

Standard Paper

A hypervolume approach to niche specialism, tested for the old-growth indicator status of calicioids

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Abstract

Certain lichen epiphytes are restricted to old-growth forest stands with long ‘ecological continuity’, explained by i) niche specialism and their dependence on microhabitats associated with old stands including veteran or senescent trees, and/or ii) dispersal limitation with probabilities of colonization being relaxed over extended time periods. ‘Calicioid’ species are among the most important old-growth indicators, yet they reproduce sexually via small spores that appear widely dispersed at ecological scales. This suggests that they should have a high level of niche specialism compared to lichen epiphytes in general, explaining their role as old-growth indicators. However, comparisons of niche specialism are challenging, and this study uses epiphytic, corticolous calicioid species as an appropriate test case. Having measured 20 variables that constrain the lichen epiphyte niche, these were collapsed into a ‘hypervolume’ representing the sampled environmental space available for occupancy by lichens in Scotland as a study system. It was then possible to examine the occupancy of this hypervolume by individual lichens (niche breadth), with the proportion/percent occupied used to estimate a niche specialism score. Consequently, epiphyte calicioid species are confirmed to have a high degree of niche specialism compared to lichen epiphytes in general, and compared to other old-growth indicators, with their niche position directed towards drier climates including locally sheltered microhabitats associated with old-growth forest structure.

Key words: niche position, old-growth structure, pin-head lichens, realized niche

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Introduction

Niche breadth is a central topic in ecology (Devictor *et al.* 2010; Slatyer *et al.* 2013; Sexton *et al.* 2017) and characterizes where species might sit on the spectrum between niche specialist and generalist. Thus, in classic ecological models a species’ niche breadth was expected to correspond to its relative commonness or rarity and the consequent structure of communities, translated into rank-abundance plots (Hutchinson 1957; Whittaker 1972). However, comparison of niche breadth among different species can be challenging when considering multiple individual species-specific niche models. Factors selected into niche models (those with the greatest explanatory power) may be contrasting, that is, because species are constrained in their distribution or abundance by different limiting effects. This has led to methods for inferring specialization-generalization without reference to ecological details, such as those based on patterns of spatial co-occurrence (Fridley *et al.* 2007; Boulangeat *et al.* 2012). Alternatively, the aim of this study was to compare niche breadth among different lichen species by constructing a model that encapsulates key constraints to lichens in general terms, being relevant to individual species though also broadly defensible when comparing all species in a habitat. The approach focuses on woodland epiphytes, using

ordination to collapse gradients relating to moisture and temperature, light, and trophic status into a hypervolume (cf. Hutchinson 1957; Whittaker 1972; Carnes & Slade 1982; Devictor *et al.* 2010; Blonder 2018), and with the proportion/percent of the hypervolume that is occupied by a given species (niche breadth) used to estimate a niche specialism score. It is tried here for an ecological guild (calicioid species) that has been repeatedly flagged as an indicator of old-growth forest structure and asks whether this status is consistent with high niche specialism.

Many studies have reported the spatial association of certain lichen species with old-growth forest stands (Tibell 1992; Goward 1994; Selva 1994), including ancient but cultural wooded landscapes (Rose 1974, 1976). These lichen species are expected to be sensitive to two processes that can explain their association with old-growth and their referral under the rubric of ‘ecological continuity’ (Coppins & Coppins 2002). First, niche specialism, with some lichens requiring structures (e.g. canopy gaps) or microhabitats skewed towards old-growth stands, such as on veteran and senescent trees (Nascimbene *et al.* 2009; Fritz & Heilmann-Clausen 2010). Second, dispersal limitation, with some lichens restricted to old-growth stands because low probabilities of colonization (Dettki *et al.* 2000; Sillett *et al.* 2000) are relaxed over time. Lichen epiphytes dependent on ecological continuity, and thus associated with old-growth, have been developed as regional indices (e.g. Nitare 2000; Coppins & Coppins 2002) which, for the highly deforested temperate biome (Hannah *et al.* 1994, 1995), provide a strong proxy for habitat

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conservation value. Although early work scoping ecological continuity or old-growth lichen indicators was based on qualitative or semi-quantitative field interpretation, recent statistical tests appear to confirm their significance (Whittet & Ellis 2013; Dymytrova *et al.* 2018; Miller *et al.* 2020). In particular, longitudinal monitoring (Öckinger *et al.* 2005; Belinchón *et al.* 2017), spatial pattern analysis (Gu *et al.* 2001; Williams & Ellis 2018) and population genetics (Walser 2004; Jürriado *et al.* 2011) support a limited dispersal of these indicators over ecological timescales.

