



Effects of Growth Form and Functional Traits on Response of Woody Plants to Clearing and Fragmentation of Subtropical Rainforest

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Abstract: *The conservation implications of large-scale rainforest clearing and fragmentation on the persistence of functional and taxonomic diversity remain poorly understood. If traits represent adaptive strategies of plant species to particular circumstances, the expectation is that the effect of forest clearing and fragmentation will be affected by species functional traits, particularly those related to dispersal. We used species occurrence data for woody plants in 46 rainforest patches across 75,000 ha largely cleared of forest by the early 1900s to determine the combined effects of area reduction, fragmentation, and patch size on the taxonomic structure and functional diversity of subtropical rainforest. We compiled species trait values for leaf area, seed dry mass, wood density, and maximum height and calculated species niche breadths. Taxonomic structure, trait values (means, ranges), and the functional diversity of assemblages of climbing and free-standing plants in remnant patches were quantified. Larger rainforest patches had higher species richness. Species in smaller patches were taxonomically less related than species in larger patches. Free-standing plants had a high percentage of frugivore dispersed seeds; climbers had a high proportion of small wind-dispersed seeds. Connections between the patchy spatial distribution of free-standing species, larger seed sizes, and dispersal syndrome were weak. Assemblages of free-standing plants in patches showed more taxonomic and spatial structuring than climbing plants. Smaller isolated patches retained relatively high functional diversity and similar taxonomic structure to larger tracts of forest despite lower species richness. The response of woody plants to clearing and fragmentation of subtropical rainforest differed between climbers and slow-growing mature-phase forest trees but not between climbers and pioneer trees. Quantifying taxonomic structure and functional diversity provides an improved basis for conservation planning and management by elucidating the effects of forest-area reduction and fragmentation.*

Keywords: dispersal and seed size, forest area reduction and fragmentation, functional diversity, growth forms, patch size, subtropical rainforest, taxonomic distinctness, woody species richness

Efectos de la Forma de Crecimiento y Atributos Funcionales en la Respuesta de Plantas Leñosas al Desmonte y Fragmentación de Bosque Lluvioso Subtropical

Resumen: *Las implicaciones para la conservación de la tala de selvas húmedas a gran escala y la fragmentación sobre la persistencia de la diversidad taxonómica y funcional permanecen pobremente entendidas. Si los atributos representan estrategias adaptativas de especies vegetales a circunstancias particulares, se*

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esperaría que el efecto de la tala de bosques y la fragmentación se viera afectado por los rasgos funcionales de las especies, particularmente aquellos relacionados con la dispersión. Usamos datos de ocurrencia de especies para plantas leñosas en 46 selvas húmedas a lo largo de 75, 000 ha en su mayoría taladas a principios de los 1900s para determinar los efectos combinados de la reducción de área, la fragmentación y el tamaño de la arboleda sobre la estructura taxonómica y la diversidad funcional del bosque húmedo subtropical. Compilamos valores de rasgos de especies por área de hoja, masa seca de la semilla, densidad de la madera y altura máxima y amplitud de nichos de especie. La estructura taxonómica, los valores de rasgos (medias, rangos) y la diversidad funcional de los ensambles de plantas trepadoras y de pie en arboledas residuales fueron cuantificados. Los parches más grandes tuvieron una mayor riqueza de especies. Las especies en arboledas más pequeñas estuvieron menos relacionadas taxonómicamente con las especies de arboledas más grandes. Las plantas que se encontraron de pie tuvieron un alto porcentaje de semillas dispersadas por frugívoros; las trepadoras tuvieron una proporción alta de semillas pequeñas y dispersadas por el viento. Las conexiones entre la distribución irregular y espacial de las especies que se encontraron de pie, tamaños más grandes de semillas y el síndrome de dispersión fueron débiles. Los ensambles de plantas de pie en los parches mostraron una estructura taxonómica y espacial mayor a la de las plantas trepadoras. Arboledas más pequeñas y aisladas retuvieron una diversidad funcional relativamente alta y una estructura taxonómica similar a la de transectos de bosque a pesar de la menor riqueza de especies. La respuesta de las plantas leñosas a la tala y la fragmentación del bosque húmedo subtropical fue diferente entre trepadoras y árboles de lento crecimiento y en fase madura, pero no entre árboles pioneros. Cuantificar la estructura taxonómica y la diversidad funcional proporciona una mejor base para la planeación y administración de la conservación al dilucidar los efectos de la reducción y fragmentación de áreas boscosas.

