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FUNCTIONAL REDUNDANCY SUPPORTS BIODIVERSITY AND ECOSYSTEM FUNCTION IN A CLOSED AND CONSTANT ENVIRONMENT

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Abstract. The role functionally redundant species play in ecosystem function has not been adequately investigated. To study this, we examined species richness and an ecosystem function, cellulose decomposition, while environmental conditions were held constant. Our hypotheses were (1) increasing species richness will have no effect on rates of cellulose decomposition and (2) species richness will decline over time in functionally redundant communities. A relatively simple microcosm-based system to manipulate complex microbial interactions was employed. Microcosms containing cellulose as the sole carbon source were inoculated at equal densities with none, one, two, four, or eight species of cellulolytic bacteria. At 5-d intervals for 25 d, community composition and cellulose decomposition were determined. We rejected both of our hypotheses. In a constant environment, greater species richness supported a greater number of individuals and subsequently greater rates of total cellulose decomposition. Furthermore, greater initial species richness maintained greater richness over time. These results provide experimental evidence that functionally redundant species may play an integral role in ecosystem function.

Key words: aquatic microcosms; biodiversity; cellulolytic bacteria; cellulose decomposition; functional redundancy; Intermediate Disturbance Hypothesis (IDH); species richness.

INTRODUCTION

In the face of declining local and global biodiversity, understanding the relationship between biodiversity and ecosystem function has been of increasing interest (Tilman and Pacala 1993, Chesson 2000, Kinzig 2001). Some studies (Hooper and Vitousek 1997, Balvanera et al. 2001, Cardinale et al. 2002) argue that a diverse biota contributes positively to ecosystem processes and that species loss will therefore have negative effects on ecosystem processes and our environment. Other studies (Naeem et al. 1994, Tilman et al. 1996, 1997, Naeem and Shibin 1997, McGrady-Steed and Morin 2000) have shown that loss of species diversity will result in little impact on ecosystem processes; whereby multiple species provide the same service to the ecosystem and this compensates for species with reduced or lost performance (i.e., insurance hypothesis; Yachi and Loreau 1999). Here we define functional redundancy as multiple species, while biologically unique, contributing with similar intensity to the same process within an ecosystem, such as energy flow or nutrient cycling.

Although factors such as spatial complexity or antibiosis may affect species diversity and ecosystem function (Kerr et al. 2002, Zhou et al. 2002), it is thought that intermediate-levels of disturbance are required for maintaining high species diversity (Connell 1975, 1978). Conversely stated, stable environments (i.e., those lacking disturbance) should yield low biodiversity. Gibert and Deharveng (2002) found this to be true in subterranean terrestrial and aquatic ecosystems, which are relatively stable environments with little colonization from surface habitats. Similarly, Kerr et al. (2002) found diversity to be low due to competitive interactions when community dynamics were not determined by a localized spatial scale or disturbance.

Understanding the role of functionally redundant species may help elucidate mechanisms underlying ecosystem stability and the underlying value of species diversity on ecosystem processes. Microorganisms are essential components of ecosystems and are ideal for such studies, since they are diverse, grow rapidly, are easily maintained in a controlled laboratory environment, and have a rapid response time to environmental changes (Hairston et al. 1968, McGrady-Steed and Morin 2000). One ecosystem process dependent on microbial activity is cellulose degradation. Cellulose is abundant in nature and insoluble in water and therefore requires enzymatic degradation. It is also a ''narrow'' physiology (Schimel 1995), and so might be expected to be sensitive to variation in the composition or diversity of cellulolytic communities. Since cellulose de-

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composition can be easily quantified and both aquatic and terrestrial environments are dependent on microbial activity for its breakdown, we selected cellulose degradation as our ecosystem function. By employing bacteria-based microcosms for study, we formed a spatially simple system with ecologically complex interactions to study cellulose decomposition (Gause 1934, Hairston et al. 1968, Connell 1975, McGrady-Steed and Morin 2000).

To determine the role functionally redundant species play in an ecosystem function, cellulose decomposition, we tested two hypotheses: that under constant environmental conditions (1) increasing species richness will have no effect on rates of cellulose decomposition and (2) species richness will decline over time in functionally redundant communities.

