

A residence time theory for biodiversity

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ABSTRACT

8 From microorganisms to the largest macroorganisms, much of Earth's biodiversity is
subject to forces of physical turnover. Residence time is the ratio of an ecosystem's size to its
rate of flow and provides a means for understanding the influence of physical turnover on
10 biological systems. Despite its use across scientific disciplines, residence time has not been
integrated into the broader understanding of biodiversity, life history, and the assembly of
12 ecological communities. Here, we propose a residence time theory for the growth, activity,
abundance, and diversity of traits and taxa in complex ecological systems. Using thousands of
14 stochastic individual-based models to simulate energetically constrained life history processes,
we show that our predictions are conceptually sound, mutually compatible, and support
16 ecological relationships that underpin much of biodiversity theory. We discuss the importance of
residence time across the ecological hierarchy and propose how residence time can be integrated
18 into theories ranging from population genetics to macroecology.

INTRODUCTION

Much of Earth's biodiversity is at the mercy of currents that drive the transport of resources and organisms through environments of greatly varying size (V) and rate of flow (Q). In nature, the turnover induced by forces of flow can vary by more than eight orders of magnitude, from minutes in the organs of some plants and animals to millennia in lakes, glaciers, and soils (e.g., Dietrich and Dunne 1978; Bell et al. 2002; James et al. 2003, Friend et al. 2014; Dey et al. 2015, Schramski et al. 2015). The duration of this physical turnover, known as residence time (τ), influences a range of biological phenomena including population growth, nutrient dynamics, and ecosystem functioning (Post et al. 1982; Valiela et al. 1997; Josefson et al. 2000; Crump et al. 2004; Beaugrand et al. 2010; Friend et al. 2014, Sibley et al. 2012, Waldron 2015). Residence time can also influence organismal health and is thought to be an evolutionary constraint on digestion (Molla et al. 1983; Castiglione et al. 2000; Franz et al. 2009; Wu et al. 2011; Flint 2012, Dey et al. 2015). Despite the relevance of τ to environmental, engineered, and host-associated habitats, no theory exists for how τ should shape the biodiversity of ecological systems.

Residence time relates to V and Q in a simple, albeit powerful way: $\tau = V/Q$. This relationship is based in probability theory and represents the average time that passively moving particles remain in a system (see Online Appendix A). At least three classic predictions related to τ have been developed and tested using well-mixed bioreactors known as chemostats where V and Q are held constant (Smith and Waltman 1995; Henze 2000; Angenent et al. 2004, see Online Appendix A). First, assuming ideal chemostat conditions, including zero immigration and constant growth, τ approximates the average time that individuals spend in the system. Second, at an equilibrium abundance, dilution rate ($1/\tau$) approximates population growth rate (μ). Third,

population size and productivity are greatest when dilution rate ($1/\tau$) is equivalent to maximum growth rate (μ_{\max}). These predictions underpin the mechanics of chemostats wherein seminal theories of resource competition and resource-limited growth were first tested (e.g., Droop 1974, Tilman 1981). However, in nature, the assumptions of chemostats are often violated: resource conditions are not optimal, populations are rarely stable, immigration is common, and organisms often resist forces of flow via active dispersal. Likewise, species in natural systems are subject to selection via the fit of their traits to the abiotic environment (i.e., environmental filtering). Consequently, it remains to be seen whether classic τ -related predictions should hold under the complex conditions found in nature. Beyond these classic predictions and despite the generality of V and Q as ubiquitous aspects of natural systems, τ has rarely been to understand the assembly and diversity of ecological communities.

In this study, we develop a τ -based theory for biodiversity. Our theory is underpinned by the idea that the physical turnover induced by τ can shape the life history strategies of individual organisms, the traits of species, and the assembly and structure of ecological communities. We propose a set of predictions for how τ influences the abundance and diversity of taxa within ecological communities and how τ acts as a force of environmental filtering on sets of traits (i.e., syndromes) that promote growth, coexistence, and persistence. At the same time, we propose that classic τ -related predictions developed for chemostats may fail in complex ecological systems. We challenge our predictions to emerge in unison alongside established patterns of biodiversity using thousands of stochastic individual-based models (IBMs). In doing so, we provide initial support for our theory and its compatibility with other ecological theories. We discuss how τ can be integrated into theories ranging from population genetics and life history to community ecology and macroecology. We also describe how τ may contribute to the

understanding of metabolism and host-microbiome dynamics. Finally, we discuss the potential
for anticipating changes in biodiversity by understanding ecological responses to changes in τ .

RESIDENCE TIME PREDICTIONS

Here, we propose predictions for how residence time ($\tau = V/Q$) should affect the
abundance, diversity, and the productivity of ecological communities, as well as the emergence
of trait-syndromes that allow organisms to persist within environments characterized by a rate of
flow or physical turnover (Q). The following predictions, which are depicted in Box 1, use a
generalized concept of an environment's size (V) that applies to the number of spatial dimensions
across which flow occurs.

Community-level predictions

Prediction 1: Total abundance (N) vs. τ — The number of individual organisms is the primary
descriptor of abundance for populations and communities. We predict that τ influences N through
its effects on immigration, emigration, and population growth. First, τ can be short enough that
individuals are removed before reproducing, a phenomenon commonly referred to as “washout”.
Second, τ can be long enough that immigration is too low to establish or maintain populations.
Under the same conditions of slow turnover, resource supply may be too low to fuel growth or to
offset metabolic maintenance. Between these extremes, resource supply can be high enough to
sustain growth, immigration can be high enough to establish populations, and physical turnover
can be slow enough to prevent washout. In this way, we expect a hump-shaped relationship
where N is greatest at intermediate τ .

Prediction 2: Productivity (P) vs. τ – The number of individuals produced per unit time should also exhibit a hump-shaped relationship to τ . At sufficiently short τ , individuals may not have enough time to reproduce. At long τ , individuals may not have the resources to grow and reproduce. The relationship between P and τ will not necessarily reflect the relationship between N and τ , as immigration and non-reproductive states of low metabolism (dormancy) can decouple how abundance relates to productivity.

