pinewood plots (sites 1 and 2 – Glen Affric and Strathspey) formed a distinctive grouping in the ordination. Lichen growth on living Scots pine is rarely as luxurious as it is on oak, mainly because the bark has a low water capacity, and a high rate of evapotranspiration (Barkman, 1958). Scots pine bark is also unstable and flakes off readily (Fletcher, 1999) so the lichen communities are often rather fragmentary and temporary assemblages, and comprise species able to tolerate drier conditions such as *Bryoria*, *Usnea* and *Cladonia* spp. The most important substrate for lichens in native pinewoods is deadwood (Fletcher, 1999). Stumps and snags provide a key habitat for crustose species, and a number of these (e.g. *Chaenotheca brunneola* and *C. trichialis*) were recorded on deadwood in the over-mature pine stands.

Both pine and spruce deadwood is recognised as a key habitat for crustose lichens in Scandinavian boreal forest (Esseen *et al.*,1997), and it is interesting to note that the upland Sitka spruce stands (particularly Clunes – site 6) share some of the species found within the native pinewoods (e.g. *Calicium viride, Cladonia glauca* and *Cetraria chlorophylla*) and are located in a similar position on the ordination. Historical map evidence supports the suggestion derived from the data that the Clunes stands were planted on sites previously occupied by ancient semi-natural woodland (see Chapter 8). Interestingly, in the bryophyte ordination, the Clunes Sitka spruce plots formed a distinctive grouping with the upland oak plots on axis 2, and shared many characteristic oakwood bryophytes such as the liverworts *Frullania dilatata*, *F. tamarsci* and *Lejeunea cavifolia*. It appears, therefore, that site history may also be an important determinant of both lichen and bryophyte diversity, as well as fungal diversity in planted stands.

The negative correlation between axis 2 of the bryophyte ordination, upper canopy cover (S4) and mean basal area (MBA), explains to some extent why over-mature pine plots (1.4, 2.4, 4.4) were grouped at the upper end of the axis with over-mature Sitka spruce plots (5.4, 9.4, 10.4) grouped at the lower end. The pine plots have an open parkland structure, with low canopy cover and basal area, whereas the spruce stands have a higher stem density (Chapter 5). Because of their open structure and dry microclimate, old-growth pine stands are not noted for their bryophyte flora (Fletcher, 1999) but even so, the Affric, Strathspey and Windsor plots were surprisingly species-poor.

Conclusions and suggested management strategies

Clearly, there is more scope for increasing the lower plant diversity of planted forests in the north and west of Britain than the south and east, and this relates to the historical effects of air pollution as well as climatic influences. Although not discussed in detail in this chapter (for a more detailed review see Humphrey *et al.*, 2002), it is clear that the planted stands have poorer lichen communities than the semi-natural stands. The differences were less pronounced for bryophyte communities, but the general principle of retaining semi-natural features within planted stands such as gaps, streams, rides, rocks and mature broadleaves will apply equally to both groups and will be of significant benefit to the conservation of lower plant diversity.

The positive correlation between the species-richness of lower plant communities and the size and quality of deadwood fills an important gap in knowledge of the value of deadwood for biodiversity in British forests (Hodge and Peterken, 1998). It is important that continuity of deadwood supply is maintained so that there is no truncation in the delivery of the more valuable later stages of decay (Kruys *et al.,* 1999). In north and west Britain, silvicultural systems such as irregular shelterwood or single-tree selection could have the potential to deliver supplies of large diameter (≥ 20 cm) deadwood within stands, thus enhancing bryophyte diversity. However, this approach would not be so appropriate in areas of high windthrow risk (Mason *et al.*, 1999).

Much could be done in both pine and spruce plantations to increase their value for lichens of early successional forest stages. Snags, stumps and logs left after clearfelling or windthrow can provide a key habitat for the Caliciales and Cladonias. Where the forest area is large enough to allow planning at the landscape scale, then a temporally continuous supply of this habitat type will be maintained through normal patch clearfelling, provided that some larger items (≥20 cm diameter) are left permanently unshaded during restocking to form a reservoir of species for potential colonisation of future stands. This type of management approach is most appropriate within the 'native pinewood zone' in the Scottish Highlands (Rodwell and Patterson, 1994) where plantations could play a major role in providing additional habitat for native pinewood species.

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SECTION THREE

Invertebrate and bird communities

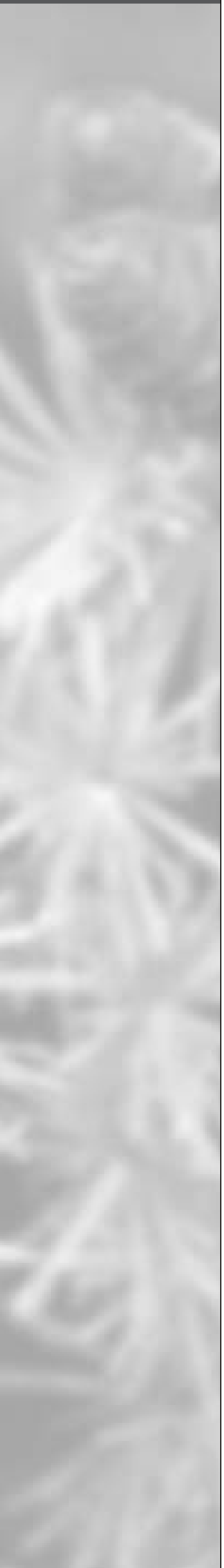
Chapter 10 Invertebrate communities in plantation forests
Martin Jukes and Andrew Peace

Chapter 11 Effects of plantation structure and management on birds
Rob Fuller and Steven Browne

CHAPTER 10

Invertebrate communities in plantation forests

Martin Jukes and Andrew Peace



Summary

Invertebrates were sampled from all biodiversity plots, but only data obtained from the pine and spruce plots are included in this chapter. Target groups, chosen for variety of function, were identified to species from pitfall traps (Coleoptera: Carabidae), Malaise traps (Coleoptera, selected families; Hemiptera: Cicadomorpha; Diptera, Syrphidae) and canopy fogging (Coleoptera). Invertebrate community composition and richness were related to a number of environmental variables. For all groups, the most significant factors affecting species-richness and community composition were tree (crop) species and latitude, with the lowland sites being more species-rich for all groups, though to a lesser extent for Malaise syrphids. Correspondence analysis showed close similarities in community composition for plots on the same site, and for sites in the same bioclimatic zone, though most plots showed a degree of uniqueness in species composition. Pitfall carabids showed a negative relationship with the degree of canopy vertical cover and increasing soil organic matter. A higher proportion of 'forest specialist' carabids were sampled from over-mature stands in comparison to younger stands. Canopy Coleoptera species-richness and abundance were influenced by chronosequence stage, related to vertical cover index, which reached a peak in the mid-rotation plots. Species-richness of Malaise-trapped syrphids and Cicadomorpha tended to be highest in the pre-thicket plots, where there was a greater variety of field-layer vegetation (Cicadomorpha) and flowers for a source of nectar (Syrphidae). Saproxylic Coleoptera from canopy or Malaise samples showed no correlation with deadwood. There was no single environmental factor which could be taken as indicative of invertebrate diversity; management for habitat variability, particularly by the inclusion of long-term retentions and open spaces, would be a useful measure to enhance the diversity of invertebrate communities in plantation forests.

Introduction

Woodland habitats support a wide variety of invertebrate species, from the familiar pests such as *Hylobius abietis* and *Bupalus piniaria,* to rare and endangered species dependent on specialised habitat niches found uniquely in semi-natural or ancient woodland sites. Many species are directly dependent on the trees themselves, feeding on foliage, bark, wood, roots, buds, flowers or seeds. An additional vast community of invertebrates is associated with the non-tree components of woodland habitats, predating or parasitising primary feeders, or utilising the understorey flora and fauna in a shaded or semi-shaded and frequently damp ecosystem. In recent years, research effort has focused on the endangered invertebrates of ancient woodland, and there is very little known about the invertebrate communities of commercial conifer plantations; the general assumption is that conifer forests have low faunal and floral diversity, and are ecologically homogeneous.

As part of the Biodiversity Assessment Project, entomological research sought to address the following questions:

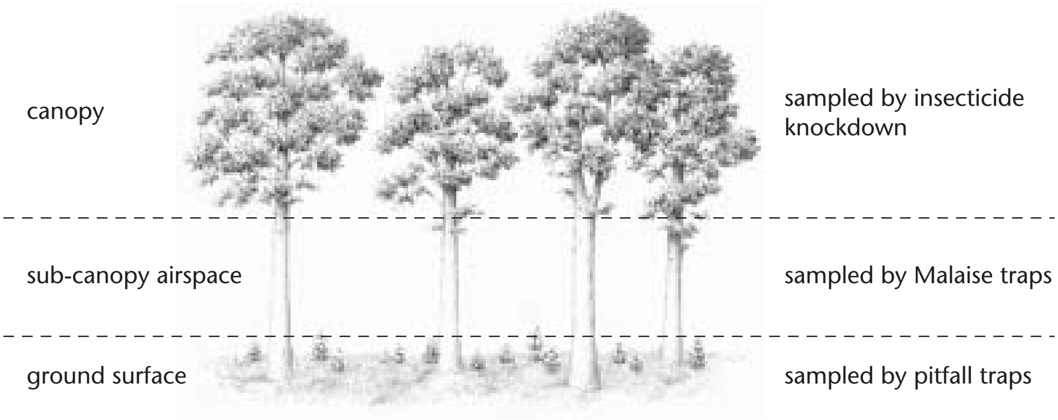
- How diverse are the invertebrate communities found in managed plantations?
- How does community structure vary within and between forests?
- Is invertebrate community composition related to other environmental factors such as plantation structure, age, understorey vegetation, deadwood volume, and could any of these factors be used as a surrogate for estimating invertebrate diversity?

Methods

Invertebrate sampling

From the outset it was decided to consider three vertical strata within the forest stand: ground surface, sub-canopy airspace and canopy (Figure 10.1). In each plot (excluding the oak sites), ground surface invertebrates were sampled using pitfall traps, operating for a 20-week period (May–September) for two consecutive years. A pitfall trap consists of a plastic beaker sunk into the ground so that the rim of the beaker is level with the ground surface. The beaker contains a small amount of 50% ethanediol which serves as a mild fixative, and is covered by a small square of galvanised steel, raised on turned-down corners, to keep rain out, and offer shelter to ground invertebrates. The traps were arranged on a north–south transect through the centre of each plot, at 10 m spacing. Samples were removed at 2-week intervals.

Figure 10.1 *Plantation strata and invertebrate sampling methods.*



Invertebrates in the sub-canopy airspace were sampled by a single Malaise trap in each plot, again operating continuously for a 20-week period for 2 consecutive years. The Malaise trap resembles a fine black nylon mesh ridge tent, with a centre partition instead of two side walls. The ridge slopes upwards to a height of 2 metres, and leads into a collecting pot containing 70% industrial methylated spirits. Flying insects are intercepted by the partition, and fly upwards, guided by the roof and sloping ridge to the collecting pot. Each trap was located in a suitable clearing close to the centre of the plot, with the ridge of the trap orientated in a N–S direction.

Canopy invertebrates were obtained by insecticide knockdown using Pybuthrin 33 from a thermal fogger. Twenty-five nylon funnels, 1 m diameter, were suspended from rope, tensioned between trees in a web-like fashion. In pre-thicket plots, funnels were suspended from higher branches. Fogging for 3–6 minutes was carried out at dawn, when the air was still, and cooler air temperatures assisted the thermal lift of the fog. Falling invertebrates were collected over a 2-hour period, and the catches from 25 funnels combined to give a single sample. One fogging sample was taken from each plot, on 2 consecutive years, during June or July.

During the first year of sampling (1995), 1000 pitfall samples, 200 Malaise samples and 20 fogging samples were processed. These totals more than doubled in the second year, as more sites were commissioned. Following examination of the first sets of samples at Alice Holt, it was apparent that sorting of complete catches, even to major groupings such as insect Order, was beyond the capability of available resources. The decision was taken to identify to species within specific ‘target’ groups (Table 10.1) of invertebrates selected to:

- Include a range of functional groups, to act as a close surrogate for the total invertebrate fauna.
- Concentrate on groups for which reliable identification keys were available, and for which reasonable ecological information could be found in the literature.
- Maximise the use of in-house identification expertise.

Table 10.1 *Target groups selected from invertebrate samples.*

Trap	Target group(s)	Comments
Pitfall	Carabidae (ground beetles)	About 350 British species, predatory on other invertebrates or general scavengers.
Malaise	Syrphidae (hoverflies)	About 260 UK species. Adult hoverflies attracted to flowers for nectar. About 50% larvae are predators on aphids and other homopterans, the rest are aquatic or general detritus feeders, some of which are saproxylic.
	Cicadomorpha (tree and leaf hoppers)	About 380 UK species. All are plant sap suckers, many are host specific or have narrow host plant preferences.
	Coleoptera (selected families: Scolytidae, Scraptidae, Cerambycidae, Curculionidae, Carabidae, Cantharidae, Cleridae, Coccinellidae, Anobiidae)	Timber borers, saproxylics and predators – potentially a large group.
Canopy fogging	Coleoptera (all)	Canopy species are mainly predators, herbivores and fungivores; many are saproxylic.

Target groups were removed and identified, and the residue retained in alcohol. In the case of pitfall traps, additional large species of Geotrupidae (dung beetles) and Silphidae (burying beetles) were identified, recorded and discarded, to reduce residue volume. Due to the large sample sizes from Malaise traps, of the 10 fortnightly collections, only collections 1, 4, 7 and 10 were sorted for Syrphidae and Coleoptera, and only collections 4 and 7 sorted for Cicadomorpha. These sorts, without any identification, took between 45 minutes and 75 minutes per sample. All records were stored in an Oracle database.

Analysis

Composition, structure and diversity of the invertebrate communities were analysed separately for each height strata. Carabid community composition was examined using correspondence analysis (CA) to identify plot similarities and underlying environmental gradients. Assessments of structural differences in the community were obtained by partitioning the carabid species into forest specialists (dependent on wooded habitats), generalists (associated with wooded habitats, though many prefer boundaries or spaces within forests) and others (habitat preferences varied or non-forest), and comparing their relative proportions. A comparison of diversity levels between and within forests was achieved by fitting linear mixed models using the method of residual maximum likelihood (REML). Similar analyses were performed at the canopy level where the interpretation of results was aided by subdividing the coleoptera species into four functional groups: saproxylics, predators, herbivores and others. At the sub-canopy level (Malaise traps) community composition relationships were examined using a combination of Venn diagrams and species association matrices. Finally, species-richness and diversity scores for all datasets were related to environmental variables measured at each sample plot.

Results

Pitfall trapped Carabidae

Fifty-one species of Carabidae and 7822 individuals were recorded. Plot species totals ranged from 19 at Kielder (pre-thicket SS) and Northants (mid-rotation NS), to 2 at Kielder (mid-rotation SS) and Northants (mid-rotation NS). Three species, *Abax parallelopipedus*, *Pterostichus madidus* and *Trechus obtusus* accounted for nearly 50% of the individuals sampled. None of the 51 species was recorded from all plots, or even all of the 12 sites. The most widely distributed species, occurring at 11 out of the 12 sites were *Carabus problematicus*, *Cychrus caraboides*, *Leistus rufescens*, *Pterostichus madidus* and *Pterostichus niger*. Twenty-five species were common to both pine and spruce.

