Microscale insight into microbial seed banks

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ABSTRACT

Dormancy is a general microbial life-history trait that leads to the emergence of seed banks across diverse ecosystems. While the primary forces driving seed banks include macroscale factors like resource supply, the importance of microscale factors such as individual encounters with resource molecules are often overlooked. Here, we used >10,000 individual based models (IBMs) to simulate energetic, physiological, and ecological processes across combinations of resource-, spatial-, and trophic-complexity. We found that increasing rates of encounter of individual organisms with resource molecules led to greater abundance, greater productivity, and larger seed banks. We also found that the chemical complexity of resource molecules reduced encounter rates, which led to increased variability in the size of seed banks. Encounter-driven 'boom and bust' dynamics also caused resource-rich environments to simultaneously host large seed banks and serve as hotbeds of microbial activity. In conclusion, microscale phenomena appear to be essential for understanding the emergence of seed banks, the energetic basis of microbial life history trade-offs, and variation in the abundance and activity of microbial communities.

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INTRODUCTION

Most microorganisms on Earth live in habitats where they experience energy limitation (Hoehler and Jørgensen, 2013). These microorganisms have evolved an expansive repertoire of traits that allow them to persist under these extreme conditions of resource scarcity (Lever et al., 2015). One strategy that is important for microorganisms experiencing energy limitation is dormancy (Aanderud et al., 2016), i.e., a reversible state of reduced metabolic activity (Jones and Lennon, 2010). Dormant microorganisms make up a seed bank, which is important for maintaining diversity (Lennon and Jones, 2011; Aanderud et al., 2015) and the functioning of ecosystems (Wang et al., 2015). Transitions into and out of dormancy are often driven by the availability of energy and nutrients (Lennon and Jones, 2011), but seed banks still tend to accumulate in otherwise resource-rich habitats. For example, >90% of microbial biomass in soils can be dormant (Alvarez et al., 1998; Lennon and Jones, 2011; Blagodatskaya and Kuzyakov, 2013). These observations suggest that seed bank dynamics may be influenced by factors other than macroscale properties such as the concentration of resources in a given habitat.

In an idealized system with few trophic interactions and where labile substrates are homogenously distributed, the encounter rate between individual microorganisms and resource molecules is governed by relatively simple physical processes such as turbulence and diffusion (Dusenbery, 2009; Rusconi and Stocker, 2015). However, these idealized conditions are rarely met in nature. Instead, microorganisms often live in complex habitats where aggregated particles of many resource types can vary in size, energetic yield, and spatial distribution (e.g., Hernández and Hobbie, 2010; Macalady et al., 2013). Such complexities modify the rate at which microorganisms encounter consumable resource particles (Kiørboe et al., 2002; Andersen et al.,

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2016; Großkopf and Soyer, 2016). Because it is challenging to integrate this fine-scale complexity into empirical studies, microorganisms are often investigated at spatial scales that exceed the scales of their individual interactions (Fierer and Lennon, 2011; Vos et al., 2013). For this reason, microorganisms may be energy- or nutrient-limited even though macroscale measurements would suggest that their habitat is replete with resources (Don et al., 2013; Allison et al., 2014). This phenomenon has led to the hypothesis that there is an advantage to maintaining large, but inactive populations (i.e., seed banks) that are able to maximize the probability of encountering resources that vary in time or space (Vaqué et al., 1989).

Encounter rates between microorganisms and resources are likely driven by interacting dimensions of ecological complexity. For example, microorganisms have a tendency to have highly aggregated spatial distributions in physically structured habitats (Raynaud and Nunan, 2014). Such patterns may reflect the non-random distribution of resources and the capacity of microorganisms to disperse (Mitchell and Kogure, 2006; Smriga et al., 2016). Encounter rates may also be affected by inherent properties of the resource pool, which is often diverse and includes substrates with complex molecular structures (Muscarella et al., 2014; Logue et al., 2016). In some cases, complex resources may only be accessible to specialized taxa that produce extracellular enzymes (Lennon, 2007), which require energy that could otherwise be used for maintenance and growth (Traving et al. 2015). Last, encounters between microorganisms and resources may be influenced by trophic interactions such as competition, predation, and parasitism (e.g., Hibbing et al., 2010). Other trophic interactions are also common, such as the consumption of dead microorganisms (i.e., scavenging) or the uptake of metabolic byproducts released by neighboring cells (i.e., cross-feeding), especially in energy-limited ecosystems

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(Rozen et al., 2009; Pande et al., 2015). Together, these different types of complexity may interact and influence encounter rates in ways that affect microbial seed-bank dynamics.

Studying complex interactions at the microscale is a profound challenge for microbial ecology (Cordero and Datta, 2016). One way to overcome this challenge is with individual-based models (IBMs), which are ideal for exploring how individual-level interactions and microscale properties give rise to higher-order phenomena at the scale of populations to ecosystems (Hellweger et al., 2016). In this study, we developed a stochastic individual-based modeling approach that explicitly simulated physiology, life history, energetics, and the metabolic activity of microorganisms. We used >10,000 IBMs to explore the influence of encounter on the emergence of microbial seed banks. We also asked whether encounters between organisms and resources are primarily driven by macroscale properties of resource concentration and supply, or whether microscale properties of spatial, trophic, and resource complexity might also be powerful factors driving encounter.

