

REPORT

The power of time: spatiotemporal scaling of species diversity

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Abstract

The species–area relationship (SAR) provides the foundation for much of theoretical ecology and conservation practice. However, by ignoring time the SAR offers an incomplete model for biodiversity dynamics. We used long-term data from permanent plots in Kansas grasslands, USA, to show that the increase in the number of species found with increasing periods of observation takes the same power-law form as the SAR. A statistical model including time, area, and their interaction explains 98% of variation in mean species number and demonstrates that while the effect of time depends on area, and vice versa, time has strong effects on species number even at relatively broad spatial scales. Our results suggest equivalence of underlying processes in space and time and raise questions about the diversity estimates currently used by basic researchers and conservation practitioners.

Keywords

Biodiversity, community turnover, species–area relationship, species–time relationship, species richness.

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INTRODUCTION

Estimating the number of species in a community or ecosystem is a fundamental problem in basic and conservation ecology. Basic researchers use biodiversity estimates to study latitudinal diversity gradients, to test differences between local and regional richness, to construct species–area relationships (SARs) across many orders of magnitude, and as a response variable in manipulative experiments. Conservation ecologists use such estimates to prioritize conservation efforts (Myers *et al.* 2000) and predict species losses following habitat fragmentation (Pimm & Askins 1995; Brooks *et al.* 1997). Most of this work relies on the SAR to scale up-field measurements of diversity to broader spatial scales. However, these estimates ignore the possibility that species number may be as sensitive to the time period of observation as to the area sampled.

Preston (1960) proposed that the relationship between species number and the period of observation, the species–time relationship (STR), should be equivalent to that between species number and area sampled, the SAR. Confirmation of his conjecture would have important implications for biodiversity assessment and also for theory, because it would suggest that similar processes determine the distribution of species in space and time. Preston suggested three

mechanisms for generating the continuous accumulation of species on a given site, each operating at a different temporal scale: ‘sampling errors’ produce turnover at a scale of individual years, ecological change, such as succession or interannual variability in weather, causes species to accumulate over decades to centuries, and evolutionary change, encompassing speciation and extinction, operates over millennia.

Preston’s conjecture contains two separate predictions. First, the Arrhenius (1921) equations $S = cA^z$, where S is the species number and A is the area, should also describe the relationship between species number and time, T . For clarity, the scaling exponent z is changed to w in the STR. Second, Preston showed by example that the rate of species accumulation in time should vary with the spatial scale of observation, so that repeated sampling in a plot of a certain size would produce an STR with a scaling exponent equal to that of the SAR.

Preston’s first prediction, concerning the form of the STR, is generally supported by the few available long-term data. STRs for very short temporal records are concave down in log–log space, as they are for SARs based on small areas (Preston 1960; Rosenzweig 1995). Records longer than 15 years show that STRs for birds (Preston 1960; E. P. White unpublished data), lepidoptera (Preston 1948;

Rosenzweig 1995, 1998) and small mammals (Hadley & Maurer 2001) fit the Arrhenius equation, producing a linear relationship in log–log space ($\ln S = \ln c + w \ln T$), although their slopes, often > 0.3 , tend to be steep with respect to SARs based on nested samples (Rosenzweig 1995, 1998). Finally, at the scale of the fossil record, STRs remain linear in log–log space but their slopes steepen considerably (Preston 1960; Rosenzweig 1998; McKinney & Frederick 1999), analogous to the steep slopes of SARs for areas that span biogeographical provinces. Preston's second prediction has never been rigorously tested despite evidence of a time–area interaction (Jacquemyn *et al.* 2001). Moreover, although Preston's work suggests that species number should scale as a function of time, area and their interaction, no quantitative form of such a relationship has been proposed.

Our objective was to evaluate both of Preston's predictions about the STR using data on plant species composition from Kansas grasslands. We tested the functional form of the STR using a 35-year data set from central Kansas. To test the interaction between STRs and SARs that Preston's conjecture implies, we used an 18-year data set from tallgrass prairie in eastern Kansas.