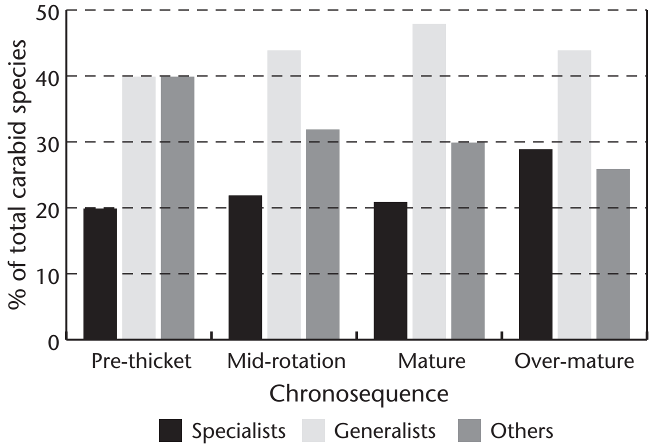


Figure 10.2

Relative proportions of carabid beetle groups associated with chronosequence stage (pine and spruce combined).

Many carabids show preferences for specific habitat types. Moist shady habitats characterise spruce plantations and support species such as *Pterostichus nigrita* and *Trechus rubens*, while pine plantations are more open and drier and are characterised by species such as *Calathus fuscipes* and *Calathus melanocephalus*. There was a significant trend for non-woodland and ubiquitous species ('others') to decrease, and for the proportion of specialist forest species (stenotopic) to increase with plantation age (Jonckheere-Terpstra test, JT^* = -1.81, $P < 0.05$; Figure 10.2). This trend was similar in both pine and spruce stands. The proportion of generalist (eurytopic) species showed little variation with plantation age.

Mid-rotation and mature pine plots were consistently more species-rich than pre-thicket plots (Figure 10.3). Estimates of diversity indices showed spruce to be more diverse than pine ($P < 0.05$). Pre-thicket plots had the highest species numbers in three out of the six spruce sites (Figure 10.3), and in most cases mid-rotation plots had the lowest species numbers (with the exception of mid-rotation Norway spruce at Fineshade, Northants from which 19 species were recorded).

Figure 10.4 shows the correspondence analysis (CA) of carabid communities with ordination of assessment plots. Plots shown in closest proximity have the greatest similarity in carabid community composition. A set of environmental variables was tested against the first two axes of the CA. From this set, the correlation coefficients which were found to be significant are given in Table 10.2. The proportion of organic matter was selected as a surrogate for available water capacity, or wetness of the soil (Pyatt *et al.*, 2001).

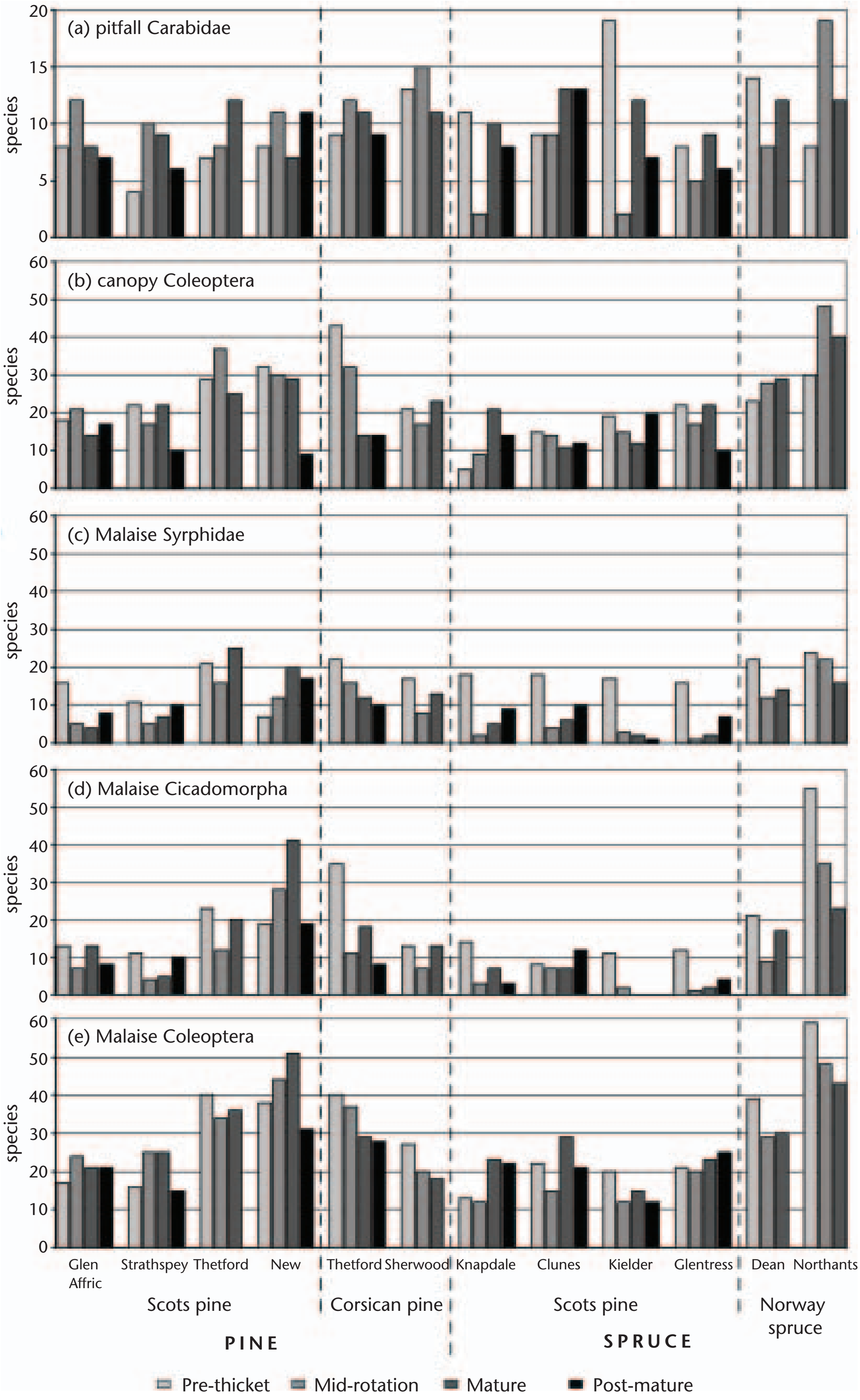
Environmental variables	CA1	CA2
Latitude	-0.75***	0.03
Mean basal area	-0.20	0.43**
Vertical cover structure (S3)	-0.37*	0.56***
Litter depth	0.39**	-0.18
Organic matter	-0.54***	-0.04
Vegetation diversity	-0.48***	0.11

Table 10.2

*Significant correlations between measured environmental variable and CA over 1 and 2. Level of significance * P < 00.5, ** P < 0.01, *** P < 0.001*

The first axis (CA1) discriminates between lowland sites at the positive end (southern latitudes) and upland/foothill sites at the negative end (northern latitudes). A possible interpretation of this axis is that it is a soil wetness gradient with plot scores negatively correlated with the percentage of soil organic matter ($r = -0.54$, $P > 0.001$). The second axis discriminates between mid-rotation/mature plots, and pre-thicket/over-mature plots, particularly on upland and foothill sites. The interpretation of this second axis as one of increasing shade is supported by a highly significant correlation with vegetation cover in the lower canopy (S3) ($r = 0.56$, $P < 0.001$) and mean basal area ($r = 0.43$, $P < 0.01$). Carabid species common in plots at the positive end of the second axis such as *Calathus micropterus*, *Trechus quadristriatus* and *Agonum assimile* are more shade tolerant than those at the negative end.

Figure 10.3 *Species-richness of pitfall, canopy fogging and Malaise trapped target groups of invertebrates.*



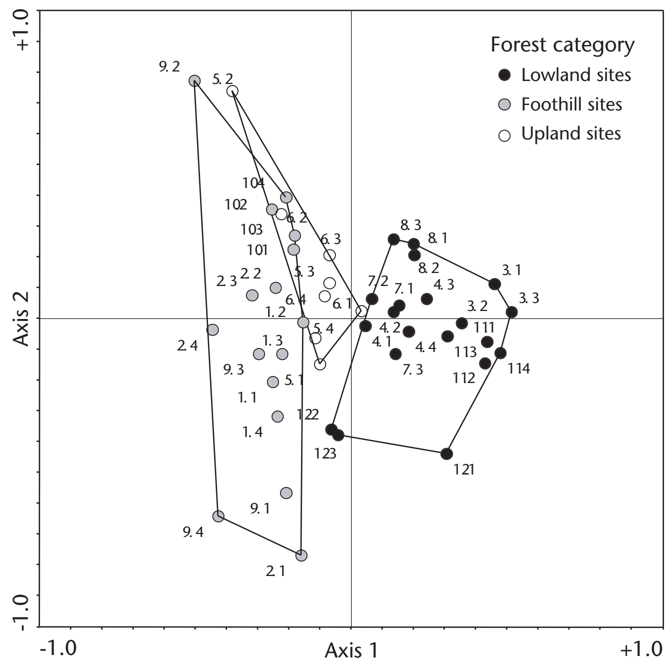


Figure 10.4

Correspondence analysis of carabid beetle communities in pine and spruce plantations, showing ordination of assessment plots.

Canopy Coleoptera

A total of 202 Coleoptera species and 11 074 individuals were recorded in the conifer stands. Pine plots had 131 species and 4456 individuals while spruce had 142 species and 6618 individuals. Only 69 species were common to both. Plot species totals ranged from 48 at Northants (mid-rotation NS) to 5 at Knapdale (pre-thicket SS). The five most common species were: *Leptusa ruficollis* (Erichson) (Staphylinidae), 2125 individuals; *Aphidecta obliterata* (Linnaeus) (Coccinellidae), 1362 individuals; *Rhynchaenus fag*i (Linnaeus) (Curculionidae), 1030 individuals; *Malthodes fuscus* (Waltl) (Cantharidae), 822 individuals; *Strophosomus melanogrammus* (Forster) (Curculionidae), 550 individuals. Most of the *R. fagi* (1020 individuals) were collected from the pre-thicket Scots pine in the New Forest (plot 4.1), due to coincidence of fogging with peak emergence from a single beech tree in the plot. This value was removed from the analyses, as it caused misleading bias in plot characterisation.

There were marked variations in community composition between the 12 sites, primarily due to tree species and latitude (Figure 10.5). Axis 1 (Figure 10.5) distinguished between pine and spruce sites, although the presence of foothills Scots pine sites (1 and 2) in an intermediate position between lowland pine (3, 4, 11, 12) and upland/foothills Sitka spruce (5, 6, 9, 10) indicates a possible latitudinal effect. Foothills Scots pine sites had species in common with upland/foothills Sitka spruce sites. The lowland Norway spruce sites (7 and 8) were distinctive, holding an intermediate position between upland/foothills Sitka spruce and lowland pine on axis 1 and, in the case of site 8 (Fineshade, Northants), separating from all other sites on axis 2. Axis 1 and 2 of the CA were significantly positively correlated with species diversity ($r = 0.62$, $n= 44$, $P < 0.001$ and $r = 0.37$, $n = 44$, $P < 0.05$ respectively), supporting the findings that the canopy Coleoptera communities of lowland sites were more diverse (and species-rich) than the communities of foothill and upland sites, particularly Sitka spruce (Figure 10.3 and Table 10.3). The Norway spruce stands, especially the Northants plots were characterised by high species-richness, including a number of abundant species which were rarely recorded elsewhere (Figure 10.7b). However no effects of chronosequence on species-richness or diversity was recorded.

Examination of axes 3 and 4 (Figure 10.6), indicated more subtle differences between sites. Groupings of similar sites and plots within sites remained, such that the foothills Sitka spruce sites (9 and 10) formed a grouping, as did the lowland Norway spruce sites (7 and 8) and the lowland Corsican pine sites (11 and 12). However, the pre-thicket Corsican pine plot at Thetford (11.1) was conspicuously separated, as it had a high number of species (43), one-third of which were unique to this plot. A number of upland Sitka spruce plots (Knapdale 5.2, 5.3 and Clunes 6.2, 6.3 and 6.4) formed a grouping to the right of axis 3. These plots were characterised by an abundance of *Leptusa ruficollis*, a saproxylic staphylinid generally associated with scolytid galleries and other sub-cortical Coleoptera burrows in deciduous trees.

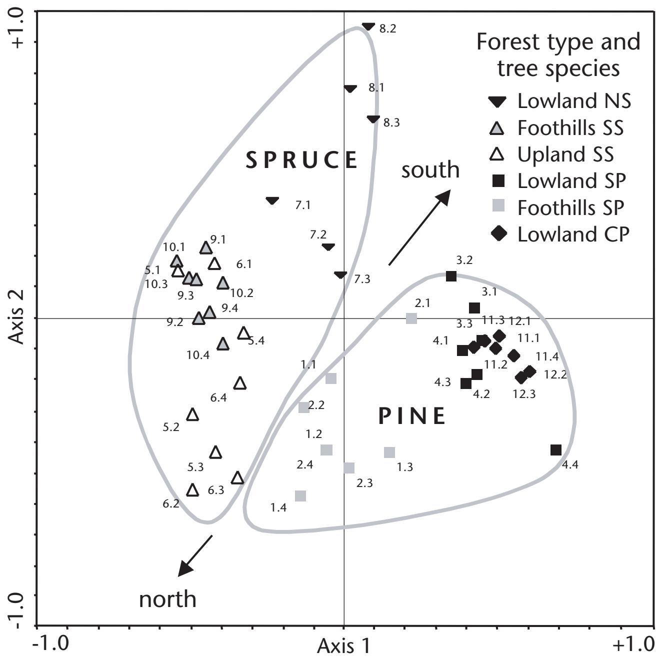


Figure 10.5

Correspondence analysis of canopy Coleoptera communities in pine and spruce plantations, axis 1 vs. axis 2.

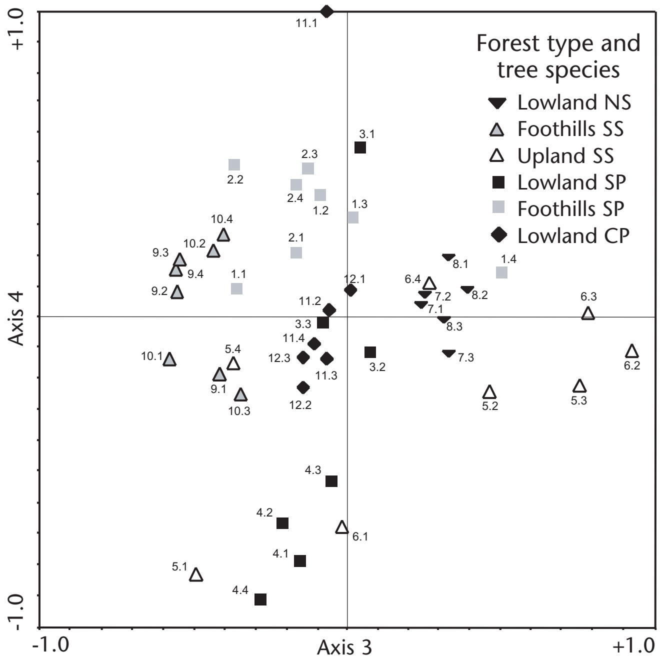


Figure 10.6

CA of canopy Coleoptera in pine and spruce plantations, axis 3 vs. axis 4.

Tree species	Mean	Standard error
Corsican pine	2.37	0.20
Norway spruce	2.60	0.21
Scots pine	2.28	0.14
Sitka spruce	1.45	0.13

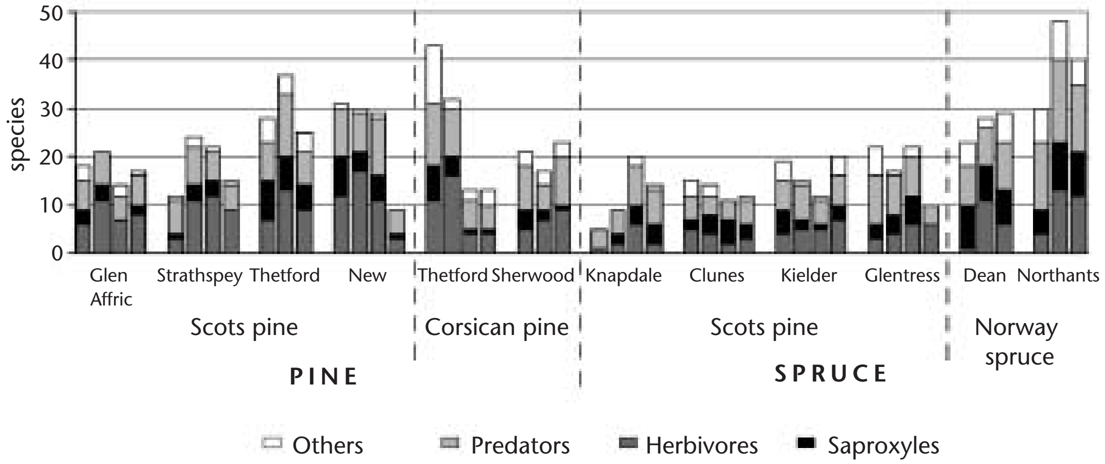
Table 10.3

Least square means of canopy Coleoptera species diversity associated with different tree (main crop) species, tested by fitting linear mixed models using the method of REML.

