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Patterns of growth, recruitment, mortality and biomass across an altitudinal gradient in a neotropical montane forest, Dominican Republic

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Abstract: We examined stand dynamics and biomass along an altitudinal gradient in a tropical montane forest (TMF) in the disturbance-prone Cordillera Central, Dominican Republic. We tested the general hypothesis that chronic disturbance by fire, wind, floods and landslides results in a landscape of relatively low above-ground biomass with high rates of mortality, recruitment and growth as compared with other TMFs. We also expected above-ground biomass to decrease with altitude in part due to declines in growth and increased biomass losses from mortality with increasing altitude. We resurveyed 75 0.1-ha plots distributed across the altitudinal gradient (1100–3100 m asl) 8 y after they were established. Our observations provided mixed evidence on these hypotheses. Turnover rates were high ($> 2\% y^{-1}$) and significantly greater on windward slopes. Above-ground biomass (mean = 306 Mg ha⁻¹, 95% CI = 193–456 Mg ha⁻¹) was highly variable but comparable to other TMFs. Altitudinal patterns of declining biomass and above-ground growth matched observations for other TMFs, whereas mortality and recruitment exhibited no altitudinal trends. More quantitative studies in a variety of TMF settings are needed to better understand how natural disturbance, complex environmental gradients and species dynamics interact to regulate carbon storage, sequestration and turnover across altitudinal gradients in TMFs.

Key Words: biomass, cloud forest, disturbance, elevation gradient, growth, mortality, recruitment

INTRODUCTION

Tropical forests harbour a large percentage of the world's biodiversity and play a major role in the global carbon cycle. Rapid conversion of these forests to other land uses, as well as their likely sensitivity to global climate change (Lewis *et al.* 2004, Phillips *et al.* 2004), threaten these valuable ecosystem services, but many uncertainties limit current understanding of patterns and trends in the tropical forest biome. Previous studies on the composition and structure of TMFs have established the general patterns of vegetation distribution and structure along the montane altitudinal gradient (Culmsee *et al.* 2010, Girardin *et al.* 2010, Homeier *et al.* 2010, Kitayama & Aiba 2002, Leuschner *et al.* 2007, Lieberman *et al.* 1996, Moser *et al.* 2011, Raich *et al.* 1997, Sherman *et al.* 2005, Tanner 1980, Weaver & Murphy 1990). However, the patterns of vegetation structure, composition and dynamics of

TMFs are exceedingly complex and variable because of local climatic, soil and topographic variation as well as regional biogeographic affinities of the available flora and the underlying causes that shape these patterns are not fully understood.

The demographics of TMF vegetation (mortality, recruitment, growth) and interactions with environmental and biotic factors are poorly elucidated. These processes may help to explain some observed patterns in forest structure along altitudinal gradients. It is clear that tree growth rates in TMFs decline with altitude (Girardin *et al.* 2010, Homeier *et al.* 2010, Kitayama & Aiba 2002, Moser *et al.* 2008, Raich *et al.* 1997, Wang *et al.* 2003, Weaver & Murphy 1990), while mortality and recruitment do not show consistent patterns across mountain slopes (Aiba *et al.* 2005, Bellingham & Tanner 2000, Herwitz & Young 1994, Lugo & Scatena 1996, Weaver & Murphy 1990).

Disturbance by windstorms, landslides, fire and other agents are common in many TMFs and can have a pronounced influence on vegetation patterns and processes (Bellingham *et al.* 1995, Boose *et al.* 1994,

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Cordillera Central, Dominican Republic: Mountain Study Area

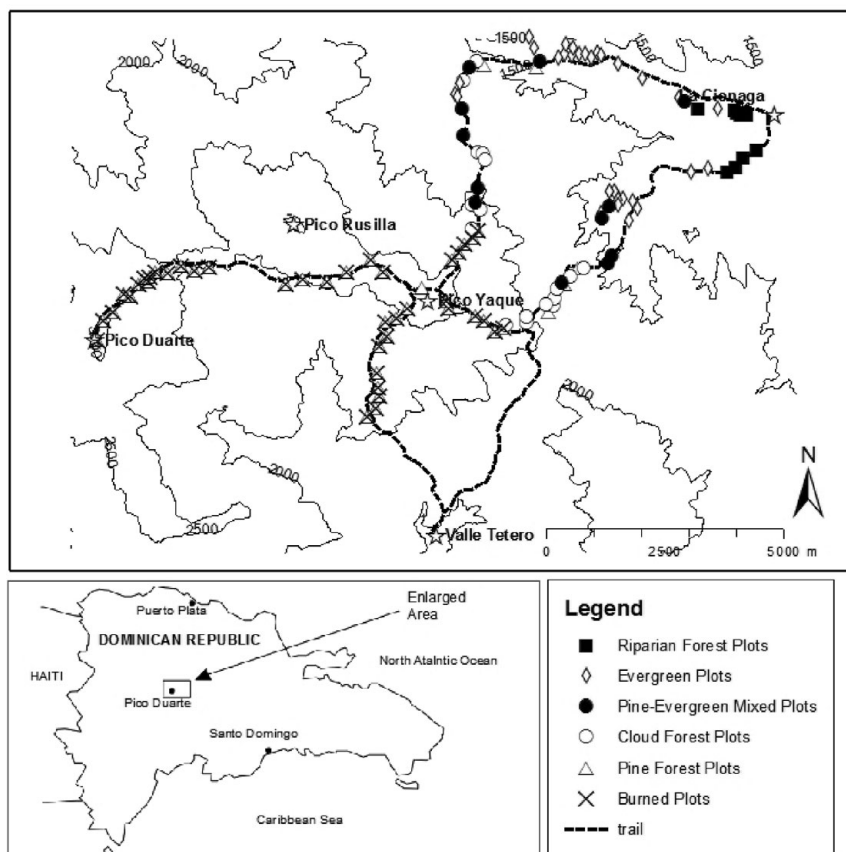


Figure 1. Map of the study area in the Cordillera Central, Dominican Republic showing the location of the permanent vegetation plots established in 1999–2000. Plots burned in the 2005 fire are indicated.

Martin & Fahey 2006, Scatena *et al.* 1996, Tanner & Bellingham 2006). The immediate impact of most disturbances is the loss of live biomass which greatly modifies subsequent forest dynamics. Patterns of forest damage are in turn influenced by topography and vegetation characteristics and as a result are highly patchy across many TMF landscapes (Bellingham 1991, Boose *et al.* 1994, Sherman *et al.* 2005, 2008). A long-term study of post-hurricane vegetation recovery in a Jamaican TMF showed that both growth and turnover rates were still elevated 30 y later (Tanner & Bellingham 2006) indicating that disturbances can create complex and long-lasting impacts on the structure, composition and dynamics across TMF landscapes.

