

SPECIES AND FUNCTIONAL DIVERSITY OF NATIVE AND HUMAN-DOMINATED PLANT COMMUNITIES

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Abstract. Despite growing attention to how human activities alter plant communities, little is known about the ecosystem consequences of these changes. We explore the relationship between species and functional diversity of herbaceous and shrubby plant communities in forested and deforested habitats in three Neotropical landscapes. We focus on six traits: pollination mechanism, dispersal mechanism, growth form, fruit type, fruit size, and seed size. We ask: (1) What is the relationship between species richness and functional diversity (trait state richness)? (2) Do species/functional diversity relationships differ between forested and deforested habitats? and (3) Are observed species/functional diversity patterns more consistent with ecological filtering or differentiation-based assembly processes? We show that species richness is often a weak surrogate for functional diversity, depending on the trait. Species/functional diversity relationships differ significantly between forested and deforested habitats, but the nature of differences is trait dependent. Dispersal mechanism and fruit type number increased more rapidly in deforested than forested habitats, but the opposite was true for most other traits. Using a null model, we found evidence of ecological filtering for most traits in both habitats. Results demonstrate that deforested habitats do not necessarily contain lower functional diversity than forest but that the ecological assembly processes influencing community function in deforested communities differ dramatically from forest.

Key words: biodiversity; community assembly; Costa Rica; deforestation; functional diversity; null models; tropical plant communities.

INTRODUCTION

The need to evaluate both societal impacts of, and response options to, human-induced ecosystem change is increasingly urgent (Alcamo et al. 2003). The relationship between species diversity and functional diversity (a proxy for ecosystem function) can be used to explore ecosystem responses to environmental change. Scientists have studied this relationship for over a decade (Schultze and Mooney 1993, Tilman et al. 1994, 1996b, Hooper and Vitousek 1997, Naeem and Wright 2003), yet a relatively limited set of ecosystem functions and traits have been explored in this context. Most such studies focus on how species richness relates to functional group or trait richness and how these relationships influence physiological processes and community productivity (Pimm 1984, Schultze and Mooney 1993, Tilman et al. 1994, Tilman and Downing 1996a). Little attention has been given to traits that contribute to other aspects of ecosystem function, such as those associated with plant–animal interactions (Naeem et al. 1994, 1995, Mabry et al. 2000, Diaz et al. 2001). Pollination and dispersal, for example, are of known importance for maintaining animal populations reliant on pollen, nectar, fruits and

seeds, and plant community composition and genetic diversity through out-crossing and dispersal between populations (Cruzan 2001, Dick 2001, Cordeiro and Howe 2003, Chapman et al. 2003, Ries et al. 2004). Yet, studies of these and related traits in an ecosystem function context are rare. Despite a lack of empirical evidence, the species/trait diversity relationships for these and related traits are generally considered to be strongly positive. Our study is one of the first to examine explicitly the species/trait diversity relationships of these ecologically significant functional traits and how they are affected by anthropogenic habitat alteration.

Given the importance of community composition to ecosystem function, it is also valuable to understand how the ecological rules that govern community composition are influenced by human landscape modification. While there is growing interest in ecological assembly rules (Weiher and Keddy 1999, Ackerly 2003), little is known about whether and how they are altered by human activities. Theoretically, ecological assembly rules can be divided into two process categories: filtering and differentiation. Ecological filtering occurs when only certain trait states are compatible with life in a particular habitat, resulting in low trait state richness (under-dispersion). Ecological differentiation occurs when competition for resources with other species results in high trait state diversity (over-

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dispersion; Weiher and Keddy 1995, Gotelli and Graves 1996, Fox 1999, Webb et al. 2002).

It is impossible to identify all traits important for community assembly. The relationship between species and functional diversity in real communities compared to null communities, however, can be used to determine the net effect of filtering and differentiation processes on trait state richness for a given trait (e.g., trait states for the trait "growth form" are herb, shrub, vine, epiphyte, treelet). By comparing species/trait state relationships in (semi-)pristine and human-altered habitats, we can also use this method to determine whether community assembly processes differ broadly between habitat types.

