

The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes

MARGARET M. MAYFIELD, DAVID ACKERLY* and GRETCHEN C. DAILY

*Center for Conservation Biology, Department of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020 USA, and *Department of Integrative Biology, 3060 Valley Life Sciences Building, University of California, Berkeley, Berkeley, CA 94720-3140, USA*

Summary

1 Human-altered landscapes dominate the planet, yet little is known about their capacity to sustain plant functional diversity. Most conservation-orientated studies of such landscapes focus on species diversity, whereas less attention is given to functional traits and their conservation.

2 We examine the functional diversity of herbaceous and shrubby plant communities in three forest habitats (understorey, tree-fall gaps and riverbanks) and three deforested habitats (pasture, roadside vegetation and pasture riverbanks), each replicated in three human-dominated landscapes in southern Costa Rica. We focus on six categorical traits related to forest regeneration, reproduction and dispersal: pollination mechanism, dispersal mechanism, growth form, fruit type, fruit size and seed size.

3 We compared trait state richness and composition of each trait in forested and deforested habitats and how three pollination states (bat, bird and bee pollination) and three dispersal states (fur, bird and monkey dispersal) of conservation interest were distributed across these landscapes.

4 Only one trait state was missing from forest, and none was missing from deforested habitats. Understorey and pasture were consistently trait state poor. Forested and deforested plots differed in trait state composition for all traits. Pasture riverbanks and road verges were compositionally similar to forest riverbanks and tree-fall gaps, for multiple traits. There were more compositional similarities between forested and deforested habitat types when abundance of individuals with a trait state was used as the basis for similarity measures than when the number of species with each trait state was used. Bat-, bird- and bee-pollinated plants and plants with bird- and monkey-dispersed fruits were most common in forest and pasture riverbanks whereas species with fur-dispersed seeds were more common in all deforested habitats.

5 Functional diversity patterns were inconsistent across habitat types and locations but overall functional similarity was high between forested and deforested communities. Patterns of functional diversity were far more variable between habitats and landscapes than the consistent patterns found previously for species diversity.

Key-words: biodiversity conservation, dispersal, functional diversity, growth form, human-dominated countryside, native herbaceous plants, native shrubs, pollination, tropical deforestation

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Introduction

Landscape modification by humans has become the rule rather than the exception over most of the planet. In modifying wild areas beyond recognition, people are creating new types of habitats and landscapes, about

which little is known. Understanding human-modified landscapes is key to understanding the ecological diversity and functioning of virtually all biomes. Because interest in human-created and modified landscapes is relatively new, even some of the most basic questions about these landscapes have yet to be answered. For instance, what species presently survive and persist in human-dominated habitats? In what ways are these elements of the biota functionally similar to and different from the wild communities they replace?

In recent years, high native species diversity has been reported in human-modified landscapes around the world. Studies have found large numbers of native arthropods, mammals, birds and plants living in agricultural and other deforested habitats in both temperate landscapes (Gondard *et al.* 2000; Soderstrom *et al.* 2001; de Blois *et al.* 2002) and tropical landscapes (Estrada *et al.* 2000; Ricketts *et al.* 2001; Mayfield & Daily 2005). Few of these studies, however, go beyond patterns of species richness and abundance, leaving much to be learned about how landscape alteration influences the functioning of plant and animal communities (Daily 1997; Alcamo *et al.* 2003; Ricketts 2004).

Studies of functional diversity do exist, with most focusing on bird (Szaro 1986; French & Picozzi 2002; Watson *et al.* 2003), plant (Diaz *et al.* 1998; McIntyre *et al.* 1999; Mabry *et al.* 2000) or marine communities (Bosman *et al.* 1987; Mathieson *et al.* 2000; Nystrom & Folke 2001). The definition of functional diversity, however, varies greatly, even in studies of the same organisms. Some authors define it in terms of species-based measurements of physiological, morphological, phenological and ecological traits of important for responses to the environment (Mabry *et al.* 2000; Diaz & Cabido 2001; Walker & Langridge 2002). Others use the term to refer to the number of distinct functional groups or types, defined by shared suites of traits or ecological strategies (Hooper & Vitousek 1997; Hulot *et al.* 2000). We use Diaz & Cabido's (2001) definition of functional traits (i.e. plant traits important for a species' response to the environment and/or important to ecosystem functioning). Because our traits are all categorical, each has a series of trait states, which are the different forms of the trait (i.e. herb, shrub and vine are trait states of the trait growth form). We define: 'functional diversity' as the richness, abundance and range of individual trait states found for individual traits in a community; 'trait state richness' as the number of trait states for a single trait in a community; and 'functional composition' as the identity and abundance of trait states found from a trait in a community.

Although studies of natural communities and their functional diversity are advancing in exciting ways, the study of how human-altered communities differ functionally from the communities they replace are still few and those are narrowly focused. There is a relatively large literature examining the relationships between physiological traits and productivity, species richness, climate change and disturbance (Chapin *et al.* 1993;

Hulot *et al.* 2000; Catovsky *et al.* 2002). There is still a need, however, for studies examining how deforestation and other types of landscape alteration affect the presence and distribution of specific traits important for non-physiological community function, such as plant-animal interactions (Diaz *et al.* 1992; Grime *et al.* 1996; Mabry *et al.* 2000). Additionally, across-site similarity of functional trait assemblages between relatively natural and human-altered plant communities has not, to our knowledge, been explored.

Recent studies of human-dominated landscapes have found patterns of plant species diversity to be remarkably consistent across landscapes (Mayfield & Daily 2005). While species diversity is generally believed to be positively related to functional diversity (Tilman *et al.* 1997; Chapin *et al.* 2000; Hector *et al.* 2001), there is little evidence from real communities that patterns of species composition are similar to patterns of trait state composition across comparable human-dominated landscapes.

The next step in understanding differences between plant communities in relatively natural and human-dominated habitats is to compare specific functional traits of importance for the long-term sustainability and function of these communities. This involves not just knowing which species live where now, but also how the surviving organisms interact functionally within their communities and how these factors vary across natural and human-dominated habitats in the same landscapes. We focus on plant communities in tropical landscapes because they contain very high levels of species diversity and because such landscapes are still being rapidly altered by human activities.

STUDIED TRAITS AND THEIR ECOLOGICAL IMPORTANCE

We focus on six traits: pollination mechanism, dispersal mechanism, growth form, fruit type, fruit size and seed size. Each trait has, or can be converted to, several discrete states (e.g. bee, bird and/or bat pollination for pollination mechanism) and we quantify diversity in terms of the number of trait states for each trait present in a plot or habitat type. Traits were chosen for their importance for understanding the types of resources available for sustaining animal life (DeVries 1987; Holl 1995; Didham *et al.* 1996), for rapid assessments of forest restoration potential (Boring *et al.* 1981; Uhl *et al.* 1988; Guimares-Vieira *et al.* 1994) and for conservation efforts in general (Buchmann & Nabhan 1996; Alcamo *et al.* 2003; Lundberg & Moberg 2003). Traits were also selected for ease of measurement, necessitated by the diverse flora of our study region (southern Costa Rica) and the breadth of this study.

