Royal
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Epiphyte Communities and Indicator Species

An Ecological Guide for Scotland's Woodlands

Christopher J. Ellis | Sally Eaton | Marios Theodoropoulos | Kathryn Elliott

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Preface

This report presents the variability of epiphyte communities in native British woodland, explores the environmental factors that control them, and provides a framework for their identification using indicator species. As far as is possible, the underpinning research was for epiphyte communities which remain intact, and for this reason it was concentrated in northern Scotland. This is a region for which, relatively speaking, the air quality has been less affected by industrial emissions, and land management is less intensive. On this basis, the report provides an introduction to Scotland's internationally important epiphytes.

Epiphytes are important in many ways. First, their physical presence and diversity remind us that a forest or woodland is more than the sum total of its trees, becoming an ecosystem of multi-layered complexity. This links to the growing awareness within conservation that a multitude of small organisms, including bryophyte and lichen epiphytes, contribute importantly to the structure and function of healthy ecosystems. Second, epiphytes are of immense cultural significance. They are indicators of clean air and provide a warning of the negative impacts of pollution on human health, and they provide a sense of place with nature. Learning to discriminate between some simple epiphyte species and communities makes it possible to orientate and understand a woodland biogeographically, for example by recognising a globally rare temperate rainforest, such as on Scotland's west coast, or a Boreal-type system allied with Scandinavian forests, such as in the higher altitude reaches of Strathspey. It also becomes possible to recognise woodlands of special interest, such as those with long ecological continuity that are biodiversity hotspots.

This report aims to have a wide appeal. In general terms, the introductory material will increase awareness of the biodiversity importance and cultural value of Scotland's epiphytes, providing an impetus for their protection. More specific suggestions of use are provided below:

- By recording species indicators for different community types the conservationist or forest/woodland manager can gather information showing the effect of habitat heteorogeneity (variability) on species diversity; more heterogeneous habitats will be represented by a greater range of community types.

- For the natural historian with some basic knowledge of bryophytes and lichens, the report can suggest focal species for field recording as part of their enjoyment of the natural world, in contribution to data gathering for monitoring, and as a framework for building further knowledge.

- For the ecologist it provides a summary of community-level information specific to epiphytes, and these field sampled data are the background from which to develop new questions for primary research.

- For the experienced lichenologist it provides a systematic epiphyte survey and ecological analysis with which to compare and contrast tried-and-tested concepts such as the '*Graphidion*' or '*Lobarion*' phytosociological communities, coupled with quantitative information on the variability of environmental conditions experienced by epiphytes in Scotland in the early 21st Century.

For those who wish to learn more, the Royal Botanic Garden Edinburgh provides introductory courses in bryophytes and lichens, while the Field Studies Council partners with specialist biologists to support identification training relevant to epiphytes. In addition, the British Bryological Society and British Lichen Society are the academic societies which support an interest in bryophytes (mosses and liverworts) and lichens through publications, field excursions and a programme of meetings and workshops for all abilities. It is our hope that readers of this report will either discover for the first time, or reappraise their knowledge of Scotland's globally significant epiphytic diversity, and help to secure its future conservation.

Introduction

Epiphyte:

> *'A plant which uses another plant, typically a tree, for its physical support, but which does not draw nourishment from it'*
>
> The Oxford Dictionary of Botany.

1.1 The Nature of Epiphytes

Epiphytes grow on the bark surface of trees, taking advantage of the physical support offered by trunk, branches and twigs as these reach upwards above the ground. They are photosynthetic organisms, which means that they produce their own food using energy from sunlight and basic raw materials (carbon dioxide, water, and nutrients), and they do not parasitise the tree on which they grow. Rather, epiphytes use trees as a scaffold, and this has proven to be an ingenious and ecologically successful strategy. Forests cover approximately 30% of the global land surface (4 billion hectares)[1] and an individual tree such as an oak, with a modest girth of 2 metres, has a bark surface area that is at least 74 times greater than the ground space it occupies[2]. Considered across forests globally, the accumulated surface area provided by a vast number of trees represents an extensive habitat to which epiphytes are adapted (*Figure 1.1*).

Figure 1.1. A. **Forests cover huge areas of the terrestrial land surface, as here in the densely forested southern Appalachian mountains of Georgia (USA).**

Figure 1.1. B. **Beneath the forest canopy, at the scale of the individual tree, an interwoven structure of trunks and branches provides an extraordinary surface area of bark for colonisation by epiphytes.**

By growing on the outer surface of structurally dominant trees, epiphytes avoid competition for space and the limitations of shading in the ground layer of forests; however, epiphytes must overcome the difficulties associated with an existence away from the soil environment, including restricted access to water, leading to periods of desiccation, and limited availability of essential nutrients[3]. Nevertheless, a tremendous diversity of plants and fungi is adapted to the epiphytic environment and can be found in forests across the planet forming an above-ground ecosystem of awe-inspiring complexity (*Figure 1.2*).

Epiphytes are a visible reminder that a forest is comprised of more than trees, which create the obvious structure. Forty percent of all known terrestrial species are associated with forest canopies, and 10% of all vascular plant species are epiphytes[4] (*Figure 1.3A*) including the celebrated orchids and ferns which adorn tropical forests. Equally impressive, though less widely known, are the cryptogamic lichens, mosses and liverworts (*BOX 1*) which are dominant on tree trunks and in the canopy of higher latitude temperate and boreal forests, including British woodland (*Figure 1.3B*).

Figure 1.2. **Vascular plant epiphytes, growing in the canopy of warm-temperate Nepalese forest.**

Figure 1.3. A. **Tropical epiphytes growing on *Anadenathera colubrina* in seasonal dry forest of the Andean piedmont in Northern Argentina.**

Figure 1.3. B. **In temperate woodland, bryophytes and lichens add significant diversity, ecosystem function and aesthetic interest, extending beyond the structure of the trees themselves; a lichen community on aspen (*Populus tremula*) at Insh Marshes NNR in north-eastern Scotland.**

Lichens, mosses and liverworts are 'poikilohydric', meaning they do not actively regulate their water status using a specialised vascular system such as the xylem and phloem of vascular plants. Instead, they respond directly to ambient environmental conditions, rehydrating when water is available and withstanding tissue desiccation during dry periods. It is this flexibility to adjust to rapid changes in the local environment, and a tolerance of environmental extremes, which make lichens, mosses and liverworts well suited to the epiphytic way of life[5].

BOX 1

'Cryptogamic' means 'hidden sex', and refers to fungi such as lichens and non-flowering plants such as bryophytes (mosses and liverworts), which reproduce to form spores contained in relatively small structures. The word cryptogam is a catch-all term for a variety of unrelated organisms which reproduce in this way using spores, and is an ecological convenience.

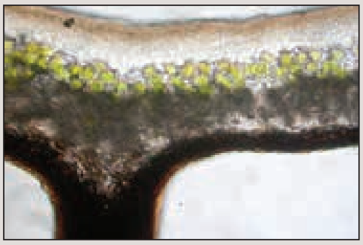
A common attribute which unites many cryptogams is that they are 'poikilohydric'. This means that they respond directly to the environment. When the atmosphere is humid or wet, the tissues of the organism become hydrated and physiologically active, and when it is dry the tissues become dormant. Cryptogamic fungi such as lichens, and plants such as bryophytes, are extremely tolerant of desiccation (drying out).

Mosses and liverworts (bryophytes) are small though ecologically very successful plants which photosynthesise to produce food using energy from sunlight, carbon dioxide and water. Mosses and leafy liverworts have stems and leaves, though 'thalloid' liverworts have a single, flattened leaf-like structure. For some species, the bryophyte plant can form asexual propagules such as gemmae, which develop directly into new independent plants. Alternatively species may develop a 'sporophyte generation', the means by which spores can be produced following sexual reproduction.

Mosses growing as epiphytes on an elder (*Sambucus nigra*). →

Lichens are composite organisms in which a fungus produces a specialised structure (the lichen thallus), within which it farms a population of photosynthetic algae, and/or nitrogen-fixing cyanobacteria, referred to as the 'photobiont'. The fungal cells of the lichen require a source of food, and they harvest some of the photosynthetic carbon compounds from the photobiont.

The distinctive lichen *Cladonia floerkeana* with bright red 'apothecia' which contain spores. ↓



← Cross-section of a lichen thallus showing the internal population of green algal cells.

← Dark brown one-septate fungal spores contained in asci (flasks) seen here in a cross-section through an apothecium.

1.1.1 Cryptogamic Epiphytes

Cryptogamic epiphytes are extremely diverse; up to around one hundred different species may occur on a single tree[6], and many hundreds of different epiphytes can coexist in a moderately sized British woodland. This epiphytic diversity should be considered as fundamental to the integrity of a forest or woodland as the trees are themselves. Nevertheless, in British forests and woodlands, trees lacking epiphytes are common in regions that have suffered air pollution, and as a largely urbanised society we have become accustomed to seeing tree bark without or with only a depauperate covering of lichens, mosses and liverworts (*Figure 1.4*).

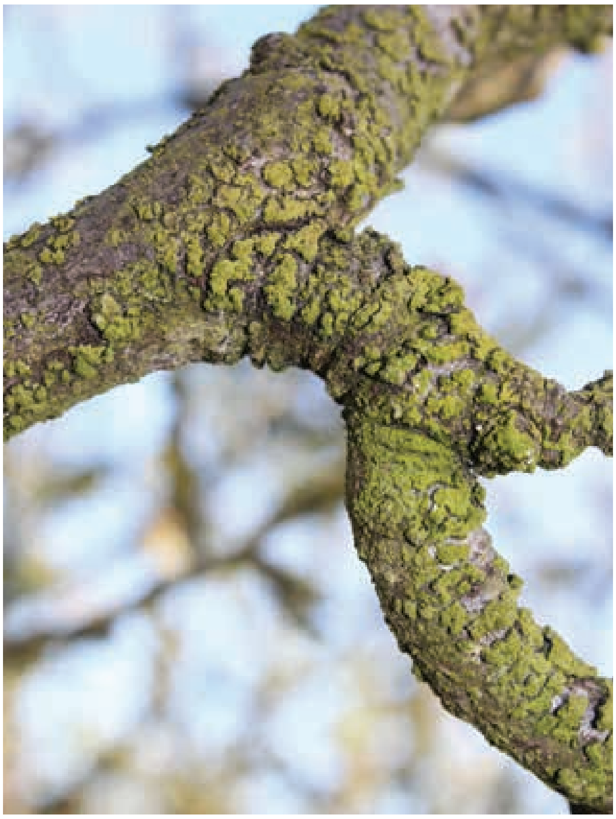


Figure 1.4. A. **A monolayer of algae is characteristic of tree bark in regions of Britain that have suffered air pollution, here on an apple tree (*Malus* sp.) in North Yorkshire.**

In contrast *Figure 1.4. B.* **The diversity of lichen epiphytes on an apple tree in a clean-air region of northern Scotland.**

This regional scarcity of epiphytes hasn't always been the case, and in the past epiphyte-covered trees were the norm across Britain:

> *'Possibly the most pervasive change which someone returning from the Middle Ages would notice in the modern countryside is the appearance of tree-trunks. Trunks everywhere used to be covered in a patchwork of grey, brown, white, green, and yellow lichens, with occasional mosses. This normal aspect of a tree-trunk is still to be seen in the remoter parts of western England, Wales, Scotland, and Ireland. To most English countrymen now, tree-trunks are grey-green with a thin layer of a single lichen,* Lecanora conizaeoides*.*
> *In suburbs tree-trunks are bright green with the alga* Pleurococcus*. In cities and downwind from industry trunks have a clean dark-brown appearance, sterilized by acid rain. The cause is air and rain pollution ...'*
>
> Rackham (1986)

This loss of epiphytic diversity as a consequence of industrial pollution is extremely well researched. In contrast, and surprisingly, the ecology of intact British epiphyte communities is relatively unexplored. To provide baseline information on the variability of epiphyte communities, and the indicator species which characterise them (presented in Chapters 4 and 5), the scope of this book is focussed geographically in a relatively clean-air region of northern Britain (Scotland). Information is drawn from a major survey of Scotland's epiphytic diversity (presented in Chapter 2) in order to provide a first assessment that is analogous to the United Kingdom's National Vegetation Classification, which already exists for ground-layer plant communities.

The work presented here builds on pioneering research examining epiphyte communities by Barkman (1958) and James *et al.* (1977), though expands on these earlier semi-quantitative assessments by: (i) using systematic sampling combined with (ii) a statistical analysis to explain how epiphyte community structure is controlled by key habitat factors (presented in Chapters 3 and 4).

1.2 Why Epiphytes Matter

Epiphytes are important in maintaining the ecosystem function of our woodlands, and provide an indicator of environmental health.

1.2.1 Ecosystem Function

The term 'ecosystem' refers to the network of interdependencies (e.g. energy flows, nutrient cycles) which unites a community of species. One of the challenges in understanding ecosystems is to think beyond the scale of human experience. For example, to fully understand the role of cryptogamic epiphytes it becomes necessary to make observations on scales of centimetres or millimetres. In this sense, lichen, moss and liverwort epiphytes are representative of an extremely diverse assemblage of small organisms (including a bewildering array of fungi, algae, and bacteria) which perform important functions in maintaining healthy and resilient ecosystems.

We know in general terms that epiphytes play an important ecosystem role in regulating forest food-webs, and in water and nutrient cycles. A mosaic of cryptogamic epiphytes increases the range of contrasting microhabitats on a tree. This positively affects the biomass and diversity of tree dwelling invertebrates, with implications across the food-web, e.g. by providing an increased food resource for forest birds. Cryptogamic epiphytes also efficiently capture atmospheric water, and act like a sponge to store and release this moisture relatively slowly into the forest system. Likewise, they capture and process atmospheric sources of nutrients which are limiting to plant productivity, such as nitrogen, performing an important role in the forest nutrient cycle. There is therefore strong evidence for a significant role of cryptogamic epiphytes in maintaining healthy forests and woodlands[7].

Despite the small-scale at which these functions operate when measured for individual organisms or within their communities, the net consequences cumulatively scale upwards and are of relevance to human society. The United Kingdom's National Ecosystem Assessment[8] – which provided a landmark examination of the health of Britain's ecosystems and the services they provide to society – emphasised that the importance of maintaining healthy communities of these small organisms far exceeds our practical understanding of their ecology.

1.2.2 Bioindicators

Cryptogamic epiphytes are indicators of environmental pollution. They have been used to indicate negative impacts on the environment resulting from the burning of fossil fuels, including the release of sulphur dioxide (SO_2) and associated acid rain, as well as excess nitrogen associated with traffic, and fertilisers and animal waste from intensive farming[9]. Air pollution has negative human health impacts, and lichen epiphytes can provide a broad index of environmental quality that has implications for human society[10]. Epiphytes can also be used to interpret landscape ecology not just in terms of pollution, but as indicators for habitat structure and quality, providing a means to determine the biodiversity value of important conservation sites[11].

1.3 Threats to Epiphytes

Given the importance of epiphytes to forest biodiversity and ecosystem function, and their usefulness as indicators of environmental health, it is of considerable human concern that epiphytic species are threatened across much of Europe. Two impacts have severely reduced the diversity of cryptogamic epiphytes: (i) the spread of settled agriculture leading to forest loss beginning long ago in prehistory, and (ii) the more recent process of industrialisation and land-use intensification.

1.3.1 Forest Loss and Fragmentation

Historically, Europe has experienced a massive loss of its native temperate forest, with the highest values of habitat alteration globally[12]. Since the mid-Holocene, persistent deforestation has followed different pathways with varying degrees of intensity across the British landscape[13]. This long process of deforestation has resulted in today's heavily managed countryside, in which trees are a relatively minor component. Epiphytes therefore occur within fragmented pockets of semi-natural woodland (or on isolated trees) which are similar to islands in an otherwise intensively managed and/or non-forested system (*Figure 1.5*).

Figure 1.5. **A landscape matrix with pockets of woodland and isolated trees set within intensively managed farmland, in the East Lothian countryside of south-eastern Scotland.**

Despite the extensive loss of forests, traditional management practices within certain remnant woodlands have ensured the continuous presence in Britain's landscape of mature, post-mature and senescent native trees, e.g. to secure a continuous supply of large timber as 'standards', or within pasture woodland to provide sheltered grazing for livestock, and as boundary trees associated with hedgerows (*Figure 1.6*). This long-standing though non-intensive management has secured a continuity of habitat for the types of epiphytic species which in 'pristine' forests may otherwise be dependent on old-growth stands[14].

Figure 1.6. **Massive veteran oak trees (*Quercus* sp.) at Woodhall Dean, south-eastern Scotland. The existence of this traditionally managed woodland provides the type of local environment which in 'pristine' forests may be associated with old-growth structure. This includes canopy gaps and glades, and specialist microhabitats on the bark of post-mature and senescent trees.**

1.3.2 Industrialisation

A stepwise change in the scale and rate at which human society is altering the natural world began with industrialisation in the mid-18th Century. So profound is this change that it has marked a new geological epoch referred to as the 'Anthropocene'[15]. Epiphytes have been decimated by the historic effects of European industrialisation, in terms of both air pollution and rapidly changing patterns of land-use. The pollution regime is dynamic, with signs of epiphyte recovery following a massive species loss associated with SO_2 pollution, though with currently high levels of nitrogen becoming an increasingly important factor in limiting epiphytic diversity[9]. The effect of land-use change on woodlands takes contrasting forms, either towards greater intensification and replanting for commercial forestry, or alternatively, with the abandonment of traditionally managed woodland which provided continuity of mature, post-mature and senescent trees with open structured canopies[16].

1.4 Scotland's Epiphyte Value

In order to provide a baseline assessment of intact British epiphyte communities this report has a regional focus on Scotland. Against a wider European background of extensive air pollution, and loss of either natural forest or the abandonment of traditional non-intensively managed woodlands, Scotland's landscape continues to provide habitat for internationally important epiphyte communities. The occurrence of these special epiphyte communities in Scotland is explained by three factors: (i) relatively low pollution loads, (ii) high environmental variability, including globally rare bioclimatic conditions, and (iii) the persistence of woodland which retains 'old-growth' characteristics. These three factors come together in Scotland's landscape to allow the continuation of intact epiphytic diversity, and are discussed below.

1.4.1 Low Pollution Loads

North of the Edinburgh-Glasgow conurbation, Scotland has a relatively clean-air environment. Westerly air-streams from the Atlantic explain the limited impact of long-distance air pollution with localised point-source effects that are restricted in extent[17]. Epiphytes in Scotland have therefore been far less impacted by widespread air-pollution than in other parts of Britain and industrialised Western Europe.

1.4.2 Environmental Heterogeneity

Scotland has an extremely varied climate and landscape. The topography of Scotland is complex, and both the climate and broad habitat types vary dramatically across the landscape. The west coast has a climate that is persistently humid and mild, and that conforms to the temperate rainforest bioclimatic zone. This climatic type is extremely restricted globally, occurring over less than 1% of the Earth's land surface[18]. The presence of a rainforest climate is consistent with unique epiphyte communities that occur along Scotland's Atlantic coastline (*Figure 1.7*), providing the pre-eminent examples of this globally rare forest ecosystem that occur within Europe. Further east in Strathspey, though only 70 kilometres from the west coast, epiphyte communities become more similar in character to those of the Scandinavian boreal forest owing to the drier climate and sub-zero winter temperatures.

Being able to identify and interpret epiphyte communities on these local or regional scales creates a profound 'sense of place', including the knowledge that in Scotland we can celebrate and we have responsibility for a natural heritage which is globally rare and internationally important.

1.4.3 Old-growth Woodland

Scotland retains areas of woodland which provide two 'old-growth' properties required for the persistence of intact epiphyte communities: (i) microhabitat heterogeneity and (ii) microhabitat persistence over time. However, these two key properties may be realised independently of one another, and can be highly variable among sites depending on patterns of woodland history. To accommodate this complexity, the important role of woodland history for epiphytes is addressed separately and in detail in Section 1.5, overleaf.

Figure 1.7. A. A Scottish oceanic hazelwood (*Corylus avellana*) in spring; an ecosystem which provides among the best examples of Scotland's 'temperate rainforest'.

Figure 1.7. B. The emblematic lichen *Lobaria pulmonaria*, a dominant species for an epiphyte community which often includes a rich diversity of cyanolichens (lichens associated with cyanobacteria as a photobiont) requiring liquid water for photosynthesis (as mist or rainfall), and species which are representative of warm-loving sub-tropical or tropical genera and that thrive in the mild climate of western Scotland, e.g. *Graphis, Pyrenula* or *Thelotrema* species.

1.5 'Old-Growth' Properties

Microhabitat heterogeneity and persistence are presented here as 'old-growth' properties, because they are the two key elements which appear to explain the difference between species-rich unmanaged, or non-intensive traditionally managed woodlands, compared to more intensively managed forest stands with reduced epiphytic diversity.

Each of these properties – heterogeneity and persistence – sets the stage for an ecological process affecting the character of epiphyte communities, in terms of: (i) the types of species found (composition), and (ii) the number of species found (richness). The first of these ecological processes – matched to habitat heterogeneity – is referred to as 'species-sorting', and describes the way in which different species occur in contrasting niches[19]. This can be seen in the way different epiphytes may grow on bark which has different roughness or chemical characteristics (*Figure 1.8*), leading to contrasting types of epiphyte community.

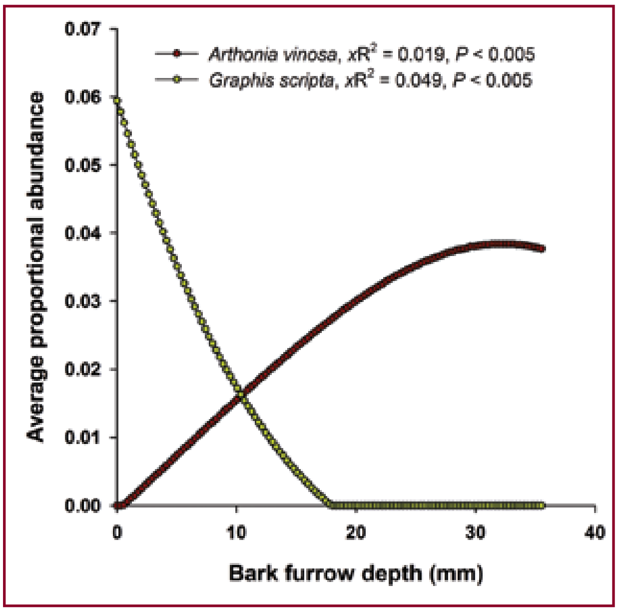


Figure 1.8. A. (Above) In the background an old oak tree (*Quercus petraea*) with rough bark, and a smooth barked rowan (*Sorbus aucuparia*) in the foreground, at a site near Taynish in south-western Scotland, and *Figure 1.8. B*. (Left) Response curves for *Arthonia vinosa* and *Graphis scripta* (derived using nonparametric multiplicative regression), showing their different niche dynamics with respect to bark roughness. Trees which have different bark characteristics will have contrasting epiphyte species, and the co-occurrence of these trees will accumulate a greater diversity of epiphytes than a monoculture of trees of the same species and age, with similar bark environments.

The second ecological process – matched to microhabitat persistence – is referred to as dispersal-limitation[20]. This refers to the fact that a species' propagules (spores, or asexual diaspores) are limited in their dispersal across the landscape (*Figure 1.9*).

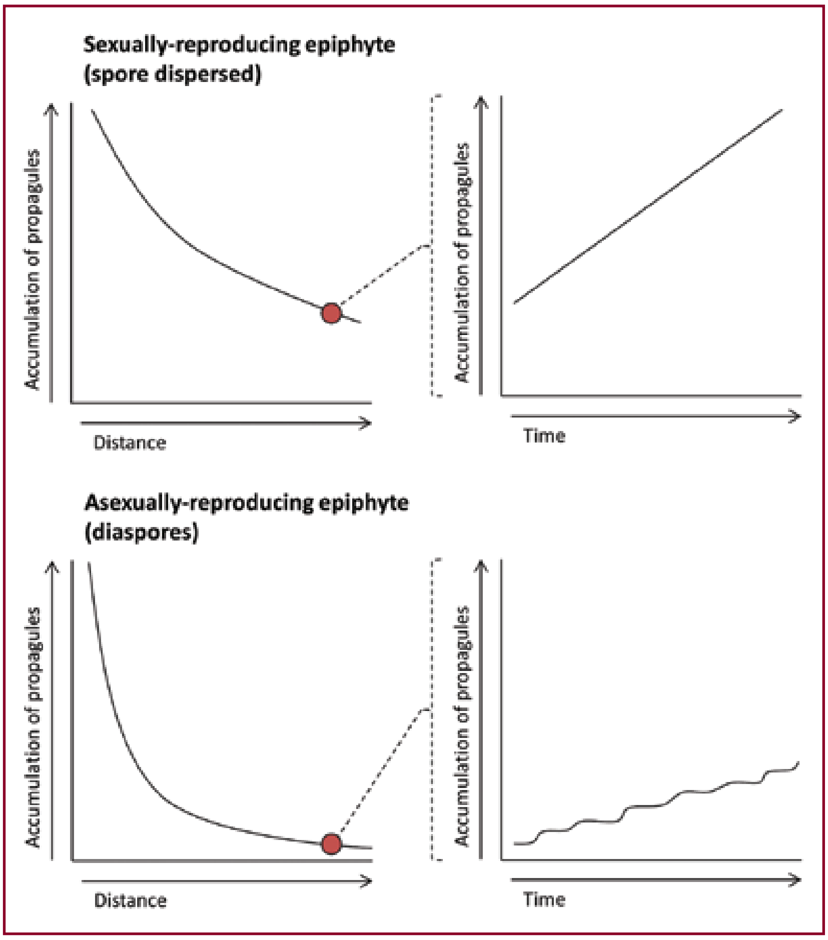


Figure 1.9. **Examples of very simplified ecological 'dispersal kernels', explaining the accumulated arrival of propagules for two contrasting species, with respect to distance and time. The net arrival of propagules into a microhabitat drops off as distance from the propagule source increases, though it may decrease at a higher rate for asexually-reproducing species with larger diaspores (e.g. isidia or soredia of lichens, or gemmae of mosses/liverworts) than for the small spores of sexually-reproducing species (see *Box 1*). However, for a given distance (e.g. at the red dot) the number of propagules arriving will accumulate over time, more rapidly and regularly for spore dispersed species, and less rapidly and irregularly for species with larger diaspores. The likelihood of colonisation into a microhabitat is therefore a function of both the distance from the source of propagules (distance from a reproductive population), and time (increasing the cumulative number of propagules arriving), with the form of this response dependent on the reproductive life-history of a species (the number and size of propagules produced).**

1.5.1 Microhabitat Heterogeneity

As outlined above, the effect of microhabitat heterogeneity is based on the observation that species sort themselves into different niches, to which they are optimally adapted. It follows that the greater the microhabitat heterogeneity (or variability) within a woodland, then the more niches are available for colonisation by a wider range of different species. Species richness will thus accumulate across contrasting microhabitats on a tree, between different trees, and between trees within different topographic settings.

Forest stands subject to natural dynamics[21] will mature to contain a mosaic of differently aged forest patches, including young pioneer and light-demanding tree species regenerating in forest gaps, mid-successional mixed patches, through to older dominant tree species along a gradient towards senescence (*Figure 1.10*). This natural sequence creates structural complexity within a relatively small area, in terms of the variety in epiphytic niche factors such as bark physical and chemical properties (related to tree species, and tree age) and the light regime (canopy structure). This successional pathway results in high levels of microhabitat heterogeneity (many different niches) compared to even-aged rotational forestry, for example[22].

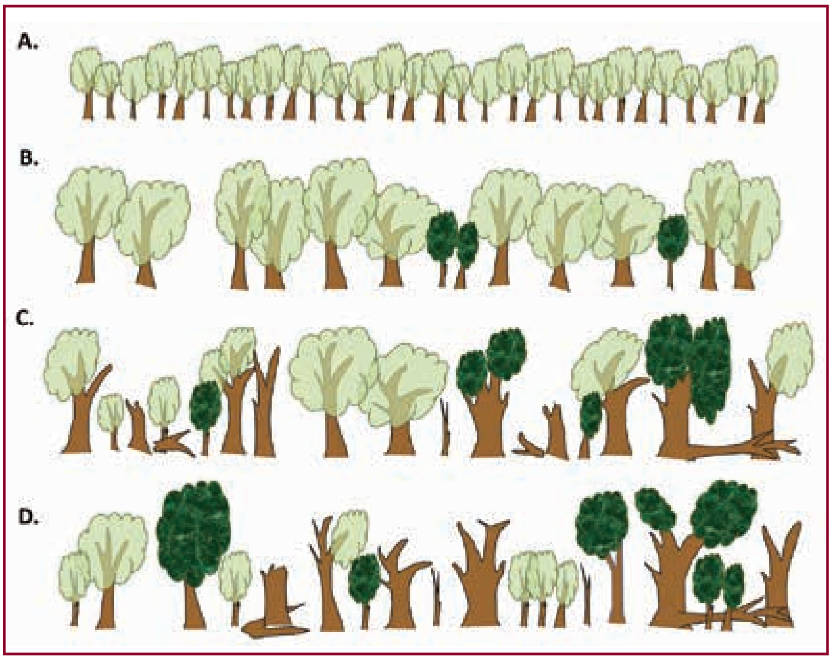
Figure 1.10. **Diversification of a hypothetical forest stand as it ages and undergoes cyclical gap-dynamics to create a mosaic of small-scale habitat patches.**

A. **Dense even-aged regeneration of light-demanding species (pale canopy trees), following stand replacing disturbance (low structural heterogeneity);**

B. **Self-thinning towards mature closed-canopy forest, with recruitment of shade tolerant species (dark canopy trees) into the understory (low-moderate structural heterogeneity);**

C. **Tree damage (e.g. wind-throw) and senescence causing canopy gaps, creating a more open and complex structure with multiple age cohorts of different tree species (high structural heterogeneity);**

D. **The cyclical process of senescence, gap formation, and regeneration recurs within the stand, allowing the temporal overlap (continuity) of specialist microhabitats within close proximity.**



1.5.2 Microhabitat Persistence

Microhabitat persistence describes the unbroken occurrence over time of specific microhabitats within a forest stand. This is important because some epiphyte species appear to be weak dispersers in colonising from one forest stand to another (cf. *Figure 1.9*). The likelihood that a given woodland will be colonised depends therefore on a species' dispersal ecology combined with spatial factors, such as the 'connectivity' or 'isolation' of the stand; connectivity measures the configuration of suitable habitat through which viable propagules must successfully travel from source populations, in order to colonise and establish new populations. Isolated stands are those with low connectivity values, i.e. with constraints to the arrival of propagules, as is the case for many woodlands in the British landscape (cf. *Figure 1.5*).

In addition to the spatial effects of connectivity or isolation, the persistence of microhabitats over time is critically important, because it weakens the effect of isolation (cf. *Figure 1.9*). If a microhabitat persists over long periods of time within a stand, then because of the increased opportunity for accumulating propagules there is a greater chance it will be colonised by dispersal-limited species, which may also tend to have lower population densities within the landscape. This principle can be seen to apply on individual trees, because the epiphyte community shifts as a tree ages to include a greater representation of dispersal- or establishment-limited though competitively dominant species[23]. At a stand-scale, it leads to the accumulation of indicator species for ecological continuity.

1.5.3 Indicator Species for Ecological Continuity

Ecological continuity is the concept which unites the two 'old-growth' properties of microhabitat heterogeneity and persistence[24]. For example, certain epiphyte species are thought to be dependent on microhabitats uniquely associated with old trees in late-successional forest patches. This may include unusual bark microhabitats found within groves of senescent trees (*Figure 1.11*). If some of these microhabitat specialist epiphytes are also dispersal-limited, then their presence would indicate not just the occurrence of unusual bark microhabitats in the here and now, but also the stand-scale occurrence of these microhabitats across time periods encompassing multiple generations of trees. When formally tested and recognised as indicator species, these epiphytes would help to pick out some of the most important habitats for protection, in terms of landscape history (non-degraded, 'old-growth-like' forest remnants) and act as substitutes for biodiversity conservation by signalling 'hotspots' for niche specialist, dispersal-limited species.

Figure 1.11. A. **Dry and powdery bark within a wound on an old aspen (*Populus tremula*) at the Insh Marshes NNR creates,**
Figure 1.11. B. **(Inset) Specialist niche space for the pin-head lichen *Sclerophora pallida.***

Figure 1.11. C. The presence of a large senescent aspen with a hollow bark structure creates habitat for,
Figure 1.11. D. (Inset) The rare epiphytic lichen *Anaptychia ciliaris* subsp. *ciliaris*.

1.5.4 **Ecological Continuity and The Cultural Landscape**

Ecological continuity, as it is defined in this report, describes the time over which individual microhabitats have persisted within a forest stand. The concept can be used as a tool, to make sense of the complex history of Scotland's woodlands (*Figure 1.12*).

First, some forest stands may have existed in the landscape for long periods of time, and with continuous tree cover throughout the post-glacial period[25]. In certain cases these so called 'ancient' woodland stands may have been subject to only low-intensity human intervention, retaining structural complexity and associated microhabitat heterogeneity, as well as microhabitat persistence across a broad variety of epiphyte niche space (*Figure 1.12A*).

Second, certain types of human management may have maintained ancient woodland stands that include key old-growth microhabitats; this may be the case for pasture woodland[26], a management situation that allowed the persistence of mature, post-mature and senescent trees with canopy gaps, as a feature of the woodland for periods beyond the lifespan of an individual tree (*Figure 1.12B*).

Third, ancient woodlands may have been subject to more intensive human management, to provide a resource for provisioning fuel, timber, roundwood, charcoal, tannin, etc.[27] For example, an increased intensification of management during the late-18th and 19th Centuries in western Scotland, including the coppicing of oak on a short rotation of c. 20 yr, had a tendency to simplify the physical woodland structure by reducing the mixture of tree species and tree ages in a stand. In this case, microhabitat heterogeneity is decreased as a consequence of historic management, and microhabitat persistence becomes relevant to only a limited suite of niches associated with younger trees, as well as fewer – economically important – tree species (*Figure 1.12C*). Microhabitat persistence is therefore curtailed across a broad spectrum of epiphyte niche space, though the woodland itself may be long-lived.

Fourth, woodland stands may have been deforested and subsequently regenerated if intensive land management is abandoned. However, the stand structural complexity and microhabitat heterogeneity is of limited age, possibly determined by the oldest trees in the stand (*Figure 1.12D*). Any specialist niches associated with post-mature and senescent trees will have existed for a limited period of time, such as within a single generation of trees. An analogous situation would be for long-established plantation sites, which are undergoing conservation management to increase structural complexity. The development of this type of stand would be encouraging from a conservation standpoint, but would possibly remain too young in the landscape for the occurrence of true indicator species of ecological continuity.

Fifth, there may be a blanket reduction in microhabitat heterogeneity as is the case in situations where there has been the uncontrolled expansion of certain non-native species, e.g. thickets of *Rhododendron ponticum* with dense shading that reduces the existing microhabitat variation to a single, severely light-limited and uniform environment (*Figure 1.13*).

Figure 1.13. A. **Rhododendron ponticum invading a native oakwood on Scotland's west coast.**

Figure 1.13. B. **The interior of a stand of *Rhododendron ponticum*, creating an environment of deep shade, which is incompatible with epiphytic diversity.**

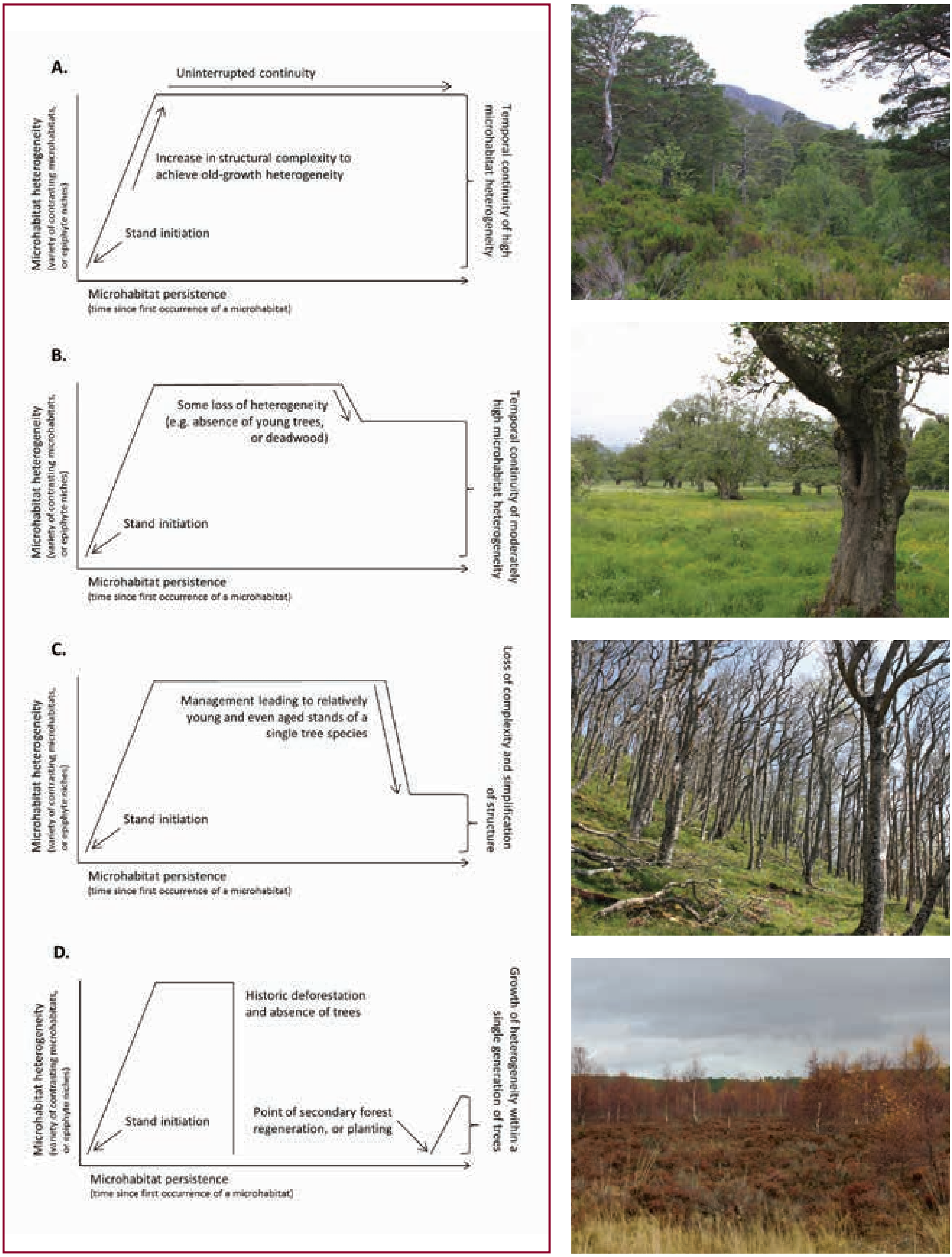


Figure 1.12. Graphs showing the relationship of microhabitat heterogeneity along the y axis, and the time over which individual microhabitat types have existed on the x axis, for different woodland stands:

A. An old-growth system, with an example of the Beinn Eighe pinewoods,

B. A pasture woodland, with an example of pasture with ancient alders (*Alnus glutinosa*) in Strathspey,

C. A coppice woodland, with an example of characteristically even aged and simplified structure from Taynish NNR (Barr Mor), and

D. A recently regenerated woodland, exemplified by birch colonisation onto abandoned moorland in Strathspey.

The key lesson emerging from the concept of ecological continuity is that the long-standing interaction between human society and Scotland's woodlands has fundamentally shaped the relationship between habitat quality and epiphytic diversity. This makes a simple dichotomy between 'natural' forest and 'managed' woodland largely irrelevant in the British context. Instead, there exists an array of local circumstances in which epiphyte communities depend to varying degrees on a legacy of human intervention. In this sense, Scotland's epiphytes are a component of our cultural landscape, providing signatures of landscape history and management.

1.6 **Future Directions**

The complex fabric of local circumstances presented in Section 1.5 is the backdrop against which our relationship with Scotland's woodlands continues to evolve, with inevitable consequences for epiphytes. The future cannot be predicted with certainty, but it seems clear that several challenges related to human-induced climate change will shape biodiversity conservation over the coming decades.

The first prevailing challenge is to widen the scale of conservation, to consider not just individual protected sites, but entire landscapes. Predictive models[28] suggest that climate change has potential to cause a reorganisation of species distributions, including epiphytic communities within Britain, consistent with observational evidence (*Figure 1.14*).

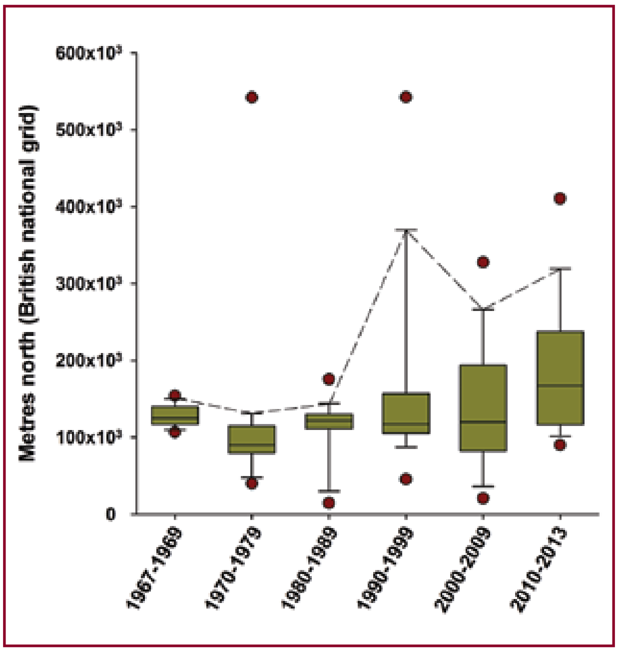


Figure 1.14. **The latitudinal distribution of records for *Flavoparmelia soredians*, as metres north within the British national grid for consecutive decades, with box-plots showing the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots). There are no definitive trends for values at the median or below (southern British range), or for the extreme outliers which possibly represent ephemeral occurrences of 'vagrant' thalli. However, the northern end of the species' consistent range appears to have expanded by c. 150 km, since the 1990s. This is demonstrated by the dotted line connecting the 90th percentile of records. Analysis used British Lichen Society data, downloaded from the National Biodiversity Gateway.**

Regardless of the exact climate future, learning how to manage biodiversity through a period of uncertainty should be attuned to the lessons of palaeoecology, which emphasises the response of species to recurrent environmental change[29]. To meet the challenge of climate change, a dynamic approach is emerging in nature conservation, which is focussed less on the protection of the status quo, and more towards the protection of habitats that are connected within a landscape, and that can accommodate changed species composition while retaining species richness. This shift recognises that the existing conservation network provides nodes of high diversity for the present-day, while also acknowledging that these sites are often small and fragmentary. Habitats across the wider landscape are likely to play a key role in securing diversity into the future[30].

The second related challenge concerns the competing demands we are likely to place on our wider landscape, alongside the biodiversity response to climate change. So called 'multifunctional landscapes' are becoming a priority (*Figure 1.15*), with society expecting a habitat to deliver multiple ecosystem services[31] in terms of carbon capture and storage, recreation, an economic return, and biodiversity conservation. Caution is required in seeking multiple benefits, as the high levels of epiphytic diversity

Figure 1.15. **A multifunctional woodland landscape in Knapdale, south-western Scotland. Commercial forestry of non-native conifer is interspersed with native semi-natural oakwoods that are important for rainforest epiphyte communities. The landscape includes a network of footpaths and mountain bike trails for recreation, and provides a resource for local community projects.**

observed in some of Scotland's woodlands today owes far more to historical contingency – and specifically a lack of economic value – than enlightened conservation over past centuries. It is possible that 'neglected' woodlands with high epiphytic diversity may become threatened during a process in which the delivery of a broad suite of ecosystem services is maximised, with biofuels providing a useful analogue of conflicted decision-making[32]. An additional concern emerges because the scaling-up of decision-making in conservation, to achieve the landscape approach, can proceed at a pace that exceeds the generation of new biodiversity knowledge at similar scales. For many groups of organisms, detailed knowledge is restricted to core areas, such as the protected site network, and the wider landscape is poorly sampled. Imminent decisions could have to be based on easily sampled structural metrics such as woodland extent and connectivity, while the consequences for biodiversity become an assumption.

Biodiversity monitoring remains essential to effective conservation. To provide information that is appropriate for managing and protecting epiphytic diversity during the era of landscape conservation, it is necessary to gather data on species distributions and ecological communities far more widely than has been possible previously. This type of extended knowledge was facilitated for vascular plants by the National Vegetation Classification, which enabled targeted survey methods such as Phase 2 habitat survey and common standards monitoring[33]. The aim of this book is to make it possible to undertake a similar targeted assessment of epiphytic diversity in Scotland, yielding ecological information through the accurate recording of robust community indicator species. This focus on a limited suite of species makes it feasible for a wider body of trained naturalists (non-specialists) to provide information on the distribution of epiphytes across the landscape. If achieved, these observational data could inform considerations in land-use decisions, helping to protect Scotland's internationally significant epiphytic diversity. This would help to ensure that epiphytes are represented in the decision-making process when developing and implementing policies in landscape management, not least by increasing public awareness and wider appreciation of this fascinating and important aspect of Scotland's natural heritage.

Figure 1.16. ***Evernia prunastri*** **on birch, at Dawyck Botanic Garden in the Scottish borders.**

Epiphyte Sampling

2.1 Community Variability

Field sampling of epiphytes was designed to capture the variability of their community composition in Scotland's native woodlands, and Chapter 2 explains the design on which the community analysis is based.

Field sampling was stratified at two scales: (i) sampling across contrasting sites (i.e. different climatic settings, and for different woodland tree composition), and (ii) sampling for contrasting habitat units within a site (i.e. different tree species, of different ages, in variable topographic settings). This approach contrasts with random sampling, which could have been used to accurately measure the abundance of different epiphyte communities. In that case, the more common community types would have been repeatedly sampled from frequently occurring habitat units (e.g. young birch (*Betula* spp.) trees), and less common community types (e.g. those occurring on old rowan (*Sorbus aucuparia*) trees) would likely have been missed.

The frequency of an epiphyte community in this study reflects the extent to which a particular community type occurs across the spectrum of different habitat units that are available (and were sampled) at a given site, rather than its true abundance. However, community types which occur across many different habitat units are likely to have been more abundant at a site, compared to those which appear restricted in their occurrence.

2.2 Site Selection

Site selection for epiphyte sampling was targeted to different woodland types nested along a steep climatic gradient from the milder and wetter oceanic west coast, through a high rainfall belt in the central Highlands, to the more continental northeast of Scotland (*Figure 2.1* and *Figure 2.2*).

Woodland National Vegetation Classification (NVC) data were used to identify sites in similar bioclimatic settings, but which had different tree compositions (*Table 2.1*). A flexible approach allowed for the sampling of important woodland types not represented within the NVC, such as Scotland's aspen woods[34]. All selected sites were Sites of Special Scientific Interest as well as Class 1a ancient woodlands (continuity ≥ 260 yr) within Scotland's Ancient Woodland Inventory[35].

In summary, epiphyte communities were sampled from: (i) ancient and semi-natural native woodlands that (ii) are protected in the conservation network (Sites of Special Scientific Interest) on the basis of their exemplary habitat quality, and which (iii) included extensive areas of ancient woodland. All sites occurred in a relatively unpolluted environment. The selected woodland sample sites are expected to contain some of the most intact epiphyte communities occurring in Britain.

