

LETTER

Extinction order and altered community structure rapidly disrupt ecosystem functioning

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Abstract

By causing extinctions and altering community structure, anthropogenic disturbances can disrupt processes that maintain ecosystem integrity. However, the relationship between community structure and ecosystem functioning in natural systems is poorly understood. Here we show that habitat loss appeared to disrupt ecosystem functioning by affecting extinction order, species richness and abundance. We studied pollination by bees in a mosaic of agricultural and natural habitats in California and dung burial by dung beetles on recently created islands in Venezuela. We found that large-bodied bee and beetle species tended to be both most extinction-prone and most functionally efficient, contributing to rapid functional loss. Simulations confirmed that extinction order led to greater disruption of function than predicted by random species loss. Total abundance declined with richness and also appeared to contribute to loss of function. We demonstrate conceptually and empirically how the non-random response of communities to disturbance can have unexpectedly large functional consequences.

Keywords

Ecosystem function, extinction, habitat fragmentation, dung beetle, bee, crop pollination, biodiversity, California, Venezuela, null model.

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INTRODUCTION

Rapid rates of global biodiversity loss are intensifying the need to understand the consequences for the functioning of ecosystems (Purvis & Hector 2000). Most studies to date have focused on the relationship between species richness and function, without including other components of biodiversity (Symstad *et al.* 2003). Species richness may indeed be important for maintaining functional processes because of interspecific differences in how species process resources, affect the physical environment, and interact with other species (Chapin *et al.* 1997; Tilman 1999). While the importance of richness has been hotly debated (Cameron 2002), two critical yet well-known observations have been lost: (i) environmental changes do not affect species composition randomly (Cardinale *et al.* 2000) and (ii) many other functionally important aspects of communities can be affected independently or in addition to species richness (Chapin *et al.* 1997).

Predicting how ecosystem function will change when species are lost from natural systems therefore requires

synthesis of factors including: the order of species extinctions (Petchey & Gaston 2002); interspecific differences in functional contribution (Symstad *et al.* 1998; Balvanera *et al.* 2005); interspecific differences in abundance/biomass (Power *et al.* 1996); spatial and temporal variability of community structure (Symstad *et al.* 2003); the immediate response of the community following species loss (Ruesink & Srivastava 2001); and the longer-term feedbacks resulting from altered community structure and function (Chapin *et al.* 2000). Although it may be experimentally impossible to generalize the functional effects of each factor independently, human-modified landscapes provide settings that allow examination of how all of these factors and functional processes are actually changing.

The majority of richness–function studies, often incorrectly referred to as diversity–function studies, have isolated species richness as the explanatory variable of interest by experimentally creating randomly assembled communities of differing richness, frequently focusing on plant communities (Loreau *et al.* 2001). While useful for determining whether species richness is inherently related to ecosystem function,

such studies do not mimic community structure in naturally occurring communities and may therefore misrepresent the impact of environmental change on ecosystem attributes (Schwartz *et al.* 2000). Two critical aspects of community response to environmental change need to be incorporated into the next generation of studies that examine the relationship between biodiversity and function.

First, changes in total and relative abundance/biomass distributions among species can affect ecosystem function, sometimes independently or concordantly with changes in species richness (Cardinale *et al.* 2000; Wilsey & Potvin 2000; Smith & Knapp 2003). The majority of experimental richness–function studies, however, have held total abundance and/or species evenness constant across richness treatments (Wilsey & Polley 2004). In nature, relative abundance distributions are uneven, and density compensation in response to local species loss may not occur for several reasons, including dispersal and recruitment limitations into vacated niches and disturbance-induced changes in factors regulating population size (Duarte 2000; Symstad & Tilman 2001; Kremen *et al.* 2002; Klein *et al.* 2003; Ricketts 2004). Whether or not density compensation occurs following species loss may greatly affect the richness–function relationship (Fig. 1).

Second, the order of species loss with disturbance in natural communities appears to have dramatic consequences for ecological function (Petchey 2000; Jonsson *et al.* 2002; Ostfeld & LoGiudice 2003; Zavaleta & Hulvey 2004). The functional consequences of extinctions will largely

depend on two different types of species-specific traits: response traits (those that determine sensitivity to disturbance) and effect traits (those that determine the functional contribution of a species) (Lavorel & Garnier 2002; Naeem & Wright 2003; Solan *et al.* 2004). If response and effect traits are independent, the order of species loss from communities will be random with respect to functional importance. However, a correlation between these traits can modify the relationship between richness and ecosystem function.