Palabras Clave: bosque lluvioso subtropical, dispersión y tamaño de semilla, distinción taxonómica, diversidad funcional, formas de crecimiento, reducción y fragmentación del área boscosa, riqueza de especies leñosas, tamaño de parche

Introduction

The clearing, destruction, and fragmentation of rainforest is now a globally pervasive phenomenon (Mayfield & Daily 2005). Plant species responses to changes in environmental conditions differ in relation to their functional attributes (traits) and ecological strategies (Rossetto & Kooyman 2005; Cornwell & Ackerly 2009). We analyzed the effects of severe reduction in forest area in combination with fragmentation (*sensu* Fahrig 2003) on the taxonomic structure and trait variation of native woody plants in different size remnant patches in a subtropical rainforest landscape.

Evolutionary history has shaped the phylogenetic structure (relatedness) of plants at global, bioregional, and local scales. In general, more closely related species have more similar taxonomic characters (traits) (Lord et al. 1995; Wiens & Graham 2005). Functional traits (such as fruit type and seed size, which affect dispersal mode) reflect the ecology of species and contribute to current-day ecological competence under different environmental conditions (Westoby et al. 2002; Kooyman et al. 2012). Understanding how plant taxonomic (characters), phylogenetic (relatedness), and functional-trait diversity are distributed across landscapes, including fragmented landscapes, is central to plant ecology (Westoby et al. 2002; McGill et al. 2006; Westoby & Wright 2006). The examination of functional traits relative to clearing and fragmentation rests on the assumption that such traits represent adaptive strategies of species (in assemblages and communities) to particular settings. This is in contrast to some

taxonomic characters (morphological traits) that signal familial or generic affinities without a clear functional role in the species' ecology (e.g., persistence of interpetiolar stipules). Details of trait compilations and rationale for inclusion are provided in Supporting Information.

Growth form underpins variation in a number of traits. To quantify the variation between life forms we explicitly separated and compared patterns of functional and taxonomic diversity between the 2 dominant rainforest forms—climbing plants (woody lianas) and free-standing species (trees, shrubs). These 2 growth forms exhibit striking differences in traits (Santiago & Wright 2007; Zhu & Cao 2010) and in patterns of community assembly (Gallagher & Leishman 2012). However, little is known about whether extensive habitat reduction and fragmentation affects climbing and free-standing species in similar ways.

The lowland (30–200 m asl) subtropical rainforest in our study area in northeastern New South Wales, Australia, once covered a basaltic plateau of more than 75,000 ha. The forest was reduced to <1% of its original extent by land clearing in the late 19th and early 20th centuries (Floyd 1990). The flora of the area is well known and fully described, and its relatively small extent makes it an ideal candidate for studies of the effects of forest clearing and fragmentation. The implications for biodiversity and ecosystem functioning from such large-scale landscape modification remain poorly understood (Thomas 2004). Despite that, actions to conserve and restore this rainforest landscape have been underway for several decades and include extensive woody weed and invasive vine control and mixed-species plantings designed to replicate or

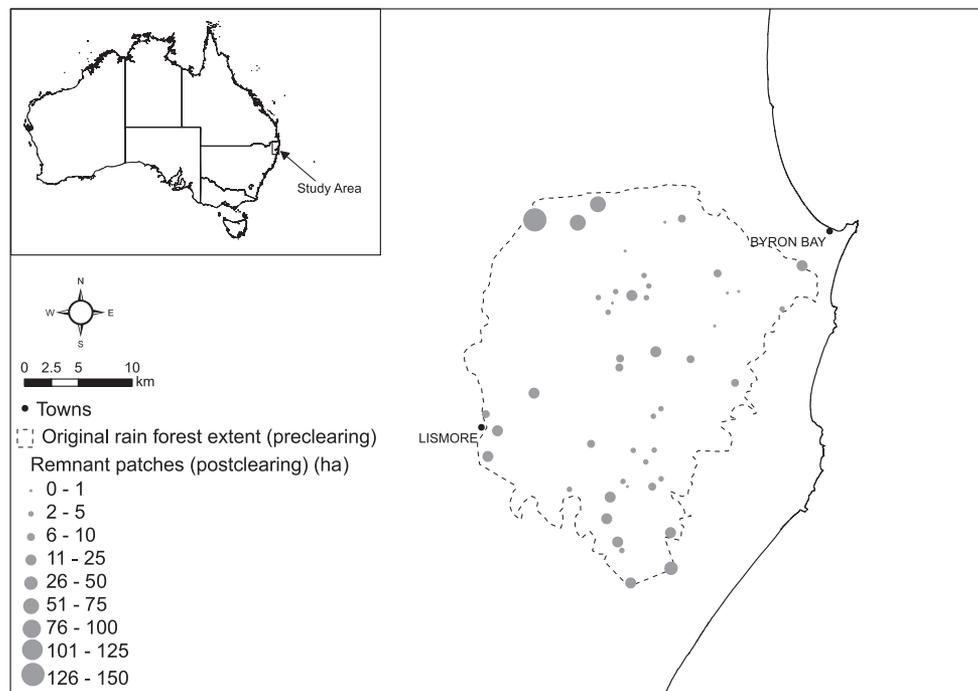


Figure 1. Map of the study area showing approximate extent of lowland rainforest, major towns, and remnant rainforest patches by relative size.

promote redevelopment of the native plant community (Kanowski et al. 2009). However, the development of quantitative evaluations and methods to guide landscape-scale conservation and restoration planning has tended to lag behind conservation actions. Filling this information gap is now recognized as imperative (Suding 2011).

