Reversal in the relationship between species richness and turnover in a phytoplankton community

BLAKE MATTHEWS¹ AND FRANCESCO POMATI

EAWAG, Aquatic Ecology Department, Center for Ecology, Evolution, and Biogeochemistry, Lucerne, Switzerland

Abstract. Negative relationships between species richness and the rate of compositional turnover are common, suggesting that diverse communities have greater stability than depauperate ones; however, the mechanistic basis for this pattern is still widely debated. Species richness and turnover can covary either because they are mechanistically linked or because they share common environmental drivers. Few empirical studies have combined long term changes in community composition with multiple drivers of environmental change, and so little is known about how the underlying mechanisms of species coexistence interact with changes in the mean and variability of environmental conditions. Here, we use a 33 year long time series (1976–2008) of phytoplankton community composition from Lake Zurich, to examine how environmental variation influences the relationship between richness and annual turnover. We find that the relationship between richness and annual turnover reverses midway through the time series (1992–1993), leading to a hump shaped relationship between species richness and annual turnover. Using structural equation modeling we show that annual turnover and diversity are independently associated with different drivers of environmental change. Furthermore, we find that the observed annual sequences of community assembly give rise to rates of species accumulation that are more heterogeneous through time than expected by chance, likely owing to a high proportion of species showing significant autocorrelation and to strong positive covariation in the occurrences of species.

Key words: community assembly; species area relationships; species time relationships; species turnover.

INTRODUCTION

A major goal of ecology is to understand what factors determine the spatial and temporal distribution of the number of species (Preston 1960, Rosenzweig 1995, Ricklefs and Jenkins 2011). Pioneering research on the biogeographic variation of species richness, for example, studies of biodiversity on islands (Losos and Ricklefs 2010) and along broad environmental gradients (MacArthur 1972, Ricklefs 1987), have revealed that the spatial structure of biodiversity results from the interaction between niche variation among species and the dynamics of colonization, speciation, and extinction (Hubbell 2001, Chase and Leibold 2003, Losos and Ricklefs 2010, Chase and Myers 2011). Positive relationships between sampling effort (e.g., area or time) and the number of species are common in ecological research, and emerge partly because of species interactions in a heterogeneous environment (Scheiner et al. 2011). Although positive species area relationships are well studied, comparatively little effort has been directed toward quantifying and explaining systematic variation in the rate of species accumulation through time

(Preston 1960, Shurin et al. 2007, White et al. 2010, Scheiner et al. 2011). Species time relationships are important for understanding spatial patterns of diversity in contemporary communities (Adler and Lauenroth 2003, Adler et al. 2005), and for predicting community responses to environmental change (Gonzalez and Loreau 2009, Shurin et al. 2010, Scheiner et al. 2011).

The study of species time relationships is embedded in the broader theories of community assembly (Law and Morton 1996, Fukami 2004, Chase and Myers 2011), compensatory dynamics (Vasseur et al. 2005, Gonzalez and Loreau 2009), and species coexistence (Chesson 2000, Mayfield and Levine 2010). In such research, a common underlying question is: how does the rate of species turnover change with species richness? There are two types of explanations for why the rate of species turnover and richness may covary. First, richness may directly influence turnover rates if niche differences among species can interact with rates of colonization and extinction at local or regional scales (Shurin 2007). High levels of local diversity, for example, can limit colonization success of invaders (Shurin 2000, Fargione et al. 2003), lead to a greater prevalence of cyclic community assembly (Fukami 2004, Steiner and Leibold 2004), and increase the likelihood of alternative stable states (Chase 2003). Whereas, in the neutral case, namely ecological drift with a constant speciation rate and size of regional species pool, the rate of local species

Manuscript received 22 December 2011; revised 13 April 2012; accepted 10 May 2012. Corresponding Editor: B. J. Cardinale.

¹ E-mail: blake.matthews@eawag.ch

FIG. 1. Four examples of how the general form of the species time relationships can change with increasing species richness. (A) Gamma richness increases while turnover stays constant (power functions: $a = 5, 10, 15, 20$; $z = 0.15$, where a and z are the parameters of the power functions describing the species time relationship). (B) Gamma richness stays constant while the turnover increases (power functions: $a = 10, 15, 20, 25$; $z = 0.10, 0.3, 0.4, 0.5$). (C) The turnover and gamma richness are positively related (power functions: $a = 10, 15, 20, 25$; $z = 0.14, 0.19, 0.22, 0.28$). (D) Turnover and gamma richness are negatively related (power functions: $a = 10, 15, 20, 25$; $z = 0.50, 0.35, 0.25, 0.18$).

turnover depends primarily on global migration rates and local rates of births and deaths (Hubbell 2001). Second, species turnover may change with richness in relation to how environmental variability influences species coexistence through time (Vasseur et al. 2005). Coexistence depends on the distribution of both fitness differences (e.g., variation in competitive ability) and niche differences (e.g., species specific resource preferences) among species in a community (Chesson 2000). Provided there is variation in resource use and competitive ability among species, environmental variability can increase or decrease species turnover either by affecting the size of the regional species pool or by shaping the distribution and co variance of environ-

mental tolerances among species (Vasseur et al. 2005, Kraft et al. 2007, Shurin 2007).

