Quantifying the biodiversity value of tropical primary, secondary, and plantation forests

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Biodiversity loss from deforestation may be partly offset by the expansion of secondary forests and plantation forestry in the tropics. However, our current knowledge of the value of these habitats for biodiversity conservation is limited to very few taxa, and many studies are severely confounded by methodological shortcomings. We examined the conservation value of tropical primary, secondary, and plantation forests for 15 taxonomic groups using a robust and replicated sample design that minimized edge effects. Different taxa varied markedly in their response to patterns of land use in terms of species richness and the percentage of species restricted to primary forest (varying from 5% to 57%), yet almost all between-forest comparisons showed marked differences in community structure and composition. Cross-taxon congruence in response patterns was very weak when evaluated using abundance or species richness data, but much stronger when using metrics based upon community similarity. Our results show that, whereas the biodiversity indicator group concept may hold some validity for several taxa that are frequently sampled (such as birds and fruit-feeding butterflies), it fails for those exhibiting highly idiosyncratic responses to tropical land-use change (including highly vagile species groups such as bats and orchid bees), highlighting the problems associated with quantifying the biodiversity value of anthropogenic habitats. Finally, although we show that areas of native regeneration and exotic tree plantations can provide complementary conservation services, we also provide clear empirical evidence demonstrating the irreplaceable value of primary forests.

biodiversity indicators | congruence | conservation | tropical forests | Amazon

High rates of deforestation have led to an unprecedented loss of biodiversity in the humid tropics (1). Although protected areas are a vital tool in preventing these losses, their coverage is currently limited (2) and their integrity is often threatened in areas undergoing widespread deforestation (3). The potential limitations of protected areas have led to a growing interest in the conservation value of the wider anthropogenic landscape (4–6), an approach that is enshrined in the Ecosystem Principles of the Convention on Biological Diversity (7). Secondary forests and tree plantations are of particular importance for biodiversity conservation as their coverage is rapidly expanding in the tropics (1, 8) and they may help to retain more forest species than alternative and more intensive agricultural land uses (6). Furthermore, it has been argued that both planted and naturally regenerating forests could provide important collateral benefits in terms of ecosystem goods and services (9), and both habitats feature prominently in ongoing carbon sequestration initiatives (10).

Unfortunately, the conservation value of these habitats cannot be easily predicted because of three widespread problems in quantifying biodiversity. First, many biodiversity studies are either poorly replicated or conducted in very small plots that are vulnerable to edge effects from adjacent primary forest (11, 12) and may systematically over-estimate the value of secondary and plantation forests for forest biodiversity (11, 13, 14). Second, our understanding of the value of these habitats for different taxa is incomplete because of a research bias toward certain groups of vertebrates and pristine habitats (15), which is exacerbated by studies reporting low levels of congruence between taxa along gradients of forest degradation (16–18). Finally, there has been a bias toward examining changes in species richness rather than community similarity and species composition (19), particularly in studies that examine congruence in response patterns (16–18).

Here, we provide a comprehensive assessment of the biodiversity conservation value of tropical primary and secondary forests and tree plantations, using a variety of focal taxa and response metrics to quantify biodiversity, and a large-scale replicated experimental design that minimized edge and fragmentation effects. The Jari forestry project, established in the 1970s in the north-eastern Brazilian Amazon, provided a landscape containing large blocks of 14- to 19-yr-old secondary forests and 4- to 6-yr-old *Eucalyptus* plantations, embedded in a largely undisturbed primary forest matrix [see supporting information (SI) Fig. 5] . We selected five study sites in each forest type (average nearest-neighbor distances between sites in primary, secondary and *Eucalyptus* forests were 30 km, 9 km, and 11 km, respectively) that were both spatially independent (SI Fig. 5 and SI Table 1) and large enough to minimize edge effects (mean size of secondary forest and *Eucalyptus* blocks were 26 km^2 and 17 km^2, and mean distances of our sample transects from primary forests were 1.3 km and 1.1 km, respectively). We sampled 15 different taxa based on the availability of standardized sampling methodologies and taxonomic expertise, and

