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Trophic Dependence of Ecosystem Resistance and Species Compensation in Experimentally Acidified Lake 302S (Canada)

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ABSTRACT

Ecosystem resistance to the impacts of diverse human insults depends on the replacement of sensitive species by ones more tolerant of the stressor. Here we present evidence from a whole-lake acidification experiment (Lake 302S, Experimental Lakes Area, Canada) that resistance and species compensation decline with increasing trophic level. Diverse and fast-growing algal and rotifer assemblages with high dispersal potentials showed significant compensatory species dynamics, resulting in the maintenance of total biomass despite 30%–80% declines in species richness. Canonical correspondence analysis showed that significant compensatory algal and rotifer dynamics were best explained by differential species tolerances of acidified chemical conditions coupled with release from resource limitation and predation. However, less diverse cladoceran, copepod, and fish assemblages showed significant declines in total biomass and weak species compensation with loss of species during acidification. In comparison, algal and zooplankton species dynamics remained relatively synchronized in a nearby unperturbed reference lake (Lake 239) during the experiment. As a result, Lake 302S showed limited ecosystem resistance to anthropogenic acidification. Therefore, we hypothesize that lost species will increase the susceptibility of acidified lakes to the adverse impacts of other environmental stressors (for example, climate warming, stratospheric ozone depletion, invasive species). Consequently, the ecosystem stability of boreal lakes is expected to decline as global change proceeds.

Key words: acidification; biodiversity; boreal lakes; dispersal; ecosystem stability; functional compensation; global change; species dynamics; trophic interactions.

INTRODUCTION

Global change and the loss of biodiversity have prompted concern over the impacts of multiple environmental stressors on freshwater ecosystems (Schindler 1990b, 1998a; Sala and others 2000). In particular, acid precipitation, climatic warming, and changing biodiversity are expected to adversely affect naturally species-poor, unproductive northern environments in which ecosystem function can depend on only a few species (Schindler 1990b, 1995). As a consequence, boreal lakes may lack the biodiversity that is necessary to maintain ecosystem

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processes such as primary production as they increasingly experience anthropogenic perturbations. For example, boreal lake ecosystems continue to be impoverished by cultural acidification (Minns and others 1990; Schindler 1990b; Arnott and others 2001), which may decrease their stability (*sensu* Pimm 1984) and increase their sensitivity to the impacts of multiple stressors (Schindler and others 1991, 1996; Yan and others 1996).

"Resistance" refers to the capacity of an ecosystem to withstand having its ecological processes displaced by a perturbation. The resistance of a group of ecologically similar species (that is, a functional group) that perform a specific ecological process depends on the presence of tolerant species and their compensatory interactions with other species (Ives 1995). Specifically, resistance and compensatory species dynamics involve tolerant species succeeding competitors that are suppressed by a perturbation and maintaining their shared ecological processes (that is, functional compensation). As a result, ecosystem processes performed by more diverse functional groups of species may show greater resistance because of an increased probability that tolerant species will be present (Ives and others 1999; Yachi and Loreau 1999). If so, higher trophic levels may show less resistance because species diversity declines with trophic rank (Rosenzweig 1995; Petchey and others 1999; Klug and others 2000). In addition, functional groups may show differential sensitivities to a perturbation depending on their species turnover rates, dispersal potentials (Schindler 1987; Finlay and Clarke 1999; Shurin 2000; Schindler and Parker 2002), and the ecological history of the ecosystem (Jenkins and Buikema 1998; Fischer and others 2001b).

In this study, we examined decade-long limnological data sets from an experimentally acidified boreal lake and a nearby reference lake for evidence of ecosystem resistance and temporal compensatory dynamics within taxonomically defined functional groups of species. We analyzed the species dynamics of phytoplankton, epilithon, rotifers, cladocerans, and copepods because each group consisted of ecologically similar species that shared certain resource needs, predation risks, and relative trophic position (Frost and others 1995). For example, phytoplankton and epilithon (rock-associated algae) biomass represented realized basal production that was potentially available to herbivores in pelagic and benthic habitats, respectively. Rotifer and cladoceran biomass represented indexes of generalist suspension feeding by micro- and macrozooplankton, respectively. Most rotifers, including *Asplanchna* species that are generally considered predatory, consume a variety of mainly algae and some protozoans and are prey for macrozooplankton (Walz 1997). In comparison, herbivorous cladoceran species were grouped into a separate functional group because they consume a wider array of items, such as bacteria, algae, protozoans, and small rotifers, and are prey for both larger zooplankton and fish (Pace and Vaque 1994). Copepod biomass served as an estimate of omnivory by raptorial-feeding planktonic macroinvertebrates that prey on an even wider prey-size spectrum (algae to macrozooplankton). In addition, copepods are very agile and are generally less susceptible than cladocerans to fish predation (Williamson and Reid 2001). Fish abundance was representative of vertebrate predation on invertebrates, because there were no piscivorous species in the lake. We did not attempt to resolve functional groups using a finer trophic scale because the potential prevalence of species-specific and ontogenetic omnivory in boreal lakes confounds the assignment of species based on limited dietary information (see Fischer and others 2001a).

Methods

Study Lakes

The study involved two small boreal headwater lakes located in the Experimental Lakes Area (ELA) (49°40′N, 93°44′W), northwestern Ontario, Canada. The study area and experimental histories of the lakes are summarized here and described elsewhere in greater detail (see Brunskill and Schindler 1971; Schindler and others 1991). Some of the lakes have been subjected to experimental manipulations of several types (Schindler 1988), including eutrophication and acidification, while long-term monitoring has been carried out on other lakes that serve as reference ecosystems. Following 2 years of premanipulation monitoring, Lake 302S was gradually acidified over 9 years (1982–90) from pH 6.8 to 4.5 using sulfuric acid. Lake 239 served as a reference for this experiment and numerous other ecosystem studies (Schindler 1990a; Schindler and others 1991).

Biological Sampling and Taxonomic Analyses

The annual sampling effort was standardized to monthly collections of phytoplankton, epilithon, and zooplankton taken from the epilimnion of each lake on closely corresponding dates during the ice-free season (May–October) from 1980 to 1990. Phytoplankton samples were collected at deep-water stations. An integrating water sampler (Shearer

1978) was used to take a composite sample from the epilimnion (Findlay and others 1999). Samples of epilithon were collected in triplicate from three 1- to 2-m deep stations along the north shore of each lake (Turner and others 1995). Algal enumerations were performed using a modified Ütermohl technique, and cell counts were converted to wet weight biomass by approximating cell volume (Findlay and others 1999). Measurements of net photosynthesis were made using ^{14}C uptake by phytoplankton (Shearer and others 1985) and by assaying dissolved inorganic carbon uptake by epilithon (Turner and others 1991).

