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Research article

Factors influencing epiphytic moss and lichen distribution within Killarney National Park

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The niches of epiphytes are widely studied and have been shown to be complex involving interspecific competition, succession and predation. This study is unique in that it applies the niche concept to moss and lichen distributions within Killarney National Park, Kerry, Ireland. We studied 75 trees between three pristine ancient woodlands and measured a range of physical and biological factors to ascertain influences on epiphyte cover. The species of tree was found as the principal determinant in community structure as it bioengineers conditions such as light, temperature and humidity that the epiphytes are reliant upon. Furthermore, the bark character and trunk circumference were important. Zonation of the epiphytes was apparent with both aspect and height on the trunk. Typically, moss dominated over lichen within a niche that was relatively sheltered. Lichen tolerated drier and lighter niches often being further up the trunk on sun facing aspects. Ultimately, there was succession up the tree mediated through competition. This study highlights the complexity and interrelatedness between biotic and abiotic factors in a relatively unstudied geographical and biological area. Understanding agents behind a population's distribution enables manipulation for conservation or sustainable exploitation.

Key words: competition, niche, epiphyte, resource availability, succession, Killarney national park

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Introduction

Mosses and lichens are abundant and ubiquitous across a diverse array of biomes and latitudes (Mezaka, Brumelis, Piterans, 2012). They fill a particularly important and often overlooked niche (Bergamini *et al.*, 2004) while displaying a complex distributional pattern determined not only by differential response to environmental conditions but also interspecific competition (Harris, 1971b). Biochemically they influence nutrient and water balances (Pypker, Unsworth, Bond, 2006; Odor *et al.*, 2013), decomposition (Liu *et al.*, 2000; Hagemann and Moroni, 2015) and soil environments (Van der Wal and Brooker, 2004). Ecologically they house and sustain rich biodiversity as habitats (Helle and Aspi, 1983; Lindo and Gonzalez, 2010). Both groups are photosynthetic autotrophs gaining water and minerals from the atmosphere (Begon, Townsend, Harper, 2006). Since neither group require soil, ground reservoirs or mychorrizal associations to survive (Nash, 1996; Bergamini *et al.*, 2004) many species are commensally epiphytic (Pojar and MacKinnon, 1994; Sterry, 2007). However, this increases their susceptibility to atmospheric pollution (Beltman *et al.*, 1980; Larsen *et al.*, 2007) that has led to their utilisation as ecological indicators of air quality, pollution, fragmentation and disturbance (Conti and Cecchetti, 2001; Mölder *et al.*, 2015).

Trees stabilise understory insolation and temperature regimes and provide microhabitats for attachment, thus engineering ideal conditions for epiphytic mosses and lichens (Mandahl-Barth, 1966; Sterry, 2007; Eaton and Ellis, 2012;

Ellis, 2012). Boreal and temperate forests are particularly cool and moist resulting in high epiphyte abundance and diversity that has attracted numerous studies (Mezaka, Brumelis, Piterans, 2012; Odor *et al.*, 2013). These include the effect of bark pH (Larsen *et al.*, 2007; Mezaka, Brumelis, Piterans, 2012), aspect (Song *et al.*, 2015), temperature (Hauck, 2011), inclination (Johansson *et al.*, 2009), humidity (Eaton and Ellis, 2012), age (Hofmeister *et al.*, 2015) and light intensity (Gauslaa *et al.*, 2008) on epiphyte distribution.

Inter-tree variation in biotic and abiotic factors has been demonstrated to be more important when compared with stand level variation. However, few have incorporated intra-tree aspects (Juriado, Liira, Paal, 2009). Even though hyper-oceanic forests create favourable conditions for rich diversity and abundance of epiphytes (Hauck, 2011; Eaton and Ellis, 2012), a lot of them have been understudied. One such example is Killarney National park in south-west Ireland, which is famed for its epiphytic flora (Cross, 1973; Cross, 1981; Kelly, 1981; Power, Igoe, Neylon, 2007), as well as being Ireland's most extensive native forest (Ratcliffe, 1968; Mitchell *et al.*, 2005).

Understanding the drivers of epiphyte distribution can inform forestry management to maximise diversity and protect these unique habitats within a changing world (Schei *et al.*, 2013). We studied factors controlling the richness, diversity and abundance of bryophytes and lichens. Here we investigate (i) whether lichen and moss richness and diversity varies between oak, holly and yew; (ii) whether moss and lichen display differential surface area cover between oak, holly and yew; and (iii) whether moss and lichen cover varied in relation to canopy cover, trunk circumference and aspect.

