A residence-time framework for biodiversity

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ABSTRACT

Residence time (τ) is the average amount of time that particles spend in an ecosystem. Often estimated from the ratio of volume to flow rate, τ equates the physical environment with dynamics of growth. Here, we propose that τ is key to understanding relationships between biodiversity and the physical ecosystem. We hypothesize that τ acts as a force of selection on traits related to growth and persistence by coupling dispersal and resource supply. We test a suite of predictions using >10,000 stochastic individual-based models that simulate resource-limited life history among ecologically distinct species within complex environments. Predicted relationships between τ and abundance, productivity, and diversity emerged alongside realistic macroecological patterns. Abundance and productivity were greatest when τ equaled an emergent property ϕ, which captures energy-based trade-offs between growth and persistence. From individual metabolism to the dynamics of bioreactors, soils, lakes, and oceans, ecological systems should inherently be governed by τ.

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INTRODUCTION

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

Residence time is a primary constraint on growth in natural, **engineered**, and experimental systems. In bioreactors, τ influences performance and stability while in experimental chemostats, τ is manipulated to control growth and to study eco-evolutionary dynamics (Smith and Waltman 1995, Henze 2000, Angenent *et al*. 2004). In both experimental and engineered systems, the inverse of τ, i.e., dilution rate ($1/\tau$), is used to approximate growth rate. In terrestrial and aquatic habitats, τ is measured with respect to the turnover of nutrients, removal of pollutants, development of algal blooms, and the global-scale consequences of altered carbon cycling (Post *et al*. 1982, Valiela *et al*. 1997, Josefson *et al*. 2000, Crump *et al*. 2004, Beaugrand *et al*. 2010, Friend *et al*. 2014). The concept of τ is even studied in medicine and microbiome research to understand the effects of disease and microbiomes on the health of host organisms (Wu *et al*. 2011, Flint 2012, Dey *et al*. 2015, Waldron 2015). Despite the importance of τ across a broad spectrum of natural, experimental, and engineered systems, it is surprisingly rare for τ to be integrated into general ecological theory (but see Schramski et al. 2015). Few, if any, studies have predicted how τ should shape the biodiversity of traits and taxa, and whether τ might approximate vital rates within complex ecological systems.

In this study, we developed a conceptual framework for how τ should influence abundance and diversity of traits and taxa, and how τ should act as a force of selection on groups of traits that promote growth or persistence, i.e., trait syndromes. We integrated established ecological relationships with resource-limited growth dynamics and the bioenergetics of physiological maintenance to test whether the predictions of our τ-based framework should hold for complex ecological systems. To do this, we developed a platform to use thousands of stochastic individual-based models (IBMs). These IBMs are capable of simulating many ecologically and physiologically unique species within spatially heterogeneous environments that are characterized by environmental gradients, resource heterogeneity, and fluctuating properties of flow, resource supply, and immigration.

PREDICTIONS

Total abundance and productivity — The number of individual organisms (i.e., total abundance; *N*) is the primary descriptor of population or community size. We predict that τ influences *N* through interactions of growth, metabolic maintenance, and resource supply. First, τ can be short enough that individuals are removed before they can reproduce, i.e., “washout”. Second, τ can be long enough that resource supply is too low to fuel growth or to offset metabolic maintenance (Pirt 1965, Droop 1983). Between these extreme values, resource resupply can be sufficient to fuel growth and flow can be slow enough to prevent washout. In simplified systems, N and productivity are expected to be greatest when dilution rate ($1/\tau$) equals maximum growth rate (μ_{max}) (Smith and Waltman 1995). In this way, we predict hump-shaped relationships of N and productivity to τ, the modes of which should occur when μ_{max} equals $1/\tau$.

***Species richness* (*S*)** — The number of species in a community (i.e., richness, S) is the foremost component of species diversity (Magurran and McGill 2011). We predict that τ affects S in two ways. While S often tends to scale with N (e.g., Locey and Lennon 2016), we expect τ to further constrain S by placing selective pressure on species to resist washout at short τ or resist starvation at long τ. Fewer species should maintain viable populations as τ becomes increasingly short or long. Based on this, we predict a humped-shaped relationship of S to τ, the mode of which should occur when μ_{max} equals dilution rate ($1/\tau$).

