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APPLYING COMMUNITY STRUCTURE ANALYSIS TO ECOSYSTEM FUNCTION: EXAMPLES FROM POLLINATION AND CARBON STORAGE

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Abstract. Human enterprise is increasingly affecting biodiversity beyond outright species losses, causing changes in ecosystem functions and the services they deliver to human beings. However, few tools are available to analyze how community attributes other than simple species richness affect ecosystem functioning, or how relative contribution to the function is distributed among the species within a community. Here, we adapted methods for describing the evenness in relative abundance among species (i.e., community structure) to the description of the evenness in species' relative contribution to ecosystem function (i.e., functional structure). We developed graphical approaches to: (1) describe the functional structure, (2) show the relationship between community and functional structures, (3) examine the influence of species identity on ecosystem function, and the relationship between species' relative functional contribution and relative abundance, and (4) determine the effects of management on the total magnitude of ecosystem function, on community and functional structures, and on individual species' contribution to the function.

We applied these methods to two contrasting ecosystem function cases: watermelon pollination by native bees in California and carbon storage in trees of a tropical humid forest in Chiapas, Mexico. Functional structure for pollination under organic management within a conserved forest matrix showed that the first two species contributed 80% of the function. Increasingly intensive management (e.g., conventional agriculture) caused the loss of 60% of the species, reductions in abundance of functionally important species, loss of 60–80% of the pollination function, and decreased evenness in functional structure. Functional structure for carbon storage of a conserved forest showed that 13% of species contributed 90% of the function. Forest under a hypothetical scenario of selective timber extraction showed a loss of 60% of carbon storage, no species loss, and an increase in evenness of the species' contribution to the function. Compared to conserved forest, secondary forests shared only 17% of species, 80% less carbon storage, but similar evenness of species' contribution to this function.

Overall, the tools developed here, and their applications, show that impacts of management regimes on functional structure vary with the analyzed function and ecosystem, differentially affecting species richness, species composition, dominance of the first-ranked species, evenness in species' functionality, and potentially the stability of the function itself.

Key words: *biodiversity conservation; community structure; carbon storage; crop pollination; diversity-function; dominance-diversity curves; ecosystem function; ecosystem service; indicator species; management; species richness.*

INTRODUCTION

Many studies have explored the relationship between ecological function and species diversity (Schulze and Mooney 1994, Loreau et al. 2001, Naeem et al. 2002); as yet, however, little has been done to describe and analyze the “functional structure” of ecosystems. Here we use functional structure to refer to the distribution of the relative contribution of species to an aggregate ecosystem function such as productivity (Hector et al.

1999b, Tilman et al. 2001), carbon cycling (Brown 1997, Clark and Clark 2000) or pollination (Herrera 1988, Kremen et al. 2002). This aggregate function results from the individual contributions of each species to the function, plus the effects of the species–species and species–environment interactions on that function (Fridley 2002, Paine 2002).

The relationship between ecosystem function and species diversity is highly debated (McCann 2000, Tilman 2000, Loreau et al. 2001, Naeem et al. 2002). Research has mainly focused on how species richness or the number of functional groups are related to the magnitude and variability of an ecosystem function (Hooper and Vitousek 1997, Hector et al. 1999a, War-

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dle et al. 2000, Tilman et al. 2001). In contrast, relatively little work has focused on the relationship between the magnitude of the function and its functional structure. Also, few initiatives have been undertaken to relate the magnitude of a function, or the species' relative contribution to the function, with species' abundances (but see Herrera 1988, Brown and Heske 1990, Lawton 1994, Sala et al. 1996), evenness (but see Purvis and Hector 2000, Wilsey and Potvin 2000), or identity (but see Jonsson and Malmqvist 2003, Ostfeld and LoGiudice 2003, Symstad et al. 2003). Understanding the consequences of gradual changes in abundances on the magnitude of the function, as opposed to abrupt changes such as species additions or deletions, could be particularly important given that disturbances (e.g., those caused by human activities) more frequently influence the abundances and evenness of species at local spatial and temporal scales (Dennis et al. 1997, Chapin et al. 2000, Scherer et al. 2000). In turn, since disturbance generally results in nonrandom patterns of species loss or reduction (Petchey and Gaston 2002), it is also important to understand the role of species identity in ecosystem function (Díaz and Cabido 2001, Symstad et al. 2003).

The development of methods for analyzing the functional structure of ecosystems would provide the basis for exploring how changes in species' abundance (due, for example, to management) affect species' functional contribution, ecosystem function, or the relation between the three. Such tools would be useful for better understanding those ecosystem functions that influence human welfare, e.g., ecosystem services (Daily 1997), and for assessing the potential coincidence or conflict between biodiversity-centered and ecosystem service-centered conservation initiatives (Balvanera et al. 2001).

Here, we first describe the functional structure in analogy to community structure by using dominance–diversity models of species contribution to total function rather than to abundance. Second, we explore the relationship between community and functional structures. Third, we examine, on a species by species basis, the relationship between species abundance and species contribution to the function. Fourth, we explore the effects of management on the magnitude of the function, on the functional structure, and on functionally sensitive species that can be used as indicators of the effects caused by management. Finally, to illustrate the use of these methods and their potential applications, we apply this four-part approach to two case studies: watermelon pollination by native bee species in California and carbon storage in trees of a tropical humid forest in Chiapas, Mexico.

CONCEPTUAL BASIS: ANALYSIS OF FUNCTIONAL STRUCTURE

We define the contribution of a given species, j , to a given aggregate ecosystem function, X , as c_{jx} . The

magnitude of the function provided by the entire community is

$$X = \sum_{j=1}^j c_{jx} \quad (1)$$

and the relative contribution of species j to aggregate functionality is

$$f_{jx} = c_{jx}/X. \quad (2)$$

In this equation, we do not explicitly consider species–species and species–environment interactions; they are assumed as part of individual species contributions.

The efficiency of a species, e_{jx} , is the species-specific per capita contribution of individuals of species j to the function. This efficiency can be constant for all individuals within the species. Then, species contribution to the function is simply the product of the efficiency and the abundance of species, n_j :

$$c_{jx} = n_j \times e_{jx}. \quad (3)$$

Otherwise, c_{jx} is the result of individual contributions of all individuals, k , of the species j to a given aggregate ecosystem function X :

$$c_{jx} = \sum_{k=1}^k e_{kix}. \quad (4)$$

The relative abundance of a given species j with respect to the total number of individuals in the community N is r_j :

$$r_j = n_j/N. \quad (5)$$

In analogy to species dominance–diversity models (Preston 1948, MacArthur 1957, Whittaker 1965, May 1975, Tokeshi 1993), which are obtained by plotting species' relative abundance (r_j) against the abundance rank of each species, we can graph species' relative functional contribution (f_{jx}) against the rank of functionality for each species. The shape of this curve reflects the way in which functional contribution is distributed across species (e.g., highly even or uneven, see Fig. 1a).

The same data can be plotted as cumulative magnitude of the function against species richness; here species are added in order of decreasing contribution to the function (Fig. 1b). As a result, a graph analogous to the widely discussed relationship between the magnitude of ecosystem function and species diversity (Vitousek and Hooper 1993, Schlapfer 1999) is obtained. When species are added at random (as they usually are in diversity–function experiments, e.g., Hector et al. 1999b), or in response to known environmental patterns (e.g., Ostfeld and LoGiudice 2003), different patterns may emerge. Thus, both the actual pattern of community assembly/disassembly and the relationship between species identity and function will greatly influence the relationship between aggregate ecosystem function and species diversity.

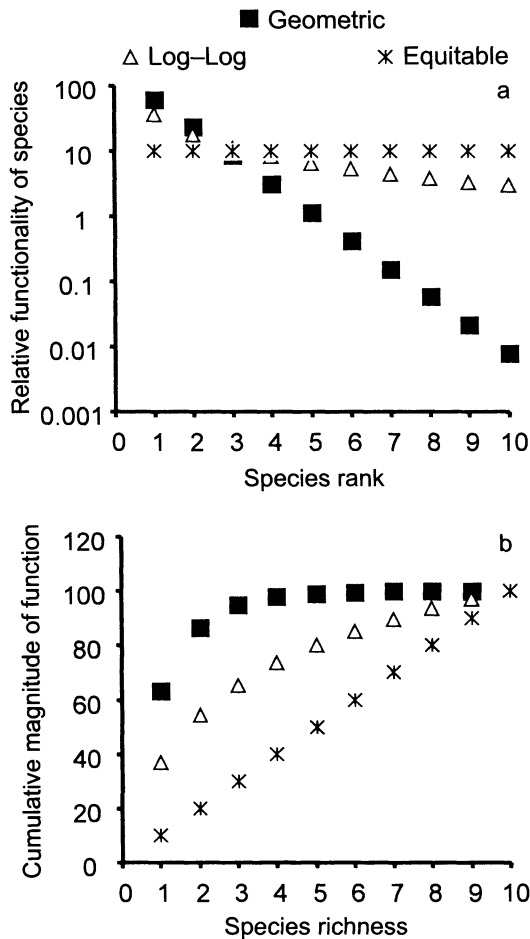


FIG. 1. Description of the functional structure of an ecosystem and the corresponding relationship between richness and magnitude of the function. (a) In analogy to species dominance–diversity curves, here the relative contribution of each species to a function, (f_{jx}) is plotted against its rank for decreasing contribution to the function. For illustrative purposes, three statistically oriented dominance–diversity models were chosen (Tokeshi 1993) to construct the curves: (1) logarithmic (May 1975), where $\log(f_{jx})$ declines constantly with each species (geometric); (2) an asymptotic model constructed with the Zipf or log–log model (Bastow 1992, Tokeshi 1993); and (3) a totally equitable model. (b) Plot of the cumulative magnitude of the ecosystem function vs. cumulative species richness (ordered by rank of decreasing functional contribution) for the three models. This graph is analogous to three alternative models proposed for the relationship between magnitude of an ecosystem function and species richness (Vitousek and Hooper 1993): (1) depending on only one or two species (logarithmic), (2) asymptotic (Zipf or log–log), and (3) linear (equitable model). Nevertheless, each model here represents a single treatment with addition of species in decreasing order of contribution to the function, rather than individual points representing independent treatments.