Zooplankton were collected from each lake by combining samples from three discrete thermal water layers using a closing net sampler (Chang and Malley 1989). *Leptodora kindtii* were excluded from the data analyses because our sampling methodology did not measure its abundance accurately in either lake. Similarly, *Chaoborus* species and zoobenthos were not included in our analyses because of insufficient sampling efforts. Also, copepodites and nauplii were excluded from the analyses due to their lack of taxonomically diagnostic features. Zooplankton species biomass was estimated using average weights derived from a variety of ELA lakes (M. Paterson unpublished).

Fish were collected in Lake 302S using the same techniques (trap nets and gill nets) described by Mills and others (1987). Lake whitefish (*Coregonus clupeaformis*) and white sucker (*Catostomus commersoni*) were weighed, measured (fork length), marked, and released. Average catch-per-unit-effort in trap nets was used to compare abundance of smaller fish species among years. A unit of effort was defined as one overnight set of trap net. Annual average effort was approximately 100 net days per year. Fish species abundance was quantified using a four-rank system (3 = original preacidification abundance, 2 = diminished abundance, 1 = some present, 0 = extirpated).

Statistical Analyses

For each algal and invertebrate group in Lake 302S, relationships among monthly species richness, function (total biomass, productivity), and environmental conditions were analyzed using backward stepwise multiple regression. Environmental conditions were defined by measured abiotic variables (pH), dissolved organic carbon (DOC) and inorganic carbon (DIC), total dissolved phosphorus (TDP) and nitrogen (TDN), epilimnetic temperature, and biotic variables (total abundance and species richness of adjacent trophic groups). Analyses were performed using StatView (SAS Institute, Cary, NC).

Ratios of the variance of total functional-group biomass to cumulative variance of member species were used to quantify compensatory dynamics within each group in both lakes during the experiment (Frost and others 1995; Klug and others 2000; Fischer and others 2001a). The variance ratio is derived from the variance of total biomass, which is equal to the sum of individual species variances, plus their covariances. If species vary independently, their covariances will equal zero and the variance ratio is one. However, if species covary negatively, then the variance ratio will be less than one, which is indicative of species compensation within the functional group. When species covary positively, the variance ratio exceeds one, which indicates that species abundances show synchronous fluctuations. Data were not transformed prior to the calculation of variance ratios. Randomization testing was used to estimate the significance of variance ratios (Manly 1997). For each functional group, species biomasses were randomized (999 permutations) among sampling dates before calculating total biomass and its variance. In each case, significance was determined by the number of randomly generated ratios that were smaller than observed ratios that were less than one (that is, compensation) or larger than observed ratios that were greater than one (that is, synchrony). Pop Tools Commonwealth Scientific and Industrial Rsearch Organization (CSIRO), Canberra, Australia version 2.1 was used to perform randomization testing. Also, observed variance ratios for each functional group in Lake 302S and Lake 239 were compared to determine the magnitude and direction of the effect of experimental acidification on temporal patterns among species abundances.

Temporal species dynamics within each functional group in Lake 302S were related to environmental changes using CANOCO version 4.0 (Microcomputer Power, Ithaca, NY, USA) (ter Braak and Smilauer 1998). For each group, a preliminary correspondence analysis (CA) was performed to determine if a unimodal species-response (for example, canonical correspondence analysis [CCA]) model was appropriate for constrained ordination. CCA is a multivariate analysis method that summarizes the maximum amount of variation in the species data set while also maximizing its correlation with linear combinations of environmental data. Each linear combination of environmental variables is represented by a CCA axis and its eigenvalue (λ), which represents the amount of explained species variance. The origin of the CCA plot represents the average environmental conditions as defined by the environmental variables that are included in the

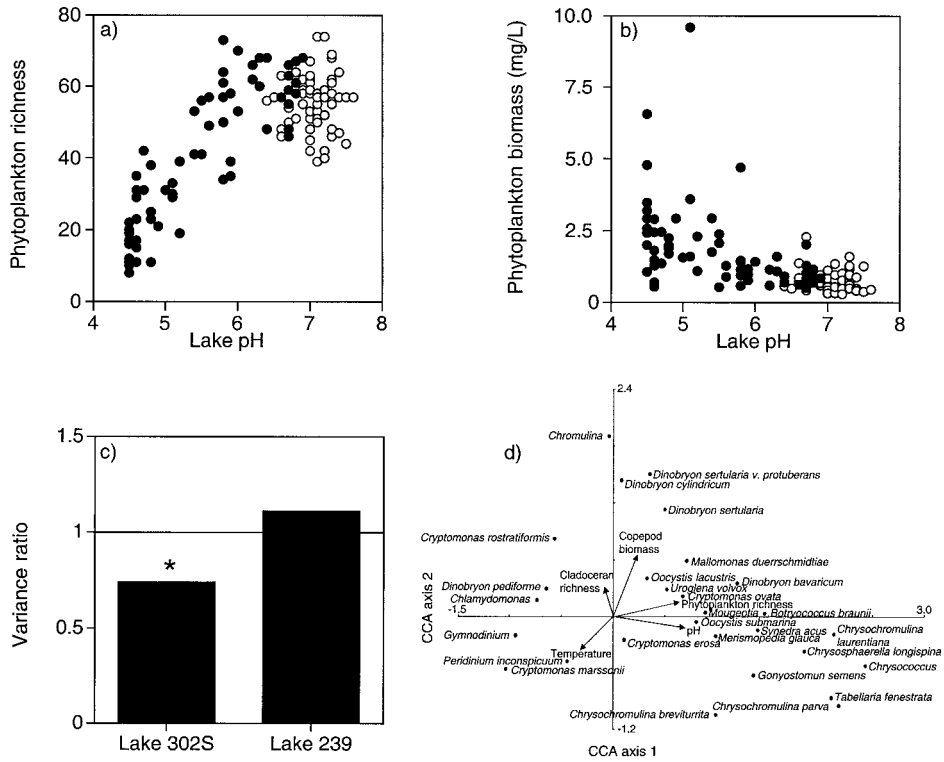

Figure 1. Phytoplankton–environmental relationships in acidified Lake 302S (*solid circles*) and reference Lake 239 (*open circles*). (**a**) Relationship between species richness and pH. (**b**) Relationship between total biomass and pH. (**c**) Variance ratios for each lake based on variance of total biomass divided by summed variance of individual species biomass. Significant levels ($*P < 0.05$) determined using randomization testing. (**d**) Association of species and environmental variables based on a CCA of species biomass and environmental conditions in Lake 302S.

ordination. The length and orientation of an environmental vector represents its magnitude and direction of maximum change in ordination space. The proximity and alignment of a species with a particular vector shows how closely the variation in its abundance is related to that environmental variable. Therefore, CCA results were used to operationally define species as being acid-sensitive or acid-tolerant depending on whether their scores were positively or negatively associated with pH, respectively.

