Effects of population-level aggregation, autocorrelation, and interspecific association on the species–time relationship in two desert communities

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ABSTRACT

Question: Can population-level patterns be used to model the species–time relationship? Which non-random patterns in population time-series are necessary for modelling the species–time relationship?

Statistical modelling methods: The presence of aggregation, autocorrelation, and interspecific association was determined using Morisita's I_M, Moran's I, and Ive's C respectively. Models for the species–time relationship were constructed from these sub-patterns using a combination of analytical models and randomization methods.

Data studied: Observational time-series of rodents and annual plants in the Chihuahuan Desert.

Conclusions: Aggregation was observed in the majority of population time-series. Most rodent species, but fewer than 10% of plant species, exhibited significant temporal auto-correlation in abundance. Models that included temporal autocorrelation as well as aggregation provided the best fit to the species–time relationship. The species–time relationship is intimately connected to the population dynamics of individual species. Models that attempt to connect the apparently general behaviour of the species–time relationship to the complex dynamics of populations are important for understanding the dynamics of ecological communities.

Keywords: aggregation, species–area relationship, species–time relationship, temporal autocorrelation, temporal turnover.

INTRODUCTION

The species–area relationship is considered to be one of the most general patterns in ecology (Rosenzweig, 1995). As a result, it has been studied extensively using observational (e.g. Rosenzweig, 1995; Chown *et al.*, 1998), experimental (e.g. Hurlbert, 2006), and modelling (e.g. Preston, 1960; Leitner and Rosenzweig, 1997; Allen and White, 2003) approaches. It has been evaluated both in terms of

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the observed species-level pattern and in terms of how the patterns in the component populations combine to generate the species-level pattern (Plotkin *et al.*, 2000; He and Legendre, 2002). The species–time relationship, on the other hand, has received relatively little attention, and work on this pattern has almost exclusively focused on the statistical description of observational, species-level data (e.g. Rosenzweig, 1995; Hadly and Maurer, 2001; Fridley *et al.*, 2006; White *et al.*, 2006).

The species–time relationship describes the observed increase in species richness as a site is observed for increasingly long periods of time (Preston, 1960; Rosenzweig, 1995). Since repeated samples tend to show relatively constant species richness at a site through time (e.g. Williamson, 1987; Ernest and Brown, 2001; Lekve *et al.*, 2002), the observed accumulation of richness results from turnover events where one species replaces another in the community between samples (Brown *et al.*, 2001; Carey *et al.*, 2007). The species–time relationship has received increasing support as a fundamental ecological pattern that provides a useful approach to understanding the dynamics of species composition (Rosenzweig, 1995, 1998; Adler and Lauenroth, 2003; White, 2004; Fridley *et al.*, 2006; White *et al.*, 2006; Carey *et al.*, 2007; Magurran, 2007; White, 2007). In addition, understanding the species–time relationship has important implications for comparative studies of species richness and for evaluating conservation priorities (Adler and Lauenroth, 2003; Chalcraft *et al.*, 2004; White *et al.*, 2006; White, 2007), and has recently played a roll in understanding diversity–stability relationships (Shurin, 2007; Shurin *et al.*, 2007).

Since the species–time relationship results from local colonization and extinction events (Carey *et al.*, 2007), it may be affected by such factors as: environmental variability, successional changes, competition, predation, metapopulation and source–sink dynamics, and demographic stochasticity (Rosenzweig, 1995; White *et al.*, 2006). One way to approach patterns resulting from large numbers of different processes is to look for statistical regularity in the observed pattern. This has been the traditional approach for exploring the dynamics of species composition, with patterns being evaluated both for the species–time relationship (Preston, 1960; Rosenzweig, 1995; White *et al.*, 2006) and for temporal turnover at different lags (Russell *et al.*, 1995; Russell, 1998). An alternative approach is to quantify and examine the phenomenological patterns in the distribution of individuals of each species that lead to the overall community-level patterns. This approach has produced valuable contributions in studies of spatial patterns (Plotkin *et al.*, 2000; He and Legendre, 2002; Green *et al.*, 2003; Harte *et al.*, 2005), but has yet to be applied to temporal patterns.

Studying the species–time relationship at the level of the population is potentially important, because the colonization and extinction events that drive turnover are generated by the birth, death, immigration, and emigration of individuals within each population. Although completely characterizing the species–time relationship using the component species' population dynamics would be extremely challenging, attempting to link the species-level species–time relationship with fluctuations in the abundance of the component populations may yield important insights. A first step in this direction is to quantify the effects of variation in the temporal distribution of individuals and their impacts on the observed species–time relationship.

Phenomenological patterns of individuals distributed along a time-series can be grouped into three categories: (1) intraspecific aggregation, where individuals tend to occur in clumps and therefore in fewer time periods than expected from random placement; (2) temporal autocorrelation, where the abundance of a species in one time period is correlated with its abundance in the previous time period (or periods); and (3) interspecific association, where individuals of one species are either more or less likely to occur in the same time

period as individuals of some other species. Because many ecological systems operate on characteristic annual time-scales, we can treat aggregation and autocorrelation as distinct patterns – with aggregation occurring within years and autocorrelation between years. Using data on the summer annual plant community and the rodent community at a long-term study site in the Chihuahuan Desert, we explore the contributions of these three processes in two ways. First, we analyse the population time-series to evaluate the statistical occurrence of aggregation, autocorrelation, and interspecific association at the species level. Then we compare the observed species–time relationships to those expected to occur based on subsets of these population properties using a combination of analytical statistical models and constrained randomizations of the observed data.