Materials and methods

Study site and habitat sampling strategy

The study was carried out in Killarney National Park (52. °0′N, −9°5′E; Fig. 1), which is characterized by ancient woodland pre-dating the 1600s (Craig, 2001; O'Sullivan and Kelly, 2006; Sterry, 2007). The region has experienced relatively little deforestation and land use change enabling more accurate observation of natural interactions (Ratcliffe, 1968; Peterken, 2001; Power, Igoe, Neylon, 2007). Killarney has Annex I status in the EU habitats directive because of its epiphyte richness and the rarity of the unique Rendianna forest dominated by English yew (*Taxus baccata*) (Smal and Fairley, 1980; Mitchell, 1990; Philip, Kelly, Mitchell, 2006). The wood is complimented by two others: Derrycunihy sessile oak wood (*Quercus petraea*) (Turner and Watt, 1939; Mitchell, 1988) and Carr wood rich in European holly (*Ilex aquifolium*) (Kelly, 1981; Mitchell and Bradshaw, 1984) centred within 10 km of each other on Lough Leane (Fig. 1). The sites were chosen to include three dominant tree species (Table 1) and for their accessibility. The distance between each sample site was relatively small reducing larger variation in precipitation, altitude and temperature that are known to effect epiphyte distributions (Ratcliffe, 1968; Kelly, 2002; Mitchell *et al.*, 2005).

Tree sampling strategy

Sampling occurred between 14th and 16th September 2011 using a transect bisecting each woodlands longest diameter. From an accessible point on the woodlands edge, a random number of steps were generated to a suitable trunk. Trunks unsuitable for surveying including those which had fallen, had obstructing branches and vines or a circumference at breast height (CBH) measuring less than 50 cm were excluded. The transect continued until 25 trees had been sampled, if the woodland edge was reached the transect reflected back towards the interior.

Moss, lichen and abiotic factor survey

Each tree's GPS grid reference (Garmin etrex H) was recorded. CBH was measured with a tape at breast height; 1.4 m from the ground. Trunks were divided into four faces corresponding to compass aspect. At each aspect, 1.4 m up the trunk and 10 cm away, air temperature (°C) and relative humidity (RH) were measured with a digital meter (Skywatch handheld) in addition to light intensity with a lux meter (Hanna portable). Canopy cover was estimated 50 cm away from the trunk using a convex spherical densitometer (Lemmon, 1956).

To assess the epiphyte cover at each of the four aspects a linear string transect consisting of seven $20 \times 20\ \mathrm{cm}^2$ quadrats was hung against the trunk 1.4 m high. This technique provided flexibility and minimised damage (Mitchell *et al.*, 2005; Fig. 2). Each tree was considered a data point composed as a sum of its four aspects; the total area of bark analysed per tree was $1.12 \times 10^4\ \mathrm{cm}^2$. Species richness and diversity were calculated for moss and lichen systematically at each quadrat. Richness was the number of moss and lichen species present that could be identified in the field using Watson (1981) and Whelan (2008). The Simpson's index of diversity ($D-1$) (see Equation 1) provided a measure of relative species abundance, or evenness, derived from richness and surface area. It is defined as the probability that two individuals randomly selected from a sample will belong to different species. This index was not affected by the large variation in site richness nor the presence of rare epiphytes and did not assume the species list was comprehensive for the habitat.

Equation 1. Calculation of Simpson's diversity index (D) where n = surface area on tree sample covered by an epiphyte species (cm^2); N = total area on tree sample covered by epiphytes. Values range from 0 to 1, where 1 is considered the most diverse sample.

$$D = 1 - \left(\sum (n/N)^2 \right) \qquad (1)$$

(Simpson, 1949)

Figure 1. Map of the woodland study sites within Killarney National Park, County Kerry, Ireland. Wooded areas around Lough Leane are highlighted in grey while dark grey areas are sampling sites. (**A**) Derrychunihy sessile oak wood; (**B**) Carr wood; and (**C**) Rendianna yew wood.

Table 1. Summary of abiotic conditions at each wood sampled Killarney National Park on the 14th–16th September 2011

Mean ± SD	Yew (*Taxus baccata*)	Holly (*Ilex aquifolium*)	Oak (*Quercus petraea*)
Grid reference of trees sampled	52. °02096′ N ± 37 −9°51754′ E ± 41	52. °01973′ N ± 49 −9°53218′ E ± 268	52. °04242′ N ± 151 −9°59697′ E ± 83
Circumference at breast height (cm)	123 ± 53	85 ± 33	256 ± 68
Canopy cover	99.2 ± 0.7	97 ± 1.5	95.5 ± 2.7
Temperature (°C)	16.6 ± 0.3	15.9 ± 0.3	15.8 ± 0.0
Humidity (RH%)	60.0 ± 0.2	57.5 ± 5	65.2 ± 0.3
Light intensity (lux)	13.3 ± 2.1	27.0 ± 3.7	20.1 ± 2.7

Figure 2. A linear string transect consisting of seven 20 × 20 cm^2 quadrats attached to the bark via pins. Every tree had transects placed on the north, south, east and west aspects hanging 1.4 m from the ground (Mitchell *et al.*, 2005; Image by Gardner 12 October 2010).

