

RESEARCH ARTICLE

Open Access



Gradient (elevation) vs. disturbance (agriculture) effects on primary cloud forest in Ecuador: floristics and physical structure

Randall W. Myster

Abstract

Background: Cloud forests are common in the Neotropics and an important part of its hydrological cycle. An investigation on how elevation and recovery from agriculture affects cloud forest floristics and physical structure in Ecuador was undertaken.

Methods: Species and diameter at a specified height (dsh) of trees were sampled in large plots in Maquipucuna and Yanacocha cloud forests in Ecuador and also in smaller plots at Maquipucuna recovering after cropping in sugarcane (*Saccharum officinarum* L.) and banana (*Musa* sp.).

Results: (1) *Palicourea* sp. was the only species found at both primary sites; *Vernonia pallens* Sch.Bip., *Erythrina megistophylla* Diels, *Nectandra* sp., and *Miconia* sp. were found in both primary and secondary plots at Maquipucuna; and *Miconia* sp. was the only species in common between the Maquipucuna secondary plots and the primary plot at Yanacocha Reserve. (2) The mean stem size was similar between the primary Maquipucuna plots and the Yanacocha plot, but the Yanacocha plot had more total stems and more stems in each size category, which lead to more basal area, above-ground biomass, and canopy closure at Yanacocha compared to Maquipucuna. (3) In the secondary plots, there were no stems larger than 29 cm dsh at breast height, which lead to a much smaller mean stem size and lower basal area, above-ground biomass, and canopy closure compared to the primary plots at both sites.

Conclusions: For the primary cloud forest at Maquipucuna, an increase in elevation changed the species-level floristics more than conversion to and then abandonment from agriculture; however, while a rise in elevation increased the number of stems, agriculture reduced stem size structure.

Keywords: Banana, LTER, Maquipucuna Reserve, Sugarcane, Yanacocha Reserve

Background

Gradients and disturbances are two of the most important forces that shape plant communities because plants often respond to cues created by or associated with them (Pickett and White 1985; Turner and Dale 1991; Whittaker 1975). Indeed, landscapes can be largely seen as a vegetative mosaic created by these two forces. Common gradients include precipitation, soil nutrients, flooding, elevation, and temperature, and disturbances range from the very severe (e.g., landslides) to the moderately severe (conversion to agriculture) to the least severe (tree fall, selective logging).

In the Andean mountains, cloud forests exist along a large elevational gradient (1300–4000 m above sea level (a.s.l.); Bushush and Silman 2004) and are important to the biogeochemical cycling of surrounding forests (e.g., the hydrological cycle; Hamilton et al. 2012). They are also subject to a variety of large-scale disturbances such as landslides (Myster 1993), conversion to agriculture (Myster 2004b; Myster 2007a; Myster 2012a), and natural tree fall (Myster 2015a). In these forests as elevation increases, net primary productivity decreases (Girardin et al. 2010), height of the canopy and of emergent trees decreases, number of strata or canopy layers also decreases, plants take on different ecotypes (Myster and Fetcher 2005), and growth forms such as buttresses and climbers give way to various kinds of epiphytes

Correspondence: myster@okstate.edu; http://www.researchgate.net/profile/Randall_Myster
Biology Department, Oklahoma State University, Oklahoma City, OK 73107, USA

(Whitmore 1998). Also as elevation increases, trees become shorter and bryophytes become more common especially where cloud condensation becomes more persistent (Grubb et al. 1963). Exposure to wind-driven fog and rain can also cause trees to take on a bent and gnarled physiognomy, and bamboos can replace palms in the understorey (Kappelle and Brown 2001).

Consequently, cloud forests offer excellent opportunities to examine how gradients (in the form of changes in elevation) and disturbances (in the form of old fields recovering after abandonment from agricultural use) affect forest structure, function, and dynamics, where those effects may actually be due to factors associated with gradients (e.g., temperature, humidity) or conversion to agriculture (e.g., soil changes, past crop). For example, Holder (2004) found, in Guatemala, that fog precipitation was greater in a cloud forest at 2550 m a.s.l. compared with a cloud forest at 2100 m a.s.l. Likewise, Veneklaas and van Ek (1990) found an increase in interception in Colombian cloud forests with an increase in elevation (2550 m a.s.l. to 3370 m a.s.l.) and Weaver (1972) found a trend of decreasing interception with increasing elevation in cloud forest of Puerto Rico, where the elevational range of sites varied from 930 m a.s.l. to 1015 m a.s.l. Recovery from agricultural uses is slow for cloud forests, similar to temperate old-field rates with small-seeded tree species arriving first followed by understorey trees (Myster and Pickett 1994). Overall richness and structure may take decades to reach primary cloud forest levels (Myster 2004b).

