A residence-time framework for biodiversity

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ABSTRACT

Much of Earth's biodiversity is at the mercy of currents and physical turnover. Residence time (τ) is the average time that particles spend in a system and is estimated from the ratio of volume to flow rate. Here, we present a framework for how τ influences biodiversity by coupling dispersal and resource supply. We test a suite of predictions with >20,000 individual-based models that impose ecological selection and energetic costs. Altogether, 24 patterns of growth, productivity, abundance, diversity, turnover, commonness and rarity, and trait syndromes simultaneously emerged across six orders of magnitude in τ. Abundance, productivity, and species richness were greatest when dilution rate, i.e., $1/\tau$, approximated basal metabolic rate. The emergence of τ-based relationships alongside realistic patterns of biodiversity and metabolic scaling suggest that manifold influences of τ, from the individual to ecosystem-levels, are powerful and congruous with ecological paradigms.

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INTRODUCTION

Much of Earth's biodiversity is at the mercy of currents and physical forces that drive the transport of resources and dispersal of organisms. In turn, these processes constrain the time that resources and individuals spend in an environment. Residence time (τ) is the average amount of time that particles spend in a system and is often estimated as the ratio of a system's size or volume (V) to its rate of flow or physical turnover (Q), i.e., $\tau = V/Q$ (Smith and Waltman 1995; Schramski et al. 2015). Residence time can drive resource resupply and individual dispersal, and can equate the physical environment with growth and productivity (Smith and Waltman 1995; Crump et al. 2004). Residence time varies over eight orders of magnitude in natural ecosystems, from several minutes within some organisms to thousands of years in some lakes, glaciers, and soils (e.g., Dietrich and Dunne 1978; Bell et al. 2002; Friend et al. 2014; Dey et al. 2015; Schramski et al. 2015). However, the field of ecology has remained largely unfamiliar with τ and its potential to shape the structure of ecological communities, the diversity of traits and life history strategies, and the strength of ecological mechanisms such as competition and drift.

Residence time is a primary constraint on growth in natural, engineered, and experimental systems. In bioreactors, τ influences performance and stability while in experimental chemostats, τ is manipulated to control growth and to study eco-evolutionary dynamics (Smith and Waltman 1995; Henze 2000; Angenent et al. 2004). In both experimental and engineered systems the inverse of τ, i.e., dilution rate also known as turnover rate ($1/\tau$), is used to approximate growth rate. In terrestrial and aquatic habitats, τ is measured with respect to the turnover of nutrients, removal of pollutants, development of algal blooms, and the global-scale consequences of altered carbon cycling (Post et al. 1982; Valiela et al. 1997; Josefson et al. 2000; Crump et al. 2004; Beaugrand et al. 2010; Friend et al. 2014). The concept of τ is also

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studied in medicine and microbiome research to understand the effects of disease and microbiomes on the health of host organisms (Wu et al. 2011; Flint 2012, Dey et al. 2015; Waldron 2015). Despite the importance of τ across a spectrum of natural, experimental, and engineered systems, it is surprisingly rare for τ to be integrated into general ecological theory (Schramski et al. 2015). Few, if any, studies predict how τ influences biodiversity or ask whether the equivalence of $1/\tau$ to species vital rates can hold outside ideal systems.

In this study, we develop a conceptual framework for how τ should influence abundance and diversity of traits and taxa, and how τ should act as a basis of selection for groups of traits that promote growth or persistence. We integrate established ecological relationships with resource-limited growth and the energetics of physiological maintenance to test whether the predictions of our τ-based framework should hold for ecological communities within stochastic and fluctuating environments. To do this, we used a platform that builds and runs thousands of stochastic individual-based models (IBMs) and leverages the power of ecological patterns that emerge in unison, i.e., simultaneously emerging relationships. This IBM platform draws from bodies of ecological theory and simulates energetically constrained life history among thousands to hundreds of thousands of individuals belonging to as many as a thousand or more ecologically unique species within spatially-explicit environments that are characterized by resource heterogeneity, ecological selection on high degrees of trait variation, and fluctuating rates of flow, resource supply, and immigration.

