Island Biogeography of Seed Plants in Lake Nipigon, Ontario

KEVIN P. TIMONEY

Department of Botany, University of Wisconsin, Madison, WI. 53706
Present Address: Department of Botany, University of Alberta, Edmonton, Alberta T6G 2E9

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Islands supporting boreal forest in Lake Nipigon, Ontario, were sampled for presence of angiosperms and gymnosperms by a timed random walk of constant duration. Sample islands were manifestly different only in size (1.5-13.5 ha) and distance to mainland (1.0-10.5 km). Island species richness was correlated positively with area and negatively with distance. A new isolation index is proposed and shown to be a reliable predictor of island species number. It is suggested that propagules of many plant species on Lake Nipigon decrease in density as 1/distance^2 from a source, and that the total number of propagules produced by a source is directly proportional to the source area. The observed species-distance relation suggests that small distances may have a significant effect on island species number. Near islands are populated by equal numbers of animal and wind-water dispersed plant species. Distant islands are characterized by a predominance of wind-water dispersed plants.

Key Words: Angiosperms, dispersal, distance, gymnosperms, island biogeography, isolation, Lake Nipigon, Ontario, species-area relation.

At what distance does an island's isolation begin to affect higher plant species richness, and how does area *per se* affect species richness? Do islands that differ in area or isolation also differ in their types of propagule dispersal?

Much research has been done on oceanic and habitat islands, and most of that work has centered on the fauna. Continental lake islands have received little attention (c.f. McNeill and Cody 1978). Recent work indicates that higher plant species richness may be affected by isolation no greater than 1.5-10 km (Nip-van der Voort et al. 1979; Crowe 1979; Linhart 1980).

The islands in Lake Nipigon, probably 8,500 to 9,500 years old (Bryson et al. 1969), are most likely near species equilibrium. The lake's islands, of varying size and isolation, provide a test of the effects of short distances, and area, on seed plant species richness. Islands were selected stringently for habitat homogeneity, and recent disturbance by fire, humans, or windstorms resulted in rejection of an island. By sampling islands equal amounts of time, the likelihood of encountering more habitats on larger islands was minimized. The more thorough sampling of small islands provided a rigorous test of the effects of island area on species richness.

The purpose of this study was to find out if distance and area are significantly related to the species richness of seed plants on boreal forest islands.

Description of the Study Area Lake

Lake Nipigon lies about 60 km north of Lake Superior in the Thunder Bay District of NW Ontario. The lake's approximate geographic center is 88° 30′W, 49° 52′N. Nipigon is nearly elliptic in outline, measuring 100 km long by 55 km wide, or about 4300 km^2 (Figure 1). Average lake level is 263 m ASL (Ontario Dept. of Lands and Forests 1965).

The lake lies within the Precambrian Shield (Zoltai 1965). Most of the islands and mainland are underlain by Late to Middle Precambrian diabase and related

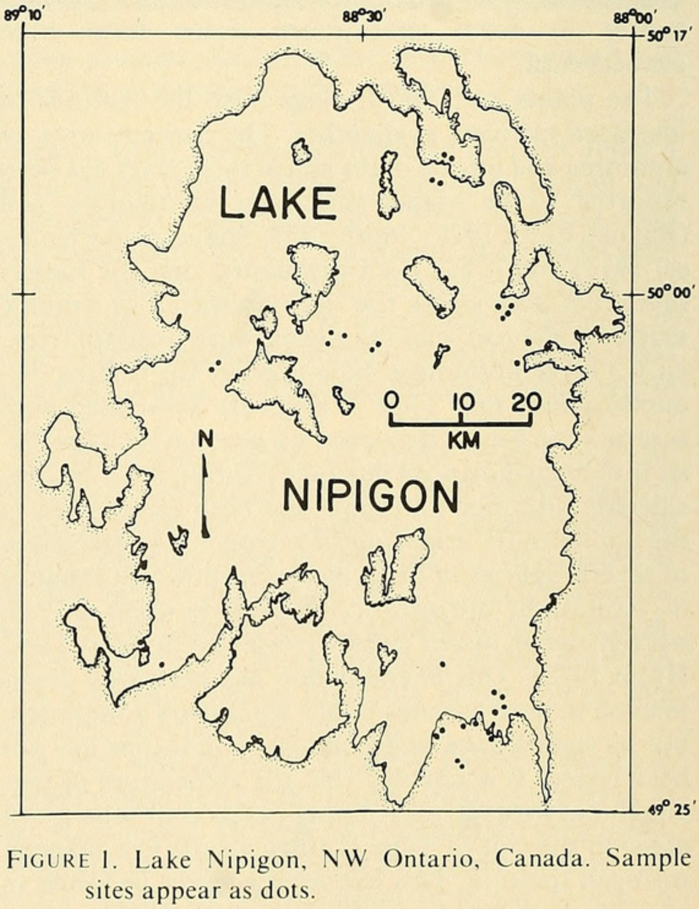

FIGURE 1. Lake Nipigon, NW Ontario, Canada. Sample sites appear as dots.