Based on these observations, we developed a conceptual framework to describe how species' response and effect traits and abundance structures can contribute to alternative richness–function relationships (Fig. 1). Previous richness–function reviews (*e.g.* Schwartz *et al.* 2000; Loreau *et al.* 2001) discuss richness–function relationships that vary between linear and saturating (Fig. 1, curves b1 and b2). We argue that both because real communities are assembled non-randomly and vary in abundance, extinctions and altered community structure can lead to alternative forms of the richness–function curve (*e.g.* Fig. 1, accelerating and sigmoidal curves, b3 and b4). Determining the form(s) of this function for communities responding to anthropogenic change is essential for developing conservation strategies that maintain ecosystem function (Kremen 2005). For example, the disassembly of communities in which functionally important species or guilds are also most extinction prone will lead to particularly rapid loss of function (Fig. 1, curve b3), as suggested by evidence from some mammal,

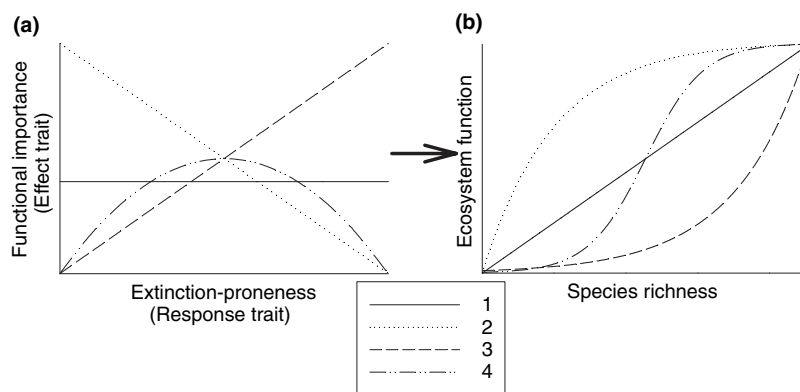


Figure 1 Hypothetical relationships between species traits, extinction order, density compensation and function: (a) the relationship between species response traits (extinction proneness) and effect traits (functional importance); (b) resulting richness–function relationship. Randomly assembled communities resulting from no response–effect correlation (*e.g.* a1) could lead to a linear increase of function with species richness (b1), although density compensation could make the curve saturating (b2). Non-random communities are assembled in rank order by extinction proneness, low to high. A negative response–effect correlation (a2) could result in a saturating functional form (b2). For example, this could arise from rare species with small population size and correspondingly small functional contributions being the most extinction prone. A positive response–effect correlation (a3) could result in a curve that is accelerating upward, indicating large loss of function with initial extinction, although this curve could approach linear (b1) with density compensation. For example, this functional form has been proposed for large vertebrate consumers that are highly sensitive to disturbance and are functionally strong interactors in food webs (Duffy 2003). Finally, a humped response–effect relationship (a4) could result in a sigmoidal richness–function relationship (b4).

bird and plant communities (Petchey & Gaston 2002; Duffy 2003; Zavaleta & Hulvey 2004). In such cases, it is especially critical to protect the most sensitive species in order to maintain ecosystem health and prevent cascading extinctions.

We tested our conceptual model by examining how habitat loss affected community structure and function for two functional guilds in two ecosystems: dung beetles in a tropical forest and bees in a temperate agro-natural landscape. Dung beetles accelerate nutrient recycling rates, increase plant yield, act as secondary seed dispersers, and help to regulate parasites of mammals (Mittal 1993; Andresen 2003). Foraging bees pollinate an estimated 60–70% of flowering plant species (Axelrod 1960) and enhance crop production by partially or fully replacing services provided by managed bee pollinators (Kremen *et al.* 2002; Klein *et al.* 2003; Kremen *et al.* 2004; Ricketts 2004). To provide a basis for interpreting our observed results and to help disentangle the effects of various variables, we also constructed artificial communities to simulate the independent effects of extinction order, density compensation, and species evenness on function. We focus on three primary research questions: (i) how do changes in species richness, evenness and total abundance/biomass affect ecosystem function? (ii) is the richness–function relationship modified by an association between species' response and effect traits? (iii) how does the observed sequence of local extinctions affect ecosystem function when compared with random species loss?

