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Non-parametric methods reveal non-linear functional trait variation of lichens along environmental and fire age gradients

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Nomenclature

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Abstract

Questions: Popular methods to analyse community–trait–environment relationships constrain community patterns by trait and environment relationships. What if some traits are strongly associated with community composition but unrelated to environmental variables and vice versa? We take a different approach, unconstrained by this assumption using non-parametric methods. We applied this technique to lichen (fungal/algal and/or cyanobacterial symbioses) communities across environmental and fire age gradients by measuring richness and cover of four important functional traits: energy generation (type of photosynthetic symbiont), water relations (inferred from growth form), dispersal capability (from vegetative propagules) and microsite specificity (measured by substrate affinity).

Location: Denali National Park and Preserve, Alaska, USA.

Methods: We ordinated plots in species space and regressed trait and environmental variables against ordination axes, resulting in one- or two-dimensional trait and environment surfaces. We then superimposed these surfaces on the ordination to create a new visual display, the ‘hilltop plot’, which enabled simultaneous measurement and display of one- and two-dimensional, non-linear community–trait–environment associations.

Results: Most traits examined show non-linear relationships with community structure. Fire favoured simple cladoniiform lichens, species with higher vegetative dispersal capacity and specificity to grow on wood, but excluded the ‘reindeer’ lichens, which had lower cover even more than 20 yrs after fire. Forests had more sorediate lichens than non-forested habitats, whereas high elevation, rocky areas had more green algal and fruticose lichens. Cyanobacterial lichen richness was positively related to shrub cover, while tripartite (cyanobacteria and green algae in a single lichen) and foliose lichen richness was highest in areas with higher moss cover.

Conclusions: Different combinations of lichen functional traits peaked along environmental and disturbance gradients, which we interpreted as balancing energy generation, water relations, vegetative dispersal and habitat specificity. Our method of trait–environment–community analysis revealed numerous one- and two-dimensional, non-linear relationships between community composition and functional traits, environmental variables and fire age gradients, which informed mechanisms behind community assembly. Our results indicate non-parametric and non-linear methods of trait–environment–community analysis have the potential to detect patterns that would have been missed using current popular techniques.

Introduction

Trait-based analyses have proven useful for understanding community dynamics (McGill et al. 2006; Adler et al. 2013; Mouillot et al. 2013), but current analytical methods make unnecessary assumptions that may mask certain trait–community or environment–community relationships. For example, most popular methods that deal with the fourth-corner problem (community–trait–environment relationships) assume community structure should be viewed through the filter of trait–environment relationships (Kleyer et al. 2012; Dray et al. 2013). However, what if some environmental variables were strongly related to the community structure but unrelated to the measured traits? Constraining the community analysis by trait–environment relationships would miss some community–environment relationships. Similarly, if the measured environmental variables are inadequate, constraining the community analysis by trait–environment relationships might then miss community–trait relationships. A more flexible approach would view community structure independently, then superimposing trait–environment relationships to the extent possible. We demonstrate this approach using non-parametric methods to explore community–trait–environment patterns unconstrained by trait–environment relationships.

Another common problem in community–trait–environment analyses is how one displays and calculates the strength of trait or environment relationships with the community. Most methods calculate or display a linear correlation between ordination axis coordinates of the sample units and traits or environmental variables. However, we expect that traits and environmental variables will have non-linear relationships with the ordination axes. Assuming linearity can result in overlooking traits or environmental variables that are actually strongly related to the community. To address this problem, we propose a simple method, the ‘hilltop’ plot, that simultaneously displays non-parametric regressions of multiple traits or environmental variables against community ordination axes.

Many studies of vascular plant communities have used functional traits to test or develop theories on mechanisms controlling community composition (Shipley et al. 2006; Laughlin 2014). While functional traits are well developed and have proven useful for vascular plants (Pérez-Harguindeguy et al. 2013), they are poorly developed for other classes of vegetation, such as lichens, which are ecologically important throughout much of the boreal, arctic and alpine zones. Lichens are symbiotic composites of fungi, algae or cyanobacteria, and provide critical ecosystem functions, such as colonizing primary successional substrates (Cutler 2010), fixing nitrogen (Gunther 1989), contributing to terrestrial vegetation biodiversity and biomass

(Lange et al. 1998) and providing critical winter forage to caribou (Heggberget et al. 1992).

Lichens present unique challenges for trait-based analyses. First, functional traits of both symbionts should be taken into account to understand lichen ecological niches. Second, lichen communities are difficult if not impossible to experimentally recreate, as can be done with vascular plants, wherein functional traits can be measured in response to controlled conditions. Third, functional trait measurements known to be useful for plants, such as specific leaf area (SLA), are scant for lichens. Those traits that have been useful, such as surface area to mass ratio (Larson & Kershaw 1976), water-holding capacity (Gauslaa 2014) or fractal dimension (Stanton & Horn 2013), are not practical to measure for even moderately diverse communities.

Ideal community data sets would have measured all of the important environmental factors and traits. Both sets of variables, however, tend to be selected more out of convenience and wishful thinking than conviction. For example, we often measure ‘easy traits’ rather than ‘hard traits’ that may be more directly relevant to organismal performance (Weiher et al. 1999). Hard traits often require long-term observations or experimental manipulation, while ‘easy’ traits can often be quickly assigned or measured. Measuring hard traits for a large number of species requires a huge investment of effort. An intermediate step towards continuous-scale hard functional trait measurements is to use a range of easy categorical traits for each species, which can then be summed to the community level and analysed using a variety of multivariate methods. Analysis of large community data sets using well chosen categorical traits could also provide guidance in developing continuous functional trait measurements by revealing connections between trait richness and abundance and abiotic and biotic environmental factors. For example, Giordani et al. (2014) used categorical functional traits to show illumination and water drainage were related to differences in lichen photobiont, growth form and reproductive mode. We also take this approach by using one of the largest, detailed landscape-scale lichen community data sets in the subarctic.

Global climate change may threaten lichens in arctic, alpine and boreal ecosystems through increased soil temperatures (Cornelissen et al. 2001), changes in fire regime (Joly et al. 2009) and consequent changes in woody vegetation (Cornelissen et al. 2001). Increasingly large and frequent fires in much of the boreal zone (Kasischke & Turetsky 2006; Beck et al. 2011) are of particular concern because they may reduce lichen cover (Joly et al. 2009), thereby negatively impacting caribou (*Rangifer tarandus*), which eat mostly lichens during the winter (Heggberget et al. 1992). Changing fire regimes and unclear lichen community responses underscore the need for long-term,

landscape-scale studies to detect functional trait shifts in response to disturbance. Our study fills part of this need in the boreal and arctic zones by using the largest, most detailed landscape lichen data set in the region to analyse lichen community responses to fire using functional traits.

We selected the following lichen traits for our analyses: (i) energy and nitrogen source determined by the photobiont (the photosynthetic partner(s) in the symbiosis); (ii) substrate affinity; (iii) growth form (which influences water relations); and (iv) vegetative propagule type, which influences dispersal ability. Lichen photobionts and growth forms vary among forests along climatic (Ellis & Coppins 2006; Giordani et al. 2012), land-use (Stofer et al. 2006; Giordani et al. 2012), water drainage and solar radiation (Giordani et al. 2014) gradients, pointing to the importance and interaction of both photobiont and growth form in determining lichen community structure. Microhabitat preference and frequency of vegetative propagules can also vary among lichen communities (Ellis & Coppins 2006; Rapai et al. 2012; Giordani et al. 2014), indicating substrate specificity and vegetation dispersal mode can explain some community patterns. We analysed these four lichen traits (photobiont, microhabitat, growth form and vegetative propagules) aggregated to communities on 569 plots arrayed over a study area of 1.28 million hectares in subarctic Alaska (Roland et al. 2013), an ecosystem where lichens feature prominently (Nelson et al. 2013).

Our general expectation was that trait–environment associations would point us toward physiological and morphological controls of lichen community structure. We also sought to describe the relationship between lichen community composition and unambiguous categorical traits that have physiological and ecological importance. Our specific goals were to further understand: (1) variation in lichen traits in response to fires of different ages; and (2) lichen trait patterns along multiple ecological gradients. We evaluated the following questions, each given as a testable statement followed by a possible primary mechanism that might produce the suggested pattern:

- 1 Lichens with the smallest vegetative propagules (soredia) will be positively associated with recent fire because having soredia allows lichens to quickly colonize new substrates post-fire.
- 2 Erect, branched fruticose lichens ('reindeer lichens') will be less abundant after recent burns because they disperse through relatively large fragments rather than soredia (small propagules), thereby impeding longer distance dispersal into recently burned areas.
- 3 Lichens with different photobionts (green algae, cyanobacteria or both) will peak in richness and cover in different habitats because green algae and cyanobacteria differ

in photosynthetic tolerances to many environmental gradients, especially light, temperature and moisture regimes. 4 Lichen growth forms will have different richness and cover maxima along environmental gradients related to water absorption, water-holding capacity and desiccation because growth form is a primary factor determining water relations in lichens.

Methods

Study area

We studied the lichen community in Denali National Park and Preserve (hereafter 'Denali'), which encompasses roughly 2.4 million hectares in central Alaska (Fig. 1a; Roland et al. 2013). Our study area included 1.28 million hectares (Fig. 1b) of Denali, located north of the Alaska Range. These mountains bisect Denali along a NE/SW line, north of which is a predominantly continental climatic regime influenced by polar air masses. Between 1971 and 2000, the mean annual precipitation (rain + snow) at Denali headquarters (63°43'19.64" N, 148°57'56.92" W) was 38.1 cm, mostly in the form of summer rain (Shulski & Wendler 2007). Average annual snowfall was 206 cm, with peak snowfall in November and December. The average temperatures in July and January were 12.7 and –16.5 °C, respectively (Sousanes 2008).

At the lowest elevations (ca. 100 m), vegetation in Denali is primarily boreal forests and taiga, giving way to shrublands at middle elevations and alpine tundra, with bare rock and ice at the highest elevations. Lichens are most abundant in alpine tundra, windswept ridges or lowland open conifer forests, but also occur in most habitats, except for dense, broad-leaf forests, alder thickets or extremely unstable rock environments, such as scree or active river terraces. Permafrost is discontinuous in Denali, where it is sporadic in south-exposed terrain and new floodplain deposits, and grading to continuous polygons in lowland basins and north-exposed terrain.