TABLE 1. Forest vegetation dominants of the sample sites.

	Dominants	Sub-dominants
Trees	*Abies balsamea* *Betula papyrifera*	*Picea mariana* *Picea glauca* *Thuja occidentalis* *Populus tremuloides* *Populus balsamifera*
Shrubs and Small Trees	Saplings of *A. balsamea* and *B. payrifera* *Rubus idaeus* *Alnus crispa* *Sambucus racemosa* *Ribes glandulosum*	*Sorbus decora* *Cornus stolonifera* *Taxus canadensis* *Alnus rugosa* *Salix humilis* *Salix phylicifolia*
Ground Layer	Seedlings of *A balsamea and B. papyrifera* *Linnaea borealis* *Trientalis borealis* *Cornus canadensis* *Moneses uniflora*	*Aralia nudicaulis* *Mitella nuda* *Pyrola secunda* *Rubus pubescens* *Fragaria vesca*

mafic igneous rocks (Ontario Geological Survey 1980). Numerous other bedrock types occur, but no sample sites were located outside the mafic igneous zone. Island and mainland sites (Figure 1) were chosen using the following criteria: homogeneous dominant tree vegetation of *Abies balsamea* (Balsam Fir) and *Betula papyrifera* (White Birch) with *Picea glauca* (White Spruce) and *Picea mariana* (Black Spruce) (Table 1; also see Cooper 1913); island size between 1.5 and 15 ha; absence of swamps, meadows, heaths, jack pine forest, and disturbance due to fires, humans, and windstorms; average slope not exceeding 25%; maximum elevation not exceeding 30 m. Bedrock outcrops, depressions, and steep areas were avoided. Differences in topography on the sample islands were so small that microclimatic differences were imperceptible. Sample islands thus differed manifestly only in area and isolation.

Silty to sandy till overlies the bedrock on the majority of mainland and island sites. Stratified and non-stratified lacustrine deposits of clay, silt, and sand are associated with the till (Ontario Dept. of Lands and Forests 1965). Till depth varies from zero on exposed bedrock to an average of 2.5 m (Zoltai 1965). The present Lake Nipigon shoreline and lower elevations, once covered by the waters of Glacial Lake Kelvin, are dominated by lacustrine deposits (D. A. Fawcett, pers. comm.). The soils of the area are broadly classed as humoferric podzols, with rockland, eutric brunisols, and gray luvisols in the rocky and stony phase (Agriculture Canada 1977). Thin soils over bedrock are common. Timber use capability, an index of plant growth potential, ranges from good to fair for the sample sites (Ontario Ministry of Natural Resources 1976).

The Lake Nipigon basin is enclosed on the north, east, and west sides by the higher land of the Central Plateau (Rowe 1972). The slope of the land is gradual in the south, with some exceptions (e.g., Nipigon River, Pijitawabik Bay, Tchiatang Bluffs, South Bay, Cook Point). In general, the topography is rolling and the relief slight, rarely exceeding 40 m above lake level. Numerous rivers and creeks drain into the lake from the north, east, and west. At Pipestone Bay in the extreme SE the lake is drained by the Nipigon River which flows into Lake Superior near the town of Nipigon.

Hundreds of islands dot the lake, the vegetated ones ranging in size from a few m^2 to about 10,000 ha (e.g., Kelvin Island). Islands are well distributed throughout the lake, though sparse near the eastern shore. The greatest distance between islands does not exceed 10 km. Typical islands appear in Figure 2.

The larger Glacial Lake Kelvin came to occupy the present Lake Nipigon basin with the retreat of the Laurentide Ice Sheet about 9,000 years B.P. (Zoltai 1965; Bryson 1969). Afterwards, water levels fluctuated due to periodic readvances of glacial ice, vertical crustal uplifts, and erosion of lake outlets (Zoltai 1965). All sample islands are similar in elevation, however, and therefore emerged from the receding lake waters at nearly the same time. Thus, all sample islands are of similar age.

