COUNTRYSIDE BIOGEOGRAPHY OF NEOTROPICAL HERBACEOUS AND SHRUBBY PLANTS

Margaret M. Mayfield[1] and Gretchen C. Daily

Center for Conservation Biology, Department of Biological Sciences, 371 Serra Mall Stanford University, Stanford, California 94305-5020 USA

Abstract. As human impacts on the environment intensify, the future of plant and animal biodiversity will depend increasingly on the floras surviving in human-dominated ''countryside'' habitats. To begin to characterize these floras for the Neotropics, we investigated the richness and composition of herbaceous and shrubby plant communities in six forested and deforested habitats, in three replicated study areas (7.5-km in diameter), of southern Costa Rica. We chose habitat types that are common throughout the tropics, to begin building a general understanding of both the habitats of origin and the diversity of countryside floras. Focal forest habitats were understory, 1- to 2-year-old tree-fall gaps, and riverbanks, all in primary forest. Focal deforested habitats were ungrazed road verges, grazed pasture, and riverbanks in grazed pasture. Non-riverbank habitats were sampled both near and far from forest edge. In total, we sampled 772 species from 79 families, ~40% of the non-tree plant diversity of the region. Only 6% of identified species are known to be exotic. In each study area, understory and pasture plots were consistently species poor, while tree-fall gaps and road verges near forest were consistently the most species-rich habitats. In each study area, we found the same proportion of species restricted to forested habitats (~45%) and deforested habitats (~37%), and the same proportion of ''countryside-habitat generalists'' (~18%) occurring in both forested and deforested habitats. However, different forested habitats supported different proportions of countryside-habitat generalists in each study area, although understory plots consistently supported the fewest generalists. Among forested habitats, riverbanks were the most similar floristically to deforested habitats. Pasture riverbanks and road verges near forest supported plant communities most similar to those in forested habitats. The uniqueness and richness of each habitat suggests that countrysides with diverse land uses can support many native herbaceous and shrubby plant species. As it becomes increasingly difficult to protect large tracts of undisturbed tropical forest, we suggest that conservation goals expand to encompass maintenance of heterogeneity in countryside landscapes.

Key words: biodiversity conservation; Costa Rica; deforestation; habitat fragmentation; human-dominated landscapes; native herbaceous plants; native shrubs; Neotropical countryside; tropical moist forest; tropical plant biodiversity.

INTRODUCTION

Deforestation and habitat fragmentation are causing dramatic changes in biodiversity throughout the tropics, yet deforestation does not leave an entirely barren, sterile land surface. Rather, it often results in ''countryside''—complex landscapes comprising diverse habitats, which vary greatly in their extent of native vegetation cover and their ability to support biodiversity. Countryside habitats include remnants of primary ecosystems (in this study, tropical forest), secondary regrowth, recently cleared land, pastures, agricultural plots, gardens, and residential areas (Daily 2001). As human activities expand throughout the tropics and preservation of large tracts of native habitat becomes more difficult, countrysides acquire greater conserva-

tion importance (Saunders et al. 1991, Daily 2001, McNeely and Scherr 2002).

The study of biodiversity in countryside of both temperate and tropical regions has traditionally been cast in island biogeographic and metapopulation frameworks. These frameworks view the world in binary terms, as comprising habitat surrounded by a uniform matrix of human-dominated non-habitat (Soulé et al. 1992, Brown and Hutchings 1997, Shahabuddin and Terborgh 1999). In reality, heavily modified countryside habitats can and do support native biodiversity, and this needs to be accounted for in forecasts of biodiversity change and in assessments of alternative conservation investments. For example, Gascon et al. (1999) found that the species richness of native small mammals and frogs was higher in the deforested habitats of their Amazonian study area than in forested habitats. Estrada et al. found diverse faunas of native carrion beetles (1998) and forest birds (2000) in deforested habitats of Las Tuxtlas, Mexico. In southern

[1] E-mail: mmayfield@stanford.edu

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Costa Rica, a series of research efforts has documented 50% or more of native species occurring in deforested habitats, for a variety of animal taxa including birds (Daily et al. 2001, Hughes et al. 2002, Luck and Daily 2003), moths (Ricketts et al. 2001), butterflies (Horner-Devine et al. 2003), mammals (Daily et al. 2003), reptiles (G. Ceballos and G. C. Daily, *unpublished data*) and amphibians (G. C. Daily and G. Ceballos, *unpublished data*).

The conservation value of tropical countryside to native plants is yet unclear. Little is known about the herbaceous (including vining species) and woody non-tree (i.e., shrubby) floras of tropical countrysides, our focus here. One of the most important and obvious differences between plants and animals is mobility. Mature plant individuals cannot escape deleterious impacts of habitat modification by moving among habitats on a daily or seasonal basis, as many animals do. If their seeds are dispersed into a deforested habitat, they must be able to complete their entire life cycle in that habitat to survive there over generations. This predicament suggests two important implications: first, fewer native forest plant species than animal species may utilize deforested habitats and, second, the common occurrence in recently deforested habitats of mature plants native to forest does not guarantee that such species will persist there over the long term. Because of their stationary nature and rapid life cycles, herbaceous and shrubby plants may offer insights into the long-term conservation value of both forested and deforested countryside habitats, for not only the flora but also the animals that depend on it.

In temperate regions of North America and Europe, the floras surviving in countryside have been well studied. Floristic diversity varies with agricultural intensity and landscape structure (Grevilliot and Muller 1996, Godreau et al. 1999, de Blois et al. 2002, Landsberg et al. 2002), with successional stage of abandoned pastures (Bazzaz 1975, Stover and Marks 1998, Gondard et al. 2000), and with the structure of hedgerow and field-margin habitats (Jobin et al. 1996, Boutin et al. 2002, Garbutt and Sparks 2002, Le Coeur et al. 2002, Tarmi et al. 2002, Thomas et al. 2002). These studies provide insights into the kinds of patterns that might occur in tropical systems (Trebino et al. 1996, Burel et al. 1998, de Blois et al. 2002), but few actually examine the entire plant communities of countryside or examine the differences between native and human-dominated habitats within them (Marks 1983, Hill et al. 2002, Schmidt and Barnwell 2002).

From the tropics there is a growing literature on trees surviving in countryside, focused largely on growth rates and reproductive success in and out of forest, and on remnant trees as habitats for other organisms or as starters for forest regrowth (Nepstad et al. 1996, Aldrich and Hamrick 1998, Guevara and Graciela 1998, Harvey and Haber 1998, Holl 2002). While remnant trees are likely to have significant ecological roles in

countryside, they do not make up the majority of plant biomass or biodiversity in these habitats. Yet most studies of forest regeneration after deforestation focus on trees and consider only the detrimental roles of some grasses and vining and shrubby species as inhibitors of tree regrowth (Buschbacher and Serrao 1988, Buschbacher et al. 1988, Gomez-Pompa et al. 1991, Cain 1999, Posada et al. 2000) rather than recognizing them as important components of regenerating forests. Multiple studies have found herbaceous and shrubby species to be integral to forest regeneration and to promoting animal-based seed dispersal (Uhl et al. 1981, 1988, Guimares-Vieira et al. 1994, Posada et al. 2000, McLachlan and Bazely 2001). Herbaceous and shrubby species are also known to play a role in nutrient sequestration, particularly in deforested countryside habitats (Boring et al. 1981, Buschbacher et al. 1988).

Despite the importance of herbaceous and shrubby species to tropical ecosystems, few studies have examined their biodiversity in tropical countryside (Fujisaka et al. 1998, Bruna 1999, Costa and Magnusson 2002, Benítez-Malvido and Martinez-Ramos 2003). Fujisaka et al.'s study (1998) investigated total plant diversity in a single agricultural settlement in the Brazilian Amazon. They found that particular land-use practices greatly influenced the flora of agricultural fields, which were dominated by exotic weeds, and that the lowest overall plant species richness was in grazed pasture. Other recent studies examine tropical understory plant communities in forest fragments of different sizes or types of disturbance. Bruna (1999) found that seeds of *Heliconia acuminata*, a native forest herbaceous species, germinated significantly less well in forest fragments than in continuous forest. Benítez-Malvido and Martinez-Ramos (2003) found that understory plant communities in forest fragments were less rich and compositionally different from understory communities in continuous forest. Finally, Costa and Magnusson (2002) found that the understory herbaceous community is not severely affected by selective logging in central Amazonia.

