

Two-phase species-time relationships in North American land birds

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Abstract

The species-time relationship (STR) is a macroecological pattern describing the increase in the observed species richness with the length of time censused. Understanding STRs is important for understanding the ecological processes underlying temporal turnover and species richness.

However, accurate characterization of the STR has been hampered by the influence of sampling.

I analyzed species-time relationships for 521 breeding bird survey communities. I used a model of sampling effects to demonstrate that the increase in richness was not due exclusively to sampling. I estimated the time scale at which ecological processes became dominant over sampling effects using a two-phase model combining a sampling phase and either a power function or logarithmic ecological phase. These two-phase models performed significantly better than sampling alone and better than simple power and logarithmic functions. Most communities' dynamics were dominated by ecological processes over scales less than 5 years. This technique provides an example of a rigorous, quantitative approach to separating sampling from ecological processes.

INTRODUCTION

Understanding the determinants of species richness is one of the major goals of contemporary ecology (Brown 1995; Rosenzweig 1995). Recent studies have shown that species richness at a site often remains relatively constant from year to year; however new species enter the system periodically while others go locally extinct, leading to an increase in cumulative richness over time (Brown *et al.* 2001; Ernest & Brown 2001; Haskell 2001; Parody *et al.* 2001). Therefore, the total number of species will increase as a site is observed for longer periods of time.

Although questions of how species accumulate with area have been well studied (Connor & McCoy 1979; Williamson 1988; Rosenzweig 1995), the manner in which species accumulate in time has received less attention (Rosenzweig 1995).

The species-time relationship (STR) describes how the number of species censused increases as a study site or area is sampled repeatedly through time. Grinnell (1922) was the first to note the regular accumulation of species with time, suggesting that the number of species of birds seen in California increased linearly with the time span sampled. Preston (1960) provided a more detailed discussion of the STR and proposed that it should be similar to the species-area relationship (SAR). As with the SAR, at short temporal scales the increase in richness should be due primarily to increased sampling of a static assemblage (Preston 1960). At intermediate time scales, the primary processes driving changes in species richness should be colonization and local extinction of species in response to succession, changing environmental conditions, demographic stochasticity, and metapopulation and source-sink dynamics (Preston 1960; Adler & Lauenroth 2003). Finally, at evolutionary time scales, speciation and extinction should exert the primary influence on the relationship (Preston 1960).

Because these processes operate at different time scales they should dominate different portions of the observed STR, leading to 3 apparent phases like those observed for the SAR (Williams 1943; Preston 1960; Rosenzweig 1995). The sampling phase results from the fact that STRs are typically constructed by grouping increasingly larger numbers of successive samples. Therefore, the number of individuals sampled tends to be directly proportional to the length of the time period. An increased sample of individuals will tend to detect additional rare species, even if the actual number of species in the community (or the pool from which the community is drawn) is static (Fisher *et al.* 1943; Bunge & Fitzpatrick 1993; Colwell & Coddington 1994; Gotelli & Colwell 2001). The sampling phase can result from two distinct processes: 1) incomplete sampling of the community by the observer; and 2) random year-to-year assembly of the community from a static pool (i.e. incomplete sampling of an unchanging pool). The first represents a methodological artifact, whereas the second represents a real pattern.

Over some longer time period, ecological processes should become more dominant than random sampling effects, resulting in a change in the form of the STR. No consensus model exists for the ecological phase of either the STR or the SAR. However, two functions have been shown to well describe STRs: power functions (McKinney & Frederick 1999; Hadly & Maurer 2001; Adler & Lauenroth 2003), and logarithmic functions (Rosenzweig 1995).

These two phases are not strictly discrete, in that at short time scales ecological processes will still be operating, and at longer time scales random processes will still influence which individuals of which species are present and sampled. However, these two processes will be of varying importance at different time scales. The different phases of the STR represent the scales at which the different processes dominate the observed pattern. Quantitatively determining where the transitions between these phases occur is important for identifying the processes generating the STR, and determining the temporal scales at which they dominate.

The Breeding Bird Survey of North America (BBS) (Sauer *et al.* 2000) provides a unique opportunity to study the STR because a large number of communities have been sampled continuously over a broad geographic area for over 20 years, thus providing a large sample of STRs for a single taxonomic group. In this study, I calculate the STRs for 521 breeding bird communities in North America. I test to see if the observed pattern is purely a result of sampling, show that it is not, and then use two-phase models to determine the time span at which the dominant processes transition from sampling to ecological.