Prediction 3: Species richness (S) vs. τ — The number of species in a community is the foremost component of species diversity (Magurran and McGill 2011). We predict a humped-shaped relationship between S and τ because of the constraining influence of N (i.e., $S \leq N$) and because a decreasing number of species should be able to persist when τ becomes increasingly short or long. Specifically, τ should constrain S by acting as an environmental filter on species that cannot resist washout at short τ or resist starvation at long τ . We expect that τ also affects S through its influence on immigration because without continued immigration (e.g., at long τ), a community can drift to a single species ($S = 1$).

Prediction 4: Species evenness (E) vs. τ — Similarity in abundance among species (i.e., evenness, E) is the second primary component of species diversity (Magurran and McGill 2011). Though measures of E are derived to be independent of S (Smith and Wilson 1996), E often scales inversely with N , $E \propto N^{-z}$ (Locey and Lennon 2016). This relationship can partly be explained as a consequence of how both N and N/S mathematically constrain E (Locey and White 2013; Xiao et al. 2015). Consequently, we expect E to be lowest at intermediate values of τ , when N and N/S are greatest.

Prediction 5: Species turnover (β) vs. τ — We predict that short τ should produce high rates of temporal species turnover (β) through a combination of low N , low S , and high rates of immigration and emigration. Species turnover should then decrease with greater τ , reflecting the dynamics of a slower moving system. However, β may increase at extremely long τ because the loss of a single species can greatly influence the value of β in communities of few species. As a result, we predict a relationship of β to τ that varies from monotonically decreasing to J-shaped.

Prediction 6: Dormancy vs. τ — Dormancy is a reversible state of reduced metabolic activity accompanied by the absence of resource consumption, growth, and reproduction. Organisms across the tree of life exhibit dormancy, particularly in response to the sparse and fluctuating availability of resources (Guppy and Withers 1999). Dormancy should be maladaptive in systems with high rates of physical turnover because individuals will have an increased probability of being washed out before reproducing (Lennon and Jones 2011). In contrast, dormancy should be favored in systems with longer residence time owing to a reduced rate of resource supply and lower probability of washout.

Trait-level predictions

Prediction 7: Individual growth vs. τ — At short τ , populations can resist washout if individuals can reproduce before being removed and if resource supply is great enough to sustain rapid growth. As τ increases, the pressure imposed by τ on individuals to grow rapidly should decrease. Because faster growth incurs greater energetic costs (Carlson et al. 2007, Lipson 2015) and

because resources may become too deplete to fuel rapid growth, environmental filtering should
134 favor slower growing organisms at longer τ .

Prediction 8: Active dispersal vs. τ — Active dispersal allows organisms to resist forces of flow
but also incurs energetic costs. At low τ , the cost of active dispersal may be compensated for by
138 high rates of resource supply. However, resources should be become increasingly limited with
longer τ and the pressure to actively disperse at rapid rates should decrease. Consequently, rates
140 of active dispersal should decrease with greater τ .

Prediction 9: Basal metabolic rate (B) vs. τ — Basal metabolic rate represents the sum of
energetic costs associated with essential metabolic functions. We predict a decrease in B with
144 increasing τ . While a higher B may be permissible in systems of high resource supply,
increasingly long τ should favor greater metabolic efficiency (e.g., maintaining a similar rate of
146 dispersal under a lower B) or greater austerity (e.g., via dormancy).

Prediction 10: Resource specialization vs. τ — Resource specialization reflects the variation in
species performance across a range of resource types (Devictor et al. 2010; Poisot et al. 2012).
150 Under the stochastic supply of several resource types, we expect the relationship between τ and
resource specialization to be hump-shaped. When τ is short, we expect that individuals reduce
152 the probability of washout by consuming a variety of resources instead of waiting to encounter a
specific resource type. As τ increases, specialists are afforded time to encounter specific resource
154 types, resulting in the emergence of species that consume largely non-overlapping sets of
resources. We expect this partitioning of resource types to promote greater S . However, we

expect that a generalist strategy may again be favored at high values of τ as the availability of each resource decreases through low resource resupply (low Q), high dilution of resources in the environment (high V), or both.

Predictions 11: Resuscitation rate vs. τ — The resuscitation of organisms from a dormant state can be highly unpredictable, a consequence of interacting life history strategies and stochastic “seed bank” dynamics (Epstein 2009). Because resuscitation exposes organisms to the costs of active metabolism, we expect rates of random resuscitation to decrease with increasing τ .

Prediction 12: Reduction of basal metabolism (B) in dormancy vs. τ — Dormancy allows organisms to persist in suboptimal environments via reduced B . Because increasingly long τ represents increasingly strong pressure on organisms to survive in the absence of resources, we expect the degree to which B is decreased in dormancy to increase with τ .

Equivalence predictions

Predictions 13 & 14: In chemostat-like bioreactors with ample resource supply, theory predicts that total abundance (N) and productivity (P) should be greatest when specific maximum population growth rate (μ_{\max}) is equivalent to the dilution rate ($1/\tau$). This classic prediction assumes a constant rate of growth, constant N , and zero dormancy; conditions that are unlikely under the stochastic and resource-limited dynamics of complex communities. Therefore, we expect the similarity between $1/\tau$ and rates of energetically costly traits (e.g., B , individual growth, active dispersal) to reflect the fit of species’ to local conditions. As a result, P and the

total abundance of active individuals (N_a) should be greatest when rates of individual growth, B , and active dispersal are equivalent to $1/\tau$.

METHODS

Overview – We tested our predictions (Box 1) using an individual-based modeling (IBM) platform that simulates stochastic and energetically constrained life history processes among thousands of highly varied and randomly parameterized IBMs. IBMs are choice tools for the aims of our study. First, IBMs are ideal for simulating changes among particles (organisms, resources) as they move through dynamic environments (Hellweger et al. 2016; Locey et al. 2017). Second, IBMs allow higher order properties (specific-growth rate, community-scale predictions) to emerge from processes operating at the individual-level (Grimm et al. 2005, Hellweger et al. 2016). For example, while specific-growth rate (μ) would typically be parameterized in most other models, μ can emerge in IBMs via the cumulative reproductive events of individuals. Finally, IBMs allow a practically unlimited number of relationships to simultaneously emerge at the individual-, population-, species-, community-, and ecosystem-level (Locey and Lennon 2017). Hence, our IBMs allowed us to examine classic predictions of τ derived from ideal conditions, novel predictions of τ derived from more realistic conditions, and well-known macroecological patterns from a single ensemble of IBMs. We describe our modeling below and provide greater details in Online Appendix B.

