

Dormancy contributes to the maintenance of microbial diversity

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Dormancy is a bet-hedging strategy used by a variety of organisms to overcome unfavorable environmental conditions. By entering a reversible state of low metabolic activity, dormant individuals become members of a seed bank, which can determine community dynamics in future generations. Although microbiologists have documented dormancy in both clinical and natural settings, the importance of seed banks for the diversity and functioning of microbial communities remains untested. Here, we develop a theoretical model demonstrating that microbial communities are structured by environmental cues that trigger dormancy. A molecular survey of lake ecosystems revealed that dormancy plays a more important role in shaping bacterial communities than eukaryotic microbial communities. The proportion of dormant bacteria was relatively low in productive ecosystems but accounted for up to 40% of taxon richness in nutrient-poor systems. Our simulations and empirical data suggest that regional environmental cues and dormancy synchronize the composition of active communities across the landscape while decoupling active microbes from the total community at local scales. Furthermore, we observed that rare bacterial taxa were disproportionately active relative to common bacterial taxa, suggesting that microbial rank-abundance curves are more dynamic than previously considered. We propose that repeated transitions to and from the seed bank may help maintain the high levels of microbial biodiversity that are observed in nearly all ecosystems.

biodiversity | ecosystem function | microbial ecology | modeling | seed bank

The biodiversity of microbial communities has important implications for the stability and functioning of managed and natural ecosystems (1–3). Therefore, it is important for ecologists to develop a theoretical basis for the factors that generate and maintain microbial diversity (4). Growing evidence suggests that biogeographic processes, such as local adaptation and patch-scale species sorting, can drive spatial patterns of microbial diversity (5). However, microbial communities are also structured by species' responses to environmental variables that fluctuate through time (6, 7). Dormancy is one trait that allows species to contend with temporal variability of environmental conditions. This bet-hedging strategy allows dormant individuals to become members of a seed bank, which can contribute to the diversity and dynamics of communities in future generations. Seed banks have been shown to structure plant and animal communities, and help explain patterns of succession and responses to perturbations (8, 9). Very little is known, however, about whether and to what degree dormancy influences the biodiversity of microbial communities.

Dormancy is a common life history strategy among microbes. Many microorganisms are capable of resisting stressors such as temperature, desiccation, and antibiotics by entering resting states or by forming spores (10–12). Because of its implications for disease, the molecular and cellular underpinning of dormancy is fairly well known for a few clinically important strains of bacteria (13). Microbial dormancy is also thought to be important in natural systems. A sometimes-large but variable fraction

(20–80%) of the bacteria recovered from environmental samples appear to be metabolically inactive (14). Although some of these cells are dead or moribund, other populations can be resuscitated with resource supplements (15). Despite evidence that dormancy is widespread, we have little theoretical expectation as to how it influences the structure of natural, complex microbial communities.

Dormancy is regulated by the interpretation of environmental cues by microbial populations. Variation in these cues may be attributed to natural or anthropogenic processes, and may be experienced at local, regional, or even global scales. Regional drivers such as air temperature or photoperiod are common dormancy cues for many plant and animal populations (16, 17). Local cues, such as resource availability or stochastic perturbations (e.g., drought and fire), also dictate when organisms enter and exit periods of reduced metabolic activity (18). As with macroorganisms, dormancy in microbes appears to be controlled by environmental cues, such as crowding, oxygen or temperature stress, and resource limitation (13). Despite the enormous complexity surrounding the interpretation of environmental cues (19), we argue that a simple theoretical framework is necessary for generating predictions about the effects of dormancy on the diversity and composition of microbial communities.

Here, we combine mathematical modeling and a molecular survey to test predictions about the role of dormancy in maintaining microbial diversity. Our model is derived from seed bank models in plant ecology (20, 21) but captures important life history features of microorganisms (*Modeling Microbial Dormancy*). To evaluate patterns observed in our model, we conducted a spatial survey of the active and total fractions of bacterial and eukaryotic microbial communities from a set of temperate lake ecosystems. Three major questions guided the development of our model and analyses of survey data: (i) To what extent does dormancy contribute to the taxon richness of microbial communities? (ii) How does dormancy shape local and regional patterns of microbial community composition? (iii) Is the “rare biosphere” (22) predominantly comprised of dormant bacterial taxa?