Plants are the primary food source for many tropical forest animals, and animals are major dispersal and pollen vectors for many plant species. Dispersal of fruits and seeds is a critical process in determining where plant species are found and in identifying what resources

are available in a given habitat to the local fauna. Although none of the traits studied here can tell us directly whether plant–animal interactions, gene flow, reproduction and dispersal within and between plant communities are maintained, they do provide evidence that there is still the possibility for these interactions to persist, a critical step in understanding our full impact on native tropical plant and animal communities.

The presence of plants producing particular types and sizes of fruits and seeds provides information about what food may be available for animals in a given habitat (Uhl *et al.* 1981, 1988; Lundberg & Moberg 2003). Fruit type provides more detailed information about the types of dispersal adaptations successful in different components of these landscapes and is known to be related to the abundance of specific plant species in other systems (Mabry *et al.* 2000). Fruit size and seed size both provide information about the types and sizes of animals likely to utilize fruit and seed resources, and seed size is a critical component of plant regeneration strategies (Grubb & Coomes 1997; Leishman *et al.* 2000). Fruit and seed sizes are correlated with a broad suite of morphological and life-history traits (Mabry *et al.* 2000; Westoby *et al.* 2002; Coomes & Grubb 2003), and thus potentially provide broad insights into patterns of functional diversity at the community level.

Pollination is not important for determining where a plant species moves to, but it is extremely important for determining whether a given plant will persist in a location. Pollination also has major impacts on gene flow and community dynamics (Didham *et al.* 1996). Additionally, information about what pollination mechanisms are present in a given plant community provides data on the types of nectar and pollen resources available for nectivorous birds and flower-foraging insects (DeVries 1987; Holl 1995; Didham *et al.* 1996).

Growth form provides information about vegetation structure, shelter options for animals and regeneration processes (Boring *et al.* 1981; Guimares-Vieira *et al.* 1994), and is also related to nutrient cycling and other physiological functions (Aerts *et al.* 1999).

OBJECTIVES

Focusing on the traits discussed above, we examine the functional diversity of herbaceous and shrubby plant communities in three forested and three deforested habitat types of three replicate landscapes in southern Costa Rica (7.5-km-diameter areas). The forest types are relatively undisturbed forest understorey, tree-fall gaps and riverbanks and the deforested habitats are actively grazed cattle pastures, roadside vegetation and riverbanks. We ask four questions about functional diversity in human-altered, tropical landscapes. We also propose several predictions about the answers to these questions based on patterns of species richness, abundance and composition found previously in these same communities (Mayfield & Daily 2005), and on general perceptions of biodiversity and ecosystem

function in forested and deforested tropical habitats. The questions we ask are:

1. Are there fewer trait states in deforested habitats than in forested habitats?
2. Does the abundance and composition of trait states differ between deforested and forested habitats?
3. Does the frequency of specific trait states differ between deforested and forested habitats?
4. Are patterns of functional composition within and across habitat types consistent with those found previously for species compositional patterns in these same landscapes?

We first predict that for all traits, there will be fewer trait states found in pasture and understorey than other habitat types, whereas road verges and tree-fall gaps will be the most trait state rich. This prediction is based on the previous finding that pasture and understorey habitats in these landscapes are the least species rich per plot and that road verges and tree-fall gaps are the most species rich per plot (Mayfield & Daily 2005). Additionally, pastures and understorey tend to have higher numbers of species from a smaller number of plant families than the other habitat types. For example, palms and species in the Araceae are over-represented in understorey plots and Asteraceae and Cyperaceae are over-represented in pastures (data not shown). Road verges, riverbanks and tree-fall gaps, by contrast, tend to contain smaller numbers of species from a broader diversity of plant families (data not shown). Because closely related species usually have more trait states in common than less related species (Darwin 1859), it follows that communities containing more closely related species will contain fewer trait states than communities with more phylogenetic diversity (Mayfield *et al.* 2005).

Building on these first predictions, we expect (for question 2) that trait state composition and abundance in forested and deforested habitats will differ for all six traits, based on known differences in the diversity and composition of animals of importance as pollinators and dispersers in forested and deforested habitats of southern Costa Rica (birds: Daily *et al.* 2001; mammals: Daily *et al.* 2003; butterflies: Horner-Devine *et al.* 2003), and on the differences in plant diversity patterns described above. At the individual habitat level, we expect that of our habitat types, riverbanks in forest and pasture will be most functionally similar, in terms of trait state composition. This prediction is based on our finding that these types are the most compositionally similar forested and deforested habitat types in terms of species composition (Mayfield & Daily 2005).

For question 3, we make predictions about the distribution of three pollination states (bat, bird and bee pollination) and three dispersal states [exozoochory (fur), bird and monkey dispersal] of particular importance to the conservation of animal diversity in tropical landscapes. The presence of higher plant species diversity in tree-fall gaps and forest riverbank habitats compared with all other habitat types leads us to predict

that all three pollination mechanisms will be proportionally more common in these habitats. We group understorey with the deforested habitat types because of its relatively low species diversity (Mayfield & Daily 2005). For dispersal, we predict that plants with seeds dispersed by birds and monkeys will be proportionally more common in forest habitats, whereas plants with fur-dispersed seeds will be most common in pasture and other deforested habitats. Fruit-eating bird species and monkeys are both known to be more common and diverse in forested than deforested habitat types in Costa Rica (Daily *et al.* 2001, 2003; Hughes *et al.* 2002). The types of seeds adapted to dispersal on animal fur (in this study) tend to be those of low-lying herbs and shrubs that catch on socks and trousers (our personal observation). Casual observation suggests that many fur-dispersed seeds are dispersed by cows and horses, which are more abundant in deforested than forested areas.

Finally, we predict that patterns of functional composition (the number and identity of trait states) will be similar to species composition patterns found previously for these plant communities (Mayfield & Daily 2005). This is because positive relationships have been shown between species richness and trait state richness per plot for each of the traits examined in this study (Mayfield *et al.* 2005), and because functional diversity, including composition, is thought to be strongly related to species diversity patterns (Hulot *et al.* 2000; Naeem 2002; Hooper *et al.* 2005).

Methods

LOCATIONS

Between June and August 2001 and January and February 2003, M.M. sampled herbaceous and shrubby plant communities in three 7.5-km-diameter study areas in southern Costa Rica [around the Las Cruces Biological Field Station of the Organization for Tropical Studies (LC) and around the towns of Puerto Jimenez (PJ) and La Palma (LP)]. The Las Cruces Forest Reserve is a small (~250 ha), mid-elevation forest (1200 m) in southern Costa Rica surrounded by cattle pastures, coffee plantations and small forest remnants (< 10 ha). The other two study areas are on the Osa peninsula, much of whose forest has been preserved in Corcovado National Park (41 788 ha). Deforested areas of the peninsula are primarily cattle pastures, rice fields and palm plantations. The LC area is separated from LP and PJ by > 50 km and 500 m of elevation: LP and PJ areas are separated by > 13 km.