METHODS

Hays data set

Albertson and colleagues (Albertson & Tomanek 1965) censused permanent 1 m² quadrats annually from 1938 to 1972 in three adjoining grassland communities near Hays, Kansas (38.8°N, 99.3° W). The shortgrass community, dominated by the C₄ grasses *Bouteloua gracilis* and *Buchloe dactyloides*, occurs on deep, loess soils on level uplands. Separated from the shortgrass by an ecotone, the little bluestem community, named for the dominant mid-sized C₄ grass *Schizachyrium scoparium*, occupies the shallow limestone soils of slopes and hilltops. During the period of record, the mean annual temperature was 12°C and the mean annual precipitation, falling mostly in April through September, averaged 577 mm.

We used digitized versions of the original Hays chart-quadrat maps and linked them to a GIS. Of the more than 60 permanent quadrats in the dataset, we used 15 with uninterrupted 35-year records. We deleted all taxa not identified to species, meaning our estimates of species number are conservative. This removed 143 individual plant records (from a total of more than 45 000 records) representing seven species, although 110 of these records belonged to one undetermined *Carex* species. Botanical synonyms were standardized according to the Great Plains Flora Association (1986). We generated STRs for individual plots, or aggregations of plots, by first calculating the mean

number of species, S_t , occurring in periods of consecutive years, t . In a 35-year record, there are 35 replicates for period $t = 1$, 34 replicates for $t = 2 \dots$ one replicate for $t = 35$. In most cases, replicate counts for each period were normally distributed.

As the species counts come from census data, and the detection probability of vascular plants in small quadrats should be uniformly close to 1, we assumed that the observed species counts are good estimates of true richness, and did not require more rigorous estimation discussed in Colwell & Coddington (1994) and Cam *et al.* (2002). We then used ordinary least squares regression to describe the linear relationship between $\ln S_t$ and $\ln t$, and compared the fit of these regressions to semi-log relationships of S_t on $\ln t$.

Note that because the data were nested, counts of species number at each time period were not independent, violating an assumption of regression. This violation does not invalidate the ordinary least squares estimator of the regression slope, which remains unbiased, but the estimate of variance in the slope is invalid. Therefore, we could not construct confidence intervals around the estimated slopes. This limitation also applies to the bivariate model we used for the Konza data, below.

To test whether the STRs were simply the result of random sampling from a stable community, species accumulation curves was constructed (Colwell & Coddington 1994, White unpublished data). We first summed all individuals by species over the plot's 35-year record (species sums), and also summed all individuals by year (year sums). For each year, we sampled individuals at random without replacement from the species sums until we had collected the appropriate number of individuals. Our choice of sampling without replacement reflects the use of census data and the corresponding assumption that the true number of individuals is known. After randomly sampling for all years, STRs were calculated as described above. Although the resulting curves were better fit by linear regressions in semi-log space, we used regressions in log–log space to enable comparison to the observed curves. We repeated this process 100 times for each quadrat and then compared the observed slope and intercept with the set of simulated parameters.

In July 2002, we sampled one Modified Whittaker plot (Stohlgren *et al.* 1998) in both the shortgrass and little bluestem communities to describe the contemporary SAR at Hays. To determine the slope of the SAR, we performed a linear regression through the mean number of species found at each scale of sampling (from 1 to 1000 m²).

Konza data set

Vegetation at the Konza Prairie Long-Term Ecological Research (LTER) site, located in eastern Kansas (39.1°N,

96.6° W), is dominated by tall warm-season grasses, primarily *Andropogon gerardii* (Knapp *et al.* 1998). Mean annual precipitation is 834 mm and mean annual temperature is 13°C. Sampling at Konza is stratified by fire and grazing treatments assigned at the watershed scale, and topographic position. We used data from the three watersheds with uninterrupted 18-year records: 1d (annual fires, no grazing), 4b (4-year fire return, no grazing), and 20b (20-year fire return, no grazing). Canopy cover of all species is estimated twice each year; we used the maximum value for each species in each year. We downloaded the Konza data from the Konza Prairie LTER website (<http://climate.konza.ksu.edu/>).

