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Investigating the relationship between non-vascular epiphytes and age structures within phorophytes on *Quercus robur* and *Pinus sylvestris*, at Dundreggan, Scotland

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Abstract

The focus of this research project was to analyse the effects of different age structures within the host phorophyte on non-vascular epiphytes in a fragmented, semi-natural forest stand in Dundreggan. Two tree species were investigated *Pinus sylvestris*, Scots pine and *Quercus robur*, oak, analysing the effect a specific tree has on epiphyte abundance and diversity. Such research is important to understand the relationship epiphytes have with different tree species, focusing on patterns of epiphytic distribution at different spatial scales, which can be later implemented into management techniques. Epiphytic functional groups were stratified vertically within the tree in three height zones, and horizontally within the branches, whether primary, secondary or tertiary. Six trees were sampled over a week. Three oak and three Scots pines were accessed using two common climbing methods; single and double rope techniques. All species of epiphytes were sampled within a quadrat on three primary, three secondary and three tertiary branches in each zone, which were later identified. The findings from the research proved that the size of the branch was the most influential component on epiphytic abundance, followed by the zone and finally the specific tree. There was a significant difference between the two tree species, with oaks epiphytic communities being more diverse and abundant than the pine, which indicated great dissimilarity between sub-plots. The main conclusion drawn from this study is the relationship between the size of the branch and epiphytic abundance, which can also correlate with maturity. There is also a distinct vertical gradient with a higher abundance of species in the lower zone. Along the horizontal gradient more species were found on the primary branches than tertiary. Further work would be viable into investigating the influence of environmental variables on epiphytic abundance.

Introduction

Caledonian forest

The Caledonian woodlands of West coast Scotland are considered to be the UK's temperate rainforest (DellaSala, 2011), due to the sheer diversity and complexity of its habitats (Rose, 1993) retaining areas of forest with a long historical continuity (Walker and Kirby, 1989; Roberts *et al*, 1992). Around 148,000 hectares of ancient woodland has been in continuous existence since the post-glacial re-colonisation (Rackham, 2006), representing approximately 27% of ancient woodland in the UK (Aspinal *et al*, 2011). These woodlands make up a small proportion of Scotland's 14% natural and semi-natural forest, of which only 1.5-2% is ancient according to the Nature Conservancy Councils Inventory of Ancient Woodlands (Roberts, 1992; Pryor and Smith, 2002). It is estimated that a mere sixth of British woodland represents ancient semi-natural woodland (Colebourn, 2009). The indigenous Caledonian forests are one of the most important habitats for wildlife (Colebourn, 2009) and one of the key biotopes (Rose, 1993) once covering the majority of the Scottish Highlands with a highly unique ecosystem (Rackham, 2006), (Figure 1). They are iconic in conservational values (Steven and Carlisle, 1959).

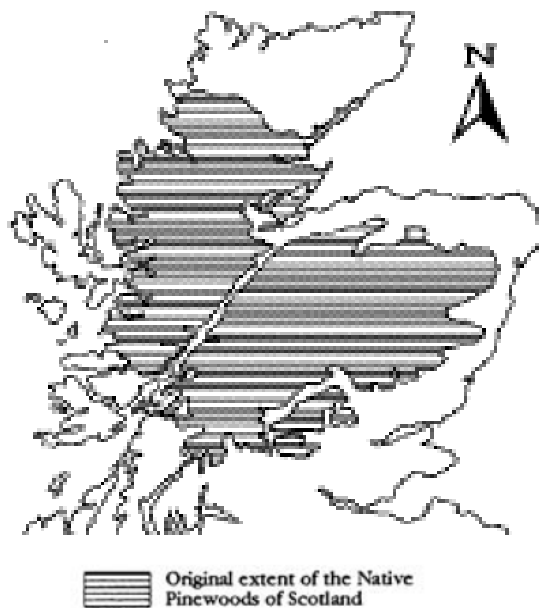


Figure 1: Represents the Caledonian forest cover at its maximum extent of 3.7million acres around 5,000 years ago (Featherstone, 1996)



Figure 2: Represents Caledonian forest now (Featherstone, 1996)

These native forests, once dominated by Scots pine (Miles, 1985) have been evolving for around 10,000 years (Colebourn, 2009) and have been subjected to constant deforestation since the Neolithic times, which is almost complete, (Figure 2) (McVean, 1962). The Scottish Highlands are described as an artificial or devastated landscape (Rackham, 2006) due to excess deforestation for fuel, clearance for agricultural land and plantations (Spencer and Kirkby, 1992), coppicing for iron works, etc., despite being one of the richest historical records we have (Colebourn, 2009). It is thought that during the 1800's the area of plantation forests overtook ancient woodland (Smout and Watson, 1997). Studies have indicated that intense logging of old growth forests reduces species diversity and assemblages, especially when replaced by plantations (Moning and Müller, 2009). Such forests cause a homogenization of the overall structure resulting in habitat loss and local extinction of sensitive species (Helioevaara and Vaeisaenen, 1984). Non-indigenous species can cause extinction of native flora and fauna by hybridization and introgression (Rhymer and Simberloff, 1996). Human behaviour has dramatically increased the rate of species extinction by around 1000 times the background level according to McVean and Ratcliffe (1962).

The Scottish government is encouraging reforestation in the interest of a shortage in domestic timber (Aspinal *et al*, 2011), therefore increasing the percentage of forest that is comprised of non-native species. This is causing a disruption of Scotland's natural heritage, as complex ancient woodlands are being replaced with monotonous plantations (Smout and Watson, 1997). A reduction in native tree species has been recognised by the National Countryside Monitoring Scheme, with recent efforts put into action to increase these populations, for example broadleaf species have seen an increase from approximately 106,000 hectares in the 1950's to 113,000 hectares in the 1980's (Aspinal *et al*, 2011). There have also been better efforts into increasing Scots pine, *Pinus sylvestris*, populations as recent recognition of their benefits in biodiversity has been appreciated (Humphrey *et al*, 2003; Humphrey, 2005). Further advent reforestation programmes from private and national parties (McVean, 1962) have been created and an overall increase in forest cover is beginning to be seen.

Dundreggan



Figure 3: Location of Dundreggan Estate shown highlighted in orange (Featherstone, 2010)

Dundreggan is a prime example of a heavily deforested area undergoing a significant amount of conservation projects in aid to restore the forest to its natural expanse. This 4,000 hectare estate is situated in North West Scotland and has been owned by the Scottish conservation charity Trees for Life since 2006 (Featherstone, 2006) (Figure 3). Trees for Life have put in a significant amount of time and effort into conserving the estate, aspiring to increase the variety of species and restore the landscape's natural forest cover (Featherstone, 2006). In this vast area of land there are only fragments of native, semi-ancient woodland found in the South, highlighted in Figure 3 in the blue shade. This area is highly overgrazed by deer and sheep preventing any further natural re-generation of woodland and vegetation communities (Featherstone, 2006). Despite this, within this confined area there is a vast array of epiphytic flora,

discovered after a detailed survey in 2007 and in 2009, which identified 266 bryophyte species (Rothero and Douglas *et al*, 2007) and 341 lichen species (Douglas, 2009), around 42 species of which are nationally scarce and 4 lichen that are nationally rare (Featherstone, 2006).

The rich and complex ecosystems found in Highland forests are rarely equalled in areas of similar size (Watling, 1997). This is resultant of geological variety, environmental conditions and the history of anthropogenic impacts (Aspinal *et al*, 2011). These factors, along with altitude and latitude, act as limiting factors strongly influencing the nature of the forest (Vincent, 1990) (Barbatti *et al*, 2007). The area experiences sub-polar and sub-tropical conditions (Gordon *et al*, 2004) due to the close proximity of the Gulf Stream. Consequently Western Scotland has a notoriously high annual rainfall, with a high percentage of wet days and a low potential water deficit, enabling flora to flourish (RBGE, 2011). At a global scale the forests are in the coastal temperate rainforest biome (RBGE, 2011), with floral communities reflecting combinations of boreal, Arctic-alpine, oceanic and Lusitanian elements (Aspinal *et al*, 2011).

Epiphytes

These combining factors and virtually non-existent pollution levels (Rose, 1993; Scottish Air Quality, 2012) create ideal conditions for vegetation to flourish, especially epiphytes. Epiphytes are vascular and non-vascular plants that grow on the stems of their associated phorophytes without deriving substance from the living tissue of their host, creating their own food via photosynthesis (Shaw, 1992; Lowman and Rinker, 2004). They are cryptogamic plants; they produce spores not seeds (Eaton and Ellis, 2012) and are dependent on the atmosphere for water and inorganic nutrients from precipitation, i.e. they are poikilohydric (Lowman and Rinker, 2004). They can also be separated into two groups vascular and non-vascular, the latter having an absence on vascularised tissue and organs such as the xylem and phloem. They can be further divided into obligate epiphytes, which are permanently attached to another plant or a facultative epiphyte, meaning that it can grow non-epiphytically too (Smith, 1982). Obligate epiphytes tend to appear at early successional stages whereas as the facultative epiphytes seem to dominate the climax communities, mostly on the trunk (Smith, 1982; Bates *et al*, 1997).

Rose (1993) suggests that for a diverse and rich epiphytic community to develop the forest must be relatively undisturbed and experience high humidity levels as found, to an extent, in the woodland of Dundreggan. The Highland forests form a reservoir of epiphytic species (Rose, 1993) and are Europe's 'hotspot' for lichen diversity (RBGE, 2011) providing internationally significant habitats for both lichens and bryophytes (Hodgettes, 1996). High epiphyte diversity and richness can also relate to the number of ancient trees, especially oaks, *Quercus spp.* (Rose, 1993).

In temperate forests bryophytes and lichens act as the dominant epiphytes (Eaton and Ellis, 2010). They're useful indicators of environmental health and are resources for arboreal invertebrates (Sillett and Antoine, 2004) for food, camouflage, oviposition sites, protection (Gerson and Seaward, 1977) (Richardson and Young, 1977) (Lowman and Rinker, 2004) and in providing micro-habitats (Eaton and Ellis, 2010). Lichens are a symbiosis between fungi and algae, whereas bryophytes are non-vascular plants, both occupying similar habitats and are frequently studied together

(Lowman and Rinker, 2004). They make up a minor part of the forests biomass but play a critical role in water relations, mineral and carbon recycling and for providing habitats (Lowman and Rinker, 2004; Toben and Dushek, 2005).

The open canopies of temperate forests constantly expose epiphytes to strong winds continually removing larger thalli, opening surfaces for re-colonisation. A general trend for temperate forests is that branches are primarily colonised by lichen followed by moss and liverwort (Lowman and Rinker, 2004). Succession of epiphytic communities involves autogenic (biotic components) and allogeneic (abiotic components) processes (Sillett and Antoine, 2004). In the canopy short-lived pioneer species grow rapidly, colonising twigs and as longer-lived species continue to proliferate as the branch matures, are displaced by later successional species (Stone, 1989; John, 1992). As the forest ages an accumulation of lichens and bryophytes develop into a community on the ever expanding tree surface. Environmental gradients, such as nutrients, temperature, height, and so on, all influence the rate of succession. Thus larger, old trees support a greater quantity and diversity of epiphytes than smaller, younger trees (Lang *et al*, 1980; Sillett and Antoine, 1994). The association these species have with old-growth stands is due to the unsuitable micro-environment or shortage of suitable substrates in young forests (Sillett and Antoine, 2004).