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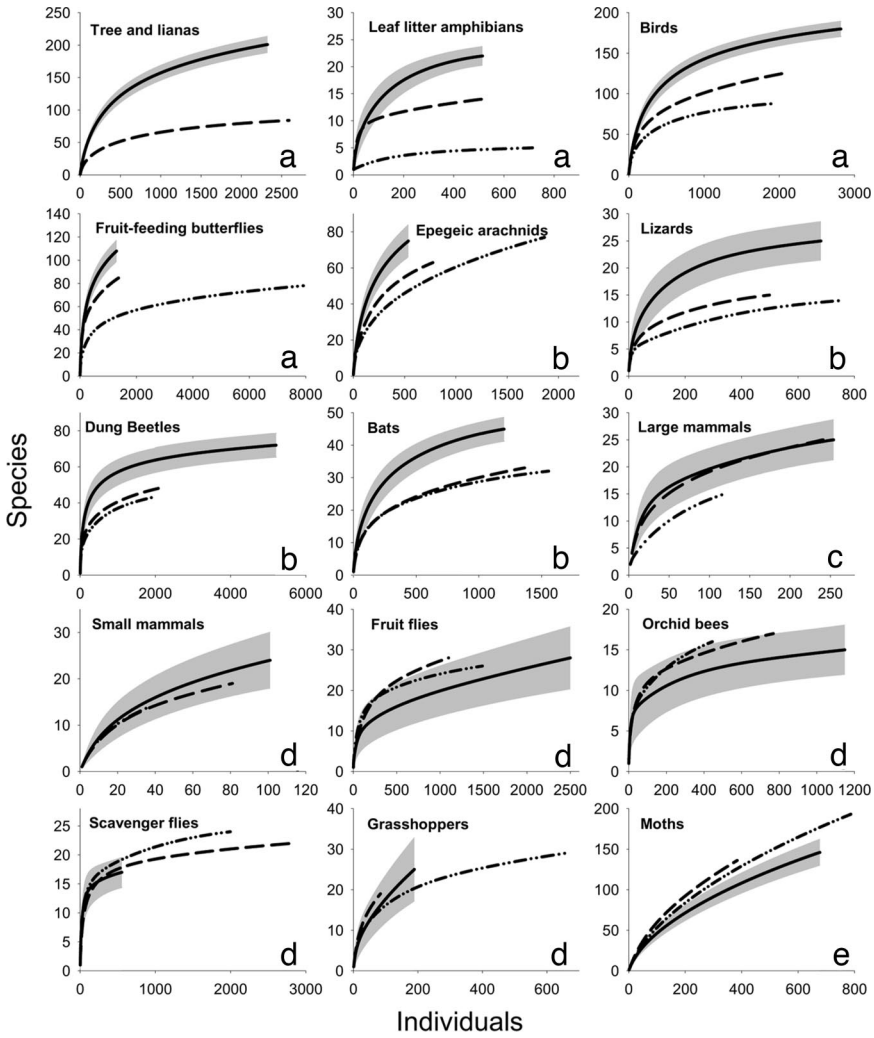

Fig. 1. Individual-based species accumulation curves for primary (unbroken line with shaded 95% confidence intervals) and secondary forests (dashed line) and *Eucalyptus* plantations (dotted-dash line). (Letters a–e) Five response types, grouping taxa according to our analytical criteria (see *Materials and Methods*) that showed the following: significant differences between samples from all habitat types (letter a), no clear significant difference between samples from secondary forest and *Eucalyptus* (letter b), no clear significant difference between samples from primary and secondary forest (letter c), no clear difference between any habitat (letter d), and primary forest appearing as less species-rich than other forest habitats (letter e).

assessed the similarity of their responses to habitat conversion using five different response metrics [overall abundance, observed richness, estimated total richness, community composition (based on species presence-absence data), and community structure (based on species composition and relative abundance data; see *Materials and Methods*)]. Taxa were grouped by sampling method rather than phylogenetic differences, reflecting the focus of the existing literature on indicator taxa (16–18), the unresolved taxonomy of some groups, and the practicalities of sampling biodiversity in tropical forests.