METHODS

Overview of individual-based modeling – We examined the influence of encounter rates and resource availability on the abundance, productivity, and activity of simulated microbial communities using over 10,000 probabilistic and information-intensive individual-based models (IBM). We constructed an automated source-code that builds IBMs from random combinations of life history parameters and ecological processes. These IBMs simulated encounters between organisms and resource particles within spatially explicit environments using varying degrees of spatial, resource, and trophic complexity. In the following sections we describe 1) how the models were parameterized with species-specific, resource-specific, and complexity-level

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constraints, 2) how the models simulated energetic costs and encounter-limited growth, 3) how we simulated levels of spatial complexity, resource complexity, and trophic complexity, and 4) our modeling workflow.

Model parameterization – Each IBM was parameterized with random values of constraints that established upper limits on growth dynamics. These constraints included maximum values for specific growth rate, maintenance energy requirements, active dispersal rate, the number of resource particles entering per time step, among others (see Table 1). The values of the parameters in the IBMs were chosen within ranges that produced computationally feasible abundances of organisms and resources within reasonable time limits. Once assembled, each IBM was populated with 10 individuals whose species identities were drawn at random from a uniform distribution. We used multi-species systems as a means to capture trophic complexity, which also allowed us to simulate a breadth of trait parameter-space. Species-specific values for maximum growth rate, active and dormant metabolic maintenance, maximum dispersal rate, environmental optimum, and growth efficiency were chosen at random (Table 1).

Simulating energetic costs and encounter-limited growth – Each IBM tracked and analyzed a large amount of information including but not limited to the identity, cell quota, physiology, location, and traits of each organism. We also tracked the identity, size, diversity, structure, and location of each resource particle (Table 1). As mentioned above, our IBMs were probabilistic, meaning that all ecological processes, such as dispersal, growth, death, reproduction, and consumption occurred via random draws. Likewise, the ability to consume resources and grow

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was directly determined by whether individuals were in simulated physical contact with a consumable resource particle.

Energetic costs to individuals were associated with cellular maintenance, growth, and dispersal. These costs lowered their endogenous resources (i.e., cell quotas) and directly determined the probabilities of reproduction, death, and transitions into dormancy. For example, a starving individual was more likely to enter dormancy or die and was less likely to reproduce than an individual that was replete with resources. Dormant individuals, while having a nonzero cell quota, were prevented from consuming and reproducing, and experienced a species-specific reduction in cellular maintenance costs (See Table 1). Individuals were also simulated in a way that, depending on the model, allowed active movement towards consumable resource particles (i.e., chemotaxis) though at an energetic cost.

Simulating ecological complexity – In addition to explicitly simulating the spatial environment and individual-level changes in organisms and resource particles, we constructed our modeling framework to allow random combinations of various levels of spatial, resource, and trophic complexity. Each IBM was parameterized at random with one of 36 combinations of complexity (4 trophic, 3 resource, 3 spatial) (Figure 1). We then explored how these dimensions of complexity affected encounter rates, along with attributes of community structure such as total number of individuals (i.e., total abundance), the abundance of active individuals, production of individuals per time step (i.e., productivity), and size of the fraction of dormant individuals (i.e. percent dormancy).

Resource complexity: We simulated three levels of resource complexity. The first level represented the simplest condition, wherein only one type of resource molecule was supplied.

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These molecules had no chemical complexity and could be consumed without extracellular enzymatic breakdown (Figure 1). Resource molecules were represented by strings of individual particles (e.g., ‘aaaa’) that could be broken down from each end when encountered by organisms. The number, size, and dispersion of resource molecules were chosen at random (Table 1). We referred to this resource complexity level as a "monoculture". The second level supplied three different types of resources (e.g., ‘aaaa’, ‘bbbb’, ‘cccc’) that could only be used by a specialist consumer (Figure 1). We referred to this as a "polyculture" resource level. The average total number of individual resource particles (e.g., ‘a’, ‘b’, ‘c’) entering the system at a given time and inflow rate was made to be consistent across levels of resource complexity.

The third level of resource complexity simulated the structural complexity of resource molecules, i.e., chemical complexity. We imposed a “lock and key” constraint on chemical complexity by requiring that consumers break down resource molecules at specific locations. For example, a molecule would have a hyphen that simulates a chemical bond separating two groups of resource particles (e.g., ‘aaaa-aaaa’). In order to consume a resource particle, i.e., ‘a’, individuals would need to cleave the ‘aaaa-aaaa’ molecule at the bond and then consume an ‘a’ from one of the two resulting ‘aaaa’ molecules. Because molecules are cleaved at random locations, there is a 1/9 chance of cleaving the ‘aaaa-aaaa’ particle and, likewise, a 1/5 chance of cleaving a ‘bb-bb’ particle, and a 2/8 chance of cleaving a ‘bb-bb-bb’ particle (Figure 1). Therefore, a molecule with a proportionately larger number of bonds requires greater time, and hence, energy to break down.