To explore the time—area interaction, we first calculated the STR for each of the 120 individual 10 m² subplots. Next, we generated STRs for larger areas by aggregating subplots by transect, soil type, watershed and the entire study area. This approach allowed us to calculate STRs for twenty-four 50 m² replicates, six 200 m² replicates, three 400 m² replicates, and one 1200 m² replicate. We also calculated SARs for time periods ranging from 1 to 18 years by taking the mean species richness found at each spatial scale in each time period. Finally, we modelled species

number as a function of time, area, and a time by area interaction.

Our model based on aggregated subplots will differ from one based on nested samples in two ways. First, the proportion of the total area sampled differs at each level of aggregation, which may introduce error. Second, because the subplots are not contiguous, the aggregations represent larger areas, and the SARs we calculated will overestimate α relative to SARs based on continuous, nested samples. We explore the consequences of underestimating α (see Discussion).

RESULTS

The form of the species–time relationship

Over the 35-year record at Hays, 103 species were recorded in the fifteen 1 m² quadrats. Species density (species richness per m² in a given year) increased over time in the shortgrass and ecotone communities, but not in the little bluestem community (Fig. 1a–c). The STRs for the individual quadrats were highly linear in log–log space: the lowest r^2

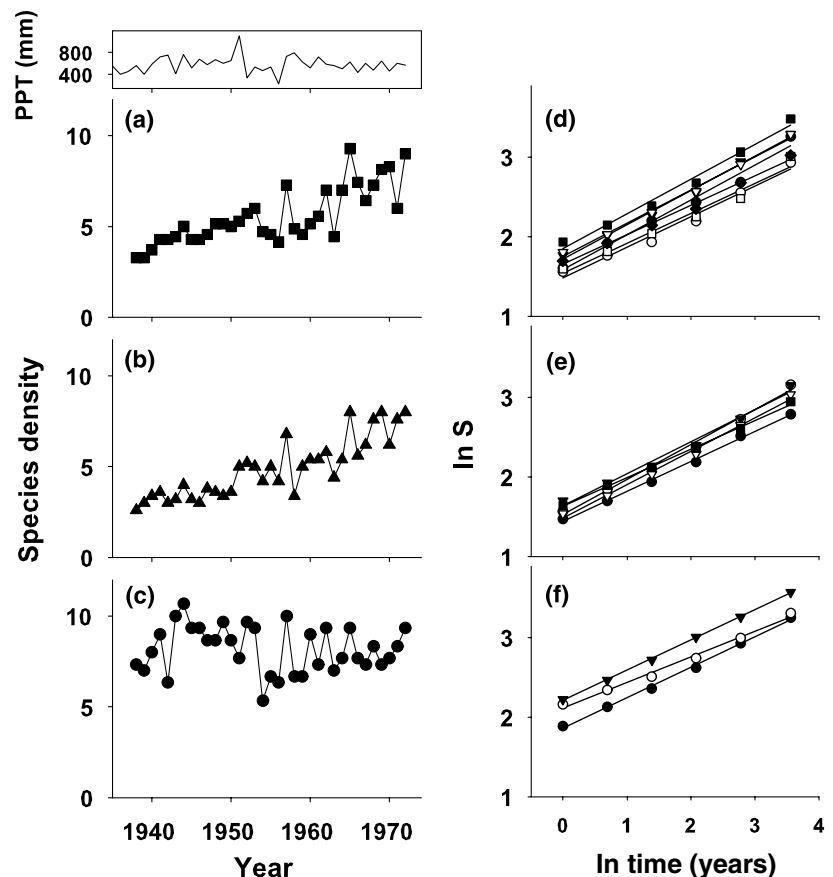


Figure 1 Species density and the species–time relationship in shortgrass (a, d), ecotone (b, e), and little bluestem (c, f) communities. Panels on the left show the mean number of species occurring in 1 m² quadrats in each year (shortgrass, $n = 7$; ecotone, $n = 5$; little bluestem, $n = 3$). For the panels on the right, symbols refer to individual 1 m² quadrats, with linear regressions shown for each quadrat. The small panel in the upper left shows annual precipitation.

from the linear regressions of $\ln S$ on $\ln t$ was over 0.96. The mean slope of the STRs was 0.42 in the shortgrass and ecotone quadrats (Fig. 1d,e), and 0.38 in the little bluestem quadrats (Fig. 1f). For every quadrat, the Arrhenius equation provided a better fit (higher r^2) than the semi-log regression of S on $\ln t$, with an average difference in r^2 of 0.11 for the shortgrass, 0.09 for the ecotone and 0.08 for the little bluestem quadrats. Another result which is true in every quadrat was that the slope of the observed STR was steeper and the intercept lower than in all simulated species accumulation curves ($n = 100$).