Methods

Microorganisms

We isolated bacteria from submerged leaf litter at a single location in the James River, Virginia, USA (77°32′ W, 37°33′ N). All bacteria were initially screened for cellulolytic activity based on their ability to grow on cellulose agar plates. Visualization of cellulolytic activity was then confirmed using a method outlined by Sirisena and Manamedra (1995), which involved inoculation of each bacterium on to carboxymethyl cellulose agar (CMC). Plates were incubated for 24 h, flooded with an aqueous solution of congo red, the congo red was poured off, and plates were then flooded with 1-mol/L NaCl. Zones of cellulose decomposition could be seen as clear areas. The 16 cellulolytic bacterial isolates were then assayed to test for redundancy of cellulase function.

Cellulase assays to screen for functionally redundant, cellulolytic bacteria were sampled on days 5 and 10. Extracellular enzyme activity was measured using three substrate analogs of cellulose (pNp-β-d-glucopyranoside, pNp-β-D-cellobioside, and pNp-β-D -cellotrioside (Sigma Chemical Company, St. Louis, Missouri, USA) in timed assays (Sinsabaugh et al. 1992). Stock solutions for each of the substrate analogs were prepared to a final concentration of 10 mmol/L. Incubation periods were 4 h, based on the findings of preliminary enzyme kinetics, where substrate concentrations tested were fit to the linear transformation of the Michaelis-Menten equation. After incubation, 0.1 mL of 1.0 mol/L NaOH was added to each aliquot and optical density at 405 nm was determined spectrophotometrically. Dissolved protein concentrations were then determined by the BCA protein assay reagent kit (Pierce, Rockford, Illinois, USA) with bovine serum albumin as the standard. An analysis of variance was used to test for significant differences in cellulolytic activity amongst the isolates (SPSS, Chicago, Illinois, USA). Based on these assays, ten isolates with comparable rates of cellulase activity on day 10 were selected for study (Table 1). Identification of the bacteria was confirmed using partial sequence analysis of the 16S rRNA gene.

Microcosms and experimental design

Microcosms were used to study functionally redundant species assemblages consisting of (1) no microorganisms (control), (2) one species, (3) a combination of two species, (4) a combination of four species, and (5) a combination of eight species. The 10 bacterial species used in this study were *Bacillus cereus*, *Deinococcus* sp. MBIC3950, *Staphylococcus simulans*, *Cellulomonas cellulans*, *Cellvibrio gilvus*, *Pseudomonas fluorescens*, *Microbispora diastica*, *Nocardia farcinica*, *Streptomyces yunnenansis*, and *Streptosporangium roseum*. These cellulose degraders coexist in nature and are diverse in terms of their phylogenetic history and physiological relationship.

In total, 276 microcosms were inoculated at t_0; for treatments of none, two, four, and eight species, there were four replicates of each treatment for each of the six sampling dates, whereas for treatment of one species, all 10 species were run with three replicates for each of the six sampling dates. Treatment replicates consisted of the same number of species, but were randomly comprised from the pool of 10 species in order to identify differences due to species diversity, not species-specific interactions. For example, a species assemblage of four functionally redundant microorganisms and four replicates might be: adel, eghi, dbgh, and bcfi; where each letter indicates a specific species. Analyses were based on averaged results of each species assemblage (none, one, two, four, or eight species) to identify differences among treatments.

Each microcosm consisted of a test tube (25 × 150 mm) containing 14 mL of minimal media (1% sodium caseinate, 0.2% $NaNO_3$, 0.2% KNO_3, 0.01% $CaCl_2$, 0.005% $MgSO_4$, 0.2% K_2HPO_4), 0.00002% yeast extract, 0.1% Hepes K buffer and 25.6 mg cellulose paper. Prior to inoculation, microcosms were sterilized by autoclaving (at 122°C for 15 min). All microcosms (with the exception of the controls) were inoculated at a total density of 2.00×10^5 cells /mL regardless of the number of species. Initial cell densities were determined using a spectrophotometer.

Microcosms were placed in an environ-shaker and experiments were run for 25 d at 25°C and 200 rpm (more than 250 generations based on a conservative estimate of a 2.5-h generation time). At 5-d intervals, microcosms were destructively sampled. On each sampling date, microbial densities, realized species richness (i.e., species richness at the time of sampling), Shannon-Weaver's index of evenness, cellulase activity, and remaining cellulose were quantified. These response variables indicated compositional and functional indices of the community dynamics in regard to cellulose decomposition.