2.3 Epiphyte Sampling

The sampling for epiphyte communities aimed to capture community variation for the lower bole (up to 2 metres) among contrasting trees within a woodland site, excluding upper bole, canopy and twig communities, or deadwood.

To quantify epiphyte community diversity, ten points were positioned approximately equidistantly within a site. Trees chosen for sampling could occur within a 15 metre radius of a point, and individual tree positions were recorded as a 10-figure grid-reference using GPS. The sampling was based on non-leaning trees (average bole lean < 5° away from vertical) without strong wounding and stem-flow effects. Trees of each species occurring within each of four different size categories were then sampled once for each site,

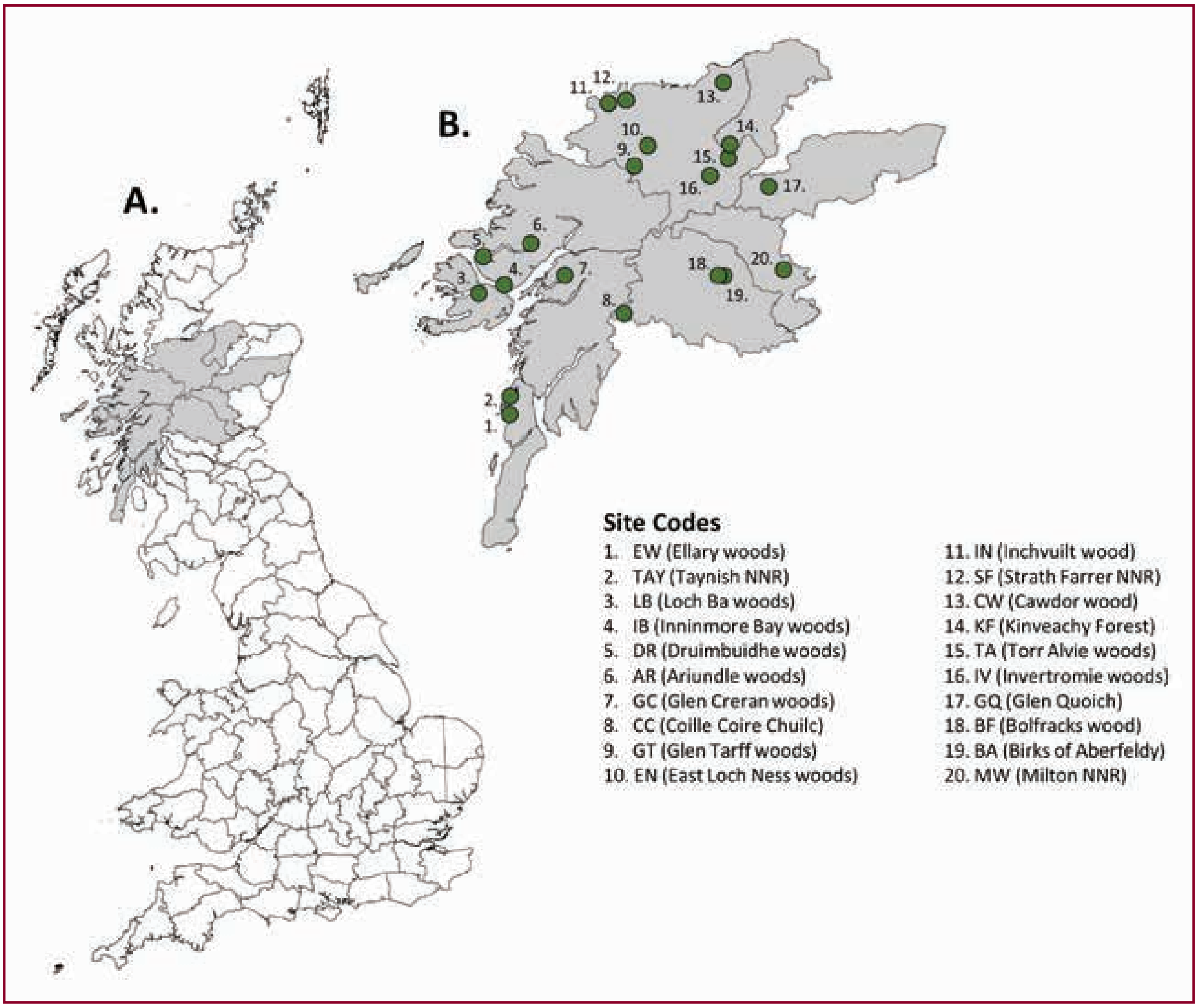


Figure 2.1. A. The regional extent of sampling in Britain, along a climatic gradient within a relatively clean-air region of Scotland, and encompassing nine botanical vice-counties: Mid Perthshire, East Perthshire, South Aberdeenshire, Moray, East Inverness, West Inverness, Argyllshire, Kintyre, and Mid Edubes, and *Figure 2.1. B*. Twenty sample sites were broadly distributed across the region (cf. *Table 2.1*).

Figure 2.2. Bioclimatic values for study sites, for annual precipitation (green symbols, solid line) and the mean temperature of the coldest month (blue symbols, dashed line), using Met Office interpolated data for the period 1961-2006.

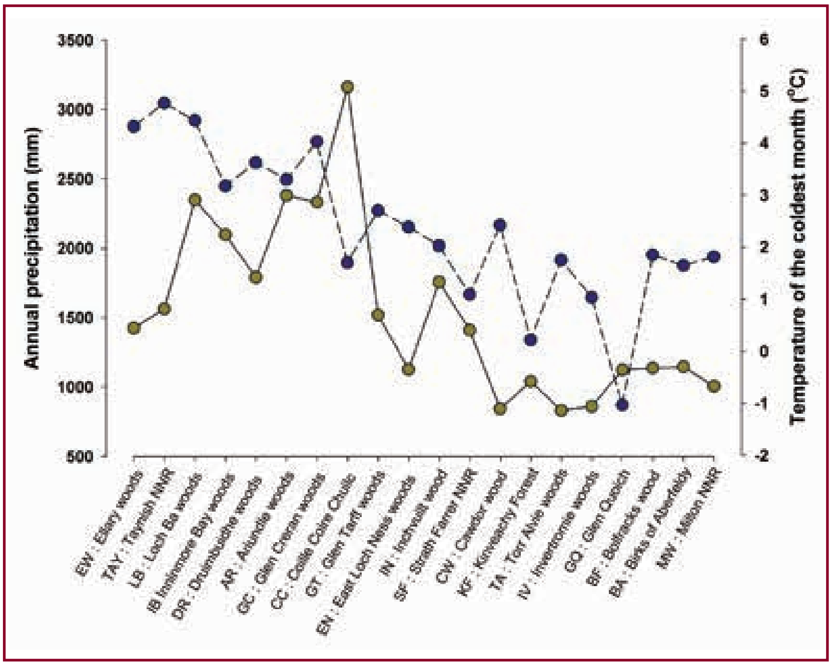


Table 2.1. Location details for woodland sample sites (cf. *Figure 2.1*), with the dominant NVC community used to target contrasting woodland types, and the size (hectares) of contiguous Class 1a ancient woodland.

Sample Site Code and Name	Grid Reference	Dominant NVC Community	Hectares
EW : Ellary woods	NR 726746	W11b : *Quercus petraea-Betula pubescens -Oxalis acetosella* woodland	47.43
TAY : Taynish NNR	NR 737848	W17b : *Quercus petraea-Betula pubescens-Dicranum majus* woodland	31.31
LB : Loch Ba woods	NM 561393	W4b : *Betula pubescens-Molinia caerulea* woodland, and W11b : *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland	56.99
IB : Inninmore Bay woods	NM 702429	W7a : *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland	41.63
DR : Druimbuidhe woods	NM 593577	W17b : *Quercus petraea-Betula pubescens-Dicranum majus* woodland	72.19
AR : Ariundle woods	NM 837641	W4b : *Betula pubescens-Molinia caerulea* woodland	60.47
GC : Glen Creran woods	NN 028490	W9a : *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* woodland	167.26
CC : Coille Coire Chuilc	NN 326275	W18b : *Pinus sylvestris-Hylocomnium splendens* woodland	55.73
GT : Glen Tarff woods	NH 378061	W9 : *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* woodland W11 : *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland	155.46
EN : East Loch Ness woods	NH 469170	W17 : *Quercus petraea-Betula pubescens-Dicranum majus* woodland	128.56
IN : Inchvuilt wood	NH 252380	W18d : *Pinus sylvestris-Hylocomnium splendens* woodland	89.03
SF : Strath Farrer NNR	NH 375402	W18d : *Pinus sylvestris-Hylocomnium splendens* woodland	89.03
CW : Cawdor wood	NH 854484	W16: *Quercus spp.-Betula* spp.*-Deschampsia flexuosa* woodland	150
KF : Kinveachy Forest	NH 885154	W18b and W18d : *Pinus sylvestris-Hylocomnium splendens* woodland	147.11
TA : Torr Alvie woods	NH 883098	W11 : *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland	85.05
IV : Invertromie woods	NH 780000	*Populus tremula-Betula* spp. woodland (no NVC community equivalent)	10.08
GQ : Glen Quoich	NO 091926	W18 : *Pinus sylvestris-Hylocomnium splendens* woodland	97.1
BF : Bolfracks wood	NN 826478	W7c : *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland	20.82
BA : Birks of Aberfeldy	NN 854478	W9a and W9b : *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* woodland	15.85
MW : Milton NNR	NO 165509	W9a : *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* woodland	38.13

on their first encounter, as consecutive points were visited: small (5-15cm dbh), intermediate-small (16-30cm dbh), intermediate-large (31-50cm dbh) and large (> 50cm dbh). Not all sites had trees of a given species in all four size categories, but the sampling aimed to capture the variation of tree species and sizes present within a given site (*Figure 2.3*: cross-reference this figure for the scientific and common names of trees).

Considered across sites, the pattern of tree sampling (*Figure 2.3*) provides a snapshot of Scotland's woodland structure and sets the context for interpreting the epiphyte communities, for example: (i) the most easily sampled trees – species which were the commonest in multiple size categories across many sites – were birches, Scots pine, sessile oak and alder; (ii) the largest trees (greatest dbh) tended to be Scots pine and pedunculate oak; (iii) the oldest trees tended to be Scots pine, elm and the oak species; and (iv) tree species diversity was contrasting, two sites had seven sampled tree species, a single site had only one sampled tree species, and the commonest number of tree species sampled per site was five.

Sampling used differently sized quadrats on trees with different sizes (*Figure 2.4*): (i) up to 10cm dbh, a 4 x 6cm quadrat divided into four subunits, (ii) 10-15cm dbh, a 6 x 9cm quadrat with six subunits, (iii) 15-

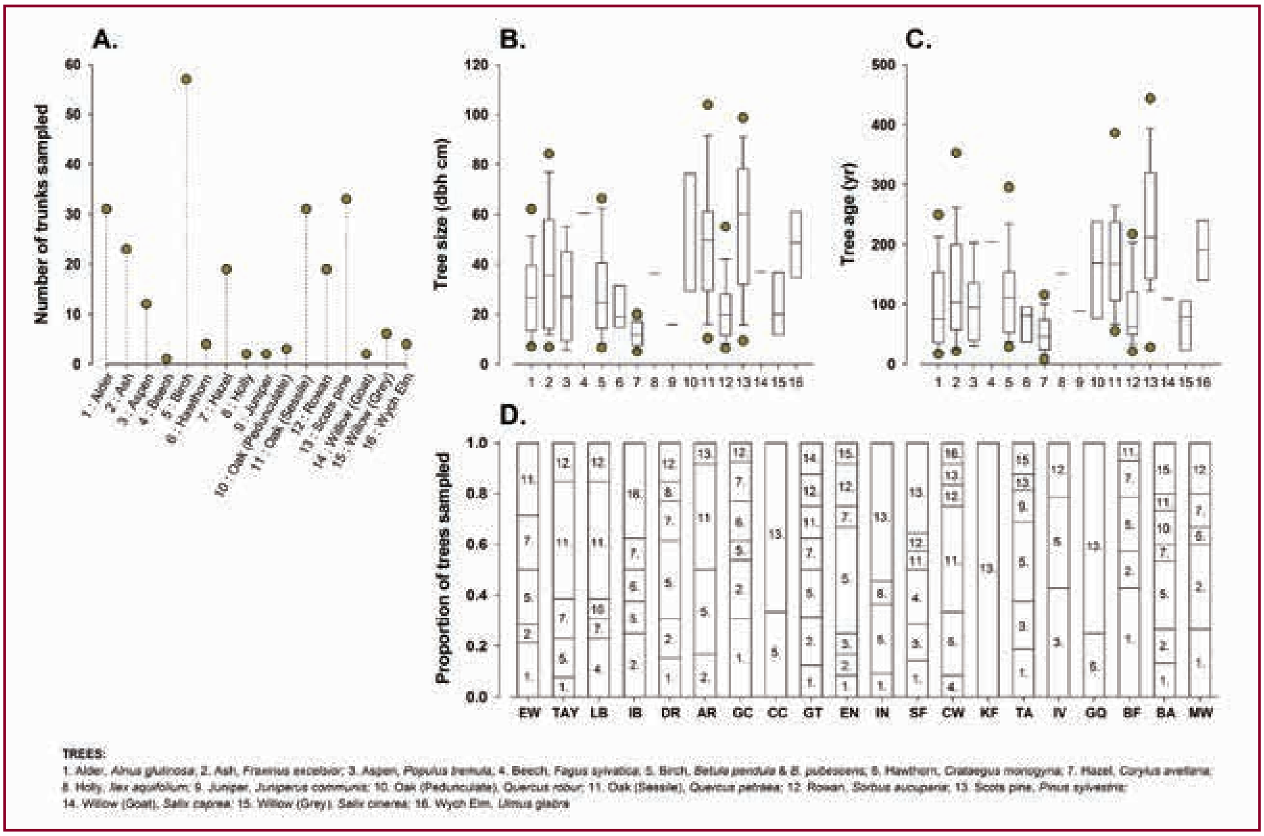


Figure 2.3. A. **The counts of different species sampled across the entire dataset of 250 trees,** *B.* **The size (dbh) of contrasting tree species, with box-plots showing the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots), and** *C.* **The age distribution of contrasting tree species (as part B).** *D.* **The proportion of different tree species sampled for each of the twenty study sites (cf.** *Figure 2.1***).**

75cm dbh, a 9 x 12cm quadrat with 9 subunits. On each tree, four quadrats were positioned at cardinal points (north, east, south and west) at random heights between 30 and 200cm. To ensure that sampling effort reflected the available habitat area, additional quadrats were added as trees became larger, e.g. five quadrats for trees 75-100cm dbh, six quadrats for trees 100-150cm dbh, and seven quadrats for trees > 150cm dbh. The additional quadrats were positioned at random heights, and at a randomised intermediate aspect (northeast, southeast, southwest, northwest).

Additionally, a single leaning tree of each species in a given size category (> 5° of lean) was sampled from a site on first encounter using two quadrats positioned at random heights onto the upper surface, and two onto the lower surface, and recording the aspect of the positioned quadrats.

Epiphyte species were recorded within each of the quadrat subunits (*Figure 2.4*), to generate a frequency of occurrence per quadrat. A bark sample was collected from each quadrat, and species that could not be identified in the field were returned to the herbarium at RBGE for identification using light microscopy (x10-x50, x100-x1000), with chemical spot tests and thin layer chromatography (lichens), and using the reference herbarium. Unless otherwise stated, nomenclature follows Smith *et al*. (2009) for lichens and Atherton *et al*. (2010) for mosses and liverworts.

Species that were identified on the sampled bark using microscopy, but which were not noted in the field, received a nominal frequency score of 0.1.

2.4 **Environmental Data**

In addition to recording quadrat height and aspect, environmental data were sampled across a wide range of habitat factors known to control epiphyte occurrence/abundance and community structure[36]. These habitat factors are described below.

Figure 2.4. **Quadrat positioned onto a tree for epiphyte community sampling.**

- **Macroclimate:** Interpolated averages for precipitation (mm) and temperature (°C) calculated at a 5km grid-scale[37] to characterise the macroclimatic setting for sampled trees (cf. *Figure 2.1*), using five variables for the period 1961-2006: (i) mean annual precipitation, (ii) mean precipitation during the summer (June, July and August), (iii) mean precipitation during the winter (December, January, February), (iv) mean annual temperature, and (v) mean temperature of the coldest month (February).

- **Landscape Matrix:** The extent of ancient woodland (hectares) surrounding a sampled tree was summarised for circular buffers with a radius of: (i) 1km, (ii) 5km, and (iii) 10km. Calculations were for 'Class 1a' ancient woodland within Scotland's Ancient Woodland Inventory[35], and therefore represented the surrounding extent of woodland stands that had a continuity of woodland cover ≥ 260 yr.

- **Topography:** Stand topography can have a strong locally-modifying influence on light availability and on the temperature and moisture regime. Potential effects were measured as: (i) altitude in metres, derived from the overlay of a sampled tree's 10-figure GPS coordinate with Ordnance Survey 1:25,000 mapping, (ii) physical exposure, measured using the Forestry Commission's ForestGALES detailed aspect method of scoring (DAMS)[38], (iii) the slope (degrees)[39] and (iv) aspect (calculated between 0-1, as deviation from north), and using standard equations[40] to estimate (v) the annual potential direct incident radiation (megajoules.cm^{-2}.yr^{-1}) and (vi) a heat load index.

- **Water Courses:** The distance to water can have a modifying influence on local climate and, in terms of distance to the sea, an additional effect on the atmospheric supply of nutrients. Distance was measured in metres for (i) distance to the sea, and up to a maximum distance of 1km for (ii) distance to and area (in hectares) of standing water, (iii) distance to a river, and (iv) distance to a stream, defined according to Ordnance Survey 1:25,000 mapping.

- **Stand Structure:** Stand structure was measured as the distance to, species identity and girth (used to calculate the basal area) of the nearest five trees to the target sampled tree. The potential influence of surrounding trees on the epiphyte community was summarised by dividing the basal area of each tree bole into the distance from the target tree (integrating the effect of tree size and distance), and summing these values for trees of the same species. This provided a multivariate response, which was reduced to two primary axes of variation using detrended correspondence analysis[41]. The analysis demonstrated a clear woodland gradient (*Figure 2.5*), from deciduous stands representative of more nutrient-rich soil conditions to the left of axis one (lower scores), characterised by the occurrence of alder as well as ash, elm and hazel for example, through an oak, rowan and holly stand structure, to the more acidic and nutrient-poor soil conditions characterised by pine, juniper and birches towards the right of axis one (higher scores). The second axis appeared to distinguish between stands with the sporadic occurrence of non-native trees such as beech and larch, with higher scores on axis two, or those characterised by native aspen clones with lower scores on axis two. Axis scores (summarising this variation in stand structure) were used as an environmental variable in explaining epiphyte communities.

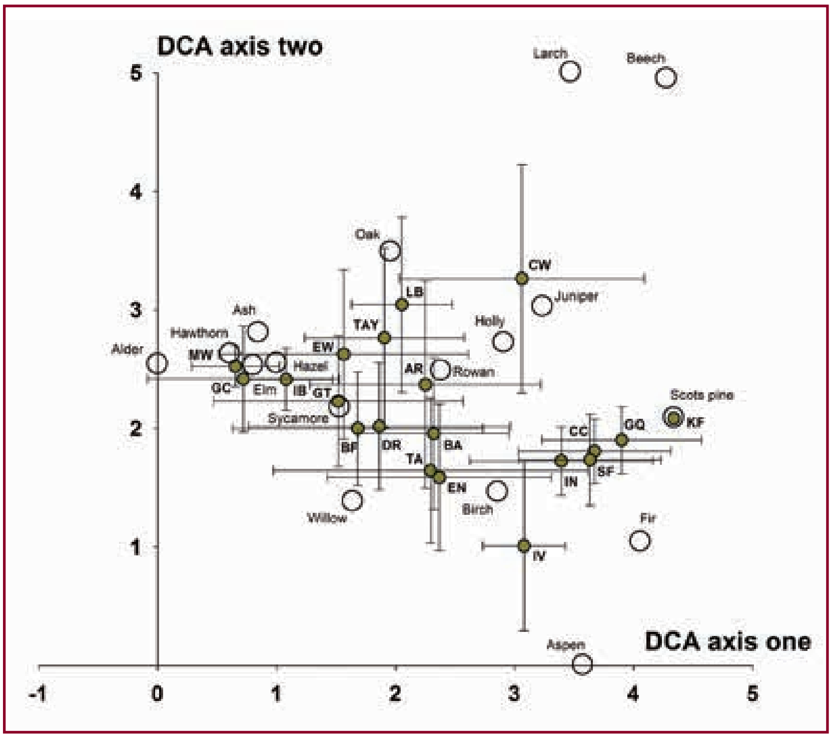


Figure 2.5. **Ordination plot to summarise graphically the stand structure surrounding target sampled trees. Coloured points (with bars) show the mean and standard deviation among the target sample trees (those sampled for epiphytes) from each site, and open circles show the averaged positions for the trees sampled as part of the surrounding woodland structure. Trees sampled for epiphytes from sites such as Milton NNR (MW), Glen Creran woods (GC) and Inninmore Bay woods (IB), tending to the left of axis one (low scores), occurred in deciduous stands (e.g. with ash and elm), while those from Kinveachy Forest (KF), Glen Quoich (GQ) and Coille Coire Chuilc (CC), tending to the right of axis one (high scores), occurred in coniferous pinewood stands (e.g. with pine and juniper). Along axis two, Invertromie woods (IV) included aspen stands, and Cawdor wood (CW) included an effect of policy plantings with non-native trees occurring alongside the target tree sampled for epiphytes.**

- **Canopy Cover:** The canopy structure was measured at a local scale as the percent canopy openness estimated using a spherical densiometer[42].

- **Soil Chemistry:** The soil pH and conductivity (µS/cm) was measured at the A horizon[43]. In each case, values were averaged for four measurements taken around each target tree at cardinal points (at a distance of c. 3 m from the base of the tree).

- **Tree Metrics:** Tree size was measured as the girth (converted to dbh) at 1.3 metres, and tree age was based on ring-counts with standard dendrochronology applied to all sampled trees, and using a Pressler-type increment borer to extract a tree core[44].

- **Microclimate and Local Light Regime:** In addition to quadrat aspect (calculated between 0-1, as deviation from north) and height (cm), the quadrat microhabitat was quantified as angle of lean, as the difference from 90° (vertical).

- **Bark Physical-Chemical Properties:** Within the area of a sampled quadrat, bark structure was quantified as the furrow depth and using an index of roughness[45], with bark chemistry calculated for a bark sample as pH and conductivity (µS/cm)[46], and with the density for a bark sample as dry weight in grams per volume (ml), and the bark water capacity in grams: (wet weight-dry weight)/dry weight[47].

Woodland Habitat for Epiphytes

3.1 Multivariate Environmental Space

Differences among the sampled epiphyte communities were explained through a comparison with a wide range of environmental variables (see Chapter 2). It is important when attempting to explain epiphyte communities in this way, to acknowledge that environmental variables are not all independent of one another.

At a landscape-scale for example, there may be a relationship between the amount of ancient woodland surrounding a site, and the climatic setting, with this correlation emerging because of differences in landscape history compared between western oceanic Scotland (with smaller more fragmented woodlands in steeper sided valleys), and north-eastern Scotland (relatively more continental, and with more extensive woodland in broader valleys). At a smaller-scale, there may be a relationship between a tree species and its size or age, and microhabitat features such as bark furrow depth. In some cases the correlations between variables of interest may be ‘accidental’ (climate and woodland history); in other cases there may be a functional dependency between variables (tree species, size/age and bark structure). Thus, the individual variables themselves, and the way they correlate with one another, define the ‘environmental space’ that is available to epiphyte species, and that shape community structure. Chapter 3 explores some of the patterns and processes which underlie this complex environmental setting.

3.2 Environmental Covariance

Strong correlations among environmental variables present a problem in understanding the drivers of community structure. For example, a statistical model to explain variability in the distribution, or ‘response’ of a community, might recognise annual precipitation as the most important variable. However, correlated variables are redundant in that case with precipitation (such as altitude or temperature), and will not contribute additional statistical power in helping to explain the community response. Therefore these will not appear to be important when generating an optimum model, i.e. in achieving the simplest model that explains sufficient variability in the community response. This is problematic, because in this example precipitation captures the potential sensitivity of an epiphyte community to altitude and temperature also, and the statistical model may be unstable; that is, if the data were sampled in a slightly different way, then temperature may have been selected over precipitation and the injudicious ecologist may jump to a different conclusion.

Carefully structured sampling can be used to break correlations, say between precipitation and temperature, and therefore separate out the relative importance of each factor by ensuring that they are ‘orthogonal’ (independent of one another, and uncorrelated). However, with many potential explanatory variables in an exploratory field setting (as in this study), orthogonal sampling becomes unrealistic. Instead, understanding the correlations among variables can be viewed as an important step in helping to visualise the complex environmental setting that is ‘experienced’ by epiphyte communities, while acknowledging that the relative importance of correlated variables in driving epiphyte community structure cannot be precisely determined.

3.3 Composite Environmental Gradients

Using ordination, it is possible to reduce the multiple correlations among continuous environmental variables to a smaller number of non-correlated axes that describe ‘composite’ environmental gradients[48]. These axes (referred to statistically as ‘principal components’) can then be used to represent the major environmental trends to which epiphyte communities are exposed.

For the analysis in this report, three ordination axes appeared to be particularly important in summarising inter-correlations among the measured environmental variables. The axes are summarised in *Table 3.1*, along with correlation coefficients which relate them back to the individual environmental variables. A correlation coefficient of 0.35 was used as a threshold to infer that a single environmental variable was appropriately considered alongside its correlated variables, as part of a composite gradient (*Table 3.1; Figure 3.1*).

Table 3.1. Statistically significant correlation coefficients (n.s. = non-significant, for 981 df), for the comparison of measured environmental variables with ordination axis scores (for the first three axes). Coefficients > 0.5 and > 0.35 are strongly and weakly shaded, respectively. Variables which do not correlate with the axis scores and which are therefore considered as individual effects, not as part of a composite gradient, are highlighted in bold.

Environmental Variable	Correlation with Principal Components (≈ Composite Gradients)		
	Gradient 1	Gradient 2	Gradient 3
Site-Scale			
Annual precip.	-0.743	0.462	-0.152
Summer precip.	-0.819	0.419	n.s.
Winter precip.	-0.676	0.466	0.195
Mean annual temp.	-0.768	-0.277	n.s.
Temp. coldest month	-0.852	-0.209	n.s.
Ancient wood – 1km	-0.357	n.s.	0.186
Ancient wood – 5km	0.472	-0.222	n.s.
Ancient wood – 10km	0.415	n.s.	-0.323
Stand-Scale			
Altitude	0.688	0.243	n.s.
Exposure (DAMS)	-0.418	0.394	-0.221
Slope	-0.244	-0.095	-0.389
Aspect	-0.363	0.22	0.33
Direct radiation	-0.231	0.176	0.567
Heat load	-0.097	0.078	0.628
Dist. sea	0.824	-0.074	n.s.
Dist. standing water	0.128	0.273	0.115
Area standing water	n.s.	-0.219	-0.337
Dist. river	-0.308	n.s.	-0.155
Dist. stream	0.128	0.186	-0.153
Stand structure DCA 1	0.439	0.511	-0.311
Stand structure DCA2	-0.47	n.s.	0.384
Canopy cover	0.247	0.312	-0.187
Tree-Scale			
Tree girth	0.182	0.604	0.422
Tree age	0.163	0.691	0.309
Soil pH	-0.113	-0.547	0.243
Soil conductivity	0.066	0.437	-0.283
Microhabitat-Scale			
Aspect	n.s.	n.s.	n.s.
Height	0.07	-0.11	n.s.
Bole lean	n.s.	n.s.	n.s.
Furrow depth	0.345	0.617	0.331
Rugosity	-0.232	-0.545	-0.338
Bark pH	0.123	-0.451	0.49
Bark conductivity	-0.118	0.435	-0.471
Bark water capacity	n.s.	-0.153	0.238
Bark density	n.s.	n.s.	n.s.

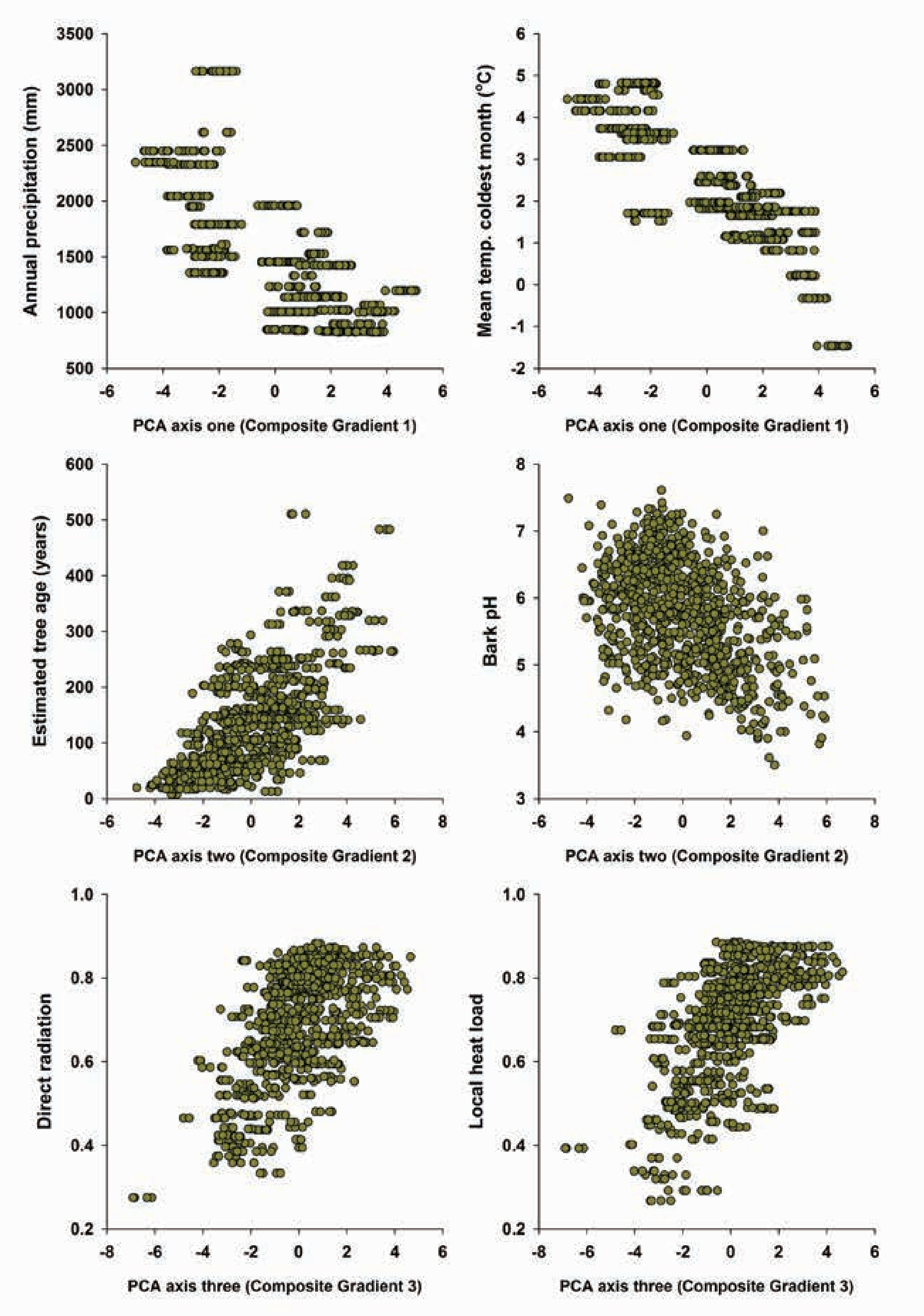


Figure 3.1. Examples of the correlation between measured environmental variables, and the ordination axes that capture summary trends among covarying environmental factors (Composite Gradients). For correlation coefficients refer to *Table 3.1.*

The composite environmental gradients (ordination axes) can be summarised as follows:

- **Composite Gradient 1:** Captures *major macroclimatic differences* between oceanic western and relatively more continental north-eastern Scotland. This climatic difference is related to the fact that western woodland sites tended to be at a lower altitude and therefore milder, while eastern woodlands were at a higher altitude with cooler minimum temperatures, e.g. in the well-wooded upper valleys of Strathspey and Deeside. Western sites were also closer to the sea, more exposed and of different aspect, with these abiotic differences reflected by trends in stand composition, from the north-eastern pine, birch and juniper woods, through to deciduous western oak woodlands characterised by the presence of ash and elm (cf. *Figure 2.5*). A further difference was in terms of the extent of ancient woodland in the landscape; at larger scales (5km and 10km buffer zones) the amount of surrounding ancient woodland was greater for the north-eastern sites, though it was locally more extensive for western sites (at a 1km buffer zone).

- **Composite Gradient 2**: Captures differences in the *tree-scale environment*. For example, tree chemistry (pH and conductivity) and bark structure (furrow depth and roughness), were broadly related to tree size and age, as well as to local soil factors (pH and conductivity). These local factors were related to the climate in terms of rainfall and physical exposure, as well as stand structure which transitioned from a broadleaf through to mixed or coniferous stands.

- **Composite Gradient 3:** Captures *differences in stand topography*, in terms of light availability and local climate (direct radiation and heat load). These topographic effects (including slope) were also related to stand structure, and to tree-scale variables of size and bark chemistry (pH and conductivity).

Tree species identity is an important factor in explaining epiphyte community structure and can affect many of the measured environmental variables such as size, age, bark chemistry, furrow depth, etc. The tree species sampled from the twenty woodland sites were significantly structured along all three ordination axes (*Figure 3.2*), and form a part of each Composite Gradient.

There were ten measured environmental variables which showed weaker inter-correlations and were not strongly related to the three ordination axes, i.e. with a correlation coefficient < 0.35 (*Table 3.1*). These can then be treated as individual effects, rather than considering them as part of a composite gradient.

3.4 The Dynamics of Tree-Scale Microhabitat

Composite Gradient 2 captured inter-correlations for the microhabitat pertaining to an individual tree. It includes variables that are known to be extremely important in determining epiphyte community structure[36], such as tree size and age, bark chemistry and small-scale physical properties such as furrow depth.

The functional relationship between several of these variables was explored in more detail.

3.4.1 Bark Chemistry (pH)

Bark pH is notoriously difficult to compare among studies, and absolute pH values should be treated as approximate, though relative values within this study can be considered reliable.

Bark pH was negatively correlated with bark conductivity (*Figure 3.3*), reflecting in general the low nutrient status of the sampled tree bark. Decreasing conductivity values are caused by a declining concentration of hydrogen ions at higher pH, without any subsequent increase in conductivity (relatively high proportional values of base saturation) which might be explained by the availability of nutrient cations (e.g. Ca^{2+}, Mg^{2+}).

In general, there was significant variability among the individuals of a given tree species in terms of bark pH (*Figure 3.4*); consequently, what might be considered a typical 'acid-barked' tree such as birch can in reality demonstrate a surprising range of pH values, though this is consistent with careful field observation (*Figure 3.5*). Birch was well sampled (data from 228 quadrats) and the variable pH measurements for

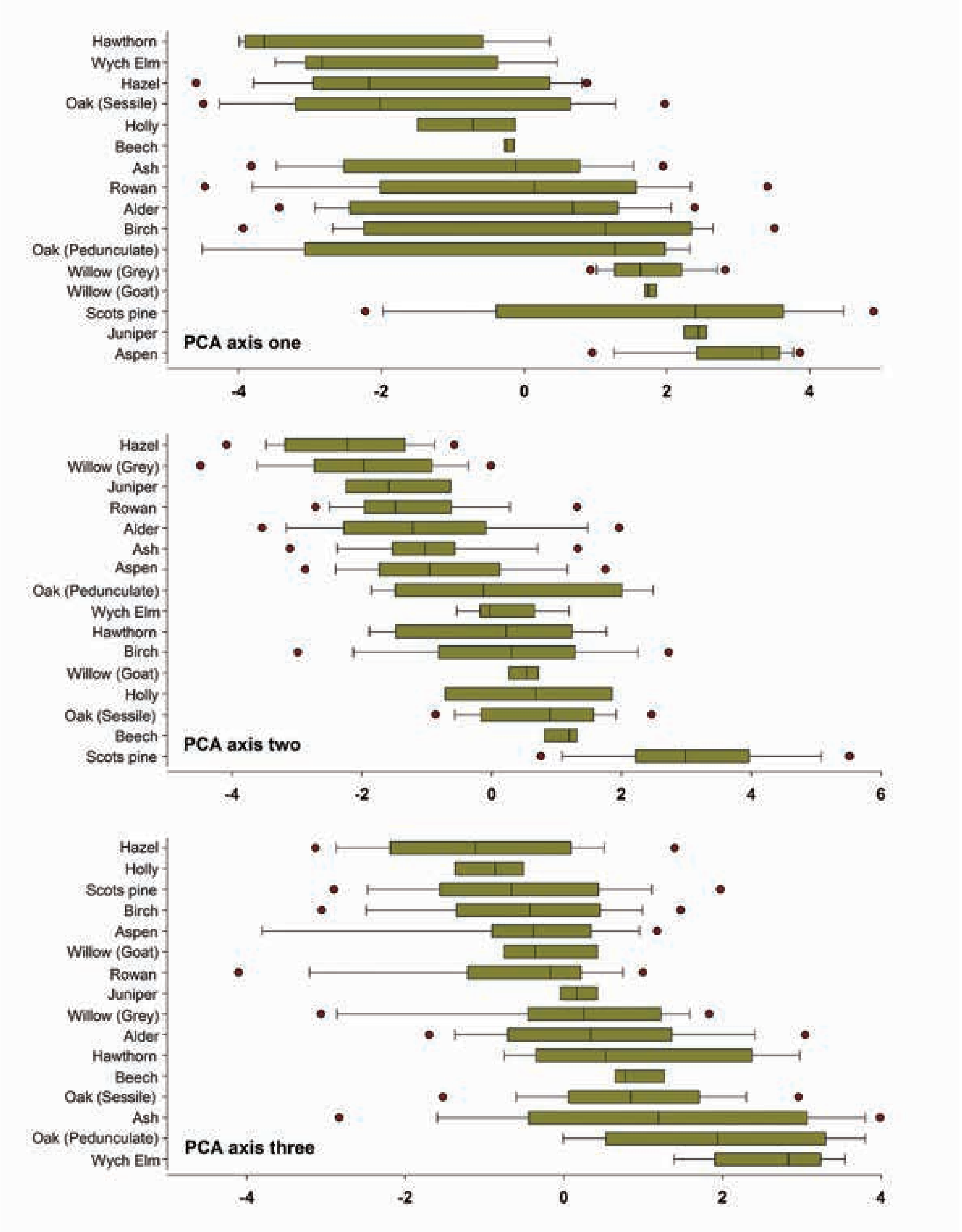


Figure 3.2. **The relationship between tree species sampled from woodland sites, and the ordination axis scores representing composite gradients (cf. *Table 3.1*). Box-plots show the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots). Tested using a Kruskall-Wallis test (df = 15), tree species occupied significantly different positions along Composite Gradient 1 (χ^2 = 312.3, $P < 0.00001$), Composite Gradient 2 (χ^2 = 508.3, $P < 0.00001$) and Composite Gradient 3 (χ^2 = 234.57, $P < 0.00001$).**

this species are likely to be representative; in contrast, juniper was less well sampled (data from only 8 quadrats), and the pH values observed for this and other less well represented species such as beech or holly (cf. *Figure 2.3*) will not capture the full range of pH microhabitats associated with these trees.

When tested statistically[50] (*Figure 3.6*), bark pH (and conductivity) was found to be influenced by a range of factors[51]: (i) tree species and tree size, (ii) climate measured as rainfall, (iii) soil chemistry, and (iv)

Figure 3.3. **The negative correlation between bark pH and bark conductivity (r = -0.956, P < 0.00001 with 1011 df).**

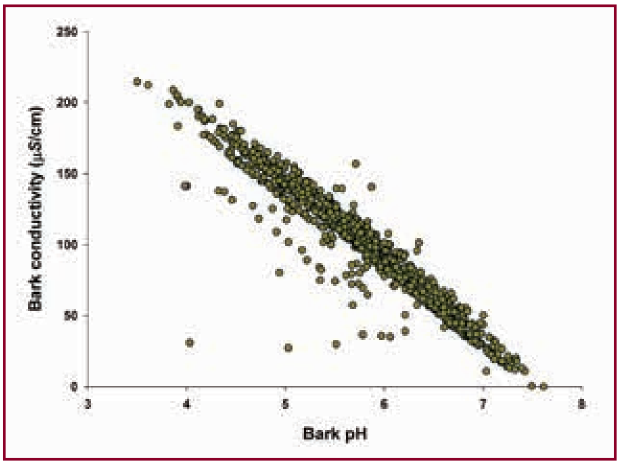
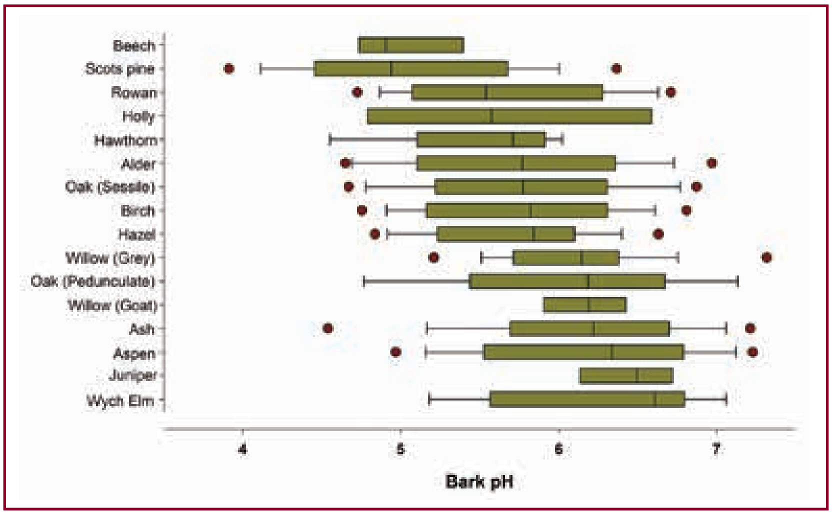


Figure 3.4. **The range of pH values associated with the different sampled trees. Box-plots show the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots). Tested using a Kruskall-Wallis test (df = 15), tree species had significantly different bark pH values (χ^2 = 160.96, P < 0.00001). Tree species with few samples do not have whiskers or dots.**



topographic effects that are captured by the related variables of direct radiation, physical exposure (DAMS), and slope. The higher than expected variability in bark pH for a given tree is therefore attributable to an interaction between tree species identity, and the multiple developmental and environmental influences that determine bark chemistry.

For example: (i) Scots pine trees in shaded environmental settings had the lowest bark pH values overall, (ii) pH values tended to be lower in leached, high rainfall environments, but (iii) within a high-rainfall environment, bark pH was higher for trees associated with less acidic soils in woodland stands that combined locally flat terrain with a sheltered and more shaded position, especially for ash, elm and willows, while (iv) in a low rainfall environment, bark pH tended to be higher for larger trees on less acidic and more nutrient-rich soils.

The key message is that bark pH shows important trends related to tree species, but natural variability is high and subject to interaction with a tree's environmental setting.

3.4.2 **Furrow Depth and Bark Roughness**

Furrow depth was correlated with the index of bark roughness (r = -0.487, P < 0.00001 with 1011 df) and these measures of bark texture were examined with respect to tree size, measured as the girth (*Figure 3.7*).

There is a difference between persistently smooth-barked trees such as hazel and rowan, and trees which have a stronger developmental relationship between tree girth and average bark roughness (furrow depth). However, for all the trees examined, there can be significant variation within a single individual stem in terms of furrow depth for the lower tree bole. Likewise, there is variation among tree species, with birches, oaks and Scots pine tending to have the highest values for bark roughness, and with alder, ash and aspen having smooth to moderately rough bark.

Figure 3.5. The vividly orange and nutrient demanding 'calcicole' lichen *Xanthoria parietina*[49] on a birch tree in Strathspey; even in a 'natural' and unpolluted environment localised effects such as wounding create exceptions to the general notion that birches have acidic and nutrient-poor bark.

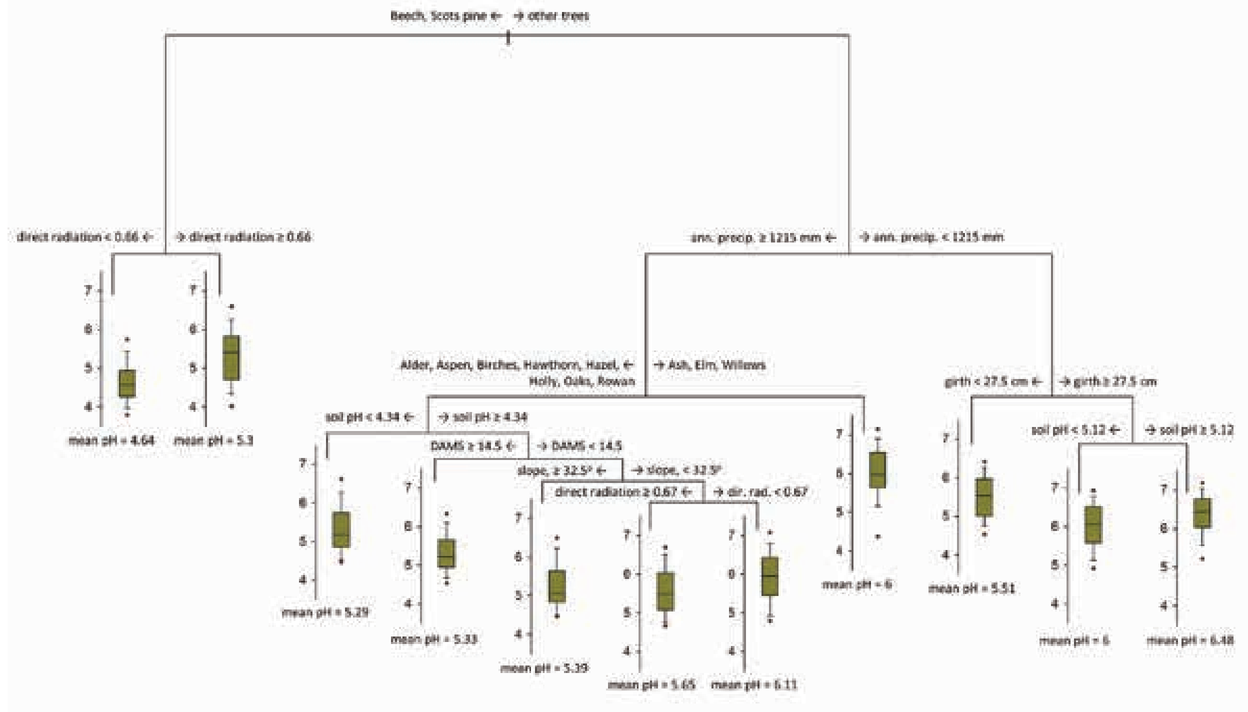


Figure 3.6. A regression tree explaining variability in bark pH. Each split in the tree can be followed into a contrasting environmental setting, and the terminal nodes represent the grouped pH values explained by the environment. For each terminal node, the mean bark pH is provided, along with box-plots to show the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots).

