

How residence time constrains diversity

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INTRODUCTION

P1—Biological and ecological change is marked by time and from rates of metabolism, growth, and evolution to the duration of seasons, succession, and life history, time is the fundamental dimension of biology. But despite its universal relevance in biological and ecological systems, time is more often used as an independent variable or to characterize rates of change, than it is treated as a primary driver of change and biodiversity. While the large lack of study into the general influence of time is recognized among some ecologists (cite), the precise importance or general influence of time is so rarely mentioned that it may be self-evident, non-existent, or commonly taken for granted. But, this is unlike the influence of other general variables such as space and abundance.

P2—Law-like patterns of space and abundance such as the species-area relationship and the species-abundance distribution are central to the ecological study of biodiversity (Hubbell 2001, McGill 2010, Harte 2011). Yet, a similarly general temporal pattern (species-time relationship) is rarely studied and is neither central to nor predicted by general ecological theory (White, Adler et al.). While area and abundance are common inputs to biodiversity theories (McGill 2010), no general theory uses time *per se* as an input. And, while at least one popular ecological subfield is devoted to spatial dynamics, i.e., spatial ecology (16000 results on Google scholar), “temporal ecology” has yet to be deemed a subfield (590 results on Google scholar) while temporal dynamics are studied along with spatial, i.e., “spatio-temporal”.

P3—Even if the general influence of time were very simple, it would be no simpler and no less profound than the most general spatial principle, i.e., “near things are more similar than far things”, also known as Tobler’s Law or Tobler’s First Rule of Geography (cite). Likewise, it might be no less straightforward, understated, and mathematically necessary than the constraining influence of total abundance and sample size on intensively studied patterns of commonness and rarity (Locey and White 2013, Xiao et al. 2015). Yet there is no general ecological rule or law relating to time. There are no studies on the general influence of time on biodiversity and, other than the species-time relationship, there are no general time-related ecological patterns. Yet, at least one aspect of time applies to all components of any biological or ecological system, i.e., the amount of time that an individual organism, resource particle, species, etc., remains in a system; residence time.

P4—Put simply, viable populations are maintained when individuals can reproduce before dying or emigrating but not so quickly that resource consumption exhausts the rate of supply. In this way, the timing of life history and population growth is constrained by residence time or perhaps even optimized for it (cite). This principle underpins chemostat theory, making residence time a master variable for controlling growth and biomass in experimental microcosms and engineered bioreactors. It also makes residence time among the most important variables influencing stability, function, and biodiversity in sensitive ecosystems like estuaries (cites). Yet, the influence of residence time is poorly known outside aquatic systems and though it is often manipulated to control growth and biomass, residence time has yet been framed as a time-related constraint common to any system, whether aquatic, terrestrial, or host-related. Yet, while many organisms are at the mercy of currents, all organisms are at the mercy of time.

P5—We examined the importance of residence time on the growth of populations, the assembly and structure of communities, and the evolution of trait combinations in highly complex systems. We propose that the residence time of a system should positively correlate with the residence times of its components (individuals, resources, species, traits, etc.). We then propose relationships of taxa and trait diversity based on the constraining influence of residence time. Finally, we propose the residence time distribution (RTD) as a general time-related ecological pattern that reveals many short-lived individuals, resources, species, etc., and few that are relatively long-lived. We examine factors influencing the RTD and test our predictions

using an information-intensive individual-based model capable of simulating communities of competitively asymmetrical and physiologically unique species and individuals operating under trait evolution, sexual and clonal reproduction, fluid and non-fluid dynamics, variable resource efficiencies, dispersal dynamics, among others.

METHODS

Quantifying residence time

Ecosystem residence time—In ideal systems (homogeneously mixed aquatic microcosms), residence time (τ) equals the ratio of volume to flow rate ($\tau = V/Q$). Volume *per se* is not critical as the size of the system could also be quantified with area (A) and distance (D); consider that a perfect cube where residence times based on V , A , or D would be equal. That is, $\tau = V/Q = D^3/Q = D^3/(D^3/\text{time}) = \text{time}$. The inverse of τ is known as dilution rate and is the portion replaced per unit time, which often approximates growth rate. If τ^{-1} exceeds growth rate, then populations can be washed out. But, if τ^{-1} is too slow (i.e., τ is too long) then the supply resources may be too low to maintain actively growing populations.

