

COVARIANCE OF LICHEN AND VASCULAR PLANT FLORAS

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ABSTRACT. The geographic relationships among taxonomic groups are important to study to determine patterns of biodiversity and whether or not associations occur between large groups, e.g., birds and vascular plants. This study was undertaken to determine relationships between higher plants and lower plants, specifically vascular plant and lichen floras in nine national parks of the Great Lakes region. No significant relationship was found between vascular plant floras and lichen floras in this area, which spans 1200 km longitudinally, or between an additional 19 areas from North America that were less than 1000 km² in area. For areas larger than 1000 km², however, a significant positive relationship existed for 33 areas that span one to approximately 150 million km². The ratio of numbers of vascular plants to lichens appeared to average just over 6 across the 33 areas. In the Great Lakes parks, between 28–30% of either the vascular plant or lichen species were singletons (occurring in only one park), but the parks that contained the most singletons were not congruent: Isle Royale had the most singleton lichens, while Indiana Dunes had the most vascular plant singletons. Fewer lichen species (2%) than vascular plants (4%) occurred in all nine parks. Latitude appeared to explain some of the variation between the two groups: vascular plants decreased with increasing latitude, while lichens increased.

Key Words: floras, lichens, vascular plants, species-area curves

The number of lichen species in North America, north of Mexico, is thought to be approximately 3600 (Esslinger and Egan 1995), while the number of vascular plant species approaches 22,000 (Kartesz 1994), a ratio of about six vascular plant species to one lichen species. Although general, ratios like this have been used to make broad biodiversity estimates (e.g., Hawksworth 1991). Such estimates can be made more useful if the geographic pattern of covariance of higher taxa can be ascertained. In recent years studies of spatial covariance of higher taxa have been conducted in order to determine patterns of biodiversity hotspots, or

the relationships among taxa, if any exist (Faith and Walker 1996; Gaston 1996). Many factors can affect spatial covariance, including scale, environmental factors, and biological properties of the taxa. Several authors have pointed out that lichen and vascular plant diversities may not track each other in general due to climate (Huston 1994) and habitat diversity (Galloway 1992; Gilbert 1977). Another study found that lichen biodiversity decreased significantly with an increase in vascular plant cover (Pharo and Beattie 1997). In addition, we suspected that the effects of air pollutants may also be a factor affecting lichen and vascular plant floras differentially because of the greater air pollution sensitivities of lichens. This paper explores all of these issues using the lichen and vascular plant floras of nine national parks in the Great Lakes region of the United States.

The lichen floras of nine national parks in the Great Lakes region of the north central United States have been well studied in recent years and are considered to be fairly complete. The parks include Apostle Islands National Lakeshore in Wisconsin (APIS), Cuyahoga Valley National Recreation Area in Ohio (CUVA), Grand Portage National Monument in Minnesota (GRPO), Indiana Dunes National Lakeshore in Indiana (INDU), Isle Royale National Park (ISRO) and Pictured Rocks National Lakeshore in Michigan (PIRO), St. Croix National Scenic River in Minnesota and Wisconsin (SACN), Sleeping Bear Dunes National Lakeshore in Michigan (SLBE), and Voyageurs National Park in Minnesota (VOYA; Figure 1). It is logical to study these floras because they should show affinities with one another, being associated geographically within the homogeneous Great Lakes/north central U. S. region. The nine parks span a region of about 1200 km longitudinally, and in the aggregate, cover a total area of 201,000 km². The vascular plant floras of these parks have been studied and were segregated into two groups by multivariate analyses (Bennett 1996a, 1996b). This study was also undertaken to determine if the same groups of parks are segregated based on the lichen floras.

The management of natural area preserves is sometimes focused on a select group of organisms, e.g., mammals, trees, rare plants, birds, or butterflies. It is often implicit in the management of these groups that the management of one group will also satisfactorily manage another group by association. This is because it is assumed that the biological groups in an area are related. For