RESIDENCE TIME PREDICTIONS

Total abundance and productivity — The number of individual organisms (i.e., total abundance; N) is the primary descriptor of population or community size. We predict that τ influences N

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through interactions of growth, metabolic maintenance, and resource supply. First, τ can be short enough that individuals are removed before they can reproduce, i.e., "washout". Second, τ can be long enough that resource supply is too low to fuel growth or to offset metabolic maintenance (Pirt 1965; Droop 1983). Between these extreme values, resource resupply can be sufficient to fuel growth and flow can be slow enough to prevent washout or local extinction. In idealized systems (e.g., well-mixed, passive dispersal, constant rate of flow or turnover, negligible effects of metabolic maintenance), N and productivity are expected to be greatest when dilution rate ($1/\tau$) equals maximum growth rate (Smith and Waltman 1995). However, natural systems are characterized by the sporadic resupply of growth-limiting resources while aspects of individual- to ecosystem-level dynamics often scale with maintenance respiration (i.e., basal metabolic rate) (e.g., Brown et al. 2004, Schramski et al. 2014). In this way, N and productivity might relate more closely to basal metabolic rate than to maximum growth rate.

Species richness (S) — The number of species in a community (i.e., richness, S) is the foremost component of species diversity (Magurran and McGill 2011). We predict that τ affects S in two ways. While S often tends to scale with N (e.g., Locey and Lennon 2016), we expect τ to further constrain S by placing selective pressure on species to resist washout at short τ or resist starvation at long τ. A decreasing number of species should be able to maintain viable populations when τ becomes especially short or long. Based on this, we predict a humped-shaped relationship of S to τ.

Species evenness (E) — Similarity in abundance among species (i.e., evenness, E) is the second primary component of species diversity (Magurran and McGill 2011). We predict that τ affects E

in two ways. First, decreases in E often scale with greater N (e.g., Locey and Lennon 2016). While this can be expected based on numerical constraints (Locey and White 2013), a more ecologically meaningful reason is found in the study of species abundance models. Specifically, models of exceptionally low E such as the dominance preemption and geometric series models result from strong competitive interactions (Magurran and McGill 2011). Because intermediate τ may allow enough time for competitive dynamics to emerge among physiologically distinct species, we expect intermediate τ to allow for the assembly of communities with low E. As a result, we predict a U-shaped relationship of E to τ.

Species turnover (β) — Temporal changes in community composition reveal how quickly the membership of a community changes. We predict that τ should drive β and produce two potential patterns. Short τ should produce high rates of β through a combination of low N, low S, and high rates of immigration and emigration. Turnover should then decrease with longer τ, reflecting the dynamics of a slower moving system. However, turnover may then increase at extremely long τ because the loss of a single species can substantially influence β at low S. As a result, we predict a J- to U-shaped relationship of β to τ.

A growth syndrome – We predict that τ acts as a force of selection on life history traits that promote growth at short τ. To maintain viable populations, organisms should either grow and reproduce before being washed out, or be physically adapted to prevent removal. Rapid rates of growth and active dispersal, as well as the capacity for physical attachment and the ability to actively forage should all contribute to the ability of individuals to grow and reproduce within environments of rapid turnover. While rapid growth can be energetically inefficient (Russell and

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Cook 1995, Carlson et al. 2007, Lipson 2015) and though active dispersal and physical attachment carry energetic investments, these shortcomings may be compensated for by high rates of resource resupply and the ability to consume resources at high efficiency.

***A persistence syndrome* –** Slow moving systems with low rates of resource resupply are characteristic of long τ. In these conditions, organisms are pressured to persist in the absence of resources. Persistence should increase if metabolic maintenance energy can be decreased, if species do not invest in energetically wasteful life history strategies, and if populations do not outgrow available resources. Additionally, the ability to enter a reversible state of decreased metabolic activity (i.e., dormancy) is a widely used life history strategy that greatly contributes to persistence. We expect organisms at long τ to more grow slowly, to use resource more efficiently (i.e., via resource specialism), to have greater capacities for decreasing metabolic maintenance, and to have greater capacities for dormancy. As transitioning between dormancy and activity is not energetically free, we expect that organisms able to persist at high τ will resuscitate less readily.

