

Outline for turnover paper:

- 1) importance for studying the relationship between biodiversity and ecosystem function
- 2) reviews suggest that this relationship is dependent upon spatial scale (e.g., Waide et al.)
- 3) Scale dependence in the relationship between richness and productivity occurs because mechanisms for generating species diversity are dependent upon scale and ANPP
- 4) proposed mechanism for spatial scale dependence (Chase and Leibold)-spatial species turnover is a function of ANPP
- 5) chase and Leibold show scale dependence and pattern of ANPP with turnover
- 6) Chase and Leibold complicates issue of spatial and temporal scale (they aggregated species occurrences in both time and space simultaneously). Raises issue of how different estimates of richness and turnover (created by aggregating data across space and time in different ways) relate to ANPP.
- 7) Describe the four measures of richness as spatial scale and/or temporal scale increases. Describe three measures of turnover-spatial, temporal, spatio-temporal (sum of independent and interactive effects). Why are these important?
- 8) Goals
 - a. Untangling the potential confounding effects of spatial and temporal scale dependence. To do this we will examine how the relationship between species richness and productivity change as i) the spatial scale increases, ii) the temporal scale increases and iii) when both spatial and temporal increase. We will also evaluate whether the patterns we see in iii for grassland systems parallel those found in the pond systems studied by Chase and Leibold
 - b. Are any of the measures of turnover a function of ANPP (also compare pattern of spatio-temporal turnover and ANPP in grassland and pond systems) ?
 - c. Are estimates of habitat heterogeneity (in terms of the variance of ANPP) correlated with mean ANPP? If so, this would indicate that turnover may be a function of heterogeneity in conditions that affect ANPP rather than alternate states at a common mean (if turnover is a function of mean ANPP).
 - d. Are the patterns (a-c) similar in grassland and shrub systems at a similar site.

Analytical questions:

Each of these analyses will be performed at each site.

A) Documentation of scale dependent patterns in the relationship between species richness and ANPP

- 1) Is there a linear or quadratic relationship between species richness and ANPP when richness is measured over small spatial and temporal scales?
 - a. Use orthogonal polynomials to relate $\overline{\alpha}_T$ with the mean of ANPP for each plot across years.
- 2) Is there a linear or quadratic relationship between species richness and ANPP when richness is measured over small spatial but long temporal scales?
 - a. Use orthogonal polynomials to relate γ_T with the mean of ANPP for each plot across years.
- 3) Is there a linear or quadratic relationship between species richness and ANPP when richness is measured over large spatial but short temporal scales?
 - a. Use orthogonal polynomials to relate $\overline{\gamma}_R$ with mean of ANPP across all plots and years for each region
- 4) Is there a linear or quadratic relationship between species richness and ANPP when richness is measured over large spatial and temporal scales?
 - a. Use orthogonal polynomials to relate γ_{RT} with mean ANPP across all plots and years for each region

-spatial scale dependence will be evaluated by comparing the results of 1 and 3

-temporal scale dependence will be evaluated by comparing the results of 1 and 2

-spatio-temporal scale dependence will be evaluated by comparing the results of 1 and 4

B) Documentation of patterns between turnover and ANPP (dissimilarity values represent measures of turnover: description of how these are estimated are provided below)

- 1) Is there a relationship between spatial species turnover and ANPP to account for comparison 1 and 3 above?
 - b. Use orthogonal polynomial to relate spatial species turnover (annual mean of the mean dissimilarity [comparing composition between all pairs of plots in a region for each year] values for all plots within a region) with mean of ANPP across all plots and years for each region
- 2) Is there a relationship between temporal species turnover and ANPP to account for comparison 1 and 2 above?
 - a. use orthogonal polynomial to relate temporal species turnover (mean of the annual dissimilarity [comparing composition of the same plot in adjacent years] measures for each plot) with mean of ANPP across all years for each plot
- 3) Is there a relationship between spatio-temporal species turnover and ANPP to account for comparison 1 and 4 above?
 - a. use orthogonal polynomial to relate spatio-temporal species turnover (mean of the dissimilarity values [comparing composition between all pairs of plots at the same and different times for each region] estimated for all plots within a region across all years) with mean of ANPP across all years and plots for each region

C) Documentation of relationship between estimates of mean ANPP and variance of ANPP

-necessary to evaluate whether changes in turnover with mean productivity is confounded with variance in productivity. A relationship between the mean and variance could indicate that turnover is not a function of high productivity but rather a function of greater heterogeneity in ANPP.