In this study, we examine species and functional trait state richness in herbaceous and shrubby plant communities in southern Costa Rica. We pose three questions, focusing on six functional traits important to the maintenance of genetic diversity, regeneration processes, and resources for animals (Buschbacher et al. 1988, Buschbacher and Serrao 1988, Uhl et al. 1988, Guimares-Vieira et al. 1994, Cruzan 2001, Dick 2001): pollination mechanism, dispersal mechanism, growth form, fruit type, fruit size, and seed size. We first ask, what is the relationship between species richness and functional diversity (measured as trait state richness)? Based on previous studies on the relationship between species and functional diversity (Schultze and Mooney 1993, Tilman et al. 1994, Hooper and Vitousek 1997), and the high levels of plant and animal diversity in forested and deforested habitats in southern Costa Rica (Denslow and Hartshorn 1994, Mayfield and Daily 2005), we anticipate strongly positive relationships between species and trait state richness for all traits.

Second, we ask, do species/trait state relationships differ between forested and deforested habitats? Deforested areas are known to be less structurally complex and to contain fewer growth forms, fruit sizes, and seed sizes than forested communities (M. M. Mayfield, G. C. Daily, and D. D. Ackerly, *unpublished manuscript*). Thus, we predict steeper (more positive) species/trait state relationships for these traits in forested than deforested habitats. Deforested habitats, however, are known to have more dispersal mechanisms and fruit types than forested habitats, seemingly due to more abiotic and large-mammal-based dispersal mechanisms in deforested than forested plant communities (M. Mayfield, G. C. Daily, and D. D. Ackerly, *unpublished manuscript*). Based on these factors, we predict that there will be steeper species/trait state relationships for dispersal mechanisms and fruit types in deforested than forested communities.

Third, we ask, are observed species/trait state patterns more consistent with filtering (trait state underdispersion) or differentiation (trait state overdispersion)? Non-tree plant communities in both forested and deforested areas of southern Costa Rica have environmental conditions that may limit the growth forms and

related structural traits viable in these habitats, such as grazing in pasture and light limitation in forest (Mayfield and Daily 2005). Accordingly, we predict that growth form, seed size, and fruit size will be underdispersed (ecological filtering) compared to a null community for both habitat types. Native consumers, including birds, butterflies, moths, and mammals, which may be important pollinators and dispersers, have been found at high diversities in both forested and deforested habitats of our same focal landscapes (Daily et al. 2001, 2003, Ricketts et al. 2001, Horner-Devine et al. 2003). Complex light-gap habitats in forest also contain the most diverse plant communities and contain species adapted to both animal and abiotic pollination and dispersal (Denslow and Hartshorn 1994). We therefore predict that pollination, dispersal, and fruit type will be over-dispersed compared to the null (differentiation). We also predict that any over-dispersion of these traits will be least apparent in the more homogeneous deforested communities.

METHODS

Plant survey

Between June and August of 2001 and January and February of 2003, M. Mayfield sampled plants in three replicate 7.5 km diameter study areas in southern Costa Rica. Study locations were around the Las Cruces Biological Field Station (LC) and the towns of Puerto Jimenez (PJ) and La Palma (LP). In total, we sampled 43 forested and 42 deforested plots, divided approximately equally among locations and among three forested and three deforested habitat types. Forested plots include forest understorey, 1-2-yr-old treefall gaps and riverbanks. Deforested plots include grazed cattle pasture, road verge vegetation along pastures, and riverbanks through pastures with no or scattered trees (see Plate 1). Each plot was 80 m² in which we recorded the number and abundance of all herbaceous, shrubby, and vining plants in 20 noncontiguous 1 × 1 m quadrats. Plots were separated by at least 400 m.

We collected 2525 specimens representing 772 morphospecies. All morphospecies were identified to family and 668 were identified to genus or species with expert assistance (see *Acknowledgments*). For a more complete description of the locations, plot types, and methods see Mayfield and Daily 2005.

Functional traits

We compiled trait state data on six functional traits using the 668 species identified to genus or species. All traits were categorical with the exception of fruit size and seed size, which we divided into size categories for comparison purposes (Table 1). Trait data were collected from published floras, herbarium specimens, and labels (Croat 1978, Stevens et al. 2001; public communication 2004 El Área de Conservación

TABLE 1. List of all trait states used in analyses for each of the six focal traits.