***Species evenness* (*E*)** — Similarity in abundance among species (i.e., evenness, E) is the second primary component of species diversity (Magurran and McGill 2011). We predict that τ affects E in two ways. First, decreases in E often scale with greater N (e.g., Locey and Lennon 2016). While this can be expected based on numerical constraints (Locey and White 2013), a more ecologically meaningful reason is found in the study of species abundance models. Specifically, models of exceptionally low E such as the dominance preemption and geometric series models result from strong competitive interactions (Magurran and McGill 2011). Because intermediate τ may allow enough time for competitive dynamics to emerge, we expect intermediate τ to allow for the assembly of communities with low E. As a result, we predict a U-shaped relationship of E to τ, the lowest point of which should occur when μ_{max} equals dilution rate ($1/\tau$).

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

Growth syndrome at short τ – We predict that τ should act as a force of selection on life history traits that promote growth at short τ. To maintain viable populations, organisms should either grow and reproduce before being washed out, or be physically adapted to prevent removal (e.g., active dispersal). Though rapid growth can be inefficient and though active dispersal carries additional energetic costs, these shortcomings may be compensated for by high rates of resource supply and the ability to consume a variety of resources (i.e., generalism). As τ increases, competition among greater S may promote greater resource specialization.

Persistence syndrome for long τ – Slow moving systems with low rates of resource resupply are characteristic of long τ. In these conditions, organisms are pressured to persist in the absence of resources. Persistence should increase if metabolic maintenance energy can be decreased, if populations do not grow outgrow available resources, and if organisms are capable of entering a reversible state of decreased metabolic activity (i.e., dormancy). We expect organisms at long τ to more grow slowly and have a greater capacity for dormancy. As transitioning between dormancy and activity is not energetically free, we expect that organisms able to persist at high τ will resuscitate less readily.

METHODS

Overview – We explored the influence of residence time (τ) on abundance, diversity, and activity using individual-based models (IBMs). IBMs simulate the interactions and behaviors of individual elements (e.g., individual organisms, resource particles) and provide a way to study how ecological relationships emerge from individual-level interactions (Grimm et al. 2005). IBMs allow bodies of theory to be incorporated through process-based rules, analytical formulas, and random sampling (Locey et al. 2017). We constructed an IBM platform that parameterized IBMs from random combinations of physical and flux-based, resource-related, community-level, and energy-based physiological parameters (Table 1). These IBMs allowed realistic dynamics to emerge from ecological selection on random variation in species traits over thousands of generations (*sensu* Locey et al. 2016).

Randomized model parameterization – The IBM source code chose parameter values at random within ranges that established limits on species-specific energetic constraints (e.g., metabolic maintenance) and vital rates (e.g., growth, dispersal) along with upper limits on the number, size, and diversity of inflowing resource particles (Table 1). Once assembled, each IBM was populated with 1,000 individuals whose species identities were drawn at random to maximize the starting diversity of trait combinations and to allow trait-syndromes and trade-offs to emerge over generations of ecological selection. In this way, our IBMs allowed the influences of τ to simultaneously emerge as robust and mutually inclusive outcomes.

***Simulating individuals, species, and resources* –** Individuals were distinguished by collections of elements within lists, where the same position in each list corresponded to the same individual. For example: IndIDs = [1, 2, 33]; SpeciesIDs = [8, 13, 1]; IndX = [45, 23, 456]; IndY = [765, 87, 21]; IndZ = [132, 68, 249]. Here, the individual with ID of 1 belongs to species 8 and is located at position x = 45, y = 765, z = 132. In addition to lists for individual IDs, species IDs, and the geographic coordinates of individuals, our IBMs also held individual-level lists for resource-specific cell quotas and whether individuals were active or dormant (Table 1). Like individuals, resource particles were also distinguished by elements within lists. When resource particles entered the system, they were assigned an individual identity, a resource identity at random, a size value between 100 and 1000, and three-dimensional spatial coordinates.

***Resource-limited life history* –** At each time step, every individual had a probability of undergoing growth, dispersal, reproduction, and transitions between dormancy and metabolic activity. The probability (p_p) of undergoing these life history processes was determined by the product of endogenous resources (i.e., cell quota; $0 \leq q_i \leq 1$) and species-specific trait values (t_s), where $p_p = q_i * t_s$. In this way, individuals with a low cell quota were more likely to enter dormancy, were less likely to reproduce, and were less likely to actively disperse as far as individuals that were replete with resources. Consumption of resources increased q_i according to the combination of species-specific maximum growth rate (μ_{max}), the ability for an individual of a specific species to convert a particular resource to biomass (i.e., efficiency), and the present value of q_i. Individuals became dormant once their value of q_i decreased below the species-specific value for maintenance energy and died once q_i reached 0.