Lichen

Lichens represent a diverse evolutionary group (Lowman and Rinker, 2004) and are an example of a biological group neglected from bio-geographic and ecological studies (Ellis and Coppins, 2006). Along with moss and liverworts, they are the dominant epiphytes in temperate and boreal forest (Eaton and Ellis, 2012). Lichen are structurally complex (Pike, 1978), composite organisms (Galloway, 1992) consisting of a usually dormant fungal partner, the mycobiont or thallus, and a photobiont, a photosynthetic partner, which form a mutualistic association (Galloway, 1992; Lowman and Rinker, 2004; Sillett and Antoine, 2004; Acton and Griffith, 2008a). The photosynthetic part is more commonly algae but sometimes cyanobacteria is found, both manufacturing food from sunlight via photosynthesis (Acton and Griffith, 2008a). This symbiosis is one of the most successful known to nature therefore is important to conserve such an individual plant group (Galloway, 1992).

Lichen species are very slow growing and long lived (Nash, 1996). They have significant effects on a forest's nutrient dynamics (Smith, 1982; Slack, 1988; Boucher and Nash, 1990; Boucher and Stone, 1992; Nash, 1996; Coppins, 2003) by expanding the surface area of the canopy (Nadkarni, 1986). They add fertility to the forest as a result of their ability to fix nitrogen from the air, which is subsequently released back into the soil when the branch falls and the lichen naturally decompose (Mitchell *et al*, 2004; Featherstone, 2011). However, it is hard to measure the concentration of nitrogen that is released as it may not be in a readily available form (Nash, 1996). They are also used by arboreal insects for food, camouflage, protection, etc. (Edwards *et al*, 1960; Gerson and Seaward, 1977; Richardson and Young, 1977)

Lichen diversity responds differently to environmental predictors which can be divided into two main areas of human impact; industrial – a source of air pollution and agriculture – increases forest fragmentation and reduces forest age (Svoboda *et al*, 2010). Lichens, especially, are sensitive to environmental disturbances and habitat

destruction (Gilbert, 1977; Seaward, 1982; Pyakala, 2004) and habitat quality (Kussinen and Slitonen, 1998), making them useful indicators for pollution monitoring (Hawksworth & Rose, 1970), in summarising community change and in identifying forest habitats that require biodiversity protection (Selva, 1994). The frequency of species occurrence can be used as an assessment of diversity thus employed as a parameter to estimate the degree of environmental stress (Asta *et al*, 1995) (Svoboda *et al*, 2010). Pollution affects species diversity of lichen quite considerably although some are more tolerant enabling indicator species to be identified (Stolte *et al*, 1993; Geiser and Neitlich, 2006). Degraded forests are identified as depauperate ecosystems, characterised by a lack in the number and variety of species and include acidophilic lichen communities (Jepson, 2000), which are normally crustose as they exhibit greater epiphyte to tree specificity than any other lichen types (Ahti, 1977). Certain lichens have limited dispersal ranges, low colonisation ability or are limited by their niches (Sillett *et al*, 2000). These species are associated with old growth stands and are used as forest age indicators (RBGE, 2011) as they grow best in old, well lit trees and dislike abrupt change in micro-climate. For example the *Lobarion* community are a natural climax epiphytic community of the prehistoric wildwood (Rose, 1993; Rackham, 2006), thus they can be used as micro-climate indicators of ancient trees (Rackham, 2006). Lichen assemblages can also show a forests history (RBGE, 2011), which is useful especially where old maps and historical records are absent (Spencer, 2009). Rose (1974) created the original Index of Ecological Continuity, IEC; a term used to ascribe value to old forest stands (Nordén and Appelquist, 2001). Coppins and Coppins (2002) created further IEC's for Woodland Epiphytic Lichen Habitats, which can be used to assess the probability of the woodland being ancient (Rose, 2003). A specific index for Western Scotland was created by Coppins (2002). The presence of 'old forest' lichen and relic species can indicate a long period of continuity (Colebourn, 2009). A study by Ellis & Coppins (2007a) suggested that epiphytic community change during the life span of a tree can be predictable in respect to epiphytic traits, for example transitioning from a community dominated by sexually reproducing crustose lichen on young trees, to one dominated by foliose lichen and bryophytes as the tree matures (Ellis and Coppins, 2007a).

Using lichen as indicators is a newly developing area with mixed views (Johansson *et al*, 2007). In recent years the concept that suggests plants can be used as ancient woodland indicators has gained considerable appraisal as the understanding of the biology of canopy flora is becoming more understood (Spencer, 2009). Research in this area shows an insight into past land use history, ecological impacts and helps develop a broader understanding of the origins of native woodlands (Spencer, 2009). However, if bio-indicators of old forests are to be put in place, species with low dispersal capacities should be chosen (Nordén and Appelquist, 2001). Although epiphytes are colonists, some studies suggest that they indicate specific microhabitats as they have a 'patch-tracking' lifestyle instead of 'old-growth' indicators, as it is difficult in separating continuity from other ecological factors (Nordén and Appelquist, 2001). A limiting factor in using bio-indicators is that old forests maybe situated in less fragmented landscapes than young forests, therefore a difference in species composition may relate to the area and separation distance, rather than time (Helliwell, 1976).

Bryophyte

Bryophytes include plants that lack true vascular tissue and vascularised organs (Lowman and Rinker, 2004); they are the largest phylum of plants and inhabit every continent. They can be divided into three taxonomic groups (Shaw, 1992):

- ❖ Moss (*Bryophyta*)
- ❖ Liverwort (*Marchantiophyta*)
- ❖ Hornworts (*Anthocerotophyta*)

Mosses are at the highest level of diversity in evolutionary history and dominate an array of habitats (Shaw, 1992). They have a heteromorphic life cycle, thus nutritionally dependent on the gametophyte. They are extremely important in the nutrient economy of ecosystems that is disproportional in relation to their modest biomass (Shaw, 1992). These species are poorly understood even though they play important roles in the Earth's ecosystems, absorbing nutrients and toxic metals, recycling carbon and in some areas are the principal harvesters of solar energy (Tobin and Dusheck, 2005).

Tamm (1953) demonstrated that mosses have higher growth rates under a forest canopy than in clearings and are often accompanied by lichens (Schofield, 2001) (Acton and Griffith, 2008 a). Growth appears to be greatest under tree boundary, as this has the highest concentration of nutrient enrichment by leachates (Asawak *et al*, 1995). Dominant species within the canopy include moss and liverwort (Lowman and Rinker, 2004) such as the *Dicranum spp.* Bryophytes are often the colonizing species, especially for clear or poor nutrient sites (Schofield, 2001) where many other species would struggle and are major contributors to the suspended soil that develops on branches (Heitz *et al*, 2002), creating shelter for arboreal insects. Moss can also be used to indicate a vast amount about the history of a wood (Colebourn, 2009) as some species, as with lichen, are seldom found in younger forests and only associated with old growth (Dettki *et al*, 2000), although typically bryophytes show little correlation with ancient woodland (Rose, 1993). They can be used in identifying polluted areas as there are some species that thrive in polluted areas and others that are more delicate to pollutants (RBGE, 2010)

Tree species

Dundreggan is a case of arrested succession with ancient birch-juniper forests dominating, as they were the primary colonisers after the last ice-age (Nash, 2006). During succession the forests slowly evolved into wildwoods (Colebourn, 2009) composed of a range of trees such as Scots pine, *Pinus sylvestris* (Miles, 1985) and broadleaves; oak, *Quercus spp.*, aspen *Populus tremula*, alder, *Alnus glutinosa* and birch, and *Betula spp.* (Featherstone, 2006). The veterans of the forest are the Scots pine and oak with some individuals estimated to be around 200 to 300 years old (Featherstone, No Date; Steven and Carlisle, 1959). They can be described as the relics of the old Caledonian forest (Colebourn, 2009). These veterans are of great value as specific lichen can only grow on the old fissured bark that is associated with them, along with other epiphytic species such as bryophyte (Rackham, 2006).

Scots pine has been endemic since the last ice age (Rackham, 2006) and is a 'key-stone' species playing a critical role in the forest. It is the largest long-lived tree in the Caledonian forest and is unique in Scotland being the only conifers (Featherstone, 1996). The bark ranges throughout maturity from papery thin at juvenile stages to a

much darker, flakier appearance (Featherstone, 1998). Trees with flaky bark rarely carry large epiphytes as the surface is ephemeral and any large species would pull the bark off (Lowman and Rinker, 2004). A Pinewood Index created by Rose and Coppins, highlights that these species are the least altered relics of ancient Scots Pine woodland (Rose, 1993), see Appendix 1. These pines have relationships with many organisms such as epiphytic lichen and moss and are the back-bone of the fragmented forest. Even though total woodland areas are experiencing a decline, Scots Pine, both planted and natural, are at a high (Steven and Carlisle, 1959), occupying 30% of the total high forest area (Pryor and Smith, 2002). The Scottish pinewoods are important on an international level and have been recognised as a priority habitat for conservation (European Community Council Directive, 1992; Featherstone, 1996)

Oak may be a relatively minor component of the forest, remaining scattered throughout the UK, but they are very important in providing habitats for many species and are characterised by diverse epiphytic communities (Ellis and Hope, 2011). They are often key stone species, without which the complex web of the ecosystem would soon undo (Shrestha, 1993). They have been recognised internationally for their conservational values and are an EEC habitat (Mitchel *et al*, 2005). The fissured bark of mature oaks support a luxurious growth of non-vascular epiphytes (Shrestha, 1993), mainly consisting of bryophytes and large foliose lichen (McVean, 1962). The UK's oaks provide habitats for over 300 species of lichen and 64 bryophyte species in the UK (Featherstone, 2011a). Oaks are home to a large diversity of species but their regenerative capacity is very poor (Anderson, 1991).

Aspen, *Populus tremula*, is distributed throughout Britain but is most common in the North and West regions of Scotland. They are of high conservational value and are the main element of Trees for Life restoration projects as they are an important component of the forest (Featherstone, 2011b). They are important for insect species, especially some moths which are restricted to this tree species (Young, 2001). Even though they are widespread, their numbers don't compare with other forest trees. They are frequently found in clumps of single-sexed trees all from the same parent tree with a few kilometres separating the individual stands. This is problematic as they reproduce by seeds, and the distance between trees of the opposite sex limits the chance of reproduction (Featherstone, 1996), which is why they are the primary focus in restoration projects.

Regeneration

A significant threat that inhibits epiphyte persistence and recolonisation are air pollutants (Hawksworth and Hill, 1984). This causes a depauperation in lichen communities throughout Europe (Werth *et al*, No Date), i.e. it arrests their growth. After coal was replaced by natural gas and legislation was brought in, such as the Clean Air Acts, the number of lichen increased significantly, even in cities such as London (Rackham, 2006) enabling recolonisation of those species with effective dispersal mechanisms (Rose, 1993). Conversely, bark acidification still remains a great threat. In areas of relatively clean air, such as the Highlands, the main threat to epiphytic species, and all other flora and fauna is unsympathetic forestry (Rose, 1993), lack of mature trees, unsuitable forest management such as coppicing, causing drastic alterations in the internal environments (Rose, 1993), deforestation resulting in a human modified cultural landscape (Ellis and Hope, 2011) and forest fragmentation (Ellis and Renhorn, 1998). This is where the canopy environment is

most prone to deleterious effects (Bierregaard *et al*, 1992), especially species with poor dispersal abilities (Hedenås and Ericsson, 2008) for example some species of lichen (Sillett and Antoine, 2004) such as *Lobaria oregano* (Sillett *et al*, 2000). Wolf (2005) deduced a shift from mesic to drought-tolerant species when forests experienced anthropogenic disturbances. It is evident that even-aged, dense stands of plantation trees and disturbed forests create unsuitable conditions for the succession of epiphytic communities (Rose, 1993).