Data analysis

Species richness and the Simpson's index of diversity were not normally distributed and could not be transformed so non-parametric Kurskall–Wallis tests on median ranks were used. Significant differences between woods were differentiated by pairwise permutations of Mann Whitney *U* tests with Bonferroni corrections applied. Similarly, the bark surface area covered by moss and lichen, the CBH and canopy cover could not be normalised via transformation consequently Spearman's rank correlations explored the relations between them across all trees. Moss and lichen surface area grouped by aspect and tree species were normally distributed were analysed using a two-way ANOVA. Statistical analyses were performed in SPSS Statistics 22 (IBM Corp, 2013). For clarity all graphical outputs were based on untransformed data.

Results

Of 8.4×10^5 cm^2 of bark sampled across 75 trees, 16 epiphyte species were identified with seven being moss (Table 2). The mean epiphyte species richness for each tree independent of species was: moss, 3.45 ± 0.12SE; lichen, 2.99 ± 0.21SE and both 6.43 ± 0.24SE. Since epiphytes were identified within the field, the number of species may be under-representative of the true community composition. However, due to a consistent sampling strategy this does not impact the overall results of the study.

The tree species effected lichen and moss richness and diversity

There was no significant variation in moss richness between the three tree species ($H_{24} = 0.63$, $p = 0.73$), the mean values were 3.52 ± 0.14SE, 3.40 ± 0.18SE and 3.44 ± 0.27SE for yew, oak and holly respectively (Fig. 3). Conversely there was significant variation in both lichen richness ($H_{24} = 59.58$, $p < 0.01$) and total richness ($H_{24} = 37.93$, $p < 0.01$) between the tree species. Holly had the most lichen species 5.16 ± 0.18SE which was over double that of oak, 2.20 ± 0.14SE ($U_{24} = 43.31$, $p < 0.01$), and yew 1.60 ± 0.29SE ($U_{24} = 33.33$, $p < 0.01$). Holly also had the greatest total richness of 8.60 ± 0.35SE which was significantly larger than oak's 5.60 ± 0.25SE ($U_{24}= 32.5$, $p < 0.01$) and yew's 5.12 ± 0.23SE ($U_{24} = 27.84$, $p < 0.01$) (Fig. 3).

The epiphyte community on holly was more even and diverse than that on oak and yew ($H_{24} = 19.6$, $p < 0.001$) (Fig. 4). Particularly holly's diversity was 0.71 ± 0.02SE being significantly higher than yew's 0.58 ± 0.02SE ($U_{24} = 13.6$, $p < 0.01$) and oak's 0.45 ± 0.04 ($U_{24}=16.5$, $p < 0.01$). Oak and yew did not differ ($U_{24} = 1.6$, $p = 0.63$) (Fig. 4).

Epiphyte community composition varied with 57% of mosses and 11% of lichens being ubiquitous between tree species. The most unique species was found on holly within this study; four lichens and one moss, whereas oak only had one and yew none. Lichens seemed more specialised to the tree species for example *Parmeliella parvula* was dominant on yew but was the rarest on oak and only *Loxospora elatina* was universal to all three.

Table 2. A record of the epiphytic bryophyte and lichen flora present on three tree species within in Killarney, County Kerry on 2011 ($N = 25$)

	Yew (*Taxus baccata*)	%	Holly (*Ilex aquifolium*)	%	Oak (*Quercus petraea*)	%
Moss	*Neckera crispa*	32.8	*Eurhynchium striatum*	13.0	*Eurhynchium striatum*	44.0
	Thamnobryum alopecurum	12.7	*Neckera crispa*	3.2	*Homalothecium sericeum* (*)	1.0
	Thuidium tamariscinum	4.8	*Homalothecium sericeum* (*)	2.5	*Neckera crispa*	0.7
			Thamnobryum alopecurum	1.7	*Thamnobryum alopecurum*	12.1
			Thuidium tamariscinum	3.3	*Thuidium tamariscinum*	6.4
Total moss	70.1		18.7		60.5	
Lichen	*Arthonia vinosa (*)*	0.1	*Arthonia cinnabarina (**)*	3.7	*Arthonia vinosa (*)*	0.8
	Arthonia vinosa (*)	1.7	*Chrysothrix candelaris (**)*	3.8	*Flavoparmelia caperata*	3.8
	Loxospora elatina	0.6	*Flavoparmelia caperata (*)*	0.4	*Loxospora elatina*	3.8
			Micarea denigrata (**)	0.7	*Parmeliella parvula (*)*	0.2
			Pyrenula dermatodes (**)	6.7	*Thelotrema lepadinum* (*)	1.6
			Thelotrema lepadinum (*)	15.3		
			Loxospora elatina	1.2		
Total lichen	1.6		28.4		5.7	
Total epiphyte	75.7		49.3		74.2	

(*) and (**) indicate species present on two and one tree species respectively. Numbers indicate the mean bark percentage cover of each (cm^2).

