Biogeographic patterns of lichens and trees on islands of the Boundary Waters Canoe Area Wilderness

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Research Article

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Abstract. Different biogeographic factors may influence the richness of lichen and tree assemblages found on islands within boreal lakes. To examine the relative importance of island area, insularity and habitat for shaping these richness patterns, we surveyed lichen and tree species on islands of the Boundary Waters Canoe Area Wilderness in northern Minnesota, USA. We hypothesized that dispersal would be a more important limiting factor for trees, whereas lichen richness would be limited primarily by habitat. Thirty islands were sampled during a one-week study in September-October 2009. For each island we measured island area, distance from lakeshore, and counted the number of habitats. A total of 51 lichen and 15 tree species were found. Lichens occurred on every island and ranged between 2 and 28 species per island. Trees were found on just 13 of the 30 islands and their richness ranged from 1-12 species. Regression analysis and structural equation modeling showed that habitat number and island size were the principle factors affecting the richness of both taxa. Insularity had a small effect on lichen richness and no effect on tree richness. When trees and lichens were examined separately, island area influenced tree richness more than did habitat, whereas lichen richness was most strongly influenced by tree richness.

Introduction

*T*he processes that shape species assemblages on islands have long fascinated ecologists. Among theories proposed to explain these patterns are ones that consider habitat availability and dispersal limitation (reviewed in Tangney et al., 1990). The Habitat Diversity Hypothesis articulated by Williams (1943) suggests that habitat availability is the primary driver of species richness because it expands niche space. This idea assumes that if a habitat is there, a species will find it, but fails to account for species' dispersal constraints. By contrast, MacArthur and Wilson's (1967) Equilibrium Theory of Island Biogeography incorporates dispersal limitation and proposes that island species richness results from a dynamic equilibrium between immigration and extinction, the former affected by island insolation, the latter by island area. These theories are not exclusive and some processes may be more important than others for certain taxonomic groups or species (Gustafson and Gardner, 1996; Burns, 2005). Some species' habitat requirements, for example, are more stringent

than others, and dispersal ability can vary widely across taxonomic groups.

Two taxa for which habitat availability and island insularity may exert different influence are trees and lichens. These taxa differ in their size and growth form, their habitat requirements, and the types of propagules they produce. Mature trees, for instance, are orders of magnitude larger than lichens, require sizeable areas of soil, and disperse by seeds. By contrast, lichens are typically small, often grow on rock substrata, and disperse via thallus fragments, soredia and diaspores (Jüriado et al., 2006; Nash, 2008). Both produce propagules that can be dispersed by wind and animals (Bailey and James, 1979; Heinken et al., 2007), but to different degrees. For example, a wind gust is likely to carry a lichen soredium much further than a pine seed (Armstrong, 1991), but that same pine seed has a higher probability of being dispersed by a bird or squirrel because it represents a food resource (Wenny, 2001; Vander Wall, 2008). These morphological and ecological distinctions likely influence the processes that shape tree and lichen assemblages on islands, potentially causing trees and lichens to "perceive" islands differently. What a tree recognizes as uninterrupted habitat, for example, may represent an archipelago of habitats to a lichen. By the same token, if lichens disperse their propagules further than trees, then distant islands become effectively "closer" for lichens.

To examine the relative importance of island area, insularity and habitat for shaping their biogeographic patterns, we studied the distribution of lichen and tree species on islands of the Boundary Waters Canoe Area Wilderness of northern Minnesota, USA. Our goal was to ascertain if particular factors influenced one taxonomic group more than the other. We hypothesized that dispersal would be a more important limiting factor for trees, whereas lichen richness would be limited primarily by habitat. Tree seeds can be dispersed by wind, but often depend on birds or animals to be carried far away from the parent (Tomback and Linhart, 1990; Siepielski and Benkman, 2007). By contrast, the wind-borne propagules of

lichens can have considerable reach (Armstrong, 1991; Armstrong and Bradwell, 2011), and may even travel continental distances (Munoz et al., 2004). Some lichens also depend on certain trees to serve as substrate (Johansson and Ehrlen, 2003; Lie et al., 2009), so we also hypothesized that lichen richness would be limited by tree species richness.