MATERIALS AND METHODS

Sites

The dung beetle study was conducted on forested islands in Lago Guri, a lake located in the state of Bolivar, Venezuela (7°20'N, 62°48'W) at 270 m a.s.l. The islands were created by the construction of a hydroelectric dam in 1986 which flooded an area of 4300 km² of semi-deciduous tropical forest (see Terborgh *et al.* 1997 for details). Studies of wild bee pollination were conducted on 14 organic and conventional watermelon farm sites in Yolo County, California that varied in proximity to natural habitat, forming a gradient of agricultural intensification (Kremen *et al.* 2002).

Diversity patterns

Beetles were sampled on the mainland and on 29 islands ranging in size from 0.16 to 181 ha. We sampled during May, June and July of 2002 and during May and June of 2003. To assess dung beetle community structure and diversity, we set human dung baited pitfall traps along linear transects with traps spaced 50 m apart (see Larsen & Forsyth 2005 for details). Transect length varied according

to island size, and we continued sampling until species accumulation curves demonstrated nearly exhaustive sampling of richness for each island (Colwell & Coddington 1994). To correct for differential transect length between islands, abundance was calculated as beetles per trap per 24 h. Data from two mainland sites and the largest island (181 ha) were averaged to represent the reference (most pristine) community. Each island was used as an independent community in the analysis. Mark-recapture experiments confirmed that movements of individuals between islands were extremely low (T.H. Larsen, unpublished data). Species collected at only one site were omitted from the analysis because it is likely that they were not widely distributed across the original unfragmented landscape.

Bee abundance and diversity were assessed in watermelon patches along 50 m transects for 10 min each half an hour from 730 to 1430 h on a single day for each farm site during allowed weather conditions. Bees were identified to the lowest taxonomic level (species or genus) and were sexed. Sampling effort was equivalent among sites. Data from the five organic farms near natural habitat were averaged as the reference condition (see Kremen *et al.* 2002 for further details on all methods related to bee study).

Ecosystem function and species traits

Dung burial rates were measured on the mainland and on 14 of the islands. Ten gram cylinders of dung were placed on the ground along linear transects beginning at 530 h. Dung cylinders were spaced at 30 m apart so that each cylinder represents an independent data point, based on studies of dung beetle movement and attraction distance in the same area (Larsen & Forsyth 2005; T.H. Larsen unpublished data). As above, transect length varied according to island size ($n \geq 3$, mean = 14), and experiments were repeated on multiple days. A visual estimation of the percentage of dung removed was recorded every 30 min for up to 3 h or until all of the dung had been buried, and then converted to grams.

To determine species-specific dung burial efficiencies (BE, the average amount of dung buried by one individual), we weighed the amount of dung removed by individual beetles for five species. Each individual was provided with more dung than it could bury and was left alone until it ceased to remove dung. The removed dung was immediately collected and weighed with a Pesola Scale. Between 1 and 8 trials were conducted for each species (median = 7). For species for which dung was not weighed, BE was estimated based on the exponential function, $BE = 0.03 \exp(0.5 \times \text{elytra width})$, (non-linear regression, $F = 198.3$, $P = 0.001$, $R^2 = 0.99$). Larger beetle species are well-known to bury more dung (Doubt 1990). Actual dung burial rates were used in all analyses, except for the simulation (described

below), which used estimated species' BE. We tested our BE estimations by comparing predicted dung burial rates from the simulation with observed dung burial rates for the 15 sites and found a strong correlation (Spearman's Rho (ρ) = 0.76, P = 0.001).

Pollination efficiencies (pollen grains deposited/individual/visit) were measured by allowing individuals of each sex of each species-group to visit a previously unvisited female watermelon flower, and then counting the pollen grains remaining on the stigma following the visit. Pollen deposition measurements were made in the morning when pollen supplies were not limiting. Total pollen deposition per farm site was then estimated by summing efficiency \times abundance (for each species-group and sex) over the time period studied, which corresponds to the period that a female watermelon flower is typically open.

To measure mean beetle biomass we preserved beetles in 70% ethyl alcohol, dried them in a laboratory hood for 3 weeks, and finally placed them in a drying oven at 105 °C for 24 h. Between three and 25 individuals were measured for each species, except for two uncommon species for which one and two individuals were measured respectively (median = 20.5). We pooled measurements for males and females, as we did not find biomass sex differences for any of the 20 species for which we had at least three males and three females (t -tests, data not shown). To estimate mean biomass for each bee species and sex, between 6 and 26 measurements of intertegular span (IT) were made on pinned, dried vouchers of female bees from our study sites (median = 14), and between 4 and 10 for male bees (median = 5). The IT were then converted to dry weights (mg) using the power function, $IT = 0.77(\text{dry weight})^{0.405}$ ($R^2 = 0.96$, Cane 1987).