Vegetation data

We collected vegetation measurements and environmental data using a multi-stage systematic grid design based on a 100-m grid with a random starting position (see Roland et al. 2013). Plots were clustered in groups of 25, called mini-grids (Fig. 1c), selected systematically from the 100-m base grid. Spacing among mini-grids was 20 km (Fig. 1c) except in two areas: (1) a 6 km buffer along the park road, and (2) in the Toklat basin ecoregion subsection where mini-grid spacing was intensified to 10 km. Within each mini-grid, plots were positioned at 500-m intervals in each cardinal direction (Fig. 1c). A single plot was a 16-m diameter circle (Fig. 1d). Fewer than 25 plots were

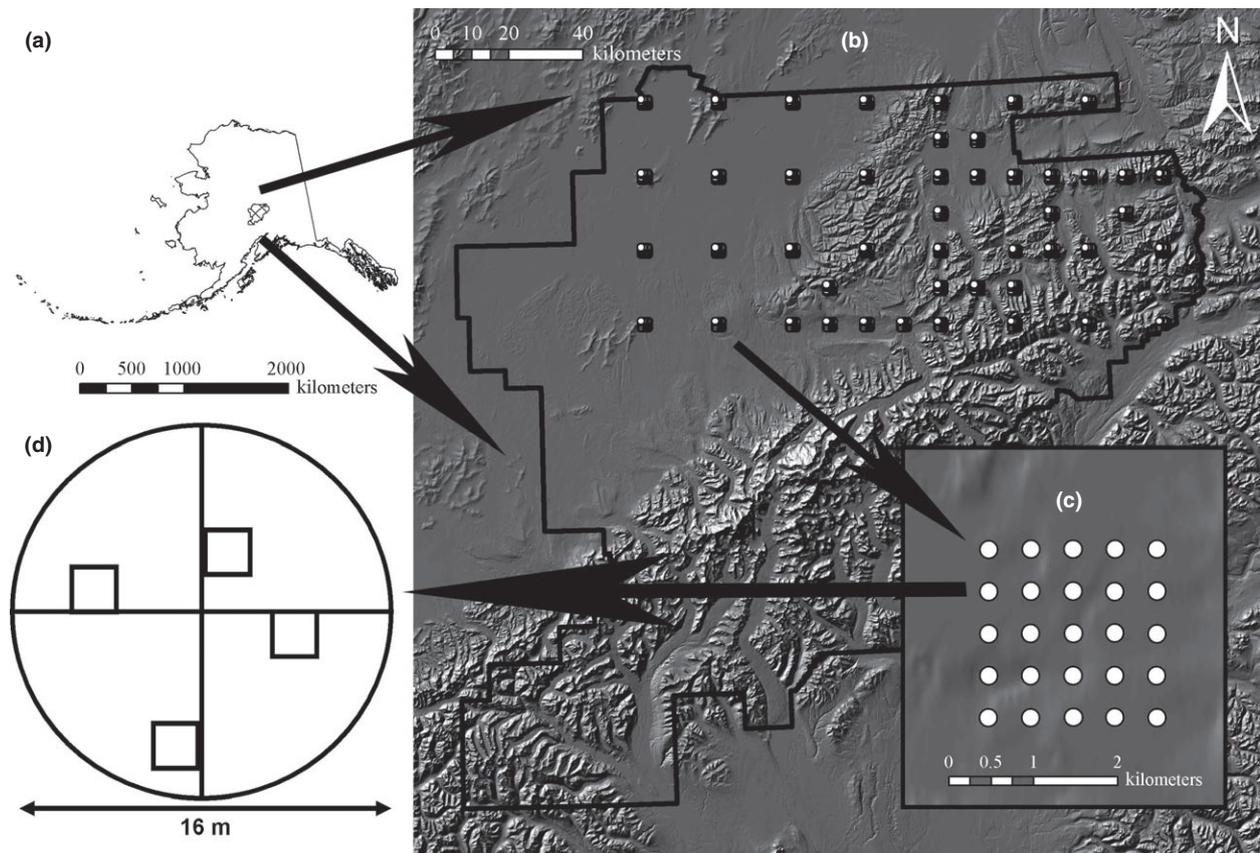


Fig. 1. Hillshade map of Denali National Park and Preserve and sampling design with (a) Alaska showing position of Denali, (b) Denali with mini-grids, (c) a single mini-grid, (d) a plot with two transects and four quadrats.

sampled in some mini-grids due to inaccessibility (e.g. plots located in lakes or on a cliff face). Sampling occurred between 2001 and 2010.

We measured species cover using two methods: (1) point intercept along transects for vascular plants, and (2) ocular estimation of cover in quadrats for lichens and mosses. The point intercept method was used along two perpendicular transects (Fig. 1d), one 16-m long running east to west, and the other segmented into two 6-m long segments oriented north to south with a 2-m gap centred on the middle of the plot. Vascular plant species presence was recorded at each intersection of the transect and an imaginary line extended vertically from the ground to the top of the tree canopy. We read transects in three different horizontal spacing categories (30, 40 or 50 cm) depending on the stature of the vegetation. For plots in forests, 50-cm spacing was used whereas in shrublands, a 40-cm spacing, and alpine tundra, a 30-cm spacing was used. Plant species cover was calculated as the percentage of the transect points where each species was present at any vertical stratum directly above the transect tape (absolute percentage cover). Plant cover was then aggregated by growth forms, including tree, shrub, dwarf shrub, forb, graminoid,

fern, horsetail, lycophyte and moss. Trees were also assigned cover by species and broad-leaved or coniferous categories.

Moss cover was estimated by species to the nearest 1% within in a series of four 1-m² quadrats per plot (Fig. 1d), averaged by species across a plot. To interpret patterns of lichens in response to the moss community, we aggregated moss species cover into growth forms (see Stehn et al. 2010) including: (1) rough mat (small- to medium-sized, horizontally sprawling but rough-textured plants forming mats, often with leaves held stiffly off the stems, e.g. *Brachythecium* sp.); (2) smooth mat (small- to medium-sized, horizontally sprawling but smooth-textured plants forming mats, often with leaves appressed to the stems, e.g. *Hypnum* sp.); (3) short turf (vertically-oriented, small plants forming turfs, e.g. *Bryum* sp.); (4) tall turf (vertically-oriented, medium to tall plants forming turfs, e.g. *Dicranum* sp. or *Sphagnum* sp.); (5) small cushion (small- to medium-sized, cushion-forming plants, e.g. *Orthotrichum* sp.); (6) thread-like (small, filamentous plants, e.g. *Calliergon* sp.); and (7) weft (medium to large plants forming airy horizontal mats, with inter-branch air spaces, e.g. *Hylocomium splendens* and *Pleurozium schreberi*).

Lichen cover, traits and diversity measures

We focused on macrolichens (those with macroscopic features used for identification) growing on the ground (terricoles), rocks (saxicoles) and logs, stumps or very decayed woody material (lignicoles) or epiphytes occasionally found at the base of trees and shrubs. We estimated macrolichen species cover in the same way as mosses. Crustose and leprose lichens (stain, crust, powdery, etc.; growth forms, hereafter referred to as microlichens) and macrolichens on trees or shrubs >0.5 m above ground level were excluded. Microlichens were excluded because they need a voucher for each species at each plot and require intensive microscopic or chemical analyses for identification. Epiphytes were excluded because forests only occur in part of the Denali landscape. We calculated lichen species richness, Shannon and Simpson diversity indices, evenness and total lichen cover for each plot.

We scored four functional traits for each species, which we converted into 19 trait dummy variables including: (1) associated photobiont; (2) mode of vegetative dispersal; (3) growth form; and (4) substrate affinity. Each trait was represented by a binary variable, where membership to a trait group was indicated by a 1 or 0. Each species could only have one state (mutually exclusive) for each trait. Photobiont trait variables included green algae, cyanobacteria or both (tripartite). To classify lichens by vegetative dispersal ability, we used the following categories: lichens with soredia (small, dust-like particles of fungal and algal tissue) or those with isidia/detachable squamules (corticate particles of fungal and algal tissue usually larger than soredia). We assigned species to the following growth forms: foliose (flattened), fruticose (filamentous, stalked or branched) and squamulose (small flattened granules). Within the foliose group, we further differentiated between erect species, such as *Cetraria islandica*, and appressed species (e.g. *Peltigera*). Within the fruticose group, we differentiated between erect forms (very branched, upright thallus, e.g. *Cladonia arbuscula*), simple cladoniiform (small pointed or cupped stalks, e.g. *Cladonia chlorophaea*) and sprawling filamentous (thread-like growing bushy or tufted, e.g. *Bryoria*). The squamulose growth form was not further divided. We assigned each lichen species to one substrate affinity group based on our field experience: epiphytes (growing on trees or shrubs), lignicoles (applied broadly to include species growing on any downed wood or stump), saxicoles (growing on rocks) or terricoles (growing on the ground).

We then aggregated lichen species-level trait data to a plot by trait matrix in two ways. First, we summed the number of species with each trait in each plot, yielding species richness in a matrix of 569 plots \times 19 traits. Each element in this matrix represents the number of species

with a given trait in a given plot. Second, we summed the cover of all species with a given trait for each plot, yielding cover in a matrix of 569 plots \times 19 traits. Each element in this matrix represents the total cover of all species with a given trait in a given plot.

Environmental covariates

We used a set of environmental variables to relate patterns in lichen community structure and trait richness and cover to habitat attributes. Those variables measured at plot centre included plot slope, elevation, latitude and longitude. Variables collected on transects (in the same manner as vegetation cover on transects) included bare ground, down woody debris, litter and water. Quadrat-level measurements were averaged to the plot level and included bare, gravel, litter, rock and woody debris. Average and maximum soil depth were calculated from depth measurements taken by driving a 1.5-m long steel rod into each of the four corners of each quadrat. Quadrat slope was measured with a clinometer. One shallow soil pit (ca. 15-cm deep) was dug at the ends of each of the transects (four pits total/plot) wherein the litter, living mat and organic mat depths were measured. Mineral soil samples (whenever possible) were taken from each pit, aggregated and analysed in the lab for percentage carbon, nitrogen and particulate fractions <2 and \geq 2 mm. Carbon to nitrogen ratio was calculated from these data.

