A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems

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Abstract. Recent meta-analyses have shown that beta diversity through space is jointly driven by species traits, geographical gradients, and ecosystem properties. Spatial variation is, however, only one aspect of beta diversity. The other component is variation in species assemblages through time, that is, temporal turnover. We examined the decrease of assemblage similarity in time in aquatic ecosystems in relation to several ecological, physical, and geographical factors using an extensive data set derived from the literature. The data set was first divided into intra-annual and interannual studies depending on the temporal extent of the studies. Sampling duration was one the most significant variables affecting the degree of temporal turnover, and we found that turnover was faster in studies with shorter temporal extent. Our results further suggested that the rate of temporal turnover increased with increasing ecosystem size, thus contradicting the general species–time–area relationship. Temporal turnover also varied among the ecosystem types: lake assemblages showed faster turnover than stream or marine assemblages in the interannual data set. We found that temporal turnover exhibited large-scale geographical variation, as there was a latitudinal gradient in turnover. Turnover was faster in the tropics in the intra-annual data set, but the pattern was reversed in the interannual data set, where turnover was faster at high latitudes. Finally, we found that the degree of temporal turnover was related to organism characteristics, as larger organisms with active mobility showed slower temporal turnover than smaller organisms. Our results suggest that the degree of species turnover in time is jointly driven by several ecological, physical, and geographical factors in aquatic ecosystems and that the turnover is not uniform across taxonomic groups. Our findings have important consequences for understanding how different biotic assemblages track temporal changes in the environment and how resilient assemblages are toward such changes.

Key words: beta diversity; latitudinal gradients; macroecology; sampling duration; species–time–area relationship; temporal variation.

INTRODUCTION

Recent meta-analyses have shown that beta diversity through space (i.e., variability in species composition) is driven by factors related to species functional traits, geographical gradients and ecosystem properties (Soininen et al. 2007a, b). Spatial variation in species assemblages is but one aspect of beta diversity. The second component is variation in assemblages through time—temporal beta diversity, i.e., temporal turnover. At least since MacArthur and Wilson’s (1963) seminal paper on the turnover of insular communities through time, studies examining temporal turnover have appeared regularly (for terrestrial ecosystems, see White 2004, Berg and Bengtsson 2007, Evans et al. 2007; for aquatic ecosystems, see Calijuri et al. 2002, Shurin et al. 2007, Wernberg and Goldberg 2008). Nonetheless, studies examining spatial turnover outnumber papers on temporal community patterns due largely to demand for long-term data, which are not easily available (Micheli et al. 1999). Studies on turnover in time do suggest, however, that the degree of temporal turnover probably varies systematically across organisms and ecosystems. The extent to which different ecological, physical or geographical factors (such as body size, trophic position, ecosystem type, or latitude) affect temporal turnover is still uncertain because a synthesis of the relative importance of these factors is lacking.

In the present analysis, we aim to synthesize the factors driving the rate of temporal turnover by analyzing vast amount of published and unpublished biological data from aquatic ecosystems. Like spatial variation in species composition, temporal turnover is likely to be driven by multiple factors allowing one to formulate specific hypotheses on patterns of temporal turnover. One of the most evident factors driving the variation in assemblage composition through time is temporal extent of the study, that is, how long a certain area is sampled. Preston (1960) suggested that there is a
species–time relationship (STR) equivalent to the species–area relationship (SAR), i.e., the longer an area is sampled, the more species are observed, but a decreasing rate with increasing temporal extent. Processes behind the STR (or equivalently, temporal turnover, sensu Adler et al. 2005) are still uncertain, but these can be classified into three major categories: sampling effect, ecological factors, and evolutionary factors (Preston 1960, Storch et al. 2007). The patterns at different timescales are usually dominated by one of these factors, therefore allowing one to separate different phases in the STR. At short timescales, the patterns in turnover are mostly driven by the sampling effect as ecological or (especially) evolutionary factors do not have enough time to shape the assemblage. At intermediate timescales, however, temporal turnover is shaped also by ecological processes, such as local colonization and local extinction that are driven by temporal variation in the environment or patterns of dispersal across sites. At long timescales, evolutionary processes such as speciation and extinction tend to dominate the increase in species richness in time (Preston 1960, Rosenzweig 1995). We emphasize that the sampling of most biological data covers intermediate timescales (from weeks to years) and therefore the variation in rate of turnover should be affected not only by sampling effect, but also by a number of ecological factors. Below, we will formulate a number of specific predictions how the rate of temporal turnover may vary across organisms and ecosystems.

