CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

IMPACT OF CURVE CONSTRUCTION AND COMMUNITY DYNAMICS ON THE SPECIES–TIME RELATIONSHIP

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Abstract. The species–time relationship (STR) describes how the species richness of a community increases with the time span over which the community is observed. This temporal scaling provides insight into theoretical questions on species diversity patterns as well as applied questions on the appropriate time scale for biodiversity assessments. To better understand STRs, we discuss the methods used to construct STRs in the literature and derive the impact of curve construction on STR properties. Using vegetation data from Mount St. Helens, Washington, USA, we illustrate the sensitivity of the STR to construction under colonization-dominated dynamics. This study highlights the importance of considering the type of STR when interpreting, comparing, and applying STRs, particularly in disturbed or successional systems.

Key words: diversity; species–area relationship; species richness; time.

INTRODUCTION

A simple measure of an ecosystem's biodiversity is its species richness, or number of species. However, the number of species observed depends on both the size of the area sampled and the length of time sampled (Adler and Lauenroth 2003, Adler et al. 2005). The positive relationship between the number of species observed and the size of the sample area is quantified by the species–area relationship (SAR), which has served as an important conceptual foundation for community ecology theories (Rosenzweig 1995). Despite extensive SAR studies, the related species–time relationship (STR), between the number of species observed and the time span over which the community is observed, had not been extensively studied until recently (White 2004, White et al. 2006).

The initial framework for STRs has been attributed to Preston (1960), who compared the increase in species richness from doubling sample area with doubling sample time. Preston proposed that similar underlying processes may influence species accumulation in space

and time based on the resemblance between a horizontal spatial transect across a lake through a marsh, grassland, and forest with a temporal transect through time as the lake fills and the landscape changes. Rosenzweig (1995, 1998) reintroduced the STR concept, stimulating interest in STRs and in testing Preston's "ergodic conjecture" that time and space have the same quantitative effects on species diversity. Recent STR studies have quantified how species richness scales with time and the interaction between spatial and temporal scaling of species richness at ecological (Adler and Lauenroth 2003, White 2004, Adler et al. 2005, Ulrich 2006, White et al. 2006) and evolutionary time scales (Rosenzweig 1998, McKinney and Frederick 1999, Hadly and Maurer 2001).

Results from species–time studies may help answer both theoretical questions on species diversity patterns and applied questions on the appropriate time scale for biodiversity assessments. However, before these questions can be addressed, it is important to understand the properties of the STR and, in particular, its possible constructions and sensitivity to its construction. Previous work (see Scheiner 2003) has examined the different methods used to construct SARs, and has found that curve construction has important implications on the shape and interpretation of these relationships. In particular, Scheiner (2003) found that different SAR
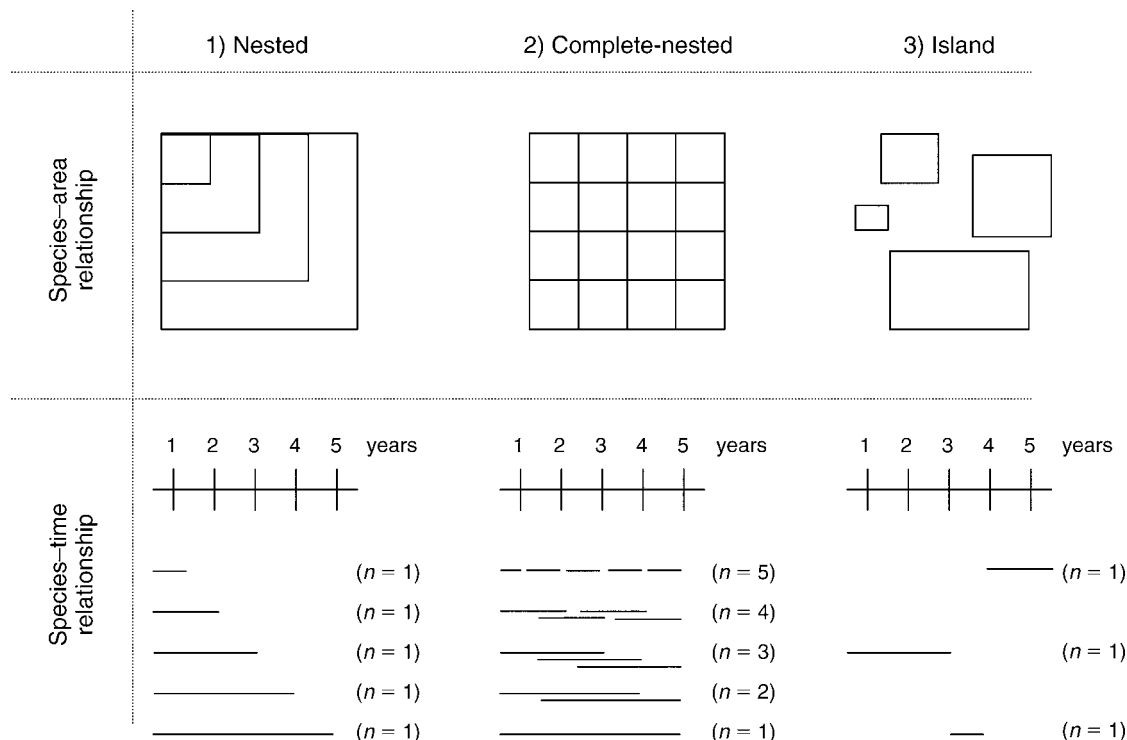
Fig. 1. Types of species–time relationships compared to species–area relationships.

