

A Residence Time Theory for Biodiversity

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ABSTRACT: 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 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 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 stochastic individual-based models to simulate energetically constrained life-history processes, we show that our predictions are conceptually sound and mutually compatible and that they support 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 into theories ranging from population genetics to macroecology.

Keywords: chemostat, dormancy, emergent properties, individual-based models, macroecology, metabolic theory of ecology.

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 eight orders of magnitude, from minutes in the organs of 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). 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; Sibley et al. 2012; Friend et al. 2014; Waldron 2015). Residence time can also in-

fluence organismal health and is thought to place evolutionary constraints on digestion and nutrition (Molla et al. 1983; Castiglione et al. 2000; Franz et al. 2009; Flint 2011; Wu et al. 2011; 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 but powerful way: $\tau = V/Q$. This relationship is based on probability and represents the average time that passively moving particles remain in a system (see appendix). Three classic predictions of τ are commonly used in the operation of continuous-flow bioreactors known as chemostats (Smith and Waltman 1995; Henze 2000; Angenent et al. 2004; see appendix). First, τ approximates the average time that individuals spend in the system. Second, 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 theories of resource competition and resource-limited growth were first tested (e.g., Droop 1974; Tilman 1981). Importantly, theory developed from chemostats assumes ideal conditions such as static V and Q , zero immigration, and constant growth, all leading to an equilibrium abundance. However, in nature, 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 used 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 τ can shape the life-history strategies of individuals, the traits of species, and the assembly and structure of communities. We propose a set of predictions for how τ influences the abundance

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and diversity of taxa and how τ acts as an environmental filter on sets of traits (i.e., syndromes) that promote growth and persistence. We also propose how classic predictions of τ developed for chemostats may fail in complex ecological systems. We challenge our predictions to emerge alongside established patterns of biodiversity using individual-based models (IBMs). These IBMs simulate the biology and dispersal of individuals and the consumption and movement of resource particles through one-dimensional environments that are characterized by length (V) and rate of flow (Q). We provide initial support for our theory and its compatibility with other ecological theories. We discuss how τ can be integrated into theories of population genetics, life history, and ecology and describe how τ may contribute to the understanding of metabolism and host-microbiome dynamics. We also 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 abundance, diversity, and productivity, as well as the emergence of trait syndromes that allow organisms to persist within flowing environments. The following predictions, which are depicted in figure 1, use a generalized concept of an environment's size (V) that can apply to length, area, or volume.

Community-Level Predictions

Prediction 1: Total Abundance (N) versus τ . The number of individual organisms is the primary descriptor of abundance. We predict that τ influences N through its effects on immigration, emigration, and growth. First, τ can be short enough that individuals are removed before reproducing, resulting in washout. Second, τ can be long enough that immigration is too low to establish populations and resource supply is too low to maintain them. 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) versus 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 nonrepro-

ductive states of low metabolism (dormancy) can decouple abundance and productivity.

Prediction 3: Species Richness (S) versus τ . The number of species 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 as τ becomes increasingly short or long. Specifically, τ should act 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. Without continued immigration (e.g., at long τ), a community can drift to a single species.

Prediction 4: Species Evenness (E) versus τ . Similarity in abundance among species (i.e., evenness, E) is the second primary component of species diversity. Though measures of E are derived to be independent of S (Smith and Wilson 1996), E often scales with N , $E \propto N^{-z}$ (Locey and Lennon 2016). This relationship can partly be explained as a consequence of how 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) versus 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 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 versus τ . Dormancy is a reversible state of reduced metabolic activity accompanied by the absence of resource consumption, growth, and reproduction (Lennon and Jones 2011). Organisms across domains of life exhibit dormancy in response to the sparse and fluctuating availability of resources (Guppy and Withers 1999). Dormancy should be favored in systems with longer residence times owing to a reduced rate of resource supply and a lower probability of washout.

Trait-Level Predictions

Prediction 7: Individual Growth versus 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 im-