Energetic costs **–** Life history processes and active metabolism were accompanied by energetic costs that depleted q_i. Our IBMs simulated these costs according to dynamics underpinned by ecological theory. Specifically, the tendency for ecological processes to be multiplicative and stochastic (Putnam 1993, Hubbell 2001), and the tendency for body size to influence vita rates (Brown et al. 2004). For example, energetic costs of active dispersal should be multiplied across distance and, within a species, should be greater for organisms that transport a larger mass. Dormant individuals, which were unable to consume or reproduce, experienced a species-specific reduction in maintenance costs, which decreased the value of q_i at which death occurred.

Realistic patterns of diversity and community structure — We evaluated whether our IBMs produced realistic species abundance distributions (SADs), i.e., vectors of species abundances. The SAD is the first pattern that theories of biodiversity should predict (McGill et al. 2007). We fit two of the most successful SAD models (i.e., Poisson lognormal distribution, log-series distribution) to the SADs of our IBMs. Historically, the Poisson lognormal and the log-series provide the best fits to empirical SADs (White et al. 2012, Baldridge et al. 2015). As an additional test, we asked whether our IBMs reproduced diversity-abundance scaling relationships. Aspects of species diversity often scale with N (Locey and Lennon 2016). These aspects include species rarity (i.e., concentration of species at low abundances), evenness, absolute dominance (i.e., greatest species abundance), and richness.

Running the models – We ran 10,000 IBMs to test the robustness of our predictions. Each IBM could result in thousands of individuals and thousands of resource particles being simulated,

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where variables related to physiology, abundance, trait and taxa diversity, as well as variables of the physical ecosystem were tracked and recorded. This computationally intensive approach required τ-adjusted run times. While IBMs at shortest τ led to few individuals persisting for more than one time step, IBMs at longest τ led to ecological selection on the capacity for individuals to resist starvation. This latter case took many thousands of time steps. Consequently, running an IBM for 1000 time steps at short τ would waste compute time while running an IBM for 1000 time steps at long τ would not allow enough time for selection to operate. We found that the minimum amount of time (t) that an IBM should run related to τ through an exponential relationship: $t = 400+5^{\tau}$. After discarding this burn-in period, we ran each model for 500 additional time steps. Altogether, run times were as low as 1000 time steps for shortest τ and as high as 79,000 time steps for longest τ.

***Quantifying abundance and diversity* –** We recorded aspects of abundance, activity, productivity, and trait and taxa diversity at either each time step or for each point after the burn-in period. We quantified species evenness using Simpson's evenness index (D^{-1}/S), where D^{-1} is the inverse of Simpson's diversity measure (Magurran and McGill 2011). Simpson's evenness is among the most robust evenness measures, being highly independent of S and giving nearly equal weight to rare and abundant species (Smith and Wilson 1996). We quantified species turnover using Whittaker's index (β_w), which quantifies the number of times that species composition changes completely between two samples (Magurran and McGill 2011).

RESULTS

Realistic patterns of biodiversity — Species abundance distributions (SADs) from our IBMs were well-fit by the two most historically successful SAD models, i.e., Poisson lognormal and the log-series (Figure S1). Our IBMs also reproduced empirical diversity-abundance scaling relationships (Figure S2). These results suggest that our IBMs, while designed to test hypotheses related to τ, were realistic enough to reproduce empirical patterns of biodiversity.

Abundance and diversity — Our IBMs produced each of our predicted relationships of abundance, productivity, diversity, and activity (Figure 1). These relationships were robust but also reflected the high degree of variability among models owing to different species compositions, differing degrees of environmental flux, and three orders of magnitude in both flow rate and system size. Contrary to our initial expectations, the modes of these relationships did not occur at the point where dilution rate ($1/\tau$) equaled maximum growth rate (μ_{max}). Instead, the modes occurred at the point where dilution rate equaled the product of persistence-promoting traits divided by the energy-corrected product of growth-promoting traits (Figure 2). This emergent property, which we refer to as the fundamental vital rate (ϕ) represents the energy-adjusted trade-off between growth- and persistence-related vital rates. Average log-transformed values of ϕ (-3.66 ± 0.005) and $1/\tau$ (-3.62 ± 0.008) from our 10,000 IBMs were extremely close; an average difference of 1.06%.

