Vascular plant community structure of regenerated Cloud Forest in the Cordillera de Talamanca, Costa Rica

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Abstract

Tropical Montane Cloud Forest of Costa Rica is a unique and species-rich habitat. After suffering severe deforestation over the 20th century, much of the forest today is secondary and in various stages of succession. This study compared the vascular plant communities of a mature secondary (>50 years recovery) and intermediate-aged secondary (20 years recovery) cloud forest. Two 1250 m² areas of forest at 1850-1950m altitude were sampled using systematic transects, and the data gathered analysed with structural and diversity metrics. It was discovered that the sites did not differ in tree density or basal area, canopy cover, plant habit distribution or height distribution of the herb and shrub layers (<2.5m). The sites did not appear to differ in terms of sample diversity or evenness, although there was insufficient data gathered and high results given for Chao's estimator of unseen species. The most abundant families recorded were *Aracaceae, Araceae, Cyatheaceae* and *Rubiaceae*, of which all were represented by understory plants except the hemi-epiphytic climbers from *Araceae*. The results appear to confirm that the new growth forest has had 20-30 years of cloud forest succession and has reached a stage where the understory is indistinguishable from mature forest. There may still be a difference between the sites at the canopy level. Although the proportion of species identified was low, there was no evidence of *Quercus* dominance and further sampling for diversity analysis of this forest type is recommended. A basic description of the plant functional traits of the most abundant genera reveals that secondary forest may be important for supporting endemic species of animals as well as a high diversity of plants.

Key Words Costa Rica, cloud forest, secondary forest, succession, vascular plant, dominance

Introduction

The tropical montane cloud forests of the Talamanca Cordillera contain huge diversity of flora (Kappelle et al., 1992). On the insulated Pacific coastal slope, a typically oak-dominated arboreal vegetation covers a band between 1000m and 3500m altitude (Bubb et al., 2004), whilst the precise community composition varies substantially (Kappelle et al., 1992). Pressure from human intervention introduces further heterogeneity in the form of both primary and secondary forest (Kappelle et al., 1994), particularly in regions recovering from pervasive deforestation in the 20th century (Sader & Joyce, 1988).

The Costa Rican National Parks authority SINAC states that water provision and the support of wildlife are amongst the essential services provided by Cloud Forests (SINAC, n.d.). The Cloudbridge Nature Reserve was established in 2002 by philanthropists Ian and Genevieve Giddy, who shared the government's goals of protection and regrowth of this unique habitat. The reserve is found on the slope of Cerro Chirripó in the Pérez Zeledón region, bordering the Chirripó National Park. It covers an altitude range of 1600m to 2000m and is host to a patchwork of old growth, naturally regenerating,

and planted forest (see **Figure 1**). The purpose of this study was to assess the success of forest restoration in one of these areas of naturally regenerated woodland.

Due to a lack of explicit records, it is difficult to say if the region of old growth forest in the Southern part of the reserve is truly primary. Secondary forest recovery from human disturbance can be rapid if it occurs in proximity to true old growth forest (Helmer, 2000) and the time taken for these landscapes to approach the same conditions of that of primary forest is not fully known (Renner et al., 2006). Primary forest is expected to have greater biomass, including at the canopy level (Helmer, 2000; Nadkarni et al., 2004), and host a greater diversity of species than secondary forest (Renner et al., 2006), although it is likely that both sites in this study have experienced some human disturbance, even if only in edge effects (López-Barrera et al., 2005) from pastureland on the other side of the Chirripó trail. This study aims to examine the differences between a secondary forest with 20 years of recovery and one with more than 50 years of recovery, referred to here as “new growth” and “old growth”. The aims are to verify the extent of regeneration possible in the shorter time, and to assess the structure of secondary forest in both conditions.

Sites are compared in terms of the density, functional and taxonomic diversity of vascular plant life. Neotropical plant species identification in the field is notoriously difficult, largely due to the high species richness (Condit et al., 2011), but also because the tropics are relatively under-studied for their contribution to global diversity (Utteridge & Bramley, 2016). A combination of structural and taxonomic descriptors creates a more complete picture of plant community composition and reduces reliance on species identification. Garnier et al. advocate for a movement away from traditional, taxonomy-based descriptors towards a more functional approach to studies of plant community structure, including more explanatory parameters such as functional traits (2015). This study attempts to consolidate the new and old standards to assess as comprehensively as is possible the vascular plant community structure in restored montane cloud forest.

Methods

Sampling

Systematic line transects were taken from two 1250 m² sites, both within 1850-1950m altitude and with the same slope aspect (SW-S), on the Cloudbridge Reserve. Site 1 (JILG) was designated “old growth” and Site 2 (MONT) new growth (see **Figure 1**). I measured five 25m transects at 5m intervals at the two sites, noting all plants that had their stem within a 5cm radius of the line (see **Figure 2**).

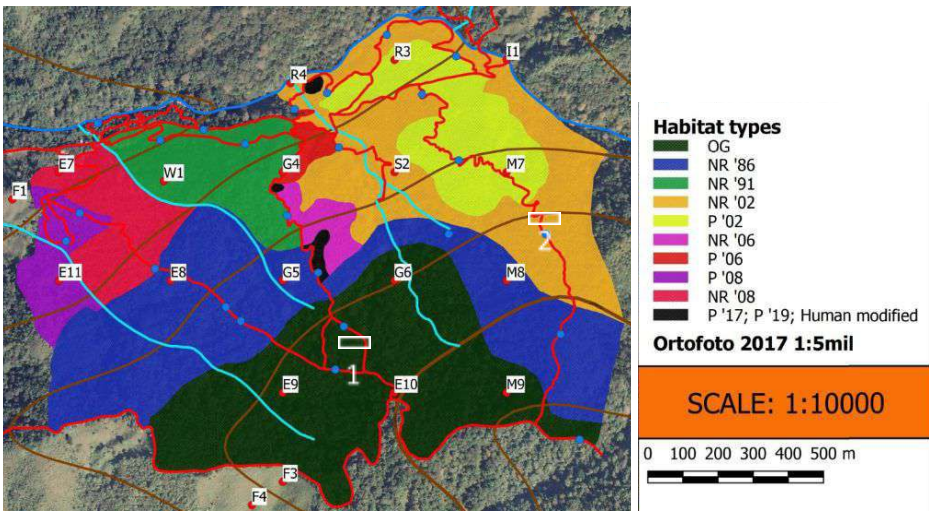


Figure 1 A map of the Southern region of the Cloudbridge Nature Reserve. Boxes show 1250m² regions in which samples were taken. Site 1 is in the 'old growth' forest, at the top of the Jilguero and Gavilan trails. Site 2 is 'new growth' forest on the Montaña trail that has been naturally regenerating since 2002. Both sites are in the range of 1850-1900m altitude.