Variables calculated in a GIS included total annual solar radiation, annual summer solar radiation, summer solar radiation broken into three blocks (April–May, June–July, August–September) and average snow-free date. Solar radiation received by each plot was calculated using the Solar Analyst tool (Dubayah & Rich 1995) in ArcGIS 10.0 (Environmental Systems Research Institute 2010), which uses input variables of slope angle, aspect, latitude, sun angles and surrounding topography (Rich et al. 1994) based on a 60-m digital elevation model (DEM) from the National Elevation Dataset (NED). Snow-free dates were calculated using the *Snowmap* algorithm (Hall et al. 2001), resulting in an average Julian date when each 30-m Landsat pixel changed from snow covered to snow-free (Macander & Swingley 2012). Aspect off 180° (absolute value of degrees away from south) was calculated in a database and equivalent latitude (Dingman & Koutz 1974) calculated in R (R Foundation for Statistical Computing, Vienna, AT). A total of 59 environmental variables were used.

Plots used in analysis

Summary statistics of lichen species cover and plot total lichen cover indicated highly variable species totals and plot totals, both of which can strongly influence

community analyses (McCune & Grace 2002). To avoid undue emphasis on nearly empty plots, we removed plots from subsequent analyses with either or both low cover and combinations of a few common species with low cover using hierarchical agglomerative cluster analysis with Euclidean distance and Ward's linkage (McCune & Mefford 2011). Based on the cluster dendrogram, we deleted 290 plots that grouped together on a single long arm of a very short branch with 96% information remaining. Deleted plots were primarily steep scree slopes, barren river bars, deep shrub thickets, wetlands/aquatic environments or very dense deciduous forests, all of which had very low lichen cover and no unique lichen communities. We used the remaining matrix of 569 plots by 160 lichen species to calculate measures of overall and trait diversity and cover.

A previous study of arctic lichen communities found an overwhelming signal of rockiness when they included saxicolous lichens in their analyses (Holt et al. 2007). Because we wished to see beyond whether or not a plot was rocky, we further limited the species matrix to include only terricolous lichens. Rare species also add noise to analyses of community structure (McCune & Grace 2002), so after calculating diversity statistics, we deleted those species occurring on fewer than 5% of plots, leaving a matrix of 569 plots \times 54 species. We then used a generalized \log_{10} transformation ($b = \log(x + x_{\min}) - \log(x_{\min})$), where x_{\min} is the smallest positive value in the data set (McCune & Mefford 2011) of species cover to reduce the influence of occasional large values and to enhance the signal from minor species.

Fire data set

To analyse variation in lichen community structure in response to differently aged fires, we randomly resampled the full pool of plots ($n = 569$) stratified by burn category, including unburned (no fire in the last 100 yrs, $n = 20$), recent burns (fire since 1982, $n = 12$) and old burns (fires between 1901–1982, $n = 20$). Old burns were determined by reviewing direct evidence of fire, such as burned logs, charcoal in the soil, etc. (Roland et al. 2013). This strategy emphasizes the signal from time since burn at the cost of reducing the sample size. Although resampling was random, we prioritized unburned plots close to old and recent burned plots, so as to minimize confounding with other habitat factors that are correlated with probability of burning. As almost all fires in Denali occurred in forests, we only used unburned plots classified as 'Forest' (Viereck et al. 1992) to avoid comparison of unburned shrublands and tundra. We again only used lichens classified as 'terricoles' in the fire analysis to minimize the influence of strictly epiphytic or lignicolous species.

Analyses

We used non-metric multidimensional scaling (Kruskal 1964) (NMS) in PC-ORD to analyse lichen community structure with both the full ($n = 569$ plots) and fire ($n = 52$ plots) data set. We used the 'slow and thorough' NMS autopilot setting, Sørensen distance and no penalty for ties in the distance matrix (Kruskal's strategy 1). We used the built-in randomization test to evaluate whether the final stress was lower than expected by chance. To interpret environmental and trait relationships with the ordination, we overlaid the second matrix of environmental variables and traits and calculated the linear correlations between them and the ordination axes. We generalized \log_{10} transformed some environmental variables or traits whose correlations with NMS axes improved r^2 by at least 0.05 after transformation.

Some second matrix variables had non-linear relationships with NMS axes or had moderately strong relationships with more than one axis. A linear correlation between these variables and NMS axes would therefore be a misrepresentation. For these situations, we used non-parametric multiplicative regression (NPMR; McCune 2006) in HyperNiche (McCune & Mefford 2009) to describe non-linear relationships of variables with the ordination axes. NPMR can recover non-linear response surfaces and automatically represents interactions among predictors (NMS axes in this case) using multiplicative weights with a kernel smoother. We used NPMR with a Gaussian kernel and forward step-wise variable selection that simultaneously optimizes the smoothing parameters (tolerances) for both NMS axes included as predictors in the model. NPMR also controls over-fitting with leave-one-out cross-validation during model selection and calculates fit using cross-validated R^2 (xR^2) so that splitting into training/validation data sets is automatically built into model development. We used the 'medium' over-fitting settings and 3% allowable missing estimates and regressed each environmental and trait variable against each NMS axis separately and all possible combinations of two axis models (e.g. axes 1 & 3, 1 & 2 and 2 & 3). We only retained NPMR models if the xR^2 improved r^2 by at least 0.05 above linear correlation, and only used two-axis models if the xR^2 improved the model fit by at least 0.05 above a one-axis NPMR model. For those variables where the NPMR models were used, we graphed the fitted response surface against the NMS axes. For two-predictor response surfaces, we overlaid contours on the ordination, in each case dividing the range of estimated response into ten contours for comparability between surfaces. To overlay multiple non-linear responses at once on the ordination, we introduce a new overlay method, the 'hilltop plot'. For each overlay

variable, we traced the second-highest contour (Fig. 2a), then superimposing them on one ordination. The resulting diagram shows the maxima of many non-linear overlay variables (in our case traits and environmental variables) in a single figure (Fig. 2a,b,d).

We tested whether the fit of linear and non-linear overlays was no better than expected by chance alone using a randomization test. The probability of Type I error was calculated by refitting linear and non-linear overlays 100 times after randomizing the rows of the NMS ordination

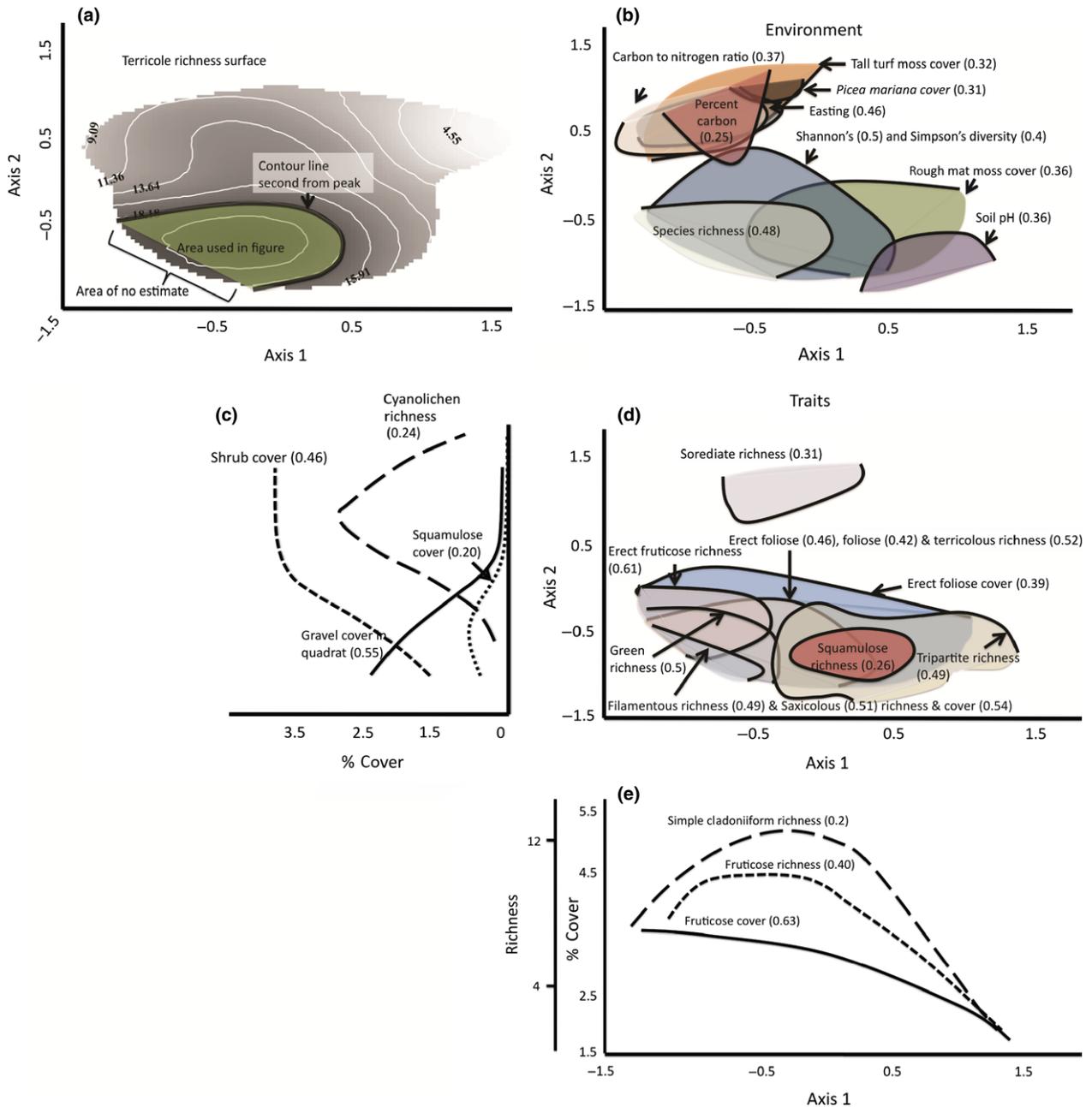


Fig. 2. NPMR of environmental variables and traits overlaid on NMS ordination axes 1 and 2. (a) Example response surface of a variable (terricole diversity) regressed against NMS axes, illustrating 'hilltop plot' method of simplifying a response surface to allow plotting multiple variables in one diagram (b, d). Bold line in (a) indicates contour (second from peak) at which all response surfaces were sliced for display. Bracket indicates area where model was not able to make an estimate, corresponding to a break in the bold line. (b) Hilltop plot of environmental variables overlaid on the NMS ordination. (c) Variables with non-linear relationships to axis 2 alone. (d) Hilltop plot of traits overlaid on the NMS ordination. (e) Variables with non-linear relationships to Axis 1 alone. Only variables with models including axis 1, 2 or both and $xR^2 \geq 0.2$ are shown. Numbers next to variables indicate xR^2 .

axes. The resulting P -value is the proportion of overlays fit to randomized data with the same number of NMS axes as predictors that had as good or better fits than with the non-randomized data.