METHODS

Analytical tools for the analysis of functional structure

Description of the functional structure.—We applied the above framework assuming that measurements of

functional contribution by species are made on replicated treatments. For each replicate, species were ranked in decreasing order of their relative functional contribution, and the among-replicates average value of the i th species contribution was then calculated, irrespective of species identity (rank_j). Cumulative magnitude was calculated by adding the average value of the i th species contribution in order of decreasing rank, and was plotted against species richness. To visualize the functional structure, values of the i th species contribution were plotted against its rank. Best fit for the shape of functional structure was obtained using the following general linear model:

$$f_{jx} = b_1 - b_2 \text{rank}_j \quad (6)$$

with log-transformation of f_{jx} and rank_j as needed (Bastow 1992, Tokeshi 1993).

Relationship between community and functional structures.—The comparison between community and functional structures can be achieved using the following model:

$$Y = b_1 - b_2 \text{rank}_j + b_3 \text{structure type} + b_4 [\text{structure type} \times \text{rank}_j]. \quad (7)$$

Here, Y is the relative contribution to either abundance or the function of species j . The “structure type” term is a categorical independent variable for “community” or “functional” structure. The parameter b_1 is the overall y -intercept, i.e., the average species relative contribution to abundance or function of the species with the highest rank. The parameter b_2 is the overall slope of the function, i.e., the evenness of the contribution of species to abundance or function. The effect of structure type, accounted for by parameter b_3 , indicates differences in the y -intercept between community and functional structures and, thus, in dominance of the first-ranked species for abundance or function. The y -intercept is equivalent to the Berger-Parker index of dominance (Magurran 1988). The effect of the interaction term “structure type \times rank $_j$,” as estimated by parameter b_4 , accounts for differences in slope, i.e., species evenness, between community and functional structures. Differences in slope are comparable to differences in the Q statistic of dominance–diversity curves (Magurran 1988). Relative values can be transformed to arcsine to meet normality criteria (Sokal and Rohlf 1995); Generalized Linear Models with normal error for the y variable can then be used (Crawley 1993).

Species classifications.—Species were classified based on their relative abundance and relative functionality (Fig. 2). A priori boundaries based on orders of magnitude intervals were defined to distinguish species with low (<1% of total individuals), intermediate, or large (>10% of total individuals) contribution to abundance, and those with low (<1%), intermediate, or high (>10%) contribution to the function. Particular

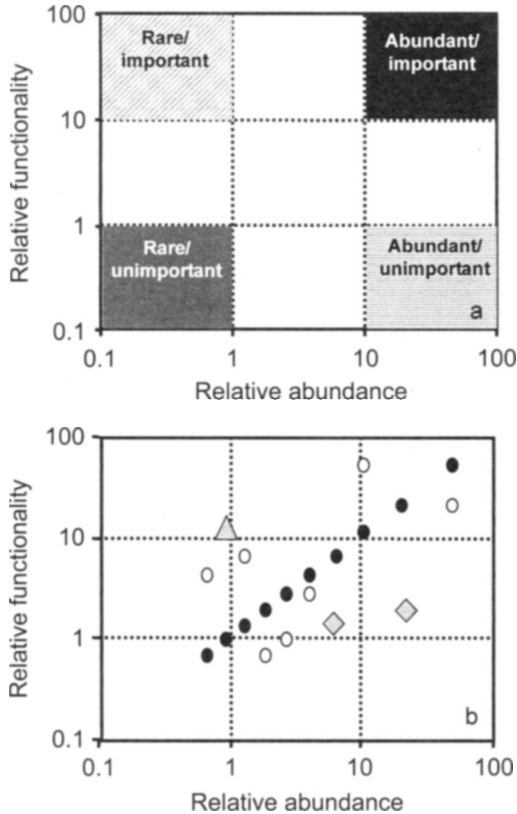


FIG. 2. Exploration of the relationship between relative functionality and relative abundance for single species within an ecosystem. (a) Species classification a priori boundaries to identify species according to both rarity and functional importance, and those that are important or unimportant for the function. (b) Examples of species classified accordingly. Solid circles indicate one-to-one correspondence between a species' relative abundance and its relative contribution to ecosystem function. Open circles represent more realistic scenarios in which relative abundance and relative functionality are identical. Among them, gray diamonds show species that contribute disproportionately less to function than expected based on their abundance; the gray triangle shows the species that contributes disproportionately more to function than expected based on their abundance.

emphasis was made on rare species that contribute disproportionately to ecosystem function, or abundant species that are disproportionately unimportant to the function. Species that contribute disproportionately to function, relative to their abundance, are identified as those that differ significantly ($\pm 95\%$ confidence interval) from the null model $f_{jx} = r_j$. An analogous procedure has been used previously to identify keystone species as those whose impacts on the ecosystem are large and greater than expected from its relative abundance (Mooney et al. 1995).

Effects of management regimes.—The above analyses can be applied to a reference treatment against which other management treatments can be contrasted. Specific effects of management can then be explored using a replicated approach.

1. *Effects on the cumulative magnitude of the function.*—For each management treatment, the average functional contribution of the i th-ranked species irrespective of species identity was plotted against species richness. The final average magnitude of the function was compared among management regimes by inspecting overlap of treatment-related confidence intervals.

2. *Effects on community and functional structure.*—Changes in community and functional structures associated with different management regimes were assessed using a modification of Eq. 7:

$$Y = b_1 - b_2 \text{rank}_j + b_3 \text{management type} + b_4 [\text{management type} \times \text{rank}_j]. \quad (8)$$

In this case, however, Y is the absolute, rather than the relative, contribution of a species to either total abundance or total magnitude of the function to explore for direct effects of management on those variables. Changes in y -intercept, i.e., the absolute contribution of the first-ranked species, among management treatments were accounted for in effects of “management type.” Such differences express the impact of the environmental changes caused by alternative management regimes on species population size, performance of individuals, and, consequently, on species functionality. Differences in steepness of the slope, i.e., in species abundance or functional evenness are accounted for in the effect of the interaction term “management type \times rank $_j$.” Such differences express the differential population and functional responses of species to the environmental scenarios operating under alternative management regimes.

To test for differences in y -intercept and slope among management treatments, we suggest the use of Generalized Linear Models. For the case of community structure, since Y measures absolute values of species abundances, a Poisson error and a log-link function, as indicated for count variables (Crawley 1987), must be used. For the case of functional structure, Y values can be counts (e.g., number of pollen grains deposited per species) and then a Poisson error must be used, or can be a continuous variable (e.g., amount of stored carbon per species) for which a normalized error can be used.

3. *Effects on single species.*—Changes in species' relative abundance and relative functionality due to management regimes are compared graphically. For that purpose a scaled relative functionality of a species under a given management regime m is defined as

$$f'_{jxm} = c_{jxm}/X_r \quad (9)$$

where c_{jxm} is the relative contribution of the species j to the function X under management regime m , and X_r is the magnitude of the aggregate function X under the reference treatment. Scaled relative abundance and scaled relative functionality of each species are compared among treatments using the among-replicates average values and their standard errors.

Functionally sensitive species are defined as those with significantly different scaled relative functionality under a certain management regime in comparison with the reference treatment. These species are identified first by pinpointing those species that disappear from management regimes relative to the reference treatment. Additional species are identified, among those that are present across all management types, by comparing average values of their scaled relative contribution to the function among management regimes using $\pm 95\%$ confidence intervals obtained from treatment replicates.

Case study systems and data collection

Watermelon pollination in California.—

1. *Farm types*.—We studied the pollination by native bees of watermelon (*Citrullus lanatus*) on farm sites in Yolo County, California, USA, that varied in agricultural management and surrounding matrix. Three contrasting farm types were considered as management treatments: organic farms within a matrix of oak woodland and chaparral, organic farms within an agricultural matrix, and conventional farms within an agricultural matrix. Organic farms were certified according to the California Organic Foods Act of 1990; conventional farms used the same three moderately to highly toxic insecticides, as well as one or more of 11 other insecticides (Kremen et al. 2002). Organic farms within oak woodland chaparral matrix (hereafter referred as Organic Near) were within 400 m of natural habitat and contained $\geq 30\%$ natural habitat within a 1-km radius of the watermelon transects. This is our reference management treatment. Organic and conventional farms within agricultural matrix (hereafter referred as Organic Far and Conventional, respectively) were further than 4 km from natural habitat and had $\leq 1\%$ of natural habitat within a 1-km radius. No Conventional farms were found close to natural habitats. Five Organic Near, four Organic Far, and five Conventional farms were studied in 2001.