constructions incorporate the effects of alpha and beta diversity in different ways. No such analysis has been carried out for STRs to our knowledge. Here we discuss the STR types present in the literature and explore theoretically how their different interpretations of time affects STR properties. These theoretical differences are then illustrated using vegetation data from Mount St. Helens, Washington, USA.

SPECIES–TIME RELATIONSHIP (STR)

The STR quantifies the increase in the number of species observed as the length of sample time increases for a fixed area. This relationship is driven by different processes depending on the time scales involved (Preston 1960, Rosenzweig 1995, McKinney and Frederick 1999). At any time scale, the total number of individuals observed increases with sample time. Therefore, at small time scales, total species richness increases due to the observation of rare species present but previously unsampled. As the length of sample time increases, additional species are observed as new species disperse or move into the area. At longer scales, new species enter the system as it undergoes ecological succession. At evolutionary time scales, richness increases from the addition of newly evolved species.

The form of the species–time equation depends on how species richness, S, scales with length of sample time, T. Some possibilities are linear, $S \sim T$; saturating, $S \sim T/(k + T)$; logarithmic, $S \sim \ln(T)$; and power law: $S \sim T^w$. While ecologists have observed and debated a

variety of SAR forms (Connor and McCoy 1979, Lomolino 2000, Tjorve 2003), the majority of species–time studies have focused on the power-law STR, $S \sim dT^w$. This equation is motivated by substituting time (T) for area (A) in the power-law SAR, $S = cA^z$ (Arrhenius 1921), and can be log-transformed to $\ln(S) = \ln(d) + w \times \ln(T)$, where d and w are constants. This form implies that total richness does not saturate at any scale. In the limit of evolutionary time, total richness continues to increase through the evolution of new species. Other forms of the STR equation have been explored by Rosenzweig (1995), White (2004), and White et al. (2006). White et al. (2006) found that little more than half of almost 1000 STR curves were fit better by a power-law than a logarithmic function.

Based on approaches used in SAR analyses, we define the STR types present in the literature ("nested," "complete nested," and "island") by their definition of sample time (Fig. 1). In all of these types, species richness is plotted as a function of increasing length of sample time; however, length of sample time depends on whether time is defined as an interval, a flow or a combination of both. In our notation, time defined as an interval is the absolute length of time from start to end (one year, two years, and so on), while time defined as a flow is the relative position of time (year 1, year 2, and so on).

First, in nested analyses, time is interpreted analogously to species–area studies constructed from areas of increasing size nested within each other (e.g., He et al.

1996, Fridley et al. 2005). The length of sample time T is defined as the total time T from the start of the initial survey. In data sets composed of annual surveys, time 1 is the first year; time 2 is the first and second years; time 3 is the first through third years, and so on. This approach defines time as both an interval and a flow. Each data point represents a single value: total species richness in the sample of length of time T calculated from the start of the initial survey. STRs of this type include McKinney and Frederick's (1999) analysis of marine fossils at evolutionary time scales where time is represented by the cumulative amount of sediment sampled.

The complete-nested design, in contrast, defines length of sample time T as the average of every possible combination of consecutive sample periods of length T. With annual survey data, time 1 is the average of all single years; time 2 is the average of all combinations of two consecutive years; time 3 is the average of all combinations of three consecutive years and so on. In an eight-year record, for example, there are eight one-year, seven two-year, six five-year, five four-year, down to one eight-year sample. Each data point represents the mean number of species across all samples of consecutive periods of length t, with time defined only as an interval. This approach is analogous to complete-nested SARs that sample all possible combinations of areas of increasing size within one area (e.g., Condit et al. 1996, Green et al. 2003, Harte et al. 2005). However, complete-nested SARs usually analyze nonoverlapping combinations of area. Applying a nonoverlapping approach to complete-nested STRs would result in eight one-year, four two-year, two four-year, and one eight-year samples in an eight-year record. Regardless of whether one uses nonoverlapping or overlapping periods, this approach removes systematic trends in total richness by averaging richness across periods. The complete-nested design is currently the dominant approach for STRs at ecological scales (Rosenzweig 1995, 1998, Adler and Lauenroth 2003, White 2004, White et al. 2006).