METHODS

I used data from the Breeding Bird Survey of North America (Sauer *et al.* 2000; USGS Patuxent Wildlife Research Center 2001) to address the above objectives. The BBS consists of approximately 3000 routes throughout the United States and Canada that are sampled annually for species presence and abundance. Each route is 40 km long and consists of 50 stops each separated by 800 m. A single observer conducts a 3 minute point count at each stop (see Bystrak 1981 for details on methodology). While this survey may contain species-specific biases, these biases should remain relatively constant from year to year and should not effect the overall results and conclusions of this paper (see O'Connor *et al.* 2000 for limitations of the survey). I selected all BBS routes with ≥ 20 -years of continuous time series between 1966 and 2000, each year of which met BBS quality standards ($n = 521$). The average route contained 52 species in a single year and 364 different species were represented in the entire study.

For each route I calculated the species richness and abundance of land birds for every possible temporal window in the time series (i.e. each single year, every possible successive pair of years, etc.). This allows maximum temporal resolution in the STRs, but requires providing greater weight to the central years in the time series. As long as the central years do not differ in some regular way this should not affect the results. A species-time relationship was then generated for each route by arithmetically averaging the richness values for each time span. This is the standard approach in nested species-area and species-time relationship analyses (e.g. SAR: Plotkin *et al.* 2000; STR: Adler & Lauenroth 2003) and avoids overemphasizing the short time spans in model fitting. This is particularly important for assessing the transition between the sampling and ecological phases where without averaging the sampling phase would exert disproportionate influence on the results. Results did not differ qualitatively if geometric averages were used.

To determine if the observed STRs were purely sampling phenomenon, the forms of the individual STRs that would be generated by sampling alone were compared to the observed patterns. This was done by first pooling abundance data from all years, and then calculating the expected richness for each data point in each STR, using a binomial-based model previously developed for area,

$$S(T) = S_0 - \sum_{i=1}^{S_0} (1 - T / T_0)^{n_i} \quad (1)$$

where $S(T)$ is the expected number of species occurring over time span T , given that S_0 species and n_i individuals of the i th species were observed over the entire T_0 years of sampling (Arrhenius 1921; Coleman 1981; Coleman *et al.* 1982). Because it uses the observed abundances, this approach does not suffer from any assumptions about the abundance distribution of the communities. If the abundance distribution happens to be log-series, this approach will produce mathematically equivalent results to those of Fisher's alpha (Coleman 1981). This model assumes that the observed individuals are placed randomly and independently into one of the observed years. This is approximately, but not precisely, equivalent to pooling all of the individuals recorded over some time period and then drawing from that pool without replacement the average number of individuals observed at each time span. The difference between the two approaches occurs because in equation (1) the number of individuals in a particular time span is a random variable, not a fixed number (Coleman 1981). All results were practically identical if a collector's curve (eq. 13 in Hurlbert 1971; as modified by Brewer & Williamson 1994; 1995) is used in place of equation (1) (see also Brewer & Williamson 1994). The sampling model is by definition constrained to equal the observed value at the maximum time span. For further discussion of the sampling model see Coleman (1981) and Coleman *et al.* (1982).

Traditionally, investigators have used Fisher's alpha to examine sampling relative to STRs (e.g. Rosenzweig 1995, 1998; McKinney & Frederick 1999; Hadly & Maurer 2001). Fisher's alpha was not used in this study because 72% of the communities had abundance distributions significantly different from log-series, and thus violated a necessary assumption of this approach (Fisher *et al.* 1943).