To determine the structure of taxonomic relations and the distribution of functional diversity (FD) in both free-standing and climbing plants in rainforest patches across a severely reduced and fragmented landscape, we tested the relative effects of patch size and patch isolation (as pairwise distance) on plant community composition; investigated the structure of taxonomic and functional (trait) diversity in and across all patches; and examined the consistency of patterns among different forms of plant growth. The rationale for the latter reflects the potential need for different conservation interventions for different growth forms (in this case, free-standing and climbing plants). Across growth forms, we expected smaller rainforest patches to have lower species diversity (fewer species) and lower taxonomic and FD (as trait variation) and larger rainforest patches to have higher species diversity (more species), greater taxonomic diversity, and greater trait variation (FD).

Methods

Study Area

The subtropical rainforest makes a good study system because it is species rich, but not so rich that species

turnover results in patches being composed of entirely different taxa. The study area was a relatively uniform basaltic plateau (30–200 m elevation) with low rolling hills. The range of variation in mean annual temperature between patches across the study area was 1.2 °C. Mean annual rainfall varied from 1400 mm in the south to south-west to 1900 mm in the north (Nightcap National Park sites).

To position the study area relative to rainforest in the broader region and to compare abundance weighted to presence–absence data, we used 42, 0.1-ha plot samples, including 7 from the actual study area. Data description and results are available in Supporting Information.

The 46 patches sampled (by compiling a full floristic inventory of each patch) in the study area ranged from 0.4 to 148 ha and included all the largest and most of the smaller remnant native vegetation patches. The 3 largest patches were connected to continuous forest and occurred in Nightcap National Park in the northern part of the study area. These connected patches represented the best available mature lowland rainforest controls, despite several having had some historic disturbance. Patches were spread across the full extent (75,000 ha) of the preclearing distribution of this once continuous lowland rainforest (Fig. 1).

Floristics

Data (species presence) for the 46 remnant rainforest patches were entered into matrices (site by species presence) of trees, shrubs, and vines; trees and shrubs; vines

only; and taxonomic relations (family, genus, species). The larger patches in the sample all had a long history of botanical collection and inventory (e.g., Floyd 1990), and all patches were exhaustively surveyed and inventoried recently (by local professional botanists) for conservation-planning purposes.

We used ordinary least-squares regression (\log_{10} values) to test the relation of species richness (woody species by patch) to patch size. We used a nonparametric Mantel-type test (RELATE in Primer version 6) to test the relation of spatial distance to floristic similarity of patches. Outputs are provided as rank correlation coefficients by permutation (P), and $P = 1$ equates with a perfect match between the elements in 2 resemblance matrices (Clarke & Gorley 2006). In this case, we ran the procedure independently for free-standing and climbing plants with the site by species data (matrix 1) and pairwise distance (Euclidean) between the 46 patches (matrix 2).

Spatial and Environmental Variables

We derived pairwise distance matrices on the basis of patch center points with the Hawth's tools plug-in for ArcGIS (version 3) (Beyer 2004). Climatic surfaces were derived by combining a digital elevation model with the bioclimatic model (ESOCIM) (Hutchinson 1989). This provided climate-surface models and site data for temperature and rainfall. We based climate details on Bureau of Meteorology records (2011) and modeled data (Supporting Information).

We tested for the effect of environmental variables on floristic variation among patches (Supporting Information). Measures of within-patch variation in environmental variables were not available.

Taxonomic Distance and Structure

To compare the 46 different sized patches, we used measures of patch taxonomic structure as average taxonomic distinctness and variation in taxonomic distinctness (Clarke & Warwick 1998; Clarke & Gorley 2006). These measures are orthogonal to species richness and unaffected by either patch size or sampling effort, are based on the relatedness of the species within a sample (at a given richness), and use a simple Linnaean tree (taxonomic matrix with equalized branch lengths that are based on species, genus, and family).

Average taxonomic distinctness is a (pairwise) measure of taxonomic distance between each pair of individuals in a sample (patch). Variation in taxonomic distinctness represents unevenness in the taxonomic hierarchy of a sample or patch. Expected values for both measures at a given species richness represent a null (no taxonomic structure) derived from 1000 random draws (iterations) from the available pool.