We resurveyed a set of 75 0.1-ha plots in a TMF in the Cordillera Central, Dominican Republic, 8 y after they were established to quantify biomass, mortality, recruitment and growth of trees across this chronically disturbed montane landscape. Our goal was to contribute to a better understanding of the patterns of variation in TMF composition, structure and demography. We hypothesized that the forest would exhibit relatively

high turnover and growth rates owing to the regime of frequent canopy disturbance. In consequence, we expected biomass and carbon storage would be relatively low at the large landscape scale and highly variable at the local scale in comparison to TMFs in less-disturbed settings. We also expected above-ground biomass to decrease with altitude in part due to correlated reductions in growth and greater biomass losses from mortality with increasing altitude.

METHODS

Site description

This study was conducted in the neotropical montane forests of the Cordillera Central, Dominican Republic (19°02'N, 71°05'W) (Figure 1). The Cordillera Central is an extensive massif that occupies the central region of the island of Hispaniola forming the highest peaks in the Caribbean. Over 1500 km² of forests from 1100 m to over 3000 m asl were placed under protection

in the late 1950s (Armando Bermúdez and Carmen Ramírez National Parks) before any major logging or farming incursions. Forest clearing was limited to lower floodplains along the two rivers (Martin *et al.* 2004). Our study area encompassed approximately 85 km² of the core area extending from the community of La Ciénaga de Manabá at the eastern park entrance at 1100 m asl to the top of Pico Duarte, the highest point in the Caribbean at 3087 m asl, and spanning the windward (north-eastern) and leeward (south-western) slopes of the central massif (Figure 1).

The climate in the study area is subtropical and seasonal: December–March is marked by drier and colder weather, and the higher altitudes of the Cordillera Central (above 2000 m asl) experience regular below-freezing temperatures (Martin *et al.* 2007). Climatic patterns on the island reflect the influence of the prevailing north-easterly trade winds and exhibit a marked rainshadow. Annual precipitation on the windward slopes averages about 1900 mm y⁻¹, and about 1300 mm y⁻¹ on the leeward slopes (Sherman *et al.* 2005). There is a pronounced 3-mo dry season from January–March when monthly rainfall averages 80 mm on windward and 31 mm on leeward slopes (Martin & Fahey 2006). The geology of these mountains is complex, dominated by Cretaceous volcanic, metamorphic and plutonic rocks (Lewis 1980). The topography is rugged, with steep and sharply dissected slopes.

Forest vegetation across the study area was classified quantitatively based on 245 0.1-ha plots. Five distinct communities were arranged along the altitudinal gradient on the windward slopes (Sherman *et al.* 2005): (1) low-elevation (1100–1250 m asl) secondary riparian forests released from agriculture in 1956; (2) lower montane evergreen forests of tall stature (up to 40 m), complex structure and high diversity was the dominant forest type between 1500–1700 m asl; (3) mixed pine–evergreen forests with varying degrees of dominance by the endemic Hispaniolan pine, *Pinus occidentalis* Sw., common throughout the altitudinal range from 1100–1900 m; (4) an upper montane cloud forest with a high abundance of tree ferns (Cyatheaceae), epiphytic bryophytes and filmy ferns on windward slopes from 1900–2200 m asl; (5) high-elevation monodominant and monospecific pine forests above 2000 m asl. Monospecific pine forests also dominated the drier, leeward slopes at all altitudes south and west of the main ridgeline.

Data collection and analysis

In January–March 2007, 75 of the 245 0.1-ha plots established in 1999–2000 were resurveyed (Figure 1). The resurveyed plots ranged in altitude from 1100 m to

3030 m asl and represented all five forest community types described above; only six of the pine-dominated plots that escaped damage from a fire in 2005 (Sherman *et al.* 2008) were included in the resurvey. All live trees ≥ 10 cm diameter at breast height (dbh) were identified, permanently tagged and measured to the nearest 1 mm in each plot (Sherman *et al.* 2005). Tree diameter measurements were taken at breast height unless the tree had a bole irregularity and the measurement was taken at a different location on the stem, noted by the tree tag. On multi-stemmed trees, all stems ≥ 10 cm dbh were tagged individually. Tree ferns and palms were counted and measured but not tagged. In the resurvey, all tagged trees were located and remeasured and any mortality or missing trees recorded. All tree ferns and palms were counted and measured. In addition, any new trees that had grown into the ≥ 10 -cm dbh size class (recruits) were tagged, measured and identified and any dead new recruits recorded.

Demography

For each plot, we calculated the annualized rate of adult tree mortality (m), recruitment (r) and population change (λ) using standard models of exponential population change that assume a constant probability of mortality and recruitment through the inventory period (% y⁻¹):

$$m = (\ln(N_0) - \ln(N_s))/t \times 100 \quad (1)$$

$$r = (\ln(N_t) - \ln(N_s))/t \times 100 \quad (2)$$

$$\lambda = (\ln(N_t) - \ln(N_0))/t \times 100 \quad (3)$$

where N_t and N_0 is the size of the population at time t and time 0, respectively, and N_s is the number of survivors at time t . Recruitment rates do not take into account trees that may have grown into the smallest size class (10 cm dbh) during the interval between census periods but did not survive to be counted in the resurvey, and thus recruitment is underestimated (Kohyama & Takada 1998).

Mortality and recruitment rates also were calculated for 36 species that had 20 or more tagged individuals across all plots that were inventoried. Relative growth rate (RGR) of those species was calculated using the following equation:

$$\text{RGR} = (\ln(\text{dbh}_{t_2}) - \ln(\text{dbh}_{t_1})) / (t_2 - t_1),$$

where dbh is the diameter at breast height of an individual tree at time t_2 and time t_1 divided by the number of years between census periods.

Biomass estimates

Tree diameter measurements were converted to above-ground biomass using two allometric regression equations reported in the literature: one for evergreen trees and one for pine trees. Chave *et al.* (2005) estimated above-ground biomass of evergreen trees based on the analysis of 1025 trees ranging in size from 10–156 cm dbh that were harvested from 15 moist tropical and subtropical forest sites from around the world. We used the polynomial model (below) from Chave *et al.* (2005) that includes wood density (ρ), tree diameter and forest type (moist forest) as predictive variables to estimate biomass:

$$\begin{aligned} \text{AGB} = \rho \times \exp(-1.562 + 2.148 \times \ln(\text{dbh}) + 0.207 \\ \times \ln(\text{dbh})^2 - 0.0281 \times \ln(\text{dbh})^3 + \varepsilon); R^2 = \\ 0.996, \text{RMSE} = 0.356 \end{aligned}$$

We also include the parameter ε which is the residual error term.

