Integrating phylogenetic community structure with species distribution models: an example with plants of rock barrens

Oluwatobi A. Oke, Stephen B. Heard and Jeremy T. Lundholm

O. A. Oke and S. B. Heard (stephen.heard@unb.ca), Dept of Biology, Univ. of New Brunswick, PO Box 4400, Fredericton, NB E3B 5A3, Canada. – J. T. Lundholm, Dept of Biology, Saint Mary's Univ., 923 Robie St, Halifax, NS B3H 3C3, Canada.

Approaches using phylogenetic pattern in ecological communities to deduce processes of community assembly have been criticised as disconnected from foundations in ecological mechanism, especially with respect to lack of data about abiotic and biotic niches. These criticisms can be addressed with analyses of organismal traits that underlie environmental filtering, competitive exclusion, and other candidate processes; however, the difficulty of assembling large trait databases means that such studies remain uncommon. We suggest a synthesis of phylogenetic community structure analysis and species distribution modeling that we believe can allow inference about community processes without prohibitive data requirements. We illustrate this method for angiosperm communities of rock barrens in eastern Canada. First, we analyzed phylogenetic community structure of four rock-barren sites at three nested spatial scales (quadrat to region). For the nine most common species in our barrens, we used regional occurrence records to build species distribution models identifying environmental drivers of the nine species' distributions. Coefficients of these models represent implicit trait data that summarize each species' response to the environmental drivers in the model. We then tested for phylogenetic signal in these traits, to ask whether ecological forces acting on them could be generating phylogenetic community structure. We found strong phylogenetic clustering at the quadrat level, while patterns at larger scales were complex. Our distribution model suggested drought stress as the dominant driver for distributions of all the species, consistent with local correlations with soil depth, and the species' responses to drought showed strong phylogenetic signal. The convergence of results from phylogenetic community structure and species distribution modeling suggests that barren communities are structured at the quadrat level by environmental filtering effects of moisture stress, to which species have phylogenetically patterned responses.

Although the theoretical groundwork is centuries old (Darwin 1859), the burgeoning availability of phylogenetic data has led to growing interest in connections between the assembly of ecological communities and evolutionary relationships of community members (Vamosi et al. 2009). Such an approach recognizes phylogenetic pattern in community structure as a product of ecological processes acting upon organismal traits, which are shaped during the evolutionary history of clades.

The most widely examined aspect of phylogenetic community structure (PCS) is whether co-occurring species are phylogenetically clustered (close relatives co-occur more often than distant ones) or overdispersed (distant relatives co-occur more often). Early discussions of PCS (Webb et al. 2002) suggested that if trait values are phylogenetically structured, then different mechanisms of community assembly should generate strikingly different patterns of co-occurrence. If communities are structured by environmental filtering (i.e. if membership in a community is determined primarily by tolerance of local environmental conditions), the result should be phylogenetic clustering as sets of close

relatives are similarly well adapted to the habitat. Phylogenetic overdispersion is expected instead if communities are structured by competition, with competition strongest and competitive exclusion possible between related, similar species. This contrast has been widely taken to provide a simple test for competitive vs environmental-filtering assembly of local communities, and one possible using easily available data: local species lists and phylogenetic hypotheses. This apparent promise led to a rapidly growing literature (Vamosi et al. 2009) reporting PCS for local communities.

Ecological inference from PCS is, unfortunately, not quite as simple as characterized above, because the mapping from process to pattern is unlikely to be one-to-one. First, environmental filtering leads to phylogenetic clustering when close relatives are most similar, but to overdispersion if it involves traits for which distant relatives are actually more similar than close ones (Webb et al. 2002). The latter pattern is possible, given extensive convergence (Cavender-Bares et al. 2006). Second, recent treatments (Vamosi et al. 2009, Mayfield and Levine 2010) have cautioned that competition might sometimes generate clustering instead of

overdispersion. In particular, competitive exclusion should remove distant rather than close relatives when it results from differences in competitive ability rather than similarity of niches, if close relatives tend to be similar in competitive ability. Thus, neither phylogenetic clustering nor overdispersion can be attributed to a single mechanism without additional data.

Our inability to diagnose process from PCS pattern alone should not be surprising. However, the methodology has been criticized (Vamosi et al. 2009, Mayfield and Levine 2010) in part because practitioners have been tempted to make such simple diagnoses. More sophisticated analyses incorporating data on the organismal traits underlying hypothesized mechanisms of community assembly (Ackerly 2003, Cavender-Bares et al. 2006, Kraft et al. 2008, Valladares et al. 2008) have been uncommon, probably because species lists and phylogenies are easily available whereas trait data may require daunting experimental work with large numbers of species. The recent intensity of debates around phylogenetic approaches to deducing ecological processes (Mayfield and Levine 2010) suggests that the field is ripe for methodological development that could more easily provide functional trait data as a context for PCS analysis, facilitating connections between phylogenetic patterns and their presumed basis in ecological mechanism.

A similar story can be told about statistical approaches to modelling species' geographic distributions. Species distribution modelling (SDM) is an important technique in biogeography and conservation biology that uses occurrence records for a species, coupled with environmental data, to predict its potential area of occurrence. SDM originally relied on presence/absence data that required intensive survey effort to confirm a species' presence or absence at each location. However, newer techniques allow the use of presence–only records, which are easy to extract from museum records and increasingly available online (Elith et al. 2006). A rapidly growing literature has resulted, but the approach has also garnered criticism for tenuous linkage to ecological theory (Austin 2007).

We asked whether PCS and SDM approaches might complement each other, jointly allowing stronger inference about ecological process while retaining manageable data requirements. Our approach is in the spirit of previous applications of SDMs to measuring niche similarity, evolution, and conservatism (Wiens and Graham 2005, Evans et al. 2009, Stephens and Wiens 2009, Diniz-Filho et al. 2010). We show how implicit functional trait data can be extracted from species distribution models and applied to the interpretation of patterns of phylogenetic community structure. Our use of SDMs to infer trait data represents an alternative (with less daunting data requirements) to approaches inferring traits or niche requirements from environmental data acquired for all sampled plots or individuals (Rabosky et al. 2011).

We demonstrate our approach with data for angiosperm communities of eastern Canadian rock barrens. Barrens are treeless areas within forested biomes, and are often characterised by rocky outcrops, shallow soil, patchy vegetation, and low nutrient and moisture availability (Stark et al. 2003). Typical barrens plants are well adapted to environmental stress, notably from heat and drought. Barrens are

an interesting system in which to investigate phylogenetic community structure, because it is not clear whether environmental filtering or competition ought to predominate in controlling local community assembly. Barrens often represent extreme edaphic conditions within the region of their occurrence (Anderson et al. 2007), and so it is plausible that fine-scale variation in abiotic factors could strongly influence the local occurrence of barrens plants. However, as a result of such filtering, barrens floras are phylogenetically clustered subsets of the regional floras from which they are drawn (Oberndorfer and Lundholm 2009). Precisely because species are strongly filtered into the barrens, we might expect competitive interactions among related and similar species to dominate community assembly within the barrens. Of these two processes, we might expect competition to matter most at the very local scales on which competitors interact, while environmental filtering could occur at any spatial scale. This logic suggests the possibility of cross-scale patterns in PCS (Vamosi et al. 2009), which could be detected with spatially nested analyses of phylogenetic community structure.

