Biodiversity of Juvenile Nitrogen Fixing *Inga Spp.* in Terra Firme Forests in Relation to Land Use at Finca Las Piedra, Madre De Dios, Peru

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Abstract

Tropical forest soils are unexpectedly nutrient poor, lacking nitrogen-based nutrients such as ammonia which are commonly limiting growth factors for plants growth. Biological nitrogen fixation (BNF) through legume-rhizobia symbiosis is amongst the most important and most efficient routes of soil nitrogen incorporation. Flora capable of BNF therefore could have added advantages in biomass buildup in nutrient poor soils. However, little is known regarding the influence of soil-nitrogen levels on the biodiversity of nitrogen fixers across mature and regenerating terra firme forests. Here, using *Inga spp*. as indicators of nitrogen fixing plants, we show that nitrogen fixer biodiversity is generally greater in mature forest than regenerating forests. We found that measures of simple species richness, relative abundance per species, and relative abundance per 100 m^2 pointed towards higher biodiversity in mature forests. Indices of the species richness, however, reveled a lack of differentiation of species richness between mature and regenerating forests. Growth variables (diameter and height) also did not point to significant differences between mature and regenerating forests.

Introduction

Although tropical forests are amongst the most diverse ecosystems on earth (Gibson et al., 2011), they have unexpectedly nutrient poor soils (Forsyth & Miyata, 1984). Plant systems constantly fight for vital nutrients such as nitrogen and phosphorus, and therefore such nutrients are not retained in rainforest soils for prolonged periods of time. Nitrogen based nutrients, such as ammonia (NH_3), are one of the most prominent nutrients that are commonly limiting growth factors for plants (LeBauer & Treseder, 2008; Elser et al. 2007). In secondary forests, where deforestation and leaching lead to rapid nutrient loss (Forsyth & Miyata, 1984), biological nitrogen fixation (BNF) through legume-rhizobia symbiosis is amongst the most efficient routes of soil nitrogen (N_2) incorporation (Gehring et al., 2005; Chapin et al., 2012). Studies on the benefits of N_2-fixation from BNF on forest regeneration have been widely debated. Some studies state that N_2-fixers help in soil nutrient replenishment (Menge & Chazdon, 2015; Gehring et al., 2005; Taylor et al., 2019), others state that N_2-fixation plays no recognizable role in regeneration (Taylor et al., 2017; Lai et al., 2018), while others state that N_2-fixers in fact inhibit forest regeneration (Taylor et al., 2017).

Table 1. *Inga* morphospecies labeled for this study, with descriptions and reference photos of both leaf top and undersides.

Morphospecies	Description	Reference Images
1	Leaf surfaces are glabrous. Leaflets are relatively long and have acuminated tips. Winged rachises are well defined and are comparatively wide. Extra floral nectaries are well defined.	
2	Leaf surfaces are coriaceous. Leaflets are elongated. Winged rachises are very thin and are widest at the middle. Extrafloral nectaries are well defined at each leaflet intersection.	
3	Leaves are pale-light green. Leaflets have acuminated tips. Winged rachises are well defined and broad. Extrafloral nectaries are surrounded by pubescence. Rachises and veins are red/brown and pubescent.	
4	Leaves are dark green and glabrous. Leaflets are short and wide with acuminated tips. Winged rachises are very thin and are widest towards the top. Extrafloral nectaries are well defined. New leaves are a much lighter green but share the same structure as mature leaves.	

5	Leaf surfaces are coriaceous. Leaflets are relatively long and acuminated. Winged rachises are very thin and are widest towards the top. Extrafloral nectaries are well defined.	
6	Leaves are dark green and glabrous. Leaflets are small, wide, and acuminated. Winged rachises are thin and are widest towards the top. Extra floral nectaries are small and well defined.	
7	Leaves are glabrous and pubescent. Leaflets are very broad and ovate and have acute tips. Winged rachises are well defined. Extrafloral nectaries are surrounded by hairs. Rachises are also pubescent.	

These contrasting results on the role of BNF make it difficult to estimate the influence of soil nitrogen levels on N_2-fixation in either mature or regenerating Terra Firme forests.

The area of study, Finca Las Piedras (FLP) in South-Eastern Peru, contains such terra firme forest. The history of human activity at FLP, such as deforestation and agriculture, has led to the formation of both disturbed mature and regenerating second growth forests (five years of regeneration). To study the potential effects of soil-nitrogen levels on the growth of N_2-fixers between these habitats, juvenile plants of the *Inga* genus were sampled as indicators. With the depletion of nutrients in second growth forests from past human activities (Forsyth & Miyata, 1984), N_2-fixing plants such as *Inga spp.* may have an advantage in soils low in nutrients, and therefore could be found in larger richness and abundance in regenerating forests compared to mature ones. This leads to the primary hypothesis, suggesting that there will be higher *Inga spp.* biodiversity in regenerating forests compared mature ones. This study will compare the species richness and relative abundance of *Inga spp.* between intact versus regenerating secondary forests at FLP to determine how soil nitrogen availability influences the biodiversity of N_2-fixing plants.