The slopes of the STRs for the Hays 1 m² quadrats are steep compared with slopes typical of published SARs (Rosenzweig 1995), and also with SARs for contemporary communities at the Hays site. Slopes of the SARs in the shortgrass and little bluestem communities determined by our field sampling were 0.23 ($r^2 = 0.98$, $P = 0.011$) and 0.22 ($r^2 = 0.97$, $P = 0.014$), respectively, much lower than the corresponding STR slopes of 0.42 and 0.38.

The species–time–area relationship

We used the Konza data set to explore how the slope of the STR would decrease as the size of the sampled plots increases. Plant species density showed no strong trends over the 18-year Konza record (not shown). Nevertheless, STRs calculated for each 10 m² plot were well-fit by power law functions, with values of w ranging from 0.19 to 0.42 (Table 1). As area sampled increased, the STRs remained linear in log–log space ($r^2 > 0.99$), but their intercepts increased and their slopes, w , decreased (Fig. 2a). This decrease in w was linear on $\ln A$ (Fig. 2c). Likewise, as the time period sampled increased, the SARs remained linear in log–log space ($r^2 > 0.98$) but their slopes decreased with $\ln T$ at virtually the same rate that w decreased with $\ln A$ (Fig. 2b,d). Modelling S as a function of time, area, and a time–area interaction, explained over 98% of the variation in

mean species number (Fig. 2e). In this model, the estimate of w at the 1 m² scale was 0.37, higher than the values for the individual 10 m² plots, and almost as high as w observed at the 1 m² scale at Hays. The significant interaction term, μ ($P = 0.0014$) gives the rate at which λ decreases with increasing time and w decreases with increasing area (Fig. 2b,d).

We emphasize that although time and area explained most of the variation in mean species number, there remained unexplained variation around the means. At a temporal scale of 1 year and a spatial scale of one plot (10 m²), the mean species number was 28.4. This mean was based on 120 plots censused in 18 periods each, or 2160 observations. Ignoring spatial and temporal correlations among these observations and treating them as independent, their SD was 10.6. Most of this variability comes from spatial sources: the SD of the 120 plots, first averaged over time period, was 9.8, while the SD of the 18 time periods, first averaged across plots, was only 1.9.

DISCUSSION

The form of the SAR and STR are equivalent

The Hays results confirm Preston's first prediction, that the form of the SAR and STR should be equivalent. The Arrhenius equation, the most widely used form of the SAR, described the increase in species number with increasing time periods of sampling better than a semi-log relationship for every Hays quadrat. This continuous accumulation of species with time is not a result of rarefaction, as the consistent differences between the parameters of the observed STRs and the simulated species accumulation curves demonstrate. The power law form of the Konza STRs and the similarity of their slopes, properly scaled, to those at Hays provide further support for the equivalence of form in the SAR and STR.

The steep slopes of the STRs in the Hays shortgrass and ecotone communities were the result of two processes, increases in species density, perhaps a recovery from the Great Drought of the 1930s, and turnover in species composition. In the Hays little bluestem quadrats and Konza plots, where species density did not increase with time, community turnover alone generated the STRs, which had slopes almost as steep as quadrats in the Hays shortgrass and ecotone communities. Such rapid turnover in species composition is striking, and illustrates the high frequency of local extinction and immigration events, at least at these fine spatial scales. Apparently, new species can easily enter a patch of established vegetation, a result with clear implications for invasions. However, it is important to recognize that in these communities, which are characterized by strong dominance, only a portion of the community

Table 1 Parameters of species–time relationships from Konza Prairie 10 m² circular permanent plots censused annually for 18 years (20 individual plots in each burning by topography treatment)

