

LETTER

Diversity–stability relationship varies with latitude in zooplankton

Jonathan B. Shurin,^{1*} Shelley E. Arnott,² Helmut Hillebrand,³ Allyson Longmuir,¹ Bernadette Pinel-Alloul,⁴ Monika Winder⁵ and Norman D. Yan⁶

¹Department of Zoology and Biodiversity Research Centre, University of British Columbia, 6270 University Blvd, Vancouver, BC, Canada V6T 1Z4

²Department of Biology, Queen's University, Kingston, ON, Canada K7L 3N6

³Institute for Botany, University of Cologne, Gyrhofstrasse 15, D-50931 Koln, Germany

Abstract

Analyses of temporal patterns of diversity across a wide range of taxa have found that more diverse communities often show smaller compositional changes over time. This generality indicates that high diversity is associated with greater temporal stability in species composition. We examined patterns of diversity and community stability in zooplankton time series data from 36 lakes sampled over a combined 483 years. The species–time relationship was flatter in more species-rich lakes in the temperate zone. However, high-latitude lakes had both low richness and low turnover. These patterns were consistent for turnover both within and among years. Daily, annual and long-term richness were all higher in large lakes while turnover was unaffected by the surface area. Richness on all time scales, as well as turnover within and among years, all declined at high latitude. Species–area relations and latitudinal gradients in richness therefore reflect different temporal components of diversity. Our results suggest that diversity shows strong associations with compositional stability that vary qualitatively across biogeographical provinces. Community stability increases with diversity among lakes in the temperate zone; however, the two are negatively correlated across latitudinal gradients. These patterns indicate that either the direct effects of diversity on stability or their covariance with environmental fluctuations vary with latitude.

Keywords

Extinction, invasion, latitudinal gradients, species–time relationship.

Ecology Letters (2007) 10: 1–8

INTRODUCTION

Ecologists have uncovered few generalities in the relationship between community diversity and stability. Elton (1958) first proposed that diversity buffers assemblages against perturbations by providing species with a range of traits and tolerances that thrive under varying conditions (see also MacArthur 1955). By contrast, May (1974) found that model communities with more species had greater chances of including unstable combinations that showed cycles, chaos or extinctions, leading to reduced stability in rich communities. However, populations in diverse communities may be more stable if most species interact weakly (Yodzis 1981; McCann *et al.* 1998). Thus, theory provides

plausible scenarios leading to either positive or negative relationships between community diversity and population stability depending on the particular configuration of species interactions. Reflecting the lack of theoretical consensus, empirical studies have shown examples where stability either increases or decreases with species diversity (McCann 2000). Virtually all studies of diversity and stability have been experimental and cover a narrow range of richness relative to natural variation due to methodological constraints on manipulating large numbers of species (Cottingham *et al.* 2001). The existing literature therefore provides equivocal evidence for a general relationship between diversity and stability. In addition, we know little about how the two co-vary in natural, unmanipulated communities.

⁴Département de Sciences Biologiques, Université de Montréal, C.P. 6128, Succ. Centre ville, Montreal, QC, Canada H3C 3J7

⁵Center for Watershed Sciences, University of California, Davis One Shields Ave., Davis, CA 95616-8803, USA

⁶Department of Biology, York University, Toronto, ON, Canada M3J 1P3, and Ontario Ministry of the Environment, Dorset Environmental Science Centre, Dorset, ON, Canada P0A 1E0

*Correspondence: E-mail: shurin@zoology.ubc.ca

Associations between diversity and population stability may manifest themselves in patterns of species turnover through time. Populations with lower mean abundance or greater variability are at greater risk of extinction (Pimm *et al.* 1988). In addition, rare taxa may be difficult to detect and show apparent colonizations and extinctions as a result of random sampling errors. If diversity affects mean population abundance or its variability, then we may expect to see associations between richness and rates of compositional change. Common environmental factors may also influence diversity and stability, leading to correlations between the two without direct causal links (Sankaran & McNaughton 1999). Compositional stability can be measured by the exponent of the relationship between the number of species encountered and the sampling period (Adler *et al.* 2005). This metric is analogous to the exponent of the species–area relationship, a measure of beta diversity or species turnover in space (Drakare *et al.* 2006), where higher exponents indicate lower stability in either space or time. White *et al.* (2006) showed that the exponents of species–time relations for diverse taxa including desert rodents, algae, birds and plants decline with increasing mean richness. Richer assemblages therefore show smaller compositional changes through time. These patterns indicate that either diversity promotes community stability or that environmental factors that enhance diversity also reduce temporal variability.