We examined patterns of angiosperm co-occurrence in rock barrens at three scales: small quadrats, sites a few kilometres apart, and regions separated by hundreds of kilometres. We attempted to connect phylogenetic pattern with trait data implicit in SDM analysis for our barren species. More specifically, we asked: 1) whether barren communities show phylogenetic clustering or overdispersion at different spatial scales; 2) what environmental factors influence distributions of the barrens species; 3) whether species' responses to distribution drivers (implicit species traits) show significant phylogenetic signal; and 4) whether the most phylogenetically structured traits also control species distributions and could thus control phylogenetic community structure. Analyses like ours may represent a productive avenue for progress in understanding community assembly, because they harness the complementary strengths of SDM and PCS approaches.

Material and methods

Our approach to understanding phylogenetic structure in rock barrens communities involves the synthesis of several analyses: calculation of PCS metrics for species assemblages of field quadrats, species distribution modeling of regional occurrence data, extraction of species traits from SDMs and their testing for phylogenetic signal, and investigation of environmental correlates of local occurrence. These analyses are outlined individually below, and the logical relationship among analyses is summarized in Fig. 1.

Field sites and sampling

We sampled plant species at four rock-barren sites in eastern Nova Scotia and southwestern New Brunswick, Canada. The Nova Scotia sites were near Halifax (Bayers Lake, 44.65°N, 63.68°W; Spryfield, 44.61°N, 63.60°W), and the New Brunswick sites near Clarendon (Clarendon North, 45.47°N, 66.40°W; Clarendon South, 45.43°N, 66.43°W).
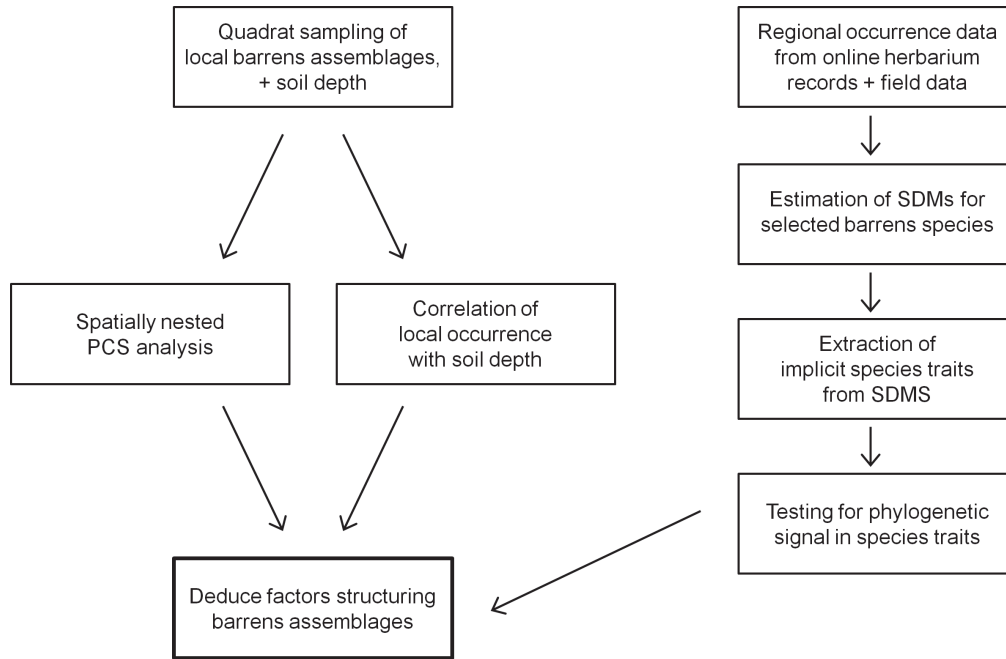
Figure 1. Summary of relationships among analyses of barrens community structure.

We treat Clarendon and Halifax as regions; sites within regions were at least 5 km apart while the regions are over 250 km apart. The two regions have distinct climates: drier and more continental (colder winters and warmer summers) in New Brunswick than Nova Scotia (Supplementary material Appendix 1).

In July 2011, we selected one barrens at each site (a treeless area with rock outcrops, or a closely spaced set of treeless patches where barrens occurred as mosaics with forest). All sampled patches were at least 10 m in length and most were less than 20 m from neighbouring patches. We placed 25×25 cm quadrats at 10 m intervals in a grid across the barrens (or patches), and measured soil depth in the centre of each quadrat. We identified vascular plants in each quadrat to species, using Hinds (2000) and Mittelhauser et al. (2010), and recorded presence/absence data for each species in all quadrats. A few individuals ($<4\%$ and with very low percent cover) were too small or damaged for identification. We sampled 97, 76, 94 and 46 quadrats at Clarendon North, Clarendon South, Bayers Lake and Spryfield. Individual quadrats included from 0 to 9 species; site-level diversities ranged from 30 (Spryfield) to 54 (Clarendon North) species, and the total plant dataset included 81 species.

Phylogenetic community structure

We analyzed phylogenetic community structure for quadrats, sites, and regions using Phylocom 4.1 (Webb et al. 2008). We considered only angiosperm species lists, for three reasons: first, because we used a phylogeny based on an angiosperm supertree; second, because other clades differ markedly in anatomy and physiology of water transport, making comparison of climate responses potentially

awkward; and third, because inclusion of very long branches such as those separating angiosperms from ferns can be problematic in PCS analysis (Kembel and Hubbell 2006). With the exception of the moss *Polytrichum commune* (67/313 quadrats), no non-angiosperm was common (*Pteridium aquilinum*, fern, 19/313; *Picea rubens*, conifer, 9/313; all others less common). Our pruned dataset included 66 species, with 26–43 species per site.

We compiled a phylogenetic hypothesis for our 66 barrens species beginning with a backbone produced, by Phylocom's Phylomatic and Bladj modules, from the angiosperm supertree of Davies et al. (2004). We resolved polytomies within families using recent systematic treatments (Asteraceae: Brouillet et al. 2009, Funk et al. 2009; Ericaceae: Kron et al. 2002, Gillespie and Kron 2010; Poaceae: Aliscioni et al. 2012; Rosaceae: Campbell et al. 2007, Potter et al. 2007; Salicaceae: Argus 2007, Hardig et al. 2010). We could not extract branch length information for these subfamilial resolutions, and so divided branch lengths from the backbone equally across internodes. The resulting master phylogeny (Supplementary material Appendix 2) retained three polytomies: in Asteraceae (*Solidago/Euthamia/Eurybia*), in Salicaceae (*Salix bebbiana/discolor/pyrifolia*) and among three families of asterids (Araliaceae/Asteraceae/Caprifoliaceae). Our results were not sensitive to the way we resolved polytomies: our literature-based resolutions support the same interpretations as does letting Phylocom resolve all polytomies (data not shown). Phylogenies for regional- and site-level species lists were obtained by deleting non-occurring species from the master tree, summing branch lengths as appropriate to maintain ultrametricity.

We calculated two metrics of phylogenetic community structure: nearest taxon index (NTI) and net relatedness index (NRI). For each metric, a positive score indicates

phylogenetic clustering of the sample relative to random sampling from the source pool, while a negative score indicates overdispersion (Webb 2000). NRI and NTI capture different aspects of community structure: NTI considers only the phylogenetic distance from each species to its nearest relative in the sample, while NRI considers distances among all pairs of species in the sample. Only quadrats with at least 3 species were included in the quadrat-level analysis: 38, 47, 56, and 34 quadrats at Clarendon North, Clarendon South, Bayer's Lake, and Spryfield. The species list for each quadrat was tested against a source pool consisting of the species in all quadrats at the site. Site-level composition was tested against a regional pool consisting of all species occurring at either site in that region ('Halifax' = Bayers Lake + Spryfield; 'Clarendon' = Clarendon North + Clarendon South). Region-level composition was tested against our overall species list (species occurring anywhere in all sampled barrens). Species lists for all source pools are provided in Supplementary material Appendix 3. We note that regional-scale PCS analyses can be difficult to interpret when filtering- and competition-based reasons for species absences may be confounded with biogeographic reasons (dispersal limitation, local speciation, etc.; Heard and Cox 2007, Vamosi et al. 2009). Such effects do not arise in our analysis, because all species in our data are members of the regional floras of both New Brunswick and Nova Scotia.