In this study we examine the herbaceous and shrubby plant communities in an array of forested and deforested countryside habitats (six in total) common throughout the tropics. We replicate our work in three study areas across southern Pacific Costa Rica. Specifically, we ask: (1) How do richness, abundance, and composition differ between forested and deforested habitats? (2) Which type of deforested habitat most resembles forested habitats floristically and vice versa? (3) How does the proximity of forest to deforested habitats influence plant richness and composition?

METHODS

Study areas

In June–August of 2001 and January–February of 2003, M. Mayfield sampled herbaceous and shrubby

plant species 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 Jiménez (PJ) and La Palma (LP). The study areas were selected as arbitrary replicates of similar countryside landscapes, all within the same general floristic province: pacific-slope tropical wet forest. The size of the study areas was established to permit sampling replicates of six habitat types at sufficient spacing.

Prior to 1960, most of southern Costa Rica, including our study areas, was covered by tropical moist forest; today it is largely deforested. The Las Cruces Forest Reserve is one of the largest remaining tracts of mid-elevation forest (1200 m) in southern Costa Rica, occupying 227 ha. Cattle pastures, coffee plantations, and small forest remnants (<10 ha) dominate the LC study area. The other two study areas are on the Osa Peninsula. Much of the tropical forest on the Osa Peninsula has been preserved in Corcovado National Park (41 788 ha). Cattle pastures, rice fields, and oil-palm plantations dominate the countryside of the peninsula. The LC area is separated from the LP and PJ study areas by >50 km and ≥500 m of elevation. The LP and PJ areas are separated by >13 km.

Sampling design

Our sampling design included four nested levels of organization in which plots were the actual sampling unit. A plot was an 80-m^2 sampling rectangle, which we describe in greater detail below. Each plot fits into four hierarchical levels of organization: level 1, study area; level 2, category; level 3, habitat type; and level 4, distance class (Table 1). Within each of the three study areas (LC, LP, PJ), we sampled plots in two categories, forested and deforested. Plots were then further distributed among six habitat types, and these split into two distance classes, near and far from forest. (That is, except for riverbanks, which were too few in either forest or pasture to achieve statistical independence in sampling, habitat types were split by distance to forest edge). Table 1 lists the four sampling levels and the number of individual plots sampled in each (85 total plots). We note that while this is a nested sampling design, levels 2, 3, and 4 are not random replicates of each higher level, but rather were selected specifically to fit the requirements described below for each sampling level. Throughout the text when we refer to ''forested habitats'' we are referring to all the plots in the forested category, including understory, tree-fall gaps, and forest riverbanks. The same is true for the term ''deforested habitats'' with the corresponding three deforested habitat types.

We used the following general criteria for situating plots within each habitat type: vegetation age, vegetation type and architecture, area of uniform habitat, and slope of terrain. Since the majority of the deforested land in our study areas was deforested between

TABLE 1. Study areas replicate our four-level hierarchical sampling design: two sampling categories each with three habitat types, which are split into two distance classes.

Category and habitat type	Distance class (m)†	Study areas‡		
		LC	LP	PJ
Forested				
Understory	far (>500)	3§	3	3
	near (<50)	3	3	3
Tree-fall gaps	far (>400)	3	3	3
	near (<50)	3	3	3
Riverbanks in forest‖	far (>400)	2	2	2
Deforested				
Pasture	near (<20)	3	3	3
	far (>300)	3	3	3
Road verges	near (<10)	1¶	3	3
	far (>300)	3	3	3
Riverbanks in pasture	far (>400)	3	3	3

† The distance of a plot from forest edge. Forest plots near forest edge are ≤50m from a pasture edge.

‡ The three tropical wet forest study areas in coastal southern Costa Rica are around Las Cruces Biological Field Station of the Organization for Tropical Studies (LC) and around the towns of Puerto Jiménez (PJ) and La Palma (LP). Data are the number of 80-m^2 rectangular plots in each study area that were sampled.

§ Understory plots in LC were 250 m from the forest edge.

‖ Only two plots for forest riverbanks were sampled in each study area because there were not enough rivers in each area to sample.

¶ Only one road-verge plot near forest was sampled in the Las Cruces area because we found no other suitable sites for replicate plots (very little forest remains along roads).

30 and 40 years ago, vegetation age refers to short-term age, i.e., last cutting or tree fall. All plots featured similar vegetation architecture and supported non-tree plant cover between 10 and 350 cm in height. All plots also comprised relatively homogeneous vegetation types for at least 100 m^2, no terrain was steeper than 25 degrees and all plots were separated by ≥400 m.

All six habitat types are common in our study areas, and throughout the tropics. Although we only have detailed land-cover data for LC, the LP and PJ study areas were similar. In the LC study area, 35% of land cover was forest and 28% cattle pasture (Sallie-Ann Bailey, *personal communication*). In forest, we sampled understory, as it is the habitat most dominated by herbaceous and shrubby species. We also sampled two common disturbed-forest habitats, tree-fall gaps and riverbanks, because one goal of our study was to determine which forest habitats are most similar floristically to deforested habitats. Among the latter, grazed pasture and ungrazed road verges are both common and superficially distinct. Our third deforested habitat type was riverbanks in pasture, to make the comparison with riverbanks in forest.

Because LC is a relatively small forest fragment (227 ha), all understory habitats there were within 250 m from forest edge, which suggests they have experienced some edge effects (Laurance et al. 1998). Understory habitats in the LP and PJ study areas were all in large

tracts of continuous forest, in or adjacent to Corcovado National Park, and >500 m from the edge of forest. In each study area, understory vegetation was 65–350 cm high and was covered by a completely closed canopy. Forest tree-fall gap plots were all 1–2 years old, with similar height and density of non-tree vegetation. Forest tree-fall gaps ranged in size from 100 to 400 m^2 and had an average understory vegetation height of 30–70 cm. Forest riverbank plots were all on sections of rivers that were wide enough that there was no canopy cover over the middle of the waterway. Deep sections of rivers with steep banks were not used because of difficulty of sampling. In LC, riverbank plots were along narrower stretches of river (5–10 m wide), and vegetation was on soil-covered rock outcroppings. In LP, forest riverbank plots were along similarly narrow stretches of rivers along muddy banks. The PJ riverbank plots were along the widest stretches of river, sometimes >20 m across, with sandbars on both sides. Rivers in LC were not used by people, except for scientific study, but the rivers in LP and PJ were used by small numbers of fisherman and gold miners, and for household activities such as washing clothes and dishes. None of the rivers was deep enough for boat traffic, and all flooded seasonally. While forest riverbanks were the most different from each other of any habitat type, they were representative of the most common forest riverbank habitats in each sampling area.

Pasture habitats were all actively grazed by cattle during the sampling period and dominated by exotic African grasses. Vegetation in pasture habitats was 10–50 cm high. The extent of pasture habitats varied, but all exceeded 1 ha and most were >5 ha or more. Road verges were also dominated by exotic African grasses but were maintained by occasional cutting rather than cattle grazing. Road-verge plots were all along paved or well-maintained dirt roads with two lanes of regular vehicle traffic. All road-verge plots were in sections of road 2–6 m wide that supported similar vegetation on both sides of the road. We did not use road verges with extensive vegetation over 80 cm high for reasons of safety. Pasture riverbanks were sampled along narrow (2–10 m wide) streams passing though actively grazed pasture. All had scant tree cover and muddy banks with mild to severe erosion caused by cattle. These streams were all too small for boat traffic.