2. *Species*.—Species were identified to the lowest possible taxonomic level possible through field observations. Nine genera and an estimated 26 species of native bees were observed at watermelon flowers: *Halictus tripartitus*, *H. farinosus*, *H. ligatus*, *Agapostemon texanus*, *Lasioglossum (mellipes or titusi)* spp., *Lasioglossum (Evylaeus)* spp. ($N = 4$ morphospecies), *Lasioglossum (Dialictus)* spp. ($N = 4$) [Halictidae]; *Bombus californicus*, *B. vosnesenskii* [Apidae], *Peponapis pruinosa*, *Melissodes (lupina, robustior, stearnsi, or tepida timberlake)* spp. [Anthophoridae]; *Hylaeus* spp. ($N = 3$) [Colletidae]. *Apis mellifera*, an introduced honey bee that is managed for pollination, occurred at all sites, but its abundance did not vary significantly between farm types. The abundance and resulting functional contribution of *A. mellifera* depends on the number and placement of managed colonies. We therefore restricted our analysis to wild bee communities because

we were interested in how changes in farm management influenced “natural,” not managed, pollination services. In addition, we previously had found no evidence supporting competitive interactions between *A. mellifera* and wild bees at our watermelon study sites; thus, leaving this species out of the analysis should not affect the conclusions (Kremen et al. 2002).

3. *Measurement of per species pollination function*.—Pollination efficiencies (e_{ij}) were calculated on a per species and per sex basis. We allowed individual bees foraging in the watermelon field to visit a female watermelon flower that had been previously protected from visitation, collected the stigma, and counted the number of pollen grains deposited per single visit. The medians of these distributions were used as the efficiency estimate (Kremen et al. 2002). Per species contributions to pollination function (c_j) were then calculated for each species on each farm based on the estimated daily visits per flower of each sex multiplied by its pollination efficiency and summed over sexes. Daily visits per flower were measured separately through 10-min transect walks conducted every half hour between 07:30 and 14:30, the period during which female flowers are open. Watermelon flowers are open for a single day; therefore, these estimates of species-specific contributions represent the entire contribution to pollination for each species per flower per day.

Carbon storage in a tropical rain forest of Mexico.—

1. *Forest types*.—We studied carbon storage of trees in the tropical rain forest in the La Selva Lacandona region (Mendoza and Dirzo 1999), southeast Mexico, in a primary forest and two different land management treatments. The reference treatment was the primary forest within the Montes Azules Biosphere Reserve (hereafter referred to as Conserved Forest). This is a diverse forest with a canopy ~ 30 m tall (Ibarra-Manríquez and Martínez-Ramos 2002). The first management treatment was a hypothetical selective logging (hereafter High-graded) of the Conserved Forest, constructed by simulating the removal of large trees (diameter at breast height [dbh] ≥ 30 cm) of species with known commercial value for timber (Echenique-Manrique and Plumtre 1990, Martínez et al. 1994, Ibarra-Manríquez and Sinaca 1995, Ibarra-Manríquez et al. 1997, Pennington and Sarukhan 1998). The second management treatment was secondary forest that had re-grown on abandoned agriculture and cattle pasture within the neighboring Marqués de Comillas region (hereafter Secondary Forest). Study fallows represented the oldest secondary forest (12–13 years old) found in the area.

2. *Forest plots*.—Data for the Conserved Forest and the simulated High-graded forest were obtained from the same five separate plots (1.5–7 km apart) all located within the dominant geomorphological unit of “low hills” (115–300 m altitude), sandy or limestone soils of low pH (3.9–5.4), and undulating landscape with slopes ranging from 0° to 30° (Ibarra-Manríquez and

Martínez-Ramos 2002). The 20 × 250 m plots were established in 1994 (total sampled area = 2.5 ha). All trees with diameter at 1.3 m above ground or above buttresses (dbh) ≥ 10 cm were identified to species, and measured for dbh in yearly censuses conducted between 1994 and 2001 (M. Martínez-Ramos, *unpublished data*).

Data for the Secondary Forest is scarcer, both spatially and temporally. We used data derived from three separate fallow sites (3–8 km apart) located within the same “low hill” geomorphological unit. The sites, all located within 5 km of the Conserved Forests, were each burned 2–4 times during 1–2 years of maize cultivation, followed by 12–13 years of fallow. No chemical or organic fertilizers were used. One of the sites was also used for two years of cattle ranching following maize cultivation. Within each site, five 2 × 50 m plots were systematically established to cover the heterogeneity within the area, and all trees with dbh ≥ 10 cm were identified and measured for dbh (Méndez-Bahena 1999). To develop qualitative comparisons against the Conserved Forest, we created one single composite Secondary Forest data pool (total area = 3 sites × 5 plots × 100 m²/plot = 1500 m²). An equivalent area was selected by randomly subsampling 20 × 75 m (1500 m²) from each of the five conserved plots. The comparison between the Conserved and the Secondary Forest is therefore based on similar total area, but is limited by the different spatial sampling design and by the lack of replicates for the Secondary Forest data.

3. *C storage calculations.*—Aboveground biomass (AGB) of each individual of a given species j , was calculated using a general model that depends on tree dbh values and average species-specific wood density (SWD), developed by Nelson et al. (1999) using Amazonian rain forest tree species:

$$\ln(\text{AGB}) = -1.4 + 2.4 \ln(\text{dbh}) + 0.8 \ln(\text{SWD}). \quad (10)$$

This model is much more sensitive to changes in dbh than in SWD. For instance, AGB for the largest individual reported here was close to 1000 times larger than that of the smallest one. Instead, AGB for a given dbh was only five times larger for the species with the highest SWD than that for species with the lowest one. Nevertheless, differences in SWD have been observed among tropical rain forest species, and the model used here emphasizes contrasts in AGB among pioneer, fast-growing, light-wooded species and canopy, slow-growing, dense-wooded species (Nelson et al. 1999). While SWD values are accessible in the literature for many of our studied species (Barajas-Morales 1987, Barajas-Morales and Gómez 1989, Carmona-Valdovinos 1995, Barajas-Morales et al. 1997, Brown 1997, Fearnside 1997), using a compilation of such values would suffer from errors associated with differences in sampling and processing techniques, tree age, tree diameter, and en-

vironmental conditions for tree growth (Fearnside 1997, Cornelissen et al. 2003). For this reason, we decided to estimate SWD of the species using field measurements of species annual relative growth rate (RGR), obtained from five years dbh census; M. Martínez-Ramos, *unpublished data*), gathered within the plots used here. The SWD values were thus calibrated using a regression between log(RGR) and SWD ($R^2 = 0.49$, $F = 15.93$, $df = 1, 16$, $P < 0.001$; $\text{SWD} = -9.71 \log(\text{RGR}) + 0.81$) for a subset of species with highly consistent SWD values in the literature, all obtained within a single tropical rain forest site and with a standard protocol (Barajas-Morales et al. 1997). The degree of significance and amount of variance explained by our regression is comparable to the ones found in the literature (Castro-Díez et al. 1998). To avoid overestimations of differences among species' SWD, maximum and minimum values were bounded within a 0.1–0.9 g/cm³ range, where 80% of SWD values found here and in the literature are concentrated (Barajas-Morales 1987, Fearnside 1997, Suzuki 1999). When a RGR value was not available for a species, the species was first classified as pioneer or slow-growing species (M. Martínez-Ramos, *unpublished data*), and then assigned the average SWD obtained for each group in the Conserved Forest (SWD = 0.443 g/cm³ for pioneer species, and 0.452 g/cm³ for slow-growing species).

Based on estimations of C content in trees in another tropical rain forest of Mexico (Hughes et al. 1999, 2000), contribution of each tree to the carbon storage function, e_{kix} was calculated as:

$$e_{kix}(\text{Mg C/ha}) = \text{AGB}_{kj} \times 0.47/\text{plot area}. \quad (11)$$

Contribution of each species to the carbon storage function was then calculated by summing the individual contributions of each tree (Eq. 4).

RESULTS

Pollination

Description of the functional structure of the reference treatment.—The aggregate pollination function in the Organic Near treatment accounted for 1757 ± 872 pollen grains-flower⁻¹·day⁻¹ (mean ± 1 SE) provided by 12 native bee species groups (eight species groups on average per farm). Nearly 80% of the function was given by the first two species; many species had intermediate to tiny contributions (Fig. 3a). The best fit for the functional structure was that of $\ln(f_{jk})$ and rank $_j$; thus, similar to a geometric function (Table 1a).

Relationship between community and functional structures for the reference treatment.—Community structure showed a best fit to the same model as functional structure. There were no significant differences between community and functional structures, neither in y-intercept (i.e., dominance of the first-ranked species) nor in slope (i.e., steepness; Table 1a, Fig. 3b).