I used a two-phase model to determine the time span at which ecological factors began to influence the STR for these communities. I allowed the break point (T_b) to vary from $T_b = 1$ to $T_b = T_0$ for each time series. I then fit the sampling function to time spans less than T_b , and used non-linear least squares to fit the ecological functions (power and logarithmic) to time spans greater than or equal to T_b , such that

$$S(T) = \begin{cases} S_b - \sum_{i=1}^{S_b} (1 - T/(T_b - 1))^{n_{i,b}} & T < T_b \\ g(T) & T \geq T_b \end{cases}, \quad (2)$$

where $g(T)$ is equal to either cT^w or $w \log T + c$ depending on which ecological function was being fit to the data, and c and w are fitted parameters representing the slope and intercept of the linearized function when plotted on log-log and semi-log axes respectively. I minimized residual sums of squares (RSS) to estimate the best value for T_b , where S_b is the average number of species occurring in a window of time span T_{b-1} and $n_{i,b}$ is the average abundance of the i^{th} ranked species in a window of time span of T_{b-1} (i.e. a rank abundance distribution was created for each T_{b-1} window and then the abundances of each rank were averaged to provide an average rank abundance distribution for that window size). The sampling portion of $S(T)$ was also calculated for all possible windows of size T_{b-1} and then averaged. The above averaging approach is equivalent to the sliding window analysis used to produce the observed STR. T_b was fit separately for the two-phase power and two-phase logarithmic functions. Simple power law and logarithmic models were also fit to the observed data for comparison.

For each route, comparisons between the overall fit of the 5 models (sampling, power, logarithmic, sampling-power, and sampling-logarithmic) were conducted using Akaike's Information Criteria with unknown variance (AIC, Burnham & Anderson 1998; Venables & Ripley 1999) with 0, 2, 2, 3, and 3 fitted parameters respectively. Because the data points in a nested STR are not statistically independent (longer time spans include shorter time spans) the standard AIC comparison may not be strictly valid. Therefore I also compared models using a proposed analog of AIC for sums of squares (Hongzhi & Lan 1989; Hilborn & Mangel 1997), and using a standard correction to the RSS ($\text{RSS}/[n-2*\#\text{parameters}]$, Efron & Tibshirani 1993; Hilborn & Mangel 1997). Results did not differ qualitatively between the model comparison techniques suggesting that they are relatively robust to the specifics of the correction for the number of parameters.

In addition to the route level statistical analyses, the general fit of the 5 models across all communities was visualized by plotting the mean and 95% confidence intervals of the combined residuals (across all STRs) for each time span. This technique has been successfully used for assessing the general quality of two-phase vs. single function fits in cases where multiple communities were analyzed (Rincon & Lobon-Cervia 2002) and provides information on systematic lack of fit across communities that cannot be provided in any other manner. I also compared the average AIC values for the different models across all routes using ANOVA with Scheffe *post hoc* comparisons (Day & Quinn 1989), effectively treating each route as a sample and its AIC value as a measure of overall quality of model fit.

RESULTS

The observed species-time relationships appear approximately linear on logarithmically scaled axes, although they often show a slight concave down trend over the first 1-5 years (Figure 1). This concave down trend caused distinctive lack of fit in the mean residuals of simple power and logarithmic functions fitted to the entire time period (Figure 2). In addition, the STRs sometimes showed slight deviations from the functional fits in the last few years. This is expected because the number of data points represented by the mean decreases linearly with the time scale (Keitt & Stanley 1998). Typically, data for a single community were poorly fit by the sampling curve, which had a higher intercept and lower slope than observed data, was obviously concave down, and always overestimated richness at all but the maximum time span (Figure 1; Figure 2).

Route level statistical comparisons between models showed that in general two-phase models performed better than one-phase models (i.e. had a lower AIC). Eighty percent of routes ($n = 521$) were best fit by one of the two-phase models (sampling-power 41%, sampling-logarithmic 38%), with the remaining 20% being better fit by the one-phase models (power 10%, logarithmic 11%). The 2-phase models also reduced the lack of fit present in the one-phase models (Figure 2). The sampling curve was the worst model for 99% of routes.

Analysis of variance of all routes together showed that there were differences between models in average AIC ($P < 0.001$). The 2-phase models had a lower average AIC than the 1-phase models (*post hoc* comparisons: all P s < 0.001). The 2-phase models were indistinguishable from one another ($P = 1$), whereas for the 1-phase models the logarithmic function performed better on average than the power function ($P = 0.003$). The sampling function performed worse than all other functions (all P s < 0.001).

For routes better fit by 2-phase models, the distribution of break points was highly right skewed regardless of which 2-phase model was superior, with the mode of the transition between the two phases for both models occurring between time spans of 2 and 3 years (sampling-power $\overline{T_b} = 4.1$; sampling-logarithmic $\overline{T_b} = 2.7$; Figure 3A-B). The slope (w) of the 2nd phase of the STR averaged 0.16 for STRs best fit by sampling-power functions (Range 0.05 to 0.40; Figure 3C) and 9.98 for STRs best fit by sampling-logarithmic functions (Range 3.76 to 22.06; Figure 3D). Slopes of sampling and logarithmic functions cannot be directly compared.