STRs can also be constructed from temporal islands, analogous to spatial islands (e.g., Diamond and Mayr 1976, Davies and Smith 1998). Here, each data point represents a unique survey (temporal island) conducted for a length of sample time T. The STR plots the total number of species observed in each survey as a function of the total length of that survey, encompassing multiple surveys of different lengths of time for the same area. Here, time is defined as an interval from isolated biological or sampling "islands." For example, Hadly and Maurer (2001) define richness on temporal islands as the number of species in a single depositional layer of fossils accumulated for various lengths of time.

Quantifying how species richness increases with sample size is also the goal of species accumulation or collector's curves. These curves plot the cumulative number of species observed as a function of survey effort, where survey effort is defined by the number of individuals sampled, or estimated by the area of survey quadrats or length of observation time (Colwell and Coddington 1994, Gotelli and Colwell 2001). In these curves, the number of species is plotted against number of samples pooled (Colwell and Coddington 1994). Sample order may be randomized, which removes any existing temporal structure, with the mean and standard deviation of species richness plotted against sample size. Species richness can then be extrapolated using either asymptotic or non-asymptotic curves. When accumulation curves are constructed from increasing sample area or sample time, they may or may not be interpreted as a type of SAR or STR depending on the theoretical background of the researcher and the questions being asked (Scheiner 2003, 2004, Ugland et al. 2003, Gray et al. 2004a, b). While population biologists tend to use species-accumulation curves to estimate actual species richness within given areas and times, theoretical ecologists and biogeographers tend to use species–area and species–time curves to understand how species richness scales with area and time. In addition, time-series studies, which examine how the number of species present at a given point in time varies through time, may be confused as a type of STR. While time-series studies analyze how species richness fluctuates through time, they do not address the fundamental species–time question of how total observed richness increases with sample time.

Of the different types of species–time constructions just described, we focus on the differences between nested and complete-nested STRs. We show that when a system is undergoing a directional change in the number of species present at a single point in time, or in the rate at which new species are encountered, the shape of the STR changes systematically depending on which of these curve constructions are used. This result is important because it is unclear which of these two versions of the STR provides more useful information for these types of systems. The complete-nested construction, which is more commonly used on ecological time scales, averages over fluctuations in richness and the encounter rate of new species. This may be appropriate for systems where these fluctuations approximately sum to zero. However, for systems undergoing directional changes in these variables, averaging may confuse the impact of time scale on diversity comparisons and may lead to inaccurate assessments of the amount of time needed to sample the majority of the species diversity.

This directional change may be particularly prominent in successional systems. Succession is one of the primary ecological processes thought to shape the relationship between species encountered and the length of time of observation (White 2004, White et al. 2006), yet the effects of successional change on the shape of the STR have not been examined. Because successional change is often accompanied by directional changes in both the number

of species present and the rate at which new species are encountered (Connell and Slatyer 1977), successional systems should exhibit differences in the STR depending on its construction, with the nested STR providing more detailed information about turnover dynamics.

Sensitivity of the STR to construction under different community dynamics

In the interest of clarity, we formulate the STR here for the case where the state of a community can be specified for an instantaneous point in time. However, we recognize that ecologists often lack knowledge of the species present at instantaneous points in time and instead specify the composition of a community over the course of a growing season or other biologically relevant time interval. As a result, we provide an alternative framework to handle this situation in Appendix A, but the results are the same as for the simpler formulation introduced here.

We take the following definitions. Let S_t be the number of species present at time t and $S(t_1, t_2)$ be the number of species present for at least some of the time between t_1 and t_2. Let $c(t_1, t_2)$ be the number of species colonization events occurring between t_1 and t_2. A species is considered to have colonized at time t if it is present when the community is sampled at time t but was not present before time t. Let $e(t_1, t_2)$ be the number of species extinction events occurring between t_1 and t_2, with extinction defined analogously to colonization. Note that we count colonization and extinction events when they are discovered through sampling, even though the actual event may have occurred at a different point in time. Last, let $n(t_1, t_2)$ be the number of new species that enter the community between t_1 and t_2, where "new" is defined with respect to the species present at time t_1. Note that $n(t_1, t_2) \neq c(t_1, t_2)$ if some species go extinct and then subsequently recolonize the community. Furthermore, note that $S(t_1, t_2) = S(t_1) + n(t_1, t_2)$ and that $S(t_2) = S(t_1) + c(t_1, t_2) - e(t_1, t_2)$.