We examined patterns of diversity and compositional stability in zooplankton data collected from 36 European and North American lakes sampled over periods of 2–42 years for a total of 483 lake-years of data and 5364 individual samples. We constructed species–time curves for each lake and tested relationships between richness at different temporal scales (daily, annual and interannual) and turnover both within and among years. As the lakes were geographically dispersed and environmentally heterogeneous, we asked how determinants of diversity such as latitude

and surface area affect richness and species turnover at different temporal scales.

METHODS

We assembled a spatially and temporally extensive data set of zooplankton samples from 35 lakes in North America and one in Europe. The lakes were sampled by relatively standard methods for periods ranging from 2 to 42 years. We included only lakes that were sampled on a minimum of four dates per year. None of the lakes were experimentally manipulated during the study period. Most were in the temperate zone between 46° N and 52° N. The exceptions were three surveys of Alaskan lakes, one from the Arctic (Toolik Lake LTER) and the other two from Kodiak island in Southeast Alaska (Alaska Department of Fish and Game, see Table 1). Although the survey represents a relatively narrow band on a global scale, the region sampled spans most of the glaciated latitudes of the northern hemisphere. As 74% of the world's lakes are of glacial origin (Kalfff 2001, p. 73), the latitudinal band includes the majority of freshwater zooplankton habitat. Most lakes were sampled at a single station. Where multiple stations were sampled, we analysed each station separately and averaged values for richness and turnover across the different stations to obtain a single value for the lake.

The lakes were sampled by hauling a plankton net through the water column from near the bottom to the surface, usually at the deepest point, followed by identification and enumeration of animals by microscopy. Samples were collected over the majority of the ice-free period in each lake. Aspects of the collection protocols varied among surveys (i.e. net diameter and mesh size, preservation method). However, most sampling protocols were designed to characterize the species composition of the crustacean zooplankton community. The degree of taxonomic resolu-

Table 1 A summary of the data sets used in the study

Survey	No. lakes sampled	Lake-years sampled	Mean samples per year	Mean sampling period (days)	Mean days between samples
North Temperate Lakes LTER (WI, USA)	7	160	8.8	271.4	38.8
Arctic LTER (Toolik Lake, AK, USA)	6	21	6.8	50.5	7.7
Dorset Lakes (ON, Canada)	8	174	8.9	173.4	22.1
Experimental Lakes Area (ON, Canada)	2	33	10.9	156.0	14.9
Coldwater (ON, Canada)	6	19	12.7	262.0	24.7
Akalura and Saltery Lakes (Kodiak Island, AK, USA)	2	21	4.7	136.3	29.9
Thoms, Kanalku and Kutalku Lakes (Kodiak, AK, USA)	3	8	4.6	142.5	31.0
Lac Lemans (France)	1	5	20.4	323.2	15.9
Lake Washington (USA)	1	42	34.1	346.6	11.4

All variables are averaged across all lakes in each data set.

tion was also variable, but the large majority of taxa were identified to species in every survey. We therefore feel confident making comparisons across studies. Table 1 shows the data sources and summary data on the surveys.

We fit species accumulation curves of the form $S = aT^x$ to zooplankton data from each lake and estimated values for a and x using nonlinear regression. S is the cumulative number of species and T is time (either in number of sampling dates for *Annual turnover*, or days for *Interannual turnover*, see below). Curves were based on species turnover both between sampling dates within years (annual turnover, x_a), and across the entire data set (interannual turnover, x_i). Richness was estimated for each date as the number of discrete taxa recorded. Nauplii and copepodid stages were counted as a distinct species only when no adult copepods of any species were identified. We fit two kinds of species–time curves.