METHODS AND MODELS

Field site and data collection

We used data from a long-term study conducted near Portal, Arizona (31.9°N, 109.1°W). The site is located at an elevation of 1330 m and is a mixture of Chihuahuan Desert shrubland and arid grassland. Within the site there are twenty-four 0.25-ha experimental plots. These plots have been censused monthly for rodents since 1977. We used the data from 1978 to 2003. Rodents were marked, which allowed us to count each individual rodent only once during each year in which it was captured. Each plot contains 16 permanently marked 0.25-m^2 quadrats that have been censused annually for plant species composition since 1989. We used data ending in 2002. [For additional details on the data and experimental design, see Brown (1998).] We used the aggregated data from the eight unmanipulated control plots for our analyses. Two plant species represented by only a single individual during the entire study were excluded from analyses because of difficulties in estimating statistical parameters from a single observation.

Population patterns

Aggregation

One reason that the Poisson model often fails to characterize the observed patterns is that it assumes no intra-annual clustering of the individuals of a species. There are a number of reasons to think that individuals of species might tend to cluster in space and time (e.g. resource heterogeneity, facilitation, dispersal limitation). We used the Morisita index of aggregation (I_M) to determine if individuals of different species are more aggregated than expected from a random distribution of individuals (Morisita, 1959; Hurlbert, 1990). The value of I_M indicates how many times more likely it is that two randomly chosen individuals of the same species will occur in the same year compared with the expected probability for a random distribution of individuals. In addition, for each population time-series we compared the fits of the Poisson distribution and the negative-binomial distribution to the distribution of abundance among years. The Poisson model assumes that individuals are randomly distributed along the time-series, whereas the negative-binomial allows for aggregation (see Appendix 1 for more details). Since these two models are nested, we determined whether including aggregation improved the fit to the data using a likelihood ratio test (Eliason, 1993; Hilborn and Mangel, 1997; Haefner, 2005), thus yielding one test for each species.

Autocorrelation

Another factor generating non-random structure in the distribution of individuals through time is temporal autocorrelation. We determined the significance of autocorrelation at different lags (up to one half the length of the time-series) by randomizing the order of the abundance values for each species 10,000 times. We then calculated Bonferroni-corrected confidence limits about zero by determining the range of autocorrelation values that includes 99.6% of the randomizations for the plants and 99.8% of the randomizations for the rodents (these values represent $100 \times [1 - 0.05/(\text{maximum lag})]$; that is, we distributed the 5% Type 1 error rate evenly across the analysed lags). Species with autocorrelation values falling outside these limits at any lag were considered to exhibit significant temporal autocorrelation. We take this randomization approach in an attempt to avoid problems associated with the relatively short length of our time-series and the resulting use of lags > $n/4$ [for a similar analysis in a spatial context, see Ganio *et al.* (2005)]. The Bonferroni correction for this type of analysis is conservative (Legendre and Legendre, 1998), and this is reflected in the fact that these results are conservative compared with a more standard approach to calculating confidence intervals on autocorrelation that assumes a large number of steps in the time-series and the analysis of lags no longer than 25% of the time-series (Diggle, 1990).

Interspecific association

The final major pattern that may be present in the distribution of individuals along a time-series is interspecific association. That is, some combinations of species may be either more or less likely to co-occur than expected by chance. We evaluate the presence of interspecific association in the time-series using Ives' C (Ives, 1988, 1991), which measures the proportional change in the number of individuals of two species co-occurring in the same patch relative to that expected if the two species were distributed independently. The significance of C-values was determined using Spearman rank correlations (Ives, 1991) controlling the false discovery rate (Benjamini and Hochberg, 1995) at 0.05 using Benjamini and Hochberg's (2000) approach to estimate the number of true null hypotheses. This approach is ideal for this study, because we are primarily interested in the number of significant C-values, not whether any particular C-value is significant [for a good introduction to false discovery rate control, see Verhoeven *et al.* (2005)].

Modelling the species–time relationship

The first step in constructing a species–time relationship is to estimate the number of species present in a given time span of observation. We used a sliding window approach where species richness was determined for every possible window of each time span (e.g. for a 20-year time-series there would be 20 one-year windows, 19 two-year windows, etc.). These values were then averaged within each time span. There are other approaches to constructing species–time relationships (Carey *et al.*, 2007). We chose this approach because it focuses on average turnover patterns, but because richness remains relatively constant at the site through time (Ernest and Brown, 2001; Goheen *et al.*, 2005, 2006), the different construction methods will produce similar results (Carey *et al.*, 2007). We then used information on patterns in the population time-series to build models of the observed species–time relationship of increasing complexity. We started with a statistical model of random placement, then allowed that model to include intra-annual aggregation, and finally we added the effects of

either inter-annual autocorrelation or interspecific association using randomization methods. We did not add both autocorrelation and association together because, given our randomization approach, it would have completely constrained the results and by definition produced the observed pattern.

Random model

The most basic null model for the species–area relationship and the species–time relationship is that individuals of each species are assumed to be distributed randomly with respect to spatial or temporal coordinates. This model has been discussed in the literature for over 80 years and is typically modelled as a sum of binomial processes (Arrhenius, 1921; Coleman, 1981; Plotkin *et al.*, 2000; White, 2004). This approach constrains the total number of individuals of each species along the time-series to be equal to the number actually observed. An alternative approach to modelling random placement is to use a Poisson-based model (Storch *et al.*, 2003). Although there is some support for random placement models at small spatiotemporal scales, they typically fail to explain the observed patterns of aggregation and hence the observed species–area relationship/species–time relationship at large spatial/temporal scales (Rosenzweig, 1995; Plotkin *et al.*, 2000; Storch *et al.*, 2003; White, 2004).

We present results for the simple Poisson model where the expectation for species richness, S, as a function of time span, T, is

$$\langle S(T) \rangle = S_0 - \sum_{i=1}^{S_0} e^{-n_i T/T_0} \tag{1}$$

where S_0 is the total number of species occurring over the time span of the entire study (T_0), n_i is the total number of individuals of the ith species over T_0, and T is the time span of observation. This is equivalent to taking Wright's (1991) simplest probability of occurrence model, assuming independent probabilities of occurrence in neighboring time periods, and then summing across species. For details of model development, see Appendix 1.