Lichens and some non-lichenized fungi predominantly with mazaedia and often stalked apothecia ('stubble' or 'pin-head' lichens), while being polyphyletic (Wedin & Tibell 1996; Prieto *et al.* 2013), are recognized by lichen ecologists as being convergent in a 'calicioid' trait group, including genera such as *Calicium* and *Chaenotheca* (lichenized) or *Microcalicium* (non-lichenized). Calicioid species have been documented as having among the strongest spatial association with old-growth forest stands (Holien 1996; Selva 2003; Nascimbene *et al.* 2010; Goward & Arsenault 2018; Malíček *et al.* 2019). Nevertheless, calicioid species have relatively small spores, typically $\leq 20 \mu\text{m}$ (fig. 11 in Tibell (1994)), which appear to be comparatively widely dispersed at biogeographical and ecological scales (Tibell 1994; Krus & Jonsson 1997). Consequently, calicioids would be expected to demonstrate a comparatively high niche specialism, since this would be the primary mechanism explaining their status as old-growth indicators. Calicioid species should therefore be more niche specialist than lichen epiphytes in general, and also more specialist than other lichen indicators of ecological continuity, a group which, overall, will include a proportion of species more constrained by dispersal-limitation relative to their niche specialism.

This study explored the use of the hypervolume approach, described above, to test the hypothesis that epiphytic and corticolous calicioid species are more niche specialist relative to other epiphytes. If this turns out not to be the case, it will be necessary to revisit assumptions about the dispersal capacity of these small-spored species, and/or invoke establishment constraints that might be explained through high specificity or selectivity towards lichen photobionts (cf. Tibell 2001; Tibell & Beck 2001; Yahr *et al.* 2004).

Methods

Field and environmental sampling

Field sampling is described in detail by Ellis *et al.* (2015) and summarized here. Twenty ancient woodland sites were selected (cf. Roberts *et al.* 1992; Whittet *et al.* 2015), positioned across a longitudinal climate gradient from oceanic western to relatively continental north-eastern Scotland, and 10 equidistant points were positioned within the boundary of each site. Points were visited in random order, to accumulate a list of contrasting tree species in contrasting size categories that were sampled for their epiphytes in a way that captured site heterogeneity (maximizing tree species and tree size differences). Sampling used quadrats of $4 \times 6 \text{ cm}$, $6 \times 9 \text{ cm}$ or $9 \times 12 \text{ cm}$ (depending on tree size), split into sub-units to record species frequency of occurrence per quadrat, with a minimum of four quadrats per tree at random heights between 30 and 200 cm for each cardinal aspect (north, south, east and west), and adding intermediate aspects as tree size increased ($> 75 \text{ cm dbh}$). Accordingly, a total of 1013 quadrats was sampled from 250 individual trees across the 20 sites.

Field sampled quadrats were each accompanied by 20 environmental variables, the selection of which was based on a literature review that had examined the constraints explaining lichen epiphyte distribution and community structure (Ellis 2012), as follows:

Macroclimate. The growth of lichens is sensitive to regional gradients in the availability of moisture and temperature (Boucher & Nash 1990; Gauslaa *et al.* 2007; Ellis *et al.* 2017), including their susceptibility to, and recovery from, cold temperatures (Solhaug *et al.* 2018). Consequently, lichen distributions are often aggregated into different bioclimatic regimes (Coppins 1976; Ellis *et al.* 2007), which correlate with an underlying growth response to climate (Braidwood & Ellis 2012). Macroclimatic variables were therefore mean relative humidity, totals for annual precipitation and precipitation during the driest quarter, mean annual and minimum temperatures, all for the 30-year period 1981–2010, interpolated from instrumental measurements at a 1 km grid-scale (Hollis *et al.* 2019).

Stand-scale microclimate. The macroclimate is modified by the topographic position of a stand, including features that can control lichen water balance, considering that lichens are both poikilohydric and only physiologically active when hydrated, enabling daytime photosynthesis (Palmqvist & Sundberg 2000; Palmqvist *et al.* 2010) and nocturnal stress recovery and tissue growth (Bidussi *et al.* 2013; Alam *et al.* 2015). Stand-scale variables were therefore a measure of physical exposure related to the drying effect of wind (detailed aspect method of scoring, DAMS: Quine & White 1994; Suárez *et al.* 1999), distance to the nearest watercourse, which has been shown to control and explain lichen occurrence/abundance (Belinchón *et al.* 2009; Rambo 2010; Stehn *et al.* 2013) and growth (Rambo 2010; Ellis 2020), and a heat load index based on latitude, slope and aspect (McCune & Keon 2002; McCune 2007).