- 1) Is there a relationship between the mean of ANPP for each plot across years with the variance in ANPP (measured across all years for each plot)?
 - a. Correlate these two variables to each other
- 2) Is there a relationship between the mean of ANPP across all plots and years for each region with the variance in ANPP (measured across all of the years and plots for a particular region)?
 - a. Correlate these two variables to each other

Sites to use for spatial patterns independent of temporal scale:

Cedar creek, Jornada (do grassy and shrub communities separately), Kellog, Konza, McLaughlin, Sevilleta (do grassy and desert communities separately), Short Grass Steppe.

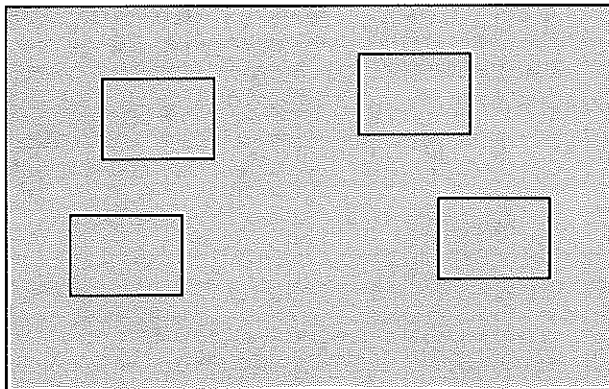
Sites to use for temporal patterns independent of spatial scale:

Jornada (do grassy and shrub communities separately), Kellog, Konza

Sites to use for spatio-temporal scale dependence:

Jornada (do grassy and shrub communities separately), Kellog, Konza

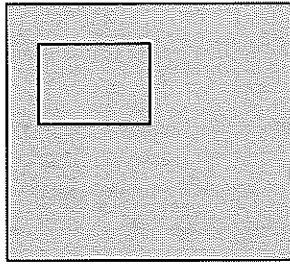
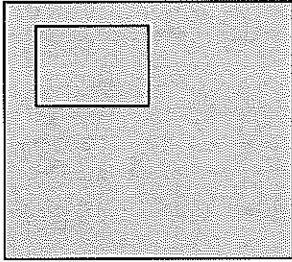
How to estimate spatial turnover for a region?



Big rectangle is a field
Small squares are plots in a field

- 1) Compute dissimilarity values for all pairwise combinations of plots in a field for each year (do not do self-pairs)
- 2) Calculate mean of all pairwise dissimilarity values for a field across all years

How to estimate temporal turnover for a plot (locality)?

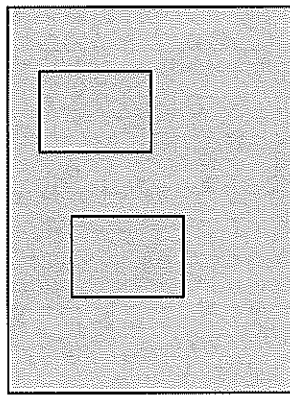
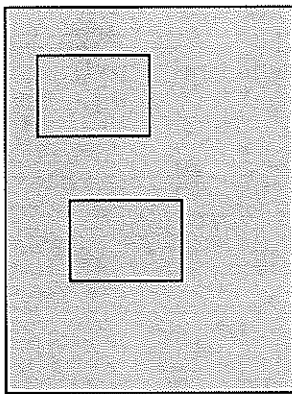


Each big square represents the same field at 2 different points in time

Each small square represents the same plot within the same field at 2 different points in time.

- 1) Compute dissimilarity values for the same plot at 2 adjacent intervals in time (i.e., one year apart). Do this for all annual intervals.
- 2) Calculate the mean of all the dissimilarity values for each of the annual intervals

How to estimate spatio-temporal turnover for a region?