PLOT SELECTION

Our sampling design included four nested levels of organization: study location (LC, LP, PJ); category (forested or deforested); habitat type (three forested and three deforested; Table 1); and sampling plot (85;

Table 1 Sampling structure by habitat category, habitat type and location. The number in each cell represents the number of individual plots sampled for each habitat type and location

Habitat category	Habitat type	Location		
		LC	LP	PJ
Forested	Understorey	6	6	6
	Tree-fall gaps	6	6	6
	Riverbanks	2	2	2
Deforested	Riverbanks	3	3	3
	Pasture	6	6	6
	Road verges	4	6	6

Table 1). All six habitat types (understorey, 1–2-year-old tree-fall gaps and riverbanks in primary forest, collectively referred to as ‘forested’, and grazed cattle pasture, ungrazed road verges and riverbanks in grazed pasture, collectively ‘deforested’) are common in the study areas, and throughout the tropics (S.-A. Bailey, personal communication).

In each habitat type at each location, we sampled 2–6 plots separated by ≥ 400 m. In each plot, sampling was conducted in 20 non-contiguous 1×1 m quadrats spaced as uniformly as possible over an 80-m² rectangular area. For each plot, we recorded the identity and abundance of all plant species with the exception of tall trees (> 5 m at maturity), pasture grasses, ferns, mosses and epiphytes that had clearly fallen from the canopy. Ferns and mosses were excluded because, as non-seed plants, they cannot be scored for most of our traits. Trees were excluded for logistical reasons (our plant survey was already extremely large) and most importantly because they represented a separate vegetation layer with a very large, distinct flora supporting a largely distinct animal fauna (Harrison 1962; Pearson 1971; DeVries & Walla 2001; Walther 2002). Most studies of tropical forests focus exclusively on the tree component, so we focused our attention on the understudied herbaceous and shrubby layer. We excluded exotic pasture grasses (~15 species) because these species are restricted to deforested habitats and represent a single trait state for each trait (they are all wind-pollinated, wind-dispersed herbs with small grain fruits). The inclusion of all pasture grasses would therefore have increased richness counts for all traits in deforested habitats by one and left forest habitats largely unchanged (although it would clearly cause much larger shifts in abundance-weighted analyses). Grasses were also excluded because they are actively managed and maintained by humans.

All collected specimens (2525) were sorted to recognizable taxonomic units (RTUs; Oliveira-Filho *et al.* 1997) and identified to family, genus and species (where possible) with the assistance of experts at the Missouri Botanical Garden, the California Academy of Sciences and Instituto Nacional de Biodiversidad (INBío) in Costa Rica (see Acknowledgements for specific contributors). For a more detailed explanation of the

Table 2 The trait states used for each trait. The number of species with each trait state is given in parentheses. Species numbers at the top indicate the total number of species used for analyses of each trait

Pollination* (649 species)	Dispersal* (647 species)	Fruit type (646 species)	Growth form (645 species)	Fruit size (383 species)	Seed size (285 species)
Bat (6)	Ants (26)	Achene (79)	Epiphytes (54)	Tiny (48)	Tiny (96)
Bee (323)	Bat (68)	Berry (168)	Herbs (284)	Small (128)	Small (93)
Beetle (126)	Bird (367)	Capsule (169)	Shrubs (199)	Medium (122)	Medium
Bird (45)	Endozoochory	Drupe (123)	Treelets (32)	Large (46)	– small (59)
Butterfly (20)	– general (32)	Follicle (18)	Vines (76)	ExLarge (24)	Medium (29)
Entomophilous	Mammal-specific	Legume (23)		Huge (15)	Large (8)
– general (169)	– endozoochory (75)	Loment (7)			
Fly (17)	Exozoochory (35)	Nutlet (8)			
Moth (20)	Gravity (56)	Pepo (11)			
Self (61)	Monkey (34)	Samara (10)			
Wasp (6)	Propulsion (46)	Schizocarp (22)			
Water (52)	Rodents (2)	Urticle (8)			
Weevil (18)	Water (19)				
Wind (106)	Wind (143)				

*Species counts for each trait state do not add to total species counts listed at top because species were allowed to have multiple trait states for these traits.

habitat types and sampling regime see Mayfield & Daily (2005).

FUNCTIONAL TRAIT DATA

Functional data were collected only for those RTUs identified to the genus or species level (of 772 RTUs, 511 were identified to species and an additional 157 to genus). RTUs identified to genus were recognizable as distinct species, but the species identification remained undetermined. Throughout the paper, the term 'species' refers to RTUs identified to species as well as RTUs that were identified to genus but were also distinguishable as unique species. Based on this sample, we collected categorical trait state data on all traits, except fruit size and seed size where continuous data were later divided into categorical states as described below. Table 2 lists all states considered for each trait. Depending on information available for each species and genus, not all 668 species were included in the analysis of each trait.

Information on plant growth form was derived from herbarium specimen labels from the Missouri Botanical Garden, the samples collected in our study and published floras of the region (Croat 1978; Huber *et al.* 2001; Stevens *et al.* 2001). In cases where plants were known to have more than one growth form, we used the growth form of the specimens we collected during this study or the growth form listed most commonly on herbarium specimens from southern Costa Rica. 'Treelets' are small trees greater than 2 m and less than 5 m in adult height. 'Vines' include woody and herbaceous species that root in the ground, and 'epiphytes' were species, including vining species, with aerial roots.

Pollination and dispersal mechanisms were determined using information on the life history of species and genera in published floras (Croat 1978; Huber *et al.* 2001; Stevens *et al.* 2001). When possible, species

with unknown pollination and dispersal mechanisms were coded as having the mechanisms most likely given their flower or fruit structures, respectively. Each species could have multiple pollination mechanisms (up to four) and dispersal mechanisms (up to three). General pollination and dispersal mechanisms, such as generally entomophilous pollination and endozoochorous dispersal, were given to those species with unknown but very general flower structures or fleshy fruits, respectively, or those known to be pollinated or dispersed by a wide range of species.

Fruit type data were collected from herbarium records and published floras (Croat 1978; Huber *et al.* 2001; Stevens *et al.* 2001). Fruit and seed size data were gathered primarily by measures made on fruits and seeds in herbarium collections and collections made during this study, or from published size data in published floras (Croat 1978; Huber *et al.* 2001; Stevens *et al.* 2001). Fruit and seed size categories are based on the length and width of dry fruit and seeds. The categories for fruit size are: 'Tiny', < 2 mm × < 2 mm; 'Small', 2–5 mm × 2–5 mm; 'Medium', 6–15 mm × 6–15 mm; 'Large', 16–25 mm × 16–25 mm; 'Extra-Large', 36–100 mm × 36–100 mm; and 'Huge', > 100 mm long in any dimension. The categories for seed size are: 'Tiny', 0–1 mm × 0–1 mm; 'Small', 1.1–3 mm × 1.1–3 mm; 'Medium-small', 4–8 mm × 4–8 mm; 'Medium', 9–12 mm × 9–12 mm; and 'Large', > 13 mm long in any dimension.