First, we expect slower turnover with increasing sampling duration because new species are found more slowly with the increasing temporal extent of the study (Fig. 1a; Preston 1960, White 2004, Anderson 2007). The most abundant species are detected first, and as sampling continues, rare species will also be sampled. Second, we expect that the rate of turnover is related to ecosystem size. Adler and Lauenroth (2003) and Adler et al. (2005) provided evidence for a general species–time–area relationship (STAR) showing that the rate of temporal turnover decreases as the area increases, and vice versa. We thus propose that temporal turnover is negatively correlated with ecosystem size (Fig. 1b; Adler et al. 2005). Third, we expect that the degree of temporal turnover is driven by the ecosystem type. Marine ecosystems are expected to be much larger and physicochemically more stable than lakes or streams. According to the STAR, marine assemblages should have slower turnover than freshwater assemblages because of the larger ecosystem size (Fig. 1c). In addition, we expect that streams will show faster temporal turnover than lakes because of their fast changes in physicochemical conditions (Allan 2008).

Fourth, temporal turnover may also show large-scale geographical variation. Therefore, one of the most intriguing factors possibly affecting the rate of temporal turnover is latitude. As low latitudes are characterized by high energy input directly affecting the organisms' rate of life cycle (reviewed by Brown et al. 2004), we expect faster temporal turnover in tropics (Fig. 1d). This negative latitudinal cline in turnover was documented by Shurin et al. (2007) who found that temporal turnover was slower at high latitudes in zooplankton communities. On the other hand, high latitudes are usually characterized by strong seasonality, which may lead to faster temporal turnover toward poles especially at the short timescales (e.g., Wolda 1988) Thus, we set an alternative hypothesis and expect that low latitudes can have slower turnover than high latitudes in data sets with a smaller temporal extent because high latitudes are characterized by larger seasonal changes in the environment (Fig. 1d). This alternative prediction is supported by at least two recent studies. White et al. (2006) suggested that communities in tropics have high stability possibly because of their high diversity (but see Tilman et al. 2006). Furthermore, British birds had slower temporal turnover in high-energy areas than in low-energy areas (Evans et al. 2007).

Fifth, temporal turnover can also be related to organisms’ intrinsic properties and can thus be driven by the organisms themselves. In contrast with the larger organisms, microbial eukaryotes (e.g., protozoa and microalgae) and prokaryotes have extremely high cell densities and small body size (Finlay 2002). We suggest that the temporal turnover and body size may be linked by at least two processes. First, the rate of life cycle is directly linked to body size through metabolic constraints (Brown et al. 2004). Second, small organisms probably show fast fluctuations in population dynamics as they have large species pools from where local sites can be rapidly colonized (Finlay 2002) thus exhibiting fast turnover. Therefore, we predict that larger organisms exhibit slower temporal turnover than smaller organisms (Fig. 1e). Finally, Schoener (1983) suggested that organisms at low trophic position have greater turnover rates than organisms at higher trophic levels. Thus, we expect that temporal turnover will decrease with increasing trophic position (Fig. 1f).

In aquatic ecosystems, relatively large number of studies have been conducted to examine, e.g., the temporal turnover of fish (Moyle and Vondracek 1985, Barletta-Bergan et al. 2002), benthic macroinvertebrates (Townsend et al. 1987, Weatherley and Ormerod 1990, Scarsbrook 2002), zooplankton (Arora and Mehra 2003, Retting et al. 2006), algae (Foster et al. 2003, Soininen and Eloranta 2004, Wernberg and Goldberg 2008), or bacterioplankton (Yannarell et al. 2003, Shade et al. 2008). Here, we conducted an analysis of temporal turnover in aquatic ecosystems. We aimed at building a model that explains the largest possible amount of variation in the temporal turnover and test the specific predictions above. These data cover broad variation in species’ major characteristics such as body sizes or trophic positions, range from small streams to oceans, and encompass geographical areas from tropics to near polar. Analysis of these data should therefore provide an
extensive meta-review of beta diversity through time and helps us to conceptually unite turnover in space and time.