In principle, we could have conducted an analysis at a higher scale still: the overall barrens flora tested against the complete flora of eastern Canada. We did not pursue this, because it is well known that the barrens flora is a non-random and phylogenetically clustered subset of the regional flora (Oberndorfer and Lundholm 2009). Our analyses remove this barrens-level effect (by using the overall barrens flora as the most inclusive species pool), and thus our focus was on whether phylogenetic clustering or overdispersion could be detected at finer scales of organization.

Tests of statistical significance for site and regional NRI and NTI used randomization methods implemented in Phylocom. However, for two reasons, we were not interested in testing significance of NRI and NTI for individual quadrats. First, with only a few species per quadrat, such tests would have rather low power. Second, at the quadrat scale we expected co-occurrences to include a considerable stochastic influence, meaning that we might see strong clumping in one quadrat and strong overdispersion in the next. Instead, we focused on detecting an overall tendency toward quadrat-scale clumping or overdispersion by tabulating quadrat-scale NRI or NTI scores for each site, and testing the hypothesis that the mean score was zero at each site (one-sample t-tests in R 2.14.1; R Core Team). Because metric distributions were significantly non-normal for some sites (Shapiro–Wilk test, 5 of 8 $p < 0.05$), we also conducted sign tests, which confirmed results of the t-tests. We checked for spatial autocorrelation in NRI and NTI scores within each site, using Mantel tests implemented in R, to ensure that degrees of freedom were not inappropriately inflated.

Inferring environmental-response traits from species distribution models

We used species distribution models to identify environmental variables that appear to determine the geographic distributions (in barrens) of some common barrens species. SDMs incorporate predictive models of species occurrence as functions of hypothesized environmental drivers, and the parameters of these models can be interpreted as traits of species, quantifying their responses to environmental factors. We built SDMs using Maxent 3.3.3e (Phillips et al. 2004, Elith et al. 2011). Maxent uses maximum-entropy methods to predict species distribution based on presence-only occurrence records and spatially extensive environmental data. Essentially, Maxent estimates the probability distribution for species occurrence across a landscape as constrained by the observed distribution and by data for environmental conditions across the study area (Pearson et al. 2007).

We built SDMs for the nine species most frequently encountered in our quadrats: *Cornus canadensis* (Cornaceae; 87 quadrats), *Danthonia spicata* (Poaceae; 47), *Gaultheria procumbens* (Ericaceae; 111), *Gaylussacia baccata* (Ericaceae; 76), *Kalmia angustifolia* (Ericaceae; 132), *Maianthemum canadense* (Liliaceae; 19), *Rhododendron canadense* (Ericaceae; 23), *Sibbaldiopsis tridentata* (Rosaceae; 47), and *Vaccinium angustifolium* (Ericaceae; 141 quadrats). This list includes shrubs, herbaceous eudicots and monocots, and a grass. In what follows, genus names without specific epithets refer to these focal species. We focused on the nine most common species for two reasons. First, these were likely to make the biggest contributions to measured pattern in phylogenetic community structure. Second, while some of our uncommon species likely occur on the barrens only as sink populations, our nine most common species are well-known, typical, and abundant on rock barrens.

Occurrence data

We compiled available field and herbarium occurrence records for our nine focal species. Field records were collected in summer 2011 by us, or prior to 2011 by other researchers in JTL's lab. We extracted herbarium records from herbaria of the Univ. of New Brunswick, Acadia Univ., and the Univ. of British Columbia and from the Northern Ontario Plant Database (< www.northernontarioflora.ca/ >). We queried these collections for records associated with the occurrence of our focal species in rock barrens; that is, we were interested in modeling distributions of the species as they occur in barrens and barrens-like habitats, not their broader distribution in other habitats. This is important because our phylogenetic community structure calculations consider only patterns of distribution among quadrats and sites in the barrens, and our SDMs can be complementary only if they consider the same patterns of distribution. We used keywords 'barren', 'rocky outcrop', 'rock', 'mountain' and 'bald' to recover herbarium records for sites having general features of the barrens. We recovered 8–9 records for 3 species (*Gaylussacia*, *Kalmia* and *Rhododendron)* and 13–30 records for each of the others. Pearson et al. (2007) demonstrated

that useful Maxent-based SDMs can be generated even from smaller sample sizes than ours.

Environmental variables

We considered a set of 24 environmental variables as potential predictors of species distribution. We began with a frequently used set of 19 climatic variables (Supplementary material Appendix 4) from BIOCLIM (< www.worldclim. org/bioclim >), a GIS-based model that summarizes the approximate energy and water balance for a location based on climate data. We supplemented the climate dataset with six other variables: altitude, plus five derived variables (slope, eastness, northness, topographic position index (TPI) and topographic wetness index (TWI)). Eastness and northness represent a breakdown of slope aspect (0–360 degrees) into two linear variables: eastness = sin(aspect) and northness = cos(aspect). TPI measures the elevation of a point with respect to its surroundings, differentiating hilltops from valleys (Weiss 2001), and TWI estimates local wetness as a function of local slope and upslope drainage area (Beven and Kirkby 1979). These variables were generated from a 1 km resolution digital elevation model (Can3d30; < www.geogratis.ca >) using the Spatial Analyst extension in ArcGIS 10 (Environmental Systems Research Inst., Redlands, CA). All environmental variables were interpolated at 1 km spatial resolution to cover the easternmost 5 Canadian provinces (Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland and Labrador). The resulting dataset had ~5.7 million environmental records, of which 10 000 were randomly selected for the SDM analyses. Our focal species have geographic ranges more extensive than this (into the northern US and further west across Canada). Because SDM results can be sensitive to the choice of background area for which environmental data are determined (Elith et al. 2011), we repeated all our SDM analyses using a dataset for all of Canada.

Because we used occurrence data only for rock barrens but environmental data for the entire area of eastern Canada, our SDMs could be interpreted as including 'habitat' and 'species' components. The habitat component, which is shared by the SDMs for each species, implicitly models the influence of our environmental variables on occurrence of rock barrens. The species component, which is distinct for each of the 9 species, then models the occurrence of plants within rock barrens. However, we would expect the habitat component to be negligible for rock barrens, as their occurrence is largely controlled by geology (rock outcrops) rather than our climate variables (with the possible exception of coastal barrens, which we do not consider here; Stark et al. 2004, Burley and Lundholm 2010). This expectation is testable: if we are wrong, and the habitat component is actually large, we would expect the SDMs to predict high probability of occurrence for environmental conditions most plausibly associated with barrens (high altitude, high TPI, and perhaps low moisture).