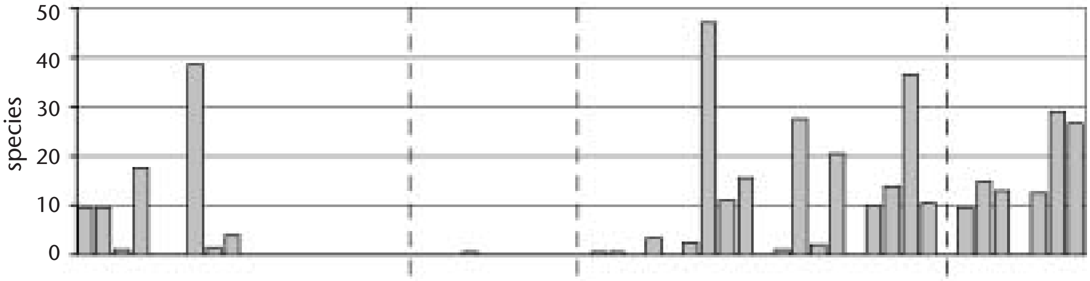
Canopy Coleoptera were categorised into four functional groups – saproxyles, herbivores, predators and others. Generally, plots with a high number of species (Figure 10.3) tended to have high numbers of species in each functional group (Figure 10.7a). However, there was considerable variation between sites. Some (e.g. Glen Affric, 1.1–1.4 and Strathspey, 2.1–2.4) were dominated by saproxyles and predators, while others (e.g. Thetford, 3.1 and Glentress, 10.3) were dominated by herbivores.

Figure 10.7 *Species-richness of pitfall, canopy fogging and Malaise trapped target groups of invertebrates.*

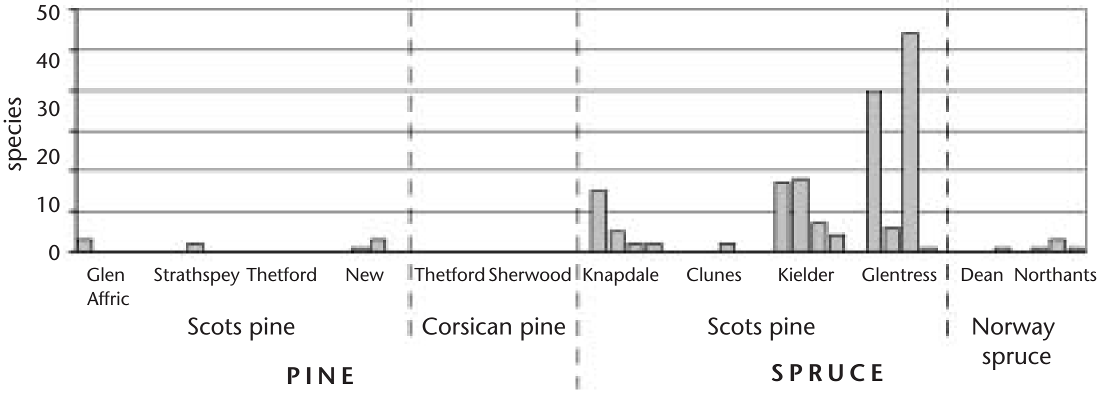
(a) Canopy Coleoptera functional groups



(b) *Aphidecta obliterata* 1996



Rhagonycha lignosa 1996



There were also differences when considering numbers of individuals within each group. High predator numbers were related to high herbivore numbers and 'others' but the numbers of saproxyles were unconnected with individuals from the other three functional groups, suggesting that as the numbers of saproxylic individuals increased, they did so for only a few dominant species. This would also be expected to be the case with predators, particularly as the prey of most species would be non-coleopteran. Individuals recorded in a single year for two predominantly aphid predators (*Aphidecta obliterata* (Linnaeus) (Coccinellidae) and *Rhagonycha lignosa* (Müller) (Cantharidae)) are shown in Figure 10.7b. In spruce plantations, both these species predate *Elatobium abietinum* (Walker), the green spruce aphid. Although high numbers of both species were present in sites 9 (Kielder) and 10 (Glentress), *R. lignosa* was unrecorded from plot 6.2 (Clunes, mid-rotation) where the highest *A. obliterata* sample was taken.

In pine stands, a number of relationships were identified between structural variables and functional groups. Stand age had a significant effect on both the abundance and species-richness of herbivores in Scots and Corsican pine stands. Both variables decreased with increasing age of chronosequence ($P < 0.001$). Herbivore species numbers were also significantly related to canopy vertical cover index

(CI), the larger the CI, the greater the number of herbivores ($P < 0.05$). Similar relationships with CI were identified for predators and saproxylic species ($P < 0.05$) while increases in numbers of saproxylic species were associated with stands of greater basal area (MBA) ($P < 0.01$).

With spruce plots, variation in counts of species and individuals in functional groups could not be explained by the underlying habitat structure. There appeared to be no effect of CI, MBA, deadwood or chronosequence in Sitka or Norway spruce stands.

Malaise-sampled invertebrates

Target groups from malaise samples were identified, recorded and the data summarised, but due to the difficulties of considering different invertebrate groups together, analysis is still progressing, and much of this account is limited to data summaries.

Target group totals, separated by tree species and latitude, are shown in Table 10.4. The most abundant species sampled in each group are shown in Table 10.5. The north/south separation splits upland and foothill sites (Scots pine, Sitka spruce) from lowland sites (Scots pine, Corsican pine and Norway spruce). Higher numbers of species were found in lowland sites for all three target groups, particularly the Cicadomorpha, with more than twice as many species and six times as many individuals recorded from southern sites than from the north. From these totals, only 17 species were exclusive to northern sites, while 73 were found only in the south.

Table 10.4 *Invertebrate target group totals sampled by Malaise trapping; (a) tree species; (b) north (foothills and uplands) vs. south (lowlands). Number of plots sampled in brackets.*

		Syrphidae	Cicadomorpha	Coleoptera	Totals
(a)					
Scots pine (15)	Species	51	86	131	268
	Individuals	1 602	2 649	3 934	8 185
Corsican pine (7)	Species	28	55	78	161
	Individuals	1 855	477	2 486	4 818
Sitka spruce (16)	Species	35	44	75	154
	Individuals	905	188	4 719	5 812
Norway spruce (6)	Species	37	72	116	225
	Individuals	1 673	2 723	3 113	7 509
Totals (44)	Species	59	134	204	397
	Individuals	6 035	6 037	14 252	26 324
(b)					
North (22)	Species	40	61	97	198
	Individuals	1 232	875	5 883	7 990
South (22)	Species	50	117	173	340
	Individuals	4 803	5 162	8 369	18 334
Totals (44)	Species	59	134	204	397
	Individuals	6 035	6 037	14 252	26 324

Species-richness values for each plot, accumulated over two sampling seasons, are shown in Figure 10.3c, d and e. It is remarkable that about 35% of the British species of Cicadomorpha were recorded from inside conifer plantations, and that a single plot, Northants pre-thicket Norway spruce, supported 14% of the British species. The chart of plot species-richness shows that for syrphids (Figure 10.3c), pre-thicket and post-mature plots in both pine and spruce tend to have the highest values. Species-richness was plotted against field layer (0.2–1.0 m) vertical structure cover, and a strong positive correlation was recorded (Figure 10.8).

Table 10.5 *Dominant species (number of individuals) in each target group of Malaise-trapped invertebrates.*

Order	Target families	Species	Individuals
Diptera	Syrphidae	*Melanostoma scalare* (F.) *Episyrphus balteatus* (Deg.) *Melanostoma mellinum* (L.) *Platycheirus albimanus* (F.) *Sphaerophoria* sp.	1465 1277 743 681 215
Cicadomorpha	Cicadellidae	*Eupteryx urticae* (F.) *Empoasca decipiens* Paoli *Hauptidia maroccana* (Mel.) *Aguriahana germari* (Zett)	2160 441 430 279
	Cercopidae	*Philaenus spumarius* (L.)	223
Coleoptera	Cleridae	*Thanasimus formicarius* (L.)	1156
	Cantharidae	*Malthodes fuscus* (Waltl) *Rhagonycha lignosa* (Müll.)	994 899
	Throscidae	*Trixagus carinifrons* (de Bonv.)	878
	Lathridiidae	*Aridius nodifer* (Westw.)	834

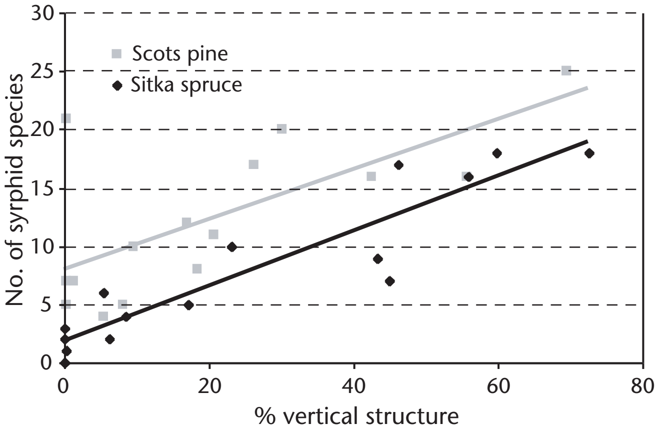


Figure 10.8

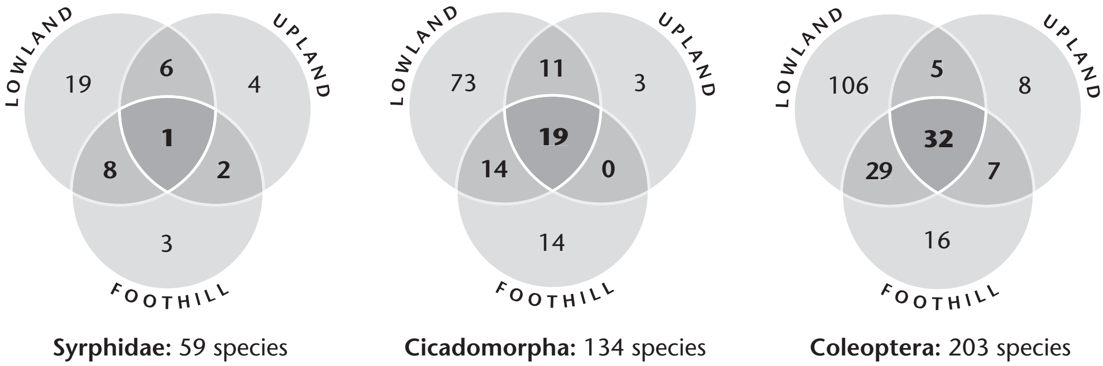
The relationship between field layer (0.2–1.0 m) vertical structure and the numbers of syrphid species sampled by Malaise traps. (All plots excluding Corsican pine and Norway spruce.)

For Sitka spruce, upland and foothills plots gave similar results and were therefore combined. Mid-rotation and mature plots are grouped to the left in Figure 10.8, with low species-richness, and a sparse field layer. Pre-thicket and post-mature plots are grouped to the right where open canopy conditions encourage a richer field layer. Scots pine plots exhibited a similar relationship between field layer vertical structure and species-richness for both lowland and foothills plots. These plots contained, on average, five more syrphid species than spruce plots for a given level of field layer vertical structure, a result which is partly explained by the inclusion of the more species-rich Scots pine lowland plots.

Pre-thicket plots had higher Cicadomorpha species-richness than the other stands (Figure 10.3d), with the exception of the New Forest Scots pine (which was at the upper age limit of the pre-thicket range and in many ways resembled a mid-rotation plot). In contrast to syrphids, the post-mature plots did not have such consistently high Cicadomorpha species-richness values. Kielder was unique in having no Cicadomorpha records for either the mature or post-mature plot. For the Coleoptera, a reduction in species-richness in the northern plots was less evident than with Syrphidae or Cicadomorpha (Figure 10.3e). Pre-thicket plots showed the highest species-richness in all lowland sites except the New Forest. Overall, there was little further discernible pattern in the Coleoptera species-richness patterns.

Venn diagrams were created to display broad community differences and similarities (Figure 10.9). The proportion of syrphid species shared between forest categories was much higher than the proportions for the other invertebrate groups.

Figure 10.9 *Broad community differences and similarities in Malaise-sampled species of Syrphidae, Cicadomorpha and Coleoptera.*



This theme was developed further by calculating Jaccard similarity coefficients for tree species and forest category (Table 10.6). For Coloeptera, high coefficient values were recorded between lowland Scots pine and lowland Corsican pine. The high values for the Cicadomorpha include all lowland Norway spruce sites, indicative of the outstandingly high species-richness at Northants Forest (i.e. these stands posses species common to other stand types as well as their own distinctive assemblages). In the case of syrphids, all of the similarity coefficients were high, with the highest values being the unlikely pairings of Norway spruce lowland with Scots pine lowland (0.67) and Corsican pine lowland with Sitka spruce foothills (0.61).

Table 10.6 *Jaccard similarity coefficients for study sites grouped by tree species and location, based on Malaise trapping.*

Coleoptera	SP foothill	SP lowland	SS upland	NS lowland	SS foothill	CP lowland
SP foothill	1.00					
SP lowland	0.29	1.00				
SS upland	0.41	0.23	1.00			
NS lowland	0.20	0.41	0.24	1.00		
SS foothill	0.38	0.28	0.43	0.28	1.00	
CP lowland	0.35	0.46	0.25	0.28	0.26	1.00

Cicadomorpha	SP foothill	SP lowland	SS upland	NS lowland	SS foothill	CP lowland
SP foothill	1.00					
SP lowland	0.21	1.00				
SS upland	0.28	0.26	1.00			
NS lowland	0.21	0.36	0.33	1.00		
SS foothill	0.23	0.17	0.25	0.15	1.00	
CP lowland	0.20	0.41	0.24	0.34	0.12	1.00

Syrphidae	SP foothill	SP lowland	SS upland	NS lowland	SS foothill	CP lowland
SP foothill	1.00					
SP lowland	0.33	1.00				
SS upland	0.46	0.38	1.00			
NS lowland	0.44	0.67	0.50	1.00		
SS foothill	0.57	0.44	0.46	0.59	1.00	
CP lowland	0.39	0.51	0.46	0.62	0.61	1.00

Discussion

There are almost 30 000 named species of British invertebrates excluding micro-organisms, of which over 22 000 are insects. All invertebrates are constrained by fairly narrow habitat requirements and many, particularly the rare and endangered species, are highly specialised and have very precise habitat requirements (Kirby, 2001). It could be argued that semi-natural forest, little disturbed by management intervention, would contain the greatest variety of habitats, including open spaces, deadwood and a variety of tree species of varying ages. Whilst this is probably true it could also be argued that managed commercial plantations create a new, different, albeit artificial habitat, supporting a unique flora and fauna which should not be ignored in favour of those habitats more charismatic by virtue of their propensity to harbour rare species.