Given these definitions, we can write an expression for how the number of species sampled depends on the length of time T over which sampling occurs. For the nested STR, $S_n(T)$, and the complete-nested STR, $S_{cn}(T)$, we have the following:

$$S_n(T) = S_0 + n(0, T) \tag{1}$$

$$
\begin{aligned}
S_{cn}(T) &= \frac{1}{N_T} \sum_{i=1}^{N_T} S(t_i, t_i + T) \\
&= \frac{1}{N_T} \sum_{i=1}^{N_T} (S_0 + c[0, t_i] - e[0, t_i] + n[t_i, t_i + T]) \\
&= S_0 + \frac{1}{N_T} \sum_{i=1}^{N_T} (c[0, t_i] - e[0, t_i]) \\
&\quad + \frac{1}{N_T} \sum_{i=1}^{N_T} n(t_i, t_i + T). \tag{2}
\end{aligned}
$$

In Eq. 2, N_T is the number of sample periods of length T used in the complete-nested approach, and t_i is the time at which the ith sample period begins. Note that at sample time of length $T = \tau$, where τ is the length of the entire study, the number of species for nested and complete-nested STRs is the same but this number may differ at other nonzero sample times.

Comparison of Eqs. 1 and 2 illustrates the differences between the nested and complete-nested STR. The first term in each equation (S_0) is the number of species present at the instantaneous start of the survey ($t = 0$). The second term in Eq. 2, which does not appear in Eq. 1, is the effect of colonization and extinction dynamics on the number of species observed at t_i, where colonization and extinction refers broadly to the addition or loss of species since the prior time period through dispersal, germination, speciation, and so on. The last term in each equation is the new species encountered as one observes the community. In Eq. 1, that term is simply the number encountered from the survey start to time T. In Eq. 2, it is the average number of species encountered over different start times t_i in the interval T. Therefore, the two sources of differences between $S_n(T)$ and $S_{cn}(T)$ are (1) community dynamics dominated by colonization or extinction, and (2) heterogeneity across the study time interval in the number of new species encountered during t.

To isolate the impact on the STR, we consider each of these sources in the absence of the other. First, consider the impact of community dynamics in the case where heterogeneity in the rate at which new species are encountered is negligible (i.e., the last terms in Eqs. 1 and 2 are effectively equal). If species turnover dominates such that colonization of new species completely displaces existing species, constant species richness results even though species composition changes between surveys. Brown et al. (2001) argue that species richness is expected to be maintained within relatively narrow limits in systems where productivity remains relatively unchanged and environmental conditions remain within the tolerances of species in the regional species pool. In this scenario, the two STR curves will be identical, and hence $w_n = w_{cn}$, where w_n and w_{cn} are the slopes of the linear regression of the nested and complete-nested STRs respectively when plotted on logarithmically transformed axes. Note that both slopes will be greater than zero if turnover is greater than zero.

Alternatively, species colonization dynamics may dominate, such as when primary succession is occurring, or when species invasions and introductions are greater than species extinctions (Sax et al. 2002, Sax and Gaines 2003). In this case of increasing richness, the second term of Eq. 2 will be greater than zero and $S_{cn}(T) > S_n(T)$ for all $T < \tau$. Short time periods will have greater mean species richness in complete-nested than nested designs, due to the averaging of high species richness at later times with low species richness at earlier times. This

shifts the left end of the complete-nested STR up. If the two STR curves are power-law, which may not be true in general but is approximately true in the case we examine, this lowers the complete-nested slope value relative to the nested slope ($w_n > w_{cn}$). This prediction for the relative slope values will also hold for non power-law STR curves as long as the difference between the nested and complete nested curves does not increase with sample time on log-log axes (Appendix B).

Finally, species extinction dynamics may dominate, such that species richness decreases through time as a result of factors such as environmental change, habitat destruction and species introductions (Sax and Gaines 2003, Thomas et al. 2004). In this case, the nested STR will be constant, because it measures the total number of species observed, which does not change as sample time increases. However, the complete-nested curve will be increasing, because the number of species sampled in small time intervals is an average of the initial number of species and the smaller number of species encountered in later sampling intervals. The second term of Eq. 2 will be negative and $S_{cn}(T) < S_n(T)$ for all $T < \tau$. This shifts the left end of the complete-nested STR down. If two STR curves are power law, this raises the complete-nested slope value relative to the nested slope ($w_n < w_{cn}$). As in the previous case, this prediction will also hold for non-power-law STR curves as long as the difference between the nested and complete nested curves does not increase with sample time on log-log axes (Appendix B).