Annual turnover

Annual turnover (x_a) was estimated based on species accumulation within years. We removed the influence of seasonal patterns from our annual species accumulation curves by calculating the number of species found for all sequential combinations of one to four sampling dates. That is, we calculated the average number of species recorded on all single dates, pairs, trios and quartets of adjacent sampling dates for each year. We took the average number of species found for each number of sampling dates for every year and fit a power function based on all years of data. This means of calculating species turnover removes the influence of seasonal patterns because it is based on the number of sampling dates regardless of when they occurred during the year. It is not influenced by differences in the length of the sampling period, which was shorter at high latitude, as the moving window width was the same between surveys. The time interval between sampling dates was similar across surveys (Table 1); therefore, turnover was calculated for a similar time window for all studies. Annual richness was calculated as the average number of species found on all possible combinations of four adjacent sampling dates a year across all years surveyed. Daily richness was the average number found per sampling date, and total richness was the number recorded across the entire sampling period.

Interannual turnover

Interannual turnover (x_i) was estimated by fitting a power function to the cumulative number of species observed against the day of sampling starting from the first day in the survey in each lake. Interannual species–time curves account for differences among surveys in the interval between sampling dates, and for phenology in species replacement

since dates are placed in temporal sequence. That is, if two lakes have the same rate of species replacement but are sampled at different frequencies, then that lake that is sampled more often will have lower annual turnover by our method, but the two will have equivalent rates of interannual turnover. By contrast, annual turnover is based on the number of adjacent sampling dates, not their separation in time, and seasonal patterns are removed by using all sequential combinations of dates between one and four within a year. Comparing the two metrics allows us to determine whether seasonal patterns, differences in sampling frequency, or length of the observation period (within or among years) influence patterns of species richness and temporal turnover.

RESULTS

Species richness was positively correlated across all temporal scales among the lakes (Fig. 1). Daily richness increased continuously with average annual richness (Fig. 1a), and annual richness with total richness across the survey (Fig. 1b). Annual and interannual turnover (x_a and x_i) were weakly positively related ($R^2 = 0.24, P = 0.002$, Fig. 1c), and species turnover was generally greater within years (x_a) than among years (x_i).

Annual species turnover (x_a) showed a unimodal relationship with average annual richness (Fig. 2a), as did interannual turnover (x_i) and total richness (Fig. 2c). The increasing portions of the curves were driven mainly by high-latitude Alaskan lakes. Exclusion of these lakes resulted in a strong negative relationship between annual richness and x_a ($r = -0.57, P = 0.001$), and a weaker negative correlation between total richness and x_i ($r = -0.31, P = 0.06$). There were no correlations between annual richness and x_a or between total richness and x_i among the Alaskan lakes. Figure 2b shows examples of annual species–time curves for a high-latitude lake with low richness and low turnover (Toolik Lake), a temperate lake with intermediate annual richness and high turnover (Allequash Lake in Wisconsin), and a temperate lake with high annual richness and low turnover (Red Chalk Lake in Ontario). Figure 2d shows the interannual species time curves for the same three lakes.

The relationships between annual and total diversity and turnover were not driven by differences in sampling intensity or duration. Annual species–time curves were standardized to include one to four adjacent sampling dates. Annual turnover was positively correlated with both sampling duration (the average number of days between the first and last sampling date within a year, $r = 0.579, P < 0.05$) and the average intersample duration ($r = 0.519, P < 0.05$). However, annual richness and its second-order term were both significant predictors of turnover in a