Spatial complexity: We simulated three levels of spatial complexity. The first level of spatial complexity was a ‘white noise’ model in which the locations of individual organisms and resource molecules changed at each time step in an uncorrelated way. Hence, every organism

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and resource particle had the same chance of moving to any location within the environment at each time step in the model. This white-noise model created a well-mixed environment with no dispersal limitation. In the second level of spatial complexity, resource molecules entered the environment in clusters but did not change locations, resulting in a system that lacked mixing. Individuals then underwent random walks. The average length of the random walk was a species-specific parameter, and larger dispersal distances carried greater energetic costs. The degree of spatial dispersion among incoming resource clusters was chosen at random (Table 1). In the third level of spatial complexity, resource molecules entered in clusters but individuals were capable of sensing resource molecules based on resource density and distance. Through this process, individuals moved toward resources via chemotaxis, a trait that can increase encounter rates between consumers and substrates in spatially structured habitats.

Trophic complexity: We simulated four levels of trophic complexity, with the last being a combination of two others (Figure 1). The first level had only one trophic interaction, which we refer to as a simple "consumer-resource" model. At this level of trophic complexity, all individuals were solely consumers of inflowing resources. The second level of trophic complexity allowed for the consumption of resources contained in dead bacteria (e.g., Rozen et al., 2009), which is a trophic interaction that we referred to as "scavenging". Our third level of trophic complexity simulated a situation in which one group of consumer species generated a metabolic byproduct that could be taken up by a second group of consumer species, which in turn generated a byproduct that served as a resource for a third group of species. This situation was meant to simulate conditions that are characteristic of cross-feeding or syntrophy (Pande et al., 2015). A final level of trophic complexity was characterized by a combination scavenging

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and cross-feeding, which we saw as more ecologically realistic and complex than scavenging or cross-feeding alone.

Modeling workflow – Each model was run to a state of mean reversion, i.e., a point where the total number of individuals (*N*) fluctuates around a given value. This burn-in period was then discarded and the models were run for at least 100 additional generations. We recorded information for each time point past the burn-in period, including, but not limited to *N*; the number of individuals produced (i.e., productivity); Morisita's index of aggregation (Hurlbert, 1990) for individual organisms and resource molecules; and the total number of resource molecules (Table 1). Once a model ran to mean reversion, we recorded its starting parameters as well as mean and variance of abundances, productivity, percent dormancy, organism and resource aggregation, and species-specific parameters related to physiology and life history (Table 1). A detailed version of the standard IBM protocol of (Grimm et al., 2006) is available on a public GitHub repository: https://github.com/LennonLab/Micro-Encounter.

RESULTS AND DISCUSSION

Dormancy allows microorganisms to persist in low-energy environments, yet seed banks emerge in other ecosystems as well (Lennon and Jones, 2011, Blagodatskaya and Kuzyakov, 2013). While it is generally assumed that energy limitation can drive transitions into dormancy, the finer details of what regulates seed bank dynamics are poorly understood and difficult to study, especially under naturally occurring conditions. Our results from thousands of individual-based models suggest that both microscale and macroscale factors are important for the development of seed banks. However, microscale factors (e.g., encounter rate and chemical

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complexity of resource molecules) did a better job of predicting microbial community attributes than macroscale properties of resources (e.g. average concentration). Contrary to expectations, we found that trophic complexity had a minimal effect on microbe-encounter rate, raising the question of whether trophic interactions, as modeled, provided enough energetic benefits to influence abundance, productivity, and the emergence of seed banks.

Importance of resource chemical complexity on encounter – Overall, the chemical complexity of resources had the strongest effect on resource encounter rates across all of our simulations. Specifically, chemical complexity suppressed encounter rates to very low levels across all combinations of spatial and trophic complexity (Figure 2a). Chemical complexity required individuals to cleave resource molecules at specific locations (i.e., "lock and key", Figure 1) in a manner analogous to enzymatic hydrolysis of a polymer like cellulose into glucose monomers. By requiring individuals to cleave resource molecules at specific locations and basing these attempts on random draws, our approach implicitly simulated concentration-dependent kinetics of enzymatic action, and thereby the greater energy lost due to the time required to break larger, more complex molecules. The strong negative influence of chemical complexity on resource encounter provides additional insight into the ways that structurally complex molecules influence the growth and activity of microorganisms within complex microbial habitats such as soil (Schimel and Weintraub, 2003; Allison et al., 2011). Chemical complexity effectively reduced the loss of energy from the resource pool by limiting encounter with consumable resource particles. Similar predictions have been made regarding the "slow release" effects of complex resources on ecosystem dynamics (e.g., Wetzel, 1999).