We used variable selection to reduce the number of intercorrelated variables in our dataset (Supplementary material Appendix 4, 5). Briefly, we excluded from the analysis one variable of any pair with correlation coefficient > 0.7, retaining the variable we considered most directly relevant to characterizing environmental conditions on rock barrens. For instance, mean temperature of the driest quarter was strongly correlated with precipitation of the driest quarter. We retained the latter because barrens soils are shallow and thus have low water holding capacity. This makes it likely that the joint action of these variables is expressed via moisture stress, which affects both nutrient uptakes and physiological processes in plants. We retained nine variables: three climate variables (precipitation of the driest quarter (PDQ), temperature annual range (TAR), and mean temperature of wettest quarter (MTWQ)), plus altitude and all five derived variables. For comparison, we also ran an SDM analysis retaining all 24 variables. We did not use principal components analysis to extract orthogonal axes of variation for two reasons: first, PCA loadings were complex and not easily interpretable; and second, PCA treatment of intercorrelated datasets may degrade the performance of SDMs using Maxent (Elith et al. 2011).

Environmental drivers from species distribution modelling

Maxent models each species' probability of occurrence as a logistic function of the environmental variables, or transformations of them. Due to limited occurrence data, we included only linear and quadratic terms in each environmental variable, and we followed the small-sample procedures of Pearson et al. (2007). We evaluated model success using a jackknife approach: omitting each presence record in turn from the occurrence dataset, and using an SDM for the reduced data to predict suitability for the location of the omitted record. The success rate is the proportion of jackknife replicates for which the location is (correctly) deemed suitable. We followed Pearson et al. (2007) in using two suitability thresholds for prediction. With the lowest presence threshold (LPT), a location is deemed suitable if its environmental characteristics are at least as suitable as the least suitable location with a presence record. With the lowest-10% threshold (T10), a location is deemed suitable if its characteristics are more suitable than the worst 10% of presence records. For either threshold, the statistical significance of a model is the probability of equal or greater prediction from random assignment of suitability (Pearson et al. 2007).

Maxent provides several ways to assess the importance of candidate environmental drivers. We calculated each variable's percent contribution, which tracks the performance gain during model-building as a single model coefficient is adjusted at each iteration step. With strongly intercorrelated variables, this measure can be sensitive to the path Maxent takes to the optimal model (Phillips 2006). While our variable selection procedure was likely to mitigate this problem, we also considered three other importance diagnostics. Permutation importance is calculated by randomly permuting values of a variable across the dataset and measuring the decrease in model performance. Omission training loss measures the decrease in model performance when it is built without each variable, while inclusion training gain measures the ability of each variable to predict occurrences by itself.

Extracting trait values

Our Maxent SDMs allowed us measure species' responses to each of our environmental variables. These responses are quantified by the coefficients of Maxent's predictive models, which can be interpreted as traits of species – for instance, as drought sensitivity (linear coefficient in PDQ) or width of wet-season thermal optimum (quadratic coefficient in MTWQ). Our analysis gave us values for 18 traits (9 environmental variables, two coefficients each) for each of our 9 focal species. We averaged the values of each coefficient across multiple jackknife models for each species.

Phylogenetic signal

We tested for phylogenetic pattern in trait values, or 'phylogenetic signal' for each trait via Blomberg's K (Blomberg et al. 2003). K measures the extent to which related species retain similar trait values due to their shared ancestry. In the absence of phylogenetic signal, $K = 0$, while $K = 1$ for signal arising when trait values evolve by Brownian motion along the phylogeny and $K > 1$ for stronger phylogenetic structure still. Note that phylogenetic signal is a pattern that can arise from a diversity of underlying evolutionary processes (Revell et al. 2008). For this reason, we avoid terms such as 'conservatism' and 'inertia' that are often used interchangeably with 'signal' but that make implications about evolutionary process. What matters for our purposes is only trait values are more similar for close relatives than distant ones, not the particular evolutionary process generating that signal.

We used the Phylosignal function in the 'picante' package of R 2.14.1 (Kembel et al. 2010) to calculate K and to test for significant overall phylogenetic signal (K significantly greater than zero). We did not attempt to break the overall pattern down to consider similarity between particular lineages (e.g. via 'traitgrams'), because our focus was on overall phylogenetic community structure rather than co-occurrence of particular species pairs.

Soil depth

Soil depth correlates with moisture availability in barrens (Oberndorfer and Lundholm 2009), and so we can use soil depth as a rough quadrat-scale measure of drought stress for comparison with larger-scale SDMs. We used logistic regression (in R 2.14.1) to ask how occurrence of our nine most common species responded to soil depth, among quadrats within sites. This analysis asks whether there is
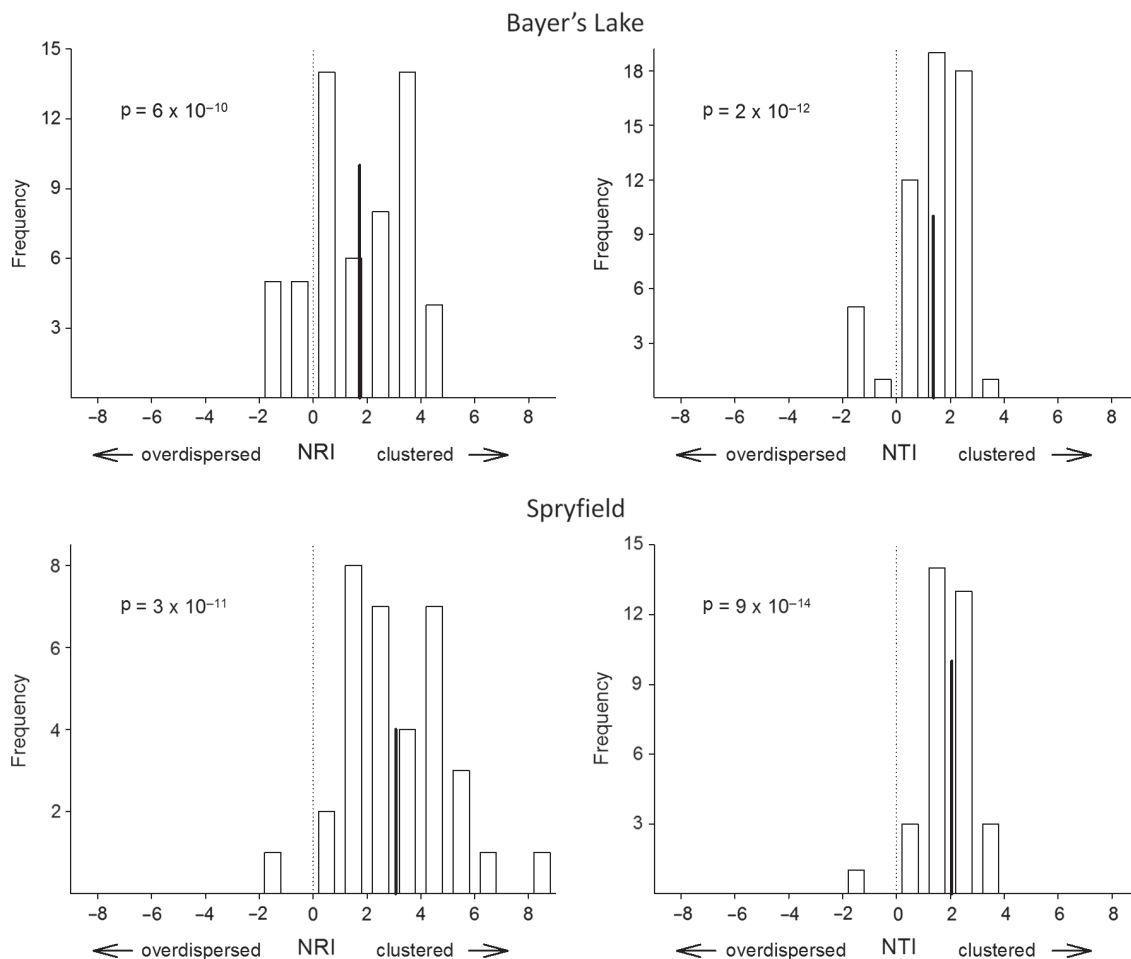

