

# The Effects of Temporal Resolution on Species Turnover and on Testing Metacommunity Models

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**ABSTRACT:** Patterns of low temporal turnover in species composition found within paleoecological time series contrast with the high turnover predicted by neutral metacommunity models and thus have been used to support nonneutral models. However, these predictions assume temporal resolution on the scale of a season or year, whereas individual fossil assemblages are typically time averaged to decadal or centennial timescales. We simulate the effects of time averaging by building time-averaged assemblages from local dispersal-limited, nonaveraged assemblages and compare the predicted turnover with observed patterns in mollusk and ostracod fossil records. Time averaging substantially reduces temporal turnover such that neutral predictions converge with those of trade-off and density-dependent models, and it tends to decrease species dominance and increase the proportion of rare species. Observed turnover rates are comparable to an appropriately scaled neutral model: patterns of high community stability can be produced or reinforced by time averaging alone. The community attributes of local time-averaged assemblages approach those of the metacommunity. Time-averaged assemblages are thus unlikely to capture attributes arising from processes operating at small spatial scales, but they should do well at capturing the turnover and diversity of metacommunities and thus will be a valuable basis for analyzing the large-scale processes that determine metacommunity evolution.

**Keywords:** temporal scale, time averaging, community turnover, metacommunity, species abundance distribution.

## Introduction

A metacommunity is a set of semi-isolated local assemblages that are either linked to other local assemblages by dispersal or surrounded by a large, panmictic species pool that acts as a source of immigrants (Wilson 1992; Leibold et al. 2004; Volkov et al. 2007). By incorporating dispersal into community processes and by distinguishing processes that operate at small (local interactions), intermediate (dis-

persal), and large (speciation-extinction) spatial scales, a wide range of metacommunity models has been developed to test and rank the effects of dispersal and niche limitation, density dependence, and equality in species per capita birth, death, and immigration rates on the assembly of local communities. For example, different metacommunity models predict different degrees of temporal constancy in species composition over ecological and evolutionary timescales (Hubbell 2001; Adler 2004; Holt and Gomulkiewicz 2004; Holyoak et al. 2005; Loeuille and Leibold 2008). However, few empirical data exist on species composition in living communities over the temporal scales appropriate for testing such predictions; monitoring programs rarely exceed a few decades.

Paleoecological time series commonly have the requisite centennial-, millennial-, and longer-scale durations (e.g., Pandolfi 1996; Cronin and Raymo 1997; Cronin et al. 1999; Clark and McLachlan 2003; Jernvall and Fortelius 2004; Hunt et al. 2005; Willis et al. 2007). However, with some exceptions of instantaneously buried remains (such as the annual laminae of some ponds), species abundances in individual fossil assemblages are time averaged to some degree: rates of population turnover typically exceed rates of net sediment accumulation, so that the skeletal remains of multiple noncontemporaneous generations can become mixed into a single fossil assemblage (on the seafloor, lake floor, streambed, or land surface) before they become permanently buried (Johnson 1972; Behrensmeier 1982; Fürsich and Aberhan 1990; Kidwell and Flessa 1995; Kowalewski 1996; Kowalewski and Bambach 2003; Lyman 2003). Radiocarbon and other dating of shells and bones from death assemblages accumulating in the surficial sediments of present-day environments indicate that skeletal remains largely reflect input from the most recent few decades but also include specimens from recent centuries and even millennia (e.g., Powell et al. 1989; Flessa and Kowalewski 1994; Martin et al. 1996; Meldahl et al. 1997; Carroll et al. 2003; Kidwell et al. 2005; Edinger et al. 2007; Terry 2008; Kosnik et al. 2009; Western and Behrensmeier

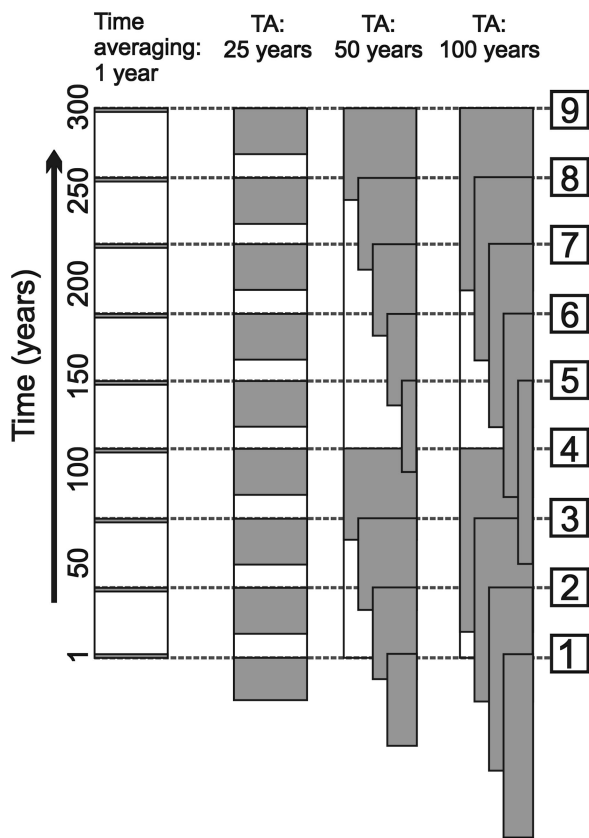
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2009). Time averaging is associated with change in three components of temporal scale, specifically (1) a decrease (coarsening) in temporal resolution, (2) an effective decrease in the temporal separation between sampling events (Russell 1998; McKinney and Frederick 1999), and (3) an increase in the temporal extent of the study (i.e., the temporal duration spanned by all sampled assemblages; fig. 1). Once time averaging per assemblage equals the separation of sampling events, the temporal separation between individual assemblages becomes 0. With a further increase in time averaging, two consecutive fossil assemblages will include some individuals that are drawn from the same pool of co-occurring living individuals. Such overlap commonly arises in natural settings because of vertical mixing of sediments over centimeter to decimeter scales by bioturbating animals and physical reworking.

The temporal dynamics apparent in a series of time-averaged assemblages may thus differ from the temporal dynamics of living (nonaveraged) assemblages because (1) community attributes such as richness or between-sample variation in composition tend to change with increasingly long windows of observation (Levin 1992) and (2) different processes act at small (population dynamics), intermediate (range limit dynamics), and large (speciation-extinction dynamics) temporal scales (Valentine and Jablonski 1993; Jablonski and Sepkoski 1996; Roy et al. 1996; Holt 2003; Harte et al. 2005; Urban and Skelly 2006; Borda-de-Água et al. 2007; Urban et al. 2008).

Analyses of paleontological time series have led to two empirical patterns that provide insights into the temporal dynamics of communities. First, temporal variation in species composition in time-averaged coral, pollen grain, and small-mammal fossil assemblages is lower than that predicted by neutral metacommunity or random-assembly models (Pandolfi 1996; Clark and McLachlan 2003; McGill et al. 2005). These findings of high community persistence indicate that trade-offs, density dependence, and niche assembly can play important roles in community dynamics at small spatial scales over long periods of time (e.g., Hubbell 2001; Chave et al. 2002; Chase et al. 2005). Some fossil communities also show unusual degrees of temporal constancy in species composition (e.g., Brett et al. 1996; Olszewski and Patzkowsky 2001; DiMichele et al. 2004; Ivany et al. 2009).

Second, temporal variation in species composition among living communities in some cases exceeds the temporal variation observed among fossil communities. For example, living coral communities exhibit high temporal variation over several decades (Tanner et al. 1994; Connell et al. 1997, 2004), whereas Pleistocene and Holocene coral reef communities are characterized by relatively constant species composition over several thousands of years (Jackson 1992; Pandolfi 1996, 2002; Pandolfi and Jackson 2001,



**Figure 1:** Time averaging (TA) is associated with change in three components of temporal scale: (1) a decrease (coarsening) in temporal resolution per sample (here, a series of nine numbered sampling events from Copano Bay; gray intervals correspond to the intervals of time encompassed by sampled assemblages), (2) an effective decrease in the temporal distance (separation) between sampling events (white intervals of time between dashed lines), and (3) an increase in the total temporal extent of the study (i.e., the duration spanned by all sampled assemblages). Once time averaging exceeds the separation of sampling events (here illustrated by 50 years of time averaging), consecutive fossil assemblages can include individuals drawn from overlapping (homogenized, nonunique) pools of dead individuals.

2006; Aronson et al. 2002, 2004, 2005). This difference is surprising, given that temporal variation in species composition increases in present-day communities as the duration of the time series increases (Lawton 1988; Pimm and Redfearn 1988; Halley 1996; Bengtsson et al. 1997; Cyr 1997). Such differences are thus thought to reflect unprecedentedly higher climatic and oceanographic variation in present-day systems related to anthropogenic disturbances (Pandolfi 2002).

The patterns of temporal species turnover observed in fossil assemblages have been tested with various types of null models. However, none of the models were scaled up

to temporal scales that correspond to the lower temporal resolution and/or smaller intersample distances that exist among multiple time-averaged fossil assemblages. Instead, null-model predictions for temporal variation in species composition are usually scaled to yearly scales that correspond to the dynamics expected for time series of non-averaged assemblages. This lack of scaling is notable because differences in temporal scale have significant effects on temporal species turnover rates (Rosenzweig 1998; Fridley et al. 2006; White et al. 2006; White 2007; McGlenn and Palmer 2009) and pooling of consecutive nonaveraged assemblages can modify several community attributes (McGill 2003; Green and Plotkin 2007; Šizling et al. 2009). Similarly, just as assemblages assessed at a low (coarse) spatial resolution are expected to exhibit less variation in composition among assemblages than those assessed at a higher (finer) spatial resolution (Wiens 1989; Gaston et al. 2007), low temporal resolution can cause averaged assemblages to be less temporally variable than nonaveraged assemblages (Gardner 1998). Several paleoecological studies have identified this likely reduction in variation among time-averaged assemblages (Peterson 1977; Kowalewski et al. 1998; Olszewski 1999; Martin et al. 2002), and we have found that time-averaged molluscan death assemblages sieved from seafloor samples are significantly less spatially variable than co-occurring living assemblages (Tomašových and Kidwell 2009).