Randomized model parameterization – Each IBM began with random combinations of traits for each species in the regional pool, along with randomly drawn values of immigration rate, resource conditions, and randomly drawn values of V and Q (Table 1). This randomized

parameterization allowed our IBMs to explore wide swaths of multivariate parameter space while allowing our predictions, realistic trait combinations, and general biodiversity patterns to emerge, as opposed to being explicitly enforced.

Simulating residence time (τ) — Flow rate (Q) was simulated as the fraction of a single unit distance covered per time step and was randomly chosen within a range of three orders of magnitude (Table 1). The length of a system across which flow occurred (V) was also randomly chosen within a range of three orders of magnitude (Table 1). These ranges of values for V and Q yielded six orders of magnitude in τ .

Immigration and resource supply – Each IBM began as an empty system into which resource particles flowed and individual organisms immigrated. The body size and species identity of each immigrant was drawn at random from uniform distributions, as were the sizes and identities of inflowing resource particles (Table 1). As a result, the probability of immigration was essentially equal among species and ensured that realistic community structures would have to emerge from the dynamics of the local community and the physical properties of the focal system (i.e., V , Q).

Life history processes: Our IBMs simulated individual-based processes of consumption, growth, reproduction, death, passive and active dispersal, and transitions into and out of dormancy. The rates at which individuals underwent these processes were determined by the products of probabilities, i.e., multiplicative interactions of random variables (see lognormal dynamics of Shoemaker et al. 2017). These probabilities were determined by species trait values along with

the metabolic state (active or dormant), body size (s), and endogenous resources (q) of individuals. Body size and q differed in that s represented the mass of individuals that could not be used to fuel metabolism. Along with basal metabolism, growth and active dispersal also incurred energetic costs (Table 1).

Resource consumption – At each time step (t), randomly sampled individuals could consume a randomly encountered resource particle from any of 10 possible resource types. Encounters with resource particles were influenced by the concentration of resource particles (D) in the system, with the probability of encounter increasing with D and equaling 0 in the absence of resources: $D/(1+D)$. Once an encounter was made, efficiency of consumption (0 to 100%) was determined by species-specific values for each of the 10 possible resource types. Consumption increased an individual's endogenous resources according to their species-specific efficiency (e) for the particular resource, the size of the resource particle (r), and s :

$$q_{t+1} = q_t + \min(r_t, e * s_t)$$

This relation prevented an individual from consuming a greater amount of resource than represented in the resource particle and allowed s to take any non-zero real number. The size of the resource particle then decreased respectively and led resource particles of zero size to be removed from the system:

$$r_{t+1} = r_t - \min(r_t, e * r_t * s_t)$$

Growth – Because our models were individual-based, they did not explicitly encode a proportional rate of population growth, also known as specific growth rate (μ). Instead, randomly

sampld individuals grew proportionally to their body size according to their species-specific rate of individual growth μ , resulting in an equivalent decrease in q :

$$s_{t+1} = s_t + \min(q_t, \mu * q_t)$$

$$q_{t+1} = q_t - \min(q_t, \mu * q_t)$$

These relationships produced proportional growth, prevented individuals from growing beyond available q , and enforced a cost of growth via reduction in q .

Reproduction – Reproduction was clonal as in other biodiversity models (e.g., Hubbell 2001) and resulted in the halving of q and body size (s). At each time step (t), randomly sampled individuals that were metabolically active could reproduce according to a probability that increased with s and the ratio (λ) of q to basal metabolic costs (B), $\lambda = q/(B)$:

$$p = \left(\frac{\lambda_t}{1 + \lambda_t} \right) * \left(\frac{s_t}{1 + s_t} \right)$$

In this way, the probability of reproducing (p) equaled 0 if q or size equaled 0. This probability also meant that reproduction was unlikely for newly produced individuals but became more likely with greater size, greater age, and with greater amounts of endogenous resources available beyond that needed to fuel basal metabolism.

Transitions between activity and dormancy – At each time step, active individuals became dormant based on the product of probabilities based on age (a) and λ :

$$p = \left(\frac{1}{1 + \lambda_t} \right) * \left(\frac{a_t}{1 + a_t} \right)$$

According to this probability, a greater amount of endogenous resource relative to basal metabolic costs decreased the probability of going dormant, while the age-related term prevented

newly produced individuals from going dormant before having the opportunity to consume and grow. Dormant individuals could transition back to activity according to a probability determined by their species-specific rate of random resuscitation (Table 1).

Metabolic maintenance and death – At each time step, randomly sampled individuals incurred a species-specific cost of basal metabolism (B): $q_{t+1} = q_t - B$. If the individual was dormant, B was reduced by a species-specific value (γ) ranging between 0.001 and 1: $q_{t+1} = q_t - \gamma B$. Active and dormant individuals died when they could no longer meet metabolic costs.

Dispersal – At each time step, individuals were passively dispersed towards the downstream edge of the system according to the rate of flow (Q). However, metabolically active individuals could actively disperse against the direction of flow according to their species-specific dispersal rate (δ) and s .

$$x_1 = x_0 - \min(x_0, q_0, \delta * s_t)$$

$$q_1 = q_0 - \min(x_0, q_0, \delta * s_t)$$

In this way, individual dispersal was limited by endogenous resources and incurred an energetic cost that was proportional to body size and the distance moved against Q . These relations also prevented individuals from dispersing beyond the upstream edge of the system.