Field Methods

Mainland exposures and islands ranging in size from 1.5 to 13.5 ha were sampled for presence of angiosperms and gymnosperms. Presence was determined during a timed random walk. Islands were divided into four quadrants which delimited NE, NW, SE, and SW exposures. Mainland sites were divided into two exposures and were sampled chiefly to determine the species present for island colonization. Fifteen minutes search time was allotted to each island quadrant and mainland aspect. Total search time on any island was one hour. Islands smaller than 1.5 ha were too small to allow one hour of random search time without sampling ground already covered. I set an upper limit of 15 ha; above 15 ha, much nonsearch time was spent travelling between quadrants.

I wrote a description of each island and mainland site immediately after sampling. The description treated the following: slope, width and nature of shoreline, moisture conditions, dominant species in the overstory, shrub and ground layers, presence of blowdowns, clearings, or depressions, and nature of the forest floor (e.g., whether moss or leaf-covered, prominence of rocks and downed trees). Descriptions

FIGURE 2. Typical islands in Lake Nipigon, June 1979.

were later used in deciding whether a site conformed to the experimental habitat type. The actual time spent on any island was at least 4-5 hours.

During random walks, I often stopped search timing to allow travel time in difficult walking on strand, downed trees, or tangles, and to allow time to record species and notes and to identify and collect plants. When 15 minutes of sampling time expired, sampling ceased until I entered a new quadrant. The walking route was random. Sampling time in deep forest, forest edge, and strand was about proportional to the area of the habitat type in each quadrant. The use of quadrants ensured stratified coverage and provided data on possible exposure effects. Species tallies by quadrant were repetitive for any island indicating that most species present were discovered (e.g., 57% of an island's species number was present in a single quadrant; the ratio of species per quadrant: total island species was unrelated to area; the average number of new species between the third and fourth quadrants equaled 3.6). The sampling method was not meant to be an exhaustive search for all higher plants in a study area; some species undoubtedly were not tallied.

At least 28 species were excluded from the study for one of three reasons. Some species, e.g., most *Carex spp.,* were impossible to identify in vegetative condition. A number of voucher specimens of rare species was misplaced by an unnamed agency; unidentified species in the lost batch were excluded. Ephemeral species, which either faded before or became visible after July 20, were excluded (e.g., *Calypso bulbosa*). I recognized one hundred species, 91 of which occurred in the samples. The limited number of species recorded for the sites can be attributed to: choice of only homogeneous *Abies-Picea-Betula* forest, inexhaustive search method, and exclusion of vegetative graminoids, lost voucher specimens, and ephemerals.

Analytical Methods

Numbers of species per island quadrant, island, mainland exposure, and mainland site were determined from field data. Frequency occurrence of each species for islands, mainland sites, and overall, and dispersal mechanisms are given in Appendix 1.

The area of each island was determined by planimeter from Canada Map Office maps (scale = 1:50000, published 1959, '66, '67, '69). Distance to the mainland was measured from an island's nearest shore to the nearest mainland shore. Islands 10 km^2 or larger were observed to support species numbers essentially identical to the mainland, and thus treated as mainland.

Thornton (1967) pointed out that simple distance to nearest neighbour ignores the contribution of other islands. He proposed that the sum or the average of distances of each island to every other island in an archipelago would provide a better index of isolation (c.f. Power 1972). Power (1972) tested two isolation indices, the latter type taking into account that near islands are more likely to contribute propagules to a recipient than are distant islands. For specified maximum distances he estimated isolation as $I = 1 - \sum_{i=1}^{k} \frac{1}{m}$ where m is in miles, and i's are islands or mainland points. Power follows Darlington (1938) in assuming that propagule density varies inversely as the distance from the source, not inversely as the square of the distance as in this study. His isolation index, moreover, does not take into account the area of each stepping stone.

The effective isolation of an island can be viewed as its distance to the mainland minus the contribution of any stepping stones (i.e., islands closer than the mainland which may contribute propagules), the latter islands effectively shortening the distance to the mainland. The stepping stone factor, S_j, was devised to approximate the effective isolation.

Calculation of S_j involved two variables: the distance in km from the recipient to each stepping stone island (D_i), and the area in km^2 of each stepping stone (A_i) estimated by planimeter. $S_j = \sum_{i=1}^{n} \left(\frac{A_i}{D_i^2}\right)$. The effective isolation in km thus $= I = W(1-K)$, where W is the distance from recipient island to mainland in km, and $K = \left(\frac{1}{S_{max}}\right)(S_j)$, where S_{max} is the maximum observed S_j. K (the correction factor for the effect of stepping stones) ranges between 0 and 1, the least isolated having a K value of 1 and therefore an effective isolation of zero, i.e., located on the mainland.