Wood specific gravity values were obtained from tables compiled by Chave *et al.* (2006) and Reyes *et al.* (1992). We used species-specific wood density values when available, but most were based on generic means. Wood density is a strongly conserved phylogenetic trait within genera and the use of generic values is usually acceptable (Chave *et al.* 2006). We used family-level wood density values for nine species as genus-specific information was not available. For unidentified trees (32 individuals) and families for which we could not find wood density values (Garryaceae), the median wood specific gravity of 0.61 g cm⁻³ was used.

An allometric equation constructed for *Pinus montezumae* Lamb. (Bonilla-Padilla 2009), which has a similar ecology and growth form as *P. occidentalis*, was used to estimate biomass of the pine. The equation developed by Bonilla-Padilla (2009) was based on 15 trees that ranged in size from 7.2–65.9 cm dbh that spanned the size range of all but two pine trees measured in the resurvey at our site:

$$\begin{aligned} \text{AGB} = \exp(-4.34 + 3.046 \times \ln(\text{dbh}) + \varepsilon); \\ R^2 = 0.990, \text{RMSE} = 0.09. \end{aligned}$$

The parameter, ε , is the residual error term.

A correction factor was applied to all observations to account for the bias involved when back transforming log-transformed data by multiplying the biomass estimate by the following equation:

$$\text{CF} = e^{RMSE^2/2}$$

where RMSE = the root mean square error of the allometric regression equation (Chave *et al.* 2005).

Finally, allometric equations for palm trees, *Prestoea acuminata* var. *montana*, and tree ferns were based on height and not diameter (Franji & Lugo 1985, Tanner 1980). We used an average height based on the measurement of 50 tree ferns (2.6 ± 0.12 m) and 30 palm trees (11.35 ± 0.47 m) and calculated an average biomass value of 86.4 kg for all palm trees using the allometric equation developed by Franji & Lugo (1985) and 6.4 kg for tree ferns using the equation of Tanner (1980).

Above-ground live tree biomass was estimated for each plot at each census period, and the biomass of mortality, recruitment and growth of survivors, excluding palm trees and tree ferns, was calculated between census periods to analyse changes over the study period. The net change in the biomass of a plot was calculated as the sum of the biomass increment of all surviving trees plus the biomass of new recruits minus the biomass of trees that died over the census period (Harmon *et al.* 2007). All data were expressed on an annual basis.

Uncertainty and statistical analysis

We calculated the regression error associated with the allometric equations as the principal source of error in AGB estimates (Chave *et al.* 2004, Harmon *et al.* 2007). We followed Yanai *et al.* (2010) to quantify the uncertainty in the biomass estimates using a Monte Carlo analysis. The RMSE of the regression model was modelled as a random error term (ε) in the equations above to propagate uncertainty in the biomass estimates.

The total biomass of live trees, recruits and trees that died was calculated for the two census periods for each plot and each of the five community types at every iteration, and the 2.5th and 97.5th percentiles based on ranking of the 200 iterations were used to determine the 95% confidence intervals of the means. Non-overlap of the 95% confidence intervals was used as the measure of statistical difference between the means.

We also used a Monte Carlo approach to evaluate whether significant linear patterns of biomass change occurred across the altitudinal gradient. Using the resampled mean plot biomass and their standard deviations from the Monte Carlo simulations above, 1000 linear regressions were run with each dependent variable of interest (total biomass, biomass of mortality, recruitment, growth and net plot change) against altitude using a random sample of the biomass from each plot based on its standard deviation. We assumed the errors were normally distributed. The regression analysis was significant when the slopes of the 95% confidence intervals were statistically different from zero.

For summaries of other metrics of forest structure (basal area and density) and demographics (mortality and recruitment rates) we report plot means and their

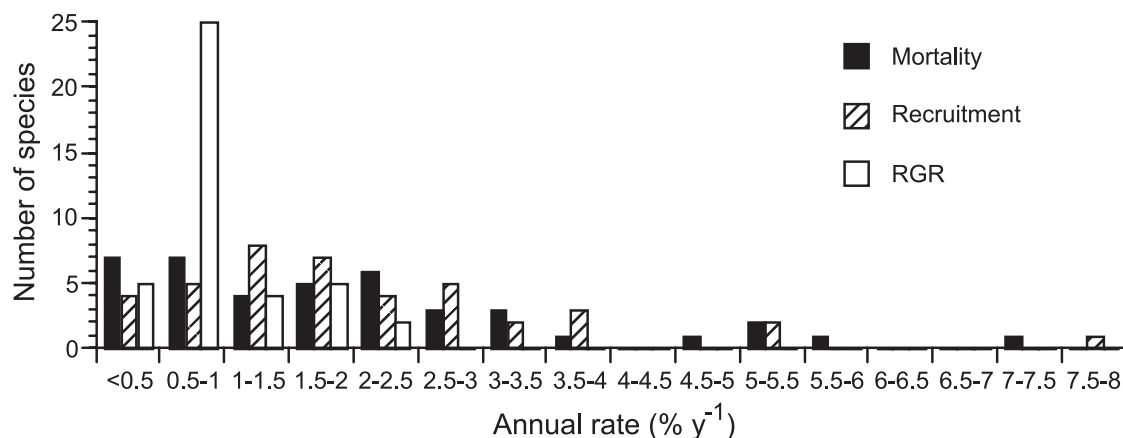


Figure 2. Frequency distribution of mortality, recruitment and relative growth rates of species in the tropical montane forest, Dominican Republic.

standard errors. Mann–Whitney tests were used to compare mean ranks between census periods and a Kruskal–Wallis test was used to test for significant differences in these parameters among forest community types. To examine the relationship between demographics (annual per cent turnover, mortality and turnover rates, and mortality and recruitment biomass) and plot-level site factors (altitude, terrain shape index, two linear indices of aspect (southness and eastness), steepness; see Sherman *et al.* 2005) and stand characteristics (basal area, density, species richness) we used a combination of general additive models (GAMs) and general linear models (GLMs) in SAS 9.2. The GAMs were used to explore the structure in the relationship among the response and predictor variables and significant relationships with second-order terms or less were subsequently parameterized using the GLM procedure.

To compare demographic characteristics among species, confidence intervals were calculated around the mean mortality, recruitment and relative growth rates of individual species, and non-overlap of the 95% confidence intervals was used as the measure of statistical difference between the means. Exact binomial confidence intervals for proportions were calculated for mortality rates (Condit *et al.* 1995). Relative growth rates were modelled as a log-normal distribution and confidence intervals were calculated using a modified Cox method (Olsson 2005). For recruitment rates, we calculated bootstrap percentile confidence intervals around the observed number of recruits of each species by resampling the population 1000 times and selecting the 2.5th and 97.5th ranked values.

