Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands

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ABSTRACT

Anthropogenic activities have resulted in extensive deforestation and forest degradation on many tropical oceanic islands. For instance, some islands in the Solomon archipelago have as little as 10% of primary forests remaining with few of these remnants protected from future land use change. We examine the plant species and functional diversity (excluding adult canopy trees) of 48 sites from four forest land use types (two types of primary forest, secondary forest and abandoned tree plantations) and two common human-maintained land use types (coconut plantations and grazed pastures) across three elevation bands on Kolombangara Island, Solomon Islands. In total, we surveyed 384 species from 86 families of which only 6.5% were non-native. Species richness was lowest in coconut plantations and grazed pastures and declined with increasing elevation across all land use types. Functional diversity was similar between primary and secondary forest (high richness, high evenness and unaltered dispersion) and lowest in coconut plantations and grazed pastures. Our results suggest that species and functional richness have had divergent responses to land use change in forest land uses indicative of a loss of functional redundancy. Despite structural and compositional similarities among primary forests and degraded forest land uses, full recovery of secondary and commercial plantations has not been achieved. We suggest that conservation of Kolombangara's forest understory flora will require reserves across the island's elevation gradient and may require active restoration in the future, particularly if degrading activities continue at the current rate.

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1. Introduction

Tropical rainforests have disproportionately high levels of biodiversity compared to other biomes (Chazdon et al., 2009; Gentry, 1992; Williams et al., 2003). Human activities such as deforestation for agriculture, logging, mining and urbanisation have increasingly threatened the Earth's tropical rainforests over the last 100 years prompting concern about the unique species held within them (Burslem and Whitmore, 1999; Fischer and Lindenmayer, 2007; Lewis, 2009). Though it is thought that many species will be lost as these forests are destroyed, altered and degraded, numerous studies have shown that human-altered components of mainland tropical landscapes support surprising amounts of native biodiversity (Daily et al., 2003, 2001; Fujisaka et al., 1998; Gascon et al., 1999; Hughes et al., 2002; Mayfield and Daily, 2005). These and similar findings, particularly in the Neotropics, have contributed to a shift in tropical conservation focusing on only protecting pristine forests towards more integrated approaches that include human-dominated landscapes (DeClerck et al., 2010). The conservation benefits of protecting heavily modified landscapes on tropical oceanic islands, however, are less well understood (Goldman et al., 2008; Sodhi et al., 2010; Woinarski, 2010).

Tropical oceanic islands are well known to have high levels of endemism, higher susceptibility to biological invasions, and different species diversity patterns than most mainland tropical rainforests (MacArthur and Wilson, 1963; Sax et al., 2002; Sax and Gaines, 2008; Simberloff, 1976). These differences may result from processes associated with isolation (Denslow, 2003; MacArthur and Wilson, 1963), which certainly contribute to the smaller number of species per area on oceanic islands due to reduced colonisation rates (MacArthur and Wilson, 1963). It may also be why, along with propagule pressure, islands accumulate additional species (rather than maintaining constant richness through extinctions) with biological invasions (Daehler, 2006; Sax et al., 2002).

Though the mechanisms and rates of plant invasions on tropical islands have been studied for some time (Denslow, 2003; Denslow et al., 2009; Sax et al., 2002; Sax and Gaines, 2008), very little is known about how human land-use activities impact the native plant diversity of tropical islands (Goldman et al., 2008). With alarming deforestation rates across the tropics, the urgency of

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understanding biodiversity on tropical oceanic islands is greater than ever (Woinarski, 2010).

In this study we examine how the conversion of forest to common land-uses has impacted the understory plant species and functional diversity of Kolombangara Island in the Solomon archipelago, a highly fragmented and human-impacted tropical Pacific island. We examine four functional traits as well as species diversity as it has been well established that functional traits can provide a more ecologically meaningful assessment of forest differences across complex landscapes (Flynn et al., 2009; Mayfield et al., 2006, 2010).

Our study focuses on understory species on Kolombangara as the tree flora of this island has already been extensively studied (Burslem and Whitmore, 1999; Burslem et al., 2000; Whitmore, 1969, 1989a, 1989b), and several of the land uses common on the island (and examined here) no longer support adult canopy trees. Using plant surveys across Kolombangara we ask the following questions:

(1) How does plant species and functional diversity vary across common land use types?
(2) Are there any floristic and functional similarities between land uses, particularly those that are undisturbed and those that were human-created?
(3) What is the potential for disturbed forests (those that were human-created) to harbour plant species and structural diversity and dispersal potential on a small oceanic island such as Kolombangara?

2. Materials and methods

2.1. Study Location

Kolombangara Island is situated at 157°E and 5°S in the New Georgia group of the Solomon Islands (Fig. 1). It is an extinct Pleistocene volcano, approximately 32 km in diameter, with a nearly symmetrical rise in elevation from the coastline to the ~1600 m high crater rim, (6.5 km in diameter) with a crater floor 300–600 m above sea level (Fig. 1; Whitmore, 1989a). Average precipitation exceeds 3000 mm yearly (Aldrick, 1993), with two rainy seasons, one from November to March and a second from July to August (Wairiu and Lal, 2003). Rainfall is quite uniform on all sides of the island (unpublished data from the Kolombangara Forest Products Ltd.'s island wide weather stations).

Kolombangara is dominated by low pH (<5.0) haplotyorx soils (Hansel and Wall, 1975) with high concentrations of organic compounds (Wairiu and Lal, 2003). Clear-cut logging in the 1960s and 1970s resulted in extensive leaching and erosion, which has resulted in increases in aluminium and iron oxide concentrations in some areas (Bruijnzeel and Critchley, 1994).

Highly fragmented agricultural landscapes, which were originally covered by tropical rainforests, dominate the island from the coastline to 400 m. Wet montane forests grow from 400 m to ~1400 m above which only scant shrubs and mosses grow. The forest in the central crater is the least disturbed (by current human activities) rainforest type on the island. There is, however, evidence of past human activities in the crater that may have been significant more than 100 years ago (Bayliss-Smith et al., 2003).