Therefore, an increase (coarsening) in temporal scale with time averaging is expected to reduce variation in species composition, biasing the outcomes of model selection toward nonneutral models and forcing time-averaged assemblages toward high community stability. The magnitude by which temporal variation is reduced and the consequences of such averaging for distinguishing different metacommunity models in paleoecological time series remain unexplored. Here, we (1) quantify the magnitude of time-averaging effects on temporal variation in species composition and abundance structure on yearly to decadal scales, (2) compare the variation in species composition observed in paleontological time series of time-averaged mollusk and ostracod assemblages with the variation predicted by neutral and nonneutral models, and (3) evaluate the effects of time averaging on our ability to distinguish metacommunity models that differ in predictions of turnover at yearly scales.

## Methods

### Data Sets

To model the effects of time averaging on temporal turnover with time-homogeneous models, estimates are needed for (1) the local-community size and dispersal lim-

itation that characterize nonaveraged living assemblages and (2) the magnitude of time averaging and the temporal extent of the counterpart paleontological time series. Such conditions can be met where (1) fossil assemblages are sampled from sediment cores taken in the same habitat where living assemblages have been sampled and (2) the temporal resolution and extent of the time series are constrained by estimates of sediment age. We use two data sets that fulfill such criteria. We analyze one mollusk data set and one ostracod data set, both of which consist of surface living assemblages and multiple subsurface fossil assemblages sampled at comparable spatial scales (several dm<sup>2</sup> to 1 m<sup>2</sup>). Mollusk assemblages were sampled in muddy sands at a 1-m water depth in Copano Bay, Texas (Powell and Stanton 1995; <http://hdl.handle.net/10255/dryad.1177>). Ostracod assemblages were sampled at a 10-m water depth in Lake Tanganyika, Tanzania (Alin and Cohen 2004).

Living mollusk assemblages of Copano Bay were sampled 14 times at 6-week intervals in 1981–1982 by sieving living individuals from the uppermost 20 cm of sediment in the habitat (Staff et al. 1985, 1986; Cummins et al. 1986a, 1986b). Fossil mollusk assemblages were extracted by sieving nine ~6–14-cm-thick sedimentary increments from a 77-cm-long core taken in the same area sampled for living assemblages (core 1 in Powell and Stanton 1995, 1996). The mean size of living assemblages is 30 individuals, and that of fossil assemblages is 1,350 individuals (table 1). Sedimentation rates of approximately 30 cm per 100 years indicate that this core corresponds to ~300 years of deposition (Shepard and Moore 1960; Powell et al. 1989). In additional cores sampled in the same region, (1) nonrandom, centimeter-scale variations in species abundances and body size demonstrate that mollusk assemblages are not affected by large-scale temporal homogenization (Powell et al. 1992), and (2) a significant correlation between relative shell age (based on concentrations of amino acids) and depth also indicates that stratigraphic order is not disturbed by sediment mixing and bioturbation (Powell et al. 1989). The estimated temporal resolution for the infaunal bivalve *Rangia cuneata* in fossil assemblages is about 20 years when concentrations of amino acids are age calibrated with museum specimens (Powell et al. 1989), and applying the sedimentation rate suggests a minimum of 23–55 years per increment, depending on its thickness. Temporal resolution on the order of 20–50 years also accounts for Powell et al.'s (1989) observation that epifaunal and infaunal species co-occurring in one depth layer can differ in postmortem age by several decades because some infaunal species burrow to depths of several decimeters.

Living ostracod assemblages were sampled monthly by sieving living individuals from the uppermost 1 cm of

**Table 1:** Metacommunity characteristics for the molluscan (Copano Bay) and ostracod (Lake Tanganyika) data sets

Data set, assemblages	Water depth (m)	Mean sample size ( $J$ )	Dispersal number ( $I$ )	Migration rate ( $m$ )	Biodiversity number ( $\theta$ )	Log likelihood
Copano Bay:						
Living assemblages	1	30	18.0	.382	6.1	-163.05
Fossil assemblages, core 1	1	1,251	306.1	.197	15.4	-1,275.48
Fossil assemblages, core 2	1	626	117.6	.158	12.5	-1,040.22
Lake Tanganyika:						
Living assemblages, site 7	10	159	26.7	.145	8.4	-472.374
Living assemblages, site 3	5	190	17.3	.084	11.4	-622.062
Fossil assemblages, core MWA-1	10	511	755.5	.597	11.4	-890.15
Fossil assemblages, core MWA-2	5	506	395.0	.439	11.0	-779.73

Note: Metacommunity parameters  $I$  (dispersal number) and  $\theta$  (fundamental biodiversity number) used in simulations were estimated with the living (nonaveraged) assemblages of Copano Bay and Lake Tanganyika (site 7). Sample sizes for simulations of death assemblages were estimated from Copano Bay core 1 and Lake Tanganyika core MWA-1. For comparison, estimates of metacommunity characteristics are also shown for the two other cores sampled in Copano Bay and Lake Tanganyika. Maximum likelihood estimates of  $\theta$  and  $I$  are based on the neutral sampling formula of Etienne (2007) for multiple samples of living assemblages in Copano Bay and Lake Tanganyika.

sediment during autumn 1997 and winter 1998 and once in July 1999 (10 sampling events, site 7, at a 10-m water depth; Alin and Cohen 2004). Fossil ostracod assemblages were derived from successive 1-cm-thick increments through a 9-cm-long interval of core MWA-1 at a 10-m water depth (Alin and Cohen 2004). All live-collected individuals (mean sample size = 200) and 500 individuals from each fossil assemblage were counted by Alin and Cohen (2004). Radiocarbon dates indicate that the core reflects 25–30 years of sediment accumulation. The minimum estimate of the temporal resolution of each fossil assemblage is thus approximately 2.5–3 years. The core is divisible into three zones that differ in organic content and grain size (Alin and Cohen 2004), and maximum bioturbation depths in Lake Tanganyika are 2–5 cm (Cohen 2000), indicating that upper bounds for estimates of the temporal resolution are about 10 years. We use 5–10 years as an estimate of temporal resolution per sample.

#### *Metacommunity Dynamics*

To evaluate the effects of time averaging, we use simulations because (1) mixing of noncontemporaneous generations violates the use of genealogical approaches that trace all individuals back to their immigrating ancestors (Etienne and Olff 2004a) and (2) species abundances in fossil assemblages are a product of species standing abundance and turnover rate. With simulations, we can incorporate additional complexity caused by the effects of reduced temporal resolution and reduced temporal separation among assemblages and also track changes in the abundance of dead individuals. We use a spatially implicit, individual-based model to simulate the dynamics of time-averaged assemblages in homogeneous habitats at two scales: the regional frozen metacommunity pool that is

determined by extinction-speciation processes at large spatial scales and the local dispersal-limited community that is determined by vital (birth, death, and immigration) rates acting at small spatial scales (Hubbell 2001).

Turnover in the composition of Copano Bay molluscan fossil assemblages is simulated for a duration of 300 years, and the turnover of the Lake Tanganyika ostracod fossil assemblages is simulated for a duration of 25 years. We simulate the effects of time averaging for a time series consisting of nine layers that correspond to nine sampling events separated by time intervals of equal duration. The nine sampling events that survey species abundances are thus separated by approximately 33 years for mollusks and 3 years for ostracods. The time intervals between the sampling events encompass any changes in species abundance that occur between sampling events (fig. 1). In addition to the minimal estimates of time averaging constrained by sediment dating (above), we simulate magnitudes of time averaging of up to 500 years per molluscan fossil assemblage and up to 50 years per ostracod fossil record.

The parameters of the simulation are (1) the metacommunity composition, as defined by the biodiversity number  $\theta$  (a measure of regional diversity that is determined by speciation rate  $v$  and metacommunity size; Hubbell 2001), (2) the size of the local living assemblage  $J$  at the sampled spatial resolution (i.e., about 1 m<sup>2</sup> in Copano Bay and about 0.06 m<sup>2</sup> in Lake Tanganyika), (3) the size of individual fossil assemblages ( $J_a$ ), (4) the species turnover rate that controls the number of individuals dying per time step, which is determined by species life span ( $G$ ), and (5) the dispersal number  $I$  (a measure of dispersal limitation defined as the potential number of immigrants that can compete with individuals in the local community; Etienne and Olff 2004a, 2004b). Dispersal number  $I$  defines the per capita immigration rate  $m$  between the local dispersal-

limited community and the metacommunity per time step. The immigration rate  $m$  per mortality event is related to  $I$  as  $m = I/(I + J - 1)$  and thus depends on both dispersal limitation  $I$  and local-community (sample) size  $J - 1$  when a spot is vacated after an individual's death (Hu et al. 2007). We obtain maximum likelihood estimates of  $I$  and  $\theta$  by using information on local living assemblages (table 1; procedure of Etienne 2007), but we also evaluate time-averaging effects for multiple values of migration rates and local-community size.