Model runs: We ran 10^4 randomly parameterized IBMs and placed no explicit ceiling on the abundance of individuals, numbers of resource particles, nor the size of individual organisms. The number of species could not exceed that of the regional pool, i.e., 10^3 . Our platform ran each IBM for $10^3 + \tau^{0.8}$ time steps before recording data. This “burn-in” time allowed models of short

τ (e.g., 10^0) a chance to form realistically structured communities while preventing models of long τ (e.g., 10^6) from running for unnecessarily large number of time steps. Each IBM ran for 10^3 time steps after burn-in and recorded 117 metrics at every 10^{th} time step (See Online Appendix B). In addition to these metrics, each IBM also recorded the abundances of each species, and the number of individuals of each species that were active or dormant at every 10^{th} time step. All modeling code and results files are available on a public GitHub repository: <https://github.com/LennonLab/residence-time>.

Measurement of select response variables:

Specific growth-rate (μ) – In experimental studies, the proportional rate of population growth is quantified during periods of population increase as: $\mu = (\ln(N_1) - \ln(N_0))/\text{time}$. At steady state conditions of chemostats, populations reach a stable abundance, allowing for $1/\tau$ (i.e., Q/V) to approximate μ . Our IBMs allowed for μ to emerge as a measurable response of populations, which we then quantified according to population growth equation (μ) above.

Species evenness and diversity – We quantified species evenness with Simpson's evenness index (D^{-1}/S), where D^{-1} is the inverse of Simpson's diversity measure (Magurran and McGill 2011) and S is species richness. This metric is considered to be independent of S (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). See Online Appendix B9 for greater details.

Resource specialization – We quantified resource specialization as the variance in resource use efficiency among species for each of the 10 resource types that could enter the system. We also calculated resource specialization in two additional ways; see Online Appendix B9.

Congruence of τ -related predictions with general biodiversity patterns:

Predictions of an ecological theory should support common ecological observations. For example, predicting the ubiquitous hollow-curve form of species-abundance distributions (SADs) is a necessary condition that theories of biodiversity must satisfy (McGill 2003, 2010). We adopted this perspective by challenging our IBMs to produce realistic forms of several ecological patterns. These patterns included SADs, four diversity-abundance scaling laws (Locey and Lennon 2016), and two other well-known ecological scaling laws. The first of these was Taylor’s law, a relationship that describes how variance in population size scales with average population size across time or space, $\sigma^2 \propto \mu^{1 < z < 2}$, where $\mu = N/S$ (Xiao et al. 2015). The second was the scaling of B with body size (M), which commonly takes the form of a $3/4$ power law, $B \propto M^{3/4}$ for plants and animals (Brown et al. 2004) but which is sometimes known to take on scaling exponents ranging from $2/3$ to $2/1$ (e.g., Glazier 2006; DeLong et al. 2010).

RESULTS

Compatibility of residence time ($\tau = V/Q$) with general biodiversity patterns — Our stochastic and randomly parameterized IBMs produced realistic general patterns of biodiversity across six orders of magnitude in τ (Fig. S1-S4). These patterns included species abundance distributions that were well-described by the maximum likelihood forms of two commonly used species-abundance models (Poisson lognormal, log-series) (Fig. S1). Our IBMs also reproduced Taylor’s

Law along with diversity-abundance scaling laws for species rarity, dominance, evenness, and richness (Locey and Lennon 2016) (Fig. S2, S3). Finally, our IBMs produced realistic scaling between metabolic rate and body size (Fig. S4), even though we did not explicitly encode any of the complex mechanisms proposed to explain metabolic scaling (e.g., fractal resource networks, genome architecture). Taken together, stochastic dynamics of resource supply, growth, and energetic costs imposed by τ reproduced general patterns of biodiversity that are rarely, if ever, produced by the same theory.

Classic predictions in complex systems – In contrast to classical predictions from chemostat theory that assume stable-state dynamics, we found that τ did not approximate the average time that individuals spent in the system (Fig. S5). The failure of this classic prediction was due to processes that classic predictions do not account for such as immigration, active dispersal, transitions to and from dormancy that lead to stochastically fluctuating population sizes (Fig. S6). For much the same reasons, we also observed no relationship between $1/\tau$ and species-specific rates of proportional growth (μ) (Fig. S7).

Community-level predictions — Our first six τ -related predictions (Box 1) emerged across six orders of magnitude in τ , despite each IBM starting as an empty system (Fig. 1). We observed unimodal relationships of total abundance (N), individual productivity (P), and species richness (S) to τ , with maximum values occurring near τ of 10^3 (Fig. 1). Responses of N , P , and S were characterized by unimodal upper bounds that were more constrained when we accounted for V and Q (Fig. 1). Species evenness (E) responded in the opposite fashion, with the lowest values of E occurring near τ of 10^3 . As expected from the formulation of τ , increasing values of V and Q

had opposing effects on N , P , S , and E (Fig. S8). We also observed that species temporal turnover (β) monotonically decreased within greater τ . In a small number of simulations, β deviated slightly from the main trend, reflecting how the gain or loss of a single species can influence β in small communities (Fig. 1). Also as predicted, the percent of individuals in a dormant state (D) increased with greater τ . Nevertheless, in some simulations, our IBMs produced relatively active communities when there was long τ , a result that can arise under relatively high immigration and when species (that) have particularly low metabolic costs, small size, and low rates of growth and dispersal.

Trait-related predictions — Our six trait-related predictions (Box 1) emerged from our ensemble of IBMs despite the random assignment of traits to species and the potential for immigration from a diverse regional pool to obscure emergent patterns. Short τ selected for a syndrome of traits that allowed species to resist washout (Fig. 2). High rates of growth, active dispersal, resuscitation from dormancy, and low resource specialization were favored in IBMs where combinations of V and Q led to rapid physical turnover, i.e., short τ .

As τ increased, we observed gradual shifts in average trait values that were consistent with a persistence syndrome emerging under decreased rates of resource supply and washout. For example, individuals grew slower, dispersed less quickly, and resuscitated less readily from dormancy (Fig. 2). Additionally, as τ increased and as individuals resuscitated less readily from dormancy, the effectiveness of dormancy in reducing B increased (Fig. 2). We also observed that resource specialization increased from low to intermediate levels of τ (10^0 - 10^3) reflecting a change in selective pressures from a growth-driven strategy of opportunistic consumption to a strategy of resource partitioning and avoidance of direct resource competition among all species.

