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More individuals but fewer species: testing the ‘more individuals hypothesis’ in a diverse tropical fauna

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A positive relationship between species richness and productivity is often observed in nature, but the causes remain contentious. One mechanism, the ‘more individuals hypothesis’ (MIH), predicts richness increases monotonically with density, as a function of resource flux. To test the MIH, we manipulated resource abundance in a community of tropical rainforest litter ants and measured richness and density responses. A unimodal relationship between richness and density most closely fitted the control and disturbance (resource removal) treatments in contrast to expectations of the MIH. Resource addition resulted in a monotonic increase in richness relative to density, a shift from the pattern in the control. In the disturbance treatment, richness was greater than in the control, opposite to expectations of the MIH. While large-scale correlations between ant diversity and net primary productivity or temperature are reconcilable with the MIH, key elements of the hypothesis are not supported.

Keywords: ants; competition; diversity; leaf litter

1. INTRODUCTION

The positive relationship between resource availability and species richness is among the most consistent patterns in ecology (Currie 1991; Hurlbert 2004; Evans & Gaston 2005; Evans *et al.* 2006). Such relationships are often attributed to species-energy theory, whereby sites with a greater resource flux have more species (Currie 1991; Wright *et al.* 1993). A major explanation for the relationship between resource flux and richness is the ‘more individuals hypothesis’ (hereafter MIH), which argues that higher productivity increases richness via lower extinction rates owing to larger population sizes (i.e. more individuals) of each species (reviewed in Evans *et al.* 2005a).

While the links between resource supply, density and richness have been the frequent subject of experiments on plants (e.g. Carson & Pickett 1990; Gough *et al.* 2000), such experiments on animals remain rare. Srivastava & Lawton (1998) experimentally manipulated productivity in tree-hole communities and observed that, although richness increased with productivity, abundance was relatively invariant.

A more recent study in pitcher plants (Kneitel & Miller 2002) concluded that, in line with MIH predictions, additions of dead ants to pitchers increased the abundance and richness of protozoans. These experiments provide insight into the plausibility of the MIH, but are from species poor, low productivity systems. Richness–density relationships and their underlying mechanistic links might be different in higher productivity, more diverse systems (Carnicer *et al.* 2007). Here, we consider how resource manipulations and disturbance affect the number of individuals and species of litter ants within one of the most diverse sites for ants worldwide (Longino *et al.* 2002).

At our study site, ant species richness increases with the density of individuals and the density of ant nests (Kaspari 1996). Ant nest density is, in turn, strongly associated with litter volume (Kaspari 1996) and litter fall rate (McGlynn *et al.* 2009), both of which are positively correlated with net primary productivity (NPP, a measure of photosynthetic energy retained in an ecosystem) available to the detrital food web, and indirectly to ants inhabiting the detrital food web (Clark *et al.* 2001). We began by quantifying the (unmanipulated) relationship between ant richness and ant density. We then manipulated resources in three ways. First, we added food resources in either clumped or widely dispersed patterns. According to the MIH, these treatments should increase the density and hence richness of ants, but the shape of the relationship should remain monotonic. Additionally, we removed leaf litter resources for detritivores (and, indirectly, their predators). In the MIH, disturbance by removing resources or making them less accessible should decrease the number of individuals and hence reduce richness. Alternatively, if there is a trade-off between dominance and disturbance, in a competitively structured community, disturbance might be expected to reduce the abundance of the most competitively superior species and increase richness for a given number of individuals (Adler *et al.* 2007). According to the MIH, our resource addition experiments are expected to increase the density of individuals and species richness. By contrast, we expect disturbance to decrease the density of individuals and consequently richness. In none of these manipulations does MIH predict that the function underlying the density–richness relationship should change.

2. MATERIAL AND METHODS

Our study was conducted in an old-growth forest at La Selva Biological Station, Heredia Province, Costa Rica, a lowland wet tropical forest (McDade & Hartshorn 1994), with more than 100 litter-dwelling ant species on site (www.evergreen.edu/ants). Plots (1 m²) were positioned across a 4 ha site 100 m east of the intersection of the Camino Circular Cercano and Sendero Suroeste trails.

Plots were randomly assigned in equal proportions to treatment (and control) categories. We supplemented food (5 g of dead *Nasutitermes corniger*) in two spatial presentations, ‘clumped’ and ‘diffuse’. ‘Clumped’ food plots received a single pile of food every 48 h in the centre of the plot, and ‘diffuse’ plots received an equivalent quantity of food at the same frequency spread evenly throughout the plot. In ‘disturbance’ plots, we removed approximately three-fourths of foliar leaf litter at the beginning of the experiment without removing ant colonies, by careful inspection of each leaf. Fifty-five plots were initiated for each treatment and the control; final numbers varied from 48–55 plots/treatment because of large branch falls.