Environmental data were screened for redundant and insignificant variables during ordination analyses (Vinebrooke and Graham 1997). First, forward selection of environmental variables was conducted by including all environmental variables in a preliminary CCA to rank variables in terms of the proportion of species variance explained by each. Second, a correlation matrix consisting of all environmental variables was used to identify sets of significant covariables. Third, a series of partially constrained ordinations was performed using pairs of environmental covariables to determine if each lower-ranked covariable exerted a significant and independent influence. Finally, an environmental variable was removed from the final ordination if its variance inflation factor (greater than 10) indicated that it was superfluous. All ordinations were tested for statistical significance using Monte Carlo permutation testing. Species abundances were not transformed prior to analysis to preserve the influence of major species that dominate both ordination results (ter Braak 1987) and compensatory dynamics in natural communities (see, for example, Frost and others 1995; Klug and others 2000; Fischer and others 2001a).

Results

Phytoplankton

In acidified Lake 302S, acid-tolerant phytoplankton species compensated for the extirpation of other species (Figure 1a, b and Table 1). Loss of phytoplankton species in Lake 302S was explained by declining pH during the experiment. Despite a loss of up to 70 taxa, total phytoplankton biomass increased significantly with declining pH in Lake 302S. In comparison, fluctuations in net phytoplankton productivity were not related significantly to pH and were best explained by changes in epilimnetic temperature during the ice-free season. In circumneutral Lake 239, phytoplankton richness, total biomass, and net productivity did not vary significantly with relatively minor fluctuations in pH.

Comparison of observed and random-generated variance ratios showed that significant compensa-

Table 1. Regression Models for the Dependence of Algal and Invertebrate Species Richness and Biomass on Environmental Conditions in Lake 302S as Determined Using Backward Stepwise Elimination Procedure

Group	Model Equation	R^2	Model F	P value
Phytoplankton	PR = 20.1pH − 69.2	0.73	167.1	<0.0001
	PB = –767.9pH + 6053.9	0.19	12.5	0.0008
	PP = 12.3Temperature − 40.6ClR −3.3RB −4.1CoB + 177.5	0.48	12.1	<0.0001
Epilithon	ER = 3.9pH − 8.8	0.59	28.3	<0.0001
	EB = 2.3DIC + 777.5	0.01	0.3	0.59
	EP = 0.03DIC + 0.3DOC − 0.9	0.44	19.4	<0.0001
Rotifers	RR = 3.3pH + 0.2Temperature − 8.2	0.52	32.8	<0.0001
	RB = –6.1pH + 1.2RR + 27.1	0.23	9.1	0.0003
Cladocerans	CIR = 0.5pH + 0.1Temperature − 0.1	0.21	7.9	0.0009
	CIB = 8.5CIR − 5.6	0.11	6.5	0.013
Copepods	CoR = 1.1pH + 0.1Temperature + 0.1RR + 0.2DOC − 3.9	0.55	17.9	<0.0001
	CoB = 1.4CoR + 0.04CIB − 0.9	0.31	13.5	<0.0001

PB, phytoplankton biomass; PP, net phytoplankton photosynthesis; PR, phytoplankton species richness; EB, epilithon biomass; EP, net epilithon photosynthesis; ER, epilithon species richness; RB, rotifer biomass; RR, rotifer species richness; ClB, cladoceran biomass; ClR, cladoceran species richness; CoB, copepod biomass; CoR, copepod species richness; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon

tory species dynamics occurred among phytoplankton in acidified Lake 302S (Figure 1c). The variance ratio for phytoplankton in Lake 239 did not differ statistically from one, indicating independent species dynamics under unperturbed conditions during the experiment. Therefore, after acidification, phytoplankton species dynamics showed a substantial shift away from independence toward compensation.

CCA axis 1 ($\lambda_1 = 0.44$, $P < 0.005$) showed that temporal variability of species abundances in Lake 302S was best explained by differential sensitivities to pH and changes in phytoplanton richness, which explained 41% and 11% of the total species variance, respectively (Figure 1d). In particular, major acid-tolerant species (*Gymnodinium*, *Peridinium inconspicuum*, *Cryptomonas* spp.) succeeded several small-celled chrysophytes (for example, *Chrysochromulina* spp., *Dinobryon* spp.) as average pH dropped below 5.5 and phytoplankton richness declined below 40 (Figure 1d). CCA axis 2 ($\lambda_2 = 0.29$) captured variance in species abundances that was correlated with copepod biomass (21%), epilimnetic temperature (15%), and cladoceran richness (12%). The second CCA axis separated several chrysophytes (*Dinobryon* spp., *Chromulina*) from *Peridinium inconspicuum* and *Cryptomonas* spp., which had been less abundant in the presence of above-average copepod abundance (more than 6.4 μg/L) and cladoceran richness (more than 3.7 species) and below-average epilimnetic temperatures (under 16.5°C).

Epilithon

Epilithic species compensated for a significant loss of species richness during acidification, and total algal biomass did not change significantly in Lake 302S (Figure 2a, b and Table 1). However, net photosynthesis did decline significantly as DIC and DOC concentrations were suppressed by acidification. In Lake 239, epilithic richness and total biomass were not related to pH.

Variance ratios showed that epilithic species exhibited marginally significant ($P < 0.10$) compensatory dynamics in Lake 302S (Figure 2c). In comparison, epilithon showed significant synchrony in Lake 239. As a result, experimental acidification suppressed synchrony among epilithon species.