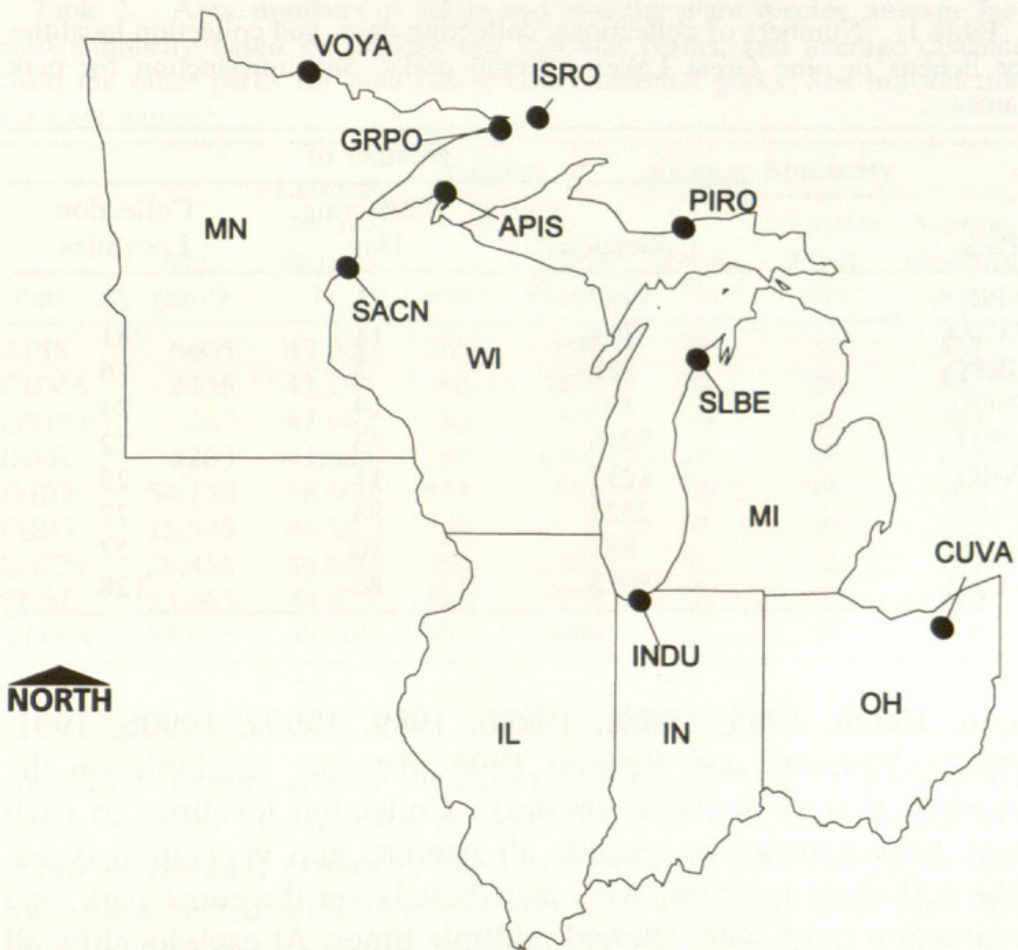


Figure 1. Map of nine Great Lakes national park units for which floras were used in this study. Park codes are explained in the introduction.

the purposes of this study, it was assumed that vascular plants and lichens are related floristically somehow, although ecologically they occupy habitats at very different scales and their floristic relationships may be obscure. From a management perspective however, it may be assumed that if there are more vascular plants in an area there will also be more lichens. This study was undertaken in order to determine the validity of this assumption by attempting to prove the hypothesis that there is no relationship between vascular plant and lichen floras.

MATERIALS AND METHODS

Lichen floristic field work in the nine parks was conducted during the summer in the years from 1978 to 1995, although collecting was not done in these particular parks every year (Wet-

Table 1. Numbers of collections, collecting days, and collection localities for lichens in nine Great Lakes national parks. See introduction for park names.

Park	Number of		
	Collections	Collecting Days	Collection Localities
APIS	1497	21	28
CUVA	304	11	31
GRPO	373	3	6
INDU	371	14	24
ISRO	5246	53	72
PIRO	1231	11	25
SACN	2327	88	77
SLBE	847	10	27
VOYA	8028	80	128

more 1983b, 1985, 1988a, 1988b, 1989, 1990a, 1990b, 1991, 1992b; Wetmore and Bennett 1996 [data are available on the Internet at www.ies.wisc.edu/brd]). Collection localities in each park were selected to include all habitats and vegetation types. The collection localities were distributed over the entire park, and vegetation types were studied multiple times. At each locality, all groups of lichens were collected (fruticose, foliose, squamulose, and crustose) and sufficient time was spent examining all substrates. At each locality all species found were collected to provide relative abundance estimates, even though the same species might have been found at previous localities. A summary of the collecting efforts is shown in Table 1. Vascular plant floras and methods were described previously (Bennett 1996a).

The nomenclature of each lichen flora was updated to the fifth checklist (Egan 1987) so as to standardize all the names. The names were then entered into a computer spreadsheet program (MICROSOFT EXCEL, Microsoft Corp., Seattle, WA) and the presence/absence of each species recorded in a field for each park. Various tallies and sorts were performed in order to perform quality control procedures and to rank species by frequencies. This file was also used to analyze the data statistically, using MINITAB (Minitab, State College, PA) and SYSTAT (SPSS, Chicago, IL). Relationships between variables were tested with Pearson's linear correlation coefficients.

Similarities between park floras were calculated using Jaccard's

Table 2. Area, numbers of lichen and vascular plant species, average Jaccard similarity based on lichens and vascular plants, and average distance from the other parks for nine Great Lakes national parks. See introduction for park names.

Park	Area (km ²)	Latitude (decimal degrees N)	Number of Species		Average Similarity		Average Distance (km)
			Lichen	Vascular Plant	Lichen (%)	Vascular Plant (%)	
APIS	6605	47.000	285	509	39	35	388
CUVA	3136	41.283	66	855	18	26	842
GRPO	287	47.967	182	279	30	23	383
INDU	5203	41.625	62	1399	19	28	638
ISRO	54,140	48.000	554	698	31	37	400
PIRO	25,545	46.567	245	723	36	39	415
SACN	26,459	46.000	282	1165	34	33	443
SLBE	23,663	44.875	182	928	33	37	426
VOYA	55,955	48.500	458	603	35	35	566

similarity index, which measures the proportion of park pairs where species are present in both parks in the pair. Details are given in Bennett (1996b). The correlation of two similarity matrices was tested with Mantel's test with PC-ORD (McCune and Mefford 1997).