Kolombangara is considered one of the most intensively logged islands in the Solomon archipelago with less than 10% of primary rainforest (excluding crater forest) remaining. Major land clearing on the island started in 1903 with virtually all accessible trees exceeding 30 cm diameter at breast height (dbh) cut by the 1980s. Remaining primary forests are largely found on ridges and steep valleys (Whitmore, 1989b), most of which are not protected from logging due to their designation as "traditional lands" (lands legally owned and managed by indigenous communities). Traditional lands can be logged if indigenous communities decide to do so. Secondary forest, tree plantations, coconut plantations, crop fields, grazed pastures and expanding human settlements now dominate the island.

2.2. Study design

We conducted surveys of understory plant diversity in 48 systematically selected sites in April and May 2009 (Fig. 1). We sampled twelve sites in each of three land use types within the submontane zone (⩽400 m). Four sites for each of these land uses were surveyed at each of three elevation bands: 0–100 m, 150–200 m, and 300–400 m. These land uses were: (1) **primary rainforest** outside of the central crater, (2) **secondary forest** and (3) single species abandoned tree plantations (**tree plantations**). We also surveyed four sites in each of three land use types that were only found within a single elevation band: (4) primary rainforest in the central crater (**crater forest**; 300–400 m), (5) **coconut plantations** (0–100 m), and (6) **grazed pasture** (0–100 m) (Table 1). Hence forth, we refer to all six categories as "land use types"; *primary forest, crater forest, secondary forest* and *tree plantations* as "forest land use types"; and *coconut plantations* and *grazed pastures* as "human-maintained land use types".

Primary forest includes remnants of tropical rainforest outside of the central crater that have not been disturbed by humans for at least 100 years. These forests are largely restricted to the well-drained alluvial soils from the coast to about 400 m elevation. They are floristically and structurally complex with the canopy reaching 20–35 m (Fig. 2a). *Crater forest* is also primary rainforest but it is structurally and floristically distinct from primary forests outside of the crater. These forests are also floristically complex, reaching 25–30 m in height. The high crater walls around this forest protect it from wind and limit direct sunlight to 4–5 h per day (Fig. 2b). Very little of the crater is accessible by foot; thus, sites were only established in the SE lower region of the crater (sites 22–25 in Fig. 1). *Secondary forests* were extensively logged at least 18 years prior to our survey (Fig. 2c). These forests have high densities of trees with smaller average dbh than in primary or crater forests (E. Katovai, personal observation). *Tree plantations* were planted more than 12 years prior to our study with monocultures of **big-leaf mahogany** (*Swietenia macrophylla)*, **plantation maple** (*Eucalyptus deglupta*) or **white teak** (*Gmelina arborea*). We selected tree plantations that were abandoned or classified as "failed" as these have more extensive understory vegetation (not actively maintained or removed) and are unlikely to be harvested in the future. None of the surveyed plantations had been slashed (understory cut back) within the five years prior to our study (Fig. 2d). *Coconut plantations* were more than 30 years old and contained widely spaced coconut palms reaching 30–40 m in height. We surveyed coconut plantations where the undergrowth had not been slashed for 2 years prior to the survey (Fig. 2e). Coconut plantations are typically slashed every two years on Kolombangara, so the plantations we surveyed represent the upper end of understory development for this land use. *Grazed pastures* were actively grazed by cattle and were dominated by stunted grasses with intermittent fig (Moraceae) trees retained for shade (Fig. 2f).

Some land use types were only surveyed on certain sides of the island due to their island-wide distributions. As described above, the consistency of weather patterns across the island make it unlikely that geography is driving any of the observed differences across land use types.

2.3. Plant survey

Each sampled site, regardless of land use type, consisted of one 50 m × 50 m plot. We positioned plots as close to the centre of
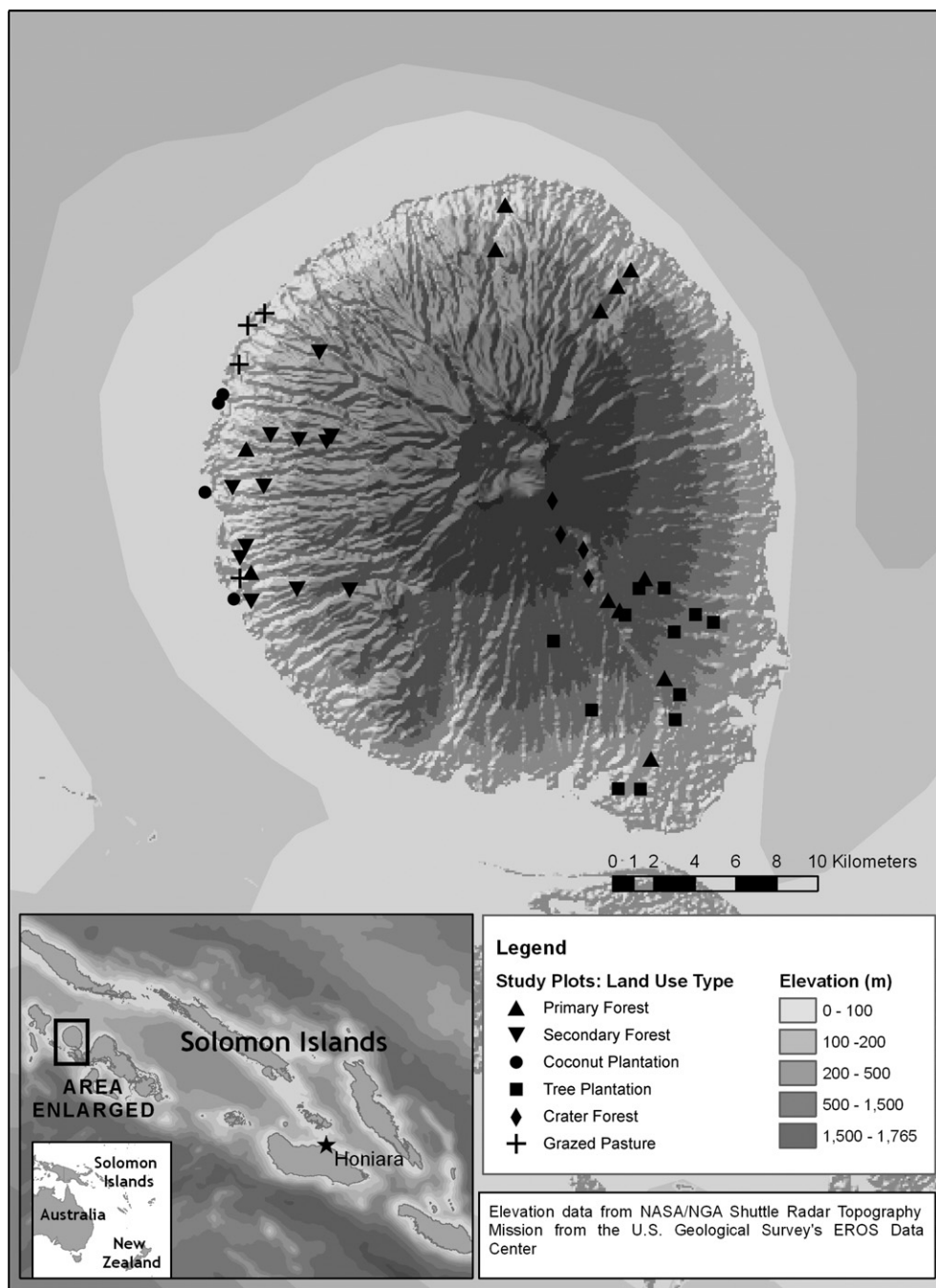
Fig. 1. Kolombangara Island in the Solomon archipelago in the southwest Pacific with topographical features. Sampled sites are shown by land use type. Distances do not always appear to be separated by 500 m due to the size of symbols and large elevational changes between some sites.