Trait syndromes — Our IBMs also supported our predictions regarding the distribution of traits along a residence-time gradient. Trait variation was greatest at extreme values of τ (Figure 3). At longest τ, individuals with suboptimal traits were able to persist within seed banks comprised of dormant individuals. Otherwise, short τ selected for combinations of traits that promoted rapid growth, reproduction, and the ability to find and use a multitude of resources (Figure 3). In contrast, long τ selected for combinations of traits that promoted persistence (Figures 3). The median range of τ produced the highest degree of resource specialization, a result of increased competition among greater numbers of individuals and species (Figure 3).

DISCUSSION

Residence time (τ) is the average amount of time that particles spend in a system and is often estimated from the ratio of a system's size to its rate of flow or physical turnover. Though often used to manage engineered and experimental systems, τ has gone unrecognized in most ecological studies. However, τ couples resource supply and individual dispersal, equates the physical environment with growth and productivity, and varies over eight orders of magnitude in natural ecosystems, from minutes within some organisms to millennia in some lakes, glaciers, and soils (e.g., Dietrich and Dunne 1978, Bell et al. 2002, Crump *et al*. 2004, Friend *et al*. 2014, Dey *et al*. 2015, Schramski *et al*. 2015). Based on thousands of stochastic and ecologically complex individual-based models (IBMs), we demonstrated that τ can be a primary constraint on the abundance and diversity of taxa and traits within complex and fluctuating ecological systems. Unlike some variables of the physical environment (e.g., area) that underpin theories of biodiversity, we suggest that τ plays multiple roles in shaping ecological systems. We found that τ time coupled the processes of resource supply and individual dispersal in ways that integrated the spatiotemporal environment with life history trade-offs. This equivalence between τ and life history traits marked transition points in abundance, activity, productivity, and diversity.

In idealized systems where passively dispersing organisms occupy well-mixed and nutrient-rich environments, total abundance (N) and productivity should be greatest when maximum growth rate (μ_{max}) equals dilution rate ($1/\tau$). However, our models, which simulated thousands of complex ecological systems, suggest an analogous but more complex relationship. Specifically, N and productivity were greatest when $1/\tau$ equals the ratio of persistence- to energy corrected growth-promoting traits, i.e., ϕ = persistence/(growth – energetic costs). When $\phi > 1/\tau$, growth was low compared to persistence, resulting in the accumulation of dormant individuals. In contrast, when $\phi < 1/\tau$, systems are dominated by individuals seeking to consume and reproduce. Only when $1/\tau$ approaches ϕ is the combination of growth and persistence potentially optimized.

The connections between $1/\tau$ and growth rate allows engineers to manage growth and optimize bioreactors, and also allows scientists to fine tune experimental chemostats, which are commonly used to study ecological and evolutionary dynamics among microbes, rotifers, and phytoplankton (Currie and Kalff 1984, Yoshida et al. 2003, Forde et al. 2004). Understanding the more complex relationship of ϕ to $1/\tau$ should empower ecologists, engineers, and microbiome biologists in similar ways. Specifically, estimates of ϕ should indicate whether a percent change in τ should produce a particular degree of increase or decrease in abundance, productivity, activity, and the diversity of traits and taxa. Consequently, knowledge of ϕ could be crucial to understanding the manifold and interrelated consequences of changing the size and rate of flow or physical turnover within terrestrial, aquatic, and host-related ecosystems.

Biological dynamics, from the scale of a cell to that of the world ocean should be influenced by τ. At the individual-scale, τ has been connected to organismal metabolism, where τ is defined in terms of body mass and the rate at which resource flow through organisms (Schramski et al. 2014). Continuing this analogy, an individual-based ϕ would represent the point where energetically based trade-offs in the life history traits of microbiota are optimized for host metabolism. At the scale of ecological communities, mechanisms of spatial dynamics such as mass effects, rescue effects, and source-sink effects are driven by individual dispersal and are central to the metacommunity paradigm (Leibold et al. 2004). However, dispersal is often linked to resource resupply and recent metacommunity theory suggests that these processes should be studied as potentially coupled (Haegeman and Loreau 2014). At the scale of trophic dynamics, the influence of τ is similar to that of "donor control", where the supply of allochthonous resources constrains consumer growth but where consumers have little-to-no effect on resource resupply (Polis et al. 1997). We suspect that changes in τ may couple or decouple trophic interactions (e.g., predator-prey, host-parasite) by either washing out particular members at short τ or by exhausting endogenous resources at long τ. Consequently, τ is relevant to all levels of the ecological hierarchy, from individual to ecosystems.