Park distances and latitudes were measured using STREET ATLAS (De Lorme, Freeport, ME), a desktop computer mapping program. Straight line distances and latitudes were calculated using the approximate park centroids for park locations. Distances were rounded to the nearest five kilometers.

RESULTS

A floristic summary of each park is shown in Table 2. Isle Royale had the greatest number of lichen species, while Indiana Dunes had the lowest. The greatest and lowest numbers of vascular plant species, however, were at Indiana Dunes and Grand Portage, respectively. Based on the lichen floras, seven of the parks were, on average, between 30 and 40% similar to all the other parks, except for Indiana Dunes and Cuyahoga Valley, which were almost 20% similar to all other parks. This is not too surprising, given that on average they are farther away from all the other parks. Overall similarity based on vascular plant floras

followed the same pattern, except for Grand Portage, which had the lowest overall similarity, lower than Cuyahoga Valley and Indiana Dunes.

Some of the variables were significantly correlated (Table 3): lichen numbers and park area (Figure 2), and average lichen similarity and average distance (Figure 3) or latitude were the strongest relationships. Number of lichens increased with latitude, while vascular plant numbers decreased (Figure 4). Numbers of lichens and vascular plants appeared to be negatively correlated, but the probability of the correlation occurring by chance was high (0.33). Park similarities based on lichens and vascular plants were comparable ($P = 0.0517$). Vascular plant similarity significantly increased with area and did not appear related to latitude, while park lichen similarity increased with latitude and was not related to area.

The lichen flora Jaccard similarity matrix for all possible 36 pairs of the nine parks is shown in Table 4. Two park pairs, Isle Royale and Voyageurs, and Apostle Islands and Pictured Rocks were greater than 50% similar, while the overall average was 31%. The comparable distance matrix (Table 5) shows that Cuyahoga Valley and Voyageurs are just over 1200 km apart, while Grand Portage and Isle Royale are the closest pair at only 60 km apart. The similarities for these same pairs were 11% and 30%, respectively (Table 4). When all 36 pairs of similarities and distances were plotted against each other (Figure 5), there was a clear negative relationship, even though the maxima and minima did not all correspond.

The overall average of vascular plant similarities was 32% (see Table 1 in Bennett 1996b), and only one park pair, Isle Royale and Pictured Rocks, was more than 50% similar. The similarities of Cuyahoga Valley and Voyageurs, and Grand Portage and Isle Royale were 23% and 30%, respectively. The overall vascular plant similarity matrix was significantly positively related to the lichen similarity matrix (Mantel $r = 0.9151$, $t = 6.3718$, $P = 0.0000$), suggesting that these parks show comparable degrees and patterns of similarity based on both vascular plant and lichen floras.

A cluster analysis of the lichen flora Jaccard similarity matrix did not reveal any significant groupings because the similarities were not very diverse. However, a cluster analysis of the presence/absence matrix of all species in the nine parks did reveal

Table 3. Pearson's linear correlation coefficients for variables given in Table 2. Significance levels of coefficients are indicated by preceding asterisks: * (0.05), ** (0.01), and *** (0.001). ¹ Number of species.

	Area	Latitude	Lichens ¹	Vascular Plants ¹	Average Lichen Similarity	Average Vascular Plant Similarity
Latitude	0.5702					
Lichens ¹	***0.9124	**0.7968				
Vascular plants ¹	-0.1671	*-0.6985	-0.3715			
Average lichen similarity	0.5214	**0.8379	0.6210	-0.4850		
Average vascular plant similarity	*0.7054	0.3882	0.5783	0.0440	0.6628	
Average distance	-0.2143	*-0.7685	-0.4796	0.4002	** -0.8083	-0.4540

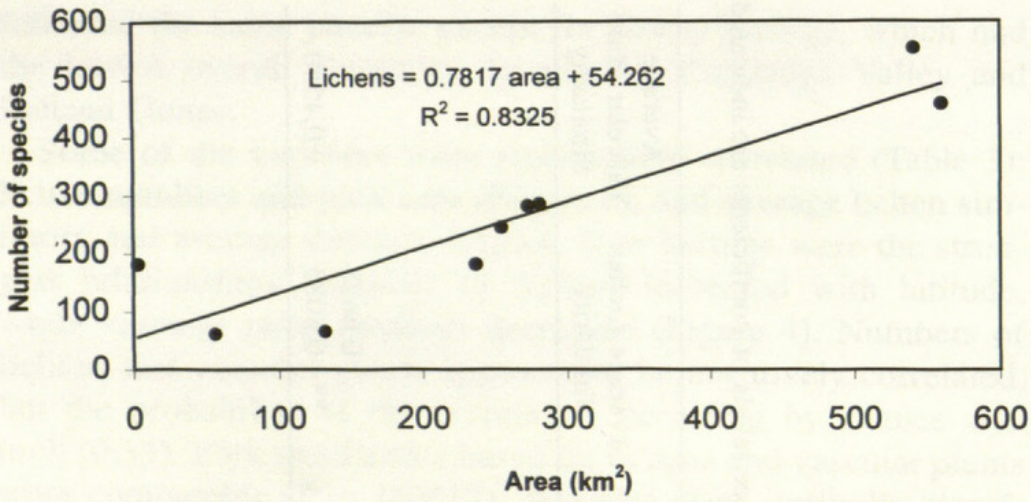


Figure 2. Relationship between number of lichen species and area for nine Great Lakes national parks, and fitted linear regression line.