To assess whether the average relative growth rates of species changed along the altitudinal gradient, we used a k-means clustering algorithm (McCune *et al.* 2002). The species were divided into five altitudinal ranges based on four descriptors of their range (median, mean, minimum and maximum), and we then calculated the mean and

95% confidence intervals for the relative growth rate of each species from 1000 randomizations. Non-overlap of the 95% confidence intervals was used as the measure of statistical difference between groups.

RESULTS

Species-specific mortality, recruitment and growth rates

A total of 36 tree species had ≥ 20 tree stems (≥ 10 cm dbh) for which we estimated mortality, recruitment and relative growth rates (Appendix 1). These 36 species accounted for over 94% of the biomass and over 80% of the stem density in all plots. Mortality rates were highly variable among species and ranged from 0 to 7.3% y^{-1} with a mean of 2.0% y^{-1} and median of 1.6% y^{-1} (Figure 2). Recruitment rates also varied greatly among species ranging from 0–7.8% y^{-1} with a mean of 2.1% y^{-1} and median of 1.8% y^{-1} (Figure 2). The average RGR of all species was 0.96% y^{-1} (median = 0.83% y^{-1}) and ranged from 0.42–2.42% y^{-1} . The modal RGR was 0.5–1% y^{-1} with 25 of the 36 species within this range (Figure 2).

Species clustered into five groups based on similarities in their altitudinal distribution ranges (Table 1). Relative growth rates of species groupings showed a strong trend of decrease with altitude and were highest among those species with the lowest median altitudinal distribution (1.34% y^{-1}), intermediate in the 17 species grouped into the second and third altitudinal groups (0.96% y^{-1}), and lowest in the 13 species that clustered into the two groups with the highest median altitudes (0.70–0.75% y^{-1}) (Table 1). In contrast, although there were significant differences in mortality and recruitment rates among the groupings of species, there was no consistent trend with altitude (Table 1).

Table 1. Changes in relative growth rates (RGR), mortality and recruitment rates of species with altitude. Species were grouped into five altitudinal groups using a k-means clustering algorithm, and the mean and 95% confidence intervals calculated for each group from 1000 randomizations are reported. Non-overlap of the 95% confidence intervals is the measure of statistical difference between groups; values with different letters are significantly different.

Median altitude (m)	Mean RGR (% y ⁻¹)	Mean mortality rate (% y ⁻¹)	Mean recruitment rate (% y ⁻¹)	No. species
1266	1.34 ^a (1.18–1.50)	1.32 ^a (0.62–2.07)	1.19 ^a (0.67–1.62)	7
1363	0.97 ^b (0.88–1.05)	1.57 ^a (1.03–2.09)	2.59 ^b (2.00–3.25)	12
1573	0.96 ^b (0.85–1.07)	3.07 ^a (1.68–4.59)	2.54 ^{a,b} (1.40–4.11)	9
1762	0.70 ^c (0.58–0.81)	1.45 ^a (0.58–2.75)	0.88 ^a (0.21–1.60)	4
1912	0.75 ^c (0.65–0.84)	2.54 ^a (1.43–3.77)	2.10 ^{a,b} (1.13–3.21)	9

Above-ground biomass and stand structure

Basal area increased significantly (Mann–Whitney test; $P < 0.001$) over the 8-y census interval by a plot average of $2.6 \text{ m}^2 \text{ ha}^{-1}$ (Table 2). Live tree above-ground biomass also increased, averaging 276 Mg ha^{-1} (CI = 175–439 Mg ha^{-1}) in 1999 across all 75 plots and forest types and increasing to 306 Mg ha^{-1} (CI = 193–475 Mg ha^{-1}) in 2007 (Table 2). However, given the large uncertainty in the biomass estimates, this biomass increase was not statistically significant. Average stem density did not change between census periods (Mann–Whitney test; $P = 0.40$).

Biomass of the secondary riparian, evergreen, pine-evergreen mixed and pine forests all increased between inventories whereas the cloud forests showed a slight decrease; however, confidence intervals around the biomass estimates overlapped and none of these changes was significant (Table 2). Changes in basal area between the 1999 and 2007 inventories tracked biomass, but none of these changes was statistically significant (Mann–Whitney test; all $P > 0.1$). Stem density remained essentially constant between census periods in all forest types (Table 2).

Biomass and basal area of the different forest community types were highest in the lower montane evergreen forests and lowest in the monospecific pine forests (Table 2). However, only the biomass stocks of the pine forests were statistically different (based on overlap of confidence intervals), being lower than all other forest types in 1999 and all but cloud forests in 2007. The basal area was not statistically different among forest types in either 1999 (Kruskal–Wallis test; $P = 0.15$) or 2007 ($P = 0.13$). Tree stem density was significantly higher in the cloud forests than all other forest types in both 1999 and 2007 (Kruskal–Wallis test; $P < 0.001$), but there were no significant differences in density among the other forest types.

Plot-level mortality, recruitment, growth and net biomass change

Mortality rates were similar among the riparian, evergreen and mixed pine-evergreen forests ranging from 1.7 – $1.9\% \text{ y}^{-1}$ and from 9.2 – $10.0 \text{ trees ha}^{-1} \text{ y}^{-1}$ (Table 3). Mortality was greatest in the cloud forest ($2.3\% \text{ y}^{-1}$) and lowest in the pine forest ($0.4\% \text{ y}^{-1}$). Recruitment rates

Table 2. Summary of above-ground biomass, basal area and density of five forest community types and the forest average based on live trees $\geq 10 \text{ cm dbh}$ measured in 75 0.1-ha plots in the Cordillera Central, Dominican Republic. Errors in parentheses are 95% confidence intervals for biomass estimates based on a Monte Carlo analysis for estimating uncertainty in allometric equations, and the plot means \pm SE are reported for basal area and density.

Forest type	Mean altitude (m asl)	Biomass 1999 (Mg ha^{-1})	Biomass 2007 (Mg ha^{-1})	Basal area 1999 ($\text{m}^2 \text{ ha}^{-1}$)	Basal area 2007 ($\text{m}^2 \text{ ha}^{-1}$)	Density 1999 (Trees ha^{-1})	Density 2007 (Trees ha^{-1})	Number of plots
Secondary Riparian	1173	252 (158–395)	309 (190–488)	23.3 ± 2.1	27.1 ± 2.4	592 ± 62	615 ± 59	10
Evergreen	1346	381 (222–612)	424 (247–682)	28.1 ± 1.7	31.9 ± 2.0	671 ± 43	681 ± 46	30
Pine–Evergreen Mixed	1642	210 (166–270)	235 (185–303)	25.3 ± 7.6	26.9 ± 8.1	594 ± 179	588 ± 177	12
Cloud	1920	211 (125–337)	209 (124–332)	26.3 ± 6.8	26.7 ± 6.9	1061 ± 274	1053 ± 272	16
Pine	2452*	111 (92–130)	131 (109–153)	18.3 ± 8.2	21.3 ± 9.5	500 ± 223	527 ± 236	6
Average	1877	276 (175–439)	306 (193–475)	25.8 ± 1.1	28.4 ± 1.2	718 ± 41	725 ± 39	74

*The mean altitude is based on all the pine-dominated plots measured in 1999; the mean altitude of the six unburned pine plots measured in 2007 is 1842 m asl.