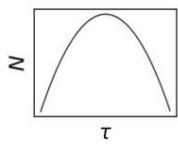
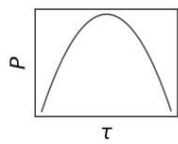
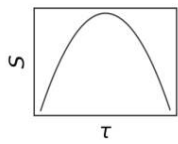
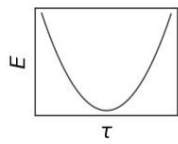
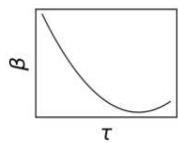
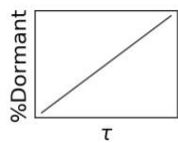
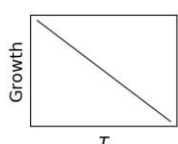
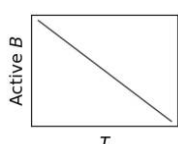
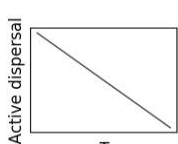
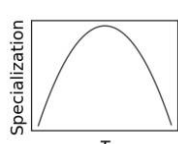
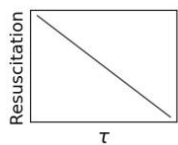
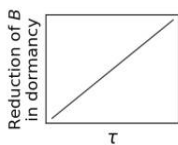
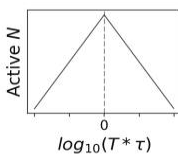
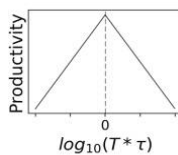
Community-level predictions			
Prediction	Pattern	Prediction	Pattern
1. Total abundance (N) should be lowest at low τ due to washout and at high τ due to low resource resupply.		2. Productivity (P) should be lowest at low τ due to washout and at high τ due to low resource resupply.	
3. Species richness (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 $T = 1/\tau$.	

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

posed 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 depleted to fuel rapid growth, environmental filtering should favor slower-growing organisms at longer τ .

Prediction 8: Active Dispersal versus 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 high rates of resource supply. However, resources should become increasingly limited with longer τ , and the pressure to actively disperse at rapid rates should decrease. Consequently, rates of active dispersal should decrease with greater τ .

Prediction 9: Basal Metabolic Rate (B) versus τ . Basal metabolic rate represents the sum of energetic costs associated with essential metabolic functions. We predict a decrease in B with 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 dispersal under a lower B) or greater austerity (e.g., via dormancy).

Prediction 10: Resource Specialization versus τ . Resource specialization reflects the variation in species performance across resource types (Devictor et al. 2010; Poisot et al. 2012). 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, individuals may reduce the probability of washout by consuming a variety of resources. As τ increases, specialists are afforded time to encounter specific resource types, which may result in the emergence of species that consume largely nonoverlapping sets of resources. As a consequence, the partitioning of resources may promote greater S . However, we expect that a generalist strategy may be favored at high τ , as the availability of resource decreases as a result of low Q and dilution in the environment (high V).

Prediction 11: Resuscitation Rate versus 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 B in Dormancy versus 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 and 14. In chemostats with ample resource supply, N and P should be greatest when maximum specific population growth rate (μ_{\max}) is equivalent to 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. Instead, we expect the similarity between $1/\tau$ and the rates of energetically costly traits (e.g., B , individual growth, active dispersal) to reflect the fit of species to τ . As a result, P and the 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 (fig. 1) using an IBM platform that simulated flowing one-dimensional environments and energetically constrained life-history processes among populations of heterotrophic asexual individuals. Each IBM began as an empty system of length V into which organisms of up to 10^3 species and resource particles of up to 10 types entered and flowed across at a rate of Q . Species identities of individuals were determined by reproduction or, in the case of immigration, by a random sample from the species pool. Species were assigned traits that determined individual-based rates of dispersal, growth, basal metabolism, reproduction, and resuscitation (table 1). These processes were fueled by the assimilation of consumed resource particles into endogenous resource quotas (q). In addition, these processes incurred energetic costs that were proportional to their rates, which could reduce q to the point that individuals would starve or become dormant. There were no free parameters for population growth or species diversity. Instead, all aspects of demography, abundance, and diversity emerged from individual-level processes and the influence of τ . We provide greater description of our modeling below and in the supplemental PDF (available online). All modeling code is available on a public GitHub repository: <https://github.com/LennonLab/residence-time>.

Randomized Parameterization

Each IBM began with random combinations of traits for each of 10^3 species in the regional pool, along with randomly drawn values of V , Q , immigration rate, and resource conditions (table 1). This randomized parameterization ensured that our IBMs explored wide swaths of parameter space while allowing our predictions, trait combinations, and general biodiversity patterns to naturally emerge, as opposed to being explicitly enforced.

Table 1: Ecosystem properties, species traits, and varying properties of individuals

	Description	Value
Ecosystem properties:		
Size (V)	Length of the environment	1–1,000
Flow rate (Q)	Units of V moved per time step	.001–1
Inflowing resource diversity	Number of inflowing resource types	10
Inflowing resource particle size	Range of sizes for inflowing resource particles	1–1,000
Species traits:		
Individual growth rate (g)	Proportional increase in individual size per time step	.001–1
Active dispersal rate (d)	Units of V traveled against direction of flow per time step	.001–1
Resuscitation rate	Probability of resuscitating per time step	.001–1
Basal metabolic rate (B)	Portion of endogenous resources lost to maintenance respiration per time step	.001–1
Reduction of B	Proportional decrease of B upon entering dormancy	.001–1
Resource efficiencies (e_1, \dots, e_{10})	For each of 10 resource types, the proportion of a consumed resource particle that is assimilated into an individual's resource quota	0–1
Varying properties of individuals:		
Resource quota (q_i)	Amount of endogenous resources	0–unconstrained
Body size (M_i)	Individual biomass (does not include q_i)	0–unconstrained
Spatial location (x_i)	Position along V	0– V
Metabolic state	Whether an individual is metabolically active or dormant	Active or dormant

Note: Values of ecosystem properties and species traits were randomly chosen within the given ranges. Resource quotas, body sizes, spatial locations, and metabolic states of individuals change throughout the course of a model, but ecosystem properties and species traits do not.