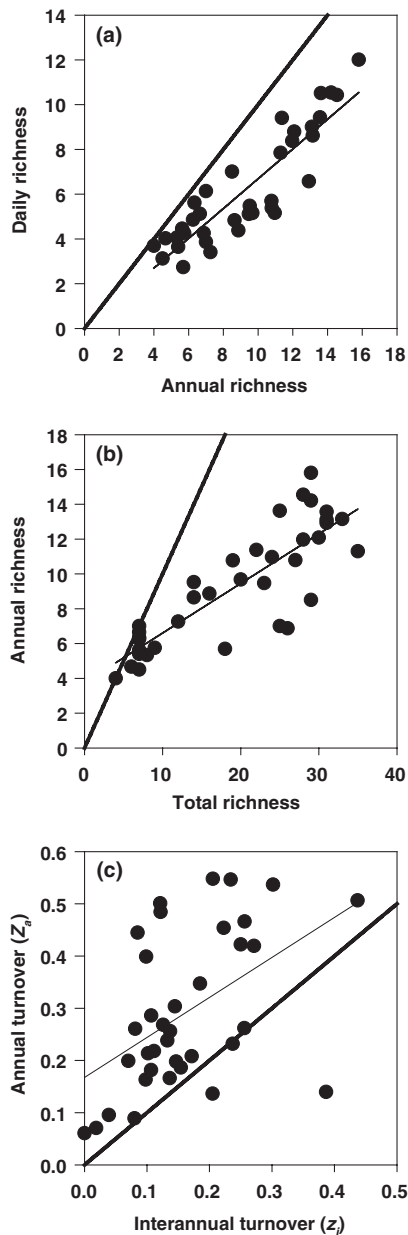


Figure 1 The relationships among: (a) daily richness and annual richness ($y = 0.04 + 0.67x$, $R^2 = 0.79$, $P < 0.0001$); (b) annual richness and total richness among years ($y = 3.76 + 0.29x$, $R^2 = 0.71$, $P < 0.0001$); and (c) annual turnover (z_a) and interannual turnover (z_i) and interannual turnover ($y = 0.17 + 0.77x$, $R^2 = 0.24$, $P = 0.002$) for zooplankton in the 36 lakes in the study. The thick lines are the 1 : 1 lines and the thin lines are the linear regressions.

multiple regression ($P < 0.03$ for both terms) after including sampling duration and the time interval between samples. The sign of the coefficients was also the same as when sampling variables were not included (i.e. positive first-order term and negative second-order term). The unimodal

relationship between interannual turnover and total richness was also significant after accounting for variation due to the length of the survey period in days ($P < 0.007$ for both terms). In addition, lakes from different surveys were found in all portions of the curve. For instance, the high-latitude Alaskan lakes with low richness and low turnover were from the Toolik Lake Arctic LTER site and two separate surveys by the Alaska Department of Fish and Game in Southeast Alaska. The lakes in the high and intermediate annual richness portions of the curve also came from a number of different surveys. Finally, there was a negative correlation between annual richness and turnover ($r = -0.654$, $P < 0.05$) and between total richness and interannual turnover ($r = -0.682$, $P < 0.05$) among lakes in the largest survey (Dorset, eight lakes), indicating that the decreasing portions of the curves were consistent within and among surveys.

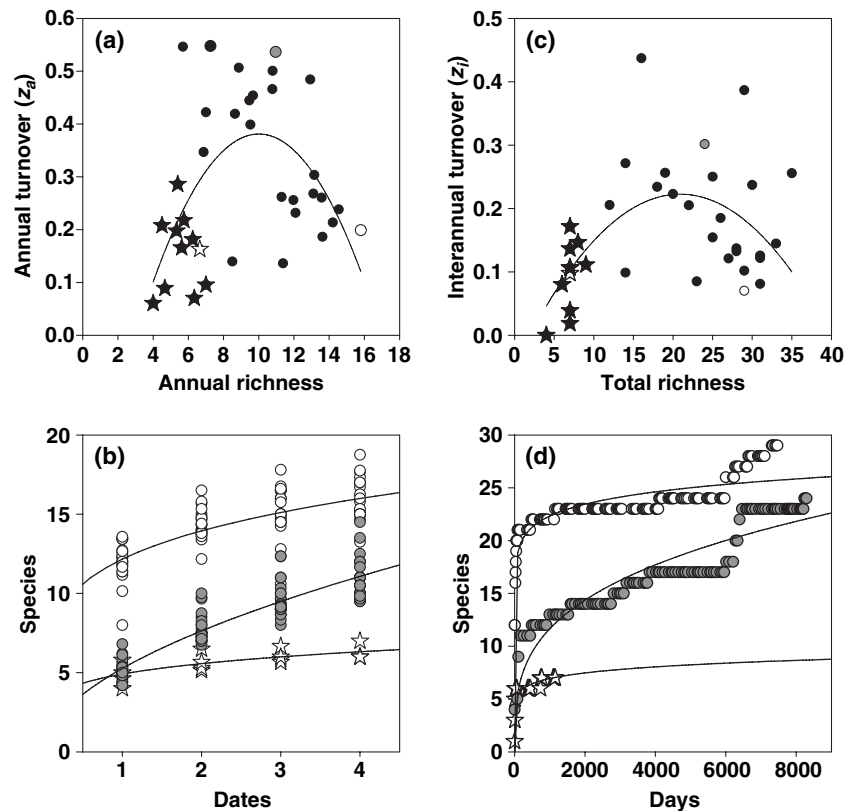
Species turnover and daily richness showed distinct relationships with lake area and latitude (Fig. 3). Daily, annual and total richness all increased with lake surface area (Fig. 3a–c), while annual and interannual turnover (z_a and z_i) were independent of area (Fig. 3d–e). By contrast, richness at all three time scales, and turnover within and among years all declined at high latitudes (Fig. 3f–j).