Results and Discussion

Our examination of 15 different taxa provided the opportunity to make novel insights into how we interpret and understand the conservation value of anthropogenic habitats. First, we examined patterns of biodiversity in the three habitats across all taxa by comparing patterns of observed species richness, the percentage of species unique to each habitat, and community turnover between habitats. We then explored how the choice of response metric could effect conclusions regarding the validity of the indicator taxa concept, and finally examined whether taxa respond in similar ways to land-use change, and identified which taxa are outliers.

In terms of species richness, five distinct response types were evident from our samples of each of the 15 taxa within each of the three forest types (Fig. 1). Only four taxa (trees and lianas, birds, fruit-feeding butterflies, and leaf-litter amphibians) followed the expected gradient with the most and least species-rich assemblages occurring in primary forest and plantations respectively. In contrast, five taxa showed idiosyncratic responses, with similar levels of species richness in primary and secondary forests (large mammals) or in secondary forests and plantations (epigeic arachnids, lizards, dung beetles, and bats). Finally, the five remaining taxa had similar levels of species richness in all habitats, although one taxon (moths) was least species-rich in primary forest (although this group also had the lowest sample representation; see SI Fig. 6).

The percentage of species unique to each habitat was also highly variable across taxa (Fig. 2). Almost 60% of tree and liana genera were only ever recorded in primary forest (and the coarser taxonomic resolution for this taxon probably greatly underestimates the number of unique species), whereas <5% of

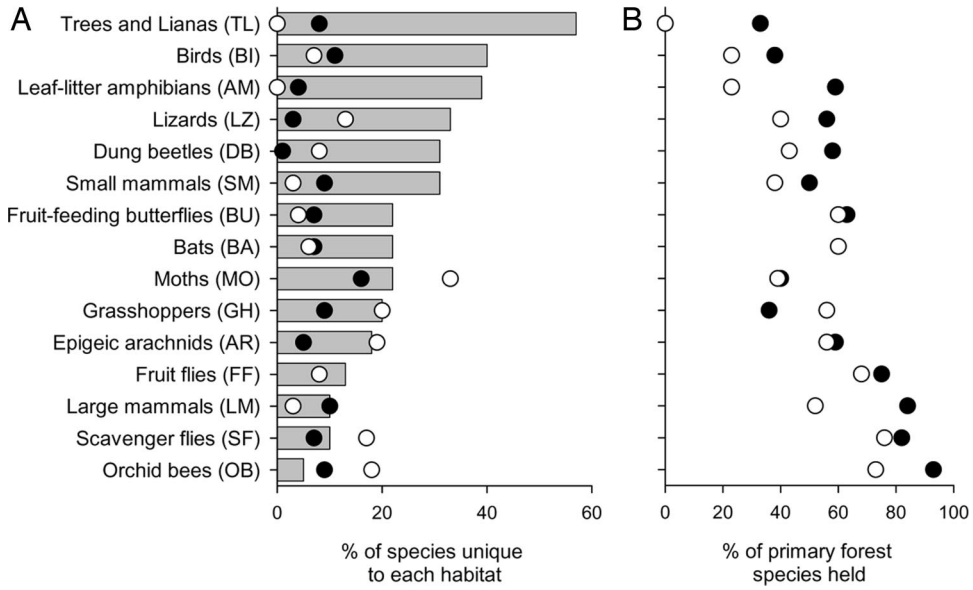

Fig. 2. The percentage of species unique to primary, secondary, and plantation forests (*A*) and the percentage of species recorded in primary forest that were also recorded in secondary forest and plantations (*B*). Primary, secondary, and plantation forests are represented by gray bars, black circles, and white circles, respectively.