ANALYSIS

To answer our first question, we ran two-way ANOVAs for each trait with habitat type as a fixed factor, location as a random factor and number of trait states per plot as the dependent factor. To determine if there was a significant difference between forested and deforested habitat types, we ran an orthogonal contrast test with

one degree of freedom. Tukey's Honest Significant Difference (HSD) *post-hoc* test was used to test for significant differences between the six habitat types for each trait (SAS 2003).

To ascertain whether trait state composition differs between forested and deforested habitats, we calculated the proportion of species and individuals with each trait state in each plot. We used both species counts and the number of individuals (abundance) with a trait state to calculate these proportions. Species-based proportions were calculated as the number of species in a plot with a trait state divided by the total number of species in that plot, including those with unknown trait states. Abundance-based proportions were calculated as the number of individuals with a trait state divided by the total number of individuals in the plot. Species with more than one pollination and/or dispersal mechanism were counted as having both of them, so proportions may add to more than 1. We did not down-weight these cases; if a plant is both beetle- and fly-pollinated, there is no *a priori* reason to assume that that plant is half as important to flies as a plant pollinated only by flies.

Using both types of proportions as dependent factors, we ran Analysis of Similarity tests based on Bray–Curtis similarity matrices on each trait, separately (ANOSIM; Plymouth Routines in Multivariate Ecological Research 5.0, Carr 1997; see also Daily *et al.* 2003). The Bray–Curtis similarity index incorporates both trait state identity and abundance. When species data are used as the basis for these analyses they indicate the trait state similarity of species assemblages in plots and habitats, whereas abundance-based analyses indicate the trait state similarity of individuals, independent of species identity, in plots and habitats.

Along with ANOSIM, we performed Multidimensional Scaling (MDS) for visual representation of similarity indices for both richness and abundance measures of each trait. We also ran Detrended Correspondence Analysis (DCA) on richness and abundance measures, using the DCA axis 1 for each trait as the dependent factor in a nested ANOVA to examine similarity of composition of trait states for each trait in each habitat type and location. Results from this technique did not differ markedly from ANOSIM results, and therefore only ANOSIM and MDS results are presented.

To determine whether the frequency of specific trait states differed between forested and deforested habitats (question 3), we ran two-way ANOVAs with habitat as a fixed factor, location as a random factor and trait state proportion per plot as the dependent factor. As above, we used a one degree of freedom orthogonal contrast test to test for differences between forested and deforested habitat types, and Tukey's HSD to test for significant differences between the six habitat types for each trait state (SAS 2003).

Our comparison of species and functional diversity patterns within and between habitats (question 4) is based on a qualitative examination of results from this

study with those of a previous study, Mayfield & Daily (2005), which used similar methods of analysis to examine patterns of species diversity rather than trait state composition. We discuss similarities in patterns of species and functional composition within and between all six habitat types and between the three locations. In Mayfield *et al.* (2005), the statistical relationship between species and functional trait state richness in the forested/deforested habitat categories was examined in the context of community assembly.

Results

TRAIT STATE RICHNESS

There were significantly more dispersal mechanisms and fruit types per plot in deforested habitats than in forested habitats (ANOVA: dispersal mechanism $Z = -3.58$, $P = 0.0004$; fruit type $Z = -5.31$, $P < 0.0001$; Fig. 1) while there were more growth forms, fruit sizes and seed sizes per plot in forested plots (ANOVA: growth form $Z = 4.23$, $P < 0.0001$; fruit sizes $Z = 2.26$, $P = 0.0239$; seed sizes $Z = 2.96$, $P = 0.0031$; Fig. 1). There was no significant difference in the mean number of pollination mechanisms per plot between forested and deforested habitats (ANOVA: pollination $Z = 0.08$, $P = 0.94$; Fig. 1).

For all six traits, we found significant differences in mean trait state richness among the six habitat types (Table 3). Pasture and understorey had the fewest trait states per plot for most traits (Table 4). Pollination and dispersal had similar numbers of trait states across all habitat types except understorey, which had significantly fewer pollination and dispersal mechanisms than all other habitat types. All other traits showed more extensive differences between habitat types (Table 4).

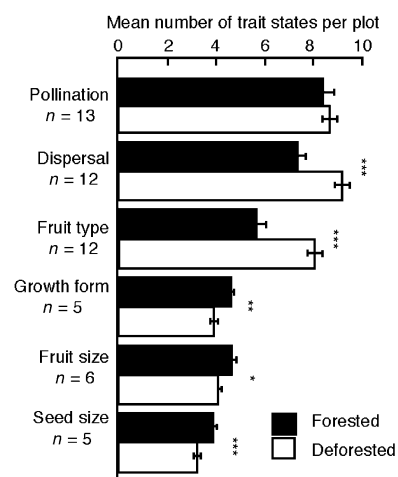


Fig. 1 The mean number of trait states per plot for each trait by habitat category. *n* is the total number of trait states for each trait and error bars represent standard errors. ***A significant difference of $P < 0.0001$, **significant difference of $P = 0.001$ and *significant difference of $P = 0.0239$. Significance was determined from orthogonal contrast tests in association with a two-way ANOVA.

Table 3 Results from a two-way ANOVA with trait state richness per plot as the dependent variable, habitat as the fixed effect and location as the random effect with an interaction term. The first value in each cell of the 'Effects tests' section is the *F* ratio and the values in parentheses are *P* values.

Trait	Whole model <i>F</i> ratio (<i>P</i> -value)	Whole model <i>R</i> ²	Effects tests		
			Habitat (d.f. = 5)	Location (d.f. = 2)	Interaction (d.f. = 10)
Pollination	3.4993 (0.0001)	0.4703	7.4017 (< 0.0001)	2.0853 (0.1323)	1.4550 (0.1762)
Dispersal	6.1406 (< 0.0001)	0.6091	17.2753 (< 0.0001)	2.2927 (0.1089)	1.3971 (0.2009)
Fruit type	8.0990 (< 0.0001)	0.6727	22.159 (< 0.0001)	2.0112 (0.1418)	1.9691 (0.0508)
Growth form	1.9293 (0.0300)	0.3286	5.1810 (0.0004)	0.6914 (0.5044)	0.4643 (0.9071)
Fruit size	4.1275 (< 0.0001)	0.5115	5.8250 (0.0002)	2.8054 (0.0676)	2.9877 (0.0036)
Seed size	5.0260 (< 0.0001)	0.5605	10.6194 (< 0.0001)	7.8594* (0.0009)	1.1323 (0.3521)

*PJ has significantly fewer trait states per plot than the other locations.