From the results shown here, it can be seen that managed conifer plantations support, or are frequented by a large variety of invertebrates, and that there are large differences in the invertebrate communities associated with different sites. These data must, however, be interpreted with care, particularly when attempting to relate invertebrates sampled by different trapping methods. Sunderland *et al.* (1995) reviewed the effectiveness of different sampling methods and showed that trap catches depend on a combination of species activity, trappability and population density. For instance, small carabids such as *Bembidion* spp. and *Harpalinus* spp. are consistently under-represented in pitfall traps whereas larger species such as *Carabus* spp. and *Pterostichus* spp. show a closer reflection of true populations.

Invertebrate activity will be influenced by short-term weather effects and the general climate of sampling sites, as well as site-dependent factors such as vegetation structure. To a large extent, variation in activity should be reduced by continuous sampling over two or more seasons, which was the case with both pitfall and Malaise samples. Canopy fogging samples should be less dependent on invertebrate activity, as resting or active individuals would be equally exposed to the insecticidal effects of the fog. With canopy fogging, larger invertebrates require a higher dose of insecticide, and take longer to fall from the canopy; the 2-hour collection period was found to be adequate for virtually all of the potential drop.

While accepting that estimates of abundance, species-richness and diversity do not reflect absolute community composition, provided that identical sampling techniques are applied and habitats are broadly similar, pitfall, Malaise and canopy-fogged samples do provide a useful comparative reference for habitat characterisation.

Pitfall carabids

Carabid species-richness and diversity have been linked to a wide variety of environmental variables such as soil moisture (Butterfield *et al.*,1995), litter depth and humus content (Butterfield and Benitez Malvido, 1992; Petit and Usher, 1998), shade and ‘openness’ (Niemelä and Halme, 1992). The carabid community of conifer plantations is generally considered to be impoverished compared to that of pasture and heathland, though conifers do support a small core of species such as *Calathus micropterus* and *Trechus rubens* with a preference for that habitat (Luff,1998).

The scale of this study extended from southern England to northern Scotland, and community composition differences are to be expected over such distances. Of the 51 species sampled, eight do not occur at latitudes north of Edinburgh (56°N; Luff,1998). The pool of available species, therefore, was not the same at each site, which is partially reflected by the CA axis 1 trend from south (+ve: many species) to north (-ve: fewer species).

From lowland plantations at least, all plots at the same site show similarities in carabid communities, regardless of chronosequence stage. Each plot, however, has its own individuality, despite similarities between related forest types. The New Forest and Thetford (lowland Scots pine) sites had very different soil and understorey vegetation types. Thetford soils are typically sand on chalk, with pH ranging from acid to basic depending on the depth of calcareous material. In contrast the New Forest has heavy brown earths and gravels, with low pH and generally high organic content. A lower rainfall and free-draining soil makes Thetford a very dry habitat compared to the New Forest. All of the New

Forest plots were dominated by the carabid *Abax parallelopipedus*, which accounted for over 50% of individuals in all plots. The species was virtually absent from Thetford plots which were dominated by *Carabus nemoralis* (pre-thicket and mature), or *Pterostichus nigra* (mid-rotation). In the foothills Scots pine chronosequences at Glen Affric and Strathspey, low numbers of forest specialist carabids were recorded from both of the over-mature plots, with a single *Cychrus caraboides* being the only representative from Strathspey. This is surprising, as both plots were ancient Caledonian pinewoods, but may reflect the wide spacing of mature pines, providing suitable habitat for both forest generalists and open heath species.

Thetford Corsican pine and Scots pine carabid communities were similar in all plots, with *Carabus nemoralis* dominant in all cases. High proportions of forest specialists were found in the mid-rotation and mature plots. Sherwood Corsican pine pre-thicket and mid-rotation plots were dominated by *Pterostichus oblongopunctatus*, and the mature plot by *Carabus violaceous*. The mid-rotation plot had the highest species count of all the pine plots and, despite being close to a forest edge bordering agricultural land, supported a high proportion of forest specialists.

Spruce sites generally displayed a higher variation in species-richness, and conspicuously low values for some mid-rotation plots. Only two species were recorded from both Knapdale and Kielder mid-rotation plots, indicative of low vegetation diversity and sparse understorey cover. In contrast, the Northants (Fineshade) mid-rotation Norway spruce had 19 species. There are several possible reasons for this anomaly: the stand age was at the upper limit of the chronosequence range; it had been planted on high pH soil unsuitable for spruce, causing self-thinning of the canopy and allowing regeneration of a diverse understorey vegetation. Also, the site had a long history of woodland cover in a small mosaic pattern, offering establishment opportunities for a variety of both ubiquitous and forest specialist carabids. The Northants site, particularly the pre-thicket and mid-rotation plots which were relatively close together, proved to be outstanding for all sampled groups of invertebrates. However, the Forest of Dean spruce plots despite being located on ancient woodland sites, supported high proportions of forest generalists as opposed to specialists (100% generalists in the case of the mature plot). The dominant carabids differed between plots, and species compositions were markedly different.

The Kielder Sitka spruce pre-thicket plot had a species count of 19 (the highest value, equalled only by Northants mid-rotation Norway spruce) comprising an even mix of forest and heathland species, including two nationally scarce species, *Trechus rubens* and *Pterostichus oblongopunctatus.* Species composition in mid-rotation and mature plots was comparable with that found by Butterfield *et al.* (1995) in an extensive survey which included mid-rotation and mature Sitka spruce plots at Kielder between 1987 and 1992. However, *Trechus obtusus*, a supposedly non-woodland species (Luff, 1998) was recorded at double the levels found in the Butterfield survey, and in fact figured highly in many of the northern plots in this study, both spruce and pine.

The increase in forest specialists with increasing plantation age, and corresponding decrease in open ground and non-forest species (Figure 10.2), was significant despite a few plots (such as Northants mid-rotation) deviating strongly from the observed progression. This changing pattern would be expected in forest habitats evolving from an open site to mature forest. Open ground species would gradually decline as the habitat became more shaded due to canopy closure, while the establishment of more stenotopic species would be expected to continue with increasing forest age. Many specialist carabid species are found outside of their optimal habitat due to small scale dispersal (Niemelä and Halme, 1992), and will be opportunistic in colonising habitats as they become available. Spence *et al.* (1996) found that old growth specialists of any invertebrate group were slow to colonise mature forest due to competition with forest generalists. Establishment will be encouraged by long-term retentions and carefully planned felling.

The carabid data show that all sites, and indeed most plots, possess a degree of uniqueness in community composition. Lowland sites show a reasonably close grouping and separation from foothills and upland sites, inferring community similarity which differs from other forest categories. Northern (foothills and lowland) sites show separation of open (pre-thicket and post-mature) and closed (mid-rotation and mature) forest plots, most probably driven by the relative abundances of open ground and shade-loving carabids.

Canopy Coleoptera

It is necessary to treat the results from canopy fogging with some caution, as many variables will influence the composition of invertebrate communities within tree canopies. As well as differences caused by aspect, climate and relative position of the study plots to other stands and forest edges, variation between months of the year have been found in the density and species-richness of Coleoptera (Simandl,1995) and the relative proportions of different functional groups (Moran and Southwood,1982; Simandl,1995). The scale of this study precluded detailed successional sampling, which may have reduced some of this variation. However, despite the limitations, the current dataset was strengthened by a degree of site replication, and by taking two successive annual samples.

In common with pitfall Carabidae and other groups of flora and fauna covered by this study, canopy Coleoptera community composition was determined primarily by latitude and tree species. Species-richness of Coleoptera was found to be greatest in Norway spruce, which was also found to be the case by Ozanne (1996). Correspondence analysis (Figure 10.5) clearly shows tree species and latitudinal differences, with the Northants site (site 8) unique in community composition, partly due to the high species-richness in all plots. The displacement of plot 2.1 (Strathspey, pre-thicket Scots pine) is believed to be caused by the inclusion of *Anatis ocellata* (Coccinellidae) which was absent from other northern Scots pine plots, but present in the Thetford (lowland) Scots pine plots.

Many specific tree associations were apparent. For example, the weevils *Phyllobius maculicornis* Germar and *Polydrusus pterygomalis* Boheman were recorded in large numbers from spruce, particularly the northern Sitka spruce sites. *Rabocerus gabrielli* Gerhardt (Salpingidae) was recorded exclusively from pine, with no latitudinal preference. *Aphthora euphorbiae* (Shrank) (Chrysomellidae) was recorded from all Norway spruce plots with the exception of the Dean pre-thicket plot, all Thetford Scots pine plots, and a single individual from Sherwood mid-rotation Corsican pine plot. This is not a conifer-feeding species, and these occurrences reflect the southern England distribution of its herbaceous host plant *Euphorbia amygdaloides* L. which occurs on damp, slightly acid soils (Rose, 1981).

There was no evidence of a relationship between Coleoptera species-richness and abundance, as found by Southwood *et al*. (1982). Where high numbers of individuals occurred, there were frequently a few, or a single, dominant species, which were often site-specific. For example, *Leptusa ruficollis* (Erichson) comprised 52.6% and 81% of the individuals sampled from Knapdale Sitka spruce mid-rotation (n = 38) and mature (n = 755) plots respectively. The species was not recorded from the pre-thicket or post-mature plots on the same site.

There was little pattern in the proportions of functional groups in each chronosequence stage, or in each forest category. With simple logic, predators would be expected to be related to herbivores, herbivores to canopy structure or cover index, and saproxyles to the volume of deadwood. In reality, this was not the case, partly explained by the fact that this study only examined the canopy Coleoptera, which represent only about 7% of canopy arthropod species (Southwood *et al*.,1982). It is probable that the functional groups of Coleoptera do not reflect proportions of functional groups in the total canopy fauna. The data shown in Figure 10.3a are from the combined samples of two consecutive years, which would tend to level out annual fluctuations. This, of course, does not reflect numbers of individuals, as shown by the examples in Figure 10.7b of two aphid predator species, *Aphidecta obliterata* (Col:Coccinellidae) and *Rhagonycha lignosa* (Col:Cantharidae), from samples taken in 1996. Although it can be seen from some plots that both species are found together in high numbers, there is little pattern to the occurrence of these species, other than a possible preference for Sitka spruce on the part of *R. lignosa*. In 1995, the pre-thicket Sitka spruce plot at Clunes Forest showed defoliation and yellowing of needles symptomatic of heavy *E. abietinum* attack. The three most abundant coleopteran species in this plot in 1995 and 1996 were the predators *Rhagonycha lignosa* (42), *Aphidecta obliterata* (34) and *Cantharis pallida* Goeze (12), which together comprised 75% of individuals in the two canopy Coleoptera samples. *E .abietinum* numbers in the 1995 sample from the same plot were estimated as 23 000 from a sub-sample count of 2900. These data would indicate that species composition of predators remains relatively constant, with populations of a few species changing dramatically in response to cyclic fluctuations in prey density.

Stand structure, particularly of the lower canopy (depicted by the cover index – CI) influences the diversity of canopy Coleoptera. A high leaf area index and closed canopy may result in a more stable microclimate, encouraging population growth (Ozanne, 1996). The negative relationship between increased cover in spruce stands and community diversity may be due to the uniformity of this habitat and reduction in niche variability. This factor is less apparent in pine stands, which show increasing diversity from pre-thicket to mature stages, but decline thereafter.

The abundance of saproxylic insects increased through the chronosequences for both pine and spruce, but this was not significantly related to deadwood volume, as might have been expected. Deadwood assessments were primarily based on fallen deadwood, and the variety of saproxyles found in the canopy may be more closely related to canopy deadwood – dead branches on living trees, and dead standing trees. Sampling in the summer is likely to disproportionately exclude saproxylic species, as many bark and timber borers are spring fliers. A third explanation is that the saproxylic community could be influenced by dispersal from adjacent or nearby stands, where the deadwood resource may be richer (such as a recent windblow or harvesting site).

As with the pitfall carabids, geographic location was found to be an important determinant of community composition of the canopy Coleoptera. Many species which are common in southern England are scarcer or absent further north, while a few species are restricted to Scotland (Luff, 1998; Twinn and Harding,1999). The Northants Norway spruce mid-rotation plot was remarkable in having the highest species-richness of canopy Coleoptera, backing up the record species-richness of pitfall carabids. The probable explanations for this are similar – a tree species grown on unsuitable soil producing gaps and structural variability due to canopy thinning. Additionally, the landscape setting may also have been a contributory factor, since the forest blocks are situated within a diverse matrix of ancient semi-natural woodland and rich agricultural land. It seems likely that this variability provides sources of additional species not recorded in other woodland sites.

Malaise Syrphidae, Cicadomorpha and Coleoptera

The data derived from Malaise samples are both extensive and complex, despite reducing the number of samples sorted and identified to four per year in the case of Syrphidae and Coleoptera, and two per year in the case of Cicadomorpha. Detailed analysis and discussion of all three groups will be the subject of a separate paper currently in preparation, while an initial comparison of Malaise syrphids and pitfall carabids has already been presented (Humphrey *et al.*, 1999). This paper indicated a negative correlation between syrphid species-richness, shrub layer diversity, and lower and upper canopy densities. Also, as expected, there was a distinction between lowland and foothills/upland communities (i.e. a latitudinal effect).

Virtually all adult hoverflies require nectar, and to a lesser extent pollen, from flowers. Some are attracted to honeydew. The larvae of about 50% of British species and many of the species recorded in this study are predatory, mainly on aphids. All of the dominant five species are predators (Table 10.5), reflecting a possible response to high aphid populations, especially *Elatobium abietinum*. The larvae of other recorded species occupy a variety of habitats, including rot holes, rotting organic matter, bogs, sap runs, bulbs, aquatic habitats and associations with ant and wasp nests. Species-richness was invariably higher, often to a marked extent, in the pre-thicket plots, where flowering plants would be more abundant, prior to canopy closure.

Watt *et al.* (1998) found that the majority of syrphid species found in northern Sitka spruce plantations were predatory (aphidophagous) species, and that while the number of individuals sampled was higher in younger plots, species diversity was higher in the older plots. This is clearly at odds with the species-richness values found in this study (see Figure10.3c), where the Sitka pre-thicket plots consistently had the highest species-richness values.

The British distributions of recorded species were examined (Stubbs and Falk,1993). Of the species trapped, 56% had a widespread distribution, and a further 14% were common in southern England, present but becoming scarcer towards northern Scotland. This would account for the high proportion of shared species between forest categories (Figure 10.9) and the unexpectedly high Jaccard similarity coefficients (Table 10.6).

A restricted number of target families were identified from the Malaise Coleoptera (largely those which could be identified in-house which included most saproxyles and predators). North/south differences in Coleopteran species-richness were apparent, though to a lesser extent than with the Syrphidae and Cicadomorpha. Pre-thicket species-richness was often, though not universally, higher than mid-rotation (Figure 10.3d). Although several families of saproxylic Coleoptera were identified, no relationships with the volume of deadwood were found. A possible reason for this is that the saproxylic beetles in flight were dispersing, and a high proportion may have been merely passing through the study plots.

The highest species-richness of Malaise Coleoptera was found in Northants (lowland Norway spruce) and the New Forest (lowland Scots pine). Of the dominant five species, predators were the three most abundant. With Malaise-sampled Cicadomorpha, all northern sites had low species-richness – a high proportion of species in this group are restricted to southern and midland England. Although most species of Cicadomorpha have specific host plant associations in the field and shrub layers, there was little correlation with the ground vegetation parameters (as described in Chapter 5).

Conclusions and management recommendations

Vast amounts of data were collected during the sampling phase of this study, and a great deal has been learned about the similarities and differences in invertebrate community composition in managed conifer plantations in Britain. The programme was ambitious in scale, providing information over a wide geographic area, partly at the expense of replication and control over other variables such as distance from the forest edge (and the variable nature of habitat beyond the forest edge), forest matrix composition at a landscape scale and previous usage and management history of the plots.

A relationship between saproxylic species and volume of deadwood was not found for any of the groups examined, and in view of the dependency of saproxylics on deadwood, the expected relationships must exist at the forest landscape scale, implying that some species associated with deadwood are highly mobile and well adapted to locating suitable habitat (or that suitable habitat was not properly recorded in this study).