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Interactions between chemotaxis and resource complexity – Chemotaxis is an important microbial trait that has strong effects on resource encounter rates (e.g., Smriga et al., 2016; Datta et al., 2016). In our simulations, the ability of organisms to use chemotaxis increased encounters in systems characterized by complex resources (Figure 2b). The energetic cost of this directed movement must have been offset by the energy saved in not encountering these complex resource molecules at random, as opposed to the white noise and random walk models. It is generally assumed that there is a trade-off between ecosystem productivity and chemotaxis. For example, chemotaxis is thought to be selected against in oligotrophic environments where searching for sparse chemically-complex resources could be energetically wasteful (Ottemann and Miller, 1997). This view is supported by genomic evidence suggesting that bacteria from copiotrophic environments tend to harbor more motility genes than bacteria from oligotrophic environments (Giovannoni et al., 2005; Lauro et al., 2009). However, unlike some of these studies we observed no relationship of productivity to either per capita or species-specific rates of dispersal in models that simulated chemotaxis (Figure S1). While the lack of a clear relationship may have been due to ways in which we encoded chemotaxis, some studies have suggested that the energetic costs of chemotaxis may also be highly scale-dependent (Stocker, 2012). Though our simulation efforts were directed at exploring the influence of chemotaxis on encounter, and were not focused on exploring chemotaxis-specific trade-offs, IBMs such as those used in this study are ideal for exploring chemotaxis related questions.

Minimal effect of trophic complexity on encounter – We focused on exploring the effects of trophic complexity on resource encounter, even though the theoretical expectations for these interactions at the miscroscale are not well developed. From this we found that trophic

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complexity had a minimal influence on resource encounter rates. We observed no effect of either scavenging or cross-feeding on resource encounter across levels of spatial and resource complexity (Figure 2). For a number of reasons, however, we do not conclude that trophic interactions are unimportant for microbe-resource encounter rate. First, we only considered a few types of trophic interactions. Besides scavenging and cross-feeding, microbial communities engage in a plethora of trophic interactions, which could affect encounter and consumer-resource interaction strength. Second, certain aspects of our model may have dampened the effect of trophic complexity on microbial encounter rates. Specifically, our models included dormancy, which reduced mortality rates. This suggests that by slowing down the turnover rate of the microbial biomass pool, seed banks may also reduce the importance of scavenging. Alternatively, scavenging may not have had an effect on encounter rates because of low microbial growth efficiencies. Per capita death rates should be highest in low resource environments. Under these conditions, energy-limited bacteria may take up microbial necromass, but there is a higher probability that these individuals will allocate energy toward maintenance rather than growth. This situation was highly likely in our models. Last, it is possible that scavenging and cross-feeding did affect resource encounter for a small cross-sections of models, but that this signal was overshadowed when all levels of spatial and resource complexity were examined together.

Microscale vs. macroscale drivers of microbial community dynamics – Rates of encounter between individual organisms and resource molecules had strong effects on the abundance, productivity, and activity of the microbial community. Greater encounters between organisms and resource particles led to increased production of new individuals and increases in the

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abundances of the entire community and its metabolically active fraction (Figure 3). While encounter rates were positively correlated with resource concentration and the rate of resource supply, encounter had a much stronger effect on productivity and abundance than either of these macroscale resource properties (Figure 4). This result reflects that encounter is not simply a consequence of resource concentration and supply, and that controls on encounter, such as chemical complexity and energetic trade-offs can be independent of macroscale resource properties. In considering the microscale heterogeneity of aquatic, terrestrial, and host-associated microbial systems, there are likely entire suites of microscale properties and microscale-level dynamics that a traditional macroscale approach has missed. Modeling provides a powerful and convenient starting point for understanding the driving influence of microscale properties. For example, animations of our IBMs suggest that "boom and bust" dynamics within spatially structured environments lead to the emergence of such seed banks and high temporal variability in abundance and productivity (see Supplemental Movie 1). These dynamics occurred in resource-rich and resource-poor systems, under all level of trophic and resource complexity.

Emergence of seed banks via micro- & macroscale interactions – The emergence of microbial seed banks appears to be driven by strong interactions between microscale and macroscale properties. At the microscale, we observed that increased encounter rates led to larger dormant fractions (Figure 3). However, large seed banks still emerged at all levels of encounter. Closer examination revealed that this relationship was partly due to interactions with total resource concentration, a macroscale property (Figures 5). Specifically, models that simulated chemical complexity resulted in characteristically low rates of encounter and highly variable seed banks (Figures 3-5a). This variability was largely due to the influence of resource concentration, where

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a greater concentration of resources led to smaller seed banks (Figure 5b). This interaction between the microscale property of encounter and the macroscale property of resource concentration was nearly absent from models that did not simulate chemical complexity.

CONCLUSION

Our study supports the general importance of microscale factors in driving ecological dynamics and the emergence of seed banks within microbial systems. Resource encounter can drive strong increases in abundance and productivity across ecologically complex systems. At the same time, the chemical complexity of resources greatly influences encounter rates. By considering the interaction of microscale and macroscale factors, our study provides insight into how otherwise resource-rich environments can host large microbial seed banks and high productivity.