Constructing species time relationships (STRs) by fitting power functions of the form ($S = aT^z$) is a useful way to quantify variation in the rate of community change through time. Variation in the shape of STRs (Fig. 1) can be used to test how the rate of species turnover (z) varies with total species richness (i.e., gamma richness, S_{gamma}), and average alpha richness (S_{alpha} , for which a is an index). In the simplest case, turnover and gamma richness might change independently from one another, such that when richness increases turnover rates remain constant (Fig. 1A) or when turnover increases species richness remains con-

stant (Fig. 1B). Alternatively, species richness and turnover rate can be either positively (Fig. 1C) or negatively (Fig. 1D) related. A recent meta analysis of STRs across a broad range of taxa found that turnover rate often declines with increasing species richness, implying that diverse communities are more stable through time (White et al. 2006). Similarly, Shurin and colleagues found a hump shaped relationship between species richness and turnover in zooplankton communities (Shurin et al. 2007). In order to achieve a comparable level of understanding of temporal vs. spatial biodiversity patterns, we need many more studies that examine turnover along broad diversity gradients and over long enough time scales to capture the range of environmental variation relevant for understanding species coexistence (Magurran et al. 2010).

To investigate how species turnover changes in relation to species richness through time (Fig. 1) we analyzed a long term data set (monthly samples from 1976 to 2008) of environmental variation and phytoplankton community composition from Lake Zurich. For each year of the time series, we calculated an STR and examined (1) how the shape of the STR changed through time in relation to variation in the environment and (2) how model fits to the STR differed between observed and randomized assembly sequences on an annual basis.

Variation in the shape of annual STRs could be influenced by several long term environmental changes in Lake Zurich associated with climate warming and re-oligotrophication (Pomati et al. 2011). More generally, there is growing evidence that changes in the mean and variability of environmental conditions can drive changes in species turnover (Jezierski et al. 2008, Shurin et al. 2010), by affecting, for example, the seasonal phenology of species (Yang and Rudolf 2010) or the size of the regional pool (Shurin 2007). To investigate this, we used structural equation modeling to examine associations between environmental variability, richness, and annual turnover over 33 years in Lake Zurich.

Comparing STRs from observed vs. randomized assembly sequences can help identify the presence of nonrandom temporal structure and determine its influence on the shape of STRs. This approach is analogous to examining how various ecological processes can alter the scale invariance of species area relationships (McGlinn and Palmer 2011). Nonrandom patterns are also useful for discriminating between niche vs. neutral based community assembly (Hubbell 2001, Chase and Myers 2011) and for elucidating the mechanisms underlying the stability of ecosystem functions in diverse communities (Allan et al. 2011). Here, we investigate how the nonrandom structure of community assembly sequences and parameters of the STRs are related to the amount of autocorrelation of species occurrences through time, and the level of interspecific temporal aggregation.

METHODS

Study system and data set structure. Lake Zurich (47°13'21.7524" N, 8°45'6.7926" E) is a large (surface area 65 km²) and deep (maximum depth 136 m) mesotrophic lake in Switzerland. The phytoplankton community and environmental conditions have been monitored for decades by the Zurich Water Supply (WVZ) at monthly sampling intervals and from multiple depths ($N = 14$ depths, 0–135 m). We examined changes in phytoplankton community composition using species presence absence matrices for every sampling date, aggregated over all sampling depths. For each sampling date, we also calculated depth averaged annual changes in the mean and coefficient of variation (CV) of the following environmental conditions: water temperature (T), phosphate concentration (P), nitrate concentration (N), conductivity (C), pH, and an index of light attenuation (L) in the water column (UV attenuation at 254 nm). Details of the phytoplankton sampling and environmental variables are described in detail elsewhere (Pomati et al. 2011). Here, we aggregated the data over the water column in order to obtain comparable time series of annual turnover, richness, and environmental conditions on an annual scale.

Quantifying species time relationships. For each year of the data set (12 monthly samples) we fit a species time relationship (STR) using a power function of the form $S = aT^z$ and used nonlinear regression to estimate a , which is a proxy for the average monthly richness over the year (i.e., S_{alpha}), and z , which is an index of the rate of species turnover on an annual basis (White et al. 2006, Shurin et al. 2007). We built the STRs for each year as follows. First, we calculated the number of species for all sequential combinations of 1–12 sampling dates over the year. For example, we calculated the number of species for all of the adjacent sampling intervals of one month, two months, three months, and up to 12 months. We then averaged the species richness for each of these intervals prior to fitting the power function. This approach removes some of the influence of seasonality on the calculated rates of species turnover, because it is based on the number rather than the specific timing of sampling dates, but it still retains information about the specific monthly sequence of community assembly, making it informative to compare with randomized assembly sequences.

The relationship between richness and annual turnover can be strongly influenced by the seasonality of plankton dynamics and environmental conditions (Shurin et al. 2007), and so we additionally quantified interannual STRs by using variation in species richness for each month over the entire 33 years. While this approach independently tests for a relationship between richness and turnover, it does so over a narrower range of both environmental conditions and richness, and leads to a reduced number of sampling points (i.e., 12 months). As a result, we did not analyze the structure of the associations between interannual turnover, richness,

and environmental variability, as we do for annual turnover.

We used linear, segmented, and quadratic regression to characterize relationships between species richness, annual STR parameters (z and a), and the sampling year. To begin, we fit a simple linear regression model and used a Davies test (Davies 1987) to test for a non-constant slope (e.g., a breakpoint) in the linear model. Then, if we detected a significant breakpoint we additionally fit a segmented regression (using the R package segmented) and a quadratic least square regression (e.g., $z = \beta_1 + \beta_2 \times S_{\text{gamma}} + \beta_3 \times S_{\text{gamma}}^2$) to the data, and selected the best model using the Akaike information criterion (AIC). All analyses were done with R version 2.13 (R Development Core Team 2011).

