ISOLATION VS. EXTINCTION IN THE ASSEMBLY OF FISHES IN SMALL NORTHERN LAKES

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Abstract.   To evaluate the roles of extinction and isolation in predicting richness and composition of fish assemblages in small forest lakes of Finland and Wisconsin, we analyzed data from 114 Finnish and 55 Wisconsin lakes 0.2–86.9 ha in area. Six isolation variables characterized properties of stream corridors, land barriers, and source pools of invading species; four extinction variables were related to habitat severity, lake area, and productivity. Two types of multivariate analyses were used: the nonparametric classification and regression trees (CART) and the parametric linear discriminant analysis (LDA).

Both types of analyses showed that extinction variables were collectively more important than isolation variables in predicting richness and composition both in Finland and Wisconsin. We interpret that the greater importance of extinction vs. isolation results, not because isolation is unimportant, but because the probability of an arrival of a new species is much less than that of an extinction. Thus, the time after an extinction event before a subsequent invasion is long relative to the time after an invasion event before a subsequent extinction; consequently, fish assemblages sampled at a given point in time more likely represent the stamp of the extinctions than of the invasions. This conclusion was robust to the differences in the geomorphic settings and fish faunas of Finland and Wisconsin.

However, the importance of individual isolation and extinction variables in determining richness and composition differed between the two regions, apparently more from differences in geomorphic settings than from differences in fish faunas. Influences of horizontal rather than vertical barriers over land and water were more apparent in Wisconsin, with its lower relief and higher incidence of lakes without stream connections; influences of the area of the nearest lake (representing the size of the available species pool) and stream gradient were more important in Finland, with its higher relief and higher incidence of lakes with stream connections. The importance of individual extinction variables also differed between the two regions, again reflecting differences in the geomorphic settings of the two lake districts and the strong influence that lake position in the landscape has in determining limnological features of the lake.

Key words: assemblages; extinction; Finland; fish; insular environments; island biogeography; isolation; lakes; species area relations; species composition; species richness; Wisconsin.

INTRODUCTION

Stephen Forbes (1887) was probably the first freshwater ecologist to emphasize the insular nature of a lake, describing it as an ''islet,'' ''a little world within itself.'' Similarities between lakes and islands have subsequently been made more explicit (e.g., Barbour and Brown 1974, Keddy 1976, Magnuson 1976, Browne

1981, Eadie et al. 1986), particularly in the context of the theory of island biogeography (Munroe 1948 as cited in MacArthur and Wilson 1963, 1967, Brown and Lomolino 1989), in which the interaction between recurrent extinction and immigration determines the species richness of the island's biota.

Among small forest lakes, differences in extinction rather than isolation have been viewed as being more important in determining community structure (Magnuson 1988, Tonn et al. 1995). Small forest lakes such as those of Finland and Wisconsin have several features that contribute to extinctions of local populations (Tonn and Magnuson 1982, Rahel 1984, Magnuson et al. 1989, Tonn et al. 1990, Bergquist 1991). High acidity, seasonally low oxygen, or both, exceed the tolerance
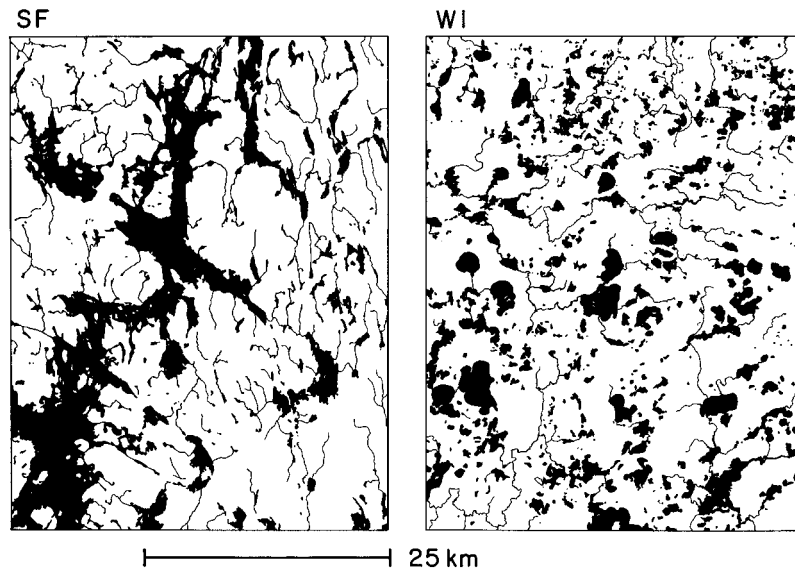
FIG. 1. Land- and lakescapes of lake districts of Finland (SF) and northern Wisconsin and the upper peninsula of Michigan (WI). The Finnish view is centered at 62°1′ N and 25°50′ E; the Wisconsin/Michigan view is at 46°3′ N and 89°41′ W. Our study lakes are some of the smallest lakes in these lakescapes; they averaged 0.33 km in diameter with a maximum of about 1 km.

ranges of many species, and piscivores frequently contribute to local extinction.

Isolation, however, also varies greatly among lakes and probabilities of an immigration, like probabilities of an extinction, also should differ greatly. Many lakes, like oceanic islands, have no direct connection for fish to enter from an adjacent lake or stream and the magnitude of land barriers between lakes varies. Other lakes have stream connections that can differ in length, gradient, and the presence of impassable barriers (e.g., waterfalls). Among small Finnish lakes, an index of isolation using the presence and gradient of connecting waters was more important in distinguishing among assemblage types than were each of four extinction factors (Tonn et al. 1990). However, in a set of Wisconsin lakes that were neither anoxic in winter nor acidic, fish assemblage composition was independent of lake connectedness (Rahel 1986); isolation by land barriers apparently did not prevent colonization. From such observations, Magnuson (1988) suggested that fish richness and composition should be more closely determined by differences among lakes in extinction rather than in isolation. The suggestion has received some support from a broadscale examination of patterns of fish assemblages in small lakes of four north-temperate regions (Tonn et al. 1995).

Our present paper examines the relative importance of isolation vs. extinction in determining the richness and composition of fishes in small forest lakes of Finland and Wisconsin and the importance of individual factors contributing to isolation and extinction. Our approach was designed to answer the following questions with respect to predicting/determining the type

and richness of fish assemblages. Are extinction parameters more important than isolation parameters? Which individual isolation and extinction variables are most important? Does the importance of individual isolation and extinction variables differ between the geomorphic settings of Finland and Wisconsin? If similar conclusions are reached with different methodologies and with two distant lake districts, then we will consider the conclusions to be robust for small north-temperate lakes that differ greatly in connectedness and environmental severity.

STUDY SITES

The Wisconsin study lakes are a part of the Northern Highland Lake District of northern Wisconsin and the upper peninsula of Michigan; all are grouped within a narrow range of latitudes (45°73′– 46°21′ N). Many are ice block lakes formed by the melting of large chunks of ice left in thick proglacial sediment during deglaciation (Attig 1984). The Finnish study lakes are more widely scattered, ranging in latitude from 60°8′ N to 67°50′ N. Many occupy basins formed by the direct action of the glacial ice on the Precambrian bedrock (Hutchinson 1957). A representative lakescape within each district (Fig. 1) illustrates the insular nature of small forest lakes, as well as some geomorphic differences between the two regions.

Individually, the 114 Finnish and 55 Wisconsin lakes were chemically and morphologically heterogeneous (Table 1). They, as groups, did not differ in surface area or water chemistry (pH and conductivity), but Finnish lakes were deeper, less isolated by land barriers, and had outlet streams with steeper gradients than

Wisconsin lakes (Tonn et al. 1990). Surface water connections to another lake were absent for 76% of the Wisconsin lakes but only 36% of the Finnish lakes; land barriers from the nearest downslope lake ranged up to 2.2 km horizontally and 30 m vertically. Gradients in streams connecting to the next lake downstream ranged up to 89 m/km in Finland but only to 12 m/km in Wisconsin. The next downstream lake was sometimes greater than 100 000 ha for Finland, but never more than 550 ha for Wisconsin. Many lakes had roads to their shores, others were less accessible to humans; the nearest road was as far as 1 km in Finland but only 270 m in Wisconsin. Many of the shallow ones become anoxic during winter ice cover (Tonn and Magnuson 1982, Rahel 1984, Holopainen and Hyvarinen 1985).

Fish assemblages are presented for reference in Table 2. Richness ranged from 0 to 12 fish species; the total species pool for these lakes was 20 in Finland and 23 in Wisconsin (Tonn et al. 1990). Scientific names of all species are given in Tonn et al. (1990). Three types of fish assemblages were delineated from relative abundance data for Finland and named by their dominant taxa as ROACH, PERCH, or CRUCIAN CARP lakes (Tonn et al. 1990). Wisconsin lakes were divided initially into three assemblage types: PIKE, BASS, or MUDMINNOW lakes (Tonn et al. 1983, 1990). We further divided MUDMINNOW lakes into MUDMINNOW-PERCH or MUDMINNOW-MINNOW lakes after Rahel (1984) and Magnuson et al. (1989). We included five FISHLESS lakes from Wisconsin (from Rahel 1984). The single FISHLESS lake from Finland was not included as an assemblage type but was included in analyses of species richness and isolation.

