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Gradient (elevation) vs. disturbance (agriculture) effects on primary Cloud forest in Ecuador: seed predation, seed pathogens, germination

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Abstract

Background: Gradients and disturbances affect plant communities. Cloud forests exist on elevational gradients and are often disturbed by being cleared for agriculture, so they present a unique opportunity for the investigation of how gradients and disturbances affect their structure, function and dynamics. The focus of the current study was on seed predation, seed pathogens and seed germination: all key factors in tree recruitment and regeneration.

Methods: Three hundred seeds of three species—*Solanum stenophyllum* Bitter (Solanaceae: bird-dispersed), *Palicourea amethystina* (Ruiz & Pav.) DC. (Rubiaceae: bird-dispersed) and *Clusia flaviflora* Engl. (Clusiaceae: mammal-dispersed) —were studied at primary (1°) cloud forest at Guandera Reserve. After 2 weeks in the field, losses due to seed predation or pathogens were counted and the remaining seeds were tested for germination. These results were then compared with similar data collected and published previously from a 1° cloud forest and a secondary (2°) cloud forest, both at Maquipucuna Reserve, Ecuador.

Results: In both closed-canopy forest and tree-fall gaps at Guandera Reserve, *S. stenophyllum* Dunal seeds suffered the greatest losses to predators, *P. amethystina* seeds had the greatest germination and *C. flaviflora* seeds had the greatest losses to pathogens. Comparison with data from Maquipucuna Reserve showed the following: (1) *Solanum* sp. suffered the greatest losses for seeds lost to seed predators in general but *Cecropia* sp. and *Ficus* sp. also had high losses in Maquipucuna 1° cloud forest; (2) for seeds lost to pathogens, species that lost the most seeds were unique to each study site: *Clusia flaviflora* seeds at Guandera 1° cloud forest, *Cecropia* sp. seeds at Maquipucuna 1° cloud forest and *Piper aduncum* L. seeds at Maquipucuna 2° cloud forest; (3) for seeds that germinated the most, species were again unique to the study site: *Palicourea amethystina* seeds at Guandera 1° cloud forest, *Otoba gordoniifolia* (A. DC.) A.H. Gentry seeds at Maquipucuna 1° cloud forest and *Solanum ovalifolium* Dunal seeds at Maquipucuna 2° cloud forest; and (4) in general, forest types differed significantly for both seed predation and seed pathogens. Within the 1° cloud forest at Maquipucuna, there was a significant difference among tree seed species for pathogens and a significant difference among the tree seed species for germination, and within the 2° cloud forest at Maquipucuna, there was a significant difference among tree seed species for pathogens.

Conclusions: As elevation increases in 1° cloud forests, the proportion of seed that germinates remain largely constant, but the major seed loss shifts from being due to predators to being due to pathogens. Conversion to agriculture also leads to seeds mainly lost to predators, but individual species loss levels depended on what crop had been planted previously.

Keywords: Banana, Closed canopy, Guandera Reserve, Maquipucuna Reserve, Pasture, Sugarcane, Tree-fall gap

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Background

Gradients and disturbances shape plant communities because plants respond to cues created by, or associated with, them (Whittaker 1975; Pickett and White 1985). A fundamental gradient in the Andean mountains is elevation, where cloud forests exist between 1300 and 4000 m above sea level (a.s.l.: Bush et al. 2004). As elevation increases in these cloud forests, net primary productivity (Girardin et al. 2010), height of emergent trees, canopy height and number of strata all decrease (Myster 2017a). Indeed, plants are more likely to be ecotypes (Myster and Fetcher 2005), and buttresses and climbers are usually replaced by epiphytes (Kappelle 1995; Whitmore 1998) in cloud forests found at higher elevations. Common cloud forest disturbances include landslides (Myster 1997; Myster 2004a, b), conversion to agriculture and pasture (see Myster 2007a) and natural tree-fall (Myster 2015). Thus, the Andes provide an opportunity to examine how gradients (here changes in elevation) and disturbances (here old fields recovering after agricultural use) affect cloud forest structure, function and dynamics. Those effects may be direct—caused by elevation and conversion to agriculture—or indirect, caused by factors associated with elevation (e.g. temperature, humidity) and conversion to agriculture (e.g. soil changes, "signature" of the past crop: Myster and Pickett 1994).