Materials and Methods

Study area and island selection

The Boundary Waters Canoe Area Wilderness of northern Minnesota, USA (BWCA or Boundary Waters) is a 441,107 ha designated wilderness area located on the U.S.-Canadian border in northern Minnesota. Characterized as a Level III ecoregion (Omernik, 1987), it has nutrient-poor glacial soils and mixed conifer-hardwood forests. The Boundary Waters forms a transition between the northern boreal and deciduous forests to the south. It is known for its abundant meso- and oligotrophic lakes. Islands within these lakes tend to be rocky, have thin soils and possess steep shorelines of exposed granite and schist bedrock (Heinselman, 2006).

We sampled 30 islands of varying size and distance from adjacent terrestrial habitats (i.e., lakeshores and other islands) on five BWCA lakes. Islands were sampled along a predetermined route by canoe between 26 September and 2 October 2009 in a region extending from Moose Lake (47° 58' 50" N; 91° 31' 17" W) to Alworth Lake (48° 00' 09" N; 91° 16' 59" W). We employed transect sampling and size-based criteria to select islands, such that all islands encountered along the planned route and having an area < 0.5 ha were examined. Our size-based criterion was chosen to facilitate rapid sampling and minimize covariance between island size and distance. Covariance is especially acute for small lakes in which larger islands occupy a high percentage of the lake surface, thereby "shrinking" the distance between lake and island shorelines. Our size-based criterion, therefore, represents a tradeoff between sampling biases for small vs. near islands.

Table 1. The eight habitat types and their attributes used to characterize island habitat richness.

Habitat type	Attributes
Bare rock	Exposed rock with no soil
Soil and moss	Soil and moss cover
Low shrub	Low woody plant cover
Grass	Graminoids with some woody plants
Forest	Mature trees growing in soil
Loose rock	Loose gravel and rock on soil
Wetland	Saturated soil with some open water
Pine needles	Pine needle ground cover

We choose the former because, in addition to minimizing island sampling time, selecting smaller islands reduced the likelihood of overlooking species and allowed more islands to be sampled within our one-week study period.

Data collection

Island distance from the nearest adjacent terrestrial habitat (i.e., lake shoreline or nearby island) was determined using a Bushnell Yardage Pro Sport 450 laser rangefinder. Island size was estimated by using a tape measure to find the island's long and short axes and then calculating the area of an ellipse. The intersection of the long and short axes was used to divide the island into four quadrats. Two people visually surveyed each quadrat to record the presence of common tree and lichen species. The survey was conducted by visually scanning the quadrant while walking a series of parallel transects until the entire quadrat area was covered. Once this was done, scans continued until species counts became asymptotic. Lichens were initially identified using a field guide (Walewski, 2007). Problematic lichen were collected and returned to the laboratory so they could be examined with a dissecting scope and identified with other taxonomic keys (e.g., Brodo et al., 2001). Trees were identified using a field guide by Brockman (2001).

After lichens and trees were surveyed, habitat richness was quantified for each island. Island habitats were categorized into eight types based on substrate, ground, and plant cover (Table 1). These categories were based on

readily discernible features that allowed for their rapid assessment and enumeration. It is important to note that our quantification of habitat types served as much an index of habitat richness as an enumeration of habitats *per se*. Defining habitat is necessarily subjective and habitat requirements for trees and lichens differ, so we intended our measure of habitat richness to be an approximation of habitat availability for each taxon.

We understood that our rapid assessment technique could result in some lichens – and to a lesser extent, some trees – being missed, underestimated or misidentified; however, our goal was not to comprehensively list all lichen and tree species, nor was this necessary for addressing our hypotheses. Rather, we intended to document the presence or absence of common, field-identifiable species across a range of islands to assess biogeographic processes.