Residence time distribution (RTD)—In ecological systems, V/Q may be a poor approximation of individual residence time and, at least, only represents one moment of an entire distribution. The amount of time that particles, individuals, etc., spend inside a system can be characterized with a frequency/probability distribution (MacMullin and Weber 1935, Danckwerts 1953). RTDs are used among engineers and hydrologists to characterize turnover, mixing, and flow and to compare the behavior of real systems to simplified models. In our individual-based modeling, we examine residence time distributions for individuals, resources, inert particles, species, traits, and any other aspect of the system that is not permanent.

Primary residence time predictions that should hold up to ecological complexity

Autocorrelated residence times—As a starting prediction, we expect residence times of individuals, resource particles, inert tracers, and most any non-permanent component of the system to be positively correlated. This is already known to be the case where τ as V/Q closely approximates the residence time of individual organisms and tracer particles. In general, without invoking any specific scenario, very short ecosystem residence times should not lead to long residence times for individual particles.

Right-skewed residence time distributions—Residence time distributions of inert tracers are generally right-skewed, often taking a lognormal or power-law form. This reveals many short-lived particles and relatively few long-lived ones; a result of turbulence and not flowing freely or homogeneously. But, whether flowing or not, we expect right-skewed distributions to characterize the life history of individuals, the presence of resource particles, and even the tenure of species.

Total abundance (N)—Chemostat models predict a unimodal relationship between biomass or total abundance (N) and residence time (τ) when accounting for maintenance energy (cites). Sufficiently low τ can exclude reproduction while sufficiently high τ can mean a slow rate of resource resupply and immigration. In this way, we expect residence time to be a primary constraint on N . In turn, N is a primary constraint on aspects of diversity related to the species-abundance distribution such as richness, evenness, rarity, dominance.

Residence time constrains N , while N constrains commonness and rarity

Richness, evenness, rarity, and dominance—Changes in N are often associated with changes in the number of species (i.e. S). Richness must change as quickly or less quickly than N , i.e., species cannot be gained or lost faster than individuals. We expect the relationship of S to τ to follow a hump-shaped relationship, the slope of which must be equal to or shallower than the relationship of N to τ . Moreover, we expect S to share a power-law-like relationship with N , i.e., $S = cN^z$, where $z \sim 0.5$, as has been observed by May (1988) and others (cite). In contrast to richness, similarity in abundance among species (evenness) should decrease with N purely because of numerical constraints (Locey and White 2013). That is, a greater portion of possible forms of the species abundance distribution reflect high rarity, low evenness, and high dominance as N increases. Consequently, greater N constrains the distribution of abundance among species to take a form that reflects greater rarity, greater dominance, and less evenness.

Species turnover— β -diversity is the heterogeneity in taxa among samples, either with respect to presence/absence or relative abundance (Tuomisto 2010). Measurements of β -diversity are generally derived to be independent of N . Because of this, and because low residence times (high dilution rates) create the most likely scenario to replace a large portion of the community in given period of time, we expect a monotonically decreasing relationship β -diversity to τ .

Residence time influences at least one general life history tradeoff

Growth rate vs. maintenance costs—Organisms with slow growth should not be favored in systems of fast turnover, while organisms with high maintenance costs should not be favored in systems of slow resource supply. Yet, unless growth rate and maintenance are directly related (high growth requiring high maintenance), the relationship between these two traits could be tenuous.