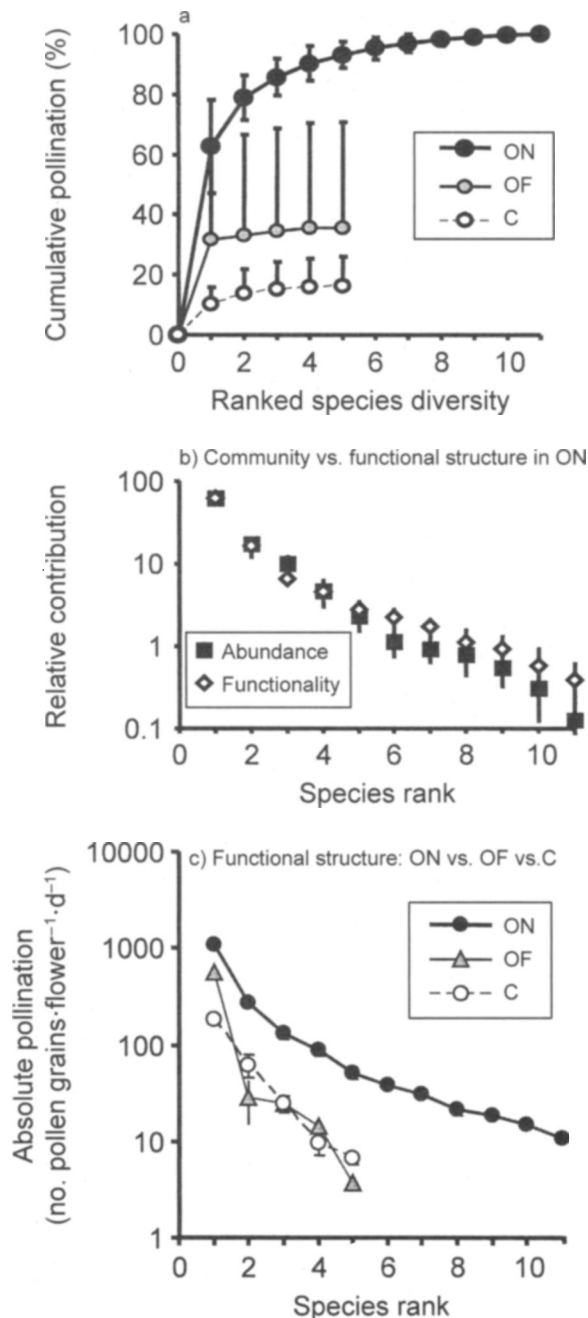


FIG. 3. Watermelon pollination function by native bees in California under three management regimes. (a) Relationship between aggregate pollination function (as a percentage of total in the reference treatment) and species richness (ordered by rank of decreasing contribution to function) for Organic Near (ON), Organic Far (OF), and Conventional (C) farms. (b) Comparison between community and functional structures for Organic Near farms (reference treatment). (c) Functional structure for pollination for each management treatment. In panels (b) and (c), values are means with 95% confidence intervals over four (OF) or five (ON, C) replicates per management treatment.

Species classifications.—*Halictus tripartitus* was the only species classified as abundant/functionally important (Fig. 4a). No rare/functionally unimportant, abundant/functionally unimportant, nor rare/functionally important species were found. Three species, however, differed significantly from the $f_{jx} = r_j$ model: the abundant tiny bee *Lasioglossum (Dialictus)* spp. contributed less to pollen deposition than expected from its abundance, while the rare medium-sized bees *Halictus farinosus* and *Lasioglossum titusi* or *mellipes* contributed more to pollination than expected from their abundance. These disproportionate cases contributed to greater evenness of the functional structure as compared to the community structure (cf. Fig. 3b), as did species that were intermediate in abundance and efficiency, such as *Bombus vosnesenskii* and *B. californicus*.

Effects of management.—Management treatments resulted in a great depression in the aggregate ecological function (Fig. 3a). Community structure differed among management treatments (Table 1b) both in y-intercept (i.e., contribution to abundance of the first-ranked species), and slope (i.e., species evenness in abundance). Organic Near farms showed significantly higher abundance of the first-ranked species than Organic Far and Conventional farms, among which there were no differences (Table 1b). The same pattern was found for the slope or evenness in species' abundances, where evenness was greater in Organic Near farms than in the two other treatments (Table 1b). There were significant effects of management in the structure of species' contribution to pollination (Table 1c), both in terms of y-intercept (i.e., contribution to pollination by the first-ranked species) and slope (i.e., species evenness in functionality). Although the tendencies were similar to those found for community structures, the contribution to pollination of the first-ranked species was significantly lower in Conventional farms, relative to Organic Near farms (Table 1c). Also, species evenness in functionality was only significantly lower in Organic Far farms, relative to Organic Near ones (Table 1c). The most important species contributed almost 90% of the pollen deposition in Organic Far and Conventional farms, while more than three species were needed in Organic Near to reach 90% of the total (cf. Fig. 3a, c). Overall, agricultural intensification caused a clear reduction in visitation rates and thus in associated pollen deposition (Fig. 3c).

The depression in the aggregate ecological function with management was due both to the outright loss of species that made small (e.g., *Halictus farinosus*) to large (e.g., *Bombus californicus*) contributions to pollination in the reference treatment (Fig. 4a), and to important reductions in abundances of remaining species (see also Kremen et al. 2002). Many bee species were identified as functionally sensitive to the management treatments. Six species recorded in the Organic Near farms disappeared in the Organic Far treat-

TABLE 1. Comparisons between community structure (distribution of species' relative abundance, r_j) and functional structure (distribution of species contribution to function X, f_j), and effects of management treatment on both, based on generalized linear models (GLMs) fit according to Eqs. 7 and 8 for watermelon pollination by native bees in California.

Source	Deviance†	df	F	R ²	P
(a) Community vs. functional structure for reference treatment. Model: $\log(\arcsine(r_j \text{ or } f_j)) = 0.282 - 0.456 \text{ rank}_j$					
Structure type (T)	0.00	1	0.02	0.00	NS
Rank _j	1.18	1	280.18	0.94	***
Rank _j × T	0.00	1	0.02	0.00	NS
Error	0.08	18			
(b) Effects of management on community structure. Models: $\ln(r_{j\text{ON}}) = 4.91^b - 0.78^b \text{ rank}_j$; $\ln(r_{j\text{OF}}) = 4.20^a - 1.46^a \text{ rank}_j$; $\ln(r_{j\text{C}}) = 3.81^a - 0.99^{\text{AB}} \text{ rank}_j$					
Management (M)	9.30	2		0.03	**
Rank _j	337.20	1		0.95	****
Rank _j × M	8.10	2		0.02	*
Error	10.20	15			
(c) Effects of management on functional structure. Models: $\ln(c_{j\text{pollinationON}}) = 6.73^b - 0.65^b \text{ rank}_j$; $\ln(c_{j\text{pollinationOF}}) = 6.24^b - 1.71^a \text{ rank}_j$; $\ln(c_{j\text{pollinationC}}) = 4.63^a - 0.68^{\text{AB}} \text{ rank}_j$					
Management (M)	14.50	2		0.09	***
Rank _j	134.50	1		0.80	****
Rank _j × M	8.79	2		0.05	*
Error	11.96	15			

Notes: Effects of structure type (T; abundance or functionality) and of management (M) account for differences in the y-intercept, and thus contribution of the first-ranked species. Effects of interaction terms rank_j × T or rank_j × M account for differences in slope between structures or among treatments, i.e., differences in evenness (steeper slopes reflect lower evenness). Parameters in the models sharing same letter (lowercase superscripts for y-intercept, uppercase for slope) did not differ statistically between structure types or among management treatments ($P > 0.05$). Models differ depending on the nature of the response variable and the best fit with alternative use of logarithmic transformations. Abbreviations for models are: ON, Organic Near farms; OF, Organic Far farms; C, Conventional farms; and c_{jx} , the contribution of a given species, j , to pollination under management treatment x .

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** = $P < 0.0001$; NS, nonsignificant.

† Deviance is used only for count variables with a Poisson distribution (number of bees, number of trees, and number of pollen grains). For parts a and c, a χ^2 test was run to test for significant differences among treatments.

ment (*Bombus californicus*, *B. vosnesenskii*, *Halictus farinosus*, *Hylaeus* spp., *Lassioglossum mellipes/titisi*, and *Melissodes* spp.; Fig. 4b). Six also disappeared in the Conventional treatment (*Agapostemon texanus*, *Bombus californicus*, *B. vosnesenskii*, *Halictus farinosus*, *Lassioglossum mellipes/titisi*, and *Peponapis pruinosa*; Fig. 4c). Two species (*Halictus tripartitus* and *Lassioglossum (Dialictus)* spp.) were found in all treatments, but presented significant reductions in their contribution to abundance and functionality (Fig. 4a, b, c). The remaining species (*Lassioglossum (Evylaeus)* spp. and *Halictus ligatus*) retained essentially the same relative positions in all treatments (except for *L. (Evylaeus)* spp. in Organic Far), tended to occur frequently across all farm types, and demonstrated relatively little sensitivity to the effects of agricultural intensification (Fig. 4a, b, c).

Carbon storage

Description of the functional structure of the reference treatment.—Total carbon storage, estimated from aboveground biomass of the 169 species present, was 94 ± 26.30 Mg C/ha in the Conserved Forest. Just 13% of the species contributed 90% of the aggregate carbon

storage; most species made intermediate to tiny contributions (Fig. 5a). The best fit for the functional structure was that of $\log(f_{jx})$ and $\log(\text{rank}_j)$, thus similar to a Zipf function (Table 2a).

Relationship between community and functional structures for the reference treatment.—Community structure also showed best fit to the $\log(Y)$ and $\log(\text{rank})$ model; the Zipf function. Differences between community and functional structures were significant for slope, with a higher evenness in community than in functional structure. There were no differences in y-intercept, i.e., in dominance of the first-ranked species (Table 2a, Fig. 5c).

The greater evenness in community as compared to functional structure is due to the fact that *Dialium guianense*, the dominant species, accounted for only $15 \pm 2\%$ of total number of individuals but as much as $28 \pm 2\%$ of carbon storage. It can also be attributed to the fact that species with similar abundance differed strongly in individual dbh and wood density, emphasizing differences in functionality among them.