Four assumptions underlie the stepping stone factor. The first and most questionable assumption is that propagule density decreases inversely as the square of the distance from the source (c.f. Johnson and Raven 1970). Such exponential dispersal may hold for water and air-borne propagules, but uniform dispersal may hold for animal borne propagules (MacArthur and Wilson 1967). Secondly, the number of potential propagules was assumed proportional to the stepping stone area. Thirdly, the maximum distance for inclusion of stepping stones equaled the distance to the mainland, with islands 10 km^2 and larger considered as mainland. Finally, dispersal was assumed equiprobable in all directions.

Regressions of island species number and independent variables were carried out. An alternate isolation factor using $\frac{1}{D}$ (thus $S_j = \sum_{i=1}^{n} \left(\frac{A_i}{D_i}\right)$ in place of $\frac{1}{D^2}$ (Darlington 1938) was regressed upon island species number. The effect of exposure (slope aspect) upon species number was tested by ANOVA. Site summaries appear in Table 2, and regression results in Table 3.

Results

Island species richness was correlated positively with area ($p < 0.01$), $\log_e$ area ($p < 0.05$), and average species richness/quadrant ($p < 0.01$), and negatively correlated with distance ($p < 0.05$) and isolation ($p < 0.05$). The $\log_e$ of island species richness was correlated positively with area ($p<0.05$) and species richness/quadrant ($p<0.01$), and negatively correlated with distance ($p<0.05$) and isolation ($p<0.05$). Species richness/quadrant was correlated positively with island area ($p<0.05$).

Isolation, distance, and the $\frac{1}{\text{distance}}$ isolation index were all strongly correlated with each other ($p<0.01$), and all were unrelated to island area.

Mainland and island exposures had no effect on species richness (ANOVA: mainland $F = 1.78$, $df1 = 2$, $df2 = 7$; island $F = 1.25$, $df1 = 3$, $df2 = 80$).

Species with animal borne propagules were numerous on near islands, whereas wind-water dispersed species outnumbered animal dispersed species on distant islands (distance $p<0.01$, isolation $p<0.01$, $\frac{1}{\text{distance}}$ index $p<0.05$). Dispersal type was unrelated to island area. (Table 3).

Of the 91 plant species which occurred in the samples, 31 were dispersed by wind and/or water, 39 by birds and/or mammals; 18 species used both wind-water and bird-mammal dispersal. The dispersal mechanism of three species could not be determined with certainty. Twenty-one of the 91 plant species found at the sample sites were restricted to islands; 14 species were restricted to the mainland, and nine of these 14 species depended on bird-mammal dispersal.

Discussion

The species richness of seed plants in Lake Nipigon is positively correlated with island area. Area *per se* as expressed through higher immigration rates and lower extinction rates of large islands may help account for the increase in species diversity with area. Immigration rate is not independent of area since large islands provide a larger catchment surface for propagules than small islands (the "sampling effect"; Power 1972). The number of wind-borne propagules landing per unit area should be the same on large and small islands. This constant immigration per unit area implies that more propagules will immigrate to larger islands. Water borne immigration should be more a function of island perimeter than area. Areas being equal, a long thin island with low shoreline would receive more propagules than a circular island with a steep margin. Larger islands also might offer more of any given resource to animals bearing propagules.

Enhancement of immigration to large islands may occur for propagules dispersed by the Woodland Caribou (*Rangifer caribou sylvestris* Richardson) during open water migration on Lake Nipigon. Caribou swim rapidly and well for distances of 5-6 km (Jackson 1961), and local fishermen have observed

TABLE 2. Name, area, log$_e$ area, total species, log$_e$ species, species/quadrant, ratio of species/quadrant tog total species, distance, isolation, isolation assuming 1/Distance dispersal, and ratio of wind and water dispersed to bird and mammal dispersed plant species of island and mainland sites. Map coordinates are available upon request.