Simulating Residence Time (τ)

Flow rate (Q) was simulated as the fraction of a single unit distance that the environment flowed downstream per time step. Resource particles and passively moving individuals were then carried downstream at a rate equal to Q . Thus, the simulated environments of our IBMs continued to flow regardless of whether resource particles or individuals were present. To reduce computational overhead, all of our IBMs were characterized by a single spatial dimension. Both the length (V) of these one-dimensional systems and the value of Q were randomly chosen within ranges of three orders of magnitude, resulting in six orders of magnitude in τ (table 1).

Immigration

Each IBM began as an empty system into which individual organisms flowed according to Q . The body size and species identity of each immigrant were drawn at random from uniform distributions (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 system (i.e., V , Q). Units of body size were considered negligible with respect to the size of environment (V).

Resource Supply

Discrete resource particles flowed into the system according to Q . The sizes and resource types represented by these particles were drawn at random from uniform distributions (table 1). Resources were not chemically or stoichiometry based but were instead abstract and differed in the efficiency by which different species could consume them. Units of size for resource particles were considered negligible with respect to the size of environment (V).

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. These probabilities were determined by species trait values along with the metabolic state (active or dormant), body size (M), and endogenous resources (q) of individuals. Body size represented the mass of individuals that could not be used to fuel metabolism.

Resource consumption. Instead of explicitly modeling energy flow, we simulated representative sources of energy (i.e., resource particles) and the use of q to build biomass and to fuel biological processes. At each time step (t), randomly sampled individuals could consume randomly en-

countered resource particles from any of 10 possible 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%–100%) was determined by species-specific values for each of the 10 possible resource types (table 1). Consumption increased an individual's q according to the species-specific efficiency (e) for the particular resource type, the size of the resource particle (r), and M :

$$q_{t+1} = q_t + \min(r_t, e \cdot M_t).$$

This relation prevented individuals from consuming a greater amount of resource than contained in the resource particle and allowed M to take any nonzero real number. The size of the resource particle decreased accordingly, with particles of zero size disappearing from the system:

$$r_{t+1} = r_t - \min(r_t, e \cdot r_t \cdot M_t).$$

Growth. At each time step, individuals grew in proportion to M and according to their species-specific rate of individual growth (g), resulting in an equivalent decrease in q :

$$\begin{aligned} M_{t+1} &= M_t + \min(q_t, g \cdot q_t), \\ q_{t+1} &= q_t - \min(q_t, \mu_i \cdot q_t). \end{aligned}$$

These relationships 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 M . At each time step (t), randomly sampled individuals that were metabolically active could reproduce according to a probability that increased with M and the ratio (λ) of q to B , $\lambda = q/B$:

$$p = \left(\frac{\lambda_t}{1 + \lambda_t} \right) \left(\frac{M_t}{1 + M_t} \right).$$

Thus, the probability of reproducing (p) equaled 0 if q or size equaled 0. Reproduction became more likely with greater size 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 :

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

Thus, a greater amount of endogenous resources relative to basal metabolic costs decreased the probability of becoming dormant, while newly produced individuals were prevented from becoming 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 B : $q_{t+1} = q_t - B$. If the individual was dormant, B was reduced by a species-specific value (γ): $q_{t+1} = q_t - \gamma B$ (see table 1). Active and dormant individuals died when they could no longer meet metabolic costs.

Dispersal. At each time step, individuals flowed toward the downstream edge of the system according to Q . However, metabolically active individuals could actively disperse against the direction of flow according to their species-specific dispersal rate (d) and M :

$$\begin{aligned} x_1 &= x_0 - \min(x_0, q_0, d \cdot M_t), \\ q_1 &= q_0 - \min(x_0, q_0, d \cdot M_t). \end{aligned}$$

Thus, 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 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 community abundance, numbers of resource particles, or the size of individual organisms. 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 prohibitively large numbers of time steps. Each IBM ran for 10^3 time steps after burn-in and recorded 117 metrics every tenth time step (see supplemental PDF). 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 tenth time step. All results files are available on a public GitHub repository: <https://github.com/LennonLab/residence-time>.

Measurement of Select Response Variables

Specific growth rate (μ). The proportional rate of population growth is often 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 $1/\tau$ to approximate μ . Our IBMs allowed for μ to emerge as a measurable response of populations.