Species classifications.—*Dialium guianense* (Fig. 6a), a very abundant and widely distributed canopy tree, was the only species in the abundant/functionally

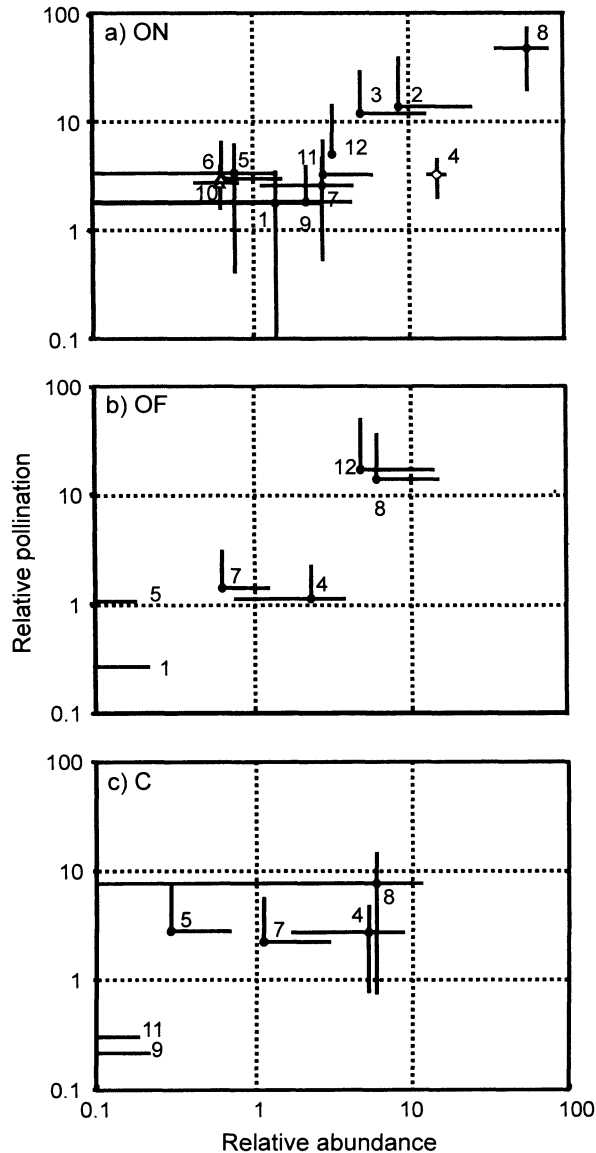


FIG. 4. Abundance-functionality species classification based on r_j and f_{jx} values for watermelon pollination by native bees in California for three management treatments: (a) Organic Near (ON), (b) Organic Far (OF) and (c) Conventional (C). Values shown are means with 95% confidence intervals over 4–5 replicates per management treatment. Open diamonds and triangles indicate species that differed significantly from the $f_{jx} = r_j$ model (see Fig. 2). Species numbers are as follows: 1, *Agapostemon texanus*; 2, *Bombus californicus*; 3, *B. vosnesenskii*; 4, *Lasioglossum (Dialictus) spp.*; 5, *Lasioglossum (Evyllaesus) spp.*; 6, *Halictus farinosus*; 7, *H. ligatus*; 8, *H. tripartitus*; 9, *Hylaesus spp.*; 10, *Lasioglossum titusi* or *mellipes*; 11, *Melissodes spp.*; and 12, *Peponapis pruinosa*.

important category, while ~95% of the species were classified as rare/functionally unimportant. No abundant/functionally unimportant, nor rare/functionally important species were found. Seven species, however, differed significantly from the model $f_{jx} = r_j$ (Fig. 6a,

star symbol). Among these species, fast-growing, pioneer species such as *Cecropia* spp. contributed less to carbon storage than expected from their abundance. In contrast, slow-growing canopy species with large individuals and dense wood contributed more to carbon storage than expected from their abundance. A clear example was *Terminalia amazonica*, which is harvested for timber.

Effects of management.—Management treatments greatly depressed the aggregate ecosystem function (Fig. 5a, b). The High-graded treatment simulated the extraction of only 11% of the individuals, with no impacts on species richness; nevertheless, the extracted trees were the larger ones, with denser woods. A reduction of 67% of carbon storage was estimated. A stronger depression of up to 80% was observed for the Secondary Forest together with a decline in species richness (68 ± 24 species per 20×75 -m plot in Conserved Forest compared to 27 species in Secondary Forest). An increase in variance of the contribution of the i th species to carbon storage is due to the higher uncertainty that any given plot will include a large tree making a large contribution to carbon storage.

The community structure of Conserved Forest and High-graded treatment did not differ either on y-intercept or slope (Table 2b). The lack of difference reflects that the extraction of 11% of the individuals did not substantially affect the abundance of the first-ranked species, or the evenness in species' abundance. The functional structures of Conserved Forest and High-graded treatments, however, differed significantly both in y-intercept and slope (Table 2c). The first-ranked species contributed significantly less to carbon storage in the High-graded treatment than in the Conserved Forest. Evenness in species' contribution to carbon storage was significantly higher in the High-graded treatment than in the Conserved Forest. Simulated selective extraction targeted species, and within those species individuals, which contributed more to carbon storage; extraction, therefore, caused higher evenness in carbon contribution. Differences in the y-intercept occurred due to the dramatic reduction in carbon storage provided by *Dialium guianense*, which dropped from 28 ± 6 Mg C/ha in the Conserved Forest to only 6 ± 1 Mg C/ha in the High-graded treatment.

The community structure of the Conserved Forest and the Secondary Forest showed a best fit to the $\log(Y)$ and rank_j model; the Geometric function (Table 2b). There were no differences in y-intercept, i.e., in the abundance of the first-ranked species. A lower evenness in abundance was found in the Secondary Forest, probably associated to the change in species composition, given that the two treatments only shared 17% of the species. The functional structure of the Conserved and Secondary Forests showed a best fit to the $\log(Y)$ and $\log(\text{rank}_j)$ model; the Zipf function (Table 2c). There were significant differences in the y-intercept among them, with lower abundance of the first-

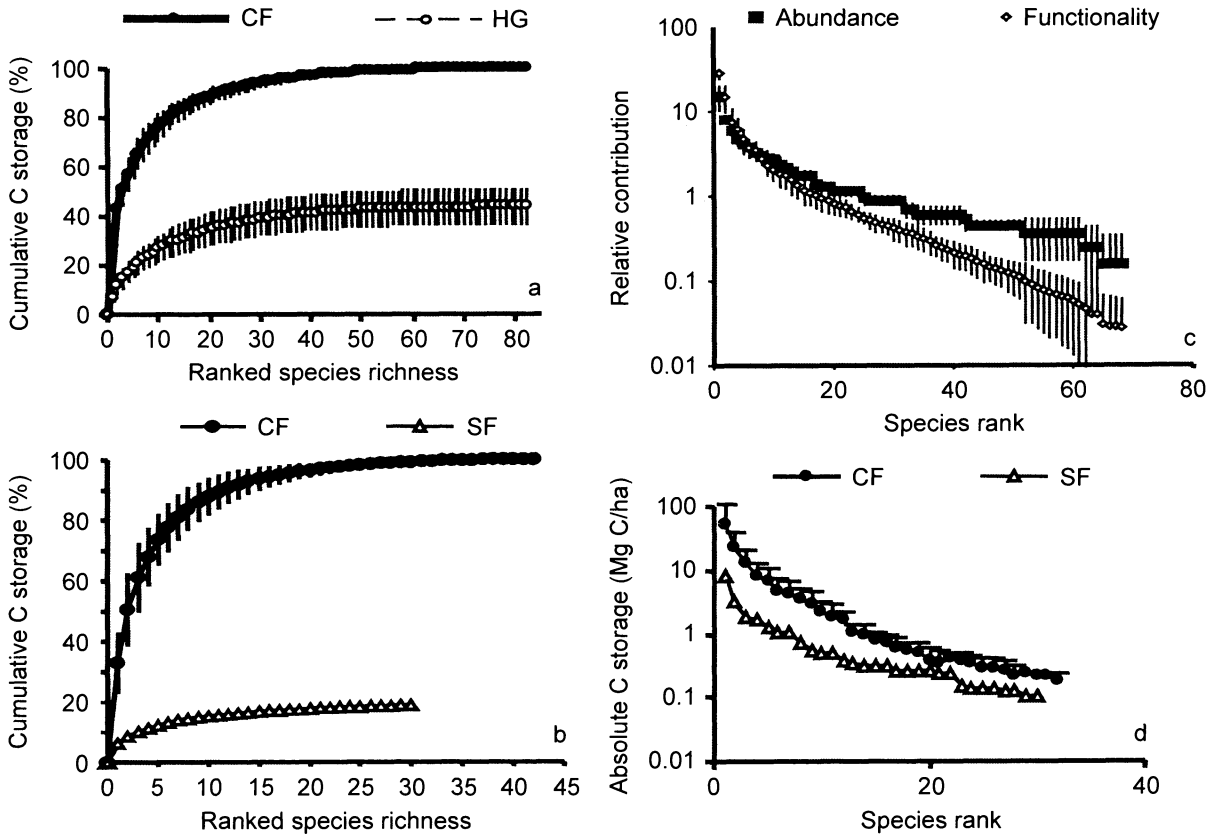


FIG. 5. Aboveground carbon storage function by tropical rain forest trees (≥ 10 cm dbh) in Chiapas, Mexico, under three management treatments. (a) Relationship between aggregate carbon storage function (as a percentage of total in the reference treatment) and species richness (ordered by rank of decreasing contribution to function) for Conserved Forest (CF, reference treatment) and High-graded Forest (HG), and (b) for Conserved and Secondary Forest (SF). (c) Comparison between community and functional structures for Conserved Forest. (d) Functional structure of carbon storage for Conserved and Secondary Forest. Vertical bars indicate 95% confidence intervals over five replicates for CF and HG (no replicates for SF).

ranked species in the Secondary Forest. There were no differences in slope, i.e., in the evenness in species' functionality.