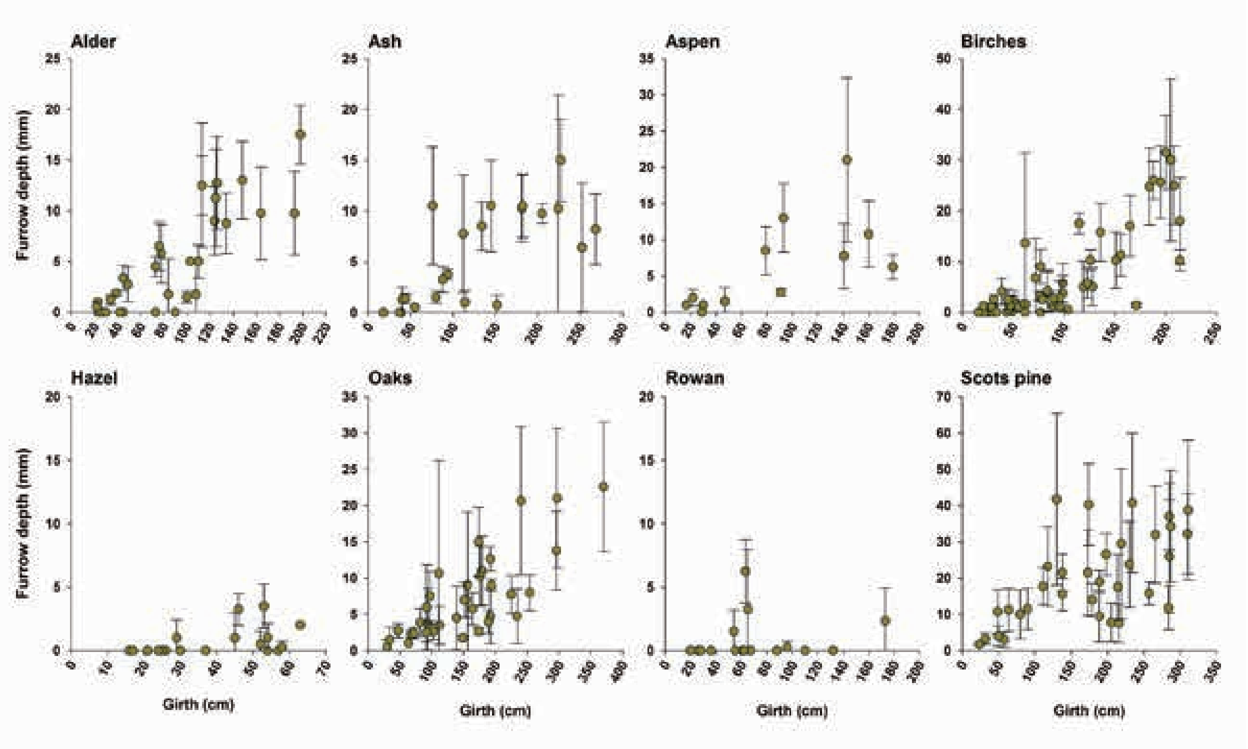


Figure 3.7. **The relationship between tree girth (at 1.3 metres) and bark roughness (furrow depth) for tree species represented by ten or more sampled individuals. Values for furrow depth are averaged across quadrats for an individual tree, with error bars showing the standard deviation. Note the different axis scales for contrasting tree species.**

3.4.3 Tree Age and Tree Girth

The relationship between tree girth (size) and age is of significant interest to epiphyte ecologists. The age-girth relationship was examined with tree species as an explanatory factor, and alongside the potential effects of climate (annual precipitation and mean temperature of the coldest month), direct radiation and heat load index, and soil pH, as proxies for growing condition. Tested statistically,[52] an optimum model identified a strong linear relationship between girth and tree age, with macroclimatic factors also significant in explaining growth (*Table 3.2*). Tree species was not a significant effect, suggesting broadly similar growth rates among the sampled tree species, and with no significant effect of topography (direct radiation or heat load), or soil effects.

Based on the strong relationship between tree girth and age, equations describing the linear trend of increasing girth can be used in a cautious assessment for the age of a tree (*Figure 3.8*).

Fixed Effect	Estimate	*r*	*P*
Intercept	25.868	1.844	0.0665
Tree age (yr)	0.683	20.818	< 0.0001
Annual precipitation (mm)	-0.017	-2.028	0.0437
Temperature coldest month (°C)	7.063	2.052	0.0413

Table 3.2. **Diagnostics for an optimised linear mixed effects model to explain tree girth, based on the three significant fixed effects (227 df) and with standard deviation for the random effect (study site identity) = 17.79. Effects dropped sequentially from the full model included:**
direct radiation (likelihood ratio = 0.436, *P* = 0.5093), heat load index (likelihood ratio = 1.055, *P* = 0.304),
soil pH (likelihood ratio = 2.739, *P* = 0.098) and
tree species (likelihood ratio = 7.022, *P* = 0.056).

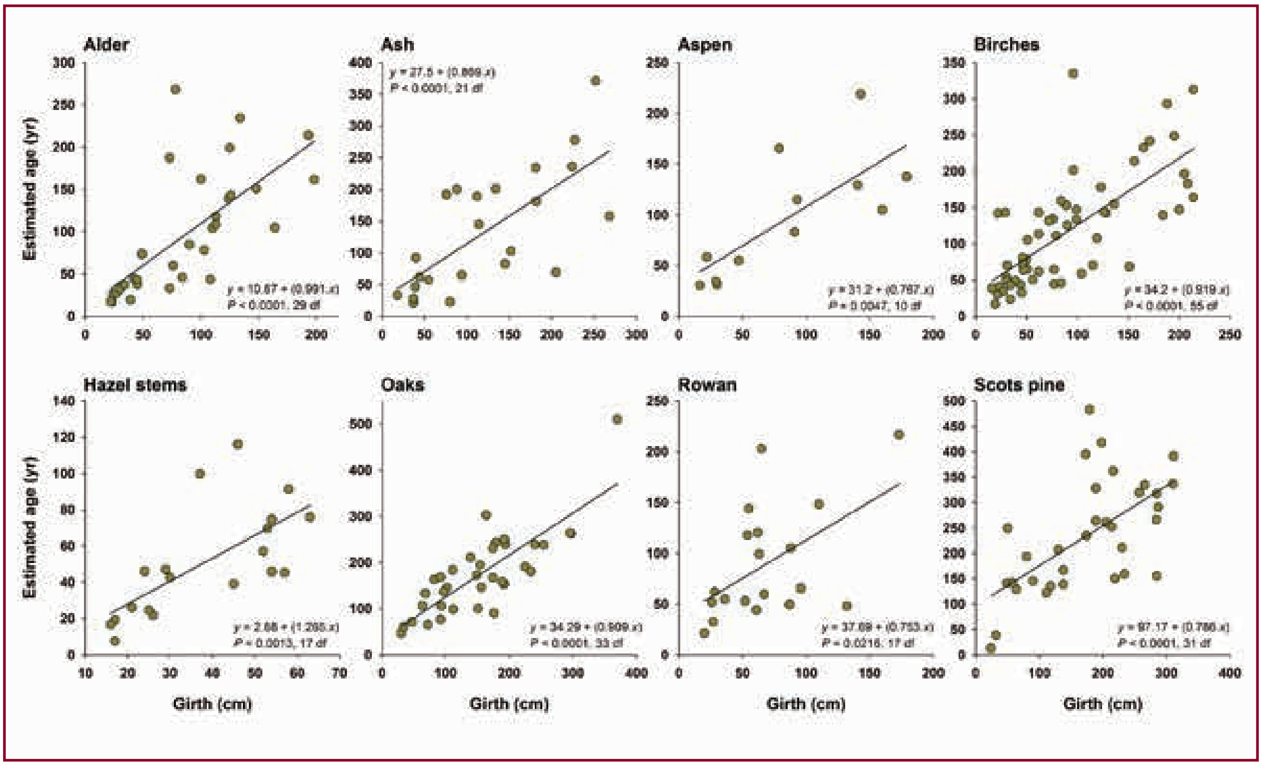


Figure 3.8. **Relationship between tree girth and estimated age for the individual tree species that were represented by ten or more samples. Equations can be cautiously used as a guide to the age of a given tree, by substituting girth in centimetres for the value *x* in the regression model (and by avoiding extrapolation, and predicting within the bounds of the sampled trees). Note the different axis scales for contrasting trees.**

3.5 The Woodland Habitat for Epiphytes – A Summary

Chapter 3 has aimed to provide an assessment of interrelated habitat factors that are useful for the interpretation of epiphyte communities. It offers a cautious summary of conditions experienced by epiphytes in Scotland's natural and cultural landscape at the beginning of the 21st Century. Accepting that there will be many exceptions to the generalisations provided here, the major trends are summarised graphically (*Figure 3.9*).

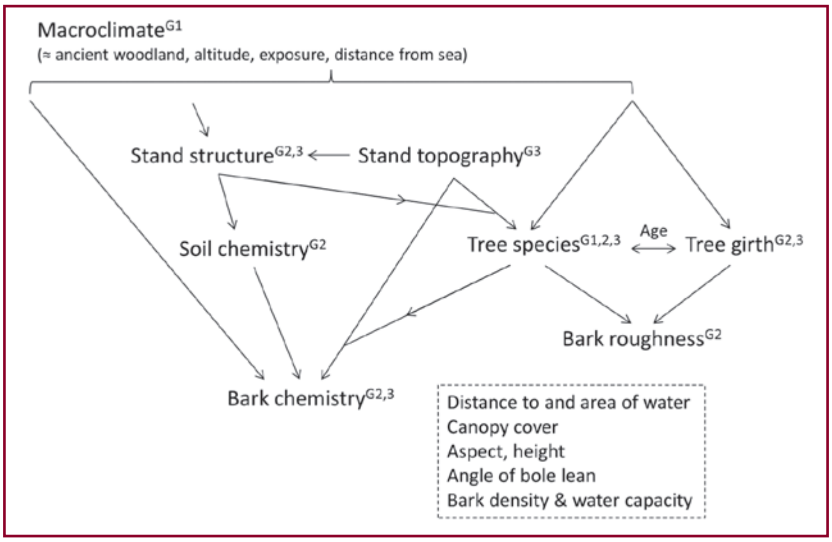


Figure 3.9. **The environmental variables used to explain epiphyte community composition and the inferred relationships between them. The variables are coded according to their correlations with Composite Gradient 1 (G1), Composite Gradient 2 (G2) and Composite Gradient 3 (G3), including those which appear to be relevant across multiple gradients. Environmental variables which appeared independent of the other measured effects are shown in the hatched box.**

Epiphyte Community Classification

4.1 **Community Analysis**

The community analysis described here in Chapter 4 is based on 1013 quadrat samples, from 250 trees across the twenty study sites. A total of 376 epiphytic taxa were recorded, including 302 lichens, 71 bryophytes and 3 vascular plants; this takes account of a small number of individual species which had to be grouped because immature specimens proved impossible to separate, e.g. *Cladonia macilenta* and *C. polydactyla*. The commonest five species encountered were *Hypnum andoi* (28% of samples), *Hypogymnia physodes* (27.5% of samples), *Frullania tamarisci* (23% of samples), *Platismatia glauca* (19.5% of samples) and *Parmelia saxatilis* agg. (17% of samples). Most species were rare, with 19% of species represented by a single record only (*Figure 4.1*).

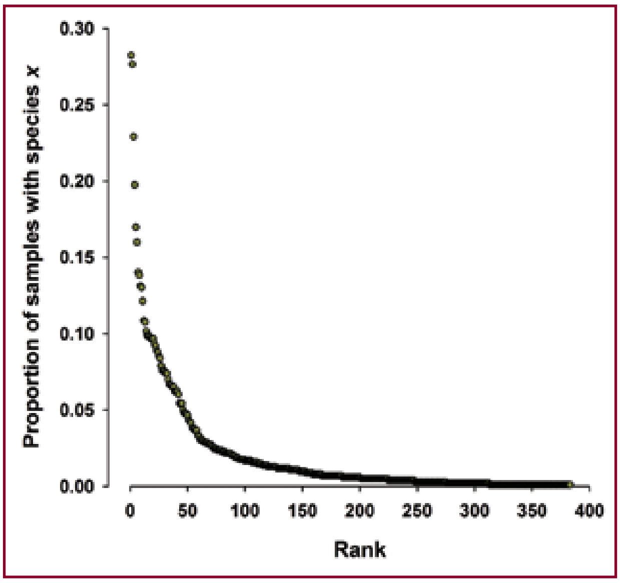


Figure 4.1. **The rank-abundance curve for 376 sampled epiphyte species.**

The analysis clustered quadrats into community types based on a degree of similarity in community composition and identified indicator species for these types[53]. Each of the communities was then compared to eleven explanatory environmental variables (see Chapter 3): Composite Gradient 1, Gradient 2 and Gradient 3, distance to water (metres), canopy openness (percent), height and aspect on the bole (cm), angle of lean (± degrees away from 90º), bark water capacity (g.dry wt) and density (g.ml), and tree species identity. A nonparametric multiplicative regression model (NPMR)[54] was used to explain the likelihood of occurrence for a given epiphyte community type, based on the environmental variables. Detailed summaries for each of the communities and their analytical results are presented in Chapter 5, with a full list of species associations for each community in Appendix 1.

4.2 **Community Types**

Fifteen epiphyte community types were recognised (referred to as Types A-O), and characterised by a total of 82 indicator species (with one to thirteen indicator species per type). It is important to be aware that these are small-scale community types sampled for quadrats, several of which may co-occur and intergrade on a single tree as an assemblage of multiple communities. The species composition of the fifteen community types was cross-compared to form seven higher-level groups (Groups I-VII). The average degree of similarity between the communities was plotted graphically (*Figure 4.2*)[55], along with the environmental controls inferred from the detailed community analyses presented in Chapter 5. The relationships of community similarities and environmental pathways were cross-referenced with previous community classifications relevant to British epiphytic diversity by James *et al*. (1977) and which have been widely adopted (Appendix 2).

This Section forms the principal result of the study (*Figure 4.2*), showing how epiphyte community types are interrelated.

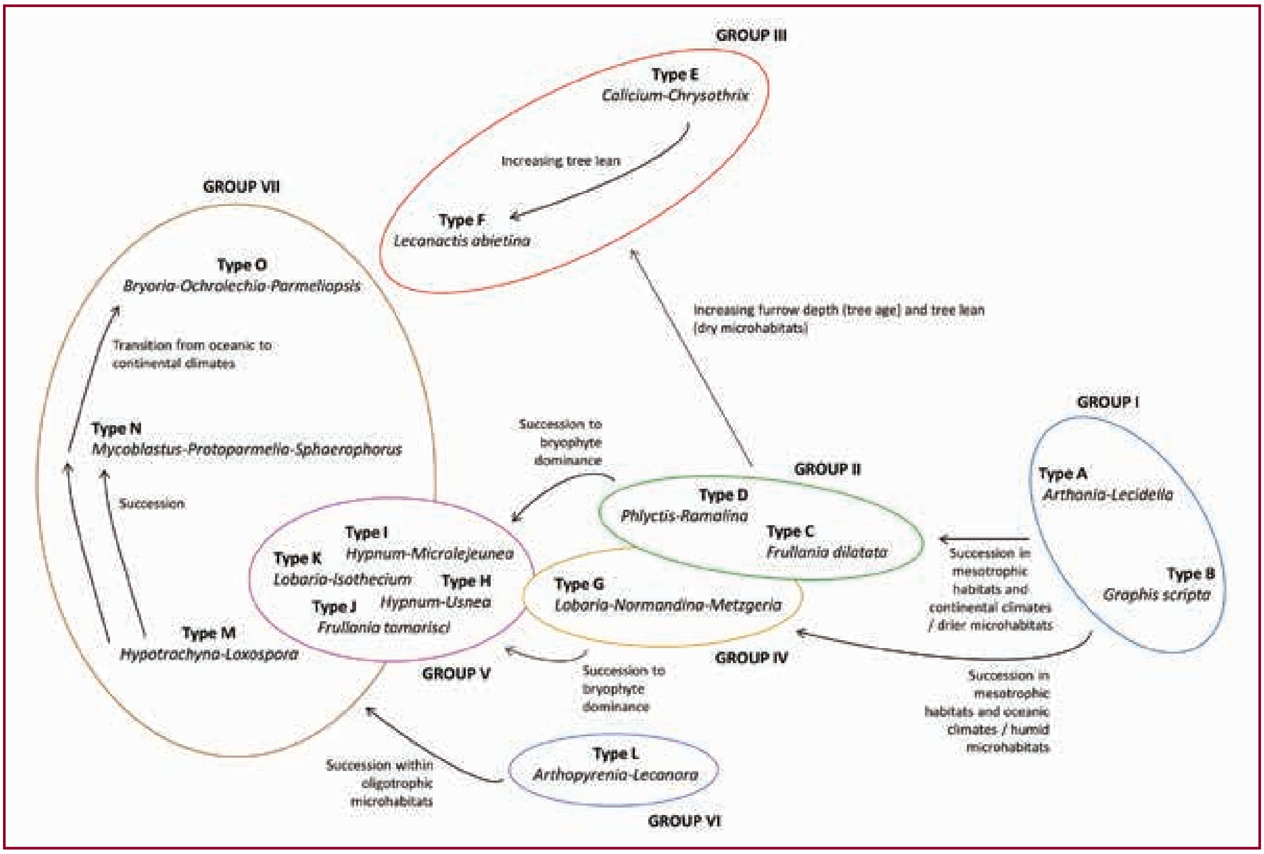


Figure 4.2. **The relative positions of fifteen epiphyte community types (A-O) plotted into ordination space. The distances between the community types in the graph represents the degree to which they share similar epiphyte species. Groups (I-VII) are therefore based on similarities in species composition as well as the environmental relationships which explained the distribution of community types.**

Group I

Early Successional (Pioneer) Communities of Smooth-Barked Mesotrophic Microhabitats

Community Type A: *Arthonia radiata-Lecidella elaeochroma* Community

Indicators: ***Arthonia radiata***, *Buellia disciformis, Lecanora chlarotera,* ***Lecidella elaeochroma***, *Pertusaria leioplaca*

Community Type B: *Graphis scripta* Community

Indicators: *Arthonia didyma,* ***Graphis scripta***, *Pertusaria hymenea, Pyrenula occidentalis*

The two communities forming an alliance in Group I were associated with younger and smooth-barked broadleaf trees with higher bark pH, though did not include the very earliest pioneer species of the smallest trees and twigs, e.g. non-lichenised *Arthopyrenia* spp., *Tomasellia* etc. The Type B *Graphis scripta* Community is narrowly defined in the analysis; in a broad sense it intergrades with Community Type A, but also for example with Community Type G (*Lobaria virens-Normandina pulchella-Metzgeria furcata* Community). Adopting the narrow definition here, the Type B Community appears highly restricted and sensitive to macroclimatic setting, such that it is marginally less common in the climatically outlying driest sites (where it intergrades with Type A) or wettest sampled habitats (where it intergrades with Type G). In contrast, the Type A *Arthonia radiata-Lecidella elaeochroma* Community is broadly distributed, though with a microhabitat preference for moderately shaded and drier local environments, e.g. away from the higher humidity associated with water courses.

Group II

Early Successional to Mature Communities in Mesotrophic Microhabitats

Community Type C: *Frullania dilatata* Community
Indicators: ***Frullania dilatata***, *Ulota bruchii/crispa*

Community Type D: *Phlyctis argena-Ramalina farinacea* Community
Indicators: *Melanelixia glabratula* agg., *Parmelia sulcata, Pertusaria amara,* ***Phlyctis argena****, Orthotrichum affine,* ***Ramalina farinacea***

The two communities forming an alliance in Group II could occur on younger broadleaf trees, though persisting (for the *Frullania dilatata* Community), and increasing (for the *Phlyctis argena-Ramalina farinacea* Community) on older and mature trees. The Type D *Phlyctis argena-Ramalina farinacea* Community is a dominant community type in mesotrophic microhabitats in relatively more continental climates, while the Type C *Frullania dilatata* Community is geographically more widespread and occurs more frequently than Type D in oceanic systems.

Group III

Mature Communities in Drier Microhabitats (Rough-Barked and/or Leaning Trees)

Community Type E: *Calicium viride-Chrysothrix candelaris* Community
Indicators: *Anisomerdium biforme, Arthonia vinosa,* ***Calicium viride****, Chaenotheca trichialis,* ***Chrysothrix candelaris****, Cliostomum griffithii, Lepraria incana*

Community Type F: *Lecanactis abietina* Community
Indicators: ***Lecanactis abietina***

The two communities forming an alliance in Group III are typical of drier microhabitats, both within deep furrows and on sheltered undersides of large leaning broadleaf trees. The Type E *Calicium viride-Chrysothrix candelaris* Community is more sensitive to macroclimate and commonest in relatively continental settings. In contrast, the Type F *Lecanactis abietina* Community is widespread geographically, but is sensitive to additional microhabitat factors including canopy openness and distance to water, and locally favours drier and more open stand conditions.

Group IV

Mature Mesotrophic Communities in Oceanic Climates (or Humid Microclimates)

Community Type G: *Lobaria virens-Normandina pulchella-Metzgeria furcata* Community
Indicators: *Frullania fragilifolia, Isothecium alopecuroides, Lepraria eburnea,* ***Lobaria virens, Metzgeria furcata, Normandina pulchella****, Opegrapha vulgata, Thelotrema lepadinum, Zygodon viridissimus*

Community Type G is the oceanic climate equivalent to Community Type D (*Phlyctis argena-Ramalina farinacea* Community), also occurring in mesotrophic broadleaf habitats. Although Community Type G may occur on relatively young trees, it is in ecological terms a later-successional element that develops from the early successional Type B (*Graphis scripta* Community) and Type C (*Frullania dilatata* Community), within the oceanic setting. Community Type G is more frequent in relatively warmer microhabitats such as sheltered south-facing wooded slopes.

Group V

Late Successional Mesotrophic Communities in Oceanic Climates (or Humid Microclimates)

Community Type H: *Hypnum cupressiforme* agg.-*Usnea flammea* Community
Indicators: ***Hypnum cupressiforme* agg.**, *Lepraria lobificans, Plagiochila punctata,* ***Usnea flammea***

Community Type I: *Hypnum andoi-Microlejeunea ulicina* Community
Indicators: *Cladonia coniocraea, Dicranum scoparium,* ***Hypnum andoi****, Lepraria rigidula,* ***Microlejeunea ulicina***

Community Type J: *Frullania tamarisci* Community
Indicators: ***Frullania tamarisci****, Harpalejeunea molleri*

Community Type K: *Lobaria pulmonaria-Isothecium myosuroides* Community
Indicators: *Hypotrachyna taylorensis,* ***Isothecium myosuroides, Lobaria pulmonaria****, Parmotrema crinitum, Parmotrema perlatum*

The alliance of four communities forming Group V is dominated by bryophytes as well as larger fruticose and foliose lichens, and is characteristic of later successional epiphyte communities in milder and/or oceanic climates. Community Type H (*Hypnum cupressiforme* agg.-*Usnea flammea* Community) and Type I (*Hypnum andoi-Microlejeunea ulicina* Community) are very similar ecologically, though with Type I possibly the more commonly occurring variant as one transitions towards drier and/or cooler habitats. It is particularly evident for Community Types J and K (*Frullania tamarisci* Community and *Lobaria pulmonaria-Isothecium myosuroides* Community), that the Group V alliance may occur in leached or slightly more oligotrophic habitats than the more mesotrophic Group IV Community Type G (*Lobaria virens-Normandina pulchella-Metzgeria furcata* Community).

The Group V community types show additional sensitivity to a range of microhabitat factors, including the angle of bole lean for Type H (*Hypnum cupressiforme* agg.-*Usnea flammea* Community) and Type I (*Hypnum andoi-Microlejeunea ulicina* Community), as well as local humidity, expressed as distance to water, for Community Type K (*Lobaria pulmonaria-Isothecium myosuroides* Community).

Group VI

Early Successional to Mature Communities in Intermediate Settings

Community Type L: *Arthopyrenia cinereopruinosa-Lecanora pulicaris* Community
Indicators: ***Arthopyrenia cinereopruinosa****, Chrysothrix flavovirens,* ***Lecanora pulicaris****, Micarea micrococca* agg., *Pertusaria pupillaris*

Community Type L is a very loosely associated grouping of crustose lichens, each of which may occur interspersed within a mosaic of more mature and competitive (foliose/bryophyte dominated) epiphyte communities. Setting aside the doubts related to its poor identity as a community, Type L has an intermediate environmental status, in the sense that it is commonest within oligotrophic woodland settings that characterise sites in the cool and wet central Highland belt, located between a warmer and more humid oceanic zone, and a cooler and drier north-eastern continental zone. However, it is not strongly restricted in terms of macroclimate, and can be geographically widespread. Locally, it occurs in drier microclimatic settings as opposed to the constant humidity of watercourses.

Group VII

Mature to Late Successional Communities in Oligotrophic Microhabitats

Community Type M: *Hypotrachyna laevigata-Loxospora elatina* Community
Indicators: *Anisomeridium ranunculosporum*, ***Hypotrachyna laevigata*, *Loxospora elatina***, *Mycoblastus caesius*, *Scapania gracilis*

Community Type N: *Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaeorophorus globosus* Community
Indicators: *Cladonia macilenta/polydactyla*, *Micarea synotheoides*, ***Mycoblastus sanguinarius***, *Ochrolechia androgyna*, *Parmelia saxatilis* agg. *Platismatia glauca*, ***Protoparmelia ochrococca*, *Sphaerophorus globosus***, *Usnea subfloridana*

Community Type O: *Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community
Indicators: ***Bryoria fuscescens***, *Hypocenomyce friesii*, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Imshaugia aleurites*, *Lecidea hypopta*, *Lecidea nylanderi*, *Lepraria jackii* agg., ***Ochrolechia microstictoides*, *Parmeliopsis hyperopta***, *Pertusaria borealis*, *Tuckermanopsis chlorophylla*, *Violella fucata (Mycoblastus fucatus)*

The alliance of three communities forming Group VII is characteristic of relatively more acid-barked and oligotrophic microhabitats. It includes the transition between Community Type M (*Hypotrachyna laevigata-Loxospora elatina*) in more oceanic climatic settings and potentially occurring on younger trees, and the later successional Community Type N (*Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaeorophorus globosus* Community) on older trees. Type N also occupies an intermediate climatic position most strongly associated geographically with the cool and wet central Highland belt. This is in contrast to the more continental Community Type O (*Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community). Of the three types, Community Type M is the most likely to occur within mesotrophic microhabitats, especially where these are shaded and moisture-retaining. The community types intergrade to varying degrees depending on the interplay of macro- and microclimatic conditions.

4.3 Expert Opinion

It is important to consider that the statistical discrimination of epiphyte communities will be affected by sampling only a sub-set of the total variability in Scotland's woodlands, creating a sampling bias. Furthermore, the analytical methods are constrained in their ability to fully capture ecological complexity. For this reason the Community Types were provided with a 'Field-Based Confidence Score' (FBCS = low, medium and high) drawing on the expert opinion of Dr Brian Coppins, who has > 40 years field experience of epiphytes in Scotland.

There may be several reasons for a lowered confidence. For example, in some cases Community Types may be recognisable, but may be considered too broad (e.g. Community Type D, *Phlyctis argena-Ramalina farinacea* Community). This may occur because the majority of sampled epiphyte species tended to be rare, and the statistical analysis could be unduly influenced by commoner species when defining community types. This situation would fail to discriminate the variability that can be recognised within a single broad category based on extensive field experience. In other cases, a disparate collection of samples may have been 'forced' by the hierarchical analysis into a weak grouping, to yield indicator species that are only loosely related within a given community type (e.g. Community Type L, *Arthopyrenia cinereopruinosa-Lecanora pulicaris* Community). In this case, there may be species which do not occur together (e.g. *Arthopyrenia cinereopruinosa* and *Chrysothrix flavovirens*), but each of which may in certain circumstances be associated to a greater or lesser extent with one of the other indicators, e.g. with *Lecanora pulicaris*, or *Pertusaria pupillaris*.

It is becoming common practice to consider a balance of statistical and expert evidence in ecological science, and referencing with expert opinion provides a useful caveat to the indiscriminate application of statistically-recognised Community Types.

4.4 Field Recording of Epiphyte Communities

Our suggestion for recording epiphyte communities recognises that mutually exclusive community types do not exist; in contrast, species will co-occur to form intergrading community patterns across a tapestry of woodland microhabitats. The epiphyte communities recognised here are statistically identified clusters of species, which form a basis for interpreting the observed variability in community structure.

The basic unit of field recording for epiphytes is a tree and its exact location, the date of sampling, and ideally the tree species and its size (e.g. girth at 1.3 metres). Species recorded from a single tree can then form the dataset for epiphyte community interpretation, or observations can be downscaled to think about contrasting parts of a tree, reflecting for example microhabitat differences in angle of lean, aspect, height on the bole, furrow depth, stem-flow patterns, wounding, etc.

The species list for the tree – or the microhabitat patch – can be used to calculate two metrics revealing information about the fifiteen epiphyte community types. This is done by extracting the significant indicator species from the total species list for the tree or microhabitat, and using these to calculate an **Indicator Strength** and **Community Contribution**. These metrics can accompany the standard reporting of all species; the additional non-indicator species can be cross-referenced against the full species listed for each epiphyte community type in Appendix 1. A theoretical worked example is provided below.

Theoretical Worked Example

Out of a total of thirty-six species, ten indicator species were recorded from a large leaning birch tree in Glen Affric. Four indicator species were for Community Type O (*Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community, n = 4), three indicator species were for Community Type N (*Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaerophorus globosus* Community, n = 3), one indicator species was for Community Type F (*Lecanactis abietina* Community, n =1) and two indicators were for Community Type E (*Calicium viride-Chrysothrix candelaris* Community, n = 2).

To calculate the **Indicator Strength** of each community type, divide the number of indicator species actually recorded for a given type, by the theoretical total number of indicator species that could be recorded for the same community type:

Community Type E (*Calicium viride-Chrysothrix candelaris* Community) = 2/7 = 0.29
Community Type F (*Lecanactis abietina* Community) = 1/1 = 1
Community Type N *Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaerophorus globosus* Community) = 3/9 = 0.33
Community Type O (*Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community) = 4/13 = 0.31

This provides an indication of the strength at which each community type is represented, for example with 33% of Community Type N indicator species present, and 29% of Type E indicator species. However, there are 100% of species for Community Type F, though this only has one significant indicator. The metric for strength is therefore accompanied by a measure of **Community Contribution**, calculated by dividing the number of indicator species recorded for each community type, by the total number of indicator species recorded:

Community Type E (*Calicium viride-Chrysothrix candelaris* Community) = 2/10 = 0.2
Community Type F (*Lecanactis abietina* Community) = 1/10 = 0.1
Community Type N (*Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaerophorus globosus* Community) = 3/10 = 0.3
Community Type O (*Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community) = 4/10 = 0.4

In this case, although Community Type F is fully represented (scoring the maximum 100% for Indicator Strength), it can be shown to contribute a minor component (10%) to the overall epiphyte assemblage, which is represented by a mix of interrelated epiphyte community types, with Community Type O and Type N together accounting for 70% of the epiphyte assemblage structure.

A field recording sheet for the epiphyte communities is provided in Appendix 3. This type of analysis can also be used as a measure which integrates the environmental heterogeneity of a woodland stand, with epiphytic diversity, as outlined in Appendix 4.

To assist in the understanding of epiphyte distributions, submit the species records for epiphyte community recording using the iRecord system (http://www.brc.ac.uk/irecord/). Once logged-in, use the ‘Record’ option to access the ‘Activity’ called ‘Scottish Epiphyte Community Survey’.

Exploratory Ecological Analysis

5.1 Type A

Arthonia radiata – Lecidella elaeochroma Community FBCS = HIGH

The 'Type A' *Arthonia-Lecidella* Community (*Figure 5.1*) is the most common pioneer community type on smooth-barked and younger broadleaf trees in mesotrophic settings (*Figure 5.2; Table 5.1*), with the allied Community Type B (*Graphis scripta* Community; see Section 5.2) seeming to be a more habitat restricted variant shared in epiphyte Group I (cf. *Figure 4.2*). The Type A Community occurs in intermediate topographic positions in terms of light and stand-scale microclimate, though may show a slight preference for partially shaded aspects rather than warmer and drier sun-exposed positions. It appears to be less frequent in microhabitats of constant high humidity, e.g. increasing with distance from water courses. Young regenerating trees in drier and gladed woodland stands represent a typical habitat (*Figure 5.3*).

Figure 5.1. **The green-tinged thallus of *Lecidella elaeochroma* (black fruits), irregular flecks of *Arthonia radiata*, and with *Lecanora chlarotera*, on smooth-barked ash.**

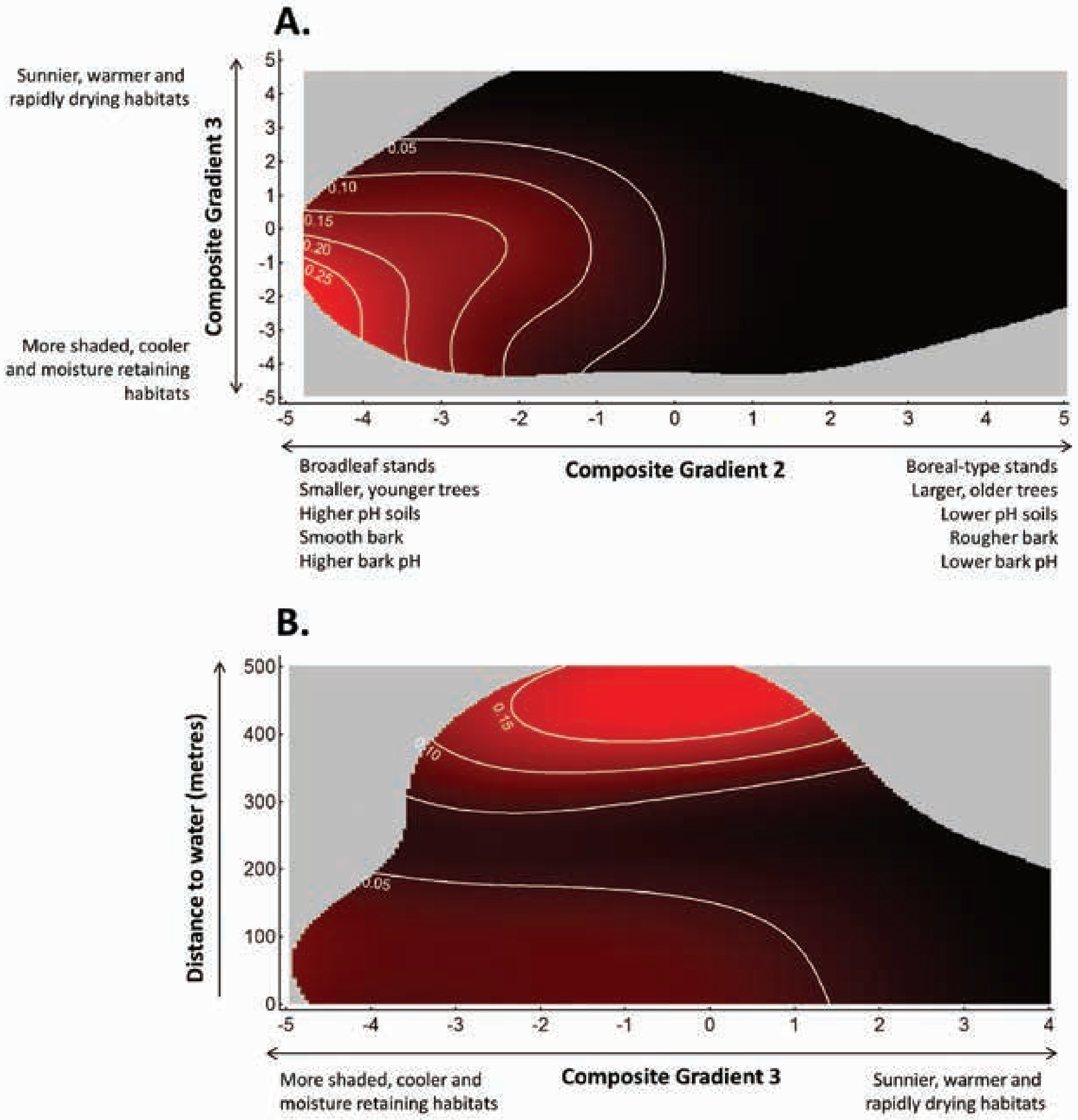


Figure 5.2. Response surfaces showing variability in the likelihood of occurrence for the Type A *Arthonia-Lecidella* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.1*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

Table 5.1. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Arthonia-Lecidella* Community in relation to the variability of Composite Gradient 2 (tree-scale environment), Composite Gradient 3 (stand topography), and distance to water (metres). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	logB	AUC	$_{MC}P$
Composite Gradient 2	1.069 (10%)	0.246	22.82	0.861	< 0.01
Composite Gradient 3	1.156 (10%)	0.124			
Distance to water (metres)	76.5 (15%)	0.075			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

Figure 5.3. **A young ash in a partially open setting represents typical habitat conditions for the *Arthonia-Lecidella* Community.**

Geographically, the Type A *Arthonia-Lecidella* Community is a common element on young trees in many broadleaved and mixed woodlands, especially in the central Highlands and eastern Scotland, and also occurs widely though less frequently at oceanic western sites (*Figure 5.4*).

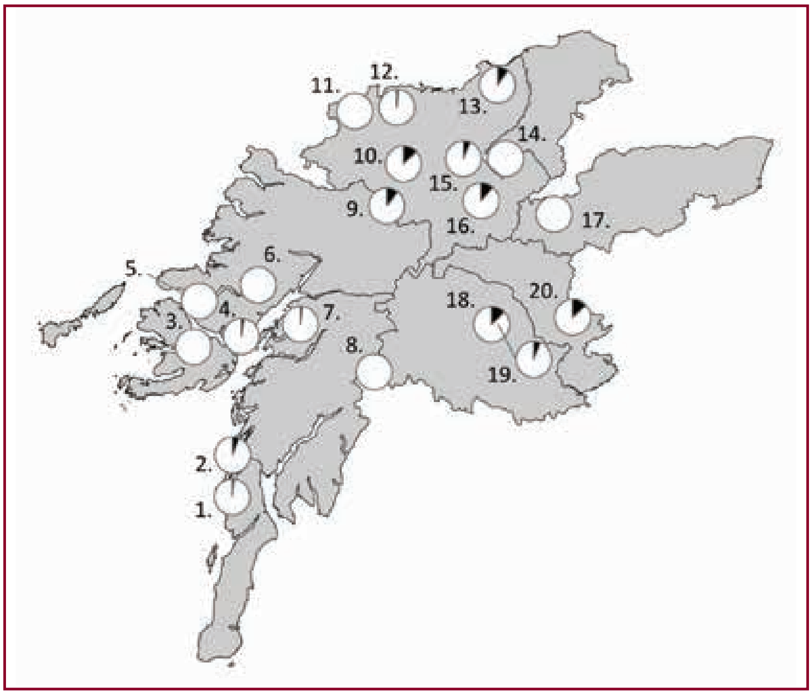


Figure 5.4. **The percent contribution (in black) of the *Arthonia-Lecidella* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods),
2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods),
5. DR (Druimbuidhe woods),
6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods),
10. EN (East Loch Ness woods),
11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood),
14. KF (Kinveachy Forest),
15. TA (Torr Alvie woods),
16. IV (Invertromie woods),
17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy),
20. MW (Milton NNR).

The *Arthonia-Lecidella* Community has five diagnostic species (*Table 5.2*). None of the species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. None of the species are strongly associated with woodlands that have ecological continuity. Bioclimatic modelling points in general to high levels of environmental suitability persisting for the *Arthonia-Lecidella* Community through to the late-21st Century (*Figure 5.5*), though with some local variability represented as small increases or decreases.

Table 5.2. **The statistically significant indicator species for the Type A *Arthonia-Lecidella* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Arthonia radiata	35%	70%	0.5			0.0001
Lecidella elaeochroma	43%	42%	0.54			0.0001
Associated						
Buellia disciformis	22%	71%	0.41			0.0001
Lecanora chlarotera	87%	34%	0.72			0.0001
Pertusaria leioplaca	52%	36%	0.67			0.0001

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

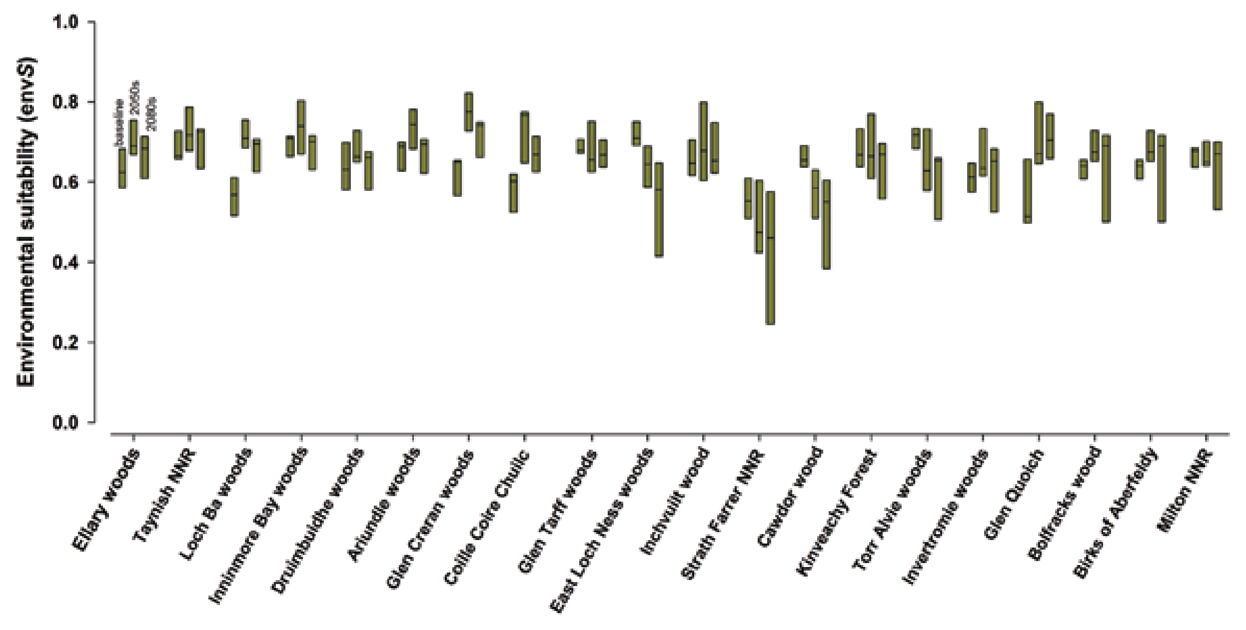


Figure 5.5. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Arthonia-Lecidella* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al*. (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

5.2 Type B

Graphis scripta Community FBCS = HIGH

The 'Type B' *Graphis scripta* Community (*Figure 5.6*) occurs most frequently on younger smooth-barked broadleaf trees in mesotrophic microhabitats (*Figure 5.7; Table 5.3*) and intermediate climatic settings. The narrow set of habitat conditions under which Type B was most frequent (*Figure 5.7*) is because it appears to exist as a unique community type only in a limited set of circumstances, and intergrades for example with Community Type A (*Arthonia-Lecidella* Community; see Section 5.1) and Community Type G (*Lobaria-Normandina-Metzgeria* Community; see Section 5.7) both of which can share similar characteristics as pioneer or early- to mid-successional systems of smooth-barked trees.

However, where the *Graphis scripta* Community matures it can become relatively species-rich in crustose lichens, including epiphytes of conservation importance such as *Thelotrema petractoides* (with an International Responsibility for UK conservation).

Figure 5.6. **The charismatic 'script lichen', *Graphis scripta*, growing on smooth bark.**

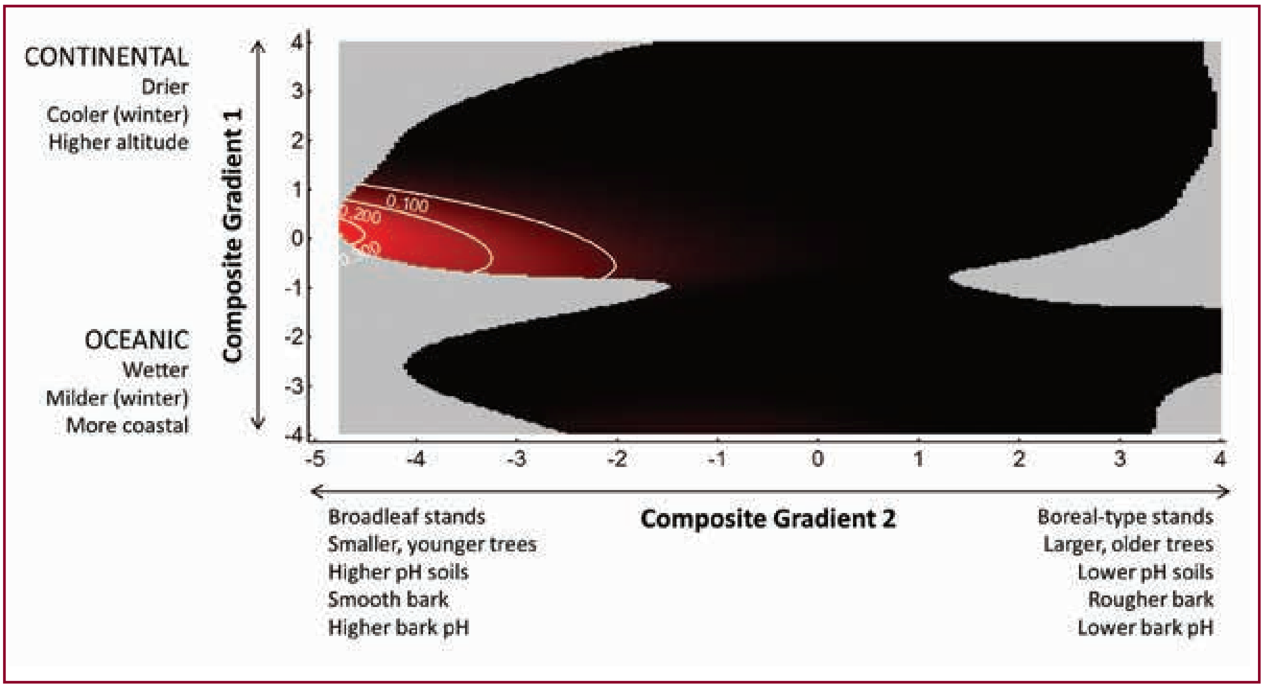


Figure 5.7. **Response surface showing variability in the likelihood of occurrence for the Type B *Graphis scripta* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.3*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.**

Table 5.3. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Graphis scripta* Community in relation to the variability of Composite Gradient 2 (tree-scale environment) and Composite Gradient 1 (macroclimate). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log$B$	AUC	$_{MC}P$
Composite Gradient 1	0.501 (5%)	0.135	12.65	0.92	< 0.01
Composite Gradient 2	1.069 (10%)	0.094			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The Type B *Graphis scripta* Community is geographically widespread, occurring at climatically contrasting sites in both the west and the east, though it was uncommon within most of the sampled woodlands and only strongly represented for lower altitude eastern sites (*Figure 5.8*). Its distribution supports the notion that it is a locally restricted variant of the more commonly occurring and widespread Community Type A (*Arthonia-Lecidella* Community; see Section 5.1), or Community Type G (*Lobaria-Normandina-Metzgeria* Community; see Section 5.7).