each selected site (vegetation fragment or plantation) as possible in order to minimise the influence of edge effects (Turner and Corlett, 1996). All sites were at least 500 m apart to ensure site independence (Fig. 1).

Within each plot, we recorded the identity and number of individuals of all plant species under 2 m high at the time of the survey in 20 evenly spaced 1 m × 1 m quadrats. We included all ferns, lycopods, epiphytes and tree seedlings in our survey but excluded mosses. We counted grass stems when present but it was not always possible to determine clonal relationships among stems thus these counts should be considered as estimates. We collected voucher specimens of all species and took them to the WWF-Solomon Island Forest Conservation Department, where M. Sirikolo, an

expert on the flora of Solomon Islands, identified them. Approximately 50% of our species were identified to species with all others identified to genus.

For all species in each plot we recorded categorical trait states for: plant growth form, dispersal mechanism, woodiness and clonality. We used the following growth forms in our analysis: epiphyte, fern, grass, herb, palm, shrub, vine and seedling (seedlings or saplings of any tree species that was less than 2 m high at the time of the survey). We considered a set of dispersal mechanism trait states that has been used in a variety of other studies: anemochory (wind dispersal), exozoochory (dispersal on the outside of animals, fur dispersal), endozoochory (dispersal involving ingestion by animals), myrmechochory (ant dispersal), ballistichory (dispersal by sudden

Table 1

Details of land use types in each elevation band. Crater forest, coconut plantations and grazed pasture were restricted to one elevation band. Numbers in () under "Total number of species" are the number of species that are not native to Kolombangara that were found at least once in plots for the indicated land use type. Mean values are given for the number of species per plot (20 1 m × 1 m quadrats totalling 20 m² sampled) and the number of stems per plot ±1 standard error. Superscript letters beside mean numbers of species indicate significant pair-wise differences across land use types and elevation bands using Tukey's HSD post hoc tests. Means with different superscript letters are significantly different. Elevation had no significant effect on the number of stems and the different letters beside the total values indicate significant pair-wise differences among land use types using Tukey's HSD post hoc tests. The "proportion of 1° forest species in common" is the percent of primary forest species that were also found at least once in the indicated land use category. Percent canopy cover is the average canopy cover for all sites sampled for the indicated land use type.

Land use type	Elevation bands (m)	Total number of species (non-native species)	Proportion of 1° forest species in common	Mean number of species per plot	Mean number of non-native species per plot	Mean number of stems per plot	Mean number of non-native stems per plot	Percent canopy cover
Primary Forest	0–100	131 (2)		67.8 ± 1.7^A	1.0 ± 0.4	565.0 ± 114.5	2.5 ± 0.9	87.5
	150–250	92 (1)		50.3 ± 2.0^{BC}	0.8 ± 0.3	386.3 ± 26.6	2.0 ± 1.1	90.0
	300–400	84 (0)		35.5 ± 1.6^{DE}	0	360.0 ± 16.2	0	89.0
	Total	189 (3)	n/a	51.2 ± 4.1	0.6 ± 0.2	437.1 ± 45.1^A	1.5 ± 0.5	88.8
Secondary Forest	0–100	98 (2)		52.5 ± 1.0^B	0.8 ± 0.5	324.3 ± 54.6	4.3 ± 2.7	93.0
	150–250	80 (0)		43.8 ± 2.3^{BCD}	0	209.8 ± 25.5	0	88.5
	300–400	43 (0)		31.3 ± 0.6^{EF}	0	125.8 ± 11.5	0	89.5
	Total	148 (2)	48.7	42.5 ± 2.7	0.3 ± 0.2	219.9 ± 30.7^B	1.4 ± 1.0	90.3
Tree Plantation	0–100	63 (7)		40.0 ± 4.1^{CDE}	5.0 ± 0.9	231.5 ± 54.6	29.5 ± 6.2	85.75
	150–250	80 (1)		36.0 ± 2.3^{DE}	0.5 ± 0.3	316.8 ± 43.3	2.0 ± 1.2	86.25
	300–400	80 (2)		36.0 ± 2.9^{DE}	1.3 ± 0.3	309.5 ± 45.9	5.8 ± 1.6	83.25
	Total	172 (8)	44.4	37.3 ± 1.8	2.3 ± 0.7	285.9 ± 22.3^{AB}	12.4 ± 4.2	85.1
Crater Forest	300–400	77 (2)	20.1	32.5 ± 1.3^E	0.8 ± 0.3	229.0 ± 27.9^{AB}	8.0 ± 5.7	92.75
Coconut plantation	0–100	52 (5)	6.9	21.0 ± 2.0^{FG}	1.5 ± 0.3	426.5 ± 127.8^{AB}	10.3 ± 4.4	68.75
Grazed Pasture	0–100	33 (10)	4.2	20.5 ± 1.0^G	5.8 ± 0.9	335.3 ± 40.9^{AB}	109.8 ± 18.2	3.75

popping or explosive action), hydrochory (water dispersal), and unassisted dispersal (Cornelissen et al., 2003; Gondard et al., 2002; and Van der Pijl, 1982; Weiher et al., 1999). To place species into dispersal categories, we examined fruit found during sampling and relied on flora information for non-fruiting species (Hancock and Henderson, 1988; Whitmore, 1966). For woodiness and clonality, we used a binary classification of woody (W) or non-woody (NW) and clonal (C) or non-clonal (NC) based on field observations and flora descriptions. For those species only identified to genus, we used general information on that genus or species complex (for example all *Piper* species are endozoochorous) or M. Sirikolo's expert knowledge. We categorised specimens as native or non-native according to Hancock and Henderson (1988) and M. Sirikolo's expert knowledge of the flora.

