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Scaling community structure: how bacteria, fungi, and ant taxocenes differentiate along a tropical forest floor

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Abstract. Taxa with smaller individuals tend to have shorter generation times and higher local abundance and diversity. The scaled specialization hypothesis (SSH) posits that taxocenes of smaller individuals should differentiate more rapidly and thoroughly along physiochemical gradients of a given age and extent. In a Panama rainforest, we evaluated how bacteria, fungi, and ants responded to two such gradients: one topographic and the other arising from nine years of NPK fertilization. Terminal restriction fragment length polymorphism (T-RFLP) delineated bacteria and fungi operational taxonomic units (OTUs); traditional taxonomy delineated the ants. Bacteria had higher local species richness than fungi and ants (averaging 48 vs. 30 vs. 6 OTUs in <0.25 m^2). Bacteria OTUs were also more widely distributed (17% of OTUs were found on $\geq$50% of sample plots compared to 3% for fungi and ants). Consistent with SSH, bacterial composition differed across short-term (+N and +P) and long-term (topographic) gradients; fungal taxocenes differed only along the long-term gradient; and ant taxocenes were homogenous across both. Body size can help predict community responses to a changing environment.

Key words: *ants; bacteria; biogeochemistry; diversity; fungi; niche; species composition.*

Introduction

The composition of taxocenes (clades of species co-occurring in a given time and place) reflects the dynamics of speciation, local adaptation, dispersal, and extinction (Hutchinson 1959, Rosenzweig 1995). These rates vary across taxa, often based on body size, making size a potentially useful trait buttressing a theory of taxocene composition across the landscape (Levin 1992, Ritchie and Olff 1999). Here we use the body size of three clades to predict their response to identical resource gradients in a Panama forest.

Bacteria, fungi, and ants are common consumers in brown (or detrital) food webs (Swift 1987). They vary orders of magnitude in size. Bacterial cells, colonies, and biofilms—measured in micrometers to centimeters (Vogel et al. 2003, Grundmann 2004)—are consistently the smallest of the three. Litter fungi range from unicellular yeasts (tens of micrometers) to filamentous hyphal cells that occupy several square meters of the forest floor (Lodge and Cantrell 1995, Redecker et al. 2001). The home ranges of ant colonies vary from a square meter to hectares (Hölldobler and Wilson 1990). Here we assume that the modal mass, and ecological footprint, of bacteria $<$ fungi $\leq$ ant colonies.

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The scaled specialization hypothesis (SSH) posits that the amount a taxocene differs in species composition along a physiochemical gradient varies with the mass of its individuals. SSH builds on the hypothesis that differentiation of taxocenes along ecological gradients should increase with the size of the species pool, the population growth rate, and the inverse of generation time (May 1975, Hendriks and Mulder 2008). SSH adds the assumption that all three are correlated to body mass. The size of the local species pool should be an inverse function of body mass given that small taxa are better passive dispersers (Martiny et al. 2006) and exist at higher local abundances with lower local extinction rates (Pimm et al. 1988, Finlay 2002, White et al. 2007). A patch of smaller taxa should thus have a larger local species pool, and higher likelihood of propagules adapted to a given environment. The maximum population growth rate and minimum inverse of generation time of taxocenes scales inversely with body mass (Peters 1983, Gillooly et al. 2002). This increases the maximum rate of species sorting through competitive exclusion, while rapid turnover and large available gene pools (through high abundance and low extinction) promote the evolution of locally adapted forms (Rainey and Travisano 1998, Ramette and Tiedje 2007). SSH predicts that for a given grain, extent, and age of an environmental gradient, taxocenes of smaller individuals should be more differentiated across that gradient.