Focal trait	Trait state list
Pollination	bat, bee, beetle, bird, butterfly, diptera, general entomophilous, moth, self, wasp, water, weevil, wind
Dispersal	ants, bat, bird, endozoochory, exozoochory, gravity, mammal-only-endozoochory, monkey, propulsion, rodents, water, wind
Growth form	epiphyte, herb, shrub, treelet, vine
Fruit type	achene, berry, capsule, cypsella, drupe, follicle, legume, loment, nutlet, pepo, samara, schizocarp, urticale
Fruit size	tiny (<2 mm ²), small (2–5 mm ²), medium (6–15 mm ²), large (16–25 mm long), ex-large (36–100 mm long), huge (>100 mm long)
Seed size	tiny (0–1 mm ²), small (1.1–3 mm ²), medium-small (4–8 mm ²), medium (9–12 mm long), large (>13 mm long)

La Amistad Pacifico, *available online*).⁴ Not all 668 taxa were included in the analysis of each trait because of limited information. Missing trait state data were not clustered by habitat or phylogenetic group, thus their absence should not bias results. Each species had one trait state for growth form, fruit type, fruit size, and seed size, and up to three for dispersal and four for pollination.

Analysis

Fig. 1 illustrates the range of biologically likely species/trait state relationships. To be biologically meaningful, species/trait state relationships must be capped at the maximum number of trait states and cannot be decreasing. Based on the observed shape of our data and mentioned biological constraints (Fig. 1), we selected a modified hyperbolic function (Eq. 1) as the simplest function for describing relationships of the nature described in this study.

$$T(x) = (N - b)[(aNx / (1 + aNx)) + b]. \quad (1)$$

In this function, $T(x)$ is the number of traits observed per plot with x species. $T(x)$ asymptotes at N , which is the maximum number of trait states possible per trait. a is the measure of curvature in the fitted line and b is the y -intercept. We refer to a as the “curvature parameter” and b as the “intercept value.” Residuals from all regressions passed tests for normality (Kolmogorov-Smirnov) and equal variances (Levene median; SPSS 2001).

To characterize the relationship between species richness and trait state richness, we ran two sets of regressions for each trait. In the first regression, we allowed intercept values to float in order to determine whether species/trait state richness relationships were positive and fit our model. We then used t tests to determine if curvature parameters differed statistically from zero. Curvature parameters that do not differ statistically from zero indicate a slow saturation of trait states. We used F tests to examine the contribution of species number to the mean number of trait states. Highly significant F values indicate that the mean num-

ber of trait states per plot increased significantly with species richness (SPSS 2001).

In the second regression, we fixed intercept values at the origin. Results from these regressions were used for Fig. 2 and comparative statistics (Table 2), to ensure realistic starting points for each curve. The majority of regressions had intercept values very near zero even when intercept values were allowed to float; exceptions are noted in the *Results*.

To determine if species/trait state relationships differed between forested and deforested habitats, we transformed the species richness data to intercept the x -axis at the grand-mean number of species per plot, 33 species. We did this by subtracting 33 from each plot's species count. Using the transformed species data, we reran our regression analysis with floating intercepts to generate predicted values (b) for each trait. Predicted values were the mean number of predicted values in a plot with 33 species. Using predicted values and standard errors, we ran ANOVAs for each trait (SAS 2003). Tested differences in species/trait state relationships at 33 species illustrate, but do not statistically test, differences in each curve's slope. We ran analyses for a fixed number of species because the mean species count per plot in forested and deforested

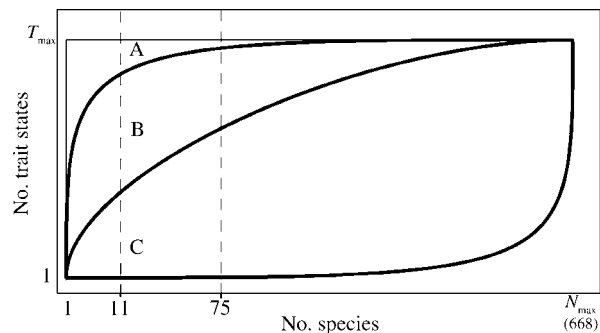


FIG. 1. Conceptual model of the relationship between species and trait state counts per plot. N_{\max} indicates the total species pool in the study area. T_{\max} is the maximum number of trait states for a given trait. A, B, and C indicate three possible species/trait state relationships in a continuum of possible relationships. The dashed vertical lines mark the actual range of our data.