Our sampling design likely includes spatial autocorrelation (Roland et al. 2013) because plots within a mini-grid may be more similar simply because they are closer to each other. However, there is no adequate way to disentangle spatial autocorrelation and community structure data without losing ecologically relevant data. We tested the amount of spatial autocorrelation left after ordinating plots in lichen species space by using a partial Mantel test, which measures the correlation between two matrices while controlling for linear relationships with a third matrix. We used the full species matrix as the main matrix, the UTM coordinates of each plot as the second (geographic) matrix and the NMS axes for each plot as the control matrix. We used Sørensen distance for the main matrix and Euclidean distance for UTMs and ordination scores. The standardized Mantel statistic ($-1 \leq r \leq 1$) after controlling for the NMS axes indicates how much spatial autocorrelation remains after accounting for the ordination structure.

We tested whether lichen communities differed between burn categories using multiple response permutation procedure (Mielke & Berry 2007; MRPP), Sørensen distance and the same matrix used for the NMS. MRPP produces an effect size of the difference between groups, the A statistic, which is equal to 1 if the members of each group are exactly the same. We also assessed differences between burn categories and lichen community traits using one-way ANOVA in R. Variables with differences of $P \leq 0.05$ between fire categories were plotted with boxplots in the ggplot2 package.

Results

The ordination of the full set of plots with terricolous lichen species (569 plots with 54 lichen species) yielded a stable three-dimensional solution (final stress = 16.7; randomization test, $P = 0.004$). All linear and non-linear overlays with $r^2 > 0.2$ had better fit than expected by chance, beating the randomization test ($P \leq 0.01$). Axis 1 represented almost a third of the community variation ($r^2 = 0.31$) and was most strongly related to an environmental gradient from acidic soils and lower total moss cover to more basic soils and higher rough mat moss cover (Fig. 2b, Table 2). Acidic soils and low total moss cover were associated with high lichen cover and species richness dominated by terricolous, green algal, fruticose (including filamentous and erect branched) and foliose species (mostly erect foliose) lichens. More basic soils and rough mat moss cover were associated with low lichen

cover but higher tripartite, appressed foliose species richness (Fig. 2b,d,e, Table 2).

Axis 2 ($r^2 = 0.27$) represented an environmental gradient from rocky and gravelly, steep, high-elevation plots with late-lying snow beds and short turf mosses to low elevation, forested plots with deep, weft moss mats and organic mats with earlier snow melt. Lichen traits and diversity measures related to axis 2 changed from species-rich and diverse saxicolous and terricolous communities at the rocky end to less diverse communities with more lignicolous, epiphytic and sorediate lichen species at the low-elevation forested end (Fig. 2b,c,d, Table 2).

Axis 3 ($r^2 = 0.18$, not shown in figures or tables) only represented a weak summer solar radiation gradient and separated plots with *Peltigera aphthosa* ($r^2 = 0.17$) in one direction and *Peltigera leucophlebia* ($r^2 = 0.67$) in the other. Since axis 3 explained the least of the variation and no environmental variables had strong correlations with it, we discuss it no further.

Without controlling for the NMS axes, there was some correlation between UTMs and the species matrix ($r = 0.18$). However, a partial Mantel test indicated almost no spatial autocorrelation remaining between the species matrix and UTMs ($r = 0.01$, $P = 0.03$), after controlling for the NMS axes. Thus most of the spatial autocorrelation in the species data was related to the environmental gradients described above.

Influence of fire

The NMS of the fire data set (52 plots with 40 terricolous lichens) yielded a three-dimensional solution (final stress = 13.1, stability <0.00001, randomization test, $P = 0.004$; Fig. 3). Similar to the full ordination, though reversed in direction, axis 1 ($r^2 = 0.42$) represented a gradient from lichen communities with higher tripartite lichen cover but overall low lichen species richness to more speciose lichen communities with more fruticose, green algal, appressed foliose and terricolous lichen species and cover (Fig. 4a,b,c). Axis 2 ($r^2 = 0.27$) represented lower-elevation, generally mossy plots with moderate lichen species richness that had not recently burned, grading into more recent burns with increased litter, downed wood and weft mosses where sorediate and simple cladoniiform lichen richness and cover increased. Soil pH, deciduous tree cover (especially *Populus tremuloides*) and woody debris within quadrats exhibited similar, double-humped shapes with respect to axis 2 (Fig. 4a,b). Similar to the full ordination, axis 3 ($r^2 = 0.16$, not shown in figure) represented a weak solar radiation gradient. Axis 3 explained the least of the variation and no environmental variables had strong

correlations with it, therefore we do not discuss it further.

Lichen communities differed between fire categories as a whole (MRPP, $A = 0.08$, $P < 0.0001$) but pair-wise com-

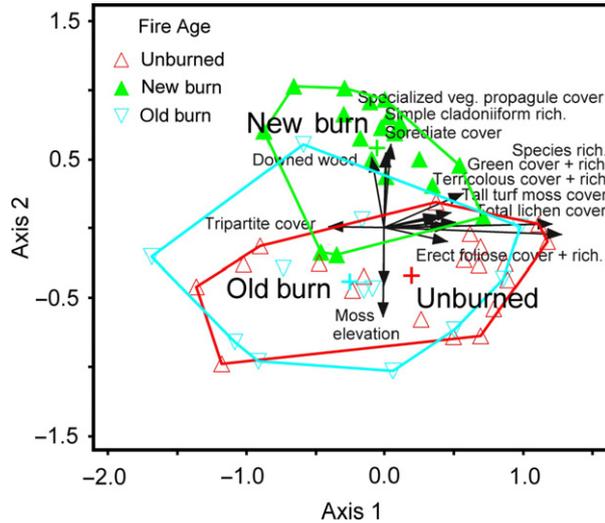


Fig. 3. NMS joint plot of fire terricole data set ($n = 52$ plots) with overlays of linearly related environmental variables and traits pointing in the direction of increasing values for each variable. Symbol coding, perimeters and centroids label plots from each fire age and their boundaries and geometric centres. Abbreviations include ‘rich.’ = richness and ‘+’ = and.

parisons between fire categories indicated unburned and old burns did not differ significantly ($A = 0.004$, $P = 0.26$), while recent burns differed from both old burns and unburned plots. Erect foliose richness and cover was lower in burns than unburned areas (Fig. 5a,b), while fruticose richness was highest in the recent burns but fruticose cover was highest in unburned areas (Fig. 5c,d). Lignicolous lichens, simple cladoniiform and sorediate lichen richness and cover were all highest in recent burns (Fig. 5e,f, h,i,j). Cyanolichen richness was also highest in recent burns (Fig. 5k). Green algal cover was much higher in unburned areas and lowest in old burns (Fig. 5l). Erect branched cover was highest in unburned areas and lowest in both old and recent burns (Fig. 5m). Shannon’s diversity was highest in recent burns (Fig. 5n).

Linear vs non-linear community–trait–environment relationships

Of the 64 environmental variables and 46 trait measures investigated (Appendix S1), only 26 had strong linear correlations with the ordination axes that were better than one or two-dimensional non-linear regressions (Table 2). Non-linear regression improved the relationship between the ordination axes and 17 environmental variables or traits. Of these, 13 environmental variables had strong two-dimensional, non-linear relationships with the ordi-

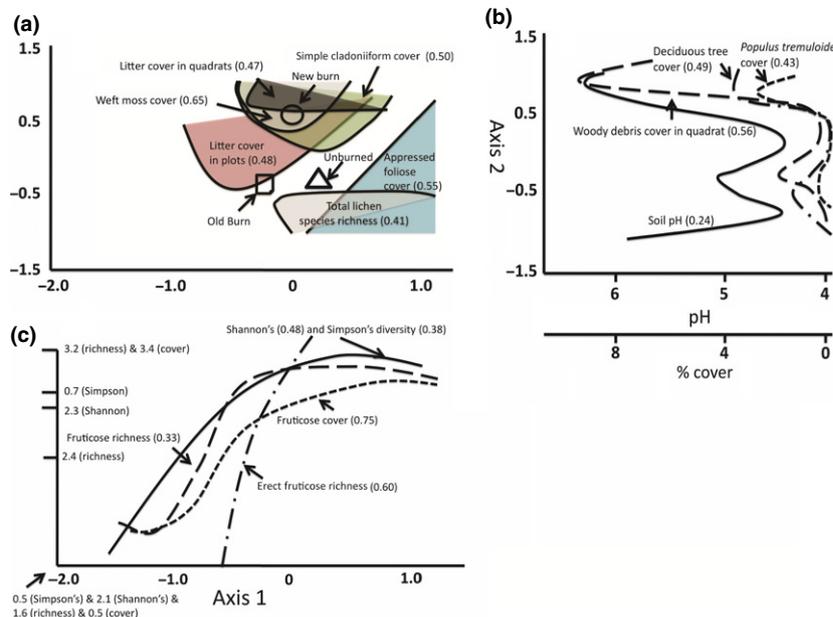


Fig. 4. NPMR of environmental variables and traits overlaid on NMS axes 1 and 2 from ordination of the fire data set. (a) Response surfaces of environmental and trait variables with different shapes marking centroids for each age of fire. (b) Variables with non-linear relationships to axis 2 alone, with x-axis labelled with pH (upper) and percentage (%) cover (lower) ticks. (c) Variables with non-linear relationships to axis 1 alone, with y-axis ticks labelled with values for richness, percentage cover and Simpson and Shannon’s diversity. Only variables with models including axis 1, 2 or both and $xR^2 \geq 0.2$ are shown. Numbers next to variables indicate xR^2 . See Fig. 2a for example response surface of variable regressed against NMS axes.