Only two species were functionally sensitive to management treatments. For the High-graded case, the selective extraction of commercially important species was reflected in an overall drop in their relative abundance and function (Fig. 6a, b), although this drop was not equal for all species. A significant reduction was only observed in relative functionality of the very abundant *Dialium guianensis* and the less abundant *Terminalia amazonica*. Both species have dense wood and high frequency of large individuals in the reference treatment. Eighty-four species in the Conserved Forest were absent from the Secondary one; 12 species not found in the Conserved Forest were present in the Secondary one. The shade-tolerant tree *Cupania belizensis*, found in both forest types, was the only functionally sensitive species with a significant decrease in its contribution to carbon storage in the Secondary Forest (Fig. 6c, d).

DISCUSSION

Pollination

The pollination function provided by native bees in the reference treatment was equivalent to that provided by managed honey bees (Kremen et al. 2002), and exceeded the minimum requirement of 1000 pollen grains for marketable fruit formation (Adlerz 1966, Stanghellini et al. 1997). Thus, it is expected to be determinant of high incidence of fruit formation, the final benefit to humans, although fruit production may also be dependent on genetic incompatibility, pollen-pollen, and pollen-pistil interactions (Stephenson 1981, Quesada et al. 2001).

The tools provided here allowed for exploration of separate contributions of species richness, relative abundance, and species identity to the pollination function. On average, pollination function proved to be highly dependent on the contribution made by the two highest ranked species at each site. Collectively across the landscape, however, many more than two species

TABLE 2. Comparisons between community (distribution of species' relative abundance, r_j) and functional (distribution of species contribution to function X , f_j) structures, and effects of management treatment on both of them, based on generalized linear models (GLMs) fit according to Eqs. 7 and 8 for carbon storage in a tropical rain forest of Mexico.

Source	Deviance†	df	F	R ²	P
(a) Community vs. functional structure for reference treatment. Models: $\log(\arcsine(r_j)) = -0.69^a - 1.19^A \log(\text{rank}_j); \log(\arcsine(f_j)) = -0.69^a - 1.36^B \log(\text{rank}_j)$					
Structure type (T)	0.01	1	1.79	0.1	NS
Rank _j	0.64	1	477.85	0.78	***
Rank _j × T	0.05	1	55.12	0.06	****
Error	0.13	132			
(b) Effects of management on community structure					
Conserved Forest vs. High-graded. Model: $\ln(r_{jCF} \text{ or } r_{jHG}) = 3.52 - 1.99 \text{ Log}(\text{rank}_j)$					
Management (M)	1.10	1		0.00	NS
Rank _j	461.9	1		0.98	****
Rank _j × M	0.37	1		0.00	NS
Error	9.30	122			
Conserved Forest vs. Secondary Forest. Models: $\ln(r_{jCF}) = 2.88^a - 0.08^A \text{ rank}_j$; $\ln(r_{jSF}) = 2.88^a - 0.12^B \text{ rank}_j$					
Management (M)	3.42	1		0.01	NS
Rank _j	252.80	1		0.83	****
Rank _j × M	10.35	1		0.04	**
Error	39.56	65			
(c) Effects of management on functional structure					
Conserved Forest vs. High-graded. Models: $\log(r_{jCF}) = 3.34^b - 2.71^B \log(\text{rank}_j)$; $\log(r_{jHG}) = 1.91^a - 0.07^A \log(\text{rank}_j)$					
Management (M)	22.00	1		0.02	****
Rank _j	1056.00	1		0.98	****
Rank _j × M	6.28	1		0.01	*
Error	7.50	132			
Conserved Forest vs. Secondary Forest. Models: $\log(r_{jCF}) = 3.92^b - 3.05^A \log(\text{rank}_j)$; $\log(r_{jSF}) = 2.13^a - 3.05^A \log(\text{rank}_j)$					
Management (M)	2077.00	1	112.21	0.62	****
Rank _j	1284.00	1	7133.00	0.38	****
Rank _j × M	0.26	1	1.42	0.02	NS
Error	12.1	68			

Note: See Table 1 for further details. Abbreviations for models are: CF, Conserved Forests; SF, Secondary Forest; HG, High-graded treatment.

† Deviance is used only for count variables with a Poisson distribution (number of bees, number of trees, and number of pollen grains). For part b, a χ^2 test was run to test for significant differences among treatments.

made significant contributions by being alternatively present at different farms. Thus, six species were ranked first or second for pollination contribution on a given Organic Near farm (*Halictus tripartitus*, *H. ligatus*, *Peponapis pruinosa*, *Bombus californicus*, *B. vosnesenskii*, and *Melissodes* spp.), and five species ranked first or second on Organic Far and Conventional farms (*H. tripartitus*, *H. ligatus*, *P. pruinosa*, *Evylaelus* spp., *Dialictus* spp.), for a total of eight out of the 12 species groups considered to be first- or second-ranked for pollination function across all farm sites. This example clearly shows the importance of considering species turnover between sites when evaluating the role of diversity in function (Schwartz et al. 2000, Symstad et al. 2003).

Depression in pollination function with management was associated with species loss, a decrease in abundance of remaining species, and a less even functional structure (Table 1c, Fig. 3c). Density compensation, either within the wild bee community or between native

and honey bees, does not appear to be occurring in this system. Both richness and abundance of native bees decreased simultaneously with management, while the abundance of honey bees was uncorrelated with the abundance of each native bee species, and with aggregate native bee abundance or diversity (Kremen et al. 2002). Instead, the same environmental factors that appear to eliminate selected native bee species from sites, leading to reduced diversity, may also be reducing the abundances of remaining species (C. Kremen, *personal observation*); therefore, there is no release from competition to mitigate the effect of species loss on function.

Carbon storage

Data shown here for aboveground carbon does not rely on actual biomass data, and was modeled from dbh data and from estimated wood density data (Nelson et al. 1999). We have emphasized differential relative contribution among species to carbon storage rather

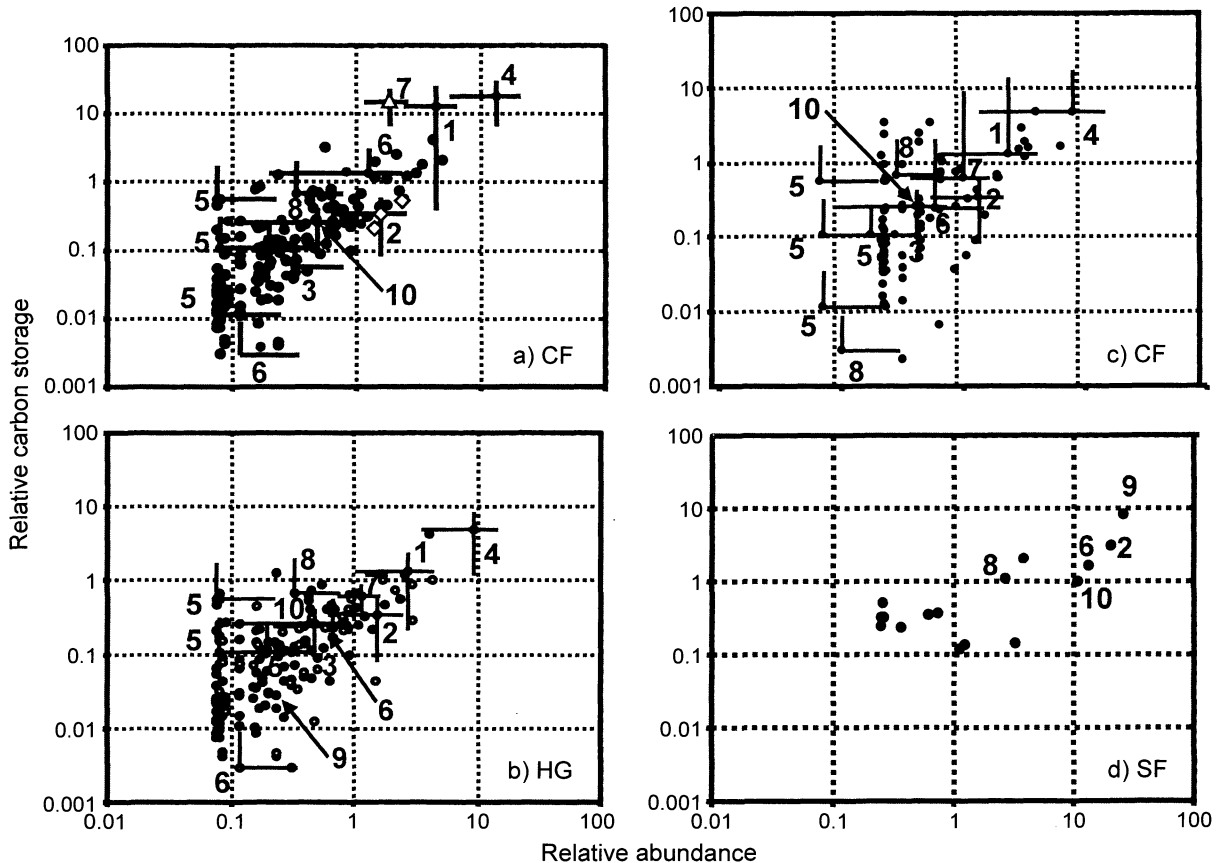


FIG. 6. Abundance–functionality species classification based on r_j and f_{jx} values for aboveground carbon storage by trees in a tropical rain forest of Chiapas, Mexico: (a) Conserved Forest (CF), (b) High-graded Forest (HG), (c) a subsample of the Conserved Forest for comparison with Secondary Forest (CF), and (d) Secondary Forest (SF). Values shown are means with 95% confidence intervals over replicates per management treatment (no replicates for SF). Gray diamonds and triangles indicate species that differed significantly from the $f_{jx} = r_j$ model (see Fig. 2). Open circles indicate species that were harvested in the hypothetical High-graded scenario. Species numbers and confidence intervals are only shown for selected species for clarity. Species names are as follows: 1, *Brosimum alicastrum*; 2, *Dialium guianense*; 3, *Cecropia* spp.; 4, *Cupania bellicenzis*; 5, *Ficus* spp.; 6, *Spondias* spp.; 7, *Terminalia amazonica*; 8, *Trichilia* spp.; 9, *Trichospermum mexicanum*; and 10, *Zanthoxylum* spp.