Lower values (outside the 95% CIs) for average taxonomic distinctness relative to random draws from the species pool occur when the individuals within a given patch are more related than expected under a null model (i.e., taxonomic values for patch biodiversity are below expectation). Higher values reflect greater taxonomic variation at a given richness relative to the null (on the basis of random draws from the pool of available species by life form). Where more stochastic processes dominate community assembly, the biological outcomes can be similar to the null model that is based on random draws from the full pool. In that case, patches occur within the expected range of values (represented by 95% CIs).

Species Traits

To investigate variation in trait values among and between species in growth-form groups and to quantify functional trait diversity across life forms in patches, we compiled data for 4 traits that are linked to key ecological processes: seed dry mass, leaf area, wood density, and maximum height at maturity (Westoby et al. 2002; Cornelissen et al. 2003; Poorter et al. 2010). To determine the effect of seed size on assembly processes that contribute to the persistence of diversity in the 46 remnant patches, we compiled information about species dispersal modes.

A single value for each trait was attributed to each species. It was neither our intention nor was it feasible to collect trait data from all locations to test the incidence of within-species (phenotypic) variation. Only seed dry mass and leaf area could be used for vines because maximum height (as length) is difficult to determine for large vines and information on wood density is mostly lacking.

We defined seed-dispersal modes for each species (frugivore dispersed, wind dispersed, and other [i.e., gravity, water, and rodent]). To investigate the relation of seed dry mass to dispersal mode and species distributions in patches for both free-standing and climbing plants, we used ordinary least-squares regression and analysis of variance (ANOVA).

To quantify and determine the range of trait variation among the 46 patches, we used patch-trait means and ranges. Traits were \log_{10} transformed for all analyses to reduce skew in the raw data. Skew was most evident for measures of leaf area and seed dry mass, which varied by several orders of magnitude. We compiled trait values for free-standing and climbing plants combined (leaf area and seed dry mass), for climbers only (leaf area and seed dry mass), and for free-standing plants only (leaf area, seed dry mass, wood density, and maximum height).

To address questions of species distributions relative to variation in trait values, we used niche breadth measured in units of the trait and implemented in trait-gradient analyses (Ackerly & Cornwell 2007; Kooyman et al. 2010, 2012; Supporting Information). A species niche breadth

represents the range of patches occupied within the study area. Niche breadth in units of the trait capture the variation in trait means by patch across the patches occupied by a species. Relations of species' seed dry mass, dispersal mode, and niche breadth to patch size were tested with ordinary least-squares regression and ANOVA.

Functional Diversity

To quantify the FD of patches, we used convex hull volume (CHV) (Cornwell et al. 2006) (Qhull program in R version 2.9.1, R Development Core Team 2006). Analyses were run for free-standing and climbing plants for leaf area and seed dry mass. Comparisons (group tests) of the relations among CHV, species richness (patch diversity), and patch area between free-standing and climbing plants were conducted with standardized major axis (SMA) tests (Warton et al. 2006). The SMA methods included group tests for common slope and for shifts above, below, or along common slopes.

To test the relation of FD to patch size and the effect of species richness, we used a range of FD measures (Laliberté & Legendre 2010; for R scripts), ordinary least-squares regression and ANOVA. We focused on functional dispersion (FDis) because it is unaffected by species richness and meets the criteria for statistical tests of difference in FD on the basis of presence-absence data (Laliberté & Legendre 2010). Tests for correlations among FD indices were undertaken.

Results

Species Richness and Patch Size

The expectation that species richness (woody species diversity) would be strongly correlated with the size of remnant patches was well supported by results of ordinary least-squares regression. Patch size explained more than half the variation across the full sample on the basis of free-standing and climbing plants combined ($r^2 = 0.58$, $p < 0.001$, $n = 46$ patches, $n = 362$ species). A similar pattern was evident for free-standing ($r^2 = 0.54$, $p < 0.001$, $n = 46$ patches, $n = 279$ species) and climbing plants ($r^2 = 0.4$, $p < 0.001$, $n = 46$ patches, $n = 83$ species).

Spatial Effects on Floristics

Spatial structuring of species diversity was evident for free-standing plants but not climbers. Mantel-type tests of pairwise floristic similarity among patches showed that for free-standing trees and shrubs geographically closer patches were more similar regardless of size (rank correlation coefficient by permutation [P] = 0.2, $p < 0.01$ after 999 permutations), but this was not the case for climbers ($P = 0.02$, $p = 0.35$ after 999 permutations).