Analysis

To determine the completeness of faunal sampling in each system, we compared the observed number of species to the expected number of species based on species estimators from species accumulation curves computed using EstimateS (Version 7, R. K. Colwell, <http://purl.oclc.org/estimates>). We used four different commonly used richness estimators (ACE, ICE, Chao1 and Chao2). Nestedness of communities (the degree to which the composition of less diverse communities represents subsets of diverse communities) was calculated using nestedness calculator software (Atmar & Patterson 1995).

To examine the form of the richness–function relationship, we used a simple power model that runs through the origin, $y = \alpha x^\beta$. This function allows for accelerating, linear and saturating relationships depending on the magnitude of the exponent and meets the logical requirement that communities with no species perform no function. To

estimate the exponent (β) we first log-transformed the power function, which normalized residuals, and then used generalized linear models with maximum likelihood to estimate parameter values and their confidence limits (Proc GENMOD; SAS, SAS Institute, Cary, NC, USA). We used bivariate linear regressions to identify the relationship between species richness and abundance/biomass, and between ecosystem function and abundance/biomass. Variables were transformed if necessary to achieve normality. We did not use multivariate analyses to disentangle the relative roles of these various aspects of community structure on function because of collinearity of some variables. Because dung burial was measured in the early morning, only the 15 diurnal and crepuscular beetle species were included in these ecosystem function regressions. Nighttime dung burial rates appeared to follow the same trend as daytime rates, as predicted daytime burial rates (based on simulation results presented below) correlated with predicted nighttime burial rates (Spearman's ρ = 0.52, P = 0.002). For both taxa, we used Spearman's rank correlations to determine the relationship of species traits with extinction proneness (response traits) and with functional efficiency (effect traits). Extinction proneness represents the proportion of sites/communities from which each species was absent.

Simulations

We used Monte Carlo simulations to examine how the order of species extinctions and species' abundance structures affected ecosystem function for artificially constructed communities as well as real beetle and bee communities. First, we isolated the functional effect of extinction order by using randomized simulations that controlled for concurrent changes in total abundance, relative abundance and species richness. We created three scenarios for artificial communities representing different relationships between response and effect traits. Each scenario consisted of 10 species and 10 sites, with each site containing a unique number of species between one and 10. Functional efficiency represents the amount of function performed by an individual of a species (Balvanera *et al.* 2005). In these scenarios, the most functionally efficient species are lost either first (perfectly positive-correlated response and effect traits), last (perfectly negative-correlated response and effect traits), or intermediately (humped relationship between response and effect traits). All species were equally abundant within a site, and total abundance decreased perfectly linearly with declining species richness, reflecting the lack of strong density compensation observed in our study (see Results) and in other real communities (e.g. Klein 1989; Klein *et al.* 2003).

For each ordered (artificial or real) community, the simulation created 250 replicate null communities by

randomly selecting a set of species from the total species pool to match the richness in the ordered community. While species evenness was maximized for artificial communities, for the real beetle and bee communities, the abundances of selected species were assigned based on observed values for those species in the baseline condition. This maintained relative species' abundances at realistic levels while allowing us to assign abundance values to randomly selected species that were not present at the observed site. For both beetles and bees, baseline habitats were those that contained the highest total richness and abundance (T. H. Larsen, unpublished data; Kremen *et al.* 2002). The assigned abundance, A_i , for each selected species i at site j is determined as:

$$A_{i,j} = \frac{n_{i,\text{ref}}}{\sum_i n_{i,\text{ref}}} \times \sum_1^k n_{i,j},$$

where $n_{i,\text{ref}}$ is the observed abundance of selected species i in the baseline community for each of the k selected species. Biomass was used instead of number of individuals for dung beetles, as it is an abundance metric more directly related to dung burial (Doubt 1990). The functional contribution of each component species was calculated as the product of that species' functional efficiency times its assigned abundance/biomass in that community, and total function for the site was calculated as the sum of this product over all species (Balvanera *et al.* 2005). We plotted the difference in total ecosystem function between ordered and randomly assembled communities among sites and used chi-squared tests to examine whether observed extinctions led to an overall gain or loss-in-function relative to random extinctions.

Second, we used the same simulations to examine the functional effects of density compensation and species evenness. As the reference for both cases, we chose the same artificial scenario described above for which the most functionally efficient species were lost first. To assess the effect of density compensation, we modified the scenario so that the total abundance remained constant across sites with species loss. To assess the effect of species evenness, we modified the scenario so that species evenness varied in two

ways. First, we made the most functionally efficient species the most abundant, with a perfect positive linear relationship between efficiency and abundance. Second, we constructed the opposite scenario with the most functionally efficient species the least abundant.