The *Graphis scripta* Community has four diagnostic species (*Table 5.4*) which support its intermediate nature; *Arthonia didyma* occurs in many smooth-barked habitats (as with Community Type A; see Section 5.1); *Pyrenula occidentalis* signals an association with oceanic temperate rainforest; and because

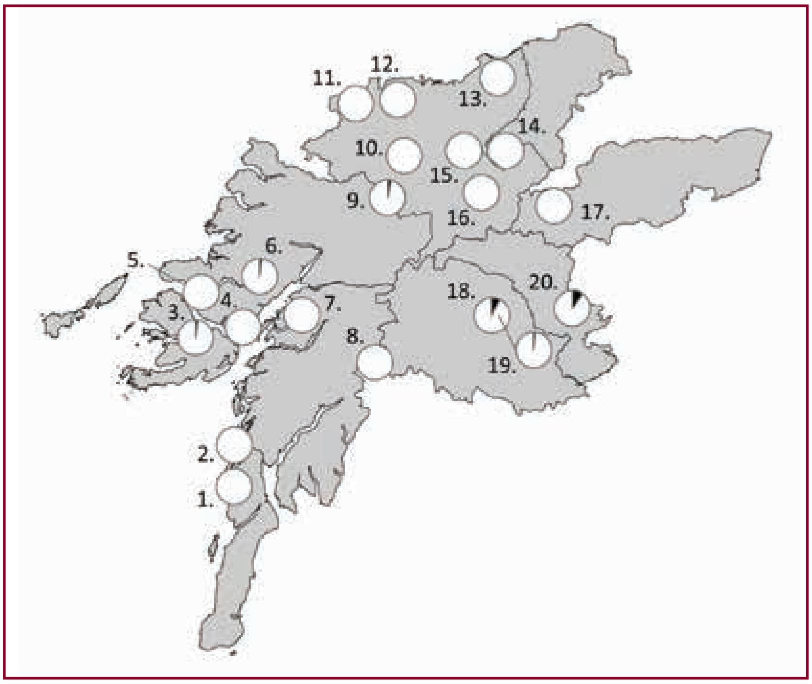


Figure 5.8. **The percent contribution (in black) of the *Graphis scripta* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

Table 5.4. **The statistically significant indicator species for the Type B *Graphis scripta* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Graphis scripta	100%	24%	0.81			0.0001
Associated						
Arthonia didyma	33%	10%	0.38			0.0004
Pertusaria hymenea	27%	17%	0.71			0.0001
Pyrenula occidentalis	13%	9%	0.67	SBL; IR	C&C = WSIEC; W&E < 0.001	0.0158

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

Pertusaria hymenea is often associated with older trees, it highlights the transitional nature of the Type B Community (*Figure 5.9*), in which pioneer crustose lichens of smooth bark undergo succession to more competitive systems dominated by larger foliose lichens and bryophytes, such as Community Type G (*Lobaria-Normandina-Metzgeria* Community; see Section 5.7).

None of the species of Community Type B are identified as threatened according to IUCN criteria, though *Pyrenula occidentalis* occurs on the Scottish Biodiversity List and has an international conservation status, as well as being associated with woodlands that have ecological continuity. Bioclimatic modelling points to locally variable trends in the environmental suitability for members of the *Graphis scripta* Community, through to the late-21st Century (*Figure 5.10*).

Figure 5.9. Successional development (clockwise) from *A. **Graphis scripta*** with young thallus of ***Pertusaria hymenea*** colonising onto a smooth-barked hazel stem.

Figure 5.9. C. ***Pertusaria hymenea*** in close-up.

Figure 5.9. B. A more mature ***Pertusaria hymenea*** thallus adjacent to the larger foliose ***Lobaria virens***, characteristic of Community Type G.

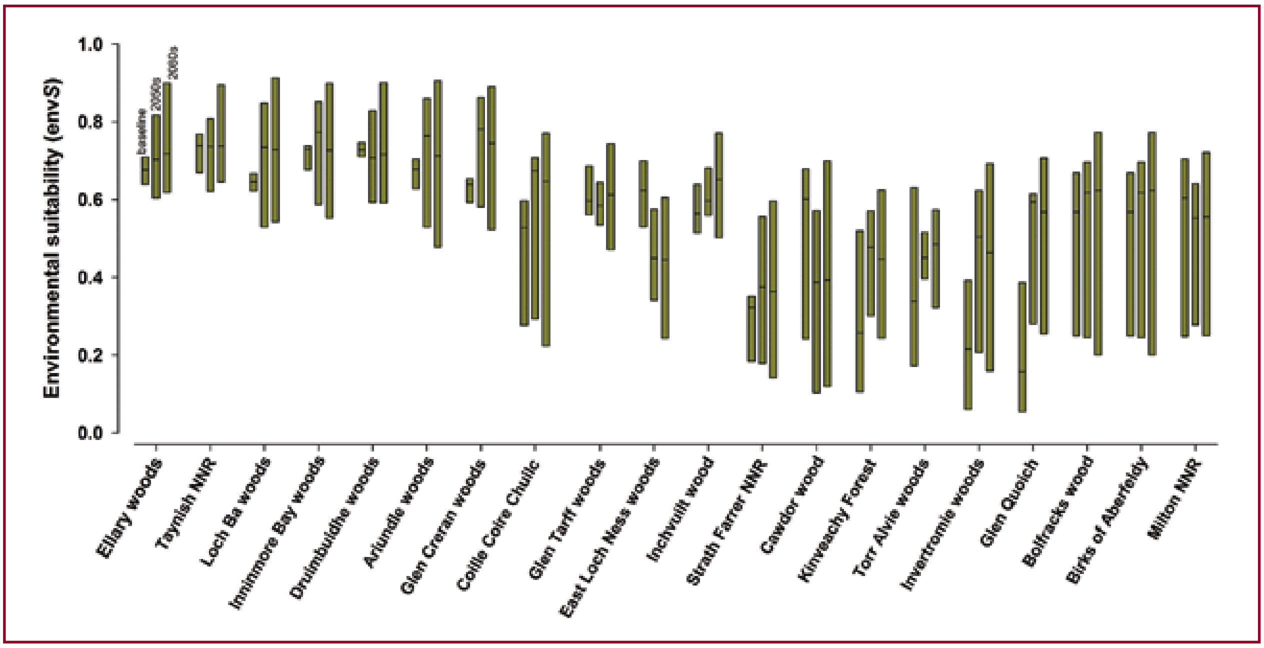


Figure 5.10. Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Graphis scripta* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al*. (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).

5.3 **Type C**

***Frullania dilatata* Community** FBCS = MEDIUM

The ‘Type C’ *Frullania dilatata* Community (*Figure 5.11 A & B*) includes early colonising bryophyte species which can persist to occur on larger and mature broadleaf trees (*Figure 5.11C; Figure 5.12; Table 5.5*), including on older hazel stems but also for example forming locally dominant patches on willows, aspen, rowan and ash (*Figure 5.13*). The community is generally reduced on the oldest trees and absent from oligotrophic microhabitats such as on birch and Scots pine.

Figure 5.11. A. **(clockwise) The common and widespread liverwort *Frullania dilatata* colonising onto a young smooth-barked hazel stem.**

Figure 5.11. C. **Persisting as the dominant local community on mature alder.**

Figure 5.11. B. **Growing with the moss *Ulota bruchii/crispa*.**

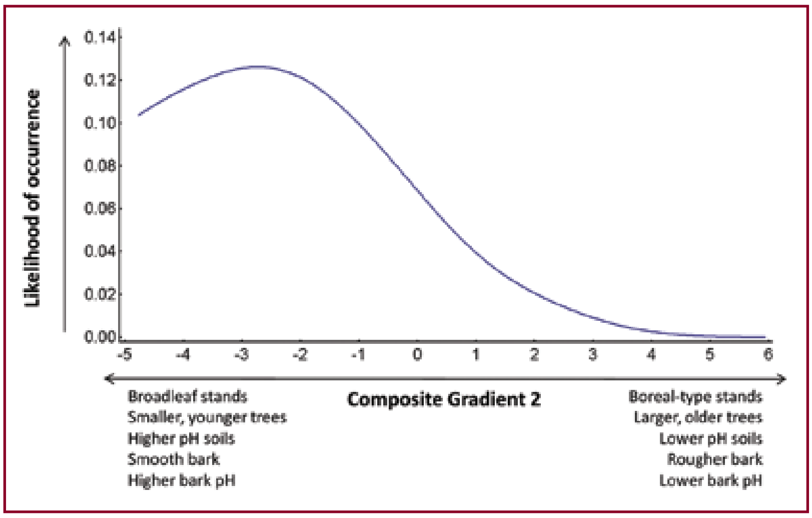


Figure 5.12. **Response curve showing variability in the likelihood of occurrence for the Type C *Frullania dilatata* Community, plotted along a composite environmental gradient related to tree-scale effects (cf. *Table 5.5*).**

Table 5.5. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Frullana dilatata* Community in relation to the variability of Composite Gradient 2 (tree-scale environment) and tree species identity. Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log$B$	AUC	$_{MC}P$
Composite Gradient 2	1.069 (10%)	0.154	23.09	0.833	< 0.01
Tree species identity					

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

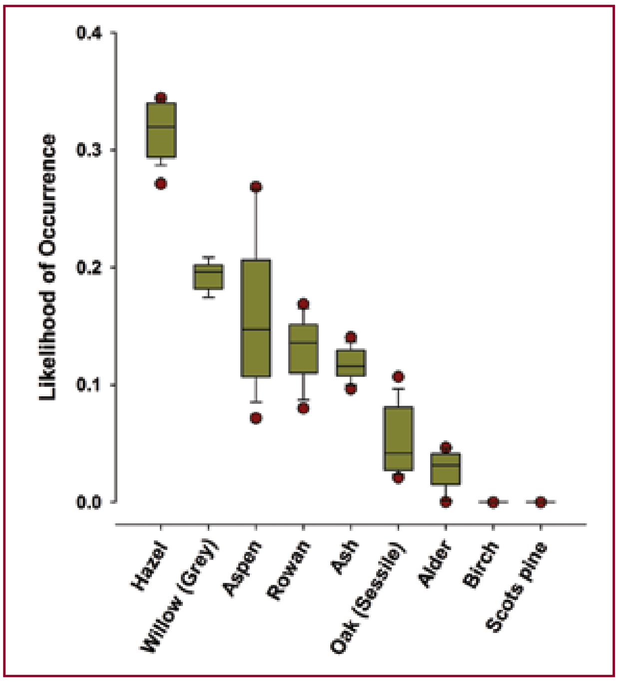


Figure 5.13. **Variability in the likelihood of occurrence for the Type C *Frullania dilatata* Community, compared to tree species identity, which was identified as an important factor in an optimised statistical model (cf. *Table 5.5*).**

The Type C *Frullania dilatata* Community is widely distributed across woodland sites in Scotland, and is sometimes among the most common community types, especially in broadleaf settings (*Figure 5.14*).

The *Frullania dilatata* Community has only two diagnostic species (*Table 5.6*). Neither of the species is identified as threatened according to IUCN criteria, or occurs on the Scottish Biodiversity List. The community includes only bryophyte species, and bioclimatic modelling was unavailable.

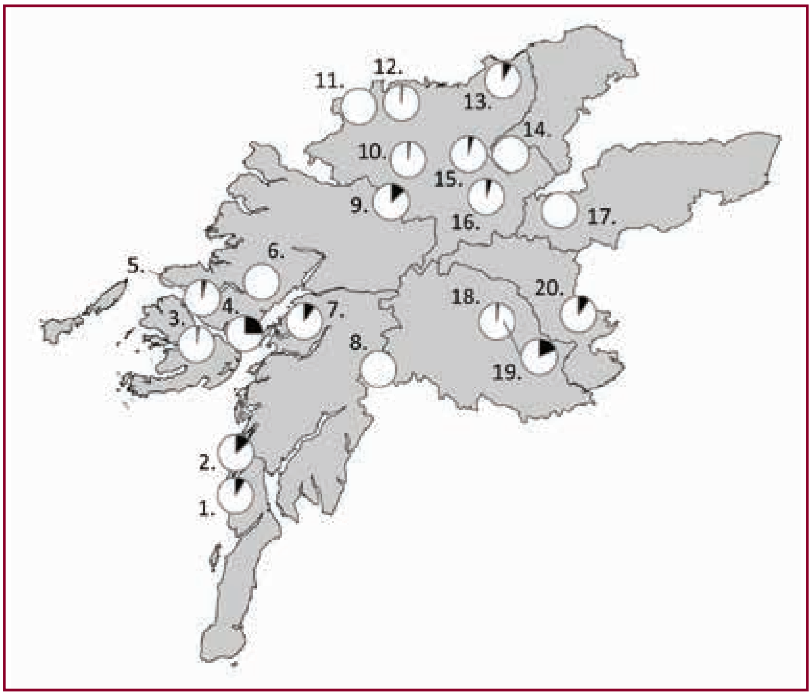


Figure 5.14. The percent contribution (in black) of the *Frullania dilatata* Community to the epiphyte assemblages in each of the twenty woodland study sites.
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

Table 5.6. The statistically significant indicator species for the Type C *Frullania dilatata* Community, with notes on the species conservation status and association with ecological continuity.

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Frullania dilatata	97%	41%	0.82			0.0001
Associated						
Ulota bruchii/crispa	25%	26%	0.27			0.0179

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

5.4 Type D

Phlyctis argena – Ramalina farinacea Community FBCS = MEDIUM

The ‘Type D’ *Phlyctis-Ramalina* Community (*Figure 5.15*) is one of the most common epiphyte communities in Scotland’s temperate woodlands. It has a similar macroclimatic response to the contrasting Community Type O (*Bryoria-Ochrolechia-Parmeliopsis*; see Section 5.15), though is differentiated at a microhabitat scale (*Figure 5.16; Table 5.7*) through its association with mature broadleaf trees in mesotrophic settings (*Figure 5.17*).

Figure 5.15. **The white crustose *Phlyctis argena*, growing below the fruticose *Ramalina farinacea* (with *Evernia prunastri* to the upper right), and with a surrounding matrix of foliose green-brown *Melanelixia glabratula* agg. and grey-blue *Parmelia sulcata* on the surrounding bark.**

Figure 5.16. **(Below) Response surface showing variability in the likelihood of occurrence for the Type D *Phlyctis-Ramalina* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.7*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.**

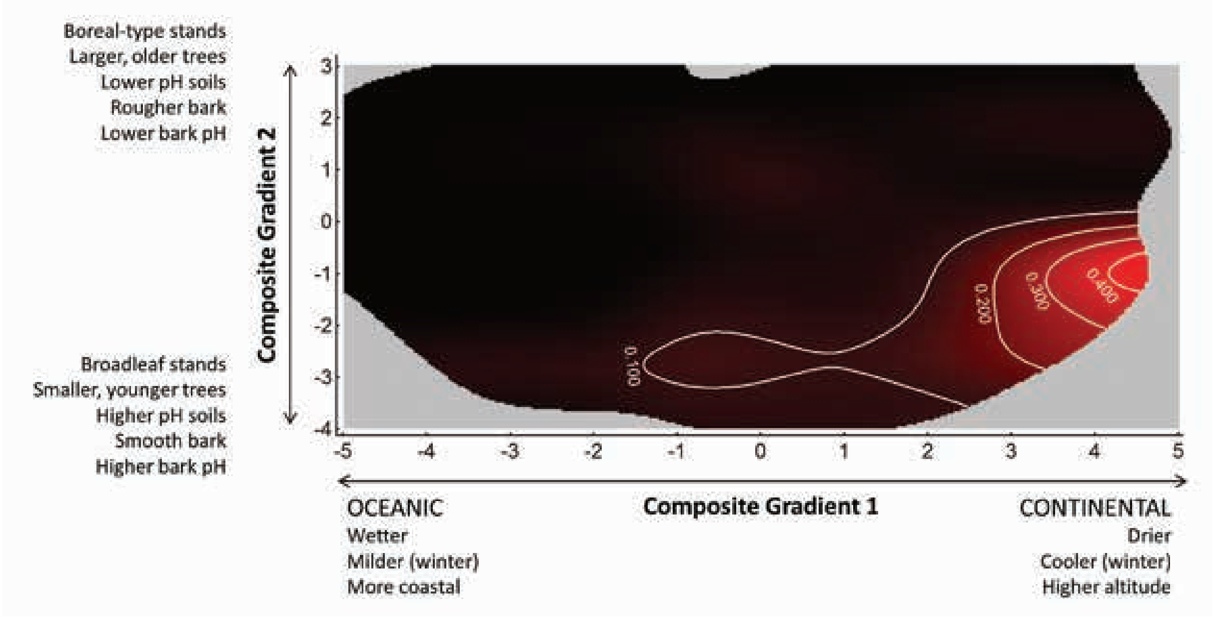


Table 5.7. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Phlyctis-Ramalina* Community in relation to the variability of Composite Gradient 1 (macroclimate) and Composite Gradient 2 (tree-scale environment). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	1.00 (10%)	0.195	15.32	0.787	< 0.01
Composite Gradient 2	0.535 (5%)	0.27			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

Figure 5.17. **A riparian alder stand on nutrient-rich soil at Woodhall Dean, typical habitat conditions for the *Phlyctis-Ramalina* Community.**

The Type D *Phlyctis-Ramalina* Community is geographically most common in broadleaf woodland sites in central and eastern Scotland (*Figure 5.18*), though also occurs to a more limited extent at oceanic western sites.

Figure 5.18. **The percent contribution (in black) of the *Phlyctis-Ramalina* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods),
4. IB (Inninmore Bay woods),
5. DR (Druimbuidhe woods),
6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods),
10. EN (East Loch Ness woods),
11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood),
14. KF (Kinveachy Forest),
15. TA (Torr Alvie woods),
16. IV (Invertromie woods),
17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy),
20. MW (Milton NNR).

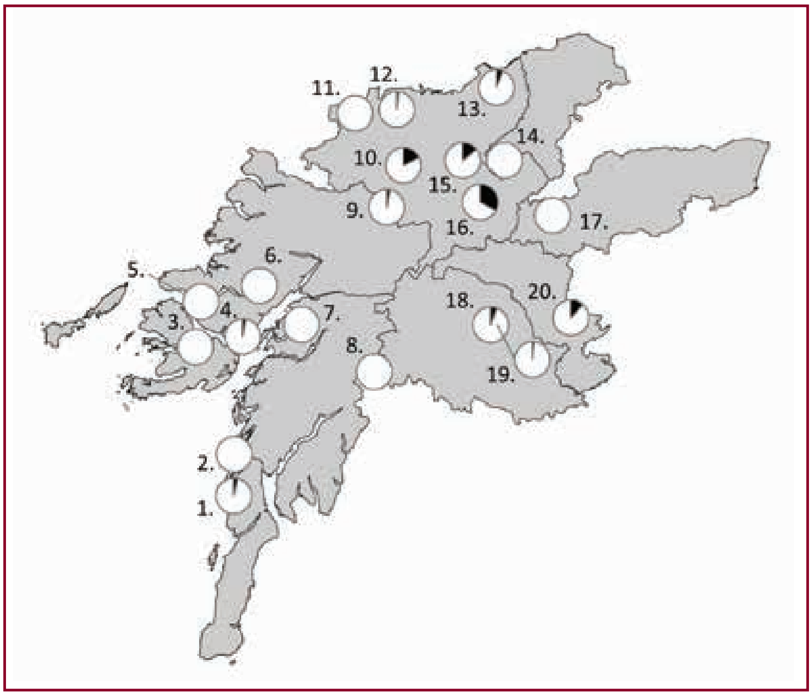


Table 5.8. **The statistically significant indicator species for the Type D *Phlyctis-Ramalina* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Phlyctis argena	35%	30%	0.74			0.0001
Ramalina farinacea	37%	36%	0.5			0.0001
Associated						
Melanelixia glabratula agg.	41%	20%	0.43			0.0001
Parmelia sulcata	22%	18%	0.59			0.0036
Pertusaria amara	43%	25%	0.53			0.0001
Orthotrichum affine	20%	61%	0.51			0.0001

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

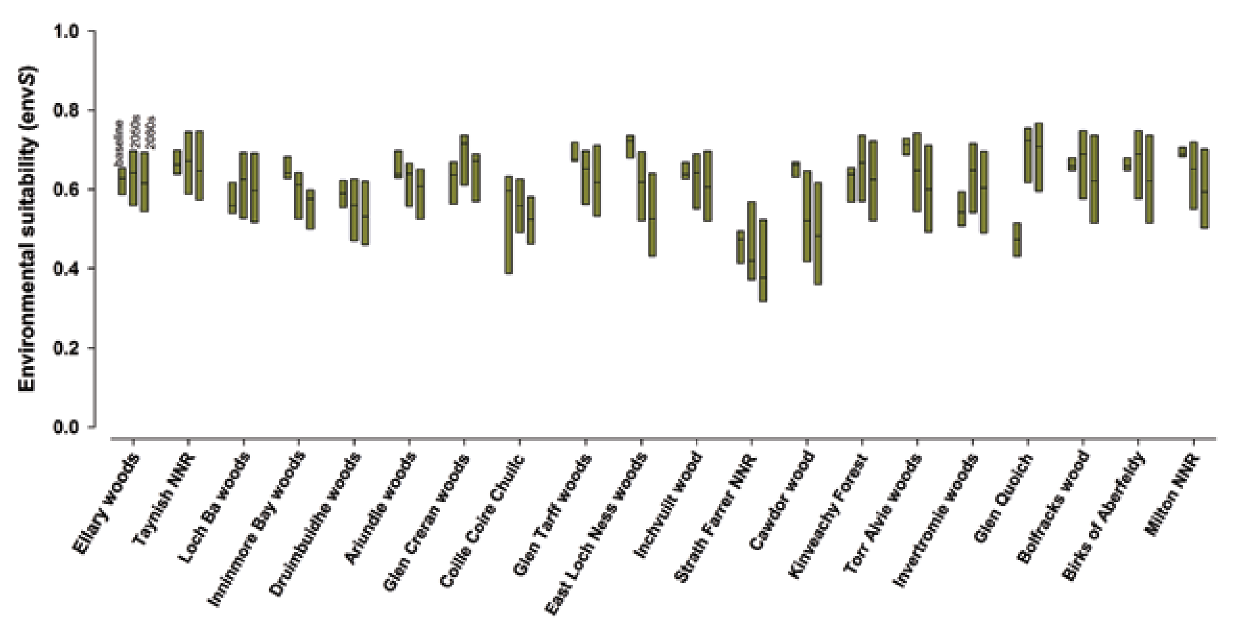


Figure 5.19. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Phlyctis-Ramalina* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al*. (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

The *Phlyctis-Ramalina* Community has six diagnostic species (*Table 5.8*). None of these species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. None of the species are strongly associated with woodlands that have ecological continuity, and the percent contribution of Community Type D to sites in southern and south-eastern Scotland may exceed our sampled observations (*Figure 5.18*) when considering 'average' sites outside the ancient woodland/conservation network. Bioclimatic modelling points in general to small future declines in environmental suitability for individual lichen species in the *Phlyctis-Ramalina* Community (*Figure 5.19*), though in most cases values of environmental suitability continue to remain relatively high through to the late-21st Century.

5.5 **Type E**

***Calicium viride* – *Chrysothrix candelaris* Community** FBCS = HIGH

The ‘Type E’ *Calicium-Chrysothrix* Community (*Figure 5.20*) has similar specialist requirements to the closely associated Community Type F (*Lecanactis abietina* Community, see Section 5.6) and both occur in drier microhabitats sheltered from direct wetting, such as on the underside of leaning trees (*Figure 5.21; Table 5.9*). However, the *Calicium-Chrysothrix* Community also increases towards the drier, cooler and more continental type climate of north-eastern Scotland, and on this basis it often co-occurs at the same sites as Community Type O (*Bryoria-Ochrolechia-Parmeliopsis*; see Section 5.15) though on broadleaf trees such as birch and oak (*Figure 5.22*).

Figure 5.20. A. **The *Calicium-Chrysothrix* Community on an old and leaning birch tree in Strath Farrer, characterised by the bright yellow powdery *Chrysothrix candelaris*.**

Figure 5.20. B. **The tiny stalked fruits of *Calicium viride* which are often nestled within deeply furrowed bark along with a community of similar pinhead lichens.**

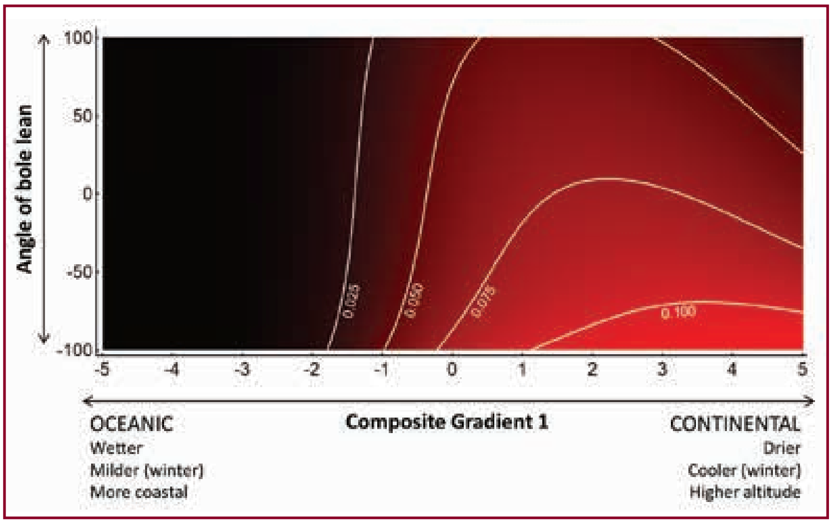


Figure 5.21. **Response surface showing variability in the likelihood of occurrence for the Type E *Calicium-Chrysothrix* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.9*). Contours show likelihood values from red (higher values), to black (lower values).**

Table 5.9. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Calicium-Chrysothrix* Community in relation to the variability of Composite Gradient 1 (macroclimate), angle of bole lean and tree species identity. Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	1.504 (15%)	0.123	21.64	0.854	< 0.01
Angle of bole lean	51.25 (25%)	0.029			
Tree species identity					

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

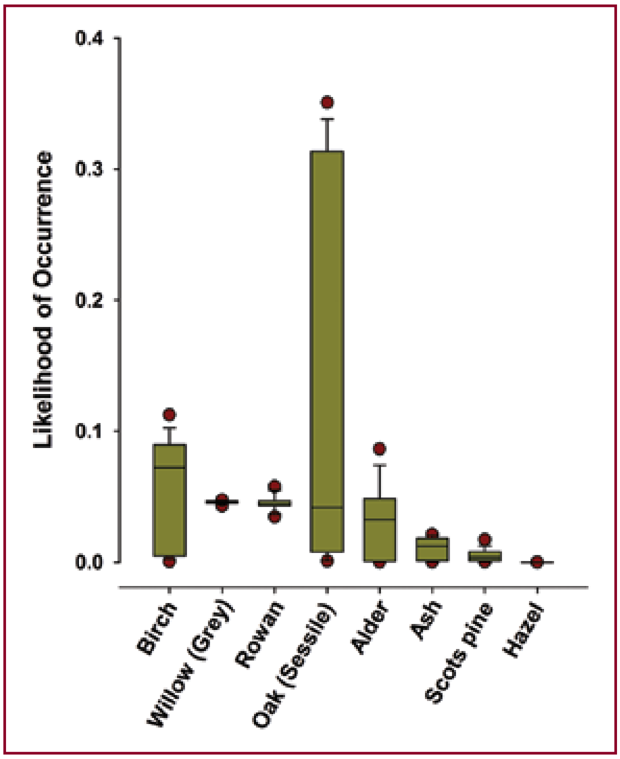


Figure 5.22. **Variability in the likelihood of occurrence for the Type E *Calicium-Chrysothrix* Community, compared to tree species identity, which was identified as an important factor in an optimised statistical model (cf. *Table 5.9*).**

Geographically, the *Calicium-Chrysothrix* Community is most common at sites in the relatively more continental eastern part of the sampled range, and especially at Cawdor wood, where there was abundantly suitable microhabitat on larger and old oak trees with deeply furrowed bark (*Figure 5.23*).

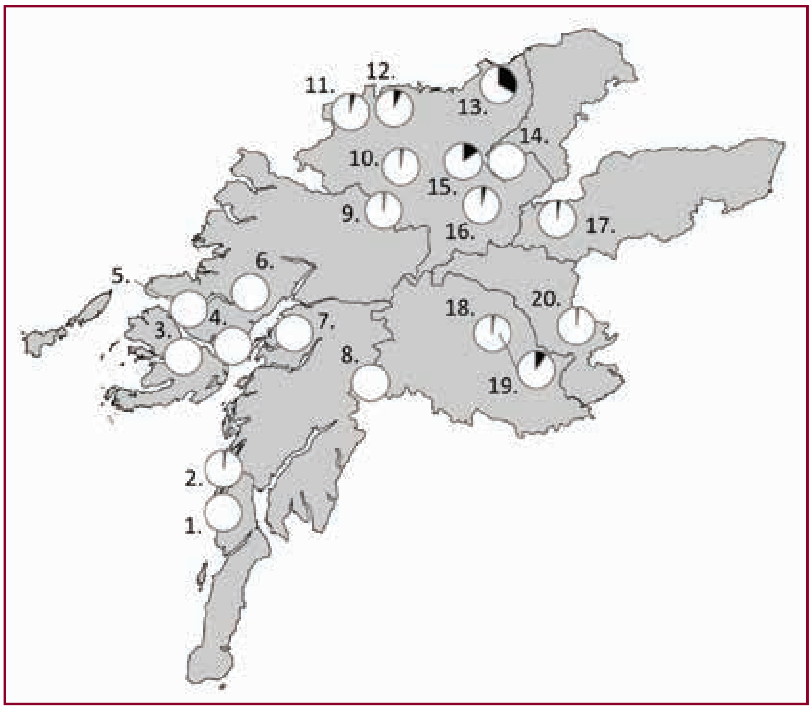


Figure 5.23. **The percent contribution (in black) of the *Calicium-Chrysothrix* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

The *Calicium-Chrysothrix* Community has seven diagnostic species (*Table 5.10*). None of these species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. However, three of the diagnostic species are thought to be strongly associated with woodlands that have ecological continuity. Bioclimatic modelling showed mixed results in the response for individual species in the *Calicium-Chrysothrix* Community (*Figure 5.24*). More oceanic western sites showed little overall shift in environmental suitability values, while central and more continental eastern sites mostly showed either an increase or a decrease through to the 2050s, and a decreased projected environmental suitability by the late-21st Century (2080s). Only the higher altitude site of Glen Quoich showed an increased environmental suitability in the long-term.

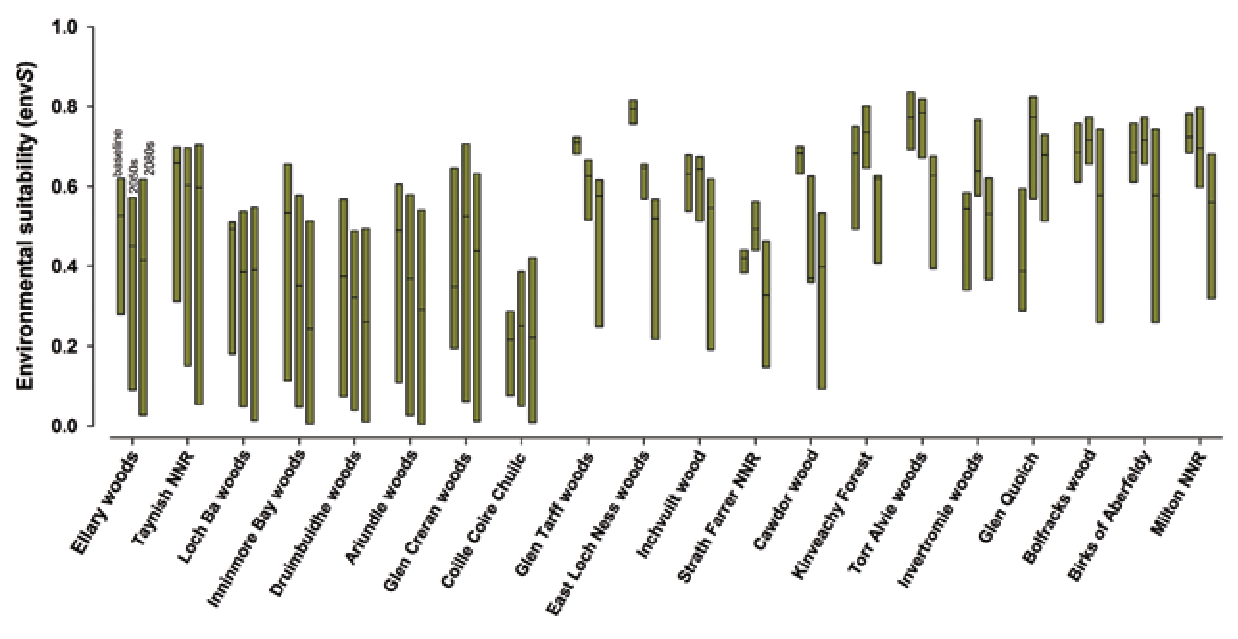


Figure 5.24. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Calicium-Chrysothrix* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al*. (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

Table 5.10. **The statistically significant indicator species for the Type E *Calicium-Chrysothrix* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	Association Values			Conservation Status	Ecological Continuity	Indicator *P*
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Calicium viride	30%	47%	0.47		C&C = ESIEC	0.0001
Chrysothrix candelaris	76%	47%	0.72			0.0001
Associated						
Anisomeridium biforme	17%	53%	0.53			0.0002
Arthonia vinosa	22%	43%	0.52		C&C = WSIEC/ESIEC/ NPIEC; E = 0.0013	0.0003
Chaenotheca trichialis	24%	52%	0.63		C&C = ESIEC/NPIEC	0.0001
Cliostomum griffithii	41%	27%	0.35			0.0001
Lepraria incana	28%	46%	0.97			0.0001

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

5.6 **Type F**

***Lecanactis abietina* Community** FBCS = HIGH

The 'Type F' *Lecanactis abietina* Community (*Figure 5.25*) is closely allied to Community Type E (*Calicium-Chrysothrix* Community; see Section 5.5) and species of these two community types often intergrade, together forming epiphyte Group III (*Figure 4.2*).

Figure 5.25. A. **The pinkish tinge that is characteristic of a population of *Lecanactis abietina* on the sheltered side of a deeply furrowed and steeply leaning oak tree at Dawyck Botanic Garden.**

Figure 5.25. B. **A closer view of *Lecanactis abietina*, with scattered colonies of *Chrysothrix candelaris* (Community Type E) appearing as yellow flecks.**

The *Lecanactis abietina* Community has clearly defined specialist requirements, and occurs in microhabitats that are not exposed to direct wetting such as on the underside of steeply leaning trees. This sensitivity extends to other factors, and Community Type F is most likely to occur in non-shaded open structured woodland and at a distance from watercourses (*Figure 5.26; Table 5.11*).

Table 5.11. Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Lecanactis abietina* Community in relation to the variability of angle of bole lean, canopy openness and distance to water (metres). Other variables were not significant.

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Distance to water (metres)	76.5 (15%)	0.037	9.18	0.716	0.0198
Canopy openness (%)	6.89 (10%)	0.029			
Angle of bole lean	10.25 (5%)	0.186			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

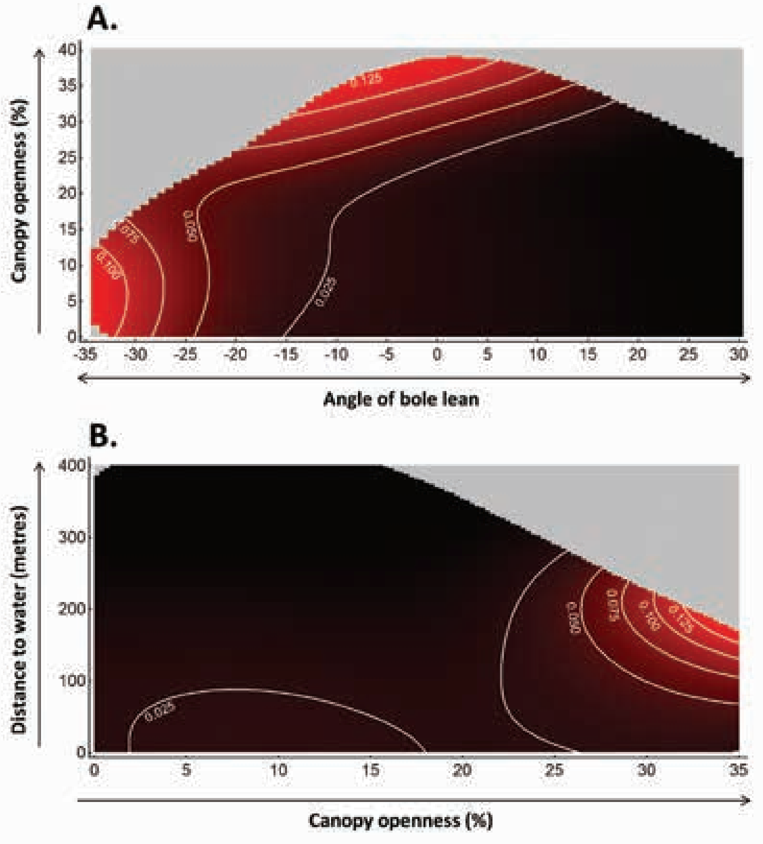


Figure 5.26. Response surfaces showing variability in the likelihood of occurrence for the Type F *Lecanactis abietina* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.11*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

The *Lecanactis abietina* Community is only locally common and was not a major element at any of the woodland sites, though it is widely distributed geographically and was recorded from sites across the sampling range (*Figure 5.27*).

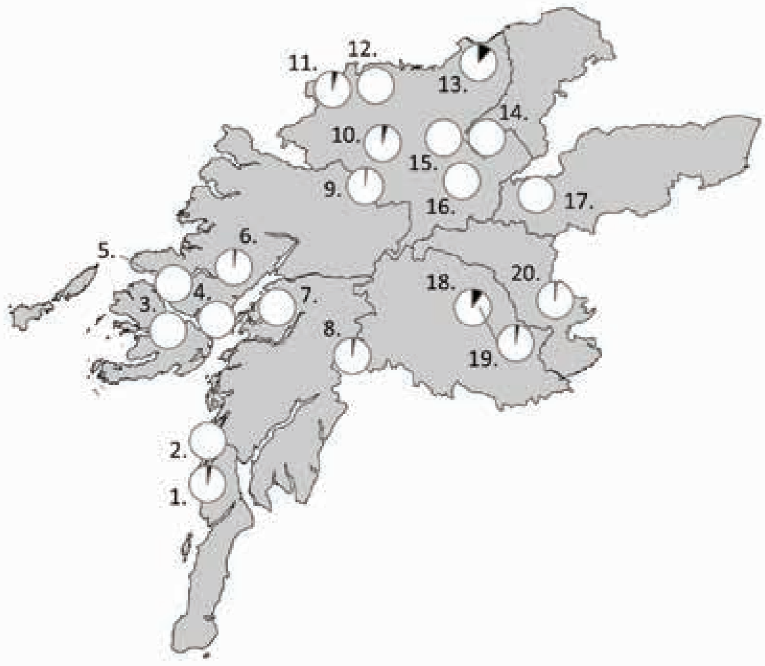


Figure 5.27. The percent contribution (in black) of the *Lecanactis abietina* Community to the epiphyte assemblages in each of the twenty woodland study sites.
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

The *Lecanactis abietina* Community is defined by itself as the single indicator species (*Table 5.12*). There are therefore circumstances in which *Lecanactis abietina* is enitrely dominant across almost the entire bark surface (*Figure 5.25*), though 66% of occurrences for the species were in other communities, and especially in contribution to Community Type E (*Calicium-Chrysothrix* Community; see Section 5.5). *Lecanactis abietina* is not threatened according to IUCN criteria, is not included on the Scottish Biodiversity List or listed as of International Responsibility, nor is it associated with woodlands that have ecological continuity. Bioclimatic modelling suggests a possible east-west split in the species response, with declining environmental suitability for eastern and more continental sites by the mid- to late-21st Century, and with less of an effect for western sites (*Figure 5.28*).

Table 5.12. **The statistically significant indicator species for the Type F *Lecanactis abietina* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Lecanactis abietina	100%	34%	0.83			0.0001

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

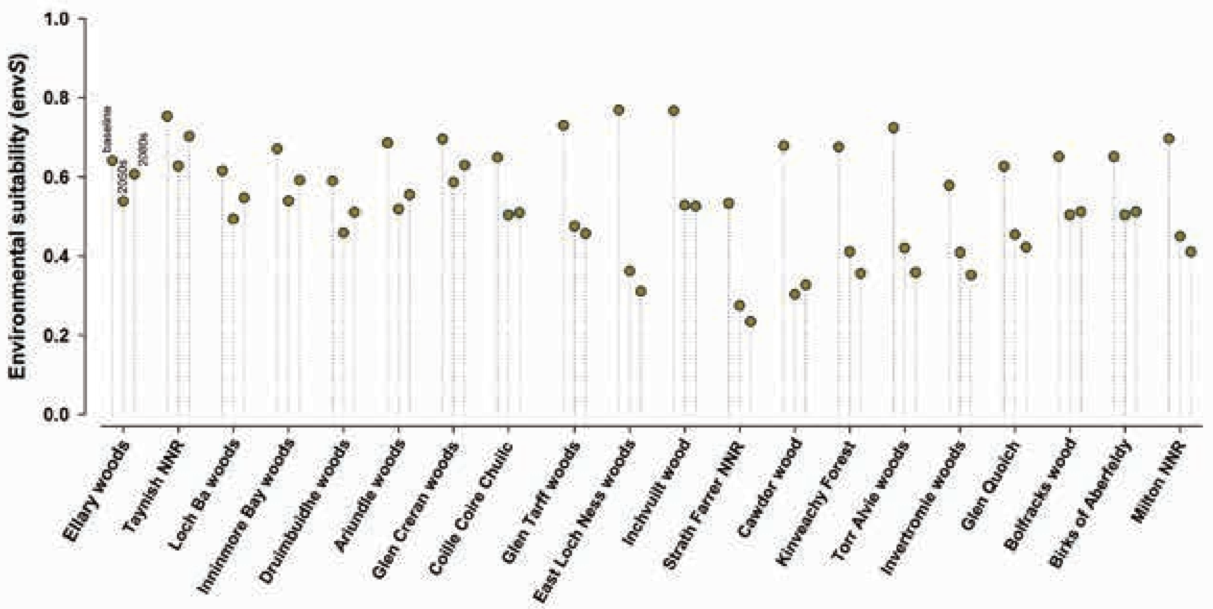


Figure 5.28. **Bioclimatic modelled values of environmental suitability (env*S*) for the *Lecanactis abietina* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Point plots for each site show the estimated value of env*S* for *Lecanactis abietina*, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s.**

5.7 **Type G**

Lobaria virens – Normandina pulchella – Metzgeria furcata **Community** FBCS = HIGH

The 'Type G' *Lobaria-Normandina-Metzgeria* Community (*Figure 5.29*) is a common epiphyte community of mesotrophic and higher pH microhabitats in oceanic climates (*Figure 5.30; Table 5.13*). It is most common in mesotrophic broadleaved woodlands, and across a wide range of stand types with respect to topography, though may be more abundant in less shaded situations subject to periodic cycles of wetting and drying.

Figure 5.29. The key indicator species for the Type G *Lobaria-Normandina-Metzgeria* Community, *Lobaria virens*.

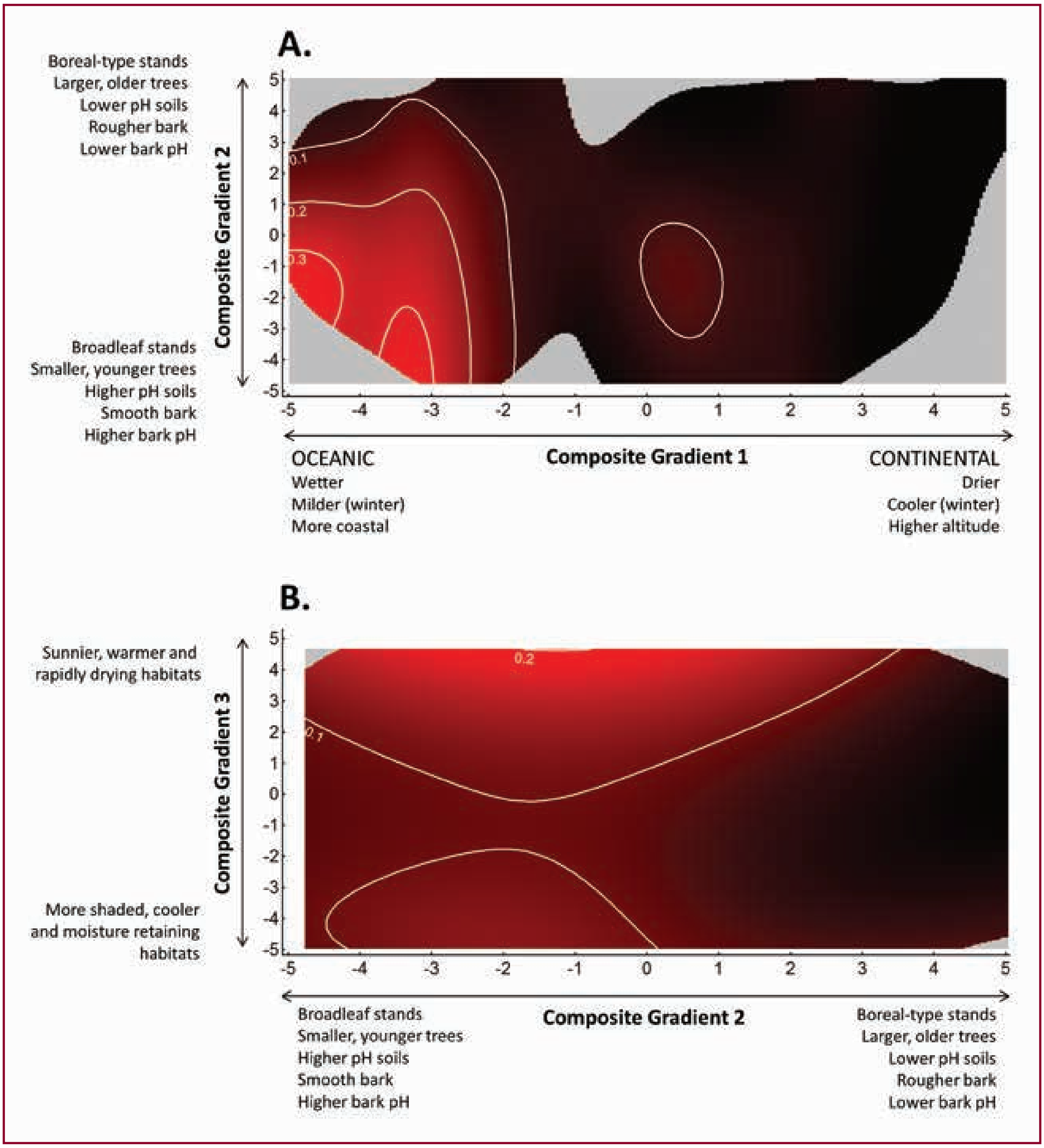


Figure 5.30. Response surfaces showing variability in the likelihood of occurrence for the Type G *Lobaria-Normandina-Metzgeria* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.13*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

Table 5.13. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Lobaria-Normandia-Metzgeria* Community in relation to the variability of Composite Gradient 1 (macroclimate), Composite Gradient 2 (tree-scale environment) and Composite Gradient 3 (stand topography). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	${}_{MC}P$
Composite Gradient 1	0.501 (5%)	0.472	16.89	0.776	< 0.01
Composite Gradient 2	1.604 (15%)	0.143			
Composite Gradient 3	1.734 (15%)	0.198			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

${}_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The Type G *Lobaria-Normandina-Metzgeria* Community is geographically most common in broadleaf woodland sites in oceanic western Scotland though also occurred in mixed woods in high rainfall areas of the central Highlands as well as in locally suitable stand types for lowland sites in eastern Scotland (*Figure 5.31*).