some interesting groups (Figure 6). At the highest similarity level, about 80%, four parks (Apostle Islands and Pictured Rocks, and Cuyahoga Valley and Indiana Dunes) were grouped into two pairs that were themselves only about 36% similar. Cuyahoga Valley and Indiana Dunes appeared to be two parks that were unrelated floristically to the other seven, which appeared to be about 50% similar overall. Isle Royale, however, was less similar to the other six northern parks, in spite of the high individual Jaccard similarity with Voyageurs. Two groups of three parks each had sim-

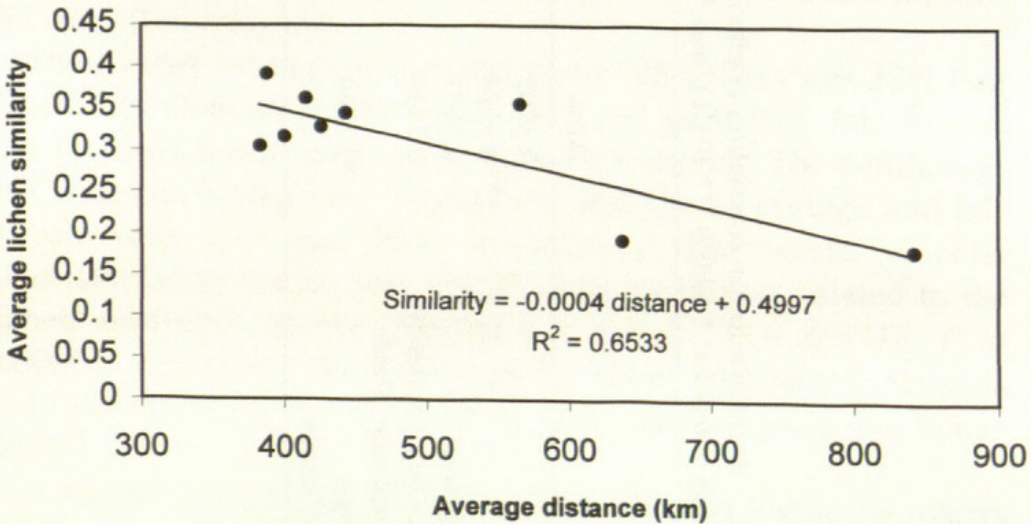


Figure 3. Relationship between average lichen flora similarity and average distance from the other parks for the nine Great Lakes national parks, and fitted linear regression line.

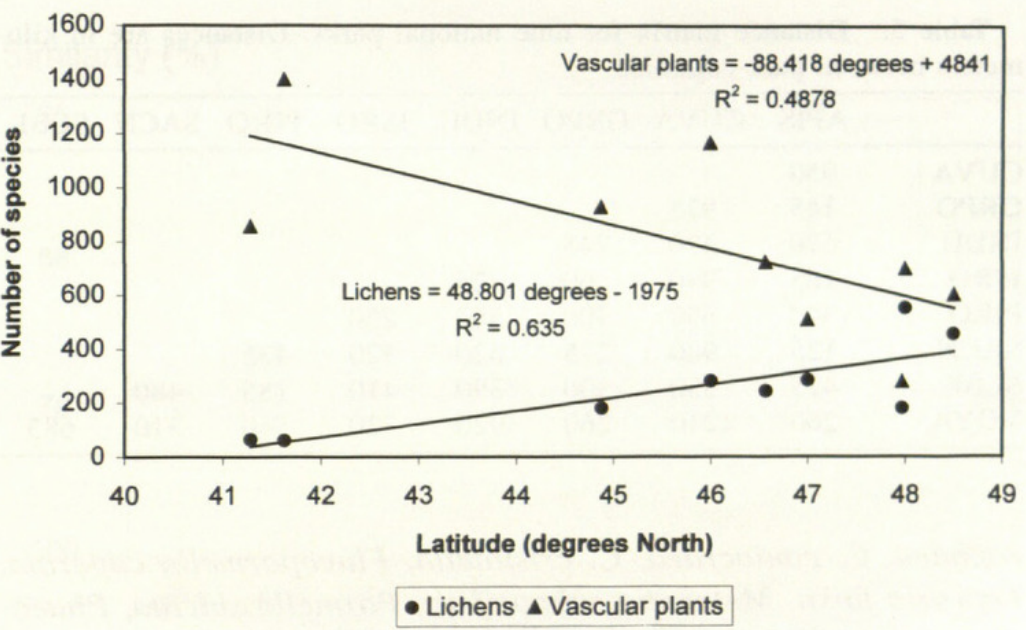


Figure 4. Relationships between number of vascular plant and lichen species and latitude for nine Great Lakes national parks, and fitted linear regression lines.

ilarities of 60–70%. One of these had two parks on the southern shore of Lake Superior and one at the northern end of Lake Michigan (Apostle Islands, Pictured Rocks, and Sleeping Bear Dunes), and the other consisted of three Minnesota parks (Grand Portage, Voyageurs, and St. Croix).