Bacteria, fungi, and arthropods are widely distributed, yet we know of no studies of how their diversity and

composition covary across the landscape (Green and Bohannan 2006, but see Bryant et al. 2008 for a plant–bacteria comparison). Toward a remedy, we evaluate SSH using a short-term fertilization gradient and a long-term topographical gradient in a Panama rainforest. We test the assumption that bacteria are both more locally species rich and more uniformly distributed across the landscape, and the prediction that bacterial taxocenes will be more differentiated across that landscape.

Materials and Methods

Bacteria, fungi, and ants were sampled from the Smithsonian Tropical Research Institute's Gigante Fertilization Experiment (9°06′31″ N, 79°50′37″ W) in the Barro Colorado Nature Monument (BCNM), Republic of Panama. Gigante is a seasonal primary forest >300 years old (Leigh and Windsor 1996) with oxisol soil low in available P and K (Yavitt and Wieder 1988).

We examined the diversity of bacteria, fungi, and ants along two gradients that differ in age. One was an NPK fertilization of 32 40 × 40 m plots, arrayed, approximately 30–40 m apart, over 27 ha. Eight treatments ($n = 4$, +N, P, K, NP, NK, PK, NPK, and control) were applied four times a year since 1998 and sampled nine years later in 2007. An additional four plots received a cocktail of micronutrients (see Kaspari et al. 2008 for a description of compounds and dosages). Fertilization enhanced leaf litter element concentrations by up to 7%, 27%, and 34% on +N, +P, and +K plots respectively. Cellulose decomposition was enhanced 49% and 30% on +P and +K plots; leaf litter decomposition was 30% higher on +P plots. All this occurred without an increase in litterfall (Kaspari et al. 2008). A second topographical gradient spanned 36 m (25–61 m above sea level) over 800 m. Four strata, each received one replicate of all fertilizer treatments. Many features of litterfall vary across strata (Kaspari et al. 2008), including the P and S content of litter, as well as the rate of leaf and twig litterfall (see Appendix A: Figs. A1 and A2).

Sampling taxocenes

Bacterial and fungal taxocenes from the forest litter were sampled from 16–20 September 2007. Five sites were sampled with a 0.09-m^2 quadrat within each fertilized plot; we report data from one central site. Litter depth was measured with a thin, scored plastic rod at the four corners, then all litter was collected down to mineral soil and sifted for 30 s through a 1 cm screen to produce a homogenous residuum. Before each collection, an equal amount of litter from an adjacent plot was used to "rinse" the sifter. Residuum was stored in plastic bags and processed within 12 hours, or stored at 3°C for 24 hours and then processed. Litter was homogenized and a 50-mL subsample was analyzed for moisture content by taking wet mass then drying to constant weight at 60°C. The pH of this sample was measured after first mixing in 30–50 mL of deionized water (in ~10 mL excess of litter volume) and incubating for 10 minutes in the dark at room temperature (22°C).

Total DNA was isolated from 0.5–1.0 g (wet mass) of homogenized litter using the MOBIO Power Soil DNA Extraction Kit (MOBIO Laboratories, Carlsbad, California, USA) using the manufacturer's protocols. DNA was extracted from two replicate subsamples, pooled for each sample, and then stored at −20°C until needed.

We used terminal restriction fragment length polymorphism (T-RFLP) analysis (Liu et al. 1997) to compare the bacterial and fungal communities. The T-RFLP method quantifies sequence variability based on the length and abundance of unique restriction fragments for a conserved sequence. While multiple taxa can share phylotypes, and underestimate total community richness (Dunbar et al. 2001), T-RFLP is well suited for quantifying large numbers of complex communities (Lukow et al. 2000). The small-subunit (16S) ribosomal RNA gene was used to characterize bacteria; the internally transcribed spacer (ITS) region between the 18S and 28S rRNA genes was used for the fungi. Details of primers and extraction techniques can be found in Appendix B.