For every vascular plant in the transect I noted the habit and height, wrote a brief morphological description, and took photos. I measured heights up to a maximum of 2.5m and approximated tree diameters by measuring the circumference and dividing by pi, as well as noting the presence of epiphytes. I used the photos and descriptions for later identification using a variety of reference material, particularly the comprehensive *Woody Plants of Northwest South America* by Alwyn H. Gentry (1996). At 5m intervals along the line (at positions 2.5, 7.5, 12.5, 17.5 and 22.5m) I took a photo of the canopy from 1.3m directly upwards and passed these photos through the application %cover (Public Interest Enterprises, n.d.) to obtain a measure of canopy cover for each 5m section.

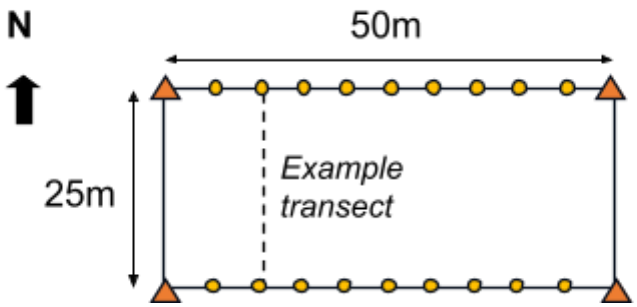


Figure 2 Site schematic. Red marker flags were placed at 5m intervals around the perimeter. Transects were measured from the North to the South side.

I generated a comprehensive catalogue of morpho-species for every apparently distinct plant that I encountered. In addition to reference material, I was assisted in identification by the citizen-science photographic database iNaturalist (*iNaturalist*, n.d.). Over the course of my study, I returned several times to each transect to reassess plant identities. For most plants, species, genus or even family level identification was very difficult from vegetative characteristics alone or for juvenile individuals. Therefore, in my analysis of diversity I have investigated the significance of the presence of certain families that were identifiable, and I have used the morpho species list to approximate overall diversity.

Data Analysis

To compare structures of the two sites, I analysed the stem density and basal area of trees with diameter ≥ 3cm. I also compared the percentage canopy cover, abundance of different plant habits and the height distribution of the herb and shrub layer. Habit distinctions follow Gargiullo and Magnuson (2008), with the exception that herbaceous and woody vines were grouped together under "Vine". "Fern" refers to both Ferns and Fern allies. The few epiphytes recorded (growing below 2.5m) were removed from analysis of habits as they did not represent the true abundance. I analysed the data using RStudio and primarily used Two-way ANOVAs under either a Gaussian or Poisson distribution to test for statistical difference between the sites. For the plant habits I used a pair-wise t-test to compare each habit at each site, and for the Boolean indicator of epiphyte presence/absence I used a Chi-squared test to compare the probability of epiphyte occurrence for any given tree at each site.

To compare diversity at the two sites, I used the VEGAN package in RStudio to calculate several diversity indices, including the Shannon-Weaver and Inverse Simpson's Index. The Shannon index is more sensitive to the presence of rare individuals due to the log transformation, whilst Simpson's index is more sensitive to dominance (Garnier et al., 2015). I also calculated the Pielou evenness (3), which aims to compare the spread of abundances across a community of given species richness (Smith & Wilson, 1996). Finally, I calculated the Sørensen Dissimilarity index (4), a form of beta diversity that assesses the proportion of unique species that occur in each new sample to the overall species richness of the site.

Diversity Equations. In (1), (2) and (3), p_i refers to the probability of randomly selecting and individual of species i, and S to the overall number of species *(Oksanen, 2022)*. In (4) b and c refer to the number of unique species in a pairwise comparison of samples and a refers to the number of species present in both samples *(Baselga, 2012)*.

$$H = -\sum_{i=1}^{S} p_i ln p_i \qquad \text{Shannon-Weaver} \qquad (1)$$

$$D_2 = \frac{1}{\sum_{i=1}^{S} p_i^2} \qquad \text{Inverse Simpson's} \qquad (2)$$

$$J = \frac{H}{ln(S)} \qquad \text{Pielou's Evenness} \qquad (3)$$

$$\beta = \frac{b+c}{2a+b+c} \qquad \text{Sørensen Dissimilarity} \qquad (4)$$

To assess the completeness of my survey, I plotted the species accumulation against sample number for both sites, using Oksanen's methods of randomised permutations for the order of samples (Oksanen, 2022). I used Chao's estimator of unseen species per site, and for the overall species pool. This method utilises the proportion of singleton and doubleton species (species which occur only one or two times over all samples) to suggest how many more could remain in the species pool (Chao, 2006).