Aggregation model

There are many approaches to quantifying and modelling aggregation within species when it exists (e.g. Krebs, 1998; Kunin, 1998; Plotkin *et al.*, 2000). Here we use one of the most popular approaches – the negative-binomial distribution (e.g. Wright, 1991; He and Gaston, 2000; He and Hubbell, 2003). If we assume that:

i.   within each year the observed number of individuals of a species at a site is a Poisson process with an expected value of λ (i.e. an average density of λ individuals occurs in a single year),
ii. λ can vary from year to year,
iii. λ values are independent between years, and
iv. that the distribution of λ values follows a gamma distribution,

then the distribution of observed abundances for each species is described by a negative-binomial distribution, since the negative-binomial is given by the combination of the gamma and the Poisson (Hilborn and Mangel, 1997). Assuming species' densities, λ_i, are independent of one another and summing the probabilities of occurrence across species, we can calculate the expected richness for a given time-scale as

$$\langle S(T)\rangle = S_0 - \sum_{i=1}^{S_0} \left(1 + \frac{n_i}{k_i T_0}\right)^{-k_i T} \tag{2}$$

where k_i is the aggregation parameter from the negative-binomial distribution (this parameter is often notated as r in other fields) for the ith species determined over the minimum time-scale (one year in this study). This parameter was estimated using maximum likelihood estimation (Appendix 1). The Poisson distribution used for random placement of individuals is the limiting case of the negative-binomial as k goes to infinity (Appendix 1). This approach represents a first-order model for temporal turnover. If the assumptions regarding the independence of λ of different species and time periods are violated, then more complex models will be necessary. For details of model development, see Appendix 1.

Equation (2) differs from previous negative-binomial-based models for species–area relationships and for changes in the probability of occupancy of individual species with scale (He and Gaston, 2000; see equation (1) in He and Hubbell, 2003). In our approach, we calculate an estimate of k at the unit time-scale and then calculate the expected species richness based on T independent draws for each species from the negative-binomial. Alternatively, He and Gaston's (2000) approach re-normalizes the data to a unit time-scale of T (i.e. for a 5-year time span it aggregates individuals into 5-year bins) and then calculates the expected species richness. However, because k will likely be dependent on the unit scale (He and Hubbell, 2003), it would be necessary to estimate k for each species for every time-scale. Alternatively, if k changes in some regular manner with time-scale, we could use a statistical model for k combined with He and Gaston's (2000) original formulation (He and Hubbell, 2003). Regardless, the annual time-scale makes biological sense for these communities (see Discussion) and this approach allows us to distinguish between annual scale aggregation and inter-annual temporal autocorrelation.

Any improvement in the fit of the negative-binomial model over the Poisson model can be attributed to the influences of intra-species temporal aggregation on the species–time relationship. We assessed whether the negative-binomial distribution provided a reasonable approximation of the temporal aggregation within the data by bootstrapping the abundance data for each species to construct species–time relationships based on randomly drawn abundance values for each year for each species from the species distribution of observed values. Having determined that the negative-binomial distribution provided a satisfactory characterization of the aggregation, we compared the fits of the negative-binomial-based species–time relationships with the fits of the Poisson-based species–time relationships using likelihood ratio tests. This was done by calculating the probability of a given number of species in a particular time span for each of the two models and taking the product of these probabilities to obtain the likelihoods for each model at the maximum likelihood estimates of each population's parameters. We used the algorithm developed by Storch *et al.* (2003) to calculate the probabilities of all species richness values for each time span and then compared the models using a standard likelihood ratio test. Richness values for all possible windows (not just the averages) were used for this test because integer richness values are necessary for the calculation of the likelihoods. Tests using rounded window averages produced similar results. It should be noted that the data points in the species–time relationship are not strictly independent, leading to potential overestimation of the degrees of freedom.

Temporal autocorrelation + aggregation model

We used randomizations of the species × year matrix to assess how temporal auto-correlation and intraspecific aggregation combine to influence observed patterns of species turnover. We randomly rotated the rows of the observed species × year matrix. We did this by making the matrix into a cylinder with the last year of the time-series neighbouring both the first year and the next to last year of the time-series and then rotating each row by a random number of positions. This preserved the temporal autocorrelation and intraspecific aggregation within each species, but removed any non-random interspecific association. We performed this randomization 10,000 times. After each randomization, we broke the cylinder and generated the species–time relationship. Results represent an average value for each time span across all randomizations. This approach preserves some of the auto-correlation structure in the original time-series but not all of it because the original series will be broken at different points depending on the randomization. On average, the propor-tion of structure preserved for any given lag will be equal to the difference between the length of the time-series and the lag divided by the length of the time-series. Because the length of the time-series can influence the amount of autocorrelation structure preserved, we analyse the rodent time-series in two ways: (1) using all 26 years of data and (2) using only the most recent 14 years of data to allow for direct comparisons with the plants (which only have a 14-year time-series).

This approach to including autocorrelation is a useful first step, but does result in the inclusion of somewhat arbitrary amounts of autocorrelation at different lags. In the future, further development of statistical models may allow for greater control over the specifics of autocorrelation. For the time being, one special case of the inclusion of autocorrelative structure is worth noting. Were we to preserve all of the autocorrelative structure, by measuring the species–time relationship on the cylinder (i.e. without breaking the cylinder measure average richness at all possible time-scales), we would get back precisely the observed relationship, because the unbroken series provides species relative occupancies at all scales, which is entirely sufficient to generate the relationship between mean species richness and time span (Sizling and Storch, 2004). The longer the time-series, the greater the amount of structure preserved and the more constrained the randomization results will be.

It is also worth noting that temporal autocorrelation can be caused by two arguably distinct sub-patterns: (1) persistence, where an individual that is present at the site in one year is also present in the following year; and (2) autocorrelated replacement of individuals, where the individuals in one year are distinct from those in the next year (White, 2007). Because we are dealing with annual plants and short lived rodents [only about 10% of the rodents persist at the site for periods longer than one year (K.M. Thibault and J.H. Brown unpublished data)], the second process is likely to be the primary contributor to observed autocorrelation (White, 2007).