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TABLE 1 | Parameter values for individual based models (IBMs). Top: Values for input
424 parameters were randomly chosen within ranges that produced computationally feasible abundances of organisms and resource particles (up to ~10^4) within reasonable simulation times
426 (up to several minutes per IBM). Mean and variances for recorded data were calculated across each time point after IBMs reached a state of mean reversion in community abundance. Bottom:
428 Recorded data from each IBM.

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Input Parameter	Range of values (per time step)
Resource molecules flowing in per time step	0 to 90
Maximum growth rate	10% to 50%
Maximum maintenance cost for active individuals	1% to 5%
Maximum dispersal rate	1% to 10%
Maximum resuscitation rate	0.1% to 1%
Maximum maintenance-reduction factor, when transitioning to dormancy	20% to 100%
Incoming resource aggregation, i.e., standard deviation of a Normal distribution	0.1 to 0.4

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Recorded data
Growth rate: specific and per capita
Metabolic maintenance: specific and per capita
Dispersal rate: specific and per capita
Aggregation of individuals and resources (Morisita's index)
Production of individuals
Death among individuals
Total individual abundance
Size of the dormant fraction, i.e., % dormancy
Resource concentration
Total resources
Number of encounters with consumable resource particles

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FIGURE CAPTIONS

FIGURE 1 | Conceptual diagram depicting dimensions of complexity simulated using individual based models (IBM) We modeled spatial complexity (top row) in the microbial habitat by simulating the distribution of resources clusters (open circles) and the movement of microorganisms (solid symbols). In the "white noise" level, the location of individual organisms and resource molecules changed in an uncorrelated way at each time step. Under these conditions, there was no dispersal limitation. In contrast, resources entered as clusters leading to spatial aggregation in the "random walk" and "chemotaxis" levels of spatial complexity. Microorganisms could encounter resource clusters via a random walk or by sensing and moving towards resources (chemotaxis), albeit with associated energetic costs. We modeled resource complexity (middle) row in three different ways. The first level of resource complexity assumed homogeneity of the resource pool ("monoculture"), while the second level supplied different resources ("polycultures") that could only be consumed by specialist microorganisms. We also simulated chemical complexity by imposing a "lock and key" constraint, such that microorganisms could only cleave a resource particle (open colored symbol) from a molecule in a cluster at a specific location (depicted by the double bond), which came at an energetic cost. Finally, we modeled trophic complexity (bottom row) by simulating different types of energy transfer among resource pools and consumers. The first level of trophic complexity assumed simple "consumer-resource" dynamics where microorganisms only consumed inflowing resources (non-dashed arrow). In the second level of complexity, the biomass of dead cells was returned to the resource pool (dashed arrow), which could be subsequently consumed by viable bacteria in a process that was intended to simulate "scavenging". Last, we simulated "cross-

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feeding" where one group of consumer species generated a metabolic byproduct that could be taken up by a second group of consumer species (dashed arrow), which in turn generated a byproduct that served as a resource for a third group of species.

FIGURE 2 | Influence of resource complexity (left), spatial complexity (center), and trophic complexity (right) on frequencies of encounter between organisms and resource particles. A: Across all 11,000 models, we found that chemical complexity substantial reduced the number of microbe-resource encounters. B: When we subsetted our simulated data to only include models with chemical complexity, we found that chemotaxis substantially increased microbe-resource encounter rates. Trophic complexity as modeled, had little-to-no influence on encounter rates.

FIGURE 3 | Encounter rate affected microbial community properties including productivity, abundance, and seed-bank size. In each plot, blue heat maps represent the results of models that simulated chemical complexity, while red heat maps represent results of models that did not. Greater heat (i.e., areas within heat maps that have lighter colors) corresponds to a greater number of models. Models with chemical complexity have characteristically lower encounter rates but do not altogether change relationships of encounter to dormancy, abundance, and productivity. The relationship of % dormancy to encounter is characterized by a strong lower constraint, where at high rates of encounter % dormancy is constrained to be high and results in the emergence of a large seed bank.

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FIGURE 4 | Microscale factors are stronger drivers than macroscale factors. Encounter rate was more strongly related to abundance and productivity than total resources and resource inflow. Greater heat (i.e., areas within heat maps that have lighter colors) corresponds to a greater number of models. While greater encounters generally led to a larger seed bank (i.e., greater % dormancy), both total resources and resource inflow generally led to lower % dormancy. The variability in relationships of % dormancy is largely due to models that included chemical complexity.

FIGURE 5 | Three dimensional heat maps reveal interactions between total resources, encounter rates, and the seed bank (% dormant). Left: The triangular relationship of % dormant to encounter, same as in Figure 3, was driven by models that included chemical complexity (blue-green heat map). Right: This relationship was in turn driven or modified by the concentration of resources in the environment. Among models that included chemical complexity, greater resource concentration led to lower % dormancy; effects which were not pronounced for other levels of chemical complexity.