Statistical analysis

We tested our hypotheses using multiple regression and structural equation modeling (SEM). Multiple regression was used to explore the main effects of island area, habitat richness and island distance on tree and lichen species numbers. SEM was used to assess the relative influences of all factors simultaneously and develop a network of putative causal relationships (e.g., Weiher et al., 2004, Harrison et al., 2006). Regression analysis allowed us to identify the factors that influenced taxon richness, and SEM allowed us to make comparisons among factors and assess their relative strength. Regression analysis was performed using JMP software (version 9), and AMOS software (version 16) was used to build and run the SEM. Goodness of fit for the SEM was evaluated using chi-square, root mean square error of approximation (RMSEA), and the comparative fit index (CFI).

Results

Sampled islands ranged $3 - 429$ m^2 in area and all but three were within 100 m of adjacent

Table 2. The location of the BWCA islands sampled, their area, distance from the nearest adjacent lakeshore or island, the number of habitats each contained, and the number of lichen and tree species observed.

Island	Lat. (N)	Long. (W)	Area (m^2)	Distance (m)	Habitats	Lichen	Trees
1	48° 2′4.95″	91°22′12.21″	154	33	1	10	0
2	48° 1′58.77″	91°21′48.85″	156	155	3	5	0
3	48° 2′10.61″	91°21′21.34″	59	44	2	2	0
4	48° 1′56.97″	91°21′9.40″	67	100	2	4	0
5	48° 2′10.41″	91°20′11.70″	283	37	2	5	0
6	48° 0′52.31″	91°17′31.01″	28	80	1	10	0
7	48° 0′54.86″	91°17′34.11″	43	17	1	9	1
8	48° 0′55.37″	91°17′34.78″	43	17	3	12	2
9	48° 1′2.05″	91°17′25.73″	15	22	2	8	0
10	48° 1′2.81″	91°17′22.13″	145	91	7	21	3
11	48° 1′3.69″	91°17′21.26″	40	94	5	15	3
12	48° 1′6.79″	91°17′18.18″	49	214	5	4	0
13	48° 1′7.25″	91°17′17.69″	189	247	4	12	4
14	48° 0′56.23″	91°17′8.41″	7	71	1	5	0
15	48° 0′56.02″	91°17′8.40″	3	70	1	4	0
16	48° 0′55.82″	91°17′8.38″	9	69	2	8	1
17	48° 0′55.70″	91°17′8.24″	4	71	1	3	0
18	48° 0′55.60″	91°17′8.33″	6	66	1	5	0
19	48° 0′22.57″	91°16′44.34″	4	14	1	9	0
20	48° 0′16.87″	91°16′37.88″	15	46	2	4	0
21	48° 0′14.16″	91°16′40.28″	314	40	7	24	2
22	47°59′55.98″	91°16′56.83″	384	50	7	20	6
23	48° 0′32.47″	91°16′58.89″	71	7	2	10	0
24	48° 0′25.40″	91°17′11.07″	14	1	3	5	0
25	48° 0′54.24″	91°17′1.88″	429	69	8	28	5
26	48° 2′52.39″	91°24′50.71″	7	62	4	11	1
27	48° 2′52.59″	91°24′55.71″	9	2	3	6	1
28	48° 2′52.57″	91°25′7.56″	18	68	4	4	0
29	48° 0′48.39″	91°28′6.17″	269	57	6	25	12
30	48° 0′28.02″	91°28′19.20″	307	94	5	28	9
Mean ± S.E.			104 ± 23	66 ± 10	3.2 ± 0.4	10.5 ± 1.4	1.6 ± 0.5

lakeshores or other islands (Table 2). Habitat types varied among islands; however, all contained Bare Rock habitat and just over half had either "Soil and Moss" or "Low Shrub" habitats (17 and 16 islands, respectively). Habitat richness was influenced by island area such that there was a significant trend for an additional habitat being added with every 42 m^2 increase in island size (F = 28.45, P < 0.001, r^2 = 0.50; Figure 1).