Modeling

Individual-based—We used a spatially explicit individual-based simulation model where individuals and information about individuals are tracked through time. Growth, reproduction, and death are simulated via weighted random sampling that simulates a probabilistic nature of environmental filtering and competition. Resources, tracer particles, and individuals enter, flow through, and exit the system according to a combination of fluid and diffusion dynamics. The model is parameterized with metacommunity, local community, ecosystem, species, and individual level parameters (Table 1). The values of the parameters determine the degree of variation among species and are chosen at random. These parameters can theoretically vary from species-neutral (i.e. all species are the same) to idiosyncratic (i.e. all species are different) but nearly always include some degree of species difference in growth rate, maintenance energy, etc. (Table 1). The model operates in two to three spatial dimensions.

Fluid flow—We used a Lattice-Boltzmann Method (LBM) to simulate movement through a fluid environment. LBMs are powerful and relatively new tools used in computational fluid dynamics, and as we show, can be used in ecology to simulate the realistic fluid flow of individuals, resource, or both (cite). LBMs discretize the environment into a lattice and attach to each position in the lattice a number of particle densities and velocities for each of nine directions of movement. Here, individual organisms and resource particle have x-y coordinates that can change (e.g. in the ideal chemostat simulation) according to the velocity of the environment at those positions (see Appendix for greater details).

Diffusion—We used simulated random walks to move resources and/or individuals through the environment via diffusion. Random walks are commonly used in ecology to model either stochastic physical movement or stochastic demographic changes where the state of an individual or population in the next time step is a random change in magnitude and direction (velocity) that is influenced by the current state; as opposed to a white-noise process where the magnitude of change in position is uniformly random and uncorrelated from step to step.

Simulated life history—In each case, the model simulated life history processes as follows: Resources and individuals flow into a system from the upstream edge of the environment. Species identities of inflowing propagules are chosen at random from a log-series distribution, which often approximates the distribution of abundance among taxa in ecological communities (Hubbell 2001, White et al. 2012). Along with a species ID and species-specific maximum rate of uptake, each propagule is given an individual ID (computer clock-time at which the individual entered), and a cell quota to represent the physiological state of internal resources.

Simulated life history—The community was sampled at random N times with replacement for each simulated time unit. This theoretically gives every individual the opportunity to grow and reproduce. Sampled individuals consume resources according to species specific rates of uptake, if there is a resource present at the individual’s location. Uptake increases the individual cell quota and decreases ambient resources within the immediate location of the individual. The individual’s quota is then decreased according to a species specific physiological maintenance cost. Individuals then reproduce with a probability equal to their cell quota and results in an equal division of the cell quota between the individual and its daughter. The daughter is given a unique individual ID which is appended to the species ID of its mother, to maintain heritage. Sampled individuals die if their cell quota is less than or equal to 0. Individuals and resource particles flow out when they pass the downstream edge of the environment.

Simulating environmental complexity—We constructed the model to capture environmental heterogeneity and the aggregation of resources and individuals. The model was parameterized with an arbitrary environmental gradient that varied regularly across a randomly chosen spatial axis in a randomly chosen direction. Barriers were constructed within the environment to prevent unhindered flow and to generate aggregation and realistic hydrological flow.

Simulating species differences—To allow species differences in physiological traits and environmental optima, we allowed species-specific values for maximum rate of uptake rate, environmental optima, and maintenance costs to be normally distributed random variables where both the means and the standard deviations of the sampling distributions were chosen at random at the start of the simulations. Whenever an individual of a new species entered the local community, values for maximum uptake rate, environmental optima, physiological maintenance cost, and minimum cell quota were chosen at random according to the respective normal distributions for those variables.

Simulating over residence time (τ)—We ran the model to quasi-equilibrium for each value of τ in a series of values spanning more than two orders of magnitude, starting with $\tau = 0.001$ and then doubling until $\tau = 0.512$. The model was run with the same combination of resource, community ecological, and environmental (thermal, physicochemical, physical complexity) values for each value of τ in the series. After running over all τ values, the model was re-parameterized at random with a new combination of resource parameters (size, number, and types of resource particles), habitat complexity parameters (size, number, and types of physical barriers), chemical environmental parameters, thermal parameters (average temperature, direction and severity of temperature gradient), and average community-level values (average specific values for uptake rate, maintenance, individual size, motility, attachment). See table 1.