Five to 10 ant colonies of only 100 workers may coexist in 1 m^2 of tropical litter (Kaspari et al. 2003). In June 2006, a pair of 0.25-m^2 plots, 14 m apart, were randomly arrayed on each of the 36 Gigante plots. Litter was sampled and arthropods were extracted for two days using a berlese funnel (Agosti et al. 2000). The ants of one randomly selected sample from each plot were identified to species using standard keys (Bolton 1994).

Statistics

We recorded local species richness in a given sample by counting bacterial and fungal phylotypes (unique T-RFLP fragment sizes) and ant species. To compare richness across the 27-ha landscape, we used the Chao 2 statistic (Colwell 1997). We compared the distribution of operational taxonomic units (OTUs) across the 36 plots using rank abundance curves. We compared the species composition of each sample using nonmetric multidimensional scaling (NMDS) to generate community profiles (Kenkel and Orloci 1986). NMDS calculates the rank distances among sample communities, and generates a nonlinear map of each taxocene in two dimensions. We used a parametric MANOVA on these community profiles to test the prediction that bacteria composition would differ along more of the four environmental gradients (N, P, and K fertilization and topographic strata, as statistical blocks) than fungi or ants (Scheiner 2001).

Results

Assumption 1: bacteria have higher local richness

Bacteria extracted from 0.09 m^2 of litter were 60% more diverse (mean = 48 phylotypes/plot, range 27–101) than fungi (mean = 30 phylotypes, range 5–49). Bacteria were eight times more diverse than ants taken from

TABLE 1. Changes in taxocene composition (tested with MANOVA) as a function of N, P, and K factorial fertilization, and blocking on topography.

Source	df	Bacteria			Fungi			Ants		
		Roy's root	*F*	*P*	Roy's root	*F*	*P*	Roy's root	*F*	*P*
N	1	0.545	8.75	0.0017	0.145	1.53	0.2403	0.0205	0.22	0.8079
P	1	0.311	3.27	0.0580	0.119	1.25	0.3071	0.0587	0.62	0.5493
K	1	0.0471	0.49	0.6166	0.0445	0.47	0.6332	0.0587	0.62	0.5495
NP	1	0.221	2.32	0.1225	0.2205	2.15	0.1409	0.0620	0.65	0.5316
NK	1	0.0439	0.46	0.6366	0.0116	0.12	0.8861	0.0151	0.16	0.8545
PK	1	0.0527	0.55	0.5833	0.106	1.12	0.3462	0.259	2.72	0.0894
Topography	3	0.850	6.24	0.0032	0.523	3.84	0.0238	0.219	1.6	0.2173
Error	22									

slightly larger 0.25-m^2 quadrats (mean = 6 species, range 1–14, $F_{2,105} = 212.56$, $P < 0.0001$; Tukey post hoc comparison, all $P < 0.05$).

The number of bacteria, fungi, and ant OTUs was uncorrelated across the 36 plots (fungi–bacteria Pearson's $r = 0.21$; fungi–ant $r = 0.11$; bacteria–ant $r = 0.03$; all $P > 0.25$), and did not vary with NPK fertilization ($P > 0.20$, see Appendix A: Table A1, Appendix C: Table C1, Fig. C1). The same was true along the topographical gradient for fungi and ant richness ($P = 0.76$, 0.10; Appendix C: Table C1), but not bacteria richness, which averaged 40 phylotypes at low strata 1 and 2, 65 on stratum 3, and 35 on the highest stratum 4; $P < 0.005$).

Assumption 2: bacteria have more widely distributed taxa

Bacteria taxa were also more widespread than fungi and ants. Six bacterial phylotypes were found on all 36 plots; 36 phylotypes (17% of the total) were found on half the plots. In contrast, only 3% of fungal and ant taxa were found on 50% or more plots (Fig. 1). Moreover, bacteria were no more diverse than fungi at the landscape scale. The total number of phylotypes of both was roughly equivalent (bacteria = 210, fungi = 236) as were the estimated number of phylotypes had sampling gone to completion (272 vs. 335, using Chao 2 with 95% CI, Fig. 1). Ant observed and estimated richness (60 and 75 species, respectively) was one-fourth to one-fifth that of microbial phylotypes.