A field study in Ecuador was implemented to expand on past samplings of Neotropical cloud forests (Myster 2014; Nadkarni et al. 1995; Tanner 1997; Weaver et al. 1986) in order to better understand the floristics and physical structure of primary cloud forests and how the natural variation of elevation and the human treatment of agriculture changed them. Plots were installed and measured as follows: (1) four 2500 m² (50 m × 50 m) plots in a primary cloud forest at Maquipucuna Reserve; (2) two 500 m² (50 m × 10 m) plots in secondary, regenerating cloud forest at Maquipucuna Reserve 17 years after sugarcane (*Saccharum officinarum*) or banana (*Musa* sp.) cultivation, and (3) one 2500 m² (50 m × 50 m) plot in a primary cloud forest at Yanacocha Reserve. Taxonomic authorities for all species referred to in this paper are available from the Plant List <http://www.theplantlist.org/>.

Three major questions were addressed: (1) how does an increase in elevation change the floristics (family, genera, species) and forest physical structure (stem density, mean stem size, four stem size classes, total basal area, above-ground biomass, canopy closure) of cloud forest in the Andean Mountains of Ecuador; (2) how does conversion to agriculture change the floristics

(family, genera, species) and forest physical structure (stem density, mean stem size, four stem size classes, total basal area, above-ground biomass, canopy closure) of a cloud forest in the Andean Mountains of Ecuador; and (3) which aspects of cloud forest floristics and physical structure are affected by which of these two forces, and does that suggest how they may interact to produce cloud forests?

Methods

Study sites and sampling

(1) Primary cloud forest at Maquipucuna Reserve (MR 0° 05' N, 78° 37' W; www.maqui.org; Sarimento 1997; Myster and Sarmiento 1998; Rhoades et al. 1998; Rhoades and Coleman 1999) located 20 km from the town of Nanegalito, Ecuador. This reserve lies between 1200 m and 1800 m a.s.l. and is classified as tropical lower montane wet/cloud forest (Edmisten 1970). It has deeply dissected drainages with steep slopes and has an annual precipitation of 3198 mm (measured from Nanegalito: Sarimento 1997). The temperature ranges yearly between 14 and 25 °C, with an average temperature of 18 °C. The reserve's fertile andisol soil is developed from recent volcanic ash deposits. The reserve is located in the Choco-Andean Corridor which is one of the top five biodiversity hot spots on earth (Sarimento 1995). In May 2012, four 2500 m² (50 m × 50 m) plots were selected as representative sites by experienced local field assistants, suggested by local field assistants, within MR primary cloud forest at 1400 m a.s.l. We then tagged and measured the diameter at a specific height (dsh) of all trees at least 10 cm dsh in each of the 25 10 m × 10 m contiguous subplots that make up each 2500 m² plot. The dsh measurement was taken at the nearest lower point where the stem was cylindrical, and for buttressed trees, it was taken above the buttresses. The tagged trees were also identified to species or to genus only when species identification was not possible.

(2) Within MR are secondary cloud forests of recovering sugarcane plantations, banana plantations, and pastures seeded with the grass *Setaria sphacelata* which is native to Africa (Myster 2014; Sarimento 1997; Zahawir and Augspurger 1999). In June 1996, 500 m² (50 m × 10 m) plots were laid out in just abandoned sugarcane plantation and in just abandoned banana plantation selected as representative sites by experienced local field assistants. In May 2011, each plot was measured using the same protocol as in (1). These plots are part of the longest and largest old-field study in the Neotropics (Myster 2004a; Myster 2004b; Myster 2007a; Myster 2007b; Myster 2009; Myster 2010a, 2010b; Myster 2014) funded by the US National Science Foundation (see Myster 2012a for details). The plots are located within a few hundred meters of each other at the lower elevations of MR (1200 m a.s.l.).