Taxonomic Structure and Distinctness

Average taxonomic distinctness of free-standing plants by patch (assemblage) was lower than expected by chance and often outside the 95% CI across the range of variation in richness (Fig. 2). This suggests that free-standing species in patches were more related than by chance. In contrast, the position of most of the climbing plant assemblages was within the 95% CIs of the null expectations (Supporting Information). This finding suggests the distribution of vine species was broad, more random, and similar to expectations under stochastic processes of community assembly. Effects of environmental variables on floristic patterns were weakly related (Supporting Information).

Traits

Climbers had a smaller range of trait variation for both leaf area and seed size than free-standing taxa (Table 1). Details for trait compilations are available in Supporting Information.

The relation of patch-level trait range to average taxonomic distinctness and variation in taxonomic distinctness showed mostly opposing trends for climbers and trees and shrubs (Table 2). The relation of patch taxonomic structure to seed size was stronger for free-standing plants and reflected a broader range of seed sizes in this group and a wider spread of larger-seeded (free-standing) taxa across the phylogeny. For leaf size the correlation values were more similar between free-standing and climbing plants and strongest for vines when measured as variation in taxonomic distinctness. The latter suggests stronger taxonomic clustering in vines for leaf size due to a concentration of large leaves in particular clades (e.g., Menispermaceae, Cucurbitaceae, Vitaceae, Smilacaceae).

Functional Diversity

FD was structured similarly between groups (free-standing versus climbing plants) in relation to patch size. Some isolated rainforest patches had high FD at lower species richness compared with the 3 largest patches that adjoined larger tracts of forest in the north of the study area (Fig. 3). Both patch size and species richness were significantly correlated with FD measured as CHV ($p < 0.0001$ in all cases); however, patch size (free-standing plants, $r^2 = 0.28$; climbing plants, $r^2 = 0.26$) explained less variation than species richness (free-standing plants, $r^2 = 0.6$; climbing plants, $r^2 = 0.63$) (Figs. 3-b).

Free-standing ($n = 279$) and climbing ($n = 83$) plants shared a common slope ($\beta = 2.68$, $p < 0.0001$) in relation to CHV and patch size. However, there was a significant difference between groups in relation to shifts along the common slope (Wald statistic $df = 1$, 49.87, $p < 0.0001$).

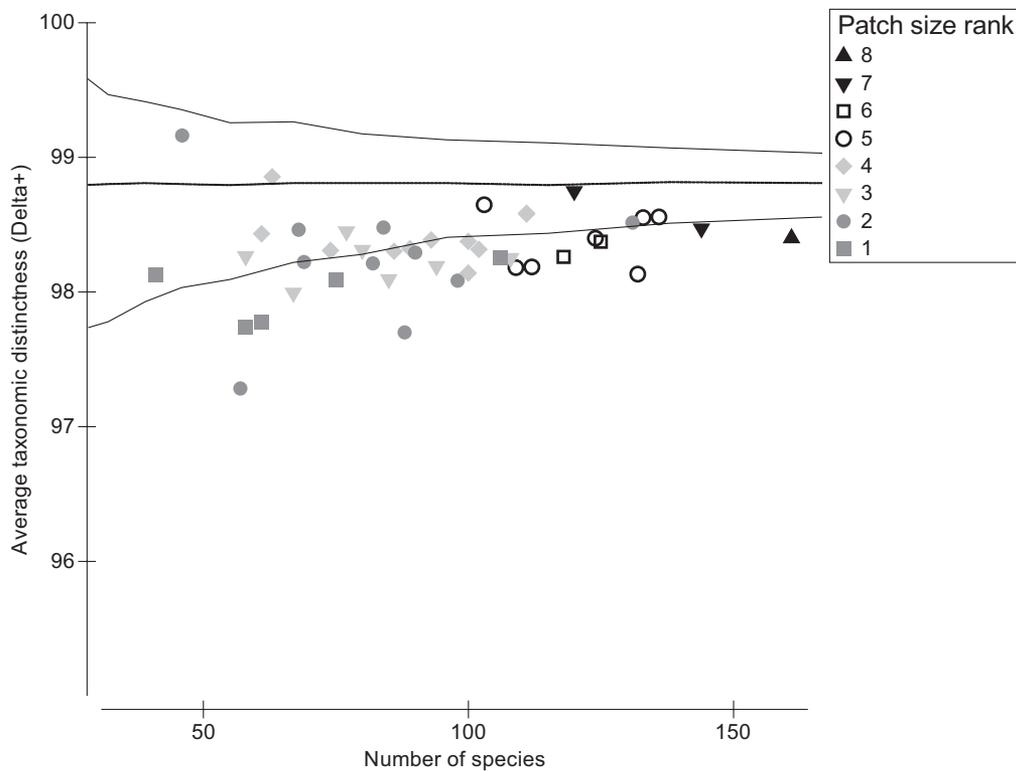


Figure 2. Average taxonomic distinctness of rainforest patches relative to species richness for 46 sites of free-standing woody plants (trees and shrubs) (patch size rank: largest, 8; smallest, 1). The funnel is bounded by 95% confidence intervals and the central black line represents the expected position of patches relative to average taxonomic distinctness at a given value of species richness.