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Figure 1

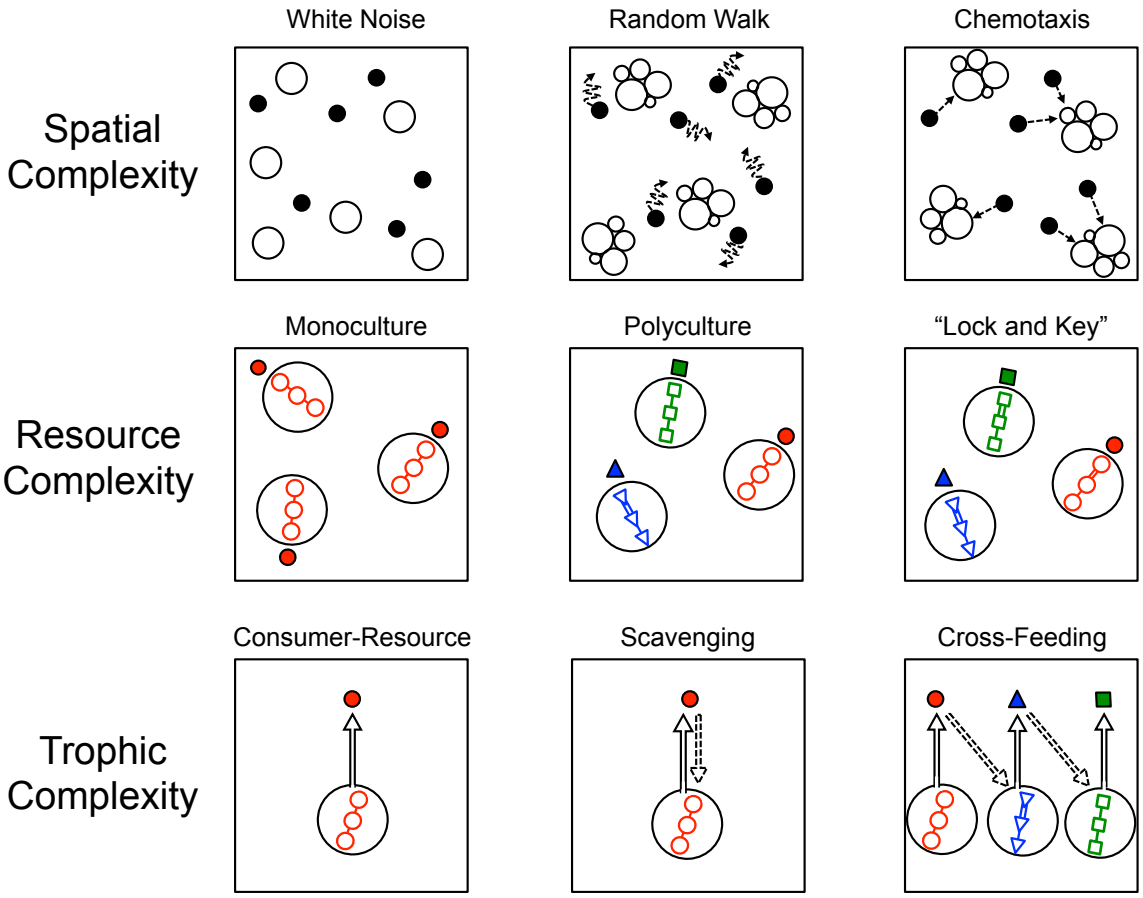

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Figure 2