TABLE 1. The 10 cellulolytic bacteria chosen for this study based on their enzyme levels (i.e., β-glucopyranosidase, cellobiosidase, and cellotriosidase) after 10 d of incubation in minimal media and the presence of cellulose.

Enzyme	*Bacillus cereus*	*Cellumonas cellulans*	*Cellvibrio gilvus*	*Deinococcus* sp. MBIC3950	*Microbispora diastica*
Gluco-pyranosidase	43.87 (1.24)	43.95 (0.89)	43.55 (0.93)	43.58 (0.93)	43.45 (1.59)
Cellobiosidase	16.45 (1.36)	17.07 (1.39)	17.10 (0.69)	17.06 (1.86)	17.20 (1.21)
Cellotriosidase	10.42 (0.92)	10.33 (1.34)	10.10 (0.79)	10.27 (1.22)	10.28 (0.93)

Notes: An ANOVA indicated that mean enzyme activities on day 10 among the 10 species did not differ significantly from each other. For each species, reported values indicate mean enzyme activity in terms of $nmol \cdot min^{-1} \cdot \mu g\ protein^{-1}$ (with 1 SD in parentheses). All F tests had df = 9, 50.

Community composition

Determinations of species richness and cell density of each species were based on plate counts with species identifications based on morphological characteristics and antibiotic markers. Of the 10 species used in the experiment, only *Cellulomonas cellulans*, *Cellvibrio gilvus*, and *Pseudomonas fluorescens* could not be identified solely on morphological properties of their colonies when grown on nutrient agar. These three organisms were screened for natural antibiotic resistance. *Pseudomonas fluorescens* was found to be resistant to tetracycline (40 μg/mL). Antibiotic resistance in *Cellulomonas cellulans* and *Cellvibrio gilvus* was induced through serial transfers of increased antibiotic resistance resulting in resistance to ampicillin (100 μg/mL) and gentamicin (50 μg/mL), respectively. Therefore, on each sampling date, media from the microcosms were plated at 100-fold dilutions from 1×10^{-1} through 1×10^{-11} onto nutrient agar plates. Any microcosms containing *P. fluorescens*, *C. cellulans*, or *C. gilvus* were also plated at the same dilutions onto nutrient agar plates with the appropriate antibiotic (i.e., tetracycline, ampicillin, or gentamicin). Plates with 30–300 colonies of any particular species were retained and counted. Cell density of each species was then determined based on colony forming units (CFUs) and the appropriate dilution.

Cellulose

Cellulose decomposition was determined by dry mass. Samples were poured into preweighed boats, dried at 55°C for 6 d, and mass recorded. Bacterial biomass was subtracted from the paper based on organism density and species-specific calculations of number:biomass.

RESULTS

Greatest density of total individuals occurred with greatest realized species richness (Fig. 1). Microcosms inoculated with more than two species had 100-fold more individuals by day 5 than other treatments (Fig. 1). Significant differences in total density between treatments of one or two species vs. four or eight species persisted from day 5 to the end of the experiment (Table 2).

In addition to differences in total densities, greater rates of cellulose decomposition were obtained with greater species richness (Fig. 2). Over the course of 25 d, mixed assemblages inoculated with four or eight species degraded approximately half of the available cellulose paper (i.e., 47.5% and 46.3%, respectively), whereas only 26.5% was removed by the two-species treatment and 30.9% by the one-species treatment. Interestingly, degradation of cellulose per individual did not differ significantly among treatments ($F_{4,39} = 1.14$, $P = 0.672$). Calculations of cellulose decomposition per cell yielded a mean of $1.10 \times 10^{-6} \pm 3.20 \times 10^{-8}$ μg cellulose/h.

Microcosms inoculated with more species maintained that species richness (Fig. 1). On day 25, 75.0% of microcosms inoculated with eight species and 87.5% of microcosms inoculated with four species had maintained initial levels of species richness. Furthermore, Shannon-Weaver index of species evenness showed that in microcosms inoculated with eight species, each species' abundance continued to contribute a comparable proportion to the total population over 25 d (Fig. 3). In the four-species microcosms, Shannon-Weaver index of species evenness was calculated to be 0.312, which indicates that unlike the eight species microcosms there was dominance amongst species. Yet, that dominance did not lead to species extinction. In contrast to the more species-rich microcosms, only 33.3% of microcosms inoculated with two species had both species present on day 25. In these two-species microcosms, one species was dominant and yielded an evenness value of 0.173 on day 25 (Fig. 3).