Interspecific association + aggregation model

To assess the combined effects of intraspecific aggregation and interspecific association on turnover, we randomized the position of single-year communities in the time-series. In other words, we randomized the position of the columns in the species × year matrix, preserving the combinations of species that were present in any given year but breaking up any relationship between the abundance/presence of a species between neighbouring years. This is equivalent to Rosenzweig's (1995) 'scattered sub-plot analysis' for the species–area

relationship. We performed this randomization 10,000 times and present an average value for each time span.

RESULTS

As expected, the Poisson model performed poorly for both communities in describing individual species distributions of abundance. This is reflected in the fact that all species of both plants and rodents at the site had I_M values greater than 1, indicating that individuals were more aggregated than expected by chance (Fig. 1). This aggregation is generally well described by the negative-binomial distribution (Fig. 1), and likelihood ratio tests confirm that the negative-binomial represents an improvement over the Poisson for the vast majority of species (90%; Appendix 2).

In addition to aggregation, there was significant temporal autocorrelation present in the abundance time-series of the majority of rodent species (57%; Fig. 2). However, autocorrelation was much less common in the plant species time-series, with only 10% of species demonstrating significant values at any lag (Fig. 2). Pairwise tests for interspecific association showed that it was detectable only rarely in both assemblages (plants: 8.5% of pairs; rodents: 6.7% of pairs).

The results of the statistical tests just described indicate what types of pattern in the abundance time-series exist and therefore have the potential to influence observed patterns of temporal turnover. However, since our goal is to evaluate the importance of these patterns in generating the species–time relationship, we need to look at how these different non-random behaviours affect the observed species–time relationship. The Poisson model provides the poorest fit to the observed species–time relationships. The model substantially overestimates species richness at short time-scales, converging on the observed pattern only at time-scales close to that of the entire time-series, which because of the finite nature of the data set is constrained to occur (White, 2004) (Fig. 3). The negative-binomial distribution provides an improvement over the Poisson model, with realistic estimates of species richness at both short and long time-scales, though in both communities it still overestimates species richness at intermediate time-scales (Fig. 3). Likelihood ratio tests comparing the fits of the observed species–time relationships to those predicted by these two models indicate that this improvement in fit to the species–time relationship is highly significant for both communities (both P-values $< 10^{-10}$). In addition, species–time relationships generated using bootstrap resampling of the observed abundance distributions look almost identical to those modelled using the negative-binomial distribution (Fig. 3). This random resampling of the observed abundances for each species removes the effects of auto-correlation and interspecific association, without assuming a particular statistical form for aggregation. As such, this result suggests that the choice of the negative-binomial to characterize observed aggregation is satisfactory for these communities.