(3) Primary cloud forest at Yanacocha Reserve (YR: <http://fjocotoco.org/reserves-yanacocha>) managed by Fundacion Jocotoco and supported by a World Land Trust land purchase and Carbon Balanced funding is located on the northeastern slope of the Pichincha Volcano about 45 min northwest of Quito along the old Nono-Mindo Road on route to the Mindo Valley. The reserve was established in 2001 to protect the black-breasted Puffleg (*Eriocnemis nigrivestis*) whose known range is restricted to the Pichincha Volcano. The YR is mainly high-elevation elfin *Polylepis* sp. forest. In May 2015, one 2500 m² (50 m × 50 m) plot was established in YR primary cloud forest at 3400 m a.s.l., in a random location suggested by local field assistants, and measured using the exact protocol as in (1).

Species identification

Voucher specimens are kept on file at the University of Georgia, USA. Plant taxonomists at the University assisted in the identification of species using Romoleroux et al. (1997) and Gentry (1993) as taxonomic sources. They also consulted the web site of the Missouri Botanical Garden (www.mobot.org).

Data analysis

Data collected from all plots were used to compile floristic tables of family, genus, and species. Also calculated were: (1) the total number of stems, the mean dsh among those stems, and the total number of stems divided into four size classes: 10 < 20 cm dsh, 20 < 30 cm dsh, 30 < 40 cm dsh, and ≥ 40 cm dsh; (2) total basal area as the sum of the basal areas of all individual stems ($\pi \cdot r^2$; where r = the dsh of the individual stem/2); (3) above-ground biomass (AGB) using the formula in Nascimento and Laurance (2001) and suggested for tropical trees of these stem sizes; and (4) canopy closure using the formula in Buchholz et al. (2004) for tropical trees.

Results

There were a total of 25 families found among all seven plots (Table 1). Chloranthaceae, Lauraceae, and Melastomataceae were the most abundant families. Actinidaceae and Melastomataceae were the only families found in all five 0.25-ha plots, but there were no families found in all seven plots (Table 1). The most abundant species in the primary cloud forest plots at MR were *Erythrina megistophylla* and *Nectandra acutifolia* (Table 2), and in the primary cloud forest plot at YR, *Hedyosman canatrecasunam* and *Miconia* sp. were the most abundant (Table 3). *Palicourea* sp. was the only species found at both primary cloud forest sites with members of the genera *Saurania* and *Miconia* also found at both sites (Tables 2 and 3).

Table 1 Details of each family that occurred in all seven plots (and their frequency) sorted in alphabetical order with the total number of stems found: in primary cloud forest at Maquipucuna Reserve (MR1), (MR2), (MR3), and (MR4); in primary cloud forest at Yanacocha Reserve (YA); and in secondary cloud forest at Maquipucuna Reserve

Family	MR1	MR2	MR3	MR4	YA	S	B
Actinidaceae	8	4	6	6	1	0	0
Araliaceae	0	0	0	0	1	0	0
Asteraceae	0	1	0	0	14	3	1
Boraginaceae	0	0	0	0	5	0	0
Bromeliaceae	1	0	0	0	0	0	0
Cecropiaceae	0	0	3	4	0	1	0
Chloranthaceae	0	0	0	0	77	2	1
Cunoniaceae	0	0	0	0	10	0	0
Cyatheaceae	0	0	0	0	1	0	0
Euphorbiaceae	0	0	0	0	0	2	0
Fabaceae	12	5	15	17	0	0	2
Lamiaceae	0	0	0	0	1	0	0
Lauraceae	28	35	37	18	0	2	2
Melastomataceae	1	1	6	2	86	0	3
Mimosaceae	3	3	0	1	0	0	0
Monimiaceae	0	0	0	1	0	0	0
Moraceae	0	2	0	0	0	0	0
Myristicaceae	3	2	4	0	0	0	0
Myricaceae	0	0	0	0	3	0	0
Myrtaceae	0	1	1	2	0	0	0
Piperaceae	2	0	2	1	0	4	0
Rubiaceae	5	0	3	3	24	0	0
Solanaceae	0	1	1	3	0	0	1
Tiliaceae	0	0	1	1	0	0	0
Urticaceae	4	3	5	0	0	1	0
Verbenaceae	8	4	8	4	0	0	0

S recovering sugarcane field, B recovering banana field

The most abundant species in the secondary cloud forest plots at MR were *Vernonia pallens*, *Nectandra* sp., and *Piper aduncum* (Table 4). *Piper aduncum* was the most abundant species in the recovering sugarcane plot, and *Miconia* sp. was the most abundant species in the recovering banana plot (Table 4). *Vernonia pallens*, *Erythrina megistophylla*, *Nectandra* sp., and *Miconia* sp. were found in both primary and secondary plots at MR as was the genera *Cecropia* and *Piper* (Tables 2 and 4). *Miconia* sp. was the only species in common between the MR secondary plots and the primary cloud forest plot at YR, but the genus *Hedyosmum* was present at both sites (Tables 3 and 4).