species of orchid bees were unique to primary forest, and both secondary forests and plantations held almost all of the species of orchid bee also found in primary forest (Fig. 2). Averaging across all taxa, many more species were unique to primary forests (25%) than secondary forests or plantations (8 and 11%, respectively), and secondary forests held more primary forest species (59%) than plantations (47%). However, there were also exceptions, and plantations held a higher percentage of primary forest grasshoppers than secondary forests, and the same percentage of bats (Fig. 2). These estimates of the uniqueness of primary habitat are likely to be highly conservative as they are influenced by the presence of vagile and transient species recorded infrequently outside primary forest and by the often disproportionate difficulties of sampling the full range of diversity found within primary habitats.

In contrast to species richness and uniqueness, all comparisons between primary forest and other habitats based on community structure were significant at $P < 0.05$, and seven taxa showed highly significant ($P < 0.01$) differences between all pairs of habitat types (SI Table 2; see SI Fig. 7 for taxon-specific ordination plots). Only three taxa (orchid bees, fruit-flies, and small mammals) showed nonsignificant interhabitat comparisons at $P < 0.05$ between secondary forests and *Eucalyptus* plantations (SI Table 2). Comparisons based on community composition (presence-absence data) were qualitatively similar to the abundance-weighted comparisons, although there were fewer significant results in the primary-secondary and secondary-plantation comparisons (SI Table 2).

In summary, the results of between-habitat comparisons were highly variable and highly dependent upon the choice of focal taxon and the value metric that was selected for analysis. To further understand this variability, we compared levels of congruency between taxa across our 15 sample sites using five different response metrics. Community structure showed the highest number of significant correlations across all taxa (79/105 possible pairwise correlations were significant at $P < 0.05$), whereas very few correlations of species richness (observed or estimated) or abundance were significant (Fig. 3). Our results help explain why previous attempts to find taxa that are effective at indicating the responses of other taxa along a gradient of structural forest modification have been unsuccessful (refs. 16 and 17; see also refs. 20 and 21), as these empirical tests of the indicator species concept have based their conclusions on univariate response metrics such as species richness, which retain little biological information, and are highly sensitive to sampling effort (22) and the invasion of degraded areas by disturbance-tolerant species that are often of least conservation concern (23, 24).

Because the highest levels of congruence were found by using community structure data (Fig. 3), we used this metric to identify which taxa shared the most similar responses to land-use change, and which were relative outliers. Mean correlation coefficients for each taxon show that fruit-feeding butterflies were the best predictor of the community responses of all other taxa (capturing 56% of the variance in community responses), closely followed by large mammals, lizards, and birds (SI Fig. 6). These patterns are demonstrated by a two-stage ordination plot (25) based on the multitaxon response correlation matrix (SI Table 3). Interpretation of this plot is intuitively straightforward, as taxa that have similar community responses group toward the center of the plot, whereas taxa that exhibit apparently idiosyncratic

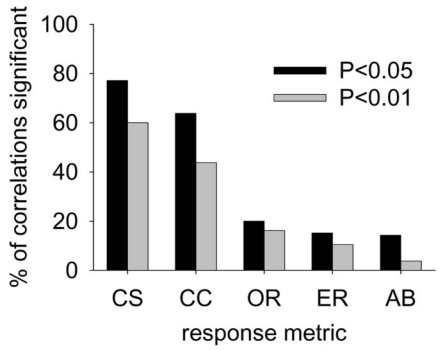

Fig. 3. The percentage of significant correlations between taxa across the 15 sites based on community structure (CS), community composition (CC), observed species richness (OR), estimated species richness (ER), and abundance (AB).