Methods

Study group

Members of the *Inga* genus were surveyed as a representative of all N_2-fixing at FLP due to their dynamic and cosmopolitan distribution (Watson & Dallwitz, 1992 onwards), and were assigned morphospecies (Table 1) for this study. *Inga* are found within the Fabaceae family where individuals are commonly found in symbiotic relationships with rhizobia. Gehring et al.'s study (2005) surveyed 35 *Inga* species, all but one of which were listed as either proven or likely to nodulate and undergo BNF. These ideas serve as the basis of this study; we assume that all sampled species of this study are capable of N_2-fixation. This ability results in the local production of nitrogen-based nutrients that have been shown to help in biomass buildup (Gehring et al., 2005). Additionally, only juvenile *Inga*s ranging from 10 to 1000 cm were surveyed as indicators of all nitrogen fixing organisms.

Study site

Ingas were sampled from FLP, Madre de Dios, Peru from both disturbed mature (DM) and regenerating secondary growth (SG) terra firme forests. The mature forest features relatively untouched local flora and fauna, although selective logging for mahogany, cedar, and most recently *shihuahuaco* has occurred. The DM terra firme habitat borders aguajal swamps as well as cleared land. The secondary forest is found in patches, fractured by either a dirt road or more cleared land. Each SG Forest patch is surrounded mainly by invasive brachiaria (*Brachiaria spp.*) grass and kudzu (*Pueraria montana*) vine. Certain patches of secondary forest also neighbour mature aguajal or terra firme forests. The SG forests themselves have been regenerating since pasture abandonment and a fire in 2016, meaning they have been continuously regenerating for five years prior to his study.

Transects

In each site, transects were positioned systematically with each initial transect being over 200 m from the habitat edge for mature forests and 10 m away for secondary growth forests as to avoid edge effects and to account for available sampling area. In the mature forest plot, successive transects were placed in alternating directions 50 m apart. In

Figure 1. Property of Finca Las Piedras, Madre de Dios, Peru, and the distribution of second growth (red) and disturbed mature (yellow) transects.

regenerating forest plots, each transect was manually positioned in accordance with aerial photographs. All transects covered a length of 25 m and spanned 2 m on each side, resulting in each transect covering 100 m^2 and each plot covering 1000 m^2. Figure 1 showcases the distribution of the transects throughout FLP.

Per transect, data on total *Inga* number, morphospecies, diameter (7 cm above the ground), height, location (0.5 m increments), and clustering observations were collected. Diameter and height variables were used as a measure of plant growth. Diameter at 7 cm above ground level was chosen over DBH because any juvenile *Inga* between 10 and 1000 cm tall was sampled, and a large majority of sampled plants were found below standard DBH. Locations of each sampled plant within a transect were rounded to half meter increments to be used only as estimations of distribution. Clustering data was also determined while sampling. Individuals are clustered when distributed ≤1 m from another individual of the same species (Appendix 1).

Data analysis

To study the differences in *Inga* biodiversity between mature and regenerating forests, species richness and relative abundance of the two forest types were measured. Species richness was measured first by a simple count of species per habitat. These values were then tested against expected distribution using a chi-squared statistic test (χ^2_{crit} = 3.84). A second measure was conducted of species richness through the species richness index (Jayaraman, 1999), the formula for which is:

$$\text{Species Richness Index} = \frac{S}{\sqrt{N}} \qquad (1)$$

where S is the number of morphospecies found per forest plot, and N is the number of individuals collected.

Relative abundance was further measured using the Shannon-Wiener index (*H*), for which the main calculating formula is:

$$\text{Shannon-Wiener Index (H)} = -\sum_{i=1}^{n} p_i \ln p_i \qquad (2)$$

where p_i is the proportion of individuals found in the *i*th morphospecies.

Relative abundance of all *Inga spp.* was also measured by utilizing the simple mean number of individuals per transect per forest type. Both measures of relative abundance were tested using a Student's t-test (t_{exp} = 2.12, df = 16; t_{exp} = 2.20, df = 11). Data regarding clustering were used at face-value to pinpoint apparent trends. Diameter and height averages per forest type were also statistically analysed using two-sample t-tests, assuming unequal variance (t_{exp} = 2.23, df = 10; t_{exp} = 2.26, df = 9).

Results

The maximum number of species found per transect (per 100 m^2) was 6 in mature forests, and the minimum number of species was two. In second growth forests, the maximum and minimum number of species found per transect was one. The average species count per transect was four in the mature forest, while in regenerating forests it was 0.2 (Fig. 2). The mature forest was found with seven species, while the regenerating forest was found with two (morphospecies *1* and *2*) (Table 2). A chi-squared test comparing species richness between the two forests was

performed; there was a significant difference between the two (df = 1, χ^2 = 4.14, 0.025 < p < 0.05).