**MATERIAL AND METHODS**

**Data**

The data comprised studies that report the raw data (i.e., species composition and abundances in tables or figures) on how species assemblages change through time. We searched the data from ISI Web of Science (1980–2007). Search strings were “seasonal succession,” “temporal turnover,” “persistence,” “seasonal dynamics,” “temporal variation,” and “long-term dynamics.” More recent papers were included if present, and papers were also derived from bibliographies of the papers that were screened. We also included some unpublished results in the analysis. In total, we scanned through ~2500 papers of which we chose 99 papers or unpublished studies concerning aquatic assemblages into closer examination. From these, we obtained 383 distance decay relationships in time, that is, relationships that describe how assemblage similarity decreases with time (for equivalent relationships in space, see Soininen et al. 2007b). For a detailed list of studies included, see the Appendix.

The relationships were classified with respect to four continuous variables (organism body size, latitude of the center of a study area, ecosystem size, and sampling duration), and four categorical variables (organisms’ trophic position, dispersal type, habitat, and type of water body). We used only studies which report community data at the species or generic levels. Taxonomic resolution did not affect the rate of turnover across the data sets (t test, $P = 0.07$).

We first divided papers into intra-annual (<365 days) and interannual (≥365 days) studies. In few cases, long-term sampling of organisms that are primarily annual was interrupted by winters at high latitudes. For example, in long-term phytoplankton studies at high latitudes, samplings occurred typically only during summers. In these cases, data were treated as separate intra-annual studies. For details of each data set, see the original publications (Appendix).

Organism body size was approximated as log-transformed wet mass (g), and derived for each organism group from Peters (1983). We acknowledge that some of the assemblages are characterized by large ranges of body sizes. However, we emphasize that while the range within groups may be large (up to five orders of magnitude), it is very small compared with the overall size range across organism groups (over 13 orders of magnitude). For more details on body size approximations and ecological classifications, see Hillebrand (2004) and Drakare et al. (2006). Latitude was scored from 0 to 90, with no distinction between the northern and southern hemisphere. Ecosystem sizes for marine studies were drawn from the papers or calculated using the areas of the whole ecosystem (e.g., North Atlantic). Lake and pond sizes were derived from original papers or by calculating areas using maps of the original studies. Based on details (e.g., areas of the sampling sites, stream orders) given in each paper, we classified streams into two categories, small (0.1 ha) and large ones (1 ha). We had to rely on this arguably coarse classification for streams because more detailed ecosys-

![Diagram](image_url)

**Fig. 1.** A conceptual figure outlining the predicted changes in slope of the linear regression across (a) sampling duration, (b) ecosystem size, (c) type of water body, (d) latitude, (e) organism body size, and (f) trophic position in a food web. The values of the slopes are negative. When the slope approaches zero, turnover slows down. Specific predictions are: (a) turnover slows down with increasing sampling duration of the study, (b) turnover slows down with increasing ecosystem size, (c) rate of turnover varies significantly among the different types of water bodies, and turnover is slowest in marine ecosystems, (d) rate of turnover decreases or increases with latitude, (e) turnover slows down with increasing organism body size, and (f) turnover is faster at lower trophic positions in a food web.
In comparison with many other metrics suggested to be immune to richness gradients (J. Oksanen, unpublished data). Third, there was no significant relationship between slope and species richness of the community ($r = 0.07, P = ns$ [not significant]) and therefore richness gradients do not drive the patterns in species turnover in the present study.