We chose these functional traits from published lists of traits considered important to plant community structural and regenerative functionality (Eriksson and Jakobsson, 1999; Vendramini et al., 2002; Weiher et al., 1999). All of these traits have also been found to be highly variable along a variety of environmental gradients (e.g. Cornelissen et al., 2003; Louault et al., 2005; Wilson et al., 1999) making them good choices for assessing ecological differences across an elevation gradient and among Kolombangara's common land uses.

2.4. Statistical analysis

2.4.1. Species richness and abundance

We used factorial analysis of variance (ANOVA) to examine if the number of species per plot differed significantly across land uses and elevation bands. We used land use type and elevation band as the explanatory variables and the number of species as the response variable with each sampling plot as an independent replicate. All analyses were performed in R (R Development Core Team, 2011). Similarly, we used a factorial ANOVA with number of stems per plot (abundance) as the response variable. Pair-wise differences for both ANOVAs were interpreted using Tukey's HSD *post hoc* tests ($\alpha = 0.05$).

2.4.2. Functional trait diversity

In this study, we examined binary and categorical functional traits. To examine functional trait diversity (richness, evenness and dispersion) among land uses and elevation bands we used the FD package in R (Laliberté and Shipley, 2011). FD computes different multidimensional indices using a Gower dissimilarity matrix and can incorporate continuous, ordinal, nominal and binary variables (Laliberté and Shipley, 2011). In these calculations, each species was allowed one growth form, and was either clonal or not, and woody or not. However, each species was allowed to have up to three dispersal mechanisms to reflect the complexity of this trait. We used FD to compute functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis) (Laliberté and Legendre, 2010). FRic represents the amount of functional space occupied by a species assemblage, FEve corresponds to how regularly species abundances are distributed in functional space (Mouchet et al., 2010), and FDis is the mean distance of individual species to the centroid of all species in the community (Laliberté and Legendre, 2010). We compared response variables FRic, FEve and FDis to the explanatory variables, land use and elevation band, using factorial ANOVAs with plots as replicates. We used Tukey's HSD *post hoc* tests ($\alpha = 0.05$) for interpretation of all pair-wise comparisons.

2.4.3. Community composition of trait states

To examine differences in trait state composition (for dispersal mechanism and growth form) across land use types we determined the proportion of species and individuals in each plot

Fig. 2. Photographs of each land use type involved in this study. Each picture was selected to illustrate the key structural differences among (a) primary forest, (b) crater forest, (c) secondary forest, (d) tree plantation, (e) coconut plantation, and (f) grazed pasture.

with each trait state. We calculated species-based proportions as the number of species in a plot with a trait state divided by the total number of species in that plot. We calculated abundance-based proportions as the number of individuals with a trait state divided by the total number of individuals in the plot. We allowed each species to have up to three dispersal mechanisms (but most had one or two) to more accurately reflect the complex dispersal dynamics of these plant communities, so proportions for this trait may add to more than one and were not down-weighted.

We used non-metric multidimensional scaling (MDS) (PRIMER v. 6) for visual interpretation of the similarity of the composition of trait states across the land use types. Using both types of proportions as dependent factors we ran analysis of similarity (ANOSIM) tests, based on Bray–Curtis similarity matrices, separately for each trait. The Bray–Curtis similarity index incorporates both trait state identity and abundance. When species data are used as the basis for these analyses they indicate the trait state similarity of species assemblages in plots and land use types, whereas abundance-based analyses indicate the trait state similarity of individuals, independent of species identity, in plots and land use types.

3. Results

3.1. Species richness and abundance

Across all 48 plots we sampled 15,278 individual plants from 86 families and 384 species. Non-native species accounted for 6.5% of all species sampled and 4.6% of the total stem count (Table 1). Non-native species were proportionally most common in grazed pastures with occurrences in descending order in abandoned tree plantations, coconut plantations, crater forests, primary forests and secondary forests (Table 1).

There was a significant interaction between land use type and elevation for the mean number of species per plot ($F = 11.75$, $p < 0.0001$; Table 1). Species richness in primary forest significantly decreased as elevation increased and a similar pattern was observed for secondary forest (Table 1). There was no significant difference in species richness with elevation for tree plantations (Table 1). The mean number of stems per plot showed no significant interaction between land use and elevation ($F = 2.30$, $p = 0.078$). A two-way additive ANOVA model showed no significant difference due to the addition of elevation ($F = 2.37$,

p = 0.107). Though elevation had no significant effect on the mean number of stems per plot (one-way ANOVA; F = 3.20, p = 0.05), land use type did, with primary forest composed of significantly more stems than secondary forest (F = 4.64, p = 0.002; Table 1). Although all other pair-wise comparisons of land use type for mean number of stems per plot were not significantly different, secondary forest, abandoned tree plantations and crater forest all had considerably fewer stems per plot than primary forest, coconut plantations or grazed pastures (Table 1).

3.2. Functional trait diversity

Functional evenness was significantly different among land uses (F = 11.54, p < 0.0001) with no significant interaction between land use and elevation (Fig. 3a). Evenness was significantly lower in coconut plantations and grazed pastures than in forest land use types. Both FRic and FDis had a significant interaction between land use and elevation (FRic: F = 6.25, p = 0.0006; FDis: F = 3.97, p = 0.009). The pattern of functional richness closely resembled that for the mean number of species (Fig. 3b, compared with Table 1) with overall highest values in the primary forest with the lowest in the coconut plantation and grazed pasture. The mean distances among individual species in trait space was evenly dispersed with the exception of significantly higher dispersion in grazed pastures (Fig. 3c). All measures of functional diversity demonstrated a high degree of similarity between primary and secondary forests, which were distinct from other land use types, including crater forest.