Modeling Microbial Dormancy

Mathematical formulation of dormancy in a variable environment has existed for decades (20, 21). Our model (Fig. 1 and Eqs. 1–3) is partially based on this theory, but we implemented the following modifications so that we could generate predictions for microbial systems: (i) we allowed for bidirectional and

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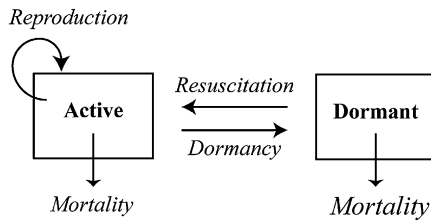


Fig. 1. Summary of multispecies microbial dormancy model structure. A portion of each taxon can occupy an active and dormant state. Active portions of populations have logistic growth and experience density-dependent mortality. Dormant individuals are inactive and can therefore not reproduce, but are subject to mortality. Transition between the active and dormant states is controlled by environmental cues at local and regional scales.

repeatable transition between active and dormant states; (ii) unlike annual plant models, we did not require passage through the dormant state for microbial reproduction; and (iii) rather than focusing exclusively on the dormant state (i.e., seeds), we explicitly simulated both the active and dormant fractions of the microbial community. By considering both active and dormant fractions of each population, we were able to make direct comparisons to our empirical measurements of active and total (active + dormant) community composition (23, 24). Although some of these components have been considered for an individual population (25), here we have developed a multispecies, microbial dormancy model.

Our model represented a landscape with spatially distributed patches (x), each with a unique position along an arbitrary environmental gradient (E_L). Within a patch, individuals from each microbial species (j) could occupy an active (A) or dormant (D) state. Change in the density of active and dormant individuals of each population were described as follows:

$$\frac{dA_{jx}}{dt} = A_{jx} \left[r \left(1 - \frac{A_{jx}}{K} \right) - (1 - R_{jx}) - m_A \right] + D_{jx} R_{jx}, \quad [1]$$

$$\frac{dD_{jx}}{dt} = A_{jx} (1 - R_{jx}) - D_{jx} (R_{jx} + m_D), \quad [2]$$

where r is the population growth rate, K is the carrying capacity, m_A is the mortality rate of microbes in the active state, and m_D is the mortality of microbes in the dormant state. Resuscitation from dormancy (R_{jx}) was described as follows:

$$R_{jx} = R_{\max} e^{-\left(\frac{E_{L,jx}^* - E_{L,x}}{\text{tol}} \right)^2 (1 - W) - \left(\frac{E_{R,j}^* - E_R}{\text{tol}} \right)^2 W} \quad [3]$$

For simplicity, we held all parameters except the environmental optima ($E_{L,jx}^*$ and $E_{R,j}^*$) constant across species (Table 1).

Table 1. Definition of parameter values used in our multispecies microbial dormancy model and values used for analyses

Parameter	Definition	Value
r	Population growth rate	0.75
K	Carrying capacity	0.5
m_A	Mortality of active individuals	0.2
m_D	Mortality of dormant individuals	(0–1)
tol	Environmental tolerance	0.2
R_{\max}	Maximum resuscitation rate	0.95
W	Weighting of local vs. regional environmental cues	(0–1)
$E_{L,jx}^*$	Local optimum for species j in patch x	(0–1)
$E_{R,j}^*$	Regional optimum for species j	(0–1)

Therefore, the proportion of dormant individuals that moved into the active state during a given time step (R_{jx}) was based on the maximum resuscitation rate (R_{\max}) and the local and regional environmental optima for a given species j . To minimize the number of parameters and environmental variables, we assumed that cues for entrance into and resuscitation from a dormant state were negatively correlated and used $1 - R_{jx}$ as the proportion of active individuals entering dormancy.