Prediction: bacteria are more differentiated along resource gradients

Fungi, bacteria, and ants varied in the way OTU composition (measured by nonmetric multidimensional scaling) mapped onto fertilization chemistry and topography (Table 1, Fig. 2). The bacterial communities on +N plots ($P < 0.0017$) and, marginally, on +P plots ($P < 0.058$) were nonrandomly arrayed across dimensions 1 and 2, as were those found across the topographic strata ($P < 0.0032$). Fungal community composition, in contrast, differed only with topography ($P < 0.02$). The composition of ant communities failed to vary with fertilization or topography.

DISCUSSION

A working hypothesis in community ecology is that species composition changes along environmental gradients because locally adapted species outcompete others (Hutchinson 1959, Rosenzweig 1995). In a time

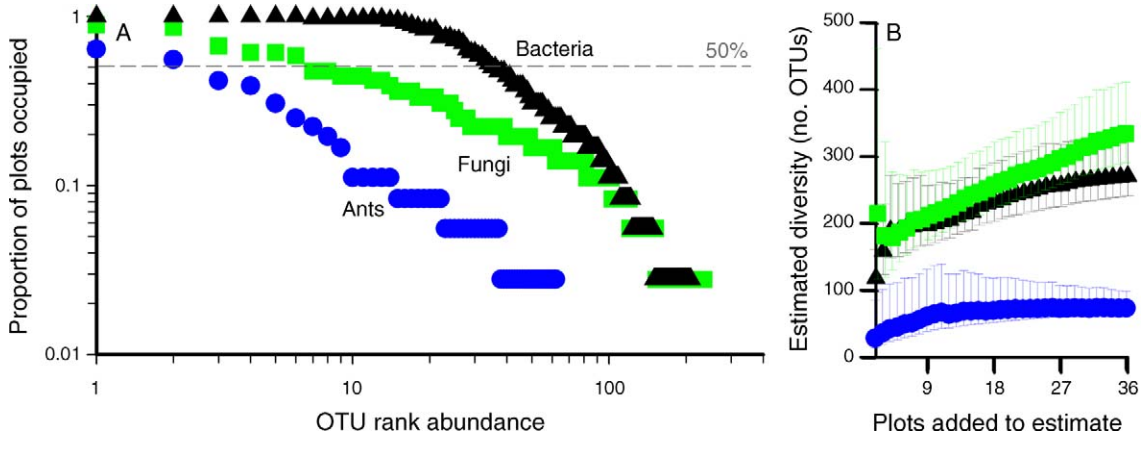

FIG. 1. Diversity patterns of bacteria (black triangles), fungi (green squares), and ants (blue circles) across 27 ha of tropical forest. (A) The abundance (by proportion of 36 plots occupied) of bacteria, fungi, and ant operational taxonomic units (OTUs) ranked from high to low abundance. Taxa above the dashed gray line were found on over half the plots. (B) Estimated diversity (±95% confidence intervals) of the OTU pool of bacteria, fungi, and ants across the sampled plots of the Gigante fertilization experiment.