3.3. Trait state composition

There were woody and non-woody, clonal and non-clonal plants in all land uses (Table 2). Coconut plantations had many fewer clonal individuals than other land uses but woodiness was consistent for species and individuals across all land uses (Table 2). The distribution of growth forms varied by land use type, with epiphytes and palms either absent or with poor representation in coconut plantations and grazed pastures. Grasses were found in all land use types but were much more prevalent in coconut plantations and grazed pastures (Table 2). Dispersal traits also varied among land uses but only "unassisted dispersal" and "myrmechochory" were entirely absent from any individual land use (Table 2). Anemochory, exozoochory and endozoochory were the most common dispersal mechanisms in all land uses (Table 2).

Trait state composition for both dispersal mechanism and growth form were significantly different between land uses for richness-based proportions (dispersal: Global R = 0.45, p = 0.001; growth form: Global R = 0.54, p = 0.001) and abundance-based proportions (dispersal: Global R = 0.28, p = 0.001; growth form: Global R = 0.50, p = 0.001) confirming MDS results (Fig. 4). Pair-wise comparisons between land uses indicated similarity of dispersal mechanisms in crater forests, coconut plantations and grazed pastures for both richness- and abundance-based measures, and a high level of similarity between primary and secondary forests based on abundance but not richness measures (Table 3). Growth forms were similar for both types of proportions between primary and secondary forests, and similar between coconut plantations and grazed pastures for abundance-based proportions only (Table 3).

4. Discussion

Similar to other studies of human-altered tropical landscapes, we found that plant communities in Kolombangara's human-created land uses differed significantly in species richness and abundance from primary forests, with a general pattern of higher overall richness in increasingly pristine forests (e.g. Connell and
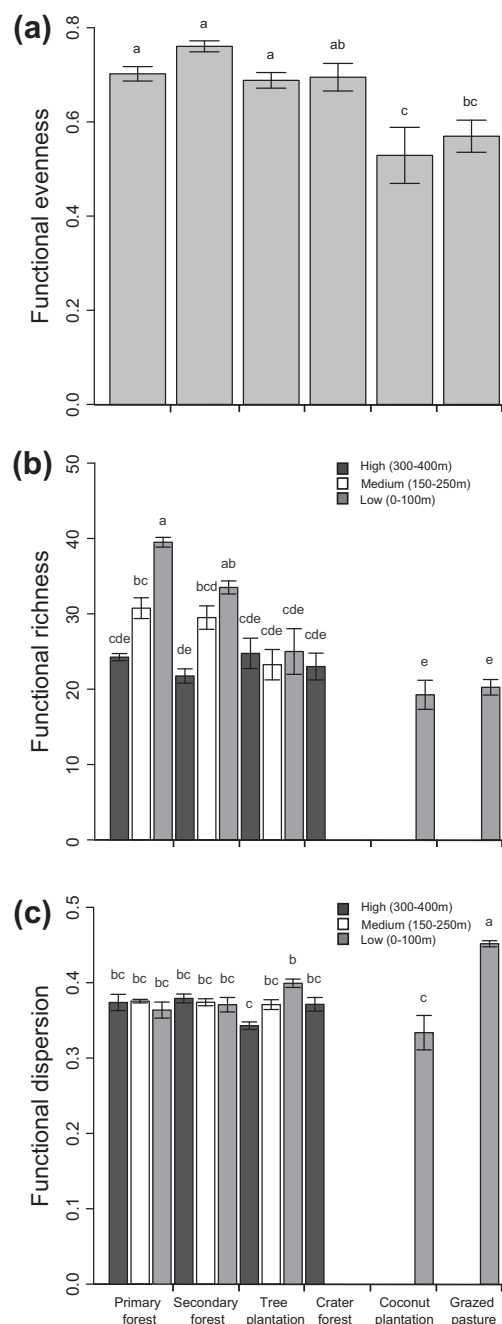

Fig. 3. Functional diversity indices of (a) functional evenness (b) functional richness and (c) functional dispersion within each elevation band within land use types (b,c). Error bars represent ±1 standard error and letters above denote significant pairwise differences across land use types and elevation bands using Tukey's HSD *post hoc* tests. Bars with the same letter above them do not differ significantly based on *post hoc* tests.

Slatyer, 1977; Goldman et al., 2008; Mayfield and Daily, 2005; Table 1). Importantly, functional diversity was similar across forest land use types within elevation bands and significantly lower in coconut plantations and grazed pastures (Fig. 3). Though there are important differences among land uses that we discuss in more detail below, overall our results suggest that species and functional trait diversity in Kolombangara's forest land uses have had a decoupled response to land use change, which may reflect fundamental differences in the processes driving community diversity and structure in these plant communities (Mayfield et al., 2010). One interpretation of this pattern is that Kolombangara's forests are resilient to disturbances associated with conversion of primary

Table 2
Proportion of species (and individuals) with each trait state in each land use type. For "Clonality" values are the proportion of species (individuals) that are clonal. Likewise for "Woodiness" the values are the proportion of species (individuals) that are woody. Species were allowed to have up to three dispersal mechanisms and thus proportions for "Dispersal' do not add to 100 within a land use.