To assess the influence of dormancy on model community structure, we varied the rate of mortality for dormant individuals. When $m_D = 0$, no dormant individuals were removed and all species persisted. In contrast, when $m_D = 1$, dormancy was effectively absent from the model, because all dormant individuals died. Because dormancy is regulated by environmental cues, we manipulated the relative strength of regional- and local-scale environmental variability with a weighting term, W . Here, we considered the local-scale environment as the physical, chemical, and biological conditions that determined the success of a species in a given patch. The regional environment was conceptualized as a seasonal variable (e.g., air temperature) that could synchronize community dynamics at a broad spatial scale. When $W = 1$, the regional cue exclusively regulated transitions between active (A) and dormant (D) states; when $W = 0$, only the local environment influenced dormancy dynamics. To characterize the response of microbial richness and composition to changes in dormancy and the scale of environmental variability, we solved Eqs. 1 and 2 at equilibrium for each population across a range of values for W and m_D (see *SI Text* and *Fig. S1* for equilibrium solutions and examples of model output).

Results and Discussion

Our multispecies model indicated that dormancy and environmental cues interact to influence the biodiversity of microbial communities. The ability to enter and successfully emerge from dormancy had a strong, positive influence on model species richness (Fig. 2). In addition, dormancy and environmental cues affected the coupling of active and total community composition. Specifically, the combination of dormancy and strong regional cues synchronized the composition of active model communities among patches (Fig. 3A) in a manner similar to the Moran effect (26). In contrast, a lack of dormancy resulted in tight coupling

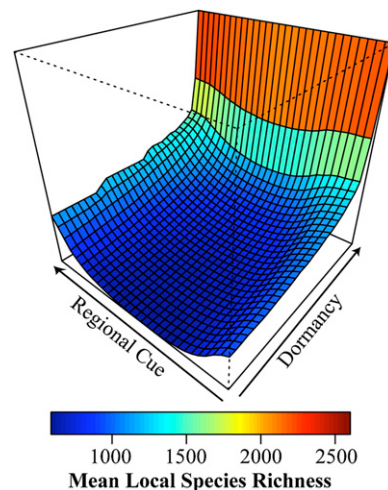


Fig. 2. Mean local richness (number of species) of model equilibrium solutions across a range of values for the strength of dormancy, manipulated using the parameter for mortality of dormant individuals (m_D), and strength of regional environmental cues, manipulated by a weighting parameter (W).

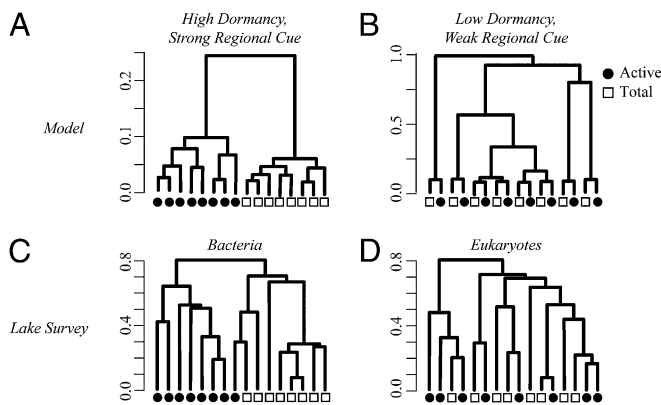


Fig. 3. UPGMA dendrograms depicting the degree of coupling between active and total (active + dormant) composition in simulated and lake microbial communities. By varying the mortality rate of dormant individuals (m_D) and the relative strength of regional and local environmental cues (W), we explored how dormancy and regional cues influenced coupling or decoupling of active and total communities. Vertical scales indicate Bray-Curtis distance. (A) Simulated communities with low mortality of dormant individuals ($m_D = 0.1$) and strong regional environmental cues ($W = 0.95$) resulted in decoupling of active and total communities. (B) In contrast, simulated communities with low persistence of dormant individuals ($m_D = 0.9$) and weak regional control ($W = 0.05$) resulted in coupling between active and total communities. (C) The composition of active (rRNA) and total (rDNA) bacterial communities in eight lakes was decoupled. (D) In contrast, the composition of active and total eukaryotic communities was more strongly coupled.

between active and total communities within each model patch (Fig. 3B).