Island		Area	Log$_e$ area	Total species	Log$_e$ sp.	Sp/quadrant	Sp/quad: total sp.	Distance	Isolation	Isolation, using 1/D	Dispersal eatio
McKee		13.2	2.58	44	3.78	27	0.61	3.1	3.0	2.5	1.06
Gypsy		1.5	0.41	33	3.50	21	0.64	3.4	3.2	2.1	1.00
Pipestone		9.7	2.27	39	3.66	20	0.51	1.5	1.4	0.4	1.54
June		1.5	0.41	34	3.53	19	0.56	1.7	1.2	0.2	1.25
Big Tchiatang		3.3	1.19	24	3.18	12	0.50	1.3	1.3	1.3	0.91
Storm		5.9	1.77	25	3.22	15	0.60	3.7	3.5	0.0	0.67
Lightning		2.8	1.03	31	3.43	17	0.55	3.1	3.0	3.0	1.40
Lone		4.4	1.48	23	3.14	11	0.48	7.2	7.1	2.4	1.38
Little Russell		5.0	1.61	38	3.64	18	0.47	1.0	0.7	0.2	1.14
Middle Tichnor		7.1	1.96	38	3.64	17	0.45	2.0	1.7	1.3	1.31
South McIvor		1.5	0.41	32	3.47	20	0.63	2.0	1.9	1.5	1.00
Middle McIvor		11.7	2.46	52	3.95	29	0.56	1.4	0.0	0.2	1.16
W.S. McIvor		1.5	0.41	24	3.18	13	0.54	1.7	1.4	1.1	1.86
Windy McIvor		5.4	1.69	29	3.37	16	0.55	1.7	1.1	1.0	1.67
Cress		1.6	0.47	31	3.43	21	0.68	2.9	2.9	2.7	1.18
Cove		2.7	0.99	36	3.58	22	0.61	2.2	2.2	1.7	1.64
East August		13.5	2.60	35	3.56	23	0.66	6.5	6.4	5.3	2.00
East Remote		3.8	1.34	28	3.33	17	0.61	9.3	9.2	5.3	1.75
West Remote		6.0	1.79	22	3.09	12	0.55	10.5	10.3	3.3	2.40
West August		12.4	2.52	35	3.56	17	0.49	4.2	4.2	3.8	1.33
South August		4.1	1.41	33	3.50	21	0.64	4.6	4.6	4.0	2.00
Mean		5.6	1.72	33	3.50	19	0.57	3.6	3.3	2.1	1.41
MAINLAND											
Cook-Col.	NE			44		36					
	NW					34					
Frenchman's Head	NE			38		33					
	NE					30					
Queen Anne Point	SE			40		37					
	NW					14					
Tchiatang	SE			45		36					
	NW					29					
Cloud	SE			43		29					
Point	SE					35					
Mean				42		31					

TABLE 3. Correlation(r) values for dependent and independent variables; regression equations listed for significant correlations, Y = a + bx, 19 d.f. error; r @ p = 0.05 = 0.433, r @ p = 0.01 = 0.549; * significant @ p = 0.05; ** significant @ p = 0.01.

	Area	Log$_e$ area	Total spp.	Log$_e$ spp.	Spp./quad.	Distance	Spp./quad. to total spp.	Isolation	Isolation, using 1/D.	Dispersal Ratio
Area	—	—	0.56** 27.0 + 1.0X	0.52* 3.3 + 0.0X	0.43* 15.7 + 0.5X	-0.13	0.11	0.08	0.19	0.08
Log$_e$ Area		—	0.45* 26.4 + 4.3X	0.40	0.27	-0.27	0.18	0.16	0.16	0.13
Total Species			—	—	0.88** 0.2 + 0.6X	0.03	-0.44* 37.0 - 1.2X	-0.48* 36.9 + 1.3X	-0.19	-0.23
Log$_e$ Species				—	0.88** -46.4 + 18.7X	0.06	-0.46* 3.6 - 0.0X	-0.49* 3.6-0.0X	-0.16	-0.23
Species/Quadrant					—	0.50* 0.4 + 0.0X	-0.29	-0.32	0.02	-0.16
Species/Quadrant Total Species						—	0.19	0.20	0.39	0.07
Distance							—	0.99** -0.3 + 1.0X	0.74** 0.5 + 0.5X	0.56** 1.1 + 0.1X
Isolation								—	0.76** 0.6 + 0.4X	0.55** 1.1 + 0.1X
Isolation, using 1/D.									—	0.54* 1.1 + 0.1X
Dispersal Ratio										—

them swimming between the large Kelvin and Shakespeare Islands, an open water crossing of about 10 km. Caribou require plentiful amounts of lichens and browse for survival; thus, their crossings must be more frequent between large islands.