DISCUSSION

Compositional stability in zooplankton species composition shows strong relationships with diversity that vary from positive within a biogeographical region to negative across a latitudinal gradient. Among lakes in the temperate zone, high annual diversity is consistently associated with slower accumulation of new species through time within and among years, indicating a positive correlation between diversity and stability. However, diversity and temporal turnover are lower in high-latitude lakes, leading to a negative correlation between diversity and stability over continental scales. This suggests that either the positive effects of diversity on stability are obscured by environmental variability at continental scales or diversity has different effects on stability at low and high latitudes. Alternatively, environmental variability may promote both diversity and stability among temperate lakes, but push the two in opposite directions across latitudinal gradients. Annual richness and turnover were uncorrelated among Alaskan lakes; therefore, associations between diversity and stability are only apparent in species-rich temperate regions.

Zooplankton richness was strongly positively correlated across all time scales (daily, annual and total across all years, Fig. 1a,b). These patterns indicate that temporal niche partitioning in zooplankton is invariant with diversity and that temporal patterns of richness mirror spatial patterns.

Figure 2 (a) Annual turnover vs. average annual richness for the 36 lakes ($y = -0.40 + 0.15x - 0.008x^2$, $R^2 = 0.28$, $P = 0.005$). Both the first- and second-order terms are significant ($P < 0.002$) in the linear regression for z_a . Lakes in Alaska are marked with stars, temperate lakes are circles. (b) Examples of species–time curves for a high-latitude lake with low annual richness and low turnover (Toolik Lake, white stars), an intermediate annual richness lake with high turnover (Allequash Lake in the Wisconsin survey, grey circles), and a lake with high annual richness and low turnover (Red Chalk Lake in the Dorset Lakes survey, white circles). (c) Interannual turnover vs. total richness across all years of sampling ($y = -0.05 + 0.03x - 0.0006x^2$, $R^2 = 0.27$, $P = 0.005$). Both the first- and second-order terms contributed significantly to the fit of the model ($P < 0.007$). (d) Examples of species accumulation curves across the entire period of sampling for the three lakes listed above.



Studies of spatial patterns found that local or within-lake crustacean richness is linearly related to regional or among-lake richness (Shurin *et al.* 2000). Such patterns are often taken to indicate that local diversity is unsaturated in that dispersal rather than local biotic interactions limit the richness of assemblages (Cornell & Lawton 1992). However, this inference has been widely criticized on the grounds that patterns of local and regional richness are inherently scale dependent and insensitive to local interactions (Srivastava 1999; Shurin & Allen 2001; Hillebrand 2005). We also found that interannual turnover was lower than annual turnover (Fig. 1c). This pattern may result from species showing consistently recurring seasonal patterns. The patterns also indicate that measures of richness at one temporal scale (e.g. daily) are a good indicator of the number of species that would be encountered with longer sampling despite the pronounced seasonal and interannual turnover observed in zooplankton communities (Arnott *et al.* 1998).

Our results showing positive associations between diversity and community stability in the temperate zone suggest several potential functional relationships between richness and turnover. First, high diversity may stabilize composition by reducing either extinction or colonization rates. Reduced extinction at high diversity may occur if species interactions are mostly weak and serve to buffer

against large population variability (McCann *et al.* 1998). Such situations can arise through community assembly as strongly interacting species combinations tend to be driven to extinction (Kokkoris *et al.* 2002; Wilson *et al.* 2003). Alternatively, high richness may repel invasion and reduce species turnover. A model where diversity inhibits invasion found that rich communities accumulate new species more slowly and therefore have flatter species–time curves at short time scales. However, rich communities also take longer to approach their asymptotic richness and therefore have higher exponents at long scales (J. B. Shurin, unpublished data). As many of the zooplankton communities in our data set were still adding new species after many years of sampling (see Fig. 2b,d), the declining exponent may indicate that diverse communities are better at repelling invasion by new species. Shurin (2000) found that natural pond zooplankton communities with more species were less susceptible to experimental introductions of new species from the region. The pattern of declining turnover in the temperate zone is consistent with reduced invasion or extinction probabilities at high richness.