Unseen Species Equations. $\hat{f}_0$ refers to the number of unseen species, f_1 is the number of singletons, f_2 the number of doubletons and N the overall population size *(Chao, 2006; Chiu et al., 2014; Oksanen, 2022)*. Note that the true Chao estimator includes observed species, such that $\hat{S}_{Chao1} = S_{obs} + \hat{f}_0$ *(Chao, 2006)*.

$$\hat{f}_0 = \{\frac{f_1^2}{(2f_2)}, \ if\ f_2 > 0 \ \frac{f_1(f_1-1)}{2}, \ \ if\ f_2 = 0$$

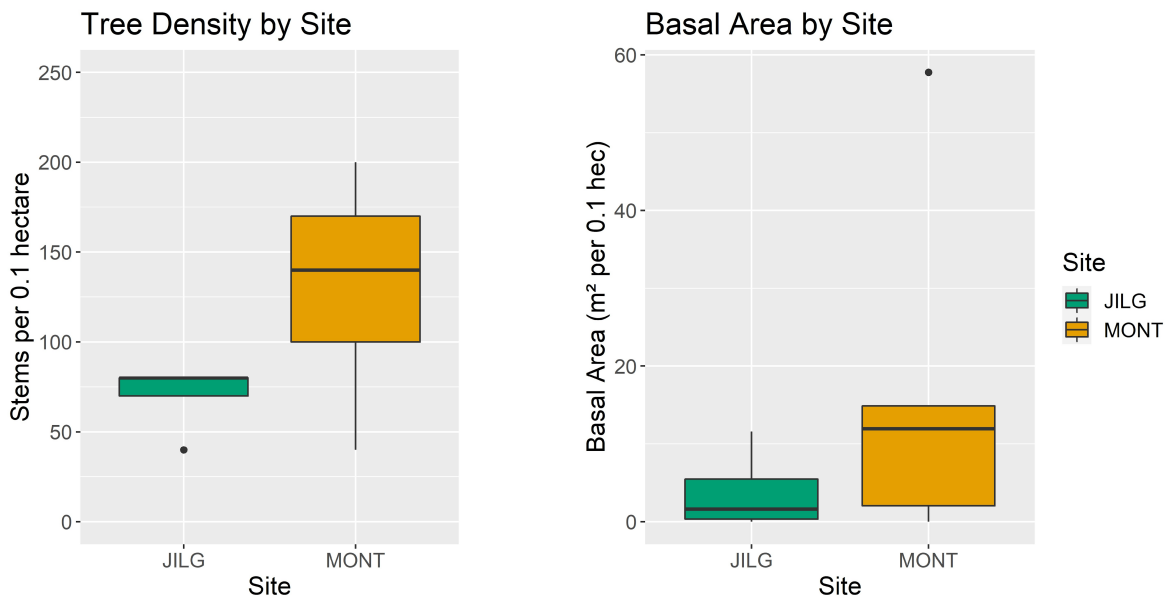
$$var\left(\hat{f}_0\right) = f_1\left(\frac{1}{4}\left(\frac{N-1}{N}\right)^2\left(\frac{f_1}{f_2}\right)^3 + \left(\frac{N-1}{N}\right)^2\left(\frac{f_1}{f_2}\right)^2 + \frac{1}{2}\left(\frac{N-1}{N}\right)\left(\frac{f_1}{f_2}\right)\right)$$

Results

Structural Measures

I found no significant difference between the density of trees with DBH ≥ 3cm (Two-way ANOVA. df = 1, F = 2.8421, p = 0.1428), the stem basal area (F = 1.5924, p = 0.2425) or the canopy cover on the two sites (F = 2.5678. p = 0.1156). Both sites had a canopy cover level designated "dense" by the %cover application standard (Public Interest Enterprises, n.d.). I noted the presence of trees of diameter greater than 50cm on the new growth site (MONT). Similarly, there was no difference found in the likelihood of a tree hosting epiphytes on either site (Chi-squared. X^2 = 0.6928, p = 0.4052).

The overall density of vascular plants on the two sites averaged at 27 per m² on Site 1 (JILG, "old growth") and 22 per m² on Site 2 (MONT, "new growth"), with distribution across plant habits as shown in **Figure 3**. A pair-wise analysis of abundance of different plant habits found no difference between the two sites (Paired t-test. t = 1.6063, df = 29, p-value = 0.1191).



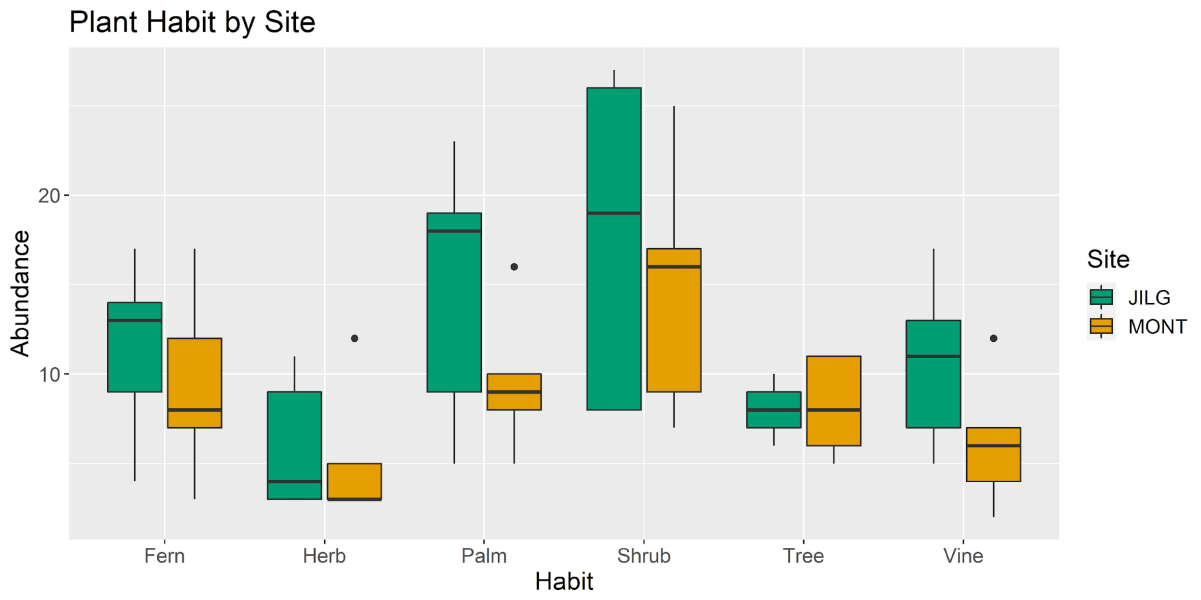


Figure 3 Top Left: Number of trees per hectare with DBH ≥ 3cm per 10m² on the two sites. Top Right: Basal area of trees (DBH ≥ 3cm) per 10m² on the two sites. One outlier on the MONT site contained two very large (DBH > 40cm) trees. Bottom: Plant habit distributions at the two sites. All three graphs take the results of 5 samples at each site. None show significant difference.