Fifty-one lichens and 15 tree species were found on sampled islands (Tables 3 and 4). Lichens occurred on every island and ranged between 2 and 28 species and averaged 10.5 species/island. The four most common lichen species were the foliose *Xanthoparmelia somloensis* Gyelnik (27 islands) and *X. cumberlandia* Gyelnik (21 islands), and the crustose

Caloplaca flavovirescens Wulfen (23 islands) and *C. arenaria* Pers. (18 islands). In contrast to lichens, only 17 of the 30 sampled islands had trees, and islands with trees averaged 3.9 species/island. Most common were *Pinus banksiana* Lamb. (jack pine; 7 islands), *Picea mariana* Mill. (black spruce; 6 islands), and the shrub *Alnus viridis* Chaix (green alder; 6 islands).

Tree and lichen richness showed a positive relationship to island habitat number and island area (Table 5; Figure 2A and B); however, the area relationship was only marginally significant for trees (P =0.069). The species/area relationship was linear rather than the logarithmic (r^2 values were 0.59 vs. 0.43 for lichens and 0.45 vs. 0.33 for trees, respectively). This was because the sampled islands were small enough
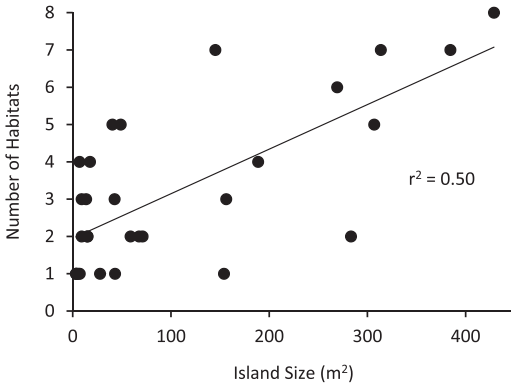
Figure 1. The relationship between habitat richness and island area for the 30 sampled islands.

not to become saturated with the available species from the regional pool, suggesting that our data represent the ascending limb of the predicted logarithmic relationship.

Island distance did not affect either taxa when examined by multiple regression, yet there was a distinct, non-linear drop in lichen richness on islands > 100 m distant (Figure 2 C). Beyond 100 m, the average lichen species number fell from 11 to 7.

Assessments of fit for our structural equation model (SEM) indicate it had an adequate to good fit to the data (following Grace, 2006, on characterizing fit). We used three measures; the Comparative Fit Index (CFI), the chi-square statistic, and the root mean square error of approximation (RMSEA). The model's CFI, in which values over 0.9 indicate good agreement between the data and model, was 0.977. The chi-square statistic was 4.936 with df =3 and P = 0.177, which suggests that there was no significant difference between the data and the model. By contrast, the root mean square error of approximation (RMSEA) was 0.149 with P = 0.203, indicating a poor fit (RMSEA values < 0.10 indicate good fit). However, RMSEA is sensitive to sample size and we had data from only 30 islands. In addition, RMSEA is sensitive to model complexity, and the model was nearly saturated with just three degrees of freedom. We also ran the SEM using log(area), but this resulted in reduced path coefficients and r^2 values.

Our SEM explained 82% of the variation in lichen richness and 52% of the variation in tree richness (Figure 3). Island area had a large effect on habitat number, which in turn influenced both tree and lichen richness. Lichen richness was most strongly influenced by tree richness and a plot of this relationship shows lichen species increasing asymptotically with tree species number (Figure 4). Tree richness was most strongly influenced by island area and less so by habitat richness. The total effect of island area on species richness was 0.67 for