Because the model is individual-based, information intensive, physiologically realistic, ecologically complex, fluid dynamic, it cannot be run over arbitrarily slow or fast residence times. During each simulation, more than a gigabyte of information is held in memory. This is unlike analytically tractable and computationally simple Markov models or closed-form analytical models, which are more useful for obtaining precise quantitative predictions according to a single theoretical framework via traditional mathematical tools, but are less useful for modeling highly complex multivariate problems and for examining how individual-level interactions lead to aggregate behaviors. In our case, we have integrated components from metabolic theory and ecological scaling, neutral and niche theory, metacommunity theory, fluid dynamics, chemostat theory, and life history theory into a self-evaluating model that tracks the life history, location, and heritage of millions of individuals.

Results

Simplistic theory supported in complex systems The probabilistic and complex modeling approach produced all primary expected results, signifying that predictions of otherwise simplistic and idealized chemostat theory could arise in a complex system.

Autocorrelated residence times—Residence times of individuals, resource particles, inert tracers, and most any non-permanent component of the system were highly correlated (Fig 1).

Autocorrelated residence times and right-skewed residence time distributions—Likewise, residence time distributions were right-skewed and well approximated by lognormal and power-law models (e.g. Pareto, Zipf, Zipf-Mandelbrot) (Fig 2).

Abundance-residence time relationship—We also observed the expected hump-shaped relationship of N to residence time, revealing that residence time could be low enough to exclude reproduction and high enough to result in a rate of resource supply that could not support optimal growth.

Predictions of abundance and species diversity

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Trait-related predictions

Growth rate vs. maintenance—A large literature suggests increasing selection for quickly growing and reproducing organisms as residence time decreases. But, as residence time decreases, selection on rapid growth and reproduction should lessen with respect to selection on a low-cost of maintenance and the ability to persist in the face of low resource supply. However, organisms that can quickly consume resources, grow, and reproduce, could continue to dominance if they can keep maintenance costs down.

Attachment vs. motility—Attachment and motility have clear costs and benefits. Motility allows organisms to seek out resources, refuge, and mates, while attachment allows weakly dispersing organisms to resist being carried away. However, structures required for motility and attachment are not energy-free and presumably come at an energetic cost.

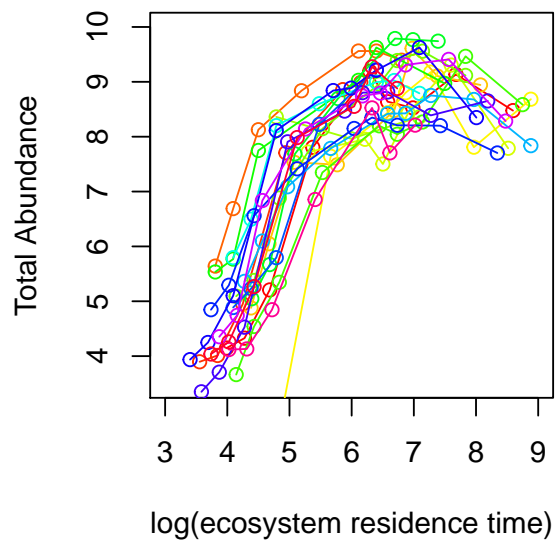
Conclusion/Discussion

We used a stochastic individual-based model that simulated a wide array of environmental and ecological conditions and species-level and individual-level traits. As much of this variation as possible was assigned at random, to explore a large swath of multi-parameter space. Rather than examine the independent influence of each of these factors, our purpose was to find whether simple relationships of residence time to total abundance and community-level characteristics should hold in ecologically complex conditions.