RESULTS

Diversity patterns

We collected 24 species of dung beetles (see Appendix S1) and 12 species-groups (species or genera) of bees (see Kremen *et al.* 2002 for identities). All four species estimators based on species accumulation curves indicated that we captured 100% of dung beetle and bee species at the sites. Species richness for beetles and bees was highly nested across sites such that less diverse sites contained subsets of the species present at more diverse sites (beetles: temperature 9.46 °C, randomized 59.52 °C; Monte Carlo, $P \ll 0.001$; bees: temperature 10.93 °C, randomized 48.63 °C, $P \ll 0.001$). Dung beetle species richness and abundance decreased sharply with declining island area (linear regression of richness on log area: $R_{\text{adj}}^2 = 0.76$, d.f. = 29, $F = 90.42$, $P \ll 0.001$; abundance, $R_{\text{adj}}^2 = 0.28$, d.f. = 29, $F = 12.32$, $P = 0.002$). Bee species richness and abundance decreased with declining proportion of natural habitat within 2.4 km (Kremen *et al.* 2004) of the farm site (richness, $R_{\text{adj}}^2 = 0.62$, d.f. = 13, $F = 22.40$, $P = 0.0005$; abundance, $R_{\text{adj}}^2 = 0.46$, d.f. = 13, $F = 12.06$, $P = 0.005$). For both beetles and bees, abundance and biomass were positively related to species richness, suggesting weak density compensation (Table 1). In addition, abundance and biomass of individual bee and beetle species either showed positive relationships with richness or were not significantly related (linear regression of abundance or biomass on richness, data not shown).

Functional changes related to richness and abundance

Beetle species richness was strongly positively associated with dung burial rates among island sites (Fig. 2a).

Dependent	Independent	R_{adj}^2	d.f.	F	P -value
Abundance	Beetle richness	0.44	29	23.35	$\ll 0.001$
Biomass	Beetle richness	0.33	29	15.14	0.0006
Abundance	Bee richness	0.37	13	8.7	0.01
Biomass	Bee richness	0.56	13	17.84	0.001
Dung burial rate	Beetle abundance	0.32	14	7.60	0.016
Dung burial rate	Beetle biomass	0.32	14	7.52	0.017
Ln (pollen deposition)	Bee abundance	0.60	13	20.11	0.0007
Ln (pollen deposition)	Bee biomass	0.48	13	13.08	0.004

Table 1 Linear regression results

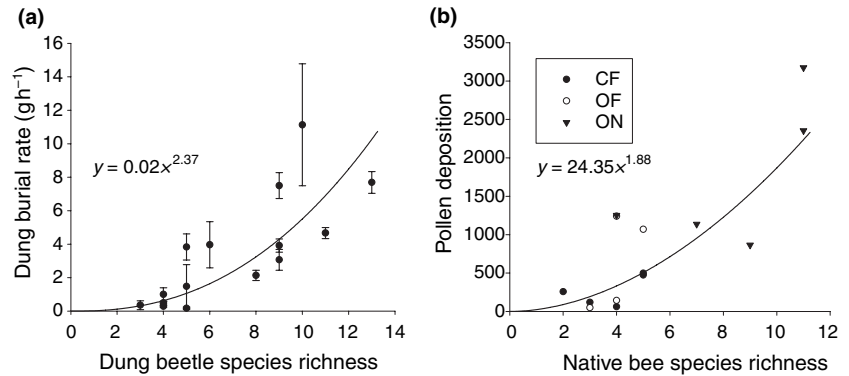


Figure 2 The relationship between species richness and function for (a) dung beetles and (b) bees, across sites using maximum-likelihood estimated power function $y = \alpha x^\beta$. Bees: CF, conventional far farms; OF, organic far; ON, organic near.

Likewise for bees, species richness was significantly related to estimated total pollen deposition among farm sites (Fig. 2b, Kremen *et al.* 2002). In both systems the most likely relation between richness and function was concave up ($\beta > 1$; parameters \pm SE and back-transformed: beetles $\alpha = 0.02 \pm 0.03$, $\beta = 2.37 \pm 0.44$; bees $\alpha = 24.35 \pm 31.22$, $\beta = 1.88 \pm 0.50$) indicating that the first species extinctions led to rapid functional loss. However, in the case of bees the 95% confidence limits overlapped 1.0 (beetles 1.46–3.29, bees 0.84–2.93). For both beetles and bees, abundance and biomass were also positively related to function in single regressions (Table 1).