***Congruence with primary ecological relationships* –** The predictions of a novel ecological framework should be compatible with universal or law-like ecological patterns. Examples are the hollow-curve nature of species abundance distributions (McGill et al. 2007), the ¾ power scaling of metabolic rate with body size (Brown et al 2004), the 0 to 0.5 scaling of species richness with area (Lomolino 2000), and the 1st to 2nd power scaling of population variance with mean population size, i.e., Taylor's Law (Xiao et al. 2015).

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METHODS

***Overview* –** We tested the predictions of our residence time framework using a stochastic individual-based modeling (IBM) platform (i.e., Locey and Lennon 2017). IBMs simulate the behaviors of individual elements (e.g., individual organisms, resource particles) and allow ecological relationships to emerge from individual-level interactions (Grimm et al. 2005). IBMs can integrate process-based rules, analytical formulas, and random sampling while providing initial testing grounds for synthetic ecological frameworks (e.g., Rosindell et al. 2015). The platform we used was designed for studying the simultaneous emergence of ecological patterns under ecological selection, energetic constraints, and complex dynamics.

***Randomized model parameterization* –** The modeling platform we used parameterizes IBMs with random combinations of parameters for physical conditions, resource conditions, and species traits (Locey and Lennon 2017). Once assembled, each IBM is populated with 1,000 individuals whose species identities are drawn at random from a uniform distribution. These randomized starting conditions allowed our τ-related predictions as well as realistic patterns of biodiversity to emerge from initially unrealistic community structures (e.g., highly even distributions of abundance) and unrealistic trait combinations (see Locey and Lennon 2017, Locey et al. 2017).

***Resource-limited life history* –** At each time step, every individual has a probability of consuming a resource particle and of undergoing growth, active dispersal, passive dispersal, reproduction, death, and transitions between dormancy and metabolic activity. The rate at which an individual undergoes a given life history process is determined, in part, by the amount of an

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individual's endogenous resources. Individuals with a low endogenous resources are more likely to go dormant, less likely to reproduce, and less likely to actively disperse. Consumption of exogenous resources increases an individual's endogenous resources according to the product of their current resources and the species-specific ability to convert a given resource to biomass. Individuals become dormant once their level of endogenous resources decreases below the species-specific active maintenance energy. Dormancy is defined here as a non-reproductive state of zero consumption and growth, where individuals incur a decreased basal metabolic rate (BMR) and hence, decreased metabolic maintenance. Dormant individuals experienced a species-specific reduction in maintenance costs. Individuals die once their level of endogenous is too low to maintain a dormant basal metabolic rate.

Congruence with iconic ecological relationships **–** The predictions of a novel ecological framework should be compatible with universal or law-like ecological patterns. In addition to testing the influence of τ on aspects of abundance and diversity in traits and taxa, we ensured that our IBMs produced realistic patterns of biodiversity. This included realistic species abundance distributions (SADs) and diversity-abundance scaling relationships (Locey and Lennon 2016). We also asked whether our IBMs produced realistic forms of three well-known scaling laws. First, the species-area relationship (SAR) describes the rate at which species are discovered with increasing area (A), often taking form of $S = cA^z$, where often $0 \leq z \leq 0.5$ (Lomolino 2000, Zinger 2014). Second, Taylor's law is a scaling relationship that describes how variance in population size varies with average population size, $\sigma^2 = \mu^z$, where typically $1 \leq z \leq 2$ (Xiao et al. 2015). Third, metabolic theory predicts that basal metabolic rate (B) relates to whole organisms body mass (M) through a 3/4 power law, i.e., $B = B_0M^{3/4}$ (Brown et al. 2004).

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Simulations – We ran more than 20,000 randomly parameterized IBMs to test the robustness of our predictions. Each IBM could simulate as many as 10^5 individuals belonging to as many as a 10,000 thousand species, and 10^4 resource particles belonging to as many as 10 resource types. Time series analysis revealed that 500 generations (tens of thousands of time steps) was enough to lose the initial signal of the starting conditions, i.e., burn-in. Each IBM was run for a total of 4,500 generations after burn-in.