than total contribution. Nevertheless, our estimate of the total AGB for Conserved Forest is half of that estimated for another conserved tropical forest in eastern Mexico at more fertile volcanic soil (Hughes et al. 2000), and is consistent with its corresponding Secondary Forest data (Hughes et al. 1999). Our High-graded scenario did not consider damage to nontarget trees (Johns 1997, Parren and Bongers 2001), and replacement of large canopy trees by low-density, small, pioneer trees (Laurance et al. 1997) for simplicity. Thus, our results are conservative, and real selective timber extraction is likely to cause much larger reductions in carbon storage than those found here.

Separate contributions of species richness, relative abundance, and species identity on carbon storage differed from the pollination example. Here the majority of function required a much larger number of species; nevertheless, as few as 12 species, out of ~80 species found in each site, contributed to 80% of the carbon

storage function (Fig. 5). This strong hierarchy in species functionality was even more dramatic when considering the entire species pool (163) found in the Conserved Forest plots for which only three species each contributed to >10% of the function (Fig. 6).

Our study confirmed the well-known difference in community structure between early and late successional forest stages. The geometric model with few dominant species frequently observed in early stages of succession was also documented here and contrast with the Zip model (similar to the “broken stick” model) typically found for mature forest stages (Bazzaz 1996), as was the case of our Conserved Forest. Beyond this, the tools provided here allowed for a description of previously unexplored components of carbon storage. While community structure of highly diverse tropical rain forests has been extensively described and modeled (Hubbell 2001), this is the first attempt to describe its functional structure for carbon storage. The

reduced evenness of functional structure contrasts with the relatively high equitability of community structure. For species with similar relative abundances, strong differences in their contribution to the function are associated with remarkable differences in dbh/age population structure of species and their maximum attainable sizes. Such differences emerge from contrasting species life histories, differential rates of biomass accumulation, and species' population dynamics (Martinez-Ramos and Alvarez-Buylla 1998).

Management greatly depressed total carbon storage for both the High-graded and Secondary Forest treatments, but the processes causing these reductions are very different. The High-graded treatment directly targeted larger trees with dense woods, those with highest carbon storage. In contrast, the Secondary Forest was primarily composed of entirely different guilds and age/dbh structure of tree species, with lighter woods and small dbh, leading to lower carbon storage. As succession progresses, we can expect that carbon storage will approach the magnitude and structure found in the Conserved Forest. Some authors propose that such magnitude may be reached after ~90 years (Hughes et al. 1999), but we do not know how these successional changes will influence the functional structure. For example, we do not know whether a return to the functional structure of the "conserved" forest is likely during this time period.

Possible uses and limitations of this approach

First, this approach allows the assessment of the potential coincidence, or lack of coincidence, between biodiversity-centered and ecosystem service-centered conservation strategies (Balvanera et al. 2001). Function-centered strategies might prioritize common species with large contributions to the function, such as the bee *Halictus tripartitus* or the tree *Dialium guianense*, but such species would be of little concern for rare species-centered biodiversity conservation. Conversely, biodiversity-centered strategies might aim at rare species such as *Halictus farinosus*, which is highly efficient for pollen deposition or the rare and light-wooded tree *Ficus* spp. While protecting the rare bee species could also contribute toward maintaining pollination services, the protection of rare tree species would not enhance a carbon storage-centered strategy. Assessing the graphs of relative functionality against relative abundance allows land managers to determine what overlaps exist between alternative goals.

Second, this approach allows the assessment of changes in evenness in species' abundance and functionality with management. Changes in species abundance along successional gradients or among management treatments have often been documented (Kremen 1992, Dennis et al. 1997, Zahawi and Augspurger 1999, Scherer et al. 2000), but comparable analyses of how the functional structure of ecosystems is affected by management are in-existent. This issue is related to the

hotly debated relationship between species diversity and the stability of the ecosystem function (sensu "insurance hypothesis"; Naeem and Li 1997, Tilman et al. 1998, Yachi and Loreau 1999). Results emerging from our two study cases suggest that very contrasting effects of management on functional evenness can occur depending on the system and function studied, with corresponding implications for functional stability. For example, in the pollination case, management reduced the evenness of functional structure; thus, the function remained strongly dependent on the first-ranked species. This change in evenness leaves managed communities increasingly dependent on the first species, and thereby more vulnerable to future change. In addition, in these depauperate systems, the stability of ecosystem function is correspondingly reduced because of the disappearance of species with different abilities to respond to future environmental fluctuations (Naeem and Li 1997, Tilman et al. 1998, Yachi and Loreau 1999, Elmqvist et al. 2003). The magnitude of the function also tends to be highly dependent on the efficiency, and thus identity, of the locally dominant species (Wilsey and Potvin 2000).

In contrast, in the carbon storage case, the evenness of the functional structure was not reduced and, in fact, increased in the High-graded treatment, without changes in species richness. Although this was a simulation, in real selective timber extraction situations, compensatory mechanisms may operate. For example, as dominant species suffer from selective extraction, a process analogous to negative frequency-dependent regulatory mechanism may occur as resources (such as space, light, water, and soil nutrients) are released to rare species. This may enable the coexistence of a highly diverse community, where redundant species may have equivalent contributions to the function, and may confer higher stability to the function under future environmental fluctuations. Nevertheless, the strong negative impact on the magnitude of the function, and its direct and indirect community and ecosystem consequences, should be emphasized. Another contrasting effect of management occurred in the case of the Secondary Forest. Despite the strong difference in species composition and the much less even community structure of this forest type, its functional structure was as even as that of the Conserved Forest. This occurred although the total magnitude of carbon storage was much lower, as was the contribution of the first-ranked species. We do not know whether comparable evenness of Secondary and Conserved Forests correspond with similarly comparable stability of the ecosystem function. All these different results indicate that impacts of different management regimes on functional structure are highly dependent of the analyzed function. Depending on this, management may differentially affect species richness, species composition, dominance of the first-ranked species, and evenness in species' functionality, with complex consequences on magnitude

and stability of the ecosystem function. Our work suggests that, even without species loss, changes in species abundances that reduce functional evenness may also reduce stability.

Third, this approach enables the identification of species that contribute disproportionately to certain ecological functions, and those that are sensitive to management. The functional/abundance classification provided here, however, is based on *a priori* boundaries for common or rare species, or for functionally important or unimportant species, and could thus have different outcomes if other boundaries are chosen. Also, the identification of a sensitive species is descriptive, not predictive; nevertheless, it can be useful to pinpoint a particularly functionally important species before it disappears from the system. These tools complement criteria already available for developing conservation priorities (e.g., rare, endangered, endemic, taxonomically distinctive species, complementary sets of species) and contribute to the search for indicators of ecosystem function.

Potential theoretical insight gained from these applications

To date, the relationship between species diversity and ecological function has been explored for only a few functions, taxonomic groups, and ecosystems (Schlapfer 1999, Schwartz et al. 2000, Loreau et al. 2002). In addition, previously published studies have been largely limited to experimentally assembled communities of plants or microorganisms, and very little is known about the provision of ecosystem services in diverse natural systems (but see Schlapfer 1999, Kremen et al. 2002). The approach developed here provides a framework for going beyond the existing diversity–function debate by emphasizing other components of species composition than richness: relative abundance, species identity (which determines efficiency values), and relative contribution to function (Symstad et al. 2003). This study contributes two examples that consider ecosystem functions that are also ecosystem services, and target different communities (bees and tropical trees) in natural, rather than artificial settings, as called for in recent reviews (Schwartz et al. 2000, Diaz et al. 2003).

Both pollination and carbon storage showed an asymptotic relationship between species richness and the aggregate ecological function, supporting the expectations for most ecosystem functions (Schlapfer 1999). Nonetheless, the two study cases contrasted strongly in the response of ecosystem function to changes in species diversity. While species diversity dropped to <40% of the original diversity in the case of bees, changes in diversity across management regimes were much less dramatic in the case of trees. Yet, in both cases, total magnitude of the function dropped to <40% of its original value. The results presented here suggest that important functional changes can occur both in

response to and independently of changes in diversity. If we are to conserve and manage our natural resources wisely in the future, then greater attention needs to be paid, both through theoretical and empirical work, to the complex relationships between species composition (rather than richness alone) and ecosystem function. The knowledge that we can gain from assessments such as these is urgently needed given the extent to which humans are transforming ecosystems (Vitousek et al. 1997).