Response and effect traits

Response traits

For beetles and bees, extinction proneness (number of local extinctions) correlated with mean body mass (beetles: Spearman's $\rho = 0.48$, d.f. = 23, $P = 0.017$; bees: Spearman's $\rho = 0.83$, d.f. = 11, $P = 0.0009$; Fig. S1a,c). Neither bee nor beetle commonness (assessed as baseline abundance), a good indicator of population size, was related to extinction proneness (beetles: $P = 0.16$; bees: $P = 0.27$).

Effect traits

Observed dung BE was positively related to dung beetle body mass ($\rho = 1.0$, $P < 0.01$; Fig. S1b). For bees, pollination efficiencies correlated weakly with body mass ($\rho = 0.55$, $P = 0.07$; Fig. S1d). There was a positive trend for beetles and a significant positive relationship for bees between extinction proneness and functional efficiency (beetles: $\rho = 0.40$, $P = 0.055$; bees: $\rho = 0.69$, $P = 0.012$; Fig. S1e,f). Therefore, for beetles, large species were simultaneously more functionally efficient and more extinction prone. For bees, the most efficient species were most extinction prone. Large bees were more extinction prone and tended to be more functionally efficient.

Simulations

Extinction order

Simulations done with artificial communities allowed us to isolate the functional effects of different variables and confirmed the expectations of our conceptual model (Fig. 1). Species extinction order strongly modified ecosystem function (Fig. 3a). When response and effect traits were perfectly positively correlated, so that the most functionally efficient species were the first to go extinct, artificial communities lost more function at all sites than predicted by random species loss and function was lost rapidly. If the most functionally efficient species were the last to go extinct, communities lost less function across all sites than predicted by random species loss. A humped relationship between response and effect traits (Fig. 1, curve a4) resulted in a sinusoidal relationship. The inflection point was shifted left or right in accordance with left or right skewness of the response–effect curve (data not shown).

The observed order of extinction for real communities resulted in larger functional loss than a random order of extinction. For the beetles, 90% of sites lost more function than expected with random species loss (Fig. 3b, $X^2 = 19.2$, d.f. = 1, $P < 0.0001$). For the bees, 86% of the sites lost more function than expected with random species loss (Fig. 3c, $X^2 = 7.1$, d.f. = 1, $P < 0.01$). The distribution of values for beetles and bees appears similar to a distribution of values for artificial communities in which the most functionally important species are among the most extinction prone.

Species evenness and density compensation

Changes in species evenness modified function, using as a reference the artificial scenario described above in which all species were equally abundant and the most functionally important species were also the most extinction prone (Fig. 4a). As we would predict, when functionally efficient species were the most abundant, the loss of these species caused a larger decrease in function across all sites. If