With all of the groups, habitat variability was a key factor in controlling species-richness. All of the plots showed a degree of uniqueness in species composition of each group, with the most influential variables being latitude, tree species, chronosequence and canopy structure. Managing forests for high invertebrate diversity, although favouring the majority of species, will impose a degree of evenness and similarity of invertebrate community composition, leading to the exclusion of some species with specific habitat requirements. A better approach would be to increase habitat variability by ensuring that the forest matrix includes long-term retentions, open spaces, deadwood and wet areas.

Many aspects of the data remain unexplainable, and are likely to be related to precise habitat requirements at the species level or the movement and exchange of species within invertebrate communities at the landscape scale. Further research is needed to address these factors.

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CHAPTER 11

Effects of plantation structure and management on birds

Rob Fuller and Steven Browne

Summary

Breeding birds were counted in all the biodiversity assessment plots excluding oak. A point count method was used which showed that, even within stands of broadly similar age, there is much variation in the overall density, number of species, diversity and composition of the bird communities. There was considerable overlap in community composition between mid-rotation, mature and over-mature stands. However, bird communities in pre-thicket stands (6–26 years), especially in upland areas, were generally distinct from those in older growth stages. This suggests that young stands make a very important contribution to bird diversity within forests. Factors influencing variation in forest bird communities are reviewed and approaches to enhancing and maintaining habitat quality for birds are outlined. Several major gaps in knowledge are identified. Improved information on the bird communities within individual forests is needed so that conservation management plans can be better targeted. There is substantial variation in the bird communities in young plantations but the causes are largely unknown. If effects of forest design on birds are to be satisfactorily predicted, a better understanding is required of responses of birds to forest edges.

Introduction

Commercially managed forests in Britain have become important habitats for a wide range of birds with diverse ecological requirements. Taken as a whole, these forests support a very high diversity of birds as well as nationally important populations of several scarce or declining species (Avery and Leslie, 1990; Petty and Avery, 1991; Fuller, 1995). An important group of species that depends on young stages of growth includes hen harrier, black grouse, short-eared owl, nightjar, woodlark, tree pipit, whinchat, grasshopper warbler and lesser redpoll. For some of these species there appear to be large differences in habitat quality between first and second generation plantations which are discussed below. Other ‘conifer specialists’ are associated with mature stands: goshawk, capercaillie, long-eared owl, firecrest, crested tit, siskin and crossbill. It has also become clear that several species of birds that have recently declined on lowland farmland have important ‘refuge’ populations within establishment or thicket stage conifer plantations. These birds include turtle dove, skylark, song thrush, linnet and yellowhammer. In addition, these forests support huge populations of many of the more widespread and common woodland birds such as blackbird, robin, coal tit, goldcrest and chaffinch. Although planted forests make a considerable contribution to the conservation of birds within Britain it is evident that there is much variation between forests in terms of their birdlife. There is a need to learn more about these differences between forests and the factors that cause them.

This Chapter outlines the major findings of fieldwork undertaken in 1996 as part of the Biodiversity Assessment Project. Breeding birds were counted in different growth stages at all 12 conifer forests forming part of the project. These forests were distributed from Glen Affric in the north of Scotland to the New Forest in the south of England (Chapter 3). The results cannot be regarded as a comprehensive account of breeding bird communities in forests. However, they do illustrate some important broad patterns and they emphasise the spatial variability of bird communities in forests. Other aims of this article are to summarise what is known about the factors that influence breeding bird communities in plantations, to indicate the broad approaches that can be taken to enhance the quality of habitats for birds within them and to identify areas where further research is needed. The emphasis is on songbird communities partly because the methods used in this study were mainly appropriate for counting small territorial songbirds and also because these make up the majority of the species and individual birds breeding in forests, though they are not necessarily among the species of highest conservation importance.

Methods

Bird counts were undertaken in the vicinity of all the 1 ha assessment plots, excluding oak. A total of 12 separate chronosequences was examined covering the broad growth stages: pre-thicket (6–26 years), mid-rotation (23–49 years) and mature (44–96 years). Additionally, a fourth sampling plot was established within some of the forests in over-mature stands (61–238). See Annexe 1 for site details.

The 1 ha plots represented extremely small samples for counting birds – a 1 ha sample will support rather few individuals and many birds occupy territories that extend over considerably larger areas. For the purposes of the bird counts, therefore, the 1 ha plots were enlarged by adding a 30 m buffer zone around the entire plot to give an extended plot size of 2.56 ha. The original 1 ha plot is termed the *core plot* and the extended area is referred to as the *whole plot*. Two basic methods were used to count the birds: point counts and territory mapping (Bibby *et al.*, 2000). Five point count locations were established at each plot, four were positioned at the corners of the whole plot and one at the centre of the core plot. Hence, a total of 220 point count locations was established. Individual point counts were of 10 minutes duration and individual records of birds were categorised as either less than or greater than 30 m from the point count location. A simple territory mapping method was used to maximise the amount of information available for each plot. A standardised route was walked which took the observer to within 50 m of every part of the whole plot and the locations of all birds heard and seen were mapped. All plots were visited twice between April and June 1996; the point counts and territory mapping were undertaken on the same visits. Unless stated otherwise, the results presented here are for the point count data derived from the whole plot.

Using the point count data, a mean count for each plot was calculated for each species by taking the highest count from each of the five locations, irrespective of which visit it was made on. The total number of birds, overall densities and numbers of species were also derived from the point count data for each plot. Densities were calculated based on counts within the 30 m radius of the count location. Patterns in bird species composition were examined by the ordination method detrended correspondence analysis (see Chapter 4) without downweighting for rare species (Jongman *et al.*, 1995).

Results

Numbers of species and individuals

In total, combining both point counts and territory mapping, 41 species were recorded in the 43 plots. This represents more than a third of the species known to use woodland and scrub habitats in Britain (Fuller, 1995). It should be noted, however, that this is an underestimate of the number of bird species known to use coniferous plantations in Britain. The plots represented very small samples of each forest and the project did not cover the earliest stages of tree growth (few plots were less than 10 years old) with which several bird species are strongly associated.

The numbers of species recorded per plot ranged from one to 15 and the number of individuals from two to 60. On average, slightly higher numbers of species and individuals were recorded in the pre-thicket and over-mature plots than in mid-rotation and mature plots but these differences were not significantly different (Figure 11.1). The large ranges in the recorded values within each growth stage indicate that there was much variation between forests in numbers of species and total numbers of birds. Species diversity, as measured by the Shannon diversity index (Magurran, 1988) also showed large variation within each growth stage and no significant difference between stages (Kruskal-Wallis test, $P = 0.76$). Furthermore, the pattern of change with forest growth stage was strikingly different between forests. For example, some forests showed a trend of increasing numbers of species and individuals with growth stage, whereas others show a decreasing trend. This suggests that generalisations about overall trends in the bird communities of plantations may be inappropriate.

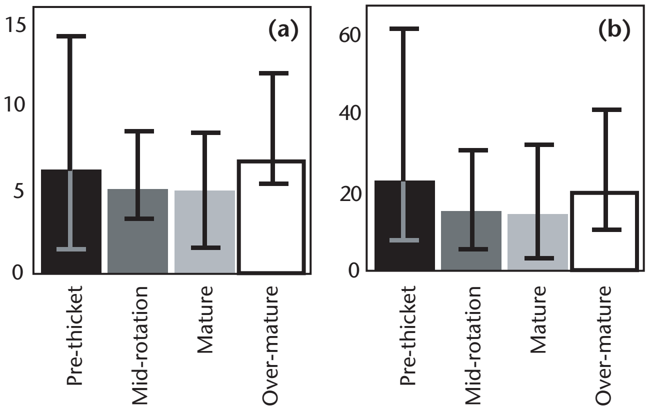

Figure 11.1

(a) The mean numbers of bird species and (b) individual birds recorded in each of the growth stages using point counts. The vertical bars show the maximum and minimum numbers. Differences between growth stages are not statistically significant (Kruskal-Wallis tests, P *> 0.50).*

Patterns in bird species composition

The five most numerous species were chaffinch, coal tit, willow warbler, goldcrest and wren (see Table 11.1 for list of species mentioned in text). These species contributed an estimated 62% of the total individuals counted and the two most abundant species, coal tit and chaffinch, contributed 31%. In terms of frequency of occurrence, the 10 most widespread species were, in decreasing order: coal tit (recorded on 79% of plots), chaffinch (79%), goldcrest (61%), wren, (60%), robin (56%), willow warbler (40%), blue tit (28%), siskin (28%), woodpigeon (28%), blackbird (26%). Of these species, three were significantly associated with a particular growth stage (chi-square tests, $P < 0.05$). Willow warbler was strongly associated with pre-thicket plots; these held 84% of the individuals. Goldcrest and woodpigeon were more abundant in mid-rotation plots than in the other stages.

Table 11.1 *Lists of bird species referred to in text.*

Common name	Latin name	Common name	Latin name
Black grouse	*Tetrao tetrix*	Long-eared owl	*Asio otus*
Blackbird	*Turdus merula*	Nightjar	*Caprimulgus europaeus*
Blue tit	*Parus caeruleus*	Lesser redpoll	*Carduelis cabaret*
Capercaillie	*Tetrao urogallus*	Robin	*Erithacus rubecula*
Chaffinch	*Fringilla coelebs*	Short-eared owl	*Asio flammeus*
Coal tit	*Parus ater*	Siskin	*Carduelis spinus*
Crested tit	*Parus cristatus*	Skylark	*Alauda arvensis*
Crossbill	*Loxia curvirostra*	Song thrush	*Turdus philomelos*
Dunnock	*Prunella modularis*	Tree pipit	*Anthus trivialis*
Firecrest	*Regulus ignicapillus*	Turtle dove	*Streptopelia turtur*
Garden warbler	*Sylvia borin*	Whinchat	*Saxicola rubetra*
Goldcrest	*Regulus regulus*	Willow warbler	*Phylloscopus trochilus*
Goshawk	*Accipiter gentilis*	Woodlark	*Lullula arborea*
Grasshopper warbler	*Locustella naevia*	Woodpigeon	*Columba palumbus*
Hen harrier	*Circus cyaneus*	Wren	*Troglodytes troglodytes*
Linnet	*Carduelis cannabina*	Yellowhammer	*Emberiza citrinella*

Patterns in the bird species composition were examined further by ordination (Figure 11.2). This analysis used all the mean counts of each species from the point count data. Plots that are relatively close together on the diagram tended to have similar bird assemblages in terms of the species that were recorded and their relative abundances. Plots that are widely separated supported rather different bird assemblages. The first two axes represented strong gradients in bird species

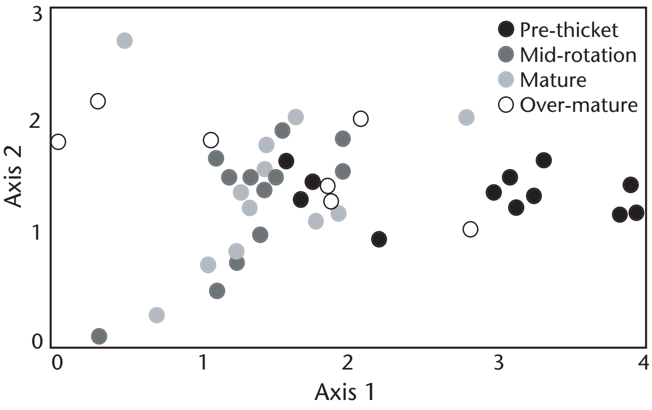

Figure 11.2

Ordination of the bird communities at the 43 plots. Plots are identified according to their growth stage.

composition as, together, they explained a very high proportion (>90%) of the variance in the data. Two main points emerge from this analysis. First, it is striking that within each growth stage there is much variation in species composition between forests. The possible causes of this variation are discussed below. Second, while there is much overlap in bird communities between the over-mature, mature and mid-rotation plots, those in the pre-thicket plots are generally distinct from those of the older stages. This finding suggests that the pre-thicket stages contribute much to the overall bird diversity of conifer forests because they support such distinctive bird communities. The ordination analysis generated no clear patterns in bird community composition with respect to tree species or geographical location. There was, however, some suggestion that bird communities in lowland pre-thicket plots may differ from those in the upland and foothills pre-thicket plots because the former are all grouped in the centre of the diagram.

Discussion

Factors influencing forest bird communities

Variation in forest bird communities can be viewed at two levels: within and between forests. The factors that influence birds at these two scales overlap but some are far more likely to be important at one scale or the other. It is well known that within any forest birds are not distributed evenly. This has been demonstrated in the case of northern spruce forests (Patterson *et al.*, 1995) and the Forest of Dean (Donald *et al.*, 1998). Factors that are likely to be relevant at the scale of the individual forest include spatial variations in growth stage, stand area, edge effects and local variations in grazing pressure and tree species composition. From the results presented above it appears that different forests vary substantially in their bird communities, perhaps more than is generally appreciated. Factors that are probably especially relevant at the 'between forest' scale include geographical location, regional population size, altitude, soil type and the relative amounts of first- and second-generation plantations.

The potential importance of these and other factors in the context of extensive coniferous forest plantations is summarised below, drawing a distinction between those that are directly affected by management practices and those that are not. For a more comprehensive review see Fuller (1995).

Fixed factors

Several of the factors that affect forest bird communities are 'fixed' and not directly affected by forest management. One of the most important is geographical location. There are strong latitudinal gradients in the diversity of birds in Britain with marked declines at higher latitudes, especially among resident species (Lennon *et al.*, 2000). Specifically within woodland, the lowest numbers of species are found in north-west Scotland. There are also longitudinal patterns, with woods in west Wales holding fewer species than woods further east (Fuller, 1995). The pool of species available to colonise potential habitat within forests will also differ from one region to another because many woodland species are not uniformly distributed within Britain. The absence or scarcity of a particular species within a forest may simply be because that forest lies outside the range of the species or in a region where the density of the species is low.

Other fixed factors of relevance to extensive plantation forests include soil fertility and altitude (Fuller, 1995). Woods situated on unproductive soils tend to hold lower densities of birds than woods on more fertile soils. The effect of land productivity probably acts through effects on vegetation structure and food availability. Densities of songbirds tend to decline with increasing altitude. This effect is probably a response to increasing climatic severity coupled with reduced soil productivity.

Factors influenced by forest management

Growth stage has an overwhelming influence on the bird community of any forest stand. The breeding birds associated with recently planted areas will obviously be very different to those found in thicket stands which, in turn, will differ from those in mature stands (as found in this current study). The responses of birds to the age of stands are driven mainly by the changing physical structure of the forest, especially the height, cover and density of foliage. However, for seed-eating species, the availability of cones is critical and consequently siskins and crossbills are mainly confined to older stands. Many species do not show a linear response to tree age. For example, Patterson *et al.* (1995), in their study of birds in stands of Sitka spruce containing trees of 0 to 50 years of age, found that most common species were least abundant in stands of trees less than eight years old but reached highest abundance in trees of nine to 25 years old. All growth stages are potentially of conservation importance for birds, though the conservation priorities may differ from forest to forest. The overall diversity of forest bird life will generally be highest where large areas of all growth stages are present. Retention of some very old areas of forest will generally be beneficial because such areas are likely to be richer in dead wood and natural tree cavities than the more intensively managed parts of the forest.

It is likely that many of the first-generation forests supported less diverse bird communities than the modern restructured forests, simply because they tended to be more uniform in their age structure. There are also more fundamental differences in the bird communities of first- and second-generation plantations. Newly afforested sites are far more attractive to hen harriers than restocked areas. On the other hand, some passerines such as tree pipit and several warblers can achieve higher densities in the second-generation forests. In Wales, the bird communities of upland restocks are more varied than those of the initial afforestation (Bibby *et al.*, 1985). These differences are probably linked with changes in the structure and composition of vegetation following changes in soil conditions and reduction in the original moorland or heathland plants.