The second source of differences between nested and complete-nested STRs is heterogeneity in the rate at which new species enter the community, which can arise from a variety of sources. For example, this rate could increase through time as species arrival improves a landscape for other species (Connell and Slatyer 1977) or decrease through time as the community contains an increasing number of the species available in the regional pool (MacArthur and Wilson 1963, 1967, Cornell and Lawton 1992). Additionally, external changes in environmental factors such as precipitation or disturbance regime could cause temporal heterogeneity in this rate. A monotonic increase in the rate of new species arrival (i.e., a rate that increases either discontinuously or smoothly, but never decreases) will lead to an average number of new species entering the community during interval T (last term of Eq. 2) that is greater than the number of new species entering during the interval T measured from the beginning of the study (last term of Eq. 1). If the community is undergoing turnover dynamics (i.e., the first source of differences is negligible), this will lead to $S_{cn}(T) > S_n(T)$ for $0 < T < \tau$. Likewise, a monotonic decrease in the rate of new species arrival will lead to $S_{cn}(T) < S_n(T)$ under the same conditions. Between these two extremes, there are a variety of possibilities. The key issue is the difference between the initial and average rate. If this average is consistently higher or lower than the initial measure-

ment, the complete-nested species richness will be less or greater (respectively) than the nested richness.

Under turnover dynamics, the nested and complete-nested curves must intersect at the two endpoints, $T = \tau$ and $T = 0$, or more typically $T = 1$, where T is measured in units of the smallest biologically meaningful sampling interval. As a result, we cannot draw any general conclusions about the relative sizes of w_n and w_{cn} under the scenarios mentioned. In fact, if there is a directional change in the rate of new species arrival, the nested and complete-nested curves cannot both be exactly power-law. If the nested curve is power law, the complete-nested curve will intersect it at the endpoints but must exhibit some curvature in between.

These differences between nested and complete-nested STRs occur because they quantify two fundamentally different processes. The nested STR quantifies how the number of species encountered in a community from a given time point depends on how long you wait or what an observer sees in a system starting at one point in time. On the other hand, the complete-nested STR quantifies how many species you will encounter when you observe a community on average for a given length of time, where the average is taken over different starting times. In other words, it describes the number of species an observer should expect to see given that they start observing the system at an arbitrary point in time. In the remainder of this study, we analyze vegetation data from Mount St. Helens, Washington, to illustrate the impact of curve construction on species–time parameters under colonization-dominated dynamics.

METHODS

Mount St. Helens, located in the Cascade Mountains in southwestern Washington, USA (46°12′ N, 122°11′ W), experienced a massive lateral eruption in May 1980. This eruption destroyed the northern half of the cone and covered surrounding landscapes with pyroclastic flows (incandescent clouds of gas and solids), pumice deposits, and lahars (mudflows) (Dale et al. 2005). One of us (R. del Moral) censused circular permanent plots (250 m^2) in several disturbed habitats since 1980 (see del Moral 1983, 2000, del Moral and Bliss 1993). We analyzed data collected on 29 of these plots, selected because they were surveyed for at least 10 consecutive years, with the first survey occurring between 1980 and 1982.

The plots analyzed encompass four disturbance intensity levels: tephra, scour light, scour heavy, and lahar. The least disturbed are the tephra plots (Butte Camp), which received coarse air-fall deposits up to 20 cm and recovered within a few years of the eruption (del Moral 2000). Next are the light (lower Pine Creek Ridge) and heavy (Butte Camp) scours, which resulted from erosion caused by rapidly melting glaciers. Finally, the most disturbed plots included in this analysis are the lahar plots (Butte Camp), where mudflows removed all vegetation and soil.
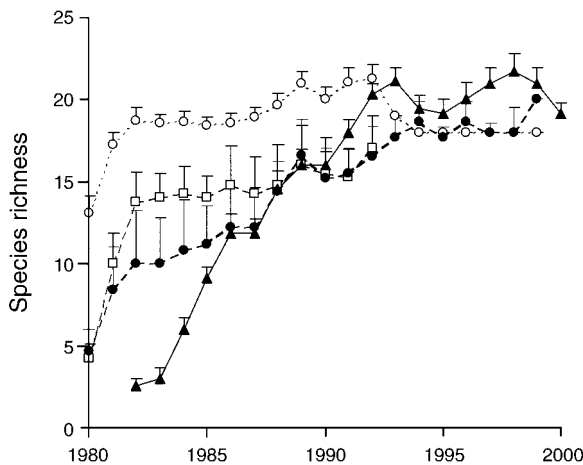
FIG. 2. Total species richness (number of species, mean + SE) in the 29 permanent plots (250 m^2) by disturbance intensity: tephra (open circles, $n = 13$), scour light (open squares, $n = 4$), scour heavy (solid circles, $n = 5$), and lahar (solid triangles, $n = 7$). The graph shows only those years included in this analysis, which was limited to consecutive surveys. Surveys continued at most plots through 2005.