Another possible explanation for the patterns we observed is that high environmental variability reduces richness and increases turnover (White *et al.* 2006). This

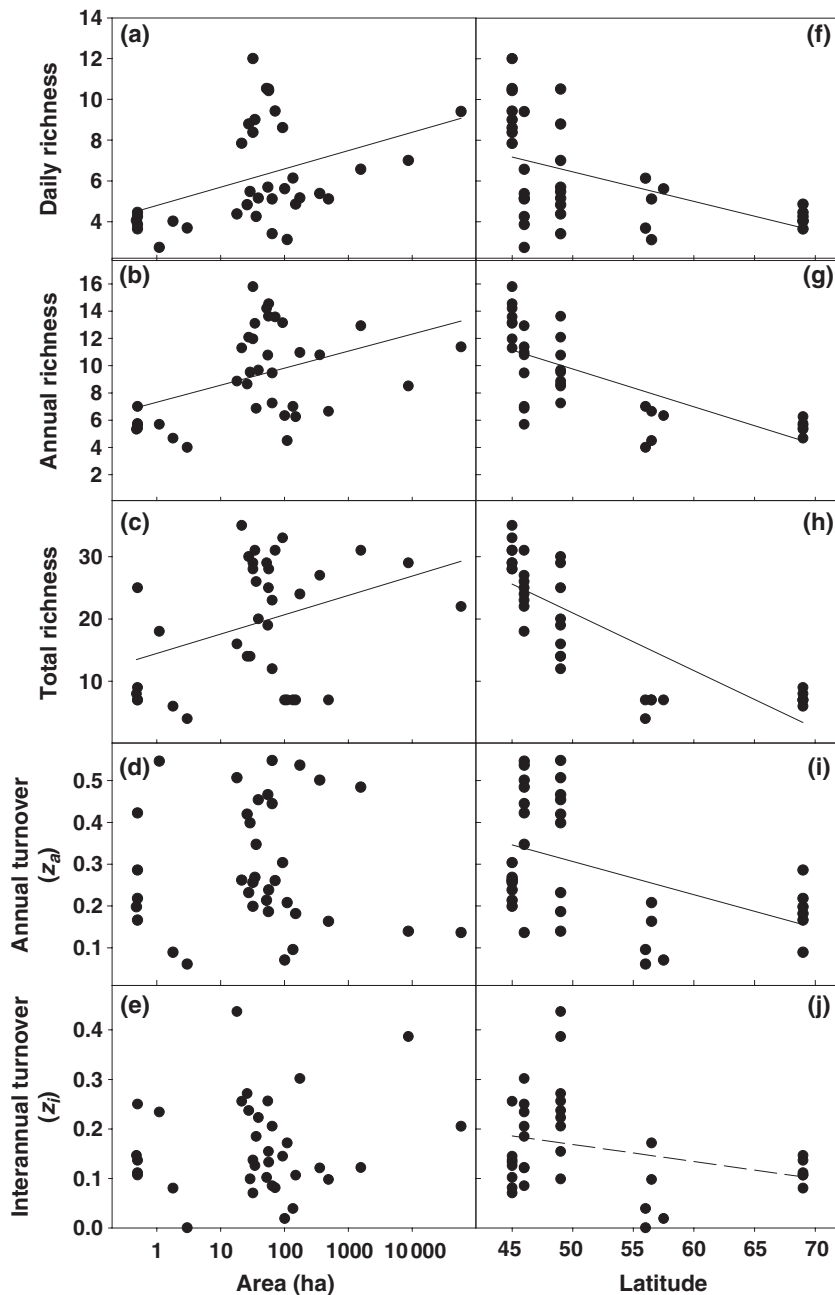


Figure 3 The relationship between lake surface area and (a) daily richness ($y = 4.79 + 0.90x$, $R^2 = 0.17$, $P = 0.01$), (b) annual richness ($y = 7.31 + 1.25x$, $R^2 = 0.18$, $P = 0.009$), (c) total richness ($y = 14.48 + 3.10x$, $R^2 = 0.13$, $P = 0.03$), (d) annual turnover ($P = 0.87$), and interannual turnover ($P = 0.40$). The relationship between latitude and (f) daily richness ($y = 13.72 - 0.15x$, $R^2 = 0.25$, $P = 0.002$), (g) annual richness ($y = 23.63 - 0.28x$, $R^2 = 0.51$, $P < 0.0001$), (h) total richness ($y = 67.24 - 0.93x$, $R^2 = 0.65$, $P < 0.0001$), (i) annual turnover ($y = 0.70 - 0.008x$, $R^2 = 0.21$, $P = 0.005$), and (j) interannual turnover ($y = 0.34 - 0.003x$, $R^2 = 0.10$, $P = 0.06$, the dashed line indicates the marginal significance).

hypothesis is based on the idea that highly variable environments experience conditions that fall outside the tolerances of many species. In this case, fluctuations in the physical environment reduce richness by excluding species and reduce stability by shifting between conditions favouring different species. However, it is also possible that environmental fluctuations favour coexistence and promote diversity through the storage effect (Chesson & Warner 1981). A model of abiotic variability and species turnover found that highly variable environments had low richness and high

turnover only when conditions exceeded the tolerances of many species (J. B. Shurin, unpublished data). If species have broad environmental niches relative to the range of conditions experienced in the habitat, then increasing variability leads to higher richness and greater turnover.

The patterns we observed give insight into the causes of species–area relationships and latitudinal gradients in diversity, two of the most familiar and well-documented patterns in ecology (Dodson *et al.* 2000; Hillebrand 2004; Drakare *et al.* 2006). Species–area relationships for zooplankton in

lakes are driven by higher diversity at all time scales, but not by greater temporal turnover in composition. This suggests that large lakes offer more potential for local coexistence but do not systematically differ in temporal niche partitioning or variability in the environment. This result contrasts with Adler *et al.* (2005) who found that α declines with increasing habitat area in a wide variety of taxa. Most of the surveys in Adler *et al.