The numbers  $I$  and  $\theta$  of nonaveraged assemblages are estimated with a genealogical approach that traces immigrating ancestors to all individuals in local communities (Etienne and Olff 2004a) and the neutral sampling formula for multiple samples (Etienne 2007), respectively. This formula constitutes the probability distribution of observing a species abundance distribution in a set of local communities with sample sizes  $J$  under the neutral model, with equal dispersal limitation and point-mode speciation in the metacommunity. This approach was developed for a spatial set of local communities, where  $I$  is assumed to be equal for all local communities sampled at comparable spatial scales (Etienne 2007). Spatially separated samples of local communities are expected to have negligible emigration from each to the others; that is, they represent independent samples of communities affected by equal dispersal limitation. Although Etienne (2009) developed a sampling formula for multiple samples by relaxing the condition of equal dispersal limitation, we use the sampling formula with equal dispersal limitation because our assemblages were consecutively sampled from the same site (i.e., dispersal limitation remains constant). We thus think that this approach can also be used for temporally separated samples from one site when temporal autocorrelation is negligible. In Copano Bay, Pearson correlations among temporal distances and all three measures of compositional dissimilarities are low ( $r < 0.15$ ) and insignificant (Mantel test). With the exception of presence-absence data at the 10-m water depth, Pearson correlations are also low and insignificant in Lake Tanganyika ( $r < 0.3$ ). Therefore, we assume that temporal autocorrelation among assemblages should not substantially affect the estimated metacommunity parameters.

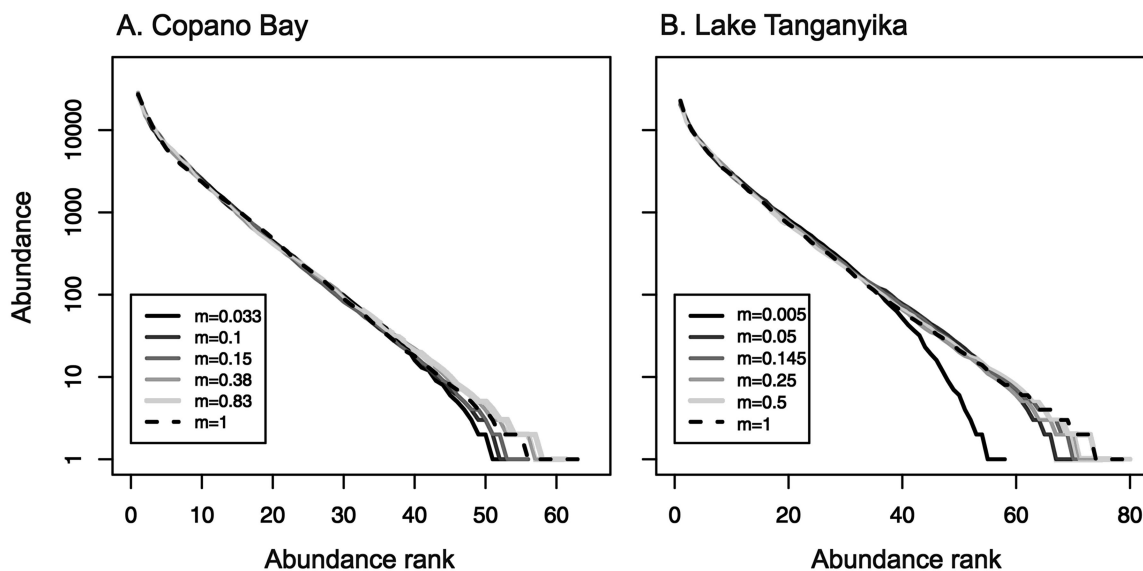
The metacommunity composition is assumed to remain static over the duration of time averaging. The spatial extent of the metacommunity species pool that represents the source of immigrants for local assemblages is on the order of 250,000 km<sup>2</sup> in Copano Bay (areal extent of the northern Gulf of Mexico ecoregion; Spalding et al. 2007) and is unknown for Lake Tanganyika (catchment area is ~230,000 km<sup>2</sup>). The composition of the metacommunity at speciation-extinction equilibrium is generated by the sequential construction algorithm (Etienne 2005), given

the biodiversity number estimated by the maximum likelihood approach and using the metacommunity size  $J_m = 100,000$  individuals (fig. 2). At  $J_m = 100,000$  individuals, differences between dispersal-limited and dispersal-unlimited metacommunity samples become relatively small (fig. 2). The composition of the local community is initialized by a random draw of  $J$  individuals from the metacommunity, and the simulation is run until local species richness attains stable values (see the R language source code, available in the online edition of the *American Naturalist*).

In the neutral model, an individual from the metacommunity migrates into the local living community with probability  $m$  and a new recruitment from the local community takes place with probability  $1 - m$  (Hubbell 2001). Individuals of all species have equal mortality probability. Therefore, our null model predicts temporal variation in species composition in fossil assemblages when species do not differ in per capita birth, death, immigration, and preservation rates (i.e., the neutral model): the expected values of diversity and temporal turnover are determined by stochasticity in these rates (Lande 1993; Hubbell 1997; Bell 2000; Sæther and Engen 2003; Maurer and McGill 2004; Hu et al. 2006, 2007). Stochasticity in birth, death, and immigration of individual species is conditioned by the abundance of species in the metacommunity, by dispersal and recruitment limitation (simulations effectively model changes in the abundances of adult individuals and dispersal limitation and thus subsume the processes that limit recruitment), and by local-community size (Hubbell 2001; for preservation rates, see "Preservation Dynamics"). To compare predictions from the neutral model with those from simple versions of a nonneutral model, we use one model with intraspecific density dependence and one model with life-history trade-offs.

In the model with negative intraspecific density dependence, per capita mortality rates of individual species increase monotonically with increasing density of conspecifics in the local community (Chave et al. 2002). The immigrants or local recruits escape density-dependent mortality with probability  $z = 1 - aq$ , where  $q$  is the proportion of conspecific individuals present in the local community at the time of immigration or local recruitment and  $a$  can vary between 0 and 1 and defines the strength of density dependence (here,  $a = 0.4$ , as in Chave et al. 2002). The probability of immigration and local recruitment is not density dependent and follows the same rules as in the neutral model.

In the trade-off model, individuals differ in predefined species-specific vital rates. Mortality rates are randomly assigned to species in the metacommunity. Fecundity and immigration rates follow life-history trade-offs, so that species with high mortality are characterized by high im-



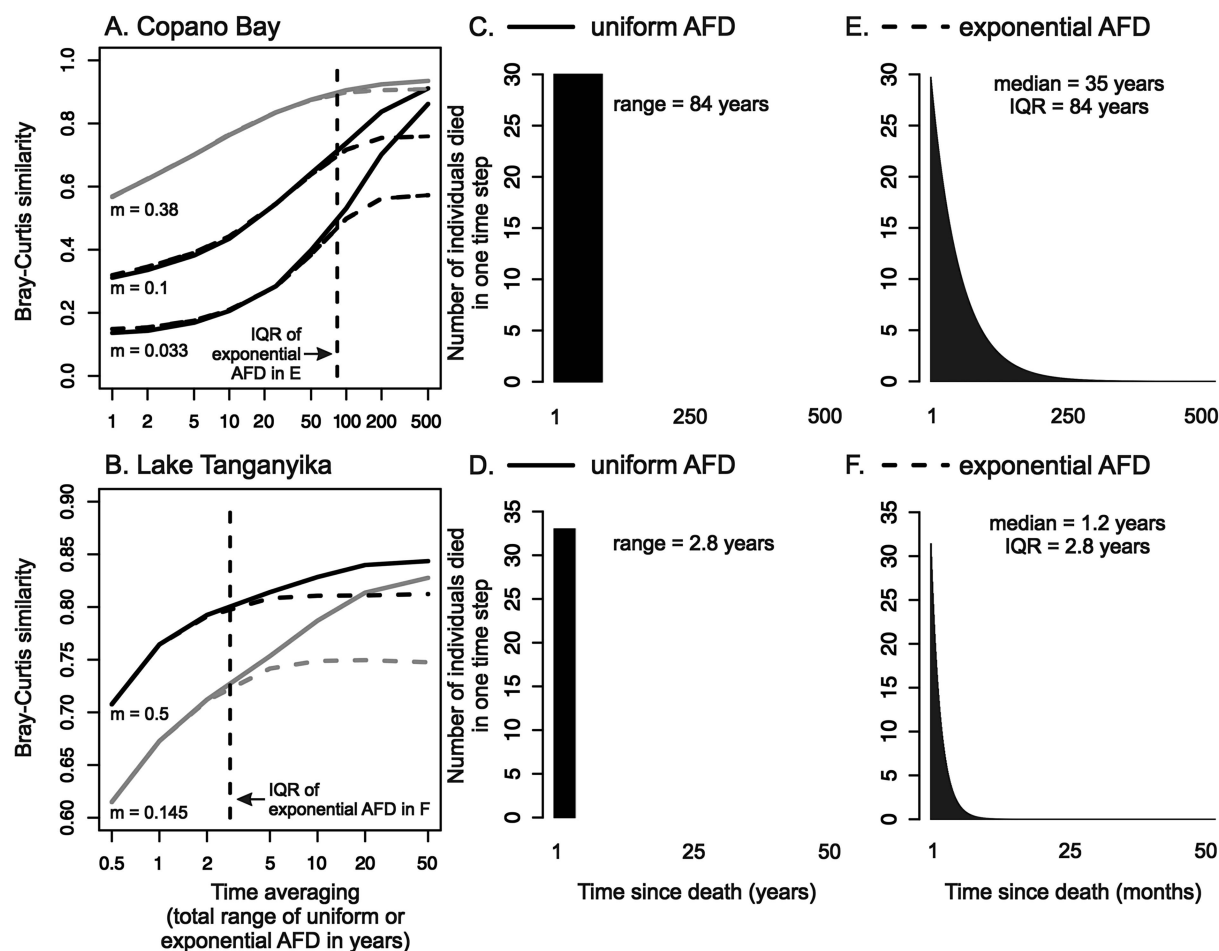
**Figure 2:** Rank abundance distributions of assemblages at large sample sizes (100,000 individuals) generated with the sequential algorithm (Etienne 2005) and used in the construction of neutral metacommunity composition at a speciation-extinction equilibrium unlimited by dispersal ( $m = 1$ ). Assemblages differing in degree of dispersal limitation (migration rates  $m$ ) and conditioned by the same biodiversity number ( $\theta = 6.05$  in Copano Bay and 8.14 in Lake Tanganyika) mostly differ in the number of rare species but become similar at  $J_m = 100,000$  individuals.

migration from the metacommunity and/or by high fecundity in the local community (e.g., Hastings 1980; Tilman 1994, 2004; Chave et al. 2002). If the species-specific mortality probability of an individual is larger than a random number drawn from a uniform distribution (in the interval from 0 to 1), then it is transferred into the pool of dead individuals. If not, the sampling is repeated until the mortality rate of some other individual is larger than a random number. An algorithm equivalent to the simulation of mortality events is used to simulate immigration and local recruitment of individuals into the local living community. For example, if the species-specific immigration probability of an individual drawn from the metacommunity is larger than a random number drawn from a uniform distribution, then it is transferred into the local living assemblage. The distribution of species abundances in the metacommunity in both the density-dependent and the trade-off models is identical to that of the neutral metacommunity. The pool of dead individuals is tracked in all three models. Variance in vital rates under high dispersal and recruitment limitation can be high in the neutral model because this model lacks regulation mechanisms, such as density dependence, and vital rates are not fixed, as in trade-off model. These three models differ in community dynamics operating at small spatial scales but are still equivalent at larger scales because they are constrained by the same metacommunity.