Data and Analyses

Data on fishes, chemistry, and morphology of 114 Finnish and 55 Wisconsin lakes come from Tonn et al. (1990), who compiled them from published and unpublished sources and from Rahel (1984). We omitted Robinson Lake because it had no isolation data. Fish species known to have been introduced by humans were excluded for the Finnish lakes because we were more interested in how geological and limnological differences influenced the assemblages than did stocking. Because stocking records were not available for Wisconsin, we could not remove that influence in our Wisconsin analyses. However, because Wisconsin was only colonized by Europeans since the mid-1800s, we think stocking effects should be less apparent than in Finland, where stocking of certain species has been routine for subsistence fisheries. The higher proportion of fishless lakes among our study lakes in Wisconsin than Finland is consistent with this view.

Lake parameters were judged to be related to either isolation (immigration) or extinction (Table 1). Features external to the lake proper and related to its accessibility to fishes were classed as isolation parameters; features within a lake that could influence the

successful establishment or maintenance of fish populations were classed as extinction parameters. We measured isolation-related features from a large set of individual-sheet, topographic maps published by 1983 by the United States and Finland (1:20 000 maps for Finland from the National Board of Survey, Helsinki, Finland, and 1:62 000 maps for Wisconsin from the U.S. Geological Survey, Washington, D.C., USA). Also, 1:250 000 maps of Finland from that country's National Board of Survey (1979) were used for longer distances. Lakes could be isolated by only land barriers, by only a stream course, or by a combination of both (Table 1).

Isolation parameters are: (1) horizontal land distance—the distance (in kilometers) over land from the next lake to the nearest surface water connection (lentic or lotic). The distance was measured in a horizontal plane, along the most likely water course during high water or floods. (2) Vertical land distance—the distance (in meters) over land from the next lake or from its nearest stream headwater to the study lake. The distance was measured in a vertical plane summing up and down over ridges and depressions. (3) Horizontal water distance—the distance (in kilometers), measured in a horizontal plane, along the water course extending upstream towards a study lake from its next lake downstream. (4) Stream gradient—the average slope (in meters per kilometer) along the water course between a lake and its next lake. (5) Area of next lake—the surface area (in hectares) of the nearest lake downstream or downhill from a study lake. This parameter is a surrogate of species richness of the next lake and thus of the species pool of most likely immigrants. (6) Distance to road—the shortest distance (in meters) from the nearest road to the shore of the study lake measured in a horizontal plane. If the road or parking area was at the shoreline, this was given a value of 1 m.

Extinction parameters are: (7) area—the surface area (in hectares) of the study lake. This parameter is a correlate of habitat heterogeneity (Tonn and Magnuson 1982, Eadie and Keast 1984) and population size (Tonn 1985). (8) Conductivity—the summer specific conductance (microsiemens per centimeter at 20°C) of near surface water. This parameter is a correlate of total dissolved solids, nutrient status, and lake productivity (Ryder 1982). (9) pH—the summer value of near surface water is a measure of acidity. (10) Depth—the maximum lake depth (m). This measure is an inverse correlate with winter dissolved oxygen levels (Tonn and Magnuson 1982).

To evaluate the importance of isolation vs. extinction on species richness and composition we used classification and regression trees (CART) (Breiman et al. 1984). CART is a flexible nonparametric multivariate analysis that provided dichotomous keys for the lakes based on their isolation and extinction characters. The CART algorithm constructs a structural tree (dichotomous key) by repeated splits of the subsets of the 10-

TABLE 1. Medians (and ranges) of isolation and extinction variables and numbers of lakes separated from the next lake downslope by land, water, or both for small forest lakes in Finland and Wisconsin; lakes are grouped by the type of fish assemblage present in the lake.

	Finland		
Variable	ROACH	PERCH	CRUCIAN CARP
Isolation variables			
Horizontal land distance (km)			
All lakes	0.00 (0.00–0.70)	0.00 (0.00–2.20)	0.13 (0.00–0.60)
Lakes with no stream	0.15 (0.05–0.65)	0.20 (0.04–2.20)	0.23 (0.02–0.60)
Horizontal water distance (km)			
All lakes	1.30 (0.00–48.00)	0.40 (0.00–13.40)	1.75 (0.00–15.20)
Lakes with stream	1.26 (0.10–48.00)	0.28 (0.10–4.90)	8.15 (1.10–15.20)
Vertical land distance (m)			
All lakes	0.0 (0.0–6.4)	0.0 (0.0–30.4)	0.6 (0.0–7.5)
Lakes with no stream	1.0 (0.0–6.4)	3.4 (0.0–30.4)	2.7 (0.0–7.5)
Stream gradient (m/km)			
All lakes	5.30 (0.00–47.00)	16.97 (0.00–88.60)	4.69 (0.87–15.00)
Lakes with stream	5.23 (0.00–47.00)	19.50 (1.00–88.60)	8.25 (1.49–15.00)
Distance to road (m)	22 (1–388)	60 (1–1000)	24 (1–382)
Area of next lake (ha)	72.5 (0.2–100 000.0)	12.1 (0.8–100 000.0)	64 000.0 (12.1–100 000.0)
Extinction variables			
Lake area (ha)	9.2 (0.9–51.8)	4.4 (0.4–64.0)	0.8 (0.2–9.2)
Lake depth (m)	9.5 (1.8–24.8)	8.7 (3.0–27.0)	3.0 (1.5–7.0)
pH	6.4 (5.5–7.5)	6.0 (4.3–6.9)	5.8 (5.0–7.1)
Conductivity (μS at 20°C)	32 (12–87)	18 (6–96)	23 (3–72)
Number of lakes with			
Water distance only	39	31	2
Land distance only	7	14	2
Land and water distances	1	13	4
Total	47	58	8

dimensional space into descendent pairs of subsets selecting the combination of parameters that does the best job of prediction. The success of the CART classification for richness can be judged by how closely the predicted richness compares with the observed, as measured by the mean squared error (MSE), by R^2, and by the frequency distribution of the residuals. For CART, MSE and R^2 are pseudo-MSE and pseudo-R^2 because CART is a nonparametric model (Brieman et al. 1984). CART classification of lakes into fish assemblage categories can be evaluated by comparing the proportion of assemblages correctly classified with the proportion expected from a random allocation of the lakes to assemblage types, constrained by the number of lakes of each type. For analyses of species richness we generated two CART models, one for Finland and one for Wisconsin. For fish assemblage composition, we generated six CART models (three for Finland and three for Wisconsin), using all extinction and isolation variables, using only isolation variables, and using only extinction variables.

The importance of an individual isolation or extinction variable was evaluated first by its use or occurrence in the classification and regression trees and second by its relative importance, which is determined by using each variable at each juncture in a tree. The variable that does the best job at classification is given a relative importance of 100%. The other variables are given an importance, as a percentage, relative to the performance of the best variable in achieving correct classifications.

We also used linear discriminant analyses (LDA), a parametric multivariate model, to classify lakes as members of predetermined assemblage types for each region. For this analysis, log transformations were applied to all environmental variables except maximum depth, pH, and conductivity, which appeared, by inspection, to be normally distributed. Four Finnish lakes with missing values were deleted. A jackknife procedure was used to classify successively each lake with the LDA model that used all the other lakes. The percentage of lakes correctly classified was an index of success. The relative importance of individual explanatory variables was judged by the magnitude of the F value required to enter or remove each variable from the model. As with CART, we generated six LDA models for assemblages, using all variables, only isolation variables, and only extinction variables.

RESULTS

Species area relations

The relation between species richness and area is considered to be central to the biogeography of isolated islands and lakes. A single species-area regression (Fig. 2) adequately represented the small, forest lakes of Finland and Wisconsin: $\log(S + 1) = 0.319 + 0.36 \log(A + 1)$, where S = species richness and A = area. R^2 was 0.41. Although the slope appeared slightly steeper for

TABLE 1. Extended.

		Wisconsin		
PIKE	BASS	MUDMINNOW-MINNOW	MUDMINNOW-PERCH	FISHLESS
0.00 (0.00–2.41)	0.44 (0.00–1.05)	0.75 (0.00–2.05)	1.08 (0.07–1.95)	0.75 (0.40–1.49)
2.41	0.50 (0.18–1.05)	1.30 (0.25–2.05)	1.08 (0.07–1.95)	0.75 (0.40–1.49)
3.30 (0.00–7.70)	0.00 (0.00–6.70)	1.16 (0.00–3.69)	0.42 (0.00–4.28)	0.0 (0.00–8.86)
3.10 (0.00–7.70)	0.16 (0.13–0.19)	1.73 (1.16–2.30)	(none)	(none)
0.0 (0.0–14.3)	1.8 (0.0–15.5)	3.4 (0.0–21.9)	2.7 (0.9–8.8)	3.5 (1.0–12.8)
14.3	2.7 (0.3–15.5)	5.2 (1.8–21.9)	2.7 (0.9–8.8)	3.5 (1.0–12.8)
0.24 (0.00–3.53)	0.00 (0.00–11.54)	0.10 (0.00–3.99)	0.42 (0.00–3.16)	0.00 (0.00–0.27)
0.20 (0.00–3.53)	1.58 (1.25–11.54)	1.80 (0.65–2.93)	(none)	(none)
1 (1–250)	25 (1–270)	30 (1–190)	60 (1–190)	120 (90–250)
73.1 (10.2–433.9)	62.6 (1.5–5481.6)	9.6 (0.2–424.6)	10.2 (1.0–1547.0)	156.4 (6.0–332.8)
45.7 (10.2–86.9)	5.8 (1.2–18.0)	4.7 (1.0–43.1)	2.0 (0.2–24.1)	1.6 (0.3–3.4)
2.4 (1.2–8.5)	5.8 (4.3–10.0)	3.0 (1.2–9.0)	3.7 (2.0–7.0)	4.8 (2.5–6.4)
7.2 (6.8–8.0)	5.8 (4.6–6.9)	6.5 (5.4–7.6)	4.6 (4.3–6.0)	5.1 (4.7–6.0)
57 (24–119)	10 (8–35)	16 (13–152)	13 (9–25)	10 (9–16)
8	3	2	0	0
0	14	4	5	3
1	4	3	6	2
9	21	9	11	5

Wisconsin (0.40) than Finland (0.33), region was not a significant source of variation nor was the interaction of region and lake area (ANCOVA, $P > 0.25$).