DISCUSSION

The species-time relationship in North American land birds was best described by two-phase models combining a short time scale sampling model with either a power or logarithmic function ecological model. This agrees with Preston's (1960) original conceptualization of the STR and mirrors the early analyses of SARs which were described qualitatively with a concave down function at small spatial scales and a power function at larger spatial scales (Williams 1943; Preston 1960). It also agrees with early STR analyses demonstrating that Fisher's alpha does not change at the shortest time scales in some communities, but at longer time scales begins to increase (Rosenzweig 1995). Failure of the sampling model to characterize the entire STR is in agreement with other studies that have shown non-sampling increases in plant (Adler & Lauenroth 2003), mammal (Hadly & Maurer 2001), and insect (Rosenzweig 1995) species richness. Thus, at ecological time scales the STR in land birds is not simply a sampling phenomenon. However, this study also demonstrates quantitatively that, at short time scales, increased sampling does have an important influence on the relationship. By using a model with both sampling and non-sampling components, it is possible to determine the time spans over which these different processes dominate the observed pattern of species richness. On average, the transition from sampling to ecological determinants of the STR occurred at approximately 4.1 years for routes best fit by sampling-power relationships and 2.7 years for routes best fit by sampling-logarithmic relationships.

To date, two statistical functions (power and logarithmic) have been proposed to describe the general form of the STR. On their own, these models perform more poorly than two-phase models combining these statistical functions with a sampling function. However, the different two-phase models appear to be indistinguishable from one another in this study. Each two-phase model has the lowest AIC in approximately 40% of the bird communities, and cross-community analyses demonstrate that the average AIC values were indistinguishable. The residual patterns also appear similar (Figure 2). This likely results because over ranges of scale equivalent to those in this study these functions can appear similar to one another and even be difficult to distinguish statistically (McGill 2003). As a result this study does not suggest that either of these statistical descriptions of the ecological phase of the STR is more appropriate. In fact, it suggests that they both perform equally well, taking similar shape (i.e. similar residual patterns in Figure 2, and approximately straight lines on log-log plots in Figure 1) and playing an equivalent role when combined with the sampling function. The slopes of the two functions were also highly correlated (Pearson's $r = 0.79$, $P < 0.001$), though it is important to remember that the power function slope represents the relative rate of species addition to community whereas the logarithmic function slope represents the absolute rate of species addition. Because the vast majority of previous STR analyses have reported only power function parameters, some of the following discussion focuses on the power function results.

The improved fit of the two-phase models is important because it may allow the use of the STR to assess ecological turnover. This is because the slope of the STR is a measure of temporal turnover in the same manner in which the slope of the SAR is a measure of spatial turnover (Lennon *et al.* 2001; Koleff *et al.* 2003). Traditional measures of temporal turnover are in general artificially elevated by sampling (Colwell & Coddington 1994). By using the slope of the STR fit after the transition between sampling and ecological processes, it is possible to focus on temporal turnover due to ecological processes by reducing the influence of sampling. The slope of the STR has the additional advantage of being essentially invariant to temporal scale (at least over the observed scales), whereas other measures change as a function of T (Diamond & May 1977; Russell *et al.* 1995). The factors correlated with the time scale at which this transition occurs should be of considerable interest because they should contribute to a broader understanding of the processes generating ecological turnover. A complete analysis of these transitions is beyond the scope of this paper. However, it is interesting to note that the transition points for the routes best fit by the sampling-power model are correlated with the post-sampling power function slope of the STR (Pearson's $r = 0.41$, $P < 0.001$), but not with either mean annual richness ($P = 1$) or with mean annual abundance ($P = 0.27$). The transition points for routes best fit by the sampling-logarithmic model on the other hand are weakly correlated with the slope of the post-sampling logarithmic function ($r = -0.16$, $P = 0.02$), with mean annual richness ($r = 0.21$, $P = 0.003$), and with mean annual abundance ($r = 0.18$, $P = 0.01$). The differences in the direction of the slope correlation may result from the fact that power slopes represent relative rates of addition and logarithmic slopes represent absolute rates of addition. It is also possible that these different correlation structures indicate real differences in the temporal structure of communities that are best fit by different ecological models. Further study will be necessary to

begin to understand correlates of the break point between sampling and ecological functions.