Quantifying abundance and diversity **–** We recorded aspects of abundance, activity, productivity, and trait and taxa diversity at every 10 generations after burn-in. We quantified species evenness using Simpson's evenness index (D^{-1}/S), where D^{-1} is the inverse of Simpson's diversity measure (Magurran and McGill 2011). Simpson's evenness is among the most robust evenness measures, being highly independent of S and giving nearly equal weight to rare and abundant species (Smith and Wilson 1996). We quantified species turnover using Whittaker's index (β_w), which quantifies the number of times that species composition changes completely between two samples (Magurran and McGill 2011). We quantified rarity using the log-modulo transformation of the skewness of the SAD as in Locey and Lennon (2016).

RESULTS

Realistic patterns of diversity — More than 20,000 stochastic, highly variable, and randomly parameterized IBMs with no hard constraints on abundance, richness, or body size produced several realistic patterns of biodiversity (Figure 1, Table 1). These included Poisson lognormal species abundance distributions (SADs), realistic nested species-area relationships, the mean-variance relationship known as Taylor's Law, the ¾ power law of metabolic scaling theory, and

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four recently documented diversity-abundance scaling relationships. Consequently, our IBMs were, at least, realistic enough to reproduce established patterns of biodiversity that have rarely, if ever, been simultaneously generated from the same models.

Abundance, productivity, and diversity — Residence time had strong effects on many community attributes in our simulations, including total abundance (N), individual productivity (P), species richness (S), species evenness, species temporal turnover, and metabolic activity related to τ as predicted (Figure 2). Each relationship was robust but also reflected the degrees of variability that were possible due to extensive randomization, different species compositions, varying environmental conditions, and three orders of magnitude in both flow rate and system size. Rather than producing strict monotonic relationships, τ appeared to place upper constraint on N, S, and P. Across all IBMs, N ranged between 1 and 90,000, P ranged between 0 and 90,000, and S ranged between 1 and 1,200. Species evenness, temporal turnover, and percent dormancy took values within the full range of possible outcomes, i.e., 0 to 100%.

The similarity of active metabolic rate to $1/\tau$ placed exponential upper constraints on N, P, and S. We found that N, P, and S were greatest when average per capita active basal metabolic rate was most similar to dilution rate ($1/\tau$) (Figure 3). We did not observe similar correspondence for any other species trait.

Trait syndromes — Species-specific maximum rates of growth, dispersal, and BMR were greatest at low τ, a syndrome of traits that prevented washout. Species-specific maxima for these trait values decreased monotonically with increasing τ, a result of decreased selection on these

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energetically costly traits and increased selection for the ability to persist in increasingly sparse resource conditions (Figure 4). As τ increased, species showed greater resource generalization, reflecting a trade-off between rapidly growing on a single resource in a highly competitive and rapidly flowing environment, versus opportunistically growing on whatever resource is encountered in a sparse environment of relatively few species. In addition to decreased rates of active dispersal, growth, and BMR, increased τ selected for other traits that promoted persistence, including an increasingly strong dormancy response, i.e., a greater decrease of BMR when transitioning to dormancy and a smaller probability of randomly resuscitating from dormancy (Figure 4).

DISCUSSION

In this study, we proposed that residence time (τ) affects biodiversity by placing constraints on growth, abundance, metabolic activity, and diversity. Residence time (τ) couples resource supply and individual dispersal, equates the physical environment with aspects of life history, and varies over eight orders of magnitude in natural systems. Although often used to manage engineered and experimental systems, τ has gone largely unrecognized in ecological studies. Using tens of thousands of ecologically complex individual-based models (IBMs) that simulated the life histories of up to one hundred thousand individual organisms, we found that τ can constrain the abundance and diversity of taxa and traits in ways that are expected from the synthesis of physiological and macroecological principles. These relationships emerged alongside some of ecology's strongest and most iconic patterns of biodiversity.