Fire frequency	Topographical position	Mean intercept	Range of		
			Mean	w	Mean r^2
1 year	Upland	3.24	0.28	0.19–0.35	0.995
	Lowland	3.17	0.30	0.23–0.37	0.995
4 years	Upland	3.42	0.34	0.24–0.40	0.995
	Lowland	3.28	0.35	0.31–0.42	0.995
20 years	Upland	3.40	0.32	0.22–0.40	0.990
	Lowland	3.29	0.35	0.27–0.41	0.995

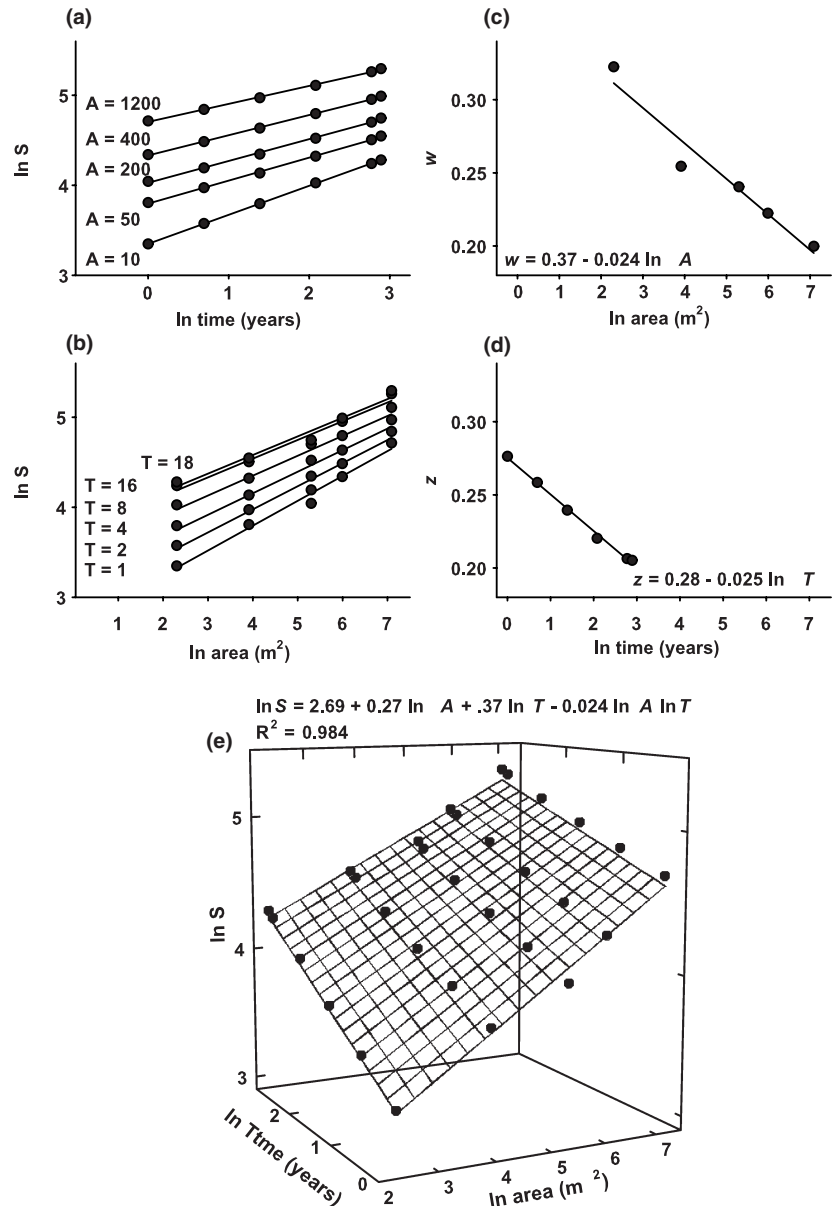


Figure 2 (a) Species–time relationships (STRs) calculated at increasing areas sampled, A , achieved by aggregating subplots at Konza Prairie. (b) Species–area relationships (SARs) for increasing periods of observation, T . (c) The relationship between area sampled and the mean slope of the STR, w . (d) The relationship between period of observation and the slope of the SAR, z . (e) Mean S as a function of time, area, and a time–area interaction term.

is turning over so rapidly. Of the 69 species that occurred over the record on the seven shortgrass quadrats, 16 appeared in only 1 year on only one quadrat, and 53 species had frequencies $< 5\%$. By contrast, the two dominant shortgrass species, with frequencies of 99 and 93%, were present in almost every quadrat in every year. Turnover of dominant species will also occur, but over longer time scales. In fact, *Andropogon saccharoides*, a native grass species never recorded at Hays during the 1938–1972 period, has expanded its range northward and now occurs in high densities in areas of the Hays shortgrass community (personal observation).