In order to take advantage of this opportunity, the current study expanded on past field experiments on the fate of the seed rain in 1° and 2° cloud forest at Maquipucuna Reserve in Ecuador (Myster 2015) by setting up a new seed experiment in closed-canopy forest and in tree-fall gaps at Guandera Reserve in Ecuador. The results of all three studies were then combined to more completely investigate how forest-type (1° cloud forest at Guandera Reserve, 1° cloud forest at Maquipucuna Reserve, 2° cloud forest at Maquipucuna Reserve), microsite (closed-canopy/tree-fall gap, recovering banana/sugarcane/pasture) and tree seed species affect seed predation, seed pathogens and seed germination, all key components of tree recruitment and regeneration (Myster 2017b) in Andean cloud forests. The aim of this study was to answer the following questions: (1) Does an increase in elevation and the formation of tree-fall gaps affect whether dispersed seeds in cloud forests are taken by predators, infected by pathogens or germinate? (2) Does conversion to agriculture, and the recovery after abandonment, affect whether dispersed seeds in cloud forests are taken by predators, infected by pathogens or germinate? and (3) How do different tree seed species respond to these different conditions?

Methods

Study sites

The current study site was the Guandera biological station (GBS:www.jatunsacha.org/guandera-reserve-and-biological-station; Cresswell et al. 1999; Bader et al. 2007; Nierop et al. 2007) situated on the inner flank of the eastern Cordillera at approximately 11 km from the town of San Gabriel in northern Ecuador (0° 36′ N, 77° 42′ W). The area is of volcanic origin and has deep dark humic Andosols developed in old volcanic ashes. Annual precipitation is 1700 mm. Diurnal temperature fluctuations range from 4 to 15 °C but annual temperature fluctuations are low (monthly means of maximum temperature vary between 12 and 15 °C: Bader et al. 2007). Within the GBS, 1° cloud forest occurs between the agricultural areas, mainly potato (*Solanum tuberosum* L.) cultivation below 3300 m a.s.l., and the páramo grasslands (Myster 2012a) above 3640 m a.s.l. The GBS consists of upper montane cloud forest at lower elevations and sub-alpine dwarf forest at higher elevations. The upper montane cloud forest is dominated by the trees *Clusia flaviflora* Engl. (Clusiaceae), *Ilex colombiana* Cuatrec. (Aquifoliaceae), *Weinmannia cochensis* Hieron. (Cunoniaceae), *Miconia tinifolia* Naudin (Melastomataceae) and *Gaiadendron punctatum* (Ruiz and Pavón) G.Don. (Loranthaceae) and the epiphytes *Tillandsia* sp. (Bromeliaceae) and *Blechnum schomburgkii* (Klotzsch) C.Chr. (Blechnaceae). The sub-alpine dwarf forest is dominated by the trees *Miconia tinifolia* and *Weinmannia cochensis*, a shrub *Gaiadendron punctatum*, a fern *Blechnum schomburgkii* and a bamboo *Neurolepis aristata* (Munro) Hitchc. (Poaceae: Cresswell et al. 1999).

Experimental design and execution

Ten 1° cloud forest areas were selected randomly at GBS in May 2015. Five had new tree-fall gaps between 100 and 300 m^2 in area (Brokaw 1982) and five were in closed-canopy forest. Ripe fruits were collected by hand (using gloves to reduce transfer of infections or human odor) from one local individual of *Solanum stenophyllum* Bitter (Solanaceae: bird-dispersed), one local individual of *Clusia flaviflora* Engl. (Clusiaceae: mammal-dispersed) and one local individual of *Palicourea amethystina* (Ruiz & Pav.) DC. (Rubiaceae: bird-dispersed). Seed species are ordered by increasing seed mass (found on www.data.kew.org/sid/). Seeds were examined for damage using a dissecting microscope and by floating them in water. Visually damaged seeds and those that floated were discarded. Ten viable seeds of each of the three test species were then placed in three separate plastic 9-cm-diameter Petri dishes spaced 50 cm apart and placed in the centre of each closed-canopy forest area and in the centre of each tree-fall gap. Three dishes per gap × ten gaps gave a total of 30 dishes and 300 seeds per species. Plastic seed mimics were also placed in each dish to examine whether seeds were removed by biotic agents (e.g. insects, birds, mammals) or by abiotic conditions (e.g. wind, rain). These mimics were constructed from plastic purchased in Quito to match seed size, shape and colour.