It was not possible to directly measure tree height above 2.5m in this study, so I removed canopy trees and assessed the height distribution of the shrub and herb layers. I found no difference in the distributions at the different sites (Two-way ANOVA. df = 1, F = 3.1399, p = 0.0869).

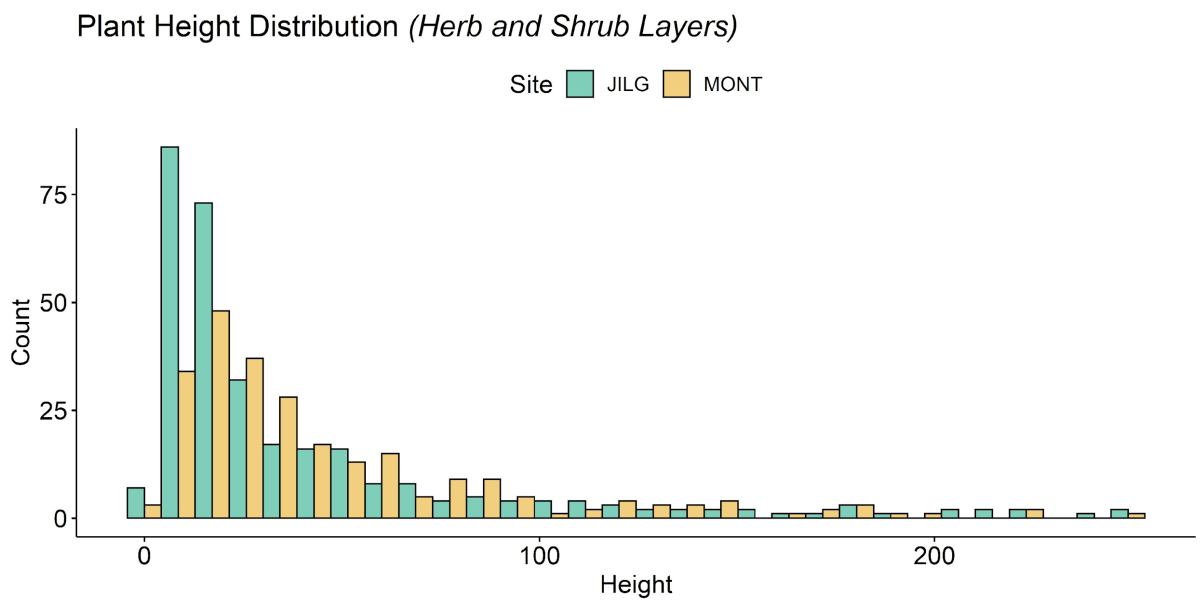


Figure 4 Plant height distribution below 2.5m (hence excluding all sub- and upper canopy trees). No significant difference in height distribution between the two sites.

Floristic Measures

I recorded 141 morpho species over the course of my survey, of which I was able to identify 31.3% to family level and 21.6% to genus level. Species level identification was not possible in the available

time frame. 97 of these morpho species were recorded on the old growth site and 81 on the new growth site.

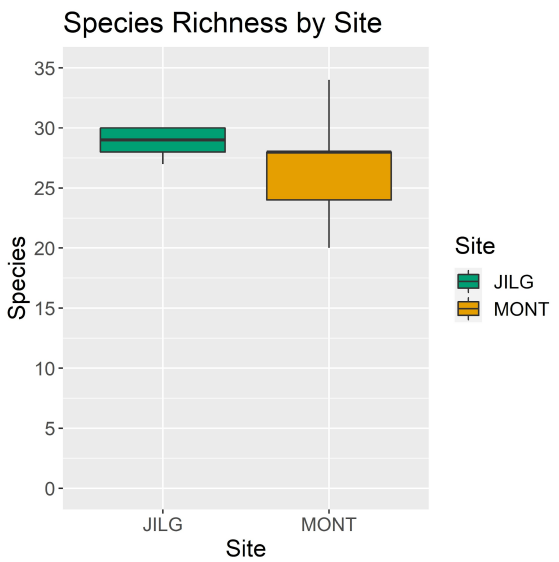


Figure 5 Species Richness averaged over the 5 samples taken from each site. Each morpho-species is approximated as representing a different species.

There was no significant difference between the species richness of the two sites (Kruskal-Wallis Test. Chi-squared = 4, df = 4, p-value = 0.406). I also calculated several diversity metrics shown in **Table 1**, none of which suggested a significant variation in sample diversity (Shannon, Simpson & Fisher), species evenness (Pielou) or between-sample diversity (Sørensen Dissimilarity) on the two sites.

Table 1

Diversity Metrics. Various diversity metrics applied to the morpho species list. Although inappropriate to test diversity metrics for significant difference, it is apparent that on a broad scale the two sites were very similar in terms of broad-scale diversity, evenness, and divergence.

	Old Growth	New Growth
Shannon-Weaver	3.75	3.68
Inverse Simpson's Index	22.08	22.92
Pielou's Evenness	0.83	0.84
Sørensen Dissimilarity	0.68	0.62

I used various metrics to estimate the species pool, primarily the Chao estimator (Chao, 2006) via the VEGAN package (Oksanen, 2022) which suggested that my sampling missed 102 $\pm$ 40 species on the old growth site and 204 $\pm$ 97 species on the new growth site, with a total species pool over both sites of 244 $\pm$ 29.