Each plot was marked with a center stake and with stakes at the end of the four radii. Species composition was recorded in six quadrats (0.1-m^2 quadrats from 1980 to 1986, 0.25-m^2 quadrats from 1986 to 2004) placed along each radius at 1-m intervals, 24 quadrats in total, each summer (del Moral 2000). All other species found within the plot, but not sampled by the quadrats, were also recorded. Total species richness and percent cover were recorded for each plot. These surveys represent the community composition over the course of the growing season, not for an instantaneous point in time. Nomenclature follows Hickman (1993).

To calculate the STR for each plot, survey years (1980, 1981, 1982, ...) were converted into sample years (year 1, 2, 3, ...). Total species richness was then calculated for each sample year, with the assumption that the observed species presences reliably estimate actual species richness. For some plots, the number of years surveyed between 1980 and 2005 is greater than the number used in this analysis as only consecutively surveyed years were analyzed. For nested STRs, total species richness was calculated for each sample length of time T from the initial sample year ($T = 1, 2, 3, \ldots$ years). For complete-nested STRs, total species richness was averaged across all possible combinations of consecutive years of sample length of time T. For both STR forms, ln(species richness, S) was plotted as a function of ln(time) and fit with a linear least squared regression line, $\ln(S) = \ln(d) + w \times \ln(T)$. Species–time slopes ($w_c$, w_{cn}) were analyzed as a function of disturbance intensity. In addition, the difference between the slopes ($w_n - w_{cn}$), was analyzed as a function of the trend in average annual richness through time, quantified here by the slope of the linear regression of

species richness against time. To illustrate heterogeneity in the encounter rate over time, we calculated the average and initial rate of new species observed in the second year of a two-year-long sampling interval.

RESULTS

A total of 52 species were observed across the 29 plots during the years examined. Of these, some species were observed in all four disturbance levels (e.g., *Agrostis pallens*, *Eriogonum pyrolifolium*, *Lupinus lepidus*, and *Polygonum davisiae*). Others were observed predominantly in the least (e.g., *Castilleja miniata*, *Fragaria virginiana*, and *Poa secunda*) or most disturbed areas (e.g., *Abies lasiocarpa*). Initial species richness varied as a function of disturbance intensity with greatest richness in the tephra (least disturbed) plots (Fig. 2). By the end of the time periods used in this analysis, total species richness approached similar levels for all four disturbance types. The average number of species colonizations per year increased with disturbance intensity from 1.06 ± 0.11 (tephra) to 1.54 ± 0.12 (lahar) species colonizations/year.