Species evenness and turnover. We quantified species evenness with Simpson's evenness index (D^{-1}/S), where D^{-1} is the inverse of Simpson's diversity (Magurran and McGill 2011)

and is species richness. 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).

Resource specialization. We quantified resource specialization as the variance in species-specific resource use efficiency for each of 10 resource types.

Congruence of τ -Related Predictions with General Biodiversity Patterns

Predictions of an ecological theory should support common ecological observations. For example, predicting the hollow-curve form of species-abundance distributions (SADs) is a condition that theories of biodiversity must satisfy (McGill 2003, 2010). We adopted this perspective by challenging our IBMs to produce realistic forms of SADs, four diversity-abundance scaling laws (Locey and Lennon 2016), and two 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, $\sigma^2 \propto \mu^{1 < z < 2}$, where $\mu = N/S$ (Xiao et al. 2015). The second was the scaling of B with 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 patterns of biodiversity across six orders of magnitude in τ (figs. S1–S4; figs. S1–S8 are available online). 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 and four diversity-abundance scaling laws (Locey and Lennon 2016; figs. 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 mechanisms proposed to explain metabolic scaling (e.g., fractal resource networks). Taken together, our IBMs reproduced general patterns of biodiversity that are rarely, if ever, produced by the same theory. Data underlying these figures and all other figures in our article and the supplemental material are deposited in the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.gr61mv4> (Locey and Lennon 2019).

Classic Predictions in Complex Systems

In contrast to 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 prediction was due to stochastically fluctuating population sizes, a phenomenon that classic chemostat theory does not account for (fig. S6). For the same reason, we also observed no relationship between $1/\tau$ and species-specific rates of proportional growth (μ ; fig. S7).

Community-Level Predictions

Our predictions (fig. 1) emerged across six orders of magnitude in τ (fig. 2). We observed unimodal relationships of N , P , and S to τ , with maximum values occurring near τ of 10^3 (fig. 2). Responses of N , P , and S were characterized by unimodal upper bounds that were more constrained when we accounted for V and Q (fig. 2); E responded in the opposite fashion, with the lowest values 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 β 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 when S is low (fig. 2). 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 have particularly low metabolic costs and low rates of growth and dispersal.

Trait-Related Predictions. Our six trait-related predictions (fig. 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. 3). 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, that is, 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 more slowly, dispersed less quickly, and resuscitated less readily from dormancy (fig. 3). As τ increased and as individuals resuscitated less readily from dormancy, the effectiveness of dormancy in reducing B increased (fig. 3). 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