Table 1. Mean and range values^a for 4 traits for free-standing and climbing plants in 46 rainforest patches.

Plant type	Leaf area mean (range)	Seed dry mass mean (range)	Wood density mean (range)	Maximum height mean (range)
Trees ^b	1.69 (2.87)	1.6 (4.44)	2.75 (0.55)	1.33 (1.56)
Vines ^c	1.64 (1.93)	1.4 (2.88)	-	-

^aBoth \log_{10} (empty cell, data not available).

^bFree-standing trees and shrubs.

^cClimbing vines and lianas.

Table 2. Correlation-coefficient values (r) representing patch-trait range values for 4 traits by 2 indices of taxonomic structure and 2 growth-form groups.

Taxonomic structure ^a	Seed dry mass ^b	Leaf area ^b	Maximum height ^b	Wood density ^b
ATD trees	0.39	0.12	0.18	0.24
VTD trees	-0.37	-0.14	-0.15	-0.22
ATD vines	0.09	-0.14	-	-
VTD vines	0.04	0.33	-	-

^aAbbreviations: ATD, average taxonomic distinctness; VTD, variation in taxonomic distinctness; trees, free-standing plants (trees and shrubs); climbing plants, vines and lianas.

^bAll \log_{10} . (empty cell, data not available).

In contrast, slopes of the relation of CHV to species richness differed significantly ($p < 0.001$) between groups (free-standing plants, $\beta = 0.055$; climbing plants, $\beta = 0.149$).

The relation of FD as FDis to patch size and species richness for free-standing plants was weaker than the relation of these factors to CHV (for FDis and species richness: $r^2 = 0.11$, $F_{1,45} = 5.29$, $p < 0.026$; for patch size: $r^2 = 0.08$, $F_{1,45} = 3.82$, $p < 0.057$). Relations were similar for vines (FDis and species richness, $r^2 = 0.18$, $F_{1,45} = 9.50$, $p < 0.004$; patch size, $r^2 = 0.07$, $F_{1,45} = 3.46$, $p < 0.07$). Consistent with results for CHV, larger patches did not have the highest FD values. Correlations among FD indices (CHV, functional evenness, FD, FDis, and Rao's quadratic entropy), measures of taxonomic structure, and the variables of patch size and species richness by plant group were investigated (Supporting Information).

Niche Breadth and Dispersal

Smaller patches had more species with higher niche-breadth values (free-standing plants, $r^2 = 0.38$, $p < 0.0001$; climbing plants, $r^2 = 0.08$, $p = 0.055$). Relations between dispersal mode and niche breadth were significant for free-standing plants ($F_{1,4242} = 21.69$, $p < 0.0001$) but not for climbing plants ($F_{1,1118} = 3.2$, $p = 0.74$).

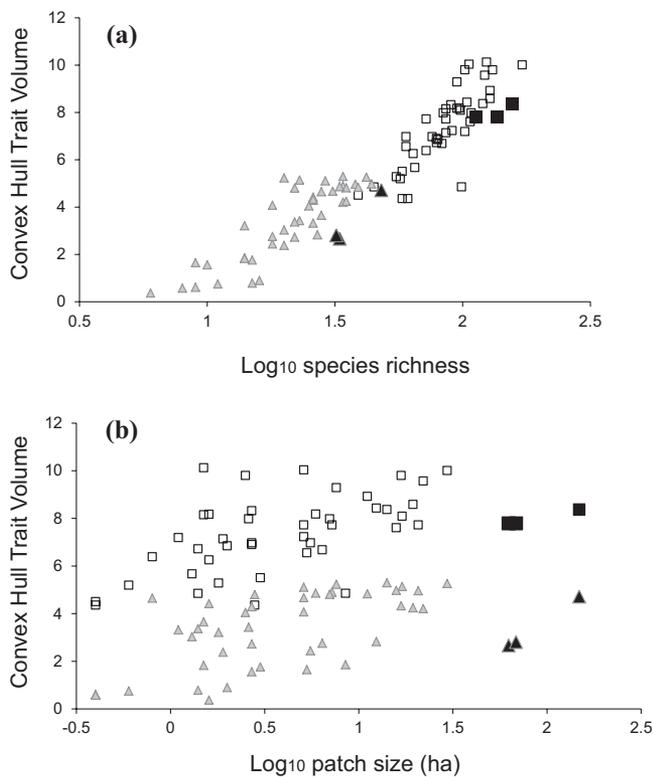


Figure 3. Convex-hull trait volume versus (a) \log_{10} species richness and (b) patch size for 46 rainforest patches, traits of leaf area and seed dry mass, trees and shrubs (open squares), and vines (shaded triangles). The largest patches represent relatively undisturbed mature forest controls associated with continuous forest (large solid black squares, trees and shrubs; large solid black triangles, vines).