The results, however, do not indicate a general enhancement of animal borne plant immigration to the larger islands. Island area on Lake Nipigon bears no relation to the type of dispersal used by the plant species. Rather, distance appears to govern dispersal type, with bird- or mammal-dispersed species comprising a smaller percentage of the flora on distant islands than on near islands. The prevailing dispersal type of species on distant islands is wind-water. This is understandable in that animal (i.e., dispersal agent) species richness has been shown to decrease with isolation, whereas wind and water can provide transport subject only to the adaptations of the plant propagule and the decrease in propagule density from the source.

Extinction rates are accepted as inverse to island size, but MacArthur and Wilson (1967) hypothesized that small islands may possess exceptionally high area-independent extinction rates. Whether Lake Nipigon's small islands exhibit the special case of area-independent extinction can only be shown experimentally. Area-independent rates or not, small populations may suffer high extinction rates (Pickett and Thompson 1978). Island populations of many species on Lake Nipigon often comprised only one to a few individuals, e.g., *Calypso bulbosa, Clintonia borealis, Cornus canadensis, Pyrola secunda, P. virens,* and *Viola nephrophylla.*

The significant decrease in plant species richness in Lake Nipigon with increasing isolation and distance may result from lower immigration rates to the distant islands. For many species on Lake Nipigon, the small isolation distances must present little barrier to dispersal. Seeds of Orchidaceae and Pyrolaceae are easily blown hundreds of km (van der Pijl 1969). Yet many species with dust-like seeds are saprophytes (e.g., *Corallorhiza trifida, Monotropa uniflora*), mycophytes, or parasites, and the special substrates they require often limit their distribution. Other wind-borne seeds are less easily dispersed but also less exacting of habitat. Löve (1963) lists average dispersal limits in km for a variety of species, some genera of which are present on Lake Nipigon: *Fraxinus* (0.03), *Abies* (0.09), *Picea* (0.3), *Betula* (1.6), *Taraxacum* (10) and *Lycopodium* (330). Some widespread species on Lake Nipigon can be dispersed by water in addition to their normal wind dispersal, e.g., *Betula papyrifera, Salix* spp., *Populus tremuloides* and *P. balsamifera* (USDA 1974). During the study I observed thousands of seeds several km from land, such as those of Paper Birch and Balsam Poplar afloat in water, and the comose seeds of Fireweed aloft in air.

Dispersal over ice from December through April must also contribute to immigration rates. For plants with winter-persistent fruits, such as birch and spruce, ice could provide a ready avenue for wind dispersal.

Isolation distances for bird-dispersed propagules, such as *Clintonia borealis* berries dispersed by Ruffed Grouse (Ridley 1930), appear trivial on first inspection. Mere flight of a bird between source and recipient islands, however, need not connote successful dispersal. The bird must first eat the fruit (or the fruit or seed become attached to the bird), the seeds must be viable, remain with the bird during the flight, and later be excreted on the recipient island in the proper habitat. Some herbivores, such as White-throated Sparrows, were very active overwater fliers, but others, such as Ruffed Grouse, appeared sedentary. Successful bird dispersal, as with any dispersal, is only one factor determining a plant's distribution; the propagule must establish itself and persist until other successful introductions.

The above discussion emphasizes the roles of area *per se* and the sampling effect in determining island species number. Other explanations exist, such as habitat diversity. Though sample time was held constant over all island sizes, a greater variety of microhabitats may have been encountered on large islands simply because large islands can contain more habitats than small islands. Although no between-island habitat differences were evident, the importance of habitat must not be overlooked. Koopman (1958) has shown that the critical factor in determining the bat species number of southern Caribbean islands is not area or isolation but vegetation. Rate of establishment is a function of the number of sites suitable for germination (Harper 1965) and the rate of immigration. On many islands in Lake Nipigon, mesic herbs are restricted to forest edge. Establishment and persistence in the moss, acidic humus, and nutrient-poor soil may be enhanced in the brighter light of the forest edge.

Competition from mosses may play a role in determining seed plant species richness on islands in Lake Nipigon. Data and observations on the frequency of forest herbs, shrubs, and seedlings in the cushion moss mats (dominated by *Dicranum fuscescens* Turn., *D. rugosum* (Hoffm.) Brid., *Hylocomium splendens* (Hedw.) BSG, and *Pleurozium schreberi* (Brid.) Mitt.) of Nipigon's islands indicate that common higher plants are able to grow in the moss mats. Whether occasional and rare species on Lake Nipigon owe their scarcity in part to moss competition can only be answered by more detailed study. Moss-seed plant competition on Lake Nipigon would not be surprising in that mosses and lichens inhibit establishment of pine, spruce, shrubs and herbs elsewhere in the boreal forest (Braun-Blanquet 1932; Wilde and Krause 1960; Savile 1963; Walter 1973).