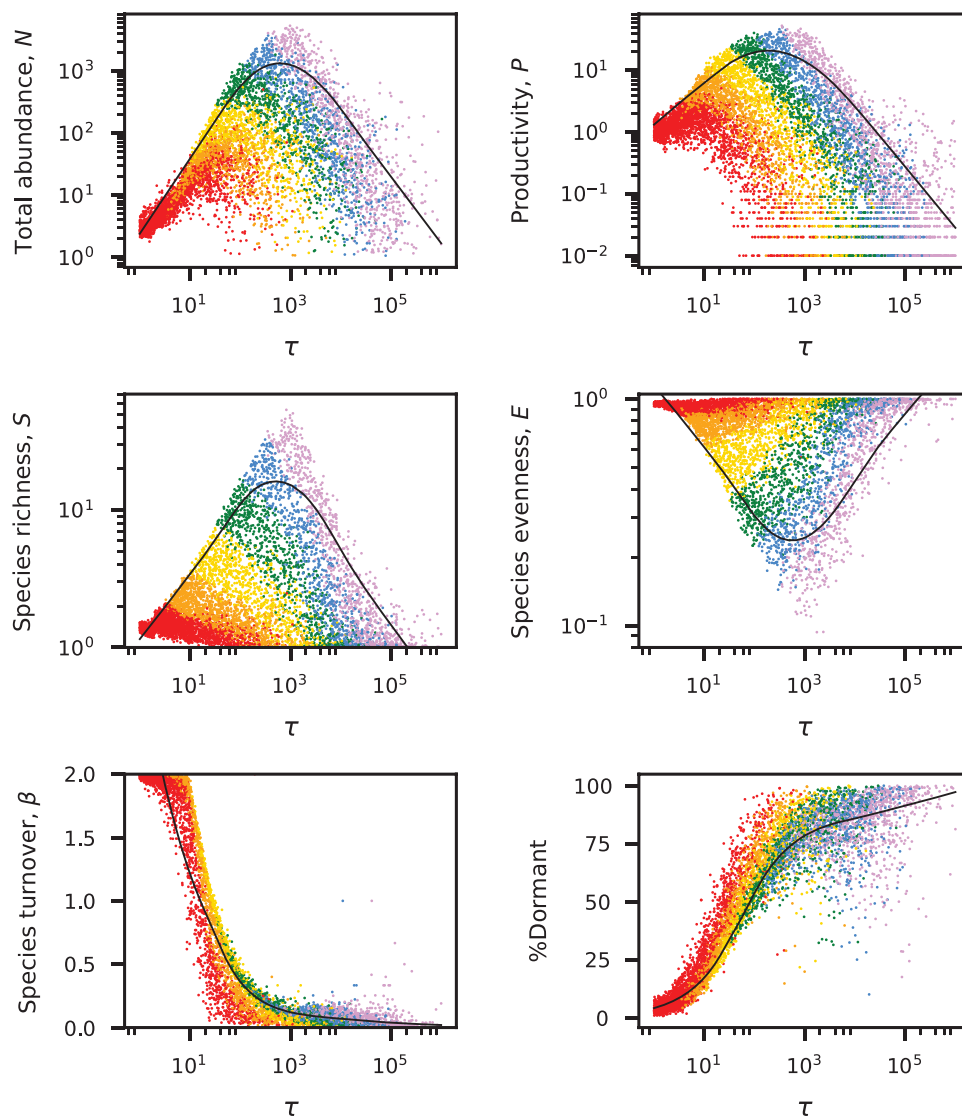


Figure 2: Shown are 10^4 stochastic and randomly parameterized individual-based models, with no explicit constraints on total community abundance (N) or species richness (S), which reveal how residence time ($\tau = V/Q$) influenced N , individual productivity (P), S , Simpson's measure of species evenness, Whittaker's measure of species turnover (β), and the percent of N individuals that were metabolically 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 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).

strategy of resource partitioning and avoidance of direct resource competition among all species. However, as τ increased past 10^3 , resource specialization decreased, resulting in a return to a more generalist strategy.

Equivalence Predictions

As predicted, P and N_a were greatest when dilution rate ($1/\tau$) approximated individual rates of basal metabolic costs, growth, and active dispersal (fig. 4). 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 τ , the ratio of V to Q , constrains growth, abundance, and metabolic activity while also acting as a force of environmental filtering on traits and taxa. We formulated a large set of τ -based predictions (fig. 1) and then