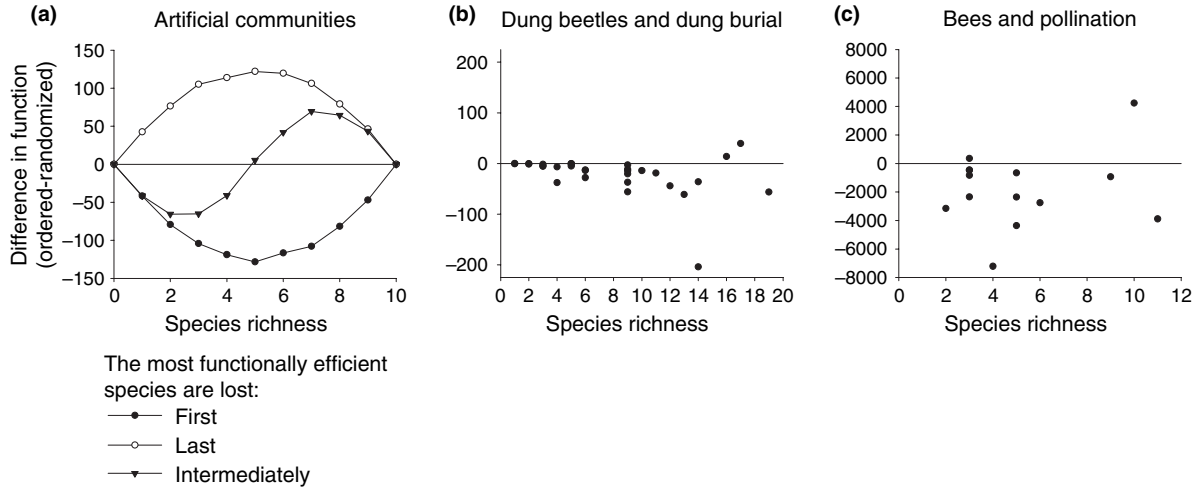


Figure 3 Functional consequences of extinction order. Y-axis represents the deviation of observed function from the function expected from a null community that is randomly assembled but maintains site-specific total abundance and species richness. Negative y-values represent sites that lost more function than predicted by random species loss, while positive y-values represent sites that lost less function than predicted with random species loss. (a) The functional consequences of extinction order for artificial communities under different extinction scenarios (perfect species evenness). (b, c) The functional consequences of extinction order for dung burial and for pollination in observed beetle and bee communities.

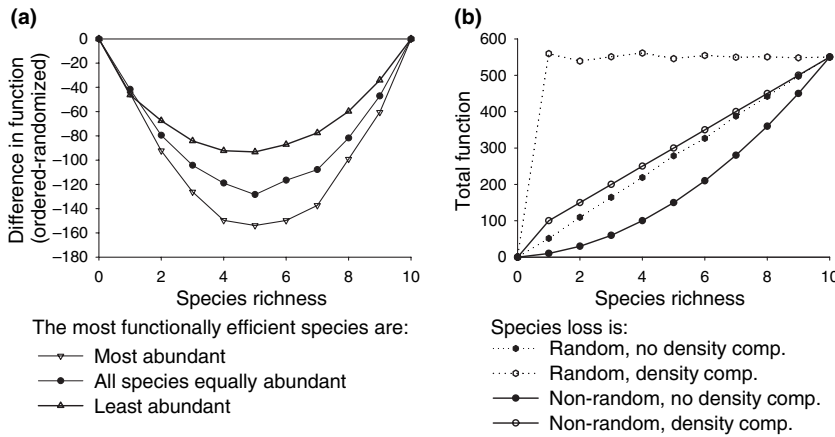


Figure 4 Effects of varying abundance on ecosystem function using artificial communities in which the most functionally efficient species are the most extinction prone. (a) The functional consequences of alterations in patterns of species evenness relative to efficiency. The most efficient species are most abundant, least abundant, or intermediate in abundance. (b) The functional consequences of density compensation on ecosystem function for randomly assembled vs. ordered communities. All species are equally abundant.

functionally efficient species were the least abundant, the absolute difference in function was reduced for all sites.

Density compensation also affected function (Fig. 4b). If species extinctions occurred randomly and there was no density compensation, ecosystem function decreased linearly with species loss. However, complete density compensation caused function to remain virtually unchanged with species loss. Based on the same artificial scenario in which the most functionally efficient species were the most extinction prone, complete density compensation caused the accelerating richness–function relationship to become linear, as predicted by the conceptual model (Fig. 1).

DISCUSSION

By studying communities that were naturally disassembled in response to disturbance, we found that changes not only in species richness but also in abundance and species composition all appear to affect ecosystem function in two systems with entirely different taxa, functional processes and habitats. Furthermore, the order of species extinctions caused function to be disrupted more rapidly than expected. With loss of natural habitat, we observed reduced pollination services by bees (Kremen *et al.* 2004) and decreased dung burial by beetles. On small, but not large islands, we

observed large accumulations of unburied howler monkey dung. Changes to dung beetle and bee communities could have serious consequences for ecosystem functions and services, lowering crop yields (Kremen *et al.* 2002; Klein *et al.* 2003; Ricketts 2004) or disrupting plant regeneration, nutrient cycling and parasite regulation (Klein 1989; Mittal 1993; Vulinec 2002; Andresen 2003). Such changes are likely to have cascading and long-term effects throughout the ecosystem (Terborgh *et al.* 2001). This suggests that previous emphasis on the relationship between species richness and function in experimentally assembled communities reveals only part of the biodiversity–function relationship.