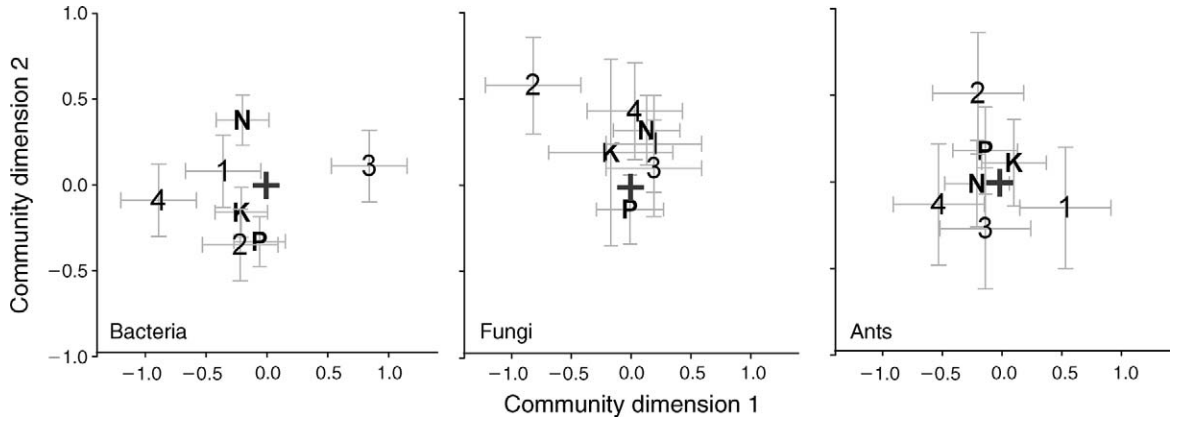

FIG. 2. Species composition of three taxa summarized by nonmetric multidimensional scaling. Each data point represents the average community composition of plots grouped by fertilization experiment (N, P, or K), or across four elevational strata (1 = high, 4 = low). The green cross in the center represents the mean composition across all 32 plots. In a factorial test, plots sharing the same treatment (e.g., N, NP, NK, NPK) are compared to those lacking the treatment (e.g., P, K, PK, control, micronutrient).

where many such physiochemical gradients are changing (Vitousek 1994), we explore how body size may help predict the dynamics of taxocene change. We find that the modal size of three key members of the brown (or decomposer) food web—bacteria, fungi, and ants—is associated with the degree that taxocenes differentiate along a recent (<10 year) fertilization gradient and long-term topographical gradient. Consistent with the size specialization hypothesis (SSH), bacteria were more locally diverse and more widely distributed (Fig. 1). Even though we recorded comparable fungi and bacteria richness across the landscape, a given bacterial phylotype was more likely to be found anywhere we sampled.

SSH is related to Beijerinck's (1913) conjecture for bacteria that "Everything is everywhere, and the environment selects." It is, at the same time, more general, adding that *for a given spatial grain and extent* clades of smaller taxa will be more widely distributed and more locally diverse. "Everything is everywhere," based on dispersal and extinction rates, must be scale dependent. It fails, for example, across the extents of biomes and continents (Green et al. 2004, Martiny et al. 2006) while it appears truer across our forest landscape. Likewise, bacteria were 50% more diverse than larger fungi at a given point in space. This set the stage for differentiation of bacteria assemblages across the Gigante plots, with artificial gradients of N and P, and a more complex topographical gradient, each generating different bacterial taxocenes. Our growing understanding of bacteria functional traits may shed light on this differentiation. For example, the growth rate hypothesis (Elser et al. 1996) predicts that +P plots should favor fast-growing, ribosome rich bacteria with more copies of rRNA operons (Klappenbach et al. 2000, Stevenson and Schmidt 2004). Likewise, the urea on +N plots should provide opportunities for ammonium oxidizing bacteria (AOB) and denitrifiers. Our results give a landscape perspective to the many lab studies (and, more recently, field studies) that show just how rapidly bacterial taxa and taxocenes evolve and sort across a changing environment (Lenski 1998, Rainey and Travisano 1998, Horner-Devine et al. 2003, Horner-Devine and Bohannan 2006, Strickland et al. 2009).

Adding N, P, and K to a Panama rainforest did little, however, to change the composition of fungi and ant taxocenes whose OTUs existed at lower local diversities and were less widely distributed across the landscape. This is not to say that N, P, and K had no effect on the fitness of individual ant colonies and fungi: P and K both enhance decomposition (Kaspari et al. 2008) with potential impacts on ant abundance (Kaspari and Yanoviak 2009). Fertilization simply did not appear to favor some fungal and ant species over others after nine years (but see Wardle 2002 and Mulder and Elser 2009 for temperate zone counterexamples). Gigante's topographic gradient, in contrast, did support different assemblages in the fungi, where strata 2, with its low carbon inputs and high availability of P and S, stood out from the other three (Fig. 2). Ants, with the perhaps the largest average footprint, were taxonomically invariant across the Gigante plots.