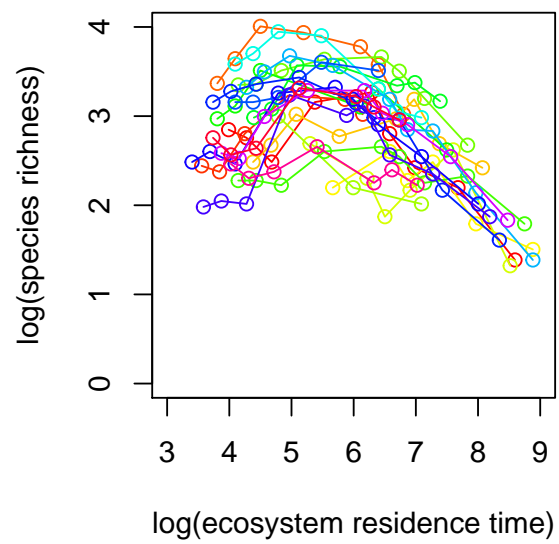
The random selection of trait values of new species (whether immigrating or evolving) allowed realistic and unreasonable trait combinations to occur. For example, a species requiring little maintenance but capable of rapid growth was possible. However, the trait combinations that persisted in the model were realistic combinations of traits that point to life history trade-offs.

Univariate relationships