Plant sampling

In each plot we recorded the number and abundance of herbaceous (including some epiphytes), vining, and shrubby (woody species up to 5 m high) plants in 20 noncontiguous 1 × 1 m quadrats spaced as uniformly as possible over an 80-m^2 rectangular area. Overhead cover was measured at four points in each plot using a spherical densiometer. We excluded grasses, ferns, mosses, and trees. Grasses were excluded because they did not contribute significantly to the richness in our plots–all were exotic except for a single individual

found on a forest riverbank. Ferns and mosses were excluded mainly for logistic reasons (the number of species sampled was already extremely high) and because, as a group, they have very different ecological roles and physiologies than species in our predominately angiosperm study taxa. Such differences would have required separate treatment, which we left for separate study. Trees were excluded because they are presently the focus of other research efforts. We did record the abundance of grasses, ferns, mosses, and tree seedlings, in those broad groupings. If epiphytes had fallen from trees above we did not count them because they were clearly not long-term members of our sampled plant communities. However, if epiphytes were rooted on the ground or on live plant tissue on the ground we did count them. In all, our sample included species in four growth forms: herbs, shrubs (woody species up to 5 m), vines (woody and herbaceous), and understory epiphytes (Table 2). We also categorized each species as exotic, cosmopolitan, or endemic. Exotic species were those with known original ranges outside of Costa Rica and a known introduction time period. Cosmopolitan species were those thought to be native to the study region but with very large distributions extending throughout Central and South America. Endemic species were those with known ranges that extend no further than northern Panama or southern Nicaragua, although most of our endemic species were endemic to even more restricted regions, mainly the Osa Peninsula.

All collected specimens (2525) were sorted to recognizable taxonomic units (RTUs; Oliveira-Filho et al. 1997) and were identified to family and genus, and species when possible (see *Acknowledgments* for contributions to plant identifications). Forty-two specimens were lost and are not included in across-plot analyses. We based growth form and categorization of species as exotic, cosmopolitan, or endemic on collected samples (for growth form only), personal communications with specialists at the Missouri Botanical Garden (Saint Louis, Missouri, USA), on collection records of the Missouri Botanical Garden, and on information provided in the *Flora of Nicaragua* (Stevens et al. 2001).

Analysis

All analyses are done at both the species and family levels given the conservation value of higher taxonomic groupings (Erwin 1991). We analyzed patterns of community diversity using species richness and species evenness of abundance ($J' = -\Sigma(p_i \ln p_i / \ln S)$; Pielou 1966) as measures of diversity. Values of J' range from 0 to 1, with 1 indicating that all species have the same abundance. We compared species and family richness per plot and per stem (log transformed for normality), measured across habitat types using a nested analysis of variance (ANOVA) with distance class nested in habitat type nested in category (JMP version 5.0.1.2;

TABLE 2. The total (and mean per plot) number of taxa sampled, and total number (and percentage) of specimens classified by growth form sampled.

Sampling hierarchy	Taxon			Growth forms			
	No. families	No. genera	No. species (RTUs)	Epiphytes	Vines	Shrubs	Herbs
Study areas							
LC	72 (22)	202 (33)	406 (40)	18 (5%)	93 (24%)	114 (29%)	167 (43%)
LP	58 (14)	177 (25)	387 (30)	17 (5%)	100 (27%)	112 (30%)	143 (38%)
PJ	68 (17)	191 (25)	362 (31)	12 (3%)	80 (23%)	111 (31%)	151 (43%)
Category							
Deforested	72 (18)	217 (29)	422 (34)	31 (7%)	98 (25%)	123 (31%)	142 (36%)
Forested	64 (16)	223 (25)	535 (33)	49 (10%)	122 (24%)	159 (32%)	173 (34%)
Habitat type							
Understory	42 (13)	78 (19)	186 (25)	19 (11%)	42 (23%)	68 (38%)	52 (29%)
Tree-fall gaps	56 (18)	161 (29)	340 (37)	36 (11%)	91 (28%)	97 (30%)	101 (31%)
Forest riverbanks	45 (21)	106 (35)	184 (45)	14 (8%)	35 (19%)	50 (28%)	82 (45%)
Pasture	53 (18)	127 (24)	201 (27)	1 (1%)	36 (18%)	51 (25%)	113 (56%)
Road verges	61 (20)	170 (36)	295 (42)	11 (4%)	60 (21%)	86 (30%)	133 (46%)
Pasture riverbanks	52 (20)	102 (27)	155 (31)	9 (6%)	38 (25%)	42 (27%)	66 (43%)
Whole study totals	79	322	772†	35	176	222	303

Notes: Numbers for taxonomic levels include only those RTUs (recognizable taxonomic units) identified to the corresponding taxonomic level. Growth-form numbers include all specimens identified at least to genus plus all RTUs that could be classified based on our collected specimens.

† This number does not include the 42 RTUs that were lost and not included in analyses.

SAS 2003). We also performed a two-way ANOVA testing the interaction between study area (LC, LP, PJ) and habitat type (all 10 types) for species richness. To examine differences in all combinations of categories and habitat types within study areas, we used Tukey honest statistical difference (hsd) post-hoc tests.

To examine species accumulation, by area, sampled within forested and deforested plots in each study area, we constructed species-accumulation curves by pooling all forested plots from a single study area and all deforested plots from a single study area and randomly drawing quadrats without replacement from each pool (Colwell 2000). The 99 curves from each analysis were then averaged to construct an accumulation curve for forested and deforested plots in each study area (six curves in total). The same randomization technique was used to create species-accumulation curves for all habitat types (Magurran 1988, Colwell 2000). To estimate total species richness in each habitat type and in all forested and deforested plots, we used a first-order jackknife richness estimator (Burnham and Overtom 1979, Smith and van Belle 1984, Hughes et al. 2002). Other studies have compared richness estimators and found the first-order jackknife consistent with several other commonly used and reliable estimators in studies of bird and plant diversity in Costa Rica (Bulter and Chazdon 1998, Hughes et al. 2002). We then used an ANOVA to test for a difference between estimated species richness in forested and deforested plots.

To examine differences in the proportions of species (or families) restricted to the forested or deforested categories, and conversely the proportions occurring in both of these categories (''countryside-habitat generalists''), we used a G test for goodness of fit (Sokal

and Rohlf 1994, SAS 2003). We also used a G test to examine the representation of countryside-habitat generalists in different habitat types. We ran these analyses with all sampled plants including singletons and doubletons and with a 10-individual cutoff (i.e., only plants observed at least 10 times were included). To examine the relationship between canopy cover and species richness, we ran a second-degree polynomial regression (Mittelbach et al. 2001).

We examined floristic similarity of habitat types in each study area with species composition and abundance, by calculating Bray-Curtis similarity coefficients (Bray and Curtis 1957). We then used a multidimensional scaling (MDS) algorithm to plot the relative similarity of plots in two dimensions (the proximity of points in the two-dimensional plot is proportional to their similarity). To calculate the probability of acquiring a given level of clustering between habitat types by chance, we conducted an analysis of similarity (ANOSIM; Plymouth routines in multivariate ecological research 5.0, Carr 1997; see also Daily et al. 2003). Because of low degrees of freedom in this test, the lowest possible P value for distance-class comparisons (three samples per habitat distance class) is 0.1, which we used as the significance level for this analysis. Global R is the level of order there is between groups and within groups, ranging from 0 (random) to 1.0 (perfectly ordered).