Although the mean stem size was similar between the primary MR plots and the YR plot (Table 5), the YR plot

Table 2 All species ≥ 10 cm dsh sampled in the four 50 m \times 50 m plots in primary cloud forest at Maquipucuna Reserve (MR1, MR2, MR3, MR4) with their number of stems

Family	Genus	Species	MR1	MR2	MR3	MR4	Mean
Actinidiaceae	<i>Saurauia</i>	<i>priannana</i>	1	2	0	1	1.0
Asteraceae	<i>Vernonia</i>	<i>patens</i>	0	0	0	1	0.25
Bromeliaceae	<i>Bromelia</i>	sp.	1	0	0	1	0.50
Cecropiaceae	<i>Cecropia</i>	sp.	2	2	3	0	1.75
Fabaceae	<i>Erythrina</i>	<i>megistophylla</i>	15	11	16	7	12.25
Lauraceae	<i>Nectandra</i>	<i>acutifolia</i>	25	34	29	30	29.50
Lauraceae	<i>Nectandra</i>	sp.	0	1	0	0	0.25
Melastomataceae	<i>Meriania</i>	<i>maxima</i>	0	1	0	0	0.25
Melastomataceae	<i>Miconia</i>	sp.	2	2	5	1	2.50
Mimosaceae	<i>Inga</i>	sp.	0	4	3	0	1.75
Monimiaceae	<i>Siparuna</i>	<i>aspera</i>	0	0	1	0	0.25
Moraceae	<i>Ficus</i>	sp.	0	0	0	1	0.25
Myristicaceae	<i>Otoba</i>	<i>gordoniifolia</i>	4	3	2	1	2.50
Myrtaceae	<i>Eugenia</i>	sp.	2	0	0	3	1.25
Piperaceae	<i>Piper</i>	sp.	1	1	1	2	1.25
Rubiaceae	<i>Faramea</i>	<i>flavicans</i>	1	0	0	1	0.50
Rubiaceae	<i>Ladenbergia</i>	sp.	0	0	2	1	0.75
Rubiaceae	<i>Policourea</i>	sp.	2	5	4	0	2.75
Rutaceae	<i>Zanthoxylum</i>	sp.	0	0	0	2	0.50
Solanaceae	<i>Cestrum</i>	sp.	2	0	2	1	1.25
Tiliaceae	<i>Triunfeta</i>	sp.	0	1	0	1	0.50
Urticaceae	<i>Urera</i>	sp.	5	3	2	2	3.00
Verbenaceae	<i>Aegiphila</i>	sp.	6	8	3	7	6.00

Table 3 All species ≥ 10 cm dsh sampled in the 50 m \times 50 m plot in primary cloud forest at Yanacocha Reserve with number of stems

Family	Genus	Species	YA
Actinidiaceae	<i>Saurauia</i>	cf <i>tomentosa</i>	1
Araliaceae	<i>Schefflera</i>	sp.	1
Asteraceae	<i>Senecio</i>	sp.	14
Boraginaceae	<i>Tournefortia</i>	sp.	5
Chloranthaceae	<i>Hedyosman</i>	<i>cauatrecasanum</i>	77
Cunoniaceae	<i>Weinmannia</i>	cf <i>fagaroides</i>	10
Cyatheaaceae	<i>Cyathea</i>	sp.	1
Lamiaceae	<i>Aegiphyla</i>	sp.	1
Melastomataceae	<i>Blakea</i>	sp.	15
Melastomataceae	<i>Miconia</i>	sp.	71
Myricaceae	<i>Morella</i>	<i>cerifera</i>	3
Rubiaceae ^a	<i>Palicourea</i>	sp.	4
Rubiaceae			20

^aSpecies also found in primary cloud forest plots at Maquipucuna**Table 4** All species ≥ 10 cm dsh sampled in the 50 m \times 10 m plots in secondary cloud forest at Maquipucuna Reserve with their number of stems