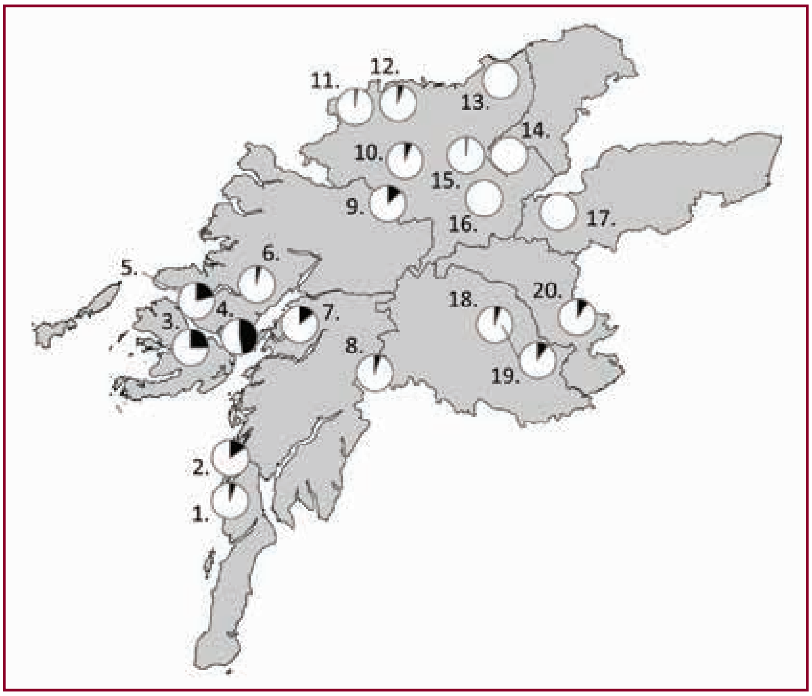


Figure 5.31. **The percent contribution (in black) of the *Lobaria-Normandina-Metzgeria* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods),
4. IB (Inninmore Bay woods),
5. DR (Druimbuidhe woods),
6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods),
10. EN (East Loch Ness woods),
11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood),
14. KF (Kinveachy Forest),
15. TA (Torr Alvie woods),
16. IV (Invertromie woods),
17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy),
20. MW (Milton NNR).

The *Lobaria-Normandina-Metzgeria* Community has nine diagnostic species (*Table 5.14*). None of these species are identified as threatened according to IUCN criteria, though *Lobaria virens* is placed on the Scottish Biodiversity List because of an International Responsibility in its conservation. Three of the species are strongly associated with woodlands that have ecological continuity, including the striking *Thelotrema lepadinum* (*Figure 5.32*).

Bioclimatic modelling points in general to locally variable patterns of decline or increase in environmental suitability for the individual lichen species in the *Lobaria-Normandina-Metzgeria* Community (*Figure 5.33*).

Table 5.14. **The statistically significant indicator species for the Type G *Lobaria-Nomandina-Metzgeria* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Lobaria virens	23%	72%	0.76	SBL; IR	C&C = ESIEC/NPIEC	0.0001
Normandina pulchella	43%	28%	0.34		C&C = ESIEC	0.0003
Metzgeria furcata	46%	32%	0.5			0.0001
Associated						
Frullania fragilifolia	9%	33%	0.86			0.0404
Isothecium alopecuroides	9%	50%	0.88			0.0179
Lepraria eburnea	9%	53%	0.78			0.0398
Opegrapha vulgata	12%	50%	0.61			0.006
Thelotrema lepadinum	20%	18%	0.49		C&C = ESIEC/NPIEC	0.039
Zygodon viridissimus	13%	39%	0.53			0.0128

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

Figure 5.32. **A characteristic indicator species for Community Type G, *Thelotrema lepadinum*.**

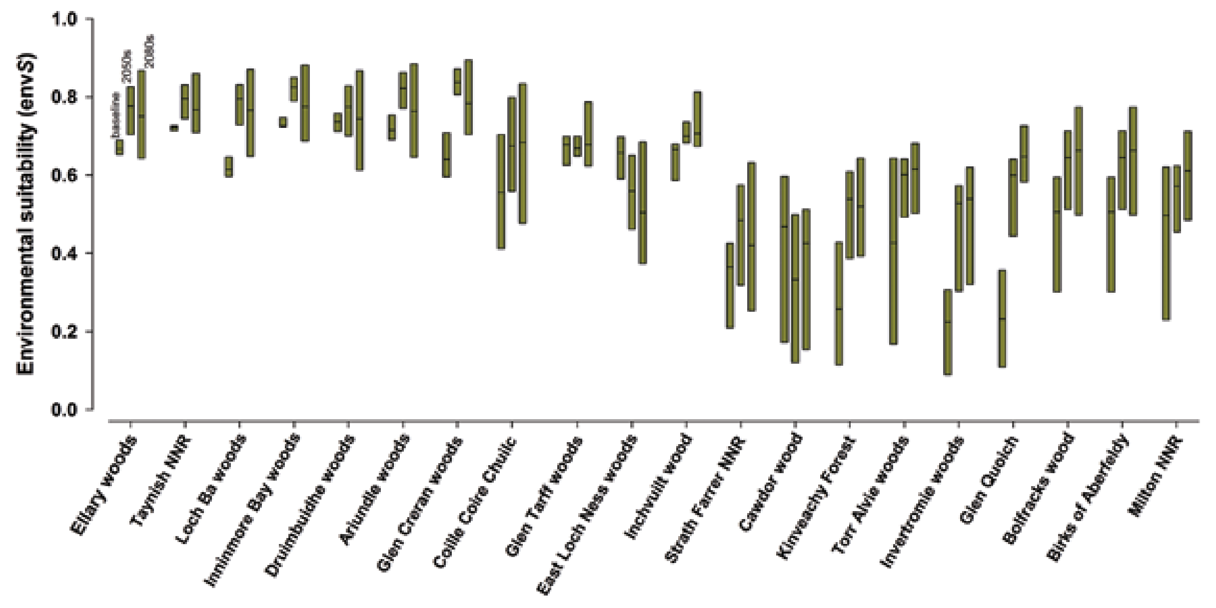


Figure 5.33. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Lobaria-Normandina-Metzgeria* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al*. (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

5.8 Type H

Hypnum cupressiforme agg. – *Usnea flammea* Community FBCS = LOW

The 'Type H' *Hypnum-Usnea* Community (*Figure 5.34*) is the least-well characterised community type in terms of habitat requirements, among three interrelated and bryophyte-dominated communities that form epiphyte Group V (*Figure 4.2*), also including Community Type I (*Hypnum-Microlejeunea* Community; see Section 5.9) and Community Type J (*Frullania tamarisci* Community; see Section 5.10). Statistical modelling of environmental effects did not meet minimum standards for confidence in the results (*Table 5.15*), though pointed to the possibility that Type H is broadly distributed while tending to be more abundant in oceanic climates (*Figure 5.35*). In terms of microhabitat, Community Type H appeared sensitive to bole lean, and occurred on a range of broadleaved trees with contrasting bark characteristics (*Figure 5.36*).

Table 5.15. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Hypnum-Usnea* Community in relation to the variability of Composite Gradient 1 (macroclimate), angle of bole lean and tree species identity. None of the tested variables were significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	2.01 (20%)	0.059	4.93	0.623	0.178
Angle of bole lean	30.75 (15%)	0.022			
Tree species identity					

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

Figure 5.34. The dominant indicator species of the *Hypnum-Usnea* Community on birch, with the fruticose *Usnea flammea* growing among a large mat of *Hypnum cupressiforme* agg.

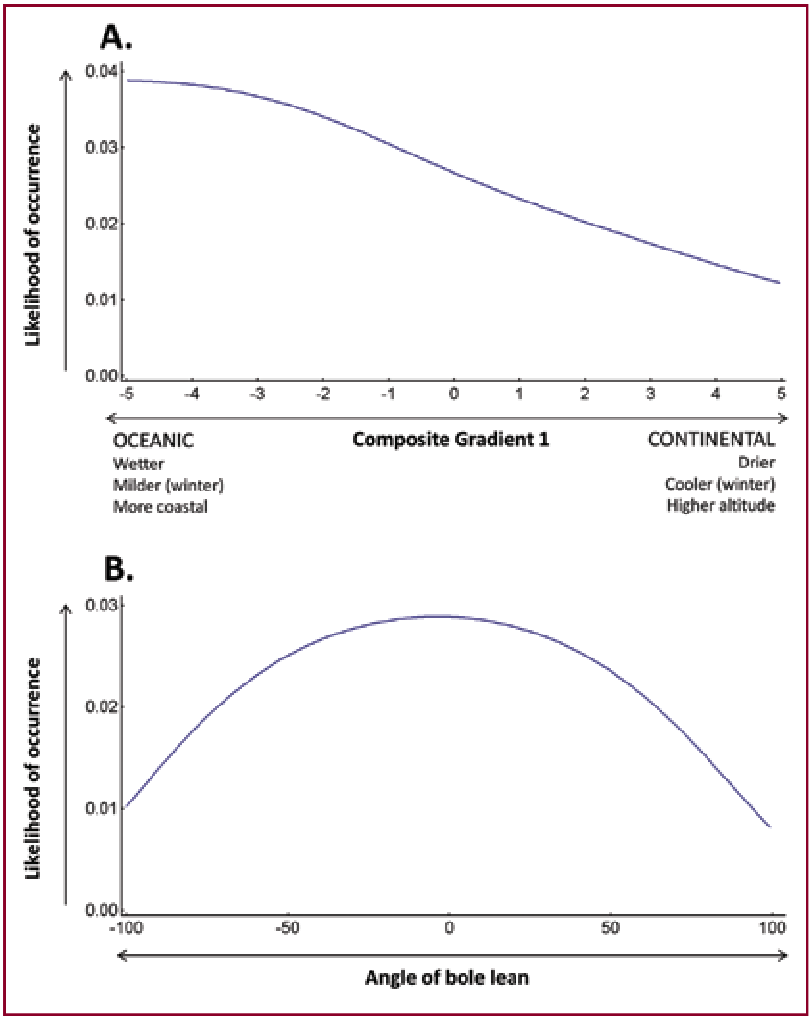


Figure 5.35. Response curves showing variability in the likelihood of occurrence for the Type H *Hypnum-Usnea* Community, plotted along the environmental gradients identified in an optimised but non-significant statistical model (cf. *Table 5.15*).

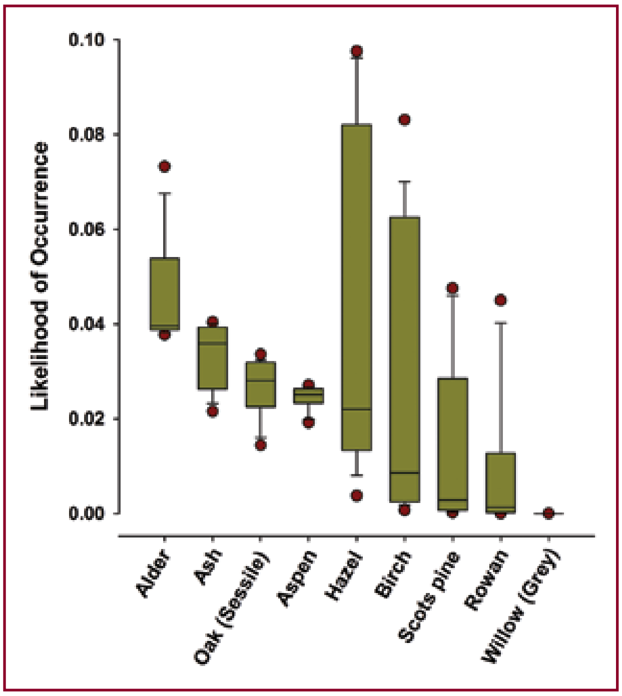


Figure 5.36. Variability in the likelihood of occurrence for the Type H *Hypnum-Usnea* Community, compared to tree species identity, which was identified as an important factor in an optimised though non-significant statistical model (cf. *Table 5.15*).

The Type H *Hypnum-Usnea* Community is geographically broadly distributed across woodland sites in different climates, and with different stand characteristics (*Figure. 5.37*).

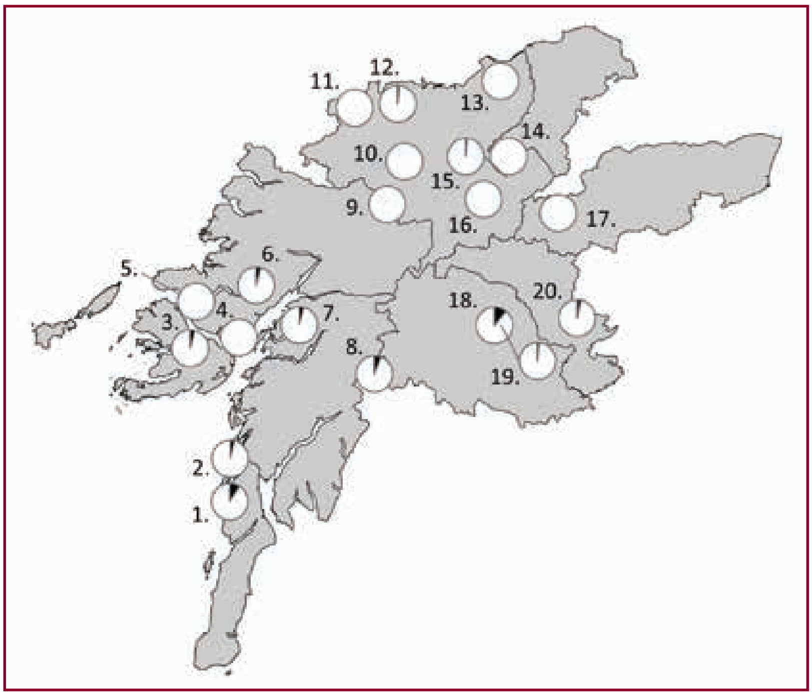


Figure 5.37. **The percent contribution (in black) of the *Hypnum-Usnea* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

The *Hypnum-Usnea* Community has four diagnostic species (*Table 5.16*). None of these species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. None of the species are strongly associated with woodlands that have ecological continuity, and the percent contribution of Community Type H may exceed our sampled observations (*Figure 5.37*) when considering ‘average’ sites outside the ancient woodland/conservation network. Bioclimatic modelling suggests a warming climate with consistent levels of precipitation/humidity could lead to increased environmental suitability for the two lichen species in the *Hypnum-Usnea* Community through to the late-21st Century (*Figure 5.38*).

Table 5.16. **The statistically significant indicator species for the Type H *Hypnum-Usnea* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Hypnum cupressiforme agg.	96%	26%	0.8			0.0001
Usnea flammea	23%	33%	0.48			0.0001
Associated						
Lepraria lobificans	31%	10%	0.6			0.0023
Plagiochila punctata	12%	12%	0.56			0.0223

Association Values : Community = % of community samples with the species present; Species = % of the species’ records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

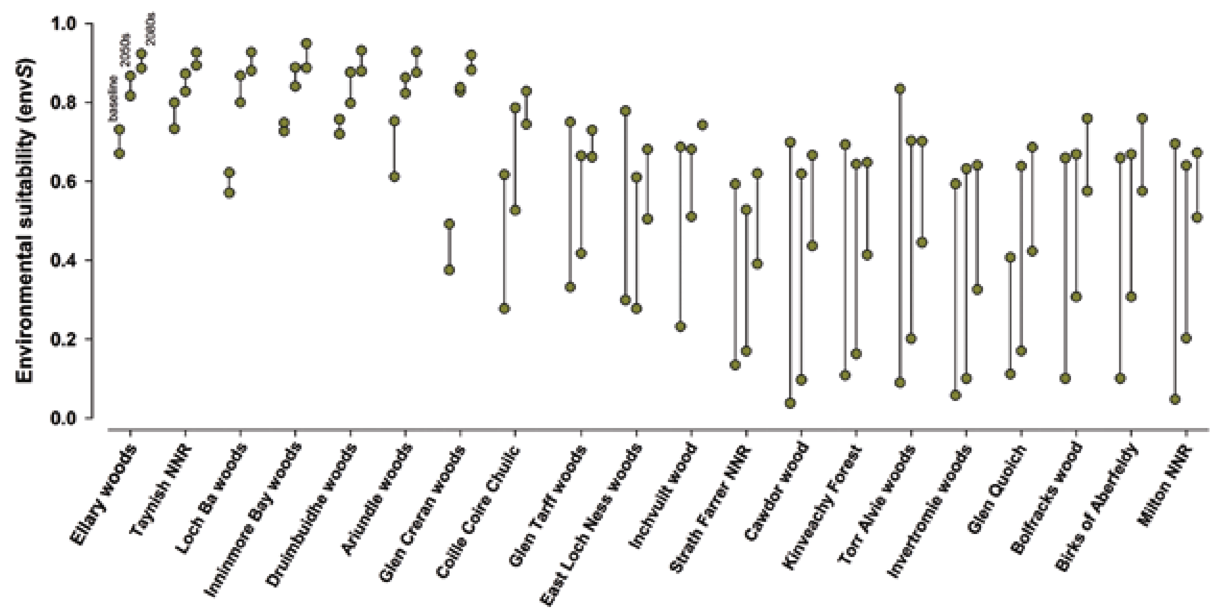


Figure 5.38. **Bioclimatic modelled values of environmental suitability (env*S*) for lichens within the *Hypnum-Usnea* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al*. (2015). Point plots for each site show the estimated values of env*S* for lichen species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s.**

5.9 Type I
Hypnum andoi – Microlejeunea ulicina Community FBCS = HIGH

The ‘Type I’ *Hypnum-Microlejeunea* Community (*Figure 5.39*) is found under two sets of environmental conditions, first within a more humid oceanic climate across a full range of stand settings, and second in an intermediate climate tending to occur within warmer south-facing stand topographies (*Figure 5.40; Table 5.17*). At a microhabitat scale, the Community Type I tends towards the upper surface of leaning trees, in contrast to Community Type H (*Hypnum-Usnea* Community; see *Section 5.8*).

Figure 5.39. **The dominant indicator species of the *Hypnum-Microlejeunea* Community, *Hypnum andoi*, forming a pendulous bryophyte mat.**

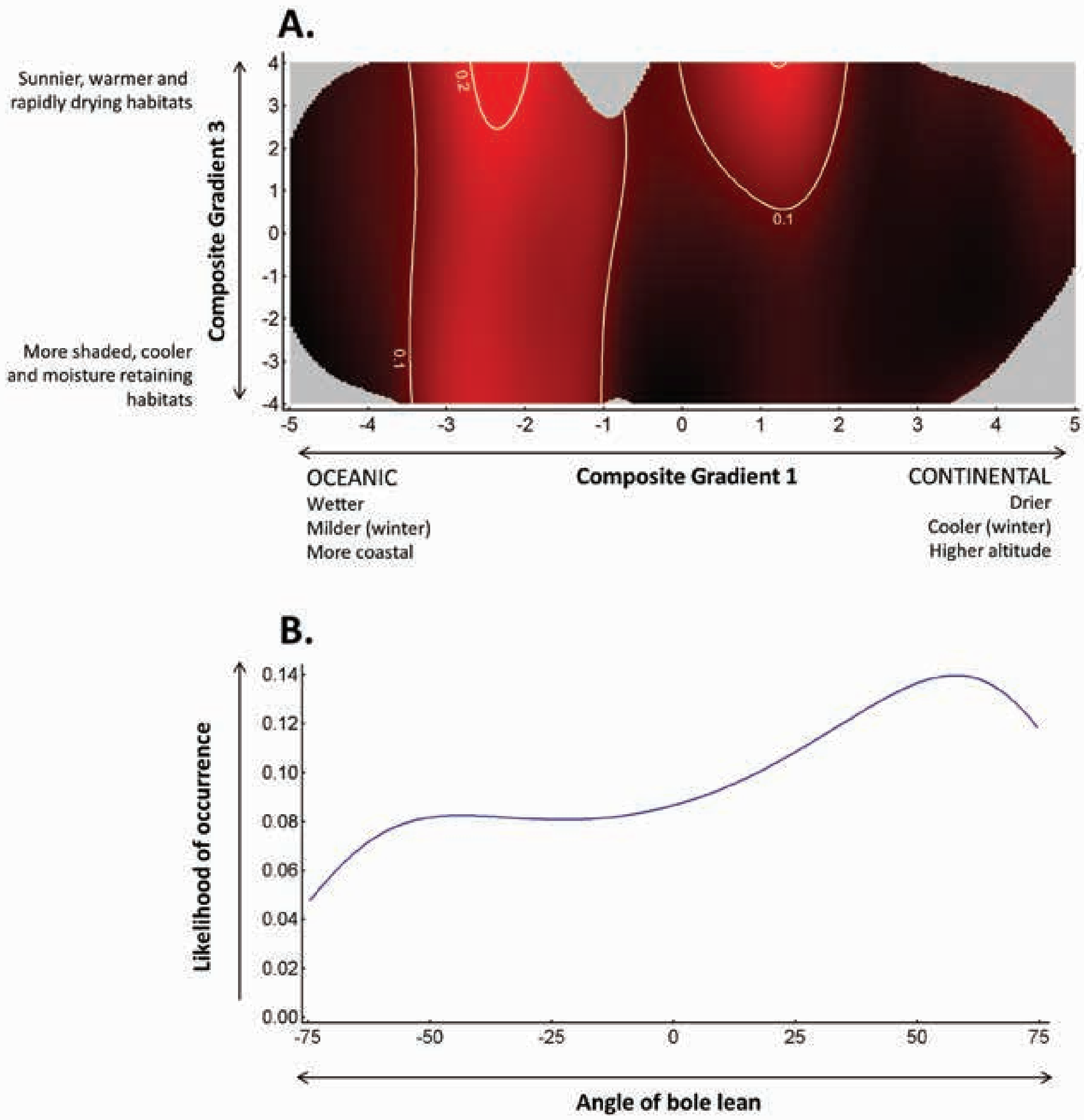


Figure 5.40. Response surface (*part A.*) and curve (*part B.*), showing variability in the likelihood of occurrence for the Type I *Hypnum-Microlejeunea* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.17*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

Table 5.17. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Hypnum-Microlejeunea* Community in relation to the variability of Composite Gradient 1 (macroclimate), Composite Gradient 3 (stand topography), angle of bole lean and canopy openness (not shown). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log$B$	AUC	$_{MC}P$
Composite Gradient 1	0.501 (5%)	0.384	10.29	0.728	<0.01
Composite Gradient 3	1.73 (15%)	0.126			
Angle of bole lean	20.5 (10%)	0.146			
Canopy openess (%)	13.78 (20%)	0.061			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The Type I *Hypnum-Microlejeunea* Community is geographically widely distributed across the sampled woodland stands in different climates, and with different stand characteristics (*Figure 5.41*).

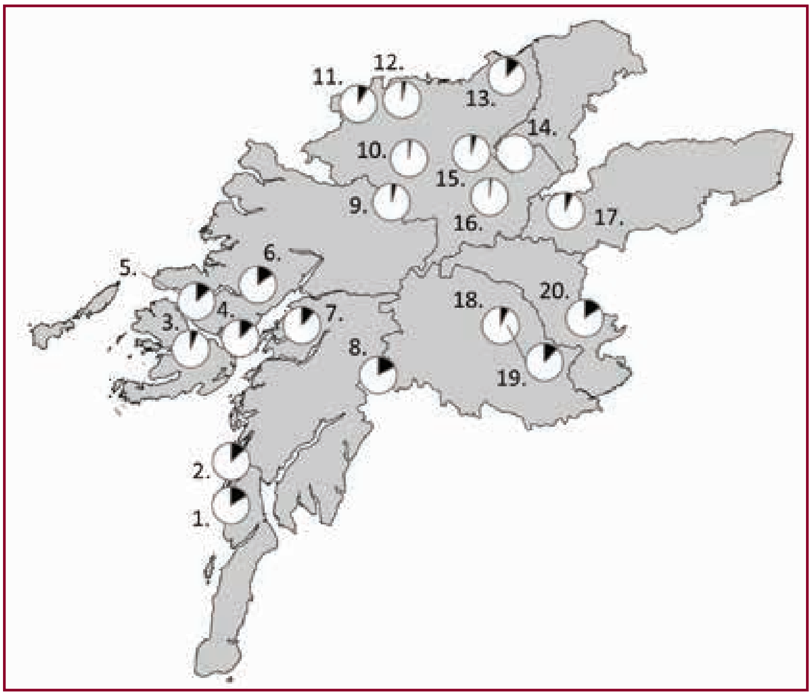


*Figure 5.41.***The percent contribution (in black) of the *Hypnum-Microlejeunea* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

The *Hypnum-Microlejeunea* Community has five diagnostic species (*Table 5.18*). None of these species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. None of the species are strongly associated with woodlands that have ecological continuity.

Bioclimatic modelling indicated mixed results, with locally variable increases or decreases in environmental suitability for the two lichen species in the *Hypnum-Microlejeunea* community through to the late-21st Century (*Figure 5.42*).

Table 5.18. The statistically significant indicator species for the Type I *Hypnum-Microlejeunea* Community, with notes on the species conservation status and association with ecological continuity.

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Hypnum andoi	85%	27%	0.75			0.0001
Microlejeunea ulicina	36%	27%	0.41			0.005
Associated						
Cladonia coniocraea	16%	31%	0.57			0.0086
Dicranum scoparium	20%	23%	0.67			0.0119
Lepraria rigidula	22%	21%	0.51			0.0398

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

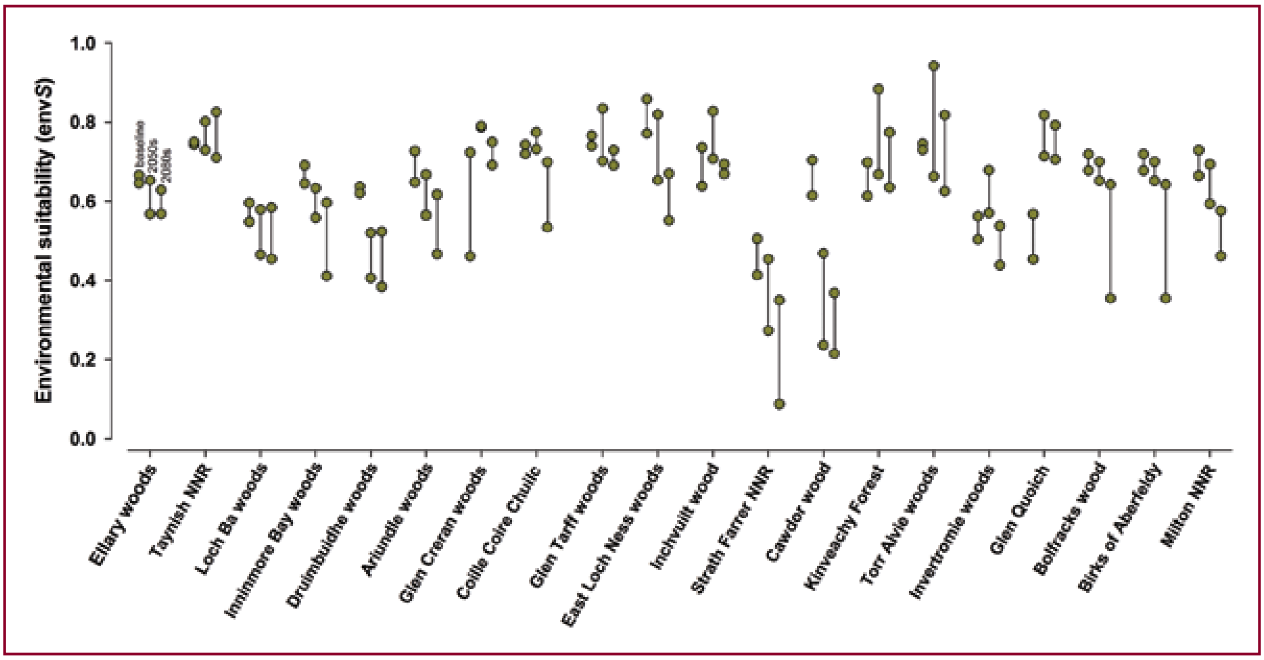


Figure 5.42. Bioclimatic modelled values of environmental suitability (env*S*) for the lichens within the *Hypnum-Microlejeunea* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Point plots for each site show the estimated values of env*S* for lichen species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s.

5.10 **Type J**

***Frullania tamarisci* Community** FBCS = HIGH

The ‘Type J’ *Frullania tamarisci* Community (*Figure 5.43*) has its maximum occurrence under two sets of environmental conditions, within an intermediate climatic zone in moderately mesotrophic stand types and microhabitats, and in an oceanic climatic zone, in relatively more oligotrophic stand types and microhabitats (*Figure 5.44; Table 5.19*). Similarly with respect to canopy cover, in an intermediate climate it appears to increase in areas of open canopy, though for oceanic climates it occurs under a wider range of canopy conditions.

Figure 5.43. **The dominant indicator *Frullania tamarisci* forming an epiphyte community on hazel.**

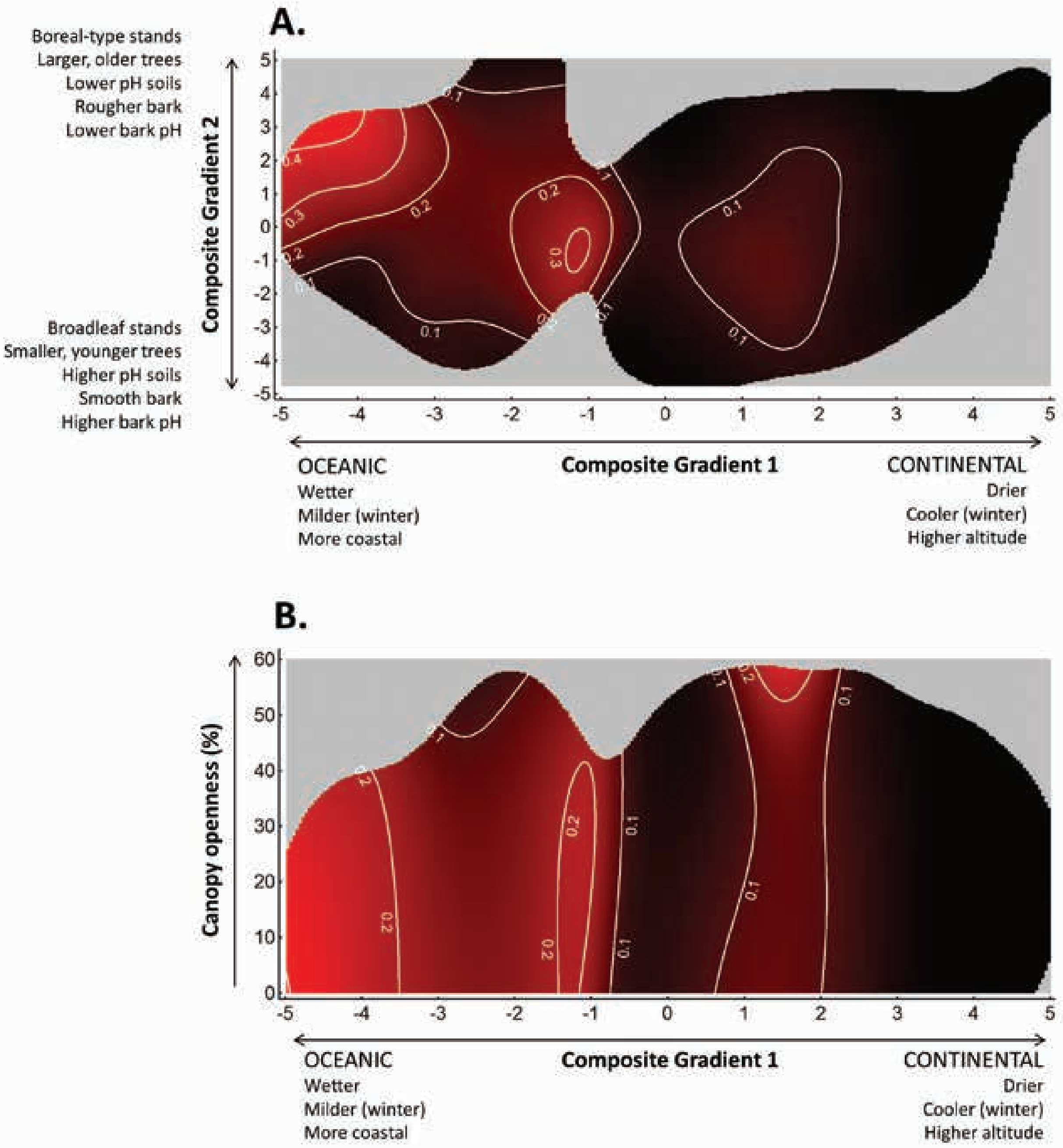


Figure 5.44. Response surfaces showing variability in the likelihood of occurrence for the Type J *Frullania tamarisci* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.19*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

Table 5.19. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Frullania tamarisci* Community in relation to the variability of Composite Gradient 1 (macroclimate), Composite Gradient 2 (tree-scale environment) and canopy openness (percent). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	0.501 (5%)	0.539	17.98	0.743	<0.01
Composite Gradient 2	1.06 (10%)	0.253			
Canopy openess (%)	17.22 (25%)	0.044			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The Type J *Frullania tamarisci* Community is geographically broadly distributed and common across woodland sites in different climates, though especially so for oceanic broadleaf settings (*Figure 5.45*).

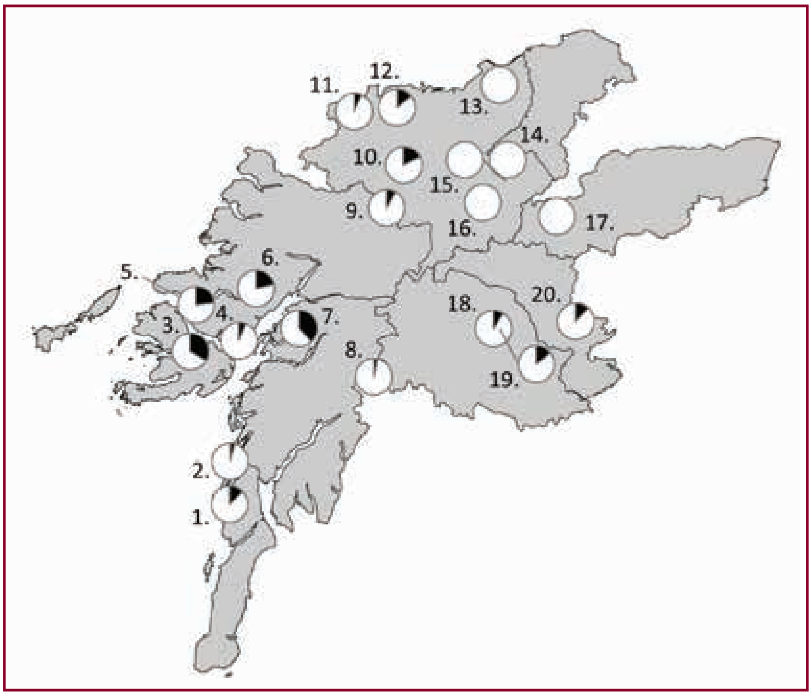


Figure 5.45. **The percent contribution (in black) of the *Frullania tamarisci* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

Table 5.20. **The statistically significant indicator species for the Type J *Frullania tamarisci* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Frullania tamarisci	86%	42%	0.77			0.0001
Associated						
Harpalejeunea molleri	10%	55%	0.64			0.0142

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

The *Frullania tamarisci* Community had only two diagnostic species (*Table 5.20*), both liverworts. Neither of the species was identified as threatened according to IUCN criteria, or occurred on the Scottish Biodiversity List. The community included only bryophyte species, and bioclimatic modelling was unavailable.

5.11 **Type K**

***Lobaria pulmonaria – Isothecium myosuroides* Community** FBCS = HIGH

The 'Type K' *Lobaria-Isothecium* Community (*Figure 5.46*), is with Community Type G (*Lobaria-Normandina-Metzgeria* Community; see Section 5.7) and Community Type M (*Hypotrachyna-Loxospora* Community; see Section 5.13) among the dominant lichen epiphyte communities in Scotland's zone of oceanic temperate rainforest. In terms of microhabitat requirements, the *Lobaria-Isothecium* Community demonstrates an interaction between the macroclimatic setting and the local climate (humidity) captured here as the distance to water. Community Type K does not appear to be as demanding of higher pH/nutrient conditions as Community Type G (*Figure 5.47; Table 5.21*), and it will more frequently grow on the relatively leached bark of older broadleaved trees on poor soils (*Figure 5.48*), especially on the upper surface of leaning trees.

Figure 5.46. **The dominant indicator species of the *Lobaria-Isothecium* Community on a recumbent hazel stem, with the foliose *Lobaria pulmonaria* embedded within a large mat of *Isothecium myosuroides*.**

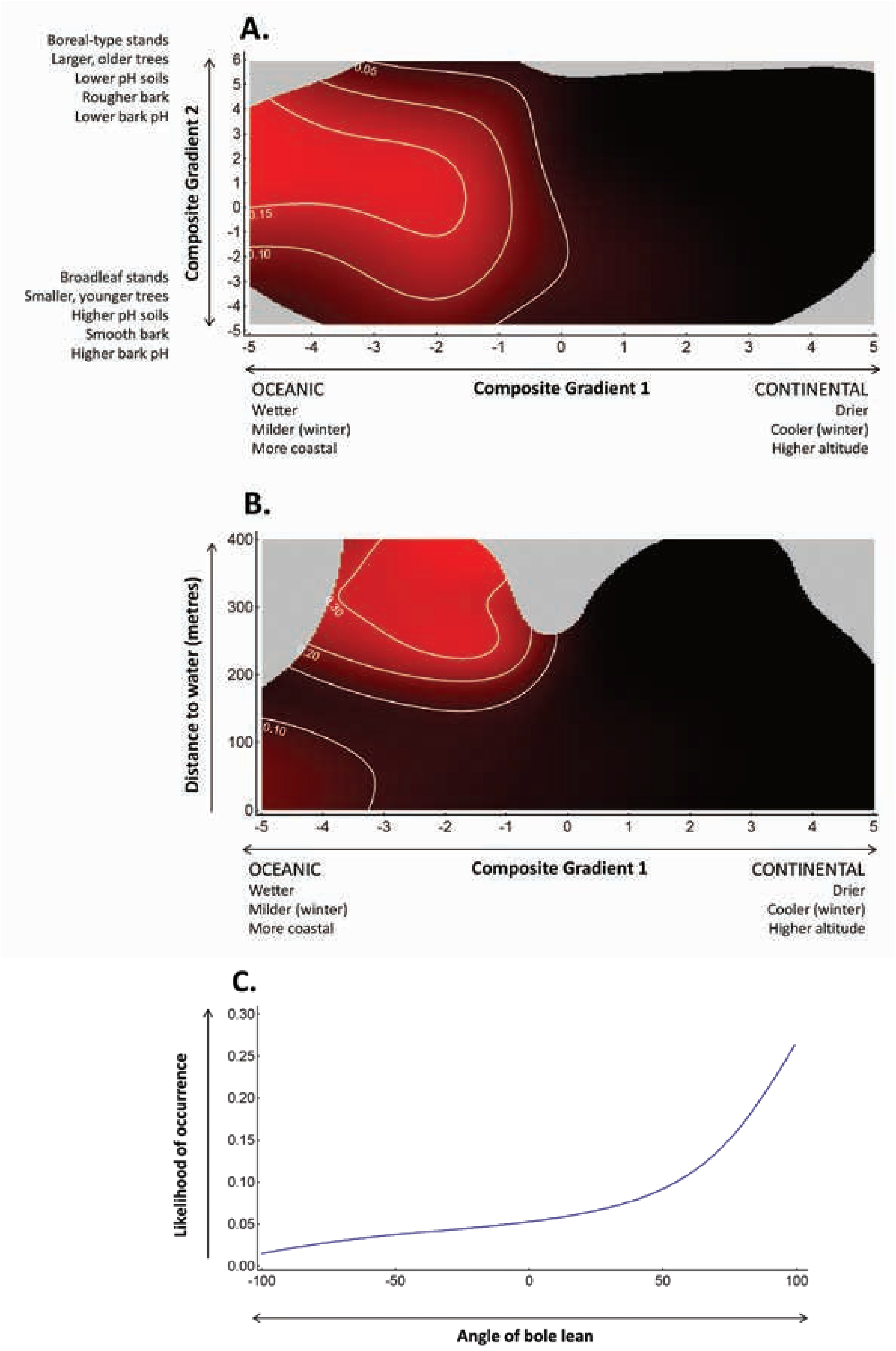


Figure 5.47. Response surfaces showing variability in the likelihood of occurrence for the Type K *Lobaria-Isothecium* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.21*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space (*parts A.* and *B.*), and a response curve (*part C.*) showing variability in the likelihood of occurrence for the angle of bole lean (cf. *Table 5.21*).

Table 5.21. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Lobaria-Isothecium* Community in relation to the variability of Composite Gradient 1 (macroclimate), Composite Gradient 2 (tree-scale environment), distance to water (metres), and angle of bole lean. Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	1.002 (10%)	0.141	25.83	0.876	<0.01
Composite Gradient 2	1.604 (15%)	0.083			
Distance to water (metres)	51 (10%)	0.096			
Angle of bole lean	30.75 (15%)	0.109			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

Figure 5.48. **A large and old oak tree with open structured canopy, representing a leached habitat type on which the *Lobaria-Isothecium* Community can be found, especially in climatically optimum oceanic regions.**

The Type K *Lobaria-Isothecium* Community is geographically most common in broadleaf woodland sites in oceanic western Scotland, though it also occurred in high rainfall areas of the central Highlands, and less commonly in suitable local microhabitats for lowland broadleaved woodlands of eastern Scotland (*Figure 5.49*).

The *Lobaria-Isothecium* Community has five diagnostic species (*Table 5.22*). None of these species are identified as threatened according to IUCN criteria, though two species are included on the Scottish Biodiversity List because of an International Responsibility for their conservation and these are strongly associated with woodlands that have ecological continuity.

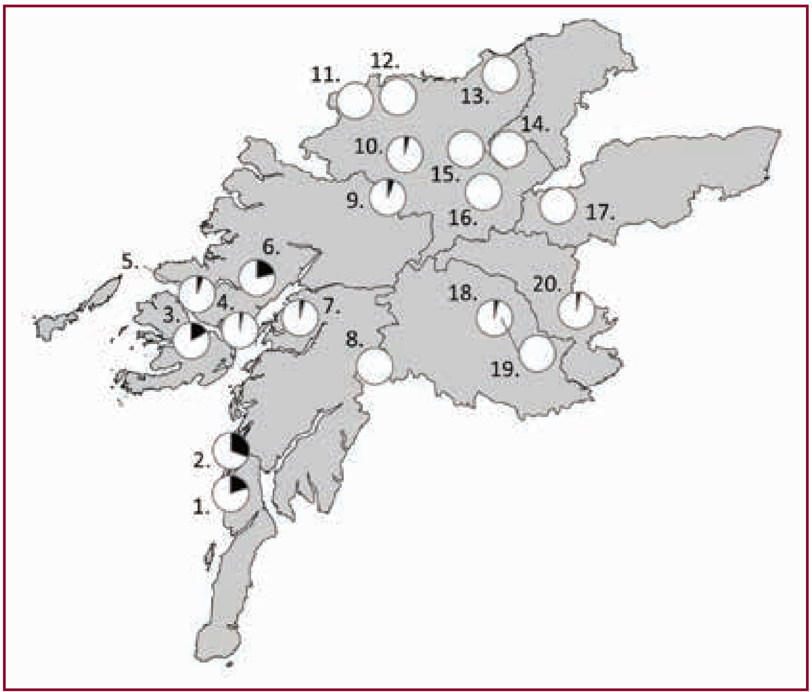


Figure 5.49. **The percent contribution (in black) of the *Lobaria-Isothecium* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

Table 5.22. **The statistically significant indicator species for the Type K *Lobaria-Isothecium* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	Association Values			Conservation Status	Ecological Continuity	Indicator *P*
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Lobaria pulmonaria	39%	36%	0.73	SBL; IR	C&C = ESIEC/NPIEC; W&E < 0.005	0.0001
Isothecium myosuroides	85%	52%	0.79			0.0001
Associated						
Hypotrachyna taylorensis	10%	38%	0.43	SBL; IR	C&C = WSIEC/ EUOCIEC; E = 0.0196	0.0217
Parmotrema crinitum	26%	36%	0.33			0.0032
Parmotrema perlatum	11%	28%	0.44			0.0323

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

Bioclimatic modelling shows the clear difference in environmental suitability as a threshold between the western oceanic and relatively continental eastern sample sites. Across all sites, though for eastern sites in particular, a warming climate with consistent levels of wetness/humidity points to increases in environmental suitability for the individual lichen species in the *Lobaria-Isothecium* Community through to the late-21st Century (*Figure 5.50*).

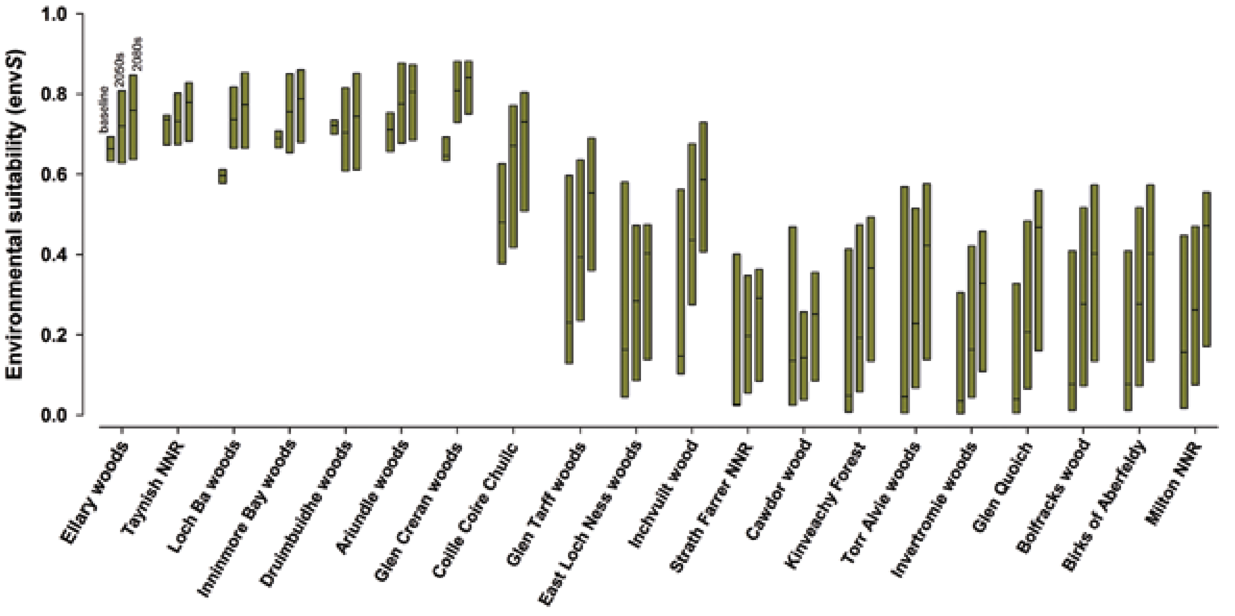


Figure 5.50. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Lobaria-Isothecium* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

5.12 **Type L**

Arthopyrenia cinereopruinosa – Lecanora pulicaris Community FBCS = LOW

The loosely defined 'Type L' *Arthopyrenia-Lecanora* Community (*Figure 5.51*) has similar environmental requirements to Community Type N (*Mycoblastus-Protoparmelia-Sphaerophorus* Community; see Section 5.14), being most common at sites with intermediate conditions falling between the more continental Boreal-type woodlands characterised by Community Type O (*Bryoria-Ochrolechia-Parmeliopsis* Community; see Section 5.15), and the temperate rainforest systems of Scotland's west coast (*Figure 5.52; Table 5.23*). Within this intermediate setting, Community Type L is locally frequent in open woodland stands that have lower levels of humidity, exemplified by its increasing occurrence away from water courses.