To test our model predictions, we determined how dormancy influenced the structure of microbial communities in eight freshwater lakes within a 3,000-km² region of southwest Michigan, United States. We assessed the composition of bacterial and eukaryotic microbial communities in the mixed surface layers of our lakes using molecular-based community fingerprinting. Community fingerprinting is commonly applied in environmental microbiology and has been widely used with ribosomal DNA (rDNA), a phylogenetically informative molecule that is stable and relatively easy to isolate. However, rDNA-based techniques only identify populations that are potentially active. Because growing cells require ribosomes for protein synthesis, ribosomal RNA (rRNA) can be used to characterize the active portion of communities (27). The simultaneous characterization of microbial communities by rRNA and rDNA fingerprinting is analogous to surveys of plant communities and their associated seed banks (28). For example, rDNA-based composition of microbial communities is akin to plant seeds, which represent propagules from past and current members of an aboveground community. In contrast, rRNA-based composition of microbial communities is equivalent to the active, aboveground members of a plant community that directly contribute to current community function.

We observed strong domain-level contrasts in the coupling of active and total community composition in our lake survey. There was tight correspondence between active and total eukaryotic composition within a given lake [multiple response permutation procedure (MRPP), $P > 0.25$; Fig. 3D], suggesting that when a population was present, it was active. Similar coupling occurred in model communities with low dormancy, regardless of the strength of regional cues (Fig. 3B). In contrast, bacterial composition was significantly influenced by the molecule used in our fingerprinting (i.e., rDNA vs. rRNA, MRPP, $P < 0.001$), suggesting that active taxa were only a subset of the total community in a given lake (Fig. 3C). We observed such decou-

pling in our model when there was high dormancy and strong regional cues (Fig. 3A).

The contribution of dormant taxa to community richness was dependent on microbial domain (i.e., bacteria vs. eukaryotes) and local-scale environment cues (Fig. 4; indicator variable multiple regression, $R^2 = 0.85$, $n = 16$, $P < 0.001$). Dormant taxa made up a constant proportion (12%) of eukaryotic microbial communities regardless of local environmental conditions. In contrast, total phosphorus (TP) concentrations influenced the proportion of bacterial community richness that was dormant. In high-TP lakes, bacterial dormancy was comparable to eukaryotic microbial dormancy, but in low-TP lakes, nearly 40% of the bacterial taxa were dormant (Fig. 4). It is well documented that phosphorus is a strong driver of aquatic microbial productivity (29), and our results are consistent with observations indicating that bacterial dormancy may be more prevalent in resource-limited ecosystems (30). Moreover, our results agree with reports that have identified strong links between resource availability and dormancy in zooplankton, insects, and mammals (31–33).

Although many eukaryotic microbes are capable of forming resting stages (34, 35), differential sinking rates may potentially explain the domain-level contrast in the apparent role that dormancy plays in structuring microbial community composition. On average, sinking velocities are 350 times greater for phytoplankton than they are for bacteria (34, 36). Moreover, inactive phytoplankton cells sink 50–1,000% faster than active individuals within the same population (34). Thus, owing to differences in body size, dormancy may be a more advantageous life history strategy for bacteria than for eukaryotic microbes, at least in aquatic ecosystems. These results suggest that there may be important differences in the factors that generate and maintain bacterial versus eukaryotic microbial diversity.