Tree-scale microclimate. Again, in relation to thallus hydrology, the macroclimate and stand-scale effects will be modified by tree-scale microclimates, and variables were therefore the height on the tree bole, which affects the growth of individual species (Antoine & McCune 2004; Merinero *et al.* 2015) and the structure of epiphyte communities (Kenkel & Bradfield 1986; Bates 1992; McCune *et al.* 2000), likewise the angle of bole lean (Kenkel & Bradfield 1986; Bates 1992; McCune *et al.* 2000; Doering & Coxson 2010), as well as bark furrow depth and cover of bryophytes which are both important in regulating lichen establishment and growth (Sillett & McCune 1998; Colesie *et al.* 2012; Rubio-Salcedo *et al.* 2015).

Light availability. The growth of lichens is physiologically constrained by light availability (Palmqvist & Sundberg 2000; Palmqvist *et al.* 2010), though species are differently adapted to light and shade (Demmig-Adams *et al.* 1990; Manrique *et al.* 1993; Gauslaa & Solhaug 1996). Variables were therefore a measure of direct radiation based on latitude, slope and aspect (McCune & Keon 2002; McCune 2007), indicative of below canopy light transmission (Liefers *et al.* 1999; Angelini *et al.* 2015) the basal area of the five nearest surrounding trees to approximate structural density, canopy openness measured around a sampled tree using a densiometer (Lemmon 1956; Englund *et al.* 2000; Paletto & Tosi 2009), and the aspect of a quadrat on the tree bole, folded around a north-south axis (cf. McCune & Keon 2002; McCune 2007).

Physical-chemical conditions. The physical and chemical bark microhabitat has been shown to control occurrence and abundance of lichen species and patterns of community composition (Gauslaa 1985; Bates 1992), and variables were therefore bark

pH and conductivity (Kuusinen 1996; Jüriado *et al.* 2009; Mežaka *et al.* 2012), as well as bark density and water holding capacity (Loppi & Frati 2004; Mistry & Beradi 2005; Kubiak & Osyczka 2020).

For detailed methods regarding measurement of environmental variables, see Ellis *et al.* (2015).

Statistical analysis

Analysis was based on the Hutchinsonian niche model (cf. Hutchinson 1957; Blonder 2018), which imagines a circumscribed environmental space or 'hypervolume' within which a species can complete its life cycle (establishment, growth and survival, reproduction). This volume is bounded by the species position along multiple axes, with the axes being environmental variables that limit the consequent occurrence or abundance of a species, and scaling to community composition.

To quantify the hypervolume concept, two ordination approaches were tested. First, a principal components analysis (PCA) was used to summarize covariance among the 20 selected environmental variables. PCA was performed using the *prcomp* package in R v. 4 (R Development Core Team 2020) with variables centred and scaled to unit variance. PCA assumes linearity among the environmental covariables. Second, non-metric multi-dimensional scaling (NMDS) was used to summarize difference among the samples with respect to environmental variables that were first standardized to avoid negatives (e.g. for minimum temperatures, or angle of bole lean). NMDS better handles non-linearity among environmental covariables (McCune & Grace 2002). NMDS was performed using PC-Ord v. 6 (McCune & Mefford 2011), based on a Bray-Curtis distance matrix; search for an optimized solution was for a maximum of six ordination axes based on 500 runs with the observed data (step length = 0.2, stability criterion = 0.00001 with 100 runs to estimate stability), and with the significance of the optimum solution estimated against 1000 runs with randomized data.

Selecting the ordination (PCA or NMDS) that yielded the greatest variation explained for the lowest number of axes, the convex hull for all samples in ordination space was calculated using the *geometry* package in R v. 4 (R Development Core Team 2020), approximating the hypervolume of sampled environmental space available for species occurrence. Convex hulls relating particularly to each species niche were then calculated using the ordination scores for the samples within which a species occurred. Mathematically, this could be achieved for all epiphyte species with occurrences \geq the number of relevant ordination axes plus one, that is the minimum number of points required to calculate a simplex; in practice, the method was applied only to species with ≥ 5 occurrences. The environmental space circumscribed by the samples within which a species occurred defined its niche breadth. Niche specialism was subsequently estimated by considering niche breadth relative to the hypervolume of sampled environmental space, that is, dividing the convex hull of the occupied samples by the convex hull for all samples, and multiplying by 100 to create a niche specialism score. Note that the lower the niche specialism score, the narrower the niche breadth with respect to sampled environmental space, and the higher the niche specialism.