Values for niche breadth for free-standing plants were higher for frugivore-dispersed than wind-dispersed seeds. However, the explanatory power of dispersal mode for niche-breadth values overall was low ($r^2 = 0.005$, $p < 0.0001$).

Relations between species' seed dry mass and dispersal mode were significant for both free-standing ($r^2 = 0.01$; $F_{1,4242} = 43.3$, $p < 0.0001$) and climbing plants ($r^2 = 0.25$; $F_{1,1118} = 36.3$, $p < 0.0001$). In contrast relations between SDM and patch size were not significant for free-standing ($p = 0.47$) or climbing plants ($p = 0.09$). This suggests that larger-seeded species were not constrained to larger patches.

Free-standing plants had a greater range of seed size than climbers in both dispersal categories (Tables 1 & 2; Fig. 4), whereas climbing plants had considerably lower seed dry mass (smaller seeds) on average and particularly for wind dispersed seeds (Fig. 4). Free-standing plants had a higher number of frugivore-dispersed species (239) than wind-dispersed species (26) and other (14) dispersal categories. Climbing plants had a higher ratio of wind-

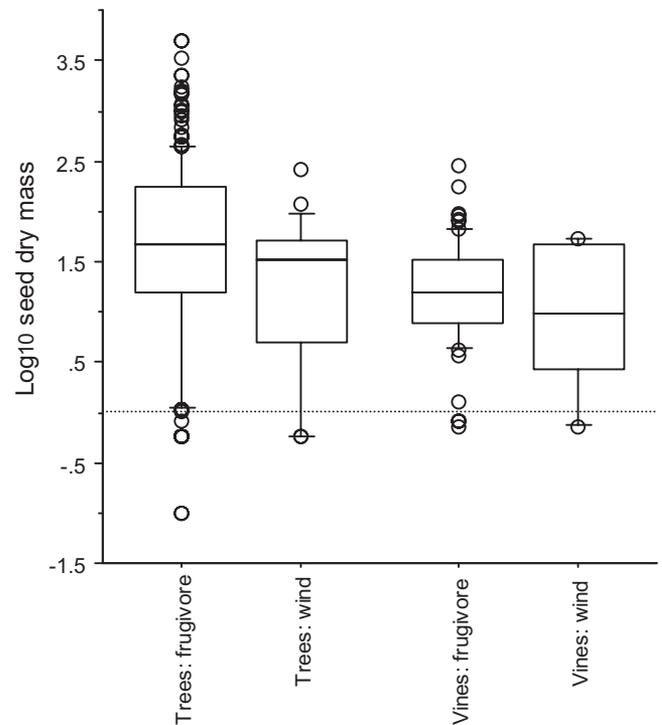


Figure 4. Cross-species relations between \log_{10} seed dry mass and dispersal mode for trees ($n = 250$ species of 260 total) and vines ($n = 74$ species of 82 in total).

dispersed (25) than frugivore-dispersed species (50) and other species (8).

Discussion

Our expectation that larger patches with higher species richness would have higher values for both taxonomic distinctness and breadth was not supported for free-standing or climbing plants. We found that mid to larger size patches with higher tree and vine species richness generally had higher values for trait breadth and CHV (Fig. 3), but not taxonomic distinctness (Fig. 2 & Supporting Information). Relations between patch size and FDis were weak. This suggests the retention of both taxonomic breadth and FD in smaller isolated rainforest patches despite species losses (Fonseca & Ganade 2001). The taxonomic patterns can be partly explained by smaller patches having lower richness made up of less related taxa, and larger patches having higher species richness and more closely related taxa. This confirms the value of taxonomic indices for measuring and interpreting patterns in diversity relative to conservation planning (Moreno et al. 2009), including in fragmented landscapes.

The stronger signal for spatial and taxonomic structuring of free-standing species may reflect the effect of spatially differentiated environmental gradients on recent community assembly or the residue of the historic

(preclearing) signal from spatially structured community assemblage and the persistence of patterns of species co-occurrence in patches since clearing occurred around them. We found only weak relations between environmental variables and floristic variation in patches (Supporting Information).