Relations among explanatory variables

Lake area, an extinction parameter, and the presence of a land barrier, an isolation parameter, are strongly related in northern forest lakes ranging from 0.2 ha to 1566 ha in area (Fig. 3). This figure includes our 169 lakes plus 100 somewhat larger northern Wisconsin lakes (Rahel 1986). Eighty percent of lakes 2 ha or smaller had no stream connection, whereas only ~20% of those 100 ha or larger did not. We note that the proportion without a stream decreased with area for all three subsets of lakes, our Wisconsin lakes, our lakes from Finland, and Rahel's (1986) Wisconsin lakes.

Overall, 12 of the 45 pairings (27%) of the 10 explanatory variables were correlated at a P level ≤0.05 both for Finland and Wisconsin (Table 3). Correlations were greatest among pairs of extinction variables (67%), least for isolation variables (15%), and intermediate for extinction-isolation pairings (23%). These percentages overestimate the dependencies among the variables. Residuals were independent in only four of the significant pairings as judged by the Durban-Watson test (Table 3). And residuals were seldom distributed equally above and below the regressions; two exceptions were "pH versus lake area" for both regions. The R^2 values from these pairings, while typically small, were >0.1 for only 7% of the Finland pairs and only 16% of the Wisconsin pairs. The strongest dependencies among explanatory variables were those among extinction pairs for Wisconsin where five of six were significant and the R^2 values ranged from 14 to 44%.

Classification and regression trees (CART)

In each CART model that used all variables (Figs. 4 and 5), extinction variables had higher relative importances than did isolation variables (Table 4). The three most important variables for both richness classifications were extinction variables. The most important variables for both assemblage classifications also were extinction variables. In the four models, 9 of the 10 variables with an importance >80% were extinction variables. Among the isolation variables and to a lesser extent among extinction variables, those that were more important in Finland tended to be less important in Wisconsin and vice versa (Table 4).

Richness.—The classification and regression trees (CART) for species richness incorporated a number of isolation and extinction variables (Fig. 4). Residuals were well distributed and did not increase or decrease with predicted richness values. The mean squared error was 0.18 species for Finland and 0.10 species for Wisconsin; standard deviations of the estimated richnesses in the terminal nodes ranged from 0.4 to 1.4 species. R^2 values of the models were 0.82 for Finland and 0.90 for Wisconsin (Table 4).

In the two CART richness trees (Fig. 4), 8 nodes were sorted with isolation variables and 11 with extinction

TABLE 2. Species structure of fish assemblages in (A) Finland and (B) Wisconsin. Species are ordered first by the nominal species in each assemblage and then by overall abundance in the assemblages. Assemblages are as defined by Tonn et al. (1990) for Finland and by Magnuson et al. (1989) for Wisconsin. Abundance values of the nominal species named to identify the assemblages are in boldface type. Species names are as in Appendix A of Tonn et al. (1990).

A) Species	Fish assemblages (Finland)†		
	ROACH	PERCH	CRUCIAN CARP
Roach	**0.50**	tr	tr
European perch	0.23	**0.86**	0.06
Crucian carp	tr	tr	**0.85**
Northern pike	0.18	0.06	0.08
Ruffe	0.02	0.04	tr
Burbot	0.02	0.02	
Bream	0.03	tr	
Bleak	tr	tr	
Tench	tr	tr	
White bream	tr		
Rudd	tr	tr	
Vendace	tr	tr	
Zander	tr	tr	
Miller's thumb	tr		
Smelt	tr	tr	
Ide	tr	tr	
Dace	tr		
Whitefish		tr	
Minnow		tr	
Ninespine stickleback		tr	
Total no. of species	17	16	5
No. of lakes	47	58	8

B) Species	Fish assemblage (Wisconsin)‡			
	PIKE	BASS	MUD-MINNOW-MINNOW	MUD-MINNOW-PERCH
Northern pike	**1.00**	0.10		
Largemouth bass	0.44	**0.81**		
Central mudminnow	0.44	0.52	**0.82**	**1.00**
Blacknose shiner	0.22		0.36	
Fathead minnow			0.27	
Finescale dace			0.36	
Golden shiner	0.44	0.19	0.55	
Pearl dace			0.18	
Redbelly dace			0.55	
Yellow perch	0.89	0.90	0.45	**0.78**
Black bullhead	0.89	0.14	0.27	0.11
White sucker	0.78	0.24	0.27	
Bluegill	0.44	0.52		
Pumpkinseed	0.67	0.24		
Black crappie	0.44	0.19		
Yellow Bullhead	0.33	0.24		
Iowa darter	0.22		0.27	
Rockbass	0.44	0.05		
Brook stickleback			0.45	
Bluntnose shiner	0.22			
Common shiner	0.11			
Mottled sculpin	0.11			
Redhorse	0.11			
Smallmouth bass		0.05		
Total no. of species	18	13	12	3
No. of lakes	9	21	9	11

† Relative biomass of individual fish species averaged for lakes in each assemblage [tr (trace) is less than 0.00].

‡ Relative frequency of occurrence of individual fish species in lakes for each assemblage.
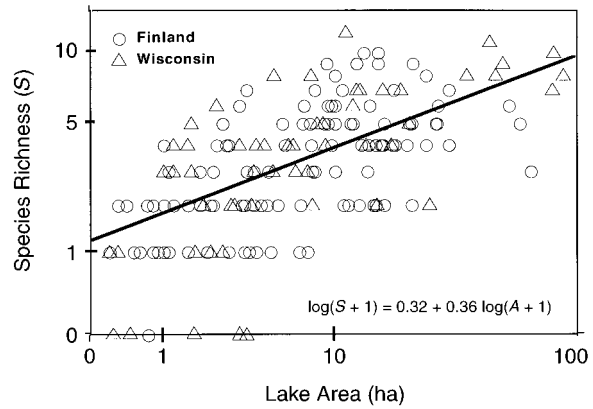

FIG. 2. Species-area relationship for 169 small, forest lakes in Finland and Wisconsin. Some points are hidden. A = area; S = number of species. $R^2 = 0.41$.

variables. For Finland, lakes >6.4 ha were sorted primarily by isolation variables, whereas those <6.4 ha were sorted exclusively by extinction variables.

Assemblages.—Classification trees correctly classified 74% of both Finnish and Wisconsin assemblages (Table 4). This compares favorably with 47% of Finnish and 27% of Wisconsin assemblages that would have been assigned correctly with a random assignment. When either isolation or extinction variables were used alone, isolation models had only slightly more correct classifications than did the extinction models, both for Finland (74 vs. 69%) and Wisconsin (67 vs. 64%).

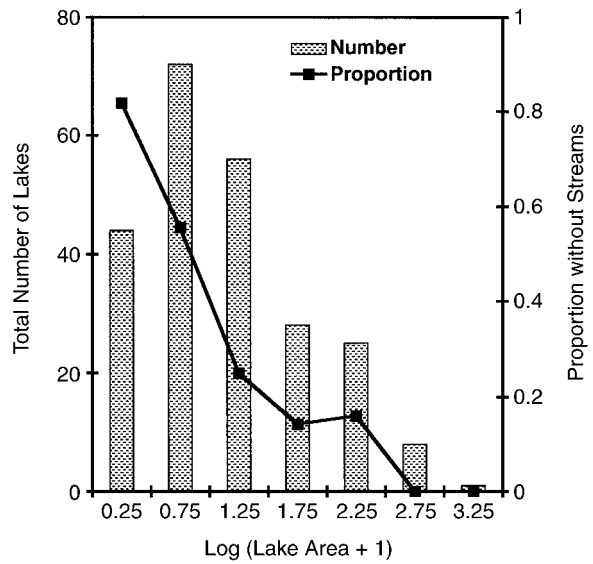Classification success of CART models with all vari-

FIG. 3. Proportion of lakes without a stream connection to a lower lake as a function of log(lake area + 1) for our study lakes in Finland and Wisconsin combined with those from Rahel (1986) in Wisconsin. Numbers of lakes in each size category are plotted as bars. Areas of the 269 lakes range from 0.2 to 1566 ha.

TABLE 3. Statistically significant correlations among the explanatory variables and residual statistics for the corresponding linear regressions for (A) Finland and (B) Wisconsin.