CCA significantly ($P < 0.005$) captured temporal variation in epilithic species abundances that was best explained by declining pH (39% of total species variance) and DOC levels (37%) in Lake 302S (Figure 2d). The first CCA axis ($\lambda_1 = 0.77$) contrasted major acid-tolerant species (*Brachysira brachysira*, *Frustulia rhomboides*, *Tabellaria quadriseptata*, *Zygogonium sp.*) from acid-sensitive taxa (*Lyngbya*, *Navicula*, *Aulacoseira*) that were favored by above-average pH (more than 5.5) and DOC levels (more than 3.9 mg/L) during the early stages of the experiment. CCA axis 2 ($\lambda_2 = 0.47$) represented a less-defined environmental gradient that separated certain cyanobacteria (*Anabaena* spp., *Lyngbya* spp.) from other epilithic taxa based on seasonality (13%) and epilimnetic water temperature (11%).

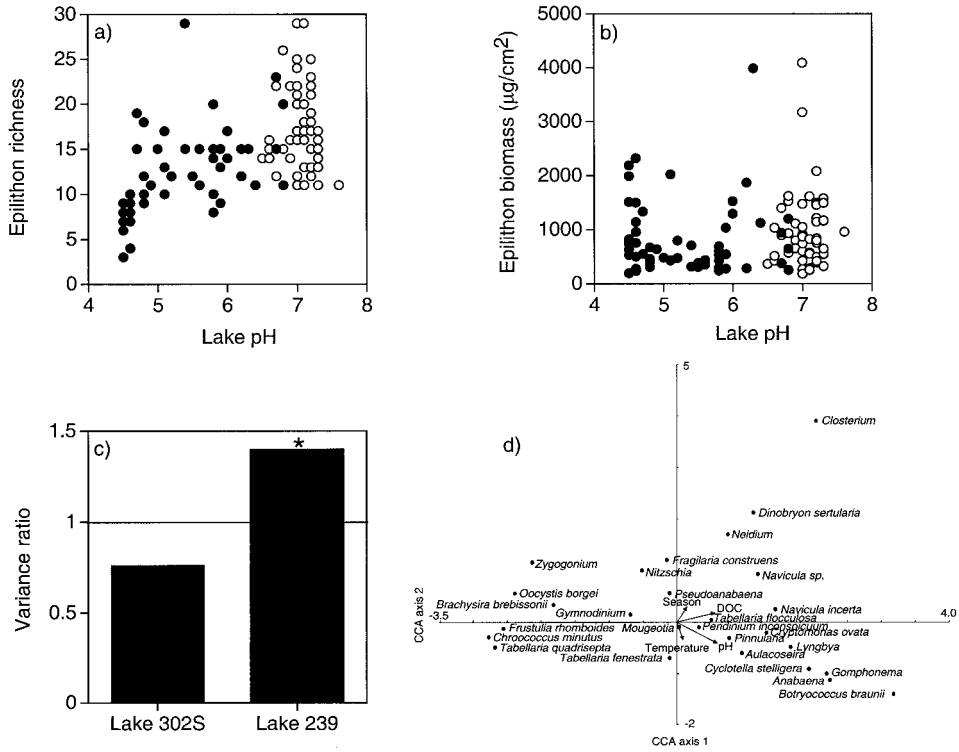

Figure 2. Epilithon–environmental relationships in acidified Lake 302S (*solid circles*) and reference Lake 239 (*open circles*). (**a**) Relationship between species richness and pH. (**b**) Relationship between total biomass and pH. (**c**) Variance ratios for each lake based on variance of total biomass divided by summed variance of individual species biomass. Significant levels ($*P < 0.05$) determined using randomization testing. (**d**) Association of species and environmental variables based on a CCA of species biomass and environmental conditions in Lake 302S.

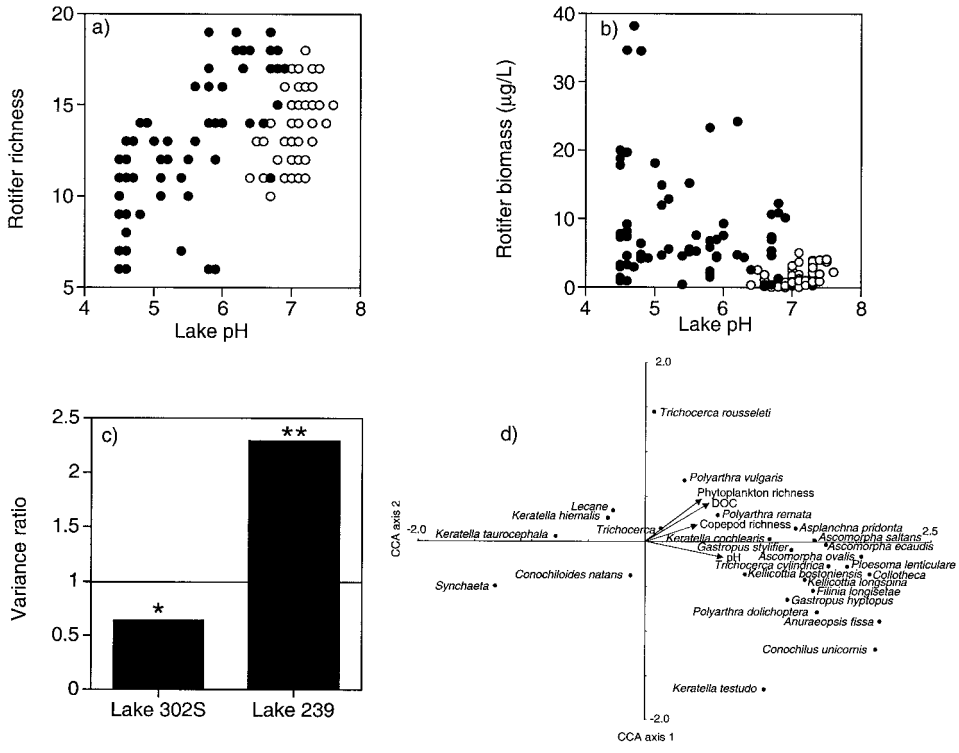

Figure 3. Rotifer–environmental relationships in acidified Lake 302S (*solid circles*) and reference Lake 239 (*open circles*). (**a**) Relationship between species richness and pH. (**b**) Relationship between total biomass and pH. (**c**) Variance ratios for each lake based on variance of total biomass divided by summed variance of individual species biomass. Significant levels ($*P < 0.05$, $**P < 0.01$) determined using randomization testing. (**d**) Association of species and environmental variables based on a CCA of species biomass and environmental conditions in Lake 302S.