Structure of the associations between richness, annual turnover, and environmental variation. We used structural equation modeling (SEM) to test specific hypotheses about the relationships between annual species richness (i.e., gamma richness), annual turnover, and environmental variation. SEM is a robust multivariate technique that is useful for testing alternate models that represent networks of association between parameters (Shipley 2002). The resulting coefficients are analogous to partial regression or correlation coefficients, and indicate how a hypothesized response variable (at the tip of an arrow) will change in response to an independent variable (at the base of an arrow). Here, we used SEM to test whether metrics of environmental variation (EV) are either directly associated with annual turnover, or whether they are indirectly associated with annual turnover via their influence on species richness. To do this, we built structural equation models based on the following three hypotheses: (H_1) EV metrics have only indirect pathways leading to annual turnover through species richness, (H_2) EV metrics have only direct pathways leading to annual turnover and are independent of richness, and (H_3) all EV metrics have both direct pathways to annual turnover and indirect pathways leading through species richness. We additionally analyzed these models with sampling year as a latent variable, in order to partially account for several unmeasured and autocorrelated characteristics of the system, such as temporal changes in the spatial distribution of environmental conditions, in the rates of migration among sites, or in the size and composition of the regional species pool.

For all SEM models, we started with a model that included all covariances among the mean environmental conditions ($N = 6$) and among the environmental fluctuations ($N = 6$), and a complete set of regression coefficients linking the environmental parameters ($N = 12$) and annual turnover and richness. We then trimmed each model by removing nonsignificant coefficients ($P < 0.01$) until we had a model where all pathways ending in annual turnover had significant coefficients. All SEM analyses were performed using R (version 2.13) with the sem package (Fox 2002).

Comparing observed to random assembly sequences.

The shape of species time relationships at a local site often reflects a truly nonrandom occurrence of different species assemblages through time (Rosenzweig 1995, 1998, Adler and Lauenroth 2003, Adler et al. 2005, White et al. 2006). To investigate this further, we compared the observed species time relationship (STR) with expected distributions for each month interval in the STR based on two separate null model randomizations. First, we randomly shuffled the sampling dates within each year and calculated STRs for each iteration. This randomization keeps the total occurrences of all species constant and preserves interspecific associations, but it makes each sampled community equally likely to occur across all months within a year. Second, we used the null model algorithm SIM 8 from Gotelli (2000), where the probability of occurrence of a given species in some month is conditional on both the observed monthly species richness and the total number of occurrences of the species across all months. This algorithm is suitable for biological situations where months (or sites) differ in their suitability and species differ in their probability of occurrence in a given year.

Nonrandom structure in the temporal distribution of species can have significant impacts on the shape of species time relationships (White and Gilchrist 2007). The frequency of autocorrelation of individual species in the community and the amount of interspecific aggregation at different time periods in the year are particularly relevant for understanding the shape of STRs. To quantify the level of autocorrelation in the community, we measured autocorrelation at lags of 1–12 months for each species (that occurred multiple times), and then randomized the order of occurrences over the entire time series for each species to generate a null distribution, which we then used to test for significant temporal autocorrelation, following White and Gilchrist (2007). To quantify patterns of interspecific aggregation through time, we used the V ratio (Gotelli 2000), which, for our application, is the ratio of the variance in species richness across all 12 months of the year relative to the total sum of the variance in species occurrences patterns over the year. We used the SIM 8 algorithm to test for significant V ratios against a null distribution. Unexpectedly high V ratios result from positive covariances among species indicating temporal aggregation of species over the year, whereas unexpectedly low V ratios result from negative covariances among species, which might reflect niche partitioning or antagonistic species interactions (Gotelli 2000). If all months have a similar number of species then both annual turnover (z) and the V ratio will be low. We might expect a relationship between annual turnover and the V ratio if the variation in z is driven by changes in the pattern of positive or negative species covariances over the time series.

RESULTS

Temporal change in STR parameter

Annual patterns. Both annual gamma richness (S_{gamma}) and average annual alpha richness (S_{alpha}) increased from 1976 to 2008, and in both cases we detected a significant breakpoint in 1993 (Fig. 2, Table 1). However, the proportional increase in the slope before β_1 and after β_2 , the breakpoint, was greater for S_{alpha} ($\beta_2/\beta_1 = 2.6$) than for S_{gamma} ($\beta_2/\beta_1 = 1.6$), suggesting that the annual partitioning of diversity changed through time. The timing of the breakpoint coincided with a clear decline in annual turnover (z) through time (Fig. 2C). Overall, the relationship between richness (both S_{gamma} and S_{alpha}) and annual turnover (Fig. 3) was hump shaped, and, in qualitative terms, it switched from being positive (as in Fig. 2C) to negative (as in Fig. 2D) over a broad gradient of species richness.

Interannual patterns. Interannual turnover (z_{inter}) was strongly negatively related to average monthly richness ($z_{\text{inter}} = 0.53 - 0.003S_{\text{alpha}}$; $P < 0.001$, $F_{1,10} = 101.7$; Appendix A). The lowest values of z_{inter} (and highest richness levels) occurred during the strongly thermally stratified period of July to October, whereas the highest values of z_{inter} (and low richness levels) tended to occur in the winter months from January to March (Appendix A).