The wood pastures have become a neglected biome (Rackham, 2006) in the past but are now the focus of conservation. In recent years there has been increasing concern regarding the loss of biodiversity in managed woodland ecosystems (Kouki, 1994) These Highland woodlands are home to many iconic species of Scottish Wildlife and priority species under UK BAP, for example Scots pine and various epiphytic species (Aspinal *et al*, 2011). It has become imperative to examine the prosperity of restoring forests (Smout *et al*, 2007). To maintain biodiversity in managed forests there must be an understanding of the patterns and processes that regulate the occurrence and dynamics of species in undisturbed ecosystems (Essen *et al*, 2006) (Franklin, 1989). Strong protection and management strategies have been put in place (Mason *et al*, 2004) in an attempt to protect these species. These techniques should be able to maintain a large fraction of the original biodiversity, whilst sustaining a continued supply of commercially valuable forest produce (Essen *et al*, 2006). Efficient landscape management would be greatly improved if there was a better autecological understanding of lichens in relation to the dynamics of their environment (Coppins, 2003). Lidén (2009) suggests that overcoming limiting factors such as dispersal and reproduction in epiphytes should be a key factor in conservation (Lidén, 2009). Common regeneration methods used to mitigate the effects of forest management operations on species abundance and diversity (Essen *et al*, 2006) include fencing to prevent grazers, increasing the distance between trees at conifer plantations (Rothero and Douglas, 2009) thus opening the canopies and increasing the light levels (Rose, 1992), using boars to control fern populations allowing tree saplings to grow etc. Another technique is to neglect (Rackham, 2006) or manipulate young, regenerating forests to encourage natural succession and epiphytic growth (Moseley *et al*, 2005; Sillett *et al*, 1995). However, it's been suggested by Rose (1992) that to gain continuity of woodland structure, it must be left for over 100 years. Sillett and Antoine (2004) imply that modifications of logging practise are essential to re-establish epiphytic communities. Within the lower canopies of plantations, young conifers are often inimical to epiphytes. This can be overcome by thinning the conifers, allowing more sunlight, etc., promoting epiphytic growth (Sillett and Antoine, 2004). It has been proven that uneven thinning increases structural complexity of regenerating forests thus increasing the diversity of microhabitats, and therefore epiphytic abundance (Neitlich and McCune, 1997). Essen *et al* (2006) suggests that prolonged rotation will be an effective method as it allows more time for epiphytic species to colonise and grow. Selective logging that will retain any lichen bearing trees, instead of cyclic-clear cutting has seen to be an effective method (Essen *et al*, 2006), which was also proven by Wolf (2005) where epiphytes showed a resilience to disturbances if the forests was selectively logged to spare larger trees. In addition it would be beneficial to attempt to attain a homogenous distribution of epiphytes in a forest (Wolf, 2005). Inoculating young stands with lichen propagules has also been suggested (Stevenson, 1990) (Neitlich, 1993) as it will give species an increased opportunity of quick colonisation by removing the factor of

chance (Benzing 1981). Recent studies have discovered the importance of wood debris in forest canopies, riparian habitats and landscape perspective (Swanson and Franklin, 1992; Franklin, 1993). These should be the primary focus when management strategies are put into place due to their considerable influence on epiphytic growth.

It has been suggested that forest age is the most simple but ecologically efficient key value that is controllable through management. Young and mature but managed forest have a far less species composition and structure, being composed of a modified species composition in comparison to semi-ancient or ancient stands (Neitlich, 1993; McCune, 1993; Goward, 1994; Read, 2000; Moning and Müller, 2008). A reduction in veteran trees would have serious consequences for Scotland's environment and biodiversity, subsequently affecting the tourism sector as these forests attract people to isolated areas that wouldn't normally be appealing. Moning and Müller (2008) proved the number of species per plot increases significantly with forest age thus stands of a semi-ancient or ancient age should not be forested. However, some species are too rare or too limited in dispersal to benefit silvicultural techniques (Sillett and Antoine, 2004), especially old-growth species as they are more susceptible to disturbances (Gausla and Solharg, 2001).

Accessing the Canopy

Researching the World's forests has been a relatively easy affair; however, accessing the treetops has proved difficult until the 1990's, progressing from basic ground based observations to modern canopy access techniques (Lowman and Rinker, 2004). The forest canopy long eluded scientists and plagued canopy ecologists due to logistic difficulties in accessing the canopies and difficulty in sampling such a diverse environment (Lowman and Rinker, 2004: Lowman, 1995). The canopy is considered one of the last frontiers in biological sciences (Moffett and Lowman, 1995). Until recently most studies related to epiphytic cryptogams have been limited in sampling to the tree trunk or below 2 metres and litter fall analysis, neither of which truly illustrate canopy communities (Lowman and Rinker, 2004). The prime importance in understanding canopy epiphytes is direct canopy access, which has been enabled in recent years due to the development of rope techniques (Lowman and Rinker, 2004). Methods need to be quick, as time in the canopy may be limited, reliable, applicable in diverse areas, simple and cheap (Lowman and Rinker, 2004). Ropes provide rapid, flexible and mobile methods of access (Mitchell *et al*, 2002). Two common rope techniques include single rope technique (SRT) and the double rope technique (DRT), developed by Canopy Access Limited (Mitchell *et al*, 2002). SRT was developed by Perry in the 1978 and is a less strenuous and safer method used to access tall, emergent canopy trees of the tropics. The technique employs a static climbing line system (Jepson, 2006) and is ideal for use in tall trees as it allows quick and easy ascent into the canopy. However, this technique leaves the climber with limited mobility in both spatial and/ or temporal aspects and the sample plot is restricted to a narrow, vertical cylinder, which becomes increasingly problematic when methods are replicated (Mitchell *et al*, 2002; Houle *et al*, 2003). The DRT enables researches to sample away from the tree trunk, broadening the sample plot and allowing the climber to swing to another branch or trunk. It is a portable and relatively cheap technique (Lowman, 1995). Once in the canopy the rope can be repositioned to suit the climbers needs (Lowman and Rinker, 2004). However, it is hard work and may be too strenuous for accessing larger trees and can also disrupt

canopy habitats (Lowman and Rinker, 2004). The DRT is a much safer and easier technique allowing access to peripheral branches (Maher, 2006) and is often used to access thick crowned deciduous trees, such as oak. The disadvantage of this method is that it's more time consuming and more energy intensive (Maher, 2006).

There have been several studies in the Scottish Highland looking at a range of variables that influence epiphytes (Walker and Kirkby, 1989; Roberts *et al*, 1992; Bates, 1992; Hampson and Peterken, 1998; Rothero and Douglas, 1999; Coppins, 2003; Ellis and Coppins, 2007 a and b). However, there have been a limited number of studies that have investigated the relationships between epiphytes and different phorophyte hosts, especially between Scots pine and oak, and the effects of different age structures within the tree, in the Caledonian forest. The factors influencing arboreal epiphytic abundance have been examined, specifically looking at different tree species and age structure within the tree. Architectural features (branch length, diameter and aspect) were documented that characterize the canopy structure and corresponding vertical zonation of epiphytic groups were observed.

Aim and Objectives

Aims

The aim of the investigation is to analyse the relationship between non-vascular epiphytes and age structures within the phorophyte, comparing Scots pine and Oak.

Objective

To understand the correlation between non-vascular epiphytes and the age structures within a tree, concentrating on tree species *Quercus robur* and *Pinus Sylvestris*, in the Atlantic woodlands of Dundreggan, Scotland.

Null Hypotheses

With an increase in maturity, there will be no significant correlation between epiphytic diversity and a complex epiphytic community.

There will be no significant correlation between tree species and epiphytic diversity.

Alternative Hypotheses

With an increase in maturity, there will be a significant correlation between epiphytic diversity and a complex epiphytic community

There will be a significant correlation between tree species and epiphytic diversity.

Methodology

Site description

Dundreggan is composed of an ombrophilous open upland habitat, heather moorland, native and non-native conifer plantations and a few fragments of native, even-aged wood in the Southern areas on the lower slopes. The dominant tree species are composed of birch and juniper, with the veterans of the forest being Scots pine and oak (Featherstone, 2006). The average annual rainfall of this area is around 2000-

3000 mm, with an average temperature averaging around -4°C to 5°C (Met Office, 2000). The site was selected on the largest fragment of semi-ancient forest, Figure 4. The topography was slightly undulated, with a south-facing slope ranging from 133m to 213m in elevation. Epiphytes thrive in forest canopies of coastal temperate zones (Lowman and Nadkarni, 1995) and this estate is renowned for its high diversity as discovered after previous surveys (Rothero *et al*, 2007; Douglas, 2009).

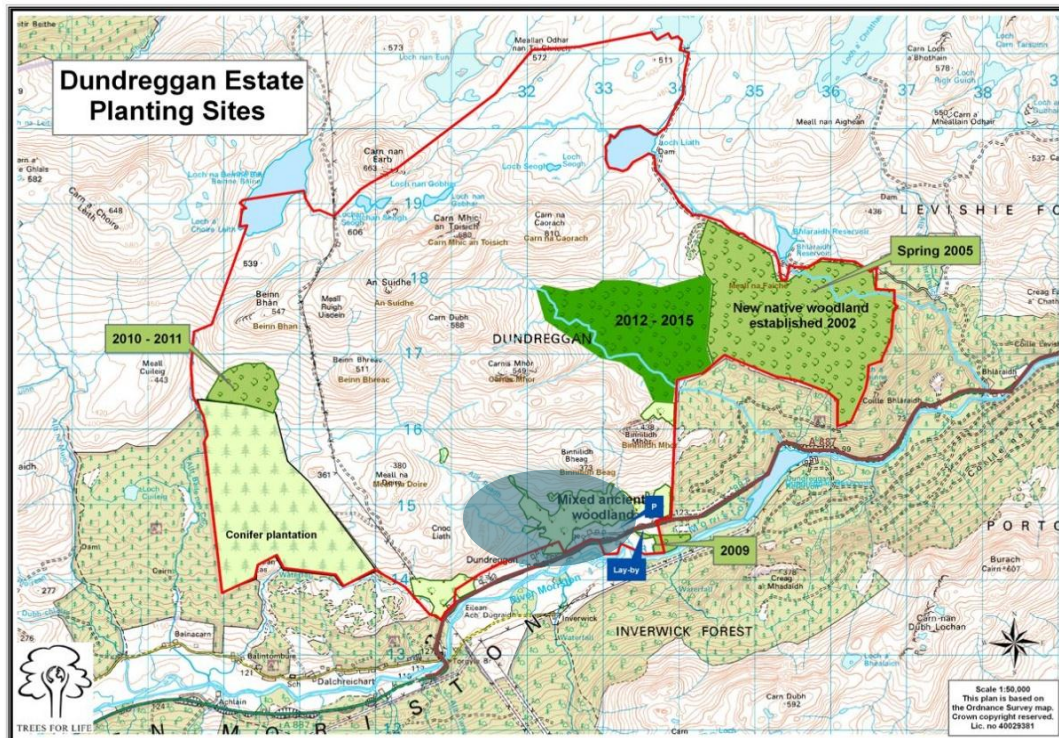


Figure 4: A map of Dundreggan estate showing the site highlighted in blue

Sampling Design

Six trees were sampled, three *Pinus sylvestris* and three *Quercus robur*, (Figure 5), to allow repetition thus increasing the reliability and validity of the data. Scots pine and oak were sampled as they are the two oldest tree species found and as background research suggests that age correlates with epiphytic diversity (Sillett and Antoine, 1994; Lang *et al*, 1980; Moning and Müller, 2008). They are also very contrasting due to different bark characteristic and as Schofield (2001) suggests epiphytes are more abundant in angiosperm forests, such as oak, than gymnosperm forests, e.g. pine (Schofield, 2001).