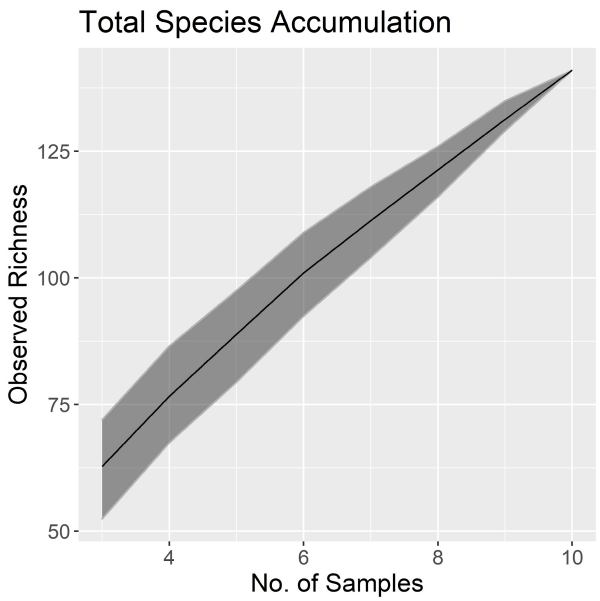


Figure 6 Total species accumulation over samples taken from both sites. Note that for a "complete" survey we would expect a logistic curve, levelling off at the total number of species present. Design credit (Sutton, 2020).

Familial Dominance

As levels of taxonomic identification were low, I analysed the groups observed for population dominance rather than diversity contribution. A summary of abundance by family on both sites is shown in **Figure 7**. Note that while "unidentified" counts for a small proportion of the abundance, it accounts for a relatively larger proportion of the diversity as many of those unidentified were singletons or doubletons.

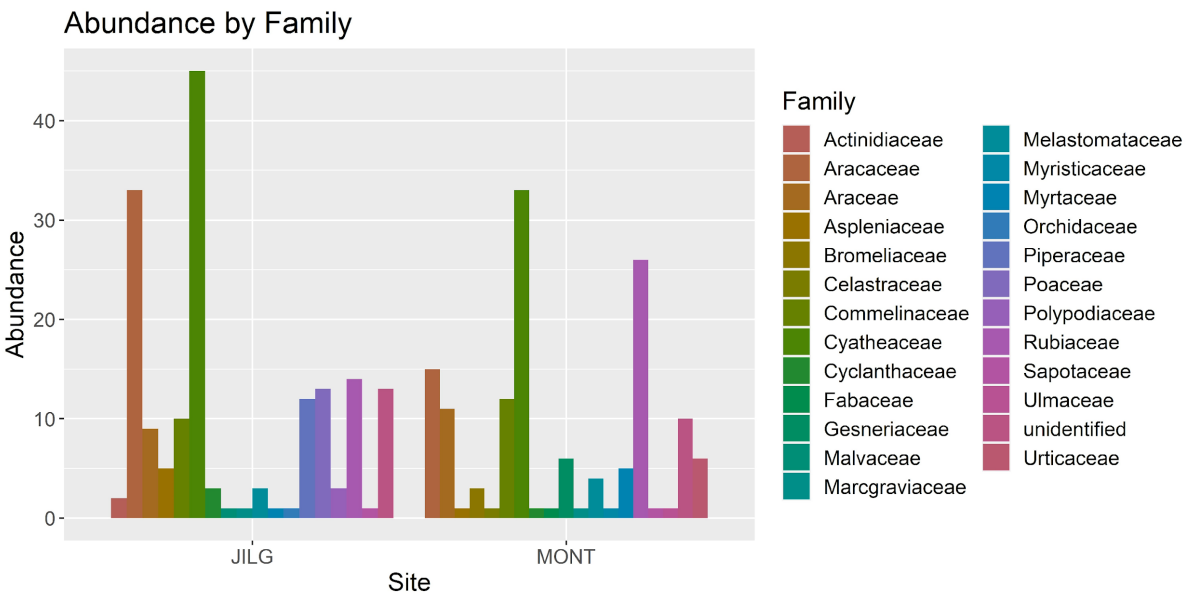


Figure 7 Total abundance of individuals by family on each site, including the 'dustbin group' of unidentified plants. Note that this graph displays number of individuals, not number of morpho-species within each family, hence describing population size rather than diversity.

With singleton and doubleton species excluded, I was able to identify 62.5% of morpho species to a family level. I modelled the difference in the abundance of Aracaceae (Palms), Araceae (Spathe-producing Vines), Cyatheaceae (Ferns) and Rubiaceae (Wild Coffee relatives) which were the four dominant families from both sites. I found no significant difference in the abundance of any of these groups (Two-way ANOVA. Aracaceae: $F = 1.8648$, $p = 0.2092$; Araceae: $F = 0.6164$, $p = 0.4550$; Cyatheaceae: $F = 0.3352$, $p = 0.5786$; Rubiaceae: $F = 0.8251$, $p = 0.3902$).

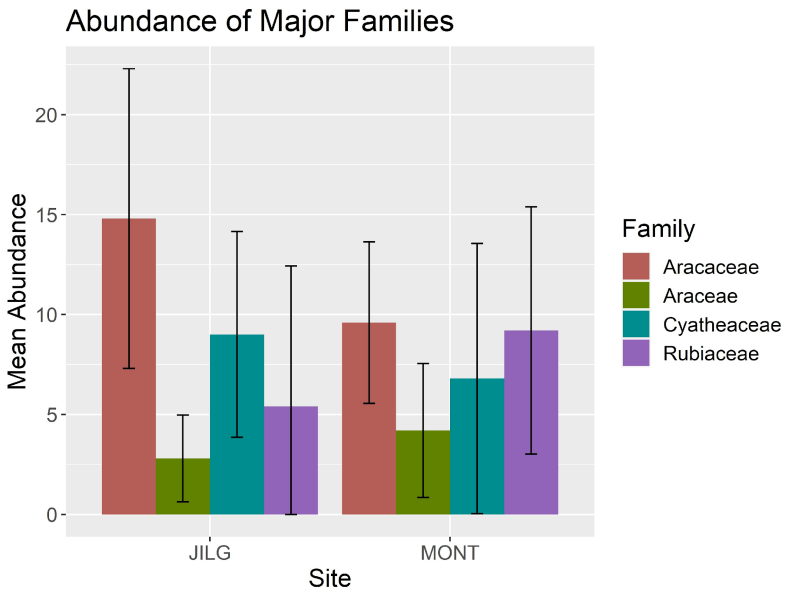


Figure 8 Mean abundance across 5 samples of each family on each site. Note significant overlap between standard deviations for any same-family comparison between the two sites.