Table 3. Mortality, recruitment and population change of the five forest community types, Cordillera Central, Dominican Republic. Reported values are the mean \pm SE based on plot-scale variation of annualized percentages and density-based rates.

Forest type	Mean altitude (m asl)	Mortality (% y ⁻¹)	Recruitment (% y ⁻¹)	Stem density change (% y ⁻¹)	Mortality (trees ha ⁻¹ y ⁻¹)	Recruitment (trees ha ⁻¹ y ⁻¹)	Stem density change (trees ha ⁻¹ y ⁻¹)
Secondary riparian	1173	1.71 \pm 0.25	2.55 \pm 0.67	0.84 \pm 0.60	9.2 \pm 1.49	11.8 \pm 1.96	2.6 \pm 1.29
Evergreen	1346	1.90 \pm 0.24	2.18 \pm 0.21	0.28 \pm 0.28	9.8 \pm 1.32	10.6 \pm 0.87	0.8 \pm 1.33
Mixed pine–evergreen	1642	1.85 \pm 0.54	1.96 \pm 0.57	0.11 \pm 0.03	10.0 \pm 2.89	8.9 \pm 2.58	-1.1 \pm 0.31
Cloud	1920	2.27 \pm 0.57	2.33 \pm 0.58	0.06 \pm 0.02	15.0 \pm 3.76	13.3 \pm 3.32	-1.8 \pm 0.44
Pine	2452*	0.42 \pm 0.17	1.13 \pm 0.46	0.71 \pm 0.63	2.4 \pm 0.96	5.5 \pm 2.25	3.2 \pm 1.29
Average	1877	1.83 \pm 0.16	2.14 \pm 0.171	0.31 \pm 0.19	10.3 \pm 1.06	10.7 \pm 0.79	0.4 \pm 0.93

*The mean altitude is based on all the pine-dominated plots measured in 1999; the mean altitude of the six unburned pine plots measured in 2007 is 1842 m asl.

were lowest in the pine forest (1.13% y⁻¹) but similar among other sites, and density-based recruitment rates were greatest in the cloud forests reflecting the higher stand density of these forests (Table 3).

There was a statistically significant linear relationship between annual per cent turnover rate and eastness ($P = 0.02$, $R^2 = 0.07$), indicating higher turnover rates on east-facing slopes, and a significant positive linear relationship of both mortality rates ($R^2 = 0.08$, $P = 0.02$) and biomass mortality ($R^2 = 0.11$, $P = 0.004$) with species richness. No other significant relationships were found between demographic parameters and site factors or stand characteristics.

A forest-wide net annual increase in AGB of 3.87 Mg ha⁻¹ y⁻¹ (CI = 2.43–6.04 Mg ha⁻¹ y⁻¹) was observed over the 8-y census interval (Table 4). The mean estimated net biomass change for the different forest community types all showed a significant rate of biomass accumulation except for the cloud forests which decreased at an annual rate of -0.32 Mg ha⁻¹ y⁻¹ (-0.66 to -0.08 Mg ha⁻¹ y⁻¹) (Table 4). Losses in biomass due to mortality were greatest in the cloud forests (4.30 (2.43–7.01) Mg ha⁻¹ y⁻¹) and lowest in the pine forests (1.26 (1.04–1.46) Mg ha⁻¹ y⁻¹) (Table 4). Biomass gains from recruitment of new individuals into the 10-cm-dbh class were similar among forest types (~0.9 Mg ha⁻¹ y⁻¹) with the exception

of the pine forests where recruitment was significantly lower at 0.15 (0.11–0.20) Mg ha⁻¹ y⁻¹ (Table 4). Gains in biomass from the growth of surviving trees averaged 5.79 (3.66–9.0) Mg ha⁻¹ y⁻¹ across all the plots (Table 4).

Above-ground biomass across altitudinal zones

Above-ground standing biomass, gains in biomass from growth and net biomass change of individual plots all decreased significantly with altitude (upper and lower 95% CI both had P values < 0.001) whereas biomass mortality (Upper CI: $P = 0.237$, Lower CI: $P = 0.996$) and recruitment (Upper CI: $P = 0.094$, Lower CI: $P = 0.758$) did not vary with altitude (Figure 3). Basal area tracked changes in biomass; both basal area increment and net basal area decreased with altitude whereas basal area mortality and recruitment were invariant with altitude.

DISCUSSION

Demography, biomass and disturbance

The forested landscape of the Cordillera Central, Hispaniola, is subject to relatively frequent natural

Table 4. Above-ground biomass contribution of mortality, recruitment and growth to net change in biomass of the different forest types, Cordillera Central, Dominican Republic. Errors in parentheses are 95% confidence intervals for biomass estimates based on a Monte Carlo approach for estimating uncertainty in allometric equations.

Forest type	Mean altitude (m asl)	Loss from mortality (Mg ha ⁻¹ y ⁻¹)	Gain from recruitment (Mg ha ⁻¹ y ⁻¹)	Gain from growth of survivors (Mg ha ⁻¹ y ⁻¹)	Net change (Mg ha ⁻¹ y ⁻¹)
Secondary riparian	1173	2.27 (1.47–3.48)	1.16 (0.65–1.90)	8.44 (4.95–13.6)	7.34 (4.12–12.0)
Evergreen	1346	2.54 (1.48–4.09)	0.75 (0.42–1.23)	7.41 (4.30–11.99)	5.62 (3.23–9.11)
Mixed pine–evergreen	1642	1.99 (1.48–2.69)	0.64 (0.37–1.04)	4.53 (3.53–5.92)	3.19 (2.42–4.27)
Cloud	1920	4.30 (2.43–7.01)	0.99 (0.59–1.59)	2.98 (1.75–4.79)	-0.32 (-0.66 – -0.08)
Pine	2452*	1.26 (1.04–1.46)	0.15 (0.11–0.21)	3.74 (3.11–4.42)	2.63 (2.19–3.07)
Average	1877	2.71 (1.68–4.25)	0.79 (0.44–1.29)	5.79 (3.66–9.00)	3.87 (2.43–6.04)

*The mean altitude is based on all the pine-dominated plots measured in 1999; the mean altitude of the six unburned pine plots measured in 2007 is 1842 m asl.