We used general linear model (GLM) with the selection of the best model to unite the effects of categorical and continuous variables on temporal turnover. We performed GLM for intra-annual ($n = 280$ studies) and interannual studies ($n = 103$ studies) separately. The most parsimonious models were identified using Akaike's information criterion (AIC; Burnham and Anderson 1998). We checked possible intercorrelations between the continuous variables and found that log sampling duration and log ecosystem size were positively correlated ($r = 0.33, P < 0.01$). There was also a positive correlation between latitude and log ecosystem size ($r = 0.33, P < 0.01$) as well as between log sampling duration and body size ($r = 0.20, P < 0.01$). The other continuous variables did not show strong intercorrelations, ($r < 0.20$ for all relationships). The general linear model was conducted using the R package (available online).4

### Results

#### Intra-annual studies

The most parsimonious model for the intra-annual data included two categorical variables (habitat and type of water body) and three continuous variables (log sampling duration, latitude, and log ecosystem size). These five variables jointly explained 59.0% of the variability in temporal turnover (Table 1). The average slope for the intra-annual studies was $-1.02 \pm 0.009$ (mean $\pm$ SE). This means that the whole assemblage turns over within a year.

The sampling duration was strongly positively correlated with the slope, as we predicted (Table 2, Fig. 3). Thus, when the sampling duration increases, temporal sizes were not always given. Ecosystem sizes (in hectares) were log-transformed. Some of the studies provided species abundances only as figures. In these cases, we used the digitizing software GrabIt (Datatrend Software, Raleigh, North Carolina, USA).

Temporal duration of the analysis was measured in days and was log-transformed. The habitat was divided into nekton, plankton, or benthos. Although we lacked a specific hypothesis on how temporal turnover would vary across the different dispersal types, we were interested in this aspect because dispersal rate is a vital species trait and a strong determinant for spatial turnover (Soininen et al. 2007a, b). We thus classified organism’s ability to disperse into four categories: mobile (e.g., fish), pelagic larvae (e.g., corals), spores (e.g., macroalgae), and passive (e.g., microalgae). Finally, the type of water body was divided into streams, lakes, and marine ecosystems.

### Analysis

A useful method to study temporal turnover is to examine how the assemblage similarity changes in time (Collins et al. 2000). We calculated the relationship between assemblage similarity (as Sorensen index) and distance in time from each pair of observations. We regressed assemblage similarity and temporal distance and obtained the slope of the linear regression as an indicator for the rate of temporal turnover. Slope was measured as a decrease in assemblage similarity per year. Steeper (i.e., more negative) slopes indicate faster temporal turnover, whereas a slope = 0 indicates no turnover in time. Although the pairwise comparison of data points inflates $N$, the estimate of the slope is not inflated.

We acknowledge that the changes in assemblage similarity in time are not necessarily linear. This is especially true for intra-annual data sets where similarities may include a seasonal signal (Fig. 2). For example, phytoplankton assemblages (see Plate 1) in spring and autumn may share more species with each other than assemblages in spring and summer. In these cases, distance decay in time may show a nonlinear pattern (Fig. 2). Therefore we examined if intra-annual data sets showed strong nonlinearity using regression modeling with Akaike's information criteria (Burnham and Anderson 1998; AIC). However, all models suggested that intra-annual data sets were best related to linear models showing no significant seasonal signal. All of the interannual data sets also showed linear patterns.

As a similarity metric, we used the Sorensen coefficient for a number of reasons. First, Sorensen is one of the most common similarity metrics in ecological literature (Magurran 2004) and facilitates comparison with many, if not most, of the papers examining species turnover in space and time. Second, although we acknowledge that Sorensen is known to be affected by species richness gradients and not only changes in species composition (Chao et al. 2005), it performs well
turnover slows down (less negative slope). Latitude also showed a positive relationship with the slope implying that the turnover was faster in tropics than in assemblages at high latitudes (Table 2, Fig. 3). Moreover, our results suggest that temporal turnover was faster in benthos than in plankton.

The most parsimonious model also incorporated log ecosystem size and type of water body, but these variables did not show significant relationship with the slope (Table 2). Due to intercorrelations between ecosystem size and other continuous variables, we also tested for whether the ecosystem size and rate of turnover would be related within a single organism group. We tested the relationship by using only the phytoplankton studies given that phytoplankton was the best-presented single organism group in both of the data sets. However, there was no significant relationship between the log ecosystem size and slope ($r = 0.002$, $P = 0.86$).

### Interannual studies

The most parsimonious model for the interannual studies included four categorical variables (dispersal type, trophic position, habitat, and type of water body) and four continuous variables (log sampling duration, log body size, latitude, and log ecosystem size). These variables jointly explained 75.2% of the variability in temporal turnover (Table 1). Mean slope of the interannual data set was $-0.095 \pm 0.10$ and it was significantly smaller than in the intra-annual data set ($t = ...$)
9.13, $P < 0.001$). The average slope means that 9.5% of the assemblage turns over between years.