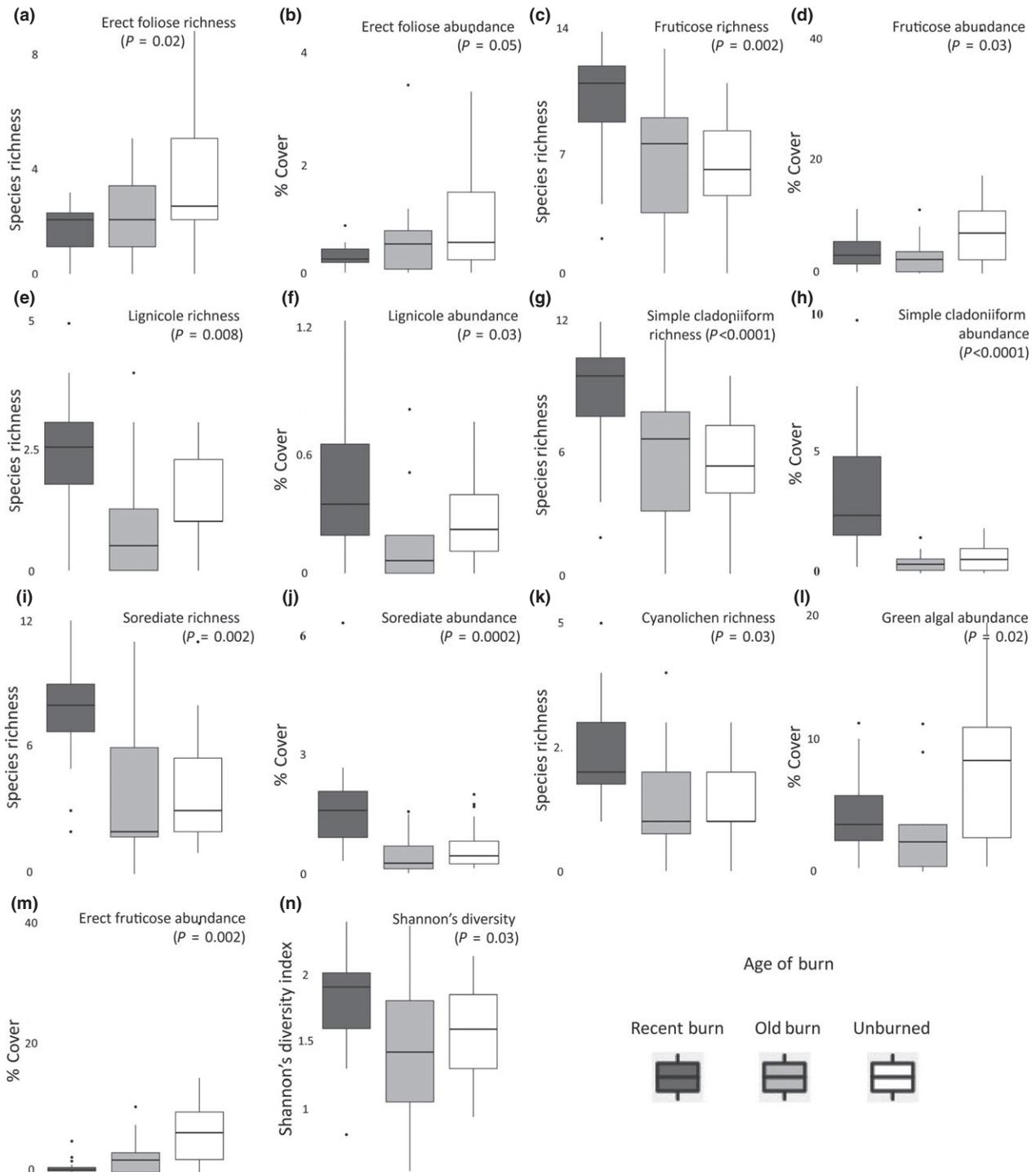


Fig. 5. Boxplots of trait richness and abundance and community diversity measures that differed ($P \leq 0.05$) between fires of different ages in chronological order (left to right; recent burn, old burn and unburned), labelled by variable and P -value from one-way ANOVA. Boxes show the 1st and 3rd interquartile ranges. Whiskers extend to $1.5 \times$ interquartile range.

nation axes (Fig. 2b,c) and four had one-dimensional, non-linear relationships with the ordination (Fig. 2c,e). Five traits and seven environmental variables had weak to no linear relationship with either axis, but had strong one-

dimensional or two-dimensional, non-linear relationships with the ordination. Two-dimensional, non-linear surfaces improved the r^2 over a single dimensional, linear correlation by between 0.08 and 0.32. Single dimensional,

non-linear surfaces made an improvement in r^2 over a linear correlation by between 0.05 and 0.16.

Discussion

Functional groups of terricolous lichens peaked in species richness and cover maxima in different parts of environmental and fire-age gradients. These maxima can be interpreted by differences in specific physiological processes likely to occur in different portions of the landscape. We interpreted the driving processes of community composition to be water relations, photosynthetic recovery and dispersal. Fire acted as an environmental filter favouring lichens with higher vegetative dispersal capacity and specificity to grow on wood, but excluded the 'reindeer' lichens, possibly due to their dispersal limitation.

Our unconstrained approach to the fourth-corner problem allowed us to see patterns in traits that were not related to trait–environment relationships. For example, species richness and cover of many functional traits were related to the dominant gradient of community composition (axis 1 in Fig. 2, Table 2). However, none of the environmental variables were strongly linearly related to that dominant gradient (Table 2). We found many traits and environmental variables linearly correlated with the community gradient on axis 2. Linear correlations with the axis 2 allowed straightforward interpretation of some traits associated with the environment, namely that forests host more epiphytic and lignicolous lichens.

Given that our community data will often carry interesting and informative patterns beyond the measured traits and environmental variables, we should use methods of community analysis that detect those patterns. Constrained ordination to solve the fourth-corner problem may be useful for appraising a given set of environmental variables and traits, but this provides an incomplete picture of community variation. As an alternative, unconstrained ordination of the community, followed by overlays from the sample unit \times environment matrix and the sample unit \times trait matrix does not sacrifice any of the community signal.

Hilltop plots successfully detected many non-linear and/or two-dimensional relationships between community composition and traits or environmental variables. Many traits and environmental variables had weak linear relationships to only one axis. For example, cyanolichen and simple cladoniiform lichen richness had strongly unimodal relationships to axes 1 and 2, respectively. By using non-linear regression of ordination axes against traits and environmental variables, these and other patterns emerged that would have been overlooked using normal linear biplot vectors. Also, some traits and environmental variables had weak or moderate correlations with both axis 1 and 2

but relatively strong relationships with the community if both axes were used together. Hilltop plots using two axes revealed many traits and environmental variables had strongly non-linear two-dimensional (Fig. 2b,d) relationships with the community. In fact, the relationship between the community composition and almost half of the traits and environmental variables had at least an improvement of $r^2 = 0.05$ if hilltop plots were used instead of linear biplot vectors.

Fire age

Fire frequency and burn area have increased across the North American boreal zone, particularly in Alaska (Kasischke & Turetsky 2006; Beck et al. 2011). Fire has been shown to decrease cover of some lichens important to winter caribou (Holt et al. 2008; Jandt et al. 2008; Joly et al. 2009). It is therefore important to better understand lichen community responses to fire, particularly through traits, which aid in understanding functional rather than species-specific responses. We found sorediate lichen richness peaked in areas with recent fires, which supports our first hypothesis. Presumably, this is because species with these smaller, more mobile dispersal propagules are able to colonize disturbances (such as burned areas) more quickly than sexually reproducing species that would have to locate a photobiont and at longer distances than species with larger asexual diaspores.

Many of the common sorediate lichens in recently burned areas were both simple cladoniiform and lignicolous (Fig. 5g,h), such as *Cladonia cenotea* (Table 1). Fire creates more abundant downed woody substrate for lignicolous species, but interpretation of the positive association of the simple cladoniiform lichens with recent fire is less clear. Simple cladoniiform lichens have a lower surface area to mass ratio compared to the majority of erect branched *Cladonia* and most possess a cortex which is lacking in most 'reindeer' lichens. We interpret these traits as adaptations to maintain hydration in the more open, dry post-fire habitat so they could continue photosynthesizing longer in comparison to erect branched *Cladonia*.

Competition no doubt also played some role in structuring the lichen community, especially as vascular plants re-established after fire, which could account for the decrease in the simple cladoniiform species in old burns and unburned areas. However, we did not attempt to measure competition beyond looking for negative associations between lichens and vascular plants and mosses. Outside the fire analysis, we saw the general trend of lichens occurring in rocky areas where vascular plants and mosses are less abundant. Smaller-scale competitive effects were likely occurring at a finer grain (e.g. sub-meter scale) than our

Table 1. Species list of the 54 more frequent terricolous lichens sorted by descending frequency on the 569 plots used in ordination, with summary statistics including frequency (Freq.), mean/max/total percentage cover, and growth form and photobiont traits.