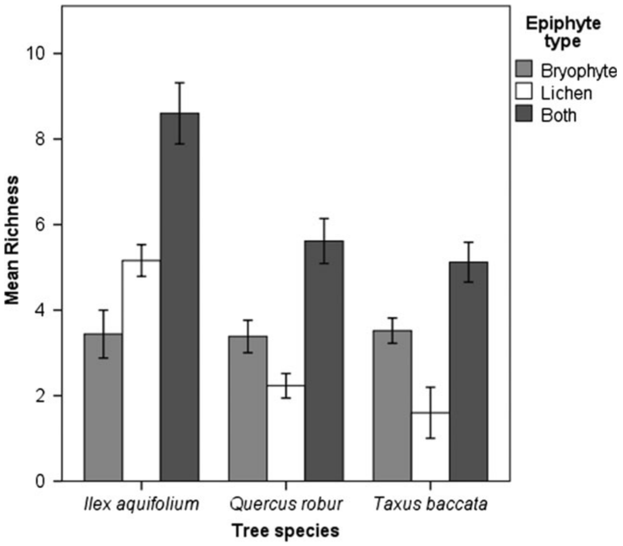

Figure 3. A comparison of epiphyte species richness between the three woodlands in Killarney National Park, County Kerry, on 14th–16th September 2011. $N = 25$. Each tree species is subdivided into lichen, moss and total richness to allow further comparison. Richness was purely the sum of different species present in the quadrats. Error bars are 95% confidence intervals.

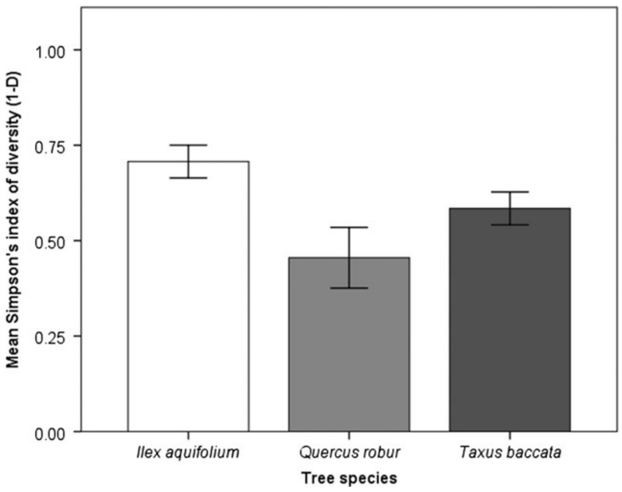

Figure 4. The mean Simpson's index of diversity of epiphytes between the three woodlands in Killarney National Park, County Kerry, on 14th–16th September 2011. $N = 25$. The index was calculated from species richness and the relative surface area of bark covered by each species. Error bars are 95% confidence intervals.

Tree species had the strongest influence on moss ($F_2 = 211.5$, $p < 0.001$), and lichen cover ($F_2 = 177$, $p < 0.001$) (Fig. 5). Overall coverage varied between species. Generally, yew had the greatest surface area covered by ephitphyes and holly the least; relatively yew had the greatest moss cover yew holly lichen cover.

Moss and lichen displayed differential growth on each tree species

Moss and lichen were negatively correlated ($r_{s\ 75} = -0.82$, $p < 0.01$) across all tree species (oak: $r_{s\ 25} = -0.40$, $p < 0.05$; holly: $r_{s\ 25} = -0.36$, $p = 0.08$; yew: $r_{s\ 25} = -0.47$, $p < 0.05$) (Fig. 6). Notable exceptions in the context of this study were the lichens *Loxospora elatina* and *Flavoparmelia caperata* that were often epiphytic on moss. Small scale distributions were observed such as *Thelotrema lepadinum*, *Arthonia cinnabarina, Pyrenula dermatodes* forming a mosaic across the smooth areas on oak while *Chrysothrix candelaris* dominated the indents in the bark. Clear vertical distributions were also observed, particularly on yew where at CBH *Neckera crispa* monopolised, midway down *Eurhynchium striatum* was prominent, then *Thamnobryum alopecurum* and finally *Thuidium tamariscinum* adjacent to the ground. On holly generally *Dicranum scoparium* dominated near ground instead of *Thuidium tamariscinum*.

Moss and lichen distribution showed differential responses to CBH, canopy cover, aspect

CBH

CBH showed a moderate positive correlation with the surface area of bark covered by moss ($r_{s\ 75} = 0.36$, $p < 0.01$) conversely, there was a weak negative correlation between lichen and CBH ($r_{s\ 75} = -0.24$, $p < 0.05$) (Fig. 7).