| Trait	Primary forest		Secondary forest		Tree plantation		Crater forest		Coconut plantation		Grazed pasture	
Clonal	21.2	(29.4)	25.0	(32.7)	24.4	(33.5)	23.4	(25.9)	25.0	(8.8)	36.4	(47.1)
Woody	48.7	(52.7)	56.8	(54.3)	46.5	(44.0)	44.2	(41.2)	55.8	(35.3)	51.5	(42.4)
Dispersal												
Anemochorous	32.8	(43.8)	32.4	(49.5)	45.9	(57.2)	39.0	(56.4)	26.9	(40.8)	36.4	(40.8)
Exozoochorous	70.9	(79.3)	70.9	(81.8)	76.2	(83.8)	70.1	(69.4)	61.5	(86.0)	54.5	(66.0)
Endozoochorous	39.2	(30.0)	41.2	(25.5)	29.7	(22.2)	29.9	(17.6)	38.5	(48.7)	24.2	(16.4)
Myrmechochorous	2.1	(2.8)	3.4	(4.5)	1.7	(2.6)	2.6	(1.5)	0.0	(0.0)	3.0	(2.5)
Ballistichorous	0.5	(0.1)	1.4	(0.3)	1.2	(0.4)	2.6	(3.4)	3.8	(0.2)	3.0	(3.9)
Hydrochorous	21.2	(24.6)	18.9	(20.8)	18.6	(17.4)	22.1	(20.7)	26.9	(14.0)	27.3	(26.1)
Unassisted dispersal	2.1	(0.7)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	1.9	(0.5)	0.0	(0.0)
Growth form												
Epiphyte	4.8	(3.8)	3.4	(3.0)	2.9	(2.7)	7.8	(10.5)	0.0	(0.0)	0.0	(0.0)
Fern	14.3	(23.0)	12.8	(27.6)	17.4	(30.1)	18.2	(34.2)	13.5	(9.3)	6.1	(6.9)
Grass	1.6	(0.4)	2.0	(0.9)	2.3	(2.2)	0.0	(0.0)	7.7	(3.8)	21.2	(33.4)
Herb	10.1	(6.5)	7.4	(5.8)	10.5	(7.5)	14.3	(13.2)	11.5	(28.0)	18.2	(17.2)
Palm	5.3	(3.4)	4.7	(3.0)	1.2	(0.3)	5.2	(3.1)	1.9	(0.5)	0.0	(0.0)
Shrub	1.6	(1.8)	3.4	(0.7)	4.1	(5.9)	1.3	(2.2)	13.5	(26.6)	6.1	(20.5)
Seedling	37.0	(34.1)	44.6	(33.8)	32.0	(17.4)	33.8	(21.5)	40.4	(6.6)	30.3	(5.5)
Vine	25.4	(27.1)	21.6	(25.2)	29.7	(33.8)	19.5	(15.4)	11.5	(25.4)	18.2	(16.6)
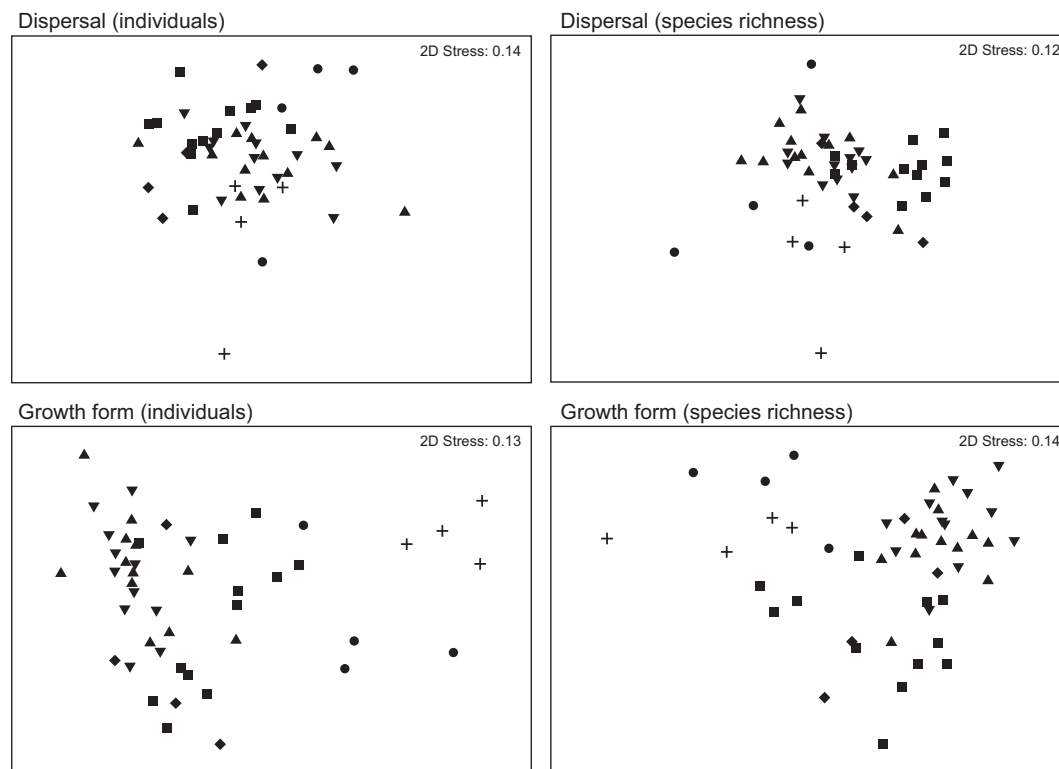
Fig. 4. Multidimensional scaling (MDS) for the functional traits of dispersal mechanism and growth form using both species richness and the number of individuals with a given trait state as the basis. MDS is based on Bray–Curtis similarity indices. The symbols represent each land use type as follows: primary forest(▲), secondary forest (▼), tree plantations (■), crater forest (♦), coconut plantation (●) and grazed pasture (+).

forest to secondary forest and tree plantations but not to those resulting in coconut plantations and grazed pastures. The loss of species but not functional traits from forest land uses also suggest that these forest types have reduced functional redundancy, at least for the studied traits (Laliberté et al., 2010; Mayfield et al., 2010). Though more studies of degraded forest recovery are needed, our results may mean that heavily modified forests on Kolombangara currently have the potential to return to a state similar to mature forest with time. The less encouraging results from

pastures and coconut plantations, however, suggest that the capacity of forest land uses to fully recover may not be maintained under indefinite extraction or more extreme degrading activities.

4.1. Species richness and abundance patterns

Consistent with studies from other tropical regions, we found Kolombangara's secondary forests and tree plantations to be more similar to primary forests in terms of species richness and

Table 3
ANOSIM results for comparisons between all six land use types for dispersal mechanism and growth form using both richness and abundance similarity measures and land use as the independent factor. p-Values < 0.05 indicate that land uses are significantly different (composition of trait states), based on Bray–Curtis similarity indices. Bolded values indicate similarity between listed land uses (i.e. non-significant p-values).