As well as the overall age structure, the internal spatial structure of the forest is relevant. We define ‘spatial structure’ as the pattern of stands with respect to their size and shape. The restructuring of the first-generation forests has generally resulted in far more complex forests containing many edges between stands of different ages. In Sitka spruce forests overall bird densities appear to be higher at the edges of stands (Patterson *et al.*, 1995). Similar data are required for other types of forest. The probable reason for such edge effects is that vegetation structure may be more complex at edges and the general productivity of the habitat greater. Although many species prefer the edges of stands, some may avoid edges, especially those associated with open clearfells (Hansson, 1983). Therefore, it is not necessarily a sensible strategy to minimise the area of all clearfells.

The density of field and shrub layer vegetation is an important determinant of bird community structure in forests. Many species use this vegetation as cover from predators, as a nest site, or as a feeding site. Species that benefit from a dense understorey include wren, dunnock, song thrush, garden warbler and willow warbler. On the other hand, some species that forage on the ground avoid areas with dense vegetation, examples being woodlark and tree pipit. Heavy grazing pressure, low soil fertility and a dense tree canopy tend to reduce the density of vegetation in the field and low shrub layers. Hence, grazing by sheep or deer will tend to reduce the numbers of warblers (Donald *et al.*, 1998; Fuller, 2001). In late thicket and mature stands, thinning can open the canopy and stimulate regeneration of field layer vegetation. The effects of this on birds have not been studied, though one would expect it to enhance numbers of many species.

Forests differ in their dominant tree species and this affects birds through differences in the types and quantity of food they offer, nest site availability and habitat structure. There have been few detailed comparisons of bird communities in stands dominated by different conifer species though in general it appears that spruce holds higher densities than pine (Newton, 1986). Broadleaved and coniferous stands differ considerably in their bird communities. In the Forest of Dean, broadleaved stands hold higher densities of hole-nesting birds than coniferous stands and mixed stands are intermediate in species composition (Donald *et al.*, 1998). The addition of moderate amounts of broadleaved woodland to conifer forests appears to be beneficial to substantial numbers of birds (Bibby *et al.*, 1989).

Approaches to improving forests for birds

It is important to recognise that birds display a wide range of requirements and that one particular management practice will not suit all species. Furthermore, there is much variation between forests in their bird communities. Therefore, it is important to establish priorities and objectives at the level of the *individual forest* when seeking to integrate conservation management into productive forestry. Nonetheless, it is possible to identify several broad principles that underpin the habitat quality for birds in forests and which will help to increase bird diversity. These should be considered alongside the special needs of rare species which are described by Currie and Elliott (1997). The following principles are based mainly on information in Ratcliffe and Petty (1986), Avery and Leslie (1990), Petty and Avery (1990) and Fuller (1995).

- Maintain a balance of growth stages within the forest so as to provide habitats for as wide a range of species as possible.

- Create a diversity of stand sizes and shapes so that : (a) a large amount of edge habitat is present and (b) suitable habitat is also available for species that require large clearfells.

- Within conifer plantations, the presence of patches of broadleaved trees is highly desirable. Maintaining some areas of European conifers (Norway spruce, Scots pine, larch) is beneficial to seed-eating birds as it diversifies cone production and seed availability.

- Allow some patches of trees to grow well beyond their commercial felling age, ideally retaining them indefinitely as minimum intervention areas.

- Wherever possible increase the amounts of deadwood. Leave standing dead trees and when thinning leave some high stumps and dying trees.

- Create networks of unplanted land to be maintained specifically as wildlife habitat, ideally covering at least 10% of the forest area. A variety of habitats and features can contribute to such a network but rides, forest roads, wayleaves and watercourses form the basis. Mosaics of open vegetation, scrub and broadleaved trees can be allowed to develop along the margins of such linear features.

Some gaps in our knowledge

Several points have emerged from the work undertaken on birds as part of the Biodiversity Assessment Project and from the brief review presented above.

- Plantations deserve far more research attention than they have received in recent years, especially as there is concern that some species of woodland birds are in decline (Gregory *et al.*, 2001) and there are increasing opportunities for integrating conservation management into the design of second-generation forests.

- Forests differ greatly in their bird communities and in the responses they show to forest growth and development. It should be noted, however, that the age class categories used in the Biodiversity Assessment Project were very broad and that some of the variation within growth stages may, in fact, be explained by tree age. Nonetheless, there is clearly a need to obtain better information about the densities of birds in forests in different parts of the country so that conservation management can be better targeted at the level of the individual forest.

- Young stages of conifer plantations make a large contribution to the diversity of woodland bird life and they appear to provide important habitats for several species that have declined outside forests. Little is known about the causes of variation in the bird communities of these young stages.

- Edge effects between stands of different ages are probably important influences on the overall population levels of many bird species within conifer forests, yet they have been studied in very few forests. Predictions of the effects of forest design on birds depend critically on this information.
- Many of the existing studies of birds in conifer plantations have been in first-generation plantations. There is a need to undertake similar studies in second-generation forests which appear to support very different bird communities.

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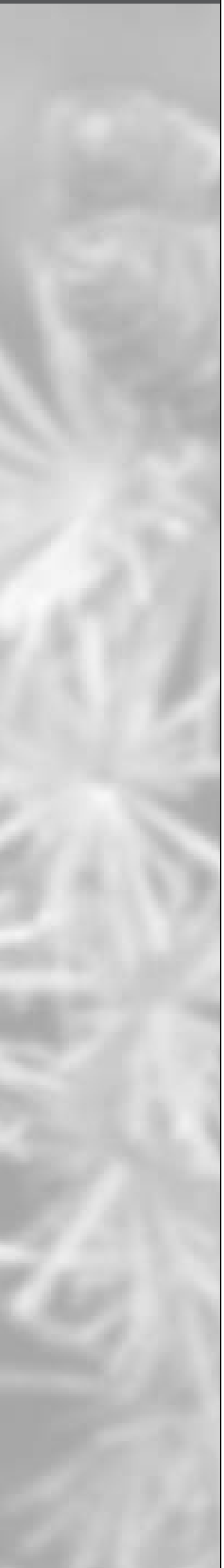
SECTION FOUR

Conclusions



CHAPTER 12

The future management of plantation forests for biodiversity

Chris Quine and Jonathan Humphrey

Summary

This brief review summarises the main findings from the Biodiversity Assessment Project and emphasises the value that Britain's planted forests already make to the conservation of biodiversity. The contentious nature of much of the upland afforestation in the latter part of the 20th century has tended to distract attention from the benefits of the creation of new forested habitats. However, much of the benefit obtained to date has been gained by chance rather than design. Further enhancement of biodiversity is possible by greater attention to structural diversity across landscapes and within stands, and applying site-specific stand management. The development of geographic information systems, and the associated codification of knowledge about sites, the habitat requirements of key species, and the identification of biodiversity indicators will provide valuable planning tools. A number of uncertainties remain to be addressed by further research, such as the level of biodiversity to seek and the appropriate balance between early seral and mature forest stages. There are few parallels to the level of ecological restoration represented by the reforesting of Britain, and while we have much to learn, we may also have much to offer other deforested countries.

Introduction – why manage for biodiversity?

As outlined in Chapter 1, the last 20 years have seen important changes in British forestry, through the 1985 Amendment to the Wildlife and Countryside Act, the 1992 Convention on Biological Diversity (The Rio Earth Summit), the 1993 Helsinki Agreement, the 1998 UK Forestry Standard, and the development of the UK Woodland Assurance Scheme (UKWAS). Management of forests in Britain must now take account of biodiversity. Some forests will be managed with biodiversity as the prime objective of management; in others, there will be several other important objectives, which in some cases may take precedence. Why should management be influenced by biodiversity considerations? Three reasons are often advanced:

- There is a fundamental value to biodiversity, and its preservation for future generations – a moral or ethical argument linked with concepts of stewardship.
- There can be financial and other benefits from preserving biodiversity – market access through certification schemes that reassure the environmentally-aware customer; long-term health and viability of the managed forest ecosystem; reduced costs of intensive management.
- There are political and legal requirements to protect and enhance some forms of biodiversity enshrined in Global, EU and national legislation and agreements.

As a consequence there are a number of requirements to be met by the forest manager – from statutory requirements, such as Sites of Special Scientific Interest, Special Protection Areas, to voluntary schemes such as UKWAS. Codes of practice, including the terms of the Woodland Grant Scheme and the UK Forestry Standard, have attempted to summarise existing knowledge and wisdom (particularly based on the precautionary principle) in order to guide the manager. It is not the intention to repeat this advice here, but rather to try and place in context the recent rapid development of interest in conserving and enhancing forest biodiversity, and provide some pointers to further management to benefit biodiversity. Some of the these pointers are based on the emerging findings from the Biodiversity Assessment Project as described in the Chapters 5–11. Another important area to consider is the cost-effective measurement of biodiversity and we suggest some potential biodiversity indicators, focusing on those which could be used by managers at the forest stand scale.

This review chapter also takes into account the outcomes from the four workshop discussion sessions held during the symposium. These workshops covered issues relating to management guidance, priority setting, biodiversity assessment and indicators and future research (see the Preface to these proceedings).

Past woodland history and biodiversity in Britain

Biodiversity lost

At present, Britain is one of the least wooded countries in the temperate regions of the world. This has resulted from a long history of human settlement, high numbers of domesticated grazing animals, and past climatic changes. The loss of woodland over the past millennia has been associated with substantial losses of woodland biodiversity. Examples of the well-known fauna are given in Table 12.1.

Table 12.1 *Loss of woodland fauna in Britain in the Holocene. Primary source: Corbet and Yalden (2001).*

Species	Timing of species loss
Reindeer (*Rangifer tarandus*)	8300 years ago
Auroch (*Bos primigenius*)	Bronze age (3500 years ago)
Elk (*Alces alces*)	Bronze age (3500 years ago)
Lynx (*Felis lynx*)	1770 in northern Scotland
Brown bear (*Ursus arctos*)	Roman times (presence doubtful after 10th century)
Wild boar (*Sus scrofa*)	End of 13th century; 16th century reintroductions for hunting
Beaver (*Castor fiber*)	Saxon times – certain presence; medieval times – probable presence
Wolf (*Canis lupus*)	1743 Scotland
Red squirrel (*Sciurus vulgaris*)	Around 1770 in southern Scotland
Red deer (*Cervus elaphus*)	End of the 18th century in Wales
Capercaillie (*Tetrao urogallus*)	1771
Greater spotted woodpecker (*Dendrocopus major*)	1850 in Scotland

Biodiversity replaced

The concerted programme of afforestation during the 20th century, frequently with fast-growing exotic species, increased woodland cover from <5 to 12%. Much of the land that became available for forestry was marginal agricultural land in the uplands. There was considerable controversy over the loss of these habitats which, although often maintained by a regime of overgrazing and frequent intervention, had become valued for their open ground flora and fauna. The potential for conflict was exacerbated by the 'blanket' nature of the afforestation, fuelled by objectives to produce a strategic reserve of timber, and to maximise financial return. This resulted in the transformation of habitats with high conservation value such as streamsides, mires and ancient woodland sites to planted forest.

The conflict between afforestation and conservation reached a head in the late 1980s over the afforestation of peatlands in the Flow Country of North Scotland. This development of an internationally valued peatland provoked a backlash from conservationists. Attention was focused on the loss of habitat caused by upland afforestation in general, and ignored the potential benefits of the creation of new habitats.

Biodiversity restored – a post-afforestation reassessment?

It now seems appropriate to reconsider biodiversity potential in view of the developments in forestry practice. In the past 10 years there has been considerable rapprochement between foresters and conservationists. As a result there have been changes to standards for new grant aid and better advice in guidelines, standards and certification. Special habitats and species are now given a higher degree of protection, and there has been substantial effort during restructuring to correct the excesses of the past and secure important habitats such as riparian zones and rocky outcrops. Restoration of particularly valuable habitats has occurred, e.g. peatland restoration such as the Border mires, lowland heath restoration, restoration of ancient woodland sites. Financial incentives have been targeted at the expansion of other under-represented habitats, such as treeline woodlands and montane scrub.

Summary of findings from the Biodiversity Assessment Project

So what of the bulk of the forest that does not comprise these special habitats? The results from the Biodiversity Assessment Project clearly illustrate that planted woodlands provide a habitat that is suitable for a wide range of different species.

Over 2000 species have been recorded to date (Table 12.2) with a large percentage of these being invertebrates. It had been expected that the native woodland stands would be considerably more species-rich than the plantations, but this was only the case for some groups such as vascular plants and lichens. These results are due in part to under-sampling of some groups in the native stands (e.g. the deadwood invertebrates), and to a lower number of stands surveyed (e.g. four upland oak stands compared to eight upland Sitka spruce stands). However, the positive value of plantations for groups such as the beetles hoverflies and other species have been substantiated by other studies in planted forests (Humphrey *et al.*, 1998). Forty-two Red Data List species were recorded in total, with highest counts in the planted and semi-natural stands Scots pine stands in the foothills. A surprisingly high number of Red Data List species (29) were recorded in the upland Sitka spruce stands.

There was a clear effect of latitude on species-counts, with the southern (lowland) plots supporting richer invertebrate and songbird communities than the northern (foothills and upland) plots (Table 12.2), but the reverse was true for lichens. Different crop types and stand ages support different species assemblages (Table 12.2). For example, the upland Sitka spruce stands had the highest diversity of mycorrhizal fungi and bryophytes whereas the lowland Scots pine had a high diversity of wood saprotroph fungi and canopy coleoptera. Pre-thicket plots were often richest for a variety of species-groups also found in non-wooded habitats such as heathland lichens (Table 12.2). In contrast, over-mature stands had a higher proportion of 'woodland specialist' species than the younger stand stages. These specialist species included bryophytes, woodland herbs and carabid beetles (Table 12.2).

There were significant effects of site type, stand structure and deadwood on the diversity of a variety of species-groups (Table 12.2). Nutrient-rich sites had more diverse vascular plant and fungal communities than the more nutrient poor sites. Stands with dense canopies had species-poor lichen, vascular plant and ground beetle communities (e.g. mid-rotation Sitka spruce stands), but had the richest mycorrhizal fungi communities. Deadwood was an important substrate for wood saprotroph fungi, lichens and bryophytes. Snags (especially in foothills pine plots) were important for lichens, with logs and stumps in Sitka spruce and oak stands providing the more optimal bryophyte habitat.

One of the other key factors affecting lower plant diversity within the planted stands was the presence of ancillary habitats such as pockets of wet and unplanted ground, remnant mature native broadleaved trees and rocky outcrops. The occurrence of native broadleaves and associated vegetation within a number of the planted stands suggests that these stands were formerly ancient semi-natural woodland. These plantations on ancient woodland sites (e.g. lowland Norway spruce stands – Northants; upland Sitka spruce stands – Clunes) appear to have higher diversity than the plantations established on previously unwooded ground (such as the foothills Sitka stands in Kielder). However, the degree of connectivity with existing ancient semi-natural woodland is an additional factor to consider as a clear link was demonstrated between the occurrence of rare and threatened native pinewood fungi and distance to existing native pinewood. Further research is needed to clarify the interrelationships between diversity, and spatial and temporal connectivity to sources of colonising species.