Sampling duration showed a positive relationship with the slope, as we predicted. Thus, temporal turnover decreased with the increasing sampling duration. Contrary to what was predicted, ecosystem size showed a negative relationship with the slope implying that turnover was faster in larger ecosystems (Table 2, Fig. 4).

The degree of turnover also varied consistently across water bodies (Table 2, Fig. 4). Lake ecosystems showed the fastest turnover, and marine and lotic assemblages showed much slower average rates of temporal turnover. The long-term turnover also showed large-scale geographical variation as latitude was negatively related to slope suggesting faster temporal turnover toward the poles.

Moreover, we found that the interannual turnover was also related to organisms’ characteristics. Organisms’ body size showed a positive relationship with the slope, as we predicted, indicating that larger organisms have slower temporal turnover. Temporal turnover was also related to organism’s dispersal as it varied significantly between dispersal types. Mobile organisms and organisms with pelagic larvae had the slowest temporal turnover. Passively dispersing organisms and organisms dispersing by spores had the fastest turnover. The most parsimonious model also included trophic position and habitat, but these factors did not show significant relationship with the slope (Table 2).

**DISCUSSION**

Our analysis showed that beta diversity in time is strongly related to several ecological, physical, and
geographical variables. This implies that temporal turnover is simultaneously driven by the variety of factors at least in aquatic ecosystems. We also emphasize that the degree of temporal turnover is not uniform across organisms and ecosystems (see White et al. 2006), but rather shows systematic variation. Our results are thus in line with the findings of recent meta-analyses examining the variation in assemblage composition and diversity in space (e.g., Hillebrand 2004, Drakare et al. 2006, Soininen et al. 2007a, b) and suggest that just as in space, ecological patterns may also vary predictably through time.

Sampling duration was one of the most significant variables affecting the temporal turnover in both data sets, as we expected. Overall, slopes were much steeper for the intra-annual data set compared to interannual
data set. This means that the difference between winter and summer, for example, is stronger than the average difference between years. Generally, this shows that turnover slows down with the increasing sampling duration because new species are found more slowly with the increasing sampling time, as predicted by STR (Preston 1960, White 2004). At first glance one may envisage that the strong effect of the sampling duration is merely related to the fact that small organisms are sampled on shorter temporal extents, that is, sampling duration covaries with the body size of the organisms. We found indeed that the sampling duration and body size were significantly positively correlated in our data sets ($r = 0.20, P < 0.01$). However, the pure sampling effect also affects the turnover since an analysis conducted exclusively on phytoplankton data revealed that almost 30% of the variation in turnover can be explained by the sampling duration ($r = 0.54, P < 0.001$).

Of the other factors considered, ecosystem size affected temporal turnover in the interannual studies. Unexpectedly, we found that the temporal turnover was faster in larger ecosystems. These data did not therefore support the general species–time–area relationship (Adler et al. 2005). Our finding may at least partly result because major part of the stream data sets that represented the smallest ecosystems consisted of fish and zoobenthos that tend to turn over relatively slowly. Environment in general may also play a crucial role in affecting the turnover rates, and much of the unexplained variation in turnover can most plausibly be related to unknown temporal variation in environment. In fact, the lack of data on environmental heterogeneity through time represents a possible caveat for our study in general, as species’ occurrences are affected by the fluctuating environmental conditions. Although we lacked specific information on temporal variation in key environmental variables in different ecosystems, we could partition part of this variance by splitting the data into three classes based on ecosystem type expected to affect the degree of turnover in time. We predicted that marine ecosystems would have slower turnover than lakes or streams because of the physicochemical stability and shorter environmental gradients in the oceans. In fact, we found that turnover varied consistently across ecosystems as lakes showed faster turnover than running waters or oceans. Contradictory to what was initially predicted, however, it seems that the marine assemblages do not turn over as slowly as we predicted. This finding resembles the results by Soininen et al. (2007) who found that the patterns in spatial beta diversity in marine ecosystems are not remarkably weaker than the patterns in freshwater ecosystems as originally suggested by Clarke (1992).