Structure of the associations between richness, annual turnover, and environmental variation

The structural equation modeling, without sampling year in the analysis, revealed that several environmental conditions are associated with the relationship between species richness and annual turnover, including average concentrations of N and P (N_{avg} , P_{avg}), average index of light attenuation (L_{avg}), and the coefficient of variation of conductivity (C_{CV} ; Fig. 4B). The best supported model included both direct and indirect pathways linking environmental conditions and annual turnover (Fig. 4B; H_3), suggesting that environmental drivers can independently affect richness and annual turnover. Although the rate of annual turnover was negatively associated with richness, annual turnover was also positively associated with two metrics of environmental variation (N_{avg} and C_{CV}) that were not strongly associated with richness (Fig. 4B; H_3). Adding sampling year to the structural equation modeling revealed similar patterns. As before, annual turnover was correlated with richness and the best supported SEM models (H_2 and H_3) included an environmental metric (N_{avg}) that was associated with annual turnover but not richness (Fig. 4C). Overall, these results suggest that annual turnover is not only driven by richness (or factors driving richness), but is also associated with other environmental drivers that are unrelated to richness.

FIG. 2. Time series of (A) the annual phytoplankton gamma richness (S_{gamma}), (B) the average annual alpha richness (S_{alpha}), and (C) the annual turnover (z).

Comparison of observed to random assembly sequences

The observed species time relationship in each year was clearly a result of nonrandom patterns of species occurrence. Regardless of the null model we used, we found strong deviations between the observed and expected STRs. Using the simpler null model algorithm that shuffled months randomly within each year, we often found lower richness than expected at the lower month intervals, and occasionally found higher richness than expected at the higher month intervals (Fig. 5). This same pattern was accentuated when using a null model algorithm (SIM 8) where species' occurrences in a given month were dependent on both the total richness

TABLE 1. Summary of regression models in Figs. 2 and 3, where S_{gamma} is annual gamma richness, S_{alpha} is average annual alpha richness, and turnover is the slope (z) of the power function.

Relationship, figure, and regression model	Breakpoint (SE)	β_1	β_2	β_3	R^2	AIC	AIC weights
$S_{\text{gamma}} \sim \text{year}$ (Fig. 2A)							
Linear		3.27			0.93	239.49	0.07
Breakpoint	1993 (3.4)	2.53	4.13		0.94	235.76	0.47†
Quadratic		1.56×10^5	160	0.041	0.94	235.82	0.46
$S_{\text{alpha}} \sim \text{year}$ (Fig. 2B)							
Linear		2			0.90	219.3	0
Breakpoint	1993 (1.7)	1.16	3.02		0.95	199.1	0.86†
Quadratic		1.90×10^5	196	0.0596	0.95	202.7	0.14
Turnover $\sim \text{year}$ (Fig. 2C)							
Linear		9.5×10^{-4}			0.11	151.8	0
Breakpoint	1992 (2.4)	0.001	0.004		0.42	163.9	0.79†
Quadratic		586	0.59	1.48×10^{-4}	0.39	161.2	0.21
Turnover $\sim S_{\text{alpha}}$ (Fig. 3A)							
Linear		7.0×10^{-4}			0.29	158.9	0.01
Breakpoint	58 (6.0)	0.003	0.001		0.44	164.9	0.28
Quadratic		0.15	0.004	3.3×10^{-5}	0.49	166.8	0.71†
Turnover $\sim S_{\text{gamma}}$ (Fig. 3B)							
Linear		2.8×10^{-4}			0.12	151.96	0.03
Breakpoint	51.3 (3.4)	0.003	0.001		0.28	156.8	0.32
Quadratic		0.11	0.003	1.2×10^{-5}	0.34	158.2	0.65†

Notes: The units of the breakpoint models are the same as the dependent variable (either years or number of species). The coefficients (β) refer to the slope of the line for linear models (β_1), the slopes before (β_1) and after (β_2) the breakpoint for the breakpoint models, and to the regression coefficients from the quadratic models (of the form $z = \beta_1 + \beta_2 S + \beta_3 S^2$). AIC is the Akaike information criterion.

† Best supported model.

and species specific occurrence frequencies across the year (Appendix B).

In nearly all of the years, this nonrandom structure of species' occurrences also led to higher than expected rates of annual turnover (black dots in Fig. 3). Such faster rates of annual turnover are not particularly surprising and likely reflect both autocorrelation of species occurrences through time and interspecific temporal aggregation within years. Indeed, more than 85% of the species that were present within each year also exhibited significant autocorrelation over the entire time series. In addition, we found a significant negative relationship between annual turnover and the proportion of species showing significant auto correlation (Appendix C; Pearson's $r = -0.45$, $P = 0.01$).

The level of interspecific aggregation within each year, measured as the V ratio, was almost always significantly higher than expected (based on the SIM 8 null model) across the entire time series (Appendix D). Such high V ratios indicate that species tend to co occur together in similar months more often than you would expect by chance. However, the relative amount of aggregation, measured as the difference between the observed and expected V ratio, was uncorrelated with annual turnover (Pearson's $r = -0.001$), suggesting that while interspecific aggregation is present, its variation is not strongly associated with variation in annual turnover through time.

DISCUSSION

The negative relationships observed between annual turnover and richness at high levels of richness (Fig. 3) and between interannual turnover and average monthly richness (Appendix A) are both consistent with the growing consensus that diverse communities exhibit less variability in aggregate community properties, such as total biomass and relative species abundances (Hooper et al. 2005, Ives and Carpenter 2007, Jiang and Pu 2009). However, there are comparatively few studies that provide good evidence that diversity is an important driver of compositional stability over long enough time scales to reasonably test alternate theories of coexistence (Agrawal et al. 2007, Levine and HilleRisLambers 2009), and even fewer studies that consider how long term changes in the environment affect the relationship between diversity and turnover. An important conclusion from our study is that richness and turnover are associated with different environmental drivers (Fig. 4), meaning that even if species richness and turnover are mechanistically linked the strength of the association will depend on the environmental context.