RESULTS

Richness and origin of the herbaceous and shrubby flora

In total, 772 recognizable taxonomic units (RTUs) from 322 genera and 79 families were collected (Ap-
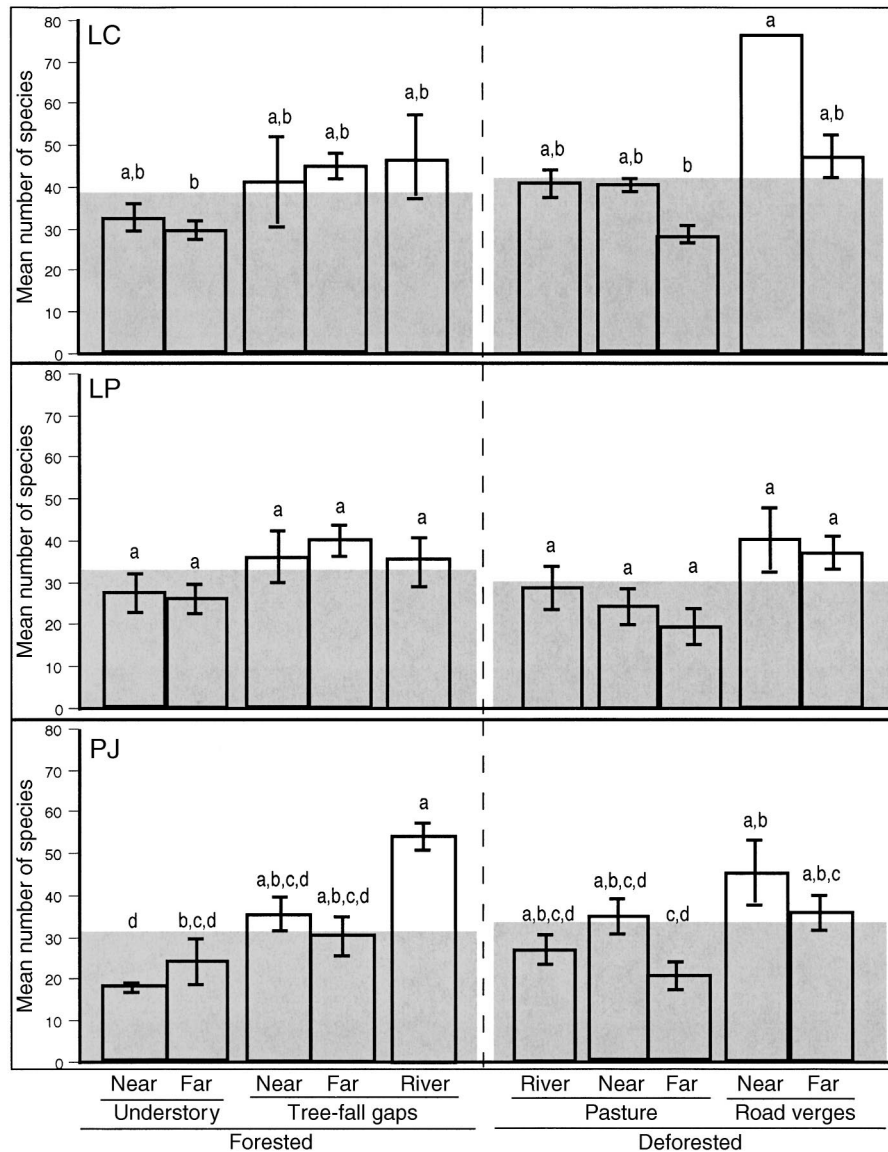
FIG. 1. Species richness (mean ± 1 SE) per plot for each habitat type, by study area. Bars with the same lowercase letters are not significantly different (Tukey's hsd test) at the $P \le 0.05$ level between habitat types within study areas. In each panel, the gray shading indicates the mean species richness over all forested or deforested plots.

pendix A); 511 RTUs were identified to species. Table 2 presents the number of taxa and common growth forms found in each study area. Our collection represents ~40% of non-tree species known to live on the Pacific Slope of southern Costa Rica. The La Amistad Pacifico region, which includes the Las Cruces study area, is well known for its high species diversity, which explains why there are more species on average in plots at this study area than the other two. In this region there are 1720 known plant species, 1084 of which are herb, shrub, vine, and epiphyte species (Hammel et al. 2004). We sampled ~40% of the non-tree flora of this region. The other two study areas are on the Osa Peninsula, which has approximately 1500 plant species.

We collected ~50% of the non-tree species of that region (Barry Hammel [Missouri Botanical Garden], *personal communication*).

Of the 511 identified species, 30 species (6%) are known exotics. In forested habitats (including plots from all three forested habitat types), ~4% of sampled species are known exotics and 54% are cosmopolitan, occurring throughout Central and South America. By contrast, in deforested habitats (including plots from all three deforested-habitat types), ~10% of sampled species are known exotics and 63% are cosmopolitan. Approximately 10% of species from forested habitats, and 3% from deforested habitats, are endemic to Costa Rica or our specific study areas.
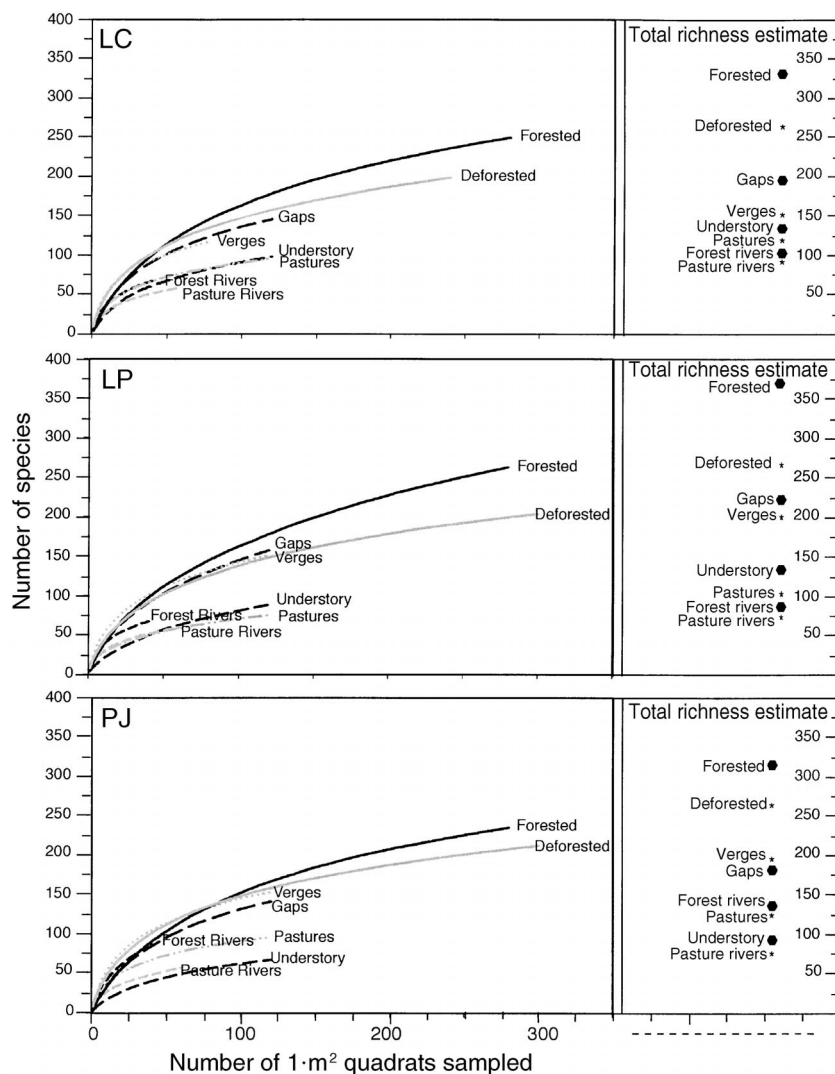
FIG. 2. Species richness accumulation across sampled quadrats and estimates of total richness in the three sample areas of southern coastal Costa Rica (see Table 1 footnote for code explanation). The top two curves in each panel are the total accumulation across all forested and deforested plots. On the right-hand side, symbols for deforested habitats (stars) and forested habitats (hexagons) indicate the estimated total species richness for each accumulation curve based on a jackknife I estimator. The dashed line below the richness estimates indicates that the scale is no longer consistent with the rest of the x-axis; it signifies that more quadrats need to be sampled, but that number is unknown.

Patterns of richness by habitat

At the family level, we found no significant differences in the sampled richness of forested and deforested plots, nor of habitat types (including distance classes) in any study area (nested ANOVA; $F = 0.7704$, $P = 0.5479$; Tukey hsd post hoc test: $P > 0.05$). However, within forested plots (pooled across study areas), family richness in forest riverbanks and understory were significantly different, the former being richer (nested ANOVA; $F = 3.4689$, $P = 0.0118$; Tukey hsd post hoc test: $P < 0.05$).

At the species level, similarly, we found no significant differences in the mean sampled richness per plot of forested and deforested plots in any of the three study areas, nor over all areas combined (nest ANOVA; $F = 0.7215$, $P = 0.3983$; Fig. 1). Estimates of total species richness, accumulated across plots, indicate, however, that forested plots are significantly richer than deforested plots (Fig. 2; ANOVA on jackknife estimator values; $F = 20.67$, $P = 0.0104$). Patterns of species accumulation were strikingly similar in each study area: pooled forested plots had higher sampled and estimated total species richness than pooled deforested plots (Fig. 2).

Both mean species richness and estimated total species richness were higher for tree-fall gaps than for understory plots in each study area (mean richness: Tukey hsd post hoc test; $P < 0.05$; estimated richness:

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TABLE 3. Patterns of community diversity as shown by evenness of abundance values (J'), reported by sampling hierarchy and study area.