Totals of 698 lichen species in 162 genera were found in the nine parks when the floras were aggregated. The most frequent species, i.e., those that were found in all nine parks (14 species, or 2% of all lichen species found), included *Arthonia caesia*, *Candelariella efflorescens*, *Cladina rangiferina*, *Cladonia chlo-*

Table 4. Jaccard similarity (%) matrix for lichen floras of nine national parks.

	APIS	CUVA	GRPO	INDU	ISRO	PIRO	SACN	SLBE
CUVA	14.3							
GRPO	43.7	13.2						
INDU	16.4	43.8	14.0					
ISRO	44.7	9.0	30.0	9.0				
PIRO	57.3	13.1	40.9	15.0	38.2			
SACN	43.5	20.0	33.7	19.0	36.4	37.2		
SLBE	42.8	20.4	31.9	25.1	25.8	45.7	39.8	
VOYA	49.8	11.0	35.6	11.1	59.1	41.7	45.7	30.6

Table 5. Distance matrix for nine national parks. Distances are in kilometers between park centroids.

	APIS	CUVA	GRPO	INDU	ISRO	PIRO	SACN	SLBE
CUVA	950							
GRPO	145	975						
INDU	670	470	745					
ISRO	185	930	60	725				
PIRO	340	690	300	560	250			
SACN	125	980	275	620	320	435		
SLBE	425	530	300	390	410	185	480	
VOYA	260	1210	260	920	320	560	310	685

rophaea, *C. coniocraea*, *C. cristatella*, *Flavoparmelia caperata*, *Lepraria finkii*, *Melanelia subaurifera*, *Parmelia sulcata*, *Phaeophysica pusilloides*, *Physconia detera*, *Punctelia rudecta*, and *Scoliciosporum chlorococcum*. Thirty percent of lichens (210 species) occurred in only one park. Most of these (129) occurred in Isle Royale. For the vascular plants, an aggregated flora of 2102 species in 691 genera was found over all the parks, with 81 (4%) occurring in all nine parks. Twenty-eight percent of the vascular

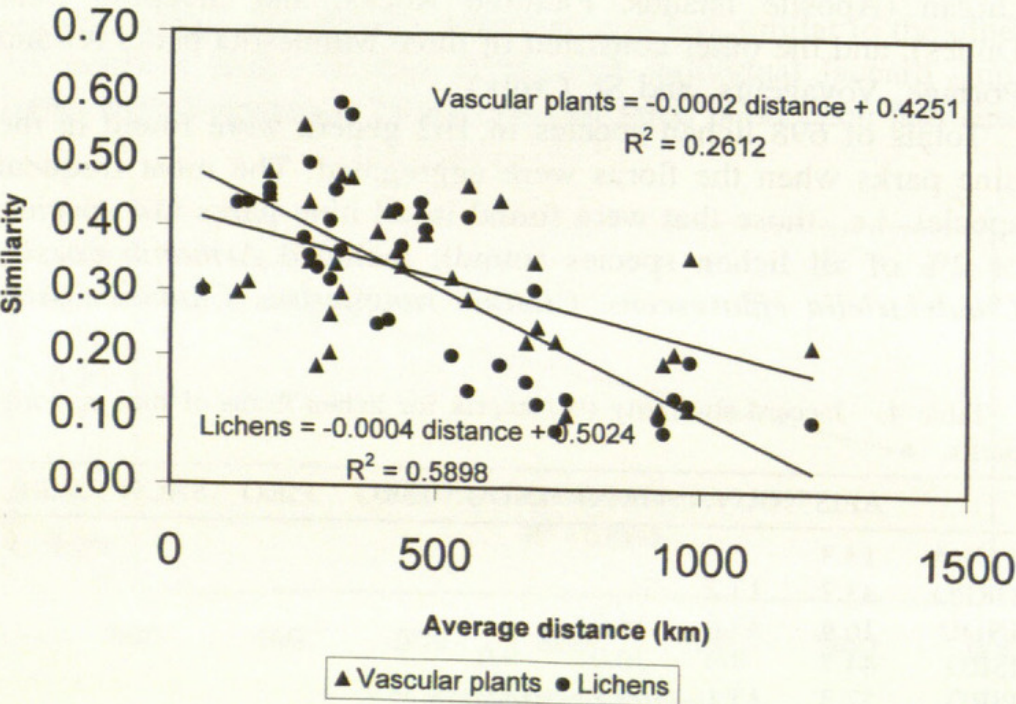


Figure 5. Relationships of vascular plant and lichen flora similarities to distance between parks for each of the 36 possible park pairs of the nine Great Lakes national parks, and fitted regression lines.