All selected trees were sampled within a small vicinity to reduce external variables (Svoboda *et al*, 2010). They were chosen based on location, accessibility and if they had an adequate amount of branches to sample. The ropes were rigged using a slingshot technique, shooting a lighter line over a branch in the canopy, which a climbing rope could be then tied to and pulled over (Maher, 2006; Houle *et al*, 2003). The canopy was accessed using two methods; Single Rope Technique (SRT) and Double Rope Technique (DRT).



Figure 5: Map showing the locations of each tree sampled, with TP representing the Scots pine and TO the oak.

Each tree was then divided into three zones: zone one - lower, zone two - middle and zone three – upper, ensuring there were at least three branches in each zone. This division allowed the tree to be split into different ages, zone one being the oldest and zone three the youngest. Within each zone of the tree three primary, three secondary and three tertiary branches were sampled, again to represent different ages.

Epiphytic Sampling

The six trees were studied over seven days from the 26th of August to the 3rd of September 2011, with 162 branches sampled for epiphytes and structural measurements. Non-vascular corticolous epiphytes were stratified vertically within the tree (zone one-three) and horizontally within the branches; on three primary, three secondary and three tertiary branches in each zone. These divisions enable a representation of the different age structures of the tree; from young to mature, for example Zone 1 Primary 1 would be the oldest branch. Repetition again allowed increased reliability and validity.

The length of the branch was measured as the horizontal distance from the beginning to the end of the branch. The sample sub-plot was determined by measuring the length of the branch and recording the circumference at the mid-point. 10% of the circumference was measured either side of this point and taped with insulation tape, for example if the circumference was 50cm, 5cm would be measured either side of the midpoint, making the sample plot 10cm in length (Figure 6). All epiphytic species within the quadrat were sampled and bagged to be later identified in the laboratories.



Figure 6: Shows the sub-plot between the red tape

Environmental Data

A range of environmental attributes were sampled from selected trees such as the elevation and spatial co-ordinates recorded using a Garmin cx60, positioned immediately adjacent to the tree to record its position (Figure 5). The height of the tree was measured using a 30m tape measure once at the top and branch aspect was recorded using a compass, to the nearest cardinal direction (North, South, East and West) for each sub-plot.

Laboratory Work - Identification

Nomenclature of epiphytes occurred at Plymouth University laboratories using a Kyowa low pressure stereo microscope following identification books (Watson, 1955; Purvis *et al*, 1992; Dobson, 2011), booklets (Acton and Griffith, 2008a; Acton and Griffith, 2008b) and chemical testing. The species were then cross-referenced with a species list found at Dundreggan created by Joe Hope and John Douglas for lichen and Gordon Rothero and Ben and Alison Aeris for bryophytes (Rothero *et al*, 2007; Douglas, 2009).

Statistical analysis

Statistical packages Primer and Minitab were used to analyse the raw data. Primer was used to create Multi-dimensional Scaling (MDS) plots for both tree species then oak and Scots pine separately. These plots detect meaningful underlying dimensions, which will show any observed similarities or dissimilarities between the investigated objects (StatSoft, 2012). Minitab was used to analyse environmental measurements, such as zone, circumference, length and aspect and how they affected epiphyte distribution, using a principal component analysis (PCA), a multivariate analysis method. A PCA reduces the number of environmental variables, therefore confining the number of control variables (Higuera, 2010).

Results

Identification

A total of 72 epiphyte species were identified with 65 lichen, 5 moss and 2 liverwort species. Those species that could not be readily classified were named as Species 1, Species 2 and Species 3. The most abundant species found on Oak were *Bryoria fuscescens*, *Isothecium myosuroides*, *Hypogymnia physodes* and *Evernia prunastri*. Scots pine had visibly fewer epiphytic species with the dominant being *Hypogymnia physodes*, *Parmelia sulcata* and *Platismatia glauca*. Scots pine had a significantly different species composition to oak, with no bryophyte species found on the pine. See Appendix 2 for a full list of species found.

Tree Diversity

Table 1 provides values for species, Shannon's diversity index and Simpson's diversity index for each tree and Appendix 3 and 4 for each quadrat. A diversity index is a mathematical measure of species diversity in a community, with the species diversity being a measure of the diversity with an ecological community that incorporates species richness and evenness (McGinley, 2010).

Table 1: Number of species and diversities for each tree

Tree	Number of Individuals	Shannon's Diversity Index	Simpson's Diversity Index
Oak 1	172	1.751337037	1
Oak 2	184	1.737398855	1
Oak 3	187	1.741475131	1
Pine 1	52	1.454211811	1
Pine 2	47	1.276090092	1
Pine 3	20	1.094677922	1

The difference in the number of individual species on each tree can be seen in Table 1, where oak has a considerably greater amount of individual epiphytes than the pine, having the highest value for species richness. On the oaks there was a very small range in the number of individual epiphytes, from 172 to 187 in each of the three trees, whereas pine seemed to have a greater variety with the number of individuals ranging from 20 to 52 species on each of the trees. The species diversity as shown using Shannon's Diversity Index suggested, unsurprisingly, that oak had greater species diversity than pine, again with a small range in oak but a larger variety in pine. After further analysis of the raw data, it clearly shows that all primary branches had a higher number of individuals per branch than secondary and tertiary, which can be seen across all zones on both tree species (Appendix 3 and 4).

Similarities between Scots pine and oak species

Figure 7 represents a multi-dimensional scaling (MDS) plot for Scots pine and oak species. It shows that there is a similarity between the numbers of epiphytic species on each of the oak quadrats as highlighted, with quite a significant dissimilarity between Scots pines as the sub-plots are widespread. This illustrates table 1, which shows similar variations between oak species.

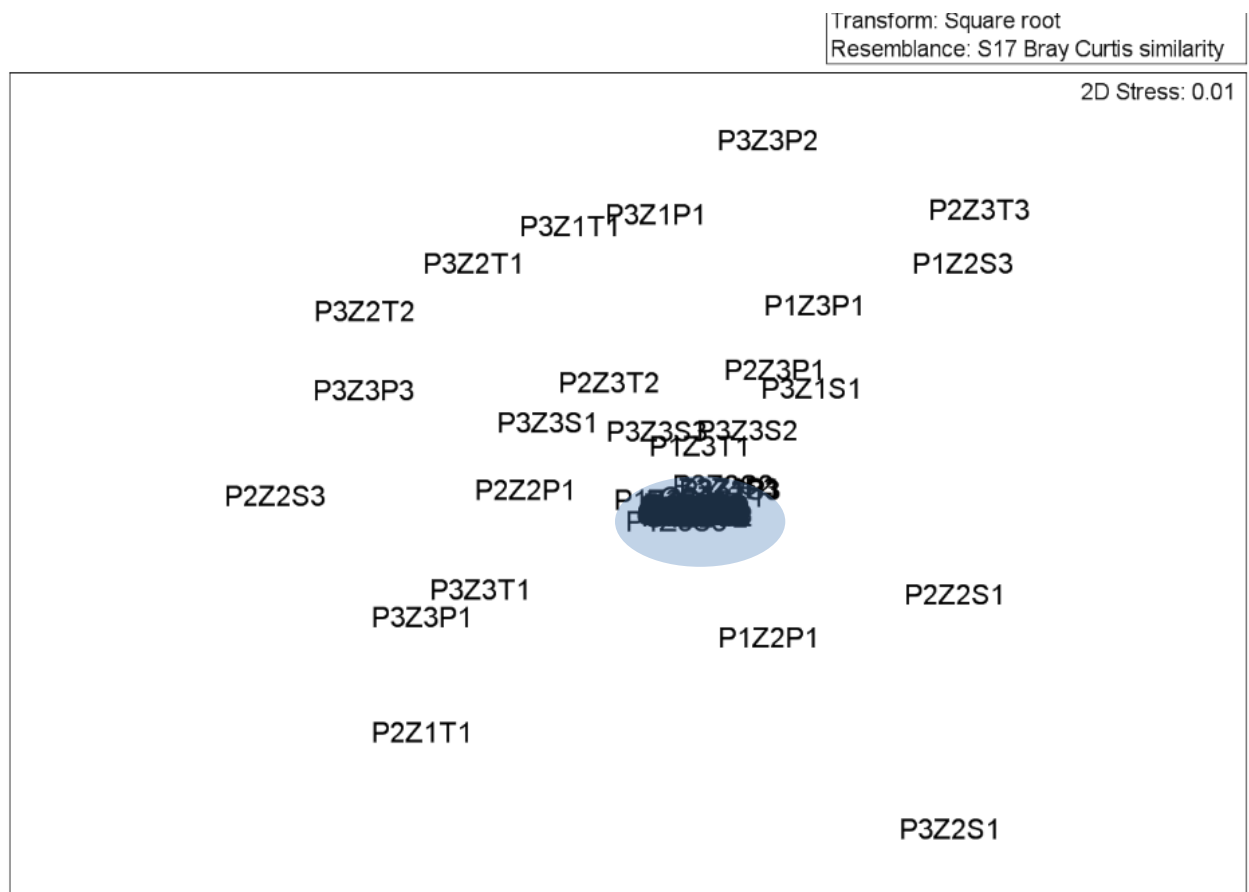


Figure 7: A MDS plot for Oak and Scots pine

This was further unpacked to look at the pine and oak species more specifically as shown in figure 8 and 9.

Similarities in Scots pine species

Figure 8 suggests that there is a similarity between sub-plots on pine one (P1), as highlighted. Dissimilarity can be seen in P2 and P3. The most dissimilar seem to be those in zone two on a secondary branch or those in zone three on a primary branch. Sub-plots from zone one in all three trees seems to be similar. The lack of similarity is further shown in Table 1 where there is an obvious difference in the number of species per tree. This dissimilarity could correlate with a higher species diversity seen in pine one in comparison to pine two and three, which had fewer species per quadrat, especially in pine three. Dissimilarities and lower diversity are most likely to be a result of the nature of the pines bark. It is very flaky and ephemeral and has low water retention, making it hard for epiphytic species to colonise (Lowman and Rinker, 2004).