	Correlations		Residuals		
Variables	r	Significance	Independent Durban-Watson	Number >0	Number <0
A) Finland					
Extinction and Isolation					
Number insignificant	18 of 23				
Road distance vs. pH	−0.33	***	no	37	74
Conductivity vs. land vertical	−0.32	***	?	48	65
Conductivity vs. land horizontal	−0.32	***	no	48	65
Conductivity vs. water gradient	−0.22	*	yes	42	54
Area lake vs. water horizontal	0.21	*	?	41	72
Extinction and extinction					
Number insignificant	3 of 6				
pH vs. conductivity	0.36	***	yes	64	49
pH vs. area lake	0.29	**	yes	57	56
Area lake vs. depth	0.28	**	no	46	67
Isolation and isolation					
Number insignificant	12 of 16				
Land vertical vs. land horizontal	0.44	***	no	20	93
Road distance vs. water gradient	0.27	**	no	27	68
Area next lake vs. water horizontal	0.22	*	yes	15	96
Water gradient vs. water horizontal	−0.21	*	no	34	62
B) Wisconsin					
Extinction and isolation					
Number insignificant	17 of 23				
Road distance vs. area lake	−0.36	***	no	23	32
Area lake vs. land horizontal	−0.32	*	?	18	37
Area lake vs. land vertical	−0.30	*	no	16	39
Conductivity vs. land vertical	−0.30	*	no	15	40
Road distance vs. pH	−0.29	*	no	21	34
Conductivity vs. land horizontal	−0.28	*	no	17	38
Extinction and extinction					
Number of insignificant	1 of 6				
pH vs. conductivity	0.66	***	no	30	25
Conductivity vs. lake area	0.54	***	no	13	42
pH vs. lake area	0.51	***	no	27	28
Conductivity vs. depth	−0.46	***	no	19	36
Lake area vs. depth	−0.38	**	no	19	36
Isolation and isolation					
Number insignificant	15 of 16				
Land vertical vs. land horizontal	0.54	***	no	17	38

Note: Significance levels for correlations are: *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$. Critical levels for the Durban-Watson residual tests are $P < 0.05$. The number of insignificant correlations are provided for each group of independent variables, i.e., extinction and isolation, extinction and extinction, and isolation and isolation.

ables differed among assemblages (Fig. 5). Some lakes were assigned without error; CRUCIAN CARP lakes in Finland and PIKE and FISHLESS lakes in Wisconsin. The poorest success was with MUDMINNOW-MINNOW lakes in Wisconsin with only 38% correct; those misclassified were placed in the MUDMINNOW-PERCH and FISHLESS categories. All other assemblage types were classified correctly 70–82% of the time.

In these CART assemblage trees, isolation variables were used less frequently than were extinction variables, especially for Wisconsin (Fig. 5). Overall, three nodes were sorted with isolation variables and seven with extinction variables. Only three of the six isolation variables were used, whereas all four extinction variables were used. Land isolation and distance to the nearest road were more influential than water distance

and stream gradient in Wisconsin CART models using only isolation variables. In the two Wisconsin CART models using only isolation variables but excluding the area of the next lake, land isolation variables were used more frequently than water isolation variables (eight vs. two nodes.

Linear discriminant analysis of assemblages

The linear discriminant analysis (LDA) models for assemblages using both isolation and extinction variables correctly classified 72% (65% by jackknifed classification) of the lakes for Finland and 78% (60% by jackknifed classification) for Wisconsin (Table 5). As with CART, extinction variables were generally selected before isolation variables. When isolation or extinction variables were used alone, the isolation model performed better for Finland, whereas the extinction

A. FINLAND RICHNESS (ALL VARIABLES)
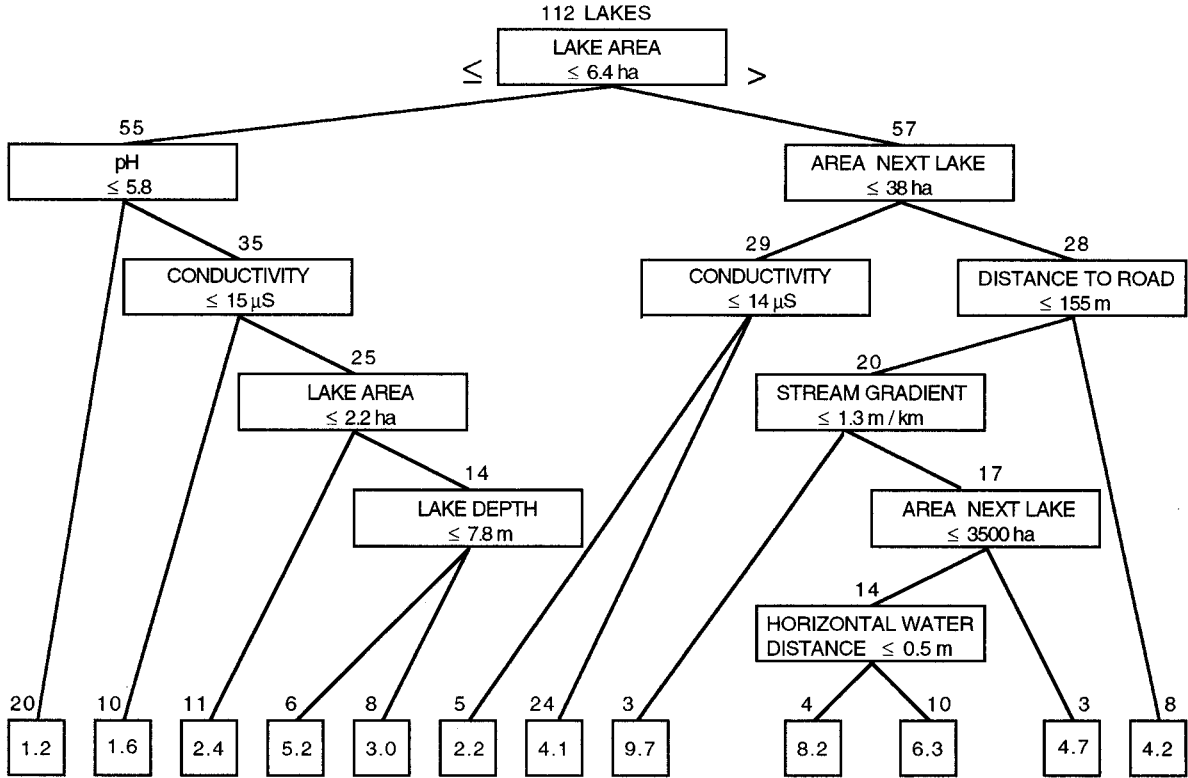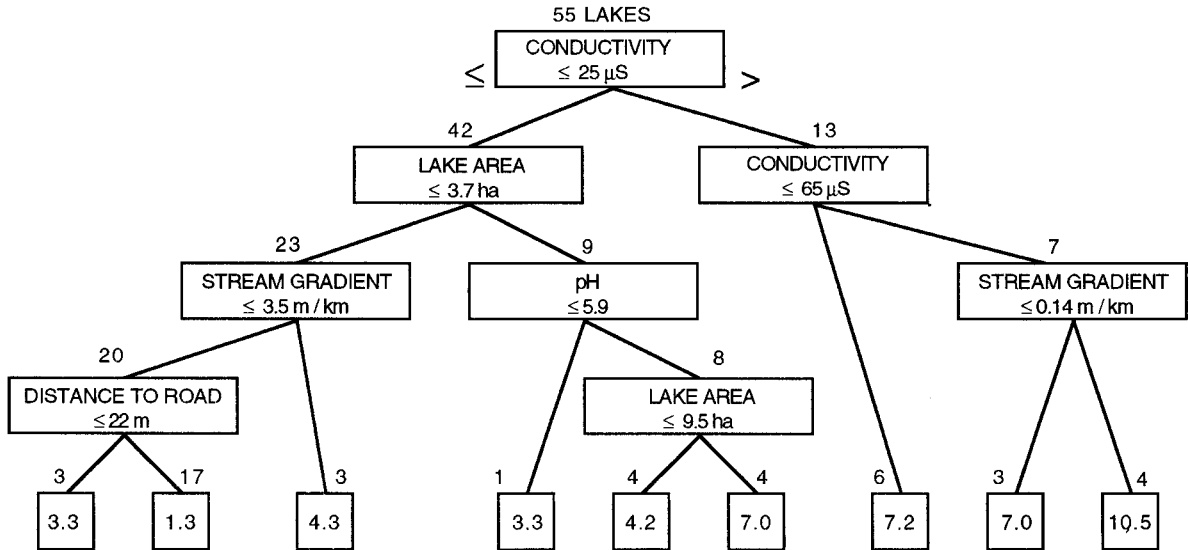

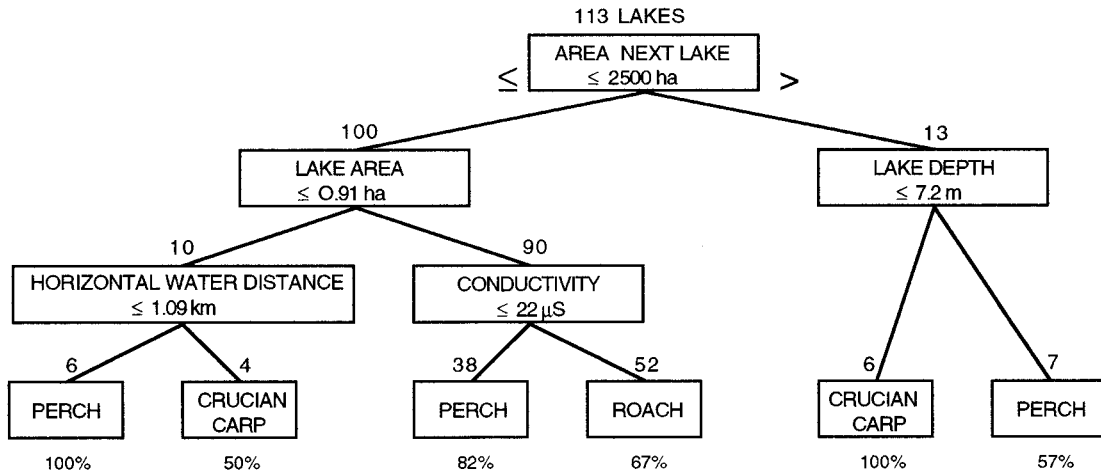## B. WISCONSIN RICHNESS (ALL VARIABLES)

FIG. 4. Classification and regression trees (CART) for fish species richness of small forest lakes in Finland (A) and Wisconsin (B) developed from 10 isolation and extinction variables. Each sorting node contains a variable and its sorting criterion. Lakes with values equal to or less than the sorting criterion go to the left; those greater than the sorting criterion go to the right. The number of lakes at each node is above the node. The mean richness for the lakes of each terminal node is given within the node. The pseudo-R^2 values for each model are 0.82 (Finland) and 0.90 (Wisconsin).