Permuting the species × year matrix to evaluate the expected patterns of temporal turnover resulting from combining aggregation with either interspecific association or temporal autocorrelation produced different results for the annual plants and the rodents. Visually comparing our randomization results to the species–time relationship for both communities suggests that incorporating interspecific association into the species–time relationship by randomizing the years of the time-series produced little improvement over aggregation alone (randomizing the years of the time-series for each species independently) in either data set (Fig. 3). Incorporating temporal autocorrelation by rotating the rows of the
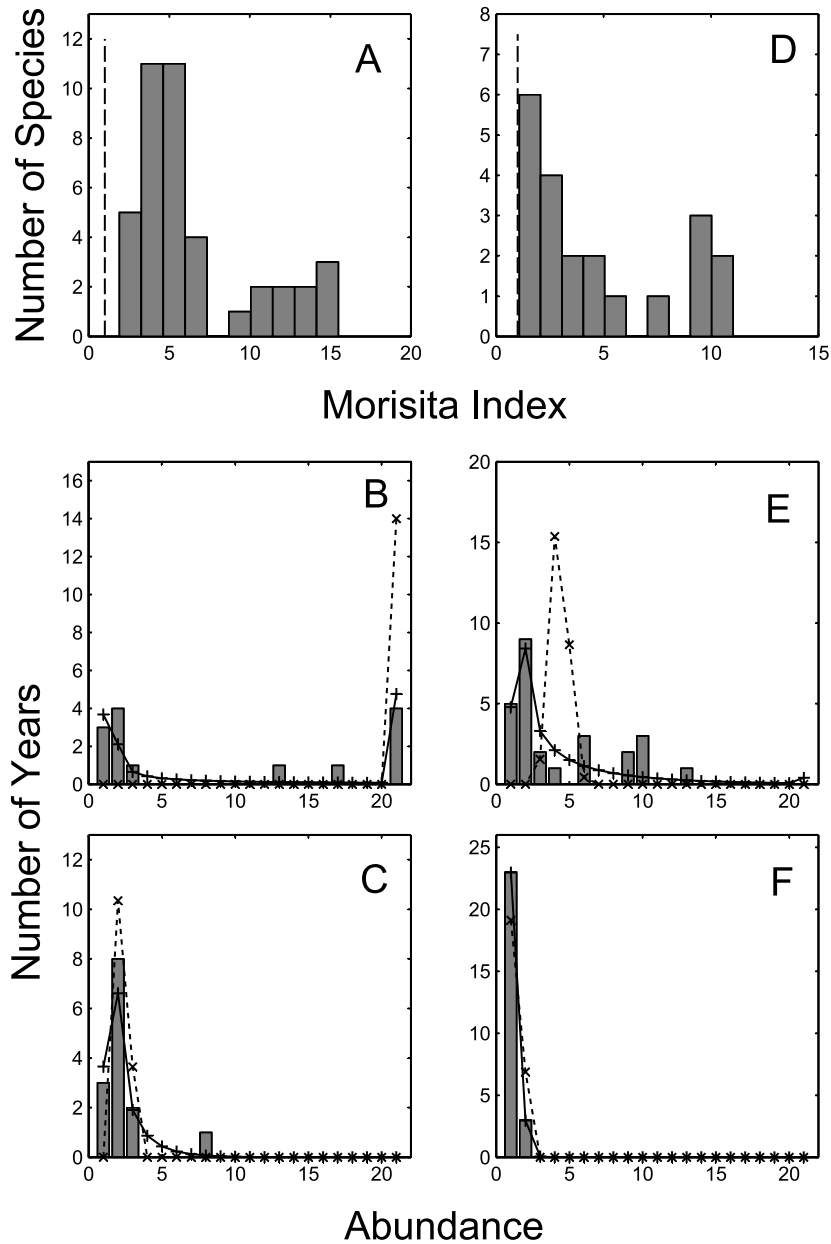
Fig. 1. Histograms of the values of the Morisita aggregation index for all species of plants (A) and animals (D) and examples of the distribution of individual species of plants (B, *Aristida adscensionis*; C, *Sida spinosa*) and rodents (E, *Dipodomys spectabilis*; F, *Chaetodipus intermedius*) and the fit of the Poisson (dotted lines and ×) and negative-binomial (solid line and +) models. In A and D the fact that all values are greater than 1 (they all occur to the right of the dotted line) shows that all species are more aggregated than would be expected from a random distribution of individuals.
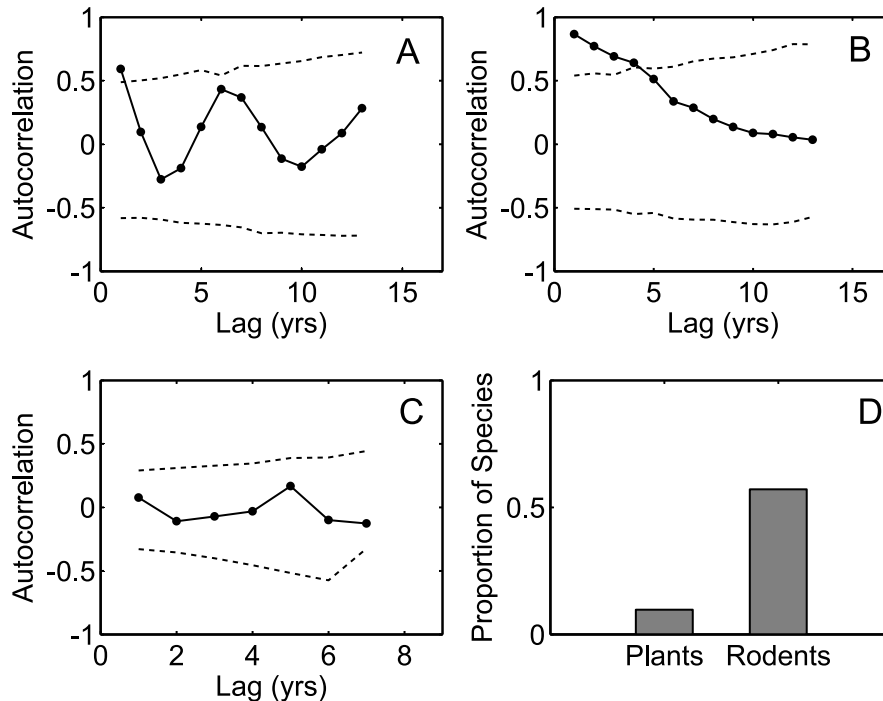
Fig. 2. Example temporal correlograms for three species (A, *Dipodomys ordii*; B, *Dipodomys specta-bilis*; C, *Tidestromia lanuginose*). The solid line is the observed autocorrelation and the dotted lines are the Bonferroni-corrected 95% confidence intervals based on randomization of the time-series. A summary of the proportion of plant and rodent species from Portal, AZ exhibiting significant temporal autocorrelation in abundance is also shown (D).

species × year matrix improved the fit of the species–time relationship somewhat in the plant community, but this randomization still overestimated species richness at intermediate time-scales. For the rodent community, however, this randomization produced an average species–time relationship very similar to that of the observed data (Fig. 3). While the fit of the randomizations to the rodent data decreased when only the most recent 14-year period was analysed, the rodent data still showed a noticeably improved fit compared with the plant data (Fig. 4).