Table 3. The 15 tree species that were identified on the 30 sampled islands. Islands are numbered by the order in which they were sampled.
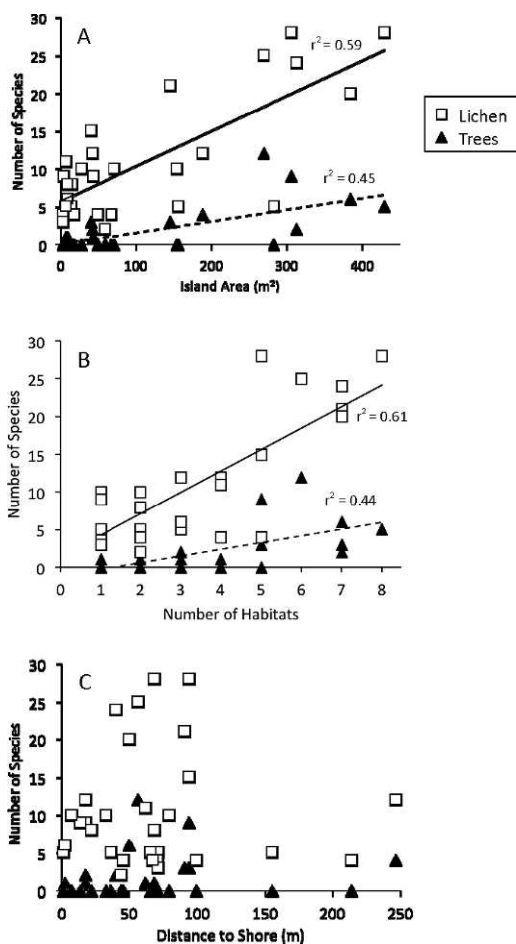
Tree species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Abies balsamea																						X							X	X
Abies fraseri																						X			X					
Acer rubrum																													X	
Alnus viridis							X														X	X			X				X	X
Betula papyrifera																						X							X	X
Cornus sp.																													X	X
Juniperus communis											X																		X	
Picea glauca																													X	
Picea mariana							X	X					X			X									X					X
Pinus banksiana										X	X		X									X			X				X	X
Pinus resinosa										X	X											X							X	X
Pinus stobus											X		X									X								X
Prunus pensylvanica																													X	
Sorbus americana																			X										X	
Thuja occidentalis													X													X	X		X	X

Table 4. The 51 lichen species that were identified on the 30 sampled islands. Islands are numbered by the order in which they were sampled.

Lichen Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Ahtiana aurescens																														X
Aspicilia cinerea						X		X		X	X	X									X	X			X					X
Baeomyces rufus																										X				
Buellia aethalea																			X			X			X				X	X
Caloplaca arenaria	X						X	X		X				X	X	X	X		X	X	X	X	X	X		X	X		X	X
Caloplaca flavovirescens							X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X
Candelariella aurella																									X		X		X	
Candelariella efflorescens																						X				X			X	X
Candelariella vitellina	X	X	X	X																										
Cladina rangiferina																									X					
Cladonia coniocraea																										X				
Cladonia amaurocraea						X																								
Cladonia chlorophaea							X	X		X			X							X		X	X	X	X	X	X		X	X
Cladonia coniocraea							X		X											X		X	X	X	X				X	X
Cladonia cristatella	X						X													X		X	X		X					X
Cladonia fimbriata						X				X												X	X							
Cladonia mitis							X	X	X	X			X									X	X	X	X			X		
Cladonia phyllophora																													X	X
Cladonia stellaris																									X				X	X
Cladonia turgida						X				X								X							X				X	X
Cladonia uncialis														X																
Dermatocarpon luridum	X							X		X		X			X	X	X			X	X	X	X							X
Dermatocarpon miniatum																								X						
Dimelaena oreina	X																													
Evernia mesomorpha																									X					
Flavoparmelia caperata										X	X											X	X		X	X	X		X	X
Imshaugia placorodia																							X		X					
Lecidea tessellata	X				X			X			X		X							X					X				X	X
Lepraria loboficans																										X			X	X
Lepraria neglecta	X	X	X	X	X			X	X	X	X	X						X		X			X	X		X			X	X
Lobaria oregana						X		X		X																			X	
Melanelixia subaurifera											X											X	X						X	X
Ochrolechia trochophora																										X				
Parmelia squarrosa											X		X			X							X		X		X		X	X
Peltigera polydactyla																					X		X						X	X
Peltigera rufescens																					X	X	X							X
Phlyctis argena										X												X	X		X	X				
Physcia stellaris																X									X					X
Pseudevernia consocians																														X
Ramalina intermedia										X															X					
Rhizoplaca chrysoleuca						X		X		X	X											X			X			X	X	
Stereocaulon saxatile								X		X	X											X	X		X					
Trapeliopsis granulosa										X																				
Umbilicaria deusta	X		X	X			X		X						X							X			X					X
Umbilicaria mammulata																													X	
Umbilicaria muehlenbergia								X		X												X			X					
Usnea hirta							X		X	X	X		X			X						X	X		X	X			X	X
Usnea subfloridana							X			X	X		X												X				X	X
Xanthoparmelia cumberlandia	X	X				X	X	X	X	X	X			X	X		X			X		X	X	X	X	X		X	X	X
Xanthoparmelia sp.		X																												
Xanthoparmelia stenophylla	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X