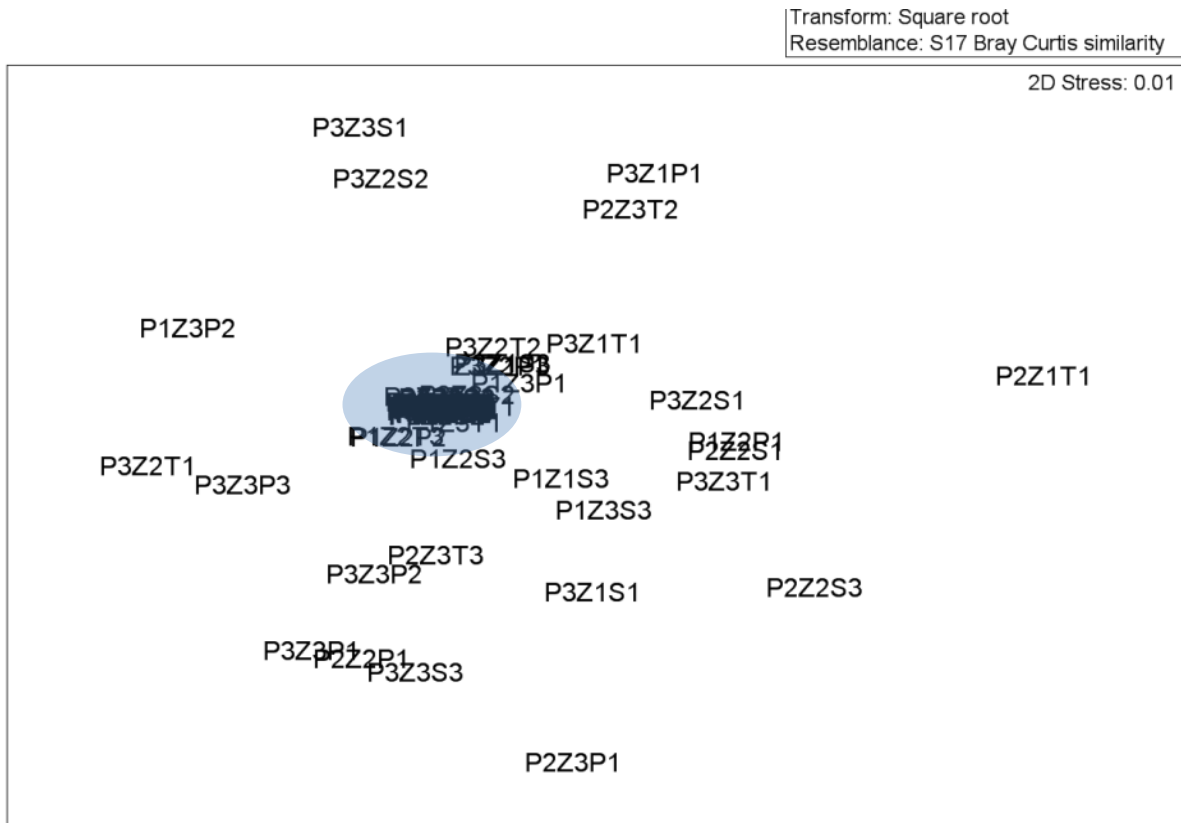


Figure 8: A MDS plot representing Scots pine species

Figure 9 indicates that all oak species are considerably similar, the epiphytic community composition were alike on all branches within each zone and tree. This is backed up by Table 1, which shows pine to have high a diversity score, with a small range between oak species. The similarity is a result of the nature of oak species and their accommodation for epiphytes, due to their barks ability to hold water. There are three sub-plots that suggest dissimilarity; O3Z1T2, O2Z1T1 and O3Z3T1. When looking at the raw-data the O3Z1T2 and O2Z1T1 quadrats have a dissimilar species composition and the Simpson's diversity index for each quadrat (Appendix 3 and 4) shows that O3Z3T1 has a lower number of species in comparison to similar sub-plots.

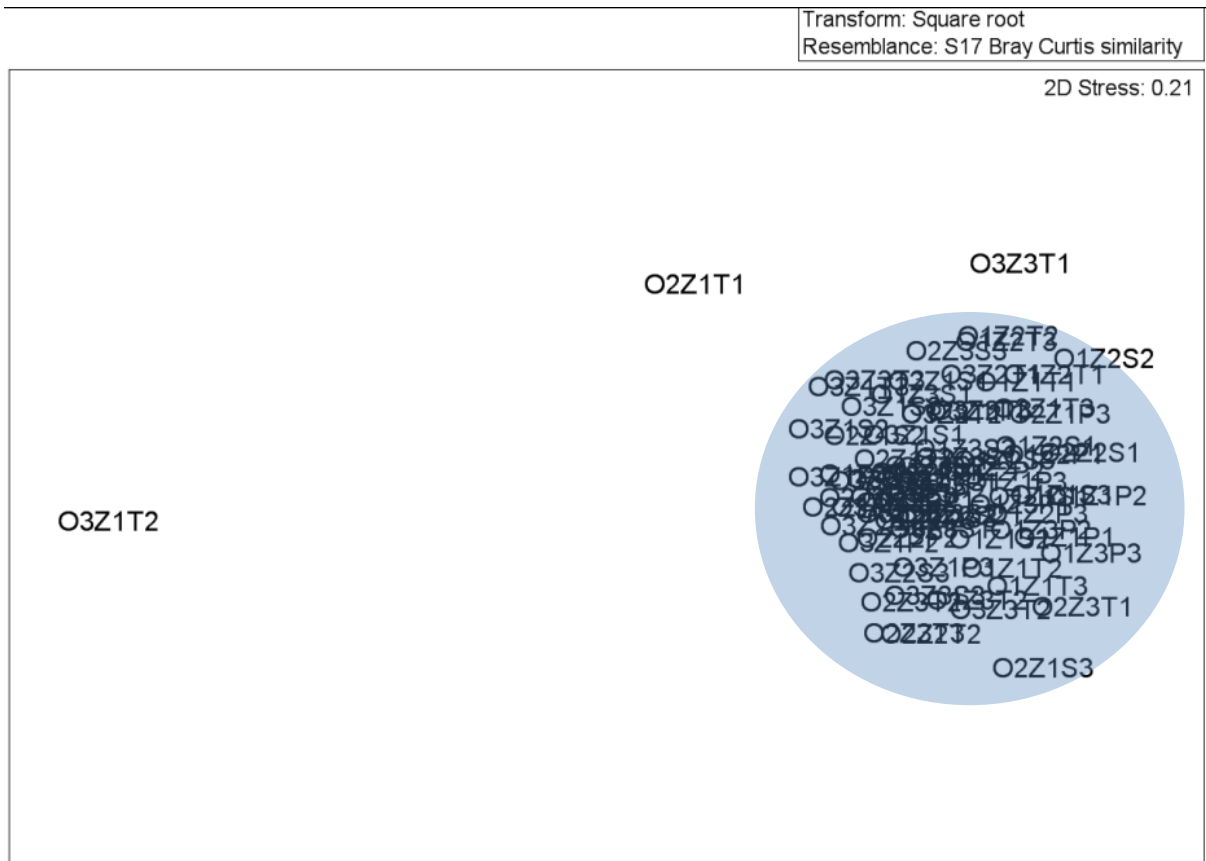


Figure 9: A MDS plot representing Oak

Principal component analysis for Scots pine

Table 2: The Principal Components of the Scots pine Species

Principal Component	Variable	Eigenvalue	Cumulative % of Data
1	Circumference and length	1.588	39.7
2	Zone	1	64.8
3	Tree	0.9573	88.7

Table 2 shows that in Scots pine species the primary principal component (PC) is a combination of circumference and length, the secondary being the zone and the tertiary the specific tree. These were determined by looking at the eigenvalue. The eigenvalue analysis is a popular method for variation decomposition and dimension reduction (Quinghong and Brekenhielm, 1995). This value of correlation matrix is equal to the variances of the PCs with PC one and two represent 64.8% of the total

data set, suggesting they're very important influences on species diversity.

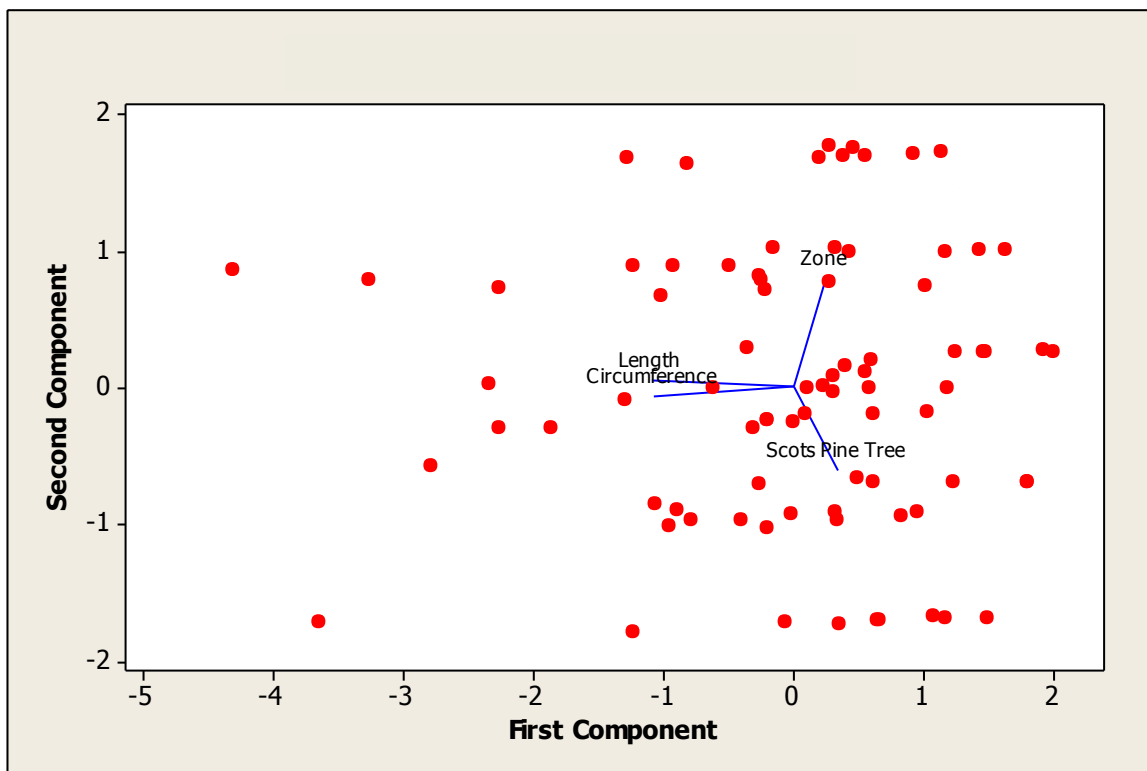


Figure 10: A bi-plot for Scots pine

Figure 10 represents a bi-plot showing the circumference and length (first component) scores plotted against the zone (second component). Those quadrats further away from the x-axis are determined by zone and those closer are so by branch length and circumference. Points that are close to the zone vector suggest that zone was the main contributing factor in those quadrats on species diversity, suggesting a possible link between branch age and epiphytic composition. Whilst those that follow length and circumference are determined by the size of the branch. Quadrats in the bottom right corner that follow the tree vector are associated with the individual tree. The branch circumference and length point in the same direction thus show an extent of similarity.