Table 1. Model selection for the relationship between ant individuals and species richness. (The most parsimonious among unimodal (quadratic) and three monotonic models were compared using AIC weights. The most parsimonious models (in bold) are presented in the text and in figure 1.)

treatment	<i>n</i>	model	residual sum of squares	AIC	Δ_i	AIC weight	r^2
control	54	unimodal	84.77	30.35	0	0.45	0.33
		log-series	89.68	31.39	1.04	0.27	
		power	90.90	32.12	1.77	0.18	
		lognormal	92.89	33.29	2.94	0.10	
disturbance	52	unimodal	117.12	48.22	0	0.38	0.32
		log-series	122.65	48.62	0.40	0.31	
		power	124.54	49.41	1.19	0.21	
		lognormal	128.06	50.87	2.65	0.10	
resources (clumped)	50	lognormal	80.04	25.25	0	0.63	0.66
		unimodal	76.68	27.32	2.12	0.21	
		log-series	86.32	29.33	4.08	0.08	
		power	83.59	29.58	4.32	0.07	
resources (diffuse)	55	log-series	165.24	64.50	0	0.35	0.37
		power	165.46	64.47	0.07	0.34	
		unimodal	162.61	65.62	1.12	0.20	
		lognormal	172.37	66.82	2.32	0.11	

All colonies were collected without replacement over a four-month period, following an 'exhaustive sampling' protocol, wherein standing litter was carefully searched for ant colonies (Bestelmeyer *et al.* 2000). Every ant was identified to species or morphospecies (using Bolton 1994; Longino & Hanson 1995; Wilson 2003). The total number of worker ants nesting within the leaf litter of each plot was used as the measure of the number of individuals. Exact counts of the number of workers are used, as opposed to estimates of colony densities because litter colonies are often polydomous (include more than one nest) and the MIH mechanism should apply independently of whether those individuals are clumped or randomly distributed.

Statistical analyses were performed using JMP 8.0.1 (SAS Institute, 2009). Considering the control and each treatment separately, we first evaluated a unimodal (quadratic) model, and three monotonic models (lognormal, log-series and a power function) for the relationship between richness and the number of individuals. Akaike's information criterion (AIC) weights were calculated to evaluate parsimony. We used analysis of variance of the best model in the untreated plots to evaluate the effect of treatments.

3. RESULTS

The unimodal model (ant richness highest at intermediate densities) was strongly supported in the unmanipulated plots and disturbance treatments (table 1, figure 1). In these cases, richness declined or plateaued at high densities. Applying this model to all samples pooled together, the unimodal curve for the richness–density relationship was well supported ($r^2 = 0.48$, $F_{10,256} = 23.6$, $p < 0.001$). In contrast to the expectation from MIH, there was a significant effect of treatment in a regression with the unimodal model ($F_{1,4} = 2.89$, $p = 0.023$), indicating differential responses among treatment and control categories. The equations for the best-supported models follow: control: richness = $1.67 + 0.0098$ individuals $- 0.000023$ (individuals $- 143.3$)²; resources (clumped): log richness = $-0.65 + 0.380$ log individuals; resources (diffuse): richness = $-1.27 + 1.03$ log individuals; disturbance: richness = $1.50 + 0.013$ individuals $- 0.000026$ (individuals $- 133.7$)².

4. DISCUSSION

The MIH predicts that as productivity increases, so too does the density of individuals and consequently

species richness. The results of our manipulations of a diverse, tropical, litter ant community deviated from these expectations in two ways. First, we found that the relationship between ant density and richness was unimodal rather than monotonic in the unmanipulated and disturbance treatments, such that adding individuals did not simply add species. These results are in contrast to the expectations of the MIH, but in line with expectations from recent studies (Tilman *et al.* 2001; Currie *et al.* 2004; Evans *et al.* 2005b), which also fail to support the MIH. Second, all of our treatments resulted in an increase in richness for a given number of individuals, not simply increases in richness owing to increases in the number of individuals. We address each treatment in turn.

(a) Resource supplementation

Under the MIH, resource supplementation should increase the density of individuals and, consequently, species richness, but should not influence the shape of this relationship. In our experiments, individual density and species richness both increased with resource supplementation, in line with the predictions of the MIH (more food = more individuals = more species). Our results are analogous to a study on the Cedar Creek long-term ecological plots (Haddad *et al.* 2001), in which increases in resource availability to plants (with fertilizers) led to increases in the abundance and consequently diversity of detritivores. On its own, these results do not deviate from MIH predictions, but because our other results did (unmanipulated and the disturbance treatment) we suspect an alternative mechanism underlies the responses we observed. We infer that at higher densities, supplemental food prevents the exclusion of other species by competitive dominants (and hence the declining phase of the richness/density relationship).