Table 12.2 *Main factors affecting the biodiversity of planted stands based on data from the Biodiversity Assessment Project. SS = Sitka spruce; NS = Norway spruce; CP = Corsican pine; PAWS = Plantations on ancient woodland sites; – = no recorded effects. Table continued on opposite page.*

	Soil	Climate	Tree (crop) species type	Vertical stand structure/ chronosequence
Canopy invertebrates (225 species)	–	North-south trend in increasing species-richness	SS much less diverse than all other crop types; NS exceptionally rich. Large variability in species counts and abundances between plots	Diversity in SP plots lower in mature and over-mature stands compared to mid-rotation stands. Diversity negatively correlated with vertical cover index (CI)
Sub-canopy invertebrates (420 species)	–	North-south trend in increasing species-richness	NS stands had high species-richness of Cicadomorpha with distinctive communities	Positive relationship between field layer vertical cover, syrphid and cycalid diversity
Ground beetles (Carabidae) (53 species)	Negative relationship between soil moisture content and diversity	North-south trend in increasing species-richness	Spruce plots more diverse than pine, especially NS	Pre-thicket SS plots important for non-forest carabids. Increase in proportion of forest specialist carabids in over-mature stands. Mid-rotation SS plots poorest of all stand types; mid-rotation SP plots richer than pre-thicket plots
Songbirds (41 species)	–	North-south trend in increasing species-richness	No recorded effects	Pre-thicket plots had distinctive communities
Ground vegetation (239 species)	Inverse relationship between available nitrogen and vascular plant and bryophyte diversity. Community composition determined by soil fertility	No direct effects; indirect effects mediated by soil fertility	No direct effects; indirect effects mediated by soil fertility. Semi-natural oak stands had more diverse communities than the planted stands	Pre-thicket plots had distinctive communities and were more diverse than denser canopied mid-rotation and mature plots (especially SS). Compared to the other stand types, mature and over-mature pine and spruce stands in the north had communities most closely matching the species-composition of semi-natural woodland
Fungi (677 species)	Positive correlation between litter saprotroph richness and soil fertility	No direct effects	Different crop types support different fungal assemblages No difference in species counts between semi-natural and plantation stands	Positive correlation between mycorrhizal species-richness and increased lower canopy cover
Lichens on deadwood (106 species)	–	North-south trend in decreasing species-richness	Northern pine and oak stands had richest lichen communities. Semi-natural stands had richer communities than planted stands	Strong negative correlation between light availability (LAI), basal area (MBA) and lichen species-richness. Pre-thicket and over-mature plots were far richer than mature and mid-rotation plots, especially in SS
Bryophytes on deadwood (77 species)	–	Effects could not be separated from effects of tree (crop) type	Spruce stands had significantly richer communities than pine stands	Over-mature spruce stands characterised by high upper canopy cover values had richer bryophyte communities than the other stand stages
Soil microbes	Negative relationship between diversity, soil moisture and organic content	–	Foothills Scots pine stands had higher fungal-derived microbial diversity than the other stand types	Mid-rotation and mature plots tended to have higher microbial diversity than the other stand stages

It is clear from the above discussion on the results of the Biodiversity Assessment Project, that in many respects, habitat development has occurred by accident rather than design, as a result of 'normal' commercial forestry practice during the 20th century. Also, the scale of these new forests means that they are significant reservoirs for biodiversity – for example, there is almost 20 times more Scots pine plantation in Britain than native Scots pinewood (Jones, 1999). Now that the conservation of the latter has been secured, it is easier to accept the the plantations can have a supplementary benefit. To what extent can this benefit be built upon in the future?

	Deadwood	Proximity to native woodland	Site history	Other
Canopy invertebrates (225 species)	–	–	–	–
Sub-canopy invertebrates (420 species)	–	–	–	–
Ground beetles (Carabidae) (53 species)	–	–	Some PAWS had a higher proportion of forest specialist carabids	–
Songbirds (41 species)	–	–	–	–
Ground vegetation (239 species)	–	Possible positive effect on the occurrence and abundance of woodland herbs and mosses	Possible positive effect on the occurrence and abundance of woodland herbs and mosses	–
Fungi (677 species)	Positive correlation between fresh (bark intact) fallen deadwood volume and wood saprotroph species-richness	Number of threatened pinewood species records negatively correlated with distance to existing native pinewood	PAWS had more threatened pinewood fungi than plantations established on non-woodland sites	Positive correlation between tree species diversity and mycorrhizal species-richness
Lichens on deadwood (106 species)	Snags had higher lichen species-richness than stumps or logs. Well-decayed snags (with loss of bark) had highest species counts	–	Remnant mature broadleaved trees supported a range of non-deadwood species on PAWS	Ancillary habitats – rocks rides and wet areas supported additional species
Bryophytes on deadwood (77 species)	Logs and stumps had higher species-richness than snags. Large diameter (≥ 20 cm) well-decayed logs had the highest species-counts	Possible positive effect on occurrence of oakwood liverworts in upland SS	–	Ancillary habitats – rocks rides and wet areas supported additional species
Soil microbes	–	–	–	Negative relationship between microbial diversity and species-richness of ericoids; positive relationship with ferns and herbs

Potential for future development – what to aim for?

In regions of the world where substantial natural forests still remain, a template or ‘reference value’ against which to compare management options is readily available. This is not the case in Britain and without the natural comparison, it is less clear what level of biodiversity is desirable or possible. The deforestation and afforestation of Britain has resulted in unique forests with little parallel worldwide. In addition, the maritime environment is rather different from that of the main forested regions of the world, and is responsible for some severe environmental gradients over short distances, underlining the need for site specificity in management. Much of the advice and standards provided in Britain to date have explicitly or implicitly reflected knowledge from regions such as Scandinavia or NW America. There is good justification for this but, equally, there has to be careful review of the validity of following such a process uncritically.

The conventional view to improve biodiversity, espoused in policy in Scandinavia and the Pacific Northwest, emphasises the need to secure and expand the contribution of high forests, particularly the mature and old-growth stages, thereby favouring forest-dwelling species and woodland specialists. When looked at over longer timescales, plantations in the UK have the potential to develop an old-growth type structure. However, this assumes there is sufficient specialist woodland flora/fauna remaining in Britain to benefit. Spatial and temporal connectivity to sources of woodland species is a key issue governing this process; the 'pool' of potential species varies considerably with locality often for very straightforward reasons, such as physico-chemical or climatic limitations (see Chapter 10 for a discussion relating to invertebrates).

A contrasting viewpoint acknowledges the contribution that forests can make in continuing to support the early successional and open ground biodiversity which is so important in upland Britain. This would include:

- Maintaining linkage between internal (permanent and transient) and external open space thereby enhancing movement of organisms between them.
- Ensuring that regeneration (planted or natural) is widely spaced; thinning and keeping rotations short to enhance survival of non-forest organisms and the soil seed bank etc.
- Developing a fine-grain mosaic of open space throughout the forest.
- Maximising the occurrence of edges.

The key to addressing such contrasting views is to avoid the slavish pursuit of either, particularly when other motives are harnessed to justify this (e.g. visual aesthetics, advocates of continuous cover forestry). It is unclear what is the appropriate balance between open ground and forest, and between early seral and late successional stages. There are dangers in being too prescriptive, particularly when there is substantial uncertainty over the functioning of forest ecosystems in British conditions. In addition, the management objectives (within the constraints of legal control) and the biophysical and social specifics of the forest/region will have important influence on opportunities and practical options. There is certainly no single optimal solution, because there is so much that remains unknown, and there are both complex interactions (e.g. deer–flora–fauna) and important external influences such as climate change.

Potential for future development – management actions

In terms of managing for biodiversity, we know what *not* to do, at least in general. However, what we *want* to do is more difficult, as this is different in different places. There is a need for diversity of end-point and objective. This means that managers are faced with a menu of options, rather than a prescription. The development of decision-support systems can help managers to make informed choices, but there will still be an element of subjectivity involved. Somebody has to make a choice between the various options, and such decisions will be based on a multitude of factors, not just driven by inherent conservation value.

Actions that will contribute to the conservation and enhancement of biodiversity can be identified at three spatial scales: national, landscape and forest stand.

Management at the national scale

At the country level, action to enhance biodiversity may include:

- Achieving an appropriate level of forest cover (national forest strategies).
- Reintroductions of lost species, e.g. beaver (as in the past with capercaillie).

- The prevention of further entry of alien and invasive organisms.
- Minimising the effects of important external effects, e.g. through climate change initiatives, and tackling pollution such as nitrogen deposition.

Management at the landscape scale

The potential for plantation forests to accrue biodiversity value is likely to be influenced by their scale. This confers a major advantage for northern conifer forests in the UK, which cover large areas and can accommodate a wider range of habitat types and management options. This permits interventions to favour biodiversity to be made at a scale which is sustainable, in terms of providing habitat networks and ensuring that the potential for dispersal between metapopulations (small distinct populations that are linked in some way) is maximised. At the larger scale, biodiversity management can support the requirements of a range of species, which may have widely different habitat patch and home range sizes.

At this scale, there are important decisions to be made, that until recently have been governed by visual aesthetics. Action to develop a biodiverse and attractive mosaic should include:

- Achieving an appropriate balance of land-use and habitat at the landscape scale.

- Developing forest habitat networks which link plantations with semi-natural wooded habitat to promote species colonisation. Evidence from the fungal survey (Chapter 8) suggests that rapid (in an ecological timescale) and long-distance dispersal is possible in some species groups. However, for many species we do not know how long this process is likely to take and, in some instances, remedial action may be required.

- Developing a planned mosaic of desirable habitats, rather than accepting what is there by accident, and incorporating valued habitats into forest design such as crags, mires, semi-natural woodland, species-rich grasslands etc.

- Tackling over-grazing by deer in both upland and lowland forests.

- Tackling alien and invasive organisms present (e.g. rhododendron, grey squirrel).

- Taking opportunities from natural forest dynamics.

- Utilising tools that enhance understanding of site potential and diversity, e.g. Ecological Site Classification – site quality; Geographical Information System (GIS) models of habitat requirements of key species – landscape ecology.

Management of individual stands

There has been relatively greater attention paid to the opportunities for enhancement of biodiversity by management at the stand level. Structural diversity can be introduced – by extending rotations and applying alternative silvicultural systems. Such silviculture now seems more feasible than, say, in the 1970s when the expectation was that rotations would be limited to around 40 years either due to the threat of windthrow, or the need to optimise economic return (Ford *et al.*, 1979). Recent work has demonstrated that the threat of windthrow is not so severe, and a broader view of values is now accepted. A range of alternatives to clearfell exist, in essence a structural gradient from clearcut to single-tree removal which provide options in different parts of the forested landscape (Kerr, 1999). Continuous cover forestry may have an important role where permanency of forest habitat is desirable, but non-intervention reserves may be even better for provision of deadwood. At present, only approximately 1/20th of the area that could be managed as continuous cover is actually managed in this way, but there are ambitious targets to redress this, e.g. in Wales 50% of Forest Enterprise woodlands are to be converted to continuous cover over the medium term. Measures for enhancing biodiversity within forest stands would include:

- Extending rotations beyond the economic optimum, maintaining tree presence by reducing the scale of harvesting, increasing the provision of deadwood and allowing some stands to develop towards old-growth within non-intervention (natural reserves), (Humphrey *et al.*, 2002).

- Increasing tree species diversity including 'intrusive' broadleaves, both within the normal patch clear-felling cycle, and in continuous cover stands. This will benefit mycorrhizal diversity (Table 12.2), but also other species groups (Humphrey *et al.*, 1998).

- Introducing other non-tree components of the forest ecosystem such as ground flora, effectively speeding-up the process of species accumulation, or adjusting composition to create a more *natural* community. For key species, such as those which may function either as keystones or flagships, this should be considered very carefully. The cost of large-scale introductions although technically feasible could be very costly.

- Increasing the area of individual stands and minimising edges to enhance the core forest habitat. Although the Biodiversity Assessment Project did not investigate specifically the influence of stand area on diversity, reviews of the evidence from other studies (Humphrey *et al.*, 2003) suggests that the expansion of core areas within old stands is a key measure in the protection and enhancement of 'woodland' related biodiversity as opposed to the biodiversity of open ground and edge habitats.

Development of management guidelines

At present, managers seeking information and practical advice on biodiversity conservation are faced with a wide range of sources, with varying levels of accessibility to the reader. The Forestry Commission's *Nature conservation guidelines* (Forestry Commission, 1990) cover nature conservation as distinct from water resources, soils, landscape, recreation and archaeology. There are also a large number of specific publications, produced by the Forestry Commission and others, which address some aspects of biodiversity, e.g. deadwood (Humphrey *et al.*, 2002). The *UK forestry standard*, while setting some benchmarks, does not provide the management guidance needed to achieve these. There is a need for information to be pulled together in a readily accessible and updatable form, providing a single state-of-the-art source. It is clearly necessary to update the existing Forestry Commission *Nature conservation guidelines,* possibly re-issuing these as holistic biodiversity guidelines.

There are a number of specific issues which need to be given greater attention in such revised management guidance. The importance of site history is recognised, and advice is needed regarding realistic biodiversity expectations and what should be considered as success in meeting restoration targets. There is also concern over the approach to be taken towards special sites, e.g. Sites of Special Scientific Interest (SSSIs) and Special Areas of Conservation (SACs). For example, how should these be buffered against changes within the wider forest landscape, and how should biodiversity objectives differ for designated sites and the generality of the forest. The need for integration of information on soils, water, and landscape is also recognised as essential for practices to more fully satisfy the requirements of sustainable forest management.

Any new guidelines need to be developed at various scales, from the stand to the landscape, and possibly using Natural Areas (England and Wales) or Natural Heritage Zones (Scotland) as a planning unit. They also need to consider a range of woodland types, incorporating native woodland HAPs, and covering plantations in both the uplands and lowlands. Furthermore, the guidelines should cover associated non-woodland semi-natural habitats, and should address both structure and composition – actual and potential (ESC will be useful in this respect as a predictive tool). It is important that inventory and monitoring are given prominence, and that the guidelines as a whole are reviewed regularly and updated as necessary.

Practitioners require backing in meeting their management obligations with respect to biodiversity, and one way that greater support could be provided would be through the appointment of an increased number of ecologists working within the state sector. An increased ecological input to forest management, at the level of individual forest districts or regions, would strengthen decision-making as part of design planning; and provide an enhanced means of feeding biodiversity information back to the policymakers.

Much of the above remains a daunting challenge but will be increasingly supported by the advent of new tools such as GIS. In addition, greater consensus amongst land-users and planning agencies, enhanced consultation with experts and the public, a willingness to experiment (adaptive management), and the product of ongoing research, give rise for optimism.

How do we measure success?

Measuring success requires that we have clearly defined targets and agreed assessment methodologies. A considerable amount of research is under way, both in the UK and on a pan-European scale, to identify key factors and associated indicators (or surrogate) measures of forest biodiversity (e.g. Larsson, 2001). These measures need to be cost-effective, ecologically meaningful, and easy-to-use. Ferris and Humphrey (1999) have reviewed potential biodiversity indicators and proposed a provisional set of compositional and structural indicators for general use within British forests. Here, we move to the next stage in the process by offering a set of parameters derived from the Biodiversity Assessment Project datasets which could be developed as potential indicators of biodiversity at the stand scale within spruce and pine plantations in Britain.

As described in Chapter 3, three components of biodiversity can be recognised: composition (e.g. tree species-richness, understorey plant communities), structure (e.g. physiognomy of forest stands and associated habitats), and function (processes, e.g. nutrient cycling). Of the three, compositional and structural indicators are more amenable to measurement by forest managers. Microbial activity could be used potentially as a functional indicator of diversity (Chapter 6), but the techniques used to characterise this activity are currently outwith the scope and expertise of forest managers. It is also important to recognise that climate and soils impose a geographical restriction on the pool of species available as potential indicators, although even within the same locality there is huge variability in species composition, particularly of invertebrate communities. One of the most robust compositional measures is simply the number of tree species within the stand. This measure was found to correlate well with mycorrhizal species-richness (Chapter 8).

Of the structural parameters, measures of deadwood volume, size and decay status show good relationships with the diversity of lower plants and fungi across all forest types (Table 12.2). Vertical stand structure is also linked with diversity in a range of species groups, and the cover index described in Chapter 3 has potential as an indicator. At the landscape scale, site history and distance to semi-natural woodland appear to influence the diversity and composition of fungi, carabid and ground vegetation communities within the planted stands. Further analysis of the Biodiversity Assessment Project datasets is planned to explore the relationships between diversity within stands, and spatial and temporal connectivity with semi-natural woodland, and a Landscape Ecology Project (Ferris *et al.*, 2000) is beginning to unravel the effects of other processes at the landscape scale.