* were spatially nested subsets; only the zooplankton survey (North Temperate Lakes LTER, Wisconsin) measured separate habitats of different area. The two methods of constructing species–area curves (nested subsets vs. comparison of patches of different size) measure different aspects of the relationship between species number and area (Rosenzweig 1995; Drakare *et al.* 2006). In addition, Adler *et al.* (2005) dealt only with interannual turnover whereas we address changes in composition within and among years. Our larger survey of zooplankton found no relationship between lake surface area and the rate of turnover. The decline in species turnover in larger habitats shown by Adler *et al.* (2005) may therefore not be a general feature of all communities. The slope of the species–area relationship was also steeper on longer temporal scales (daily = 0.90, annual = 1.25, interannual = 3.10, Fig. 3).

The patterns indicate that species turnover in both space and time decrease with latitude so that species have broader temporal and spatial niches. In addition, our patterns agree with Hillebrand (2004) who showed that latitudinal declines in diversity are strongest at broad temporal and spatial scales (e.g. compare Fig. 3f–h). MacArthur (1972) proposed that a more stable environment allows lower latitudes to support greater species diversity. However, our data indicate that temperate lakes showed higher species turnover in time, suggesting that if environmental variability changes with latitude, it is greater further from the poles. Another possible explanation is that the high-latitude lakes in our survey have few species because of their recent geological origin and slow post-glacial dispersal (Stemberger 1995), or because their rate of diversification is lower (Jablonski *et al.* 2006). Higher spatial turnover at low latitudes may be caused by niche compression in the face of more intense interactions in diverse communities (MacArthur 1972). Our results indicate that temporal turnover declines with increasing latitude (Fig. 3i,j). High-latitude lakes may have lower turnover because weaker interactions allow them to persist for longer periods. Alternatively, low temperatures may slow demographic rates and cause interactions to proceed towards extinction more slowly, resulting in slower turnover. Our results indicate that temporal turnover in species composition mirrors patterns of spatial turnover (Koleff *et al.* 2003; Hillebrand 2004; Drakare *et al.* 2006) in that both decline at high latitudes.