When this two-phase approach is used to examine the slopes of the ecological portion of the STR, the values for BBS data were lower than most power function slopes reported in the literature (most $w \approx 0.3$; Rosenzweig 1995, McKinney & Frederick 1999, Hadly & Maurer 2001, Adler & Lauenroth 2003). This may result for several different reasons. First, some of the published curves are for fossils and may be in the evolutionary phase of the STR where the slope should be higher (Rosenzweig 1995; McKinney & Frederick 1999). Second, there may be taxonomic differences in the slopes of STRs, due to differences in body size, dispersal ability, and other natural history characteristics. The only other STR reported for birds has a power function slope very similar to those in the BBS ($w = 0.12$; Preston 1960, Rosenzweig 1995). Third, some of the previously reported STRs were measured at smaller spatial scales than that of a BBS route, and there is empirical evidence that decreasing the spatial scale increases the slope of the STR (Preston 1960; Adler & Lauenroth 2003). At larger spatial scales, a greater proportion of the species in the regional pool are identified at short time scales, thus reducing the relative rate of the accumulation of new species. However, the details of this scale dependence are likely specific to the taxon and census technique, confounding the comparison of different taxa sampled in different ways. Fourth, lower slopes of the SAR have been associated with higher local species richness (Lennon *et al.* 2001; Lyons & Willig 2002). In this study, there is a similar cross-community correlation between mean annual richness and the power function slope of the ecological STR (Pearson's $r = -0.58$, $P < 0.001$) suggesting that perhaps differences in richness between different STRs may result in differences in observed slopes. Finally, previous studies have not excluded data in the sampling phase of the relationship before fitting the power function, which should in most cases artificially elevate the slope of the STR.

While the two-phase model represents an improvement for describing the STR, it is still restricted by the fact that it takes a strictly hierarchical approach to the problem of separating sampling and ecological processes, allocating each process to a distinct set of scales. The discrete nature of this approach likely explains the remaining lack of fit of the 2-phase model (i.e. mean residuals significantly different from zero at some scales; Figure 2), because around the estimated transition point the two processes are likely having approximately equal influence on the pattern, causing the single process fits to deviate regularly. In addition, the specifics of the transition from sampling to ecological processes probably differ for different parts of the community based on size, dispersal distance, and differences in natural history. This should also result in the transition between processes occurring over some range of time scales, not at a single point. A better characterization of the pattern and its associated processes may eventually be achieved by allowing the processes to gradually transition across a range of scales.

It is also possible that the second phase of the STR is well described by functions other than the power and logarithmic functions used here. In particular, it is conceivable that there is an eventual asymptote. However, there is no indication of an asymptote at the maximum time scale for these data where the average residuals are, if anything, positive (Figure 2). It is also possible that a temporal equivalent of recent theoretical SAR models (e.g. McGill & Collins 2003; Sizing & Storch 2004) may describe the ecological phase of the STR eliminating the need for fitting statistical functions to this portion of the relationship.

The proposed technique for separating the sampling and ecological phase of the STR is equally applicable to the SAR, though it is limited to studies in which the abundance of the species present is also available. In cases where abundance data has not been collected it may be possible to use presence/absence sampling models (e.g. Colwell & Coddington 1994; Cam *et al.* 2002) to estimate this portion of the curve. This approach should also prove useful in quantifying the transition between the ecological power function and theoretical models for the broad-scale upturn of the SAR (Allen & White 2003; McGill & Collins 2003).

Dealing with the influence of sampling on observed patterns has been a major problem in ecology (Colwell & Coddington 1994). By modeling ecological patterns in such a way as to explicitly include sampling, it should be possible to then set sampling aside and focus on the portion of the pattern that is driven by ecological processes. The two-phase approach to the STR presented here provides an example of a rigorous, quantitative way in which to separate sampling from ecological processes, and demonstrates that the STR mirrors the SAR not only in its general ecological form, but also in the influence of sampling and the transition between scales at which ecological and random processes dominate.