A growing number of studies have demonstrated that the biodiversity of microbial communities is primarily comprised of rare species (22, 37), but the metabolic status of these taxa is unclear. Theory suggests that rare species are prone to extinction due to stochastic events or biological processes that create positive density dependence (38). Alternatively, rare taxa may represent a reservoir of genetic diversity that actively responds to environmental change (22, 39). To test these contrasting hypotheses, we used tag-encoded pyrosequencing to deeply sample the rDNA and rRNA from bacteria residing in two of our lakes. We classified each taxon as active or inactive based on its recovery in rDNA and rRNA samples. We scored a taxon as

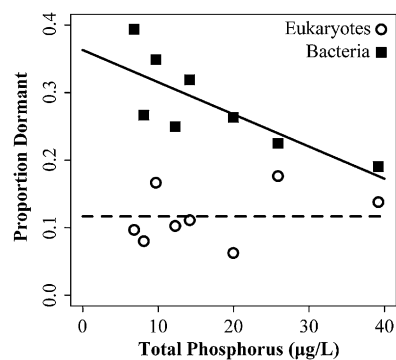


Fig. 4. The contribution of dormant taxa to microbial richness along a total phosphorus (TP) gradient in our lake survey. Dormant taxa were identified from terminal restriction fragments that were recovered in rDNA fingerprint profiles but not in rRNA fingerprint profiles. The proportion of dormant bacterial taxa decreased with increasing TP (a proxy for ecosystem productivity), but this was not the case for eukaryotic microbes. Together, the proportion of dormant taxa (D_T) could be predicted for different microbial domains (M ; 1 for bacteria, 0 for eukaryotes) with the following multiple regression model: $D_T = 0.12 + 0.25M - 0.005(M)(TP)$ ($R^2 = 0.85$, $n = 16$, $P < 0.001$).

active if the rRNA relative recovery was greater than its recovery from rDNA. Conversely, a taxon was scored as inactive if the relative recovery of rRNA was less than the relative recovery of rDNA. In both lakes, there was an inverse relationship between the probability of a taxon being active and its rDNA rank (logistic regression, $P < 0.001$; Fig. 5), indicating that, on average, rare taxa are more likely to be active than common bacterial taxa. These results support the idea that microbial rank abundance curves may be highly dynamic (39, 40). For example, if we assume no change in environmental conditions, populations that were scored as active are likely to increase in abundance and move to the left on the rDNA rank abundance curve, whereas the opposite would be true for inactive populations. In addition, we observed strong taxonomic contrasts in the distribution of active and inactive operational taxonomic units (OTUs). Specifically, 48% of Bacteroidetes OTUs and 69% of the α -Proteobacteria OTUs were scored as active, whereas almost all of the Actinobacteria and Acidobacteria OTUs were scored as inactive (89% and 93%, respectively). Our findings provide evidence that many rare bacterial taxa are active and thus have the potential to increase when rare, which is an important criterion when evaluating species coexistence and the assembly of food webs (41). Moreover, as has been found with macroorganisms (42), rare taxa may have important implications for the contribution of microbial diversity to ecosystem functioning.

The identification and enumeration of dormant populations in complex communities is of great interest to microbial ecologists but is also challenged by some conceptual and technical difficulties. For example, microbial dormancy is commonly identified via morphological features such as endospores, cysts, or conidia. However, microbes can enter reversible states of reduced metabolic activity without investment in specialized cellular struc-

tures (12, 43). Persister cells, which are capable of surviving antibiotic treatment without resistance mutations, represent one example of this form of dormancy (13). Here, we define dormancy based on reduced metabolic activity inferred from the detection of a population in the total community (measured using rDNA) and an inability to detect the population among the active members of the community (measured using rRNA). It is unlikely that our approach perfectly discriminated between dormant populations and extremely slow-growing populations (44, 45). However, there is some evidence that dormant and slow-growing populations can respond similarly to favorable environmental change (45, 46). Although there is potential for refined definitions and improved measurements, we view our approach as a reasonable approximation for quantifying the contribution of dormancy to microbial diversity.