The relationship between phytoplankton species richness and annual turnover in Lake Zurich (Fig. 3) switched from positive (Fig. 1C) to negative (Fig. 1D) over a time period in which species richness more than doubled (from ~ 70 to 170; Fig. 2A). This result is similar to a recent analysis of zooplankton diversity in 36 North American lakes that revealed a similar hump

shaped relationship between turnover and richness (Shurin et al. 2007). Shurin et al. (2007) found that the annual turnover of zooplankton communities peaked ($z_a \sim 0.3$ – 0.4) in temperate lakes with an intermediate level of species richness (approximately 9–12 species), but was lower in both high latitude lakes with low diversity and in temperate lakes with high diversity.

In comparison to annual turnover (z), interannual turnover (z_{inter}) can reveal variation in the phenology of species replacement through time, assuming a fixed sampling frequency. Our analysis of interannual patterns reveals two differences from the results of Shurin et al. (2007). First, we found that the rates of interannual turnover were always greater than rates of annual turnover (Fig. 3, Appendix A). In our study, this is consistent with the observation of long term shifts in the species composition of phytoplankton in Lake Zurich (Anneville et al. 2004) that has likely occurred in response to changing environmental conditions (Pomati et al. 2011). Such a pattern would not be expected in lakes that have strong seasonality in terms of their species composition and richness relative to their long term trends. Second, we found that z_{inter} was strongly negatively related to average monthly richness (Appendix A), whereas Shurin et al. (2007) found a hump shaped relationship between z_{inter} and richness. However, this pattern is difficult to compare directly, because Shurin et al. (2007) calculated z_{inter} from a single STR for each lake (sequentially along the entire time series), whereas we calculated z_{inter} for each month in a single lake. Nevertheless, these two studies, along with others (White et al. 2006), provide strong evidence that richness and turnover are often correlated, but that their form may vary across spatial, temporal, and environmental scales.

Reversals in the relationship between annual turnover and richness (Fig. 3) could result from changes in the stabilizing effects of diversity on species turnover through time (Shurin 2007), or from changes in the interaction between environmental variability, diversity, and turnover (Ives and Carpenter 2007). High diversity can stabilize species composition (i.e., reduce turnover) either by directly reducing colonization rates, for example by repelling invasions of new species from the regional to the local pool, or by reducing extinction rates in local or regional species pools (Shurin 2007). If high diversity is also associated with weak interactions among species then population variability may decrease and lower the probability of stochastic extinction (Doak et al. 1998, McCann 2000). Such reasoning can partly explain the observed changes in turnover through time, but it does not address how long term changes in the mean and variability of environmental conditions might affect the relationship between species richness and turnover (Ernest et al. 2008, Shurin et al. 2010, Allan et al. 2011). If diversity and stability are subject to the same environmental drivers then they may co vary positively

FIG. 3. Change in annual turnover (z) in relation to (A) the average annual alpha richness (S_{α}) and (B) the annual gamma richness (S_{γ}). Coefficients of the quadratic functions are found in Table 1. Open circles denote years where the rate was not significantly different from randomized assembly sequences in which months were shuffled within each year.

or negatively without being mechanistically linked (Ives and Carpenter 2007).

Environmental variability, annual turnover, and richness in Lake Zurich

Our SEMs provide the strongest support for our third hypothesis (Fig. 4; H_3), namely that variation in annual turnover is best explained by both direct and indirect associations between environmental variation and richness. The indirect pathways leading from environmental variables to annual turnover through richness were both positive and negative. This is consistent with the idea that variability in the environment can indirectly affect annual turnover either by promoting or eroding diversity (Shurin et al. 2010). On one hand, increased environmental variability can promote diversity and increase rates of annual turnover (Fig. 1C), provided that species vary in their fitness in relation to the contrasting environmental conditions experienced over

A) Alternate hypotheses

B) Path analysis model (without year)

C) Path analysis model (with year)

FIG. 4. (A) A simplified schematic of the structural equation models for the three different hypotheses about the relationships between annual turnover, richness, and environmental conditions. (B) The best fitting structural equation models, without sampling year in the analysis, for each hypothesis shown in panel A. The asterisks denote the P values for the models, based on Bayesian information criterion (BIC; Table 2). The weights of the arrows are proportional to the size of the coefficients. Only significant coefficients were included in the final model. (C) The best fitting structural equation models, with sampling year in the analysis, for each hypothesis shown in panel A. Models depicting hypotheses 2 and 3 converge on the same final model and have identical statistical support. Sampling year (time) was included in the model as a latent variable leading from it to all other variables in the model (not depicted in panel A for clarity). Numbers next to the arrows in panels B and C are coefficients of the structural equation model. Abbreviations are: Env_{avg} , an average environmental condition; Env_{CV} , the coefficient of variation of an environmental condition; L_{avg} , the average index of light attenuation; P_{avg} , the average phosphate concentration; T_{avg} , the average water temperature; N_{avg} , the average nitrate concentration; C_{CV} , the coefficient of variation of conductivity.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

FIG. 5. Examples of annual species time relationships for years where species richness is (A) only lower than or (B) both lower and higher than expected for a given time interval based on the null model. Open circles indicate significant departures from the null distribution for each month interval, and the gray bars indicate 95% of the null distribution. (C) The proportion of years in the entire data set where there is a significant departure from the null distribution for each monthly interval. These lines are truncated at 1 and 12 month intervals because there is no variance generated by the null model randomization for these intervals.

the time period. For example, environmental variation might prolong beyond ecologically relevant timescales the deterministic outcomes of competitive exclusion, either by varying the density independent rates of mortality or the rank order of competitive abilities among community members. Alternatively, environmental variation can promote coexistence by allowing species to partition their use of resources through time, for example via storage effects (Chesson and Warner 1981, Hairston and Ellner 1996). On the other hand, environmental variability can create conditions that exceed the tolerances of species to persist in the environment (i.e., conditions exceed the fundamental niche requirements of species), leading to an erosion of diversity along with an increase in annual turnover (follow curves from top to bottom in: Fig. 1D). In Lake Zurich, it seems that environmental variation is having both direct and indirect effects on annual turnover, but more research is need to identify which aspects of environmental variation are important for understanding changes in the mechanisms of species coexistence in

phytoplankton communities (Mayfield and Levine 2010).