Similarity (%)

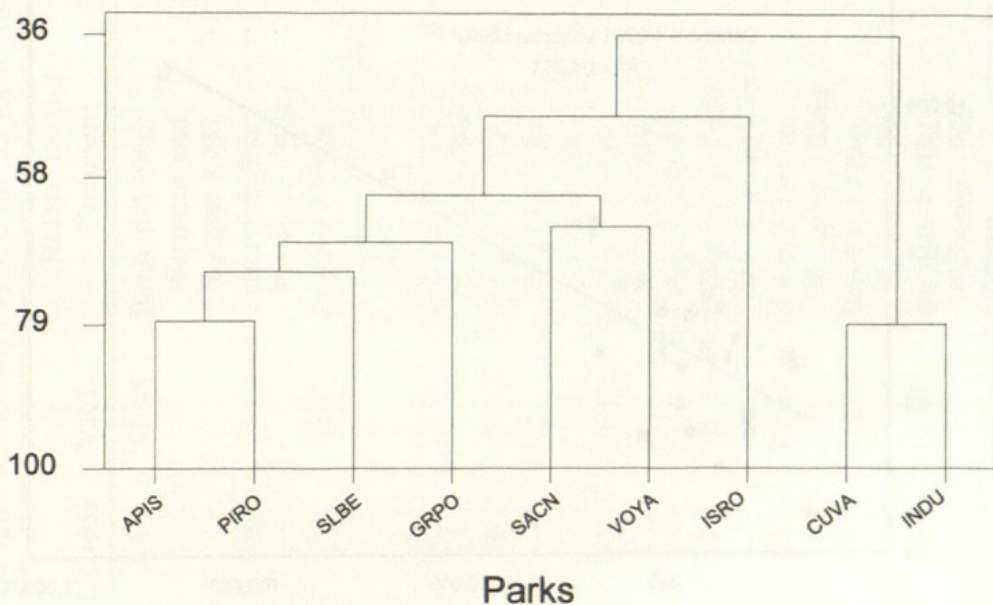


Figure 6. Cluster dendrogram for nine Great Lakes national park lichen floras, using Ward's linkage and correlation for the distance measure.

plants (596 species) occurred in just one park each. Most of these (221) were found in Indiana Dunes.

DISCUSSION

At first glance it appears that for this set of nine park floras there was no obvious relationship between vascular plants and lichens. However, further examination of the parks sheds more light on the problem. Two parks, Cuyahoga Valley and Indiana Dunes, are in locations that have been subject to oxidant and sulfur oxide pollution fumigations for many years, and studies have shown that the lichen floras of these parks have decreased to about 80% of their historical floras (Wetmore 1988a, 1989). However, if these two parks were to be omitted from the analysis there would not be enough data points to draw justifiable conclusions about the vascular plant/lichen relationship. When the historical total numbers of species were used instead of current species numbers (205 for Cuyahoga Valley and 154 for Indiana Dunes), there was still no clear relationship. This appears due to the vascular plant flora numbers rather than the lichen flora numbers. The vascular plant flora numbers were not linearly related to area (Table 3). This is probably due to confounding effects of

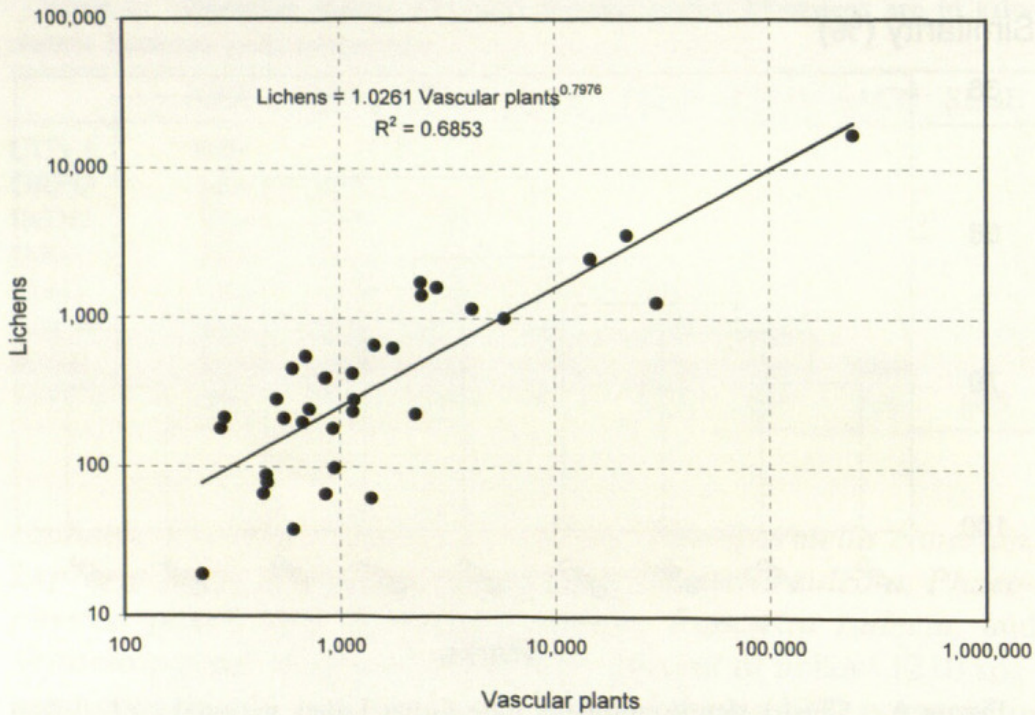


Figure 7. Relationship between numbers of lichen and vascular plant species for 33 areas, and fitted non-linear regression line.

latitude, as vascular plant diversity decreases with increasing latitude, the opposite of what happens with the lichen diversity (Huston 1994).