⁴ <http://www.inbio.ac.cr/ecomapas/aclap.htm>

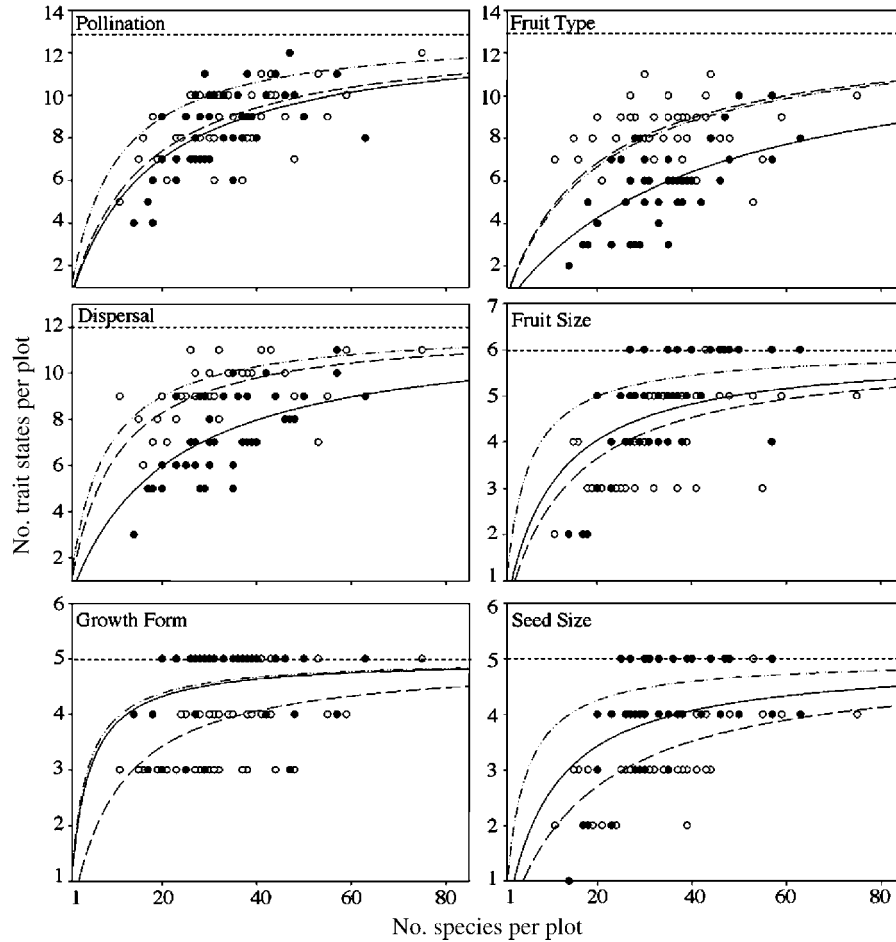


FIG. 2. Species/trait state relationships by trait. Solid symbols and curves indicate observed species counts per plot and regression curves for forested plots; open symbols and the simple dashed curves indicate species counts and regression curves for deforested plots. The long-short-short dashed curve shows the regression line for the null pseudocommunity. All curves saturate at the maximum number of trait states possible, indicated by the dotted horizontal line.

habitats did not differ significantly (32.9 ± 1.89 and 33.8 ± 1.89 , respectively). This indicates that differences in species/trait state relationships between habitats are due to trait state and not species patterns, and that comparison of these relationships at a fixed number of species is appropriate.

To explore what community assembly processes were predominantly acting on focal traits, we determined whether trait states (for each trait) were over- or under-dispersed in comparison to null models. Under-dispersion occurs if there are few trait states per plot relative to random samples assembled from the regional species pool (null), and provides evidence of ecological filtering (Webb et al. 2002). Traits are over-dispersed if there are more trait states present compared to a regional sample (Gotelli and Graves 1996, Weiher and Keddy 1999).