Figure 5.51. ***Lecanora pulicaris*, one of the characteristic species of the *Arthopyrenia-Lecanora* Community.**

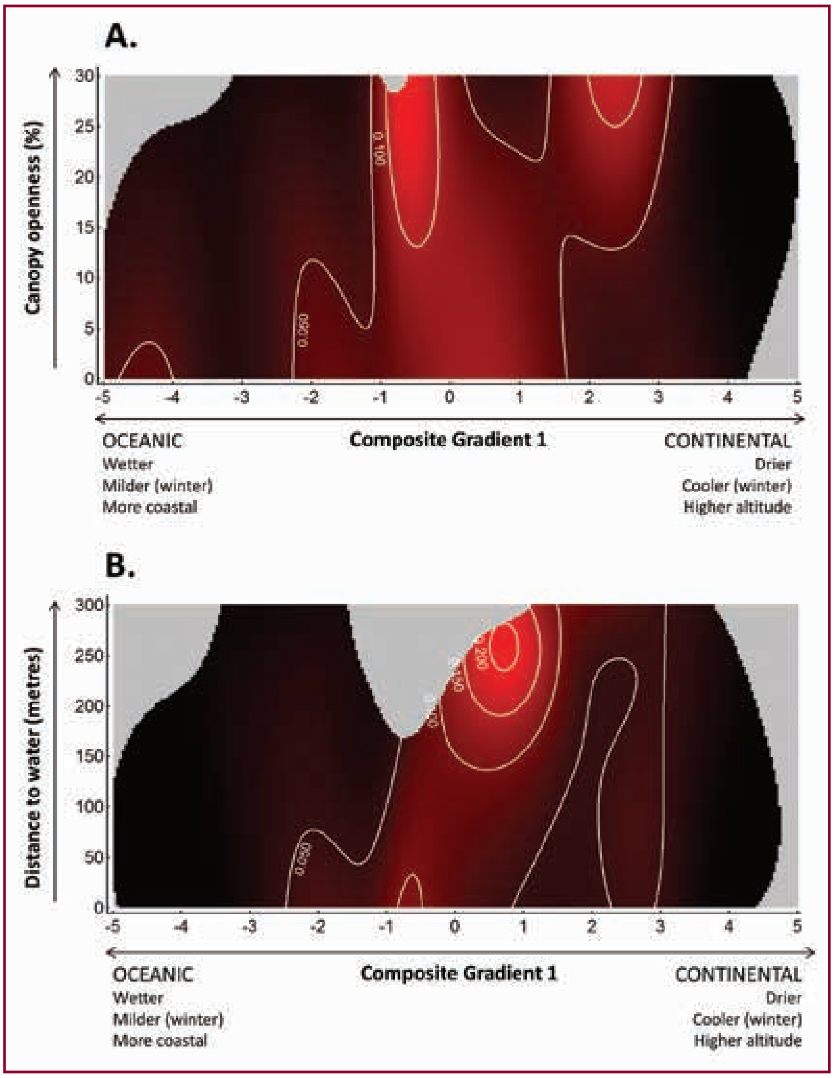


Figure 5.52. Response surfaces showing variability in the likelihood of occurrence for the Type L *Arthonia-Lecanora* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.23*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

Table 5.23. Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Arthopyrenia-Lecanora* Community in relation to the variability of Composite Gradient 1 (macroclimate), distance to water (metres) and canopy openness (percent). Other variables were not significant.

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	0.501 (5%)	0.255	7.63	0.704	0.0198
Composite Gradient 2	76.5 (15%)	0.076			
Canopy openness (%)	10.34 (15%)	0.056			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The Type L *Arthopyrenia-Lecanora* Community is geographically widespread, with its sampled distribution extending to sites lying east and westwards of a core range in the central Highlands (*Figure 5.53*).

The *Arthopyrenia-Lecanora* Community has five diagnostic species (*Table 5.24*). None of these species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. None of the species are strongly associated with woodlands that have ecological continuity. The relatively low Association Values for indicator species, with the samples identified as belonging to Community Type L, suggests the *Arthopyrenia-Lecanora* Community is less easily defined and represents a far less reliable grouping than for some of the other epiphyte community types.

Figure 5.53. **The percent contribution (in black) of the *Arthopyrenia-Lecanora* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods),
4. IB (Inninmore Bay woods),
5. DR (Druimbuidhe woods),
6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods),
10. EN (East Loch Ness woods),
11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood),
14. KF (Kinveachy Forest),
15. TA (Torr Alvie woods),
16. IV (Invertromie woods),
17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy),
20. MW (Milton NNR).

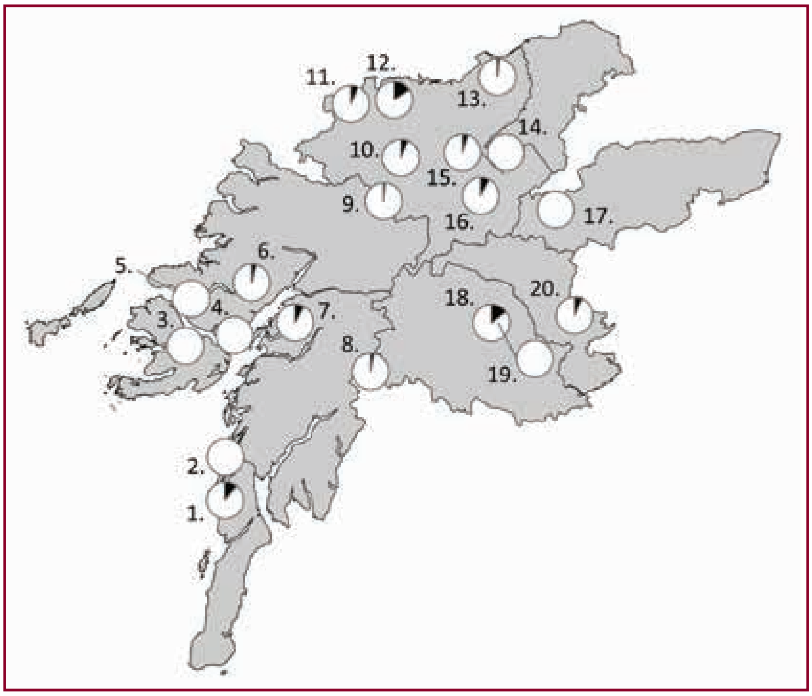


Table 5.24. **The statistically significant indicator species for the Type L *Arthopyrenia-Lecanora* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Arthopyrenia cinereopruinosa	22%	65%	0.56			0.0001
Lecanora pulcaris	22%	38%	0.63			0.0003
Associated						
Chrysothrix flavovirens	12%	30%	0.72			0.0012
Micarea micrococca agg.	18%	9%	0.39			0.0248
Pertusaria pupillaris	18%	24%	0.44			0.0011

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

Bioclimatic modelling points to a potential decline in environmental suitability for individual species in the *Arthopyrenia-Lecanora* Community (*Figure 5.54*), although this potential decline is more apparent for sites in the central Highlands and north-eastern Scotland.

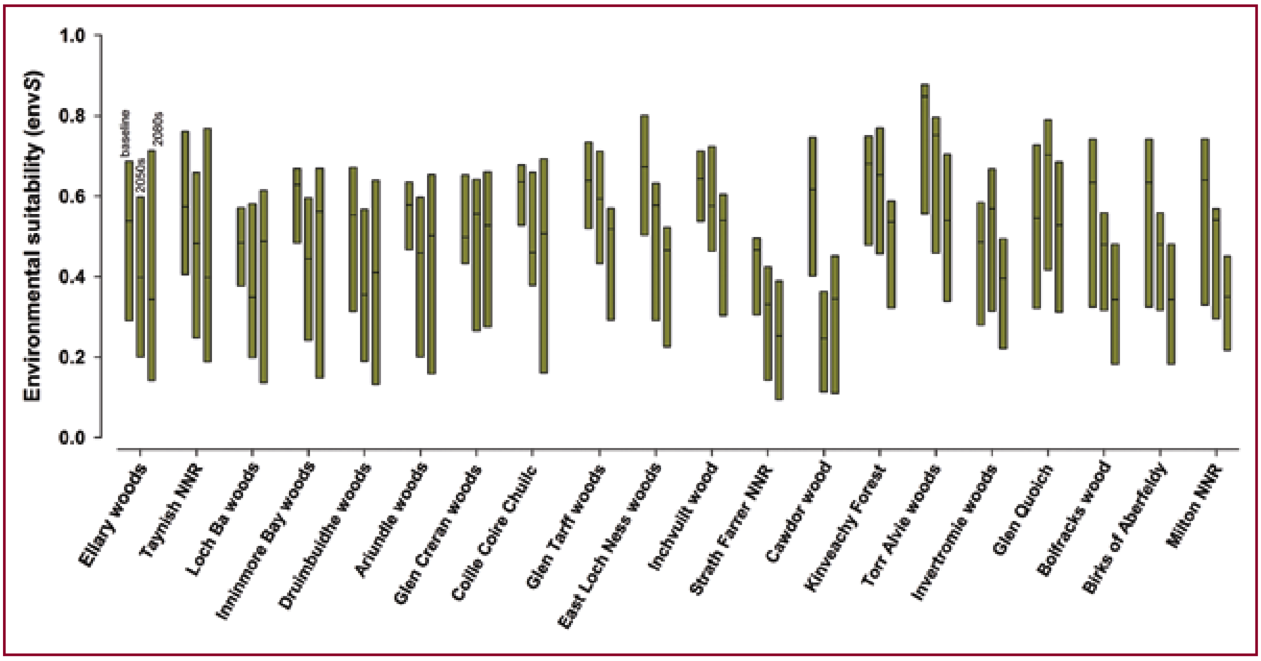


Figure 5.54. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Arthopyrenia-Lecanora* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

5.13 **Type M**

***Hypotrachyna laevigata – Loxospora elatina* Community** **FBCS = HIGH**

The ‘Type M’ *Hypotrachyna-Loxospora* Community (*Figure 5.55*) is a common community type in oceanic and intermediate climates, where it shows a preference for oligotrophic microhabitats in mesotrophic broadleaved or mixed woodlands (*Figure 5.56; Table 5.25*). It also tends to be more abundant in stands which are shaded and less sun exposed and not prone to frequent drying.

Figure 5.55. **The *Hypotrachyna-Loxospora* Community on a mature alder, with the white crustose *Loxospora elatina* with pale yellow-green coloured soralia, and the blue-grey foliose *Hypotrachyna laevigata* with characteristic deep sinuses to the lobes, and terminal soredia at the lobe ends.**

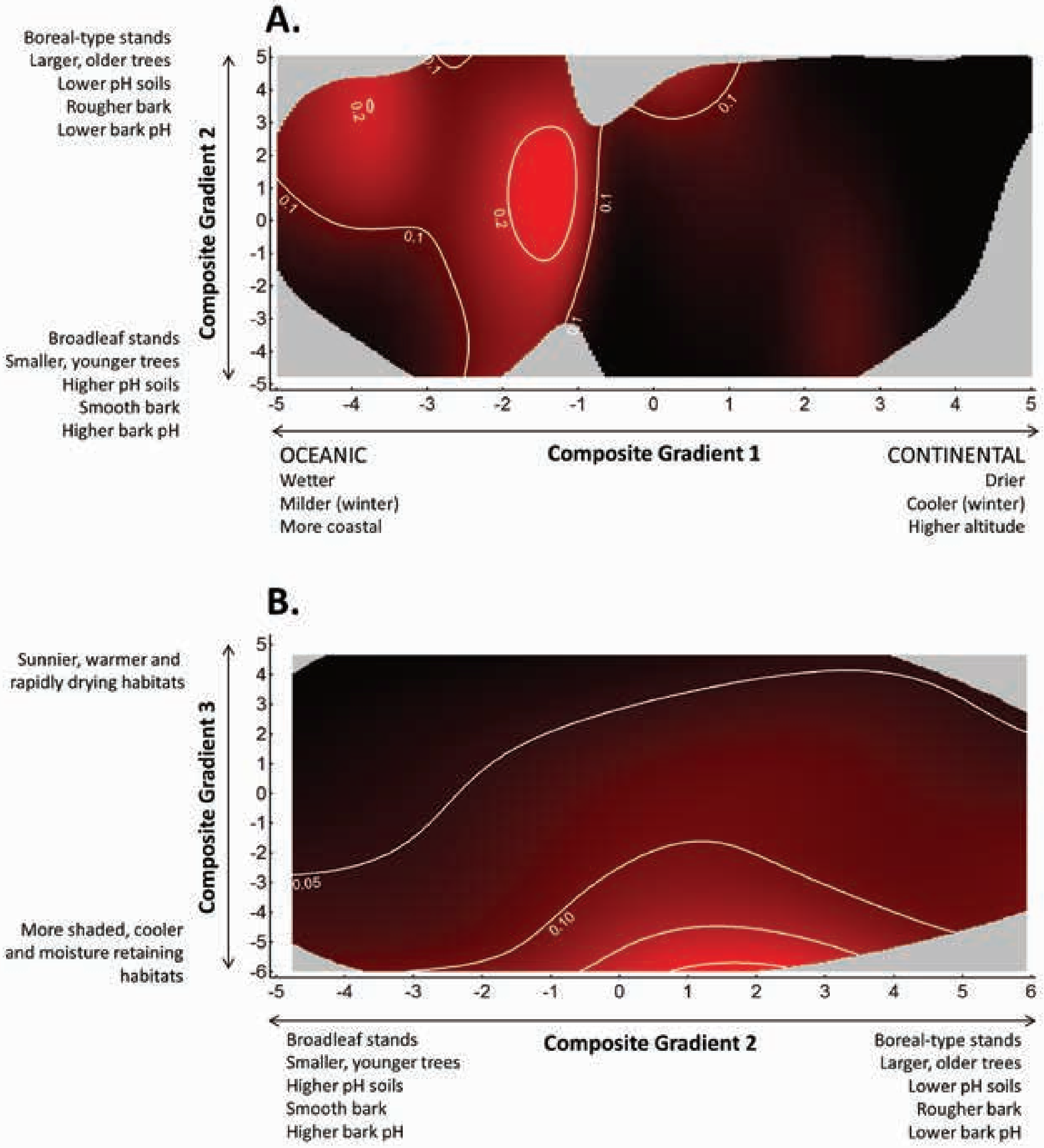


Figure 5.56. Response surfaces showing variability in the likelihood of occurrence for the Type M *Hypotrachyna-Loxospora* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.25*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.

Table 5.25. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Hypotrachyna-Loxospora* Community in relation to the variability of Composite Gradient 1 (macroclimate), Composite Gradient 2 (tree-scale environment) and Composite Gradient 3 (stand topography). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	0.501 (5%)	0.342	13.82	0.764	<0.01
Composite Gradient 2	1.604 (15%)	0.116			
Composite Gradient 3	1.734 (15%)	0.105			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The Type M *Hypotrachyna-Loxospora* Community is geographically most common in broadleaf woodland sites in oceanic western Scotland and also occurs in mixed woods in high rainfall areas of the central Highlands (*Figure. 5.57*). It is absent from drier lowland sites in eastern Scotland, and is less common at sites within the most continental climatic zone in north-eastern Scotland.

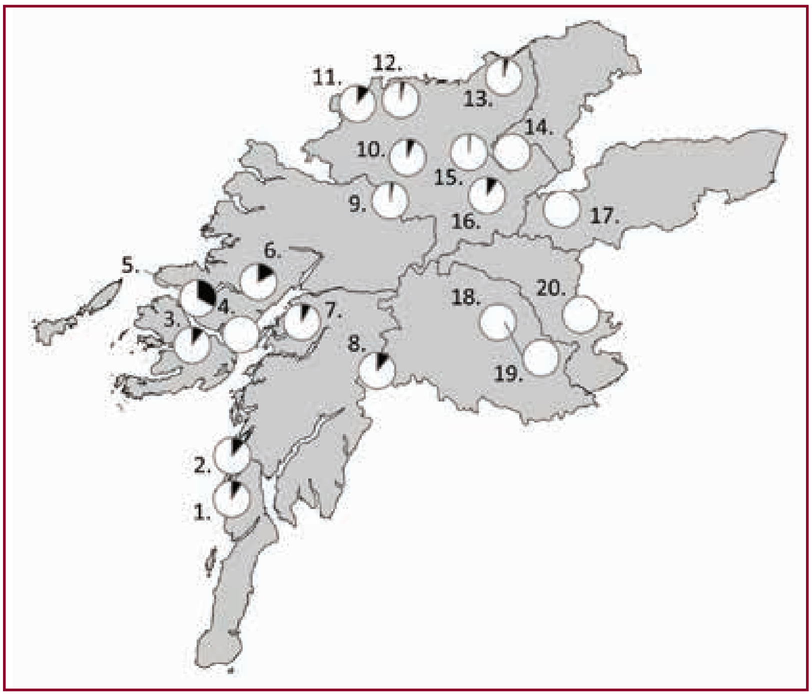


Figure 5.57. **The percent contribution (in black) of the *Hypotrachyna-Loxospora* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

The *Hypotrachyna-Loxospora* Community has five diagnostic species (*Table 5.26*). None of these species are identified as threatened according to IUCN criteria, occur on the Scottish Biodiversity List, or carry a level of International Responsibility. However, three of the species are strongly associated with woodlands that have ecological continuity, including *Hypotrachyna laevigata*.

Bioclimatic modelling points in general to locally variable small declines or increases in environmental suitability for the individual lichen species in the *Hypotrachyna-Loxospora* Community (*Figure 5.58*).

Table 5.26. **The statistically significant indicator species for the Type M *Hypotrachyna-Loxospora* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Hypotrachyna laevigata	29%	54%	0.55		C&C = EUOCIEC/NPIEC; E = 0.0051	0.0001
Loxospora elatina	25%	20%	0.44		C&C = EUOCIEC/NPIEC; E = 0.0034	0.0045
Associated						
Anisomeridium ranunculosporum	17%	24%	0.47			0.0065
Mycoblastus caesius	19%	24%	0.36		C&C = EUOCIEC; E = 0.034	0.0109
Scapania gracilis	12%	42%	0.28			0.0249

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

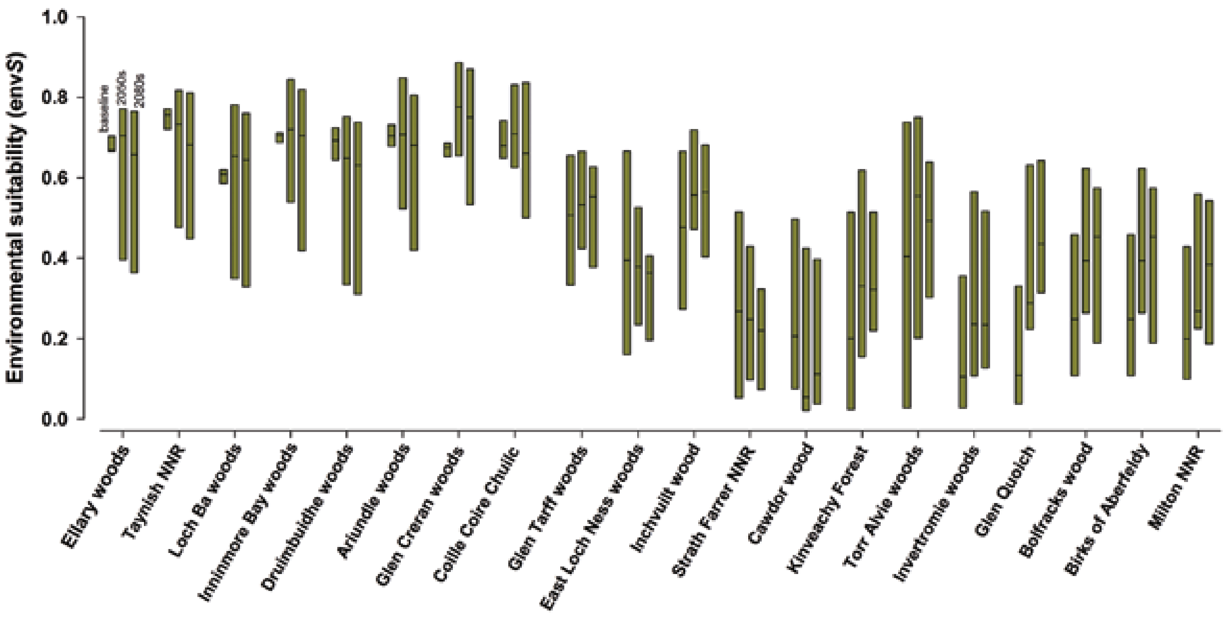


Figure 5.58. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Hypotrachyna-Loxospora* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line) and the interquartile range (box).**

5.14 **Type N**

***Mycoblastus sanguinarius – Protoparmelia ochrococca – Sphaerophorus globosus* Community** FBCS = HIGH

The ‘Type N’ *Mycoblastus-Protoparmelia-Sphaerophorus* Community (*Figure 5.59*) tends to occur in more humid environments than the similar Community Type O (*Bryoria-Ochrolechia-Parmeliopsis* Community; see Section 5.15), and it is locally frequent especially on older and relatively acid-barked trees (*Figure 5.60; Table 5.27*). There is a clear association with Scots pine and birch, though also with aspen and alder where these occur in oligotrophic habitats (*Figure 5.61*).

Figure 5.59. **The indicative members of the *Mycoblastus-Protoparmelia-Sphaerophorus* Community.**

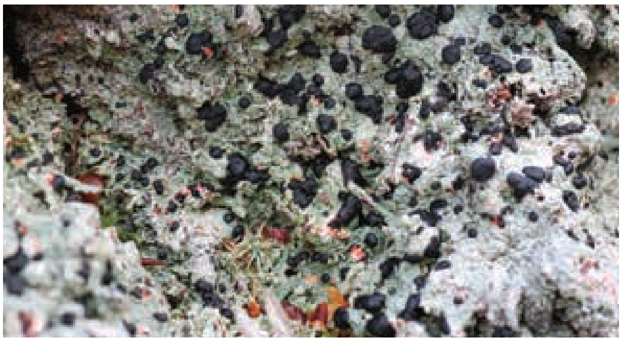


Figure 5.59. A. ***Mycoblastus sanguinarius***

Figure 5.59. B. ***Protoparmelia ochrococca***

Figure 5.59. C. ***Sphaerophorus globosus***

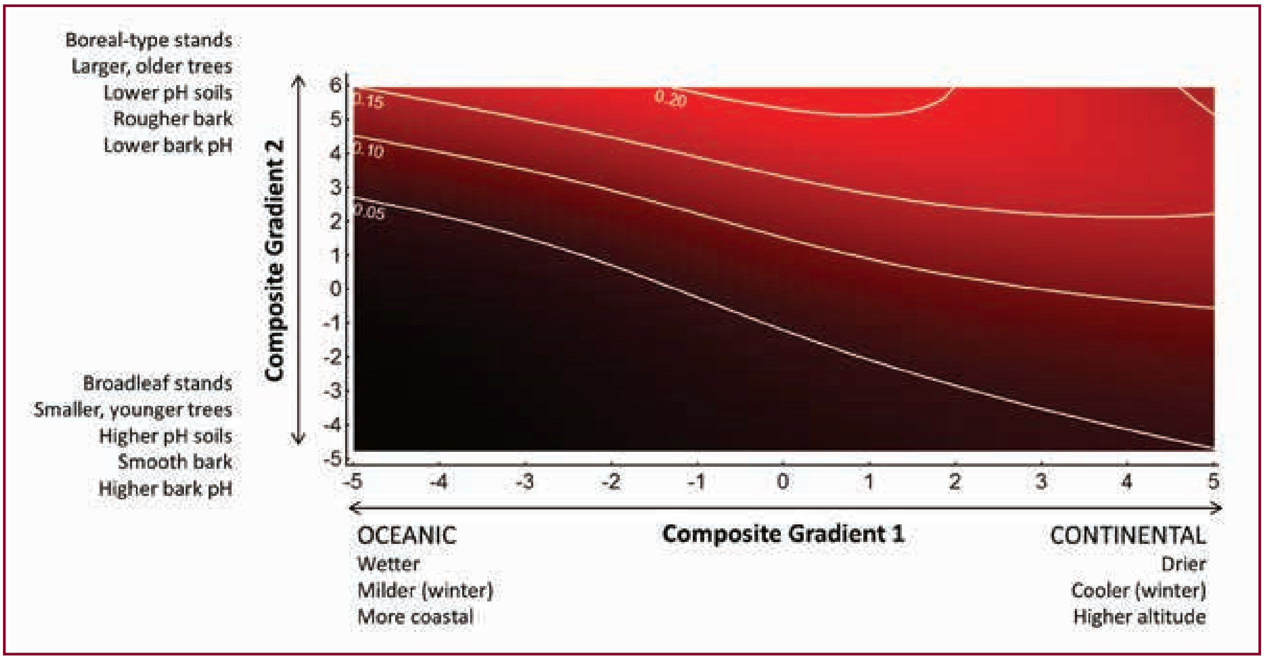


Figure 5.60. **Response surface showing variability in the likelihood of occurrence for the Type N *Mycoblastus-Protoparmelia-Sphaerophorus* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.27*). Contours show likelihood values from red (higher values), to black (lower values).**

Table 5.27. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Mycoblastus-Protoparmelia-Sphaerophorus* Community in relation to the variability of Composite Gradient 1 (macroclimate, Composite Gradient 2 (tree-scale environment), and tree species identity. Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	2.507 (25%)	0.072	26.56	0.863	<0.01
Composite Gradient 2	2.139 (20%)	0.082			
Tree species identity					

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

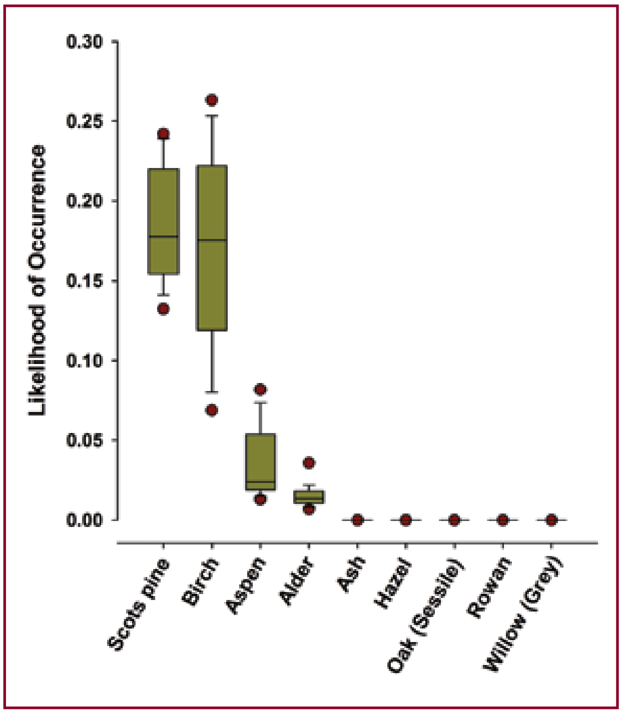
Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

Figure 5.61. **Variability in the likelihood of occurrence for the Type N *Mycoblastus-Protoparmelia-Sphaerophorus* Community, compared to tree species identity, which was identified as an important factor in an optimised statistical model (cf. *Table 5.27*).**



The *Mycoblastus-Protoparmelia-Sphaerophorus* Community is distributed beyond the relatively more continental climatic zone of north-eastern Scotland, towards the central Highlands, where it occurs in mixed woodlands in a wetter climate (*Figure 5.62*).

The *Mycoblastus-Protoparmelia-Sphaerophorus* Community has nine diagnostic species (*Table 5.28*). As is the case for *Hypogymnia physodes* in Community Type O (*Bryoria-Ochrolechia-Parmeliopsis* Community; see Section 5.15), the *Mycoblastus-Protoparmelia-Sphaerophorus* Community was dominated by a relatively widespread species, *Platismatia glauca* (*Figure 5.63*); 99% of samples had *P. glauca*, which on average occupied > 66% of the bark space within the community. However, *P. glauca* also occurs in a range of other community types, and although this species provides a useful guide to the possible occurrence of the *Mycoblastus-Protoparmelia-Sphaerophorus* Community, it is not diagnostic unless accompanied by at least one of the key indicators (*Mycoblastus sanguinarius, Protoparmelia ochrococca* and/or *Sphaerophorus globosus*), as well as associated specialist species such as *Micarea synotheoides, Ochrolechia androgyna* or *Parmelia saxatilis* agg. (*Figure 5.64*).

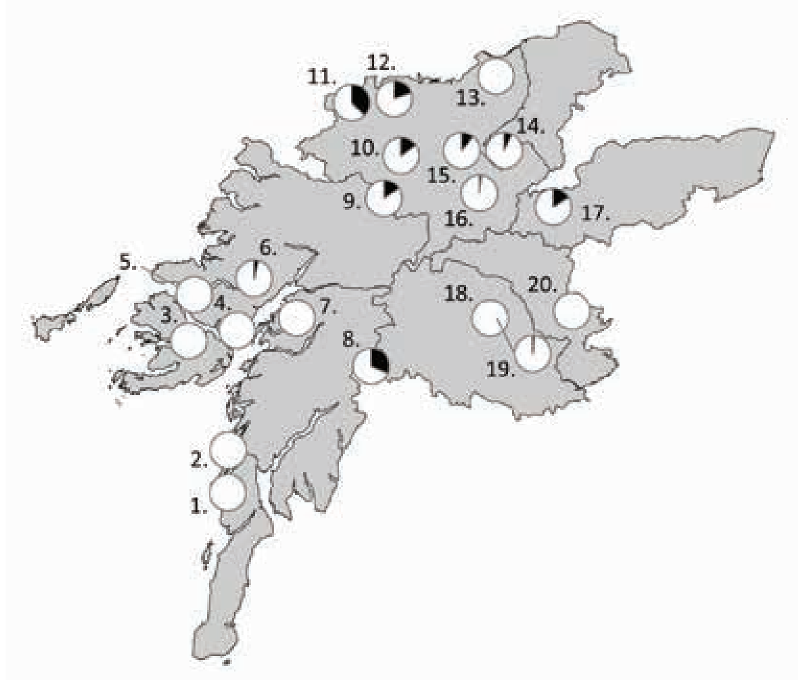


Figure 5.62. The percent contribution (in black) of the *Mycoblastus-Protoparmelia-Sphaerophorus* Community to the epiphyte assemblages in each of the twenty woodland study sites. Site Codes: 1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

Table 5.28. The statistically significant indicator species for the Type N *Mycoblastus-Protoparmelia-Sphaerophorus* Community, with notes on the species conservation status and association with ecological continuity.

SPECIES	Association Values			Conservation Status	Ecological Continuity	Indicator *P*
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Mycoblastus sanguinarius	45%	44%	0.35		C&C = EUOCIEC; W&E < 0.05; E = 0.0031	0.0001
Protoparmelia ochrococca	31%	37%	0.2		C&C = NPIEC	0.0004
Sphaerophorus globosus	26%	44%	0.43		C&C = EUOCIEC; E = 0.0016	0.0002
Associated						
Cladonia macilenta/ polydactyla	28%	25%	0.31			0.0335
Micarea synotheoides	15%	46%	0.17	SBL; IR	C&C = NPIEC	0.0057
Ochrolechia androgyna	27%	22%	0.4			0.001
Parmelia saxatilis agg.	47%	20%	0.37			0.0001
Platismatia glauca	99%	37%	0.66			0.0264
Usnea subfloridana	11%	36%	0.33			0.0087

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

Figure 5.63. **The common lichen *Platismatia glauca*, with a crinkled foliose structure and brown underside.**

Figure 5.64. **Two easily identified species which are closely associated with the *Mycoblastus-Protoparmelia-Sphaerophorus* Community, (Left)** *Figure 5.64. A*. ***Ochrolechia androgyna*, and (Right)** *Figure 5.64. B.* ***Parmelia saxatilis* agg.**

The *Mycoblastus-Protoparmelia-Sphaerophorus* Community has no species identified as threatened according to IUCN criteria. However, *Micarea synotheoides* is included on the Scottish Biodiversity List, and signalled as having an international conservation obligation for the UK, while four of the diagnostic species are thought to be strongly associated with woodlands that have ecological continuity. Bioclimatic modelling suggests that individual lichen species in the community are likely to experience reduced climatic suitability throughout Scotland by the mid- to late-21st Century (*Figure 5.65*), especially in the central Highland region, representing a potential long-term risk to this community type in Scotland.

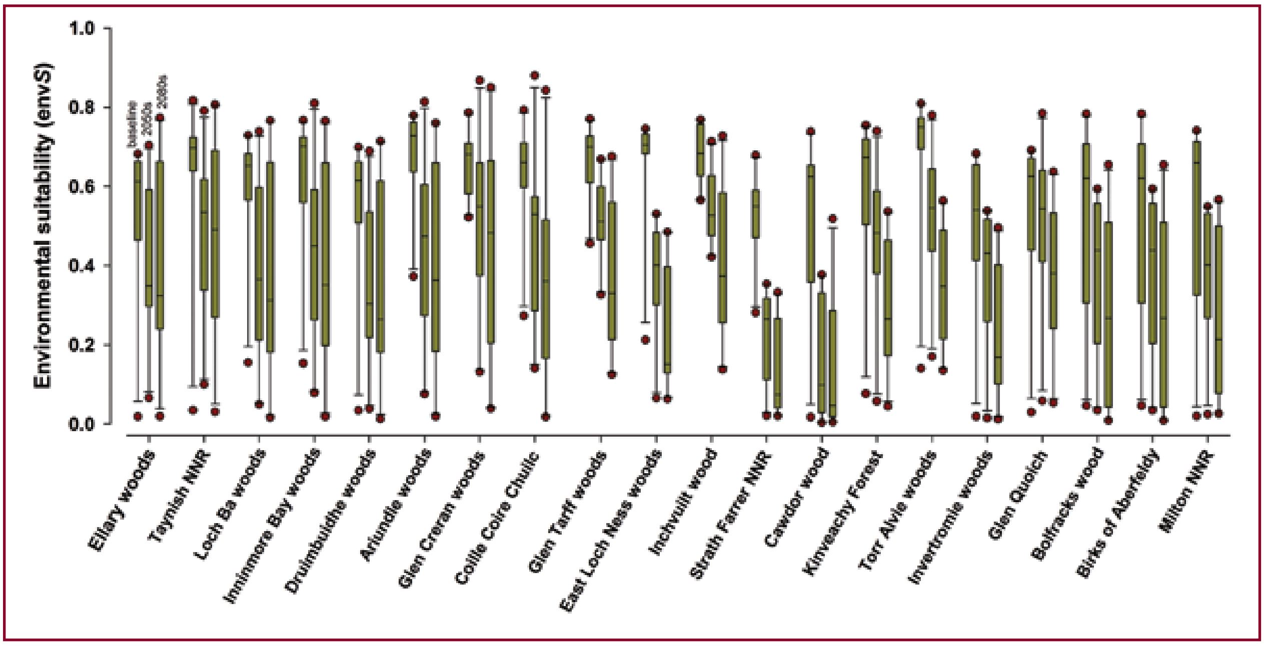


Figure 5.65. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Mycoblastus-Protoparmelia-Sphaerophorus* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots).**

5.15 Type O

Bryoria fuscescens – Ochrolechia microstictoides – Parmeliopsis hyperopta Community FBCS = HIGH

The 'Type O' *Bryoria-Ochrolechia-Parmeliopsis* Community (*Figure 5.66*) is the one of the commonest epiphyte community types in the drier and more continental climatic region of north-eastern Scotland, especially on older and relatively acid-barked trees (*Figure 5.67; Table 5.29*).

Figure 5.66. **The *Bryoria-Ochrolechia-Parmeliopsis* Community, with (Left)** *Figure 5.66. A.* **Fruticose and pendulous *Bryoria fuscescens* growing with the white sterile crustose *Ochrolechia microstictoides*, and (Right)** *Figure 5.66. B.* **The foliose and sorediate *Parmeliopsis hyperopta*.**

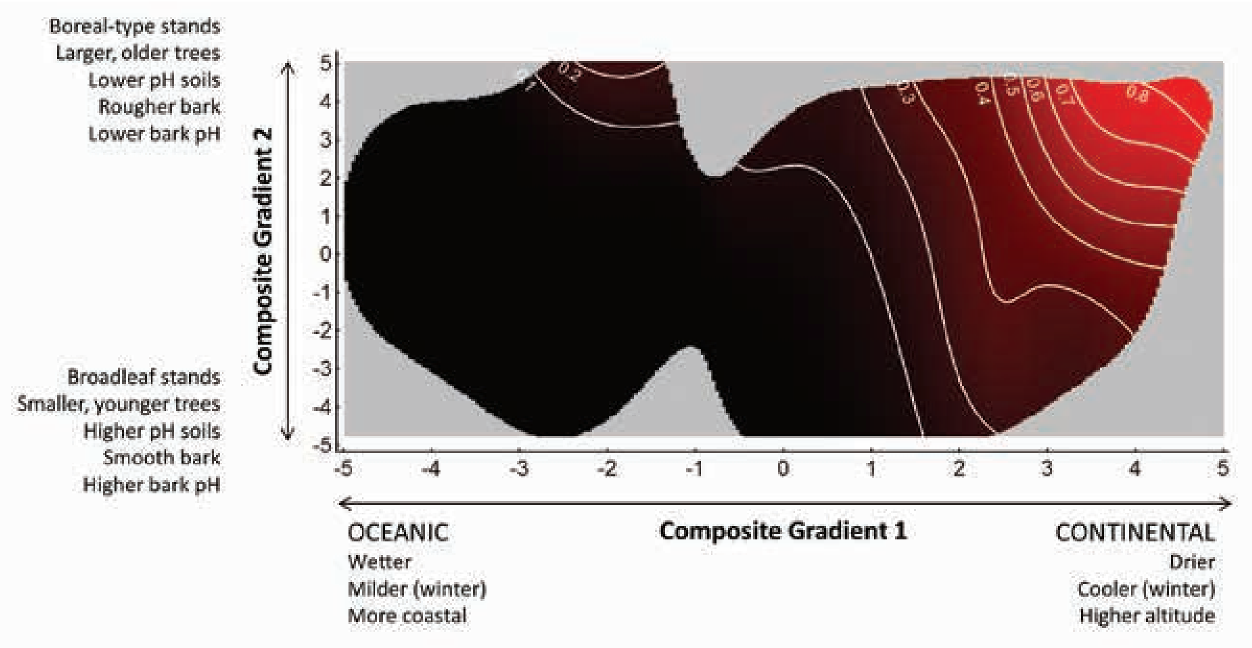


Figure 5.67. **Response surface showing variability in the likelihood of occurrence for the Type O *Bryoria-Ochrolechia-Parmeliopsis* Community, plotted along the environmental gradients identified in an optimised statistical model (cf. *Table 5.29*). Contours show likelihood values from red (higher values), to black (lower values), with surrounding grey showing the unmodelled environmental space.**

Table 5.29. **Diagnostics for an optimum ecological response model (NPMR), which explained the occurrence of the *Bryoria-Ochrolechia-Parmeliopsis* Community, plotted in relation to the variability of Composite Gradient 1 (macroclimate) and Composite Gradient 2 (tree-scale environment). Other variables were not significant.**

Explanatory Variable	Tolerance	Sensitivity	log*B*	AUC	$_{MC}P$
Composite Gradient 1	0.501 (5%)	0.659	60.27	0.865	<0.01
Composite Gradient 2	1.069 (10%)	0.279			

Tolerance : the width of a local weighting function (as a percentage of the environmental data range), which is used as a smoother to fit the modelled response surface.

Sensitivity : the mean difference when nudging each of the predictors by 5% of their range, expressed as a proportional shift in the range of the response variable.

log*B* : the log likelihood ratio for the improvement of the fitted model over a naïve model, which assumed a response based on the average likelihood of occurrence across all samples.

AUC : a measure of predictive performance, in which 1 = perfect, 0.5 = no better than random, with 0.7 and 0.9 considered reasonable and excellent, respectively.

$_{MC}P$: the statistical significance of the fitted model, when compared to multiple fitted models generated under a permutation test (number of randomisations = 100).

The *Bryoria-Ochrolechia-Parmeliopsis* Community is especially characteristic of Scotland's Boreal-type pine and birch woods in the higher altitude north-eastern valleys such as Strathspey and Deeside (*Figure 5.68*), and this was reflected in its sampled distribution (*Figure 5.69*). It is closely allied to Community Type N (*Mycoblastus-Protoparmelia-Sphaerophorus* Community; see Section 5.14), and species of these two communities are often found intergrading together (forming epiphyte Group VIII in *Figure 4.2*). However, the *Bryoria-Ochrolechia-Parmeliopsis* Community appears in general to be less tolerant of higher precipitation climates and moist microhabitats, compared to the more moisture demanding *Mycoblastus-Protoparmelia-Sphaerophorus* Community.

Figure 5.68. **Typical habitat for the *Bryoria-Ochrolechia-Parmeliopsis* Community occurring (Left)** *Figure 5.68. A.* **On pine bark, and (Right)** *Figure 5.68. B.* **In pine, birch and juniper woodland with a boreal character such as in the Rothiemurchas forest, Strathspey.**

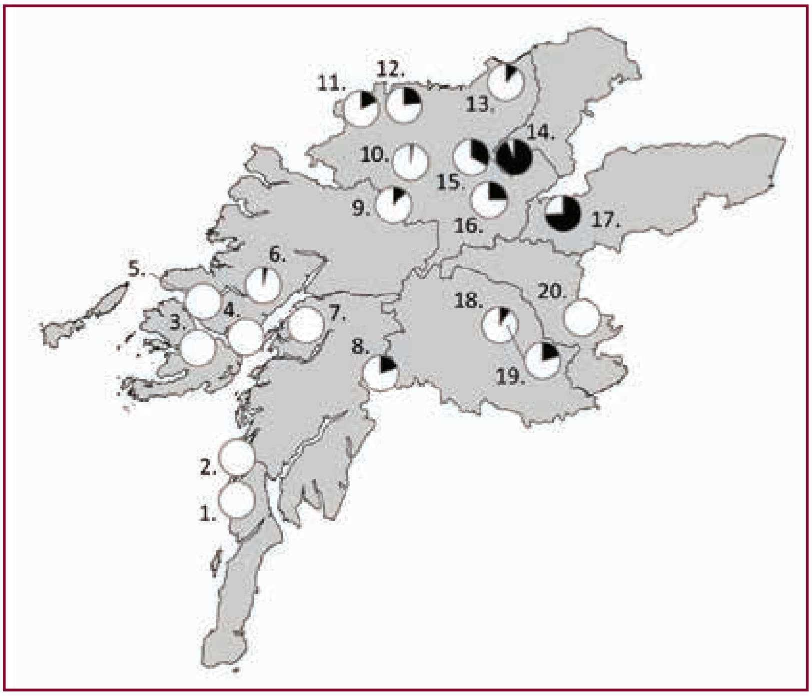


Figure 5.69. **The percent contribution (in black) of the *Bryoria-Ochrolechia-Parmeliopsis* Community to the epiphyte assemblages in each of the twenty woodland study sites.**
Site Codes:
1. EW (Ellary woods), 2. TAY (Taynish NNR), 3. LB (Loch Ba woods), 4. IB (Inninmore Bay woods), 5. DR (Druimbuidhe woods), 6. AR (Ariundle woods), 7. GC (Glen Creran woods), 8. CC (Coille Coire Chuilc), 9. GT (Glen Tarff woods), 10. EN (East Loch Ness woods), 11. IN (Inchvuilt wood), 12. SF (Strath Farrer NNR), 13. CW (Cawdor wood), 14. KF (Kinveachy Forest), 15. TA (Torr Alvie woods), 16. IV (Invertromie woods), 17. GQ (Glen Quoich), 18. BF (Bolfracks wood), 19. BA (Birks of Aberfeldy), 20. MW (Milton NNR).

The *Bryoria-Ochrolechia-Parmeliopsis* Community has thirteen diagnostic species (*Table 5.30*). It is often dominated by the relatively widespread *Hypogymnia physodes* (*Figure 5.70*); 97% of samples included *H. physodes*, which on average occupies > 50% of the bark space within the community. However, *H. physodes* occurs in a range of other community types, and while it is a useful guide to the possible occurrence of the *Bryoria-Ochrolechia-Parmeliopsis* Community, it is not diagnostic unless accompanied by at least one of the key indicators (*Bryoria fuscescens, Ochrolechia microstictoides* and/or *Parmeliopsis hyperopta*), as well as associated specialist species such as *Lecidea hypopta, Pertusaria borealis* or *Tuckermanopsis chlorophylla*.

Table 5.30. **The statistically significant indicator species for the Type O *Bryoria-Ochrolechia-Parmeliopsis* Community, with notes on the species conservation status and association with ecological continuity.**

SPECIES	**Association Values**			**Conservation Status**	**Ecological Continuity**	**Indicator *P***
	Community	Species	Abundance	SBL; IUCN; IR	C&C (2002); W&E (2013); E (2015)	
Indicative						
Bryoria fuscescens	48%	68%	0.43		C&C = EUOCIEC; E = 0.036	0.0001
Ochrolechia microstictoides	42%	68%	0.37			0.0001
Parmeliopsis hyperopta	33%	79%	0.43			0.0001
Associated						
Hypocenomyce friesii	9%	81%	0.29		C&C = NPIEC	0.003
Hypocenomyce scalaris	18%	96%	0.37			0.0001
Hypogymnia physodes	97%	51%	0.7			0.0001
Imshaugia aleurites	22%	76%	0.27		C&C = NPIEC	0.0003
Lecidea hypopta	19%	85%	0.33		C&C = NPIEC	0.0002
Lecidea nylanderi	10%	74%	0.18			0.0171
Lepraria jackii agg.	34%	46%	0.61			0.0016
Pertusaria borealis	15%	88%	0.17	SBL; IR	C&C = NPIEC	0.0007
Tuckermanopsis chlorophylla	15%	79%	0.25			0.001
Violella fucata (Mycoblastus fucatus)	31%	46%	0.25			0.0043

Association Values : Community = % of community samples with the species present; Species = % of the species' records associated with the community type; Abundance = species mean abundance in the community (for the patches in which it occurs).

Conservation Status, according to Woods & Coppins (2012) : SBL= Scottish Biodiversity Priority List; IUCN = categorisation according to IUCN criteria; IR = considered to be of International Responsibility for UK conservation.

Ecological Continuity : C&C (2002) = cited as an indicator by Coppins & Coppins (2002); W&E = statistically significant indicator in Whittet & Ellis (2013), or E = Ellis (2015).

Indicator *P* = species significance as a community indicator, under a permutation test (10,000 randomisations).

Figure 5.70. **The common lichen *Hypogymnia physodes*, a frequent species in the *Bryoria-Ochrolechia-Parmeliopsis* Community,** *Figure 5.70. A.* **Multiple thalli growing in a dispersed community on Scots pine.**

Figure 5.70. B. **A single thallus of *Hypogymnia physodes* on a young birch tree.**

The *Bryoria-Ochrolechia-Parmeliopsis* Community has no species which have been identified as threatened according to IUCN criteria. However, *Pertusaria borealis* is on the Scottish Biodiversity List, signalled as having an international conservation obligation for the UK, and five of the diagnostic species are thought to be strongly associated with woodlands that have ecological continuity. Bioclimatic modelling suggests that individual species in the community are likely to experience severely reduced climatic suitability in their core region of occurrence (i.e. the sites with high levels of env*S* for the baseline climate) by the mid- to late-21st Century (*Figure 5.71*), representing a potential long-term risk to this community type in Scotland.