Given this approach, it was important to test whether a species niche specialism was consistent with a deterministic niche model. In contrast, a neutral model (Hubbell 2001; Etienne & Alonso 2007) would predict that the number of occurrences, and therefore the extent to which a species is calculated to be a niche specialist or generalist, would scale with a process of random selection given the species abundance in a regional species pool. Niche specialists could therefore be identified as those with a niche specialism exceeding that of a null taxon with equivalent occurrence. Accordingly, null taxa were constructed at different occurrence levels, being randomly assigned to the samples in environmental space. Niche specialism scores were calculated for null taxa, repeated 10 000 times for each different occurrence level. Species with deterministic niches were identified in a one-

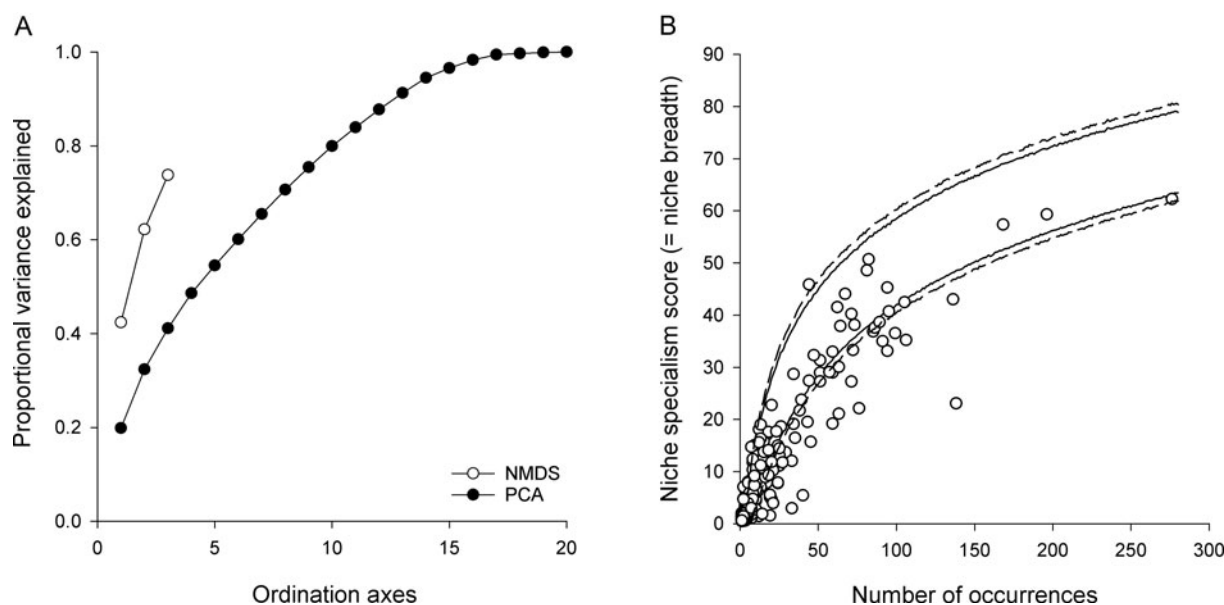


Fig. 1. A, comparison of environmental variance explained with the number of ordination axes for alternative methods of PCA and NMDS. B, comparison of a species calculated niche specialism (circles), with thresholds for niche specialism based on randomization for a given number of occurrences, at the 5th to 95th (solid lines) and 2.5th to 97.5th percentiles (dashed lines). Circles below the 95th percentile show species with niche specialism exceeding null expectation for a one-tailed test ($P < 0.05$).

tailed test as those with a niche specialism score exceeding the 5th percentile of their null taxa with equivalent occurrence ($P < 0.05$).

Species passing the null model test were grouped as follows: i) all lichens excluding ecological continuity indicator species relevant to the study area (Coppins & Coppins 2002) and by default excluding calicioid species, ii) ecological continuity indicator species, excluding calicioid species, iii) broadly defined calicioid species including fruticose lichens such as *Sphaerophorus globosus* (Huds.) Vain., and iv) calicioids including only the pin-head morphology. The niche specialism scores were compared among groups by resampling their component species with replacements (10 000 times) to calculate their bootstrapped means, plotted as boxplots.

Furthermore, to aid interpretation of niche constraints, the mean (weighted average) position of calicioid species was calculated along individual ordination axes for the samples in which they occurred, and plotted into the sampled environmental space, while ordination axes were interpreted through Spearman's rank correlation with the 20 environmental variables.

Results

Analysis of the 20 environmental variables by PCA suggested that a large number of axes would be required to adequately represent environmental variation (15 axes to explain $\geq 95\%$), while NMDS identified a statistically significant ($P < 0.001$) optimum solution with three axes (stress = 18.96, instability < 0.00001). The three NMDS axes explained 73.8% of environmental variation, while nine PCA axes would be required for a comparable result (Fig. 1A). NMDS was therefore adopted as a parsimonious method that summarized non-linear relationships among the environmental variables.