After 2 weeks in the field, seed loss from each dish was counted. Animals were assumed to be the agents of removal because chewed seeds and husks and small-mammal faeces were found in or near the dishes and because plastic seed mimics in the dishes were not taken. It was also assumed that the seeds taken did not germinate later (Notman and Gorchov 2001), and there is, to date, no reason to question this (Myster 2007a; Myster 2014b). The remaining seeds were placed on moist paper, in sealed plastic Petri dishes, in a shade house at GBS for incubation. After 4 weeks, seeds that germinated, seeds that did not germinate and had extensive fungal infection (i.e. lost to pathogenic attack: Myster 2004b) and "other" seeds were counted after being viewed under a dissecting microscope.

Data analysis

Data collected previously (Myster 2015) were included in the analysis. That study site was the Maquipucuna Reserve (MR:www.maqui.org: Sarmiento 1997; Myster and Sarmiento 1998, Rhoades and Coleman, 1999, Rhoades et al., 1998, Myster 2015) between 1200 and 1800 m a.s.l. in elevation and 20 km from Nanegalito, Ecuador (0° 05′ N, 78′ 37″ W). The MR has a mean temperature of 18 °C and an annual precipitation of 3198 mm (measured from Nanegal: Sarmiento 1997). The MR consists of 1° cloud forest (Myster 2014b) and 2° cloud forest of old fields recovering from cultivation of sugarcane (*Saccharum officinarum* L.) and banana (*Musa* sp.) and pastures seeded with the grass *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. Ex Moss (native to Africa: Sarmiento 1997; Zahawi and Augspurger, 1999). Common tree species in the 1° cloud forest include *Erythrina megistophylla* Diels (Fabaceae), *Nectandra acutifolia* (Ruiz & Pav.) Mez (Lauraceae) and *Aegiphila* sp. (Verbenaceae: Myster 2014b). There are permanent plots in those old fields, which comprise the longest and largest old-field study in the Neotropics (Myster 2004a; Myster 2004b; Myster 2007a; Myster 2007b; Myster 2014b), funded by the US National Science Foundation (see Myster 2012b for detail). The same protocol was used at MR in both 1° and 2°, cloud forest and some of those data (Myster 2015) were used here.

Because different tree seed species were used in all three forest types, the species and microsite data were pooled before a one-way ANOVA (SAS 1985) was performed to examine how seed predation, seed pathogens and germination were affected by forest type (1° cloud forest at Guandera vs. 1° cloud forest at Maquipucuna vs. 2° cloud forest at Maquipucuna). The species were then pooled, and a two-way ANOVA was performed to examine how seed predation, seed pathogens and germination were affected by the main effect of forest type (1° cloud forest at Guandera vs. 1° cloud forest at Maquipucuna), by the main effect of the microsite (closed-canopy vs. tree-fall gap) and by the interaction of forest-type × microsite. Finally, each forest type was analysed using three separate two-way ANOVAs to determine how seed predation, seed pathogens and seed germination were affected by:

1. The main effect of microsite (closed-canopy vs. tree-fall gap for both 1° cloud forests, recovering sugarcane field vs. recovering banana field vs. recovering seeded pasture for the 2° cloud forest)
2. The main effect of species and
3. The interaction of microsite × species

A generalised linear model was not needed for any of the ANOVAs because microsites were not paired. When results from ANOVA were significant, means testing was conducted using the Tukey procedure (SAS 1985) to find those treatment levels that were most significant. Prior to statistical analysis, all data were examined and found to be normally distributed.