A. FINLAND ASSEMBLAGES (ALL VARIABLES)

113 LAKES

AREA NEXT LAKE
≤ 2500 ha

≤   >

100   13

LAKE AREA
≤ 0.91 ha

LAKE DEPTH
≤ 7.2 m

10   90

HORIZONTAL WATER DISTANCE
≤ 1.09 km

CONDUCTIVITY
≤ 22 µS

6   4

PERCH   CRUCIAN
CARP

100%   50%

38   52

PERCH   ROACH

82%   67%

6   7

CRUCIAN
CARP   PERCH

100%   57%

B. WISCONSIN ASSEMBLAGES (ALL VARIABLES)

55 LAKES

pH
≤ 6.7

≤   >

40   15

DISTANCE TO ROAD
≤ 75 m

LAKE AREA
≤ 8.6 ha

24   16

LAKE DEPTH
≤ 4 m

pH
≤ 4.6

8   16

MUDMINNOW
PERCH   BASS

62%   94%

4   12

MUDMINNOW
PERCH   FISHLESS

100 %   42%

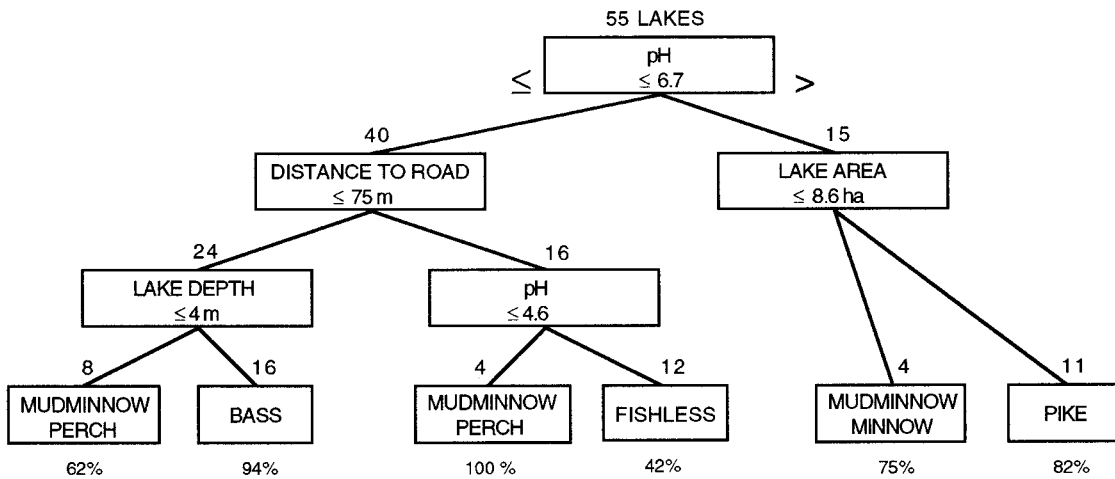4   11

MUDMINNOW
MINNOW   PIKE

75%   82%

FIG. 5. Classification and regression trees (CART) for fish assemblages of small forest lakes in Finland (A) and Wisconsin (B) developed from 10 isolation and extinction variables. Each sorting node contains a variable and its sorting criterion. Lakes with values equal to or less than the sorting criterion go to the left; those greater than the sorting criterion go to the right. The number of lakes at each node is above the node. Each terminal node has an assigned assemblage type; the same assemblage type can be reached by several routes. The percentages of lakes that were correctly classified in each terminal node are given below the node. Overall percentages of correct classification were: for Finland—all = 74%, roach = 76%, perch = 70%, and crucian carp = 100%; for Wisconsin—all = 74%, pike = 100%, bass = 71%, mudminnow-perch = 82%, mudminnow-minnow = 38%, and fishless = 100%.

model performed slightly better for Wisconsin. Isolation variables with higher F values in Finland tended to have lower F values in Wisconsin and vice versa (Table 5).

Meta-analysis of multivariate results

In all models that included both isolation and extinction variables, extinction variables were more im-portant than isolation variables. The average rank of importance (1 to 10 with 1 high) was markedly higher for extinction variables (3.6) than for isolation variables (6.8). The ranks in each group were similar among the six models, with a range of 3.0–4.3 for extinction and 6.3–7.2 for isolation; there was no overlap between groups.

The relative importance of individual isolation and

TABLE 4. Isolation variables (**I** and in boldface type) and extinction variables (E) listed in order of relative importance from CART analysis for richness and assemblage in small, forest lakes of Finland and Wisconsin. For assemblage type, three pairs of analyses were conducted for each region: with all variables, with isolation variables alone, and with extinction variables alone. Letters following the E or **I** indicate the same variables that differed by more than one rank between regions.

	Finland			Wisconsin		
Importance rank	Variable	Relative importance (%)	Variable type	type	Relative importance (%)	Variable
Richness						
1	conductivity	100	E	E	100	pH
2	pH	96	E	E	94	conductivity
3	lake area	88	E	E	65	lake area
4	**stream gradient**	62	**Ia**	**Ic**	60	**vertical land distance**
5	**horizontal land distance**	56	**I**	**I**	57	**horizontal land distance**
6	**area of next lake**	55	**Ib**	Ea	34	lake depth
7	**horizontal water distance**	44	**I**	**I**	30	**horizontal water distance**
8	**vertical land distance**	42	**Ic**	**I**	28	**distance to road**
9	**distance to road**	28	**I**	**Ia**	19	**stream gradient**
10	lake depth	26	Ea	**Ib**	10	**area of next lake**
Assemblages						
All variables						
1	lake area	100	E	E	100	lake area
2	lake depth	86	Ea	**Ic**	94	**horizontal land distance**
3	**area of next lake**	67	**Ia**	Eb	91	pH
4	**stream gradient**	53	**Ib**	Ea	78	lake depth
5	conductivity	48	E	E	73	conductivity
6	pH	37	Eb	**I**	71	**vertical land distance**
7	**vertical land distance**	37	**I**	**I**	48	**horizontal water distance**
8	**horizontal water distance**	35	**I**	**Ia**	44	**area of next lake**
9	**distance to road**	31	**I**	**I**	39	**distance to road**
10	**horizontal land distance**	23	**Ic**	**Ib**	26	**stream gradient**
Isolation variables alone						
1	**stream gradient**	100	**Ia**	**Id**	100	**horizontal land distance**
2	**area of next lake**	94	**Ib**	**Ie**	69	**distance to road**
3	**vertical land distance**	79	**I**	**I**	65	**vertical land distance**
4	**horizontal water distance**	79	**Ic**	**Ia**	54	**stream gradient**
5	**horizontal land distance**	66	**Id**	**Ib**	54	**area of next lake**
6	**distance to road**	59	**Ie**	**Ic**	37	**horizontal water distance**
Extinction variables alone						
1	lake depth	100	Ea	Eb	100	lake area
2	lake area	90	E	E	99	pH
3	conductivity	81	E	E	91	conductivity
4	pH	58	Eb	Ea	71	lake depth

Note: For Finland and Wisconsin, respectively, the pseudo-R^2 values for richness are 0.82 and 0.90, and the percentages correctly classified are 74% and 74% using all variables, 74% and 67% using isolation variables alone, and 69% and 64% using extinction variables alone.

extinction variables differed between Finland and Wisconsin (Fig. 6; Tables 4 and 5). Among the six isolation variables, stream gradient and area of the next lake were consistently important for Finland, whereas the horizontal land and water distances were consistently more important for Wisconsin. Among the four extinction variables, lake area was consistently important for both Finland and Wisconsin; the other important extinction variables included conductivity for Finland and pH for Wisconsin. Lake area and conductivity were more important than lake depth and pH in Finland, while pH and lake area were more important than conductivity and lake depth in Wisconsin. Rankings among all 10 models were more similar for extinction variables than for isolation variables; none of these differences altered the overall differences between regions or the importance of individual variables.

Discussion

Necessity of a multivariate approach

The positive species–area relations we observed are consistent with expectations from island biogeography. The relation between species richness and lake area for small forest lakes of Finland and Wisconsin was moderately strong (Fig. 2). This slope is similar to the steeper slopes observed for more distant island archipelagoes, more isolated islands, less vagil species (Brown 1971, Lomolino 1984), or islands within the same province (Rosenzweig 1995). However, slopes of species–area regressions have a variety of possible interpretations rather than a unique interpretation in terms of the importance of isolation and extinction to species richness. Caution should be applied when making mechanistic interpretations from slopes of species–area regressions (Connor and McCoy 1979, Abbott 1983).