Each big square represents the same large field at 2 different points in time

The two small squares represent 2 different plots within the same field

- 1) Compute the dissimilarity among all pairwise combinations of plots in a field (region) regardless of their spatial or temporal relation (exception: do not self-compare plots within the same point in time)
- 2) Calculate the mean of all the dissimilarity values obtained in 1)

Given a site with M plots/region, N censuses, and Q regions, the total number of observations is MxNxQ, where each observation represents a unique combination of a plot and a census. The potential measures of richness include:

Symbol Number of Points Definition

Small Space, Short Time

α_{PT}	MxNxQ	α -richness, for each unique observation
$\overline{\alpha}_T$	MxQ	temporal mean of α -richness across years for each plot (<i>Our figure A</i>)
$\overline{\alpha}_R$	NxQ	mean α -richness across plots within a region, for each year

Big Space, Short Time

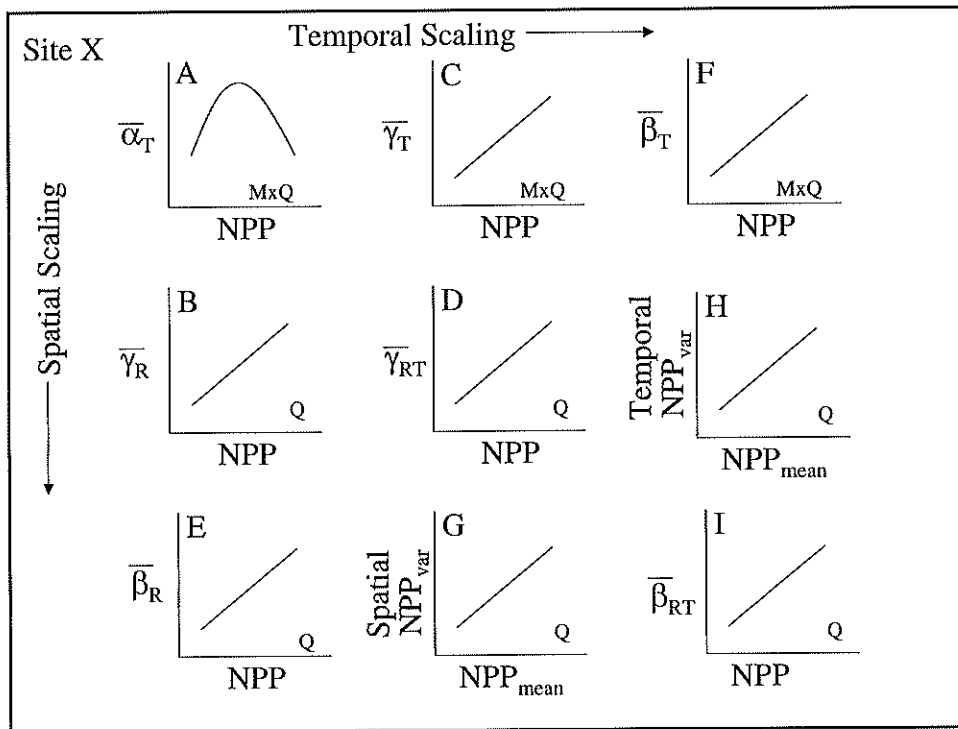
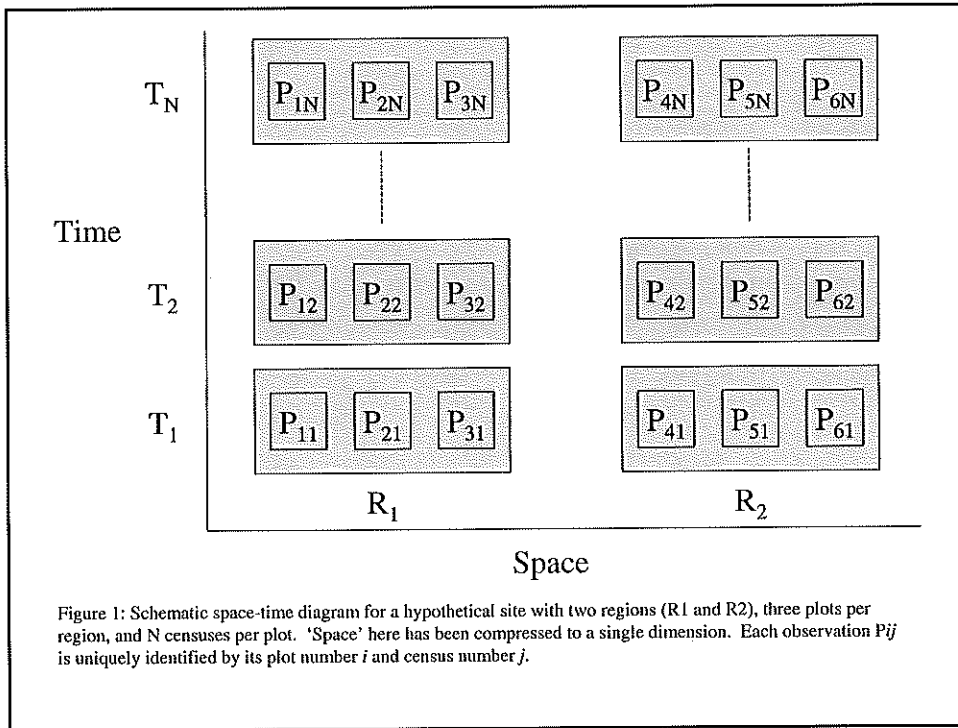
γ_R	NxQ	aggregate species richness across all plots in a region, calculated for each year (<i>spatial gamma diversity</i>)
$\overline{\gamma}_R$	Q	temporal mean of spatial gamma diversity (<i>Our figure B</i>)
β_R	NxQ	dissimilarity among plots within a region, calculated for each year (<i>spatial turnover</i>)
$\overline{\beta}_R$	Q	temporal mean of spatial turnover (<i>Our figure E</i>)