Aspect

Aspect did not have any effect on cover in isolation ($F_2 = 0.23$, $p > 0.05$). However, when taken into account with the tree species it was significantly different ($F_6 = 3.1$, $p < 0.001$) (Fig. 5). The mean moss cover on holly across the aspects was ~500 cm^2, being one third of oak and yew cover ($p < 0.05$) and displayed no difference ($p > 0.05$). Holly shows the greatest cover of moss in the north while oak in the west. The variability between aspects of lichen was the inverse of the moss cover for example, yew had the greatest moss cover in the east but the lowest lichen there too.

Canopy cover

Canopy cover had a moderate positive correlation with moss ($r_{s\ 75} = 0.32$, $p < 0.01$) and moderate negative correlation with lichen ($r_{s\ 75} = 0.32$, $p < 0.05$).

Discussion

The tree species affected lichen and moss richness and diversity

The relation between tree species and the diversity, richness and distribution of moss and lichen species is a known phenomenon (Juriado, Liira, Paal, 2009; Nascimbene *et al.*, 2009a, 2009b, Kiraly *et al.*, 2013). On a stand level heterogeneity in age and size of trees as well as abundance of dead wood has been repeatedly emphasised (Fritz, 2009; Odor *et al.*, 2013; Hofmeister *et al.*, 2015). However, when comparisons are made between specific tree species a more complex distribution of moss and

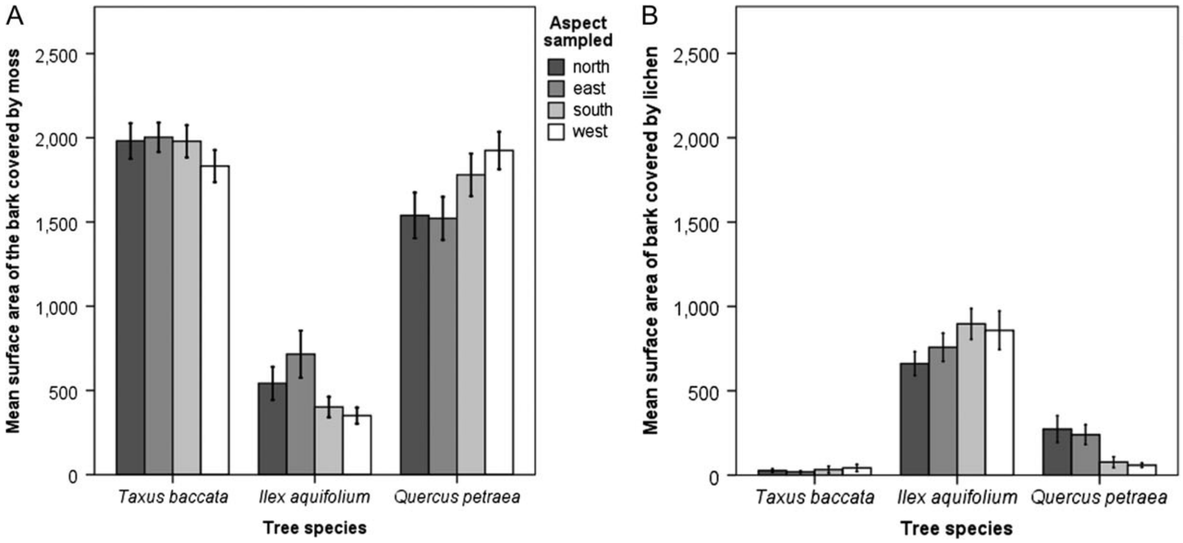

Figure 5. The difference in area of bark covered by epiphytes in relation aspect with reference to the four point compass where (**A**) total moss coverage and (**B**) total lichen coverage. Trees were sampled within the three woodland types in Killarney National Park, County Kerry, on 14th −16th September 2011.

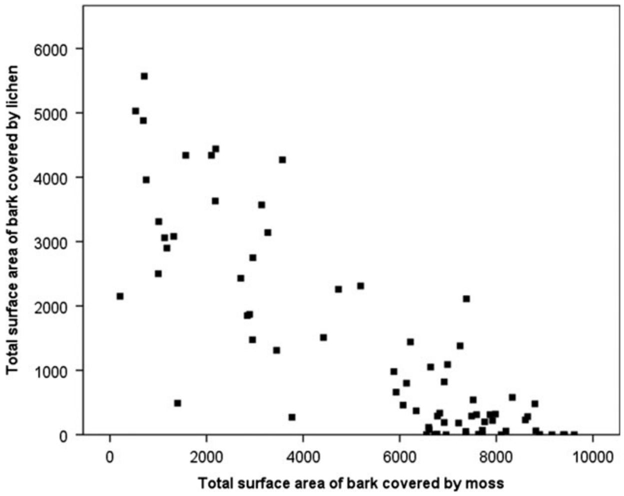

Figure 6. The correlation between moss and lichen on tree bark in Killarney National Park, County Kerry, 14th–16th September 2011. *N* = 75. Each point accounts for a single tree, the totals are the sums of the individual species cover within the epiphyte group.