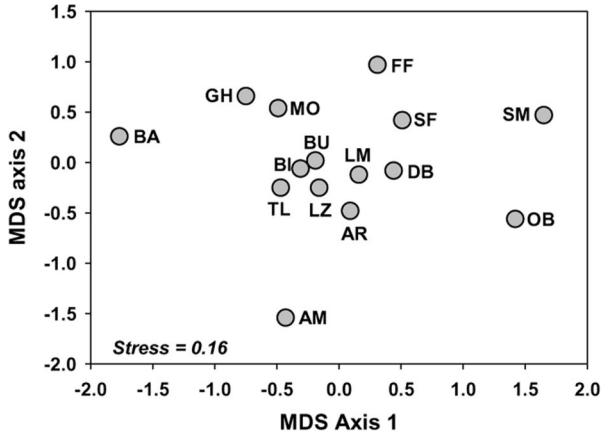

Fig. 4. Multidimensional scaling ordination of the correlation coefficients between taxa (based on community structure; see SI Table 3). The similarity of responses of any given taxon to land-use change across the 15 sites is represented by their relative proximity on the plot. See Fig. 2 for taxa codes.

responses appear as outliers (Fig. 4). The distinct responses of these outlying taxa might be attributed to their high vagility [e.g., orchid bees and bats can travel very long distances to locate ephemeral resources (26, 27), or the difficulty in achieving adequate sample representation at the site level (small mammals; see SI Fig. 6]. Contrary to previous suggestions (16), our analysis based on community structure rather than species richness shows that well studied taxa (such as trees and woody lianas, birds, large mammals, fruit-feeding butterflies, lizards, dung beetles, and epigeic arachnids) do seem to share broadly similar community responses to land-use change (Fig. 4; and see ref. 19), and the average matrix correlation coefficient between this subset of taxa was 0.70. Furthermore, the generality of this result is supported by four independent lines of evidence (see *SI Text*), and these selected taxa also clearly distinguish between different forest types (SI Table 2), providing support for their potential value as indicators of structural habitat integrity (28, 29). Nevertheless, these data also reinforce the need for focused research on other taxa that seem to have more unique and less predictable response patterns, as well as those that are particularly difficult to sample (30).

Conservation science can help inform political decision-making regarding land-use strategies by providing clear answers to questions regarding the biodiversity value of different habitats. This study demonstrates that surprisingly high numbers of primary forest species can be found in areas of native regeneration and exotic tree plantations with an understorey of native shrubs (Fig. 2), and suggests these habitats can provide important conservation services that are complementary to strictly protected areas (4–6). However, the intact nature of the forest matrix surrounding the plantations and secondary forests mean our results should be seen as a best-case scenario, and we also provide some of the clearest empirical evidence available regarding the unique importance of undisturbed primary forests (Fig. 2), highlighting the importance of retaining comprehensive reserve networks as part of a wider landscape management strategy. Finally, we provide insights regarding the complexities involved in answering simple questions about the biodiversity conservation value of degraded habitats and caution against drawing firm conclusions from studies that focus on a limited number of taxa or inappropriate response metrics.

Materials and Methods

Study Area. The study was conducted within the 17,000-km^2 Jari landholding located in the State of Pará in north-eastern Brazilian Amazonia (00°27′00′′–01°30′00′′ S, 51°40′00′′–53°20′00′′ W). Fifteen transects were established in April 2004, with five replicate sites in each of three forest types (primary, secondary, and plantation forests). Although 130,000 ha of Amazonian primary forests were converted to fast-growing tree monocultures, 80% of the primary forest was left virtually intact. The Jari landholding currently contains 53,000 ha of *Eucalyptus urograndis* plantations and a similar amount of regenerating native vegetation in areas where *Eucalyptus* or *Gmelina* stands were once planted and harvested but subsequently abandoned (SI Fig. 5).

After a detailed landscape structure analysis using the company GIS database and a recent Landsat image, 15 transects were preselected and then established across the Jari landscape, comprising five replicate sites in each habitat type (primary, secondary, and plantation forests; SI Fig. 5). Transects in primary forests were selected to reflect regional-scale differences in soil type and topography, thereby capturing the highest amount of baseline regional diversity represented before forest clearance. Primary forest plots had experienced minimal levels of anthropogenic disturbance, although a few stems of commercially valuable timber (*Manilkara* sp. and *Dinizia* spp.) were felled 30–40 years ago for latex or wood. Floristically, primary forest tree plots were dominated by the Burseraceae, Sapotaceae, Lecythidaceae, and Leguminosae (Caesalpinioideae).