Family	Genus	Species	S	B
Asteraceae	<i>Vernonia</i>	<i>pallens</i>	3	1
Cecropiaceae	<i>Cecropia</i>	<i>monostachyma</i>	1	0
Chloranthaceae	<i>Hedyosmum</i>	sp.	2	1
Euphorbiaceae	<i>Acalypha</i>	<i>platyphylla</i>	1	0
Euphorbiaceae	<i>Croton</i>	<i>eluterin</i>	1	0
Fabaceae ^a	<i>Erythrina</i>	<i>megistophylla</i>	0	1
Fabaceae	<i>Inga</i>	sp.	0	1
Lauraceae ^a	<i>Nectandra</i>	sp.	2	2
Melastomataceae ^a	<i>Miconia</i>	sp.	0	3
Piperaceae	<i>Piper</i>	<i>aduncum</i>	4	0
Solanaceae	<i>Solanum</i>	sp.	0	1
Urticaceae	<i>Pilea</i>	sp.	1	0

S recovering sugarcane field, B recovering banana field

^aSpecies also found in primary cloud forest plots at Maquipucuna

Table 5 Physical structure parameters for all trees ≥ 10 cm dsh sampled in the four 2500 m² plots, primary cloud forest Maquipucuna Reserve (MR1, MR2, MR3, MR4) in May 2012, and in the one 2500 m² plot, primary cloud forest Yanacocha Reserve (YR) in May 2015

Parameter	MR1	MR2	MR3	MR4	YR
Stem density					
Total	68	70	81	75	193
10 < 19 cm dsh	45	39	38	31	91
20 < 29 cm dsh	24	21	18	19	56
30 < 39 cm dsh	14	9	11	12	24
40 cm or greater	3	3	5	2	22
Mean dsh (cm)	22.0	22.1	23.8	22.8	23.1
Family richness	11	12	13	13	11
Genus richness	14	13	13	17	13
Species richness	14	14	13	17	13
Basal area (m ²)	2.2	3.2	2.4	3.2	5.2
Above-ground biomass (Mg)	49.0	49.7	48.3	51.4	87.2
Canopy closure (%)	45.2	45.9	46.2	47.7	65.2

had more total stems and more stems in each size category which lead to more basal area, AGB, and canopy closure at YR. All five plots had a reverse J stem size distribution pattern. Richness of families, genera, and species were slightly less in the YR plot compared to the MR primary plots (Table 5).

At MR, the secondary cloud forest plots are one quarter the size of each of the primary cloud forest plots. When adjusting for these differences in area by multiplying by four, the total number of stems and the number of stems in the first two size classes were slightly smaller than any of the primary cloud forest plots. But the largest difference was that there were no stems larger than 29 cm dsh in either the sugarcane or the banana plot (Table 6), which led to a much smaller mean stem size in the secondary plots. Richness of families, genera, and species were all less here when compared to both the MR plots and the YR plot but similar between past crops (sugarcane vs. banana). Given the smaller number of stems and stem size, the basal area, AGB, and canopy coverage were much lower in the sugarcane and banana fields compared to the primary plots at MR and YR (Table 6).

Discussion

There were several more species in common between the primary Maquipucuna cloud forest and the secondary Maquipucuna cloud forest than between the primary Maquipucuna cloud forest and the primary Yanacocha cloud forest. This suggests that cloud forest floristics is affected more by an increase in elevation (here 2000 m) than by past sugarcane and banana cultivation (here 17 years after abandonment). In terms of forest physical

Table 6 Physical structure parameters for all trees ≥ 10 cm dsh sampled in the four 2500 m² plots and in sugarcane fields (S:500 m²) and in banana fields (B:500 m²). All plots are located at Maquipucuna Reserve

Parameter	MR1	MR2	MR3	MR4	S	B
Stem density						
Total	68	70	81	75	15	10
10 < 19 cm dsh	45	39	38	31	11	7
20 < 29 cm dsh	24	21	18	19	4	3
30 < 39 cm dsh	14	9	11	12	0	0
40 cm or greater	3	3	5	2	0	0
Mean dsh (cm)	22.0	22.1	23.8	22.8	5.6	4.6
Family richness	11	12	13	13	7	6
Genus richness	14	13	13	17	8	7
Species richness	14	14	13	17	8	7
Basal area (m ²)	2.2	3.2	2.4	3.2	0.76	0.69
Above-ground biomass (Mg)	49.0	49.7	48.3	51.4	14.87	15.24
Canopy closure (%)	45.2	45.9	46.2	47.7	11.22	8.95

structure, with an increase in elevation, there is a gain in tree stems of all sizes but a loss of some diversity, especially at the species level. This leads to a more closed and structurally (but not floristically) complex cloud forest at the higher elevations. Large trees are absent in the recovering sugarcane and banana plots, which produces large differences in physical structure, and thus, the secondary forest at MR may reach floristic similarity before structural similarity.