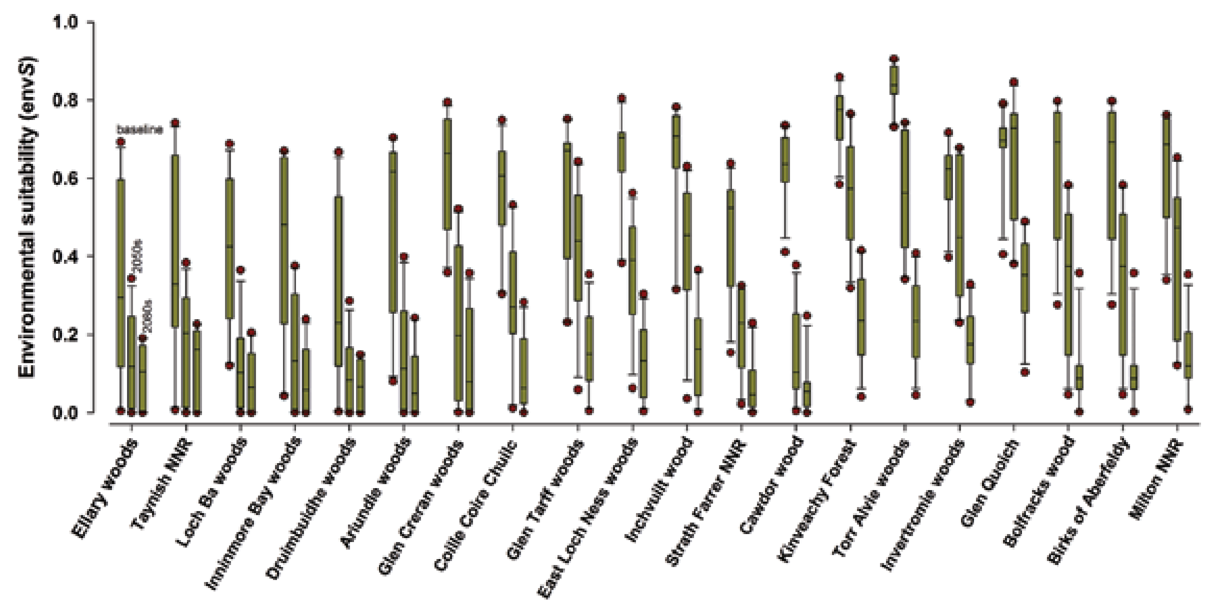


Figure 5.71. **Bioclimatic modelled values of environmental suitability (env*S*) for members of the *Bryoria-Ochrolechia-Parmeliopsis* Community across each of the twenty study sites, with bioclimatic data derived from Ellis *et al.* (2015). Box-plots for each site show the estimated values of env*S* for species in the community, comparing the baseline climate (1961-2006), with climate change scenarios for the 2050s (medium greenhouse gas emissions) and 2080s (high greenhouse gas emissions). Climate scenarios are grouped into triplets for each site in the order baseline, 2050s and 2080s, and box plots show the median (line), the interquartile range (box), the 10th and 90th (whiskers) and 5th and 95th percentiles (dots).**

List of Species Associated with Epiphyte Community Types

Values show the percentage of samples for each community type (Types A-O) in which an epiphyte species occurred. Indicator species are highlighted; note that their status as indicators was based on their relative abundance within a community, and not just their patterns of occurrence.

Key to Epiphyte Community Tables

Community Type A	*Arthonia radiata-Lecidella elaeochroma* Community
Community Type B	*Graphis scripta* Community
Community Type C	*Frullania dilatata* Community
Community Type D	*Phlyctis argena-Ramalina farinacea* Community
Community Type E	*Calicium viride-Chrysothrix candelaris* Community
Community Type F	*Lecanactis abietina* Community
Community Type G	*Lobaria virens-Normandina pulchella-Metzgeria furcata* Community
Community Type H	*Hypnum cupressiforme* agg.-*Usnea flammea* Community
Community Type I	*Hypnum andoi-Microlejeunea ulicina* Community
Community Type J	*Frullania tamarisci* Community
Community Type K	*Lobaria pulmonaria-Isothecium myosuroides* Community
Community Type L	*Arthopyrenia cinereopruinosa-Lecanora pulicaris* Community
Community Type M	*Hypotrachyna laevigata-Loxospora elatina* Community
Community Type N	*Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaerophorus globosus* Community
Community Type O	*Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS															
Acrocordia cavata	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acrocordia gemmata	0.00	0.00	1.47	0.00	0.00	0.00	1.09	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Anisomeridium biforme	0.00	0.00	2.94	1.85	17.39	8.70	1.09	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Anisomeridium polypori	3.70	0.00	1.47	1.85	0.00	0.00	0.00	7.69	1.09	1.75	6.56	2.04	0.00	0.00	0.00
Anisomeridium ranunculosporum	0.00	0.00	2.94	0.00	0.00	4.35	3.26	7.69	6.52	17.54	1.64	2.04	17.39	1.35	0.00
Anisomeridium viridescens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Arctomia delicatula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	1.35	0.00
Arthonia anombrophila	0.00	0.00	1.47	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Arthonia arthonioides	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthonia cinnabarina	3.70	0.00	2.94	0.00	0.00	0.00	3.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthonia didyma	27.78	33.33	10.29	5.56	4.35	0.00	2.17	0.00	2.17	1.75	4.92	8.16	0.00	0.00	2.05
Arthonia elegans	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.88	3.28	0.00	0.00	0.00	0.00
Arthonia ilicina	0.00	6.67	0.00	0.00	0.00	0.00	3.26	0.00	0.00	2.63	0.00	0.00	2.90	0.00	0.00
Arthonia leucopellaea	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	1.09	0.00	0.00	0.00	0.00	2.70	0.00
Arthonia muscigena	0.00	6.67	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthonia radiata	35.19	6.67	1.47	0.00	2.17	0.00	0.00	0.00	0.00	0.00	1.64	8.16	0.00	0.00	0.00
Arthonia spadicea	0.00	0.00	0.00	3.70	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00
Arthonia vinosa	0.00	0.00	0.00	1.85	21.74	8.70	0.00	3.85	1.09	0.00	0.00	4.08	0.00	1.35	3.42
Arthonia sp.	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthopyrenia analepta	12.96	0.00	0.00	0.00	2.17	0.00	0.00	0.00	1.09	0.88	0.00	0.00	0.00	2.70	0.00
Arthopyrenia cerasi	1.85	0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	1.75	0.00	0.00	0.00	0.00	0.00
Arthopyrenia cinereopruinosa	3.70	6.67	4.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.45	0.00	0.00	0.00
Arthopyrenia fraxini	1.85	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthopyrenia punctiformis	7.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthopyrenia salicis	0.00	0.00	2.94	0.00	0.00	0.00	1.09	0.00	0.00	0.88	1.64	0.00	0.00	0.00	0.00
Bacidia absistens	0.00	0.00	5.88	7.41	2.17	0.00	0.00	0.00	2.17	3.51	1.64	0.00	0.00	0.00	1.37
Bacidia arceutina	1.85	0.00	2.94	5.56	2.17	0.00	1.09	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.68
Bacidia beckhausii	1.85	0.00	2.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bacidia biatorina	0.00	0.00	2.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	1.45	0.00	0.00
Bacidia caesiovirens	0.00	0.00	2.94	0.00	2.17	0.00	4.35	0.00	2.17	0.88	0.00	2.04	1.45	1.35	0.00
Bacidia circumspecta	0.00	0.00	1.47	1.85	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS															
Bacidia laurocerasi	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bacidia rubella	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.88	1.64	0.00	0.00	0.00	0.00
Bacidia subincompta	0.00	0.00	1.47	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bacidia sulpherella	0.00	0.00	2.94	3.70	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bacidia vermifera	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Biatora britannica	0.00	0.00	2.94	0.00	0.00	0.00	2.17	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Biatora chrysantha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	1.09	0.88	0.00	0.00	0.00	0.00	0.00
Biatora vernalis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	2.90	0.00	0.00
Biatora sp. A	0.00	0.00	0.00	1.85	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Biatora sp. B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Bryoria fuscescens	0.00	0.00	0.00	1.85	0.00	4.35	2.17	0.00	1.09	0.88	0.00	0.00	2.90	33.78	47.95
Bryoria subcana	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	4.35	4.05	0.68
Buellia disciformis	22.22	0.00	1.47	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.04	1.45	0.00	0.68
Buellia erubescens	0.00	0.00	0.00	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buellia griseovirens	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	1.09	1.75	0.00	2.04	0.00	4.05	2.74
Buellia schaereri	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calicium glaucellum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.37
Calicium lenticulare	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calicium parvum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	4.11
Calicium salicinum	0.00	0.00	1.47	3.70	8.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.37
Calicium viride	0.00	0.00	0.00	0.00	30.43	8.70	0.00	0.00	2.17	0.00	0.00	4.08	0.00	0.00	6.85
Caloplaca cerina	1.85	0.00	0.00	5.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caloplaca ferruginea	1.85	6.67	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Candelariella xanthostigma	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Catillaria chalybeia	0.00	0.00	1.47	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Catillaria nigroclavata	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.68
Catinaria atropurpurea	0.00	0.00	2.94	0.00	0.00	0.00	3.26	0.00	1.09	2.63	6.56	2.04	0.00	0.00	0.00
Catinaria cf. *atropurpurea*	0.00	0.00	1.47	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Catinaria neuschildii	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chenotheca brunneola	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	1.37
Chenotheca chrysocephala	0.00	0.00	0.00	0.00	6.52	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	1.37

Chenotheca ferruginea	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	4.08	0.00	1.35	6.85
Chaenotheca stemonea	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chenotheca trichialis	0.00	0.00	0.00	0.00	23.91	13.04	1.09	0.00	1.09	0.00	0.00	2.04	0.00	1.35	2.05
Chenothecopsis nigra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Chaenothecopsis pusilla	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Chaenothecopsis savonica	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chrysothrix candelaris	0.00	0.00	2.94	5.56	76.09	30.43	0.00	0.00	3.26	1.75	3.28	6.12	1.45	5.41	8.90
Chrysothrix chrysophthalma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.00
Chrysothrix flavovirens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.24	0.00	0.00	8.90
Cladonia chlorophaea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	2.17	0.88	1.64	0.00	0.00	2.70	0.00
Cladonia coniocraea	0.00	0.00	2.94	0.00	0.00	4.35	0.00	15.38	16.30	6.14	0.00	6.12	0.00	9.46	6.16
Cladonia cornuta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Cladonia digitata	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	2.17	0.00	0.00	0.00	2.90	2.70	4.11
Cladonia diversa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Cladonia fimbriata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.90	1.35	0.68
Cladonia humilis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Cladonia macilenta/polydactyla agg.	0.00	0.00	1.47	1.85	0.00	8.70	1.09	3.85	20.65	10.53	3.28	0.00	4.35	28.38	15.07
Cladonia ochrochlora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	3.28	0.00	1.45	1.35	0.00
Cladonia pyxidata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.28	0.00	0.00	0.00	0.68
Cladonia ramulosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Cladonia rangiformis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.00
Cladonia squamosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	2.17	1.75	1.64	0.00	2.90	9.46	1.37
Cladonia sp.	0.00	0.00	11.76	1.85	0.00	4.35	6.52	30.77	17.39	18.42	19.67	0.00	23.19	6.76	4.11
Cliostomum flavidulum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	1.64	0.00	0.00	0.00	0.00
Cliostomum griffithii	12.96	0.00	7.35	24.07	41.30	13.04	0.00	0.00	3.26	3.51	0.00	4.08	5.80	1.35	6.85
Cyphelium inquinans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Degelia atlantica	0.00	0.00	5.88	0.00	0.00	0.00	3.26	0.00	1.09	0.88	3.28	0.00	0.00	0.00	0.00
Degelia cyanoloma	0.00	0.00	1.47	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Degelia plumbea	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Dimerella lutea	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.09	0.88	8.20	0.00	1.45	1.35	0.00
Dimerella pineti	0.00	0.00	2.94	3.70	2.17	4.35	7.61	11.54	7.61	9.65	6.56	0.00	1.45	2.70	4.11
Enterographa crassa	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Evernia prunastri	7.41	0.00	2.94	3.70	8.70	0.00	0.00	0.00	4.35	0.00	0.00	2.04	4.35	4.05	9.59
Fellhanera duplex	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS															
Flavoparmelia caperata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	5.43	0.88	3.28	2.04	7.25	0.00	0.00
Fuscidea lightfootii	7.41	0.00	2.94	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	6.12	1.45	0.00	1.37
Fuscopannaria ignobilis	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Fuscopannaria mediterranea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gomphilus calycioides	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Graphis elegans	0.00	0.00	1.47	1.85	0.00	0.00	0.00	3.85	4.35	3.51	0.00	0.00	8.70	0.00	0.00
Graphis scripta	14.81	100.00	25.00	1.85	0.00	0.00	8.70	7.69	4.35	3.51	0.00	8.16	0.00	0.00	0.00
Gyalecta derivata	0.00	0.00	2.94	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Gyalecta truncigena	0.00	0.00	2.94	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypocenomyce friesii	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.09	0.00	0.00	0.00	0.00	1.35	8.90
Hypocenomyce scalaris	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	18.49
Hypogymnia farinacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Hypogymnia physodes	9.26	0.00	4.41	11.11	8.70	30.43	2.17	26.92	17.39	10.53	0.00	20.41	21.74	68.92	97.26
Hypotrachyna laevigata	0.00	0.00	0.00	0.00	0.00	0.00	1.09	19.23	6.52	3.51	0.00	0.00	28.99	1.35	0.00
Hypotrachyna revoluta agg.	0.00	0.00	0.00	0.00	0.00	0.00	3.26	0.00	8.70	7.02	3.28	0.00	2.90	0.00	0.00
Hypotrachyna sinuosa	0.00	0.00	0.00	1.85	0.00	0.00	0.00	3.85	1.09	1.75	0.00	0.00	0.00	0.00	0.00
Hypotrachyna taylorensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	1.09	3.51	9.84	0.00	5.80	0.00	0.00
Imshaugia aleurites	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	1.45	9.46	21.92
Jamesiella anastomosans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	2.90	0.00	0.00
Japewia subaurifera	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.76	4.79
Lecanactis abietina	0.00	6.67	0.00	3.70	10.87	100.00	4.35	3.85	6.52	0.88	0.00	10.20	8.70	6.76	6.16
Lecania cyrtella	1.85	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lecania dubitans	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lecania naegelii	5.56	0.00	0.00	3.70	0.00	0.00	0.00	0.00	1.09	0.88	0.00	0.00	0.00	0.00	0.00
Lecanora alboflavida	0.00	6.67	0.00	0.00	0.00	0.00	2.17	0.00	2.17	1.75	0.00	0.00	0.00	0.00	0.00
Lecanora cadubriae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.85
Lecanora carpinea	3.70	0.00	1.47	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Lecanora chlarotera agg.	87.04	6.67	41.18	35.19	17.39	0.00	8.70	3.85	1.09	9.65	1.64	10.20	2.90	0.00	5.48
Lecanora confusa	0.00	0.00	2.94	0.00	0.00	0.00	0.00	0.00	1.09	0.88	0.00	0.00	1.45	0.00	0.00
Lecanora dispersa agg.	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lecanora expallens	11.11	0.00	13.24	14.81	21.74	13.04	2.17	3.85	5.43	4.39	4.92	6.12	4.35	1.35	11.64

Lecanora intumescens	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lecanora jamesii	5.56	0.00	5.88	0.00	0.00	0.00	0.00	0.00	2.17	0.88	0.00	0.00	1.45	0.00	0.00
Lecanora populicola	3.70	0.00	1.47	7.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lecanora pulicaris	1.85	0.00	0.00	3.70	2.17	0.00	0.00	0.00	1.09	0.00	0.00	22.45	2.90	2.70	6.16
Lecanora sambuci	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lecanora symmicta agg.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Lecidea hypopta	0.00	0.00	0.00	0.00	2.17	0.00	1.09	0.00	2.17	0.00	0.00	0.00	0.00	1.35	19.18
Lecidea nylanderi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	5.41	9.59
Lecidea turgidula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	6.16
Lecidella elaeochroma f. *eleaochroma*	42.59	0.00	23.53	16.67	4.35	0.00	4.35	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Lecidella elaeochroma f. *soralifera*	1.85	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lepraria eburnea	0.00	0.00	2.94	0.00	0.00	0.00	8.70	7.69	0.00	0.88	1.64	0.00	0.00	0.00	0.68
Lepraria elobata	0.00	0.00	0.00	0.00	2.17	4.35	0.00	3.85	2.17	0.00	0.00	0.00	4.35	0.00	2.74
Lepraria incana	0.00	0.00	1.47	7.41	28.26	4.35	1.09	0.00	5.43	0.00	0.00	0.00	0.00	0.00	2.05
Lepraria jackii agg.	1.85	0.00	5.88	1.85	13.04	30.43	1.09	7.69	10.87	1.75	6.56	2.04	15.94	12.16	34.25
Lepraria lobificans	0.00	0.00	8.82	5.56	6.52	13.04	7.61	30.77	8.70	27.19	16.39	0.00	1.45	0.00	0.00
Lepraria membranacea	0.00	0.00	0.00	0.00	0.00	0.00	1.09	3.85	1.09	1.75	0.00	0.00	0.00	0.00	0.68
Lepraria rigidula	1.85	0.00	16.18	12.96	6.52	13.04	4.35	11.54	21.74	14.04	4.92	2.04	5.80	9.46	8.22
Lepraria umbricola	0.00	0.00	0.00	3.70	2.17	0.00	8.70	0.00	1.09	1.75	3.28	0.00	0.00	6.76	9.59
Lepraria sp.	3.70	0.00	10.29	20.37	6.52	4.35	11.96	23.08	11.96	10.53	9.84	46.94	7.25	6.76	19.86
Leptogium burgessii	0.00	0.00	0.00	0.00	0.00	0.00	3.26	0.00	1.09	2.63	0.00	0.00	0.00	0.00	0.00
Leptogium cyanescens	0.00	0.00	1.47	0.00	0.00	0.00	3.26	0.00	0.00	0.00	3.28	0.00	0.00	0.00	0.00
Leptogium lichenoides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Leptogium teretiusculum	0.00	0.00	1.47	0.00	0.00	0.00	1.09	0.00	0.00	4.39	3.28	0.00	0.00	0.00	0.00
Leptorhaphis atomaria	3.70	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leptorhaphis epidermidis	5.56	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lichenomphallia umbellifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.69	1.09	1.75	0.00	0.00	1.45	2.70	0.00
Lobaria amplissima	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	3.28	0.00	0.00	0.00	0.00
Lobaria pulmonaria	0.00	0.00	13.24	1.85	4.35	0.00	13.04	3.85	6.52	6.14	39.34	0.00	4.35	2.70	0.00
Lobaria scrobiculata	0.00	0.00	0.00	1.85	0.00	0.00	1.09	0.00	0.00	2.63	6.56	0.00	0.00	0.00	0.00
Lobaria virens	1.85	0.00	1.47	0.00	0.00	0.00	22.83	0.00	0.00	0.88	8.20	0.00	0.00	0.00	0.00
Lopadium disciforme	0.00	0.00	0.00	0.00	0.00	4.35	1.09	0.00	5.43	7.89	0.00	2.04	4.35	6.76	0.68
Loxospora elatina	0.00	0.00	1.47	5.56	2.17	8.70	0.00	7.69	6.52	15.79	3.28	8.16	24.64	20.27	10.27
Megalaria grossa	1.85	0.00	7.35	1.85	0.00	0.00	0.00	3.85	1.09	0.00	0.00	0.00	0.00	0.00	0.00

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS															
Megalaria pulverea	1.85	0.00	4.41	1.85	0.00	0.00	13.04	11.54	6.52	13.16	4.92	6.12	7.25	5.41	6.85
Megalospora tuberculosa	0.00	0.00	2.94	0.00	2.17	0.00	0.00	3.85	1.09	1.75	0.00	0.00	0.00	0.00	0.00
Melanelixia glabratula agg.	12.96	0.00	22.06	40.74	2.17	0.00	5.43	11.54	9.78	9.65	3.28	12.24	20.29	6.76	6.85
Melanelixia subaurifera	3.70	0.00	1.47	0.00	4.35	0.00	2.17	0.00	2.17	1.75	3.28	2.04	1.45	0.00	2.74
Melaspilea sp.	0.00	0.00	4.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Menegazzia subsimilis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.68
Menegazzia terebrata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.64	0.00	0.00	0.00	0.00
Micarea adnata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	2.70	0.00
Micarea alabastrites	0.00	0.00	0.00	0.00	0.00	0.00	1.09	7.69	4.35	2.63	1.64	0.00	4.35	5.41	2.05
Micarea botryoides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.05
Micarea cinerea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.88	0.00	0.00	0.00	4.05	0.00
Micarea denigrata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.42
Micarea leprosula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	1.45	1.35	0.00
Micarea melaena	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Micarea micrococca agg.	0.00	0.00	4.41	9.26	0.00	17.39	6.52	26.92	18.48	14.91	3.28	18.37	4.35	14.86	10.27
Micarea peliocarpa	0.00	0.00	0.00	1.85	0.00	0.00	1.09	0.00	0.00	4.39	0.00	6.12	4.35	2.70	1.37
Micarea prasina	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	2.63	0.00	0.00	1.45	1.35	0.68
Micarea stipitata	0.00	0.00	0.00	0.00	0.00	0.00	1.09	7.69	5.43	7.02	0.00	4.08	8.70	0.00	0.00
Micarea subviridescens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00
Micarea synotheoides	0.00	0.00	0.00	1.85	0.00	4.35	2.17	7.69	0.00	1.75	0.00	0.00	4.35	14.86	1.37
Micarea viridileprosa	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Microcalicium ahlneri	0.00	0.00	0.00	0.00	2.17	4.35	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Microcalicium disseminatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	8.16	0.00	0.00	0.00
Mycobilimbia epixanthoides	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.88	0.00	0.00	2.90	0.00	0.00
Mycobilimbia pilularis	0.00	0.00	0.00	0.00	0.00	0.00	5.43	0.00	1.09	0.88	0.00	0.00	1.45	0.00	0.00
Mycoblastus affinis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.63	0.00	0.00	1.45	1.35	0.68
Mycoblastus caesius	1.85	0.00	5.88	0.00	0.00	4.35	0.00	7.69	10.87	7.89	0.00	2.04	18.84	14.86	2.05
Mycoblastus sanguinarius	0.00	0.00	0.00	1.85	2.17	4.35	0.00	3.85	3.26	5.26	0.00	0.00	7.25	44.59	16.44
Mycomicrothelia confusa	0.00	6.67	4.41	0.00	0.00	0.00	2.17	0.00	0.00	0.88	0.00	2.04	0.00	0.00	0.00
Mycomicrothelia wallrothii	1.85	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mycoporum antecellens	1.85	6.67	1.47	0.00	0.00	0.00	0.00	0.00	2.17	1.75	1.64	0.00	5.80	0.00	0.00

Nephroma laevigatum	0.00	0.00	1.47	0.00	0.00	0.00	3.26	0.00	0.00	0.88	0.00	0.00	2.90	0.00	0.00
Nephroma parile	0.00	0.00	0.00	0.00	0.00	0.00	2.17	7.69	4.35	4.39	3.28	0.00	0.00	0.00	0.00
Normandina acroglypta	0.00	0.00	5.88	0.00	0.00	0.00	1.09	0.00	0.00	0.00	3.28	0.00	0.00	0.00	0.00
Normandina pulchella	0.00	0.00	36.76	1.85	0.00	0.00	43.48	11.54	13.04	28.95	22.95	12.24	11.59	0.00	0.00
Ochrolechia androgyna	1.85	0.00	1.47	5.56	2.17	4.35	2.17	11.54	4.35	10.53	4.92	0.00	24.64	27.03	14.38
Ochrolechia inaequatula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Ochrolechia microstictoides	0.00	0.00	1.47	1.85	8.70	0.00	0.00	0.00	3.26	1.75	0.00	2.04	7.25	16.22	41.78
Ochrolechia subviridis	0.00	0.00	1.47	1.85	0.00	0.00	3.26	0.00	1.09	1.75	4.92	0.00	0.00	1.35	1.37
Ochrolechia szatalaensis	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ochrolechia tartarea	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	3.26	1.75	0.00	0.00	2.90	4.05	0.68
Ochrolechia turneri	0.00	0.00	2.94	7.41	0.00	0.00	0.00	3.85	1.09	0.88	1.64	0.00	1.45	1.35	0.00
Opegrapha atra	1.85	0.00	1.47	0.00	4.35	0.00	0.00	0.00	1.09	0.88	0.00	0.00	0.00	0.00	0.00
Opegrapha fumosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Opegrapha herbarum	1.85	13.33	1.47	0.00	6.52	0.00	1.09	0.00	0.00	0.00	1.64	2.04	1.45	0.00	0.00
Opegrapha niveoatra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Opegrapha ochrocheila	0.00	0.00	2.94	0.00	4.35	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Opegrapha rufescens	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Opegrapha sorediifera	0.00	0.00	0.00	11.11	2.17	0.00	2.17	0.00	0.00	0.00	1.64	0.00	0.00	0.00	1.37
Opegrapha varia	0.00	0.00	1.47	1.85	0.00	0.00	3.26	3.85	0.00	0.00	0.00	2.04	0.00	0.00	0.00
Opegrapha vermicellifera	0.00	0.00	0.00	1.85	0.00	4.35	1.09	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.00
Opegrapha vulgata	0.00	0.00	2.94	3.70	2.17	4.35	11.96	0.00	2.17	0.88	1.64	2.04	0.00	0.00	0.00
Pachyphiale carneola	0.00	0.00	2.94	0.00	0.00	0.00	1.09	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Pannaria conoplea	0.00	0.00	1.47	0.00	0.00	0.00	3.26	0.00	1.09	1.75	0.00	0.00	0.00	0.00	0.00
Pannaria rubiginosa	0.00	0.00	2.94	0.00	0.00	0.00	4.35	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Parmelia sulcata	7.41	0.00	0.00	22.22	8.70	0.00	0.00	0.00	6.52	1.75	0.00	6.12	1.45	16.22	15.75
Parmelia saxatilis agg.	1.85	0.00	4.41	14.81	2.17	13.04	3.26	19.23	25.00	27.19	19.67	6.12	40.58	47.30	10.96
Parmelia sp.	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	2.04	0.00	0.00	0.00
Parmeliella parvula	0.00	0.00	5.88	0.00	0.00	0.00	1.09	0.00	7.61	11.40	11.48	0.00	7.25	2.70	0.00
Parmeliella testacea	0.00	0.00	0.00	0.00	0.00	0.00	3.26	0.00	0.00	2.63	1.64	0.00	0.00	0.00	0.00
Parmeliella triptophylla	0.00	0.00	10.29	0.00	0.00	0.00	3.26	3.85	0.00	3.51	3.28	0.00	1.45	0.00	0.00
Parmeliopsis ambigua	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.70	0.00
Parmeliopsis hyperopta	0.00	0.00	0.00	0.00	0.00	4.35	1.09	0.00	2.17	0.00	0.00	0.00	2.90	9.46	32.88
Parmotrema crinitum	0.00	0.00	2.94	0.00	0.00	0.00	4.35	19.23	4.35	3.51	26.23	4.08	10.14	0.00	0.00
Parmotrema perlatum	0.00	0.00	7.35	0.00	0.00	0.00	1.09	3.85	6.52	1.75	11.48	2.04	2.90	0.00	0.00

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS															
Peltigera collina	0.00	0.00	2.94	0.00	0.00	0.00	1.09	0.00	1.09	0.00	1.64	0.00	0.00	0.00	0.00
Peltigera degenii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Peltigera hymenina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Peltigera praetextata	0.00	0.00	1.47	0.00	0.00	0.00	0.00	3.85	1.09	0.00	6.56	0.00	0.00	0.00	0.00
Pertusaria albescens	0.00	0.00	5.88	0.00	0.00	4.35	3.26	7.69	4.35	7.89	9.84	0.00	0.00	1.35	0.68
Pertusaria amara	1.85	0.00	10.29	42.59	4.35	21.74	3.26	0.00	10.87	10.53	4.92	6.12	10.14	10.81	6.16
Pertusaria borealis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.05	15.07
Pertusaria coccodes	0.00	0.00	0.00	3.70	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.68
Pertusaria coronata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Pertusaria flavida	0.00	0.00	0.00	0.00	13.04	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.00
Pertusaria hemisphaerica	1.85	0.00	1.47	3.70	4.35	0.00	3.26	0.00	3.26	8.77	0.00	0.00	4.35	2.70	2.05
Pertusaria hymenea	1.85	26.67	8.82	3.70	0.00	0.00	2.17	0.00	2.17	0.00	6.56	0.00	4.35	0.00	0.00
Pertusaria leioplaca	51.85	33.33	30.88	0.00	8.70	0.00	6.52	3.85	2.17	4.39	3.28	4.08	0.00	0.00	0.68
Pertusaria multipuncta	7.41	0.00	4.41	5.56	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	7.25	0.00	0.00
Pertusaria pertusa	1.85	0.00	10.29	7.41	10.87	0.00	0.00	0.00	3.26	2.63	1.64	0.00	1.45	4.05	0.68
Pertusaria pupillaris	1.85	0.00	5.88	1.85	0.00	0.00	3.26	3.85	3.26	2.63	0.00	18.37	0.00	4.05	6.85
Phaeophyscia orbicularis	0.00	0.00	0.00	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phlyctis agelaea	0.00	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phlyctis argena	3.70	0.00	10.29	35.19	19.57	0.00	2.17	7.69	4.35	13.16	0.00	0.00	1.45	0.00	1.37
Phyllopsora rosei	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	1.75	0.00	0.00	1.45	0.00	0.00
Physcia adscendens/tenella agg.	1.85	0.00	2.94	12.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Physconia distorta	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Placynthiella dasaea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	1.09	0.88	0.00	0.00	4.35	5.41	0.68
Placynthiella icmalea	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	5.43	4.39	0.00	0.00	2.90	1.35	2.74
Placynthiella uliginosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	4.05	0.68
Platismatia glauca	0.00	0.00	0.00	14.81	0.00	4.35	2.17	30.77	22.83	9.65	3.28	6.12	18.84	98.65	39.73
Porina aenea	5.56	0.00	5.88	0.00	2.17	0.00	3.26	0.00	0.00	0.00	3.28	0.00	0.00	0.00	0.00
Porina coralloidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.00
Porina leptalea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.35	1.75	0.00	0.00	0.00	0.00	0.00
Protopannaria pezizoides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	2.70	0.00
Protoparmelia ochrococca	0.00	0.00	1.47	0.00	2.17	4.35	0.00	3.85	4.35	0.00	0.00	0.00	4.35	31.08	19.86

Pseudevernia furfuracea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.70	8.22
Psoroma hypnorum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Pycnora sorophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	2.70	1.37
Pyrenula coryli	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pyrenula laevigata	0.00	6.67	0.00	1.85	0.00	0.00	3.26	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Pyrenula macrospora	1.85	0.00	7.35	1.85	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.00
Pyrenula occidentalis	7.41	13.33	5.88	0.00	0.00	0.00	6.52	0.00	0.00	2.63	0.00	4.08	1.45	0.00	0.00
Pyrrhospora quernea	1.85	0.00	1.47	0.00	2.17	0.00	0.00	0.00	2.17	0.00	0.00	0.00	1.45	0.00	0.00
Ramalina farinaria	3.70	0.00	10.29	37.04	10.87	0.00	2.17	0.00	0.00	1.75	4.92	0.00	2.90	2.70	6.85
Ramalina fastigiata	5.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Rhaphidicyrtis trichosporella	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Rinodina efflorescens	1.85	0.00	0.00	1.85	0.00	0.00	1.09	3.85	1.09	0.88	0.00	0.00	0.00	2.70	6.16
Rinodina griseosoralifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Ropalospora viridis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.68
Schaereria corticola	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	2.04	0.00	0.00	1.37
Schismatomma graphidioides	0.00	0.00	1.47	1.85	8.70	4.35	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.68
Schismatomma quercicola	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sclerophora peronella	0.00	0.00	0.00	0.00	2.17	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphaerophorus globosus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.26	11.40	4.92	0.00	4.35	25.68	1.37
Stenocybe nitida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Sticta canariensis	0.00	0.00	1.47	0.00	0.00	0.00	3.26	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Sticta fuliginosa	0.00	0.00	1.47	0.00	0.00	0.00	1.09	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Sticta limbata	0.00	0.00	2.94	0.00	0.00	0.00	2.17	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Sticta sylvatica	0.00	0.00	2.94	0.00	0.00	0.00	5.43	0.00	2.17	3.51	9.84	0.00	5.80	0.00	0.00
Strangospora microhaema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.00
Strigula jamesii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Strigula phaea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Tephromela atra	0.00	0.00	2.94	5.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thelotrema lepadinum	3.70	0.00	17.65	9.26	0.00	4.35	19.57	3.85	7.61	23.68	11.48	6.12	15.94	1.35	2.05
Thelotrema macrosporum	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	1.75	0.00	0.00	0.00	0.00	0.00
Thelotrema petractoides	0.00	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trapelia corticola	0.00	0.00	0.00	5.56	0.00	0.00	4.35	7.69	8.70	14.04	0.00	2.04	10.14	6.76	3.42
Trapeliopsis flexuosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.88	0.00	6.12	4.35	4.05	1.37

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS															
Trapeliopsis pseudogranulosa	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	1.09	0.88	0.00	0.00	0.00	0.00	0.00
Tuckermanopsis chlorophylla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.90	5.41	15.07
Usnea cornuta	0.00	0.00	1.47	0.00	0.00	0.00	0.00	3.85	3.26	0.00	1.64	4.08	5.80	0.00	0.68
Usnea dasypoga	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68
Usnea flammea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.08	5.43	3.51	1.64	0.00	2.90	0.00	0.00
Usnea fragilescens var. *mollis*	0.00	0.00	2.94	0.00	0.00	0.00	0.00	3.85	1.09	1.75	0.00	0.00	5.80	1.35	0.00
Usnea hirta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.42
Usnea subfloridana	0.00	0.00	0.00	1.85	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	1.45	10.81	7.53
Usnea wasmuthii	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	1.37
Usnea sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	1.75	0.00	0.00	17.39	1.35	3.42
Violella fucata (Mycoblastus fucatus)	0.00	0.00	1.47	0.00	2.17	8.70	3.26	3.85	13.04	4.39	0.00	6.12	15.94	18.92	30.82
Xanthoria parietina	0.00	0.00	2.94	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BRYOPHYTES															
Anastrophyllum hellerianum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	1.45	0.00	0.68
Brachythecium velutinum	0.00	0.00	2.94	0.00	0.00	0.00	2.17	0.00	1.09	3.51	3.28	2.04	2.90	0.00	0.00
Calypogeia fissa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.00
Campylopus flexuosus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	2.70	0.00
Cephalozia bicuspidata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.88	0.00	0.00	4.35	1.35	0.00
Cephalozia sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.68
Cephaloziella divaricata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.63	0.00	2.04	2.90	0.00	0.00
Ctenidium molluscum	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dicranella heteromella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.64	0.00	0.00	0.00	0.00
Dicranoweisia cirrata	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Dicranum fuscescens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.26	0.88	0.00	0.00	0.00	4.05	0.68
Dicranum majus	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	1.09	0.00	1.64	2.04	0.00	0.00	0.00
Dicranum montanum	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	1.09	1.75	0.00	0.00	1.45	10.81	0.00
Dicranum scoparium	0.00	0.00	1.47	0.00	0.00	0.00	7.61	11.54	19.57	18.42	6.56	0.00	11.59	8.11	6.16
Douinia ovata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	1.09	2.63	0.00	0.00	0.00	0.00	0.00
Drepanolejeunea hamatifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.28	0.00	1.45	0.00	0.00
Eurhynchium striatum	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Frullania dilatata	20.37	13.33	97.06	27.78	10.87	4.35	25.00	19.23	10.87	6.14	11.48	6.12	0.00	5.41	2.05
Frullania fragilifolia	0.00	0.00	0.00	3.70	0.00	0.00	8.70	0.00	6.52	0.88	0.00	2.04	2.90	4.05	0.68
Frullania tamarisci	1.85	0.00	2.94	7.41	4.35	8.70	14.13	23.08	23.91	85.96	55.74	8.16	43.48	16.22	1.37
Frullania teneriffae	0.00	0.00	0.00	0.00	0.00	0.00	6.52	0.00	0.00	0.88	4.92	2.04	1.45	0.00	0.00
Harpalejeunea molleri	0.00	0.00	2.94	0.00	0.00	0.00	5.43	0.00	0.00	9.65	1.64	0.00	1.45	0.00	0.00
Homalothecium sericeum	0.00	0.00	1.47	0.00	0.00	0.00	4.35	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Hypnum andoi	3.70	20.00	41.18	22.22	10.87	34.78	16.30	3.85	84.78	57.89	13.11	18.37	23.19	29.73	8.90
Hypnum cupressiforme agg.	5.56	13.33	7.35	11.11	2.17	4.35	6.52	96.15	3.26	7.89	9.84	6.12	14.49	13.51	5.48
Hypnum resupinatum	0.00	0.00	0.00	0.00	2.17	0.00	4.35	0.00	0.00	2.63	4.92	2.04	0.00	0.00	0.00
Isothecium alopecuroides	0.00	0.00	0.00	0.00	2.17	0.00	8.70	3.85	0.00	4.39	1.64	0.00	0.00	0.00	0.00
Isothecium myosuroides	0.00	0.00	2.94	0.00	2.17	4.35	10.87	3.85	6.52	12.28	85.25	2.04	11.59	2.70	1.37
Kindbergia praelonga	0.00	0.00	0.00	1.85	0.00	4.35	0.00	0.00	1.09	0.88	1.64	0.00	0.00	0.00	0.00
Lejeunea cavifolia	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lejeunea lamacerina	0.00	0.00	0.00	0.00	0.00	0.00	3.26	0.00	1.09	0.00	1.64	0.00	0.00	0.00	0.00
Lejeunia patens	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	1.09	0.00	3.28	0.00	0.00	0.00	0.00
Lepidozia reptans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.64	0.00	0.00	1.35	0.68
Lophocolea bidentata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00
Lophocolea fragrans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	2.90	0.00	0.00
Lophocolea heterophylla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00
Lophozia longidens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85	0.00	2.63	0.00	0.00	0.00	1.35	0.00
Lophozia ventricosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.68
Metzgeria furcata	5.56	0.00	38.24	11.11	2.17	0.00	45.65	7.69	14.13	14.04	37.70	0.00	0.00	0.00	0.68
Microlejeunea ulicina	0.00	0.00	11.76	3.70	0.00	0.00	10.87	23.08	35.87	25.44	16.39	6.12	28.99	0.00	1.37
Neckera complanata	0.00	0.00	1.47	0.00	0.00	0.00	7.61	3.85	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Neckera pumila	0.00	0.00	7.35	0.00	0.00	0.00	7.61	0.00	1.09	3.51	4.92	0.00	1.45	1.35	0.00
Orthotrichum affine	0.00	0.00	4.41	20.37	0.00	0.00	0.00	7.69	0.00	1.75	0.00	0.00	0.00	0.00	0.00
Orthotrichum lyellii	1.85	0.00	7.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orthotrichum stramineum	0.00	0.00	1.47	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orthotrichum striatum	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orthotrichum sp.	1.85	0.00	1.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plagiochila atlantica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	1.75	0.00	0.00	0.00	0.00	0.00
Plagiochila porelloides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Plagiochila punctata	0.00	0.00	0.00	0.00	0.00	0.00	4.35	11.54	4.35	9.65	0.00	4.08	1.45	0.00	0.00
Plagiochila spinulosa	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00

	Epiphyte Community Type														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
BRYOPHYTES															
Plagiothecium curvifolium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Plagiothecium denticulatum	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plagiothecium undulatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Porella arboris-vitae	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Porella cordaeana	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pseudotaxiphyllum elegans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Pterogonium gracile	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ptilidium pulcherrimum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Radula complanata	0.00	0.00	7.35	9.26	0.00	0.00	13.04	11.54	1.09	3.51	6.56	0.00	0.00	0.00	0.00
Rhytidiadelphus loreus	0.00	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saccogyne viticulosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Scapania gracilis	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	2.17	0.88	0.00	0.00	11.59	6.76	1.37
Tetraphis pellucida	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00
Thuidium tamariscinum	0.00	6.67	0.00	1.85	0.00	0.00	0.00	0.00	1.09	0.88	4.92	0.00	1.45	0.00	0.00
Ulota bruchii/crispa agg.	7.41	6.67	25.00	7.41	2.17	0.00	11.96	7.69	6.52	7.02	3.28	4.08	1.45	1.35	4.11
Ulota drummondii	1.85	0.00	0.00	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	0.00	0.00
Ulota phylantha	0.00	0.00	7.35	0.00	0.00	0.00	3.26	0.00	0.00	0.88	3.28	0.00	0.00	1.35	0.00
Zygodon conoideus	0.00	0.00	0.00	1.85	0.00	0.00	2.17	3.85	1.09	0.88	0.00	0.00	1.45	0.00	0.00
Zygodon rupestris	0.00	0.00	0.00	0.00	0.00	0.00	3.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Zygodon viridissimus	1.85	0.00	10.29	0.00	0.00	0.00	13.04	0.00	1.09	6.14	3.28	0.00	0.00	0.00	0.68
VASCULAR PLANTS															
Polypodium vulgare	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00	0.00
Vaccinium myrtillus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	1.35	0.00
Vaccinium vitis-idaea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.35	0.00

Epiphyte Community Comparison with James *et al*. (1977)

Group I

Early Successional (Pioneer) Communities of Smooth-Barked Mesotrophic Microhabitats

Community Type A: *Arthonia radiata-Lecidella elaeochroma* Community
Indicators: ***Arthonia radiata***, *Buellia disciformis, Lecanora chlarotera,* ***Lecidella elaeochroma***, *Pertusaria leioplaca*

Community Type B: *Graphis scripta* Community
Indicators: *Arthonia didyma,* ***Graphis scripta***, *Pertusaria hymenea, Pyrenula occidentalis*

The Type A *Arthonia radiata-Lecidella elaeochroma* Community corresponds most closely to the *Lecanorion subfuscae* (*Lecanoretum subfuscae* sub-division) of James *et al*., which they identify as a pioneer community with *Arthonia radiata* and *Lecidella elaeochroma* as indicators. The fact that the *Lecanorion subfuscae* can include *Graphis scripta* also, supports the close association between the Type A and Type B Communities found here.

Other Type A species, including *Lecanora chlarotera* and *Pertusaria leioplaca*, are consistent with the *Lecanorion subfuscae*, while *Buellia disciformis* possibly indicates an overlap for nutrient-rich bark situations, with James *et al*.'s *Xanthorion parietinae*.

The Type B *Graphis scripta* Community corresponds to the *Graphidion scriptae* of James *et al*. The variety of species associated with Community Type B points to a wide variability around the use of *Graphis scripta* as an indicator. However, this variability supports the close alignment of Types A and B together in Group I, because the Type A indicators *Lecanora chlarotera* and *Lecidella elaeochroma* are also included in James *et al*.'s early successional *Arthopyrenietum punctiformis* sub-division of the *Graphidion scriptae,* along with the Type B indicator *Arthonia didyma* (included by James *et al.* as *A. lurida*).

Of the other Type B species, *Pertusaria hymenea* is an indicator in James *et al*.'s *Pertusarietum amarae* sub-division of the *Graphidion scriptae*, while *Pyrenula occidentalis* is consistent with a hyper-oceanic sub-division, which was noted by James *et al*. but not formally described. *Pyrenula occidentalis* points to the transitional relationship between Community Type B, and the oceanic Type G *Lobaria virens-Normandina pulchella-Metzgeria furcata* Community.

Group II

Early Successional to Mature Communities in Mesotrophic Microhabitats

Community Type C: *Frullania dilatata* Community
Indicators: ***Frullania dilatata***, *Ulota bruchii/crispa*

Community Type D: *Phlyctis argena-Ramalina farinacea* Community
Indicators: *Melanelixia glabratula* agg.*, Parmelia sulcata, Pertusaria amara,* ***Phlyctis argena***, *Orthotrichum affine,* ***Ramalina farinacea***

The recognition of the Type C *Frullania dilatata* Community, which includes *Ulota bruchii/crispa*, matches broadly with the description by James *et al*. of a successional development towards increasing bryophyte presence in the *Graphidion scriptae*, particularly in humid microhabitats.

The Type D *Phlyctis argena-Ramalina farinacea* Community matches most closely with James *et al*.'s description of the *Parmelion perlatae*, and its role as a dominant community type on mature broadleaf trees. Lichen species associated with Type D, such as *Melanelixia glabratula* agg., *Parmelia sulcata, Pertusaria amara*, as well as *Phylctis argena* and *Ramalina farinacea*, are all listed as indicators by James *et al*. for the *Parmelion perlatae* (*Parmelietum revolutae* sub-division). The moss *Orthotrichum affine* is shared with and links the Type D Community with successional development from the *Graphidion scriptae*.

However, the namesake for the *Parmelion perlatae, Parmotrema perlatum*, was not found to be associated with Type D, but instead with the Type K *Lobaria pulmonaria-Isothecium myosuroides* Community. This forces a distinction within James *et al*.'s description of the *Parmelion perlatae*, between (i) a meostrophic community occurring on mature trees in relatively drier and cooler (winter) climates (Type D) and (ii) a separate community type of mature mesotrophic settings, occurring in warmer winter climates, or microhabitats (Type K), which included *Parmotrema perlatum* as an associate alongside dominant foliose lichens such as *Lobaria pulmonaria* and pleurocarpous mosses such as *Isothecium myosuroides*.

Group III

Mature Communities in Drier Microhabitats (Rough-Barked and/or Leaning Trees)

Community Type E: *Calicium viride-Chrysothrix candelaris* Community
Indicators: *Anisomerdium biforme, Arthonia vinosa,* ***Calicium viride****, Chaenotheca trichialis,* ***Chrysothrix candelaris****, Cliostomum griffithii, Lepraria incana*

Community Type F: *Lecanactis abietina* Community
Indicators: ***Lecanactis abietina***

The Community Types E and F match extremely well with the distinct habitat characteristics described by James *et al*. for their *Calicion hyperelli* Community, confirming their observation that the associated species are microhabitat specialists and relatively faithful to a narrow set of ecological conditions.

Species associated with Community Type E are consistent with James *et al*.'s *Calicietum hyperelli* sub-division of the *Calicion hyperelli*, e.g. *Calicium viride, Chrysothrix candelaris, Cliostomum griffithii* and *Lepraria incana*. It is consistent with the biogeographic scope of our sampling that James *et al*. recognised the occurrence of *Chaenotheca trichialis* as a distinct community indicator for a variant of the *Calicietum hyperelli* in central Scotland, i.e. it is also an indicator for Type E within our Scottish samples. The association of *Anisomeridium biforme* and *Arthonia vinosa* suggests Type E may also operate as a northern equivalent to James *et al*.'s *Arthonietum impolitae* sub-division of the *Calicion hyperelli*, i.e. in the absence of the more southern *Schismatomma decolorans*.

Our analysis recognised the separate identity of the Community Type F, with *Lecanactis abietina* as an indicator, and matching with James *et al.*'s contrasting *Lecanactidetum abietinae* sub-division of the *Calicion hyperelli*.

Group IV

Mature Mesotrophic Communities in Oceanic Climates (or Humid Microclimates)

Community Type G: *Lobaria virens-Normandina pulchella-Metzgeria furcata* Community
Indicators: *Frullania fragilifolia, Isothecium alopecuroides, Lepraria eburnea,* ***Lobaria virens, Metzgeria furcata, Normandina pulchella****, Opegrapha vulgata, Thelotrema lepadinum, Zygodon viridissimus*

In terms of its species composition, the Type G Community corresponds most closely to the *Lobarion pulmonariae* of James *et al*. However, the absence of *Lobaria pulmonaria* with dominant pleurocarpous bryophytes suggests that Type G represents an earlier successional and species-rich variant of the *Lobarion pulmonariae*, which was recognised for western Scotland by James *et al*., for example in contrast to the communities in Group V. This early successional effect is suggested by the indicators *Metzgeria furcata* and *Opegrapha vulgata*, which are shared with the *Graphidion scriptae*, and which link to the pioneer Type B *Graphis scripta* Community.