TABLE 5. Isolation variables (**I** and in boldface type) and extinction variables (E) listed in order of the F value to enter or remove the variable in a linear discriminant analysis for fish assemblage type in small, forest lakes of Finland and Wisconsin. Three pairs of analyses were conducted for each region: with all variables, with isolation variables alone, and with extinction variables alone. Letters following the E or **I** indicate the variables that differed by more than one rank between regions.

Rank	Finland Variable	F to enter or remove	Variable type		Wisconsin F to enter or remove	Wisconsin Variable
All variables						
1	lake area	11.9	E	Eb	22.9	pH
2	**area of next lake**	10.4	**Ia**	E	6.5	lake area
3	conductivity	5.5	Ea	E	6.1	lake depth
4	lake depth	3.9	E	**Id**	2.9	**horizontal water distance**
5	**horizontal land distance**	2.2	**Ib**	**I**	2.0	**stream gradient**
6	**stream gradient**	2.0	**I**	**Ia**	2.2	**area of next lake**
7	**vertical land distance**	1.9	**Ic**	**Ib**	1.7	**horizontal land distance**
8	**horizontal water distance**	2.2	**Id**	Ea	⋯	conductivity
9	pH	3.0	Eb	**Ic**	⋯	**vertical land distance**
10	**distance to road**	⋯	**I**	**I**	⋯	**distance to road**
Isolation variables alone						
1	**area of next lake**	10.5	**Ia**	**Ic**	5.0	**horizontal water distance**
2	**vertical land distance**	5.5	**Ib**	**Ie**	3.4	**horizontal land distance**
3	**stream gradient**	4.1	**I**	**Id**	3.4	**distance to road**
4	**horizontal water distance**	4.2	**Ic**	**I**	1.8	**stream gradient**
5	**distance to road**	1.5	**Id**	**Ia**	⋯	**area of next lake**
6	**horizontal land distance**	⋯	**Ie**	**Ib**	⋯	**vertical land distance**
Extinction variables alone						
1	lake area	11.6	E	Eb	22.9	pH
2	conductivity	5.5	Ea	E	6.5	lake area
3	lake depth	2.5	E	E	6.1	lake depth
4	pH	1.6	Eb	Ea	⋯	conductivity

Note: For Finland and Wisconsin, respectively, percentages classified correctly from the classification matrix (with corresponding percentages for jackknife classifications in parentheses) are 72% (65%) and 78% (60%) using all variables, 68% (65%) and 58% (44%) using isolation variables alone, and 58% (56%) and 66% (60%) using extinction variables alone. Ellipses indicate variables that were not statistically significant at $P < 0.05$.

Furthermore, it is important to acknowledge that lake area itself is correlated with the rich array of isolation and extinction properties of small forest lakes (Fig. 3; Table 3). Thus, a multivariate approach is needed in comparative studies to sort out the possible role of isolation and extinction.

In addition to the correlations involving lake area, a number of other isolation and extinction variables were correlated. Some of these are expected from limnological or geomorphic principles, such as the relation between "pH and conductivity" or between "vertical land distance and horizontal land distance." Others are easily rationalized such as the negative correlation between "road distance and pH" for Wisconsin, where
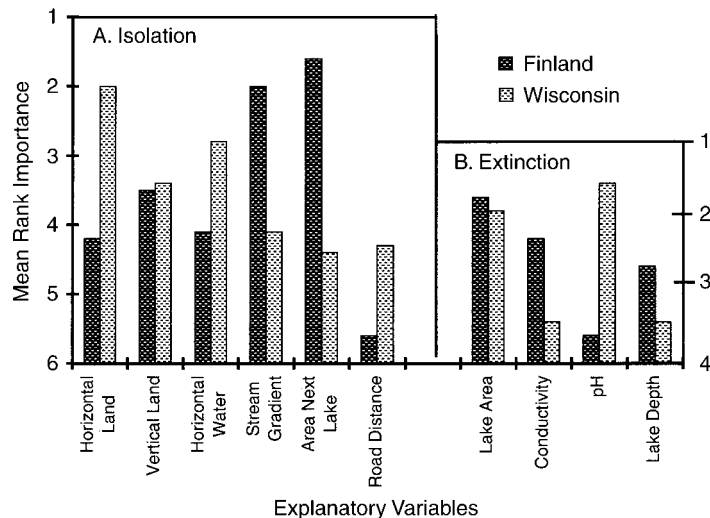

FIG. 6. Mean rank importance of each isolation variable and extinction variable averaged across individual ranks for all 14 models for Finland and Wisconsin, richness and assembly, CART and LDA, and for isolation and extinction treated together or separately. For isolation (on the left), the highest mean rank would be 1 and the lowest 6. For extinction (on the right), the highest mean rank would be 1 and the lowest 4.

the most acidic lakes are dystrophic bogs surrounded by sphagnum wetlands that prohibit the close approach of a road. The same negative correlation is apparent but weaker in Finland because the road density is lower in Finland.

The greatest correlations among explanatory variables were for extinction variables in Wisconsin. These result because all of the variables are partially determined by an overarching geomorphic control on limnology, namely the position of the lake in the landscape (Kratz et al. 1997), which was established by the geomorphic template set down as the glaciers retreated (Riera et al., *in press*). Lakes high in a groundwater flow system tend to be smaller, more acidic, less fertile, and less likely to be connected by a stream to another lake than are lakes lower in the landscape. Multivariate approaches are especially useful in teasing apart the potential relative importance of individual variables on fish species richness and assembly. The concern, of course, is that the importance of one explanatory variable may be masked by its strong correlation with another explanatory variable. For example, is the importance of lake depth (winterkill) in Wisconsin masked by pH through the common associations that lake depth and pH have with lake area? While this is possible, in the multivariate analysis (Tables 4 and 5), pH is chosen before lake depth in all five Wisconsin models, both parametric and nonparametric for richness and assemblages. We favor the conclusions reached through the multivariate analysis.

Importance of isolation vs. extinction

We designed the present analyses to assess whether extinction was more important than isolation in determining richness and composition of fish assemblages in small forest lakes. Our earlier analyses (Tonn and Magnuson 1982, Tonn et al. 1983, 1990, 1995, Magnuson et al. 1989) indicated that both extinction and isolation variables contributed to statistical models explaining differences in richness or assemblages; some of these studies suggested that extinction was more important than isolation. The present analysis greatly strengthens the evidence for the importance of extinction over isolation in prediction of richness and assembly.

Extinction variables were consistently more important than isolation variables in our multivariate analyses (Table 3 and 4; Figs. 4 and 5); this was true for both Finland and Wisconsin, for richness and assembly, and for CART and LDA analyses. This does not mean that isolation is unimportant, but rather that the observed patterns of richness and assembly of fishes in small forest lakes more closely reflect the local conditions for extinction (or failure to establish) than the local conditions of isolation.

A key question is: Why are the relations of richness and assembly stronger with extinction variables than with isolation variables? We suggest that the explanation for this robust result lies in the difference between the relative probabilities of immigration and extinction events rather than in the effect each has in its own right. Operationally, differences in potential rates of extinction and invasion translate into how soon an extinction occurs after an invasion event vs. how soon an invasion event occurs after an extinction. The last imprint on species composition and richness of a lake would more likely reflect the higher probability (potentially more frequent) process than the lower probability (potentially less frequent) process.

Evidence reviewed below suggests that the immigration rate of new species into a lake is low, normally requiring decades to centuries or millennia, but that a local extinction can occur relatively quickly, months to a few years or to a few decades after an invasion. Recent studies that have measured local extinction and (re-)colonization from historical evidence indicate that extinctions occur more frequently than (re-)colonizations in lakes (Bergquist 1991, Eckmann 1995).

Immigration.—The occurrence of fishless lakes in our data set suggests that immigration rates of new taxa can be slow. It has been ~10 000 yr since the glaciers receded, yet six of the lakes were FISHLESS, even though each appears capable of supporting fish. For Wisconsin, two should be suitable for the BASS assemblage, two for the MUDMINNOW-PERCH assemblages and one for the MUDMINNOW-MINNOW assemblage (Magnuson et al. 1989). None of the six had a stream connection and as a group they tended to have the longest and highest land barriers and the longest distance to a road (Table 1). Thus, even with tornadoes, migratory aquatic birds, and humans for transport (Magnuson 1976), low arrival rates apparently have excluded fish from 1% of the Finnish and 9% of the Wisconsin study lakes, or 2 and 12%, respectively, if only lakes without stream connections are considered. More directly, no new species were observed over 13 yr of annual sampling in two small, isolated forest lakes (Crystal Bog and Trout Bog) at our Wisconsin site.

In North America and Wisconsin, estimates of recent colonization rates are much higher in larger lakes where human influences are more apparent than in the small forest lakes (see Magnuson and Lathrop 1992, Cisneros 1993, Mills et al. 1993, Magnuson et al. 1994). These estimates of a new species every 6–25 yr for intensively used lakes such as Lake Mendota, Wisconsin, the Laurentian Great Lakes, and five larger lakes frequented by tourists at the Wisconsin study site, clearly overestimate colonization for the small forest lakes, which are more isolated and less visited by humans.

Extinctions.—In our study lakes, three factors operate repeatedly and at frequent intervals that result in local extinction or prevent successful establishment following an immigration event. These factors are winterkill owing to low winter oxygen levels in the shallow lakes, low pH effects in dystrophic bog lakes, and predation by northern pike or largemouth bass in small

lakes with low habitat heterogeneity (reviewed in Magnuson et al. 1989). Because of their frequent or continuous operation, these factors can occur soon after an immigration.