Comparing the two study primary cloud forests to the primary cloud forest at Monteverde, Costa Rica, also sampled for all trees at least 10 cm dsh, there was a similar number of stems (555/ha) but more basal area (62 m²/ha: Nadkarni et al. 1995) but the same reverse J size distribution. There were many families in common: Asteraceae, Cecropiaceae, Fabaceae, Lauraceae, Melastomataceae, Moraceae, Myristicaceae, Myrtaceae, Myrtaceae, Piperaceae, Rubiaceae, Solanaceae, Tiliaceae, Urticaceae, and Verbenaceae, but only Fabaceae and Lauraceae were abundant. *Cecropia* was the only genus in common as well.

The stem density for all trees at least 10 cm dsh in another primary cloud forest sampling in Costa Rica was comparable to YR (553/ha: Heaney and Protor 1990), but low in Jamaica (Tanner 1997) and Ecuador (Grubb et al. 1963), which puts the MR sampling somewhere in between. In Puerto Rican "dwarf" cloud forest, there were many small stems (3671/ha) but the basal area was comparable to Monteverde in Costa Rica (49.1 m²/ha: Weaver et al. 1986). In cloud forests closer to Ecuador (Venezuela) sampled to a dsh of at least 10 cm, the stem density (365–850/ha) and species richness (9–14/ha) was also comparable (Schwarzkopf et al. 2011).

Previous studies of the sugarcane and banana plots have compared floristics and physical structure like in this study (Myster 2007a); for example, relationships between richness and productivity (Myster 2009) and dominance-diversity curves (Myster 2010a, 2010b). These studies have also included field experiments into regeneration mechanisms and tolerances at MR (Myster 2004a; Myster 2015a) and have shown that seed predators took most of the seed and had their greatest effect in closed-canopy primary cloud forest, a medium effect in tree-fall gaps in primary cloud forest, and least effect in secondary cloud forest (Myster 2015a).

Field experiments into how elevation affects seed processes were also done at Guandera biological station also in Ecuador (also at 3400 m a.s.l.) and at MR (Randall Myster: unpub. data). In that study, I found: (1) the two study sites were significantly different for all three seed processes but where seed predation dominated Maquipucuna, seed pathogens dominated Guandera; (2) closed-canopy vs. tree-fall gap variation was only significant for germination; (3) species were significantly different for both seed predation (*Solanum stenophyllum* [11%], *Palicourea amethystine* [16%], *Clusia flaviflora* [13%] Engl., *Cecropia* sp. [79%], *Ardisia websteri* [83%], *Prestoea acuminata* [84%], *Ficus* sp. [85%], *Otoba gordoniiifolia* [69%]) and for seed pathogens (*Solanum stenophyllum* [43%], *Palicourea amethystine* [52%], *Clusia flaviflora* [68%] Engl., *Cecropia* sp. [14%], *Ardisia websteri* [7%], *Prestoea acuminata* [4%], *Ficus* sp. [4%], *Otoba gordoniiifolia* [7%]); and (4) there were significant interaction terms for elevation \times species seed predation, where it was driven by the differences between study sites and the tree seed species *Palicourea amethystine*, and for elevation \times species seed pathogens, where it was driven by the differences between study sites and the tree seed species *Otoba gordoniiifolia*. Thus, cloud forest recruitment and regeneration is affected less by predation and more by pathogens, as elevation increases.

Conclusions

In conclusion, (1) elevation affects both floristics and physical structure in these Andean cloud forests and I continue my work at other high-altitude sites in order to examine these differences in more detail and, (2) after 17 years while the old fields have species in common with the primary MR forest, they are not floristically similar and differences suggest that there may continue to be a lingering effect of the past crops of sugarcane vs. banana (a crop signature: Myster 2004b). Structural differences are consistent with trends in successional vs. primary vegetation studies elsewhere (see chapters in Myster 2007b). These permanent plot studies, and others like them, provide baseline data on forest dynamics (i.e., plant-plant

replacements: Myster 2012c) and fluctuations of forest structure.