Sampling hierarchy	Distance class†	J', by study area		
		LC	LP	PJ
Category				
Deforested[a]		0.461 ± 0.017	0.442 ± 0.042	0.418 ± 0.014
Forested[a]		0.402 ± 0.022	0.375 ± 0.023	0.370 ± 0.047
Habitat types				
Understory[b]	far[b,c]	0.377 ± 0.030	0.373 ± 0.048	0.302 ± 0.111
	near[b,c]	0.327 ± 0.021	0.313 ± 0.071	0.384 ± 0.213
	all	0.352 ± 0.020	0.343 ± 0.099	0.343 ± 0.247
Tree-fall gaps[a]	far[a,b]	0.476 ± 0.012	0.412 ± 0.044	0.263 ± 0.024
	near[a,b]	0.408 ± 0.066	0.365 ± 0.025	0.464 ± 0.004
	all	0.442 ± 0.033	0.389 ± 0.061	0.363 ± 0.113
Forest riverbanks[a]	all[a]	0.432 ± 0.113	0.431 ± 0.115	0.470 ± 0.048
Pastures[b]	far[c]	0.415 ± 0.015	0.333 ± 0.021	0.347 ± 0.033
	near[a,b,c]	0.417 ± 0.034	0.373 ± 0.026	0.411 ± 0.024
	all	0.416 ± 0.040	0.353 ± 0.042	0.379 ± 0.057
Road verges[a]	far[a]	0.497 ± 0.0121	0.435 ± 0.032	0.447 ± 0.002
	near[a]	0.600‡	0.572 ± 0.155	0.470 ± 0.022
	all	0.523 ± 0.59	0.503 ± 0.189	0.458 ± 0.028
Pasture riverbanks[a,b]	all[a,b,c]	0.469 ± 0.020	0.496 ± 0.227	0.416 ± 0.024

Notes: Data are means ± 1 SE. Lowercase-letter superscripts on habitat types and distance categories indicate significant differences in species richness based on a Tukey hsd post hoc test. Categories, habitat types, and distance classes with the same superscript are not significantly different at the 0.05 level. For study area codes, see Table 1 footnote.
† For distance class, "far" and "near" refer to distance from forest edge, as summarized in Table 1.
‡ There was only one road verge near forest in LC.

ANOVA of jackknife estimator values $F = 18.67$, $P < 0.05$). Moreover, road verges were consistently the richest deforested habitat type, as rich as tree-fall gaps by either measure (Tukey hsd post hoc test: $P < 0.05$; ANOVA of jackknife estimator values, $F = 18.67$, $P < 0.05$; Figs. 1 and 2).

Patterns of relative abundance and diversity

On average, forested plots contained 321 (range: 141–575) individual herbaceous and shrubby plants (in the 20 quadrats sampled). By contrast, deforested plots had an average of 920 (range: 286–2036) individual plants. When species per stem was used as a diversity index, pastures, road verges, and pasture riverbanks had significantly fewer species on average than did forest tree-fall gaps and understory, which had the same number of species per stem on average (ANOVA, $F = 10.14$, $P = 0.0001$, Tukey hsd post hoc test, $P < 0.05$).

In all study areas, measures of evenness of abundance (J') yielded patterns similar to those of species richness (Table 3).

Community composition

Within and across all study areas, forested habitat types were more similar in species composition to each other than to any deforested habitat type (Fig. 3, Appendix B). All forest plots clustered separately from deforested plots, with forest riverbanks and tree-fall gaps the most similar to deforested habitats (ANOSIM, global $R = 0.670$, 0.579, and 0.557 for LC, LP, and PJ, respectively, and $P = 0.012$, 0.024, and 0.100, re-

spectively, for comparisons of tree-fall gaps with pasture river banks; see Appendix B for other comparisons). Both forest riverbanks and pasture riverbanks, and also forest riverbanks and road verges were similar at the family level (Fig. 3; Appendix B).

Patterns of similarity in community composition at the species level reflected those at the family level (Fig. 3). The forested habitat type most similar to deforested habitats was forest riverbank (Fig. 3, Appendix B). All forested and deforested plots had significantly different species compositions, with the exceptions of forest riverbanks and pasture riverbanks, and forest riverbanks and road verges (Fig. 3, Appendix B).

Species distributions across habitats

In all study areas (around Las Cruces Biological Field Station [LC] and the towns of La Palma [LP] and Puerto Jiménez [PJ]), nearly half (LC: 45%, LP: 49%, PJ: 42%) of all species were found exclusively in forest and over a third (LC: 39%, LP: 34%, PJ: 38%) were restricted to deforested habitats. Overall, 16–20% of species were found to live in both forested and deforested habitats. We call these species "countryside-habitat generalists" (Fig. 4). When rare species were excluded, the pattern across plots was similar, but a higher proportion were found to be countryside generalists (LC: 26%, LP: 37%, PJ: 38%), only a quarter of species were restricted to forest (LC: 29%, LP: 22%, PJ: 21%), and ~40% restricted to deforested habitats (LC: 45%. LP: 41%, PJ: 40%).
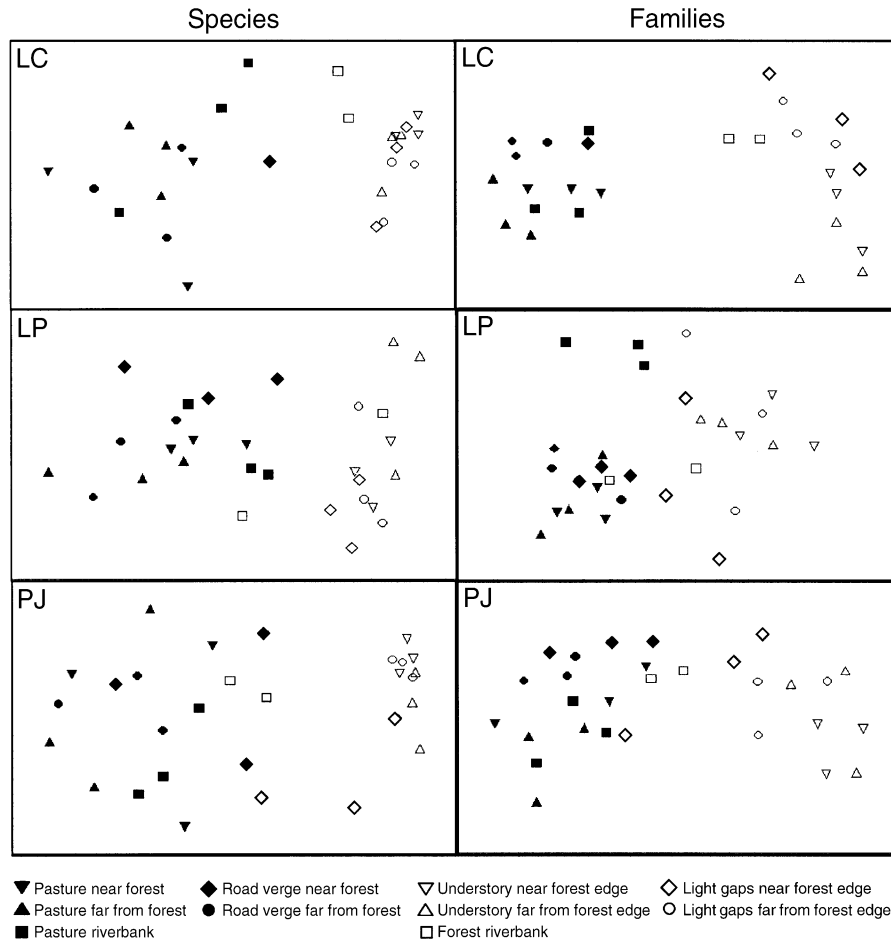
FIG. 3. Multidimensional scaling (MDS) using Bray-Curtis similarity indices for species composition and abundance. Solid symbols are deforested plots, and open symbols are forested plots. Each habitat type and distance class is marked with a different symbol. The stress values for each area are: LC species stress = 0.1, LP species stress = 0.14, PJ species stress = 0.13, LC families stress = 0.11, LP families stress = 0.17, PJ families stress = 0.09. Stress is a measure of how close the two-dimensional configuration of points is to the numerical dissimilarities between samples (e.g., if <0.15 it is a good representation and if <0.10 it is a very good match). For study-area codes, see Table 1 footnote.