DISCUSSION

Observed differences in treatment densities and cellulose degradation, as early as day 5 in this experiment, are noteworthy. Finite resources, as one finds in a closed system, theoretically have a maximum number of individuals they can support with disregard to species richness or redundancy (Roughgarden 1979). Our hypotheses, based in part on the intermediate-disturbance hypothesis and insurance hypothesis, predicted that in the absence of disturbance, species richness should decline as a result of competitive interactions, while cellulose decomposition remains constant. However, only in microcosms inoculated with two species was competitive exclusion evident, where elimination of one species occurred rapidly. Had the experiment been extended beyond 25 d, we would predict that in

TABLE 1. Extended.

Nocardia farcinica	*Pseudomonas fluorescens*	*Staphylococcus simulans*	*Streptomyces yunnenansis*	*Streptosporangium roseum*	*F*	*P*
43.66 (1.43)	43.55 (1.53)	43.53 (0.74)	43.77 (0.97)	43.95 (1.22)	0.146	0.998
16.80 (1.53)	16.47 (1.89)	17.15 (0.66)	16.40 (1.45)	16.70 (0.92)	0.325	0.963
10.82 (1.07)	9.9 (0.94)	10.28 (0.75)	10.30 (1.11)	9.95 (1.53)	0.336	0.959

a short time all two-species microcosms would have a single species given the finite resources, absence of disturbance and overlapping similarity (Roughgarden 1979). Competitive exclusion however was not evident in microcosms containing more than two species. In these microcosms, we found species richness to facilitate species coexistence. In the four-species microcosms, more than 85% of the replicates maintained all four species over the 25-d duration. In the eight-species microcosms, not only was diversity maintained in the absence of disturbance in these treatments, but also the frequency distribution of all eight species remained similar to the initial inoculation after ~250 generations. Furthermore, in both the four- and eight-species treatments there were more individuals per microcosm and greater rates of cellulose decomposition than in any single-species microcosm (Figs. 1 and 2). Were competition present, we would expect decreased cell densities and decreased rates of cellulose decomposition, as observed in the two-species microcosms. Yet, when multiple species were present, there was an elevated numeric and functional response than observed in the single-species microcosms. Therefore, we contend that this is not an example of competitive exclusion proceeding more slowly in a diverse system due to longer transient dynamics; rather it is the inherent diversity of multiple species (i.e., genetic variability amongst species and therefore different mechanisms and pathways to exploit different resources) that supports the maintenance of diversity over time.

To further support our claim that the maintenance of species diversity over time is due to differences between species, we must examine other possibilities. An alternative explanation to competitive exclusion, but a possibility given the finite resource base of a closed system, is that the lower density of individuals observed in microcosms inoculated with only one or two species are limited by the production of inhibitory compounds (Connell 1975, Czárán et al. 1989). Production of such inhibitory compounds however, should continue to impact mixed assemblages, as well. Yet, there was a positive numerical response observed with greater species richness, as well as an increase in ecosystem function. The possibility that these inhibitory compounds are consumed or degraded within the mixed assemblages does exist, as well. However, we would have expected to see two-species interactions that were positive, which we did not observe. These findings lead us to believe that the populations were not limited by the production of such inhibitory compounds.

A third possible explanation is the ''complementarity effect,'' which states that increasing species richness increases the number of species exploiting nonoverlapping resources (i.e., complementary interactions) instead of interacting competitively (Naeem et al. 1999). Here the different rates of total cellulose decomposition in the different treatments were a direct response to the number of individuals per microcosm. Since individual microorganisms were selected based on similar cellulolytic activities (i.e., redundant function), one can assume that all individuals were producing cellulases. These extracellular β 1–4 glucanases, endo- and exohydrolases, were required to break down cellulose to its monomeric form (cellobiose). Given the extracellular nature and activity of these enzymes, we did not determine specific enzymatic activity per individual cell