Our initial theoretical exploration of microbial dormancy portrayed a simplified scenario where all populations were equally likely to enter and emerge from a dormant state. Despite being a taxonomically widespread phenomenon (13, 34), it seems unlikely that all microbes are capable of using dormancy as an adaptive life history strategy. In addition, the cues that trigger entrance into and emergence from a resting state are likely to vary among populations. This interpopulation heterogeneity represents a level of complexity beyond our current mathematical formulation of microbial dormancy. Under more realistic scenarios, we expect that populations with the capacity to become dormant would experience a higher probability of persisting through inhospitable periods and thus make a larger contribution to microbial richness.

Of course, the ability to maintain a dormant state is only useful if more favorable environmental conditions return before intracellular reserves are depleted or the dormant cells fall victim to some other source of mortality. If the return interval of optimal conditions is relatively short, investment into dormancy may prove unnecessary and costly (20). However, populations with the capacity to enter a dormant state would likely realize benefits in systems that experience gradual or predictable environmental change (47). The optimization of reproductive behavior in the face of environmental variation has been explored for plant and insect populations (20, 21) and the findings are likely to apply to microbial communities, as well.

Dormancy has the potential to explain numerous ecological patterns observed in microbial systems over the past decade, including repeated seasonal succession (6), the rare microbial biosphere (22), and the apparent resilience to disturbance of microbially mediated processes (48). In addition, the dormancy-driven decoupling of active and total composition observed in our study raises the question of whether we must consider the use of rRNA-based approaches to link microbial community structure and function. However, dormancy does not appear to be equally important for all microbes. Our findings suggest that ecosystem features (e.g., productivity) or species traits (e.g., body size) may explain the relative importance of dormancy in microbial communities. Together, our findings provide evidence that dormancy is likely to play a key role in the maintenance of microbial diversity, and our theoretical framework paves the way for microbial dormancy research in a variety of natural and managed systems.

Materials and Methods

Limnological Methods. We sampled from the surface mixed-layer of eight lakes in southwest Michigan, United States, between 8 and 12 September 2008. The discrete boundaries of lakes create spatially distinct patches with a range of local environmental conditions (Table S1). We sampled all lakes over a short time period (<1 week) to help ensure that the microbial communities experienced similar regional cues (e.g., photoperiod and weather). Water temperature and pH were measured on-site with a Hydrolab Quanta probe (Hach Environmental). TP was measured by persulfate oxidation of organic

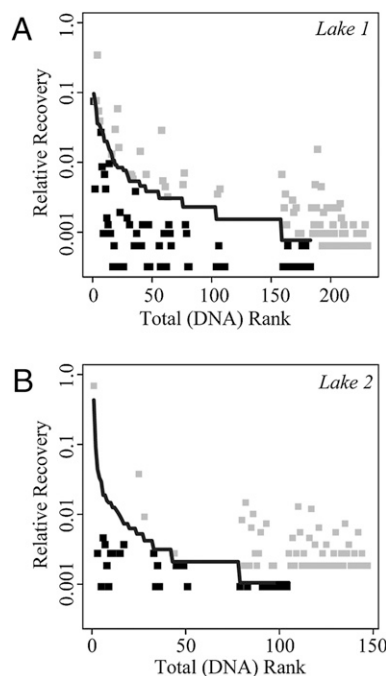


Fig. 5. Rank-abundance curves for the total (rDNA-based) community of bacteria from two lakes. Points indicate the relative recovery of the corresponding OTUs (97% sequence identity) in the active community (rRNA-based). Gray squares indicate OTUs that were scored as disproportionately active, and black squares indicate OTUs that were scored as disproportionately inactive. Logistic regression revealed that with each increasing rank, the probability of a taxon being active increased by 6% and 2% for Lake 1 and Lake 2, respectively.

phosphorus to phosphate followed by colorimetric analysis of phosphate (49). Total nitrogen (TN) and dissolved organic carbon (DOC) were measured by oxidation and subsequent chemiluminescence or nondispersive infrared (NDIR) detection, respectively, using a Shimadzu TOC-V equipped with a TNM-1 unit. For measurement of chlorophyll *a* concentrations, plankton were captured on 0.7- μm glass fiber filters and frozen at -20°C . Chlorophyll *a* was extracted from filters in 95% ethanol overnight at 4°C and quantified via fluorometry (50). Finally, plankton from 250 mL of lake water were captured onto 0.2- μm filters and stored at -80°C until processing for molecular-based microbial composition.