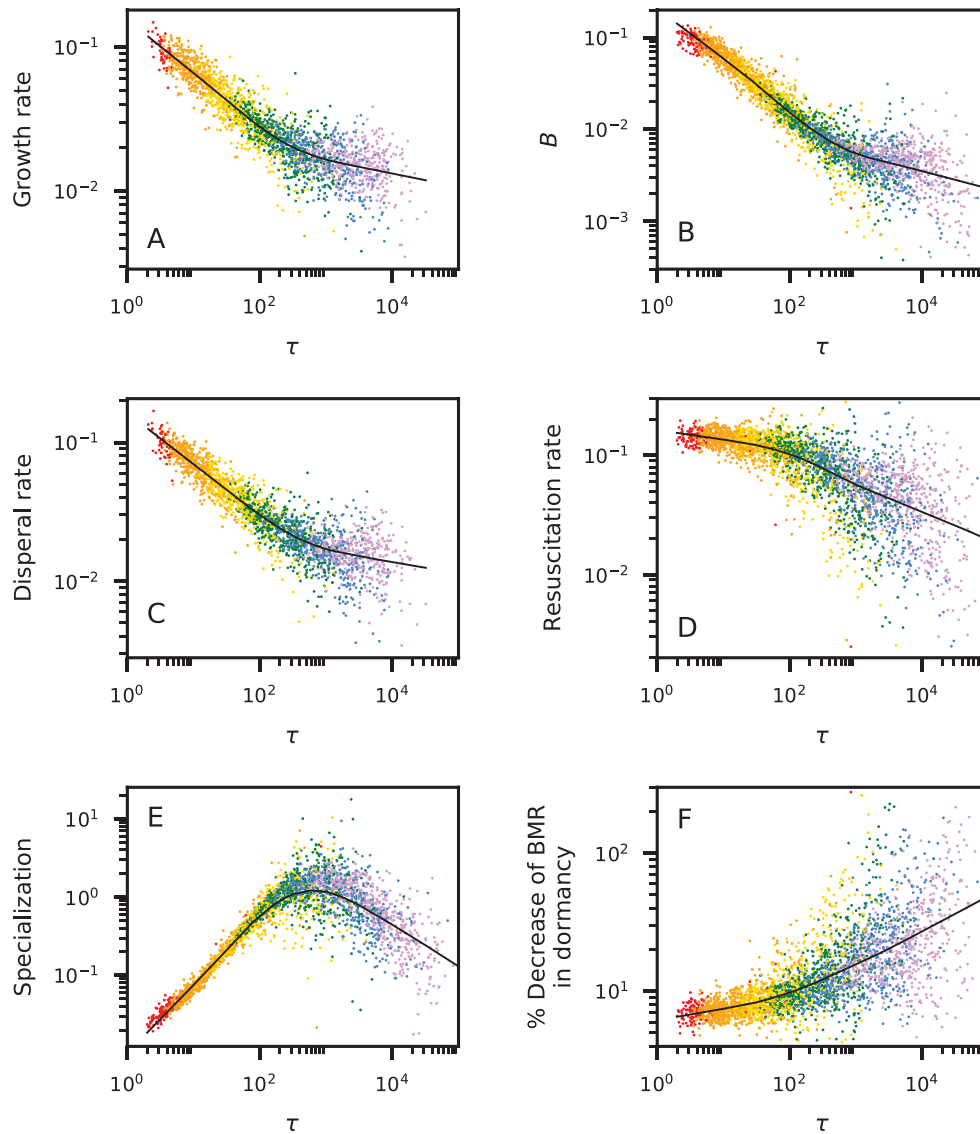


Figure 3: Shown are 10^4 stochastic and randomly parameterized individual-based models, with no hard constraints on abundance or richness, which reveal how residence time ($\tau = V/Q$, where V is size and Q is flow rate) influenced species traits of individual growth rate, basal metabolic rate (B), active dispersal rate, the rate of random resuscitation from dormancy, resource specialization, and the degree to which B is decreased when individuals become dormant. Each of these relationships agrees with our predictions (fig. 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.

challenged an ensemble of 10^4 IBMs to produce each predicted relationship alongside general patterns of biodiversity. These models imposed no explicit relationships among traits, between τ and traits, or between metabolic costs and body size. Despite this, 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, $1/\tau$ often approximates μ (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, the models and predictions of our τ -based theory were derived with the complexity and openness of ecological systems in mind. As a result, our predictions and modeling reveal how τ may influence abun-