Acknowledgements

I thank Arcenio Barras, Bernardo Castro, Jorge Reascos, Rebeca Justicia, and the staff of Maquipucuna Reserve for their help in executing this research. I also thank E. Bruna, D. Bonte, A. Chiarucci, P. Campanello, P. Bernier, and A. Austin for commenting on a previous draft of the manuscript.

Competing interests

The author declares that he has no competing interests.

Received: 27 June 2016 Accepted: 23 December 2016

Published online: 20 January 2017

References

- Buchholz, T., Tenggigkeit, T., & Weinreich, A. (2004). *Maesopsis emini*—a challenging timber tree species in Uganda—a production model for commercial forestry and smallholders. Proceedings of the international union of forestry research organizations (IUFRO) conference on the economics and management of high productivity plantations, Lugo, Spain.
- Bushush, M. B., & Silman, M. R. (2004). 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, *303*, 827–829.
- Edmisten, J. (1970). Some autoecological studies of *Ormosia krugii*. In H. T. Odum & R. F. Pigeon (Eds.), *A tropical rain forest*. Springfield: National Technical Information Service. Chapter D-8.
- Gentry, A. A. (1993). *Field guide to woody plants of northwest South America (Colombia, Ecuador, Peru)*. Washington, DC: Conservation International.
- Girardin, C. Y., Malhi, L., Aragao, M., Mamani, W., Huaraca-Huaraca, W., & Durand, L. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*, 3176–3192.
- Grubb, P. J., Lloyd, J. R., Pennington, T. D. A., & Whitmore, T. C. A. (1963). Comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. *Journal of Ecology*, *51*, 567–601.
- Hamilton, L. S., Juvik, J. O., & Scatena, F. N. (2012). *Tropical montane cloud forests*. Berlin: Springer-Verlag.
- Heaney, A., & Protor, J. (1990). Preliminary studies on forest structure and floristics on Volcan Barva Costa Rica. *Journal of Tropical Ecology*, *6*, 307–320.
- Holder, C. D. (2004). Rainfall interception and fog precipitation in a tropical montane cloud forest of Guatemala. *Forest Ecology and Management*, *190*, 373–384.
- Kappelle, M., & Brown, A. D. (2001). *Bosques nublados del Neotropico*. Heredia, Costa Rica: Instituto Nacional de Biodiversidad.
- Myster, R. W. (1993). Spatial heterogeneity of seed rain, seed pool, and vegetative cover on two Monteverde landslides, Costa Rica. *Brenesia*, *39–40*, 137–145.
- Myster, R. W. (2004a). Regeneration filters in post-agricultural fields of Puerto Rico and Ecuador. *Plant Ecology*, *172*, 199–209.
- Myster, R. W. (2004b). Post-agricultural invasion, establishment and growth of neotropical trees. *The Botanical Review*, *70*, 381–402.
- Myster, R. W. (2007a). Early successional pattern and process after sugarcane, banana and pasture cultivation in Ecuador. *New Zealand Journal of Botany*, *46*, 101–110.
- Myster, R. W. (2007b). *Post-agricultural succession in the neotropics*. Berlin: Springer.
- Myster, R. W. (2009). Are productivity and richness related consistently after different crops in the neotropics? *Botany*, *87*, 1–6.
- Myster, R. W. (2010a). Testing dominance-diversity hypotheses using data from abandoned plantations and pastures in Puerto Rico and Ecuador. *Journal of Tropical Ecology*, *26*, 247–250.
- Myster, R. W. (2010b). Flooding gradient and treefall gap interactive effects on plant community structure, richness, and alpha diversity in the Peruvian Amazon. *Ecotropica*, *16*, 43–49.
- Myster, R. W. (2012a). Long-term data from fields recovering after sugarcane, banana and pasture cultivation in Ecuador. Dataset papers in Ecology Volume 2013, Article ID – 468973.10 pages, DOI 10.7167/2013/46873.
- Myster, R. W. (2012a). Post-agricultural ecotones in Puerto Rico. In R. W. Myster (Ed.), *Ecotones—between forest and grassland* (pp. 147–166). Berlin: Springer-Verlag.
- Myster, R. W. (2012b). Plants replacing plants: the future of community modeling and research. *The Botanical Review*, *78*, 2–9.