All secondary forest and plantation sites were cleared, burned, and bulldozed between 1970 and 1980. We selected even-aged second-growth sites of similar age (14–19 yr) that contained a high basal area of palms, *Inga* spp., and other pioneers. Transects in *Eucalyptus* stands were located in 4- to 6-yr-old plantations (stands are harvested at ages 5–7 yr), which were commercially managed, and the native vegetation in the understorey is periodically cleared or suppressed by using a herbicidal treatment (Glyphosate and Isoxaflutole). However, all areas were characterized by dense understorey vegetation, consisting of annuals (including many Rubiaceae and Piperaceae), lianas (e.g., *Davilla* sp. Dilleniaceae), and small trees such as *Vismia* spp. (Clusiaceae), *Jacaranda copaia* (Bignoniaceae), *Cecropia* spp.(Cecropiaceae), *Mabea taquari*, and *Aparisthmium cordatum* (Euphorbiaceae). Our results are not explained by the spatial layout of the sampling transects, and all Martel-type RELATE test correlations between community structure and the geographic distance between sites were insignificant (SI Table 1).

Sampling Methodologies. Detailed sampling methodologies are available from the authors on request. Where collections were necessary, specimens were first sorted to morphospecies, and voucher specimens were later identified by an expert taxonomist. Unless stated otherwise, all within-site trapping stations were 100 m apart along a 1-km transect. All sampling was carried out between May 2004 and June 2005. Samples were repeated during different seasons wherever possible, and all sampling was randomly alternated across habitat types. In the following, numbers in parentheses relate to the number of individuals and species sampled.

Leaf-litter amphibians (1,739; 23). Each forest type was sampled by using a combination of pitfall traps (35- and 62-liter buckets in four-trap arrays, a total of 3,150 and 630 array-nights, respectively), funnel traps (6,300 trap-nights), and transect walks (153 h). All sites were sampled in both 2004 and 2005.

Bats (4,125; 54). Each site was sampled for seven nights by using ten 12-m mistnets that were set at 100-m intervals in the understorey, and two 12-m mistnets set in the subcanopy. Mistnets were moved after two consecutive sampling nights, and an interval of at least 4 weeks was maintained before resampling any site. Sampling was conducted during the wet and dry seasons of 2005.

Birds (6,865; 255). Point counts (ten 10-min counts spaced 200 m apart) and mist netting (twenty-four 12-m mistnets strung along the transect) were used at all sites. Each primary forest site was sampled for 3 days. Each secondary forest and plantation site was sampled for 2 days.

Large mammals [1,227 (direct and indirect observations); 30]. Monthly diurnal transect walks (0630 hours to 1030 hours) were made along 2- to 5-km transects at each site for 12 months.

Lizards (1,937; 30). See leaf-litter amphibians for methods, with additional use of glue traps (3,324 trap-nights).

Small mammals (219; 32). Individuals were captured from the same pitfall traps as the herpetofauna. A total of 160 baited (Sherman and Tomahawk) live-traps were deployed for a 10-day period at each site during 2005, contributing an additional 24,000 trap-nights.

Epigeic arachnids [Arachnida; orders Amblypygi, Araneae, Opiliones, Scorpiones, and Uropygi (3,176; 116; adults only)]. Individuals were trapped by using the same pitfall traps as the herpetofauna (samples collected in 2005 only).

Scavenger flies [Diptera; Calliphoridae, Mesembrinellidae, and Sarcophagidae (5,365; 30)]. Each forest type was sampled in the dry (2004) and wet season (2005) by using suspended traps baited with a piece of 24-hour-old cow lung. Five traps were used at each site, sampled across two nights in each year (300 trap-nights in total).