Of an initial 294 fully identified species sampled as epiphytes (Ellis *et al.* 2015), there were 183 with ≥ 5 occurrences. Of these, 113 (62%) passed the null model test for niche specialism (Fig. 1B), including 30 lichens assumed to be indicators of ecological continuity (Coppins & Coppins 2002), plus an additional six calicioid species: *Calicium salicinum* Pers., *C. viride* Pers., *Chaenotheca ferruginea* (Turner ex Sm.) Mig., *Ch. trichialis* (Ach.) Th. Fr., *Microcalicium disseminatum* (Ach.) Vain. and *Sphaerophorus globosus*. When the mean scores for niche specialism were bootstrapped, it was clear that indicators of ecological continuity are more niche specialist than lichen epiphytes in general (Fig. 2). When including the fruticose *Sphaerophorus globosus*, the calicioid species had similar niche specialism to other ecological continuity indicators, but when restricting to pin-head calicioids there was a further shift towards higher levels of niche specialism than other ecological continuity indicators.

Niche position could be interpreted alongside niche specialism by considering how calicioid species plot into environmental ordination space (Fig. 3), and the relationship of ordination axes with environmental variables (Table 1). Thus, *Sphaerophorus globosus* appeared to occur under higher moisture conditions than the pin-head calicioids, which were closely grouped towards negative axis one scores representing drier and cooler climates, well-lit stand positions, and sheltered microhabitats (e.g. deeper bark furrows), being conditions that strongly contrasted with bryophyte-dominated communities, for example. However, there was wider spread in niche position encompassing positive and negative scores for axis two, representing differences between species tending to occur on a relatively more acidic (*Chaenotheca ferruginea*, *Microcalicium disseminatum*) or a less acidic (*Calicium*

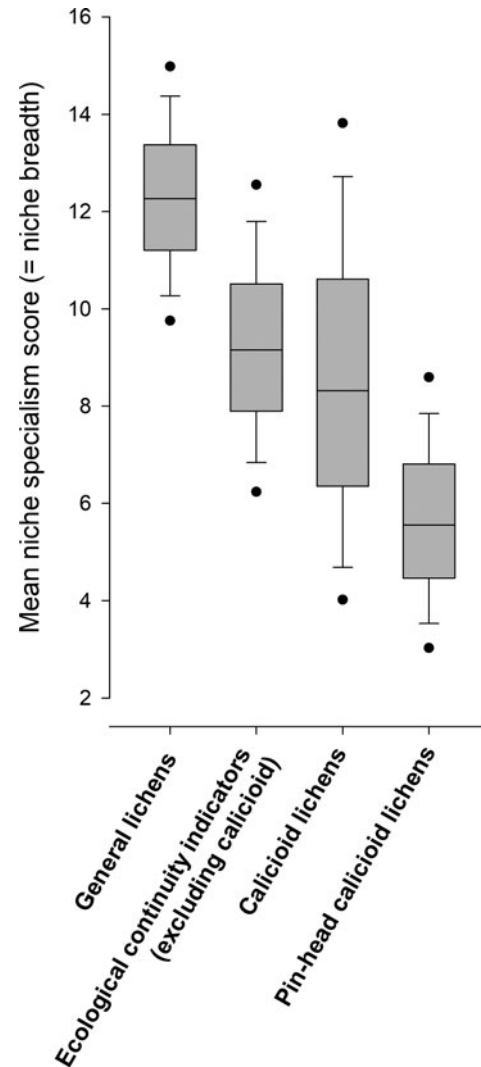


Fig. 2. Bootstrapped mean of niche specialism scores for four different lichen groups. Boxplots show the median (line), 25th to 75th percentiles (box), 10th to 90th percentiles (whiskers), and 5th and 95th outliers (symbols). Note that the lower the niche specialism score, the narrower the niche breadth with respect to sampled environmental space, and the higher the niche specialism.

viride, *C. salicinum*, *Chaenotheca trichialis*) bark substratum. Axis three was most strongly related to tree bole aspect, though without a clear pattern in niche position among the different calicioids (data not shown).

Discussion

Comparison of niche breadth, to establish whether species have specialist or generalist niches, poses a series of conceptual and methodological challenges. This study attempted a hypervolume approach to estimate the niche specialism of lichens, with calicioid species as a test case, since these are putative old-growth indicators (Holien 1996; Selva 2003; Nascimbene *et al.* 2010; Goward & Arsenault 2018; Malíček *et al.* 2019). It used ordination to construct a hypervolume (Carnes & Slade 1982; Devictor *et al.* 2010) that aimed to represent the environmental space available for lichen epiphytes within the study area. Niche specialism was subsequently estimated as the proportion/percent of environmental space that is occupied by different species, including calicioids.