The larger eukaryotic genomes of fungi and ants, by favoring generalists, may also play a role in decreasing differentiation across the landscape. A single bacterial cell can only use the resources directly surrounding it; it is similarly limited to the suite of enzymes encoded in its prokaryotic genome. If confronted with a pectin, and such a unicell lacks the gene for a pectinase enzyme or (for example) the molybdenum required to build it, that unicell will be denied access to that resource. If a basidiomycete's hyphal cell encounters the same pectin, it may uptake molybdenum atoms from the soil anywhere within the reach of its mycelial network, and translocate it to the point of need. There, its eukaryote genome is more likely to find and upregulate the appropriate pectinase. In this way, the larger genomes and greater footprint of ants and fungi pre-adapt them to the opposite end of the

gradient posited by Beijerinck, which might be called "never everywhere—but plastic and adaptable."

Comparing diversity gradients between kingdoms: caveats

Species concepts for microbes are poorly defined relative to ants and require arbitrary sequence-based phylotypes. As more than one microbial population likely shares the same restriction fragment, the absolute value of bacterial and fungal diversity reported here is doubtless underestimated. T-RFLP is best at comparing diversities across sites: Fierer and Jackson's rainforest surveys, from their global survey of bacterial diversity, generated values similar to ours (Fierer and Jackson 2006, Lauber et al. 2009). It is also possible the higher abundance of fungal phylotypes is an artifact arising from our use of different sequences to characterize OTUs. However it need not be so. Leaf litter—plates of carbon defended with phenolics and lignins, periodically drying and discontinuous—is primarily attacked by fungi, while bacteria dominate in the fine organic carbon of the soil (de Boer et al. 2005).

One of the challenges of ecological scaling is understanding how the answer to the question "which is more diverse?" co-varies with the interaction of spatial grain and body size. SSH predicts that bacteria are more diverse than fungi or ants at grains of $\sim$0.1 m^2, as their small size allows them to recognize (due to their small footprint) and act on (due to their higher abundance and "evolvability") a given amount of heterogeneity. But that same abundance also allows more OTUs to be collected. Some of our differences in the local diversity of ant, fungi, and bacteria may thus arise as a sampling effect. A common way to control for sampling effects is to vary plot sizes so as to eliminate abundance bias (Gotelli and Colwell 2001). Note, however, to sample the same number of ants as bacterial colonies in 0.1 m^2 of tropical litter (1.37×10^{12} cultivatable colonies; Witkamp 1966) would require a plot roughly the size of Ecuador (Appendix D).

If SSH is true, any consistent variation in modal mass among taxa should generate the same predicted patterns. The fungi and arthropods both possess taxa that vary orders of magnitude in mass, providing opportunities for side by side comparisons of coexisting taxocenes on the same physiochemical gradients. Detecting such differences, as we have for bacteria across the forest floor, is a first step toward exploring their functional ecology and genomics. Given how little is known about tropical brown food webs, considerable, unexpected discoveries will likely result.

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APPENDIX A

A description of the Gigante plots (*Ecological Archives* E091-156-A1).

APPENDIX B

Additional methods for the description of the bacterial and fungal communities (*Ecological Archives* E091-156-A2).

APPENDIX C

Analysis of diversity gradients on the Gigante plots (*Ecological Archives* E091-156-A3).

APPENDIX D

Given the density of bacterial clones in 0.1 m^2 of forest litter, how large a plot would you need to sample the same number of ant colonies? (*Ecological Archives* E091-156-A4).