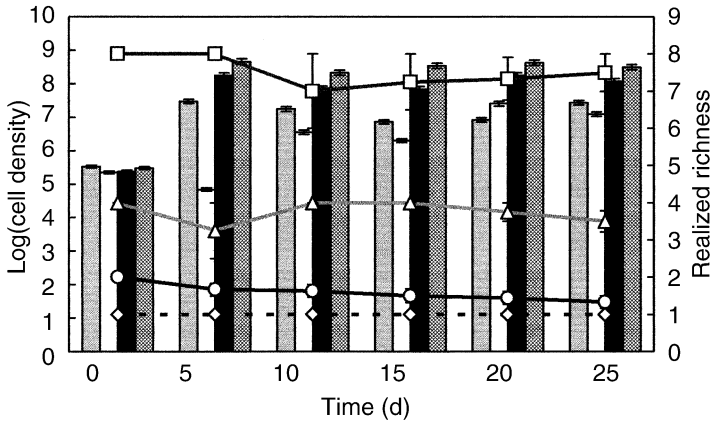

FIG. 1. Density of microorganisms (log-transformed no. cells/L, shown as histogram bars) and realized species richness (lines) for each sampling date in the 25-d experiment. All microcosms were inoculated with 2×10^5 cells/mL at time 0. Error bars depict ±1 SE. The treatment number equals the number of species at the start: treatment 1 (gray bar and open diamond), $n = 30$; treatment 2 (open bar and open circle), $n = 9$; treatments 4 (solid bar and open triangle) and 8 (cross-hatched bar and open square), $n = 4$. Controls are not shown, but were 0 throughout the experiment.

TABLE 2. Summary of least significant difference (LSD), post hoc multiple comparison *P* values for the effects of species richness on density (cells/mL) in treatment comparisons.

Treatment comparisons (no. species)	Day 0	Day 5	Day 10	Day 15	Day 20	Day 25
1–2	0.349	0.001*	0.726	0.679	0.020*	0.019*
1–4	0.629	0.057	0.030*	0.010*	<0.001*	0.014*
1–8	0.322	0.018*	0.006*	0.001*	0.001*	0.003*
2–4	0.324	<0.001*	0.075	0.043*	0.061	0.057
2–8	0.337	<0.001*	0.025*	0.009*	0.062	0.033*
4–8	0.354	0.548	0.806	0.579	0.876	0.261

Notes: Density data were log transformed before ANOVA to improve normality. An asterisk indicates a *P* value of ≤0.05, which was considered significant. All treatments (i.e., 1, 2, 4, 8) paired with the control, on all sampling dates, had a *P* value of <0.001.

in mixed microcosms. The ''complementarity effect'' would suggest that although the 10 isolates selected for this study have an overlapping function, they each contribute differently to cellulose degradation or other ecosystem processes. While we do not refute this possibility, we believe that facilitation is occurring where the different species contribute additional resources such as enzymes or dissolved organic carbon to the system. These additional resources, not solely the partitioning of available resources, are responsible for the positive numeric response and elevated rates of cellulose decomposition in microcosms with greater species richness.

Diversity between species, despite a redundant function, appears to be crucial to ecosystem function and long-term sustainability. Yet we must ask if this positive numerical response observed with greater species richness is a ''hidden treatment effect'' (Huston 1997). Limited by the number of functionally redundant, cellulolytic bacteria we could collect, identify and manipulate for this experiment, mixed assemblages of eight species had overlapping species composition. This overlap could lead to a pairing or grouping that may explain this positive response. We contend that it does not. No single species yielded the high cell densities or rates of cellulose decomposition that we see in treatments of four or eight species. In our four-species assemblages, only *Pseudomonas* and *Nocardia* were present in two of the four replicates and in the two species treatment, *Nocardia* outcompeted *Pseudomonas* by day 5. Therefore, the elevated numerical and functional response in our four-species treatment is not a function of a ''hidden treatment effect.'' Furthermore, the constancy of species over time in the eight species assemblages suggest that even in the absence of disturbance these cellulolytic bacteria isolated from the James River benefit from greater species richness and their inherent diversity.