Results

Results of the current study are presented here along with those of the previous study mentioned earlier (all in Tables 1, 2 and 3). For seeds lost to seed predators, (1) the smallest seeds of *Solanum stenophyllum* had the greatest losses both in closed-canopy forest and in tree-fall gaps in 1° cloud forest at Guandera, (2) *Cecropia* sp. had the greatest losses in closed-canopy forest and

Table 1 The percentage (mean ± standard error) of the total seeds remaining put out: in closed-canopy forest/in tree-fall gaps in 1° cloud forest, Guandera biological station

Species	% lost to predators	% lost to pathogens	% germinated	% other
Solanum stenophyllum	15 ± 2/17 ± 1	60 ± 1/63 ± 1	20 ± 3/10 ± 2	5 ± 2/10 ± 2
Palicourea amethystina	11 ± 2/13 ± 2	44 ± 3/47 ± 1	35 ± 2/27 ± 2	10 ± 2/13 ± 1
Clusia flaviflora	10 ± 2/9 ± 1	71 ± 2/75 ± 1	15 ± 1/12 ± 1	4 ± 2/4 ± 2
Mean % (rounded)	12/13	58/62	23/16	

Table 2 The percentage (mean ± standard error) of the total seeds remaining put out: in closed-canopy forest/in tree-fall gaps in 1° cloud forest, Maquipucuna Reserve

Species	% lost to predators	% lost to pathogens	% germinated	% other
Cecropia sp.	88 ± 1/70 ± 2	8 ± 2/19 ± 1	4 ± 1/6 ± 1	0 ± 1/5 ± 2
Ardisia websteri	85 ± 1/81 ± 1	4 ± 1/10 ± 1	11 ± 2/9 ± 1	0 ± 1/0 ± 1
Prestoea acuminata	80 ± 3/88 ± 2	3 ± 2/5 ± 2	10 ± 2/6 ± 2	7 ± 2/0 ± 1
Ficus sp.	82 ± 2/92 ± 1	5 ± 1/3 ± 3	8 ± 1/4 ± 3	5 ± 1/1 ± 1
Otoba gordoniifolia	70 ± 1/68 ± 1	4 ± 2/10 ± 3	20 ± 1/10 ± 2	6 ± 2/12 ± 1
Mean % (rounded)	81/80	5/9	11/7	

Ficus sp. had the greatest losses in tree-fall gaps in 1° cloud forest at Maquipucuna and (3) *Solanum ovalifolium* had the greatest losses in banana and sugarcane fields and tied for greatest losses in seeded pasture 2° cloud forest at Maquipucuna. For seeds lost to seed pathogens, (1) *Clusia flaviflora* had the greatest losses both in closed-canopy forest and in tree-fall gaps in 1° cloud forest at Guandera, (2) *Cecropia* sp. had the greatest losses both in closed-canopy forest and in tree-fall gaps in 1° cloud forest at Maquipucuna and (3) *Piper aduncum* had the greatest losses in banana and sugarcane fields and tied for greatest losses in seeded pasture in 2° cloud forest at Maquipucuna. For seeds that germinated, (1) the largest seeds of *Palicourea amethystina* had the greatest germination both in closed-canopy forest and in tree-fall gaps in 1° cloud forest at Guandera, (2) *Otoba gordoniifolia* had the greatest germination both in closed-canopy forest and in tree-fall gaps in 1° cloud forest at Maquipucuna and (3) *Solanum ovalifolium* had the greatest germination in banana fields, in sugarcane fields and in seeded pastures in 2° cloud forest at Maquipucuna.