In idealized systems where actively growing and passively dispersing organisms occupy well-mixed resource-rich environments, total abundance (N) and individual productivity (P)

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should be greatest when $1/\tau$ equals maximum specific growth rate (Smith and Waltman 1995). However, most natural systems are unlikely to obey such ideal conditions. In contrast, and despite orders of magnitude of variation in species traits, system size, flow rate, and resource supply, we found that N, P, and S were greatest when $1/\tau$ approximated the average per capita basal metabolic rate (BMR). Deviations of $1/\tau$ from BMR produced exponentially lower N, S, and P. The importance of BMR is well-recognized as underpinning the life histories and vital rates of all organisms (Brown et al. 2004). BMR can also drive the residence times of nutrients within ecosystems, resulting in strong scaling relationships (Schramski et al. 2014). Our findings suggest that, in ecosystems where the movement of individuals and resources are influenced by physical turnover, the magnitude of τ should be a strong selective force on BMR and, in turn, the many physiological and ecological processes that BMR determines.

Residence time was a strong driver on the emergence of growth and persistence related trait syndromes, which were initiated from random conditions. In this way, τ acted as a force of ecological selection on traits that underpin general life history strategies, e.g., r/K selection. We expect that the strength of τ depends on how greatly it couples resource supply and individual dispersal, and whether populations and species have the capacity and diversity to adapt. We did not explore the point at which the driving influence of τ on species traits breaks down. This threshold may arise through the lack of sufficient trait diversity or via the decoupling and independence of resource supply and individual dispersal. Though we did not model scenarios where resource supply and individual dispersal are decoupled or independent of τ, there are conditions and systems where this occurs. For example, sessile occupants of intertidal zones experience a flow through of resources and highly motile occupants of swamps, marshes, and open aquatic environments can actively forage. However, traits that allow certain organism (e.g., sessile crustaceans) to attach, filter feed, and achieve larval dispersal are perhaps adaptive responses to τ. That is, such traits would seem to allow organisms to simultaneously overcome wash-out, to take advantage of planktonic resources, and produce planktonic larvae or gametes.

Residence time should be relevant at all levels of the ecological hierarchy, from individuals to ecosystems. At the individual-scale, τ is defined in terms of body mass and the rate at which resources flow through organisms (Schramski et al. 2014). At the scale of populations, τ should influence population size, and hence, effective population size and the strength of drift versus selection. Among ecological communities, mechanisms of spatial dynamics such as mass effects, rescue effects, and source-sink effects are driven by individual dispersal and are central to the metacommunity paradigm (Leibold et al. 2004). Recent metacommunity work also suggests that the dispersal of individuals and resources should often be studied as coupled processes (Haegeman and Loreau 2014). At the scale of trophic dynamics, the influence of τ is similar to that of "donor control", where the supply of allochthonous resources constrains consumer growth but where consumers have little-to-no effect on resource resupply (Polis et al. 1997). We suspect that changes in τ may couple or decouple trophic interactions (e.g., predator-prey, host-parasite) by either washing out particular members at short τ or by exhausting endogenous resources at long τ.

In our study, we focused on τ as a variable of the physical ecosystem that can shape biodiversity and even approximate metabolic rates. However, both τ and metabolic rates can be influenced by other variables of the physical ecosystem. For example alterations in hydrological processes (e.g., melting permafrost and variable precipitation) can increase flow rate and volume, which changes τ. These alterations can be driven by temperature, which also directly influences metabolic rates and the breakdown of nutrients. Physical factors that influence both τ also apply

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to host organisms, where changes in diet and the occurrence of disease can alter τ in ways that change host health (Molla et al. 1983). Examples are bacterial overgrowth resulting from an increase in τ driven by Crohn's disease (Castiglioni et al. 2000) and the removal of microbiota and nutrients resulting from a decrease in τ driven by Cholera (Sack et al. 1978). In this way, understanding the influences of τ on abundance, activity, productivity, and the diversity of traits and taxa also begs for an understanding of the physical factors that drive the magnitude and variability of τ and its relationship to metabolic rate.