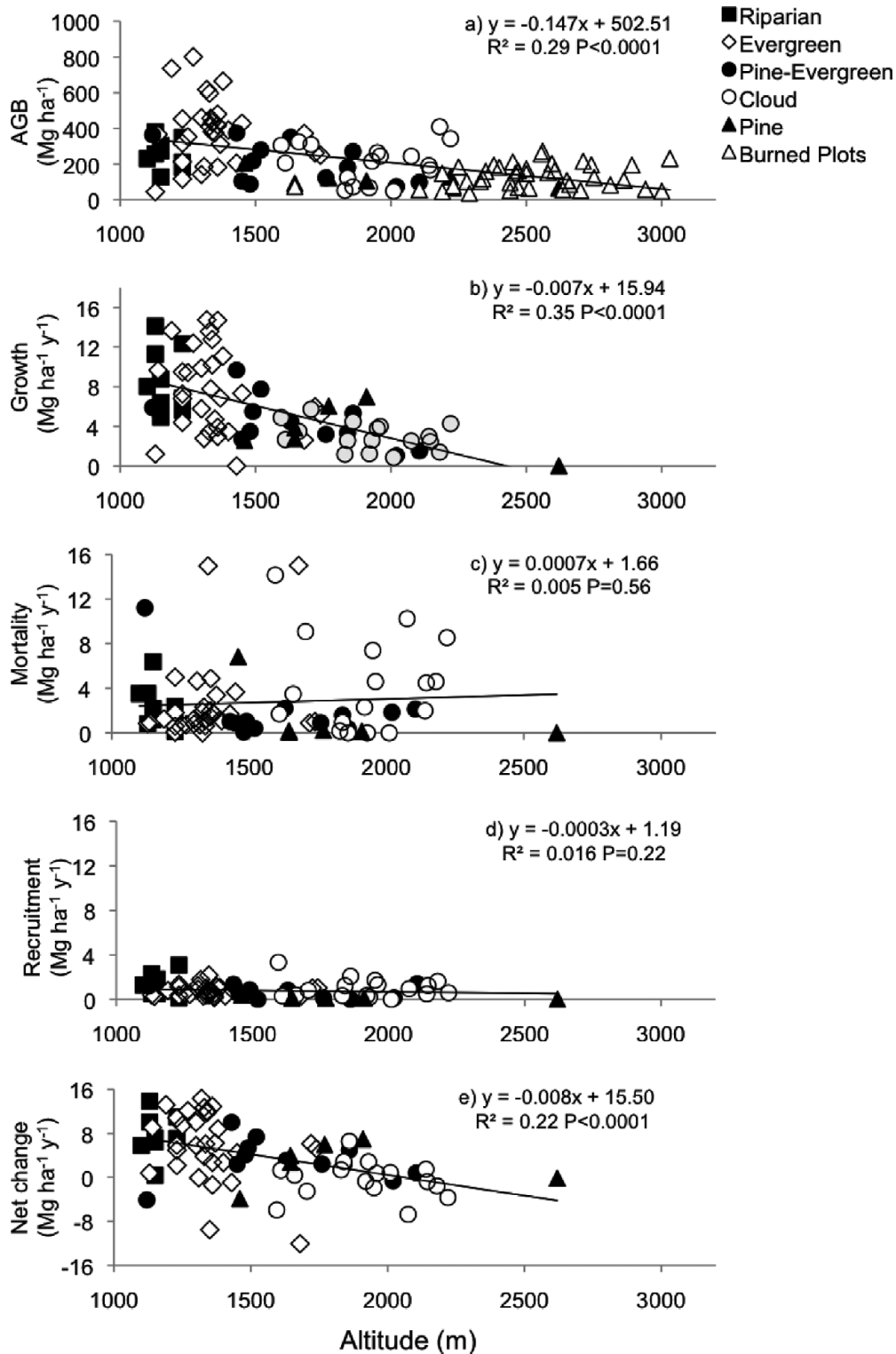


Figure 3. Changes in above-ground biomass with altitude in a tropical montane forest, Cordillera Central, Dominican Republic: standing stocks (a); stem wood growth (b); mortality (c); recruitment (d); and net change (growth + recruitment – mortality) (e). Above-ground standing stocks are 1999 values and include the pine-dominated stands that burned in the 2005 fire and not included in the 2007 re-census.

disturbances owing to its position in the pathway of hurricanes and to seasonal drought favouring wildfire. Recent hurricanes (David and Frederic in 1979, Georges in 1998) have been marked by intense winds, landslides and severe floods all resulting in canopy disturbance, albeit patchy on the landscape. The fire regime is mixed with both surface and crown fires, particularly in the pine-dominated forests (Martin & Fahey 2006); in recent major fire years (1965, 2005) both stand-replacing and lighter surface fires occurred over extensive portions of the landscape, especially above the cloud-forest zone (>2300 m) and on dry leeward slopes. The fire return interval averages 42 y on the windward slopes (Martin & Fahey 2006), and the hurricane frequency averages five to nine per decade (Reading 1990). We hypothesized that this chronic disturbance regime maintains the landscape in a shifting-mosaic steady state characterized by high demographic rates (mortality, recruitment and growth) and low biomass and C storage that varies markedly across the landscape.

Our demographic observations provided some evidence supporting this hypothesis. Canopy turnover (average of relative mortality and recruitment) exceeded $2\% \text{ y}^{-1}$ in the evergreen, mixed pine-evergreen and cloud-forest zones. Moreover, turnover rates tended to be higher on east-facing (windward) slopes which receive the highest hurricane winds (Boose *et al.* 2004). Tanner & Bellingham (2006) reported similarly high turnover rates in a Jamaican TMF both for the period following a major hurricane and for a longer disturbance-free interval (> $2\% \text{ y}^{-1}$ for stems ≥ 3 cm dbh). In the less disturbance-prone mountains of Borneo, average turnover rates (< $1.5\% \text{ y}^{-1}$ for trees ≥ 10 cm dbh) were substantially lower than at our site (Aiba *et al.* 2005). Somewhat surprisingly, average mortality rates for the Luquillo mountains of Puerto Rico ($1.5\% \text{ y}^{-1}$ for trees ≥ 10 cm dbh) (Lugo & Scatena 1996) were lower than at our site ($2\% \text{ y}^{-1}$ for the evergreen, pine-evergreen, cloud-forest zone) even though the two sites have a similar wind disturbance regime. The overall average turnover rate for 38 lowland rain forests ($1.6\% \text{ y}^{-1}$) appears lower, but many of those sites had values exceeding $2\% \text{ y}^{-1}$ (Phillips & Gentry 1994).