Microbial Community Composition. We extracted DNA and RNA from cryo-stored filters using commercially available kits and protocols (DNA FastPrep purification kit from BIO 101; RNeasy isolation kit from Qiagen). We synthesized cDNA from RNA using random hexamer primers and a SuperScript III first-strand synthesis kit (Invitrogen). Terminal restriction fragment length polymorphism (T-RFLP) was conducted on both DNA and cDNA using general 16S [8F and 533R (51)] and 18S [Euk1Af and Euk516r (52)] rRNA primers. Fragment analysis was conducted at the Research Technology Support Facility at Michigan State University. In addition, the DNA and cDNA from two lakes were used as template in PCR reactions with barcoded primers targeting the V4 region of bacterial 16S rDNA. PCR products were sequenced using an Illumina Genome Analyzer II at the Research Technology Support Facility. Both T-RFLP profiles and tag-encode pyrosequences are available from the authors upon request.

16S rDNA and rRNA tag sequences were assigned to operational taxonomic units (97% sequence identity) using RDP 10 (53). To avoid interpreting random sequencing errors as rare community members, we only considered OTUs that possessed two or more tag sequences. This resulted in 231 and 147 observed OTUs from Lake 1 and Lake 2, respectively. After scoring each tag sequence-based OTU as active or inactive based on the relative recovery of sequences from rRNA and rDNA, we tested whether rDNA-based rank (a proxy for abundance) was a significant predictor of activity using logistic regression. Logistic regression was implemented using the *glm* function in the R Statistics Environment with a binomial distribution family. A significant positive slope would indicate that low-ranking (i.e., rare) OTUs were more likely to be active, whereas a significant negative slope would indicate that common OTUs tended to be more active.

As in all biodiversity studies, sampling depth may have influenced some of our conclusions. However, the probability of detecting a given population is proportional to its abundance relative to other community members. Of course random sampling error and molecular techniques can impart bias in

our recovery rates, but tag-encoded pyrosequencing should help avoid these issues by providing greater sampling depth and using short amplicons with uniform length.

Model Details. To mirror our lake sampling, we used a model landscape comprised of eight patches. The local environmental conditions of the patches were evenly spaced from 0 to 1. We seeded a total of 2,601 microbial species, representing all combinations of local and regional environmental optima spanning from 0 to 1 by increments of 0.02, into each patch. The qualitative results, however, were robust to the number of species added to a simulated patch (36–2,601). We did not include dispersal among patches in our model. An explicit exploration of the consequences of dormancy in a microbial metacommunity would be a logical extension of the current model. Although all species were initially present in all patches, environmental cues and the strength of dormancy determined the persistence of a species in a given patch. The total equilibrium density ($A^*_{jx} + D^*_{jx}$) was used as an analog for the total (rDNA-based) community, and A^*_{jx} was taken as the active (rRNA-based) community. We assessed patterns of community composition using cluster analysis (*Statistical Analyses*).

Statistical Analyses. All statistical analyses, including UPGMA cluster analysis, indicator variable regression, logistic regression, and multiple response permutation procedure (vegan package), were performed in the R Statistical Environment. Pairwise Bray-Curtis distance matrices were used to summarize difference in both model and T-RFLP-based community composition. The distance matrices were used for visualization of compositional patterns of active and total communities by UPGMA clustering. In UPGMA clustering, the most similar communities (dendrogram tips) are joined by a branch with total length equal to their Bray-Curtis dissimilarity, the most similar communities' entries in the distance matrix are combined by averaging, and the process is repeated until all communities are included in the dendrogram. We used the multiple response permutation procedure (MRPP) to test for significant differences in composition between active and total communities. Indicator variable regression was fit using negative log likelihood minimization in R.

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