Trait	Land use type	Richness		Abundance	
		R statistic	p-Value	R statistic	p-Value
Dispersal	Primary, Secondary	0.169	0.017	**−0.026**	**0.677**
	Primary, Tree plantation	0.478	0.001	0.192	0.007
	Primary, Crater	**0.223**	**0.070**	0.417	0.015
	Primary, Coconut	0.481	0.012	0.381	0.021
	Primary, Grazed	0.542	0.010	0.324	0.067
	Secondary, Tree plantation	0.451	0.001	0.130	0.034
	Secondary, Crater	0.444	0.010	0.454	0.004
	Secondary, Coconut	0.848	0.002	0.559	0.001
	Secondary, Grazed	0.723	0.002	0.373	0.041
	Tree plantation, Crater	0.286	0.031	**0.282**	**0.056**
	Tree plantation, Coconut	0.852	0.001	0.586	0.001
	Tree plantation, Grazed	0.798	0.001	0.564	0.002
	Crater, Coconut	**0.323**	**0.057**	**0.427**	**0.114**
	Crater, Grazed	**0.042**	**0.400**	**0.198**	**0.171**
	Coconut, Grazed	**0.266**	**0.057**	**0.271**	**0.143**
Growth Form	Primary, Secondary	**0.022**	**0.283**	**-0.065**	**0.947**
	Primary, Tree plantation	0.549	0.001	0.318	0.001
	Primary, Crater	0.322	0.046	0.428	0.014
	Primary, Coconut	0.903	0.001	0.893	0.002
	Primary, Grazed	0.954	0.001	0.998	0.002
	Secondary, Tree plantation	0.590	0.001	0.391	0.001
	Secondary, Crater	0.408	0.023	0.487	0.005
	Secondary, Coconut	0.889	0.002	0.944	0.001
	Secondary, Grazed	0.971	0.001	1.000	0.002
	Tree plantation, Crater	0.359	0.013	0.358	0.006
	Tree plantation, Coconut	0.630	0.001	0.621	0.001
	Tree plantation, Grazed	0.662	0.001	0.883	0.003
	Crater, Coconut	0.688	0.029	0.729	0.029
	Crater, Grazed	0.958	0.029	1.000	0.029
	Coconut, Grazed	0.432	0.029	**0.375**	**0.057**

composition than any human-maintained land use types (Lugo, 1992; Lugo et al., 1993; Parrotta, 1993; Srivastava, 1986; Table 1). Though commercial tree plantations can be highly controlled environments with little if any understory, most of the plantations surveyed here were abandoned and those still in operation had extensive native-dominated understory communities (Fig. 2c). Studies of tree plantations in Puerto Rico found that plantations with similar species and functional attributes were important in speeding the recovery of adjacent secondary forest (Lugo et al., 1993; Parrotta, 1992, 1993). Thus, the high species and functional richness of this land use is encouraging for forest regeneration and conservation on Kolombangara.

Species richness per plot decreased with elevation for all forest land use types (Table 1). Factors such as reduced area, colder conditions and lower disturbance rates are all likely contributors to this pattern (Drakare et al., 2006; Karger et al., 2011; MacArthur and Wilson, 1963; Rahbek, 1995; Stevens, 1992). Though the high-elevation primary, secondary and plantation forests (300–400 m) may face such conditions, the forest in the crater is protected by the high crater walls, potentially leading to fewer tree falls and less disturbance in general than forest outside the crater (E. Katovai, personal observation; Whitmore, 1989b). Crater forests are floristically distinct from other forest types in the 300–400 m elevation band (21% of high elevation primary forest species were also found in the crater forest; Table 2) supporting the idea that distinct processes may be driving observed species richness patterns in the high elevation band in and out of the crater.

Stem density (number of plants per plot) did not differ by elevation for any land use type and was similarly high for primary forest, tree plantations, coconut plantations and pastures (Table 1). Canopy cover is well known to impact stem density in rainforest understory (Montgomery and Chazdon, 2001); however, canopy cover did not differ substantially among the four forest land use types (Table 1). On Kolombangara it seems likely that species composition, regeneration processes, and historical factors unique to each land use also heavily influences understory stem density. For instance, high stem densities in grazed pastures are certainly related to the prevalence of grasses (Table 2), while in primary forest, seedlings of the common tree Calophyllum sp. were four times more abundant in primary than secondary forest plots, which was the only forest type with significantly lower stem densities (Table 1).

4.2. Functional diversity indices and trait composition

Functional diversity patterns for primary and secondary forests suggest that these forest types are quite similar in terms of structure and dispersal attributes (Figs. 3 and 4; Table 3). However, about 50% of species in secondary forests are distinct (in terms of identity) from those found in primary forest (Table 1). Non-overlapping species may differ substantially for important but unmeasured traits. In particular, traits associated with life history, such as specific leaf area (SLA), shade tolerance, and nutrient acquisition strategies are worth exploring in the future.

Tree plantations were also similar to primary and secondary forest for all functional indices except at low elevations (Fig. 3b). More extensive fragmentation and persistent human disturbance at lower elevations (see Section 2.1) may limit the structural and dispersal trait states found in these plantations. These functionally depauperate low elevation plantations may be more reflective of what will occur in plantations that are maintained for harvest and replanting. The understory communities of such plantations are likely to enter into cycles of succession, but persistent disturbance may lead to stronger environmental filters (reflected in

changes in the distribution of some traits), leading to decreased functional diversity over time.

Crater forests were surprisingly functionally depauperate, having greater similarity in dispersal traits with grazed pastures and coconut plantations than other forest land uses. This may result from restrictions on dispersal from certain types of plants into the crater from the outer forests. The same features of the crater forest that we speculated to result in low species richness in this forest system are thus also likely to contribute to lower functional diversity (see Section 4.1).

Coconut plantations and grazed pastures had significantly lower functional evenness (FEve) and reduced functional richness (FRic) than forest land uses (Fig. 3a and b). These patterns indicate greater functional dominance (a few species driving functional diversity patterns) in these more intensively modified land uses. An absence of some trait states (e.g. palm and epiphyte growth forms) in grazed pastures also indicates a significant increase in the dispersion (FDis) of the existing traits (Fig. 3c; Table 2). These patterns suggest that not only are coconut plantations and grazed pastures functionally less diverse than forest land uses, but that the conditions in these land uses have shifted the types of species that persist there. Functional dispersion patterns in particular are consistent with the greater influence of competitive exclusion (in the context of community assembly theory; Webb, 2002) in human-maintained land uses than in forests, where trait space is more evenly filled by a range of species.