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FIGURE CAPTIONS

Figure 1. Over 20,000 stochastic, highly variable, and randomly parameterized individual based models (IBMs) with no hard constraints on abundance, richness, or body size produced realistic patterns of biodiversity. Top left: The Poisson lognormal (PLN) explained >80% of variation in abundance among taxa. Simulated data were less similar to the log-series distribution. Top right: Species-richness often scaled with system size at rates (z) similar to nested species-area relationships (i.e., $0 < z < 0.5$). Bottom left: Basal metabolic rate (BMR) scaled to the ¾ power of body size. BMR includes the percent by which BMR decreases in dormancy. Bottom right: Taylor's Law predicts that variance (σ^2) in abundance scales with mean abundance, $1 < z < 2$. Different colors represent systems of different orders of magnitude in residence time (τ), with red being smallest and violet being greatest.

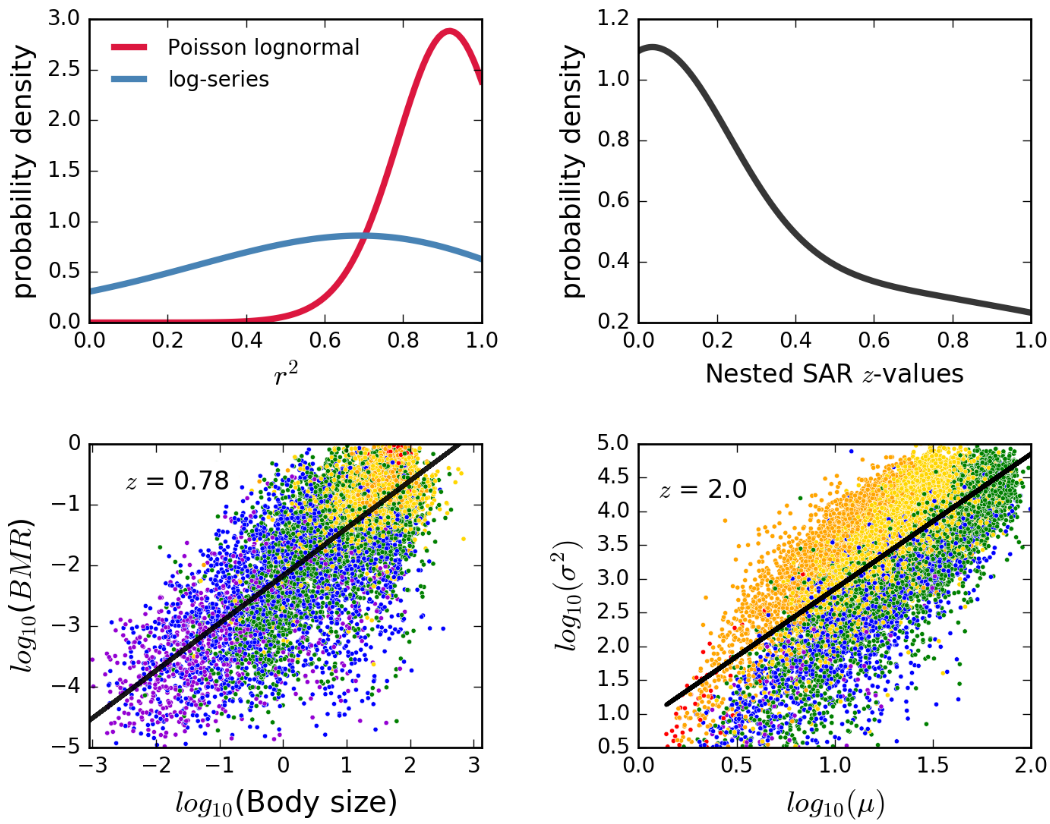

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Figure 2. More than 20,000 stochastic and randomly parameterized IBMs with no hard constraints on abundance or richness reveal how residence time (τ) influenced total abundance (N), individual productivity (P), species richness (S), species evenness, species turnover (β), and the percent of N individuals that were metabolically inactive or dormant. System size and flow rate both varied over three orders of magnitude. The form of each relationship matches our conceptual predictions. Different colors represent systems of different size, with red being smallest and violet being greatest.