The relationship between diversity and stability remains controversial and poorly understood in ecology (McCann

2000; Cottingham *et al.* 2001). Our results indicate that high annual diversity in temperate zone lakes is consistently associated with lower temporal turnover in composition. This suggests that either diversity stabilizes population dynamics or greater environmental stability increases annual richness. However, diversity and stability are negatively correlated over a latitudinal gradient, suggesting that either environmental variability across broad scales reduces richness and turnover or high-latitude species show less temporal niche compression than those in the temperate zone. Therefore, diversity and stability appear linked in associations that vary qualitatively from positive to negative with spatial scale.

ACKNOWLEDGEMENTS

Orlanne Anneville, Jean Marcel Dorioz, Switgard Duesterloh, Hal Geiger, Renate Riffe, James Rusak and Frank Wallis generously provided access to data sets. Peter Adler, John Bruno, Howard Cornell, Blake Matthews, Sandra Nicol, Russ Markel, Mark Vellend, Laura White and Spencer Wood provided helpful comments on the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada, the Alaska Department of Fish and Game, and the US Long-Term Ecological Research network.

REFERENCES

- Adler, P.B., White, E.P., Lauenroth, W.K., Kaufman, D.M., Rassweiler, A. & Rusak, J.A. (2005). Evidence for a general species–time–area relationship. *Ecology*, 86, 2032–2039.
- Arnott, S.E., Magnuson, J.J. & Yan, N.D. (1998). Crustacean zooplankton species richness: single- and multiple-year estimates. *Can. J. Fish. Aquat. Sci.*, 55, 1573–1582.
- Chesson, P.L. & Warner, R.R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.*, 117, 923–943.
- Cornell, H.V. & Lawton, J.H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.*, 61, 1–12.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.
- Dodson, S.I., Arnott, S.E. & Cottingham, K.L. (2000). The relationship in lake communities between primary productivity and species richness. *Ecology*, 81, 2662–2679.
- Drakare, S., Lennon, J.T. & Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecol. Lett.*, 9, 215–227.
- Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.*, 163, 192–211.
- Hillebrand, H. (2005). Regressions of local on regional diversity do not reflect the importance of local interactions or saturation of local diversity. *Oikos*, 110, 195–198.

- Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314, 102–106.
- Kalff, J. (2002). *Limnology: Inland Water Ecosystems*. Prentice Hall, Upper Saddle River, NJ.
- Kokkoris, G.D., Jansen, V.A.A., Loreau, M. & Troumbis, A.Y. (2002). Variability in interaction strength and implications for biodiversity. *J. Anim. Ecol.*, 71, 362–371.
- Koleff, P., Lennon, J.J. & Gaston, K.J. (2003). Are there latitudinal gradients in species turnover? *Glob. Ecol. Biogeogr.*, 12, 483–498.
- MacArthur, R.H. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology*, 36, 533–536.
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton, NJ.
- May, R.M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.
- McCann, K.S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.
- McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988). On the risk of extinction. *Am. Nat.*, 132, 757–785.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Sankaran, M. & McNaughton, S.J. (1999). Determinants of biodiversity regulate compositional stability of communities. *Nature*, 401, 691–693.
- Shurin, J.B. (2000). Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology*, 81, 3074–3086.
- Shurin, J.B. & Allen, E.G. (2001). Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.*, 158, 624–637.
- Shurin, J.B., Havel, J.E., Leibold, M.A. & Pínel-Allouf, B. (2000). Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology*, 81, 3062–3073.
- Srivastava, D.S. (1999). Using local–regional richness plots to test for species saturation: pitfalls and potentials. *J. Anim. Ecol.*, 68, 1–16.
- Stemberger, R.S. (1995). Pleistocene refuge areas and post-glacial dispersal of copepods of the northeastern United States. *Can. J. Fish. Aquat. Sci.*, 52, 2197–2210.
- White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M. *et al.* (2006). A comparison of the species–time relationship across ecosystems and taxonomic groups. *Oikos*, 112, 185–195.
- Wilson, W.G., Lundberg, P., Vazquez, D.P., Shurin, J.B., Smith, M.D., Langford, W. *et al.* (2003). Biodiversity and species interactions: extending Lotka–Volterra community theory. *Ecol. Lett.*, 6, 944–952.
- Yodzis, P. (1981). The stability of real ecosystems. *Nature*, 289, 674–676.

Editor, Howard Cornell

Manuscript received 16 November 2006

Manuscript accepted 23 November 2006