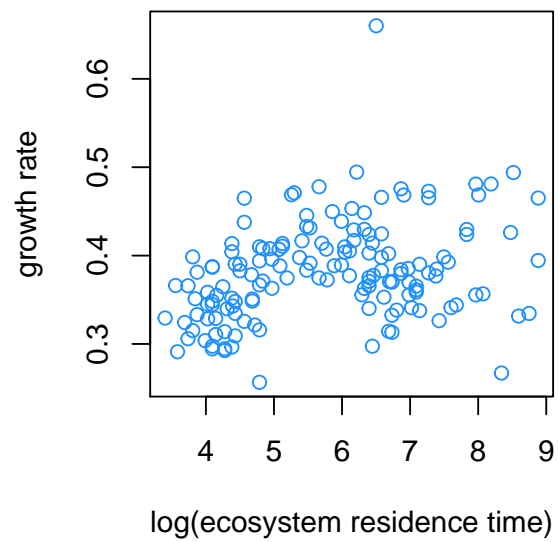
N vs. Tau



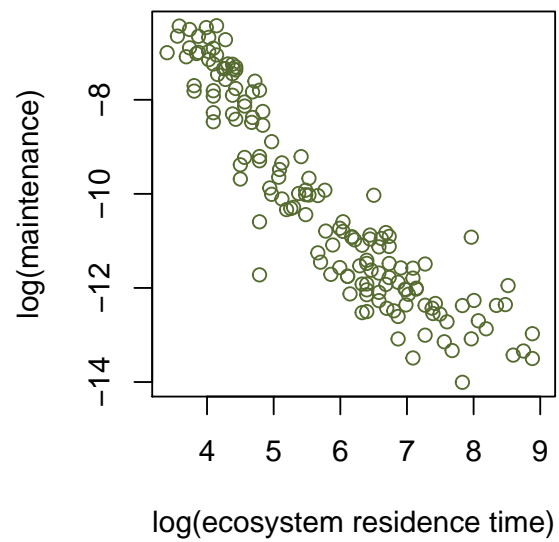
S vs. Tau



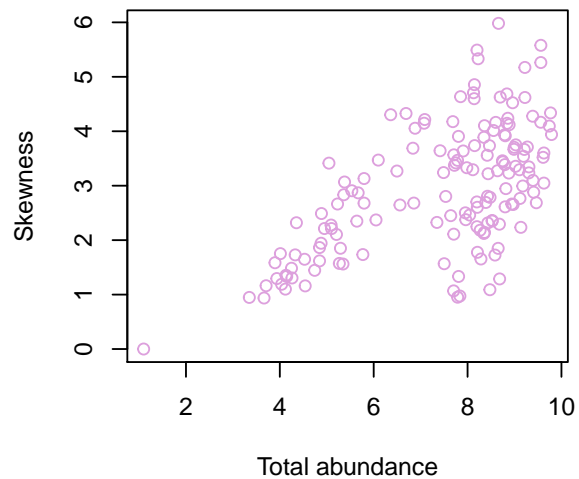
Per capita growth vs. Tau



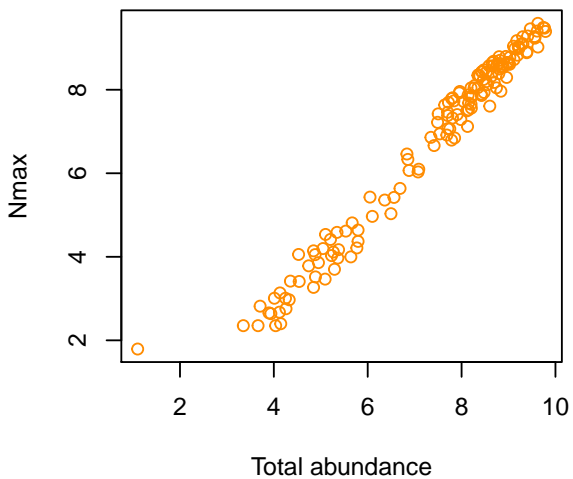
Per capita maintenance vs. Tau



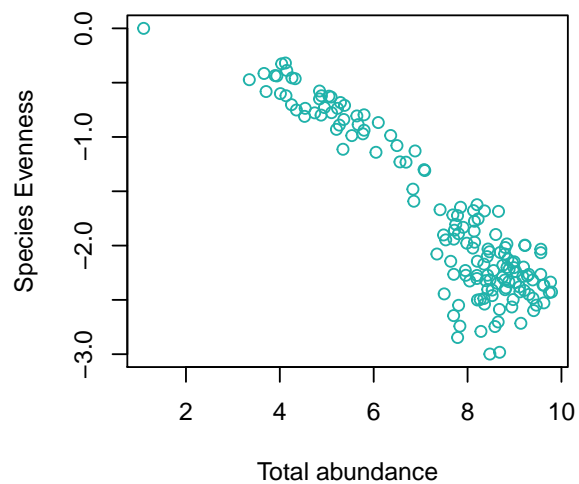
Rarity vs. N



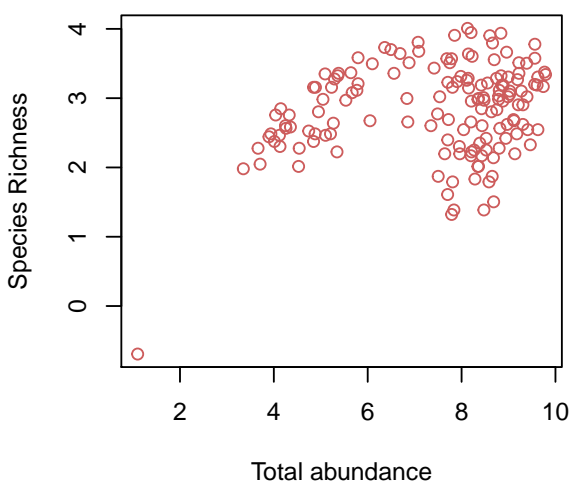
Nmax vs. N



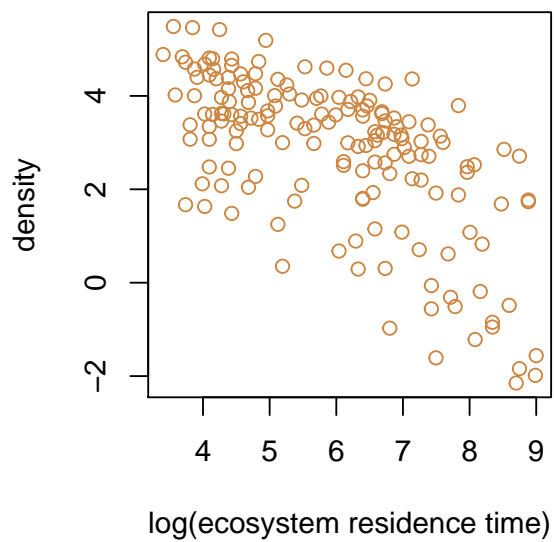
Evenness vs. N



S vs. N



Resource density vs. Tau



Resource richness vs. Tau