Rotifers

In Lake 302S, rotifers overcompensated for a significant 75% loss of species and total biomass increased during acidification (Figure 3a, b and Table 1). Reduced rotifer richness was explained by a decreased pH and was associated with periods of colder epilimnetic temperatures. Increased total rotifer biomass was best explained by decreasing pH

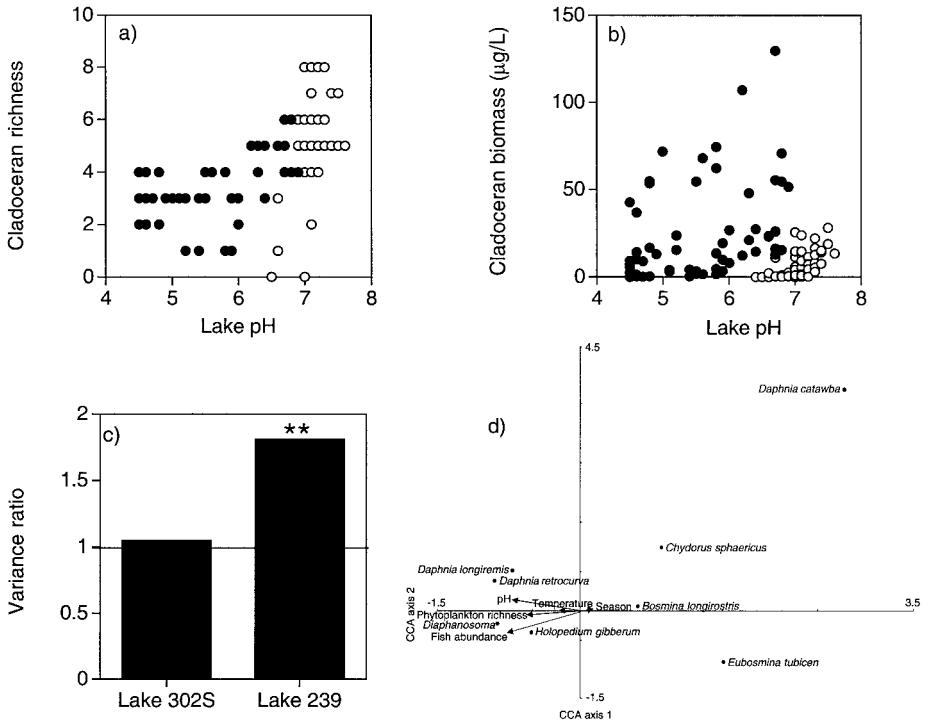

Figure 4. Cladoceran–environmental relationships in acidified Lake 302S (*solid circles*) and reference Lake 239 (*open circles*). (a) Relationship between species richness and pH. (b) Relationship between total biomass and pH. (c) Variance ratios for each lake based on variance of total biomass divided by summed variance of individual species biomass. Significant levels ($^{**}P < 0.01$) determined using randomization testing. (d) Association of species and environmental variables based on a CCA of species biomass and environmental conditions in Lake 302S.

and rotifer richness. In comparison, rotifer richness and biomass remained relatively low in Lake 239 during the experiment.

Variance ratios showed that rotifer species displayed significant compensatory dynamics during the acidification of Lake 302S (Figure 3c). In contrast, temporal variations in rotifer species abundances were significantly synchronous in Lake 239 during the experiment (Figure 3c). Therefore, acidification resulted in a pronounced departure from synchrony toward compensation by rotifer species.

CCA axis 1 ($P < 0.005$) showed that differential pH tolerances (49% of total variance) and changes in copepod richness (7%) best explained compensatory rotifer species dynamics during acidification (Figure 3d). The first CCA axis ($\lambda_1 = 0.49$) contrasted major acid-tolerant species (*Keratella taurocephala*, *Synchaeta*) from several acid-sensitive species (*Polyarthra remata*, *Gastropus stylifer*, *Keratella cochlearis*), which were more abundant during periods of above-average (more than 4.5 species) copepod richness (Figure 3d). CCA axis 2 ($\lambda_2 = 0.17$) was best defined by increasing DOC (16%) and phytoplankton richness (14%), which favored *Polyarthra remata* and *Polyarthra vulgaris* (Figure 3d).

Cladocerans

Acid-tolerant cladocerans did not compensate for extirpated species, and total biomass declined significantly during the acidification of Lake 302S (Figure 4a, b and Table 1). Loss of species richness was best explained by declining pH and epilimnetic temperature. The only significant predictor of declines in total cladoceran biomass was loss of species richness. In Lake 239, cladoceran species richness was highly variable, and total biomass remained relatively low between 1980 and 1990.

Cladocerans showed independent (variance ratio = 1) temporal fluctuations in abundance in Lake 302S but significant species synchrony in Lake 239 (Figure 4c). Therefore, an effect of acidification on cladoceran species dynamics was suppression of synchronous behavior during the experiment.

CCA showed that cladoceran species dynamics were primarily attributable to declines in pH (51%), fish abundance (33%), and phytoplankton richness (10%) in Lake 302S (Figure 4d). Epilimnetic temperature and seasonality explained an additional 6% of the variance within the species data set. The first CCA axis ($\lambda_1 = 0.37$) contrasted abundant acid-sensitive species (*Daphnia retrocurva*, *Holopedium gibberum*) from major acid-tolerant species (*Bosminia longirostris*, *Eubosmina tubicen*, *Daphnia catawba*), which were disproportionately less abundant prior to the decline of fish abundance in 1988 (Figure 4d). CCA axis 2 ($\lambda_2 = 0.15$) further separated *Daphnia catawba* from the other cladocerans based primarily on its strong negative association with fish abundance (Figure 4d).