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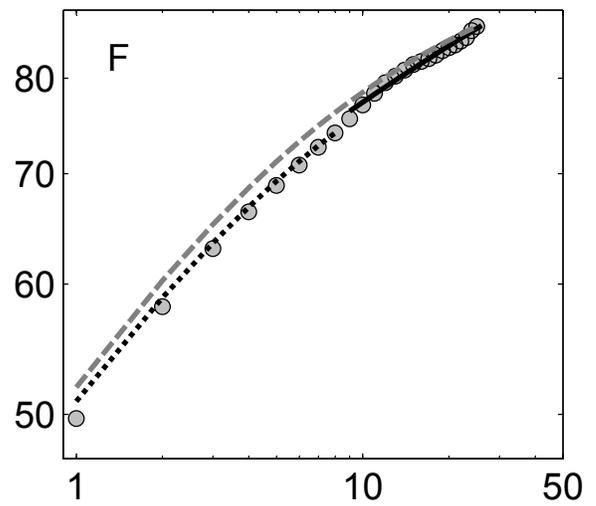
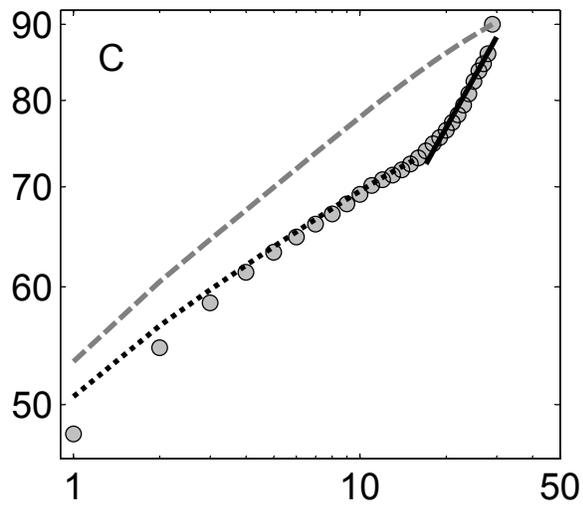
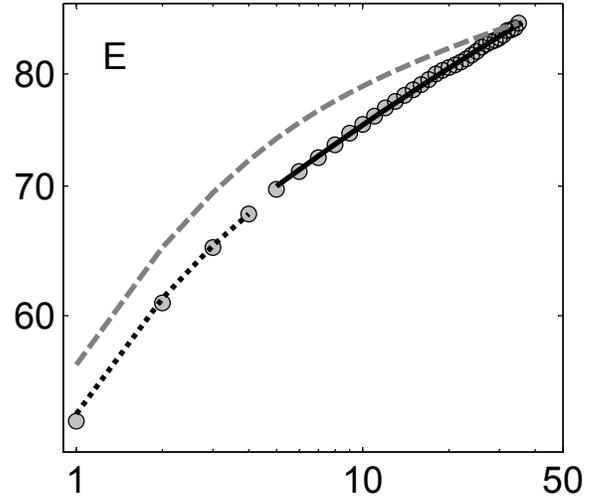
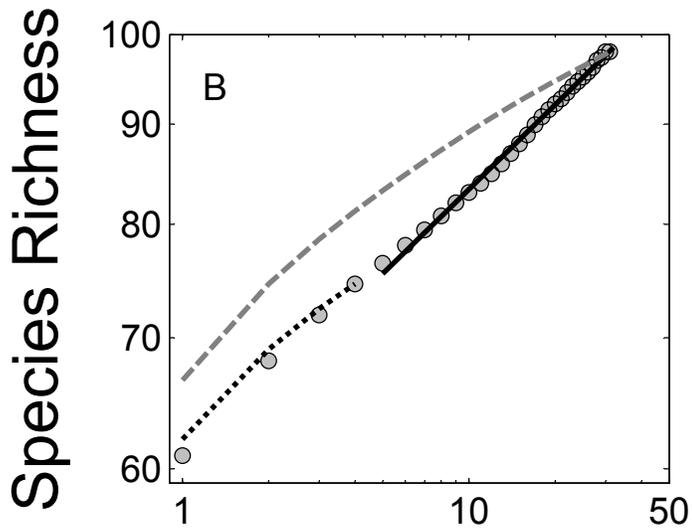
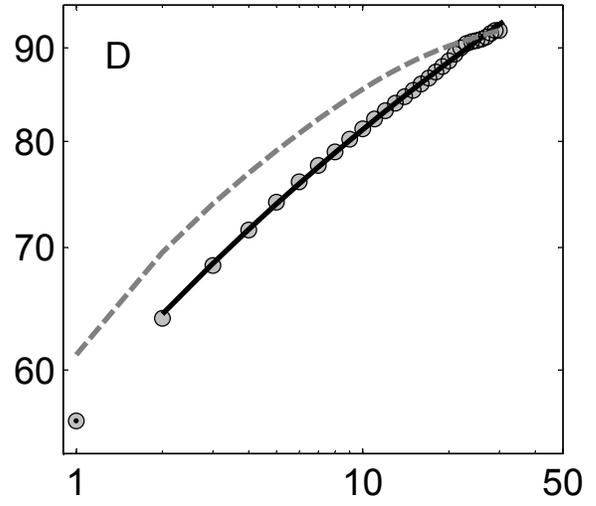
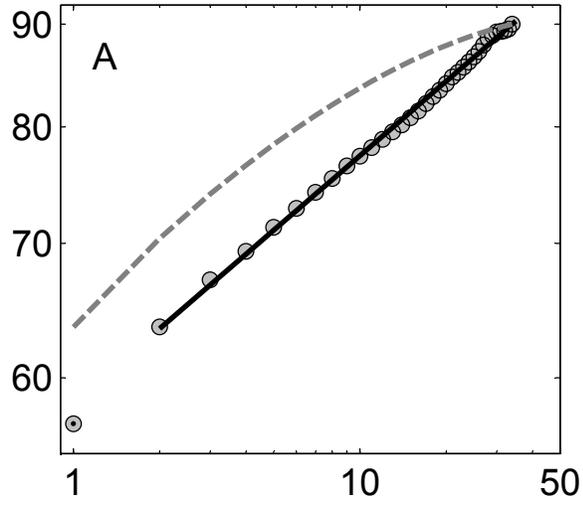
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FIGURE LEGENDS