Table 4 HSD *post-hoc* tests comparing mean trait state richness in the six habitat types. Habitat means are significantly different from each other at the $P < 0.05$ level, if they have different superscript letters. Values are mean (standard error)

Traits	Understorey	Gaps	FR	PR	Pasture	Verges
Dispersal	5.94 ^b (0.304)	8.00 ^a (0.304)	9.33 ^a (0.527)	9.22 ^a (0.430)	9.17 ^a (0.304)	9.28 ^a (0.328)
Pollination	7.06 ^b (0.336)	9.44 ^a (0.336)	9.67 ^a (0.582)	8.78 ^a (0.475)	8.06 ^{ab} (0.336)	9.28 ^a (0.363)
Growth form	4.39 ^{ab} (0.303)	4.78 ^a (0.175)	4.33 ^{ab} (0.303)	4.22 ^{ab} (0.247)	3.67 ^b (0.247)	3.81 ^b (0.189)
Fruit type	4.33 ^c (0.318)	6.28 ^b (0.318)	8.00 ^{ab} (0.551)	8.22 ^a (0.450)	8.06 ^a (0.318)	8.25 ^a (0.34)
Fruit size	4.11 ^{bc} (0.212)	5.06 ^a (0.212)	5.00 ^{ab} (0.367)	4.22 ^{abc} (0.300)	3.67 ^c (0.212)	4.88 ^{ab} (0.229)
Seed size	3.33 ^{bc} (0.165)	4.33 ^a (0.165)	4.33 ^a (0.286)	3.22 ^{bc} (0.234)	2.83 ^c (0.165)	3.69 ^{ab} (0.178)

Few trait states were completely missing from any habitat type. All growth forms and fruit sizes were found in all habitat types, while rodent-dispersed species were missing from all habitats except pasture and road verges. Fruit type had the most trait states missing from various habitats, with loment-, nutlet- and pepo-bearing species missing from understorey plots and samara-bearing species missing from road verges. Bat-pollinated species were absent from both pasture and road verges and weevil-pollinated species were absent from pasture riverbank plots (supplementary Appendix S1).

There were no location effects on the mean number of trait states per plot except in the case of seed size, where there were significantly fewer sizes present per plot in PJ than in LC and LP (Table 3). There were interaction effects between habitat type and location for fruit type and fruit size (Table 3), although these effects varied by trait and never reflected significant differences between the same habitat types or locations.

COMMUNITY COMPOSITION OF TRAIT STATES

When we compared all forested plots combined with all deforested plots (as habitat categories) for trait state composition, forested and deforested habitat categories were significantly dissimilar for all traits, whether using species or individuals as the basis for Bray–Curtis indices (all $P < 0.001$; Figs 2 & 3). The same comparison yielded weaker but similar results when we used habitat type nested in habitat category (forested/deforested) as the dependent factor (Appendix S2; $P = 0.1$).

Compositional similarity between all six habitat types varied depending on whether species richness or trait state abundance was used as the basis for Bray–Curtis indices (Figs 2 & 3, Appendix S3). The only similarities between forested and deforested habitat types for both measures were among forest riverbanks, pasture riverbanks and road verges for growth form and

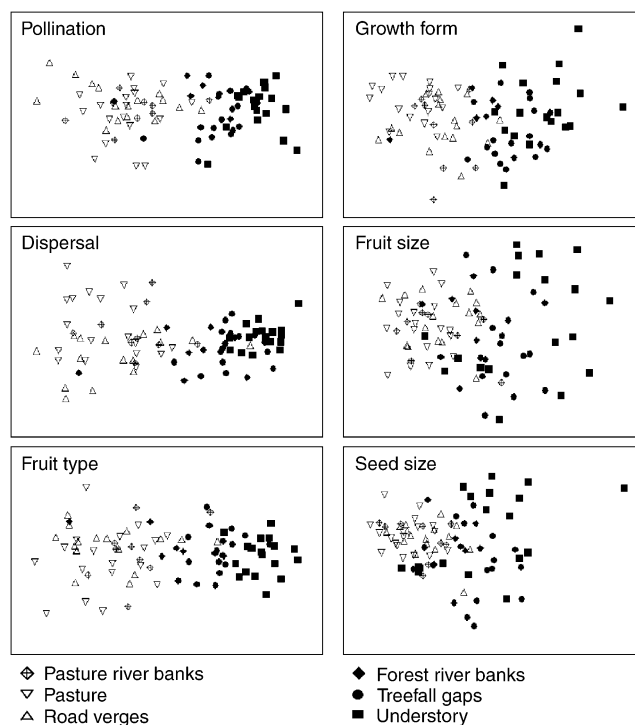


Fig. 2 Multidimensional Scaling (MDS) plots for each of the six traits using species richness as the basis. MDS is based on Bray–Curtis similarity indices. Closed symbols are forested plots and open symbols are deforested plots. Symbols for individual habitat types are listed in the key.

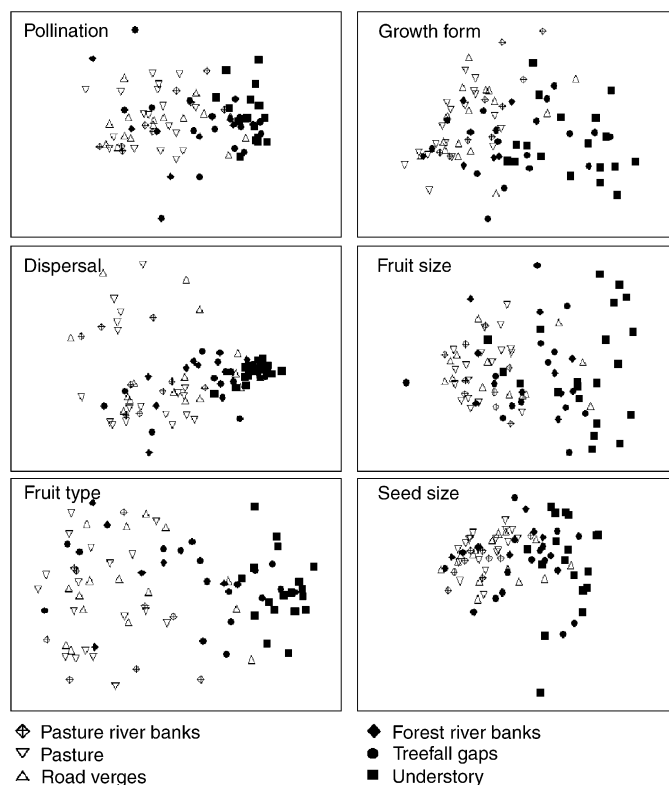


Fig. 3 Multidimensional Scaling (MDS) plots for each of the six traits using the number of individuals with a given trait state as the basis. MDS is based on Bray–Curtis similarity indices. Closed symbols are forested plots and open symbols are deforested plots. Symbols for individual habitat types are listed in the key.

forest riverbanks and road verges for fruit size. When we used richness-based indices, we found significant similarity between forest riverbanks and pasture riverbanks for fruit size and seed size (Fig. 3, Appendix S3).