To create each null pseudocommunity (for each trait), we generated null data sets by averaging the number of trait states counted in 1000 non-replacement

draws of species from respective data sets. We then calculated the average number of trait states present for pseudo-plots containing between 12 and 75 species, our observed species range. The probability of sampling a species was based on the actual number of plots in which that species was observed.

For growth form, fruit type, fruit size, and seed size, each species had one trait state. Pseudocommunities of these traits were generated from species draws that corresponded to single trait states. For dispersal and pollination mechanisms, each species could have up to three or four trait states, respectively. In the generation of the pseudocommunities for these traits, all associated trait states for a drawn species were added to the total trait state count for that draw.

Using pseudocommunities, we ran a third set of regressions. We compared the null regression curves for each trait with those for forested and deforested habitats. Using the transformed species data (minus 33) we repeated our ANOVAs as described previous-

TABLE 2. Results from nonlinear regressions using Eq. 1 with b fixed at the origin; values are means \pm SE.

Traits, category	Model		Observed no. trait states	Predicted no. trait states	ANOVA	
	$a \pm$ SE	r^2			F	P
Pollination						
Forested†	0.0045 \pm 0.0003	0.4639	8.11 \pm 0.343	8.81 ^b \pm 0.233	26.81	<0.0001
Deforested*	0.0051 \pm 0.0001	0.3549	8.66 \pm 0.337	8.84 ^b \pm 0.208		
Null	0.0085 \pm 0.0000	0.9920		10.24 ^a \pm 0.013		
Dispersal						
Forested†	0.0057 \pm 0.0005	0.4776	7.11 \pm 0.314	7.58 ^c \pm 0.218	57.95	<0.0001
Deforested	0.0156 \pm 0.0018	0.2417	9.21 \pm 0.308	9.34 ^b \pm 0.192		
Null	0.0125 \pm 0.0001	0.9775		10.06 ^a \pm 0.006		
Growth form						
Forested	0.0640 \pm 0.0153	0.0841	4.61 \pm 0.137	4.63 ^a \pm 0.107	81.15	<0.0001
Deforested	0.0216 \pm 0.0025	0.2203	3.83 \pm 0.134	3.83 ^b \pm 0.193		
Null	0.0713 \pm 0.0024	0.8733		4.66 ^a \pm 0.010		
Fruit type						
Forested*	0.0024 \pm 0.0002	0.4054	5.25 \pm 0.347	5.83 ^b \pm 0.246	37.26	<0.0001
Deforested	0.0059 \pm 0.0005	0.0000	8.17 \pm 0.341	8.17 ^a \pm 0.216		
Null	0.0040 \pm 0.0000	0.9835		8.25 ^a \pm 0.026		
Fruit size						
Forested	0.0171 \pm 0.0024	0.3646	4.36 \pm 0.229	4.86 ^b \pm 0.128	57.07	<0.0001
Deforested	0.0129 \pm 0.0014	0.3254	4.17 \pm 0.225	4.36 ^c \pm 0.143		
Null	0.0411 \pm 0.0010	0.9235		5.40 ^a \pm 0.011		
Seed size						
Forested§	0.0217 \pm 0.0031	0.3179	3.61 \pm 0.172	4.14 ^b \pm 0.103	133.93	<0.0001
Deforested†	0.0118 \pm 0.0010	0.3289	3.21 \pm 0.169	3.29 ^c \pm 0.103		
Null	0.0569 \pm 0.0016	0.9019		4.56 ^a \pm 0.011		

Notes: Curvature parameters (a) that were significant when intercept values were not fixed are marked next to the category designation with a † ($P < 0.10$) or * ($P < 0.05$). F tests for all curves were significant at $P \leq 0.01$. Observed no. trait states is the mean number of trait states observed in all forested ($x = 32.9$ spp.) and all deforested ($x = 33.8$ spp.) plots. The “predicted no. trait states” is the mean predicted intercept value (b) with an x -intercept of 33 species. ANOVA results are for tests comparing the predicted intercept values between categories (forested, deforested, and null). Predicted numbers for each trait with different superscripts are significantly different at $P \leq 0.05$ (hsd post hoc test). Degrees of freedom were 2 and 139 for all F tests.