The environmental conditions of Lake Zurich have changed dramatically over the past three decades (Pomati et al. 2011), and this might partly explain the reversal in the relationship between phytoplankton

TABLE 2. Summary of model selection for the path analysis.

Model formulation and alternate hypotheses	Chi square	<i>P</i>	BIC
SEM without year (Fig. 4B)			
<i>H</i> ₁ : only indirect paths	201.7	<0.001	95.5
<i>H</i> ₂ : only direct paths	250.1	<0.001	47.1
<i>H</i> ₃ : direct and indirect paths	183.9	<0.001	106.3†
SEM with year (Fig. 4C)			
<i>H</i> ₁ : only indirect paths	237.1	<0.001	112.58
<i>H</i> ₂ : only direct paths	228.63	<0.001	117.52†
<i>H</i> ₃ : direct and indirect paths	228.63	<0.001	117.52†

Notes: The alternate hypotheses about the structural equation models (SEM) are indicated in Fig. 4A. BIC stands for Bayesian information criterion.

† Best supported model.

diversity and annual turnover. Lake Zurich has undergone a long period of re oligotrophication, such that levels of phosphorus (P) have fallen from around 80 to 20 $\mu\text{g P/L}$ concurrently with a significant decrease in annual P variability through time and an increase in variability over depth (Pomati et al. 2011). Over the same time period, mean water column temperature increased by about 0.5°C , but this warming has had only marginal effects on annual variability of temperature over the water column. Our pattern of high phytoplankton species richness at low phosphorus levels is opposite to the findings of two recent large scale spatial surveys of phytoplankton diversity, both of which found positive relationships between total phosphorus (TP) levels and species richness (Ptacnik et al. 2008, Stomp et al. 2011). However, our observations of negative associations between phosphorus levels and annual turnover are in agreement with the observation that lakes with higher phosphorus have greater rates of compositional turnover (Ptacnik et al. 2008). We need many more of such comparisons across studies in order to reach an integrated perspective on species time and species area relationships in phytoplankton communities (White et al. 2010, Scheiner et al. 2011).

Our results also indicate that annual turnover is directly influenced by long term changes in both the mean and variability of environmental conditions. A recent meta analysis of zooplankton reached a similar conclusion, namely that long term changes in both the average and variability of environmental conditions in lakes can influence levels of species richness (Shurin et al. 2010). Shurin and colleagues found that temperature variation promoted species richness, whereas chemical variability excluded species, implying that increasingly variable climatic conditions might have implications for biodiversity. In Lake Zurich, we found no evidence for effects of changing environmental variability on species richness, but did find a positive association between chemical variability (i.e., conductivity) and annual turnover. Changes in the variability of conductivity over the season could indicate changes in patterns of thermal stratification, or in how the lake is coupled with exchangeable cations in the surrounding catchment. It is still an open question how changes in the mean and variability of chemical and thermal conditions in lakes can affect biodiversity dynamics (Jeziorski et al. 2008, Shurin et al. 2010).

Community assembly: comparing observed to random sequences

The observed assembly sequences produced species time relationships that differed strongly from those generated from our randomized assembly sequences (Fig. 5, Appendix B). In studies of species area relationships such randomizations are analogous to generating "random landscapes" to compare with parameters from species area curves (Coleman 1981, Carey et al. 2006). Here we used two contrasting null

models to the detect the temporal scales over which the observed and random patterns of community assembly differed (Fig. 5). Comparing the observed STRs to STRs generated from different null models revealed a qualitatively similar pattern, namely that observed richness at small time intervals in the STR was significantly lower than expected (Fig. 5, Appendix B). This illustrates that the nonrandom patterns of species occurrences through time can affect the shape of the STR, as has been observed in other studies (White and Gilchrist 2007).

The deviations between the observed and randomized STRs notably increased when we used a null model that broke apart interspecific associations. Our simplest null model, that randomized the sampling dates within a year (e.g., Fig. 5), randomized annual phenology of different communities, but did not change the phenology of species' co occurrences. By comparison, randomizing species co occurrence patterns, along with some constraints (i.e., by using SIM 8), led to STRs with higher levels of species richness at low month intervals than in the observed STRs. This suggests that the shape of the observed STRs is strongly influenced by underlying processes that govern the nonrandom patterns of species occurrences. White and Gilchrist (2007) came to a similar conclusion by analyzing how contrasting null models of population level processes affect STRs of plants in the Chihuahuan Desert. In particular, they emphasize the intimate connections between STRs and levels of aggregation, autocorrelation, and interspecific association (White and Gilchrist 2007). We used a similar approach as White and Gilchrist (2007) to measure the level of autocorrelation, and found a negative relationship between annual turnover the proportion of the species in the community that show significant autocorrelation (Appendix C). This is an admittedly coarse way to link the rich variation of autocorrelation patterns among species with measures of annual turnover, but it does suggest a connection between the identity and phenology of species and the observed rates of annual turnover. We were unable to find a similar relationship between annual turnover and the extent of interspecific temporal aggregation within each year (measured by the V ratio), even though such aggregation was significant in nearly all of the sampling years (Appendix D).