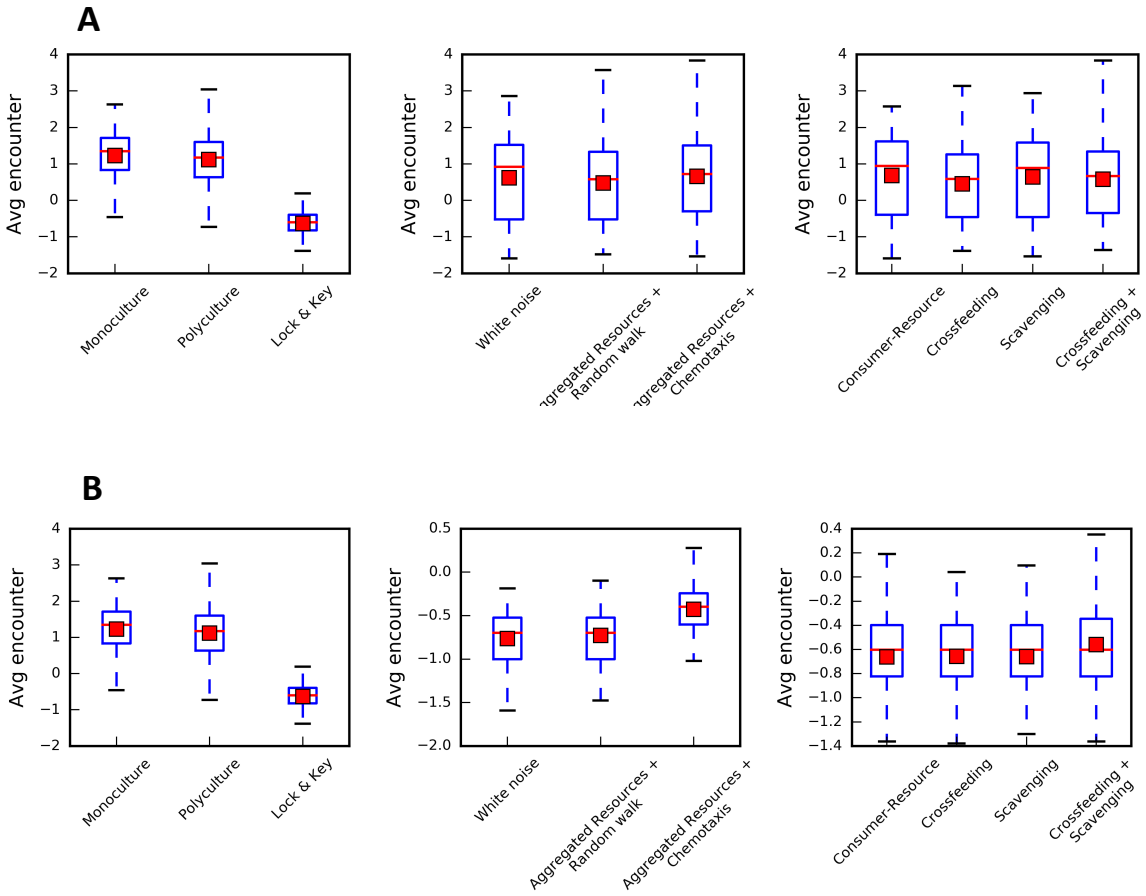

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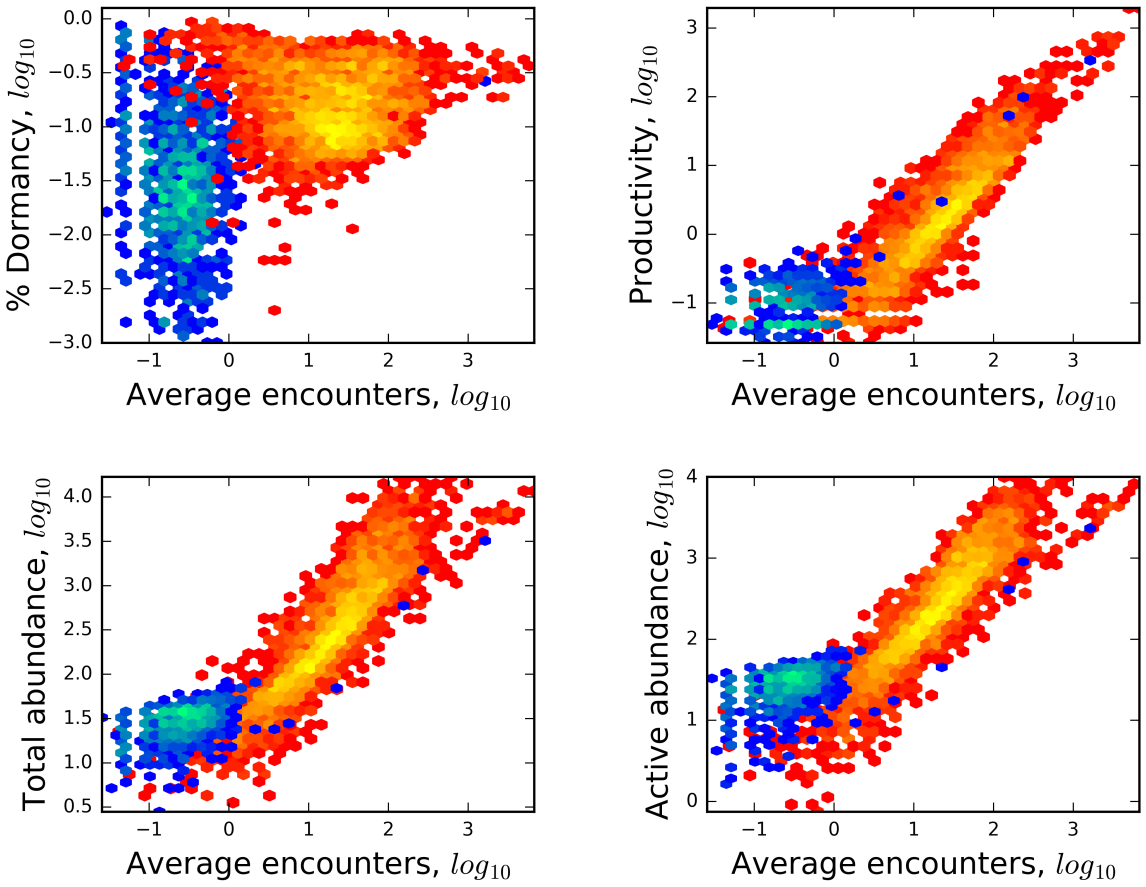
Figure 3