A power-law STR fit nested and complete-nested STRs with adjusted $r_n^2 = 0.54$–0.98 and $r_{cn}^2 = 0.67$–0.99 (Appendix C). The nested species–time slope ranged from $w_n = 0.06$–1.03, while the complete-nested slope ranged from $w_{cn} = 0.03$–0.28. The nested species–time intercept ranged from $\ln(d_n) = 0.52$–2.90, while the complete-nested intercept ranged from $\ln(d_{cn}) = 1.93$–3.10. In all plots, nested slopes were steeper than complete-nested slopes (Figs. 3 and 4), as would be expected under colonization-dominated dynamics where species richness increases through time. Additionally, the nested and complete-nested slope values, as well as the difference between them ($w_n - w_{cn}$), increased with disturbance intensity from tephra to lahar. In other words, the difference between the two STR methods was small in low disturbance plots (tephra, 0.10 ± 0.02 [mean $\pm$ SE]) but large in the heavily disturbed plots (lahar, 0.68 ± 0.05), which were more influenced by colonization dynamics (Fig. 4a). This is also illustrated by the positive relationship between the difference in slope values and the slope of the linear regression of species richness against time (Fig. 4b). The average number of new species observed across all plots when the length of the study was extended from one to two years was 1.3 ± 0.1 species, less than initial rate of new species observed from year one to year two of 3.5 ± 0.6 species. As mentioned above, we cannot derive general predictions of how directional changes in the rate at which new species are observed will impact the relative magnitudes of w_n and w_{cn}. However, it is worth noting that while our calculations indicate that there may be a decrease in the rate at which new species are encountered in this system, this directional change did not impact the success of predictions made based on colonization-dominated dynamics in the absence of this heterogeneity.
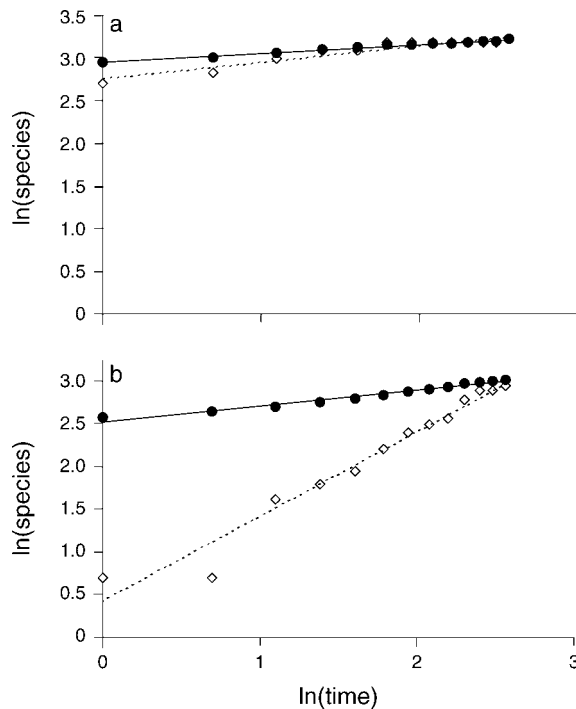
FIG. 3. Nested (open diamonds) and complete-nested (solid circles) STRs (species–time relationships) for two sample plots, where S is species richness and T is time: (a) Butte Camp A3, tephra plot [for nested, $\ln(S) = 0.19 \times \ln(T) + 2.75$, adjusted $r^2 = 0.90$; for complete-nested, $\ln(S) = 0.10 \times \ln(T) + 2.95$, adjusted $r^2 = 0.98$]; (b) Lahar 5, lahar plot [for nested, $\ln(S) = 0.92 \times \ln(T) + 0.52$, adjusted $r^2 = 0.96$; for complete-nested, $\ln(S) = 0.18 \times \ln(T) + 2.53$, adjusted $r^2 = 0.98$]. See *Methods* for discussion of disturbance intensity levels.

DISCUSSION

Species–time relationships are emerging as an important ecological concept. Specifically, they may be useful for establishing the role of time scale in diversity comparisons needed to establish patterns such as the latitudinal gradient in diversity, or to make decisions about conservation priorities. However, as demonstrated here, STR construction has important implications on conclusions drawn due to fundamental differences between STR types. At Mount St. Helens, nested STR slopes were greater than complete-nested slopes in agreement with our expectation under colonization dynamics. In addition, the difference between the nested and complete-nested slopes increased with disturbance intensity, which is related here to changes in species richness or the importance of colonization dynamics. The relationship between the difference in slopes and rate of change in species richness illustrates the importance of considering STR construction in disturbed and/or successional systems, where the significant changes in species richness might occur. As Fig. 4b illustrates, the two constructions produce similar results when richness dynamics approach equilibrium.