#### *Preservation Dynamics*

The size of the death assemblages sampled from the simulated pool of dead individuals is constrained by the average size  $J_d$  observed in fossil assemblages of Copano Bay and Lake Tanganyika. Therefore, under fixed sample size, sampling rates must decrease with increasing time averaging to compensate for the increasing total number of individuals that have died over the duration of time averaging. Sampling rates are defined by the number of sampled individuals relative to the total number of individuals produced over the period of time averaging. In sampling dead individuals, we assume a uniform frequency distribution of the postmortem ages of all individuals (age frequency distribution [AFD]; fig. 3), where the sampling probabilities of each individual do not depend on its postmortem age. Therefore,  $J_d$  individuals are sampled at random from the total pool of individuals that died during this period of time averaging. The range of ages in this uniform AFD defines the temporal resolution of a death assemblage, which is an unbiased sample of species composition integrated over the period of time averaging.

Strictly speaking, such sampling is appropriate only when the per capita preservation rate of each individual in a death assemblage is equal to 1, that is, when there is no loss of individuals to postmortem processes during the interval of time averaging. In models with constant per



**Figure 3:** The shape of change in similarity with increasing total range of the postmortem age frequency distributions (AFDs) differs between uniform (*solid curves*) and exponential (*dashed curves*) AFDs (here using selected examples of the neutral model for Copano Bay assemblages and the density-dependent model for Lake Tanganyika assemblages, with several migration rates  $m$ ). Patterns of similarity change start diverging once the interquartile range (IQR) of the unveiled exponential AFD is approximately equal to the total range of uniform AFD (*vertical dashed lines*; A, B). When the exponential AFD is fully unveiled, the similarity expected under sampling from a uniform AFD with time averaging defined by the total age range (C, D) is comparable to the similarity expected under sampling from an exponential AFD with an approximately similar IQR (E, F). Therefore, our simulation results for total age ranges assuming uniform AFDs are approximately comparable to those generated when the temporal resolution is defined by the IQRs of exponential AFDs. Patterns of similarity change expected under sampling from the exponential AFD (*dashed curves*; A, B) become flat and do not converge because the total age ranges are in the extreme tails of the exponential AFDs, where the increase in the effective temporal resolution is 0.

capita preservation rates that are less than 1—that is, where postmortem destruction does occur—the total probability of preservation of each individual is expected to decrease with time. In such cases, dead individuals are sampled from an exponential AFD (fig. 3). Indeed, natural molluscan death assemblages frequently show right-skewed AFDs and tend to be dominated by recently dead individuals (Flessa et al. 1993; Olszewski 1999, 2004; Kidwell 2002; Kosnik et al. 2007, 2009).

For these nonuniform distributions, temporal resolution is best estimated by the median or the interquartile

range (IQR) of postmortem ages rather than by the total range (exponential distributions tend to infinity, although AFDs of real fossil assemblages are constrained by sediment accumulation rates). Even when the total temporal ranges of uniform and exponential AFDs are equal, the effective temporal resolution of exponential AFDs is smaller. Simulations indicate that, notwithstanding the likely nonuniform AFDs of natural death assemblages, we can still assume a uniform AFD if we set its range as the IQR (effective temporal resolution) of the nonuniform AFD (fig. 3). At low time averaging, both AFDs show the

same patterns of change in similarity because the exponential AFD is strongly truncated and thus quite comparable to the uniform AFD (fig. 3A, 3B). Patterns of similarity change start diverging once the IQR of the unveiled exponential AFD is approximately equal to the total range of the uniform AFD (fig. 3A, 3B). When the exponential AFD is fully unveiled, the similarity expected under sampling from a uniform AFD with time averaging defined by its total range (fig. 3C, 3D) is comparable to the similarity expected under sampling from an exponential AFD with an approximately similar IQR (fig. 3E, 3F). For example, for a uniform AFD with a total range of postmortem ages of 84 years, community attributes of time-averaged assemblages will be comparable to those expected for an exponential AFD with an IQR of 84 years (fig. 3C, 3E). Our estimates based on uniform AFDs should thus apply to the effective range of time averaging (IQR) when underlying distributions are exponential. The temporal resolutions estimated for the Copano Bay (20–50 years) and Lake Tanganyika assemblages (5–10 years) correspond to such effective age ranges.

We evaluate the effects of increasing temporal scale at fixed sample size  $J_a$ , thus discriminating the effects of increasing scale (which covaries with changes in dispersal limitation and metacommunity size) from effects that are purely related to sampling (White et al. 2006; McGlenn and Palmer 2009). The number of individuals dying in the local community per year ( $R$ ) is defined by the average species life span in years ( $G$ ) as  $R = J/G$ . We estimate that the average life span of mollusks in Copano Bay falls in the range of 6 months to 1 year because a substantial portion of species is represented by juveniles and small size classes (Powell et al. 1984). The average life span of ostracods in Lake Tanganyika is unknown (A. S. Cohen, personal communication) but in general is estimated to range between a few months and 1–2 years. We run these simulations using life spans of 3 and 6 months.

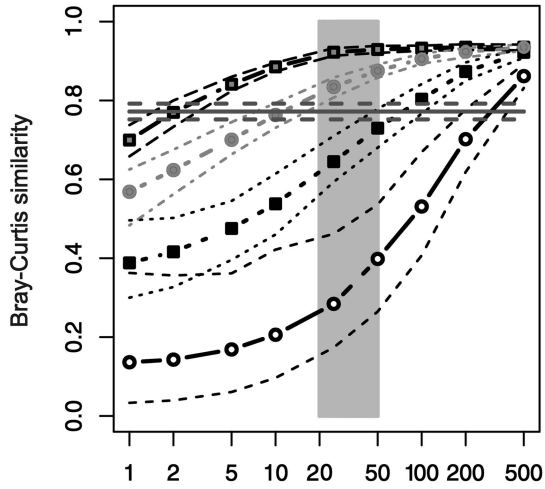
We measure temporal variation in species composition as a median of Bray-Curtis similarities, a median of Horn-Morisita similarities, and a median of Jaccard similarities (e.g., Russell et al. 1995; Condit et al. 2002; Ellingsen and Gray 2002; Dornelas et al. 2006). All three indices give qualitatively identical results, so we plot results for Bray-Curtis similarity only (see the appendix in the online edition of the *American Naturalist*). Average similarity values and error bars observed in fossil assemblages denote means and 95% confidence intervals of 100 medians of similarities based on sample-size-standardized data sets. In simulations, 100 replicate sequences were run for each combination of parameter values. We plot the expected similarities for simulated fossil assemblages against time averaging in semilog plots. Temporal species turnover rate is measured as the slope of the species-time relationship in log-log space: the exponent of the power function ( $w$ ) is related to the proportional increase in species richness for each doubling of the temporal grain (White 2007). Changes in temporal variation in composition owing to time averaging are also linked to changes in diversity and in the abundance structure of averaged assemblages (McGill 2003). Therefore, we measure time-averaging effects on (1) species richness and the Gini-Simpson index at alpha spatial scales of local assemblages (i.e., about 1 m<sup>2</sup> in Copano Bay and about 0.06 m<sup>2</sup> in Lake Tanganyika) and (2) the shape of the species abundance distribution (as the Akaike Information Criterion [AIC] weight of a lognormal model relative to the weights of preemption and Zipf models; Wagner et al. 2006; Harnik 2009). The preemption model produces a straight line in semilog rank abundance plots (with abundance on the log scale), the lognormal model forms an S-shaped curve in semilog rank abundance plots, and the Zipf model forms a straight line in log-log rank abundance plots.