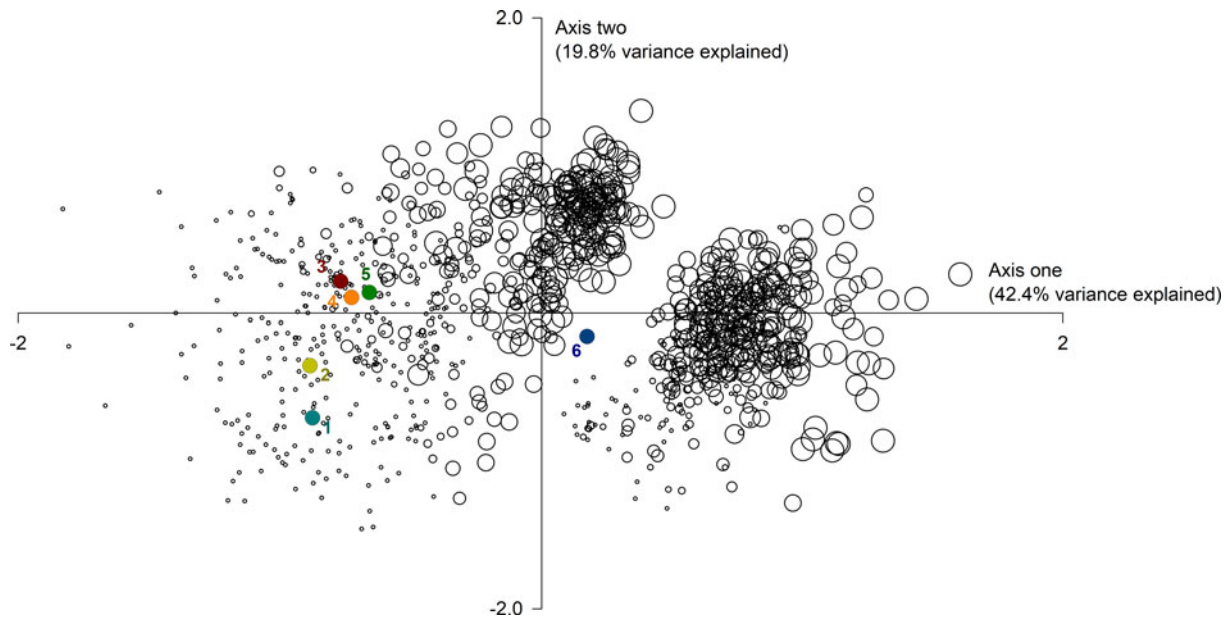


Fig. 3. Plot for two NMDS ordination axes (points = samples), with the mean niche point of calicioid species positioned into the sampled environmental space (cf. Table 1). 1 = *Microcalicium disseminatum*, 2 = *Chaenotheca ferruginea*, 3 = *Calicium salicinum*, 4 = *Calicium viride*, 5 = *Chaenotheca trichialis*, 6 = *Sphaerophorus globosus*. Symbol size shows the frequency of bryophytes as a proxy for microhabitat conditions linked to community structure. In colour online.

The validity of the approach depends on a series of caveats outlined below, and which form targets for methodological improvement.

First, there may be unsampled environmental space (the hypervolume may be too small), and/or species occupancy may be under sampled (niche breadth may be truncated). The extent of these problems depends on the sampling design. Here, the sampling sought to capture environmental heterogeneity for ancient mixed temperate woodlands (between and within sites, between and within trees), positioned across a steep climatic gradient, while aiming for sufficient effort to recover an adequate representation of each species' niche based on a structured random sampling. The focus on the calicioid test case is therefore context specific (cf. Sætersdal *et al.* 2005), relevant only to the limits of the sampling regime. Second, the use of convex hulls to quantify niche breadth makes a set of simplifying assumptions, principally that the outer limits of a species occurrence circumscribe the breadth of its deterministic realized niche; thus i) it reconstructs niche topography without bimodal or more complex responses (Austin & Smith 1989; Smart *et al.* 2010), and ii) it considers empty samples (missing occurrences) within the boundaries of the niche as unoccupied niche space, for example because of dispersal limitation (Pulliam 2000; Wild & Gagnon 2005), though not accounting for other stochastic processes that could extend niche breadth, such as mass effects (Pulliam 2000; Warren *et al.* 2012). Third, the choice of relevant environmental variables is critically important, ensuring a link to ecological performance (establishment, growth and survival, reproduction) which will ultimately determine the sampled patterns of epiphyte occurrence. The choice for each of the environmental variables is outlined in detail as part of the Methods (see cited literature in 'Field and environmental sampling', above); they captured the key constraints of moisture availability at contrasting scales, temperature, light availability, and trophic status with respect to bark chemistry. Fourth, because niche breadth measured with a convex hull will scale to the number of occurrences, evidence for deterministic

niche specialism needed to be tested against null expectation and *c.* 38% of species failed to meet a significance threshold of 0.05 (including two calicioid species: *Calicium parvum* Tibell and *Chaenotheca chrysocephala* (Ach.) Th. Fr.). This could be for various reasons, including weak initial specification of environmental variables that determine the lichen epiphyte niche (see cited literature in 'Field and environmental sampling', above), if irrelevant or redundant variables are included, and with possible improvement by considering a weighting for variable importance, or variable interactions. A further reason may be redundancy among the lichen species. That is, if the niche position of lichen epiphytes is broadly overlapping so that different species can replace one another stochastically in an epiphyte community, consequently a measured volume could be large relative to the number of occurrences. These caveats notwithstanding, sufficient species appeared to pass the null model test to cautiously estimate the comparative niche specialism of calicioid epiphytes.