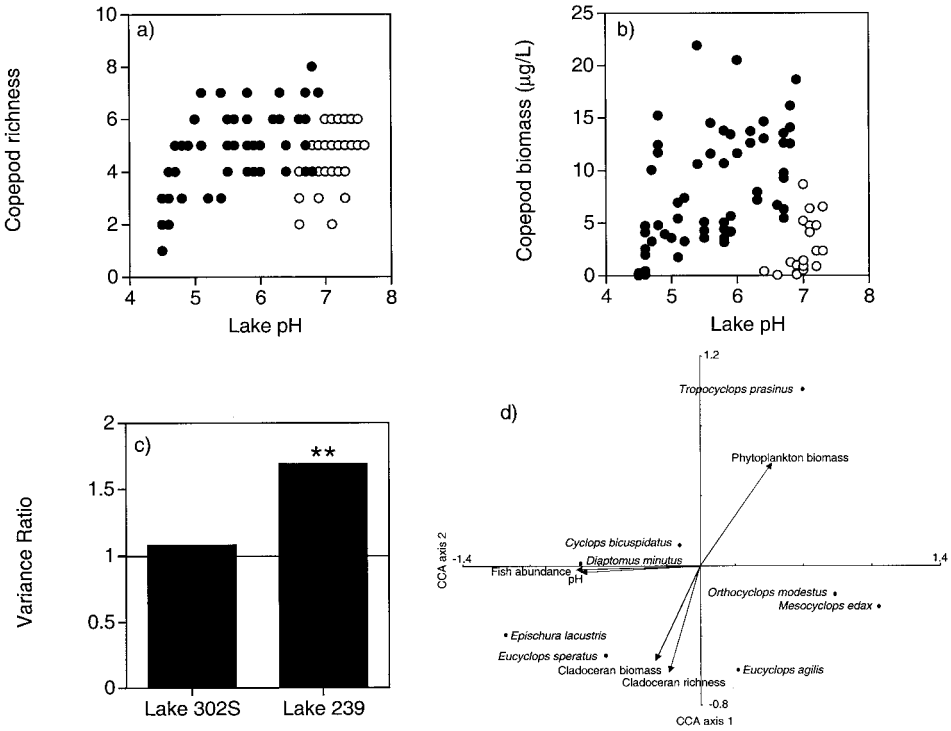

Figure 5. Copepod–environmental relationships in acidified Lake 302S (*solid circles*) and reference Lake 239 (*open circles*). (a) Relationship between species richness and pH. (b) Relationship between total biomass and pH. (c) Variance ratios for each lake based on variance of total biomass divided by summed variance of individual species biomass. Significant levels ($^{**}P < 0.01$) determined using randomization testing. (d) Association of species and environmental variables based on a CCA of species biomass and environmental conditions in Lake 302S.

Copepods

In Lake 302S, copepod species were also unable to maintain total community biomass as species richness declined significantly during acidification (Figure 5a, b and Table 1). Significant environmental predictors of declining copepod richness were pH, epilimnetic temperature, rotifer richness, and DOC. Decreases in total copepod biomass were best explained by loss of copepod richness and cladoceran biomass in Lake 302S. Copepod biomass remained relatively low in Lake 239.

Variance ratios indicated that copepod species abundances fluctuated independently in Lake 302S but showed significant synchrony in Lake 239 (Figure 5c). Comparison of variance ratios for copepod assemblages from both lakes showed that acidification reduced synchronous species dynamics observed in the reference lake during the experiment.

CCA axis 1 ($\lambda_1 = 0.39$, $P < 0.01$) captured temporal variance in copepod abundances related to changes in fish abundance (61% of total species variance) and pH (15%) in Lake 302S (Figure 5d). In particular, major acid-tolerant copepods (*Orthocyclops modestus*, *Mesocyclops edax*) succeeded the dominant acid-sensitive species (*Diaptomus minutus*) as fish abundance declined during acidification. Temporal variance in copepod species abundances was also explained by CCA axis 2 ($\lambda_2 = 0.10$), which represented an environmental gradient of increasing phytoplankton biomass (10%) and decreasing cladoceran richness (9%) and total biomass (5%) (Figure 5d).

Fish

Fish abundance also declined during acidification of Lake 302S with the loss of five of seven species (Table 2). Loss of fish species richness began with the elimination of smaller prey fish (northern redbelly dace, fathead minnow, slimy sculpin) in 1988. Subsequently, larger species (lake whitefish, white sucker) were extirpated during the later stage of experimental acidification.

Discussion

We found evidence of limited ecosystem resistance to experimental acidification and significant loss (30%–80%) of species in a boreal lake over a 10-year period. Fast-growing speciose algal and rotifer groups with wide dispersal potentials were resistant, exhibiting significant compensatory species dynamics and functional compensation during acidification. However, species-poor cladoceran, copepod, and fish assemblages with relatively lower dispersal potentials did not compensate for extirpated species, and their total biomass declined significantly. In contrast, algal and invertebrate species displayed synchronous or independent dynamics in

Table 2. Estimated Annual Species Richness and Ranked Abundance of Fish Species in Lake 302S during Experimental Acidification

	1982	1983	1984	1985	1986	1987	1988	1989	1990
Lake whitefish	3	3	2	2	2	1	1	0	0
White sucker	3	3	2	2	2	2	2	1	0
Redbelly dace	3	3	1	1	1	1	1	0	0
Fathead minnow	3	3	3	2	2	2	1	0	0
Slimy sculpin	3	3	3	3	3	3	3	1	0
Finescale dace	3	3	3	3	3	3	3	3	2
Pearl dace	3	3	3	3	3	3	3	3	2
Species richness	7	7	7	7	7	7	7	4	2

Fish abundances were based on total number of fish caught for large species (lake whitefish, white sucker) and catch-per-unit-effort for smaller species. Rank categories defined as follows: 3 = original preacidification abundance, 2 = diminished abundance, 1 = present, 0 = extirpated

a nearby circumneutral reference lake (Lake 239). Here we will discuss the potential ecological mechanisms that result in differences in resistance and species dynamics between trophic groups in perturbed and unperturbed boreal lake ecosystems.

Strong resistance of algal abundance to anthropogenic acidification (see, for example, Schindler and others 1991; Brezonik and others 1993; Havens and Carlson 1998; Findlay and others 1999; Klug and others 2000) requires highly responsive and tolerant species. The presence of acid-tolerant species among dozens of phytoplankton and epilithic taxa in an acid-sensitive boreal lake is not surprising given the expected high probability of tolerant species within speciose communities (Ives and others 1999). In addition, tolerant algal species from other naturally acidic water bodies (for example, bogs) should be able to readily colonize Lake 302S and compensate for extirpated species given their relative high dispersal potentials and fast growth rates (Schindler 1987; Williams and others 1994; Finlay and Clarke 1999). However, algal assemblages in atmospherically acidified lake regions may be less resistant to acidification because of widespread impoverishment of the algal species pool (Minns and others 1990). For example, phytoplankton required 7 years to recover taxonomically from a reacidification event that occurred in a lake located in a region of high acid deposition (Arnott and others 2001).