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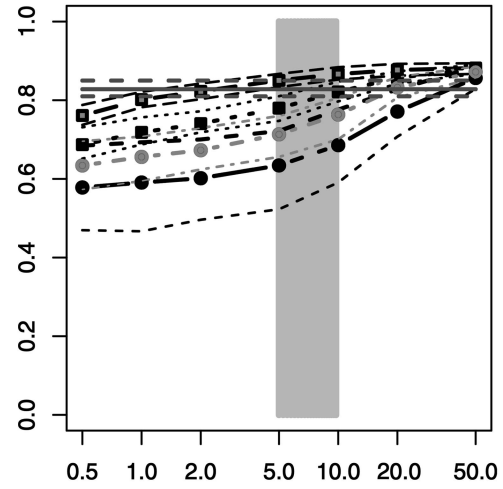
**Figure 4:** In simulations, community similarity markedly increases with increasing time averaging of Copano Bay molluscan assemblages and Lake Tanganyika ostracod assemblages (life spans of 6 months) using neutral, trade-off, and density-dependent models. Thin dashed lines represent 95% confidence intervals on estimates of median similarity based on 100 simulations. The three models, which differ in dynamics at small spatial scales and 1 year of temporal resolution, become indistinguishable under high time averaging, where they converge on the single similarity level that is expected under random sampling of assemblages from the same metacommunity. The levels of median similarity observed among fossil assemblages in Copano Bay core 1 (*horizontal gray line*, with dashed 95% confidence intervals; see “Methods”) are comparable to the similarities predicted by the neutral model using the migration rate estimated from living assemblages (*gray circles*;  $m = 0.38$ ) and the range of time averaging estimated from sediment accumulation rates (20–50 years; *vertical gray bars*). Observed similarity among Lake Tanganyika fossil assemblages in core MWA-1 is also comparable to that predicted by the neutral model using the migration rate estimated from living assemblages ( $m = 0.145$ ) and the range of time averaging estimated for fossil assemblages (5–10 years). The migration rates  $m$  used in the Copano Bay core simulations were chosen with respect to the local-community size  $J = 30$  individuals:  $m = 0.033$  corresponds to one migrant,  $m = 0.1$  corresponds to three migrants,  $m = 0.15$  corresponds to five migrants, and  $m = 0.83$  corresponds to 25 migrants per 6 months or per 1 year, depending on the life span model. In Lake Tanganyika, simulations were chosen with respect to local-community size  $J = 200$  individuals:  $m = 0.05$  corresponds to 10 migrants,  $m = 0.25$  corresponds to 50 migrants, and  $m = 0.5$  corresponds to 100 migrants per 6 months.



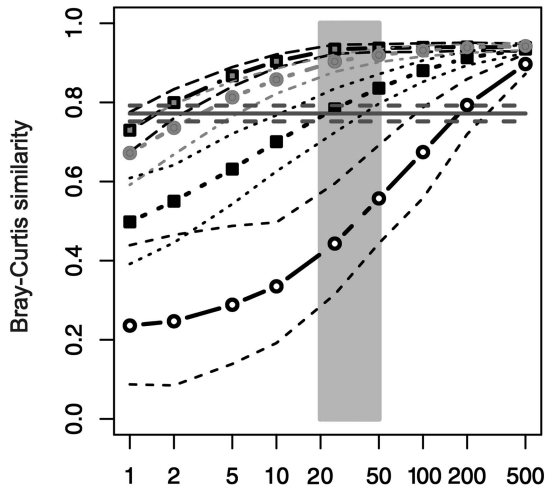
A. Copano Bay - neutral model



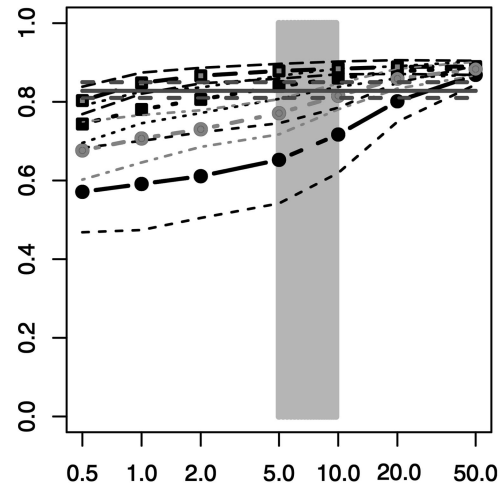
D. Lake Tanganyika - neutral model



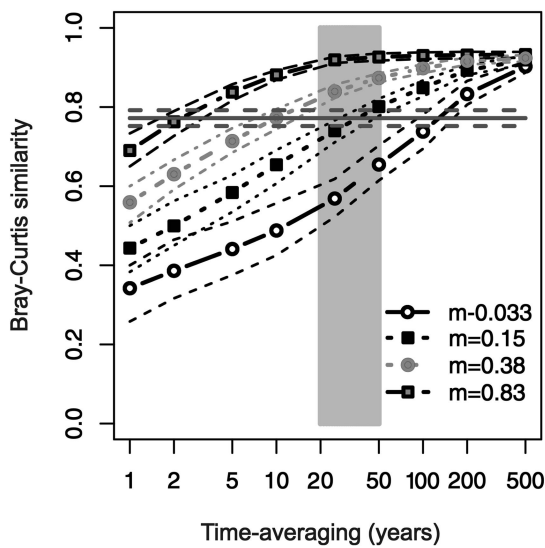
B. Copano Bay - trade-off model



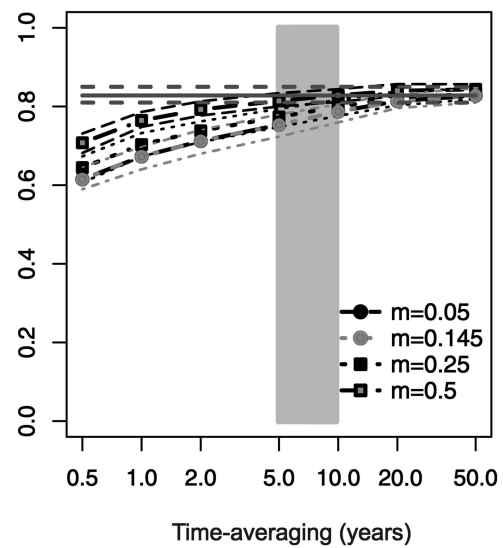
E. Lake Tanganyika - trade-off model



C. Copano Bay - density dependence



F. Lake Tanganyika - density dependence



## Results

### *Predicted Effects of Time Averaging on Temporal Variation in Species Composition*

All three indices of similarity show either a monotonic or a sigmoidal increase in semilog plots as temporal resolution per sampled assemblage decreases from 1 to 500 years in Copano Bay assemblages and from 1 to 50 years in Lake Tanganyika assemblages (fig. 4). Under constant meta-community structure and constant local-community size, the rate of increase in similarity depends on migration rate: low-migration models are characterized by an initially slow change in similarity that accelerates with higher time averaging (curves have an initially concave form). High-migration models start at fairly high similarities that are close to the asymptote and show decelerating rates of change in similarity (entirely convex curves). All models asymptotically converge on equally high similarity when the magnitude of time averaging corresponds to complete averaging of all nine of the consecutive events that form the time series. This level of similarity is expected when individuals are randomly sampled from a pooled set of multiple local assemblages or from one metacommunity (fig. 5).

Turnover  $w$ —the slope of the species-time relationship—in local averaged assemblages is also minimized ( $w = 0.05\text{--}0.1$ ) under high time averaging (fig. 6A). The strongest reduction characterizes the low-migration models that have the highest turnover under negligible time averaging (fig. 6). Even when the composition of the meta-community is static, the turnover rate  $w$  does not fall to 0 under high time averaging because consecutive averaged assemblages are derived from intervals that do not overlap completely, as a result of lengthening of the total extent of the time series (fig. 1).

The trade-off and density-dependent models mostly predict higher similarity among time-averaged assemblages than does the neutral model (fig. 7). These differences are small and decrease with increasing migration rate, although in some cases neutral models do predict higher similarity values than nonneutral models under high migration rates (fig. 7). Longer life spans (1 year in Copano Bay and 0.5 years in Lake Tanganyika) lead to higher similarity among averaged assemblages for any given magnitude of time averaging, with the exception of the lowest migration rates ( $m = 0.033$ ; fig. A3 in the online edition of the *American Naturalist*).

Neutral models predict that, over the course of time averaging up to the range estimated for Copano Bay fossil assemblages (20–50 years), between-assemblage similarities will increase on the order of about 0.1–0.3 over those expected among nonaveraged assemblages (fig. 4A; also fig. A1 in the online edition of the *American Naturalist*).

The increase in similarity with time averaging is slightly slower in trade-off and density-dependent models because the initial community similarity among nonaveraged assemblages under those models is mostly higher (fig. 4B, 4C). Neutral models predict that similarities among Lake Tanganyika fossil assemblages will increase by 0.05–0.1 with time averaging up to 5–10 years (fig. 4D). The magnitude of increase in similarities is comparable in trade-off models (fig. 4E) and slightly smaller in density-dependent models (fig. 4F).

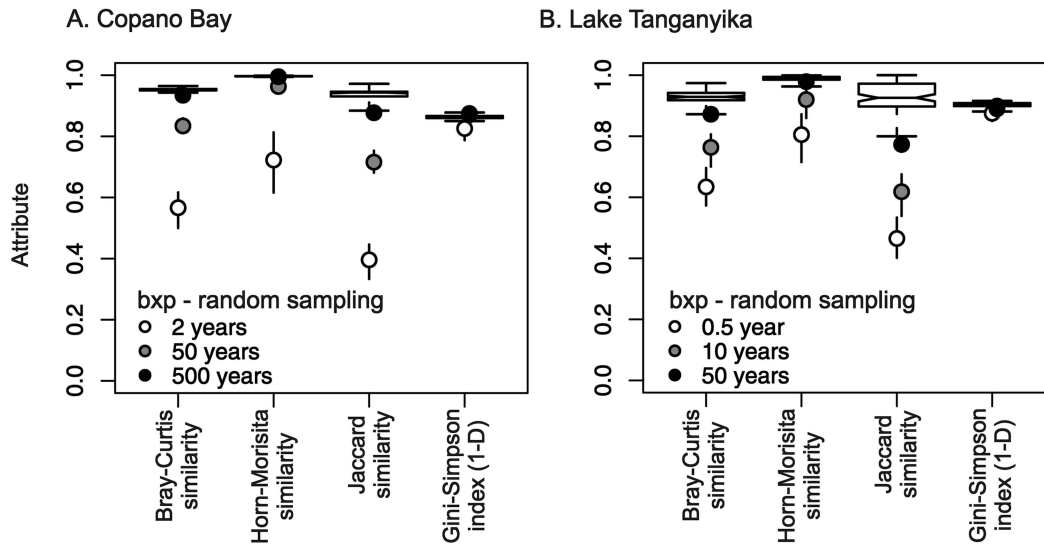
### *Predicted Effects of Time Averaging on Diversity and Species Dominance*

In simulations, species richness increases with increasing time averaging in both data sets, notwithstanding fixed sample size (fig. 8). Richness increases at a higher rate in low-migration models because it starts at a lower value (i.e., tends to be lower in nonaveraged assemblages under those conditions).