Besides varying across ecosystems, temporal turnover exhibited large-scale geographical variation as latitude was included in the most parsimonious model for both data sets. We found that turnover was faster in tropics for the intra-annual data set. However, this pattern was reversed in the long-term data set where turnover was faster at high latitudes. Both of these outcomes are somewhat unexpected, but they show surprising similarity to the paper by Soininen et al. (2007b), which documented strikingly similar scale dependency in
latitudinal gradient of spatial turnover. First, the finding that turnover was faster in tropics at short timescales is probably because of higher energy input in low latitudes. Energy input affects organisms’ rate of life cycle, which is in turn directly linked to organisms’ generation times and longevity (Brown et al. 2004). In addition, low latitudes are typically characterized by higher species diversity, which may have a destabilizing effect on population stability (Tilman et al. 2006). In the present data, however, temporal turnover was not affected by species richness gradients as we did not find any correlation between species richness and latitude (r = 0.07, P = ns) and between species richness and slope of the turnover (r = 0.07, P = ns). Second, the finding that the turnover was faster at high latitudes at long timescales concurs, for example, with Evans et al. (2007) who found that birds at low latitudes have slower temporal turnover compared with their northern counterparts. White et al. (2006) also suggested that the more species rich assemblages in tropics, for example, have slower rate of temporal turnover due to low environmental heterogeneity. In fact, it may well be that year to year variation is large in a seasonal environment (Berg and Bengtsson 2007). Put together, we found that the latitudinal gradient in temporal turnover is scale dependent: turnover is faster in tropics at short timescales but slower at long timescales. The mechanisms behind this remain speculative at present but we suggest that these outcomes result because of the interplay between energy input and temporal variation in environment.

The long-term turnover was not only driven by ecosystem properties or geographical gradients, but was also related to organism characteristics. We found that the body size was positively correlated with the slope, i.e., large organisms had slower long-term temporal turnover than the small organisms. We suggest that this is because of two major reasons. First, microscopic organisms may be widely or some even globally dispersed due to their high abundances and efficient dispersal (Finlay 2002). Therefore, the local assemblage compositions of small organisms may change fast as species pools contain huge number of potential colonist species. Second, the negative relationship between the body size and slope can be due to the direct linkage between organisms’ size and rate of life cycle suggested by the metabolic theory (reviewed by Brown et al. 2004). The strong influence of body size was also reflected in patterns of turnover among the different dispersal types as smaller organisms that are typically passive had faster turnover than larger, mobile organisms.

Bearing in mind the vast heterogeneity of our data, we could explain a surprisingly high percent of the variation in temporal turnover using only a few key variables described above. For example, Soininen et al. (2007b) found that the comparable model for the halving distance reflecting spatial turnover explained only 37.6% of the variance. Considering that we could explain a higher percentage of the variation at the longer timescales, we suggest that the longer sampling durations are essential for the understanding of the underlying mechanisms driving temporal turnover in ecosystems.

In conclusion, we showed that beta diversity in time is simultaneously governed by ecological, physical, and geographical variables. First, turnover decreased substantially with the increasing temporal extent of the study. Second, we found that turnover was faster in larger ecosystems. Our results also suggested that the long-term temporal turnover is faster at high latitudes perhaps implying larger long-term variation in environment toward the poles. On the contrary, short-term temporal turnover was slower at high latitudes possibly because of higher energy input in the tropics. Finally, turnover was faster for small-sized and passive organisms than for the large and mobile organisms. We acknowledge that our data only comprised aquatic organisms and encourage researchers to test the generality of our findings also in terrestrial ecosystems. Nonetheless, we feel that these results have important consequences for understanding how different biotic assemblages track temporal changes in the environment and how resilient assemblages are toward such changes. We emphasize that examining not only spatial beta-diversity, but also temporal beta diversity is highly important because predicted broad-scale environmental changes in the future are expected to cause tremendous shifts not only in spatial species distribution but also in assemblage turnover in time (see, e.g., Schiel et al. 2004).

Acknowledgments

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Literature Cited


APPENDIX

A list of the studies included in our analysis (Ecological Archives E091-037-A1).