Our findings support the hypothesis that compensatory algal dynamics are driven by a coupling of differential species sensitivities to acidity and competitive release (Klug and others 2000). Compensatory species shifts by phytoplankton and epilithon were best explained by differential tolerances to changes in pH in Lake 302S. Similarly, overcompensation by phytoplankton in an acid-press experiment was attributed primarily to chlorophytes being less sensitive than diatoms to low pH (Klug and others 2000). However, changes in the diversity and abundance of crustacean zooplankton also explained temporal variance of phytoplankton species in Lake 302S. Algal species dynamics in acidified lakes can involve tradeoffs between resistance to acidity and herbivores because slow-growing, acid-tolerant species are more susceptible to grazing (Graham and Vinebrooke 1998). Therefore, acid-tolerant phytoflagellates (*Cryptomonas rostratiformis*, *Gymnodinium*, *Peridinium inconspicuum*) and epilithic species (*Frustulia rhomboides*, *Tabellaria quadriseptata, Zygogonium tunetanum*) probably compensated for acid-sensitive, fast-growing chrysophytes (*Chrysochromulina* spp., *Dinobryon* spp.) and Cyanobacteria (*Lyngbya*) because of release from both competition and grazing by impoverished herbivore assemblages in Lake 302S (Vinebrooke and others 2001). Indeed, overcompensation by acid-tolerant phytoplankton probably required a release from grazing pressure because phosphorus concentrations did not increase during acidification (Schindler and others 1991).

Compensatory algal dynamics were more pronounced in Lake 302S than in acidified mesocosms in a temperate lake (Trout Lake) in Wisconsin (Klug and others 2000). One possible explanation for this discrepancy between the two studies involves differences in experimental scale. In Lake 302S, several nonresident, or possibly rare, species (for example, *Cryptomonas rostratiformis*, *Dinobryon* spp., *Frustulia rhomboides*, *Tabellaria quadriseptata*, *Zygogonium tunetanum*) increased in abundance during the decade-long acidification experiment. Compensatory algal dynamics required that these tolerant species either be present as resting structures in lake sediment (see, for example, Hansson 1996) or that they be able to migrate from local water bodies

(Figuerola and Green 2002). Enclosure walls impede the migration of tolerant species (Carpenter 1996; Leibold and others 1997; Schindler 1998b), which would limit species compensation in acidified mesocosms (see, for example, Klug and others 2000). Species compensation may also have been better expressed in Lake 302S than in the well-buffered Trout Lake (pH 8.1, acid neutralizing capacity = 829 μeq/L) (Klug and others 2000) because a greater proportion of species in poorly buffered boreal lakes are likely adapted to acidity.

Total rotifer biomass also did not decline significantly with loss of species in Lake 302S, supporting other evidence of rotifer compensation in experimentally acidified lakes (Frost and others 1995). In particular, rare rotifer species (*Keratella taurocephala*, *Synchaeta*) increased in abundance to compensate for several extirpated rotifers during acidification. Compensatory shifts by rotifer species in Lake 302S were significantly associated with differential tolerances to decreases in pH and DOC, which is the primary attenuator of damaging UVB radiation in boreal lakes (Schindler and others 1996). In comparison to crustacean zooplankton, rotifer species exhibited a relatively high capacity for compensation, in part because they are faster and more prolific as colonists (Jenkins and Buikema 1998). The importance of these rare rotifers to functional compensation in acidified lakes could not be predicted from observations of Lake 239 and other reference lakes (Frost and others 1995) where these species were likely suppressed by competitors, which exhibit synchronous species dynamics. In fact, compensatory shifts by rotifer assemblages in acidified Lake 302S were also associated significantly with changes in phytoplankton and copepod richness. Therefore, acid-tolerant rotifers may compensate for extirpated species because they are better adapted to resource limitation under conditions of reduced predation by copepods and acid-sensitive rotifers, such as *Asplanchna*.

For larger herbivorous cladocerans, differences in variance ratios suggested that species showed weak compensatory dynamics in Lake 302S and strong synchrony in Lake 239. Compensatory shifts in cladoceran assemblages primarily involved differential species tolerances to pH and fish, and were characterized by acid-tolerant species (*Daphnia catawba*, *Bosmina longirostris*, *Eubosmina tubicen*) replacing *Holopedium gibberum* and *Daphnia retrocurva* as the major species. As a consequence of a size shift from large-bodied (10 μg/individual) *Holopedium gibberum* to smaller (1–7.5 μg/individual) *Bosmina longirostris* and *Daphnia catawba*, weak compensatory dynamics resulted in a significant decline in total cladoceran biomass.

In Lake 302S, food limitation and predator limitation could account for the temporal dynamics of major cladoceran species. Clearly, increased acid-tolerant species abundances could not be attributed directly to declines in pH because acidity is not a resource. Instead, *Daphnia catawba* is hypothesized to increase in abundance in acidified lakes because of competitive release from acid-sensitive *Holopedium gibberum* and *Daphnia dubia* (Fischer and others 2001a). Our findings suggest that smaller, acid-tolerant cladocerans, such as *Daphnia catawba*, can also tolerate reduced phytoplankton richness. Nocturnal migration by *Daphnia catawba* can enable them to better exploit dense metalimnetic phytoplankton layers (Tessier 1986), which develop in acidified lakes during leaching of DOC and increased light penetration (Findlay and others 1999). Smaller cladocerans may also cope better with food limitation in acidified lakes because they have relatively lower metabolic costs than larger species (Moore and others 1996). In addition, fish abundance as a surrogate measure of zooplanktivory helped explain cladoceran dynamics in Lake 302S. In particular, *Holopedium gibberum* declined during lake acidification, possibly because of increased predation by *Chaoborus*, a larval midge that is suppressed by acid-sensitive planktivorous fish and the cyclopod *Mesocyclops edax* (Yan and others 1991; Fischer and Frost 1997; Fischer and others 2001a). Unfortunately, the abundance of *Chaoborus* and certain other predatory macroinvertebrates in Lake 302S were not determined accurately during the experiment and therefore could not be used to help explain shifts in cladoceran species composition. Nevertheless, the potential positive indirect effect of fish on *Holopedium gibberum* via the suppression of predatory macroinvertebrates (for example, *Chaoborus, Leptodora*, coleopterans, hemipterans, odonates) was reflected in its strong association with fish abundance in Lake 302S. Interestingly, cladoceran dynamics that involved *Daphnia catawba* succeeding *Holopedium gibberum* were also attributable to increases in food limitation and decreases in fish predation in a nonacidified softwater lake (Tessier 1986).