All increases in richness are associated with a change in the shape of the species abundance distribution. First, species dominance is reduced, as shown by the increasing Gini-Simpson index of diversity (fig. A4 in the online edition of the *American Naturalist*); that is, rank abundance distributions (RADs) become flatter on their left side. Species dominance decreases faster when migration rates are low because dominance is relatively high in nonaveraged communities under those conditions. With increasing time averaging, local assemblages approach the Gini-Simpson diversity expected from sampling the meta-community (not limited by dispersal) rather than the diversity exhibited by the local dispersal-limited community (fig. 5). The increase in species richness is also related to an increase in the proportion of rare species that have little effect on dominance. Second, the weight support of the lognormal model of the species abundance distribution increases with time averaging at the expense of support for the preemption and Zipf models, although assemblages time averaged under low migration rates show lower initial support for a lognormal model and never converge on the levels attained under high migration (fig. 8). Both Preston plots and RADs indicate that although species of intermediate abundance increase in commonness with time averaging, rare species are still common in the tail of the RAD (fig. A5 in the online edition of the *American Naturalist*, using an intermediate migration rate).

### *Observed versus Predicted Temporal Variation in Species Composition and Turnover*

Observed levels of similarity among sequential fossil assemblages in the Copano Bay core (fig. 4; table 2) are



**Figure 5:** With increasing time averaging, local-community attributes (three measures of community similarity and the Gini-Simpson index of diversity) converge toward those expected under random sampling from one metacommunity. Data points represent means and 95% confidence intervals predicted by simulations of time averaging for  $m = 0.38$  (A) and  $0.145$  (B). Box plots (*bxp*) summarize the distribution of attributes under random sampling of one metacommunity, without replacement. The expected values are based on the neutral model.

comparable to the similarities predicted by the neutral model using the migration rate predicted for living assemblages (*gray circles*;  $m = 0.38$ ) and the range of time averaging that was estimated from sediment accumulation rates (20–50 years; *vertical gray bars*). The observed turnover  $w$  is also comparable to the temporal turnover predicted by the neutral model (fig. 6A). Fossil assemblages of Copano Bay would thus have to be less time averaged than they are thought to be in order to reject the neutral or other models that predict low similarity at fine temporal resolution.

Lake Tanganyika yields similar results. Within the range of estimated time averaging (5–10 years), observed similarities among fossil assemblages are comparable to those predicted by the neutral model under intermediate migration rates ( $m = 0.145$ ; fig. 4D; table 2), and the observed temporal turnover  $w$  is comparable to that predicted by the neutral model (fig. 6B).

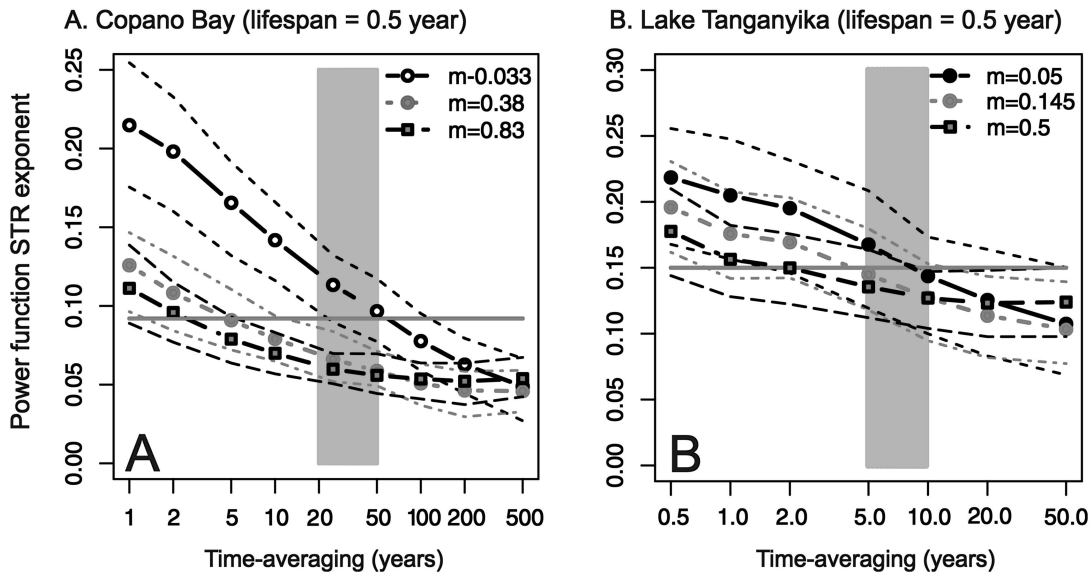
Temporal turnover  $w$  and variation in species composition observed in mollusk and ostracod assemblages thus basically match the scaled predictions of turnover for averaged assemblages. Therefore, in both data sets, the low persistence in species composition that characterizes non-averaged assemblages (related to the lack of density dependence in neutral-model simulations) is expected to be modified by time averaging alone into a relatively high persistence. The similarities predicted by neutral, trade-off, and density-dependent models differ only slightly and

can be difficult to distinguish, even under moderate degrees of time averaging (fig. 7).

## Discussion

### *Similarity-Time Relationship: Time Averaging Reduces Temporal Turnover*

The relatively low values of temporal variation and turnover in species composition observed in Copano Bay and Lake Tanganyika are mostly within the bounds predicted by neutral, trade-off, and density-dependent models for the estimated ranges of time averaging. Two components of increasing temporal scale likely account for the reduced temporal variation in species composition. First, the reduction in temporal resolution leads to reduced variation in the vital rates and preservation rates of individual species (same principle as Levin 1992); that is, the magnitude of short-term fluctuations in abundance is minimized under high averaging. Second, the decrease in separation among averaged assemblages effectively reduces the unsampled time between two sampling events and thus limits the potential species accumulation that can occur between two sequential assemblages. The decrease in temporal turnover with increasing time averaging is analogous to the reduction in the slope of a species-time relationship with increasing spatial scale (Adler et al. 2005; Adler and Lauenroth 2003): the increase in spatial scale is coupled



**Figure 6:** Decrease in the power-function exponent (turnover rate  $w$ ) of the species-time relationship (STR) with increasing time averaging in simulated assemblages from Copano Bay and Lake Tanganyika (thick lines represent means, and thin lines represent 95% confidence intervals). The horizontal gray lines represent the power-function exponents observed in Copano Bay (core 1) and Lake Tanganyika fossil assemblages (core MWA-1).

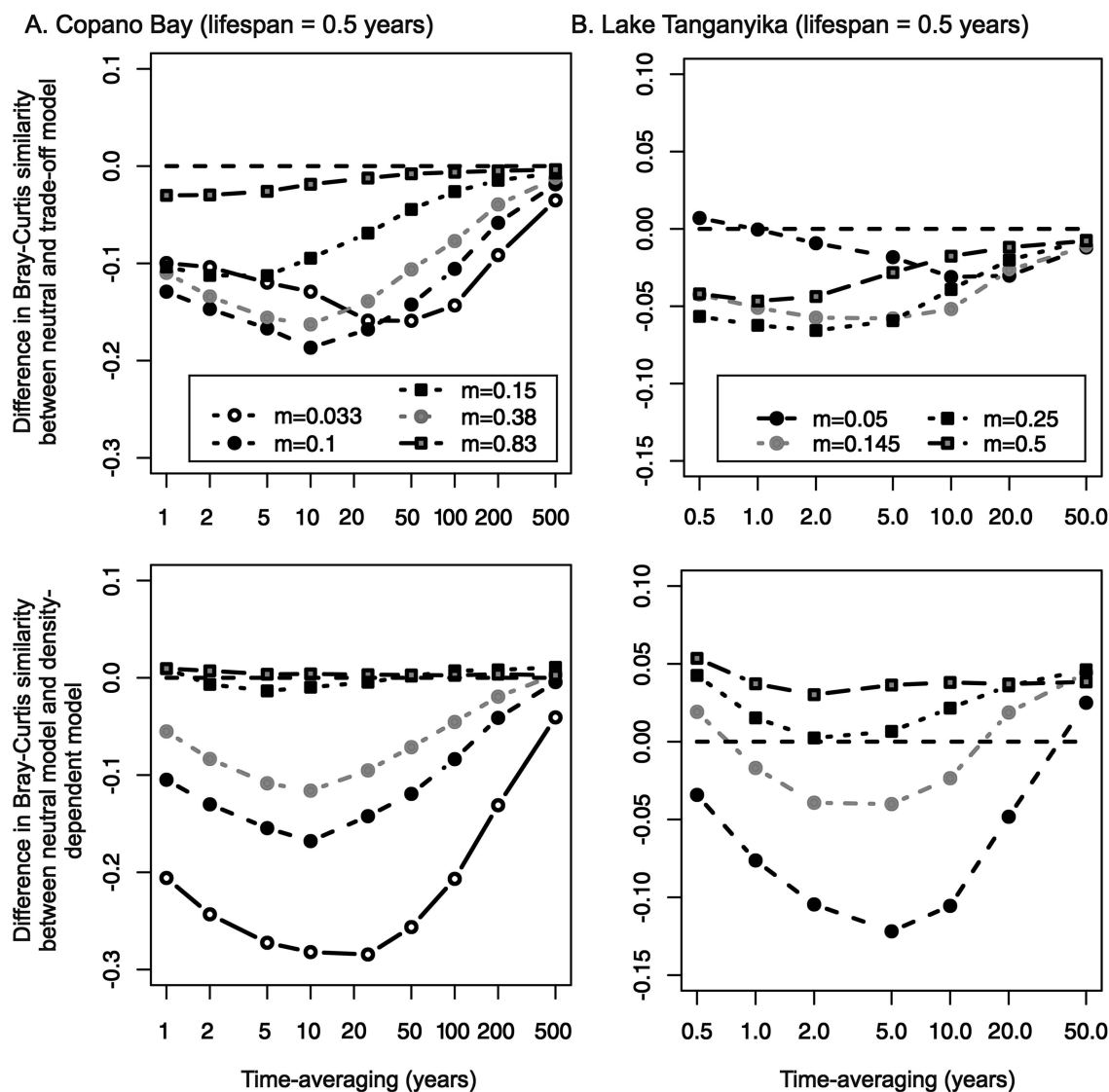
with an increasing probability of immigration, just as with an increase in temporal scale. The increase in spatial scale also affects the scaling of temporal turnover with increasing time averaging: with increasing spatial scale (accommodated here by increasing the local-community size  $J$ ), the rate of change in temporal turnover  $w$  is reduced (fig. 9). Variations in life span also affect temporal turnover: shorter life spans decrease variation among averaged assemblages because they increase the mixing of successive generations relative to models where individuals have longer life spans.