Figure 2. Quadrat-scale NRI and NTI values. Dotted vertical line is the null expectation (NRI/NTI = 0); heavy vertical line is the sample mean for the site.
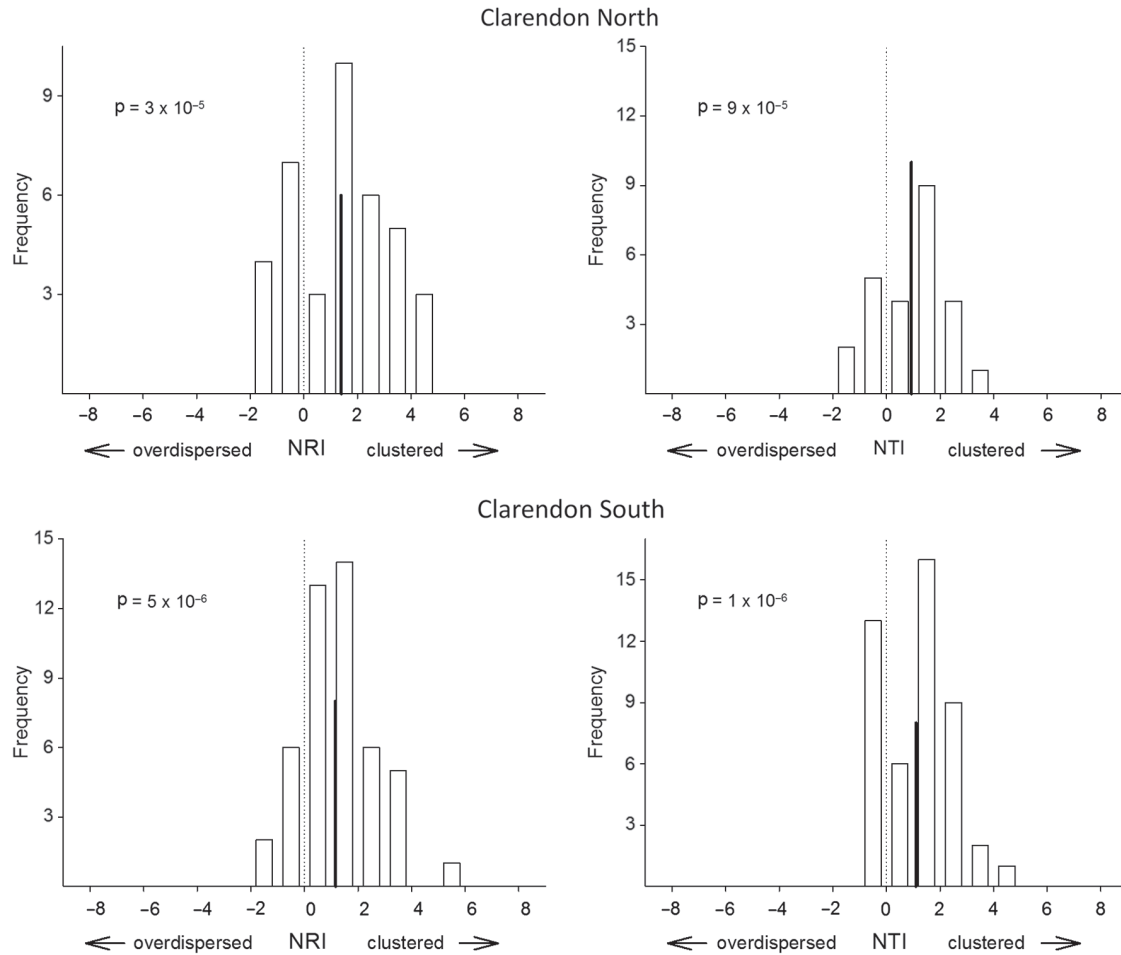
Figure 2. (Continued).

local-scale pattern in species response to the environment that is consistent with the larger-scale pattern detected by SDMs. If there is, then it is plausible that environmental filtering could operate at our most local scale. We carried out regressions for the 16 (of 36) site × species combinations with occurrence rates between 20 and 80% and thus with reasonable power for logistic regression. We used Stauffer's z to combine the 16 p-values into a single overall test of the null hypothesis that plant distributions are independent of soil depth. We calculated two versions of Stauffer's z. The first (trend-insensitive z) is based on the raw p-values from the logistic regression and tests the null against the alternative that soil depth influences plant distributions in some way, perhaps differently among site × species combinations. The second (trend-sensitive z) is based on right-tail p-values and tests the null against the stricter alternative that soil depth influences plant distributions in the same direction for all site × species combinations.

Results

Phylogenetic community structure

At the quadrat scale, barrens communities showed strong phylogenetic clustering at all sites, whether measured via NRI or NTI (Fig. 2). While a few individual quadrats had NRI/NTI scores suggestive of overdispersion, mean scores were always positive (all $p < 0.0001$). These analyses were not affected by spatial non-independence of community structure across quadrats: NRI scores showed significant but weak autocorrelation (Mantel $r = 0.17$, $p = 0.006$) at Clarendon North, while autocorrelation was weaker and nonsignificant for all other metric × site combinations.

In contrast, at site and regional scales phylogenetic community structure was variable and more subtle (Table 1). At the site scale, we detected clustering at Clarendon North (NRI significant, NTI suggestive), but overdispersion at Clarendon South (both metrics significant). The Halifax sites showed weak overdispersion at narrower

Table 1. NRI, NTI and p-values for each site and region. Bold: significant ($p < 0.05$) phylogenetic structure versus random null; italic, suggestive ($p < 0.10$) phylogenetic structure.

Sites and regions	NRI	p	NTI	p
Clarendon North	**2.48**	**0.02**	1.31	0.10
Clarendon South	**−1.64**	**0.03**	**−1.69**	**0.03**
Bayers Lake	1.15	0.14	*−1.52*	*0.06*
Spryfield	0.84	0.20	−0.47	0.33
Clarendon	0.15	0.41	0.61	0.27
Halifax	0.53	0.98	**−1.81**	**0.02**

Table 2. Environmental variables and their respective contributions to the species distribution. PDQ = precipitation of driest quarter, TAR = temperature annual range, MTWQ = mean temperature of wettest quarter, TWI = topographic wetness index and TPI = topographic position index. C.c. = *Cornus canadensis*, D.s. = *Danthonia spicata*, G.p. = *Gaultheria procumbens*, G.b. = *Gaylussacia baccata*, K.a. = *Kalmia angustifolia*, M.s. = *Maianthemum canadense*, R.c. = *Rhododendron canadense*, S.t. = *Sibbaldiopsis tridentata*, V.a. = *Vaccinium angustifolium*.