Discussion

My results seem to indicate that the two study sites were of the same forest type. The similarity is seen across structural measures including tree density, basal area, canopy cover and herb/shrub layer height distribution. An abundance of Palm and Fern plant habits is typical of a lower montane cloud forest understorey below 2000m, as is a tree density within a range of 600 - 800 stems per hectare (Kappelle & van Uffelen, 2006). The overall density of canopy cover should be partly attributed to low sensitivity in the analysis, and investment in an accredited densiometer is recommended for future studies in this area. However, the 70-80% canopy cover found on both sites does broadly reflect the observed near total shading of forest floor from the combination of upper canopy, sub-canopy and shrub layers.

If there were a difference between sites at the canopy level, this would not have been detected in my investigation. Inability to engage with canopy flora was one of the major limitations of this experiment, as the layering and epiphytic foliage of the canopy are diagnostic features of forest maturity (Holz, 2006; Kappelle, 2006a). According to Kapelle, early-successional secondary forest (10-year recovery period) in this region has an upper canopy of 5 - 14m, late-successional forest (32-years) reaches 11-18m and a mature forest has a distinct 3-20m subcanopy and upper canopy of primarily *Quercus* species reaching 20 – 40m (2006a). I estimate that the upper canopy within the study areas in question did not exceed 20m, but further investigation is required.

Although it is not unknown for tropical studies to utilise morpho-species in diversity estimates (Husson et al., 2018; Lodge & Cantrell, 1995; Pither & Kellman, 2002), low levels of family and genus

identification introduce considerable uncertainty to my calculated metrics of diversity. Like Husson et al., I preferred to aim for a metric as close as possible to true diversity rather than narrowing the scope of the study to only identified groups (2018). The species richness estimates correspond most closely to the upper end of Kappelle's montane forest succession gradient (30-32 years) although Kappelle presents a notably higher Shannon-Weaver and Reciprocal Simpson's diversity (2006a). My results are likely lower because of the incompleteness of my species count, as suggested by the steep species accumulation gradient in **Figure 7** and the suspected high numbers of unseen species.

The mass ratio hypothesis predicts that the most abundant species will have a disproportionate effect on ecosystem functioning (Grime, 1998). Therefore, the broad functional traits of genera represented from these groups could be informative of overall ecosystem functioning. I have noted the abundance of the families *Aracaceae, Araceae, Cyatheaceae* and *Rubiaceae*, within which the genera *Geonoma, Chamaedorea, Monstera, Cyathea (sensu latu.* including *Alsophila), Palicourea* and *Psychotria* were most prominent.

From the *Aracaceae* group, the most abundant genera were the *Geonoma* and *Chamaedorea* palms. *Geonoma* palm species in particular are thought to be understory specialists which occur only in late-secondary or mature forest (Groot et al., 2006; Kappelle et al., 1995). It is perhaps surprising then that they coexisted in abundance with *Cyathea* fern species, which tend to be more abundant and speciose in disturbed habitat (Arens & Baracaldo, 1998). The ferns often take advantage of open canopy, but can persist through stages of secondary forest succession and remain in very reduced in diversity and abundance in mature forest (Arens & Baracaldo, 1998). This suggests that the forest type represented here was in a late secondary stage of succession, where residual species from the initial disturbed stages are still present alongside mature-forest species.

From the Araceae, a group of entire-leaved *Monstera* was best represented, and from the *Rubiaceae* I found an abundance of *Palicourea* and *Psychotria* species. Whilst less diagnostic of forest maturity, the response traits of the *Monstera* may have implications for the hydraulic function of the forest as studies of other *Araceae* indicate that the life stages of the group may be sensitive to drought (Groot et al., 2006). Similarly *Palicourea* and *Psychotria* are not thought to be particularly sensitive to forest maturity but do have many pollinator species (Theim et al., 2014) giving them a functional value in the plant-pollinator ecology of the forest.

Few total vascular plant species counts have been carried out in the neotropics, but they offer an insight into the true diversity of vascular plants that could potentially be hosted there (Linares-Palomino et al., 2009). For example, a total species count by Whitmore in 1985 recorded 233 species in just 100m² of tropical forest (Whitmore et al., 1985). I recommend similar intensive studies be carried out in the Costa Rican Cloud Forest, so that potentially endemic species of the primary and secondary rainforests be recorded, and their protection status assessed. The plant-keys I was able to source for the habitat either displayed only a sub-set of species present, or were collated from nearby regions and better applied lowland forest studies (Condit et al., 2011; Gentry, 1996). Therefore, studies in the region may suffer from lack of accessible information and leading to continued understudying of this globally significant region (Utteridge & Bramley, 2016).

In the wider context of cloud forest regeneration, this study offers some insight into the importance of semi-mature secondary forest. At a structural level, I found the shrub and herb layers of secondary forest to be indistinguishable from older or primary forest after just 20-30 years, although the extent to which primary forest edge effects (Castillo & Ríos, 2008) have contributed to the rate of recovery is not explored. Furthermore, secondary forest at this altitude hosts a greater diversity of tree species than the climax state (Kappelle et al., 1995), including plants that support endemic birds (Powell et

al., 2022). As Costa Rica is a tectonically active country that experiences hurricanes, flash-flooding and wildfires (Quesada-Román & Villalobos-Chacón, 2020; Rozario et al., 2018), disturbance and regeneration are a natural part of the ecosystem and many species are adapted to thrive in a post-disturbed habitat (Lawton & Putz, 1988). However, the oak-dominated cloud forest is a unique and threatened plant community (Kappelle, 2006b), so conservation efforts may be directed towards restoring or protecting the climax forest state. Secondary forest does have the capacity to develop that characteristic upper-canopy oak layer at 2000m altitude, but requires a much longer time scale, in the range of 50 to 80 years of recovery (Kappelle et al., 1995). Whether or not this justifies the protection of secondary forest as a "bank" from which future *Quercus*-forest can develop is a context-dependent decision to be made by land managers and conservationists.