Differences in the shape of the similarity-time relationship among different migration models are related to differences in abundance structure because rank abundance distributions (RADs) affect between-sample similarities and the exponent of species-time relationships (as in Hubbell 2001; He and Legendre 2002; Pueyo 2006*b*). Uneven RADs, corresponding to low migration rates, are characterized by concave-up similarity-time relationships. Under such conditions, the identity of the dominant species generally changes between sequential nonaveraged assemblages because of demographic stochasticity; the initial temporal similarity of assemblages is low and grows slowly because only dominant species in individual samples are initially sampled. With increasing time averaging, more of these consecutive generations are mixed, thus increasing the probability of sampling individuals from all of these sequentially dominant species and reducing temporal var-

iation in species composition. The more even RADs that characterize communities subject to high migration rates are expected to have convex-up similarity-time relationships. Similarity in nonaveraged assemblages is initially higher because of lower variance in vital rates, and temporally sequential assemblages are expected to share more species even under low time averaging. Increasing time averaging thus has less of an effect on turnover and similarity than it does on less even RADs.

#### *Time Averaging Flattens the Abundance Structure*

Time averaging reduces the proportional abundance of dominant species, because species undergo stochastic dynamics in models where the total community size is bounded but the RADs of the local nonaveraged communities are in steady state. Therefore, any temporal decrease in the abundance of one (dominant) species is compensated for by an increase in the abundance of another species. The lower temporal turnover observed among time-averaged assemblages thus is fundamentally associated with changes in (specifically, a flattening of) the abundance structure of assemblages at alpha spatial scales. In addition, although abundant species switch in dominance while remaining temporally persistent, different rare species arrive in the local community at each time step; new species in neutral metacommunities with point-mode speciation are initially rare and thus susceptible to extinction (e.g., Zillio and Condit

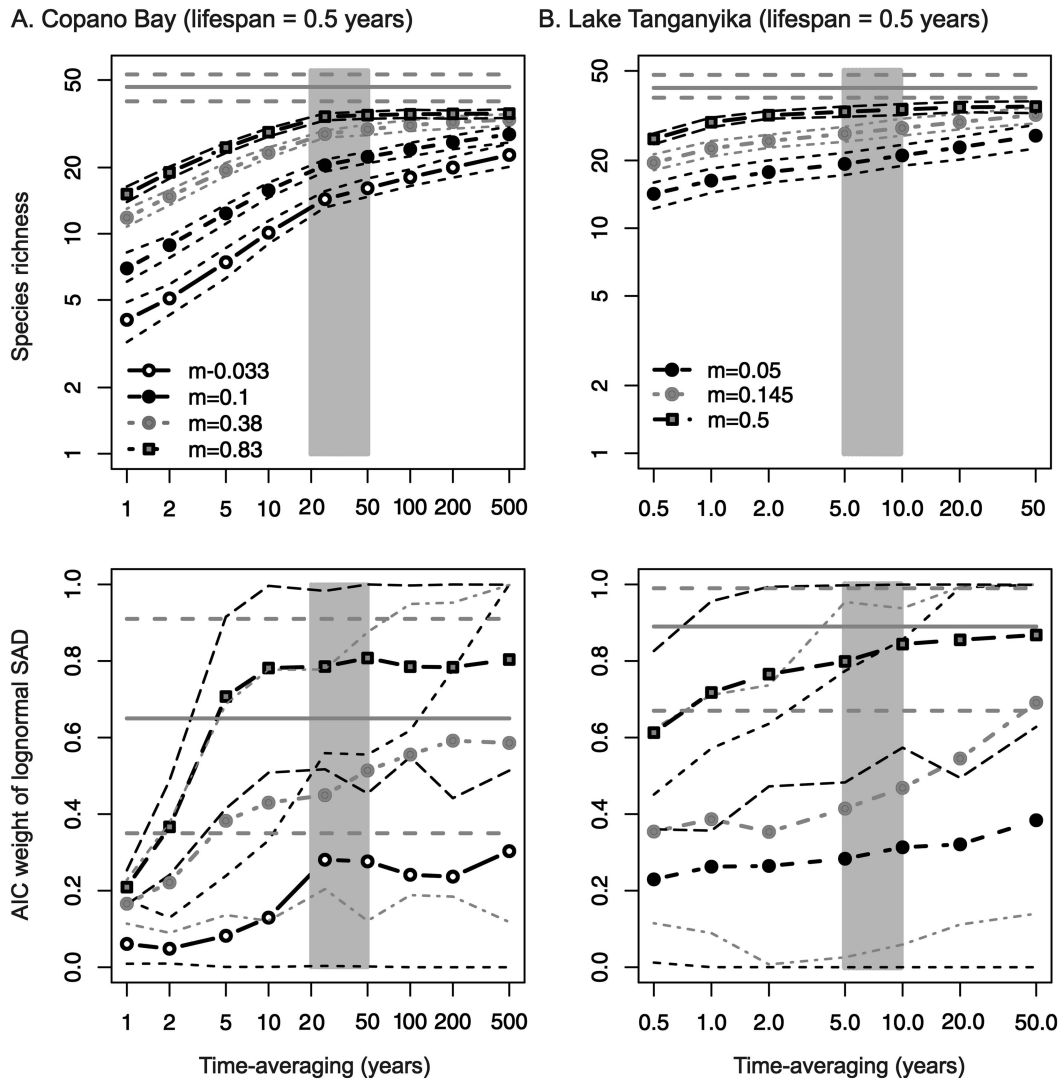


**Figure 7:** Difference in community similarity between neutral and trade-off models (*top row*) and between neutral and density-dependent models (*bottom row*) with increasing time averaging. The predicted differences between neutral and nonneutral models are relatively small for both Copano Bay and Lake Tanganyika (life span = 6 months for both) and ultimately decrease with time averaging. The 95% confidence intervals are relatively wide, with the upper and lower endpoints being 0.05–0.1 units from mean values.

2007). Increasing time averaging thus also leads to an increased proportion of rare species and to a shift from straight (geometric) to J-shaped RADs. This difference in population dynamics between common and rare species parallels the difference between core (temporally persistent) and satellite (temporally sparse) species (Hubbell 2001; Magurran and Henderson 2003; Magurran 2007).

As predicted by species-time relationships (Preston 1960), species richness increases with time averaging because of several mechanisms (White 2007). Here, our sim-

ulations incorporate local colonization and extinction in dispersal-limited communities in the absence of ecological successions or temporal environmental variability. As the total number of individuals increases, the probability of species immigration inevitably increases with elapsed time, which in turn increases species richness. Importantly, the increase in sampled species richness with increasing time averaging is conditioned by the change in RADs toward flatter curves, because sample sizes of local assemblages remain fixed in our simulations.



**Figure 8:** Expected changes in species richness and the shape of the species abundance distribution (measured as Akaike Information Criterion [AIC] weight of a lognormal species abundance distribution [SAD]) with increasing time averaging at alpha spatial scales for Copano Bay (core 1; A) and Lake Tanganyika (core MWA-1; B) assemblages. Thick lines represent means, and thin lines represent 95% confidence intervals. The horizontal gray lines denote means and 95% confidence intervals estimated from the species richness and AIC weights observed in Copano Bay and Lake Tanganyika fossil assemblages (nine samples each).