	C.c.	D.s.	G.p.	G.b.	K.a.	M.c.	R.c.	S.t	V.a.
PDQ	65.7	50.7	40.9	42.1	86.4	62.3	55.0	63.4	64.9
Altitude	27.1	13.0	21.4	0.6	2.1	4.3	20.0	20.8	16.3
TAR	0	0.2	0.3	0.1	0	0	0	0.1	0.5
MTWQ	0.4	9.7	23.6	42.5	4.9	0.1	0	3.0	10.7
Easting	0.1	7.7	0.9	0.5	2.1	7.5	0	5.1	0
Northing	1.7	9.1	6.4	7.5	1.2	17.9	20.0	0.8	1.8
Slope	4.7	0.2	6.5	0.2	0.2	4.0	1.9	1.6	2.0
TPI	0	1	0	0	2.0	0	3.3	0.1	3.2
TWI	0.4	8.4	0	6.6	1.0	3.8	0.1	5.2	0.6

phylogenetic scales (NTI) but weak clustering at broader scales (NRI), but neither result was significant. At the regional scale, we found significant overdispersion for NTI at Halifax, but otherwise no strong pattern.

Species distribution drivers

All Maxent SDMs had high success rates, and most were statistically significant for both LPT and T10 thresholds (Supplementary material Appendix 6). However, the model for *Vaccinium* was significant only for T10, and models for *Danthonia* and *Maianthemum* were not significant at either threshold (p > 0.05). Model significance did not depend on number of occurrence records.

Among our nine candidate environmental variables, precipitation of the driest quarter (PDQ) had consistently high percent contribution (41–86%; Table 2). This strongly suggests that PDQ (or an aspect of precipitation correlated with it) is the most important driver of barrens distributions for all nine species. Permutation importance, omission training loss and inclusion training gain all supported this inference (results not shown). Altitude made substantial contributions for six species (Table 2), although permutation importance supported this inference only for *Cornus* and *Gaultheria* (results not shown). Mean temperature of the wettest quarter made substantial contributions for three species. Other variables made only small contributions. Occurrence of all species increased with PDQ and declined with altitude (Supplementary material Appendix 7), although the strength of both influences varied among species (compare slopes and elevations of response curves). We can rule out the possibility that our SDMs are predicting the occurrence of barrens, rather than of our plant species, because the influences of PDQ and altitude were opposite in direction to those expected for prediction of barrens (and TPI lacked influence).

SDM analysis retaining all 24 environmental variables yielded models with importance spread across many more variables (results not shown). However, PDQ and altitude remained among the most important predictors, making this analysis broadly consistent with our preferred analysis of the reduced variable set. Analysis using an environmental dataset for all of Canada differed little from our eastern-Canada analysis (results not shown).

Phylogenetic signal

PDQ, which was the most important driver of species distributions, showed strong phylogenetic signal (Table 3): significant for its linear coefficients ($K = 1.02$, p = 0.01), and nearly so for its quadratic coefficients ($K = 1.39$, p = 0.07). Thus, responses of our barrens species to drought stress are more similar among close relatives than among distant ones. Among the other variables, only TWI coefficients showed statistical evidence for phylogenetic signal in trait values, although a few other K estimates were reasonably large (> 0.8).

Soil depth

Of 16 species × site combinations tested, three showed plant occurrence related positively to soil depth (p < 0.05; Supplementary material Appendix 8). Overall, the 16 datasets show strong evidence that plant distributions respond to soil depth (trend-insensitive Stauffer's $z = 3.43$, p < 0.001). However, several site × species combinations showed negative (but nonsignificant) dependence of occurrence on soil depth. As a result, we have only weak evidence (trend-sensitive Stauffer's $z = 1.15$, p = 0.125) for an occurrence–depth relationship consistent among sites.

Discussion

Quadrat-scale phylogenetic community structure and its likely mechanism

At the quadrat scale, we detected strong phylogenetic clustering at every site. Clustering was equally strong via NRI and NTI, which emphasize different aspects of phylogenetic community structure. Positive NTI indicates that barrens species co-occur with their closest relatives more often than expected by chance. Positive NRI indicates that this pattern extends to average relatedness of all species in the quadrat. Thus, clustering is not due only to frequent co-occurrence of a few congener pairs (e.g. *Vaccinium angustifolium/myrtilloides*, *Solidago juncea/puberula*), nor is it due only to infrequent co-occurrence of distant relatives (e.g. of monocots with eudicots).

Table 3. *K*-statistics (phylogenetic signal) for environmental-response traits (linear and quadradic coeffcents from Maxent SDMs). Bold: significant phylogenetic conservatism (p < 0.05); italic: suggestive phylogenetic conservatism (p < 0.10).

Variables	K_{linear}	p	$K_{quadratic}$	p
PDQ	**1.02**	**0.01**	*1.39*	*0.07*
TWI	**1.11**	**0.03**	0.28	0.88
Altitude	0.38	0.69	0.55	0.31
TAR	0.49	0.49	1.11	0.39
MTWQ	0.34	0.80	0.97	0.37
Easting	0.81	0.15	0.43	0.52
Northing	0.30	0.88	0.36	0.74
Slope	0.32	0.79	0.36	0.76
TPI	0.33	0.77	0.31	0.76

Because multiple mechanisms can generate phylogenetic clustering (Vamosi et al. 2009, Mayfield and Levine 2010, HilleRisLambers et al. 2012), including both environmental filtering and competition, we cannot directly infer ecological process from the strong clustering evident in our PCS analyses. Can we draw on additional data to ask whether clustering in our barrens communities is more likely an outcome of environmental filtering or of local competition?

Arguments that competition could drive phylogenetic clustering depend on competitive exclusion resulting from differences in competitive ability (not similarity in niche), and on competitive ability showing phylogenetic signal. We do not have comprehensive data on competitive ability for our barrens species. However, Cahill et al. (2008) addressed this question more generally, with a meta-analysis of data for 142 plant species (including 12 genera and 6 species occurring in our dataset). If competitive ability is similar for close relatives, then competitive impact should be greater for pairs of distant relatives (that will differ in competitive ability). Cahill et al. found little evidence for stronger competitive impact of distant relatives, at least within major angiosperm clades (monocots and eudicots). Instead, competitive impact was strongest for close relatives within monocots, and there was no pattern within eudicots. It is thus unlikely that local competition can generate phylogenetic clustering of close relatives (measurable via NTI) among angiosperms. Mayfield and Levine (2010) interpreted Cahill et al.'s (2008) data as suggesting conservatism of competitive ability at deeper phylogenetic scales, with eudicots as a group competitively superior to monocots. If this interpretation is correct, we might expect competition to generate a clustering signal measurable via NRI but not via NTI. Our results are inconsistent with this expectation, as we measured equally strong quadrat-scale clustering via both metrics. We therefore reject the hypothesis that competition could have driven clustering in our barrens communities.

Environmental filtering, in contrast, is a strong candidate as a mechanism for phylogenetic clustering in the barrens. Significant SDMs with high success rates suggest that distributions of common barrens species are determined in part by drought stress (represented in our SDMs by precipitation of the driest quarter). Our soil depth data are broadly consistent with an influence of drought: overall, plant occurrence responded significantly to quadrat

soil depth. Unfortunately, we cannot clearly establish whether these local relationships are all in the same direction (a few site × species combinations had a trend, albeit nonsignificant, towards occurrence on shallower soils). This is not entirely unexpected: we would expect species to vary in the strength (and perhaps even direction) of their local association with soil depth, because the SDMs show that they vary in the strength of their regional association with PDQ. In any event, our SDMs and soil depth together clearly indicate that barrens plants have restrictive niche requirements with respect to environmental characteristics that vary across our study area. For filtering to generate phylogenetic clustering, however, niche requirements must differ among species, and the traits underlying niche requirements must show phylogenetic signal. We were able to measure niche-related traits for our species (coefficients of environmental variables in the SDMs), and we found strong phylogenetic signal (consistent with phylogenetic niche conservatism sensu Wiens and Graham 2005, Wiens et al. 2010) for traits underlying response to drought. That SDMs identified a drought-related variable (precipitation of the driest quarter) as driving the distributions of our barrens species is reasonable. In our study area the driest quarter is summer, when the open barrens habitat experiences high solar flux. The shallow barrens soils (usually < 10 cm) hold little water, and that water is quickly depleted through evapotranspiration. In addition, exposed rocks are quickly warmed by direct solar radiation, and heat released to the atmosphere (Hall et al. 2005) can drive convective mixing of the cooler air above the vegetated patches with warmer air above exposed rocks. This convection is likely to further increase the moisture deficit in vegetated parts of the barrens.