Figure 11 suggests that the second component, zone, was dominated by a low species count, ranging from 0-3 species. Specific tree had an even lower species count with a range from 0-2. However, the size of the branch equates to a moderate-high species number, from 0-6 species found in that quadrat, which backs up interpretations from Table 2 and Figure 10.

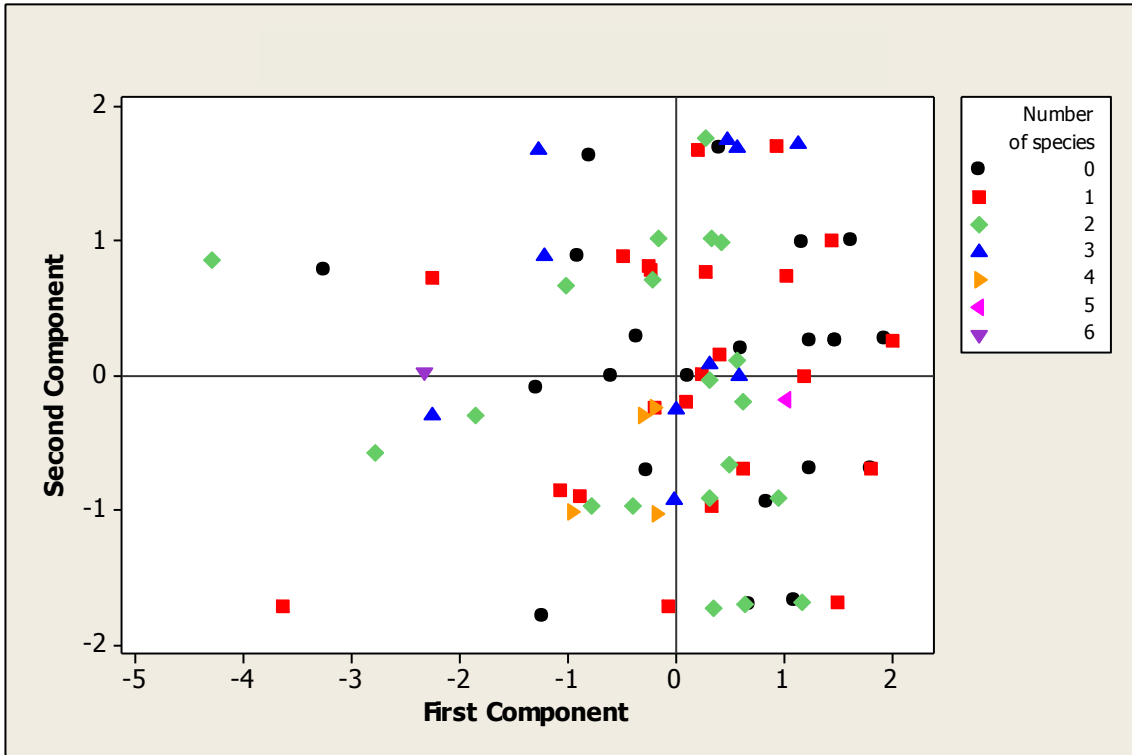


Figure 11: A scatter plot of the first two components in relation to the number of epiphytic species

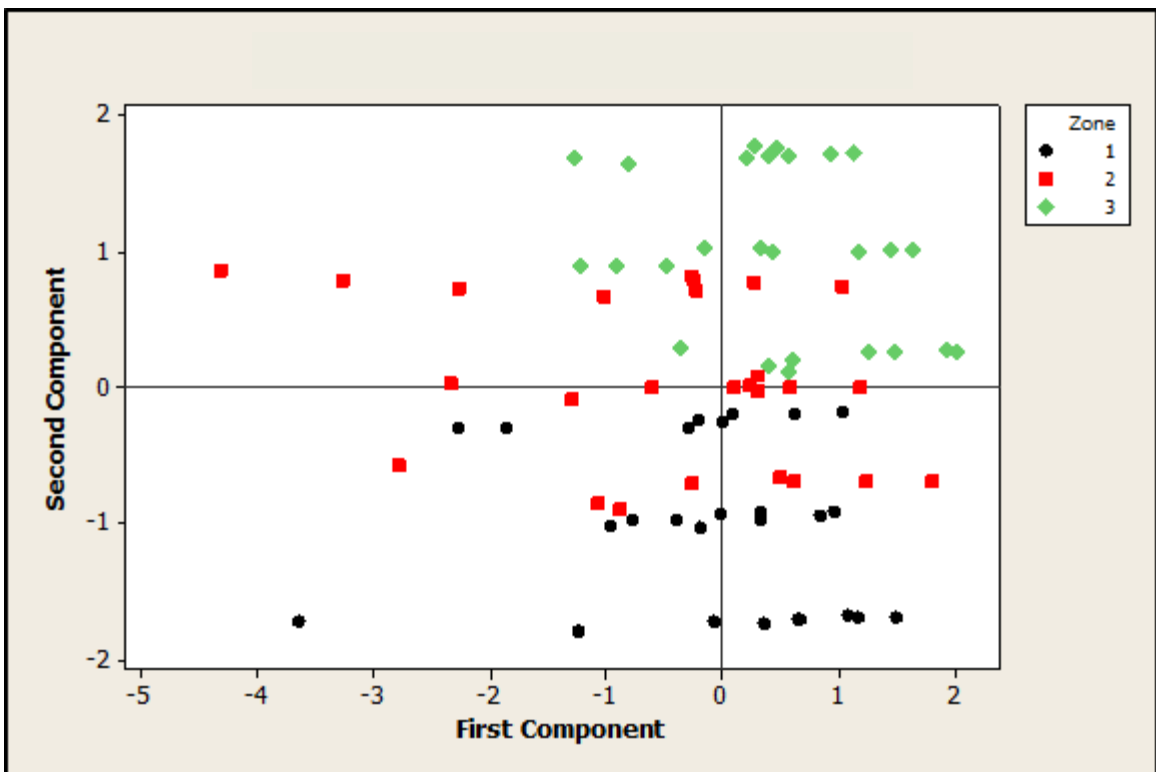


Figure 12: Species diversity in respect to zones on Scots pine

Figure 12 shows that circumference and length of branch were most influential in zones one and two. Zone aligns well, fundamentally with zone three and for tree species zone one and two are the dominant feature.

The graphs suggest that the highest number of species was found in zone one followed by zone two and zone three, which is a natural characteristic as the lower zones are of older age and would have a larger total area, in comparison to younger branches (Essen and Renhorn, 1996).

Principal component analysis for Oak

Table 3: Eigenanalysis of the correlation matrix

Principal Component	Variable	Eigenvalue	Cumulative % of Data
1	Circumference and Length	1.539	39.0
2	Zone	1.102	66.1
3	Tree	0.9109	88.8

Table 3 shows the three principal components (PC), with a combination of branch circumference and length as the first component; zone the second and the specific tree being the third, and were again determined by looking at the eigenvalue. A combination of the first and second PC represents 66.1% of the data set suggesting these two variables are important influences on species diversity.

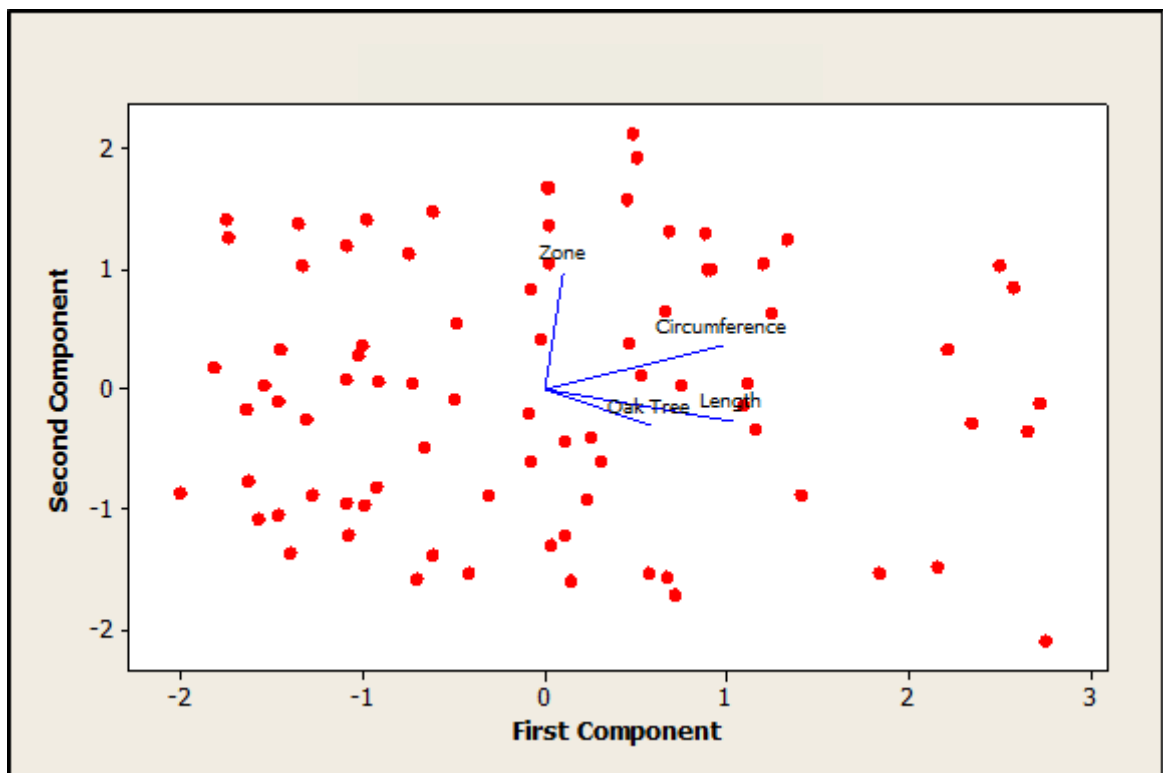


Figure 13: A Bi-plot of Oak species

The bi-plot for Oak, Figure 13, represents circumference and length plotted against zone. The graph backs up the theory that circumference, length and zone are important factors in influencing diversity as most points lie near the x-axis suggesting a correlation with branch size and the y-axis, suggesting an association with zone. Those points that follow the tree vector represent sub-plots that were influenced by the specific tree. Points that follow zone suggest that zone was the main influence on epiphytic distribution and the same with length and circumference.