- Myster, R. W. (2014). *Primary vs. secondary forests in the Neotropics: two case studies after agriculture*. Pp 1–42 in *forest ecosystems: biodiversity, management and conservation*. NY: Nova publishers.
- Myster, R. W. (2015). Seed predation, pathogens and germination in primary vs. secondary cloud forest at Maquipucuna Reserve, Ecuador. *Journal of Tropical Ecology*, 31, 375–378.
- Myster, R. W., & Fetcher, N. (2005). Ecotypic differentiation and plant growth in the Luquillo Mountains of Puerto Rico. *Journal of Tropical Forest Science*, 17, 163–169.
- Myster, R. W., & Pickett, S. T. A. (1994). A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology*, 75, 387–392.
- Myster, R. W., & Sarmiento, F. O. (1998). Seed inputs to microsite patch recovery on tropicandean landslides in Ecuador. *Restoration Ecology*, 6, 35–43.
- Nadkarni, N. M., Matelson, T. J., & Haber, W. A. (1995). Structural characteristics and floristic composition of a neotropical cloud forest, Monteverde, Costa Rica. *Journal of Tropical Ecology*, 4, 481–495.
- Nascimento, H. E. M., & Laurance, W. F. (2001). Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecology and Management*, 157, 1–11.
- Pickett, S. T. A., & White, P. S. (1985). *The ecology of natural disturbance and patch dynamics*. NY: Academic Press.
- Rhoades, C. C., & Coleman, D. C. (1999). Nitrogen mineralization and nitrification following land conversion in montane Ecuador. *Soil Biology and Biochemistry*, 31, 1347–1354.
- Rhoades, C. C., Eckert, G. E., & Coleman, D. C. (1998). Effect of pasture trees on soil nitrogen and organic matter: implications for tropical montane forest restoration. *Restoration Ecology*, 6, 262–270.
- Romoleroux, K., Foster, R., Valencia, R., Condit, R., Balslev, H., & Losos, E. (1997). Especies Lenosas (dap => 1 cm) encontradas en dos hectareas de un bosque de la Amazonia ecuatoriana. In R. Valencia & H. R. Balslev (Eds.), *Estudios Sobre Diversidad y Ecología de Plantas* (pp. 189–215). Quito, Ecuador: Pontificia Universidad Católica del Ecuador.
- Sarimento, F. O. (1995). Naming and knowing a tropicandean landscape: the Maquipucuna Reserve as a case study. *The George Wright Forum*, 12, 15–22.
- Sarimento, F. O. (1997). Arrested succession in pastures hinders regeneration of tropicandean forests and shreds mountain landscapes. *Environmental Conservation*, 24, 14–23.
- Schwarzkopf, T., Riha, S. J., Fahey, T. J., & Degloria, S. (2011). Are cloud forest tree structure and environment related in the Venezuelan Andes? *Austral Ecology*, 36, 280–289.
- Tanner, E. V. J. (1997). Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *Journal of Ecology*, 65, 883–918.
- Turner, M. G., & Dale, V. H. (1991). Modeling landscape disturbance. In M. G. Turner & R. H. Gardner (Eds.), *Quantitative methods in landscape ecology* (pp. 323–351). Berlin: Springer-Verlag.
- Veneklaas, E. J., & van Ek, R. (1990). Rainfall interception in two tropical montane rain forests, Colombia. *Hydrological process*, 4, 311–326.
- Weaver, P. L. (1972). Cloud moisture interception in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*, 12, 129–144.
- Weaver, P. L., Medina, E., Pool, D., Dugger, K., Gonzales-Liboy, J., & Cuevas, E. (1986). Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. *Biotropica*, 18, 79–85.
- Whitmore, T. C. (1998). *An introduction to tropical rain forests*. Oxford: Clarendon Press.
- Whittaker, R. H. (1975). *Communities and ecosystems*. NY: MacMillan.
- Zahwir, R. A., & Augspurger, C. K. (1999). Early plant succession in abandoned pastures in Ecuador. *Biotropica*, 31, 123–129.

Submit your manuscript to a SpringerOpen[®] journal and benefit from:

- Convenient online submission
- Rigorous peer review
- Immediate publication on acceptance
- Open access: articles freely available online
- High visibility within the field
- Retaining the copyright to your article

Submit your next manuscript at ► springeropen.com