Responses of ants to resource addition were independent of how resources were added, with one exception. Ant density explained nearly twice as

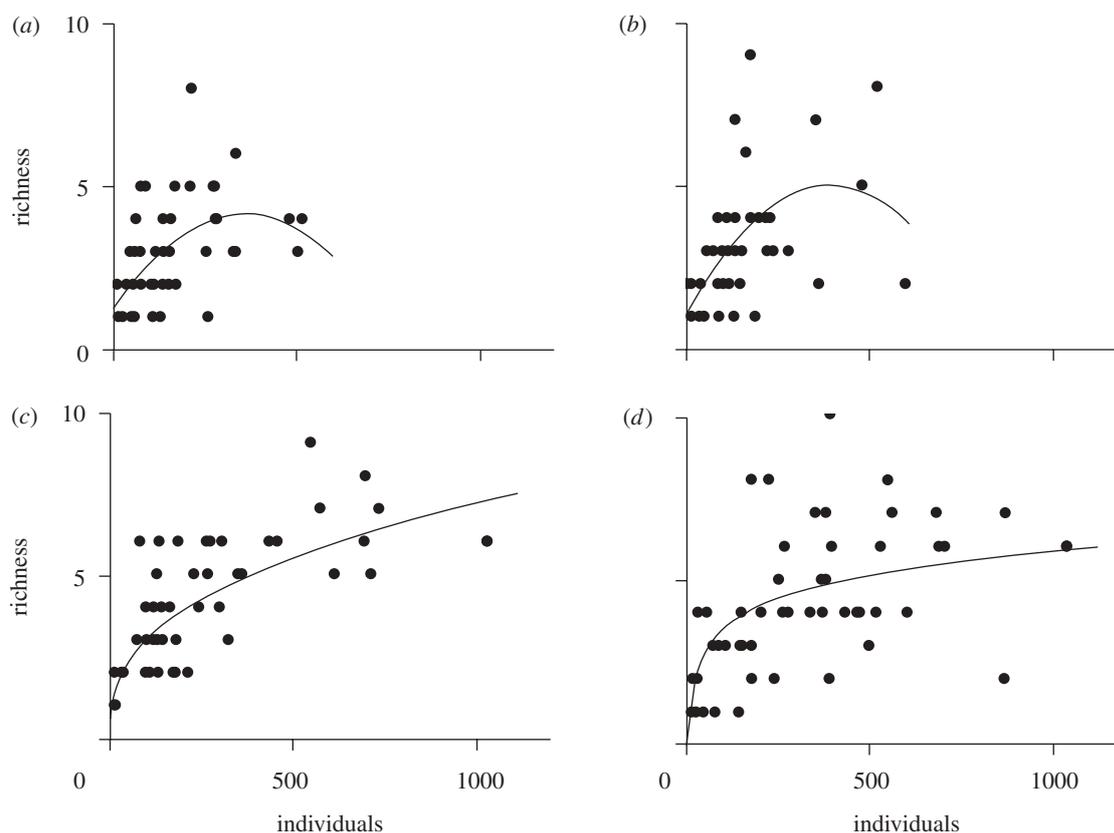


Figure 1. Most parsimonious models, from table 1, of regression of ant species richness by ant density (number of adult workers). Each circle represents an independent 1 m² plot. (a) Control; (b) disturbance; (c) resources (clumped); (d) resources (diffuse).

much of the variation in richness when food was added in clumps, compared with just over one-third when food was added in a diffuse fashion. One interpretation of this pattern is that the influence of competition on the shape of this relationship is stronger where resources are patchier and competition is more intense (McGlynn & Kirksey 2000).

(b) *Disturbance*

The disturbance created by litter removal should, under the MIH, reduce richness by reducing the number of individuals. By contrast, in models that emphasize the role of competition, disturbance is predicted to increase richness for a given productivity or number of individuals (Proulx & Mazumder 1998). This increase is predicted to occur via reductions in the abundance of the most competitively dominant species, particularly where productivity is high, as in our sites (Proulx & Mazumder 1998). In our experiments, disturbance did not have the effect predicted on the basis of the MIH (a decrease in individual density and associated decrease in richness). Instead, we saw a modest increase in richness for a given number of individuals.

(c) *Conclusions*

To summarize, resource addition yielded responses only partially reconcilable with MIH and disturbance produced the opposite response of that predicted by the MIH. Our results seem reconcilable with a model

whereby richness is limited by competition when resource levels (and individual densities) are low, but not necessarily when they are high. If our results generalize, a key question becomes, what sets the point at which richness begins to decline or plateau with increases in resources and individual density? Within a site, disturbance and resource supply rates both appear important. However, across sites it may be that regional species pools limit richness. If so, and if the balance between extinction and speciation is spatially coupled with NPP or related variables, then linear productivity–richness relationships might be common (Kaspari *et al.* 2000) even if the MIH does not operate at local scales.

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