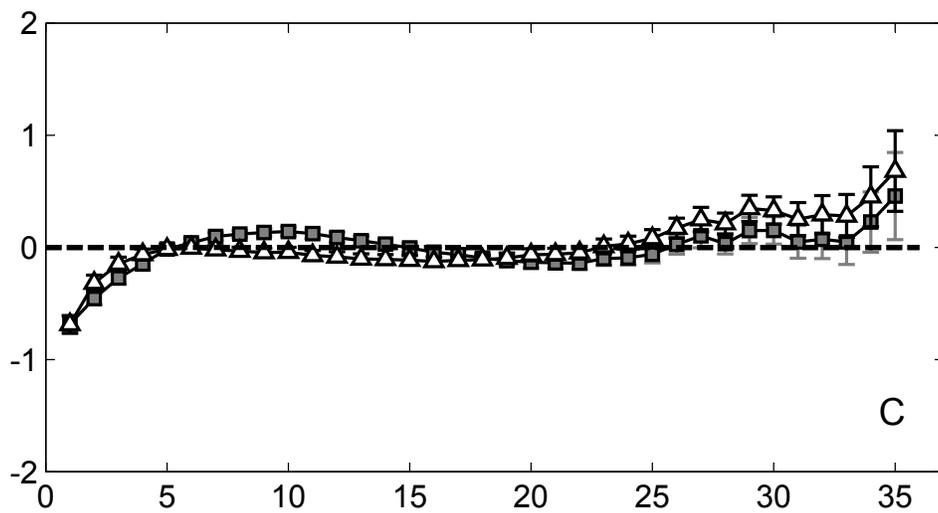
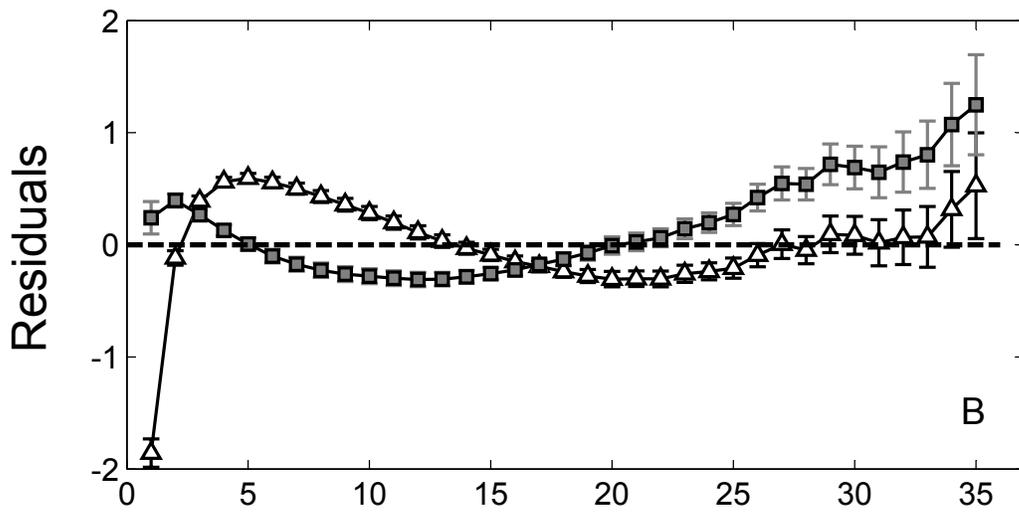
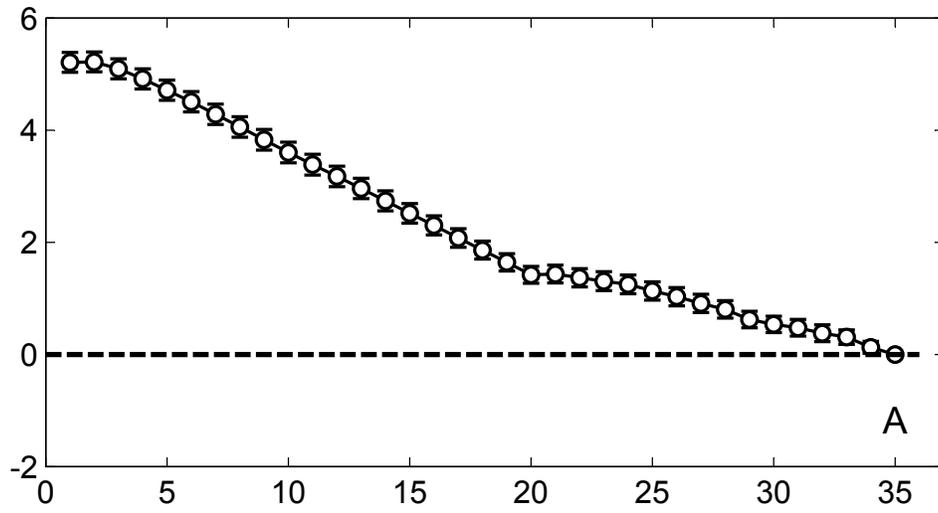
Figure 1. Examples of species-time relationships from the Breeding Bird Survey of North America (Arkansas Route #4 (A), Wisconsin Route # 55 (B), Connecticut Route #10 (C), Illinois Route #37 (D), West Virginia Route #38 (E), and Quebec Route #21 (F)). Observed data (gray circles) are plotted with the best fitting model as determined by minimum AIC. Best fitting models are sampling-power (A-C) and sampling-logarithmic (D-F). The sampling portion of the models is represented by the dotted line and the ecological portion by the solid line. Sampling only models (gray dashed line) are presented for comparison. Axes are scaled logarithmically. Examples were chosen to represent routes that were best fit by each of the two-phase models across the range of observed break points.

Figure 2. Mean residuals of all species-time relationships combined for the sampling only model (A), the simple power function model (B, white triangles), the simple logarithmic function model (B, gray squares), and for the sampling-power (C, white triangles) and sampling-logarithmic (C, gray squares) 2-phase models. Error bars represent 95% confidence intervals and in some cases are difficult to see because of their small extent. Note that the y-axis has the same extent for B and C, but is twice as large for A. The dashed line indicates 0 mean residual.

Figure 3. Histograms of the frequency of different transition points between sampling and ecological functions (A: routes best fit by sampling-power functions; B: routes best fit by sampling-logarithmic functions) derived by minimizing residual sums of squares for the 2-phase models of the species-time relationship, and slopes of the ecological phase of the STR (C: routes best fit by sampling-power functions; B: routes best fit by sampling-logarithmic functions) for 521 communities of breeding birds in North America.



Time Span



Time Span (yrs)