Do lichen and vascular plant floras co-vary? At the scale of the Great Lakes no relationship could be seen, but what about at other scales? The flora data for the nine parks were combined with comparable data for 24 other geographic areas, including the world, and are shown in Figure 7 (Table 6). It appears that when larger geographic areas were included, a significant, positive relationship was found between the two floras ($r = 0.9808$), even when the floras of the world were omitted ($r = 0.7037$). When only areas less than 1000 km² were considered, the relationship broke down ($r = 0.0896$). Area was obviously a factor when all 33 areas were considered (Figure 8), but may not have been with areas under 1000 km² for the reasons given above. This finding differs significantly from an older study of lichens and area where no relationship was found above 1000 km² (Wetmore 1967), which was based on incomplete inventories.

We conclude that any relationship between vascular plant and lichen floras is scale-dependent. For natural areas under approximately 1000 km², no relationship was found for the national

Table 6. Areas, numbers of vascular plant (VP) and lichen (L) species, and the ratio of the two (VP/L), for 33 locations.

Location	Area (km ²)	Vascular Plants	Lichens	VP/L	Reference and Comment
Homestead National Monument, NE	1	227	19	11.95	Bennett 1996a; Wetmore and Bennett 1997
George Washington Carver National Monument, MO	1	605	38	15.92	Bennett 1996a; Wetmore 1992a
Pipestone National Monument, MN	1	439	66	6.65	Bennett 1996a; Wilson and Vinyard 1986
Grand Portage National Monument, MN	3	279	182	1.53	Bennett 1996a; Wetmore 1992b
Effigy Mounds National Monument, IA	6	458	79	5.80	Bennett 1996a; Wetmore and Bennett 1997
Wilson's Creek National Battlefield, MO	7	454	88	5.16	Bennett 1996a; Wetmore and Bennett 1997
Tuxedni Wilderness, AK	23	290	214	1.36	Talbot et al. 1995; Talbot et al. 1992
Indiana Dunes National Lakeshore, IN	52	1399	62	22.56	Bennett 1996a; Wetmore 1988a
Apostle Islands National Lakeshore, WI	66	509	285	1.79	Bennett 1996a; Wetmore 1990a
Cuyahoga Valley National Recreation Area, OH	131	855	66	12.95	Bennett 1996a; Wetmore 1989

Table 6. Continued.

Location	Area (km ²)	Vascular Plants	Lichens	VP/L	Reference and Comment
Nantucket Island, MA	140	939	99	9.48	Dunwiddie and Sorrie 1996 (species not seen after 1960 omitted)
Acadia National Park, ME	190	858	397	2.16	Anonymous 1997b; Wetmore 1984
Sleeping Bear Dunes National Lakeshore, MI	237	928	182	5.10	Bennett 1996a; Wetmore 1988b
Pictured Rocks National Lakeshore, MI	255	723	245	2.95	Bennett 1996a; Wetmore 1990b
St. Croix National Scenic Riverway, MN and WI	265	1165	282	4.13	Bennett 1996a; Wetmore 1991
Theodore Roosevelt National Park, ND	285	550	212	2.59	Anonymous 1997b; Wetmore 1983a
Chiricahua National Monument, AZ	485	672	200	3.36	Anonymous 1997b; Wetmore and Bennett 1992 (Lichen number is doubled because flora is 50% known.)
Isle Royale National Park, MI	541	698	554	1.26	Bennett 1996a; Wetmore 1985
Voyageurs National Park, MN	560	603	458	1.32	Bennett 1996a; Wetmore 1983b

Table 6. Continued.

Location	Area (km ²)	Vascular Plants	Lichens	VP/L	Reference and Comment
Glacier National Park, MT	4,102	1147	425	2.70	Anonymous 1997b; Debolt and McCune 1993
Yellowstone National Park, WY	8,983	1150	236	4.87	Anonymous 1997b; Eversman 1990
Israel	21,946	2250	229	9.83	Zohary 1962; Kondratyuk et al. 1996
Netherlands	41,784	1781	633	2.81	Statistics Netherlands 1997; B. Wit, pers. comm.
Tasmania	67,858	1456	655	2.22	Chapman 1997; Galloway 1992
United Kingdom	229,979	2397	1,730	1.39	Palmer 1996; Galloway 1992
New Zealand	268,114	4167	1,162	3.59	Allan 1961; Moore and Edgar 1970; Healy and Edgar 1980; Webb et al. 1988; Galloway 1985
Finland	338,148	2423	1,420	1.71	Anonymous 1997a; O. Vit- kainen, pers. comm. 1997

Table 6. Continued.