At the family level, ~18% (LC: 19%, LP: 18%, PJ: 19%) of all families were restricted to forested plots and ~26% (LC: 24%; LP: 17%, PJ: 37%) of families were found only in deforested habitats. Overall, ~44–65% of plant families were countryside-habitat generalists, with at least one representative species in one or more forested and deforested plots (Fig. 4). When families represented in our plots by fewer than 10 individuals were removed, we see a similar shift in proportions as at the species level: only 3–10% of families are restricted to forest, 10–16% to deforested habitats, and a higher fraction, ~75–87%, are habitat generalists. There were no significant differences between study areas in the number of species or families found exclusively in forested habitats (all forest habitats combined), in pasture and pasture riverbanks combined, or in road verges, nor in the number of countryside-habitat generalists (whether or not rare species were included; Fig. 4).

In all study areas, understory plots had the fewest countryside-habitat generalists, although this was not a significant pattern (Fig. 5; Appendix C). There were, however, significant differences between study areas in the fraction of the flora made up by countryside-habitat generalists in forest riverbanks, understory, and tree-fall gaps (*G* test; $P < 0.001$; Fig. 5). For example, tree-fall gaps had more countryside-habitat generalists in LC than in any of the other study areas (Fig. 5). Other relationships can be seen in Fig. 5 and are detailed in Appendix C.

Landscape context and overhead cover

There were few striking patterns associated with distance class. Pasture plots far from forest were species poor as compared to those near forest, but this trend was not always significant (Fig. 1). In terms of community composition, road verges near forest were similar to some forested habitat types (ANOSIM, $P = 0.10$;

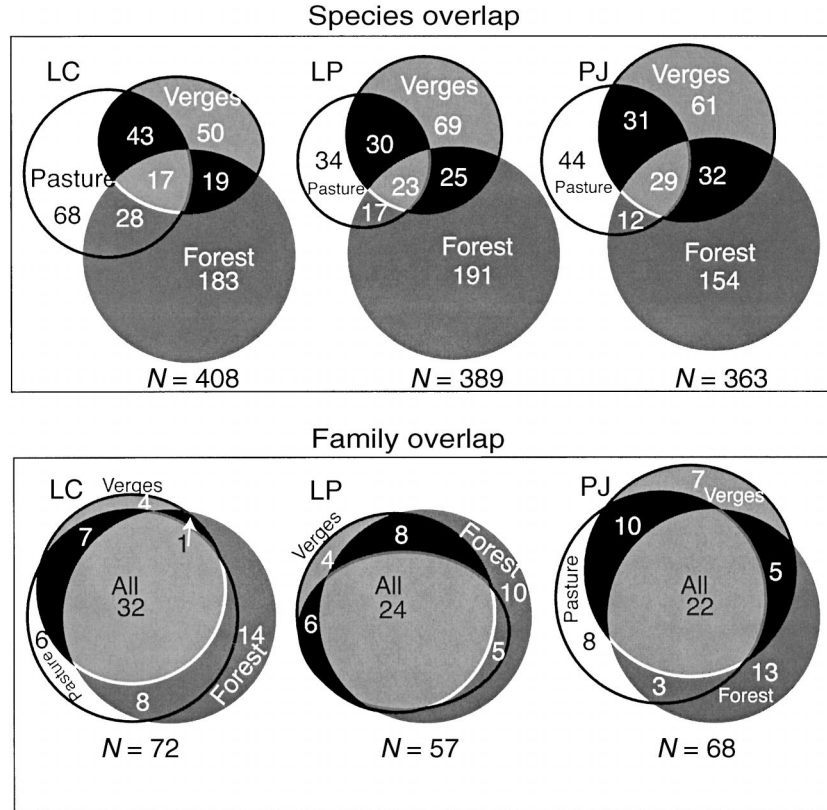## Species overlap

Family overlap

FIG. 4. Contribution of habitat types to total species pool in each study area. The numbers in the overlapping circle segments indicate the number of species or families found in that combination of habitat types. In this figure, forest includes all three forested habitat types: understory, tree-fall gaps, and forest riverbanks. ''Pasture'' includes pasture and pasture riverbanks, and ''Verge'' only includes the road-verge habitat type. Numbers in the nonoverlapping portions of the circles indicate the number of species or families found only in that habitat type.

Appendix B) whereas those far from forest were not (ANOSIM, $P > 0.2$; Appendix B). There were no other cases where landscape context was statistically important.

Based on a second-degree polynomial regression, we found a significant hump-shaped curve relating species richness of each plot (all 85 plots) to overhead cover, a proxy for disturbance level ($R = 0.2249$, $P < 0.0001$;
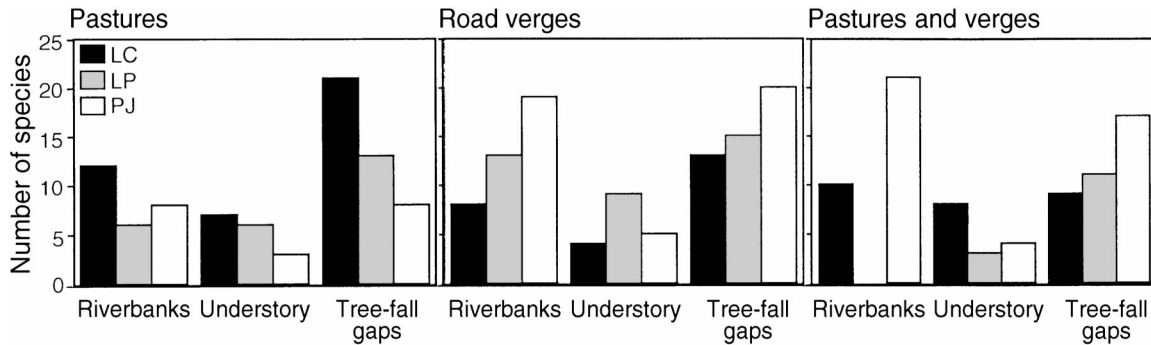

FIG. 5. The number of countryside-habitat generalists found in each forested habitat type. In each panel, the numbers of species found living in both the indicated deforested habitat type and each of the three forest habitat types are shown separately. The ''pastures and verges'' panel shows those generalists that are found in forested habitat types and both road verges and pasture. The separate pasture and verge panels show the number of species found only in pasture (or verges) and some forested habitat types. For study-area codes, see Table 1 footnotes.
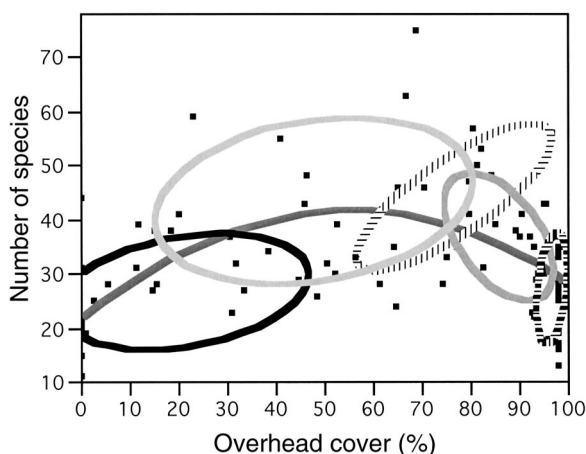
Fig. 6. Relationship between species richness and the percentage of overhead cover of all plots, in all study areas combined. The bold black curve is a second-degree binomial curve. Ovals surround the majority of plots from each category. The solid black oval is for pasture plots, the solid light-gray oval is for road verges, the hatch-marked oval is for forest riverbanks, the dark-gray oval is for tree-fall gaps, and the heavy- and light-striped oval is for pasture riverbanks. All understory plots were coded at 98% overhead cover so they would not fall directly on the 100% line; no oval is shown for this category because they are all the same.

Fig. 6). Overhead cover was significantly correlated with habitat type, with understory plots having the highest overhead cover, pastures very low overhead cover, and tree-fall gaps, riverbanks, and road verges having intermediate levels of cover (Fig. 6).