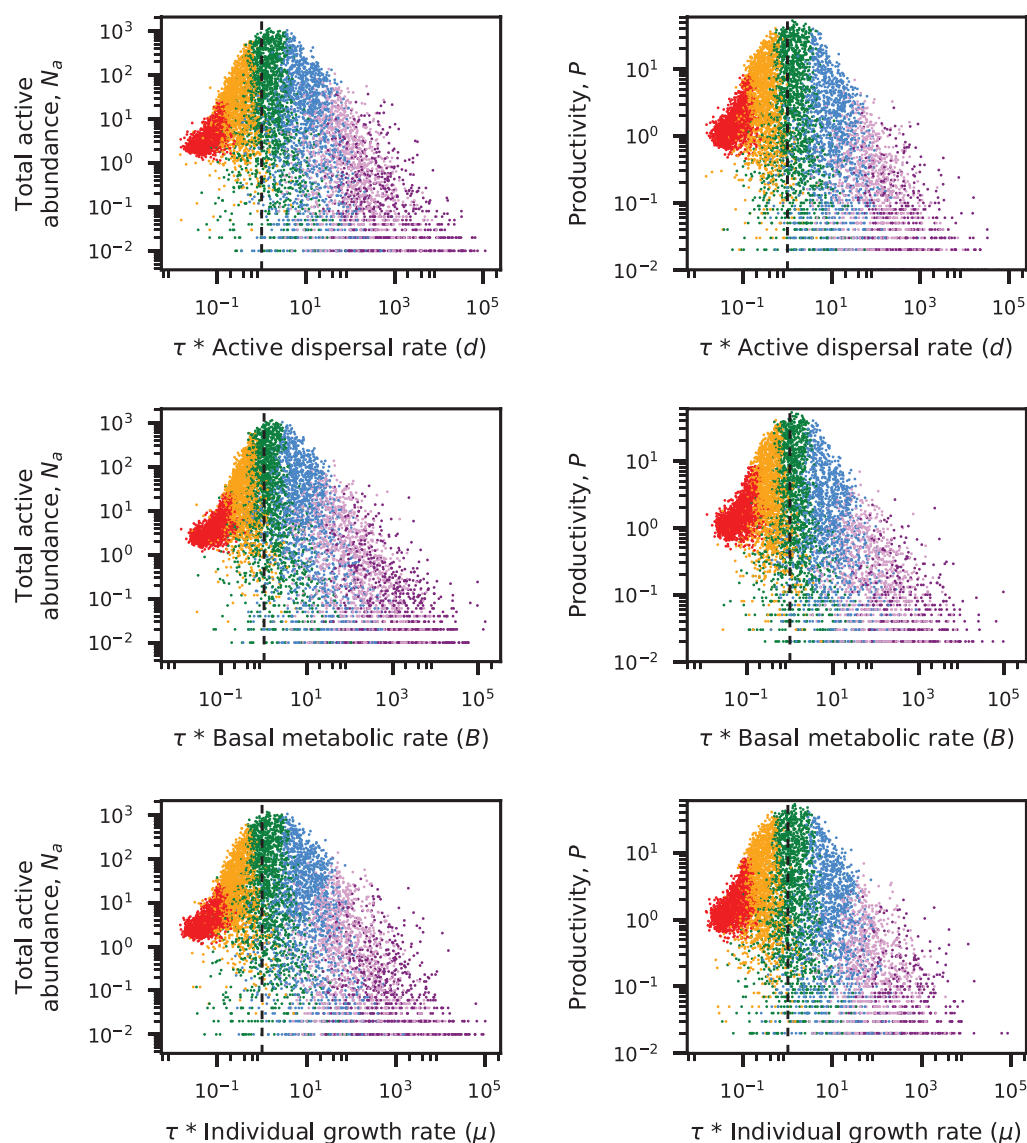


Figure 4: Greater similarity between dilution rate ($1/\tau = Q/V$, where V is size, Q is flow rate, and τ is residence time) and species traits led to greater maximum values of active total abundance (N_a) and individual productivity (P). These traits included rates of individual growth (g), basal metabolism (B), and active dispersal (d). The vertical dashed line represents the point where average values g , B , and d equal dilution rate ($1/\tau$). For example, if $B = 1/\tau$, then $\log_{10}(B \cdot \tau) = 0$. 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.

dance, productivity, and the diversity of traits and taxa in complex ecological systems even when classic predictions fail.

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 typically at the mercy of flow. 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 ecosystem processes

(Schramski et al. 2015). Such an approach could be extended to understand host-microbiome interactions within environments such as gastrointestinal (GI) tracts. While theoretical work on GI tracts has focused on aspects of V (length, surface area) and their relation to M (e.g., Franz et al. 2009; Sibly et al. 2012), little focus has been given to Q . Our *in silico* tests suggest that V and Q should 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 (Molla et al. 1983; Castiglione et al. 2000; Flint 2011; Wu et al. 2011; Dey et al. 2015; Waldron 2015).

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, the influences of τ on abundance (fig. 2) suggest 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, that is, $N\mu \propto f(\tau)\mu$.

Life History. Our theory reveals 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 disperse sufficiently fast to resist washout, resulting in decreased reproductive investment (figs. 1, 3A, 3C). 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. 3A). 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 zero reproductive efforts (fig. 3D, 3F).

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 $1/\tau$ (fig. 4). 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 population and community dynamics such as temporal changes and stability, coexistence and competition, and dispersal-related aspects such as mass effects. For example, longer τ reflects a slower-moving system and, as a result, slower rates of change in species composition and the accumulation of a 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.

Competition is central to the study of ecological communities. The simulated 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 greater than individual abundance. Consequently, resource competition was perhaps less influential than the pressures imposed by potential washout. At high τ , resources were supplied more slowly and seed banks comprised nearly all individuals in the community. Under such conditions, the few remaining metabolically active individuals may have had relatively low interspecific competition for resources. However, at intermediate τ , large and diverse communities of many active individuals tended toward a greater partitioning of resources (fig. 3E). This trend was the consequence of larger, more diverse communities being likely to assemble when species consumed largely nonoverlapping sets of resources.

Dispersal is also key to the dynamics of populations and communities. In much of population and community ecology, organisms are assumed to actively disperse (Levins 1969; Hubbell 2001; Leibold et al. 2004; McGill 2010). Our theory and modeling accounted for active dispersal and its energetic costs but also the reliance of organisms on passively flowing resources. 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). In contrast, our theory places primary importance on the flow of resources into and through the environment as a means by which resource limitation influences active dispersal.

Biodiversity and Biogeography. Biodiversity theories often focus on 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 (d ; 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 and theories of

biodiversity and biogeography, consider how A/d resembles V/Q in that both place the size of a system over a rate of flow. With little modification, τ as A/d could be used to derive new predictions from island biogeography theory, ecological neutral theory, and others. For example, the maximum entropy theory of ecology (METE) predicts more macroecological patterns than most any other ecological theory (Harte 2011). While the predictions of METE are “snapshots” in time, the inclusion of τ as a state variable could add a temporal dimension to METE. In fact, the expectation that τ approximates the time that inert particles spend in a system is, by first principles, a maximum entropy solution (see appendix).

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, and other 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). While our theory accounts for one variable that is central to ecosystem science (i.e., productivity), we had not included nutrient cycling, stoichiometry, photosynthesis, and trophic dynamics. Still, we suspect that τ may serve as a conduit for linking the ecology of communities to the dynamics of ecosystems. For example, organisms that form the base of food webs (e.g., soil microorganisms, cyanobacteria) are more subject to flow than the larger-bodied consumers. However, the dependence of consumers on the organisms they consume inextricably connects the lives of consumers to physical forces of flow. This cross-trophic effect 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 such as changes in temperature that induce precipitation and the melting of ice and permafrost. All of these processes lead to changes in both V and Q . Human-induced physical changes within watersheds and 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 influences of τ on abundance, activity, productivity, and biodiversity also begs for an understanding of the physical factors that drive the magnitude and variability of τ .