Exposure did not affect species richness on either islands or mainlands, due perhaps to the low elevations and gentle slopes of the sample sites.

Conclusions

The results indicate that seed plant species richness of Lake Nipigon islands is affected both by area and by isolation distances less than 10 km. The larger catchment surface of large islands may permit higher immigration rates than those of small islands.

Lower species richness on distant islands may result from lower immigration rates than those of near islands.

Island area in Lake Nipigon bears no relation to plant dispersal type. Wind-water dispersal is the primary means by which plants disperse to distant islands. Near islands are populated by equal numbers of animal and wind-water dispersed plant species.

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APPENDIX 1. Recognized species found at the sample sites, their site frequencies, and probable dispersal mechanisms. Nomenclature follows Scoggan 1978.

Species	Islands	Mainlands	Overall	Probable Dispersal[1]
Abies balsamea	1.00	1.00	1.00	wind[3,5] Red Squirrel[2] birds?, water[2]
Acer spicatum	0.33	0.71	0.43	wind, birds?
Achillea millefolium	0.38	0.00	0.29	wind, water, birds
Actaea rubra	0.05	0.57	0.18	birds?
Agrostis perennans	0.57	0.00	0.43	birds?, wind?, water?
Alnus crispa	0.76	0.86	0.79	wind, water[2]
Alnus rugosa	0.43	0.71	0.50	wind, water?
Amelanchier sanguinea	0.29	0.43	0.32	birds
Anaphalis margaritacea	0.05	0.00	0.04	wind?
Aralia nudicaulis	0.43	1.00	0.57	birds (e.g., Pine Grosbeak, Red-bellied woodpecker)
Arctostaphylos uva-ursi	0.05	0.00	0.04	birds (e.g., Blue Grouse), mammals
Aster macrophyllus	0.00	0.71	0.18	wind?, birds?
Betula papyrifera	1.00	1.00	1.00	wind, water[2,3,4], birds
Bromus ciliatus	0.05	0.00	0.04	birds (e.g., Crow)
Calamagrostis canadensis	0.86	1.00	0.89	birds?, wind?, water?
Cardamine pensylvanica	0.24	0.00	0.18	water?, birds?
Carex disperma	0.43	0.57	0.46	birds?, water?, mammals?
Clintonia borealis	0.05	1.00	0.29	Ruffed Grouse
Coptis trifolia	0.14	0.57	0.25	gravity?
Corallorhiza trifida	0.00	0.43	0.11	wind[3]
Cornus canadensis	0.57	1.00	0.68	birds (e.g., Pine Grosbeak, Crow)[4]
Cornus stolonifera	0.95	0.71	0.89	birds (e.g., Crow[4], American Redstart)
Deschampsia caespitosa and *D. flexuosa*	0.19	0.00	0.14	wind[7]
Diervilla lonicera	0.00	0.57	0.14	?
Eleocharis compressa	0.00	0.14	0.04	birds (e.g., ducks and Killdeer[6])
Epilobium angustifolium	0.95	0.57	0.86	wind[2]
Fragaria vesca	0.43	0.29	0.39	birds (e.g., Crow, Starling, Eastern Kingbird)
Fragaria virginiana	0.00	0.29	0.07	birds (e.g., Crow)
Galium triflorum	0.14	1.00	0.36	birds, mammals
Gaultheria hispidula	0.05	0.43	0.14	birds?
Goodyera repens	0.10	0.14	0.11	wind
Hierachloe odorata	0.05	0.00	0.04	wind?, water?
Hydrocotyle americana	0.00	0.14	0.04	birds?
Ledum groenlandicum	0.14	0.00	0.11	birds (e.g., Rock Ptarmigan), reindeer
Linnaea borealis	0.38	1.00	0.54	mammals (e.g., humans[2], deer, hare), birds
Lonicera canadensis	0.00	0.71	0.18	birds?
Lonicera hirsuta	0.00	0.29	0.07	birds (e.g., Grey Vireo, Red-eyed Vireo)
Maianthemum canadense	0.24	1.00	0.43	birds (e.g., Magpie)
Mentha arvensis	0.48	0.14	0.39	water
Mertensia paniculata	0.05	0.86	0.25	gravity?
Mitella nuda	0.29	1.00	0.46	gravity?
Moneses uniflora	0.62	0.43	0.57	wind
Monotropa uniflora	0.24	0.43	0.29	wind?
Oryzopsis asperifolia	0.00	0.14	0.04	birds?
Phalaris arundinacea	0.19	0.00	0.14	birds (e.g., Killdeer, Mallards[6], Reed Bunting), water, wind
Physocarpus opulifolius	0.14	0.00	0.11	wind?[3]
Picea glauca	0.95	0.86	0.93	wind[3,5], rodents?, birds?, water[2]
Picea mariana	0.71	1.00	0.79	wind[3,5], rodents?, birds?, water[2]
Pinus strobus	0.00	0.14	0.04	wind[3,5], birds?, water?
Poa glauca	0.62	0.43	0.57	wind?, water?
Poa palustris	0.52	0.00	0.39	birds?, wind?, water?
Polygonum sp.	0.43	0.14	0.36	birds (e.g., Killdeer and ducks[6])
Populus balsamifera	0.86	0.71	0.82	wind, water[4]