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LITERATURE CITED

- Adlerz, W. C. 1966. Honey bee visit numbers and watermelon pollination. *Journal of Economic Entomology* **59**:28–30.
- Balvanera, P., G. C. Daily, P. R. Ehrlich, T. H. Ricketts, S. A. Bailey, S. Kark, C. Kremen, and H. Pereira. 2001. Conserving biodiversity and ecosystem services. *Science* **291**:2047.
- Barajas-Morales, J. 1987. Wood specific gravity in species from two tropical forests in Mexico. *International Association of Wood Anatomists Bulletin* **8**:143–148.
- Barajas-Morales, J., G. Angeles-Alvarez, and P. Solis-Sanchez. 1997. Anatomía de maderas de México: especies de una selva alta perenifolia. Universidad Nacional Autónoma de México, Mexico City, Mexico.
- Barajas-Morales, J., and C. L. Gómez. 1989. Anatomía de maderas de México: especies de una selva baja caducifolia. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.
- Bastow, W. J. 1992. Methods for fitting dominance/diversity curves. *Journal of Vegetation Science* **2**:35–46.
- Bazzaz, F. A. 1996. Plants in changing environments. Cambridge University Press, Cambridge, UK.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert grassland transition by a keystone rodent guild. *Science* **250**:1705–1707.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. Food and Agriculture Organization (FAO), Rome, Italy.
- Castro-Díez, P., J. P. Puyravaud, J. H. C. Cornelissen, and P. Villar-Salvador. 1998. Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia* **116**:57–66.
- Chapin, F. S., III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, and M. C. Mack. 2000. Consequences of changing biodiversity. *Nature* **405**:234–242.
- Clark, D. B., and D. A. Clark. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* **137**:185–198.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**:335–380.

- Crawley, M. J. 1993. *Glim* for ecologists. Blackwell Scientific, Oxford, UK.
- Daily, G. C., editor. 1997. *Nature's services: societal dependence on natural ecosystems*. Island Press, Covelo, California, USA.
- Dennis, P., M. R. Young, C. L. Howard, and I. J. Gordon. 1997. The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. *Journal of Applied Ecology* **34**:433–443.
- Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16**:646–655.
- Echenique-Manrique, R., and R. A. Plumptre. 1990. *A guide to the use of Mexican and Belizean timbers*. Oxford Forestry Institute, Oxford, UK.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* **1**:488–494.
- Fearnside, P. M. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology and Management* **90**:59–87.
- Fridley, J. D. 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia* **132**:271–277.
- Hector, A., B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Gillier, and J. Good. 1999a. Plant diversity and productivity experiments in European grasslands. *Science* **286**:1123–1127.
- Hector, A., et al. 1999b. Plant diversity and productivity experiments in European grasslands. *Science* **286**:1123–1128.
- Herrera, C. M. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* **35**:95–125.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302–1305.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Hughes, R. F., J. B. Kauffman, and V. J. Jaramillo. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* **80**:1892–1907.
- Hughes, R. F., J. B. Kauffman, and V. J. Jaramillo. 2000. Ecosystem-scale impacts of deforestation and land use in a humid tropical region of Mexico. *Ecological Applications* **10**:515–527.
- Ibarra-Manríquez, G., and M. Martínez-Ramos. 2002. Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology* **160**:91–12.
- Ibarra-Manríquez, G., M. Ricker, G. Angeles, S. Sinaca-Colin, and M. A. Sinaca-Colin. 1997. Useful plants of the Los Tuxtlas Rain Forest (Veracruz, Mexico): considerations of their market potential. *Economic Botany* **51**:326–376.
- Ibarra-Manríquez, G., and C. S. Sinaca. 1995. Lista florística comentada de la Estación de Biología Tropical “Los Tuxtlas”, Veracruz, México. *Revista de Biología Tropical* **43**:75–115.
- Johns, A. G. 1997. *Timber production and biodiversity conservation in tropical rain forests*. Cambridge University Press, Cambridge, UK.
- Jonsson, M., and B. Malmqvist. 2003. Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia* **134**:554–559.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**:203–217.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* **99**:16812–16816.
- Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de Merona, C. Gascon, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. *Science* **278**:1117–1118.
- Lawton, J. H. 1994. What do species do in ecosystems? *Oikos* **71**:367–374.
- Loreau, M., S. Naeem, and P. Inchausti. 2002. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, New York, New York, USA.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- MacArthur, R. H. 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences (USA)* **43**:293–295.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey, USA.
- Martínez, E., C. H. Ramos, and F. Chiang. 1994. Lista florística de la Lacandona, Chiapas. *Boletín de la Sociedad Botánica de México* **54**:99–177.
- Martínez-Ramos, M., and E. R. Alvarez-Buylla. 1998. How old are tropical rain forest trees? *Trends in Plant Science* **3**:100–105.
- May, R. M. 1975. Patterns of species abundance and diversity. Pages 81–120 in M. L. Cody and J. D. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- McCann, K. S. 2000. The diversity–stability debate. *Nature* **405**:228–233.
- Méndez-Bahena, A. 1999. Sucesión secundaria de la selva húmeda y conservación de recursos naturales en Marqués de Comillas, Chiapas. Thesis. Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, Mexico.
- Mendoza, E., and R. Dirzo. 1999. Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. *Biodiversity and Conservation* **8**:1621–1641.
- Mooney, H. A., J. Lubchenco, R. Dirzo, and O. E. Sala. 1995. Biodiversity and ecosystem functioning: basic principles. Pages 275–326 in V. H. Heywood and R. T. Watson, editors. *Global biodiversity assessment*. United Nations Environment Programme (UNEP), Cambridge University Press, Cambridge, UK.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507–509.
- Naeem, S., M. Loreau, and P. Inchausti. 2002. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. Pages 3–11 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspective*. Oxford University Press, New York, New York, USA.
- Nelson, B. W., R. Mesquita, J. L. G. Pereira, S. G. Aquino de Souza, T. G. Batista, and L. B. Couta. 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecology and Management* **117**:149–167.
- Ostfeld, R. S., and K. LoGuidice. 2003. Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* **84**:1424–1427.

- Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science* **296**:736–739.
- Parren, M., and F. Bongers. 2001. Does climber cutting reduce felling damage in southern Cameroon? *Forest Ecology and Management* **141**:175–188.
- Pennington, T. D., and J. Sarukhan. 1998. *Arboles tropicales de Mexico. Manual para la identificacion de las principales especies*. Universidad Nacional Autonoma de Mexico (UNAM) and Fondo de Cultura Economica, Mexico City, Mexico.
- Petchey, O. L., and K. J. Gaston. 2002. Extinction and the loss of functional diversity. *Proceeding of the Royal Society of London, Series B* **269**:1721–1727.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* **29**:254–283.
- Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. *Nature* **405**:212–219.
- Quesada, M., E. Fuchs, and J. A. Lobo. 2001. Pollen load size, reproductive success, and progeny kinship of naturally pollinated flowers of the tropical dry forest tree *Pachira quinata* (Bombacaceae). *American Journal of Botany* **88**: 2113–2118.
- Sala, O. E., W. K. Lauenroth, S. J. McNaughton, G. Rusch, and X. Zhang. 1996. Biodiversity and ecosystem functioning in grasslands. Pages 129–149 in H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E. D. Schulze, editors. *Scope 55. Functional roles of biodiversity: a global perspective*. John Wiley and Sons, International Council of Scientific Unions, Scientific Committee on Problems of the Environment, Chichester, UK.
- Scherer, G., D. Zabowski, B. Java, and R. Everett. 2000. Timber harvesting residue treatment. Part II. Understorey vegetation response. *Forest Ecology and Management* **126**: 35–50.
- Schlapfer, F. 1999. Expert estimates about effects of biodiversity on ecosystem processes and services. *Oikos* **84**: 346–352.
- Schulze, E. D., and H. A. Mooney, editors. 1994. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. v. Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**:297–305.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry. The principles and practice of statistics in biological research*. Third edition. W. H. Freeman, New York, New York, USA.
- Stanghellini, M. S., J. T. Ambrose, and J. R. Schultheis. 1997. The effects of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon. *American Bee Journal* **137**:386–391.
- Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* **12**:253–279.
- Suzuki, E. 1999. Diversity and specific gravity and water content of wood among Bornean tropical rainforest trees. *Ecological Research* **14**:211–224.
- Symstad, A. J., F. S. Chaping, D. H. Wall, K. L. Gross, L. F. Huenneke, G. G. Mittelbach, D. P. C. Peters, and D. Tilman. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *BioScience* **53**:89–98.
- Tilman, D. 2000. Causes, consequences and ethics of biodiversity. *Nature* **405**:208–211.
- Tilman, D., C. Lehman, and C. Bristow. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence. *American Naturalist* **151**:277–282.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* **294**:843–845.
- Tokeshi, M. 1993. Species abundance patterns and community structure. *Advances in Ecological Research* **24**:111–186.
- Vitousek, P. M., and D. U. Hooper. 1993. Biological diversity and terrestrial ecosystem. Pages 3–14 in E. D. Schulze and H. A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Wardle, D. A., K. I. Booner, and G. M. Barker. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos* **89**:11–23.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* **147**:250–260.
- Wilsey, B. J., and C. Potvin. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology* **81**:887–892.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem functioning in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Science (USA)* **96**:1463–1468.
- Zahawi, R. A., and C. K. Augspurger. 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica* **31**: 540–552.