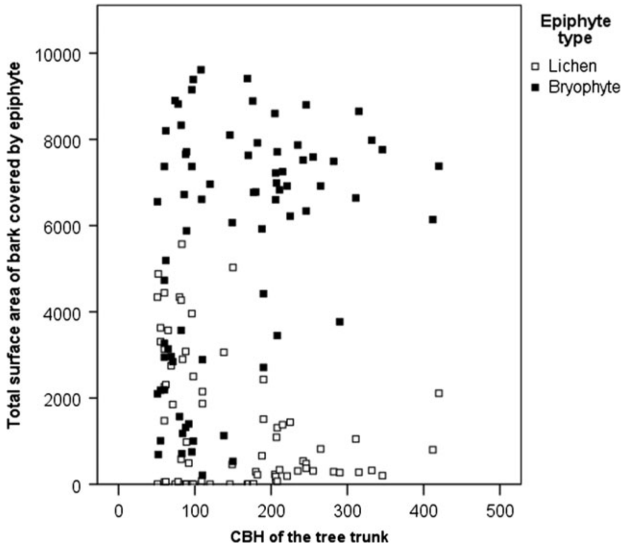

Figure 7. Correlation between circumference at breast height (CBH) and epiphyte coverage of trees sampled in Killarney, County Kerry, on 14th–16th September 2011 (*N* = 75). CBH is an indicator of a trees age, larger trees having greater trunk size (White, 1998).

lichen is revealed. Of the epiphytes identified, holly was found to have the highest epiphyte total richness and diversity while oak and yew displayed similar, lower diversity levels. Furthermore, holly was characterised by the highest number and coverage of lichen species compared to oak and yew which were dominated by mosses. This is in contrast with Kiraly *et al.* (2013) who found an increase in lichen species richness with increased proportion of oaks within mixed forests.

Many of the epiphytes identified were unique to a single tree species which is consistent with other studies in boreal woodlands (Nascimbene *et al.*, 2009a, 2009b; Hauck, 2011; Odor *et al.*, 2013). This could be related to species specific characteristics including bark pH and texture (Armstrong and Welch, 2007; Nascimbene *et al.*, 2013). Highly textured bark provide shelter, increased humidity, protection from predation and attachment security (Armstrong and Welch, 2007; Ranius *et al.*, 2008). However, the textured yew bark was dominated by shade loving *Chrysothrix candelaris,* perhaps due to the lower light intensity (Whelan, 2008; Seawright, 2011).

Epiphytes have a narrow pH tolerance controlling colonisation of bark surfaces (Watson, 1981; Pojar and MacKinnon, 1994; Hocking *et al.*, 2008). Oak and holly prefer acidic sandstone and so their bark is expected to have a lower pH (Peterken, 2001) in comparison to yew that prefers basic limestone thus higher pH. *Dicranum scoparium* and *Bartramia pomiformis* favour low pH and therefore were absent from yew (Watson, 1981; BBS, 2005). *Flavoparmelia caperata* was more abundant on oak and holly being adapted to acidic environments (Larsen *et al.*, 2007). Despite this four calcicole mosses including *Neckera crispa* and *Thamnobryum alopecurum*, were found in ‘acidic woods’ studies suggesting other factors are significant. Compensation can occur when the majority of resources are ideal, *Thuidium tamariscinum* and *Thamnobryum alopecurum* have been found in less basic woods if they are extremely humid (Ratcliffe, 1968; Watson, 1981) whereas *Eurhynchium striatum* in ion rich environments (Watson, 1981; BBS, 2005).

Variation of the epiphytic communities between tree species may also be due to overall lifespan, for instance holly has one tenth the lifespan of oak and yew trees (Hocking *et al.*, 2008). The general lichen complexity on holly could be at an intermediate point in succession, the four native species being adapted to quick growth in the relatively ephemeral habitat (Richards, 1938; Harris, 1971b; Hocking *et al.*, 2008). Studies have shown that community is also dependant on age. *Homalothecium sericeum* is found on wood around 250 years old whereas *Micarea denigrata* on 100 years (Ireland, 1975; Fritz, Niklasson, Churski, 2008). Older trees are generally more textured and have greater surface areas providing more suitable epiphytic habitat (Matthews, 1994; Fritz, Niklasson, Churski, 2008; Ranius *et al.*, 2008). They may also reach an epiphytic climax community that many not be as diverse but often is characterised by specialist species (Molder *et al.*, 2015).