By design, our IBMs allowed the potential for groups of species to consume different sets of resources. However, as τ increased past 10^3 , resource specialization decreased, resulting in a return to a more generalist and opportunistic strategy.

As predicted, productivity (P) and the abundance of active individuals (N_a) were greatest when dilution rate ($1/\tau$) approximated the values of individual rates of basal metabolic costs, growth, and active dispersal (Fig. 3). An increasingly large difference between each of these traits and $1/\tau$ led to greatly decreased values of N and P . These relationships were also characterized by upper bounds, revealing that a closer match between $1/\tau$ and the rates of energetically costly traits allows, but does not necessitate, greater P and greater N_a .

DISCUSSION

We proposed that residence time (τ), the ratio of a system's size (V) to its rate of flow (Q), constrains growth, abundance, and metabolic activity while also acting as a force of environmental filtering on the diversity of taxa and traits. We formulated a large set of τ -based predictions (Box 1) and then challenged an ensemble of 10^4 ecologically complex individual-based models to simultaneously produce each predicted relationship alongside general patterns of biodiversity that are rarely, if ever, predicted by the same theories. Each IBM began as an empty system within which realistically structured communities were allowed to assemble. These models imposed no explicit relationships among traits, between τ and traits, between metabolic costs and body size, nor between abundance and species richness. Despite these randomized and highly uncontrolled conditions, our predictions and general biodiversity patterns emerged in unison from the simulation of energetically constrained life history processes acting

within flowing and resource-limited environments. Altogether, our models and findings provide the foundation for a formal τ -based theory for biodiversity.

The influence of τ in complex systems:

In idealized and simplified systems with stable-state dynamics and no immigration, dilution rate ($1/\tau$) often approximates the specific growth rate (μ) of a population (Smith and Waltman 1995).

It is reasonable to assume that this and other classic τ -based relationships should fail outside of idealized stable-state conditions. In contrast to this and other τ -based expectations, the

predictions of our τ -based theory were derived with the complexity and openness of ecological systems in mind, which was reflected in our modeling by allowing for high degrees of

variability, instability, and stochasticity. As a result, our predictions and modeling reveal how τ may still influence abundance, productivity, and the diversity of traits and taxa in complex

ecological systems that violate assumptions of traditional residence-time theory.

Importance of τ across the ecological hierarchy

Microbiomes and their hosts — Residence-time theory may be particularly useful for

understanding the ecology of microorganisms, which are almost always at the mercy of flow and physical turnover. At the scale of individual microorganisms, τ has been defined in terms of cell

size and rate of consumption, and then integrated into metabolic scaling theory to predict

processes in terrestrial and aquatic ecosystems (Schramski et al. 2015). Such an approach could

be extended to understand host-microbiome interactions within physically dynamic

environments such as the gastrointestinal (GI) tracts. While theoretical work on GI tracts has

often focused on aspects of V (length, surface area) and their relations to body size (e.g., Franz et

al. 2009, Sibly et al. 2012), little focus has been given to flow rate (Q). Our *in silico* tests of residence time theory suggest that V and Q have opposing influences on microbiome abundance, activity, and diversity (Fig. S8). In turn, these aspects of microbiome structure can greatly influence the metabolism and health of hosts. For example, Q of the GI tract can vary according to diet and disease, in some cases reducing τ to the point of washout, which can alter a host's ability to absorb and retain nutrients (Castiglione et al. 2000; Dey et al. 2015; Flint 2011; Molla et al. 1983; Waldron 2015; Wu et al. 2011).

Evolution of populations — In the study of population genetics, population size directly influences the strength of genetic drift and natural selection, which influences the rate at which mutations are lost or become fixed. For example, the number of new mutations (m) expected per generation is known from the simple relation: $m \propto N_i\mu$, where N_i is population size and μ is the site-specific mutation rate. While our modeling did not incorporate evolutionary processes or genetic information, the influences of τ on abundance (Fig. 1) suggests a natural connection between τ and population genetics. That is, if τ can be used to predict changes in productivity and abundance, then the accumulation of mutations or evolution of populations could be understood to be driven, in part, by a physical aspect of the environment (i.e., $N\mu \propto f(\tau)\mu$).

Life history – Our findings reveal connections between life history and aspects of the abiotic environment such as τ . Life history theory focuses on strategies that cause organisms to vary in growth rate, energetic efficiency, and reproductive investment. From early theory of r/K selection (e.g., MacArthur and Wilson 1967; Pianka 1970) to continuum theories of fast-slow life-history strategies (e.g., Salguero-Gómez et al. 2016), biologists often investigate strategies

that allow species to achieve high growth in unstable environments or that allow long-lived species to maintain stable population sizes. Our theory is consistent with the continuum view of fast-slow life history theory. For example, at extremely low values, τ places demands on organisms to grow and disperse sufficiently fast to resist washout, perhaps resulting in a decreased investment in reproduction (Box 1, Fig. 2A,C). As τ increases, advantages of active dispersal may be reduced relative to traits that allow populations to maintain competitively large populations (via rapid growth and reproduction) (Fig. 2A). At even greater τ , when rapid rates of dispersal, growth, and reproduction cannot be supported, pressure increases on the ability to persist in stable but resource-deplete conditions via dormancy-related strategies that result in greatly decreased reproductive efforts (Fig. 2D,F).

In addition to supporting a continuum of life history strategies across magnitudes of τ , we suggest that energetically costly life history traits may be most effective at maintaining large populations when those traits are well-matched to the physical environment. For example, productivity and the abundance of active individuals was greatest when individual rates of growth, basal metabolism, and dispersal were similar to dilution rate ($1/\tau$) (Fig. 3). The result of this match between energetically costly life history traits and $1/\tau$ allowed individuals to grow and reproduce fast enough to maintain large populations, but not so fast as to outstrip rates of resource supply and the ability of resource consumption to offset energetic costs.