Frequency of winterkill has rarely been measured directly, but should depend on a lake's depth, productivity, altitude, latitude, and the severity of the winter; occurrences range from annually to never. For the Wisconsin lakes, local experience (Tonn and Paszkowski 1986) suggests that the probability of extinction for an intolerant species in a susceptible lake is in the range of 0.05–0.2/yr, or an extinction every 5–20 yr.

The pH strongly filters the distribution of fish species among lakes (Rahel and Magnuson 1983, Magnuson et al. 1984, Rask 1987, Bergquist 1991). Those not killed directly by low pH may have problems with osmoregulation, reproduction, or survival of eggs and larvae (Craig and Baksi 1977, Haines 1981, Nelson 1982, Chuklakasem et al. 1989, McCormick et al. 1989, McCormick and Jensen 1992). Direct lethal effects can occur in days, whereas local extinction caused by effects on reproduction or recruitment occur over the duration of a fish's 2–20 yr life span. When Swedish lakes were being acidified by acid deposition, average richness declined from 4.7 to 3.6 fishes (Bergquist 1991). Sensitivity varied among species; European minnow disappeared from 70% of the lakes, whereas only 2% of European perch populations disappeared. Annual extinction probabilities for sensitive species could range from 0.05 (one species in 20 yr) for long-lived, to 0.5 (one in 2 yr) for short-lived species, and even 1.0 (one in 1 yr) for those for which low pH is a direct lethal factor.

Predation by northern pike, largemouth bass, and even yellow perch can eliminate the mudminnow and minnows (cyprinids) from small forest lakes in Wisconsin (Tonn and Magnuson 1982, Magnuson et al. 1989, Tonn et al. 1990). This results both from direct predation in closed systems and a combination of direct predation and emigration in open systems (He and Kitchell 1990, He et al. 1993, Kitchell et al. 1994). Additional evidence of predation's effectiveness comes from attempts to stock minnows as forage for northern pike and largemouth bass in small Wisconsin lakes (Rahel 1982); in five such lakes with moderate pH, minnows (golden shiner, bluntnose minnow, fathead minnow, and redbelly dace) were not found 7–19 yr later. The annual extinction probability for sensitive taxa following their arrival in a lake with piscivores, or after a successful invasion of a piscivore, appears to be in the same range as for winterkill and pH. In Finland, minnows persist more readily with northern pike because most European cyprinids grow large enough to reach a body-size refuge from predation (Tonn et al. 1990). However, even with this refuge, northern pike are known to influence the abundance and size distributions of crucian carp and tench (Brönmark et al. 1995).

Isolation vs. extinction.—Extinction and immigration intrinsically depend on each other. To go extinct, a species must first have arrived at a lake or returned following a previous local extinction. We suspect that recurrent invasions and extinctions are more frequent than novel invasions. Regardless, the greater the lag in arrival after an extinction vs. the lag in extinction after an arrival, the more important extinction variables will be identified relative to isolation variables in analyses such as ours. Thus, somewhat counterintuitively, the greater the isolation is among insular sites, the more important extinction will be in determining patterns of richness and assembly. Extinction factors are more important than isolation factors for Wisconsin relative to Finland even though (or because) isolation by land barriers was more common in Wisconsin.

Because differences in time lags between extinction and immigration events appear to determine observed species richness and composition for a lake, the more frequent process will be more important. In some cases, the action of what we are calling an extinction factor can be so frequent that an arriving taxon may not even have the opportunity to reproduce. Thus, even well-connected lakes, such as the PIKE lakes in Wisconsin, can have an assemblage determined by frequent extinction factors, e.g., predation by northern pike on small spineless species. High frequencies of extinction can only occur if (re-)invasions continue to supply species. In a sense, when invasions are rare, it is the potential frequency of the extinction factor that is important; the actual extinction rate may be low simply because the rate of invasion is low owing to strong isolation factors.

This phenomenon may be general for aquatic and terrestrial insular environments and not unique to fish in small forest lakes. When comparing lakes as islands (and oceans as continents), Magnuson (1988) suggested that "for the same spatial scale, recruitment in lakes may be best predicted by extinction models whereas recruitment in oceans may be best predicted by colonization models." In open systems extinction events may be erased quickly by reinvasion, whereas in lakes or on islands extinction events are not soon erased by invasion events. In a wide variety of studies, differences in extinction variables have been more important than differences in isolation variables in explaining species richness. Examples include vascular plants in ponds (Moller and Rordam 1985), butterflies, birds, and mammals on montane islands (Wilcox et al. 1986, Davis et al. 1988), and mammals on islands (Crowell 1986, Peltonen and Hanski 1991). This generality is not to say that differences in isolation are not important, they are, but that the signals left to observe on the richness and composition of the biota are those of extinction rather than isolation.

Differences between Finland and Wisconsin

We also examined the individual contributions of six isolation and four extinction variables after accounting

for their associations with each other in CART and LDA multivariate analyses. In earlier papers, our index of isolation combined stream gradient and vertical distance over land between the lakes (Tonn et al. 1990). Although that index did indicate an important role for isolation, our present analyses have shown that the two variables were not necessarily the most important of the isolation variables and that the importance of individual variables differed between Finland and Wisconsin. Differences in the importance of individual isolation variables were related to differences in geological settings between Finland and Wisconsin (Fig. 1; Table 1).

In Finland, immigrants need to swim up steep gradient streams from large lake sources or refugia. Not surprisingly, the highest ranked isolation variables for Finland were the area of the next downstream lake and the gradient of the connecting stream (Fig. 6A). Because of species–area relations, the area of the downstream lake is an index of the number of species available for movement to the upstream lake whereas stream gradient is a measure of difficulty of traveling up the stream. Owing to the relatively high topographic relief, vertical distances were more important than horizontal distances, i.e., vertical land distance was more important than horizontal land distance and stream gradient was more important than the length of the stream (Fig. 6A).

In contrast to Finland, the Northern Highlands of Wisconsin are relatively flat and more lakes are separated from their NEXT LAKE by a land barrier. Consistently, the highest ranked isolation variable for Wisconsin was horizontal land distance, a measure of difficulty for transport across a land barrier, whereas the area of the source lake was relatively unimportant (Fig. 6A). Similarly, stream length was more important than stream gradient (Fig. 6A).

Because of more complete stocking records, we were able to exclude stocked species from the Finnish analyses but not from the Wisconsin analyses; interestingly, this facilitated identification of the human role in moving fishes across geomorphic barriers. Not surprisingly, road distance was more important in Wisconsin than Finland (Fig. 6A). In addition, including road distance contributed to the correct classifications from isolation variables for Wisconsin. The percentage of correctly classified assemblages (67%) declined to 53% when road distance was not included in a CART analysis, mainly because only 14% of the BASS lakes were then classified correctly, compared with 62% if road distance were included (J. J. Magnuson, *unpublished data*). Stocking of largemouth bass would appear to be functionally related to proximity of these geomorphically isolated lakes to a road, although we cannot exclude the alternate hypothesis that roads were built to lakes containing largemouth bass. However, in a separate analysis of stocked fish in Finland (J. J. Magnuson, *unpublished data*), numbers of stocked fishes decreased with road distance ($G = 23.7$, df = 2, $P \ll 0.001$ [Sokal and Rohlf 1981]). A greater proportion of lakes with only 0–2 stocked species were farther than 100 m from a road than were lakes with as many as 3–6 stocked species. Regardless, although stocking apparently did influence some of the Wisconsin results and could have influenced the Finland results had we included stocked fish in the overall analyses, its influence was relatively minor and evidence for the influence of geomorphic differences between Finland and Wisconsin on richness and assembly is strong.

Extinction factors have been important in both regions (Tonn and Magnuson 1982, Rahel 1984, Magnuson et al. 1989, Tonn et al. 1990, 1995), but again differences between regions occur (Fig. 6B). Conductivity and lake depth were more important in Finland, whereas pH was more important in Wisconsin; lake area was important in both regions (Fig. 6B). As with the isolation variables, some of the differences between Finland and Wisconsin in the importance of individual extinction variables appear related to differences in the geomorphic settings of the regions. In Wisconsin, fish species richness and at least two of our extinction variables (conductivity and lake area) are related to the position of the lake in the landscape (Kratz et al. 1997). Lakes higher in the landscape (higher in the flow system) are smaller and have lower conductivities than lakes lower in the landscape (lower in the flow system). For these and related reasons (e.g., lower pH and a greater likelihood of no connecting streams), lakes higher in the landscape have fewer fish species than those lower in the landscape (Kratz et al. 1997). We have not formally compared the influence of position in the landscape on the relative importance of individual extinction factors between the two regions, but such an analysis would appear to have promise given the difference in the geomorphic settings and the strong relations observed in Wisconsin. Such inter-regional analyses are underway at the North-Temperate Lakes Long-Term Ecological Research Site in Wisconsin.

Conclusion

Multivariate statistical models used to predict species richness and assembly in small forest lakes of Finland and Wisconsin consistently indicated that extinction factors were more important than isolation factors. The greater importance of extinction is not because the isolation of a lake is unimportant, but because extinction events are expected to occur sooner following an invasion, than invasion events occur following an extinction. This conclusion is not altered by differences in the geomorphic settings of Finland and Wisconsin nor by the use of parametric or nonparametric statistical models. The differences between the geomorphic settings of the two lake-rich regions are reflected in differences in the importance of individual isolation variables. The most important extinction variables also dif-

fer between regions; these differences may be set by the geomorphic differences between the two regions.