DISCUSSION

Tropical countryside habitats differ markedly in floristic terms from the native forest habitats that they have replaced. We found about 24–45% of herbaceous and shrubby plant species restricted to forested habitats, and thus likely to disappear entirely from our study areas—and broader regions that they represent—if remaining native forests are destroyed.

We nonetheless found deforested habitats supporting 37–42% of all herbaceous and shrubby plants surveyed. There was little overlap of species between forested and deforested habitats: only 16–20% of all sampled species and 26–38% of common species (more than 10 individuals) were countryside-habitat generalists, living in at least one forested and one deforested habitat. (Estimated proportions of habitat generalist species and families with habitat generalists vary depending on whether rare species are included. We include rare species to yield more conservative estimates and to prevent the exclusion of known rare generalists.) In forest, generalists were best represented in riverbank and tree-fall gap habitats. Given the low number of generalist species found in multiple deforested habitats, the fate of these elements of the flora is likely tied to future land use: ongoing intensification is likely to diminish the diversity of the open countryside flora.

In both forested and deforested habitats, more than 50% of species are found throughout Central and South America. Only 10% of plants from deforested habitats and 4% from forested habitats are known exotic species. These proportions of exotics were very similar in our three study areas, suggesting that they may hold over broader tropical regions. Few other studies have reported the number of exotic species in non-island tropical locations and those that do report the presence of individual exotic species rather than percentages of sampled floras (Rejmanek 1996, Fine 2002). Surprisingly low numbers of exotic species have been reported in both disturbed and undisturbed tropical forest (Rejmanek 1996), and one analysis found an average of 13% exotic species in a sample of multiple sites in South America, a number within the range of our results (Lonsdale 1999). While many exotic species are noxious weeds in Costa Rica, the exotics in our sample were not. Our most common exotics (≥1000 individuals) were *Phyllantus urinaria* (Euphorbiaceae), which is largely known for its medicinal properties not as a noxious weed, and *Mimosa pudica* (Fabaceae), which is a noxious weed in some areas, but was found predominantly in pasture and was found only in small numbers on forest-edge plots and forest riverbanks in our study areas.

Our study, although providing only a lower-bound estimate of the herbaceous and shrubby floristic diversity of tropical countryside, offers an important baseline for future comparison. Forty years after extensive forest clearance, a substantial fraction of the native flora persists in our study regions. We attribute its continued survival to several factors: the substantial proportion of countryside remaining in forest remnants; the apparent conservation value of active pastures, road verges, and other deforested countryside habitats; and the lack of harvesting of most herbaceous and shrubby plants (a factor that does not apply to trees).

Patterns of diversity

There are many physical differences between the habitats sampled in our study that likely contribute to the patterns of species richness observed in them. The high-light, high-disturbance environments of deforested pastures and road verges are obviously extremely different from the cool undisturbed understory of tropical moist forest. While our analysis of species accumulation over sampled area indicates significantly higher species richness in all forested plots than deforested plots, our analysis of average species richness per plot does not. One cause of similar average richness and evenness (J') found in forested and deforested plots is the differences in plant abundances. There were much higher densities of plants in all deforested habitat types of our study than in forested habitat types. When analyses were conducted on the basis of species richness per stem, instead of species richness per plot, there were significantly fewer species in deforested habitat

types (Zobel and Liira 1997). In most conservation contexts, however, species richness per area measured is more relevant than number of individual plants supported; land conservation is never done on a per-stem basis.

The lower densities of plants in rainforest than in cattle pastures are not surprising, nor is it surprising that species richness and evenness of abundance (J') are equally low in pasture and forest understory. While understory and open pasture are extremely different habitats, they are similar in their (in)hospitability for most plants. Extremely low light levels in forest understory make survival difficult even for shade-loving plants (Cornwell and Grubb 2003). While rainforests are renowned for their rich plant life, most plants wait for a gap to open in the canopy before germinating or growing to reproductive size (Brokaw 1985, Collins et al. 1985, Canham 1989, Hubbell et al. 1999). Pastures do not suffer from a lack of light, but pose other challenges to survival. Actively grazed pastures have, by definition, high levels of herbivory as well as intense solar exposure, high winds, large diurnal shifts in temperature and humidity, extreme soil compaction, and competition from exotic grasses. Both forest understory and pasture have relatively simple physical architectures. Clearly, tropical forests have very complex vegetative architectures, but the understory alone is much simpler. Closed understory with a single architectural layer is likely to have fewer niches available for plants than more complex habitats such as tree-fall gaps and road verges.

Tree-fall gaps and road verges were consistently the most species rich, rarely differing from each other in the three study areas. Tree-fall gaps in primary rainforest are well known to be diverse, relatively dense forest communities (Denslow and Hartshorn 1994, Hubbell et al. 1999). Although these habitats are usually ephemeral, they often represent the best opportunity for tree seedlings and vines to reach the canopy, as well as the best location for light-tolerant understory shrubs and herbs.

Road verges are similar to pasture in their lack of trees but different in several major ways. They are not being compacted or actively grazed by large mammals and thus they typically support some amount of vertical structure, creating a lightly shaded habitat. While they are periodically cut, plants living in road verges have a greater chance to reach maturity and reproduce than do their neighbors in pastures. These differences likely contribute to the higher richness of road verges than pastures.

Studies of plant richness in temperate rangeland have found surprisingly little effect of grazing on species richness (Stohlgren et al. 1999, Todd and Hoffman 1999, Landsberg et al. 2002). These studies generally find that species richness is increased by grazing at the scale of sampling plots and decreased at the regional scale, while showing no overall difference between grazed and ungrazed land. Differences between grazed and ungrazed pasture tend to be changes in the abundance of certain species and in the community composition. In our study, there is a clear difference in grazed and ungrazed deforested land, although it is important to point out that our road verges were more dissimilar from grazed pasture than the ''ungrazed pasture'' used in the temperate studies cited above. Notably, soils in our road verges were somewhat disturbed, and all received additional water due to their proximity to ditches and roads. The road verges sampled in our study may be more analogous to hedgerows than ungrazed pastures.

There is a large literature examining the species conservation value of hedgerows in temperate regions around the world (e.g., Burel 1996, Jobin et al. 1996, 1997, Burel et al. 1998, McCollin et al. 2000, Boutin et al. 2002, Garbutt and Sparks 2002, Thomas et al. 2002). It is well established that both planted and unplanted hedgerows support much higher levels of plant species richness than open pasture or cultivated land in the same countryside.

Several studies of plant diversity patterns have found hump-shaped relationships between richness and disturbance (Grime 1973, Thompson and Grime 1979, Molino and Sabatier 2001). In our study, the two most species-rich habitat types, road verges and tree-fall gaps, are generally characterized by intermediate overhead cover, a plausible proxy for level of disturbance, while our least species-rich habitats are the most disturbed and least disturbed habitats, pastures and understory, respectively (Fig. 6).

The origin of the deforested flora

One of the concerns about human-induced habitat alteration is that the corresponding disturbance will result in a new unsaturated flora, and thus an opportunity for exotic species to invade (Levin 2003). If this were true, we would expect to see few native species in deforested habitats. However, if there are enough native forest species adapted to forest-disturbance habitats to fill the new disturbance habitats of pastures and road verges, we would likely see a large number of native forest species, originating from forest-disturbance habitats, in newly created deforest habitats. According to Marks' 1983 study of the origin of old-field plants in the northeastern United States, plants surviving in old fields mainly originate from long-term or permanent marginal natural disturbances such as landslides and riverbanks. These permanent marginal disturbance habitats are more likely to include permanent high light, wind exposure, and similar soil conditions to human-created disturbance habitats. In accordance with Marks' study, we predicted that tropical countryside-habitat generalists would mainly originate from our permanent marginal forest habitats, the forest riverbanks.

Although few species in deforested habitats were also found in forested habitats, those that were did fit our prediction and Marks' (1983) findings. With the exception of the planted exotic African grasses that dominated the deforested habitats, there were few exotic species (10% of species) in the deforested areas. In total, there were 13 exotic species in forested habitats and only 10 exotic species in deforested habitats. These exotics ranged from some of the most common species to some of the rarest (range: 2–4000 individuals, mean = 263 individuals per exotic species counted). Additionally, only 16–20% of species were habitat generalists living in both forested and deforested habitats. This leaves in deforested habitats ~70% of the species native but with unexplained origin. There was considerable variation in which forested habitats shared the most habitat generalists with deforested habitats, but the majority of habitat generalists were found along forest riverbanks as well as some deforested habitats (Fig. 5). This was also supported by our ANOSIM analysis examining the similarity of categories taking composition and abundance into account (Fig. 3). The very small number of habitat-generalist species suggests that there were more available niches in the deforested countrysides than were filled by compatible native forest species.