Other key Type G indicators suggesting an oceanic species-rich *Lobarion pulmonariae* include *Thelotrema lepadinum*, as well as *Lobaria virens* and *Normandina pulchella*. *Lepraria eburnea*, *Isothecium alopecuroides* and *Zygodon viridissimus* are suggestive of mesotrophic microhabitats, e.g. with *Zygodon viridissimus* an indicator for James *et al*.'s *Xanthorion parietinae* (*Physcietum ascendentis* sub-division).

Group V

Late Successional Mesotrophic Communities in Oceanic Climates (or Humid Microclimates)

Community Type H: *Hypnum cupressiforme* agg.-*Usnea flammea* Community
Indicators: ***Hypnum cupressiforme* agg.**, *Lepraria lobificans, Plagiochila punctata,* ***Usnea flammea***

Community Type I: *Hypnum andoi-Microlejeunea ulicina* Community
Indicators: *Cladonia coniocraea, Dicranum scoparium,* ***Hypnum andoi****, Lepraria rigidula,* ***Microlejeunea ulicina***

Community Type J: *Frullania tamarisci* Community
Indicators: ***Frullania tamarisci****, Harpalejeunea molleri*

Community Type K: *Lobaria pulmonaria-Isothecium myosuroides* Community
Indicators: *Hypotrachyna taylorensis,* ***Isothecium myosuroides, Lobaria pulmonaria****, Parmotrema crinitum, Parmotrema perlatum*

Cross-referenced with James *et al*., the Group V communities show an intergradation between the *Lobarion pulmonariae* and *Parmelion laevigatae*. For example, the Type J indicator *Frullania tamarisci* is recognised within both the *Lobarion pulmonariae* and *Parmelion laevigatae*, with the associated *Harpalejeunea molleri* providing an additional indicator for oceanic settings.

The Type K *Lobaria pulmonaria-Isothecium myosuroides* Community is identified as a late-successional and species-poor variant of the *Lobarion pulmonariae*, with *Lobaria pulmonaria* as a key indicator, alongside *Isothecium myosuroides* as a spatially dominant bryophyte. However, several of the associated indicator species align the community with leached and relatively more nutrient-poor or acidic-bark conditions within oceanic climates, such as *Hypotrachyna taylorensis* and *Parmotrema crinitum,* which James *et al*. associated with the *Parmelietum laevigatae*. These occur alongside the indicator *Parmotrema perlatum* which was shown to be distinct from James *et al*'s *Parmelion perlatae*, by not associating with the mesotrophic Type D (*Phlyctis argena-Ramalina farinacea* Community).

The leached microhabitat conditions for Group V, relative to Community Type G (*Lobaria virens-Normandina pulchella-Metzgeria furcata* Community ≈ species-rich *Lobarion pulmonariae*), are further highlighted through the close association of the Type I *Hypnum andoi-Microlejeunea ulicina* Community. This community can develop to be fully dominated by *Hypnum andoi* and includes oceanic indicators such as *Microlejeunea ulicina*, though also species within the *Parmelietum laevigatae*, including *Cladonia coniocraea* and *Dicranum scoparium*, with *Lepraria rigidula* recognised as an additional indicator.

Finally, the importance of *Cladonia coniocraea* within the Type I *Hypnum andoi-Microlejeunea ulicina* Community supports the link through to the Type H *Hypnum cupressiforme* agg.-*Usnea flammea* Community. The role of *Usnea flammea* as indicator for the Type H Community suggests a similarity to the acid-barked *Cladonieto-Usneetum tuberculatae* sub-division in the *Usneion barbatae* of James *et al*., which includes

Cladonia species as a component. However, Type H also includes *Hypnum cupressiforme* agg. as a dominant bryophyte, along with *Plagiochila punctata* as indicative of a milder and wetter oceanic climate, and with *Lepraria lobificans* as a further indicator species.

In summary, Group V represents a complex suite of species in communities where bryophytes are important, at the interface of the *Lobarion pulmonariae* where this is late-successional and relatively species-poor. In contrast, in the *Parmelietum laevigatae* the environment for lichens transitions away from the mesotrophic to become too oligotrophic for the typical members of the *Lobarion pulmonariae*. Finally, a bryophyte dominated element provides links to the *Usneion barbatae*.

Group VI

Early Successional to Mature Communities in Intermediate Settings

Community Type L: *Arthopyrenia cinereopruinosa-Lecanora pulicaris* Community
Indicators: ***Arthopyrenia cinereopruinosa***, *Chrysothrix flavovirens*, ***Lecanora pulicaris***, *Micarea micrococca* agg., *Pertusaria pupillaris*

For Community Type L there is no suitable equivalent community identified by James *et al*., though *Lecanora pulicaris* was indicative of their *Lecanorion subfuscae*. However, the key indicators of the Type L *Arthopyrenia cinereopruinosa-Lecanora pulicaris* Community are either relatively small such as *Arthopyrenia cinereopruinosa*, or are placed in taxonomically difficult genera, e.g. *Micarea micrococca* agg., including the sterile crusts *Chrysothrix flavovirens* and *Pertusaria pupillaris*. In the last 35 years knowledge of these species has grown. The association of species identified as Community Type L appears relatively weak, however, and in general it may represent a poorly defined community whose species occur as scattered elements among dominant fruticose/foliose lichens or bryophytes.

Group VII

Mature to Late Successional Communities in Oligotrophic Microhabitats

Community Type M: *Hypotrachyna laevigata-Loxospora elatina* Community
Indicators: *Anisomeridium ranunculosporum*, ***Hypotrachyna laevigata, Loxospora elatina***, *Mycoblastus caesius*, *Scapania gracilis*

Community Type N: *Mycoblastus sanguinarius-Protoparmelia ochrococca-Sphaerophorus globosus* Community
Indicators: *Cladonia macilenta/polydactyla*, *Micarea synotheoides*, ***Mycoblastus sanguinarius***, *Ochrolechia androgyna*, *Parmelia saxatilis* agg. *Platismatia glauca*, ***Protoparmelia ochrococca, Sphaerophorus globosus***, *Usnea subfloridana*

Community Type O: *Bryoria fuscescens-Ochrolechia microstictoides-Parmeliopsis hyperopta* Community
Indicators: ***Bryoria fuscescens***, *Hypocenomyce friesii*, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Imshaugia aleurites*, *Lecidea hypopta*, *Lecidea nylanderi*, *Lepraria jackii* agg., ***Ochrolechia microstictoides, Parmeliopsis hyperopta***, *Pertusaria borealis*, *Tuckermanopsis chlorophylla*, *Violella fucata (Mycoblastus fucatus)*

Community Type M is aligned with James *et al*.'s *Parmelion laevigatae*, because of the key indicator role of *Hypotrachyna laevigata*. However, *Loxospora elatina* appears as a pioneer species in the *Pertusarietum amarae* sub-division of the *Graphidion scriptae* in old-growth forests (linking to the Group I communities), or as a member of the *Loborion pulmonariae* and linking therefore to the more mesotrophic Type G (*Lobaria virens-Normandina pulchella-Metzgeria furcata* Community). Nevertheless, *Scapania gracilis* occurs within the *Parmelion laevigatae* and is also indicative of oligotrophic habitats in oceanic climates, with *Anisomerdium ranunculosporum* and *Mycoblastus caesius* as additional indicators for Type M. Community Type N is also clearly identified as equivalent to the *Parmelion laevigatae*, including the indicators *Mycoblastus sanguinarius, Sphaerophorus globosus, Ochrolechia androgyna, Parmelia saxatilis* agg., *Platismatia glauca* and *Usnea subfloridana*, with *Micarea synotheoides* and *Protoparmelia ochrococca* identified as additional species. The occurrence of *Cladonia macilenta/polydactyla* suggests that the Type N Community can share a similarity with the *Cladonietum coniocraeae* sub-division of the *Cladonion coniocraeae*, which according to James *et al*. can also include *Sphaerophorus globosus*.

The Community Type O is aligned to the *Pseudevernion furfuraceae* of James *et al*., and these share indicator species including *Bryoria fuscescens, Ochrolechia microstictoides* (included by James *et al*. as *O. turneri*), *Parmeliopsis hyperopta*, as well as *Hypocenomyce scalaris, Hypogymnia physodes* and *Tuckermanopsis chlorophylla*. Additional species recognised here include *Hypocenomyce friesii, Imshaugia aleurites, Lecidea hypopta, Lecidea nylanderi, Lepraria jackii* agg., *Pertusaria borealis*, and *Violella fucata (Mycoblastus fucatus)*. There are several species included in James *et al.'s Pseudevernion furfuraceae* which are shared among other community types, such as: (i) for the Type N Community, including *Mycoblastus sanguinarius* and *Parmelia saxatilis* agg., and (ii) for the more mesotrophic but continental Type D *Phlyctis argena-Ramalina farinacea* and Type E *Calicium viride-Chrysothrix candelaris* Communities, e.g. *Melanelixia glabratula* agg., *Parmelia sulcata*, and *Phylctis argena*, and *Calicium viride* and *Lepraria incana*, respectively.

Pro Forma for the Field Recording of Epiphyte Communities

These pages provide a recording sheet for the fifteen epiphyte communities (Types A-O), and a simplification of the statistical analysis (box-plots) as a reminder of the habitat conditions under which the different community types were recorded.

To assist in our understanding of epiphyte distributions, submit the species records for epiphyte community recording using the iRecord system (http://www.brc.ac.uk/irecord/). Once logged-in, use the 'Record' option to access the 'Activity' called 'Scottish Epiphyte Community Survey'.

Date:	**Location:**	**Code:**
Tree Species:	**Tree Girth:**	
Habitat Notes:		

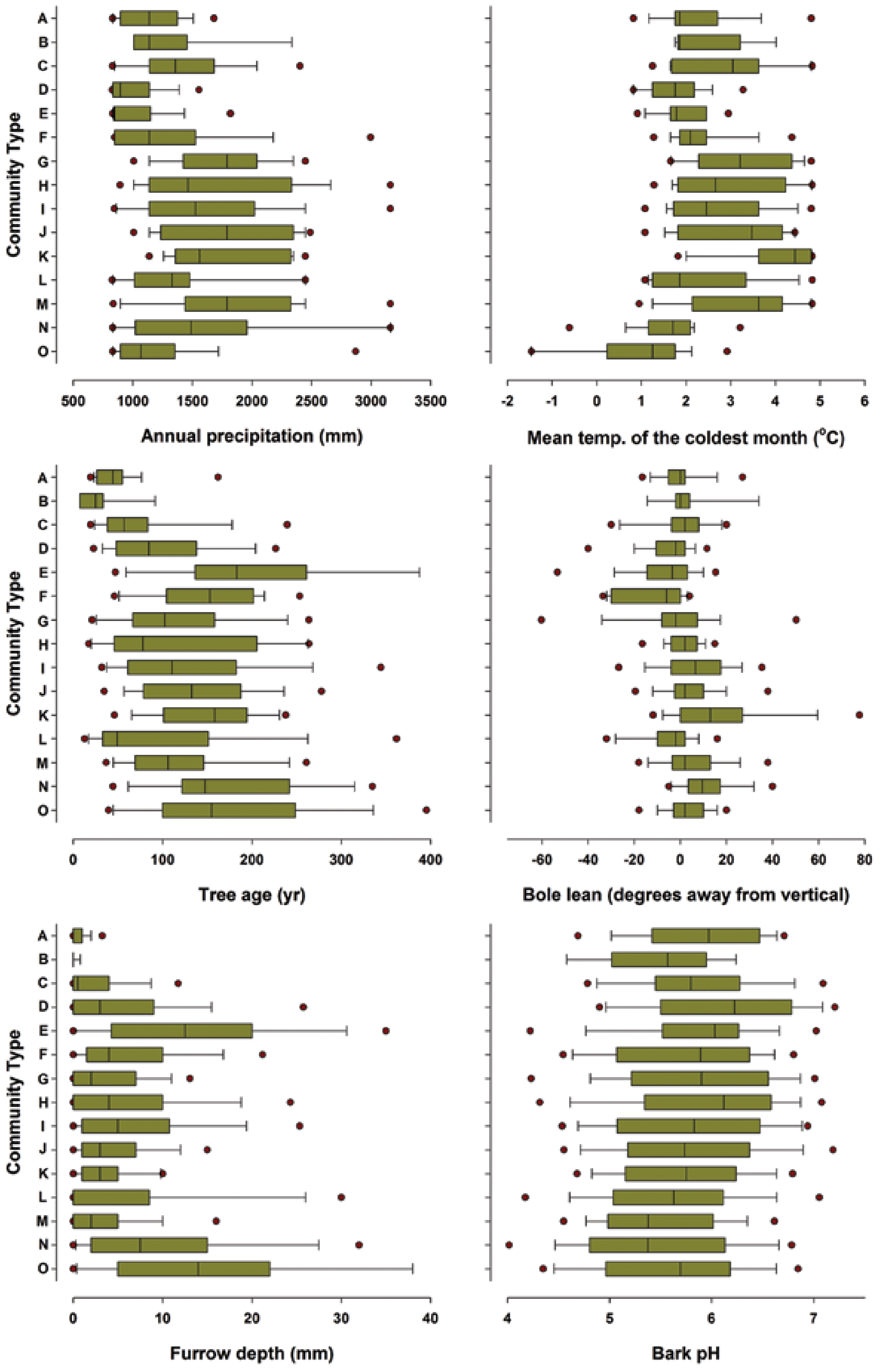
	Community Types:														
	I		**II**		**III**		**IV**	**V**				**VI**	**VII**		
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**
LICHENS															
Anisomeridium biforme					▨										
Anisomerdium ranunculosporum													▨		
Arthonia didyma		▨													
Arthonia radiata	▨														
Arthonia vinosa					▨										
Arthopyrenia cinereopruinosa												▨			
Bryoria fuscescens															▨
Buellia disciformis	▨														
Calicium viride					▨										
Chaenotheca trichialis					▨										
Chrysothrix candelaris					▨										
Chrysothrix flavovirens												▨			
Cladonia coniocraea									▨						
Cladonia macilenta/polydactyla														▨	
Cliostomum griffithii					▨										
Graphis scripta		▨													
Hypocenomyce friesii															▨
Hypocenomyce scalaris															▨
Hypogymnia physodes															▨
Hypotrachyna laevigata													▨		
Hypotrachyna taylorensis											▨				
Imshaugia aleurites															▨
Lecanactis abietina						▨									
Lecanora chlarotera	▨														
Lecanora pulicaris												▨			
Lecidea hypopta															▨
Lecidea nylanderi															▨

	Community Types:														
	I		II		III		IV	V				VI	VII		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
LICHENS *continued*															
Lecidella eleaochroma	■														
Lepraria eburnea							■								
Lepraria incana					■										
Lepraria jackii agg.															■
Lepraria lobificans								■							
Lepraria rigidula									■						
Lobaria pulmonaria											■				
Lobaria virens							■								
Loxospora elatina													■		
Melanelixia glabratula agg.				■											
Micarea micrococca agg.												■			
Micarea synotheoides														■	
Mycoblastus caesius													■		
Mycoblastus sanguinarius														■	
Normandina pulchella							■								
Ochrolechia androgyna														■	
Ochrolechia microstictoides															■
Opegrapha vulgata							■								
Parmelia saxatilis agg.														■	
Parmelia sulcata				■											
Parmeliopsis hyperopta															■
Parmotrema crinitum											■				
Parmotrema perlatum											■				
Pertusaria amara				■											
Pertusaria borealis															■
Pertusaria leioplaca	■														
Pertusaria hymenea		■													
Pertusaria pupillaris												■			
Phyctis argena				■											
Platismatia glauca														■	
Protoparmelia ochrococca														■	
Pyrenula occidentalis		■													
Ramalina farinacea				■											
Sphaerophorus globosus														■	
Thelotrema lepadinum							■								
Tuckermanopsis chlorophylla															■
Usnea flammea								■							
Usnea subfloridana														■	
Violella fucata (Mycoblastus fucatus)															■
BRYOPHYTES															
Dicranum scoparium									■						
Frullania dilatata			■												
Frullania fragilifolia							■								
Frullania tamarisci										■					
Harpalejeunea molleri										■					
Hypnum andoi									■						

	Community Types:														
	I		**II**		**III**		**IV**	**V**				**VI**	**VII**		
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**
BRYOPHYTES ***continued***															
Hypnum cupressiforme agg.								▨							
Isothecium alopecuroides							▨								
Isothecium myosuroides											▨				
Metzgeria furcata							▨								
Microlejeunea ulicina									▨						
Orthotrichum affine				▨											
Plagiochila punctata								▨							
Scapania gracilis													▨		
Ulota bruchii/crispa			▨												
Zygodon viridissimus							▨								
A - Number of recorded indicators per community:															
B - Theoretical total per community:	**5**	**4**	**2**	**6**	**7**	**1**	**9**	**4**	**5**	**2**	**5**	**5**	**5**	**9**	**13**
C - Total number of recorded indicators (sum of A):															
Indicator Strength[1] **=**															
Community Contribution[2] **=**															

[1] divide the Number of recorded indicators per community (A), by the Theoretical total per community (B)
[2] divide the Number of recorded indicators per community (A), by the Total number of recorded indicators (C)

Additional Species:


Community Type
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
500
1000
1500
2000
2500
3000
3500
Annual precipitation (mm)
-2
-1
0
1
2
3
4
5
6
Mean temp. of the coldest month (°C)
0
100
200
300
400
Tree age (yr)
-60
-40
-20
0
20
40
60
80
Bole lean (degrees away from vertical)
0
10
20
30
40
Furrow depth (mm)
4
5
6
7
Bark pH

Calculation of Habitat Heterogeneity and Biodiversity

One of the important contributions that recording community indicator species can make, is to provide an assessment of habitat heterogeneity in explaining epiphytic diversity, as a complement to the recording of rare and threatened species. For example, woodland with a simple structure (a monoculture of similarly aged trees) will be dominated by relatively few community types. Heterogeneous woodland with a mosaic of different tree species and stand ages will have a greater diversity of community types. A development provided by this report, is to link epiphyte community types to key habitat factors, providing a degree of statistical confidence in the interpretation of the communities, and their response to an environmental setting and habitat dynamics. It should be possible to set management goals in terms of the types and diversity of communities appropriate to a given site, as part of recording habitat quality and monitoring change.

When using the epiphyte community indicators in this way, it is important to consider the sampling regime, whether this is spatially random, aiming for accurate representation of the abundance of different communities at a site, or aiming to detect the full range of habitats that are available to epiphytes at a site (as presented in Chapter 2). Either way, it would be necessary to record communities from multiple trees at a stand-, or site-scale. Consider an example analysis: for each sampled tree, the Indicator Strength and Community Contribution (see Chapter 4 and/or Appendix 3) of each different epiphyte community type could be multiplied together, providing a single value per community type, per tree. These values could then be summed for each community type across the sampled trees, calculated as relative proportions, and combined with a suitable diversity metric (e.g. Shannon-Weiner's *H*').

A simplified example, which imagined sampling five trees for two theoretical woodlands, is provided below:

Figure Appendix 4.1. **Surveying epiphyte communities from aspen-birch pasture woodland in north-eastern Scotland.**

Woodland 1: A hypothetical species-poorer woodland in western Scotland, dominated by few old oak trees (Trees 1 & 2) and very young hazel (Trees 3-5).

	Community Type														
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**
Tree 1															
IS											0.4				
CC											1				
IS x CC											**0.4**				
Tree 2															
IS											0.2				
CC											1				
IS x CC											**0.4**				
Tree 3															
IS	1	0.25													
CC	0.833	0.166													
IS x CC	**0.833**	**0.042**													
Tree 4															
IS	0.8	0.5													
CC	0.666	0.333													
IS x CC	**0.533**	**0.166**													
Tree 5															
IS	0.8	0.5													
CC	0.666	0.333													
IS x CC	**0.533**	**0.166**													
Sum IS x CC	1.899	0.374									0.8				
Proportion (*p*)	0.618	0.122									0.26				
(*p*) x log(*p*)	-0.129	-0.111									-0.152				
H′	**0.392**														

IS = Indicator Strength; CC = Community Contribution
H′ = -1 x [∑ {(*p*) x log(*p*)}]

Woodland 2: A hypothetical species-richer woodland in eastern Scotland, with young rowan (Tree 1), mature (Tree 2) and old oak trees (Trees 3 & 4) and pine (Tree 5).

	Community Type														
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**
Tree 1															
IS	1	1	0.5												
CC	0.625	0.25	0.125												
IS x CC	**0.625**	**0.25**	**0.063**												
Tree 2															
IS			0.5	0.666					0.6		0.4				
CC			0.1	0.4					0.3		0.2				
IS x CC			**0.05**	**0.266**					**0.18**		**0.08**				
Tree 3															
IS					0.714	1					0.6				
CC					0.555	0.111					0.333				
IS x CC					**0.396**	**0.111**					**0.2**				
Tree 4															
IS					1	1					0.2				
CC					0.777	0.111					0.222				
IS x CC					**0.777**	**0.111**					**0.044**				
Tree 5															
IS															0.692
CC															1
IS x CC															**0.692**
Sum IS x CC	0.625	0.25	0.113	0.266	1.173	0.222			0.18		0.324				0.692
Proportion *(p)*	0.163	0.065	0.029	0.069	0.305	0.058			0.047		0.084				0.18
(p) x log*(p)*	-0.128	-0.077	-0.045	-0.08	-0.157	-0.072			-0.062		-0.09				-0.134
H'	**0.846**														

IS = Indicator Strength; CC = Community Contribution
H' = -1 x [∑ {*(p)* x log*(p)*}]

End Notes

[1] The estimated global forested area of 4 billion hectares was reported by the United Nations Environment Programme for 'forests' that meet the following standard criteria: (i) a minimum threshold for the height of trees of 5 metres, (ii) at least 10 percent crown cover (measured as shaded ground) and (iii) a minimum extent of 0.5 hectares. The assessment excluded agro-forestry systems such as orchards. The data was originally sourced by the Global Forest Resources Assessments (FRA) of the Food and Agriculture Organization of the United Nations (FAO). Information accessed from: http://www.unep.org/vitalforest/Report/VFG-01-Forest-definition-and-extent.PDF (January 2015).

[2] Estimates for bark surface area are based on a study published in the British Lichen Society's Bulletin (Pentecost 2010) which used fractal relationships to estimate the surface area available for colonisation by epiphytic cyanobacteria, at a scale of c. 10 μm, and using smooth-barked beech (*Fagus sylvatica*) and rough-barked oak (*Quercus robur*) as case-study tree species.

[3] An example of evolutionary adaptation to survive in the epiphytic environment is provided by the vascular plant family Bromeliaceae (bromeliads) which includes familiar epiphytes such as 'Spanish moss'. Evolution of a successful epiphytic strategy among bromeliads, includes an increased water-use efficiency through the development of photosynthesis by crassulacean acid metabolism (Crayn *et al.* 2004) as well as physiological mechanisms for the efficient uptake, utilisation and storage of growth-limiting nutrients such as nitrogen and phosphorus (Winkler & Zotz 2009).

[4] A review by the leading journal *Science* documented the diversity and ecosystem function of the forest canopy, of which epiphytes are a fundamental component (Ozanne *et al.* 2003). It concluded that although the forest canopy plays a key role in the biosphere, e.g. intercepting up to 25% of precipitation and controlling rainfall patterns, ecologically it remains one of the least known ecosystems.

[5] As an example of poikilohydry, lichens are particularly well-adapted to epiphytic habitats. They are able to efficiently sequester growth-limiting nutrients directly from rainfall or stem-flow (Lang *et al.* 1976); they can, depending on their photobiont type, reactivate physiologically using only water vapour (Lange *et al.* 1986), and they have evolved a range of mechanisms to tolerate extreme and prolonged periods of desiccation (Kranner *et al.* 2008).

[6] In tropical ecosystems the values of epiphytic diversity may be even higher, and to date the greatest number of lichen species recorded for an individual tree is one-hundred and seventy-three, from Papua New Guinea (Aptroot 2001).

[7] The occurrence of cryptogamic epiphytes on a tree creates 'a world within a world'; mathematically, it has been suggested that the community of epiphytic lichens may be viewed as a miniature woodland on the surface of a tree itself (Shorrocks *et al.* 1991), increasing the food resource for birds (Petterson *et al.* 1995) by providing key habitat for invertebrates (Stubbs 1989; Gunnarson *et al.* 2004). Epiphytes may increase canopy water uptake by around 50% (Knops *et al.* 1996) and lichen-fungi associated with cyanobacteria make growth-limiting nutrients such as nitrogen biologically available in the forest ecosystem (Forman 1975; Antoine 2004).

[8] The UK National Ecosystem Assessment (NEA 2011) drew a distinction between species which provide cultural service value, e.g. salmon and deer, or eagles and dolphins, about which a great deal is known, compared to the myriad species which go unnoticed by society at large, and which are less well known scientifically, but which form the building blocks of ecosystems and are essential to the delivery of 'supporting services' for human well-being.

[9] Archaeobotanical studies have shown that lichen communities from before the Industrial Revolution were much more diverse than they are today (Ellis *et al.* 2011; Yahr *et al.* 2011). The local or regional decline of lichens because of air pollution, and their potential as an environmental health indicator, was noted in scientific publications from the mid-19th Century onwards (reviewed in Hawksworth 1971). By the early 1970s the empirical use of lichens as indicators of SO_2 pollution (Hawksworth & Rose 1970) was supported by experimental work to demonstrate the functional basis for toxicity (Hill 1971). More recently, as SO_2 pollution has declined (Vestreng *et al.* 2007), nitrogen pollution has increased (Fowler *et al.* 2004), and lichens have been used as indicators for the processes of nitrogen acidification and hypertrophication (van Herk 1999; Van Herk *et al.* 2003).

[10] The United Kingdom's Environmental Audit Committee Fifth Report (2010) estimated that air pollution in the UK reduces life expectancy by an average of 7-8 months, though this reaches 9 years for people exposed

to the poorest quality air, costing the health service a conservative estimate of £8.5-20 billion p.a. in 2005. Lichen epiphytic diversity provides a metric that links pollution with human wellbeing (Cislaghi & Nimis 1997), by making it possible for local government, community groups and individual citizens to gauge the health of the environment in which they live.

[11] Lichen and bryophyte epiphytes ('signal species') are used in the Scandinavian conservation system to identify 'woodland key habitats', which are pockets of biodiversity-rich habitat associated with ecologically-important natural or semi-natural woodland structure (Gustafsson *et al.* 1999; Timonen *et al.* 2010), and which deserve protection within a commercial forest landscape. A similar indicator value has been proposed for lichen epiphytes in the United Kingdom (Ferris & Humphrey 1999) and is applied in a broadly comparable manner using 'indicators of ecological continuity' (Coppins & Coppins 2002).

[12] Intact temperate broadleaf forest is (in relative terms) the rarest biome globally; particularly in Europe, it has suffered among the highest disturbance levels, based on the conversion of natural habitat to an intensive human land-use such as agriculture (Hannah *et al.* 1995).

[13] The trend of permanent deforestation in the British lowlands dates to the end of a 'forest maximum' at approximately 5000 yr BP, and in the uplands to c. 2500 yr BP. However, particularly in upland regions, the progression of deforestation was discontinuous and spatially variable (Birks 1988).

[14] Ancient woodlands in Britain have been moulded into a cultural landscape, but in some cases are also the direct descendants of the original 'wildwood' (Rackham 2003). Examples such as 'coppice with standards', pasture woodlands or deer parks have provided a recurrent supply in the landscape of larger and older trees with an open and more gladed woodland structure, similar to that of old forest stands. The pioneering lichen ecologist Francis Rose noticed that certain epiphytic species were restricted to Britain's ancient woodland habitats and were indicators of woodland structure and historical longevity (Rose 1974, 1976). It is therefore expected that some managed types of ancient woodland may have allowed the survival of epiphytes in Britain that would otherwise be dependent on old-growth forest.

[15] The concept of the Anthropocene (Crutzen 2002; Steffen *et al.* 2007) was developed to mark a new phase in Earth's history, in which human activities have become a major driver of global geophysical and biological processes. The start of the Anthropocene is conventionally placed at the beginning of the Industrial Revolution.

[16] Some traditional management practices in ancient woodlands may have allowed the survival of epiphytic species otherwise associated with old forest stands, within a highly modified and deforested landscape[14]. The abandonment of this management can lead to secondary succession with changed microclimates and over-shading (light-limitation) in ancient woodland, causing a shift in the types of epiphytes found there (Leppik *et al.* 2011) and a loss of diversity (Jönsson *et al.* 2011).

[17] The most recent review of United Kingdom transboundary air pollution (RoTAP 2012) provides spatial analysis of data to show that upland Scotland beyond the central-belt, and away from major urban conurbations such as Glasgow, tends to have the lowest levels of air pollution in Britain; at a local scale, values for pollutants are consistent with the occurrence of intact epiphyte communities.

[18] There is a continuum of rainforest types, transitioning from tropical rainforest, to higher-latitude boreal or temperate rainforest of the type occurring in western Scotland. The bioclimatic conditions for temperate rainforest have been defined (Alaback 1991) as: (i) annual precipitation > 1400 mm, at least 10% of which occurs in summer, (ii) cool summers with a July isotherm < 16 °C, and (iii) with a dormant (winter) season caused by lower temperatures. Mapping and modelling the distribution of boreal/temperate rainforests (DellaSala 2011) has indicated that this ecosystem type covers as little as c. 0.07% of the global land area, with c. 17% of the suitable rainforest bioclimate occurring within Europe, and with Britain accounting for c. 39% of the European rainforest resource.

[19] The niche is one of the fundamental concepts in ecology. As a theoretical basis (Volterra 1928; Levin 1970) niche differences are required for long-term species coexistence (for biological communities to exist under stable equilibrium), because competition becomes focussed intra-specifically 'within a species'. This intra-specific competition suppresses the population growth of one species (through a process referred to as density dependence) more than it limits the population of other co-occurring species that have different environmental or resource requirements, i.e. which have a different niche. Alternatively, if two species share the same or very similar niche requirements, one of them (the better competitor) will eventually suppress the other. This niche postulate formed an early mechanism for explaining species diversity (Whittaker 1972). On the other hand, increasing refinement through criticism of its limitations has led to a very rich canon of ecological research.

[20] Experimental evidence has demonstrated that a lichen species does not occupy all its available niche space (Sillett *et al.* 2000; Keon & Muir 2002), and it follows that suitable niches are not colonised because of limits

to dispersal. The rate of dispersal for a propagule is controlled importantly by its shape, size and mass (Greene & Johnson 1993; Tackenberg 2003) and studies for lichens (e.g. *Lobaria pulmonaria*) with both larger asexual and smaller sexual propagules (spores) have indicated that there are stronger patterns of spatial aggregation generated by larger asexual propagules than for more widely distributed smaller sexual spores (Werth *et al.* 2006).

[21] The standard model of succession used here recognises the disturbance regime as a key driver for forest structure. Disturbance occurs along a continuum from stand replacing disturbance, such as fire or disease outbreaks which operate over a larger area, through to nested smaller-scale gap dynamics such as wind-throw or tree senescence (Lorimer 1989). This model of gap dynamics has been quantified for old-growth temperate forests in North America (Lertzman *et al.* 1996; Fraver *et al.* 2009) and fits with a mosaic-cycle observed for 'near-natural' European temperate forests (Emborg *et al.* 2000). We favour gap dynamics here to alternatives such as the 'wood pasture' hypothesis, which has inferred a more open 'parkland' type European landscape maintained by large herds of grazers. Wood pasture is an important outcome of traditional human management (Kirby *et al.* 1995), though it lacks convincing support from the palaeoecological record as the predominant natural forest structure in north temperate Europe (Birks 2005; Mitchell 2005).

[22] Natural forest old-growth stands have been shown to have greater environmental heterogeneity leading to higher levels of epiphytic diversity, compared to more intensively managed forest systems (Lesica *et al.* 1991; Brunialti *et al.* 2010).

[23] At the scale of an individual tree, the community of epiphytes on the lower bole transitions from one dominated by pioneer species, such as fast-growing crustose lichens reproducing sexually and dispersing with small spores, during early succession, to an increasing number of larger and more competitively dominant species (foliose lichens and bryophytes) which are more likely to reproduce asexually (Ellis & Ellis 2013).

[24] The use of lichens as indicators of woodland ecological continuity has been developed and refined since the 1970s (Rose 1974, 1976; Coppins & Coppins 2002), though there is a requirement for further critical research (Whittet & Ellis 2013) to understand: (i) the parameters which define ecological continuity and by which it can be independently measured, and (ii) the biological mechanisms which explain why certain epiphyte species (indicators) are sensitive to these parameters.

[25] Palaeoecological studies have demonstrated continuous post-glacial forest cover at certain sites over thousands of years; for Scotland's pinewoods this includes the area around Abernethy in Speyside (Birks 1970), and the eastern portion of Glen Affric (Froyd & Bennett 2006).

[26] The structure of ancient woodland in Scotland is often consistent with independent forms of evidence pointing to extensive pastoralism, which maintained the historically widespread occurrence of open structured woodland (Holl & Smith 2007).

[27] The influence of 19th Century woodland management on Scotland's oakwoods has been well documented (Smout 2005), in creating a cultural landscape with a simplified woodland structure.

[28] Regional trends in epiphyte distributions can be explained by climatically sensitive growth rates (Eaton & Ellis 2012) lending support to bioclimatic models which demonstrate the control of epiphyte distributions by climate (Braidwood & Ellis 2012), including scenarios of future climate change (Ellis *et al.* 2007).

[29] The environment is dynamic over time, and vegetation is responsive. Large-scale analyses of pollen data during the late Quaternary have emphasised the dynamic properties of vegetation in relation to climate change, with variable (non-stationary) plant associations structured by individualistic species responses (Williams *et al.* 2004).

[30] This wider landscape perspective is necessary to protect the processes which maintain biodiversity, especially during a period of environmental change. This includes broader habitat connectivity to facilitate meta-population dynamics and range shifting (Pressey *et al.* 2007).

[31] Ecosystem services are the benefits that human society derives from nature, and which are often considered 'free' and therefore discounted in classic economic models. Biodiversity has a multifaceted relationship with ecosystem services (Mace *et al.* 2012), with a great diversity of species often unnoticed but essential to ecosystem function (supporting services), while other 'charismatic' organisms provide a cultural service, such as in recreational fishing or bird-watching. However, the ecosystem service framework (NEA 2011) includes agricultural crops, or timber, outdoor recreational activities etc., and the delivery of some 'high value' ecosystem services can directly conflict with species conservation, especially for 'non-charismatic' taxa.

[32] Deforestation for biofuels is the classic example of good intentions gone wrong. Biofuels have led to the loss of > 13 million hectares of tropical forests and associated diversity, to make way for a new 'green' economy in

oil-palm production, which could take between 75-93 years to recover the carbon lost through deforestation, and up to 600 years where there was the conversion of tropical peatlands (Danielsen *et al.* 2008).

[33] The National Vegetation Classification (NVC) provides a common standard among the United Kingdom's nature conservation agencies, and has been widely adopted across sectors by ecologists, land managers, and conservationists. The influence of the NVC has been substantial, and it acts as the main terrestrial habitat classification in the Guidelines for the Selection of Biological Sites of Special Scientific Interest, for UK Common Standards Monitoring Guidance, for UK Interpretation of Annex I habitats listed under the EC Habitats Directive, and for detailed (Phase 2) ecological site survey and assessments.

[34] Some important woodland types in Scotland are not adequately represented in the UK National Vegetation Classification (NVC). This is the case for aspen woods, which have only recently been recognised for their biodiversity importance (Cosgrove & Amphlett 2002; Parrott & MacKenzie 2009), as well as for unmanaged hazel stands (Coppins & Coppins 2012). A single aspen-dominated woodland was sampled, from the core area of distribution in north-eastern Scotland (Strathspey), though sampling for hazel tended to be in areas where it was dominant within 'standard' NVC woodland types.

[35] Scotland's ancient woodland inventory (AWI) used cartographic evidence to identify woodland sites which had existed continuously in the landscape over long periods of time (Walker & Kirby 1987; Roberts *et al.* 1992). Class 1 sites are thought to have existed continuously over at least 260 years, as they consistently appear on maps produced since c. 1750.

[36] There are many studies that have examined the response of epiphyte species and communities to woodland and tree microhabitat factors. In preparation for field sampling this literature was reviewed for lichen epiphytes (Ellis 2012, 2013) to ensure that environmental variables with the potential to explain epiphyte community structure were considered.

[37] Monthly averages for a range of bioclimatic variables are made publicly available by the UK's Met Office. Values at a 5km grid-scale are based on statistical interpolation between instrumental recording sites (Perry & Hollis 2005), using c. 540 stations for temperature variables, and c. 4400 stations for precipitation. Long-term averages (1961-2006) are used to reflect trends in the regional climate.

[38] ForestGALES (Gardiner *et al.* 2006) provides a scoring system for the degree of topographic exposure, related to the mean wind-speed (Detailed Aspect Method of Scoring, or DAMS). The scoring was originally developed by comparing the attrition of tatter flags, which is correlated with wind condition (Jack & Savill 1973), to geographic parameters including position, aspect, slope, elevation, valley shape and direction, and positive angle to the sky-line within a distance of 10km (Quine & White 1994; Suárez *et al.* 1999). The scoring system was extended to sites across Britain using digital terrain modelling, with predicted values verified against observed data (Suárez *et al.* 1999). Values range from a score of 5 (very sheltered) up to approximately 32 (severely exposed).

[39] The slope angle was measured using an Abney level set between two markers at one metre height above the ground, and positioned three metres above and below the sampled tree, along the line of steepest slope.

[40] Values for calculating potential direct incident radiation and heat load index are based on published standard equations that integrate latitude, aspect and slope (McCune & Keon 2002).

[41] Ordination by detrended correspondence analysis (Kent & Coker 1992; Kent 2012) is used to summarise trends in multivariate data (e.g. a species x sample data matrix), and provide a graphical representation that averages the relationships observed among species (measured across samples) and samples (which contain different communities of species). Points representing individual species and samples can be plotted along orthogonal axes, of descending importance, and each of which summarises some of the variability in the original data matrix. Plotted for two axes (e.g. the most important axes one and two) the distance between sample points in ordination space reflects the difference in terms of species composition, while the position of species can be related to the samples in which they occur. The analysis for stand composition was performed in CANOCO v. 4.5 (Ter Braak & Šmilauer 2002; Lepš & Šmilauer 2003), with axes one and two describing 11.2% and 9.5% of variability in the data matrix, respectively.

[42] At four cardinal positions around the sampled tree, canopy openness (the reciprocal of canopy closure) was measured using a spherical densiometer (Lemmon 1956) and averaged. This measurement is based on a standardised concave mirror used to examine the sky in a series of 96 points over a network of sub-divisions (multiplied by 1.04). It is a relatively simple though effective tool for stand assessments, generating results that compare favourably with more complex techniques including hemispherical photography (Englund *et al.* 2000).

[43] Soil chemistry was assessed separately for four samples per tree, and an average calculated. Analysis followed a standard protocol in which 5g of sieved and oven-dried soil (30 °C for 24 hours) was mixed into 20ml distilled water over a period of 10 minutes. Analysis used a Sartorius bench-top pH/conductivity meter, which was re-calibrated at least once per hour against standard buffers at pH 4 and 7.

[44] The Pressler-sampled tree cores were stored in plastic straws in the field, and glued and strapped into wooden grooved splints for preparation. Cores were sectioned longitudinally using a scalpel, and were sanded before counting rings under a dissecting microscope (x10 - x50). If the centre of the tree core was not visible, a growth index was calculated based on the average ring width and dividing this into the radius of the tree bole. This was then cross-referenced against a second estimate, which aligned the sectioned core to an acetate sheet with evenly spaced concentric circles, corresponding to the average ring width for the earliest sampled 10 years of growth, and then estimating the number of missing tree rings.

[45] An index of bark roughness was measured as the ratio of furrow habitat, to bark ridge habitat, using Pythagorean geometry (Ellis & Coppins 2007). This approach provides an index of surface roughness, but could yield high values even if the absolute depth of furrows was small (so long as the furrows accounted for a relatively large area of the quadrat, compared to ridges); it was therefore accompanied by a simple measure of vertical furrow depth per quadrat.

[46] Bark samples were prepared by removing epiphytes and surface debris with a scalpel blade and stiff brush. The bark was sectioned into multiple fragments (each < 5 x 5 x 5 mm). The bark fragments were oven-dried at 30 °C until a constant weight was achieved. The dried bark was added to distilled water at a ratio of 1:20 (0.1g bark to 2 ml water), and soaked for 12 hours. Analysis used a Sartorius bench-top pH/conductivity meter, which was re-calibrated at least every 60 samples against standard buffers at pH 4 and 7.

[47] The bark volume was calculated for air-dried samples following the surface cleaning, by placing the sample into a laboratory cylinder with 10ml water, and calculating the immediate displacement. This made it possible to estimate water-holding capacity and density, based on the difference between the dry weight and the saturated bark weight, following a 12 hour suspension in distilled water.

[48] Ordination by principal components analysis (PCA) was used to handle collinearity among the multiple environmental variables (Kent & Coker 1992; Kent 2012), quantifying composite environmental gradients as sample scores along orthogonal PCA axes. Continuous environmental variables (excluding the categorical tree species identity) were summarised using PCA, implemented with the base package in R (R Development Core Team 2013). Data were log-transformed to achieve normality prior to analysis where required (values for the landscape matrix at 1km, 5km, and 10km, altitude, distance to the closest river and stream, canopy openness, tree girth and age, and furrow depth). PCA was performed on data that were standardised and centred to derive a correlation cross-product matrix. The first three PCA axes explained 17.1%, 11.6% and 8.1% of variation in the environmental data matrix, respectively.

[49] Carefully controlled experimental studies have demonstrated that *Xanthoria parietina* benefits physiologically from a combination of higher pH combined with cation sources such as for calcium and magnesium, compared for example to the more 'oligotrophic' *Parmelia saxatilis* (Armstrong 1990).

[50] A regression tree (Maindonald & Braun 2010) was used to compare bark pH with the putative explanatory factors that were also correlated with PCA axes two and three (Composite Gradients 2 and 3): (i) tree species, (ii) annual precipitation (to capture the climatic effect), (iii) physical exposure (DAMS), (iv) stand structure (DCA axes 1 and 2), (v) slope, (vi) direct radiation, (vii) heat load, (viii) tree girth, (ix) tree age, (x) soil pH, and (xi) soil conductivity. Regression trees split the gradient of an explanatory factor into discrete sets which maximise homogeneity of variance in the response group. Splitting proceeds in a hierarchical fashion to produce a branching structure with end nodes (a tree) that allows interactions among multiple explanatory variables to be examined. Fitted trees which increase in complexity (increasing number of branches/nodes measured using a 'complexity parameter') are tested using a cross-validated error, in which a subset of data are left out of the tree calculation process, and the ability of the fitted tree to successfully predict the values of these set-aside data is tested. By convention, the simplest tree with a cross-validated error that is within one standard error of the tree with the lowest rate of cross-validated error is selected. Analysis used the package '*rpart*' in R (R Development Core Team 2013), with the end nodes restricted to a minimum of 30 samples ('minbucket'), run 100 times, and with the most frequently produced optimum tree used to explain bark pH. In 66% of cases the best tree had a complexity parameter of 0.011, with a cross-validated error of 0.715.

[51] Previous research has also shown that bark pH is controlled by multiple interacting variables, including tree species (Jüriado *et al.* 2009; Lewis & Ellis 2010) and age/size (Fritz *et al.* 2009; Jüriado *et al.* 2009), and the soil environment (Gauslaa 1985; Gustafsson & Eriksson 1995) which may itself be related to the stand topography (Gauslaa 1995). The results here also invoke an effect of the climate, pointing to increasingly leached (lower pH) bark in high rainfall and exposed settings.

[52] A mixed-effects model (Zuur *et al.* 2009) was used to compare tree girth to seven explanatory variables including: (i) tree species, (ii) tree age, (iii) annual precipitation, (iv) mean temperature of the coldest month, (v) direct radiation, (vi) heat load and (vii) soil pH. The mixed model is used to account for the fact the measurements are clustered within the 20 different sites, and in this sense are not independent of one another, affecting the statistical degrees of freedom. The identity of the site was used as a 'random effect' to control for this nested sampling design. Analysis proceeded backwards from the full model (with all seven explanatory variables), using log-likelihood tests to sequentially remove the least significant variables (Zuur *et al.* 2009). Mixed-effects analysis used the package '*lme4*' in R (R Development Core Team 2013).

[53] Because of the very large number of sampled quadrats (n = 1013), and many rare species occurrences, the dataset was simplified to reduce 'noise' by removing those species reported from < 15 quadrats. This resulted in the removal of 30 samples which had no species, i.e. samples for which all recorded species had < 15 occurrences, and on this basis the analysis was reduced to $n = 983$. To emphasise variability in species composition (McCune & Grace 2002), samples were standardised by the maximum recorded species value (frequency of occurrence) in each quadrat. Samples were then compared to produce a pairwise matrix using Bray-Curtis dissimilarity, which was applied in constructing a dendrogram using flexible beta linkage with $\beta = -0.25$ (McCune & Grace 2002). The dendrogram was split at successive points to produce a consecutive number of different community groups, from 2 to 100. For each of these 99 splits, Indicator Species Analysis (Dufrêne & Legendre 1997) was used to test the degree to which species were indicators for a given group, using a permutation test with 10,000 randomisations to assess a species' significance. An optimum number of community groups was selected at the cut-off point which minimised the mean indicator species P-value, following the procedure recommended by McCune & Grace (2002). All analysis used PC-ORD v. 6 (McCune & Mefford 2011).

[54] Sampled quadrats were uniquely assigned to a given community type[53], providing a presence-absence structure to the dataset. The occurrence of each community type was then compared to 11 explanatory variables: Composite Gradient 1, Gradient 2 and Gradient 3, distance to water, canopy openness, height and aspect on the bole, angle of lean, bark water capacity and density, and tree species identity. The comparison used nonparametric multiplicative regression (NPMR), implemented in the program Hyperniche v. 2 (McCune & Mefford 2009). NPMR uses a local model 'window', the width of which can vary with respect to an environmental gradient, and with the width referred to as the 'tolerance', to calculate the value of a central data point, based on weightings for response values sampled across the window (McCune 2006). The estimated value of the response also includes an automated interaction which is achieved by simultaneously sampling the windows for a progressively larger number of additional environmental variables (McCune 2006). Given multiple possible sizes of each window, and many possible combinations of different environmental variables, the NPMR procedure is computationally intensive, and uses cross-validation to seek an optimum model from among the large number of potential alternatives, with a set of rules for parsimony, e.g. a threshold for the data:predictor minimum. The analysis used a Gaussian structure to weightings within the window, and the default 'medium' settings in Hyperniche, to seek for each community type the best model, and disallowing increasingly complex models which did not improve the measure of fit ($\log B$) by ≥ 8%.

[55] The species mean frequency of occurrence was calculated for the sampled quadrats assigned to a given community type, and these summary values standardised by the maximum mean species value (frequency of occurrence) per community type. Ordination by detrended correspondence analysis (DCA)[41] was used to summarise variability among the different community types and infer environmental relationships. The first two DCA axes explained 29.4% and 19.5% of variation in the community matrix, respectively.

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Botanic Garden
Edinburgh

Epiphyte Communities and Indicator Species

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