The most similarities in trait state composition between forested and deforested habitats were found using abundance-based similarity indices (i.e. the number of stems with a given trait state per plot) with similarities

between pasture riverbanks and road verges and various forest habitats for numerous traits (Appendix S3). For example, using abundance-based similarity indices we found significant similarity between road verges and forest riverbanks for all traits and among tree-fall gaps, understorey, road verges and pasture riverbanks for seed size (Appendix S3). It should be noted that the exclusion of grasses from our sample is likely to have substantially altered abundance-weighted measures, as grass traits such as wind pollination are under-represented in pastures given this exclusion.

In comparing trait state composition of each trait across the three study locations, we found that the mean number of trait states in each habitat type differed between PJ and LC and LP for fruit type and fruit size and between LC and the two Osa locations for all other traits. Specific patterns for each trait varied depending on whether richness or abundance was used as the basis of similarity indices (Appendix S4).

SPECIFIC TRAIT STATES

Significant and extensive differences in the frequency of individual trait states were found for all traits. For

the sake of brevity, we do not report on all of these patterns here; they are available online as supplementary Appendices S1, S5 and S6 for readers interested in specific trait states.

Both bee- and bird-pollinated species were significantly less common in deforested than forested habitats ($F = 58.2$, $P < 0.0001$; $F = 12.2$, $P = 0.0009$, respectively), whereas there was no difference in the frequency of bat-pollinated species in forested and deforested plots ($F = 3.26$, $P = 0.076$). When abundance was used as the basis of proportions, however, there were no significant differences in the number of individuals with bat-, bee- or bird-pollinated flowers in forested or deforested habitats. Species with fur-dispersed seeds (exozoochory) were significantly more common in deforested than forested habitats ($F = 90.6$, $P < 0.0001$) and species with bird- or monkey-dispersed seeds were found more frequently in forested habitats ($F = 121$, $P < 0.0001$; $F = 23.9$, $P < 0.0001$, respectively). These patterns were the same when abundances were used as the basis of proportions (Fig. 4, Appendix S5).

Pastures and verges had almost no bat-pollinated plants (species or individuals) and forest tree-fall gaps had the most bat-pollinated species (Fig. 4, Appendix

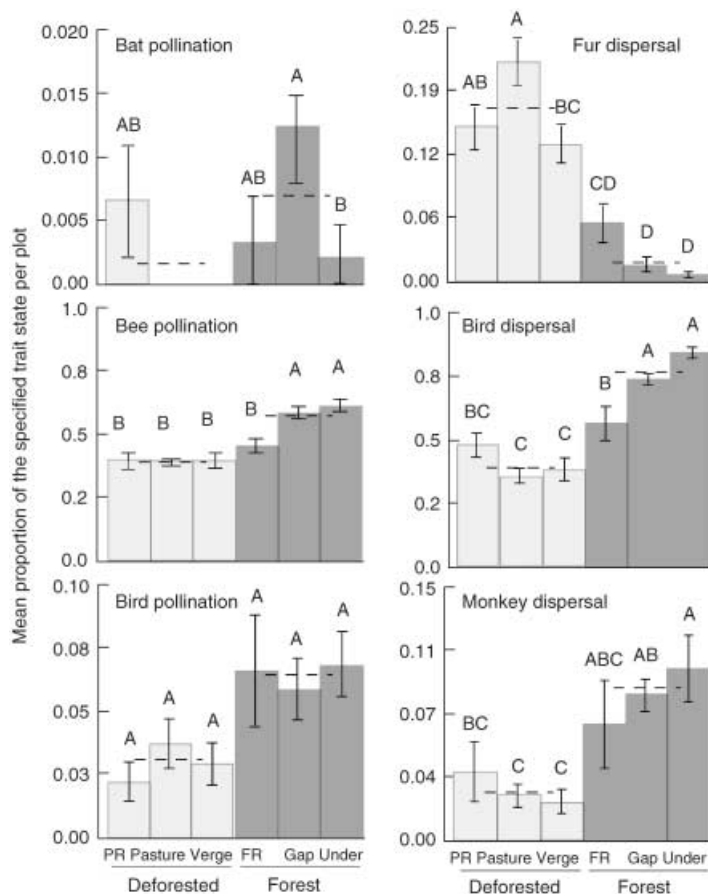


Fig. 4 Mean number of species per plot with bat-, bee- and bird-pollinated flowers in the first column and fur-, bird- and monkey-dispersed seeds in the second column. Error bars are standard errors. Horizontal dotted lines indicate the mean number of species with the specified trait state across all forested and all deforested plots. Bars with different letters are significantly different at the $P = 0.05$ level. Significant differences are based on Tukey HSD *post-hoc* tests in association with two-way ANOVAS.

S1). Bee-pollinated plants were significantly more common in tree-fall gaps and understorey with significantly fewer species in all deforested habitat types and forest riverbanks (Fig. 4, Appendix S1). There were no differences in the number of species or individuals with bird-pollinated flowers in any habitat type (Fig. 4, Appendix S1). Fur-dispersed species were significantly more common in pasture than all other habitats, with these species being least common in tree-fall gaps and understorey (Fig. 4, Appendix S1). Plants with bird-dispersed seeds were most common in understorey and tree-fall gaps, with pasture and road verges having the fewest species with this dispersal vector (Fig. 4, Appendix S1). Plants with monkey-dispersed seeds were most common in the understorey, with the fewest in pasture and road verges (Fig. 4, Appendix S1). None of these patterns changed when abundances were used for proportions except for bat pollination, for which there were then no significant differences between any of the habitat types.

Discussion

We find that the functional diversity of herbaceous and shrubby plant communities in deforested habitats is not lower than for their counterparts in remnant forest habitats in the same landscapes. In fact, there is higher functional richness (mean number of trait states per plot) in deforested than in forest communities for traits such as dispersal mechanism and fruit type. These results suggest that certain types of ecosystem function may be maintained in tropical human-altered landscapes, on the assumption that functional diversity influences ecosystem functions (Hulot *et al.* 2000; Díaz & Cabido 2001; Naeem 2002; Hooper *et al.* 2005). Other functions, however, may be in decline in deforested habitats. Importantly, habitat heterogeneity in deforested components of human-altered landscapes may be of particular importance for preserving a diversity of ecosystem functions, as evidenced by the dissimilarity of trait state compositions in deforested habitat types for different traits.