Moss and lichen displayed differential growth on each tree species

A clear vertical gradient was observed from the tree base to breast height. Tree bases are more sheltered with higher humidity and lower light intensity (Richards, 1938; Harris, 1971b; Hocking *et al.*, 2008). Here, climax communities of *Thamnobryum alopecurum* and *Thuidium tamariscinum* or

Dicranum scoparium occur (Thomas and Polwart, 1958; BBS, 2005; Mitchell *et al.*, 2005; Armstrong and Welch, 2007). These mosses are several centimetres tall and form dense blankets completely smothering competition (Thomas and Polwart, 1958; Ratcliffe, 1968). With height mosses are shorter and more able to cope with lower moisture like *Eurhynchium striatum* (Ratcliffe *et al.*, 1968). One study recorded double the richness in the upper trunk, perhaps due to less stable conditions, greater habitat variation or competitor fitness equality (Thomas and Polwart, 1958). At the highest points pioneering stress resistant lichens like *Micarea denigrata* are concentrated where they cannot be outcompeted (Armstrong and Welch, 2007).

Competitive, offensive or defensive strategies in both specialized oceanic and generalist moss and lichen have been recognised (Ratcliffe, 1968; Watson, 1981; Begon, Townsend, Harper, 2006). Lichens have a wider range of tolerance to moisture than moss however, they are outcompeted in wetter areas by moss through indirect shadowing and physical displacement (Begon, Townsend, Harper, 2006; Ranius *et al.*, 2008). Intraspecific competition is often more intense as the niches have greater overlap (Holt, 1977; Bonsall and Hassell, 1997). Direct competition where one species has specific characters to hinder others is quite controversial in lichens and mosses, but from previous studies it is apparent in certain species, especially in woodlands (Lisci, Monte, Pacini, 2003; Armstrong and Welch, 2007). Competitive strategies gear the metabolism to a fast growth rate, mass and fecundity at the sacrifice of hardiness whereas, stress resistant strategists are the reverse. Mosses tend to adopt an offensive strategy being fast growing, dense and tall although this has also been adopted by some lichen species also (Bergamini *et al.*, 2004). Although rare within the current study, lichen may also use moss as a substrate where space limited, intensifying competition further. As observed on holly, lichen competition is more complex (Whelan, 2008; Seawright, 2011). Foliose species, such as *Flavoparmelia caperata*, are able to dominate large areas midway up the tree by smothering competitors via thick semidetached growth (Armstrong and Welch, 2007). Some actively engage in allelopathy producing enzymes and antibiotics to dissolve tissue as well as phenolic secondary metabolites like vulpinic acid which prevent germination and herbivory (Begon, Townsend, Harper, 2006; Armstrong and Welch, 2007). Crustose species, *Thelotrema lepadinum*, *Arthonia cinnabarina* and *Pyrenula dermatodes*, cling to the bark tightly and find it difficult to suppress other species with mass (Whelan, 2008; Seawright, 2011). Instead they are often pioneers withstanding drier conditions and commonly secrete defensive metabolites (Armstrong and Welch, 2007). Frequently in areas where more than two species occur truce margins are formed to conserve energy amongst a highly antagonistic environment (Armstrong and Welch, 2007).

Competition between epiphytes for light and moisture is mediated by wider interactions which can reset succession and create heterogeneous mosaics (Peterken, 2001; Begon, Townsend, Harper, 2006). Large areas of the woodland floor was covered in moss blankets greater than 1 cm thick which are relatively unpalatable compared to many other understory plants like wood-sorrel (*Oxalis* spp.) and bilberries (*Vaccinium* spp.) (Cross 1973; Cross, 1981). Consequently a prominent 1.2 m browsing line exists from grazers like the introduced sika (*Cervus nippon*) and indigenous red deer (*Cervus elaphus*) which can damage trunks by clipping and antler stripping. Browsing damage has intensified since the loss of predators like golden eagle (*Aquila chrysaetos*) and grey wolf (*Canis lupus lupus*) (Philip, Kelly, Mitchell, 2006). Direct herbivory pressure on epiphytes occurs despite the presence of defensive alkaloid cardio-toxins (Kelly, 1981; Mitchell, 1990; Kelly, 2002; Tiwary *et al.*, 2005). Lichens can be consumed by footmen moths (*Eilema* spp.) and Kerry slugs (*Geomalacus maculosus*) (Mandahl-Barth, 1966; Townsend, Waring, Lewington, 2004) whereas accounts of ants (*Formicidae* spp.), slugs (*Veronicelloidea* spp.) and voles (*Arvicolinae* spp.) have been recorded (NPWS, 2007; Monthey and Dudzik, 2010).