Continued

APPENDIX 1. Concluded.

Species	Islands	Mainlands	Overall	Probable Dispersal[1]
Populus tremuloides	0.81	0.86	0.82	wind, water[4]
Potentilla anserina	0.29	0.14	0.25	water, mammals, birds (e.g., domestic goose)
Potentilla norvegica	0.86	0.29	0.71	birds (e.g., domestic chicken), water?
Potentilla palustris	0.10	0.00	0.07	water?, birds?
Primula mistassinica	0.48	0.00	0.36	wind?
Prunus pensylvanica	0.14	0.43	0.21	birds (e.g., Crow, Robin[4]), mammals
Pyrola secunda	0.67	0.71	0.68	wind
Pyrola virens	0.43	0.29	0.39	wind
Ranunculus pensylvanicus	0.29	0.86	0.43	birds?, water?
Rhamnus alnifolia	0.00	0.14	0.04	birds?
Ribes glandulosum	0.95	0.86	0.86	birds
Ribes hudsonianum	0.19	0.00	0.14	birds
Ribes lacustre	0.00	0.57	0.14	birds
Ribes oxyacanthoides	0.43	0.29	0.39	birds (e.g., Catbird, towhee, Blue Jay, Cedar Waxwing, Robin, etc.)[8]
Ribes triste	0.00	0.14	0.04	birds, reindeer
Rosa acicularis	0.38	1.00	0.54	birds (e.g., Prairie Chicken), mammals
Rubus idaeus	0.90	0.43	0.79	birds (e.g., Crow, Magpie)
Rubus pubescens	0.33	0.86	0.46	birds
Salix humilis	0.90	0.57	0.82	wind, water[4]
Salix phylicifolia	0.67	0.86	0.71	wind, water[4]
Sambucus racemosa	0.52	0.14	0.43	birds (e.g, Crow, Robin, Red-headed Woodpecker)
Schizachne purpurascens	0.05	0.00	0.04	birds?, wind?, water?
Sium suave	0.05	0.00	0.04	water
Solidago graminifolia	0.67	0.00	0.50	wind?, water?
Sorbus decora	0.95	1.00	0.96	birds, mammals
Streptopus roseus	0.00	0.86	0.21	birds?
Taraxacum sp.	0.19	0.00	0.14	wind, birds, water
Taxus canadensis	0.90	0.43	0.79	birds
Thuja occidentalis	1.00	0.86	0.96	wind?, birds?
Trientalis borealis	0.81	1.00	0.86	mammals?
Typha latifolia	0.10	0.14	0.11	wind[7], water
Urtica dioica	0.10	0.00	0.07	wind, birds (e.g., Magpie), mammals
Vaccinium angustifolium	0.14	0.29	0.18	birds, humans[2]
Vaccinium myrtilloides	0.10	0.43	0.18	birds, humans[2]
Viburnum edule	0.29	1.00	0.46	birds
Viola macloskeyi	0.19	0.14	0.18	birds?, ants?
Viola nephrophylla	0.10	0.00	0.07	birds?, ants?, water?
Viola renifolia	0.14	0.86	0.32	birds?, ants?

[1]Source is Ridely (1930) unless otherwise noted
[2]Personal observation
[3]van der Pijl (1969)
[4]USDA Forest Service (1974)
[5]Löve (1963)
[6]de Vlaming and Proctor (1968)
[7]Praeger (1911)
[8]Cooper (1922)
Some dispersal agents listed are not present at Lake Nipigon, but related species are, e.g., domestic goose — Canada Goose.
"?" denotes that dispersal agent is documented for a plant species related to that at Lake Nipigon.

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