Conclusion

Despite 8 weeks of surveying the vascular plant community of two Cloud Forest sites of different ages on the Cloudbridge Nature Reserve, I was not able to distinguish the age difference (if one exists) between the old and the new growth forest. Structurally, and from the limited data I was able to gather on the diversity and abundance of plant families, the two sites appeared the same. However, several key factors can be drawn from the information gathered:

The new growth forest has had a minimum of 20-25 years recovery from deforestation (as suggested by the Cloudbridge records), but also contains trees older than this period. Therefore, I am confident that the previous phase of deforestation was not total, and the secondary forest that exists there today may be influenced by the presence of older forest patches. These trees are thought to be significant in increasing rates of seedling recruitment and overall rate of succession into mature forest (Castillo & Ríos, 2008; López-Barrera et al., 2005).

Although the proportion of family and genera identified is low, high levels of evenness suggest that both sites are of the lower-montane secondary forest habitat as described by Kappelle (Kappelle, 2006a; Kappelle & van Uffelen, 2006), just below the altitude threshold for oak-dominated forest with bamboo understory. It is important to note the canopy at this level is not yet oak-dominated but rather a great diversity of tree species. Further research is recommended to understand the canopy composition in this forest type, as it may be neglected from studies that focus on upper oak forest (>2000m) or lowland tropical forest (<1000m).

In absence of a more comprehensive species list for the area, a functional analysis of the dominant families reveals that the presence of understory species significantly contributes to the structure and cover of the shrub and herb layers in secondary Cloud Forest. Hemi-epiphytic climbers may impact the hydraulic circulation of the forest (Groot et al., 2006), and abundant shrub-layer plants interact with a host of other species including endemics such as the Northern Emerald Toucanet (observed eating *Geonoma* palm fruits) and the White-throated Mountain Gem hummingbird (observed feeding from *Psychotria* flowers).

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References

Arens, N. C., & Baracaldo, P. S. (1998). Distribution of Tree Ferns (Cyatheaceae) across the Successional Mosaic in an Andean Cloud Forest, Nariño, Colombia. *American Fern Journal*, *88*(2), 60–71. https://doi.org/10.2307/1547225

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*(12), 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Bubb, P., May, I. A., Miles, L., & Sayer, J. (2004). *Cloud forest agenda*.

Castillo, R. F. del, & Ríos, M. A. P. (2008). Changes in seed rain during secondary succession in a tropical montane cloud forest region in Oaxaca, Mexico. *Journal of Tropical Ecology*, *24*(4), 433–444. https://doi.org/10.1017/S0266467408005142

Chao, A. (2006). Species Estimation and Applications. In S. Kotz, C. B. Read, N. Balakrishnan, B. Vidakovic, & N. L. Johnson (Eds.), *Encyclopedia of Statistical Sciences* (p. ess5051). John Wiley & Sons, Inc. https://doi.org/10.1002/0471667196.ess5051

Chiu, C.-H., Wang, Y.-T., Walther, B. A., & Chao, A. (2014). An improved nonparametric lower bound of species richness via a modified good-turing frequency formula: An Improved Nonparametric Lower Bound of Species Richness. *Biometrics*, *70*(3), 671–682. https://doi.org/10.1111/biom.12200

Condit, R., Pérez, R., & Daguerre, N. (2011). *Trees of Panama and Costa Rica*. Princeton University Press. https://press.princeton.edu/books/ebook/9781400836178/trees-of-panama-and-costa-rica

Gargiullo, M., & Magnuson, B. (2008). *A Field Guide to Plants of Costa Rica*. Oxford University Press.

Garnier, E., Navas, M.-L., & Grigulis, K. (2015). 5 A functional approach to plant community structure . In *Plant Functional Diversity: Organism traits, community structure, and ecosystem properties* (pp. 94–118). Oxford University Press.

Gentry, A. H. (1996). *A Field Guide to the Families and Genera of Woody Plants of Northwest South America: With Supplementary Notes on Herbaceous Taxa*. University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/F/bo3683584.html

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*(6), 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Groot, T. V. M., Stift, M., Oostermeijer, J. G. B., Cleef, A. M., & Kappelle, M. (2006). Population Structures of Two Understory Plant Species Along an Altitudinal Gradient in Costa Rican Montane Oak Forests. In M. Kappelle (Ed.), *Ecology and Conservation of Neotropical Montane Oak Forests* (pp. 191–206). Springer. https://doi.org/10.1007/3-540-28909-7_15

Helmer, E. H. (2000). The Landscape Ecology of Tropical Secondary Forest in Montane Costa Rica. *Ecosystems*, *3*(1), 98–114. https://doi.org/10.1007/s100210000013

Holz, I. (2006). Epiphytic Communities of Bryophytes and Macrolichens in a Costa Rican Montane Oak Forest. In M. Kappelle (Ed.), *Ecology and Conservation of Neotropical Montane Oak Forests* (pp. 83–98). Springer. https://doi.org/10.1007/3-540-28909-7_7

Husson, S. J., Limin, S. H., Adul, Boyd, N. S., Brousseau, J. J., Collier, S., Cheyne, S. M., Arcy, L. J. D., Dow, R. A., & Schreven, S. (2018). Biodiversity of the Sebangau tropical peat swamp forest, Indonesian Borneo. *Mires and Peat*, *22*, 1–50. https://doi.org/10.19189/MaP.2018.OMB.352

iNaturalist. (n.d.). iNaturalist. Retrieved 27 August 2023, from https://www.inaturalist.org/

Kappelle, M. (2006a). Changes in Diversity and Structure Along a Successional Gradient in a Costa Rican Montane Oak Forest. In M. Kappelle (Ed.), *Ecology and Conservation of Neotropical Montane Oak Forests* (pp. 223–233). Springer. https://doi.org/10.1007/3-540-28909-7_17

Kappelle, M. (2006b). *Ecology and Conservation of Neotropical Montane Oak Forests* (M. M. Caldwell, G. Heldmaier, R. B. Jackson, O. L. Lange, H. A. Mooney, E.-D. Schulze, & U. Sommer, Eds.; Vol. 185). Springer Science & Business Media.