§ When examined separately, results for the LC (Las Cruces) region differed from combined results (all three locations combined) and results from the Osa peninsula locations (LP and PJ) alone. For LC, $a = 0.0614 \pm 0.0250$, $R^2 = 0.000$, predicted number of traits with 33 species = $4.50^a \pm 0.654$.

ly, along with Tukey Honest Significant Difference (HSD) post hoc tests comparing all three curves for each trait.

All analyses used data from all 85 plots combined, and for two separate regions: LC (27 plots), and OSA (PJ and LP, 58 plots). PJ and LP are separated by only 14 km and have no major floristic differences, unlike LC, which is 50 km away, 500 m higher in elevation, and floristically somewhat distinct. Results from separate regions did not differ from those for combined plots, with the exception of seed size in forest communities. We present results only from the combined analysis, with the exception noted in Table 2.

RESULTS

Species/trait state relationship

We found that species/trait state relationships are very trait dependent and often weak (insignificant a values; Fig. 1, Table 2). All traits do have positive asymptotic species/trait state relationships, evidenced by reasonable fits to our model (r^2 values range 0.24 to 0.47; Table 1) and intercept values close to zero

(when allowed to float; Table 2). Despite consistently positive relationships, few species/trait state regressions had curvature parameters that differed statistically from zero (Table 2), indicating weakly saturating relationships, most similar to curve B (Fig. 1). Pollination mechanism was the only trait to have statistically significant saturation parameters for both habitat types indicating a rapid accumulation of trait states per added species (Table 2). Growth form had insignificant curvature parameters (likely a statistical artifact) but the strongest positive species/trait state relationship, similar to curve A (Fig. 1), evidenced by the largest curvature parameters (Table 2).

Forest/deforested comparison

There were significant differences between the species/trait state relationships in forested and deforested habitats for all traits except pollination (Fig. 2, Table 2). Not all traits, however, were more diverse in forested habitats. For growth form, fruit size, and seed size, there were more trait states per added species in forested than deforested habitats. The opposite was true



PLATE 1. The intersection of representative forest and cattle pasture habitats on the Osa peninsula, Costa Rica. Photo credit: M. Mayfield.

for dispersal and fruit type, for which there were more trait states per species in deforested than forested habitats (Fig. 2, Table 2).

Fruit types in deforested habitats fit our model poorly ($r^2 \approx 0$). It is difficult to determine whether this trait exhibits a rapid addition of trait states with added species, delayed addition of trait states (curve C, Fig. 1), or a step-type relationship. Other traits fit our model well for both habitat types.

Pollination, dispersal, and fruit types in deforested plots had floating intercept values that differed substantially from zero (intercept (b) = 2.6, 4.5, 6.6, respectively). The lowest species diversity per plot was 11 species, indicating that these trait states are added quickly at low species counts.

Ecological assembly processes

For all traits, the null species/trait state relationship predicted higher or equal numbers of trait states per species than was observed in either forested or deforested communities (null curves predicted more rapid addition of trait states than most observed communities). Differences between real and null communities were trait dependent (Table 1, Fig. 2). The null models for pollination, dispersal, fruit size, and seed size predicted significantly more trait states per species than were observed in either habitat type. For growth form the null predicted more trait states per species than were observed for deforested habitats but not forest habitats and the opposite was true for fruit type (Fig. 2, Table 2).

DISCUSSION

One major goal of conservation research is to understand how human activities alter natural communities. In tropical areas, there is concern that deforestation will dramatically alter the functioning of ecosystems. Our results show that deforestation does alter species/trait state relationships, indicating fundamental changes in how forested and deforested communities are assembling on ecological time scales. This pattern is very trait dependent, however, suggesting that deforestation alters components of ecosystem function in different ways.