LITERATURE CITED

Abbott, I. 1983. The meaning of z in species/area regressions and the study of species turnover in island biogeography. Oikos **41**:385–390.

Attig, J. W. 1984. The Pleistocene geology of Vilas County, Wisconsin. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.

Barbour, C. D., and J. H. Brown. 1974. Fish species diversity in lakes. American Naturalist **108**:473–489.

Bergquist, B. C. 1991. Extinction and natural recolonization of fish in acidified and limed lakes. Nordic Journal of Freshwater Research **66**:50–62.

Breiman L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth International Group, Belmont, California, USA.

Brönmark, C., C. A. Paszkowski, W. M. Tonn, and A. Hargeby. 1995. Predation as a determinant of size structure in populations of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*). Ecology of Freshwater Fish **4**:85–92.

Brown, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. American Naturalist **105**:467–478.

Brown, J. H., and M. V. Lomolino. 1989. Independent discovery of the equilibrium theory of island biogeography. Ecology **70**:1954–1957.

Browne, R. A. 1981. Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. Journal of Biogeography **8**:75–83.

Case, T. J., and M. L. Cody. 1987. Testing theories of island biogeography. American Scientist **75**:402–411.

Chulakasem, W., J. A. Nelson, and J. J. Magnuson. 1989. Interaction between effects of low pH and low ion concentration on mortality during early development of medaka, *Oryzias latipes.* Canadian Journal of Zoology **67**:2158–2168.

Cisneros, R. O. 1993. Detection of cryptic invasions and local extinctions of fishes using a long-term database. Master's thesis. University of Wisconsin, Madison, Wisconsin, USA.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. American Naturalist **113**:791–833.

Craig, G. R., and W. F. Baksi. 1977. The effects of depressed pH on flagfish reproduction, growth, and survival. Water Research **11**:621–626.

Crowell, K. L. 1986. A comparison of relict versus equilibrium models for insular mammals of the Gulf of Maine. Biological Journal of the Linnean Society **28**:37–64.

Davis, R., C. Dunford, and M. V. Lomolino. 1988. Montane mammals of the American Southwest: the possible influence of post-Pleistocene colonization. Journal of Biogeography **15**:841–848.

Eadie, J. M., T. A. Hurly, R. D. Montgomerie, and K. L. Teather. 1986. Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. Environmental Biology of Fishes **15**:81–89.

Eadie, J. M., and A. Keast. 1984. Resource heterogeneity and fish species diversity in lakes. Canadian Journal of Zoology **62**:1689–1695.

Eckmann, R. 1995. Fish species richness in lakes of the northeastern lowlands in Germany. Ecology of Freshwater Fish **4**:62–69

Forbes, S. A. 1887. The lake as a microcosm. Bulletin of the Peoria Scientific Association 1887:1–15 (see also 1925 Bulletin of Illinois State Natural History Survey **15**:537–550).

Haines, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Transactions of the American Fisheries Society **110**:669–707.

He, X., and J. F. Kitchell. 1990. Direct and indirect effects of predation on a fish community: a whole lake experiment. Transactions of the American Fisheries Society **119**:825–835.

He, X., R. A. Wright, and J. F. Kitchell. 1993. Fish behavioral and community responses to manipulation. Pages 69–84 *in* S. R. Carpenter, and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Holopainen, I. J., and H. Hyvarinen. 1985. Ecology and physiology of crucian carp [*Carassius carassius* (L.)] in small Finnish ponds with anoxic conditions in winter. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **22**:2566–2570.

Hutchinson, G. E. 1957. A treatise on limnology. Volume 1. Wiley, New York, New York, USA.

Keddy, P. A. 1976. Lakes as islands: the distributional ecology of two aquatic plants, *Lemna minor* L. and *L. trisulca* L. Ecology **57**:353–359.

Kitchell, J. F., L. A. Eby, X. He, D. E. Schindler, and R. A. Wright. 1994. Predator-prey dynamics in an ecosystem context. Journal of Fish Biology **45** (supplement A):209–226.

Kratz T. K., K. E. Webster, C. J. Bowser, J. J. Magnuson, and B. J. Benson. 1997. The influence of landscape position on lakes in northern Wisconsin. Freshwater Biology **37**:209–217.

Lomolino, M. V. 1984. Mammalian island biogeography: effects of area, isolation and vagility. Oecologia **61**:376–382.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of island biogeography. Evolution **17**:373–387.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology **1**.

Magnuson, J. J. 1976. Managing with exotics—a game of chance. Transactions of the American Fisheries Society **105**:1–9.

———. 1988. Two worlds of fish recruitment: lakes and oceans. American Fisheries Society Symposium **5**:1–6.

Magnuson, J. J., J. P. Baker, and F. J. Rahel. 1984. A critical assessment of effects of acidification on fisheries in North America. Transactions Royal Society of London B **305**:501–516.

Magnuson, J. J., B. J. Benson, and A. S. McLain. 1994. Insights on species richness and turnover from long-term ecological research: fishes in north temperate lakes. American Zoologist **34**:437–451.

Magnuson, J. J., and R. C. Lathrop. 1992. Historical changes in the fish community. Pages 193–231 *in* J. F. Kitchell,

editor. Food web management: a case study of Lake Mendota. Springer-Verlag, New York, New York, USA.

Magnuson, J. J., C. A. Paszkowski, F. J. Rahel, and W. M. Tonn. 1989. Fish ecology in severe environments of small isolated lakes in northern Wisconsin. Freshwater wetlands and wildlife, 1989, CONF-8603101, Department of the Environment Symposium Series Number 61. *In* R. R. Sharitz and J. W. Gibbons, editors. U.S. Department of the Environment Office of Scientific and Technical Information, Oak Ridge, Tennessee, USA.

McCormick, J. H., and K. M. Jensen. 1992. Osmoregulatory failure and death of first-year largemouth bass (*Micropterus salmoides*) exposed to low pH and elevated aluminum, at low temperature in soft water. Canadian Journal of Fisheries and Aquatic Sciences **49**:1189–1197.

McCormick, J. H., K. M. Jensen, and L. E. Anderson. 1989. Chronic effects of low pH and elevated aluminum on survival, maturation, spawning and embryo-larval development of the fathead minnow in soft water. Water, Air, and Soil Pollution **43**:293–307.

Mills, E. L. J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crisis and anthropogenic introductions. Journal of Great Lakes Research **19**:1–54.

Moller, T. R., and C. P. Rordam. 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. Oikos **45**:8–16.

Munroe, E. G. 1948. The geographical distribution of butterflies in the West Indies. Dissertation. Cornell University, Ithaca, New York, USA.

National Board of Survey. 1979. Fennia, Suuri Suomi-kartasto Finland in maps 1:250,000. Weilin+Göös, Helsinki, Finland.

Nelson, J. A. 1982. Physiological observations on developing rainbow trout, *Salmo gardneri* (Richardson), exposed to low pH and varied calcium ion concentrations. Journal of Fish Biology **20**:359–372.

Peltonen, A., and I. Hanski. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. Ecology **72**:1698–1708.

Rahel, F. J. 1982. Fish assemblages in Wisconsin bog lakes. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.

―――. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology **65**:1276–1289.

―――. 1986. Biogeographic influences on fish species composition of northern Wisconsin lakes with applications for lake acidification studies. Canadian Journal of Fisheries and Aquatic Sciences **43**:124–134.

Rahel, F. J., and J. J. Magnuson. 1983. Low pH and the absence of fish species in naturally acidic Wisconsin lakes: inferences for cultural acidification. Canadian Journal of Fisheries and Aquatic Sciences **40**:3–9.

Rask, M. 1987. Effects of acid deposition on fish populations in small lakes of southern Finland. Pages 528–532 *in* R. Perry, R. M. Harrison, J. N. B. Bell, and J. N. Lester, editors. Acid rain: scientific and technical advances. Selper, London, UK.

Riera, J. L., J. J. Magnuson, T. K. Kratz and K. E. Webster. *In press.* A geomorphic template for the analysis of lake districts applied to Northern Highland Lake District Wisconsin, USA. Freshwater Biology (Special Issue: The Organization of Lake Districts).

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York, New York, USA.

Ryder, R. A. 1982. The morphoedaphic index—use, abuse, and fundamental concepts. Transactions of the American Fisheries Society **111**:154–164.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, USA.

Tonn, W. M. 1985. Density compensation in *Umbra-Perca* fish assemblages of northern Wisconsin lakes. Ecology **66**:415–429.

Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology **63**:1149–1166.

Tonn, W. M., J. J. Magnuson, and A. M. Forbes. 1983. Community analysis in fishery management: an application with northern Wisconsin lakes. Transactions of the American Fisheries Society **112**:368–377.

Tonn, W. M., J. J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small forest lakes: fish assemblage patterns in Finland and Wisconsin. American Naturalist **136**:345–375.

Tonn, W. M., and C. A. Paszkowski. 1986. Size-limited predation, winterkills, and the organization of *Umbra-Perca* fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences **43**:194–202.

Tonn, W. M., R. E. Vandenbos, and C. A. Paszkowski. 1995. Habitat on a broad scale: relative importance of immigration and extinction for small lake fish assemblages. Bulletin Francais de la Peche et de la Pisciculture **337/338/339**:47–61.

Wilcox, B. A., D. D. Murphy, P. R. Ehrlich, and G. T. Austin. 1986. Insular biogeography of the montane butterfly faunas in the Great Basin: comparison with birds and mammals. Oecologia **69**:188–194.