Species	Freq.	Total Cover	Max Cover	Mean Cover	Growth Form	Photobiont
<i>Cladonia gracilis</i>	0.74	170.1	16	0.3	Fruticose	Green
<i>Cladonia rangiferina</i>	0.61	477.5	19.5	0.84	Fruticose	Green
<i>Cladonia amaurocraea</i>	0.61	274.5	10.25	0.48	Fruticose	Green
<i>Cladonia arbuscula</i>	0.6	696.5	30.25	1.22	Fruticose	Green
<i>Cetraria cucullata</i>	0.6	142.7	3	0.25	Foliose	Green
<i>Peltigera aphthosa</i>	0.53	475.3	18.75	0.84	Foliose	Tripart
<i>Cetraria islandica</i>	0.48	84.75	2.25	0.15	Foliose	Green
<i>Cladonia chlorophaea*</i>	0.46	34.19	0.75	0.06	Fruticose	Green
<i>Cetraria laevigata</i>	0.45	75.38	6.56	0.13	Foliose	Green
<i>Cladina stygia</i>	0.41	402.4	17.5	0.71	Fruticose	Green
<i>Peltigera leucophlebia</i>	0.37	275	10	0.48	Foliose	Tripart
<i>Cladonia cornuta*</i>	0.36	33.62	1.12	0.06	Fruticose	Green
<i>Peltigera scabrosa</i>	0.34	136.1	4.31	0.24	Foliose	Cyano
<i>Peltigera malacea</i>	0.34	102.5	6	0.18	Foliose	Cyano
<i>Thamnolia vermicularis</i>	0.33	37.06	1.38	0.06	Fruticose	Green
<i>Lobaria linita</i>	0.26	187.8	21	0.33	Foliose	Tripart
<i>Cladonia uncialis</i>	0.25	81.75	11.25	0.14	Fruticose	Green
<i>Cladonia scabriuscula*</i>	0.25	18.12	2.06	0.03	Fruticose	Green
<i>Dactylina arctica</i>	0.24	35	2.5	0.06	Fruticose	Green
<i>Cladonia cyanipes*</i>	0.23	14.81	0.56	0.03	Fruticose	Green
<i>Cladonia pyxidata</i>	0.23	21.31	1.06	0.04	Fruticose	Green
<i>Nephroma expallidum</i>	0.21	42.75	3.25	0.08	Foliose	Tripart
<i>Peltigera didactyla*</i>	0.2	19.75	1.31	0.04	Foliose	Cyano
<i>Stereocaulon paschale</i>	0.2	237.3	25	0.42	Fruticose	Tripart
<i>Cetraria nivalis</i>	0.19	46.19	11.56	0.08	Foliose	Green
<i>Cladonia cenotea*</i>	0.19	11.94	0.56	0.02	Fruticose	Green
<i>Cladonia crispata</i>	0.18	14.94	1.38	0.03	Fruticose	Green
<i>Cladonia borealis</i>	0.18	15.12	1.06	0.03	Fruticose	Green
<i>Cladonia deformis*</i>	0.18	12.94	0.81	0.02	Fruticose	Green
<i>Cladonia stellaris</i>	0.17	188.4	35.25	0.33	Fruticose	Green
<i>Nephroma arcticum</i>	0.16	155.8	18	0.27	Foliose	Tripart
<i>Peltigera rufescens</i>	0.15	49.25	4.75	0.09	Foliose	Cyano
<i>Masonhalea richardsonii</i>	0.15	15.12	0.81	0.03	Foliose	Green
<i>Stereocaulon tomentosum</i>	0.14	66.19	11	0.12	Fruticose	Tripart
<i>Peltigera canina</i>	0.12	52.62	7.75	0.09	Foliose	Cyano
<i>Psoroma hypnorum</i>	0.1	7.69	0.62	0.01	Squam.	Tripart
<i>Alectoria ochroleuca</i>	0.1	23.94	9.56	0.04	Fruticose	Green
<i>Peltigera polydactylon</i>	0.1	23.62	2	0.04	Foliose	Cyano
<i>Hypogymnia austerodes*</i>	0.1	6.56	0.44	0.01	Foliose	Green
<i>Peltigera neopolydactyla</i>	0.09	28.25	5.5	0.05	Foliose	Cyano
<i>Cetraria aculeata</i>	0.08	6.56	0.81	0.01	Foliose	Green
<i>Bryocaulon divergens</i>	0.08	18.38	4.75	0.03	Fruticose	Green
<i>Cladonia phyllophora</i>	0.08	7.38	1.56	0.01	Fruticose	Green
<i>Cladonia squamosa #</i>	0.08	4.12	0.25	0.01	Fruticose	Green
<i>Cladonia coniocraea*</i>	0.07	4.75	0.56	0.01	Fruticose	Green
<i>Peltigera praetextata #</i>	0.07	10.69	3	0.02	Foliose	Cyano
<i>Parmelia omphalodes</i>	0.07	13.94	3	0.02	Foliose	Green
<i>Hypogymnia physodes*</i>	0.07	5.12	0.25	0.01	Foliose	Green
<i>Dactylina ramulosa</i>	0.06	5.5	0.88	0.01	Fruticose	Green
<i>Peltigera lepidophora #</i>	0.06	6.44	1.25	0.01	Foliose	Cyano
<i>Pannaria pezizoides</i>	0.06	3.75	0.5	0.01	Fruticose	Cyano
<i>Cladonia pleurota*</i>	0.06	3.88	0.88	0.01	Fruticose	Green
<i>Physconia muscigena</i>	0.05	3.31	0.44	0.01	Foliose	Green
<i>Cetraria ericetorum</i>	0.05	5.75	0.81	0.01	Foliose	Green

*, sorediate; #, isidiate; Tripart, Tripartite; Cyano, Cyanolichens; Squam., Squamulose.

lichen community data were collected and are therefore not discussed here.

Our hypothesis that 'reindeer' lichens would be less abundant after fire was supported by our finding that in both old and recent burns, these lichens had much lower cover compared to unburned areas (Fig. 5m). Previous studies showed the very branched growth form (high surface area to mass ratio) of these lichens makes them prone to rapid desiccation, which they mitigate by growing in dense mats (Larson & Kershaw 1976; Larson 1981). We suspect habitat changes caused by fire, such as increased solar radiation or physical damage to the continuous lichen mat, may account for the diminished erect branched lichen cover post-fire. Dispersal limitation may also play a role as all species of the erect branched growth form in Denali lack vegetative reproductive propagules, although thallus fragmentation can result in dispersal. However, thallus fragmentation appears an effective dispersal strategy only for shorter distances (Heinken 1999), which may in part explain the slow colonization of recent fires by erect branched 'reindeer' lichens. Our results support that the long regeneration times published elsewhere (Coxson & Marsh 2001; Jandt et al. 2008) hold true in Denali, as the old fires in our study still had lower erect branched lichen cover than unburned plots (Fig. 5m).

Variation in other environmental factors between study areas, such as average monthly temperature, may explain why others have found more rapid recovery of lichen species richness after fire (Holt et al. 2008). For example, small variations in winter temperatures can change the probability of lichen occurrence (Glavich et al. 2005). Holt et al. (2008) reported a peak in lichen species richness 20 yrs after burns in Bering Land Bridge National Preserve, Alaska, which has a maritime climate that may account for the faster recovery in lichen communities there. Fire intensity may be another reason for differences between regeneration times, although this has yet to be investigated.

Shannon diversity increased after recent fires since fruticose, lignicolous, simple cladoniiform and cyanolichen richness all increased (Fig. 5c,e,g,k). We interpret this increase in Shannon diversity as the result of fires creating a heterogeneous habitat of many types of new, unoccupied surfaces for lichens to colonize, including rock, soil and wood. Some species, such as *Cladonia botrytes* are thought to be transient and adapted to fire (Yahr et al. 2013) so perhaps other species are also.

The interaction between vegetative dispersal, photobiont and growth form traits created an unexpected outcome of increased cyanolichen richness in recently burned plots, although others have also seen higher cyanobacterial lichen richness in some exposed habitats (Giordani et al. 2014). A cyanobiont allows a lichen to fix its own nitrogen,

which would be an advantage because most of the soil nitrogen volatilizes after fire (Raison et al. 1985). However, this deviates from the general tendency of cyanolichens to be more abundant in areas of stable humidity and temperature (Marini et al. 2011), where the liquid water required for cyanolichen photosynthesis is more available. Forests after burns are usually quite open and thereby receive more sunlight. We would expect this would impede cyanolichens in maintaining sufficient hydration for photosynthesis. However, desiccation tolerance may not always be lower for all cyanobacterial lichens in comparison to green algal lichens (Gauslaa & Solhaug 1996), and water-holding capacity is generally higher for cyanolichens than green algal species (Gauslaa & Coxson 2011). Indeed, further examination of species-specific responses to fire age showed several cyanobacterial *Peltigera* species were more abundant after fire, especially *Peltigera didactyla* (Table 2), which commonly colonizes mineral soil. *P. didactyla* may survive in the open, dry post-fire environment by reducing desiccation via its appressed foliose growth form, which would minimize surface area relative to fruticose growth forms. It also has soredia, giving it better mobility to colonize new substrates after fire. This

Table 2. Environmental or trait variables with squared correlation coefficients (r^2) and direction of correlation ('+' = positive, '-' = negative) with NMS axes from full terricole data set (569 plots by 54 species). Blank cells indicate $r^2 < 0.2$ between variables and NMS axis.

Environmental or Trait Variable	Axis 1	Axis 2
Appressed Cover	+0.21	
Conifer Cover		+0.22
Elevation		-0.65
Epiphyte Cover		+0.25
Epiphyte Richness		+0.24
Erect Branched Cover	-0.6	
Green algal Cover	-0.63	
Soil Particles <2 mm		+0.41
Total Lichen Cover	-0.22	
Lignicole Cover		+0.26
Lignicole Richness		+0.25
Living mat Thickness		+0.21
Mineral Cover		-0.51
Soil Particles >2 mm		-0.41
Total Moss Cover		+0.36
Organic Mat Depth		+0.38
Quadrat Bare Cover		-0.25
Quadrat Rock Cover		-0.51
Quadrat Slope		-0.32
Plot Slope		-0.34
Small Cushion Moss Cover		-0.36
Average Snow-free Date		-0.31
Sorediate Cover		+0.22
Tree Cover		+0.31
Tripartite Cover	+0.21	
Weft moss Cover		+0.33

demonstrates the importance of considering multiple traits, as photobiont, growth form and dispersal traits interacted to produce a counterintuitive community pattern if photobiont was considered alone.

Photobionts

Modes of energy generation (lichen photobionts) strongly varied along environmental gradients within our terricolous community data set, pointing to the importance that energy production plays in explaining community composition. Specifically, our results support the hypothesis that cyanobacterial, tripartite and green algal lichens have different ecological maxima. We expected this because photobionts impose different physiological constraints while also imparting different advantages to the lichen symbiosis. Others have found ecological separation of the same photobiont categories along a daily solar radiation gradient (Giordani et al. 2014), although our coarser bimonthly solar radiation measures showed no such trend. Nonetheless, we did see green algal lichen cover and species richness peak in high-elevation, rocky areas with deeper snow, perhaps attributable to the ability of green algae to photosynthesize without liquid water (e.g. snow or mist) in contrast to cyanolichens (Lange et al. 1986) and their ability to quickly restart photosynthesis upon rewetting (Groulx & Lechowicz 1987). Surface area also likely plays a role in favouring green algal lichens in snowy areas, as all sprawling filamentous species (e.g. species with high surface area to mass ratio) in Denali possess green algae which would allow them to quickly rehydrate (Larson 1981) (see 'Growth form' discussion).