TRAIT STATE RICHNESS (QUESTION 1)

Herbaceous and shrubby plant communities differed in functional richness (for the traits studied here) between forested and deforested habitat categories (all habitat types combined for each), but not consistently. Analysis of specific forested and deforested habitat types illustrated that there are major differences in functional richness for these traits at finer-scale habitat levels.

Fifty-two of the 53 trait states from the six traits examined were found at some frequency in both forested and deforested habitats. The one exception was rodent dispersal, which was absent from all forest habitats. This result is, however, likely to be an artefact of limited dispersal information and of the exclusion

of trees, many of which have rodent-dispersed seeds. Specific rodent dispersal was only recorded for two species of *Physalis* (Solanaceae), which were restricted to road verge and pasture plots, although numerous species living in both forested and deforested habitats, and categorized as 'generally endozoochorous' in this study, are dispersed by a variety of animals including rodents. Observed losses of other trait states from specific forested and deforested habitats, such as the absence of bat-pollinated species from pastures and road verges, are probably more biologically meaningful.

Although no trait states were lost from deforested areas, growth form, fruit size and seed size had fewer trait states per plot (on average) in deforested than forested habitats, following our predictions. The opposite pattern was observed for dispersal and fruit type, counter to our predictions. Compositional patterns for dispersal and fruit type indicate that the addition of abiotic dispersal mechanisms and fruits dispersed on the fur of large mammals in deforested habitats may largely explain this pattern.

At the habitat level, understorey and pasture had the fewest trait states per plot and road verges and tree-fall gaps had the most, results that matched our predictions. Understorey and pasture plots probably have low numbers of trait states due to low species richness, extreme light limitation (understorey only), competition with the dominant grasses (pasture) or other restrictive environmental conditions (Mayfield & Daily 2005). The high functional richness in tree-fall gaps and forest riverbanks is probably due to high species richness and structural and environmental complexity in these habitat types (Denslow & Hartshorn 1994; Mayfield & Daily 2005).

FUNCTIONAL COMPOSITION (QUESTION 2)

Patterns of trait state composition indicated low levels of similarity when combined forested and deforested habitat types were considered, but there was surprisingly high trait state similarity between specific forested and deforested habitat types for some traits. Although there was more trait state similarity in forested and deforested habitats than expected, many forested and deforested habitat types were compositionally distinct for all traits in terms of trait state identity and abundance, indicating that many trait states found commonly in forested habitats are rare in deforested habitats and vice versa.

Counter to our predictions, road verge and pasture habitats were compositionally similar to some forest habitat types, most commonly forest riverbanks and tree-fall gaps, for some traits. As predicted, forest riverbanks and pasture riverbanks are functionally similar for most traits using both richness and abundance as the basis for similarity indices. Notably, we also found that pastures and forest riverbanks are compositionally similar in terms of dispersal mechanisms

and fruit types. Dispersal mechanism and fruit size are the two traits most likely to be directly influenced by animal behaviour in these habitats. Other studies of animals in similar human-altered landscapes have found high numbers of native forest animals moving through pasture environments (Estrada *et al.* 2000; Daily *et al.* 2001; Horner-Devine *et al.* 2003). Although we cannot determine if these animals transport seeds between pastures and forest riverbank habitats, our results, in combination with animal diversity studies, suggest a connection between the fruits and animals found in both habitat types.

One of the most interesting findings from our examination of functional composition was that richness and abundance-based similarity indices revealed dramatically different results regarding functional composition in forested and deforested plant communities. One possibility for greater compositional similarity between forested and deforested plots when using abundance rather than richness indices is that certain trait states are present in a few species that are found commonly in both forested and deforested habitats. However, of the 18 species with more than 300 individuals observed across the study, all but two were absent or had fewer than ten individuals in understorey and tree-fall gap habitats (Appendix S7). This suggests that whereas trait state abundance is similar between forested and deforested habitats, the underlying frequency distributions of species with these traits are substantially different. Deforested habitats appear to have a few common species with the same trait states whereas forested habitats have multiple less-common species that share trait states.

Trees are a major component of the plant communities in all forest habitats. Although we did not include this interesting portion of the flora in our study, it should be noted that there are probably numerous pollination and dispersal mechanisms, fruit types and, possibly, fruit and seed sizes that are unique to the tree component of forest habitats. Because this group of plants is so large and distinct from the herbaceous and shrubby plant flora of southern Costa Rica, we do not feel comfortable speculating about exactly how the inclusion of trees would have altered our results, particularly in terms of trait state composition. Given that this group of plants is largely restricted to the forest components of these landscapes, however, any trait states restricted to trees, including the growth form 'tree', would certainly have been found only in forest habitats, and compositional differences between forested and deforested components of these landscapes would have been more extreme. Detailed study of functional traits in the canopy layer of tropical forests would probably highlight the more obvious biodiversity and functional losses associated with deforestation in the tropics. Our results illustrate that the non-tree components of tropical plant communities are perhaps not as severely altered by deforestation, for some types of functional traits, as once thought.

SPECIFIC TRAIT STATES (QUESTION 3)

Although general patterns of functional richness and composition are valuable for understanding community-wide differences in functional diversity in human-altered landscapes, the distribution of individual trait states provides more specific information about the differences in ecological function and the availability of floral, fruit and protective (growth form) resources available for animals in different components of these landscapes. There are too many trait states in this study to discuss individually and thus we discuss only six of particular interest here. Results from all the trait states are presented in Appendices S1, S5 and S6.

Our general *a priori* predictions about the six specific traits were met. Bat-, bee- and bird-pollinated plants were most common in forested habitats, as were plants with seeds dispersed by birds and monkeys. Only species with seeds dispersed on animal fur were found to be more common in deforested habitats. When we examined patterns at the specific habitat level, however, our predictions were less consistently upheld.

Bat-pollinated plant species were all but absent in pasture or road verges. Although this finding was not surprising for pasture, we had anticipated that road verges would contain more species attractive to bat pollinators than other deforested habitats. The bat-pollinated species in this study include members of numerous plant families, including Cucurbitaceae, Fabaceae, Acanthaceae and Marcgraviaceae, suggesting that the observed exclusion of bat-pollinated species is not a sampling artefact but the result of an ecological filter or community assembly process. Relatively little is known about bat-habitat associations in the tropics but some bats are known to forage in deforested habitats while roosting (and thus dropping seeds) and nesting only in forest (Reis & Muller 1995; Duncan & Chapman 1999; Evelyn & Stiles 2003). Bat foraging patterns are unlikely to determine directly where bat-pollinated plant species are found. Individual plants in habitats more suitable or attractive to foraging bats may, however, be more likely to persist than individuals dispersed to or growing in habitats in which bats will not forage, perhaps pastures and road verge vegetation. Thus, our findings suggest that an association with trees is important for the long-term persistence of bat-pollinated species.