Population and community ecology — Our theory suggests that τ should influence aspects of population and community dynamics such as temporal changes and stability, coexistence and competition, spatiotemporal resource dynamics, and dispersal-related aspects such as mass-effects and source-sink dynamics. For example, longer τ reflects a slower moving system and, as

a result, slower rates of change in species composition along with the accumulation of a
 472 persistent seed bank. In contrast, shorter τ reflects a system of faster dynamics, greater numbers
 of transient species, and lower degrees of population and community stability. Within individual
 474 IBMs, we did not simulate changes in V or Q that would have restructured communities or that
 may have promoted coexistence strategies. For example, varying V or Q across time may have
 476 fostered coexistence and greater diversity via storage effects and the temporal separation of
 competing species. However, by the same token, rapid changes in V or Q could have also led to
 478 less stable communities and the local extinction of populations.

Competition is central to the study of ecological communities. The simulated
 480 communities that assembled across magnitudes of τ were subject to varying degrees of resource
 competition. At extremely short τ , resource resupply was rapid and resource abundance was
 482 greater than individual abundance. Consequently, resource competition was perhaps less
 influential than the pressures imposed by potential washout. At high τ , resources were supplied
 484 more slowly and were more dilute, and seed banks comprised nearly all of individuals in the
 community. Under such conditions, metabolically active immigrants were introduced into largely
 486 dormant communities for which resuscitation was infrequent, and competition for highly limited
 resources was relatively low. However, at intermediate τ , large and diverse communities of many
 488 active individuals tended towards a greater partitioning of resources (Fig. 2e). This trend was the
 consequence of larger and more diverse communities being more likely to assemble when
 490 species consumed from largely non-overlapping resource pools.

Dispersal is also key to the dynamics of populations and communities. In much of
 492 population and community ecology, organisms are assumed to actively disperse (Levins 1969;
 Hubbell 2001; Leibold et al. 2004; McGill 2010). Our theory and modeling accounts for the

influence of active dispersal but also suggests the importance of passive dispersal and energetic constraints on active dispersal. For example, in rapidly flowing systems, rates of active dispersal opposed the rate of passive dispersal (i.e., flow rate) but also required an inflow of passively flowing resources great enough to support the energetic costs of active dispersal. While resource limitation is also fundamental to the study of populations and communities, resources in nature are spatiotemporally dynamic and their movement through environments is often overlooked (Polis et al. 1997; Haegeman and Loreau 2014). However, our theory places primary importance on the dispersal of resources into and through the environment as a means by which resource limitation occurs and influences rates of active dispersal.

Biodiversity and biogeography — Biodiversity theories often focus on the understanding of space, but generally lack a comparable emphasis on time. Theories of biodiversity and biogeography often incorporate area (A) and a rate of dispersal or immigration (m) (e.g., Hubbell 2001, McGill 2010, Harte 2011). However, these theories rarely consider explicit aspects of time outside the rates of biological processes (Wolkovich et al. 2014). In drawing connections between residence time theory and general theories of biodiversity and biogeography, consider how A/m resembles V/Q in that both place the size of a system over a rate of flow. With little modification, we suspect that τ as A/m could be used to derive new predictions from island biogeography theory, ecological neutral theory, stochastic resource limitation theory, and others. For example, the maximum entropy theory of ecology (METE) predicts more patterns of abundance, distribution, and diversity than most any other ecological theory (Harte 2011). However, METE's predictions are effectively “snapshots” in time. The inclusion of τ as a state variable could add a temporal dimension to METE and bring it closer to a dynamical theory. In

fact, the expectation that τ should approximate the time that inert particles spend in a simplified system is, by first principles, a maximum entropy solution (see Online Appendix A).

Ecosystem science — Residence time should have far-reaching effects on ecosystem dynamics (e.g., Copeland 1966). Historically, τ is recognized as an important variable with regard to nutrients, biomass, or other bulk ecosystem variables (e.g., Post et al. 1982; Valiela et al. 1997; Josefson et al. 2000; Crump et al. 2004; Beaugrand et al. 2010; Friend et al. 2014, Schramski et al. 2015). While our theory accounts for at least one variable that is central to ecosystem science (i.e., productivity), we have not yet developed our theory for nutrient cycling, stoichiometry, and trophic dynamics. Still, we suspect that τ may serve as a conduit for linking the ecology of populations and communities to the dynamics of ecosystems. For example, organisms that form the basis of food webs (e.g., soil microorganisms, cyanobacteria) are more prone to physical forces of flow than the larger-bodied consumers that occupy higher trophic levels. However, the dependence of consumers on the smaller organisms they consume inextricably connects the lives of consumers to physical forces of flow. This cross-trophic effect 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 the resupply of resources (Polis et al. 1997).

In presenting our theory, we focused on τ as a variable of the physical ecosystem that can shape biodiversity and drive biological rates. However, the value of τ is, in turn, driven by other properties of the physical environment. For example, changes in temperature induce the melting of ice, permafrost, and the occurrence of precipitation. All of these processes lead to changes in both V and Q . Temperature also influences metabolic rates and the breakdown of nutrients within ecosystems via chemical kinetics. Human-induced physical changes within watersheds and

540 across landscapes can also influence τ by changing V and Q of water bodies, and the loss of litter
and erosion of soils through deforestation and agriculture. In this way, understanding the
542 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 .