We note that these issues are not isolated to STRs. Analogous differences would exist between nested and complete-nested SARs if constructed across a spatial gradient in species richness, or in the rate at which new species are encountered as one moves in space. Scheiner (2003) pointed out that nested SAR curves quantify alpha and beta diversity starting from one spatial location through their intercept and slope on log–log scales, respectively, whereas complete-nested SAR curves quantify average alpha and beta diversity over the entire plot. But this averaging would cause complete-nested SARs to have z values, where z is the slope of the SAR relationship on log–log axes, that are systematically lower than nested SAR z values if alpha diversity is higher on other parts of the plot than in the starting location. Likewise, the opposite trend would result if alpha diversity is lower on other parts of the plot (analogous to the impact of colonization and extinction dynamics on STRs, respectively). It would also lead to complete-nested SARs that curve either above or below nested SARs depending on whether average beta
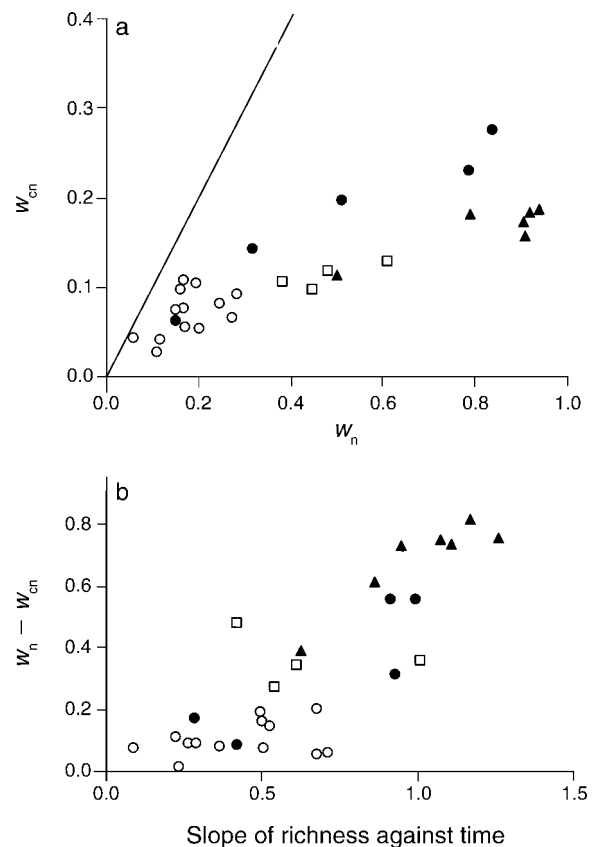

FIG. 4. (a) Nested and complete-nested STR slopes by disturbance intensity. The solid line is a one-to-one line. (b) Difference between nested and complete-nested STR ($w_n - w_{cn}$) slopes as a function of the slope of the linear regression of species richness against time. In both panels, each data point represents one plot: tephra (open circles), scour light (open squares), scour heavy (solid circles), and lahar (solid triangles).

diversity is higher or lower in other parts of the plot (analogous to the impact of a higher or lower rate of encounter of new species on STRs).

The nested and complete-nested constructions have different benefits depending on the research question and study system. The complete-nested STR has the advantage of averaging over fluctuations in richness and arrival rates. Hence, it can give us information about the average relationship between species sampled and sample time in the system. However, in systems where changes in species richness and the rate of new species arrival are integral to the system dynamics and question at hand, the nested construction may be more relevant. For example, in studies involving systems undergoing disturbance and succession, one gains important information by considering how diversity depends on the length of a sampling interval started after a disturbance event (a nested STR) instead of how it depends on the length of a sample averaged over different starting points (a complete-nested STR). Two systems with completely different nested STRs (for example one reflecting an increasing rate of encounter and the other a decreasing rate) could have similar complete-nested STRs. In that case, an analysis of complete-nested STRs would lead to the inaccurate conclusion that time scale impacts diversity in the same way in both systems and that the diversity of these two systems could be compared equally at any time scale. Similar issues may be relevant when extending comparisons to broader scales in order to establish geographic patterns across systems where species richness may be increasing or decreasing with time. However, if one wants to establish broad-scale patterns across all systems, most of which will likely have relatively constant species richness (Brown et al. 2001), then the complete-nested construction would be more useful.

The STR could also be useful in conjunction with the SAR for considering the correspondence between processes influencing diversity in space and processes influencing it in time. In systems undergoing disturbance and succession, the most biologically interesting analysis may be a search for correspondence between nested STRs and nested SARs, which would reflect the fact that the dynamics of these systems are undergoing depend on time since disturbance and distance away from undisturbed patches. Furthermore, in these systems, the nested version of the species–time–area relationships (STAR), which is meant to quantify the interactive effects of temporal and spatial scale (Adler and Lauenroth 2003, Adler et al. 2005, Ulrich 2006), could provide more biologically interesting information than the complete-nested version, as it quantifies directional influences on this interaction. For example, distance from an undisturbed patch may matter more soon after a disturbance than later in the successional sequence. On the other hand, the complete-nested STR would be of interest where the average scaling of richness with time is of interest. This would be important when establishing large-scale patterns that are free of the effects of small-scale heterogeneity.

We raise these issues here to stimulate further discussion on the appropriate definition of sample time and STR construction. We believe that once these issues are resolved, STRs have the potential to play an important theoretical role in understanding diversity patterns, as well as an applied role in biodiversity assessments.

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CONCEPTS & SYNTHESIS

APPENDIX A

Nested and complete-nested species–time relationship (STR) examples (*Ecological Archives* E088-128-A1).

APPENDIX B

Relative sizes of nested and complete-nested slopes for non power-law STRs (*Ecological Archives* E088-128-A2).

APPENDIX C

Table of nested and complete-nested STRs observed for Mount St. Helens (*Ecological Archives* E088-128-A3).