Small Space, Long Time

γ_T	MxQ	aggregate species richness across all censuses for each plot (<i>temporal gamma diversity, plot focus</i>) (C&L <i>Figure 1a; Our figure C</i>)
$\overline{\gamma}_T$	Q	regional mean of plot-scale temporal gamma diversity
β_T	MxQ	differences in species composition between years, calculated for each plot (<i>temporal turnover</i>)
$\overline{\beta}_T$	Q	regional mean of temporal turnover (<i>Our figure F</i>)

Big Space, Long Time

$\overline{\alpha}_{RT}$	Q	mean α -richness across all observations in a region
γ_{RT}	Q	spatiotemporal gamma diversity, calculated by compiling the regional species composition and aggregating across years (C&L <i>Figure 1b; Our figure D</i>)



Attempts to relate ecological patterns and the mechanisms driving these patterns are hindered by the lack of overarching and integrated programs for the collection of relevant data (Huston 1999). Programs to collect or archive specific measurements abound (e.g., FLUXNET, ORNL DAAC), but our ability to combine these data in meaningful ways is severely constrained by mismatches between the spatio-temporal domains of data collected to identify patterns and those collected to determine causation. Even programs that attempt to address these issues at local scales (e.g., LTER) are less consistent about matching the domains of measurements across sites. The inadequacy of existing data to address controls on the generation and maintenance of biodiversity led Huston (1999) to comment that “the number of hypotheses about species diversity far outstrips the data that are available to test these hypotheses.” Our present ad hoc approach to the collection of ecological data needs to be closely examined in the light of proposed major investments in infrastructure to enhance measurement and monitoring of ecological processes.

Chase and Leibold (2002) present an example of the importance of matching measurement domains. Data that they collected from small ponds showed a hump-shaped relationship between productivity and species richness when viewed at a local scale (among ponds). However, the same data viewed at a regional scale (among watersheds) produced a positive linear relationship, suggesting that the mechanisms that produce patterns are scale dependent. These results confirm earlier studies in lakes (Dodson et al. 2000) and grasslands (Gross et al. 2000). However, in the grassland study, linear patterns were found at the local scale and humped patterns at larger scales. Searching for similar or conflicting patterns in other systems is hampered by the lack of matching measurement domains, which restricts our ability to examine the effects of scale the relationship between dependent and independent variables.

Thompson et al. (2001) indicated that defining the spatial-temporal domains of ecological processes was one of the most important issues in ecology, one that would require a reevaluation of the way ecologists bound their conceptual models. The existence of a set of domains of causality that vary in spatial and temporal extent complicates these models and requires a clear topology of ecological causative factors (Thompson et al. 2001). Once this topology is established, measurements protocols need to be instituted to assure that relevant data are collected for each domain. Since different kinds of ecological questions might require data from different measurement domains, the establishment of new monitoring programs will require careful attention to matching key ecological questions with long-term measurements.