Thus, it seems odd that deforested habitats contain so few exotic species and large numbers of unaccounted-for native species. One possibility is that many of these native species come from habitats we did not sample, such as swamps, or the canopy, or other rare marginal habitats. We are confident that we sampled the major non-agricultural terrestrial-habitat types in each study area. Based on ground-truthed Landsat TM (thematic mapper) data (Landsat images that have been corrected to match habitats mapped out on the ground) from the LC area (such data are currently unavailable from the LP and PJ areas), forest covers ~35% of the study area and grass-dominated pasture covers ~28% (Sallie-Ann Bailey, *personal communication*). However, species restricted to marginal and rare forest habitats are likely to contribute at least some of the species found in our study to be restricted to deforested habitats. Most of the remaining land cover in our study areas is large-scale agriculture and urban areas, which are not likely to supply many native forest species to the pasture (Fujisaka et al. 1998). While shade and traditional coffee plantations have been shown to act as refuges for native species (Soto-Pinto et al. 2001, Perfecto et al. 2003), traditional coffee plantations no longer exist in our study areas and most other crops are also grown with highly mechanized cultivation techniques. There is little evidence that large-scale mechanized tropical agriculture, including coffee, allows many native plant species to survive in the fields themselves (Fujisaka et al. 1998, O'Brien and Kinnaird 2003, Rappole et al. 2003). Additionally, it seems unlikely that many species persisting in the seed banks

of agricultural fields would not be present at all in any of our sampled forest habitats.

Another possible explanation is that these unaccounted-for native species are regional migrants or ancient exotics. The majority of our ''native'' species not found in the forest are found to live throughout the New World tropics. There is very little known about the original range of most of these species. Clement and Horn's (2001) recent study examining pollen records from a lake near the Las Cruces reserve (LC) found convincing evidence that human populations have been burning and cultivating the land around LC for at least the last 3000 years. If indeed this area was first deforested over 3000 years ago, many of the plants we now consider native to the area could easily have been introduced long ago, surviving in the presence of human activity until the present. If this is the case, the species we found in our recently deforested habitats could mainly be ancient exotic species that are better adapted to these habitats than newly arrived exotic species or the presumably fewer native forest species also adapted to disturbance.

Landscape context

One of the goals of our study was to obtain better information about the importance of landscape structure to the preservation of herbaceous and shrubby plant diversity in tropical countryside. Our results indicate that the proximity of deforested habitats to forested habitats had minimal and inconsistent effects on the number and composition of species supported in the deforested habitats. In similar studies on animal taxa, distance to forest has been found to be very important to species richness in deforested areas (Ricketts et al. 2001, Horner-Devine et al. 2003). As discussed earlier, plants differ from animals in their immobility, and their ability to survive depends on first being dispersed to an appropriate habitat and, second, surviving once they arrive. Although there are likely to be some positive shading effects of forest edges, pasture 10 m from a forest edge is unlikely to be better protected from grazing, soil compaction, and sun exposure than pasture 100 m from forest. Other studies have found both dispersal and environmental factors, even close to forest edge, to severely limit the number of native species growing in pasture (Otero-Arnaiz et al. 1999), suggesting that the lack of a distance effect for these plants is not surprising.

We found no statistical difference of edge effects (near and far from forest edge) on the richness, evenness (J'), or species composition on herbaceous and shrubby species living in forest understory or tree-fall gaps. There are numerous studies showing significant edge effects on tree species diversity in tropical forests (Laurance et al. 1997, Oliveira-Filho et al. 1997, Williams-Linera et al. 1998, Tabarelli et al. 1999) but little is known about edge effects on understory herbs, vines, and shrubs. There are known differences in temperature

and soil chemistry at the edges of tropical forests, but understory plants are likely to be less affected by exposure (such as to wind and sun) than trees, because of their small size and the protection by the canopy. In Watkins et al.'s (2002) study of the effects of roads on temperate understory flora, they found high numbers of exotic species close to roads—but all effects on native species richness disappeared at 5 m from the road, a much shorter distance than observed for tropical trees. Another recent study on the impact of forest fragmentation on understory plant richness (Benítez-Malvido and Martinez-Ramos 2003) found that herbs and shrubs had similar species richness in forest fragments as in continuous forest except in very small fragments (1 ha), while tree seedlings were significantly affected by fragmentation, even when the fragments were large (100 ha).

In recent years there has been increasing interest in the importance of landscape heterogeneity to species richness in agricultural fields. In several temperate systems landscape structure and agricultural practices have been found to have significant impacts on the diversity of animal and plant species living in agricultural countryside (Burel et al. 1998, Alard and Poudevigne 1999, Benton et al. 2003). Benton et al. (2003) reviews this idea in depth. Although we did not directly compare homogeneous and heterogeneous countryside we did find only low levels of species overlap among all habitat types. This suggests that removing a habitat type would also remove the majority of the plant species found in that habitat type from the countryside.

Conservation implications and recommendations

The first and most obvious implication of continued, and ultimately complete, deforestation is that many forest plant species will be lost. Conservation of species based on phylogenetic placement and evolutionary potential has been suggested as a better approach to conservation for ensuring a broad evolutionary basis in the future (Erwin 1991). We found that species loss was fairly evenly spread across families, with 44–65% of surveyed families with species representatives in both forest and deforest habitats. This figure increased to 75–87% of families when only common species were considered. This suggests that the compositional losses in this system are the tips of phylogenetic trees rather than major branches, a positive finding for this view of conservation.

Our finding that the total number of species living in deforested habitats is very similar to the number of species living in forested habitats brings up an interesting and important conservation question about the value of species identity. Certainly one of the most important goals of conservation is to protect and preserve individual endangered species. However, herbaceous and shrubby plants are not only worth protecting in their own right, but they also provide many resources for other organisms (DeVries 1987, Gui-

mares-Vieira et al. 1994) and play a significant role in forest regeneration (Uhl et al. 1981, 1988) and nutrient sequestration in deforested areas (Boring et al. 1981, Buschbacher et al. 1988). In many cases ecosystem services provided by herbaceous and shrubby species can be provided by a wide variety of species. For example, many tropical butterflies appear to be host specialists at the family rather than species level, using multiple species within the same plant families as larval host plants (DeVries 1987). In our study areas, many individual species are missing from any given habitat type, but most plant families are preserved, suggesting that these countrysides may be surprisingly high in resources for native butterflies.

Herbaceous and shrubby plant species do not provide the same level of carbon sequestration as trees, but rich herbaceous and shrubby plant communities such as in our deforested countryside are likely to provide similar levels of relevant services (e.g., habitat for pollinators and pest enemies) as comparably rich forest plant communities.

Not surprisingly, our first recommendation for landscape-level conservation in southern Costa Rica is to protect remaining native forest. Given that most of the original forest has already been removed, we suggest that the high species richness found in our three study areas is largely due to the diversity of habitats within them. There is a trend around the world to increase agricultural efficiency by making larger monocultural crop fields, which homogenizes the countryside (Burel et al. 1998, DeFries et al. 2004). Our results suggest that such activities would result in decreased herbaceous and shrubby plant richness in deforested habitats of countryside. Such a decrease is likely to compound the loss of species by decreasing plant-based resources for animals. We recommend that conservation investments be designed and implemented to foster landscape heterogeneity in managed areas of tropical America.

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APPENDIX A

A list of plant families and the number of species in each family found in forested or deforested habitats or both is available in ESA's Electronic Data Archive: *Ecological Archives* A015-012-A1.

APPENDIX B

ANOSIM results for species- and family-level analyses are available in ESA's Electronic Data Archive: *Ecological Archives* A015-012-A2.

APPENDIX C

The total number and percentage of habitat-generalist species and families, by habitat type, for each of the three study areas are available in ESA's Ecological Data Archive: *Ecological Archives* A015-012-A3.