The occurrence of strong filtering-driven phylogenetic clustering on rock barrens is at first glance surprising. After all, our analyses partition out the known filtering of plant species into barrens, considering instead the distribution within barrens of a species pool already strongly weighted toward the inclusion of close relatives. With our species pools thus enriched in close relatives with similar trait values, it would seem reasonable to anticipate strong local competition and hence phylogenetic overdispersion. That we found no such pattern could suggest that competition is unimportant on the barrens, that competition occurs but that its impact does not depend on relatedness (Cahill et al. 2008), or that competitively generated overdispersion is simply swamped by much stronger environmental filtering. Without detailed experiments, it is difficult to distinguish these possibilities. Our study is not the first to detect local environmental filtering even within a flora already filtered at a coarser scale: Ojeda et al. (2010) found that local heath- and scrubland communities demonstrated local filtering by tolerance to fire, despite being drawn from a flora already regionally fire-filtered.

Cross-scale patterns in phylogenetic community structure

While clustering at the quadrat scale was consistent and strong, phylogenetic community structure at site and

regional levels was quite complex and sometimes differed markedly between sites just a few kilometers apart (e.g. clustering for Clarendon North, overdispersion for Clarendon South). At the regional scale, we detected no pattern for Clarendon, while for Halifax there was apparent overdispersion measured via NTI but no pattern via NRI. If there is an overall conclusion to be drawn, it is that the strong signal of environmental filtering identified at the quadrat scale weakens at larger spatial scales. This is something of a surprise, for two reasons. First, habitat heterogeneity, and thus the potential for filtering, is often assumed to increase with spatial scale. Second, if competitive exclusion drives overdispersion, it is likely to do so primarily on local scales, with its influence declining at larger scales (Vamosi et al. 2009). For this reason, it seems intuitive to expect phylogenetic overdispersion at fine scales (e.g. Slingsby and Verboom 2006) and clustering at larger scales – opposite to the pattern for our barrens. However, empirical evidence for the expected cross-scale pattern is weak (Vamosi et al. 2009), and other studies have attributed quite local phylogenetic clustering to fine-scale environmental filtering (Kraft et al. 2008, Ojeda et al. 2010).

It is striking that our SDMs were generated at a 1 km resolution, and yet they were able to identify the likely driver of environmental filtering that is strongest at the quadrat scale (25 cm). This suggests that the same environmental variables that predict species occurrence at larger scales are involved in sorting them into quadrat-scale patches. Our soil-depth analysis is consistent with this suggestion, although soil depth is likely to capture only some of the within-site variation in local moisture (which will also depend on aspect, drainage, and other features). Such variation is undoubtedly strong in the barrens, and this fine-scale variation in the driver of larger-scale distributions accounts for our ability to interpret local phylogenetic clustering.

Linking phylogenetic community structure and species distribution models: a path forward

The invention of techniques for measuring phylogenetic community structure (Webb 2000) was rapidly followed by their enthusiastic application to a broad range of systems (Vamosi et al. 2009). Part of the appeal of PCS metrics is that they have been seen as promising inference about community assembly via data that are easily obtained: species lists and phylogenies. However, the step from clustering or overdispersion to the mechanisms of community assembly is not an easy one (as for any attempt to infer process from pattern). Early enthusiasm for PCS analyses has been tempered to some degree by warnings that more than one process can generate any given pattern in phylogenetic community structure (Vamosi et al. 2009, Mayfield and Levine 2010), making it hazardous to draw conclusions from pattern alone. Much stronger inferences are possible in studies that combine PCS metrics with data on the species traits that underlie processes such as competition and environmental filtering. For instance, Cavender-Bares et al. (2006) detected phylogenetic overdispersion of Florida oak communities, but used trait data to show that this resulted

not from competition but from filtering – on traits that evolved convergently during adaptive radiation in different oak lineages. Such studies have remained uncommon, probably because it is difficult to gather the necessary trait data, especially in floras with high species richness or broad phylogenetic representation.

Our work suggests that the use of trait data implicit in species distribution models may provide a productive avenue for progress. SDMs are typically used to explain current distributions of species occurrence, and to predict changes in those distributions in response to anthropogenic stressors such as climate change and species introductions (Kellermann et al. 2012, Mbatudde et al. 2012). However, a few studies have instead taken advantage of the ability of SDMs to provide implicit estimates of species traits. For example, Diniz-Filho et al. (2010) used Maxent models to measure niche similarity between species, using a metric based on the Euclidean distance between habitat suitabilities across landscape cells. Our approach differs from Diniz-Filho et al.'s in that we provide direct estimates of traits for individual species, in the form of model coefficients that capture responses to selected environmental variables. Evans et al. (2009) also used Maxent to model niche occupancy and overlap, but did so in a way that produced detailed, non-parametric estimates of occurrence functions with respect to each environmental variable. These occurrence functions could be reparameterized to provide trait values comparable to ours, although it is not clear whether the additional complexity of this approach would yield additional insight.

The species traits extractable from SDMs are more ecologically integrative than those typically measured in the field or lab (e.g. seed mass, leaf area, wood density; Cavender-Bares et al. 2006, Kraft et al. 2008), because they represent the plant's response to the environment as a result of an entire suite of physiological, anatomical or other traits. This may be a shortcoming in that it is more difficult to connect analyses of SDM-derived trait data to experimental work such as manipulation of plant traits in competition experiments. However, a compensating virtue of defining traits via SDMs is that the traits are not chosen simply for measurability; instead, we can be assured of their ecological importance, as they are inferred from distributional data. In addition, the increasing availability of occurrence records as museum collections are digitized and placed online should provide a rich source of trait data even for species that are ecologically or physiologically unstudied.

One important empirical question is how often traits determining broader-scale species distributions – and thus accessible to our SDM-based approach – will also determine occurrence on finer spatial scales. In our barrens system, it seems that drought stress influences occurrence on both the 1-km-and-up scale of our Maxent models and on the 25 cm scale of our quadrat surveys. This need not always be true, and if processes at the two spatial scales are frequently decoupled, our approach will be less useful. For instance, we might measure strong local clustering without detecting environmental constraints on occurrence in SDMs (or if constraints were detectable, they could lack phylogenetic signal and thus fail as explanations for the observed local pattern; Valladares 2008). Because our study is the first,

to our knowledge, to link phylogenetic community structure to implicit traits from SDMs, we cannot yet know whether all, or most, analyses will be as successful as ours. We are eager to find out.

Conclusion

By integrating conventional analysis of phylogenetic community structure with implicit trait data from species distribution modeling, we assembled a clear picture of plant community structure in our rock barrens. Our barrens communities showed strong phylogenetic clustering at the quadrat scale. We can identify a likely trait-based mechanism for this clustering: at least for our most common barrens species, distributions responded strongly to environmental characteristics related to drought stress, and implicit species traits describing those responses showed strong phylogenetic signal. But most traits did not show this signal. Thus, we suggest that barrens communities are phylogenetically clustered because the environmental variables that most influence plant distributions happen to interact with plant traits that are phylogenetically structured. The result is environmental filtering of rock-barren plants in response to quadrat-scale environmental variation. The combination of PCS and SDM perspectives on species distribution and co-occurrence may represent a powerful new approach to understanding community assembly.