Scaling species number with time and area

The Konza data demonstrate that, as Preston suggested, the relative rate of species accumulation in space vs. time depends on scale: at small spatial scales, species accumulate faster in time than in space, but as the area sampled increases, species accumulation in time slows. The dependence of z on time scale and w on spatial scale makes Preston's prediction that these exponents will be equivalent somewhat trivial: in any system, we should be able to find a combination of scales at which $z = w$. However, identifying the spatial scale at which time–space equivalence occurs will

still be useful for cross-system comparisons, and also for marking the threshold at which time gives way to space as the dominant control on species turnover. For the Konza data, the interaction parameter w allows us to estimate the spatial scale at which the rate of accumulation of species in time and space is equal or, more formally, when the slope of the STR, w , equals the slope of the SAR for time periods of one, which we will label ζ_0 (as the log of one is zero). Using the model based on aggregated subplots, $w = \zeta_0 = 0.27$ when area is 47 m^2 , or when approximately five 10 m^2 plots are sampled.

How would this result change given data from a continuously sampled landscape? The spatial scale of time–space equivalence is extremely sensitive to the value of ζ_0 . Our estimate of $\zeta_0 = 0.27$ based on the aggregated Konza subplots is at the upper end of the range of values for ζ_0 estimated by field sampling in the central grassland region of North America, and some reported values of ζ_0 are as low as 0.17 (data from Stohlgren *et al.* 1999). To approximate a hypothetical species–time–area relationship (STAR) for continuously sampled data, we needed to generate models with lower values of ζ_0 . To this end, we adjusted the areas represented by the aggregated subplots by increasing the log of their areas 20%. Fitting the model to these altered data produced $\zeta_0 = 0.21$, and the area at which w equals ζ_0 rose to *c.* 2400 m^2 , or *c.* 0.25 ha . With an even lower ζ_0 of 0.17, obtained by increasing the aggregated areas by 40%, the spatial scale of time–area equivalence increased to 12 ha. Such extrapolations emphasize that in these grasslands, time has a strong influence on species richness at all spatial scales that can be directly censused. To be meaningful, any estimate of species richness must clearly specify the area and the time period of sampling (Fig. 3).

Future challenges

The glimpse of a STAR offered by our data poses challenges for basic and conservation ecology. The first challenge for basic ecology concerns the generality of the form and parameter values of the STAR. We know that the slope of the single-year area relationship, ζ_0 , is similar for many taxa in many ecosystems. Is this also true for the slope of the time relationship, w , and the value of the interaction parameter, w ? Or do these parameters vary widely and systematically among ecosystems and taxa, suggesting large differences in the relative influence of space and time? We might expect steeper STRs in ecosystems subject to greater environmental variability because different species will be favoured at the extremes of the environmental distribution. If this were true, species richness estimates based on snapshot samples would be negatively biased relative to estimates for less variable systems. On the other hand, in ecosystems or at spatial scales