There were more significant differences in the composition of growth forms and dispersal mechanisms among most forest land use types than expected given the mature stage of all forest types (Table 3; Fig. 4). This expectation was based on Mayfield et al.'s (2006) finding that for both dispersal traits and growth forms, there were few trait state compositional differences among rainforest understory communities in disturbed or mature forest environments in Costa Rica. The trait state compositional differences observed in our study indicate that despite similar values for functional diversity (most trait states are present in most land uses), the distribution of growth form and dispersal mechanism trait states still vary extensively across most land use types (Tables 2 and 3). Across forest types, there was no single growth form or dispersal mechanism that seems to be driving this pattern (Table 2) but clearly the absence or near-absence of epiphytes and palms and the prevalence of grasses are important for the observed trait compositional differences with human-maintained land uses (i.e. coconut plantations and grazed pastures; Table 2). The similarity in dispersal trait state composition among crater forest and high intensity land uses is unlikely due to any land use change factors given what else is known about these land use types (Fig. 2; Table 2).

4.3. Potential for colonisation and recolonization of non-native and native species

Kolombangara is part of a large archipelago (Fig. 1), however, overall species richness patterns suggest that even a geographically well-connected island is more negatively impacted by land use change than comparable landscapes in the mainland tropics. Using similar studies of degraded and fragmented tropical landscapes in Hawaii and Costa Rica we make a rough comparison of results from Kolombangara (Goldman et al., 2008; Mayfield et al., 2005). In Costa Rica, grazed pastures had 34% of the richness found in primary forest understory (based on total richness across all sampled sites; Mayfield et al., 2005), with only 14% of species in common across these land use types. On the islands of Kolombangara and Hawaii, grazed pastures had 17% and 16% of the overall surveyed richness of primary forests respectively (Table 1 in this study; Goldman et al., 2008). Additionally, Kolombangara's grazed pastures had only 4% of species in common with its primary forests (Table 1).

Sampling in all three of these studies focused on understory and pasture species but each had various restrictions on which species were counted (for example grasses and ferns were excluded in Mayfield and Daily, 2005). Though proper meta-analytical comparisons are warranted, this simple comparison suggests that intensive land use change may have more extreme consequences for understory diversity on oceanic islands than we expect in mainland tropical landscapes. Limitations to both long- and short-distance dispersal on these islands seem likely to play an important role in driving this pattern (Goldman et al., 2008; MacArthur and Wilson, 1963). Certainly, there is no evidence that islands are more targeted for deforestation than mainlands, rather complete deforestation happens much more quickly on islands than on continents, purely as a function of area and accessibility. Though Kolombangara is a relatively well-connected tropical oceanic island, dispersal from other islands is unlikely to be as fast as across a continuous landmass, especially for species dispersed by wind, terrestrial animals or gravity. Dispersal on islands themselves could conceivably also be more limited than in mainland tropical landscapes due to historical extinctions of specialised seed processing or dispersing animals (e.g. Temple, 1977) and the absence of any large forest patches acting as sources of less common forest-restricted species.

Comparisons of the proportion of invasive species found in these three studies, suggest that not all tropical islands are more invaded than mainland tropical sites. As expected, non-native species were most prevalent in the human-maintained land uses of Kolombangara (coconut plantations and grazed pastures). The overall proportion of non-natives was, however, more similar to the proportion of non-natives found in the tropical mainland site in Costa Rica (6.5%) than on the other island, Hawaii (40% non-natives; Goldman et al., 2008; Mayfield et al., 2005). Again, though more rigorous meta-analyses of more sites are warranted, this suggests that a complicated interaction of factors such as dispersal limitation, geographic isolation and the history of human habitation may all be important in determining the realised invasibility of tropical countryside landscapes (Denslow et al., 2009).

5. Conclusions

In this study, we show that high-intensity land uses on Kolombangara have significantly lower within- and across-site plant diversity than remnant primary forest and secondary forests. Functional diversity was maintained within the forest land uses (including tree plantations), while the more disturbed human-maintained land uses (coconut plantations and grazed pastures) have less functional diversity for measured traits. In forest land uses, it appears that structural and dispersal traits are maintained at near pre-disturbance levels even though species richness has declined and the composition of these communities only partially overlap. Though it is encouraging that functional richness (as measured) has been retained in all but the most heavily modified land uses, evidence suggests that functional redundancy has been reduced in secondary forests and tree plantations. Low elevation tree plantations, coconut plantations and grazed pastures may have changed so much that they are of little direct value for the conservation of Kolombangara's native forest plant diversity nor are they likely to regenerate to forests resembling mature forest even if abandoned.

Dispersal limitation due to distances from source populations, constraints on the capacity of island natives to compete for resources with more aggressive invaders and propagule pressure from non-natives are prominent theories proposed to explain diversity and invasibility patterns observed on oceanic islands (Daehler, 2006; Denslow, 2003; Denslow et al., 2009; MacArthur and Wilson, 1963; Sax et al., 2002). Kolombangara is part of a large archipelago that is relatively close to mainland Asia (Fig. 1). There

is high species overlap among the islands of the archipelago suggesting the potential for cross-island dispersal and colonisation of rainforest plants, at least across large time scales (Hancock and Henderson, 1988; Whitmore, 1966). Despite this, our results suggest that land use changes on Kolombangara have been more detrimental to the native rainforest flora than in similarly structured fragmented tropical mainlands.

To conserve and sustain plant diversity on Kolombangara and similar islands, we strongly recommend that patches of remnant primary forest across a range of elevations be protected. Forest communities show distinct diversity patterns across elevation bands and are all likely key to the trajectory of secondary forest and abandoned tree plantation recovery. We found the intensive land uses (coconut plantations and grazed pastures) had little in common (in terms of species and functional diversity) with primary forest species, but that patches of well-established secondary forests and mature tree plantations support elements of the species and functional diversity of primary forests. These less pristine forests are considerably more common than primary forest and thus should also be protected as the basis of forest recovery for the future. We feel that commercial activities on Kolombangara and similar Pacific tropical islands should be selected carefully to allow for economic gains while maximising the biodiversity value of human-altered regions of these botanically unique islands, especially due to evidence that recovery of island forest systems may be slow and incomplete without assistance.

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