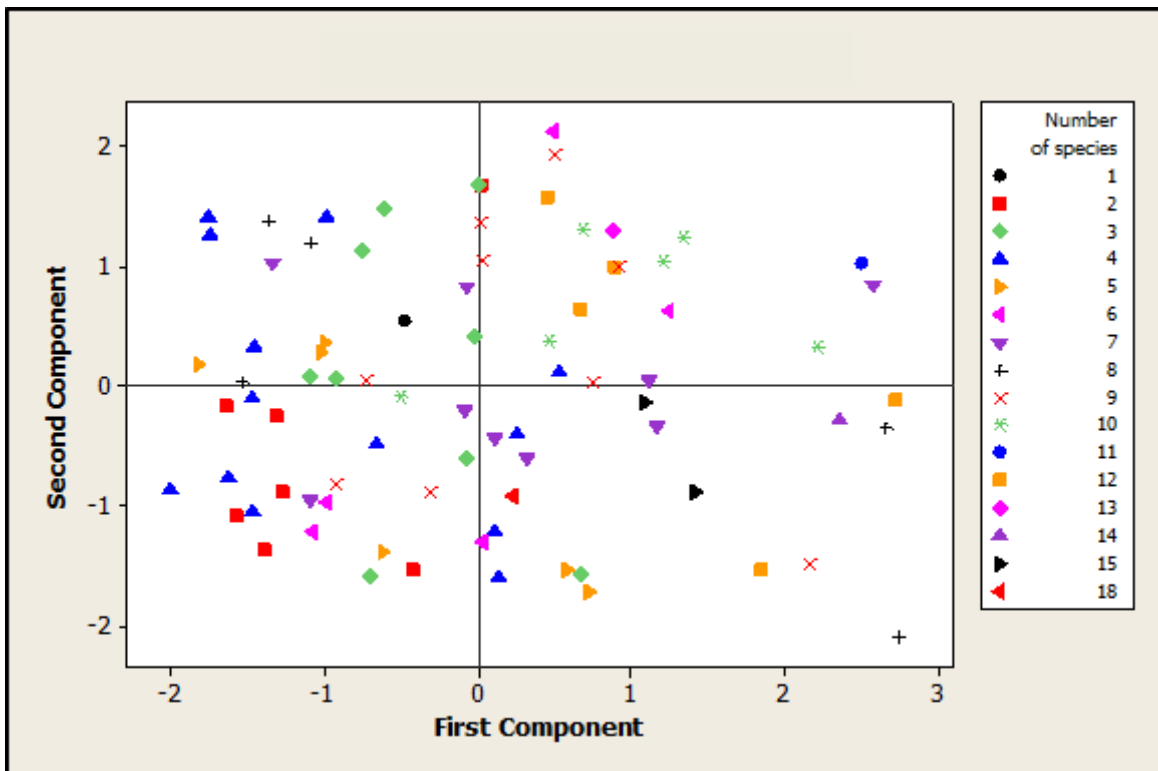


Figure 14: A scatterplot of the first two components in relation to the number of epiphytic species

Figure 14 shows the relation between the number of species and the branch circumference, length and zone. It suggests that branch circumference and length has the most amount of individual species, ranging from 4-15. Zone has a fairly high species count, with quadrats having a lower number of individual species, with the specific tree having the lowest number of species per quadrat. Both zone one and two quadrats have significantly high number of species, which can be correlated with age.

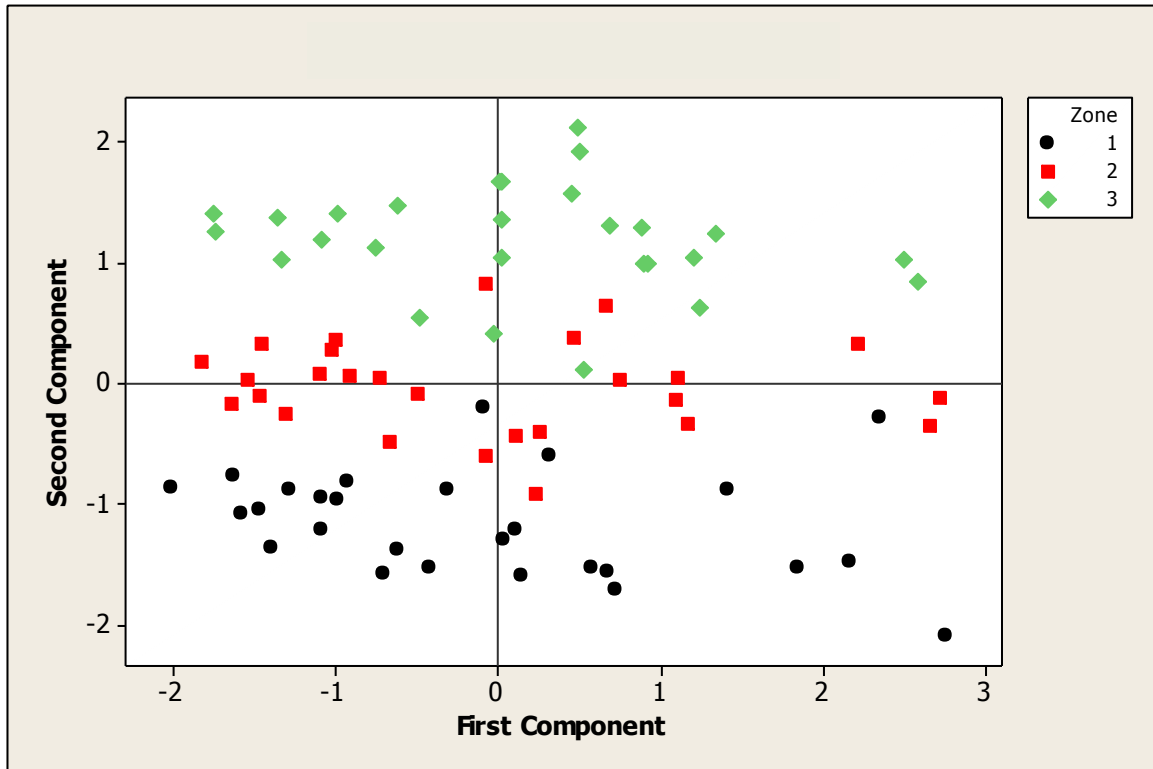


Figure 15: A scatterplot showing the relation between zone and species diversity

Figure 15 shows that zone aligns well with zone three. Length and circumference correlates with zone one and two, and that the specific tree relates to zone one. All quadrats fit into distinct zones, which correlates with different species diversity.

Species distribution on oak seem to be quite similar to that of Scots pine, but have a much more diverse epiphytic sample.

Species distribution along a horizontal transect

Table 4: Number of species per branch for Scots pine

Tree	Zone	Primary	Secondary	Tertiary
1	1	9	8	7
	2	2	6	2
	3	3	6	8
2	1	16	7	4
	2	7	2	6
	3	5	4	1
3	1	3	1	3
	2	3	3	1
	3	0	0	4
Average		48	37	36

The data in Table 4 suggests that within Scots pine hosts there are overall more individual epiphytes found on primary than secondary by looking at Table 4. However, the results in some branches which appear to be reversed, for example Tree 1, Zone 3, where the largest number of individuals is found on the tertiary branch, then secondary with the least on the primary, the same goes for Tree 3, Zone 3.

Table 5: Number of species per branch for oak

Tree	Zone	Primary	Secondary	Tertiary
1	1	24	24	11
	2	32	15	15
	3	31	20	16
2	1	36	13	10
	2	31	23	13
	3	31	20	9
3	1	29	12	10
	2	41	22	11
	3	28	27	9
Average		283	176	104

Table 5 shows an apparent differentiation between the number of individuals and the branch location, i.e. whether it was a primary, secondary or tertiary. In all the zones a clear hierarchy is seen with primary having the most species, then the secondary with tertiary having the least amount, which is obvious when looking at the average values.

Discussion

Host differentiation

Figure 7 indicates that the two tree species differ in their suitability as hosts for epiphytes and such species-specificity suggests relatively high levels of interdependence with their communities. It is apparent that community composition in Scots pine and oak was very different, with the pine trees showing a great amount of dissimilarity in the species composition in contrast to the oak which showed great similarity. This is further evident when looking at the number of species per tree, where oak had a total of 542 individual epiphytes in comparison to Scots pine which had 118. The Shannon diversity index figures in Table 1 also show this trend as there is a much higher variation on pine than oak. Lowman and Rinker (2004) found similar results suggesting that patterns of change vary depending on the physical characteristics of the phorophyte, e.g. flakiness of maturing bark on Scots pine and the seasonal leaf loss of oak. It has been further demonstrated that relationships between a species and their phorophyte has a high correlation with the water-holding capacity of the host tree's bark and Callway *et al's* (2002) research shows that *Quercus spp.*, oak, bark is one of the most efficient in water holding capacity. This high efficiency is associated with diverse arboreal flora communities, as it increases humidity near the tree and reduced leaf-to-air vapour pressure differences, i.e. the bark ameliorates xeric, dry, conditions (Callway *et al*, 2002). Pines, on the other hand, appear to be a poor host for epiphytic species as they have a low water holding capacity and retained virtually no water after 24 hours (Callway *et al*, 2002). They

also suggest that bark characteristics, such as stability, rugosity and adherence, promote successful colonization, again suggesting that oak would have a higher epiphytic abundance as the bark is very fissured and rough (Shrestha, 1993) in comparison to pines ephemeral bark (Lowman and Rinker, 2004), which is an unsuitable substrate for epiphytes (Schlesinger and Marks, 1977). Pugnaire (2002) suggested that species-specificity in plant-plant interactions, such as that seen with epiphytes and their phorophytes, can develop as plants interact simultaneously via competition for resources, facilitation and allelopathy. This is further evident when looking at the number of species per tree and at the figures from Shannon diversity index on Table 1, which shows a much higher variation on pine than oak.

Similarity in Scots pine

The raw data was unpacked further to look at each tree species more precisely as Figure 7 was difficult to fully interpret. Figure 8 shows dissimilarity in all the pine trees as a result of pines ephemeral and poor quality bark (Schlesinger and Marks, 1977; Lowman and Rinker, 2004), as mentioned previously. Nadkarni (2000) found that once bark had been stripped, the variety of species recolonising differ strikingly from the original. This could be a significant reason for such variation in species composition between the quadrats as seen in Figure 10 and when looking at Shannon's figures, Table 1, ranging from 1.09 to 1.45. After further analysis of the raw data, the species composition was defiantly dominated by lichen, with no bryophyte species; this can be backed up by Löhmus *et al* (2006) whose research provided similar results.

Similarity in oak

The epiphytic composition in oak species was very similar with one another as displayed in Figure 9 and Table 1, where the diversity ranged from 1.74-1.75. A major contributing factor to the similarity found could be the favourable characteristics of the oaks bark. Oaks are renowned for high epiphytic growth due to features such as the barks high water holding capacity (Callway *et al*, 2002), their fissured and course bark (Shrestha, 1993) (Nelson and Halpern, 2005) creating shade (Kussinen, 1996) and acts as protection against direct rain (Lukošienė and Naujalis, 2006). Oak is also a hardwood and has a high density, which help moderate microclimate changes and enhances epiphytic survival (Nelson and Halpern, 2005). Bates (2001) noticed in his study that most epiphytic species were strongly selective for *Quercus spp.*

The primary principal component

From the biplots and scatterplots, Figures 10-15, and the Shannon Diversity Index figures in Table 1, it is evident that the three main factors that control the abundance of epiphytes on Scots pine and oak are in this study are; a combination of branch length and circumference (the size of the branch), followed by zone and finally the specific tree. It is known from previous research that within height class, the absolute position within the canopy and the relative position within individual trees and branches are important factors in influencing epiphytic abundance (Lyons *et al*, 2000). In this study the size of the branch was the structural variable most influential to epiphytic abundance, as it had the closest correlation to the quantity of epiphytic species as shown in figures 10 and 13. This concurs with other studies; (Hilmo, 1994; Clemet, 1995; Essen *et al*, 1996; Essen and Renhorn, 1996; Wolf, 2005) who stated that epiphytes are strongly influenced by the structural characteristics of the phorophyte, e.g. branch size. Lyons *et al* (2000) suggests that branch size is an

important predictor of total epiphytic abundance and a strong correlation between the size of the branch and an epiphytes ability to intercept propagules, nutrients and moisture is found, as does Catling *et al* (1986). It is one of the most important determinants of epiphytic cover within the individual tree crowns, along with relative position (Lyons *et al*, 2000). This observation is in agreement with Lui *et al* (2000) whose research showed a relatively strong relationship between branch basal diameter and lichen abundance. However, structural and positional variables do not have a direct influence on epiphytic growth but serve as partial surrogates for other direct environmental variables such as light, temperature and humidity (Parker, 1995). The correlation between branch size and the number of species can be seen further in Figure 11 and 12 for Scots pine, and 14 and 15 for oak. This relation between epiphytic abundance and branch size can be assumed that they're good predictors of the amount of substrate available, as suggested by Essen and Renhorn (1996). This explains why smaller branches have a restricted diversity as there is a limited amount of substrate available (Essen and Renhorn, 1996). Areas closer to the trunk will have a higher epiphytic abundance as there is a more moderate microclimate (Lyons *et al*, 2000) and are protected from extremities. However, there are cases in two of the pine trees where the tertiary branch has the highest number of species, with the primary branch having the least, as shown in Table 4 for trees one and three. This can be explained due to the pines ephemeral bark as the more mature bark has increased chance of flaking off, taking any epiphytic species with it (Lowman and Rinker, 2004).