Table 5. Species richness as a function of the three biogeographic parameters (i.e., island area, distance from shore, and habitat richness) based on multiple regression analyses. A separate regression model was constructed for each taxon, and the adjusted R^2-values were 0.70 and 0.46 for lichen and trees, respectively. The β^* values are the standardized partial regression coefficients for each factor.

Taxon	Parameter	df	β^*	F-value	P-value
Lichens	Area	1	0.41	8.25	0.008
	Distance	1	-0.17	2.74	0.111
	Habitat	1	0.53	13.08	0.001
Trees	Area	1	0.41	20.27	0.069
	Distance	1	-0.01	0.029	0.938
	Habitat	1	0.38	16.56	0.046

trees and 0.52 for lichens (following the laws of path coefficients; Grace, 2006), suggesting a greater importance of area for trees. Distance had a small negative effect (-0.17) on lichen richness and no effect on trees. Distance and island size were positively correlated to a small degree (0.13), indicating that more distant islands tended to be slightly larger. Islands that were < 100 m (n = 28) averaged 104 m^2 in area whereas those > 100 (n = 3) averaged 131 m^2.

Discussion

Island size and habitat were the principle factors affecting lichen and tree richness on the islands studied. By contrast, island distance (i.e., insularity) had only a small effect on lichen richness and no effect on tree richness. These results lend support to the Habitat Diversity Hypothesis (e.g., bigger islands support more

Figure 2. The relationship between tree and lichen species richness and island area (A), habitat richness (B), and distance from the nearest lakeshore (C). The trend line is solid for lichens and dashed for trees. Lines are not shown in (C) because no linear relationships were detected.
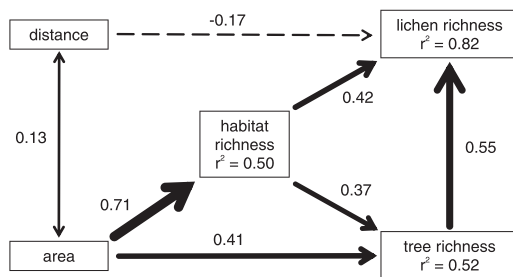
Figure 3. Structural equation model for factors influencing lichen and tree richness for the Boundary Waters islands sampled. Single-headed arrows represent putative causal relationships, and path coefficients are standardized partial regression coefficients (which can be interpreted as independent partial correlations). The double-headed arrow represents a simple correlation.
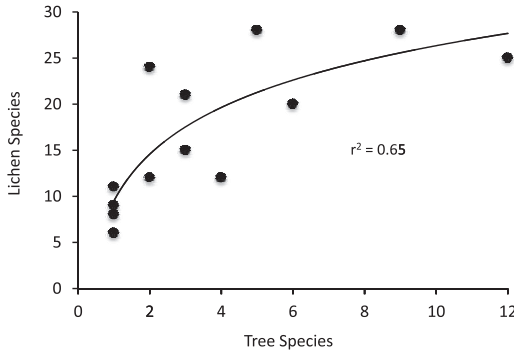
Figure 4. The relationship between lichen and tree richness for the 17 islands that had trees. The fitted, logarithmic line (y = 7.32*$\ln$x + 9.5) shows the asymptotic trend in the data.

habitat types); however, trees and lichens responded to habitat availability differently.