Dung beetles [Coleoptera; Scarabaeinae (9,203; 85)]. Pitfall traps were baited with human dung. Trapping protocol was as for scavenger flies.

Fruit-feeding butterflies [Lepidoptera; Nymphalidae (10,987; 128)]. Cylindrical traps were baited with fermented banana. Eight traps were placed in each site, each 100 m apart. Eight additional canopy traps were suspended in primary forest. Sampling was conducted for 20 days in each site, spaced over four seasonal replicates.

Fruit flies [Diptera; Drosophilinae (5,085; 38; males only)]. Ten traps baited with fermented banana were suspended for 2 days in each site during the wet season in 2004.

Grasshoppers [Orthoptera; Acridiidae (932; 44; adults only)]. Sweep-netting was conducted once along each 1-km transect and within a 10×10-m plot at each site during the wet season of 2005. We also collected all grasshoppers attracted to light traps (see *Moths*).

Moths [Lepidoptera; Arctiidae, Saturniidae and Sphingidae (1,848, 335)]. We conducted two nights of light-trapping in the wet season of 2005 at each site (with 30 days between repeated surveys) using sheets suspended next to two mercury vapor lamps and one UV lamp, held 100 m apart. Sheets were checked hourly from 1800 hours to 0600 hours.

Orchid bees [Hymenoptera; Apinae, Euglossini (2,363, 22)]. Eight traps baited with the attractant Methyl Salicylate were suspended for 2 days at each site, repeated over two seasonal replicates in both 2004 and 2005 (480 trap-days in total).

Trees and woody lianas [8,077; 219 (genera)]. All trees $\geq$10 cm and lianas $\geq$5 cm in diameter at breast height (DBH) were measured and identified to genus within 1-ha plots at all native (primary and secondary) forest sites.

Overall Survey Effort. We spent a total of 18,200 person-hours (excluding all travel time) sampling and identifying specimens and recorded >2,000 vertebrate, invertebrate, and plant species from >60,000 registration events. Habitat level sample representation was >75% in 34 of 44 cases (see SI Fig. 6).

Data Analysis. Patterns of species richness between different forest types were compared by using a sample-based rarefaction procedure within the program EstimateS (v.7) (31), where individuals are set as samples and the curves are then calculated by using the Mao Tao estimator (31). This approach allowed direct comparison of results between groups that differ in patterns of abundance and were sampled by using very different techniques. Results were qualitatively indistinguishable from patterns shown using sample-based curves. The significance of observed differences in species richness between habitats (at $P < 0.05$) was evaluated by visually comparing rarefaction curves and their associated 95% confidence intervals. If the total observed richness (for a given taxon) of a more species-poor habitat fell outside the 95% confidence interval of a more species-rich habitat, then we inferred that the former sample contained significantly fewer species than the richer community. Estimated richness was calculated by using the abundance-based coverage estimator (ACE) (31). Ordination analyses were implemented in Primer v. 5 (25) using nonmetric multidimensional scaling (MDS) and the Bray–Curtis similarity index. There are many different options for standardizing data, and we decided on two frequently used alternatives. First, we used square-root transformed and site-standardized the data, which retains some abundance information but reduces the contribution of the most abundant species to the overall pattern (a strategy recommended by ref. 25). Second, we performed the most severe possible transformation of abundance data by converting each species-site abundance matrix into presence/absence data (community composition) (SI Table 4). Analyses of Similarity (ANOSIM) (a nonparametric permutation test) were used to test for significant differences in community structure between disturbance treatments. Congruence between taxa across the 15 sites was compared by using five different response metrics. We used nonparametric Spearman's correlations to evaluate congruence for observed species richness, estimated species richness, and abundance. Abundance data were corrected by sample effort where this differed across sites. Nonparametric RELATE tests were used to evaluate congruence and correlate distance matrices based on community structure (defined as site-standardized and square-root transformed data) and community composition (presence-absence data). The correlation coefficients from the RELATE tests based on community structure formed the basis of the MDS ordination of response similarity (Fig. 3).

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