Some of the patterns of biomass change also appeared to reflect the effects of disturbance; however, hurricane damage patterns are difficult to reconstruct at small spatial scales because of the complex effects of terrain on wind flow combined with the fact that successive storms obscure damage from previous storms (Boose *et al.* 2004). Most of our plots exhibited a net gain in biomass over the census period with an overall net AGB accumulation rate of $3.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ (95% CI = $2.4\text{--}6.0 \text{ Mg ha}^{-1} \text{ y}^{-1}$) or $3.3 \text{ Mg ha}^{-1} \text{ y}^{-1}$ (CI = $2.2\text{--}5.1 \text{ Mg ha}^{-1} \text{ y}^{-1}$) when the secondary riparian forests are excluded. Stem wood accumulation rates across the altitudinal gradient in our

study area are among the highest reported for TMFs but comparable to a site in Malaysia (Kitayama & Aiba 2002; see Figure 2b in Moser *et al.* 2011), while exceeding those for sites in Hawaii (Raich *et al.* 1997), Ecuador (Moser *et al.* 2011), Puerto Rico (Wang *et al.* 2003, Weaver & Murphy 1990), and all but one site in Jamaica (Tanner 1980). The 'gap' forest in the Jamaican TMF had AGB accumulation rates of $3.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$ whereas three other forest types had lower rates of 2.0, 1.0 and $0.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$ (Tanner 1980). We propose that the high AGB accumulation rates at our site reflect in part recovery from past disturbances such as the relatively recent severe hurricanes of 1979 and 1998. Similar patterns were seen after Hurricane Hugo in the Luquillo Experimental Forest of Puerto Rico where AGB accumulation rates increased from about $5 \text{ Mg ha}^{-1} \text{ y}^{-1}$ to values as high as $16.3 \text{ Mg ha}^{-1} \text{ y}^{-1}$ in a census 5 y after the hurricane (Scatena *et al.* 1996). The patchy nature of this disturbance history appears to be reflected in extremely high spatial variation in AGB at the scale of 0.1-ha plots (range = $50\text{--}897 \text{ Mg ha}^{-1}$; SD = 183 Mg ha^{-1}). Although some of this spatial variation is undoubtedly associated with edge effects and large-tree effects from using small plots (Chave *et al.* 2004, Clark *et al.* 2001), much is clearly associated with disturbance and local topographic variation (Bellingham & Tanner 2000, Boose *et al.* 1994, Scatena *et al.* 1996).

We also expected relatively low landscape-scale AGB given chronic disturbance in this TMF, but our values are within the range observed for many other TMFs (Culmsee *et al.* 2010, Girardin *et al.* 2010, Kitayama & Aiba 2002, Tanner 1980), and comparable to those across a similar altitudinal range (1050–3060 m) in the less disturbance-prone Ecuadorian Andes (AGB declined from 285 to 112 Mg ha^{-1} ; Moser *et al.* 2008, 2011) but much higher than AGB estimates for the chronically disturbed mountains of Puerto Rico ($80\text{--}190 \text{ Mg ha}^{-1}$; Weaver & Murphy 1990) as well as Hawaii (Raich *et al.* 1997) and Costa Rica (Lieberman *et al.* 1996). Hence, support for our hypothesis that high disturbance frequency maintains the landscape at lower steady-state biomass is not conclusive.

Another indicator of disturbance in our site was the prominence of several species with traits of pioneer tree species (e.g. high relative growth rates and low wood density, Appendix 1). In addition to fire-adapted *Pinus occidentalis* (Martin & Fahey 2006), other common species were abundant in plots with evidence of historical disturbance, including *Brunellia comocladifolia*, *Alchornea latifolia*, *Garrya fadyenii* and *Clusia clusioides*. In contrast, a lack of species with pioneer traits was noted in infrequently disturbed Andean TMFs (Schwartzkopf 2003). Other studies of disturbance recovery in the Caribbean region have noted high sprouting ability of related TMF species following both windstorms (Bellingham *et al.* 1995, Zimmerman *et al.* 1994) and fire (Kennedy & Horn 2008), as well as regeneration from seed

after fires in cloud forests (May 2000). As noted for other Caribbean TMFs, adaptive traits of the dominant trees help them to survive even intense hurricanes (Bellingham *et al.* 1995, Zimmerman *et al.* 1994). Together, these features may help to account for the observation that all 36 of the principal species in these forests exhibited successful recruitment into ≥ 10 -cm-dbh class during the 8-y interval (Appendix 1).

Altitudinal patterns in demography and biomass

Our observations for 1999–2007 indicate no clear altitudinal pattern in mortality and recruitment whereas AGB and biomass accumulation clearly declined with increasing altitude in our study area. Aiba *et al.* (2005) demonstrated that forest turnover rates, productivity and species richness inter-correlated and declined with increasing altitude on Mt. Kinabalu, Borneo. Although mortality did not show any pattern with altitude at our site, there was a significant increase in both mortality rates and mortality biomass with species richness suggesting that productivity may covary in a similar pattern. In contrast, relative mortality rates were constant across an altitudinal gradient in Venezuela but absolute mortality rates increased with altitude as a result of increasing tree density (Lugo & Scatena 1996), and neither relative nor absolute tree mortality rates changed with altitude in Puerto Rico (Lugo & Scatena 1996). Net biomass accumulation rates declined with altitude at our site, a pattern that can be attributed entirely to decreased AGB growth rates with increasing elevation.

The general trend of declining above-ground biomass with altitude is a common feature of TMFs (Girardin *et al.* 2010, Kitayama & Aiba 2002, Moser *et al.* 2011, Raich *et al.* 1997, Wang *et al.* 2003, Weaver & Murphy 1990); however, the underlying mechanisms responsible for these patterns are not fully understood and have been attributed to declining soil nutrient supplies (Kitayama & Aiba 2002, Raich *et al.* 1997), decreased solar insolation (Wang *et al.* 2003), and increased below-ground carbon allocation (Girardin *et al.* 2010, Moser *et al.* 2011) with increasing altitude. Altitudinal trends of decreased biomass and biomass accumulation rates also are accompanied by changes in the forest community composition that can influence forest structure and processes (Culmsee *et al.* 2010). At our site, there is a continuous turnover of tree species along the altitudinal gradient (Martin *et al.* 2007, Sherman *et al.* 2005), and our analysis showed that species growing at higher elevations had lower RGRs suggesting that slower growing species may replace faster-growing species across the altitudinal gradient. Undoubtedly, changes in species composition combine with environmental constraints to regulate patterns of AGB and accumulation rates across

TMF landscapes, but experimental work is needed to disentangle environmental controls and species effects on AGB patterns.

Because tropical montane forests store large amounts of carbon, they are an important component of the tropical forest contribution to the global carbon budget. Global climate change may exert profound effects on the disturbance regime of many TMFs by increasing the frequency and intensity of hurricanes (Webster *et al.* 2005) and fires (Loope & Giambelluca 1998) with consequent impacts on forest and carbon dynamics. Understanding the underlying mechanisms that control how AGB pools and uptake rates vary across TMF landscapes and forest types will help us predict how they might respond to climate change which is critical for improving our understanding of the magnitude and variation in AGB pools in tropical regions, a poorly quantified component of the global carbon budget (Houghton *et al.* 2009). More quantitative studies in a variety of tropical montane settings are needed to better understand how natural disturbance, complex environmental gradients and species dynamics interact to regulate carbon storage and sequestration across altitudinal gradients in TMFs.