Moss and lichen distribution showed differential responses to canopy cover, CBH and aspect

Canopy cover

Canopy cover had a moderate positive correlation with moss and moderate negative correlation with lichen. The positive association between canopy cover and moss could be explained in terms of local humidity where shaded conditions protect moss from wind and desiccation (Kiraly *et al.*, 2013). At a broader scale is the canopy type; denser canopies are correlated with greater humidity and thermal stability at the expense of light intensity and maximum temperature. Holly-dominated woods have sparse canopies, often being found in clearings (Peterken, 2001). Oak wood is intermediary being taller and having denser leaves whereas yew wood casts intense shade due to rot resistant lateral growth (Smal and Fairley, 1980). It should be noted that holly and yew are more stable environments for moss and lichen as they are evergreen.

CBH

Trees with a larger CBH were colonised by more moss than lichen. Larger trees have been shown to have higher lichen biomass (Arseneau, Sirosis, Ouellet, 1997), however, this is a complex relationship as CBH is often representative of age that is interrelated to surface area, bark texture, microclimate and time of colonisation. Within the current study, yew had the greatest CBH but was dominated by moss suggesting that CBH is not always the dominating factor.

Aspect

The thick canopies of oak and yews may have diminished differences between aspects in moss and lichen cover. Because, holly showed the greatest variation between the aspects the canopy is less dense, allowing more radiation on the southern and western bark as the sun passes over the horizon. This favours species more resistant to desiccation and larger abiotic fluctuations (Ratcliffe, 1968). It is a common misconception that the north and east sides are always the most shaded and humid areas in the northern hemisphere because topography is also important (Matthews, 1994). This is demonstrated by the fact that there is a large mountain range to the west blocking the sun.

At the more exposed sites lichen cover dominated while moss was retarded. Many lichen species are adapted to drier environments compared to moss which has a reduced competitive ability in these areas. The capacity to withstand aridity might be a mixture of morphology being low lying to surface where there is greater moisture and less exposed surface area for loss (Hocking *et al.*, 2008). Likewise, in shaded sides moss grows relatively faster and can reach greater heights that can hinder lichen through reducing area and light intensity (Thomas and Polwart, 1958). However, at an individual level the pattern was not necessarily consistent, sometimes the side farthest from the sun leant toward the ground. Moss and lichen found attachment here difficult.

Conclusion

Bryophytes and lichens are incredibly important not just phylogenetically but environmentally (Mitchell *et al.*, 2005), as indicators of pollution, nutrient recycler and fixers, producers in food webs and invertebrate habitat providers (Peterken, 2001; Oksanen, 2006; Monthey and Dudzik, 2010). Economically they can be beneficial through medicine, dyes and as a food source (Knowles, 1929; Oksanen, 2006; Monthey and Dudzik, 2010). Therefore, improvement of moss and lichen diversity by forest management increasing tree species diversity is likely to benefit forest function (Nascimbene *et al.*, 2013). The niches of moss and lichens are highly complex and interlinked, however, the tree species is paramount as it defines the abiotic conditions of the substrate and atmosphere as well as other populations interacting with the epiphytes. pH is fundamental to the community but there are homologous variables across the woods. Sub-patterns that act on the humidity, light and temperature across individual trees include aspect, age, bark texture and height from ground. Niches are wettest and darkest in the crevasses at the tree base on the side receiving the least insolation, frequently the north. As one travels up the tree more light penetrates through but wind currents and evaporation lower the humidity. Ultimately, a continuous change in niche gradient occurs. Moss tend to have a niche that require greater humidity and light requirements than lichen (Lisci, Monte, Pacini, 2003). Succession is apparent since moss tends to outcompete lichen due to its mass and growth limiting space available (Thomas and Polwart, 1958; Harris, 1971a). Consequently, lichens are generally found in less hospitable upper reaches. Within similar niches there is intense competition, particularly between the defensive crustoses and offensive folioses, through allelopathy and mechanical destruction. This increases with richness which is constantly moderated by predation and competition.

Further study could consider whether these findings persist across a wider sample of forest type and could benefit with a more extensive identification method. Controlled experimental design could determine the successional hierarchy of moss and lichen under differing conditions.

Author biography

Following his MNatSci, Kris Sales has remained at UEA as a PhD student to study how the fertility of male Coleoptera and Lepidoptera is affected by climate change. He designed the epiphyte study during the assessment period of a second year Field Ecology module. Moreover, he assisted with all aspects of the project, particularly planning, analysis, figure creation and writing the transcripts.

Jessie Gardner also studied Natural Sciences and has just embarked on a PhD with the British Antarctic Survey focusing on the effect of ocean acidification and warming on pteropods. She assisted through all aspects of the project, particularly epiphyte identification, reviewing literature, writing transcripts and editing them.

Laurie Kerr completed her ecology degree at UEA and currently is in France teaching English. She assisted with the data collection, some analysis and reviewed the first transcript.

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