Location	Area (km ²)	Vascular Plants	Lichens	VP/L	Reference and Comment
California	411,049	5862	1,000	5.86	Hickman 1993; Tucker and Jordan 1979
British Columbia	948,600	2850	1,600	1.78	British Columbia Ministry of Environment, Land, and Parks 1997
Australia	7,682,341	14,679	2,499	5.87	Chapman 1997; Galloway 1992
China	9,596,961	30,000	1,274	23.55	Harvard University Herbaria 1997; Wei 1991
United States and Canada	21,479,211	21,757	3,600	6.04	Kartesz 1994; Esslinger and Egan 1995
World	149,702,000	243,893	17,000	14.35	Mabberley 1987; Thorne 1992; Galloway 1992

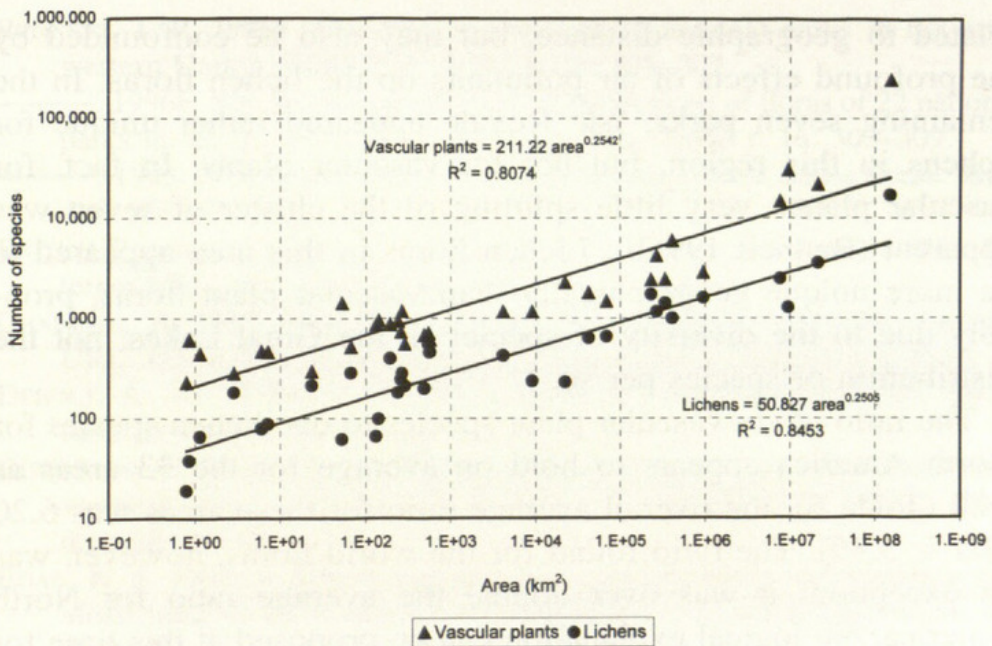


Figure 8. Relationships between numbers of lichen and vascular plant species and area for 33 areas, and fitted non-linear regression lines.

parks and areas in this study. This is partly due to the confounding effect of latitude, which affects vascular plant and lichen richness in opposite ways. A second reason is that we deliberately chose a set of natural areas in a relatively homogeneous ecological region so as not to introduce significant habitat diversity. The third reason is that vascular plants and lichens occupy microhabitats that are unrelated because of the scale differences between the two groups of plants. Lichens occupy habitats at the centimeter scale, while vascular plants could be said to occupy habitats at the meter scale. In addition, lichens can grow in some microhabitats where vascular plants are not found, e.g., house roofs or rocks. However, when the range of natural areas was expanded to include those larger than 1000 km², a relationship between vascular plant and lichen floras was found. This is most likely due to the effect area has on increasing ecosystem diversity, which produces more overall habitat diversity and hence species diversity.

The similarity clusters of the parks based on the two types of floras were not completely congruent. Both separated Indiana Dunes and Cuyahoga Valley from the other seven parks, although St. Croix was grouped with them for the vascular plants. This separation of Cuyahoga Valley and Indiana Dunes is probably

related to geographic distance, but may also be confounded by the profound effects of air pollutants on the lichen floras. In the remaining seven parks, Isle Royale appeared rather unique for lichens in this region, but not for vascular plants. In fact, for vascular plants, very little splitting of the cluster of seven was apparent (Bennett 1996b). Lichen floras in this area appeared to be more unique geographically than vascular plant floras, probably due to the diversity of species in the Great Lakes, not the distribution of species per se.

The ratio of six vascular plant species to one lichen species for North America appears to hold on average for the 33 areas as well (Table 6): the overall average ratio for these areas was 6.20 (SD = 5.89). The ratio found for the world floras, however, was an exception: it was over double the average ratio for North America. No logical explanation can be proposed at this time for this anomaly.

In conclusion, although average similarities of these nine parks, based on vascular plants and lichens, were comparable (just over 30%), this generalization hides the fact that the two types of floras do not appear related to one another at this scale. There was a closer relationship among the vascular plant floras than among the lichen floras, suggesting that geographic affinities between them are weaker for lichens. Thus, management strategies to conserve the vascular plant floras may not conserve the lichen floras on an equal basis. Lichen biodiversity may have to be managed differently than vascular plant biodiversity.

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