There are numerous examples of nonrandom assembly sequences in ecological communities, including classical descriptions of seasonality (Sommer et al. 1986), directional species sorting in response to changing environmental conditions (Leibold et al. 1997), and cyclic assembly trajectories oscillating between multiple groups of species (Steiner and Leibold 2004). Such nonrandom assembly sequences would likely change the shape of STRs, and often increase the rate of species turnover relative to randomizations of the same assembly sequence. For example, observed z will typically be greater than expected z if changes in diversity through time are sustained for a long enough

period to be included in multiple time intervals of the STR. Slower than expected rates can also occur, for example, if there are multiple short bursts (e.g., 1–2 months) of high diversity throughout the year that are surrounded by periods of low species diversity. These patterns would lead to unexpectedly slow rates because they elevate the average species richness for multiple intervals in the randomized sequences, but affect fewer intervals in the observed sequence. In natural populations, such variation in the rate of species accumulation over the year could result from the temporal grain of environmental heterogeneity in lakes, as has been argued previously for species area relationship (McGlenn and Palmer 2011). Previous research on phytoplankton community assembly in lakes has described several phases of the year that are dominated by different functional groups of species (Sommer et al. 1986, Anneville et al. 2004). We propose that quantifying the rates of species turnover could reveal how time scales of community assembly differ among lakes with different phenologies and species assemblages (Pacnik et al. 2008).

Future directions

The diversity of phytoplankton communities in lakes has inspired some of the most fundamental questions about the maintenance of species diversity (Hutchinson 1961). Here, we have examined the relationship between diversity and turnover in a single community over decades of changing environmental conditions, and have revealed patterns that are complementary to previous large scale spatial surveys of plankton diversity (Shurin et al. 2007, Pacnik et al. 2008). Admittedly, however, such comparative studies (ours included) often use relatively coarse environmental metrics compared to the known complexities about how niche differentiation among phytoplankton species can influence coexistence (Tilman et al. 1982, Huisman et al. 1999, Stomp et al. 2004). Furthermore, we have little information about how diversity and turnover might change in response to long term trends in the size and composition of the regional species pool or in the rates of migration within metacommunities of lakes. Nevertheless, our analyses reveal strong associations between diversity, annual turnover and environmental change and identify temporal scales over which the observed community assembly differs from random patterns. These are two critical steps toward explaining how niche differences among species can explain the temporal and spatial patterns of community assembly of phytoplankton communities in lakes.

ACKNOWLEDGMENTS

We thank O. Koster and R. Forster (WVZ) for providing access to the data set and for insights into the analysis of phytoplankton taxonomy. F. Pomati was supported by Eawag action project Aquaprobe. The long term monitoring was financed by the Zurich Water Supply and the AWEL (Amt für Abfall, Wasser, Energie und Luft).

LITERATURE CITED

- Adler, P. B., and W. K. Lauenroth. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecology Letters* 6:749–756.
- Adler, P., E. White, W. Lauenroth, D. Kaufman, A. Rassweiler, and J. Rusak. 2005. Evidence for a general species time area relationship. *Ecology* 86:2032–2039.
- Agrawal, A. A., et al. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5:145–152.
- Allan, E., W. Weisser, A. Weigelt, C. Roscher, M. Fischer, and H. Hillebrand. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences USA* 108:17034–17039.
- Anneville, O., S. Souissi, S. Gammeter, and D. Straile. 2004. Seasonal and inter annual scales of variability in phytoplankton assemblages: comparison of phytoplankton dynamics in three peri alpine lakes over a period of 28 years. *Freshwater Biology* 49:98–115.
- Carey, S., J. Harte, and R. del Moral. 2006. Effect of community assembly and primary succession on the species area relationship in disturbed ecosystems. *Ecography* 29:866–872.
- Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia* 136:489–498.
- Chase, J., and M. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Chase, J., and J. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B* 366:2351–2363.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Chesson, P., and R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923–943.
- Coleman, B. 1981. On random placement and species area relations. *Mathematical Biosciences* 54:191–215.
- Davies, R. B. 1987. Hypothesis testing when a nuisance parameter is present only under the alternative. *Biometrika* 74:33–43.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Ernest, S. K. M., J. H. Brown, K. M. Thibault, E. P. White, and J. R. Goheen. 2008. Zero sum, the niche, and metacommunities: long term dynamics of community assembly. *American Naturalist* 172:E257–E269.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA* 100:8916–8920.
- Fox, J. 2002. *An R and S PLUS companion to applied regression*. Sage Publications, Thousand Oaks, California, USA.
- Fukami, T. 2004. Community assembly along a species pool gradient: implications for multiple scale patterns of species diversity. *Population Ecology* 46:137–147.
- Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* 40:393–414.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.
- Hairton, N., Jr., and S. Ellner. 1996. Overlapping generations: the storage effect and the maintenance of biotic diversity.