Plants pollinated primarily by bees were more common in tree-fall gaps and understorey than in any other habitat type. There is growing evidence that bees survive in forest fragments and forage actively in both forested and deforested components of these landscapes (Feinsinger *et al.* 1987; Klein *et al.* 2002; Ricketts 2004). There is, however, little information about what bees surviving in forest fragments forage on or how floral resources are distributed between forested and deforested habitats. Although our results do not suggest that bee-pollinated plants are clustering entirely in forest habitats, it does appear that more specialized bee resources (species pollinated primarily by bees rather

than a wide range of insects including bees) are more common in forest habitats.

Bird-pollinated plants were equally common in forested and deforested habitats, although there was a trend for more bird-pollinated plants in forested habitats. This trend suggests that although there has been a decrease in bird-pollinated plant species in deforested habitats, some deforested areas still have numerous resources, in the non-tree flora, for nectar-eating birds surviving or foraging out of the forest.

Exozoochory, or dispersal on fur, is more common in deforested than forested habitats, with more of these plants in forest riverbank plots than any other forest habitat type. These patterns correspond to movements of cattle and horses, which are probably the main vector of seeds from these species and are common in pastures and move between pastures along roads and waterways (our personal observation).

Plants with bird- and monkey-dispersed fruits were found more frequently in forested than deforested habitats. Pasture riverbanks had more plants with these dispersal mechanisms than the other deforested habitats, suggesting that trees may be an important component of communities dispersed by these animals. This is not surprising given the reliance of birds and monkeys on trees for foraging and nesting habitat.

Many factors influence the ability of plants to survive in different components of human-altered landscapes. It is often assumed that physiological limitations of plant species are the most important factors in determining which species can survive in which habitats. Although this is not the first study to show evidence contrary to this belief (Mabry *et al.* 2000; Coomes *et al.* 2002), our results do provide evidence that animal-mediated dispersal may also play a major role in the community assembly of native plants throughout such landscapes. These results do not indicate whether animal dispersers cause plant distribution patterns or vice versa, but they do illustrate the importance of plant/animal interactions in community assembly and the effects of human landscape alteration on the ecology of native plant and animal communities.

FUNCTIONAL DIVERSITY VS. SPECIES DIVERSITY (QUESTION 4)

Given that conservation efforts in the tropics are usually under-funded and data collection can be time consuming and expensive, it would be useful if broad studies of species diversity could be used to inform conservation managers about the functional diversity, both richness and composition, in different habitats within tropical human-dominated landscapes. Although theoretical studies, and research in temperate systems, have suggested a strong positive correlation between species diversity and functional diversity (Hooper & Vitousek 1997; Tilman *et al.* 1997; Díaz & Cabido 2001), these results provide no information about how and whether species and trait state compositional pat-

terns relate. In a separate analysis of our data, we found that trait state richness generally increased with species richness, although relationships were weak for all traits except growth form (Mayfield *et al.* 2005). As shown by the results presented above, however, specifics about trait state composition likely provide more revealing information about how deforestation impacts functional diversity in these landscapes.

To determine whether patterns of species and trait state composition correspond across these landscapes, we qualitatively compared results from this study with those from a previous study examining species composition in the same landscapes and plots (Mayfield & Daily 2005). In this study, we found that few trait states were lost from forested or deforested habitats but that the functional composition of deforested habitats was largely distinct from forested habitats. This seems to fit with observed species richness patterns, for which we also found similar numbers of species per site in forested and deforested habitats, but distinct community compositions (Mayfield & Daily 2005). Functional and species diversity patterns diverge more dramatically, however, when we examine the specifics of these patterns.

Although only a few trait states were completely absent from any habitat type, only 16–20% of species were found both in a forested and in a deforested habitat, indicating that there is far more functional similarity between communities (the same trait states found in different habitats) than species overlap in forested and deforested components of these landscapes. There was also far more compositional similarity of trait states than species when we examined patterns for each trait using both richness and abundance-based similarity analyses. Only pasture riverbanks and forest riverbanks were compositionally similar for species diversity, while forest riverbanks, road verges, pasture and pasture riverbanks were all compositionally similar for trait states from numerous traits (Mayfield & Daily 2005).

Finally, we expected functional diversity patterns to be consistent across locations, as was found for species diversity patterns. Unlike species composition, however, patterns of functional trait state composition differed significantly between locations (Appendix S4). These differences were not always even between LC and the two Osa locations, which would have been easily explained given differences in the floras and climates of these areas. The observed inconsistency of trait state patterns across locations suggests that communities may be compositionally and ecologically influenced by microenvironmental conditions, animal diversity patterns and other environmental factors more than was evident in a study of species diversity alone.

Conclusions

Functional trait state diversity patterns can be extremely valuable for understanding the conservation

potential of countryside landscapes and the habitats that comprise them. Results from this study provide information about these specific communities, and suggest how functional trait states are likely to be distributed in other countryside landscapes around the world. We found that few trait states common in forest remnants are completely absent from deforested components of these landscapes. The frequency of individual trait states for each of the studied traits, however, varied greatly between habitat types, with few trait states equally common in both forested and deforested habitats. The diversity of deforested habitat types also appeared to be important in the preservation of primarily forest trait states, such as bat pollination, in deforested areas. Although our results paint a fairly optimistic view of the future of ecosystem function in tropical human-dominated landscapes, they should not be used to suggest that other types of ecosystem function respond similarly to deforestation. Additionally, the exclusion of trees from the study removes from discussion some of the most extreme changes that obviously occur in tropical deforested regions. The removal of trees from these landscapes is likely to have much more extreme impacts on ecosystem functions, such as carbon sequestration and nutrient cycling, than on the types of floral resources available for pollinator species and on the other functional traits examined in this study. Additionally, animal diversity is strongly influenced by structural complexity of vegetation, and loss of the medium- and tall-stature tree growth will dramatically influence many animal species (Harrison 1962; Pearson 1971; DeVries & Walla 2001; Walther 2002).

Comparisons of species and trait state compositions illustrate that care should be taken in using studies of species diversity to determine the types of functional diversity found in a given landscape. Functional trait diversity patterns are far more variable across and between landscapes than species diversity patterns. Overall, the patterns reported here provide insight into the complexity of community function and the impacts deforestation has on plant and animal communities surviving in increasingly common human-dominated landscapes.

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com:

Appendix S1 Mean proportion (and standard error) of each trait state by habitat type using richness as the basis

Appendix S2 Results for the Multidimensional Scaling (MDS) analyses shown in Figs 2 & 3 in the main text

Appendix S3 ANOSIM results for comparisons between all six habitat types for each trait using both richness and abundance similarity measures with habitat type as the independent factor

Appendix S4 ANOSIM results for each trait with location as the independent factor

Appendix S5 Comparison of trait state frequencies in forested and deforested habitat categories

Appendix S6 General model results from two-way ANOVAs with habitat type and location as independent variables and the proportion of each trait state as the dependent factor

Appendix S7 The most common species (per individual) sampled across the entire study with trait state for each trait