DISCUSSION

Attempts to understand the species–time relationship and other temporal turnover patterns have thus far focused primarily on species-level patterns (e.g. Diamond and May, 1977; Rosenzweig, 1995; Russell *et al.*, 1995; Adler *et al.*, 2005; White *et al.*, 2006; Carey *et al.*, 2007; White, 2007). However, recent work on the species–area relationship suggests that examining patterns in the abundance of individuals of the component species can allow for additional insights into the under-lying processes (e.g. Plotkin *et al.*, 2000). These spatial studies have concentrated on the spatial aggregation of individuals (He and Legendre, 2002; Green and Ostling, 2003). They suggest that com-bining the abundance distribution with aggregation may be sufficient to characterize observed spatial patterns (Plotkin *et al.*, 2000; Harte *et al.*, 2005). Here we have applied this general
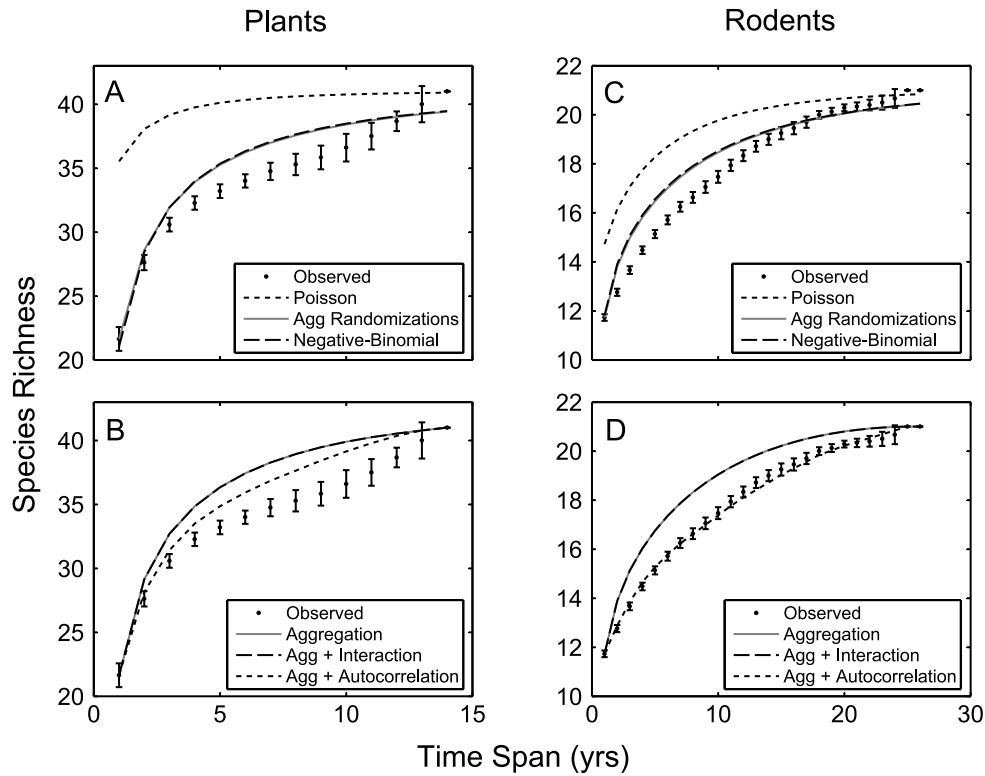
Fig. 3. Species-time relationship patterns for the summer annual plant and rodent communities at Portal, AZ, from 1989 to 2002 and 1977 to 2003 respectively. (A, C) Observed pattern and statistical models. (B, D) Observed pattern and randomizations for aggregation, aggregation + interspecific association, and aggregation + temporal autocorrelation.
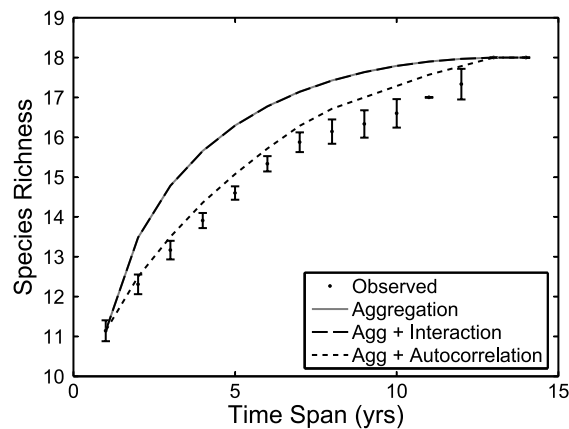

Fig. 4. Species–time relationship pattern for the rodent community at Portal, AZ, including the observed pattern and randomizations for aggregation, aggregation + interspecific association, and aggregation + temporal autocorrelation, from the most recent 14 years of the study.

approach of evaluating patterns in the distribution of individuals in an attempt to better understand the temporal structure of two desert communities.

Three primary patterns governing the distribution of individuals can be expected to influence the species–time relationship: (1) non-random aggregation/dispersion of individuals (at the unit time-scale); (2) temporal autocorrelation in the abundance of individual species; and (3) interspecific association. Our analyses suggest that intraspecific aggregation and temporal autocorrelation have important influences on the species–time relationship. There are many reasons to expect non-random aggregations of individuals in time. These include social behaviours, variability in environmental conditions, and population processes. However, it appears that this aggregation alone is insufficient to describe the observed species–time relationship. The importance of autocorrelation is not surprising since population processes should generate autocorrelations in abundance, and substantial data demonstrate non-random autocorrelation patterns in population time-series (e.g. Inchausti and Halley, 2001).

Although significant autocorrelation was present in some species of both plants and rodents, a much greater percentage of the rodent community exhibited autocorrelation (Fig. 2). In addition, incorporating the influence of temporal autocorrelation into randomizations of the time-series produced results very similar to observed values for the rodent species–time relationship, but not the plant species–time relationship (Fig. 3). The difference likely results from differences in the life histories of annual plants and mammals. By definition, individual annual plants do not persist from year to year in the community. The community in any one year is tied to the community in previous years through the seed bank. This results in the ability of plant communities to respond rapidly to changes in environmental conditions. Consequently, if the environment (broadly interpreted to include animal influences on the plant community) is not temporally autocorrelated, then the plant community would not be expected to be strongly autocorrelated. On the other hand, the population of a rodent species in any particular year is more directly related to that in the previous year, because many of the new individuals in the community will be the offspring of the individuals that were present in the community in the previous year. In addition, some of the individuals from the previous year will still be alive, resulting in additional autocorrelation. In general, we may expect temporal autocorrelation in individual populations to be more important for generating turnover patterns in animal communities than in plant communities, and to be more important in communities that have overlapping generations and long life spans.

We have treated aggregation and autocorrelation as two distinct patterns (He and Gaston, 2000). For temporal analyses, especially of short-lived species, this makes sense because processes generating these two patterns could operate fairly independently. For example, if environmental conditions were not temporally autocorrelated, inter-annual environmental variation could produce aggregation without autocorrelation. However, these patterns could also be related to one another and studies of spatial aggregation sometimes generate both aggregation within cells and autocorrelation between them (Plotkin et al., 2000; Sizling and Storch, 2004; Harte et al., 2005). As such, these patterns are not necessarily independent of one another. Future models should attempt to address this relationship more directly.

Our analyses suggest that in general correlated abundances among species were not important in generating the observed species–time relationship in these two communities. Non-random associations between species can result from several processes, including competition, mutualistic interactions, and similar or dissimilar environmental tolerances

(Diamond, 1975). Resulting correlations between species abundances were observed in less than 10% of species pairs. In addition, analyses of the relative strength of intraspecific aggregation and interspecific association (see Ives, 1991; Jaenike and James, 1991; Shorrocks and Sevenster, 1995 for methodological details) show that aggregation is more important for the vast majority of species (plants: 98%; rodents: 95%). Therefore, even in cases where interspecific correlations are present, they may be too weak to have a detectable impact on the species–time relationship. However, it should be noted that interactions among species can be difficult to detect using these types of simple statistical approaches because they can be far more complex than simple pairwise interactions. For example, multiple species can interact in triplets, quadruplets, and so on, and there can be time lags in these interactions. Future attempts to model the species–time relationship should consider these possibilities.