Cyanobacterial lichen cover peaked at middle elevations where shrub cover was high. Shrubs provide canopy cover and shading, which would keep humidity higher for cyanolichens living on the ground or on the shrub bases. Moderate shading can benefit cyanolichens, but dark, closed shrub thickets have few cyanolichens in Denali. Indeed, cyanolichen richness increases with shrub cover and then drops off as shrub cover plateaus. The physical structure of shrubs may deliver liquid water to cyanolichens via throughfall and stemflow. It is also possible that shrubs, many of which are in the Salicaceae, chemically enhance cyanolichens with sugar-rich leaf exudate (Campbell et al. 2013), an alternative carbon source that might offset the lichen's need to photosynthesize. However, scatterplots between cyanolichen and *Salix* species cover show no strong relationship, at least when all plots are included in the comparison. Several *Salix* species are low-growing, alpine species (e.g. *Salix arctica* or *S. reticulata*), which would likely not contribute leaf exudates for cyanolichens.

Tripartite lichen species richness and cover peaked where appressed foliose growth form, rough mat mosses

and soil pH also peaked, reflecting the tendency of *Peltigera* and *Nephroma* species to grow over the top of common xeric to mesic rough mat mosses (most frequently *Abietinella abietina* and *Rhytidium rugosum*). Tripartite lichens may have an advantage over lichens with only cyanobacteria or green algae in that situation, since they produce their own nitrogen in the nutrient-poor moss surface. Tripartite lichens may also be favoured by their primary photosynthetic partner, a green alga, which can utilize more forms of precipitation (e.g. dew and mist; Lange et al. 1986) than cyanobacteria. For these reasons, the tripartite lichens may be the optimal solution for both nutrition and photosynthesis in the nutrient-poor but open moss mat environment.

Growth form

Different lichen growth forms represent varying adaptations to solving the problems of water relations while balancing other constraints such as maximizing photosynthetic area (Larson & Kershaw 1976; Lange et al. 1986). As we hypothesized, lichen growth forms had different richness maxima in relation to environmental gradients. Our results show ecological separation of some growth forms (erect foliose, appressed foliose and cladoniiform form), whereas many growth forms overlap where lichen species richness peaks. We see the overlap of the species richness of many growth forms as affirmation of the long-standing assertion that most lichens specialize in harsh, drier or rockier environments (Grime 1977), while the former indicates nuanced ecological differences between growth forms along water gradients.

Fruticose, erect branched and sprawling filamentous lichen richness all peaked in high elevation, rocky and gravelly areas where snow persists longer. Fruticose lichens have a high surface area to mass ratio (Larson & Kershaw 1976) and can rehydrate quickly relative to other growth forms (Larson 1981); perhaps as an adaptation to take advantage of moisture sources more frequent at high elevations, such as light, ephemeral snow or dew. Since all fruticose species in Denali contain green algae, which do not require liquid water to photosynthesize, as do cyanolichens (Lange et al. 1986), green algal fruticose species may be an ideal combination of hydration and energy traits for frequent wetting/drying cycles at higher elevations.

In contrast to fruticose lichens, peak foliose lichen richness and cover occupied a broader swathe of environmental space (Fig. 2d). Appressed foliose cover peaked at the extreme right side of axis 1 (Table 2), opposite to most lichen growth forms. These foliose lichens may compete better with mosses that often dominate that ecological space (Fig. 2b,d). We suspect the surface area to mass of

foliose lichens to be generally lower than that of fruticose species, which would confer the ability to maintain optimal moisture levels and thereby tolerate more variable conditions, although there is significant inter- and intra-specific variation of both surface area and mass (Larson & Kershaw 1976). Foliose lichens may also maintain higher water content by growing more embedded in the boundary layer compared to most fruticose lichens, thereby trapping moisture between thallus and substrate. The disadvantage to this growth form may be slower moisture absorption (Larson 1981) and therefore a lower capacity to take advantage of wetting/drying cycles than the more absorbent (high surface area to mass) fruticose species. The ecological differences in growth form lend some support to our hypothesis that surface area to mass explains part of this variation.

Moderate water content is optimal for photosynthesis in many lichens (Lange et al. 1993, 2001), which is why we based our morphological categories primarily on the physiological importance of water absorption. However, it is important to note desiccation is also necessary for lichen survival (Farrar 1976a), as thallus saturation impedes gas exchange and photosynthesis (Lange et al. 1993) and can lead to cellular damage, especially at higher temperatures (Farrar 1976a). Beyond mitigating negative effects of thallus saturation, the beneficial aspects of drying are not entirely clear. Desiccation also comes with its own negative effects, including production of reactive oxygen species (Kranner et al. 2003). As many lichen characteristics seem to optimize water absorption (Larson & Kershaw 1976; Larson 1981; Stanton & Horn 2013) and retention (Gauslaa & Coxson 2011; Gauslaa 2014), the beneficial role of desiccation needs further study to better quantify water relations strategies using lichen traits. Future studies should use traits associated with water-holding capacity, desiccation and water absorption to understand how these parts of lichen water relations interplay and scale up in influencing lichen community structure.

Water relations in lichens involves other traits not included in our analyses, such as biochemical pathways that scavenge free radicals or maintain protein integrity (Kranner et al. 2008). Internal thallus anatomy, especially cortex and photobiont thickness, are also strongly related to water relations (Gauslaa & Coxson 2011). Furthermore, growth form (and photobiont) showed no relationship to extremely wide differences in net photosynthetic rates at different levels of thallus hydration (Lange et al. 1993), although that study occurred in a temperate rain forest covering a small number of taxa. These complications belie the need for a large, collaborative effort, similar to those for vascular plants (Kattge et al. 2011), to find lichen quantitative traits for use in community ecological studies.

Vegetative dispersal

Asexual dispersal propagules, such as soredia and isidia, may facilitate wider dispersal than sexual spores (Bowler & Rundel 1975), which must encounter the right photobiont to re-associate into a new lichen. Lichens with the smallest vegetative dispersal propagules were strongly associated with disturbance, perhaps because this trait facilitated relatively rapid colonization of newly opened habitat without having to re-synthesize the lichen symbioses as in sexual reproduction. Specifically, our results support the hypothesis that sorediate lichens are positively associated with recent fire. Sorediate lichens were also more frequent in forests than middle or high elevations, a finding supported elsewhere (Rapai et al. 2012). However, we did not sample the full suite of epiphytic lichens, rather only noting those that occurred below 0.5 m on trunks and stems of shrubs and trees. Despite this, we believe the pattern of more epiphytic species having soredia than terricolous species would be sustained had we done so, based on our experience elsewhere in Alaska in similar forests. However, terricolous species also reproduce asexually (Table 2) and by fragmentation (Heinken 1999) so the difference in the number of sorediate species between substrates is a matter of degree. Sorediate lichens may be more common in forests, since trees present more unoccupied surface area for colonization compared to the ground, which is frequently occupied by other plants, mosses or lichens. While further study is needed to understand the link between soredia and subarctic forests, it is a significant finding to see a major form of vegetative dispersal being so clearly associated with lichens from one substrate.

Conclusion

Categorical lichen functional traits showed distinct and different richness and cover maxima along environmental gradients associated with physiological factors controlling lichen community assembly. Disturbance favoured lichens with the most motile vegetative dispersal propagules and affinities for the woody substrate created by fire. Many of categorical traits were overlapping, indicating interacting trade-offs between traits, such as water relations strategies conferred by growth form and photobiont type, controlling the lichen's ability to restart photosynthesis. More than half of the traits and environmental variables had non-linear two-dimensional relationships with the community ordination, indicating non-parametric non-linear methods recovered many community-trait-environment associations that may have been missed by most other currently used methods.

Our study is one of the few that takes a broad view of lichen traits to examine factors affecting community

structure. Other studies that have looked at lichen community-level traits have also found important relationships between lichen traits and disturbance, solar radiation, water drainage, land management and climatic gradients (Ellis & Coppins 2006; Rapai et al. 2012; Koch et al. 2013; Giordani et al. 2014). Organisms similar to lichens, such as coral and bryophytes, showed analogous functional traits were important in determining community structure, such as water relations for bryophytes (Michel et al. 2012) and autotrophic partners and growth forms for corals (Bell 2007; Stat et al. 2008). We see reason to continue using categorical traits to understand community–trait–environment relationships while the search continues for readily measured continuous lichen traits.

Lichen functional trait theories will hopefully coalesce with more studies like ours, coupled with improved continuous functional trait measurement methods. When such theories and measurement techniques exist for lichens, new predictive frameworks could then be constructed using traits rather than single species to address important management, conservation and scientific questions.