For trees, island area influenced richness more than did habitat; for lichens, tree richness was the single most important factor. These results are intuitive because trees are larger and require more space, and hence, island area constitutes an aspect of tree habitat that we did not formally assess. For lichens, trees comprise critical habitat (Johansson and Ehrlen, 2003; Morley and Gibson, 2010). This was well illustrated by the relationship found between lichen and tree richness (Figure 4), which looks similar to a species-area curve, but one in which tree species are the "area". Indeed, trees are known to provide niche space for lichens (Antoine and McCune, 2004; Gauslaa et al., 2008) and lichens are frequently associated with particular tree species and forest community types (Sillett et al., 2000; Lie et al., 2009). Trees may also modify local environmental conditions to favor lichens (Jonsson et al., 2009). For example, trees can provide shade, act as windbreaks, and buffer temperature extremes to help reduce lichen desiccation stress (Kalapos and Mazsa, 2001; Gignac and Dale, 2005; Ranius et al., 2008). With these other aspects of habitat considered, it might be said that we actually examined two habitat parameters for each taxa, one defined by us (Table 1), and the other defined by area for trees, and tree

richness for lichens. Of these two, the latter were better predictors of species numbers.

We had hypothesized that tree richness would decrease on distant islands because they would be limited by dispersal, but this was not the case. Instead it was lichens that showed a small response to island insularity (Figure 3); in particular, our data suggest that lichen richness declined beyond 100 m (Figure 2C). Although lichens have a potential for long-range dispersal, some have effective dispersal ranges of 100 m or less (Armstrong, 1987; Heinken, 1999; Dettki et al., 2000; Ockinger et al., 2005; Jüriado et al., 2011). For example, Ockinger et al. (2005) found the mean dispersal distance for *Lobaria pulmonaria* in Swedish forests was 35 m, with a recorded maximum of 75 m. In another study, Jüriado et al. (2011) found a dispersal range of only 5-30 m. The type of propagule being dipersed can also be important (Armstrong, 1987; Heinken, 1999); for example, Heinken (1999) found that thallus fragments of *Cetraria muricata* and *Cladonia* spp. traveled distances that were typically < 1 m. These studies and others suggest that boreal lichens are limited by local dispersal and we speculate that island insularity becomes a more critical factor structuring the lichen assemblages on islands > 100 m). Unfortunately, our sample size of distant islands was small.

Only three (10%) of the islands sampled were more than 100 m from lakeshores and adjacent islands. Had we sampled more islands at greater distances we might have seen an enhanced insularity effect for lichens and perhaps trees as well. The primary reason we did not survey a greater number of distant islands was that they were rare in the Boundary Waters lakes we sampled. These lakes were typically only a few hundred meters wide, and lake dimension necessarily constrains island insularity. Also, the most isolated part of a lake is often the deepest, and consequently, less likely to have islands.

We chose to sample islands < 0.5 ha in area for reasons of sampling efficiency and to help counteract a bias towards "near" islands. Larger islands tend to be nearer to the shorelines by virtue of their "lake-filling"

effect. Had we sampled bigger islands an inverse relationship between island size and distance may have confounded our analyses. This did not occur; in fact, our data show a slight trend in the opposite direction – that distant islands were slightly larger. Even so, the constraints imposed by our study system made it difficult to locate islands > 100 m from shorelines and our data largely reflect the processes occurring on near islands where insularity effects were minimal. Our results indicate that these islands are essentially habitat patches to lichens and trees and their richness is determined by habitat availability, which included aspects of area (for trees) and the presence of other species (for lichens).

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