To date almost all of the work on the species–time relationship has been based on purely statistical descriptions of the observed patterns (Rosenzweig, 1995; Adler and Lauenroth, 2003; White *et al.*, 2006). Although this approach has proved useful in quantifying patterns of turnover (Rosenzweig, 1995; Russell *et al.*, 1995; Fridley *et al.*, 2006; White *et al.*, 2006), it has done little to elucidate the underlying processes (White, 2007). Given the large number of processes that go into determining the dynamics of single species, we might expect the observed species–time relationship to be largely dependent on the specific configuration of the community and ecosystem. However, it appears that the species–time relationship behaves in a surprisingly regular way across different taxonomic groups and ecosystems (Adler *et al.*, 2005; White *et al.*, 2006; White, 2007). The challenge then becomes understanding how these fairly general patterns of turnover can emerge from the complex behaviours of multiple species' populations. This study suggests that observed patterns of turnover are generated predominantly by intraspecific aggregation at the time-scale of a single year. As such, regularity in the degree of temporal aggregation among different communities could result in the consistent behaviour of temporal turnover. These conclusions represent an important bridge between population and community patterns, suggesting that mechanistic models of the species–time relationship should focus on processes generating aggregation. In addition, it could be that making predictions about community turnover patterns may not require a strictly mechanistic understanding of how aggregation is generated, but simply a reasonable understanding of what the distribution of aggregations across species in a community will look like based on knowledge about life history and the environment.

Understanding the species–time relationship is essential for a broader understanding of the dynamic nature of ecological systems. Here we have attempted to offer new insights into the processes underlying the species–time relationship by evaluating how this community-level pattern results from the non-random behaviour of the composite populations. It is our hope that an increased understanding of how patterns in the population dynamics of individual species combine to generate observed patterns of temporal turnover will eventually allow us to determine the ecological processes underlying community dynamics.

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APPENDIX 1: DETAILED MODEL DEVELOPMENT

Poisson

We assume that the individuals of each species are randomly distributed (Poisson) along the time-series. Therefore, the probability of N individuals of a species occurring in a time span of length T (i.e. the probability density function for the Poisson) is

$$\Pr(n_{i,T} = N \mid n_i, T) = \frac{(n_i T/T_0)^N}{N!}\, e^{-n_i T/T_0},$$ (1)

where n_i is the total number of individuals occurring over the entire time-series, and T_0 is the length of the time-series being analysed. Therefore, the probability that no individuals of a particular species will occur in a time span of T years is

$$\Pr(n_{i,T} = 0 \mid n_i, T) = e^{-n_i T/T_0},$$ (2)

and the probability that the species i is present in a time span of T years (i.e. the probability that $n_{i,T} > 0$) is

$$\Pr(n_{i,T} > 0 \mid n_i, T) = 1 - e^{-n_i T/T_0}.$$ (3)

Since the expected species richness is simply the sum over the probabilities that each species will be present,

$$\langle S(T) \rangle = S_0 - \sum_{i=1}^{S_0} e^{-n_i T/T_0},$$ (4)

where S_0 is the total number of species occurring over the entire time-series.

Negative-binomial

For this model, we assume that individuals are distributed based on a negative-binomial process, based on assumptions given in the text. Therefore, the probability of N individuals of a species occurring in a time span of length T (i.e. the probability density function for the negative-binomial distribution) is

$$\Pr(n_{i,T} = N \mid n_i, k_i, T) = \frac{\Gamma(k + N)}{\Gamma(k)\Gamma(N + 1)} \left(1 + \frac{n_i}{k_i T_0}\right)^{-k_i T},$$

and the probability that no individuals of a particular species will occur in a time span of T years is

$$\Pr(n_{i,T} = 0 \mid n_i, k_i, T) = (1 + n_i/(k_i T_0))^{-k_i T}, \tag{5}$$

where k_i is the aggregation parameter of the negative-binomial distribution determined using Nelder-Mead maximum likelihood estimation (implemented in Matlab's fminsearch function). Therefore, the probability that the species i is present in a time span of T years (i.e. the probability that $n_{i,T} > 0$) is

$$\Pr(n_{i,T} > 0 \mid n_i, k_i, T) = 1 - (1 + n_i/(k_i T_0))^{-k_i T}. \tag{6}$$

Since the expected species richness is simply the sum over the probabilities that each species will be present,

$$\langle S(T) \rangle = S_0 - \sum_{i=1}^{S_0} \left(1 + \frac{n_i}{k_i T_0}\right)^{-k_i T}. \tag{7}$$

Likelihoods

For statistical purposes, we need to know the probability of all possible species richness values for a given set of n_i. The probability of species richness S is equal to the probability of all possible combinations of S and only S species occurring in span T given the probabilities of occurrence of each individual species, or

$$P_{S,T} = \sum \left[\prod_{i=1}^{S} \Pr(n_{i,T} > 0) \prod_{j=S+1}^{S_0} (1 - \Pr(n_{i,T} > 0)) \right], \tag{8}$$

where Σ is related to all possible combinations of S species. [See Storch *et al*. (2003) for a more detailed description of the calculation of these probabilities. These probabilities were calculated using the counting method derived and implemented by Storch *et al*. (2003) (see their appendix).]