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References

- Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. 2013. Trait-based tests of coexistence mechanisms. *Ecology Letters* 16: 1294–1306.
- Beck, P.S.A., Goetz, S.J., Mack, M.C., Alexander, H.D., Jin, Y., Randerson, J.T. & Loranty, M.M. 2011. The impacts and implications of an intensifying fire regime on Alaskan boreal forest composition and albedo. *Global Change Biology* 17: 2853–2866.
- Bell, J.J. 2007. Contrasting patterns of species and functional composition of coral reef sponge assemblages. *Marine Ecology Progress Series* 339: 73–81.
- Bowler, P.A. & Rundel, P.W. 1975. Reproductive strategies in lichens. *Botanical Journal of the Linnean Society* 70: 325–340.
- Campbell, J., Bengtson, P., Fredeen, A.L., Coxson, D.S. & Prescott, C.E. 2013. Does exogenous carbon extend the realized niche of canopy lichens? Evidence from sub-boreal forests in British Columbia. *Ecology* 94: 1186–1195.
- Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M. & Michelsen, A. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89: 984–994.
- Coxson, D.S. & Marsh, J. 2001. Lichen chronosequences (post-fire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. *Canadian Journal of Botany* 79: 1449–1464.
- Cutler, N. 2010. Long-term primary succession: a comparison of non-spatial and spatially explicit inferential techniques. *Plant Ecology* 208: 123–136.
- Dingman, S.L. & Koutz, F.R. 1974. Relations among vegetation, permafrost, and potential insolation in central Alaska. *Arctic and Alpine Research* 6: 37–47.
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S. & ter Braak, C.J.F. 2013. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95: 14–21.
- Dubayah, R. & Rich, P.M. 1995. Topographic solar radiation models for GIS. *International Journal of Geographical Information Systems* 9: 405–419.
- Ellis, C.J. & Coppins, B.J. 2006. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Journal of Biogeography* 33: 1643–1656.
- Environmental Systems Research Institute 2010. *ArcGIS 10.0*. Redlands, CA, USA.
- Esslinger, T.L. 2012. *A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada*. North Dakota State University, Fargo, ND. <http://www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm> (First Posted 1 December 1997, Most Recent Version (#19) 23 March 2014).
- Farrar, J.F. 1976a. Ecological Physiology of the Lichen *Hypogymnia physodes*. I. Some Effects of Constant Water Saturation. *New Phytologist* 77: 93–103.
- Gauslaa, Y. 2014. Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *The Lichenologist* 46: 1–16.
- Gauslaa, Y. & Coxson, D. 2011. Interspecific and intraspecific variations in water storage in epiphytic old forest foliose lichens. *Botany-Botanique* 89: 787–798.
- Gauslaa, Y. & Solhaug, K.A. 1996. Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Functional Ecology* 10: 344–354.
- Giordani, P., Brunialti, G., Bacaro, G. & Nascimbene, J. 2012. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecological Indicators* 18: 413–420.
- Giordani, P., Incerti, G., Rizzi, G., Rellini, I., Nimis, P.L. & Modenesi, P. 2014. Functional traits of cryptogams in Mediterranean ecosystems are driven by water, light and substrate interactions. *Journal of Vegetation Science* 25: 778–792.

- Glavich, D.A., Geiser, L.H. & Mikulin, A.G. 2005. Rare epiphytic coastal lichen habitats, modeling, and management in the Pacific Northwest. *The Bryologist* 108: 377–390.
- Grime, J. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169–1194.
- Groulx, M. & Lechowicz, M.J. 1987. Net photosynthetic recovery in subarctic lichens with contrasting water relations. *Oecologia* 71: 360–368.
- Gunther, A.J. 1989. Nitrogen Fixation by Lichens in a Subarctic Alaskan Watershed. *The Bryologist* 92: 202.
- Hall, D.K., Riggs, G.A., Salomonson, V.V., Barton, J.S., Casey, K., Chien, J.Y.L., DiGirolamo, N.E., Klein, A.G., Powell, H.W. & Tait, A.B. 2001. Algorithm theoretical basis document (ATBD) for the MODIS snow and sea ice-mapping algorithms. *Hydrological Science Branch NASA*. Available at: neptune.gsfc.nasa.gov/hsb/
- Heggberget, T.M., Gaare, E. & Ball, J.P. 1992. Reindeer (*Rangifer tarandus*) and climate change: importance of winter forage. *Rangifer* 22: 13–31.
- Heinken, T. 1999. Dispersal Patterns of Terricolous Lichens by Thallus Fragments. *The Lichenologist* 31: 603–612.
- Holt, E.A., McCune, B. & Neitlich, P. 2007. Succession and community gradients of arctic macrolichens and their relation to substrate, topography, and rockiness. *Pacific Northwest Fungi* 2: 1–21.
- Holt, E.A., McCune, B. & Neitlich, P. 2008. Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, U.S.A. *The Bryologist* 111: 68–83.
- Jandt, R., Joly, K., Meyers, C.R. & Racine, C. 2008. Slow recovery of lichen on burned caribou winter range in Alaska tundra: potential influences of climate warming and other disturbance factors. *Arctic, Antarctic, and Alpine Research* 40: 89–95.
- Joly, K., Jandt, R.R. & Klein, D.R. 2009. Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. *Polar Research* 28: 433–442.
- Kasischke, E.S. & Turetsky, M.R. 2006. Recent changes in the fire regime across the North American boreal region – Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters* 33: 9.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P.B., (...) & Wirth, C. 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935.
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* 23: 805–821.
- Koch, N.M., de Azevedo Martins, S. M., Lucheta, F. & Müller, S.C. 2013. Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. *Ecological Indicators* 34: 22–30.
- Kranner, I., Zorn, M., Turk, B., Wornik, S., Beckett, R.P. & Batič, F. 2003. Biochemical traits of lichens differing in relative desiccation tolerance. *New Phytologist* 160: 167–176.
- Kranner, I., Beckett, R., Hochman, A. & Nash, T.H. 2008. Desiccation-tolerance in lichens: a review. *The Bryologist* 111: 576–593.
- Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27.
- Lange, O.L., Kilian, E. & Ziegler, H. 1986. Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia* 71: 104–110.
- Lange, O.L., Büdel, B., Heber, U., Meyer, A., Zellner, H. & Green, T.G.A. 1993. Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO₂ exchange. *Oecologia* 95: 303–313.
- Lange, O.L., Hahn, S.C., Meyer, A. & Tenhunen, J.D. 1998. Upland tundra in the foothills of the Brooks Range, Alaska, U.S.A.: Lichen long-term photosynthetic CO₂ uptake and net carbon gain. *Arctic and Alpine Research* 30: 252–261.
- Lange, O.L., Green, T.G.A. & Heber, U. 2001. Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance? *Journal of Experimental Botany* 52: 2033–2042.
- Larson, D.W. 1981. Differential wetting in some lichens and mosses: the role of morphology. *The Bryologist* 84: 1–15.
- Larson, D.W. & Kershaw, K.A. 1976. Studies on lichen-dominated systems. XVIII. Morphological control of evaporation in lichens. *Canadian Journal of Botany* 54: 2061–2073.
- Laughlin, D.C. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* 102: 186–193.
- Macander, M.J. & Swingley, C.S. 2012. *Mapping snow persistence for the range of the western Arctic caribou herd, northwest Alaska, using the Landsat archive (1985–2011)*. National Park Service, Fort Collins, CO, US.
- Marini, L., Nascimbene, J. & Nimis, P.L. 2011. Large-scale patterns of epiphytic lichen species richness: Photobiont-dependent response to climate and forest structure. *Science of the Total Environment* 409: 4381–4386.
- McCune, B. 2006. Non-parametric habitat models with automatic interactions. *Journal of Vegetation Science* 17: 819–830.
- McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR, US.
- McCune, B. & Mefford, M.J. 2009. *HyperNiche v.2.1.3, Non-parametric multiplicative habitat modeling*. MjM Software, Gleneden Beach, OR, US.
- McCune, B. & Mefford, M.J. 2011. *PC-ORD version 6.0., multivariate analysis of ecological data, Users guide*. MjM Software Design, Gleneden Beach, OR, US.

- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.
- Michel, P., Lee, W.G., During, H.J. & Cornelissen, J.H.C. 2012. Species traits and their non-additive interactions control the water economy of bryophyte cushions. *Journal of Ecology* 100: 222–231.
- Mielke, P.W. & Berry, K.J. 2007. *Permutation methods: a distance function approach*. Springer, Dordrecht, NL.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28: 167–177.
- Nelson, P.R., Roland, C., Macander, M.J. & McCune, B. 2013. Detecting continuous lichen abundance for mapping winter caribou forage at landscape spatial scales. *Remote Sensing of Environment* 137: 43–54.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., (...) & Cornelissen, J.H.C. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.
- Raison, R.J., Khanna, P.K. & Woods, P.V. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. *Canadian Journal of Forest Research* 15: 132–140.
- Rapai, S.B., McMullin, R.T. & Newmaster, S.G. 2012. The importance of macrolichen traits and phylogeny in forest community assemblage along a high elevation gradient in southwestern British Columbia. *Forest Ecology and Management* 274: 231–240.
- Rich, P.M., Dubayah, R., Hetrick, W.A. & Saving, S.C. 1994. Using viewshed models to calculate intercepted solar radiation: applications in ecology. *American Society for Photogrammetry and Remote Sensing Technical Papers*. 524–529.
- Roland, C.A., Schmidt, J.H. & Nicklen, E.F. 2013. Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska. *Ecological Monographs* 83: 19–48.
- Shipley, B., Vile, D. & Garnier, É. 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* 314: 812–814.
- Shulski, M. & Wendler, G. 2007. *The climate of Alaska*. University of Alaska Press, Fairbanks, AK, US.
- Sousanes, P.J. 2008. *Annual climate summary 2006*. National Park Service, Fort Collins, CO, US.
- Stanton, D.E. & Horn, H.S. 2013. Epiphytes as “filter-drinkers”: life-form changes across a fog gradient. *The Bryologist* 116: 34–42.
- Stat, M., Morris, E. & Gates, R.D. 2008. Functional diversity in coral–dinoflagellate symbiosis. *Proceedings of the National Academy of Sciences of the United States of America* 105: 9256–9261.
- Stehn, S.E., Webster, C.R., Glime, J.M. & Jenkins, M.A. 2010. Elevational gradients of bryophyte diversity, life forms, and community assemblage in the southern Appalachian Mountains. *Canadian Journal of Forest Research* 40: 2164–2174.
- Stofer, S., Bergamini, A., Aragón, G., Carvalho, P., Coppins, B.J., Davey, S., Dietrich, M., Farkas, E., Kärkkäinen, K., (...) & Scheidegger, C. 2006. Species richness of lichen functional groups in relation to land use intensity. *The Lichenologist* 38: 331–353.
- Viereck, L.A., Dyrness, C.T., Batten, A.R. & Wenzlick, K.J. 1992. *The Alaska vegetation classification*. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, US.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.
- Yahr, R., Coppins, B.J. & Coppins, A.M. 2013. Transient populations in the British conservation priority lichen, *Cladonia botrytes*. *The Lichenologist* 45: 265–276.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Environmental and trait variables used in analysis including units of measure, mean standard deviation, minimum and maximum values from 569 plots. “-” indicates field does not apply to that trait or environmental variable.