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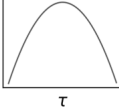
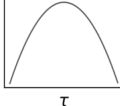
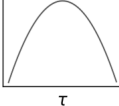
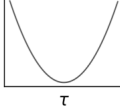
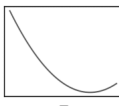
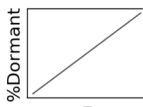
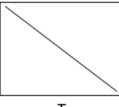
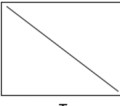
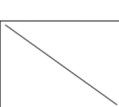
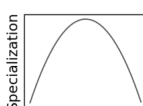
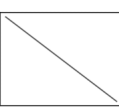

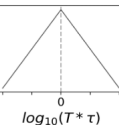
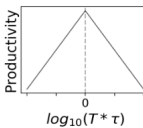
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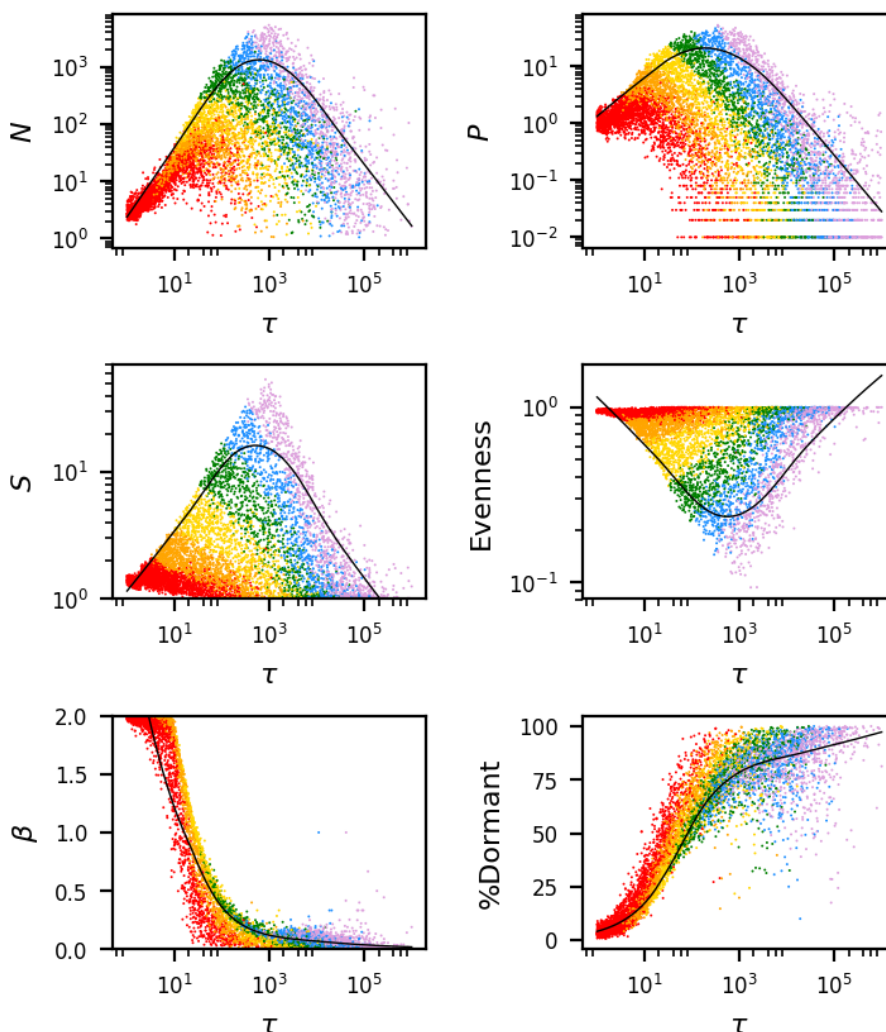
Table 1. Parameters, traits, and variables for each of 10^4 individual-based models. Values of each were randomly chosen within the noted ranges. See Methods and Online Appendix A for full descriptions of IBMs and their analysis.

Model-specific parameters		
Parameter	Description	Value
Size (V)	Length of the environment	1 - 1000
Flow rate (Q)	units of V moved per time step	0.001 - 1
Resource diversity (R)	number of inflowing resource types	10
Resource particle size	Range size for inflowing resource particles	1 - 1000
Immigration rate	per capita probability of immigration per time step	Q
Inflowing resource concentration	probability of a resource particle flowing in per time step	Q
Species-specific traits		
Trait	Description	Value
Intrinsic growth rate	proportional increase per time step	0.001 - 1
Active dispersal rate	units of space traveled against direction of flow per time step	0.001 - 1
Resuscitation rate	probability of resuscitating per time step	0.001 - 1
Basal metabolic rate (BMR)	proportion of endogenous resources lost to maintenance respiration per unit time	0.001 - 1
Reduction of BMR	proportional decrease of BMR when entering dormancy	0.001 - 1
Resource growth efficiencies	proportion of consumed resources assimilated in biomass	0 - 1
Individual-specific variables		
Variable	Description	Value
Resource quota (q_i)	amount of endogenous resources	0 - unconstrained
Body size	Individual biomass (does not include q_i)	0 - unconstrained
x	position along V	0 - V
Species	species of an individual	unconstrained
State	metabolic state	active or dormant

676 **Box 1.** Predictions for how abundance, productivity, activity, the diversity of taxa, and traits
 should relate to residence time (τ), the ratio of a system's size (V) to its average rate of flow or
 678 physical turnover (Q), $\tau = V/Q$.

Community-level predictions			
Prediction	Pattern	Prediction	Pattern
1. Total abundance (N) should be lowest at low τ due to washout and at high τ due to low resource resupply.		2. Productivity (P) should be lowest at low τ due to washout and at high τ due to low resource resupply.	
3. Species richness (S) should be lowest at low τ due to selection to resist washout and at high τ due to selection on persistence.		4. Species evenness (E) should be lowest at intermediate τ , reflecting competition and the constraining influence of N and S .	
5. Species turnover (W) should decrease with greater τ , reflecting less immigration and greater persistence. W may then increase, due to loss of species at low S .		6. The percent of individuals in a dormant state should increase with greater τ due to insufficient resource resupply and decreased threat of washout.	
Trait-level predictions			
Prediction	Pattern	Prediction	Pattern
7. Intrinsic rates of growth should decrease with greater τ , reflecting of growing quickly in rapidly moving systems and of growing less quickly in resource deplete conditions.		8. Active basal metabolic rate (B) should decrease with greater τ , reflecting pressures to accomplish similar rates of energetically costly processes at lower energetic costs.	
9. Rates of active dispersal should decrease with greater τ , reflecting advantages of strong dispersal in rapidly moving systems and the costs of active dispersal in resource deplete systems.		10. Resource specialization should be low at short and long τ . Specialization should increase as resource partitioning emerges among greater numbers of competing species.	
11. Rates of resuscitation from dormancy should decrease with greater τ , reflecting the disadvantage of being dormant at short τ and the costs of active metabolism at long τ .		12. Increasing τ should select for a greater reduction of basal metabolic rate (B) when individuals go dormant.	
Equivalence predictions			
Prediction	Pattern	Prediction	Pattern
13. The difference between the rates of energetically costly traits T and $1/\tau$ represents the match between resource supply and energetic costs. N should be greatest when $T = 1/\tau$.		14. The difference between the rates of energetically costly traits T and $1/\tau$ represents the match between resource supply and energetic costs. P should be greatest when $T = 1/\tau$.	