The likelihoods of the random and aggregation models where calculated as

$$L(\text{model} \mid \hat{\theta}) = \prod_T P_{S,T}(S \mid \hat{\theta}, T).$$

The likelihoods of the Poisson and negative-binomial models were calculated by taking the product of $P_{S,T}$ over all of the data points in the species–time relationship (not the averages for the windows), because integer richness values are necessary for the calculation, so we actually calculate the likelihood as

$$L(\text{model} \mid \hat{\theta}) = \prod_T \prod_a P_{S,T}(S \mid \hat{\theta}, T),$$

where a indexes the different windows for each time span, and $\hat{\theta}$ is the vector of the maximum likelihood estimates of the parameters for either the Poisson or negative-binomial model. We also calculated likelihoods based on the average richness values by rounding richness to the nearest integer, and by selecting a single richness value for each time span. The results of these two analyses were qualitatively similar to those reported (i.e. highly significant).

Clearly, the different time spans are not independent of one another, causing problems for this approach as well as more conventional statistics (White, 2007). However, the results are so significant that it is extremely unlikely that this influences the conclusions of the analysis.

APPENDIX 2: RESULTS OF THE STATISTICAL ANALYSES OF THE DISTRIBUTION OF ABUNDANCES

The likelihood ratio P-value is from likelihood ratio tests comparing the fits of the Poisson and negative-binomial distributions to individual population time-series. The null hypothesis is that the negative-binomial model does not provide an improved fit to the distribution compared with the Poisson model. The test is based on a chi-square approximation of the likelihood ratio (Eliason, 1993). Autocorrelation lags are the time lags at which significant temporal autocorrelation exists for each species. [See text for details of how significant autocorrelation was determined.]

Table A1. Results of statistical analyses of the distribution of abundances through time for the rodent community at Portal, Arizona

Species	Abundance	Likelihood ratio P	Autocorrelation time lags
Baiomys taylori	3	1.36×10^{-1}	—
Dipodomys merriami	3118	$\leq 10^{-10}$	1
Dipodomys ordii	1092	$\leq 10^{-10}$	1
Dipodomys spectabilis	743	$\leq 10^{-10}$	1–4
Neotoma albigula	368	5.16×10^{-10}	1
Onychomys leucogaster	332	$\leq 10^{-10}$	1–5
Onychomys torridus	766	$\leq 10^{-10}$	1
Chaetodipus baileyi	543	$\leq 10^{-10}$	1–2
Chaetodipus hispidus	8	5.64×10^{-2}	—
Chaetodipus intermedius	8	5.47×10^{-5}	—
Chaetodipus penicillatus	1084	$\leq 10^{-10}$	1–3
Perognathus flavus	342	$\leq 10^{-10}$	1
Peromyscus leucopus	3	1.36×10^{-1}	—
Permomyscus eremicus	253	$\leq 10^{-10}$	—
Peromyscus maniculatus	112	$\leq 10^{-10}$	—
Reithrodontomys fulvescens	5	1.82×10^{-3}	—
Reithrodontomys megalotis	346	$\leq 10^{-10}$	11
Reithrodontomys montanus	3	1.36×10^{-1}	—
Sigmodon fulviventer	27	4.44×10^{-10}	13
Sigmodon hispidus	42	3.17×10^{-9}	—
Sigmodon ochrognathus	8	8.13×10^{-3}	—

Table A2. Results of statistical analyses of the distribution of abundances through time for the plant community at Portal, Arizona

Species	Abundance	Likelihood ratio P	Autocorrelation time lags
Amaranthus palmeri	647	$\leq 10^{-10}$	—
Ambrosia artemisifolia	31	3.00×10^{-4}	—
Aristida adscensionis	8992	$\leq 10^{-10}$	1
Bahia biternata	11	2.07×10^{-3}	—
Baileya multiradiata	111	$\leq 10^{-10}$	—
Boerhaavia intermedia	2450	$\leq 10^{-10}$	—
Boerhaavia coulteri	52	$\leq 10^{-10}$	—
Boerhaavia torreyana	598	$\leq 10^{-10}$	—
Bouteloua aristidoides	106386	$\leq 10^{-10}$	1
Bouteloua barbata	4111	$\leq 10^{-10}$	—
Cassia leptadenia	24	3.66×10^{-15}	—
Chenopodium fremontii	19	2.55×10^{-5}	—
Crotalaria pumila	439	$\leq 10^{-10}$	—
Dalea brachystachys	357	$\leq 10^{-10}$	—
Dithyrea wislizenii	3	7.24×10^{-3}	—
Eragrostis arida	42	$\leq 10^{-10}$	—
Eragrostis cilianensis	10	$\leq 10^{-10}$	—
Erigeron divergens	18	1.52×10^{-9}	—
Eriochloa lemmoni	120	$\leq 10^{-10}$	—
Eriogonum abertianum	2996	$\leq 10^{-10}$	—
Erodium cicutarium	76	$\leq 10^{-10}$	—
Euphorbia ?	8	8.49×10^{-2}	—
Euphorbia micromera	193	$\leq 10^{-10}$	—
Euphorbia serpyllifolia	1840	$\leq 10^{-10}$	—
Euphorbia serrula	218	$\leq 10^{-10}$	—
Haplopappus gracilis	4098	$\leq 10^{-10}$	—
Ipomoea costellata	18	$\leq 10^{-10}$	—
Kallstroemia grandiflora	53	$\leq 10^{-10}$	—
Machaeranthera tanreafolia	41	$\leq 10^{-10}$	—
Mollugo cerviana	1177	$\leq 10^{-10}$	—
Mollugo verticillata	222	$\leq 10^{-10}$	—
Panicum arizonicum	462	$\leq 10^{-10}$	—
Panicum hirticaule	683	$\leq 10^{-10}$	—
Panicum miliaceum	95	$\leq 10^{-10}$	—
Pectis papposa	1412	$\leq 10^{-10}$	1
Portulaca parvula	3352	$\leq 10^{-10}$	1
Sida spinosa	122	$\leq 10^{-10}$	—
Tidestromia lanuginosa	780	$\leq 10^{-10}$	—
Tragus berteronianus	3	2.79×10^{-1}	—
Trianthema portulacastrum	9	2.61×10^{-5}	—
Verbesina encelioides	8	2.45×10^{-3}	—