The niche specialism of calicioid epiphytes depended on whether the guild included the fruticose *Sphaerophorus globosus*, appearing more highly specialized than other ecological continuity indicators when restricted to pin-head calicioids only (excluding *Sphaerophorus*). This is despite the morphological differences that exist among the pin-heads themselves, being lichenized or non-lichenized, or contrasting in the form of their stalk, capitulum and mazaedium etc. (Van Dort & Horvers 2021). The results are therefore consistent with previous studies that have highlighted the specialist niche requirements of calicioid species, which when lichenized will require uptake of ambient moisture for photosynthetic activation (Palmqvist & Sundberg 2000; Palmqvist *et al.* 2010) except for pin-heads with an avoidance of direct wetting so that their occurrence is often skewed to drier climates and microhabitats comprising dry bark surfaces in furrows, crevices and overhangs (Van Dort & Horvers 2021). Thus, niche specialism combines with niche position (cf. Vela Díaz *et al.* 2020), which has an association with older trees, for example where these are characterized by deeply fissured bark

Table 1. Interpretation of NMDS ordination by correlating axis scores for samples against respective environmental variables; axis scores were used to define the convex hull for the sampled environmental space (hypervolume), and for epiphyte niche breadth (samples within which a species occurred). Statistically significant correlations are shown in bold, with the strongest relationships ($r \geq 0.7$) shaded.

Scale of Analysis	Spearman's rank coefficient; statistical significance (<i>P</i>)		
	NMDS 1	NMDS 2	NMDS 3
Environmental variable			
Macroclimate			
Annual precipitation	<i>r</i> = 0.727; <i>P</i> < 0.0001	<i>r</i> = -0.521; <i>P</i> < 0.0001	<i>r</i> = -0.0169; <i>P</i> = 0.591
Precipitation driest quarter	<i>r</i> = 0.760; <i>P</i> < 0.0001	<i>r</i> = -0.424; <i>P</i> < 0.0001	<i>r</i> = 0.012; <i>P</i> = 0.692
Relative humidity	<i>r</i> = 0.793; <i>P</i> < 0.0001	<i>r</i> = -0.191; <i>P</i> < 0.0001	<i>r</i> = 0.059; <i>P</i> = 0.062
Mean annual temperature	<i>r</i> = 0.583; <i>P</i> < 0.0001	<i>r</i> = 0.114; <i>P</i> = 0.0003	<i>r</i> = 0.081; <i>P</i> = 0.01
Mean minimum temperature	<i>r</i> = 0.798; <i>P</i> < 0.0001	<i>r</i> = 0.077; <i>P</i> = 0.014	<i>r</i> = 0.07; <i>P</i> = 0.025
Stand-scale microclimate			
Exposure	<i>r</i> = 0.344; <i>P</i> < 0.0001	<i>r</i> = -0.486; <i>P</i> < 0.0001	<i>r</i> = 0.081; <i>P</i> = 0.01
Distance to watercourse	<i>r</i> = -0.149; <i>P</i> < 0.0001	<i>r</i> = -0.205; <i>P</i> < 0.0001	<i>r</i> = 0.079; <i>P</i> = 0.012
Heat load index	<i>r</i> = 0.136; <i>P</i> < 0.0001	<i>r</i> = -0.007; <i>P</i> = 0.829	<i>r</i> = -0.024; <i>P</i> = 0.437
Tree-scale microclimate			
Height on bole	<i>r</i> = -0.063; <i>P</i> = 0.044	<i>r</i> = 0.029; <i>P</i> = 0.354	<i>r</i> = 0.074; <i>P</i> = 0.019
Angle of lean	<i>r</i> = 0.057; <i>P</i> = 0.068	<i>r</i> = 0.044; <i>P</i> = 0.161	<i>r</i> = -0.055; <i>P</i> = 0.08
Furrow depth	<i>r</i> = -0.249; <i>P</i> < 0.0001	<i>r</i> = -0.051; <i>P</i> = 0.102	<i>r</i> = -0.01; <i>P</i> = 0.759
Bryophyte cover	<i>r</i> = 0.678; <i>P</i> < 0.0001	<i>r</i> = 0.401; <i>P</i> < 0.0001	<i>r</i> = -0.13; <i>P</i> < 0.0001
Light availability			
Direct radiation	<i>r</i> = 0.293; <i>P</i> < 0.0001	<i>r</i> = -0.152; <i>P</i> < 0.0001	<i>r</i> = -0.059; <i>P</i> = 0.06
Stand density	<i>r</i> = -0.058; <i>P</i> = 0.066	<i>r</i> = 0.093; <i>P</i> = 0.003	<i>r</i> = -0.037; <i>P</i> = 0.234
Canopy openness	<i>r</i> = -0.252; <i>P</i> < 0.0001	<i>r</i> = -0.146; <i>P</i> < 0.0001	<i>r</i> = 0.06; <i>P</i> = 0.07
Aspect on bole	<i>r</i> = -0.025; <i>P</i> = 0.427	<i>r</i> = -0.068; <i>P</i> = 0.03	<i>r</i> = 0.893; <i>P</i> < 0.0001
Physical-chemical condition			
Bark pH	<i>r</i> = -0.009; <i>P</i> = 0.765	<i>r</i> = 0.727; <i>P</i> < 0.0001	<i>r</i> = 0.214; <i>P</i> < 0.0001
Bark conductivity	<i>r</i> = 0.003; <i>P</i> = 0.916	<i>r</i> = -0.718; <i>P</i> < 0.0001	<i>r</i> = -0.233; <i>P</i> < 0.0001
Bark density	<i>r</i> = 0.137; <i>P</i> < 0.0001	<i>r</i> = -0.145; <i>P</i> < 0.0001	<i>r</i> = -0.021; <i>P</i> = 0.512
Bark water capacity	<i>r</i> = -0.007; <i>P</i> = 0.835	<i>r</i> = 0.289; <i>P</i> < 0.0001	<i>r</i> = 0.039; <i>P</i> = 0.212