The one-way ANOVA found that forest types differed significantly ($F = 7.2$, $P = 0.01$) for seed predation (12.5% in 1° cloud forest at Guandera, 80.5% in 1° cloud forest at Maquipucuna, 64.2% in 2° cloud forest at Maquipucuna) and differed significantly ($F = 5.2$, $P = 0.03$) for seed pathogens (60.1% in 1° cloud forest at Guandera, 7.5% in 1° cloud forest at Maquipucuna, 19.2% in 2° cloud forest at Maquipucuna). Within the 1° forest at Guandera, ANOVA found a significant difference ($F = 4.5$, $P = 0.04$) among tree seed species for pathogens (61% for *Solanum stenophyllum*, 45% for *Palicourea amethystina*, 73% for *Clusia flaviflora*) and a significant difference ($F = 3.3$, $P = 0.05$) among the tree seed species for germination (15% for *Solanum stenophyllum*, 31% for *Palicourea amethystina*, 13% for *Clusia flaviflora*). Within the 1° cloud forest at Maquipucuna, ANOVA found a significant difference ($F = 4.1$, $P = 0.03$) among tree seed species for pathogens (13% for *Cecropia* sp., 7% for *Ardisia websteri*, 4% for *Prestoea acuminata*, 4% for *Ficus* sp., 7% for *Otoba gordoniifolia*) and a significant difference ($F = 5.3$, $P = 0.03$) among the tree seed species for germination (5% for *Cecropia* sp., 10% for *Ardisia websteri* Pipoly, 8% for *Prestoea acuminata* (Willd.) H.E.Moore, 6% for *Ficus* sp., 15% for *Otoba gordoniifolia*). Within the 2° cloud forest at Maquipucuna, ANOVA found a significant difference ($F = 6.2$, $P = 0.02$) among tree seed species for pathogens (27% for *Cecropia monostachya* C.C.Berg, 29% for *Piper aduncum*, 11% for *Cestrum megalophyllum* Dunal, 8% for *Solanum ovalifolium*).

Discussion

The results obtained from both the current study and that of Myster (2015) showed large significant differences between the two cloud forests sites, which are near the two ends of the elevational ranges for Andean cloud forests (Bush et al. 2004). Pathogens were the major seed mechanism limiting forest recruitment for 1° cloud forest at Guandera (Myster 1997; Myster 2003), and predation was the major seed mechanism limiting forest recruitment for both 1° and 2° cloud forest at Maquipucuna (see reviews in Myster 2004a; Myster 2007a). If a seed could survive both of those two filters, it had a high probability of germinating (Myster 2003; Myster and Everham, 1999). Variation in how effective

Table 3 The percentage (mean ± standard error) of the total seeds remaining put out: in fields recovering from banana cultivation/in fields recovering from sugarcane cultivation/in fields recovering after use as seeded pasture in 2° cloud forest, Maquipucuna Reserve

Species	% lost to predators	% lost to pathogens	% germinated	% other
Cecropia monostachya	66 ± 1/67 ± 2/50 ± 1	24 ± 2/25 ± 1/29 ± 3	10 ± 2/6 ± 1/10 ± 1	0 ± 1/2 ± 1/11 ± 1
Piper aduncum	50 ± 1/50 ± 2/49 ± 2	30 ± 1/30 ± 1/29 ± 2	11 ± 3/10 ± 1/12 ± 1	9 ± 1/10 ± 2/0 ± 1
Cestrum megalophyllum	74 ± 2/69 ± 1/71 ± 2	13 ± 1/11 ± 2/10 ± 1	10 ± 2/9 ± 2/9 ± 1	3 ± 1/11 ± 3/9 ± 1
Solanum ovalifolium	77 ± 2/75 ± 1/71 ± 3	9 ± 1/9 ± 1/8 ± 3	14 ± 1/14 ± 2/13 ± 1	0 ± 1/2 ± 2/7 ± 2
Means % (rounded)	67/65/60	19/19/19	11/10/11	

seed predation and seed pathogens (Myster 2004b), among forest types, microsites and species, determines the pattern and process of recruitment and regeneration in cloud forests. It should also be remembered that seed predators (insects, birds, mammals) differ in species preference and behavior, and also fungi (e.g. *Colletotrichum* sp. attacked *Palicourea riparia* Benth. seeds in another Neotropic Montane forest study: Myster 1997).