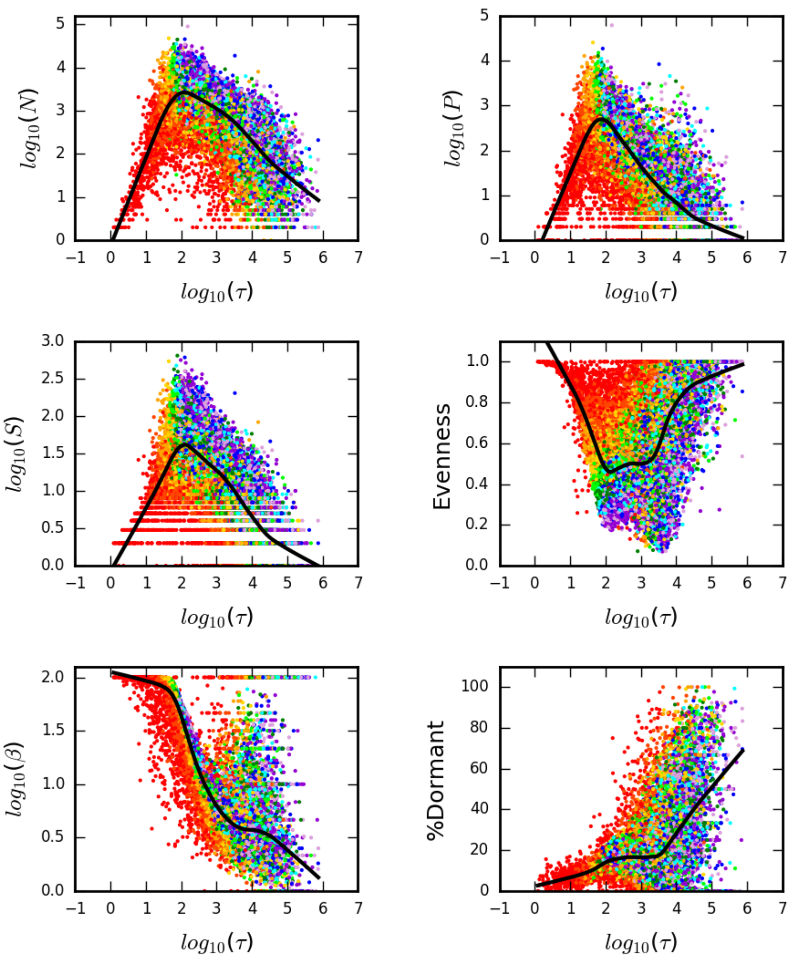

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Figure 3. Scatter plots of results from more than $2{\cdot}10^4$ IBMs that were initialized with 1000 individuals from a regional pool of 10,000 species, each with randomly chosen basal rates of active metabolism (BMR). The dashed line represents the point where BMR equals dilution rate ($1/\tau$). That is, if BMR = $1/\tau$, then $\log(\text{BMR})/\log(\tau) = -1$. This is the point where overall greatest total abundance (N), productivity (P), and species richness (S) occurred and away from which N, P, and S, appear to exponentially decrease, i.e., nearly linear on log-scale. Different colors represent systems of different orders of magnitude in residence time (τ), with red being smallest and violet being greatest.