Copepods also showed relatively weak compensatory species dynamics and only partial compensation of total copepod biomass in Lake 302S. Major acid-tolerant species (*Mesocyclops edax*, *Orthocyclops modestus*) succeeded but did not match the abundance of *Diaptomus minutus*, which had been the most abundant copepod during the early stages of acidification (pH more than 5). Similarly, Frost and

others (1995) showed that copepods as a taxonomic group could not achieve functional compensation because species fluctuated independently during the acidification of Little Rock Lake. However, Fischer and others (2001a) reported that only predatory copepods exhibited independent species dynamics, whereas herbivorous copepods showed significant compensatory dynamics in Little Rock Lake. The probability of detecting compensatory dynamics within a functional group is inversely related to the fidelity of its assigned members, which is complicated by factors such as omnivory (Fischer and others 2001a) and lack of knowledge of the ecology of individual species and their complete life histories (for example, naupliar and copepodid stages). In other words, greater ecological resolution of component species should increase the probability of detecting compensatory dynamics within a defined functional group.

Copepod species dynamics in Lake 302S were best explained by differential tolerances to predation, pH, and resource availability. For example, the major acid-sensitive copepod (*Diaptomus minutus*) showed a strong positive association with fish abundance. *Diaptomus minutus* probably benefited from acid-sensitive fish and cyclopoids that suppress *Chaoborus* and its predation on diaptomids (Yan and others 1991; Fischer and Frost 1997; Fischer and others 2001a). In contrast, relatively abundant and acid-tolerant copepods (*Mesocyclops edax*, *Orthocyclops modestus*) were negatively associated with fish abundance. Although these species were not strongly associated with cladoceran variables in our study, Fischer and others (2001a) used autoregression analysis to show that the availability of small cladoceran prey positively influenced the abundance of *Mesocyclops*. In Lake 302S, *Tropocyclops prasinus* was strongly associated with low cladoceran diversity and increased phytoplankton biomass, which agreed with this omnivore relying primarily on a diet of algae and rotifers (Adrian and Frost 1993).

Fish also did not achieve functional compensation during acidification. The relative species-poor fish assemblage in Lake 302S consisted of functionally distinct species (for example, littoral-foraging cyprinids versus deep-water pelagic lake whitefish), which is typical of fish communities in boreal lakes. Consequently, many boreal fish communities likely contain low functional redundancy and poor resistance to environmental perturbations (Schindler 1995). Poor dispersal potential and physical barriers (for instance, no inflow or outflow) would also have prevented acid-tolerant fish (*Lepomis gibbosus*, *Perca flavescens*, *Umbra limi*) from colonizing Lake 302S.

Conclusions

Clearly, ecosystem resistance depends on compensatory species dynamics and declines with the trophic rank of a functional group. Our correlative approach identified patterns between environmental variables and temporal variance of species abundances, which enabled us to develop testable hypotheses of the ecological mechanisms that drove compensatory species dynamics and determined functional compensation in Lake 302S. We agree with the hypothesis that a coupling of differential species tolerances and competitive release can explain compensatory dynamics in acidified systems (see Klug and others 2000; Fischer and others 2001a), but ecological tradeoffs between competitive ability and vulnerability to predation should also be considered as a potential mechanism. Also, we hypothesize that functional compensation is more probable at lower trophic levels in acid-sensitive boreal lakes because these groups have relatively faster growth rates, wider dispersal potentials, and greater species diversity, which results in a higher probability of the presence of tolerant species.

A comparison of variance ratios across Lake 302S and Lake 239 suggested that experimental acidification suppressed synchronous species dynamics within the different functional groups. In particular, rotifer dynamics showed the most pronounced difference by being synchronous in Lake 239 and compensatory in Lake 302S. Synchrony among epilithon, cladoceran, and copepod species in Lake 239 was also not detected in Lake 302S; instead, it was replaced by independent species dynamics. Therefore, anthropogenic acidification of boreal lakes may disrupt synchronous species responses to benign environmental fluctuations affected by other regional factors (for example, climate).

In summary, our findings demonstrate that boreal lake ecosystems have limited resistance to anthropogenic acidification because higher trophic groups cannot compensate functionally for significant loss of species. Collectively, the different resistances of the functional groups to anthropogenic acidification and species loss in our study (Figure 6) correspond with the asymptotic relationship between ecosystem function and species richness, which is expected to be most common in natural communities (Vitousek and Hooper 1993). Therefore, higher trophic processes are likely less resistant than is primary production to ecosystem stress

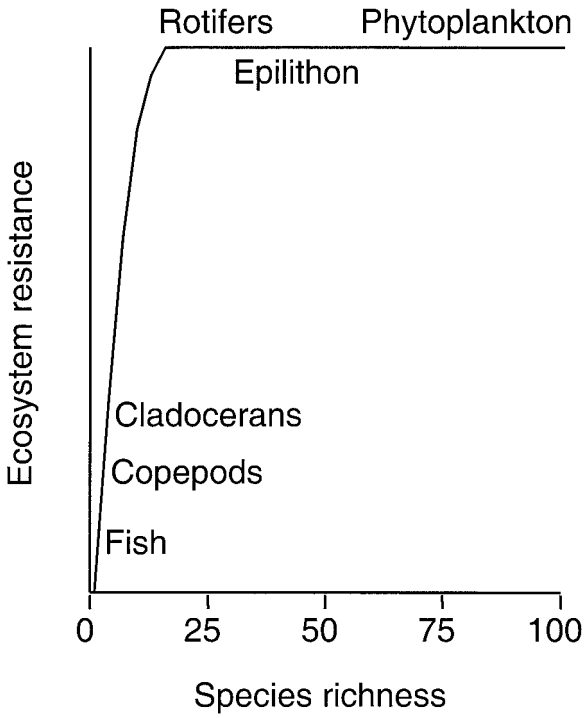

Figure 6. Hypothesized trophic dependence of ecosystem resistance in anthropogenically perturbed boreal lakes. Highly dispersive speciose algal and rotifer groups show greater resistance of total biomass and compensatory species dynamics in response to acidification and loss of species richness. Less dispersive species-poor macrozooplankton and fish groups are less resistant and exhibit weak compensation during acidification of boreal lakes.

(Odum 1985; Petchey and others 1999; Klug and others 2000). However, even ecosystem processes performed by resistant functional groups in boreal lakes may ultimately be jeopardized by the cumulative impacts of multiple stressors if global change and the loss of biodiversity are allowed to proceed (Schindler 1998a).

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