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590 Figure 4

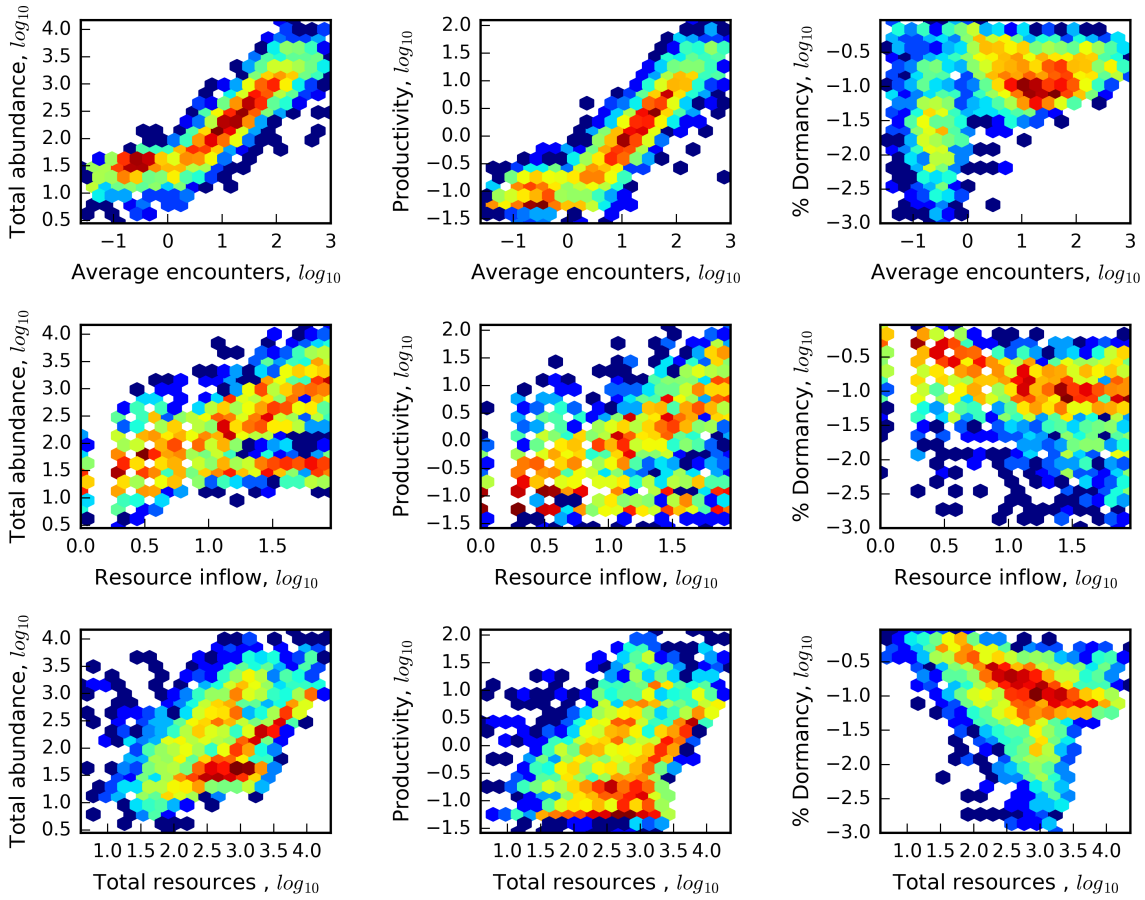

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Figure 5

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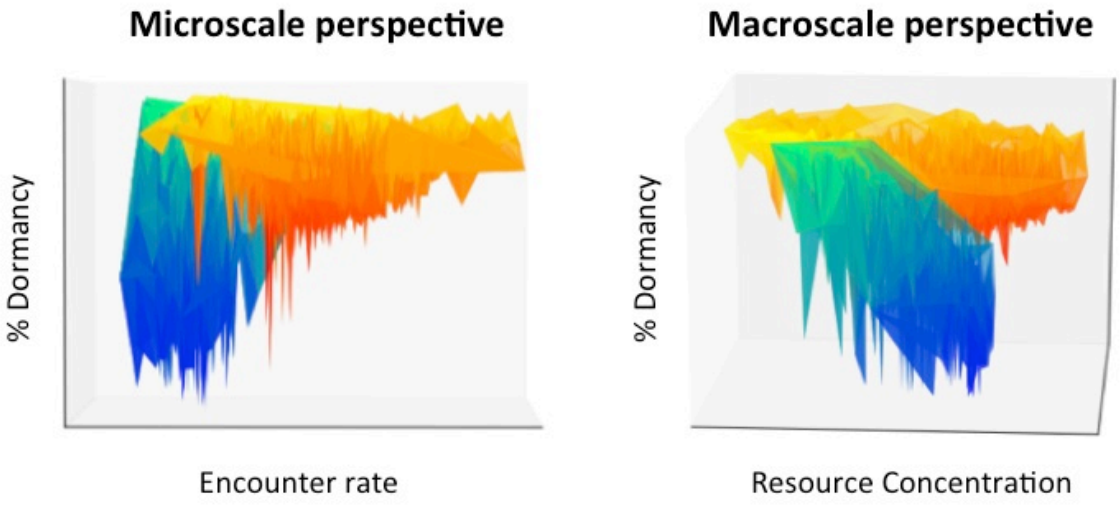

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