The second principal component

The second principal component, zone, correlates with age, as lower branches on all trees are the oldest (Lyons *et al*, 2000). Figures 10-15 show the same relationship for both tree species, with more individual species found in zones one than two and three. There was a total of 276 species in zone one, 170 in zone two and 98 in zone three for all the oak combined. The examination of epiphytic abundance in different regions of the canopy provided necessary information on the interactions between canopy positions on epiphytic abundance, as well as branch location. The limited number of species in the higher zones is a result of a combination of many environmental variables, for example with increased height the humidity decreases, wetting and dry cycles become more rapid, reduced protection from solar radiation and wind, a less moderated microclimate, etc. (Lyons *et al*, 2000) creating unfavourable conditions for epiphytic growth. The observation that epiphyte abundance is strongly related to age can be backed up by Wolf (2005) and Essen and Renhorn (1996), who discovered the same correlation with lichen. Lyons *et al* (2000) suggested that the lower branches have a consistently higher cover than those branches in corresponding middle and upper zones. This corresponds well with other studies (Trynoski and Glime, 1982; Ingram and Nadkarni, 1993; McCune, 1993; Hilmo, 1994; Clement, 1995; Essen *et al*, 1996; Platt *et al*, 1997). Figures 14 and 15 confirm this as a higher species diversity is found on the lower zones for oak. McCune (1993) proposed that there is a pronounced vertical difference in species composition from lower zones to upper. Ellis and Hope (2011) back this up as they suggest a shift in epiphytic composition and richness is controlled by tree age. There is much evidence to suggest that phorophytes support a succesional progression of communities as they age (Tewari *et al*, 1985; Stone, 1989; Freiberg, 1996; Lara and Marimipaka, 1998). Rose (1993) illustrated a strong interaction between stand age and light availability, which are very important for lichen growth. Smith (1982) suggest

that more mature trees support distinct vertical zones of communities, which can be seen in the results as all the trees showed distinct zones and they were all of a mature age. It is suggested that this differentiability could be a result of the branch surfaces age (Lowman and Rinker, 2004). However, there are some who disagree; Svoboda (2010) suggests that forest age has a weak influence on diversity in comparison to other ecological variables. Natural abiotic factors such as the mean annual precipitation are the leading effects of predictor lichen diversity followed by altitude then radiation. A study by Slack (1976) in America showed that tree species showed no great change in epiphytic diversity with the age of the branch. Essen *et al* (2006) suggest that it's hard to interpret the effect of branch age on species abundance as there are many indirect variables, as the influence of the age of the branch integrates the effects of many possible causal factors, such as the microclimate, tree structure, sun radiation (Gauslaa and Swretholhaug, 1999) etc. and because a description of a pattern of epiphytic distribution on a specific stand will differ greatly to patterns deduced from other stands as they vary in structure, stand age and local climate (McCune, 1993). Therefore environmental and successional variables should be speculated (McCune, 1993). For example, many species restricted to tree tops in temperate rainforests are found in drier climates but only on lower trunks on mesic sites (McCune, 1993).

The third principal component

A distinct difference in epiphyte abundance and composition was found between the two different hosts, with oak having a greater variety and larger number of species individuals in comparison to Scots pine which had significantly fewer species. In total oak had 543 individual epiphytes whereas pine had 119. Freiberg (1996) found similar results in his study looking at the distribution of vascular epiphytes. Barkman (1958) suggests that bark characteristics of the host exert quite a large influence on the establishment of epiphytes. As previously stated both tree species had quite significantly different bark, oaks being very rough and fissured, encouraging epiphytic growth (Bates, 1992; Shrestha, 1993; Kussinen, 1996; Lukošienė and Naujalis, 2006) whilst the pine was flaky and ephemeral and was a limited substrate for growth in comparison (Lowman and Rinker, 2004; Schlesinger and Marks, 1977). Beaver (1984) relates to this as he suggests that the clearest case of host specificity is attributed to its bark properties, i.e. the hosts' substrate (Barkman, 1958). Wolf (1993) suggested that species assemblages differ among tree host trees independently from the other variables in his research, which can be seen in this study as when the third component, specific tree, is separated from other variables, such as zone and branch size, it still has an effect on the number of species and the overall epiphytic diversity. Palmer (1986) proposes that in temperate areas the relationships between the phorophyte and epiphytic species is clearly visible when comparing broadleaf trees and gymnosperm, for example Scots pine. Epiphytic communities appear to be composed of ecologically equivalent species (Schofield, 1972) within host species. Another reason for the differences could be as a result of chance, for example the arrival of propagules leading to spatial aggregation (Greene and Calogeropoulos, 2002), which is a major factor in determining species composition and can account for high variability between the same tree species at similar habitats (Benzing 1981). The importance of dispersal has previously been recognised by Barkman (1958) for good development of epiphytic communities, as this is the primary way propagules are transported (Greene and Calogeropoulos, 2002).

Species distribution along a horizontal transect

A strong composition gradient along a horizontal transect showed a distinct difference in the abundance of epiphytic functional groups. It is evident that more epiphytic species are found on the primary branches than secondary and tertiary, as shown in Tables 4 and 5, presenting an association between a species and its horizontal location. This observation agrees with that reported by Lyons *et al* (2000) found a similar correlation, as by Johansson (1974) who deduced theoretical distribution patterns along large branches. He found two groups of environmental influences; decreasing factors, such as roughness of the substrate, humus deposits, nutrients and humidity and increasing factors for instance temperature, light, wind and velocity. This correlation can also relate to different age structures within the tree as the primary branches are more mature than the secondary and tertiary. One of the major environmental variables that effect epiphytic abundance is the position within the host tree (Frahm, 1990; Wolf, 1993) with Lyons *et al* (2000) suggesting it was the most important. This is almost certain to be as a result of variables such as the variations in the quality of microclimates, which are known to change in quality and quantity of a substrate along a gradient thus the species distribution (Freiberg, 1996). This is reinforced by Essen *et al* (1996) who suggests that a limited amount of substrate, i.e. if the branches are small, available to epiphytes and are young, then there is a only a short time for colonization and will be limited until the branch matures and gets larger. Lyons *et al* (2000) are in similar agreement as they found that inner plots along a horizontal transect had a higher epiphytic cover than the outer plots. Another reason for this relationship is that newer, tertiary branches colonise slower and have less time to do so than those near the trunk (Lyons *et al*, 2000). The correlation between epiphytic abundance and branch age is said to be predictable by the Island Biogeography Theory, (Barkman, 1958) which was a proposition by MacArthur and Wilson stating that the number of species on an island will reflect a balance between the rate of new species colonizing it and the rate of which populations of established species will become extinct (Ehrlich *et al*, 1988). This theory can be reflected in woodland systems, which emphasises the aspects of colonization as well as seed dispersal (Barkman, 1958). However, Clement (1995) suggests the biomass is greatest in foliage than on the inner branch base. This discrepancy is possible due to the differentiation between the phorophytes, difference in habitat characteristics and their sampling strategy (Lyons *et al*, 2000).

Conclusion

This study has investigated the effect of tree branch maturity on non-vascular epiphytes, comparing the two tree species Scots pine and oak in a fragmented, semi-natural forest stand in Dundreggan estate. Returning to the hypotheses posed at the beginning of this study, the alternative can be accepted and the null rejected. It is possible to state that non-vascular epiphytes exhibit varying distribution patterns within the tree phorophyte along vertical and horizontal gradients. The horizontal gradients were established by identifying different branch positions, whether primary, secondary or tertiary, which showed obvious distribution patterns with the primary branch having the highest species abundance and tertiary the lowest for both species, bar two sub-plots in pine one and pine three where the tertiary branch had the highest number of species. One of the most important findings to emerge is the succession of epiphytic functional groups on Scots pine and oak showing a strong correlation with the size of the branch, a combination of the branch length and circumference, with larger branches having a greater abundance of epiphytic species.

The second most influential component for both oak and Scots pine was zone, the vertical positioning in the tree. Results indicated that there were a greater number of epiphytes on those branches in the lower zone compared to those on the middle or upper. Both size of the branch and zone have been well documented in past studies (Pike *et al*, 1977; Clement, 1995; Lyons *et al*, 2000). The two different tree species had significantly different species composition and abundance due to varying bark characteristics. When analysing each tree species individually, the epiphytic composition on Scots pine seemed very dissimilar whereas oak was very similar, as suggested in other sections of the result.

This research project was not specifically designed to evaluate factors related to specific environmental variables that influence epiphytic abundance, mainly due to time constraints. A factor that was not addressed by this study was the measurement of the tree trunk, whether circumference or diameter, as different trunk sizes of the same tree species normally represent their maturity and have found a correlation with the degree of epiphytic diversity (Bennett, 1986) and its specific associations (Catling and Lefkovitch, 1989). Examining the beneficial effects of nutrients and detrimental effects of other chemical was also lacking and would have been beneficial as Benzing (1974) discovered in his research that that they are primary factors in explaining epiphyte-host specificity. Hosokawa *et al* (1964) found in his study that moisture availability and radiation intensities can be very influential in determining the vertical distribution of epiphytic species within the phorophyte. Further experimental investigation into the effects of environmental variables, such as light intensity, humidity, nutrients available, etc., would help establish a greater understanding of the effects these variables have on epiphytic growth and distribution. A few authors have stated the importance of tree height as it is a good predictor for tree age and epiphytic cover. Lyons *et al* (2000) suggested that the change in abundance corresponds with different relative positions, regardless of tree age. Unfortunately some of the data for tree height was lost in transit so any analysis on the effect of height was not viable. Additional work could involve more intense analysis of the raw data to investigate the distribution of specific epiphytic species. This would give an insight into the succession of epiphytes by comparing younger tertiary branches through to secondary and finally to more mature primary as Essen *et al* (2006) deduced that branch age has a stronger influence on fruticose species than foliose. Old-growth epiphytes could also be determined. In addition further statistical analysis could be used to determine the significance of the results. This research will serve as a basis for future studies, which will fabricate more comprehensive research proposals as there is only limited research investigating the canopies of the Scottish Caledonian forests.

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