In our study, we focused on τ as the primary variable of the physical ecosystem and on ϕ as a multivariate property that capture trade-offs between traits related to persistence and growth. However, both τ and ϕ can be influenced by other variables of the physical ecosystem. For example alterations in hydrological processes (e.g., melting permafrost and variable precipitation) can increase flow rate and volume, which changes τ. Likewise, temperature influences metabolic rates and the breakdown of nutrients via chemical kinetics, hence changing the vital rates and energetic costs in ϕ. Physical factors that influence τ and ϕ also apply to host organisms, where changes in diet and the occurrence of disease can alter τ in ways that decrease host health (Molla et al. 1983). Examples are bacterial overgrowth resulting from an increase in τ driven by Crohn's disease (Castiglioni et al. 2000), and the removal of microbiota and nutrients resulting from a decrease in τ driven by Cholera (Sack et al. 1978). In this way, understanding the influences of τ on abundance, activity, productivity, and the diversity of traits and taxa also begs for an understanding of the factors that drive τ and ϕ.

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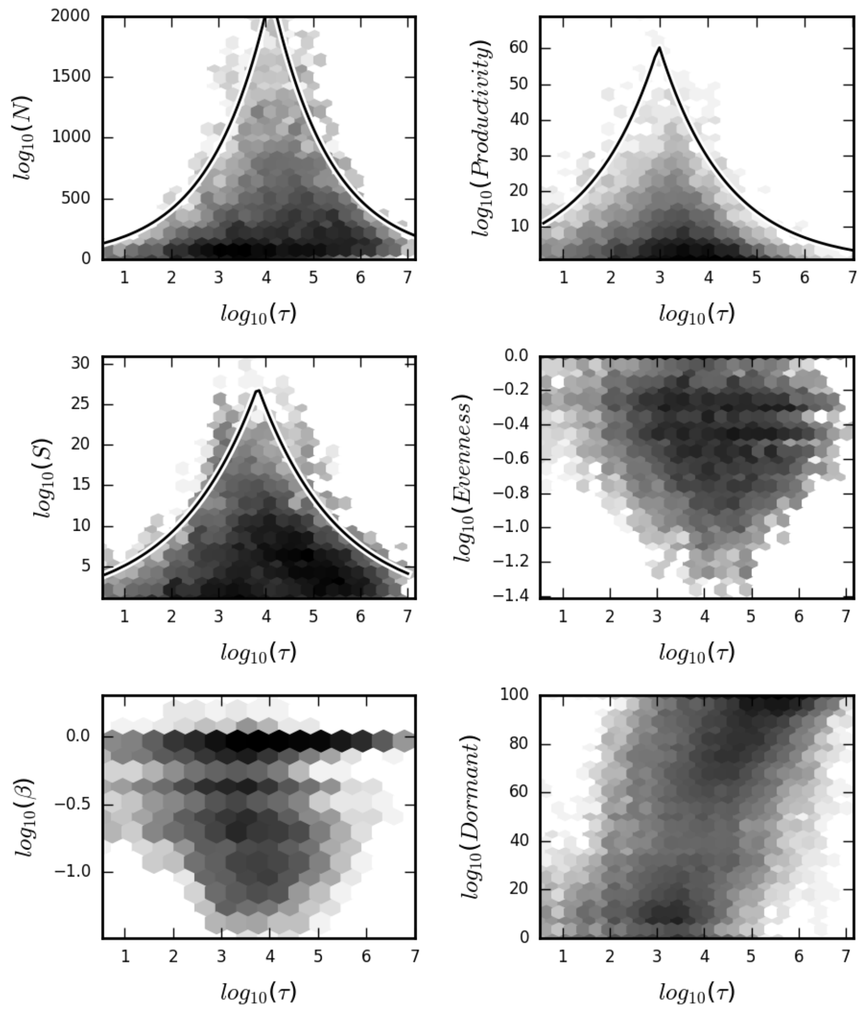
FIGURE CAPTIONS

Figure 1. Gray-scale heat maps for 10,000 IBMs that varied by 4 orders of magnitude in both volume and flow rate reveal how residence time (τ) influenced total abundance (*N*), individual productivity, species richness (*S*), species evenness, species turnover, and the percent of *N* individuals that were metabolically inactive (i.e., dormant). Each colored hexagon represents the average value (e.g., *N*, *S*, etc.) among one or more models. Darker colors representing a greater density of models. The form of each relationship matches our conceptual predictions. Black lines within plots *N*, productivity, and *S* are maximum likelihood fits of the double exponential curve (i.e., Laplace distribution) to the 99% percentile, revealing a strong exponential upper constraint.