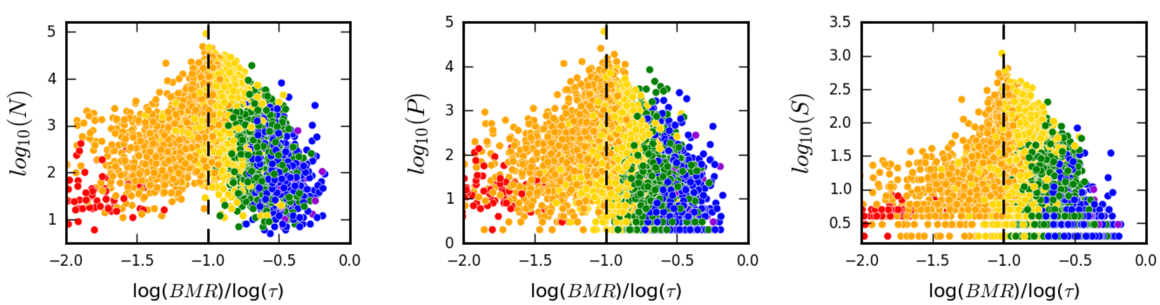

Figure 4. Scatter plots for >2·10^4 IBMs that were parameterized with random combinations of species traits and no explicitly enforced trade-offs. The value of each trait could vary across two orders of magnitude. Residence time (τ) influenced specific growth rate, maintenance energy, rate of active dispersal, the probability of random resuscitation from dormancy, resource specialization, and the strength of the dormancy response (i.e., factor by which maintenance energy was reduced by the transition to dormancy). The form of each relationship matches our conceptual predictions. Different colors represent systems of different size, with red being smallest and violet being greatest.

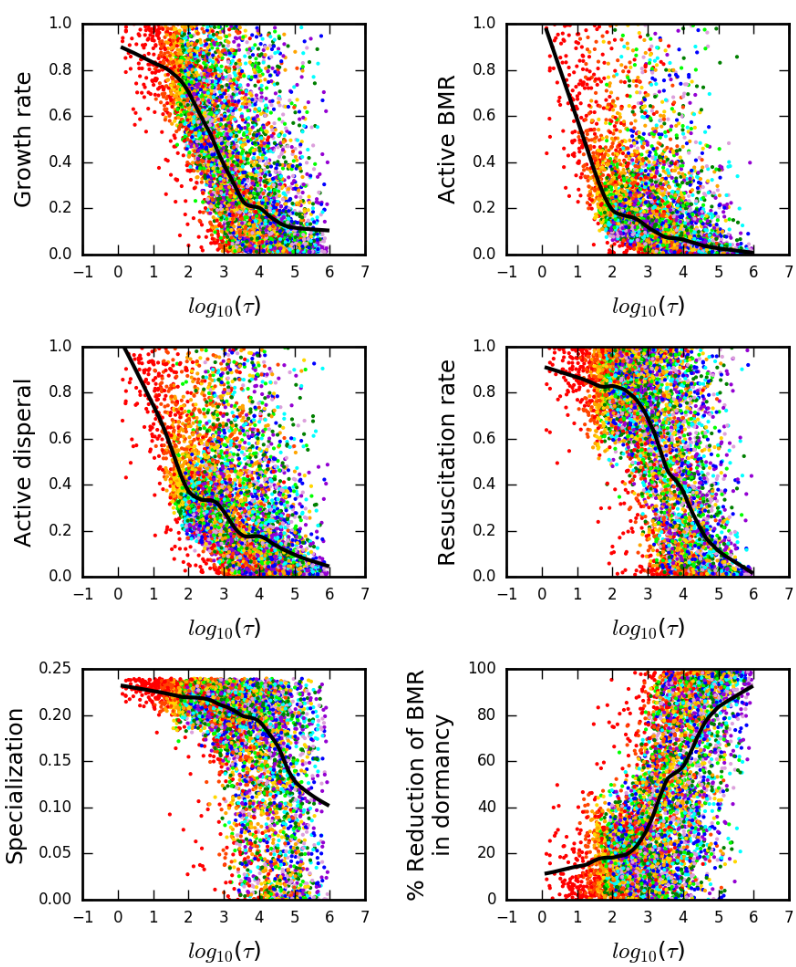

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Table 1. The scaling of species rarity, dominance, evenness, and richness with total community abundance (N) from $2{\cdot}10^4$ stochastic and randomly parameterized IBMs with no hard constraints on abundance or richness. These simulation-based scaling relationships are similar to those previously documented in a study using tens of thousands of community level data on microorganisms and macroscopic plants and animals (Locey and Lennon 2016).

Relationship	**Locey and Lennon (2016)**	**Current Study**
Rarity vs. N	$R \approx N^{0.21}$	$R \approx N^{0.14}$
Dominance vs. N	$N_{max} \approx N^{0.96}$	$N_{max} \approx N^{1.04}$
Evenness vs. N	$E \approx N^{-0.35}$	$E \approx N^{-0.36}$
Richness vs. N	$S \approx N^{0.44}$	$S \approx N^{0.33}$

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