Researchers (Schimel 1995, Brussaard et al. 1997, Groffman and Bohlen 1999) have determined that the species-specific composition of microorganisms typically does not affect general ecosystem processes, but does affect ''narrow'' processes. Due to the specific physiology that is possessed by a limited group of microorganisms, cellulase production has been defined as a narrow process (Schimel 1995). Therefore in a natural environment, where only a small percentage of the microbial species possess the ability to produce cellulases, species composition should impact the rate of this narrow ecosystem function. In our experiment however, all of the microorganisms present were able to degrade

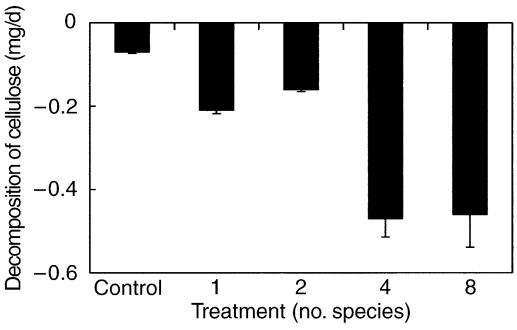

FIG. 2. Rate of cellulose decomposition for each treatment over the course of the 25-d experiment. The control was not significantly different from 0 ($P < 0.332$). Error bars represent 1 SE.

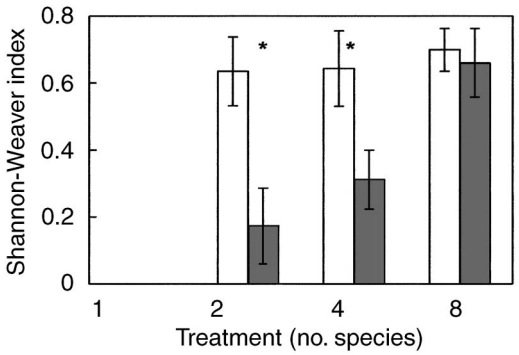

FIG. 3. Shannon-Weaver index of species evenness. A one-way ANOVA was calculated to determine the significance between day 0 (open bars) and day 25 (filled bars) for each treatment ($P \leq 0.050$ was considered significant, as indicated by an asterisk). The one-species treatment index could not be calculated. Error bars depict ±1 SE.

cellulose. Given this condition, we demonstrate that it is the number of species present (i.e., species richness), which is the primary factor affecting rates of cellulose degradation. Although the microcosms were comprised of functionally redundant species (i.e., cellulose degraders), treatment replicates consisted of randomly selected species in order to identify differences due to species richness, not species-specific interactions. Regardless of species composition, microcosms with more than two species yielded a positive numerical and subsequently an ecosystem response. Interactions resulting from this diversity are complementary and contribute additional resources such as enzymes or dissolved organic carbon to the system (Loreau and Hector 2001). Such additional resources in turn support greater cell densities and subsequently greater ecosystem function. Studies that examine coexistence, species facilitation, or complementarity support our findings that multiple species will persist due to the interaction of the parts (Loreau and Hector 2001, Kerr et al. 2002).

This emergent property is noteworthy. We assert that multiple-species interactions may inhibit antibiosis and create additional resources and resource heterogeneity in this closed system for the total community. Furthermore, while a single species may produce a specific suite of enzymes to degrade a compound or produce secondary metabolites that may have inhibitory compounds, it appears that communities can gain advantage from interactions between species. We see mixed assemblages to be better equipped for cellulose decomposition than individual species. These results provide experimental evidence that greater initial species richness maintains greater species richness over time by means of facilitation. More over, these findings indicate that environmental variability is not required to explain the coexistence of functionally redundant species.

While our findings are based on the complex ecological interactions of one-, two-, four-, and eight-species microcosms of bacteria, they are still very simple relative to a natural environment where the number of microbial species may be many times greater (Torsvik et al. 1990). Therefore, to further explain the dynamics causing this elevated numerical and subsequent functional response to diversity, future efforts will focus on a series of microcosm studies performed in conjunction with field tests. Microcosm studies offer us an environment that can be manipulated to understand dynamics of organism interactions (e.g., stable vs. stochastic environment, analysis of cellular by-products, and species interactions), whereas field studies provide a system with natural scales of variables such as space, time, and biological complexity. Using more sophisticated molecular data to analyze species composition and functional genes we can better understand how species richness and population dynamics of the microbial community scale up, while further exploring the role of species richness and ecosystem stability in terms of diversity and function.

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