The lack of spatial structure in the distribution of climbing plants relative to most of the free-standing taxa in the study area likely reflects differences between growth forms in relation to plant ecological strategies and the seed size and dispersal dimension (Fig. 4). Our results were similar to those of Moles et al. (2005a, 2005b) that showed climbing plants generally had a higher proportion of small wind-dispersed seeds. In continuous forest, climbing plants use light gaps created by tree falls and the support of trees to climb into the canopy (Laurance et al. 2001). The small and plentiful seeds of vines allow them to be widely dispersed, including to the spatially and temporally shifting gap regeneration opportunities created by tree falls (e.g., Denslow 1987). A subset of trees in the study area that have small widely dispersed seeds and grow in disturbed environments (Givnish 1988; Kariuki & Kooyman 2005) had a similar signal to the vines (i.e., widespread distribution and no spatial clumping) (Supporting Information).

If one assumed a relation between seed size and dispersal potential the expectation might reasonably be for a clear signal of persistence of larger-seeded taxa in larger patches and the absence of such taxa in smaller more disturbed patches. There was no such signal across the study landscape. However, both vines and trees with smaller seeds were more widespread (regardless of dispersal mode). This suggests that the persistence since clearing (approximately 100 years BP) of larger-seeded tree taxa in both small and large patches at least partly explained the weak signal for spatial structuring relative to seed size.

Conservation Planning Implications

Forest area reduction and fragmentation created abundant opportunities for a suite of small-seeded free-standing and climbing species to establish along patch edges and in disturbed areas. However, of significant interest for restoration and management were the results that showed smaller, isolated patches can (at least for a time, 100 years) retain relatively high FD and similar taxonomic distinctness at lower species richness relative to the lowland rainforest patches still connected to larger tracts of midelevation to upland forest. The taxonomic structure of the smaller remnant patches showed they retained high levels of taxonomic distinctness despite having fewer species. This is a consequence of species being less closely related in small patches than in the larger remnants. Similarly, despite having fewer species,

functional trait variation remained high. This suggests that the retention of functional and taxonomic diversity in small remnants is at least partly independent of species richness. It follows that restoration of functional attributes and taxonomic structures in constrained forest patches may not require full representation of all the (woody) species in a complex forest community.

From a broader landscape restoration perspective, the importance of protecting and retaining all forest patches (small and large) and tree species populations across patches remains evident (Rossetto & Kooyman 2005). However, if diversity is maintained in smaller patches only because of the persistence (longevity) of a few adults and there is no recruitment, species will eventually be lost. This signals the need for more extensive demographic (and genetic [Rossetto et al. 2008]) surveys of species in remnant patches to determine population structures and to guide interventions such as population expansions (e.g., by increasing remnant size and promoting natural regeneration of long-lived tree species). This is particularly the case for rare, threatened, or endangered species (Kooyman & Rossetto 2008).

Divergent results at the trait level between climbers and many but not all free-standing species identified in this study point to the need for both growth-form and trait-specific restoration strategies to be developed. For instance, differences in seed characteristics may play an important role in determining taxonomic composition of climbers and free-standing species in remnants. Climbers appear to be more adept at moving around the landscape and colonizing remnants by virtue of their small, wind-dispersed seeds than most free-standing species that rely heavily on frugivorous birds. However, some small-seeded frugivore-dispersed trees appear to behave similarly to climbers. Thus, although declines in frugivorous bird abundance may adversely affect colonization opportunities for large-seeded, animal-dispersed trees in the study region by increasing dispersal limitation (Moran et al. 2009), this is not the case for climbers or the subset of trees with a preference for disturbed habitats. From that perspective and for climbers and trees, our results showed that functional ecology (seed size and dispersal capacity) was more important to species distributions than differences between life forms.

Mature-phase forest trees comprise most of the (woody) diversity in rainforest and are the most likely to need management interventions in fragmented landscapes (e.g., efforts to expand populations), whereas vines and disturbance-related (pioneer) trees can largely be expected to look after themselves. The planning of landscape-scale management and restoration actions will benefit substantially from the development of a deeper understanding of community assembly processes and how taxonomic and FD are structured, distributed, and retained in remnant vegetation through time.

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Supporting Information

Data-collection details, comparisons of presence-absence versus abundance-weighted data, and floristic and landscape context of the study-area rainforest (Appendix S1); spatial and environmental variables of study area (Appendix S2); trait compilation details and trait gradient analysis methods (Appendix S3); taxonomic distinctness of patches for climbing species (Appendix S4); list of widely dispersed free-standing (tree) taxa (Appendix S5); tree-persistence discussion (Appendix S6); correlation values for patch size and richness by taxonomic and functional indices (Appendix S7); regression equations for relations of patch size and richness to functional diversity, niche breadth, and life forms and means and standard deviations for selected traits and indices (Appendix S8); and additional literature (Appendix S9) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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