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Appendix 1. Characteristics of the most abundant species (≥ 20 individuals) from the Cordillera Central, Dominican Republic arranged in order of the median altitudinal distribution range.

Species	Family	Origin	Forest community	Median altitude (m)	stems	RGR (% y ⁻¹)	Annualised mortality	Annualised recruitment	Turnover rate (% y ⁻¹)	Wood Density (g/cm ³)
					≥ 10 cm dbh 2007		rate (% y ⁻¹)	rate (% y ⁻¹)		
<i>Inga vera</i> Willd.	Fabaceae	Native	Riparian	1150	55	1.79	2.49	1.19	1.84	0.59
<i>Tabebuia berteroi</i> (DC.) Britton	Bignoniaceae	Endemic	Evergreen	1230	362	0.88	0.40	0.93	0.67	0.77
<i>Ocotea floribunda</i> (Sw.) Mez	Lauraceae	Native	Riparian	1230	28	2.42	0.51	1.93	1.22	0.4
<i>Syzygium jambos</i> (L.) Alston	Myrtaceae	Non-native	Riparian	1230	118	0.57	0.12	1.22	0.67	0.79
<i>Prunus occidentalis</i> Sw.	Rosaceae	Native	Evergreen	1300	74	2.01	0.43	3.26	1.85	0.97
<i>Ocotea leucoxydon</i> (Sw.) Mez	Lauraceae	Native	Evergreen	1300	301	0.84	1.45	2.62	2.04	0.46
<i>Citharexylum</i> sp.	Verbenaceae	Native	Riparian	1300	47	0.97	2.23	1.71	1.97	0.63
<i>Sideroxylon cubense</i> (Griseb.) T. Pennington	Sapotaceae	Native	Riparian	1300	54	1.66	0.00	2.00	1.00	0.66
<i>Nectandra coriacea</i> (Sw.) Griseb.	Lauraceae	Native	Evergreen	1333	121	0.98	2.86	1.77	2.32	0.48
<i>Oreopanax capitatum</i> (Jacq.) Decne. & Planch.	Araliaceae	Native	Evergreen	1340	52	1.5	3.18	3.92	3.55	0.52
<i>Turpinia occidentalis</i> (Sw.) Don	Staphyleaceae	Endemic	Riparian and Evergreen	1340	53	0.94	1.56	2.05	1.80	0.42
<i>Alchornea latifolia</i> Sw.	Euphorbiaceae	Native	Riparian	1340	169	1.28	2.02	1.66	1.84	0.34
<i>Sloanea ilicifolia</i> Urb.	Elaeocarpaceae	Endemic	Evergreen	1350	46	0.68	0.82	0.56	0.69	0.8
<i>Meliosma impressa</i> Krug & Urb.	Sabiaceae	Endemic	Evergreen	1360	116	0.74	1.65	1.98	1.82	0.48
<i>Myrsine coriacea</i> (Sw.) R. Br.	Myrsinaceae	Native	All	1360	28	0.74	7.35	7.80	7.57	0.65
<i>Byrsonima lucida</i> (Miller) L.C. Rich	Malpighiaceae	Native	Evergreen	1370	39	0.7	0.34	1.00	0.67	0.65
<i>Ilex impressa</i> Loes. & Eckman	Aquifoliaceae	Endemic	All but Riparian	1395	64	0.75	5.30	2.36	3.83	0.56
<i>Myrcia deflexa</i> (Poirot) DC.	Myrtaceae	Native	Evergreen	1440	45	0.44	4.43	1.47	2.95	0.78
<i>Coccoloba wightii</i> Lindau	Polygonaceae	Native	Evergreen	1595	30	0.6	1.60	3.88	2.74	0.69
<i>Rondeletia ochracea</i> Urb. & Eckman	Rubiaceae	Endemic	Evergreen	1630	21	0.86	4.82	2.64	3.73	0.66
<i>Pinus occidentalis</i> Sw.	Pinaceae	Endemic	All	1645	417	1.2	0.94	0.68	0.81	0.58
<i>Didymopanax tremulus</i> Krug & Urb.	Araliaceae	Endemic	Cloud	1675	30	1.47	1.04	3.32	2.18	0.74
<i>Chionanthus domingensis</i> Lam.	Oleaceae	Native	Evergreen	1680	64	0.62	1.64	1.45	1.54	0.86
<i>Brunellia comocladifolia</i> H. & B.	Brunelliaceae	Native	All	1682	176	1.58	3.62	2.60	3.11	0.3
<i>Clusia clusioides</i> (Griseb.) D'Arcy	Clusiaceae	Native	Cloud	1720	82	0.75	2.55	1.12	1.83	0.68
<i>Chaetocarpus domingensis</i> G. Proctor	Euphorbiaceae	Endemic	Cloud	1730	68	0.97	0.42	1.99	1.21	0.61
<i>Lyonia alainii</i> Judd	Ericaceae	Endemic	Evergreen	1740	107	0.74	0.74	1.10	0.92	0.7
<i>Torrolbasia cuneifolia</i> (C. Wr.) Krug & Urb.	Celastraceae	Native	Cloud	1740	86	0.63	2.15	0.90	1.53	0.72
<i>Tabebuia vinosa</i> A.H. Gentry	Bignoniaceae	Endemic	Cloud	1840	30	0.59	1.23	0.42	0.83	0.77
<i>Ocotea cicatricosa</i> C.K. Allen	Lauraceae	Endemic	Cloud	1840	24	0.42	1.09	1.09	1.09	0.54
<i>Weinmannia pinnata</i> L.	Cunoniaceae	Native	Cloud	1849	39	0.65	5.96	1.00	3.48	0.53
<i>Garrya fadyenii</i> Hooker	Garryaceae	Native	All	1860	47	1.27	3.42	3.68	3.55	0.61
<i>Ilex repanda</i> Griseb	Aquifoliaceae	Native	Cloud	1930	31	0.68	0.61	5.48	3.04	0.56
<i>Ocotea wrightii</i> (Meissn.) Mez	Lauraceae	Native	Cloud	1950	35	0.49	1.98	0.00	0.99	0.54
<i>Antirhea oligantha</i> Urb.	Rubiaceae	Endemic	Cloud	1950	52	0.82	0.60	2.97	1.78	0.76
<i>Podocarpus aristulatus</i> Parl.	Podocarpaceae	Endemic	Cloud	2140	24	0.88	2.00	0.53	1.27	0.5