References

Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. – Int. J. Plant Sci. 164: S165–S184.

Aliscioni, S. et al. 2012. New grass phylogeny resolves deep evolutionary relationships and discovers C4 origins. – New Phytol. 193: 304–312.

Anderson, R. C. et al. 2007. Savannas, barrens, and rock outcrop plant communities of North America. – Cambridge Univ. Press.

Argus, G. W. 2007. *Salix* (Salicaceae) distribution maps and a synopsis of their classification in North America, north of Mexico. – Harvard Papers Bot. 12: 335–368.

Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. – Ecol. Model. 200: 1–19.

Beven, K. J. and Kirkby, M. J. 1979. A physically based, variable contributing area model of basin hydrology. – Hydrobiol. Sci. Bull. 24: 43–69.

Blomberg, S. P. et al. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. – Evolution 57: 717–745.

Brouillet, L. et al. 2009. Astereae. – In: Funk, V. A. et al. (eds), Systematics, evolution, and biogeography of Compositae. International Association for Plant Taxonomy, pp. 747–777.

Burley, S. T. and Lundholm, J. T. 2010. Environmental predictors of forest expansion on open coastal barrens. – Biodivers. Conserv. 19: 3269–3285.

Cahill, J. F. Jr et al. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? – Perspect. Plant Ecol. 10: 41–50.

Campbell, C. S. et al. 2007. Phylogeny of subtribe Pyrinae (formerly the Maloideae, Rosaceae): limited resolution of a complex evolutionary history. – Plant Syst. Evol. 266: 119–145.

Cavender-Bares, J. et al. 2006. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. – Ecology 87: S109–S122.

Darwin, C. 1859. The origin of species. – Penguin Books, 1968 reprint.

Davies, T. J. et al. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. – Proc. Natl Acad. Sci. USA 101: 1904–1909.

Diniz-Filho, J. A. F. et al. 2010. Hidden patterns of phylogenetic non-stationarity overwhelm comparative analyses of niche conservatism and divergence. – Global Ecol. Biogeogr. 19: 916–926.

Elith, J. et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. – Ecography 29: 129–151.

Elith, J. et al. 2011. A statistical explanation of MaxEnt for ecologists. – Divers. Distrib. 17: 43–57.

Evans, M. E. K. et al. 2009. Climate, niche eEvolution, and diversification of the "bird-cage" evening primroses (*Oenothera*, Sections Anogra and Kleinia). – Am. Nat. 173: 225–240.

Funk, V. A. et al. 2009. Compositae metatrees: the next generation. – In: Funk, V. A. et al. (eds), Systematics, evolution, and biogeography of Compositae. International Association for Plant Taxonomy, pp. 747–777.

Gillespie, E. and Kron, K. 2010. Molecular phylogenetic relationships and a revised classification of the subfamily Ericoideae (Ericaceae). – Mol. Phylogenet. Evol. 56: 343–354.

Hall, K. et al. 2005. Rock albedo and monitoring of thermal conditions in respect of weathering: some expected and some unexpected results. – Earth Surf. Proc. Land. 30: 801–811.

Hardig, T. M. et al. 2010. A phylogenetic analysis of *Salix* (Salicaceae) based on matK and ribosomal DNA sequence data. – J. Bot. 2010: 1–12.

Heard, S. B. and Cox, G. H. 2007. The shapes of phylogenetic trees of clades, faunas, and local assemblages: exploring spatial pattern in differential diversification. – Am. Nat. 169: E107–E118.

HilleRisLambers, J. et al. 2012. Rethinking community assembly through the lens of coexistence theory. – Annu. Rev. Ecol. Evol. Syst. 43: 227–248.

Hinds, H. R. 2000. Flora of New Brunswick. – Dept of Biology, Univ. of New Brunswick.

Kellermann, V. et al. 2012. Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. – Proc. Natl Acad. Sci. USA 109: 16228–16233.

Kembel, S. W. and Hubbell, S. P. 2006. The phylogenetic structure of a neotropical forest tree community. – Ecology 87: S86–S89.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. – Bioinformatics 26: 1463–1464.

Kraft, N. J. B. et al. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. – Science 322: 580–582.

Kron, K. A. et al. 2002. Phylogenetic classification of Ericaceae: molecular and morphological evidence. – Bot. Rev. 68: 335–423.

Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – Ecol. Lett. 13: 1085–1093.

Mbatudde, M. et al. 2012. Modelling the potential distribution of endangered *Prunus africana* (Hook.f.) Kalkm. in east Africa. – Afr. J. Ecol. 50: 393–403.

Mittelhauser, G. H. et al. 2010. The plants of Acadia National Park. – Univ. Maine Press.

Oberndorfer, E. C. and Lundholm, J. T. 2009. Species richness, abundance, rarity and environmental gradients in coastal barren vegetation. – Biodivers. Conserv. 18: 1523–1553.

Ojeda, F. et al. 2010. Soil shapes community structure through fire. – Oecologia 163: 729–735.

Pearson, R. G. et al. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. – J. Biogeogr. 34: 102–117.

Phillips, S. J. 2006. A brief tutorial on Maxent. – < http://www.cs.princeton.edu/˜schapire/maxent/ >.

Phillips, S. J. et al. 2004. A maximum entropy approach to species distribution modeling. – In: Proceedings of the 21st International Conference on Machine Learning. ACM Press, pp. 655–662.

Potter, D. et al. 2007. Phylogeny and classification of Rosaceae. – Plant Syst. Evol. 266: 5–43.

Rabosky, D. L. et al. 2011. Species interactions mediate phylogenetic community structure in a hyperdiverse lizard assemblage from arid Australia. – Am. Nat. 178: 579–595.

Revell, L. J. et al. 2008. Phylogenetic signal, evolutionary process, and rate. – Syst. Biol. 57: 591–601.

Slingsby, J. A. and Verboom, G. A. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae : Schoeneae) of the Cape Floristic Region, South Africa. – Am. Nat. 168: 14–27.

Stark, K. E. et al. 2003. Relationships between seed banks and spatial heterogeneity of North American alvar vegetation. – J. Veg. Sci. 14: 205–212.

Stark, K. E. et al. 2004. Arrested development of soils on alvars of Ontario, Canada: implications for conservation and restoration. – Nat. Area. J. 24: 95–100.

Stephens, P. R. and Wiens, J. J. 2009. Bridging the gap between community ecology and historical biogeography: niche conservatism and community structure in emydid turtles. – Mol. Ecol. 18: 4664–4679.

Valladares, F. et al. 2008. Functional traits and phylogeny: what is the main ecological process determining species assemblage in roadside plant communities? – J. Veg. Sci. 19: 381–392.

Vamosi, S. M. et al. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. – Mol. Ecol. 18: 572–592.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – Am. Nat. 156: 145–155.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Webb, C. O. et al. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. – Bioinformatics 24: 2098–2100.

Weiss, A. 2001. Topographic position and landform analysis. – Poster presentation, ESRI Conference, San Diego, CA.

Wiens, J. J. and Graham, C. H. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. – Annu. Rev. Ecol. Evol. Syst. 36: 519–539

Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – Ecol. Lett. 13: 1310–1324.