#### *Time Averaging Affects Estimates of Biodiversity and Dispersal Numbers*

Paleontological observations of variation in the fundamental biodiversity and dispersal numbers might reflect community dynamics on long (evolutionary) scales (Olszewski and Erwin 2004), but with the caveat that analyses of  $\theta$  and  $I$  in the fossil record must be constrained to fossil assemblages having comparable degrees of time averaging. An increase in time averaging will effectively increase the size of the metacommunity needed to encompass all in-

dividuals that died during that time period relative to the metacommunity size needed to accommodate dynamics over shorter time periods. Metacommunity diversity ( $\theta$ ) is expected to increase with increasing  $J_m$  ( $\theta = 2J_m v$ ), and  $I$  is also expected to increase because  $J$  of the local averaged community increases ( $I = m(J - 1)/(1 - m)$ ; Etienne 2005; Etienne and Alonso 2007). This simple expectation is met by our observed estimates. The value of  $\theta$  is generally higher in fossil (time-averaged) assemblages than in living (nonaveraged) assemblages in both the Copano Bay and

**Table 2:** Summary of observed attributes and attributes predicted by the neutral model for Copano Bay (core 1) and Lake Tanganyika (core MWA-1) assemblages for empirically estimated values of time averaging

	Copano Bay			Lake Tanganyika		
	Observed	Predicted: 25 years	Predicted: 50 years	Observed	Predicted: 5 years	Predicted: 10 years
Horn-Morisita similarity	.92 (.90–.94)	.96 (.94–.98)	.98 (.97–.99)	.96 (.95–.97)	.88 (.83–.92)	.92 (.86–.95)
Bray-Curtis similarity	.83 (.81–.85)	.83 (.81–.86)	.88 (.86–.89)	.83 (.81–.85)	.71 (.66–.76)	.76 (.7–.81)
Jaccard similarity	.61 (.57–.64)	.72 (.67–.75)	.78 (.75–.80)	.65 (.63–.67)	.55 (.49–.61)	.62 (.54–.68)
Power-function						
STR exponent	.092	.066 (.051–.084)	.059 (.049–.071)	.15	.14 (.12–.18)	.13 (.09–.15)
Species richness	47 (40–53)	28 (27–29)	30 (28–31)	42 (38–48)	26 (24–28)	28 (26–31)
Gini-Simpson diversity	.885 (.868–.899)	.87 (.86–.88)	.87 (.86–.88)	.912 (.918–.924)	.88 (.86–.9)	.89 (.86–.91)
AIC weight of lognormal	.65 (.35–.91)	.45 (.20–.78)	.51 (.12–.88)	.89 (.67–.99)	.43 (.11–.89)	.48 (.037–.98)

Note: Mean similarity values and 95% confidence intervals (in parentheses) observed in fossil assemblages are based on medians of similarities derived from 100 sample-size-standardized data sets. Mean similarity values and 95% confidence intervals (in parentheses) in simulated assemblages are based on 100 simulated medians of similarities. AIC = Akaike Information Criterion; STR = species-time relationship.

the Lake Tanganyika study areas, and  $I$  is higher by an order of magnitude (table 1).

#### *Bias toward Models Predicting Low Turnover*

Testing the neutrality of metacommunity dynamics using measures of temporal variation in species composition is analogous to testing whether two local communities derived from the same metacommunity and separated by a known distance are more similar in composition than predicted by a neutral model that does not incorporate conspecific density dependence, trade-offs, or storage effects (Chesson 2000; Chave and Leigh 2002; Tuomisto et al. 2003; Leibold et al. 2004; Etienne and Alonso 2005; Etienne 2007; Munoz et al. 2007; Driscoll and Lindenmayer 2009). Approaches that use neutral models as the null model for more complex explanations must assume that environments remained stable through time. Under such an assumption, the observed patterns of temporal variation in species composition in Copano Bay and Lake Tanganyika would indicate that neutral processes were sufficient to explain community assembly. However, these mollusk and ostracod fossil records almost certainly reflect some degree of environmental change over the course of their accumulation. For example, Copano Bay is subject to seasonal fluctuations in salinity and decadal-scale rainfall cycles (Powell and Stanton 1995), and Lake Tanganyika sediments reflect a history of changes in both climate and human landscape use, affecting soil erosion and sedimentation rates (Cohen et al. 2005).

Such instability in environment should increase temporal turnover in species composition. This turnover can be greater than that predicted by neutral models for non-averaged assemblages (e.g., see Dornelas et al. 2006 for a spatial analog). However, time averaging is expected to damp such turnover. This damping effect will be stronger when consecutive assemblages are weakly autocorrelated

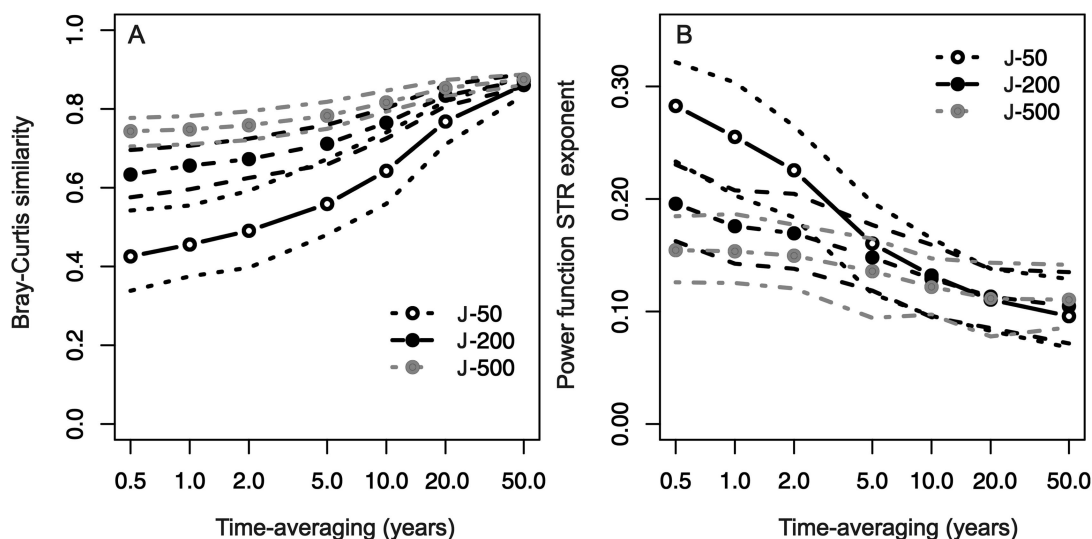
(as in the case of compositional changes in niche models driven by external environment) and will be weaker when assemblages are strongly autocorrelated (because of density dependence or dispersal limitation; Levin 1992; Gardner 1998). Therefore, the observed patterns in time-averaged assemblages agree with both the predictions for neutral model and the expectations for nonneutral communities at that same scale of time averaging.

Regardless of the model that determines community dynamics, the differences in the predictions of models tend to decrease with increasing time averaging because model predictions will tend to converge on the levels of similarity that are expected under random sampling of multiple assemblages from one metacommunity (fig. 5). These findings agree with other studies that demonstrate that the differences in community attributes predicted by neutral and more complex models are scale specific because pooling tends to equalize species abundances at larger (spatial) scales by averaging out the effects of local small-scale processes (Chave et al. 2002; Purves and Pacala 2005; Pueyo 2006a; Ruokolainen et al. 2009).

Finally, we emphasize that an increase in temporal scale has clear directional effects: temporal variation among local assemblages is reduced, thus biasing the outcome of model selection toward models that predict low variation. Distinguishing neutral and nonneutral dynamics will thus be most challenging in groups and environmental settings subject to the greatest time averaging, and time averaging reduces our ability to distinguish different metacommunity models that differ in predictions at small spatial scales.

#### *From Local-Community Attributes to Metacommunity Attributes*

In local species abundance distributions drawn from a variety of regional species abundance distributions (implicitly determined by processes at large scales), the tails



**Figure 9:** Expected effects of changing the spatial scale of analysis (proxied by size  $J$  of local living community) on temporal variation in composition (A) and on the power-function exponent of the species-time relationship (B), based on the neutral model for Lake Tanganyika assemblages (life span = 6 months). Lines with circles represent means, and dashed or dash-dotted lines without circles represent 95% confidence intervals.

of both rare and abundant species are known to thicken with increasing dispersal limitation and other forms of temporal autocorrelation at small scales (McGill 2003; Green and Plotkin 2007). In such models with processes operating at two temporal scales, time averaging pushes community structure toward an abundance distribution governed by processes at larger spatial scales (such as speciation and extinction). In neutral metacommunity models, community attributes of increasingly averaged assemblages thus converge toward the attributes of log series-like metacommunities with many rare species (fig. 5). In models where processes operate at local spatial scales only, the averaging of assemblages is governed completely by local processes. They thus inevitably converge on lognormal abundance distributions (e.g., Šizling et al. 2009). Although local-scale processes are unlikely to be captured by time-averaged assemblages in both model cases, the two-scale models predict that time series with consecutive averaged assemblages should be more informative about the processes governing metacommunity turnover than about the processes driving turnover among local communities. The differences in the predictions of neutral and various nonneutral models at local scales tend to diminish as time averaging increases and, for these modeled benthic communities, to converge on the parameters of the metacommunity within a few decades or centuries of time averaging. Therefore, this loss of resolution on local processes of community assembly is compensated for by the ability of time-averaged assemblages to provide insights into processes that act over larger spatial and temporal scales, such

as the evolution of niches and dispersal, range limit dynamics, taxon cycles, and speciation modes. Such large-scale phenomena are difficult to evaluate by using non-averaged assemblages of live-collected individuals unless life spans are very short.

#### *Effects of the Duration of Time Series*

We note that the total length of time series and the temporal distances among individual ostracod and mollusk assemblages evaluated here were relatively short (several decades to centuries), given the temporal resolution of the assemblages within the time series (years to decades). Therefore, the simulated increase in time averaging per assemblage led to zero temporal separation among assemblages and even to some mixing of consecutive assemblages (case 3 in fig. 1). In time series where the series duration is more than an order of magnitude greater than the resolution of fossil assemblages, the effects of time averaging on our ability to discriminate metacommunity models will be smaller because the rate of community change over the full duration of the time series should substantially exceed the rate of community change that occurs within the window of time averaging that characterizes assemblages within those time series.

The ratio of the total duration of the time series to the temporal resolution of individual sampling units will almost certainly determine our ability to distinguish the roles of different metacommunity models. These effects must be explored because a range of favorable ratios clearly



exists in the fossil record. For example, pollen assemblages in the sedimentary records of stratified lakes commonly have decadal (and in some cases annual) resolution within time series spanning thousands of years, deep-sea foraminiferal and ostracod assemblages can have decadal to centennial resolution within time series that are hundreds of thousands to millions of years long, and coral assemblages have centennial resolution within time series that are tens of thousands to millions of years long (e.g., Pandolfi 1996; Yasuhara et al. 2008). Because effective time averaging in fossil assemblages is probably constrained to these decadal to centennial scales regardless of geologic age, the long-duration time series available in the fossil record are particularly promising for evaluating large-scale temporal species turnover.

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