The level of losses for predation and pathogens in 2° forest was intermediate to losses for the two 1° cloud forests. This result suggests that the effects of seed predators and seed pathogens in 2° cloud forest at Maquipucuna may be similar in 1° cloud forest located between Guandera and Maquipucuna in elevation, and so gradients and disturbances may have comparable effects under certain circumstances (see Myster 2014a for another example where the gradient was black-water flooding and the disturbance was natural tree-fall). Thus, the proportion of seed that germinates remain largely constant as elevation increases in these cloud forests, but the major cause of seed loss shifts from being due to animal predators to being due to fungal pathogens. When the lower elevation cloud forest was converted to agriculture and then allowed to revert back to cloud forest, seeds were still lost mainly to predators but individual species loss levels corresponded with the crop that had previously been planted.

Results from previous Neotropic 1° cloud forest studies conducted by several different groups have identified a number of effects relating to seed loss, i.e. (1) predators take larger seeds in preference to smaller seeds (Pringle et al. 2007); (2) 2° dispersal is rare (Culot et al. 2009); (3) litter reduces seed predation (Cintra 1997), and after bat defaecation, seed were eaten at a rate of 8% per week with possible satiation (Romo et al. 2004); (4) seed predation can be reduced more by loss of soil fertility (i.e. in palm forest) than by increased flooding (i.e. in igapó forests: Myster 2014a); (5) standing water in palm forest leads to the greatest losses to pathogens, but increased flooding in igapó forests also increases loss of seeds to pathogens; and (6) seeds mainly germinate if they escape predators and pathogens (Myster and Everham 1999).

The results of the current study were also similar to those from several Neotropic 2° forest studies: (1) over 75% of seeds were lost to predators in Peru old fields (Notman and Gorchov 2001); (2) more seeds were lost to predation than pathogens in Puerto Rico pasture, banana and sugarcane fields (Myster 2004a) and in their coffee fields and pastures as well (50–75% predation, 20%–45% pathogens, 15%–35% germination: Myster 2003); (3) a reduction of seed predation from the forest into clear-cut logged areas in Peru (Notman et al. 1996); and (4) pathogens affected more seeds (16%) than predators (9%) in landslides at a cloud forest in Costa Rica with 69% germination (Myster 1997). Further, for tree seedlings in the MR old fields, there was no survival in pastures, 15% survival in sugarcane fields and 25% survival in banana fields (Myster 2007b) and the species with the smallest seeds (i.e. those of the genera *Piper*, *Vernonia* and *Cecropia*) survived best.

A previous study of how these same two factors (elevation vs. agriculture) affect cloud forest floristics and physical structure (Myster 2017a) found (1) *Palicourea* sp. was the only species found at both 1° sites (Yanacocha Reserve 3400 m a.s.l, Maquipucuna Reserve 1200 m a.s.l), *Vernonia pallens* Sch.Bip., *Erythrina megistophylla*, *Nectandra* sp. and *Miconia* sp. were found in both 1° and 2° plots at Maquipucuna and *Miconia* sp. was the only species in common between the Maquipucuna 2° plots and the 1° plot at Yanacocha Reserve; (2) the mean stem size was similar between the 1° Maquipucuna plots and the Yanacocha plot, but the Yanacocha plot had more total stems and more stems in each size category, which led to more basal area, above-ground biomass and canopy closure at Yanacocha compared to Maquipucuna; and (3) in the secondary plots, there were no stems larger than 29-cm diameter at breast height (dbh) which lead to a much smaller mean stem size and lower basal area, above-ground biomass and canopy closure compared to the 1° plots at both sites. For the 1° cloud forest at Maquipucuna, an increase in elevation changed the species-level floristics more than conversion to, and then abandonment from, agriculture; however, a rise in elevation increased the number of stems, while agriculture reduced stem size structure (Myster 2017a).

Conclusions

The proportion of seed that germinates remains largely constant as elevation increases in these cloud forests, but the major cause of seed loss shifts from being due to predators to being due to fungal pathogens. Seeds are still lost mainly to predators when cloud forests are converted to agriculture and then allowed to revert back to cloud forest, but there are important interactions between species and past crop (here banana and sugarcane), and this type of regeneration may be faster than after tree-fall (Myster 2017a). Finally, elevation made more of a difference in recruitment and regeneration in these cloud forests than conversion to agriculture, but the key mechanism may change from predation to pathogens as elevation increases. Species differences also remain important.

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