Kappelle, M., Cleef, A. M., & Chaverri, A. (1992). Phytogeography of Talamanca Montane Quercus Forests, Costa Rica. *Journal of Biogeography*, *19*(3), 299. https://doi.org/10.2307/2845453

Kappelle, M., Kennis, P. A. F., & de Vries, R. A. J. (1995). Changes in diversity along a successional gradient in a Costa Rican upper montane Quercus forest. *Biodiversity & Conservation*, *4*(1), 10–34. https://doi.org/10.1007/BF00115312

Kappelle, M., & van Uffelen, J.-G. (2006). Altitudinal Zonation of Montane Oak Forests Along Climate and Soil Gradients in Costa Rica. In M. Kappelle (Ed.), *Ecology and Conservation of Neotropical Montane Oak Forests* (pp. 39–54). Springer. https://doi.org/10.1007/3-540-28909-7_4

Kappelle, M., van Velzen, H. P., & Wijtzes, W. H. (1994). Plant communities of montane secondary vegetation in the Cordillera de Talamanca, Costa Rica. *Phytocoenologia*, 449–484. https://doi.org/10.1127/phyto/22/1994/449

Lawton, R. O., & Putz, F. E. (1988). Natural Disturbance and Gap-Phase Regeneration in a Wind-Exposed Tropical Cloud Forest. *Ecology*, *69*(3), 764–777. https://doi.org/10.2307/1941025

Linares-Palomino, R., Cardona, V., Hennig, E. I., Hensen, I., Hoffmann, D., Lendzion, J., Soto, D., Herzog, S. K., & Kessler, M. (2009). Non-woody life-form contribution to vascular plant species richness in a tropical American forest. In A. G. Van der Valk (Ed.), *Forest Ecology: Recent Advances in Plant Ecology* (pp. 87–99). Springer Netherlands. https://doi.org/10.1007/978-90-481-2795-5_8

Lodge, D. J., & Cantrell, S. (1995). Diversity of litter agarics at cuyabeno, ecuador: Calibrating sampling efforts in tropical rainforest. *Mycologist*, *9*(4), 149–151. https://doi.org/10.1016/S0269-915X(09)80003-7

López-Barrera, F., Newton, A., & Manson, R. (2005). Edge effects in a tropical montane forest mosaic: Experimental tests of post-dispersal acorn removal. *Ecological Research*, *20*(1), 31–40. https://doi.org/10.1007/s11284-004-0016-7

Nadkarni, N. M., Schaefer, D., Matelson, T. J., & Solano, R. (2004). Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecology and Management*, *198*(1–3), 223–236. https://doi.org/10.1016/j.foreco.2004.04.011

Oksanen, J. (2022). *Vegan: Ecological diversity*.

Pither, R., & Kellman, M. (2002). Tree species diversity in small, tropical riparian forest fragments in Belize, Central America. *Biodiversity & Conservation*, *11*(9), 1623–1636. https://doi.org/10.1023/A:1016831916994

Powell, J. R., Slifkin, J. P., Spooner, F. T., Roth, J., Allnatt, L., Andrews, R., & Smokoska, M. (2022). Bird species inventory in secondary tropical montane cloud forest at Cloudbridge Nature Reserve, Talamanca Mountains, Costa Rica. *Check List*, *18*(1), 17–65. https://doi.org/10.15560/18.1.17

Public Interest Enterprises. (n.d.). *Percentage Cover – Ecological Survey App*. Retrieved 27 August 2023, from https://percentagecover.com/

Quesada-Román, A., & Villalobos-Chacón, A. (2020). Flash flood impacts of Hurricane Otto and hydrometeorological risk mapping in Costa Rica. *Geografisk Tidsskrift-Danish Journal of Geography*, *120*(2), 142–155. https://doi.org/10.1080/00167223.2020.1822195

Renner, S. C., Waltert, M., & Mühlenberg, M. (2006). Comparison of Bird Communities in Primary vs. Young Secondary Tropical Montane Cloud Forest in Guatemala. *Biodiversity and Conservation*, *15*(4), 1545–1575. https://doi.org/10.1007/s10531-005-2930-6

Rozario, P. F., Madurapperuma, B. D., & Wang, Y. (2018). Remote Sensing Approach to Detect Burn Severity Risk Zones in Palo Verde National Park, Costa Rica. *Remote Sensing*, *10*(9), Article 9. https://doi.org/10.3390/rs10091427

Sader, S. A., & Joyce, A. T. (1988). Deforestation Rates and Trends in Costa Rica, 1940 to 1983. *Biotropica*, *20*(1), 11–19. https://doi.org/10.2307/2388421

SINAC. (n.d.). *Mission and Vision*. Sistema Nacional de Areas de Conservacion Costa Rica. Retrieved 29 August 2023, from https://www.sinac.go.cr/EN-US/conozca/Pages/misvis.aspx

Smith, B., & Wilson, J. B. (1996). A Consumer's Guide to Evenness Indices. *Oikos*, *76*(1), 70. https://doi.org/10.2307/3545749

Theim, T. J., Shirk, R. Y., & Givnish, T. J. (2014). Spatial genetic structure in four understory Psychotria species (Rubiaceae) and implications for tropical forest diversity. *American Journal of Botany*, *101*(7), 1189–1199. https://doi.org/10.3732/ajb.1300460

Utteridge, T., & Bramley, G. (Eds.). (2016). *The Kew Tropical Plant Families Identification Handbook: Second Edition*. Royal Botanic Gardens, Kew. https://press.uchicago.edu/ucp/books/book/distributed/K/bo23404167.html

Whitmore, T. C., Peralta, R., & Brown, K. (1985). Total species count in a Costa Rican tropical rain forest. *Journal of Tropical Ecology*, *1*(4), 375–378. https://doi.org/10.1017/S0266467400000481