Loss of function with local extinctions of dung beetles and bees is most likely greatest for initial extinctions (Fig. 1, curve b3; Fig. 2), although the richness–function form for bees did not differ significantly from linear (Fig. 1, curve b1). Both forms represent more rapid functional loss with species extinctions than are often found in experimental communities (Schwartz *et al.* 2000). Two main factors correlated with the loss of ecosystem function in beetle and bee communities: the non-random loss of species and the lack of strong density compensation following species loss. Three lines of evidence support the importance of non-random species loss in exacerbating effects of species extinction on function. First, dung beetle and bee species did not disappear randomly from disturbed sites; instead species were lost in an ordered fashion leading to nested community sets. Second, the rapid decline of function likely reflects the correlation between response and effect traits (Fig. 1, curves a3 and b3), as the most functionally efficient species tended also to be the most extinction prone. Third, simulations using null communities of randomly assembled species composition indicated that fragmentation and agricultural intensification may be causing much greater functional loss than would be expected under random loss of species. Over 85% of sites for both bees and beetles lost more function than expected; the few sites that exhibited higher function than expected were among the most species rich, having lost only one or two species that were so low in abundance as to contribute little to function (Fig. 3b,c).

Correlations between response and effect traits may exist in many communities influenced by disturbance. Large species often tend to be more extinction prone (Gaston & Blackburn 1995) and more functionally important (Duffy 2003). Although this trend may be more common for animals (Duffy 2002), it has also been observed in some plants (Duarte 2000). As most studies have focused on plants and/or artificially assembled communities that do not take extinction order into account, the rapid loss of function with initial species extinctions may therefore be more widespread than previously thought. Examining artificial

communities, we found that species evenness and the role of species' abundance as a response or effect trait can also modify function (Fig. 4a). For real beetle and bee communities, species' baseline abundance was not related to extinction proneness. However, when rare species are the most extinction prone, communities may lose function much less rapidly than we found in this study, as has been found for the non-random loss of some plant species (Wilsey & Polley 2004). On the contrary, other studies show that even if rare plants are extinction prone, rare species can be disproportionately important for maintaining invasion resistance (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004).

Even if communities do lose the most functionally important species first, simulation of artificial communities showed that density compensation can buffer against functional loss and shift the form of the richness–function relationship from accelerating to linear (Fig. 1, curves b1, b3; Fig. 4b). However, neither bees nor beetles demonstrated much density compensation (Table 1); thus with the loss of species there was a concomitant decline in total abundance and biomass, which was also related to reduced function. Many communities, particularly those strongly affected by human disturbances, show a lack of density compensation with species loss (Klein 1989; Vulinec 2002; Klein *et al.* 2003; Ricketts 2004). Agricultural landscapes with repeated annual disturbance provide one example of how disturbance may prevent compensatory increases in abundance following species loss. In addition to differing degrees of density compensation, systems in which competition and species interactions strongly influence ecosystem function may increase the complexity of richness–function relationships and lead to different results than those found in our study (Tilman 1999).

In summary, the large and rapid functional losses in bee and beetle communities probably resulted from the dual effects of (i) positive correlation between response and effect traits and (ii) weak or no density compensation. Rather than finding that function saturated with higher species richness, we found that beetles showed an accelerating richness–function relationship, and bees showed a linear to accelerating relationship. For similar communities in which sensitive species also tend to be more functionally important, such as communities containing top predators, it may be critical to target the requirements of the most sensitive species in order to maintain ecosystem integrity. This finding is contrary to predictions made by traditional richness–function models which are based primarily on artificially assembled communities or communities with very few species. There are several other ways in which species richness can be important for maintaining function (Schwartz *et al.* 2000), including temporal and spatial

turnover (Herrera 1988; Kremen *et al.* 2002; Balvanera *et al.* 2005), increased efficiency of resource use (Tilman 1999), and the occurrence of specialized functional relationships between species, such as between plants and their pollinators (Linder 2003). With environmental change and biodiversity loss occurring so rapidly, it is now imperative to examine how all aspects of community structure are changing in response to various kinds of disturbance, and how these changes then affect functional processes (Kremen 2005).

Two commonly used approaches to examine functional diversity are random assembly experiments and removal experiments (Diaz *et al.* 2003). We propose that examining naturally assembled communities across disturbed landscapes combines many useful aspects of both approaches by providing settings where the rules for changing community structure have already been applied. While it may be more difficult to address mechanisms directly, this approach in combination with field experiments and simulations such as those we provide here, is providing startling but urgently needed information about how attributes of real communities are changing and affecting functional processes (see also Solan *et al.* 2004; Zavaleta & Hulvey 2004; Kremen 2005). Understanding these patterns of change in biodiversity and their functional consequences should improve our ability to predict and mitigate future responses and protect the processes that sustain ecosystems in the long-term.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE749/ELE749sm.htm>

Figure S1 Response and effect traits for dung beetles and bees.

Appendix S1 Forest dung beetle species collected at Lago Guri, Venezuela.

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