680 **Figure 1.** 10^4 stochastic and randomly parameterized IBMs with no explicit constraints on total
community abundance (N) or species richness (S) reveal how residence time ($\tau = V/Q$)
682 influenced N , individual productivity (P), S , Simpson's measure of species evenness, Whittaker's
measure of species turnover (β), and the percent of N individuals that were metabolically
684 dormant. System size (V) and flow rate (Q) each varied over three orders of magnitude. The form
of each relationship matches our predictions. Rainbow spectrum data points represent systems of
686 different Q , with red being fastest and violet being slowest. Black lines are locally weighted
polynomial regressions fitted to the 95th percentile of binned data (5th percentile for evenness).



688

Figure 2. 10^4 stochastic and randomly parameterized IBMs with no hard constraints on

abundance or richness reveal how residence time ($\tau = V/Q$) influenced species traits of individual growth rate, basal metabolic rate (B), active dispersal rate, the rate of random resuscitation from dormancy, resource specialization, and the degree to which B is decreased when individuals go dormant. Each of these relationships agrees with our predictions (Box 1). Rainbow spectrum data points represent systems of different flow rates, with red being fastest and violet being slowest. Black lines are locally weighted polynomial regressions.

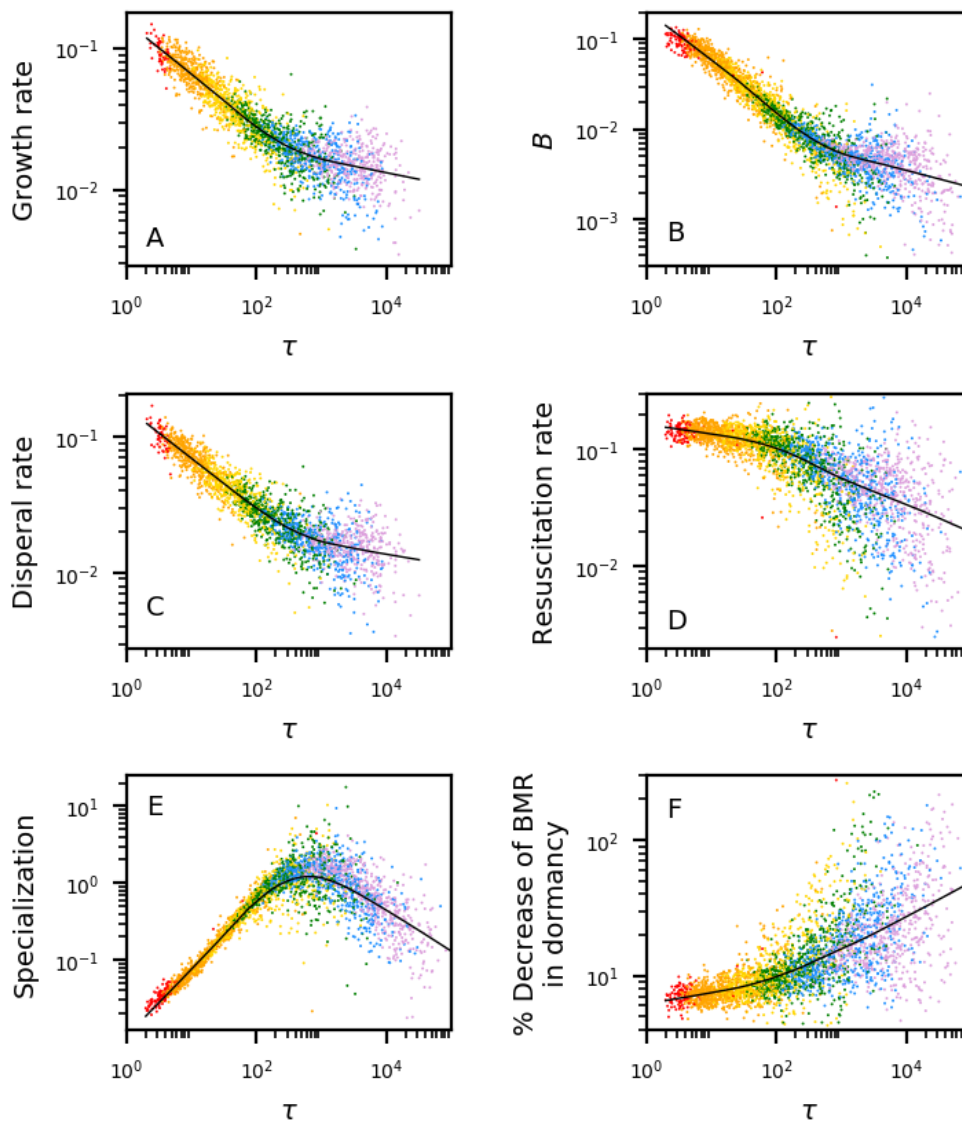


Figure 3. Greater similarity between dilution rate ($1/\tau = Q/V$) and species traits led to greater

maximum values of active total abundance (N_a) and individual productivity (P). These traits

included rates of individual-growth (μ), basal metabolism (B), and active dispersal (d). The

vertical dashed line represents the point where average values μ , B , and d equal dilution rate

($1/\tau$). For example, if $B = 1/\tau$, then $\log_{10}(B*\tau) = 0$. As expected, this is the point where greatest N_a

and P occurred. Rainbow spectrum data points represent systems of different τ , with red being

shortest and violet being longest.