Results from this study indicate that (1) species/trait state relationships are generally only weakly positive, (2) that forested and deforested components of tropical landscapes have different species/trait state relationships for the same traits, and (3) that the contribution of filtering and differentiation in directing the functional composition of communities differs between forested and deforested plant communities, with filtering the dominant process for all traits. While species/trait state relationships are positive, they are less strongly positive than expected based on studies of physiological traits. More importantly, the strength of these relationships is habitat dependent for most traits, highlighting the need for care when drawing conclusions about the effects of deforestation on other functional traits not directly studied.

Growth form number, not surprisingly, increased rapidly in both habitat types. This is likely due to the presence of all growth forms in forested and deforested

habitats (Mayfield and Daily 2005). Growth forms in these landscapes have been found to have different distributions across habitat types, but none are rare in either forested or deforested areas (M. M. Mayfield, G. C. Daily, and D. D. Ackerly, *unpublished manuscript*).

All other traits had less positive species/trait state relationships than predicted. Trait states for all traits in forested and deforested communities were also always under-dispersed or neutral compared to null expectations (Table 2, Fig. 2). This suggests that most of these traits are strongly influenced by ecological filtering processes in at least one habitat type. The traits that do not differ from the null are likely being influenced by both habitat filtering and differentiation processes, or are largely unselected for in these communities.

Consistent with our predictions, growth forms, fruit sizes, and seed sizes were added more rapidly to plant communities in forested than deforested habitats, providing evidence that forested habitats are more structurally complex than deforested habitats. While forests have been extensively examined for structural complexity (Denslow and Hartshorn 1994) deforested habitats are assumed to contain less structural complexity, but few studies empirically support this observation. The removal of trees clearly decreases structural complexity, but our results suggest that this decreased complexity in deforested habitats extends to the herbaceous and shrubby plant communities of these landscapes, a less obvious pattern. Structural complexity is important to many animals for protection, nesting, roosting, and foraging. Decreased vegetative structure in herbaceous and shrubby plant communities may prevent many animal species from residing in deforested areas or may restrict their use of these habitats. Thus, while many animal species are found in deforested areas (Estrada et al. 1998, Daily et al. 2001, 2003, Horner-Devine et al. 2003), their relationships with plants may be very different in forested and deforested components of these landscapes.

As predicted, dispersal mechanisms and fruit types were added more quickly in deforested than forested habitats. Significant differences in the assembly processes directing these patterns likely mark a shift in the distribution of dispersal mechanisms and fruit types in deforested compared to forest plant communities. Such shifts may be linked to a decreasing diversity of animals dependent on these species' fruits and seeds, which may in turn alter dispersal patterns through deforested habitats or alter the seed bank available for forest regeneration. Previous observations that the composition of species, fruit types, and dispersal mechanisms differ between forested and deforested communities support the likelihood that such changes are occurring (Mayfield and Daily 2005; M. M. Mayfield, G. C. Daily, and D. D. Ackerly, *unpublished manuscript*). While we cannot say whether plants or animals cause these changes in community assembly and com-

position, our results do indicate that changes are occurring.

Pollination was the only trait for which there was no difference in how quickly trait states were added to communities between forested and deforested habitats. This suggests that deforestation does not affect the diversity of pollination mechanisms in these landscapes. This is surprising given that deforestation negatively influences pollinating animals throughout the tropics (Aizen and Feinsinger 1994, Ricketts 2004). Pollination may be a trait for which redundancy maintains ecological function, although results may also be an artifact of using broad trait states, or indicate that trait state diversity does not translate into direct effects on consumers for this trait.

Species establishment largely depends upon dispersal traits and regeneration ability. Traits observed in adults, such as pollination mechanism, will not directly influence initial establishment, though they are clearly important for long-term persistence. Traits do not disperse into habitats independently, but rather come in packages, as parts of complete species. Thus, some patterns may be caused by correlations with other traits. This is likely true for dispersal and fruit type, which have similar patterns. Such correlations are not, however, always as expected, as seen by differences between fruit size and dispersal and fruit type.

From a conservation perspective, results from this study provide evidence that deforestation changes the nature of species/trait diversity relationships and the assembly rules underlying functional community compositions. Understanding functional diversity patterns in forests and how people are changing them is a critical step in understanding native plant and animal communities and in developing a basis for protecting them.

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