- Pages 109–145 in O. Rhodes, R. Chesser, and M. Smith, editors. Population dynamics in ecological space and time. The University of Chicago Press, Chicago, Illinois, USA.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hubbell, S. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Huisman, J., R. R. Jonker, C. Zonneveld, and F. J. Weissing. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology* 80:211–222.
- Hutchinson, G. 1961. The paradox of the plankton. *American Naturalist* 95:137–145.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
- Jezierski, A., et al. 2008. The widespread threat of calcium decline in fresh waters. *Science* 322:1374–1377.
- Jiang, L., and Z. Pu. 2009. Different effects of species diversity on temporal stability in singletrophic and multitrophic communities. *American Naturalist* 174:651–659.
- Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* 170:271–283.
- Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762–775.
- Leibold, M., J. Chase, J. Shurin, and A. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467–494.
- Levine, J. M., and J. HilleRisLambers. 2009. The importance of niches for the maintenance of species diversity. *Nature* 461:254–257.
- Losos, J., and R. Ricklefs, editors. 2010. The theory of island biogeography revisited. Princeton University Press, Princeton, New Jersey, USA.
- MacArthur, R. 1972. Geographical ecology. Princeton University Press, Princeton, New Jersey, USA.
- Magurran, A. E., S. R. Baillie, S. T. Buckland, J. M. Dick, D. A. Elston, E. M. Scott, R. I. Smith, P. J. Somerfield, and A. D. Watt. 2010. Long term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology and Evolution* 25:574–582.
- Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13:1085–1093.
- McCann, K. S. 2000. The diversity stability debate. *Nature* 405:228–233.
- McGlinn, D. J., and M. W. Palmer. 2011. Quantifying the influence of environmental texture on the rate of species turnover: evidence from two habitats. *Plant Ecology* 212:495–506.
- Pomati, F., B. Matthews, J. Jokela, A. Schildknecht, and B. W. Ibelings. 2011. Effects of re oligotrophication and climate warming on plankton richness and community stability in a deep mesotrophic lake. *Oikos*, *in press*.
- Preston, F. W. 1960. Time and space and the variation of species. *Ecology* 41:611.
- Ptácnik, R., A. G. Solimini, T. Andersen, T. Tamminen, P. Brettum, L. Lepisto, E. Willén, and S. Rekolainen. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proceedings of the National Academy of Sciences USA* 105:5134–5138.
- R Development Core Team. 2011. R version 2.13. R Project for Statistical Computing, Vienna, Austria. www.r-project.com
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167–171.
- Ricklefs, R., and D. Jenkins. 2011. Biogeography and ecology: towards the integration of two disciplines. *Philosophical Transactions of the Royal Society* 366:2438–2448.
- Rosenzweig, M. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Rosenzweig, M. 1998. Preston's ergodic conjecture: the accumulation of species in space and time. Pages 311–348 in M. McKinney and J. Drake, editors. Biodiversity dynamics: turnover of populations, taxa, and communities. Cambridge University Press, New York, New York, USA.
- Scheiner, S. M., A. Chiarucci, G. A. Fox, M. R. Helmus, D. J. McGlinn, and M. R. Willig. 2011. The underpinnings of the relationship of species richness with space and time. *Ecological Monographs* 81:195–213.
- Shipley, B. 2002. Cause and correlation in biology. A user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge, UK.
- Shurin, J. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086.
- Shurin, J. B. 2007. How is diversity related to species turnover through time? *Oikos* 116:957–965.
- Shurin, J. B., S. E. Arnett, H. Hillebrand, A. Longmuir, B. Pinel Alloul, M. Winder, and N. D. Yan. 2007. Diversity stability relationship varies with latitude in zooplankton. *Ecology Letters* 10:127–134.
- Shurin, J. B., M. Winder, R. Adrian, W. B. Keller, B. Matthews, A. M. Paterson, M. J. Paterson, B. Pinel Alloul, J. A. Rusak, and N. D. Yan. 2010. Environmental stability and lake zooplankton diversity contrasting effects of chemical and thermal variability. *Ecology Letters* 13:453–463.
- Sommer, U., Z. M. Gliwicz, W. Lampert, and A. Duncan. 1986. The PEG model of seasonal succession of planktonic event in fresh waters. *Archiv für Hydrobiologie* 106:433–471.
- Steiner, C. F., and M. A. Leibold. 2004. Cyclic assembly trajectories and scale dependent productivity diversity relationships. *Ecology* 85:107–113.
- Stomp, M., J. Huisman, F. De Jongh, A. J. Veraart, D. Gerla, M. Rijkeboer, B. W. Ibelings, U. I. A. Wollenzien, and L. J. Stal. 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature* 432:104–107.
- Stomp, M., J. Huisman, G. Mittelbach, E. Litchman, and C. Klausmeier. 2011. Large scale biodiversity patterns in freshwater phytoplankton. *Ecology* 92:2096–2107.
- Tilman, D., S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics* 13:349–372.
- Vasseur, D. A., U. Gaedke, and K. S. McCann. 2005. A seasonal alternation of coherent and compensatory dynamics occurs in phytoplankton. *Oikos* 110:507–514.
- White, E., P. Adler, W. Lauenroth, R. Gill, D. Greenberg, D. Kaufman, A. Rassweiler, J. Rusak, M. Smith, J. Steinbeck, R. Waide, and J. Yao. 2006. A comparison of the species time relationship across ecosystems and taxonomic groups. *Oikos* 1:185–195.
- White, E. P., S. K. M. Ernest, P. B. Adler, A. H. Hurlbert, and S. K. Lyons. 2010. Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society B* 365:3633–3643.
- White, E. P., and M. A. Gilchrist. 2007. Effects of population level aggregation, autocorrelation, and interspecific association on the species time relationship in two desert communities. *Evolutionary Ecology Research* 9:1329–1347.
- Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* 13:1–10.

SUPPLEMENTAL MATERIAL

Appendix A

Relationship between interannual turnover and monthly richness (*Ecological Archives* E093 229 A1).

Appendix B

Analysis of the deviation between the observed annual species time relationships and a null model (SIM 8) (*Ecological Archives* E093 229 A2).

Appendix C

Relationship between annual turnover and autocorrelation of species (*Ecological Archives* E093 229 A3).

Appendix D

Time series of the observed annual V ratio relative to a null model (SIM 8) (*Ecological Archives* E093 229 A4).