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APPENDIX

Definitions of Residence Time and Dilution Rate

Residence time (τ) is the average amount of time that passively moving particles remain in a system and is estimated from the ratio of a system's volume or size (V) to its rate of flow or physical turnover (Q), $\tau = V/Q$. This concept is used in studies of fluid dynamics, geology, chemostat bioreactors, and probability theory (see Whitten 1975; Schwartz 1979; Smith and Waltman 1995) and is explained as follows. Consider a perfectly mixed environment of volume (V) containing a constant number of N inert particles and operating at a constant rate of flow ($Q = v/t$), where v is a subvolume of V and t is time. The ratio of v to V represents the fraction of the environment that is lost and replaced per unit time, that is, the dilution rate ($1/\tau = Q/V = v/Vt$). Because the N particles are perfectly mixed within the environment, $1/\tau$ also represents the fraction of N lost per unit time and, hence, the probability (p) that a given particle will be lost in an amount of time equal to t . According to the geometric distribution, which gives the probability of x successes in repeated Bernoulli trials, a particle can expect to remain in a system for an amount of time equal to $1/p$. Hence, under ideal conditions, dilution rate ($1/\tau = Q/V = p$) is the inverse of residence time ($\tau = V/Q = 1/p$). Because $\tau = V/Q = Vt/v$, units of volume cancel out, and only units of time remain.

Relationship between Dilution Rate and Growth Rate

Dilution rate is used to control the rate of proportional population growth (μ) in bioreactors (see Smith and Waltman 1995). Consider a theoretically ideal chemostat: a perfectly mixed environment of volume (V) with a constant rate of flow (Q) of nutrient media and that supports a constant population size (N) in the absence of immigration and death. To maintain N individuals, the population must grow at a rate ($\mu = n/Nt$) equal to the rate of removal, that is, $1/\tau = v/Vt$. Hence, under ideal chemostat conditions, relative (or specific) growth rate (μ) comes to equal dilution rate ($1/\tau$). However, once $1/\tau$ exceeds the maximum population growth rate (μ_{\max}), the system loses organisms faster than they can be replaced, and a process of “washout” ensues, with the eventual loss of the population.

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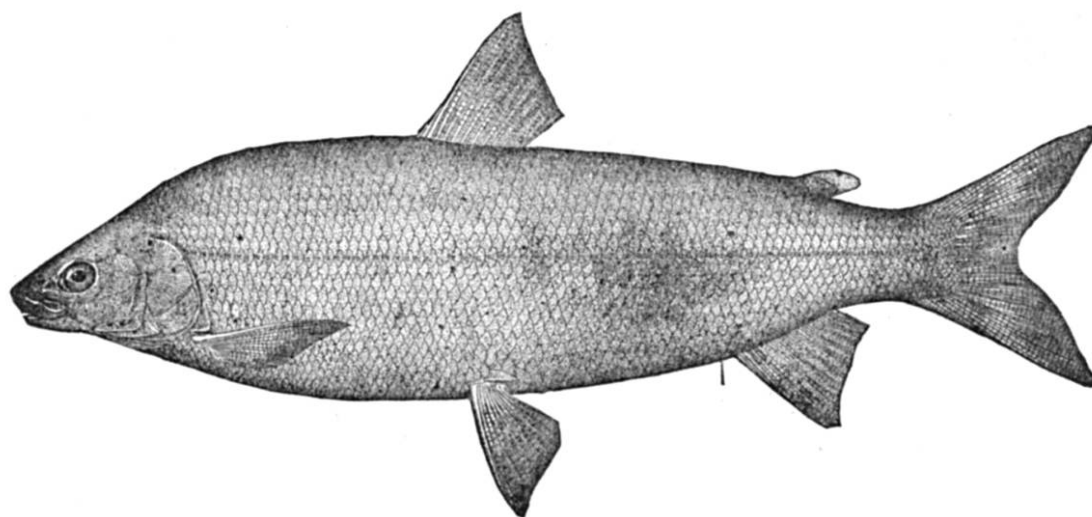
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“The family of Salmonidæ—embracing the white fishes, the salmons, and the trouts—is one of the most important of the temperate and arctic regions of the world.” Figured: “Common White-fish (*Coregonus clupeiformis*). Ecorse, Michigan.” From “Distribution and Some Characters of the Salmonidæ” by Tarleton H. Bean (*The American Naturalist*, 1888, 22:306–314).