Research priorities

Based on the results of the Biodiversity Assessment Project to date, a wide range of research priorities can be identified, recognising that progress so far has only begun to answer the key questions concerning forest biodiversity. To fully understand the complex interrelationships between organisms, within and between habitat patches, a much longer timeframe is required. The need for rapid dissemination of data, interpreted in the form of readily usable management advice, means that researchers are unlikely to be given such opportunities for long-term studies. Instead, there will be an increasing requirement for interim advice, based on available data coupled with ecological wisdom. While the current project represents the most extensive biodiversity evaluation of British forests ever undertaken, it did not span all species and site types. More information is needed on soil types, ground flora, and the relationships between them. Further assessment of mammals, birds, reptiles, fungi (possibly using molecular markers) and invertebrates is also needed. Links need to be made to the landscape scale, necessitating the use of GIS-based tools. The inception of the Landscape Ecology Project (Ferris *et al.,* 2000) aims to address these issues. However, the question of genetic diversity needs to be addressed, and research has only just begun in relation to biodiversity.

In addition to looking at research concerned with compositional aspects of biodiversity, functional aspects require attention (in relation to the resilience or sustainability of the system). These have possibly been avoided due to problems of tractability of the research involved. Key areas identified include the following:

- Herbivore interactions.
- Experimental exclusions or additions to the system.
- Implications of changing management practices for biodiversity, e.g. continuous cover.
- Catchment level interactions.
- Ecological hierarchies.
- Carbon-nitrogen balance.
- Spatial heterogeneity (assessment of landscape pattern and flows – validation of forest habitat network concepts).
- (Meta)-population dynamics.
- Changes in habitat quality over time.

Recognising the importance of below-ground biodiversity, particularly in terms of site potential (as borne out by the work outlined in Chapter 6), there is the potential for developing methods for evaluating soil microbial communities. Microbial profiling is an emerging technology, which can be utilised to make comparisons between numerous site types. The following represent potentially valuable avenues for further work:

- Comparisons of PAWS, Ancient Semi-Natural Woodland and restored Ancient Woodland;
- NVC types.
- Forest chronosequences (and first generation forests v subsequent generations).
- New woodlands.
- Effects of management impacts.

If we can begin to gain an improved understanding of microbial succession, this could help to provide management advice with implications for restoration of PAWS, and the establishment of new woodland.

A revised view of the biodiversity potential of planted forests?

The findings of the Biodiversity Assessment project, and a revised view of an afforestation process that no longer threatens special habitats, goes a long way to refuting the notion that plantations are ecological deserts, or irrelevant for biodiversity. Many native species find the forest conditions to their liking. The large area of planted (productive) woodland means a significant contribution can be made to species survival, even if the densities are lower, and communities differently configured than those found in natural forests. In the future, it is reasonable to expect planted forests to have a diverse structure at a range of spatial scales. They will make a significant contribution to conservation and enhancement of woodland and open habitat biodiversity (as well as providing for other values), and be valued in their own right, perhaps as ‘long-established’ rather than ‘non-native’ species and ecosystems.

Trying to identify objectives, set targets and then assess whether these have been met is a difficult task, in part because of the multiple stakeholders involved. Each stakeholder group will have a different perspective, both in terms of defining biodiversity and its position in a hierarchy of management objectives and outputs from forest management. The audience for this Symposium was largely composed of professionals employed in forestry and forestry-related fields; all have an appreciation of the importance of biodiversity, although levels of knowledge inevitably vary. However, the views of this group are by no means representative of the wider public, which raises the issue of consultation. Just how far should we go to ensure that expectations are met? This is a question which needs to be addressed as part of the growing social forestry agenda.

There are clearly many uncertainties in the management of forests for biodiversity. The following appear to be of greater importance:

- How should protection and management respond when rare species become more common? Or when the needs of two rare species conflict?
- What effect will climate change have directly on trees and indirectly on wider flora and fauna?
- How will public perception of 'wildlife' develop and what impact will that have on wildlife management (i.e. harmful biodiversity)?
- How will managers reconcile biodiversity objectives with economic and social objectives?

Conclusion

From an earlier meeting on the ecology of planted forests:

'The great accomplishments of foresters in deforested Great Britain are admirable... The first step was to establish the material base of the forest, i.e. to create biomass. It is possible to progress only after such a base has been created.'

Professor D. Mlinšek, 1979

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Annexe 1

Details of assessment sites

Details of assessment sites. Pyear is planting year, n/a indicates that stands were unlikely to have been established by planting but site history is not known. NR = stand established by natural regeneration. DAMS = detailed aspect Method of Scoring (Quine and White, 1993 – see Chapter 3); AT = accumulated temperature; MD = moisture deficit (Pyatt et al.*, 2001 – see Chapter 3).*

Site No.	Site	Crop species	Pyear	Age	Rotation	Previous land-use	Grid ref.	Long/lat	Elevation (m.asl)	Wind exposure DAMS	AT (>5°C)	MD (mm)	Continentality (Conrad Index)
1	**Glen Affric**												
1.1	Lochan Dubh, Cannich	Scots pine	P84	12	1	Heath/grassland	NH363317	57°23´N 4°48´W	220	12	1045	70	5
1.2	Knockfin	Scots pine	P61	35	1	Heath/grassland	NH279261	57°18´N 4°51´W	300	15	954	48	5
1.3	Plodda Falls	Scots pine	P1900	96	1	Native pinewood	NH273237	57°17´N 4°55´W	190	13	1089	77	5
1.4	Loch Beinn a' Mheadhoinn	Scots pine	n/a	238[a]	n/a	Native pinewood	NH238258	57°16´N 4°52´W	300	13	955	48	5
2	**Strathspey**												
2.1	Moor of Alvie	Scots pine	P88	8	2	Native pinewood	NH853084	57°9´N 3°54´W	235	12	1039	78	6
2.2	An Slugan	Scots pine	P64	32	1	Native pinewood	NH943129	57°12´N 3°45´W	350	10	893	49	6
2.3	Glenmore Lodge	Scots pine	P32	64	1	Native pinewood	NH988101	57°10´N 3°40´W	450	14	772	25	6
2.4	Airgiod-meall	Scots pine	n/a	165[a]	n/a	Native pinewood	NH966074	57°9´N 3°43´W	450	14	773	24	6
3	**Thetford**												
3.1	Lynford	Scots pine	NR 78	18	1	Heath/grassland	TL833901	52°29´N 0°42´E	30	12	1781	220	11
3.2	Horsford Woods	Scots pine	P59	37	1	Heath/grassland	TG197180	52°43´N 1°15´E	30	13	1748	225	10
3.3	High Lodge	Scots pine	P28	68	1	Heath/grassland	TL825846	52°26´N 0°41´E	40	12	1768	217	11
4	**New Forest/Windsor**												
4.1	Knightwood Inclosure	Scots pine	P70	26	1	Native oakwood	SU254064	50°51´N 1°38´W	40	11	1969	197	9
4.2	Denny Lodge	Scots pine	P47	49	1	Native oakwood	SU333052	50°51´N 1°32´W	20	10	2011	203	9
4.3	Denny Lodge	Scots pine	P30	66	1	Native oakwood	SU341038	50°50´N 1°31´W	20	10	2012	204	9
4.4	The Look Out, Windsor	Scots pine	P30	66	1	Native b/l woodland	SU883656	51°23´N 0°44´W	110	12	1760	188	11
5	**Knapdale**												
5.1	Dunardy	Sitka spruce	P87	9	2	Heath/scrub	NR814907	56°4´N 5°31´W	160	18	1246	83	4
5.2	Dunardy	Sitka spruce	P72	24	2	Heath/scrub	NR814910	56°4´N 5°31´W	130	15	1287	91	4
5.3	Gortonronach, Kilmichael	Sitka spruce	P52	44	1	Heath/scrub	NR937925	56°5´N 5°19´W	150	18	1257	88	4
5.4	Dunardy	Sitka spruce	P34	62	1	Heath/scrub	NR817912	56°4´N 5°30´W	130	11	1287	91	4
6	**Clunes**												
6.1	South Laggan	Sitka spruce	P88	8	2	Heath	NN257938	57°0´N 4°52´W	90	14	1238	104	5
6.2	Clunes	Sitka spruce	P68	28	1	Heath/native woodland	NN185908	56°58´N 4°59´W	350	16	917	36	5
6.3	Clunes	Sitka spruce	P34	62	1	Heath/native woodland	NN189892	56°58´N 4°59´W	150	16	1169	87	5
6.4	South Laggan	Sitka spruce	P29	67	1	Heath	NN248936	57°0´N 4°53´W	130	11	1189	93	5
7	**Forest of Dean**												
7.1	Ruddle Marsh	Norway spruce	P81	15	1	Native woodland	SO608130	51°49´N 2°34´W	120	11	1713	157	8
7.2	Cannop	Norway spruce	P65	31	1	Native woodland	SO612106	51°48´N 2°34´W	80	9	1794	167	8
7.3	Ruardean	Norway spruce	P43	56	1	Native woodland	SO637164	51°51´N 2°32´W	260	16	1437	121	8
8	**Fineshade**												
8.1	Fineshade	Norway spruce	P79	17	1	Native woodland	SP982978	52°34´N 0°33´W	80	13	1692	190	10
8.2	Fineshade	Norway spruce	P57	39	1	Native woodland	SP977976	52°34´N 0°34´W	80	13	1692	189	10
8.3	Fermyn Woods	Norway spruce	P31	65	1	Grassland	SP985837	52°27´N 0°33´W	80	13	1706	190	11

Site No.	Site	Crop species	Pyear	Age	Rotation	Previous land-use	Grid ref.	Longitude/ latitude	Elevation (m asl)	Wind exposure DAMS	AT (>5°C)	MD (mm)	Continentality (Conrad Index)
9	**Kielder**												
9.1	Falstone	Sitka spruce	P90	6	2	Grassland	NY715860	55°10´N 2°27´W	260	15	1162	101	8
9.2	Falstone	Sitka spruce	P73	23	2	Grassland	NY708838	55°9´N 2°27´W	280	15	1133	96	8
9.3	Falstone	Sitka spruce	P39	57	1	Grassland	NY671849	55°9´N 2°31´W	300	14	1103	90	7
9.4	Archie's Rigg	Sitka spruce	P27	69	1	Grassland/mire	NY704830	55°8´N 2°28´W	305	15	1096	90	8
10	**Glentress**												
10.1	Glentress	Sitka spruce	P86	10	2	Heathland	NT277421	55°40´N 3°9´W	380	13	954	58	7
10.2	Glentress	Sitka spruce	P68	28	1	Heath/grassland	NT288408	55°39´N 3°8´W	310	13	1055	77	7
10.3	Glentress	Sitka spruce	P41	55	1	Heath/grassland	NT279428	55°40´N 3°9´W	400	14	925	54	7
10.4	Cardrona	Sitka spruce	P35	61	1	Grassland	NT305368	55°37´N 3°6´W	300	10	1072	80	7
11	**Thetford**												
11.1	Kings Forest	Corsican pine	P88	8	2	Heath/grassland	TL815761	52°21´N 0°40´E	50	12	1758	215	11
11.2	Kings Forest	Corsican pine	P63	33	1	Heath/grassland	TL809763	52°21´N 0°40´E	50	12	1758	215	11
11.3	Kings Forest	Corsican pine	P37	59	1	Heath/grassland	TL810747	52°20´N 0°39´E	40	12	1778	218	11
11.4	High Lodge	Corsican pine	P27	69	1	Heath/grassland	TL815845	52°26´N 0°40´E	40	12	1769	217	11
12	**Clipstone**												
12.1	Clipstone	Corsican pine	P87	9	2	Heath/grassland	SK606621	53°9´N 1°6´W	105	14	1591	172	10
12.2	Clipstone	Corsican pine	P53	43	1	Heath/grassland	SK632627	53°9´N 1°3´W	75	13	1643	180	10
12.3	Clipstone	Corsican pine	P47	49	1	Heath/grassland	SK613644	53°10´N 1°5´W	90	13	1615	176	10
13	**Alice Holt**												
13.2	The Straits	Oak	P35	62	n/a	Native b/l woodland	SU794401	51°9´N 0°51´W	70	10	1866	198	10
13.3	Goose Green	Oak	P1820	177	n/a	Native b/l woodland	SU807403	51°9´N 0°50´W	95	10	1814	191	10
14	**New Forest**												
14.2	Salisbury Trench	Oak	P36	61	n/a	Native b/l woodland	SU255147	50°55´N 1°38´W	110	13	1815	178	9
14.3	Fletcher's	Oak	P1829	168	n/a	Native b/l woodland	SU272043	50°50´N 1°36´W	25	11	2002	201	9
15	**Taynish**												
15.2	Taynish	Oak	n/a	104[a]	n/a	Native oakwood	NR732849	56°0´N 5°38´W	50	14	1404	110	4
15.3	Taynish	Oak	n/a	112[a]	n/a	Native oakwood	NR762853	56°0´N 5°35´W	40	12	1417	113	4
16	**Beasdale/Moidart**												
16.2	Beasdale	Oak	n/a	111[a]	n/a	Native oakwood	NM707847	56°53´N 5°45´W	90	15	1254	94	4
16.3	Moidart	Oak	n/a	131[a]	n/a	Native oakwood	NM705729	56°47´N 5°45´W	40	15	1329	107	4

[a] Semi-natural stand, mean age. Ages range were: plot 1.4: 183–270; plot 2.4: 100–242; plot 15.2: 39–150; plot 15.3: 60–140; plot 16.2: 19–154; plot 16.3: 55–201.

Annexe 2

Methods for extraction and analysis of soil microbial PFLAs (see Chapter 6)

The current extraction process is a relatively passive technique and is an adaptation of a well-established method for lipid extraction (Bligh and Dyer, 1959). It uses the principle of initial extraction into a single phase mixture of trichloromethane, methanol and buffer (taking into account the residual moisture in the sample) which is then split into organic and aqueous phases by the addition of more trichloromethane and buffer. The extracted lipids (neutral, glyco- and polar lipids) partition into the organic (lower) layer. The extracted lipids were then separated into classes according to their polarity by adsorption to activated silica and selective elution with progressively more polar solvents. Polar lipids, including phospholipids, are eluted last with the most polar eluant, methanol.

The fatty acid components of the isolated phospholipids must then be cleaved from the glycerol backbone and their carboxylic acid groups derivatised by the addition of a methyl group to reduce their polarity and enable them to be analysed by gas chromatography. Extracts were transmethylated using potassium hydroxide in dry methanol (mild alkaline methanolysis) (Christie, 1989). The resulting extracts were reconstituted in HPLC-grade hexane, and 0.5–1.0 µl of this injected onto a capillary gas chromatograph where they were separated (essentially on the basis of their boiling point) and detected using a flame ionization detector. Two Gas Chromatographs, a Shimadzu 9A and a Pye-Unicam PU4550, fitted with 60 m x 250 mm i.d SE54 (0.25 µm δf) capillary columns, were used for the analyses (see Morris, 2000 for further details).

A bacterial fatty acid methyl ester (FAME) mix (Supelco Inc., Bellefonte, PA and Matreya Inc., Pleasant Gap, PA) was used as a qualitative reference standard and comprised 26 FAMEs of bacterial origin. Initial identification of soil extract FAME peaks was made by retention time correlation with peaks in this bacterial standard mix. Peak identities were confirmed using a Varian Saturn GC with ion trap mass selective detection. Further validation of the extraction and analytical procedures was also carried out. This included injection reproducibility, limit of detection and quantification, linearity of derivatization, solid phase extraction, and linearity of PLFA recovery from high and low humus content forest soils (from which PLFAs had been pre-extracted) at two moisture levels. Although this showed the extraction to be linear it also indicated that the efficiency of the extraction process decreased with increasing lipid content (inverse log relationship, $R^2 = 0.943$). Chromatograms were acquired and manipulated using a Kontron 450 MT2/DAD data handling system.

References

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