(cf. Ellis 2012; Ellis *et al.* 2015; Van Dort & Horvers 2021). Extending this consideration, there is also evidence of community succession among lichen epiphytes as trees age (Lewis & Ellis 2010; Ellis & Ellis 2013) that possibly includes a mid-age peak in species richness, while pin-heads appear to occupy a later stage in epiphyte community succession as species richness, density and inter-thalline competition decline.


The results here add support to the role of pin-head calicioids in particular as indicators of ecological continuity and old-growth status owing to their dependency on a limited set of realized niche conditions (specific climate or microclimate, bark condition, low competition) being associated with microhabitats found especially on veteran or senescent trees. Consequently, there is no reason to invoke alternative explanations for the role of calicioids as old-growth indicators. There is currently a lack of strong evidence to suggest that calicioid species are dispersal-limited (Wiersma & McMullin 2022). Furthermore, it has been proposed that production of mazaedia and loose spore mass facilitates dispersal by animals, including birds (Johansson *et al.* 2021), providing effective long-distance dispersal at ecological scales (Tibell 1994;

Rikkinen 2003; Prieto *et al.* 2013). Instead, calicioid diversity has been associated with microhabitat heterogeneity of old-growth stands, rather than its temporal continuity *per se* (Kruys & Jonsson 1997; Löhmus & Löhmus 2011), with this diversity extending beyond the few corticolous species examined here when considering epixylic species accumulated onto old-growth deadwood volume and structure (Kuusinen & Siitonen 1998; Löhmus & Löhmus 2011; Goward & Arsenaault 2018). Nevertheless, because the niche position of calicioid species is centred on old-growth microhabitats that are now rare in nature, arguably population sizes and consequent spore densities may also be low, thus acting through meta-population processes (cf. Hanski 1999, 2002) to restrict their wider dispersal (and abundance) in the landscape. However, this meta-population constraint is potentially weakened by the high fecundity (spore production) of calicioid species (Tibell 1994). With respect to the potential effect of photobiont specificity and selectivity, although photobiont selectivity has been suggested as a constraint to the establishment of certain cyanolichens (Rikkinen *et al.* 2002; Fedrowitz *et al.* 2011; Belinchón *et al.* 2015), experiments on

niche specialist chlorolichens do not convincingly report the same pattern (Svensson *et al.* 2016).

In summary, calicioid species have been widely documented as ecological continuity old-growth indicators and they appear to provide an example of a trait group that has high niche specialism relative to other lichen epiphytes, and a niche position towards specific microhabitats associated with veteran and senescent trees. The hypervolume approach tried here is consistent with and strengthens evidence that calicioid epiphytes provide examples of old-growth indicators strongly determined by niche specialism rather than dispersal limitation. The hypervolume approach needs further testing and method development, though in principle it could also be used to estimate the degree to which species are dispersal-limited, by comparing the proportion of samples falling within the boundary of a species niche that is occupied compared to unoccupied, giving potential for widely dispersed species to occupy a greater proportion of suitable and available niche space.

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