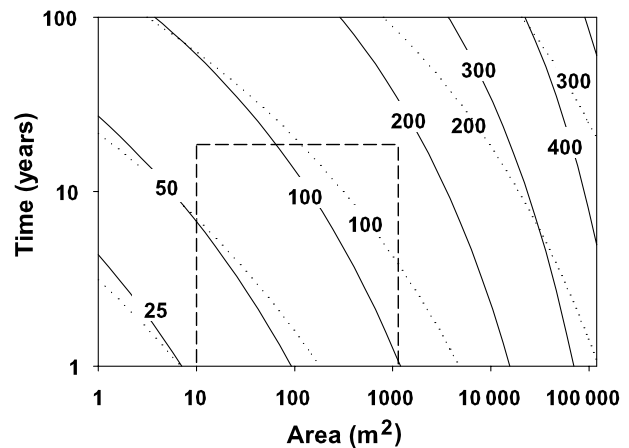


Figure 3 Isopleths of species number in time and space. The solid isopleths are based on the species–time–area relationship generated by aggregating 10 m^2 subplots at Konza Prairie, producing a ζ_0 of 0.27 (Fig. 2e). The dashed box outlines the domain of the data; extrapolation outside the domain assumes no change in the model parameters at these broader scales. The dotted isopleths are based on a model of the same form for a hypothetical continuously sampled landscape with a ζ_0 of 0.21.

where values of w are very low, we could safely ignore the influence of time on species number. Other priorities for empirical research are testing scale dependence in the model parameters and understanding how variability in species number scales with time and area. Answering these questions will require multiscale sampling and long-term research programmes in a variety of ecosystems.

The second important challenge for basic ecology is identifying the mechanisms that underlie the SAR and STR. The similarity of patterns in space and time is intriguing because it suggests the equivalence of underlying processes. If spatial and temporal processes are indeed equivalent, then space-for-time substitutions (Pickett 1988) may offer an efficient and valid approach for exploring long-term dynamics. Preston (1960) made a case for such equivalence by suggesting spatial analogues for the three processes that he proposed to generate the STR. The most relevant to our study is the comparison of temporal environmental changes because of disturbances or extreme weather events with spatial habitat heterogeneity. The assumption is that environmental conditions vary through time on the scale of decades to centuries much as they do through space on the scale of ha to km^2 .

Ecological patterns such as the STAR, however, are not the result of environmental variability, but of the interaction between environmental variability and biological processes operating at the scale of individual organisms, populations and communities. Storch *et al.* (2003) presented evidence that SARs for central European birds are the result of spatial

population processes superimposed on habitat heterogeneity. Because those population processes may not respond to spatial and temporal environmental variability in the same way, mechanisms underlying spatial and temporal patterns may not be equivalent. For example, the way that organisms move from one location to another may not be analogous to their 'movement' through time (Rosenzweig 1998). An extremely unfavourable year is likely to have significant lag effects on the density of a population, whereas an unfavourable site may have little effect on population density in neighbouring sites. However, extended dormancy could allow an organism to bridge unfavourable time periods just as long distance dispersal would allow it to pass over unfavourable habitat. Whether or not the spatial and temporal processes are equivalent, they are clearly linked: temporal dynamics, represented by a time series for a population in a given site, depend on mechanisms of dispersal from surrounding sites (Johst *et al.* 2002), while spatial dynamics, represented by the spatial structure of a population at one time, depend on mechanisms of temporal persistence. Metapopulation theory offers a potential framework for these dynamics (Matter *et al.* 2002).

The strong links between spatial and temporal processes suggest that future theoretical work on the SAR, whether based on statistical patterns (May 1975; Harte *et al.* 1999), niche interactions (Shmida & Wilson 1985), or neutral processes (Bell 2001; Hubbell 2001), should address the STR as well. Confronting theoretical models with spatio-temporal data will focus the search for underlying processes by providing a more stringent test, making it easier to reject candidate models.

The questions that the STAR raises for conservation are more philosophical. What is the appropriate temporal scale for biodiversity assessment? Should conservation priorities be determined by the number of species found in a community in 1 year, or over longer time periods? If, as we have suggested, STRs vary systematically along environmental gradients, then use of 1-year sampling to establish conservation priorities may not provide adequate information. Finally, how should restoration goals be identified if communities are in constant, and even rapid, flux?

CONCLUSION

The strong influence of time on species richness raises questions to challenge basic and applied ecologists. We need basic researchers to test for cross-ecosystem patterns in the relative effects of area and time on species number and to explore the possible equivalence of underlying spatial and temporal processes. Conservation practitioners must determine appropriate temporal scales for assessing biodiversity and identifying restoration targets. Although these questions will not be answered quickly, evidence of a STAR

should have immediate implications for basic and applied ecology. While the importance of scaling estimates of species number by area is now widely appreciated, our results demonstrate that they must also be scaled by the time period of sampling.

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