406 **Figure 2.** Scatter plots for results of 10,000 IBMs that varied by seven orders of magnitude in residence time (τ). Greatest values of total abundance (*N*), species richness (*S*), and individual

408 productivity coincided with the point where dilution rate ($1/\tau$) and the fundamental vital rate (ϕ) were equal, i.e., where $\phi * \tau = 1$. In contrast, the equivalence between $1/\tau$ and ϕ corresponded to

410 the lowest values of species evenness, species turnover, and the percent of *N* represented by dormant individuals. The fundamental vital rate captures the trade-off between growth and

412 persistence trait syndromes and at $1/\tau = \phi$, represents a highly productive and stable system that is well-adapted to dilution rate, and hence τ.

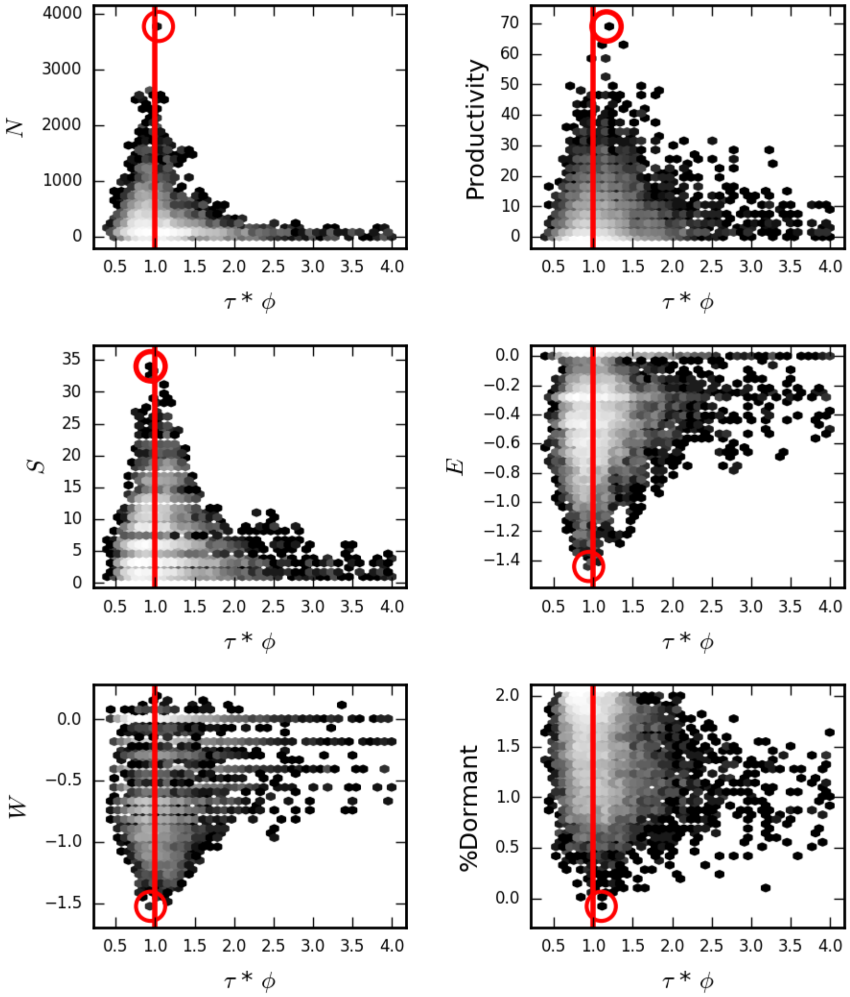


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Figure 3. Heat maps reveal how residence time (τ) influenced traits related to growth (e.g., high rates of growth and active dispersal) and traits related to persistence (e.g., lower maintenance energy, lower chance of randomly resuscitating from dormancy, greater decrease in maintenance energy while in dormancy). Colored heat maps are plotted over gray-scale heat maps. Each pixel in gray-scale heat maps is the average of one or more models, while each pixel in the colored heat map is the average among 50 or more models. Thus, gray-scale heat maps reveal the variation among all 10,000 models, while colored heat maps reveal the central tendency. The relationship of resource specialization was humped-shaped, revealing that highest specialization coincided with the point of highest richness and total abundance (see Figure 1).