Figure 2. Mean species richness per 100 m^2 across the disturbed mature forest and secondary growth forest (R Core Team, 2021).

In mature forests, the largest number of individuals per transect was 26, and the lowest was six. In regenerating forests, the largest number of individuals per transect was five, and the lowest was four. Relative abundance within each transects (Fig. 3) averaged 16.1 individuals for mature forests and 0.9 for regenerating forests. Utilizing a two-sample t-test assuming unequal variance, we found a significant difference between the two forest habitats (p = 1.06E^{-5}, t_{exp} = 2.20, t = 7.60, df = 11).

Values for the species richness index were 0.55 in mature forests and 0.67 in regenerating forests (Table 2). It is important to take note that the species richness function (1) considers sample size.

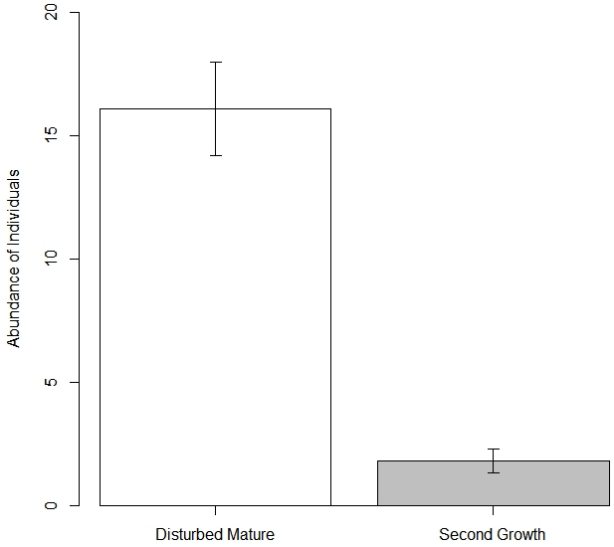

Figure 3. Mean number of individuals per transect per forest type (R Core Team, 2021).

As a measure of relative abundance, the Shannon-Wiener index (*H*) (Table 3) resulted in 1.59 for mature forests, and 0.69 in regenerating forests. Student's t-test was applied with 16 degrees of freedom, resulting in significant differences in *H* between mature and regenerating forests (p < 0.05, t_{exp} = 2.12, t = 8.98). Mature forest samples resulted in a variance of 0.0026, while regenerating forests gave 0.0075.

Morphospecies *1* was the most abundant both collectively and per habitat. Within the DM habitat, it represented 34.2% of all morphospecies, while within the SG habitat it represented 55.6%. The least abundant morphospecies was *4*, with only one sample collected from the mature forest, while morphospecies *3* through *7* were absent in the

Table 2. Simple species richness per forest type, and the applied chi-squared test for those values where df = 1, and χ2 = 4.14. The calculated species richness index per forest type was also calculated, which accounts for sample size.

Forest Type	Morphospecies							No. of species	Species Richness Index
	1	2	3	4	5	6	7		
DM	55	27	37	1	7	29	5	7	0.5517
SG	5	4						2	0.6667

Table 3. Relative abundance per forest type, as showcased though the Shannon-Wiener index (H). Student's t-test was applied to evaluate significance of H, where df = 7, and texp = 2.12. Variance per forest type was also calculated.

	Shannon-Wiener Index (*H*)	p-value	Variance
DM	1.588764	< 0.05	0.002556
SG	0.686962		0.007539

regenerating forest transects. Outliers were identified for morphospecies *3* and *6* in mature forests – one transect sampled an above average number of eight individuals in morphospecies *3*, and another transect sampled an above average of 11 individuals in morphospecies *6*. Figure 4 illustrates the simple abundance per morphospecies between the two forest types.

Data on clustering, diameter, and height were also measured. Clustering was observed for 60% of all sampled individuals. In the regenerating forest, all samples were clustered. Appendix 2 gives a visualization of the physical distribution of sampled individuals, where location information was collected in half meter increments.

Diameter (at height of 7 cm) and height (Appendix 3) were also compared per morphospecies (Fig. 5). From the regenerating forest plots, morphospecies *1* had the largest mean diameter of 2.93 cm. The same species sampled from mature forests averaged to 0.61 cm. In the mature forest, the morphospecies *4* averaged the greatest diameter of 1.27 cm. For height data, morphospecies *1* sampled the tallest of 438.6 cm in the regenerating forest. In mature forests, the same species averaged 32.63 cm. The tallest of the mature forest was morphospecies *4*, averaging 121 cm.

Collectively, average diameter was lower in second growth forests, while height was lower in the mature forest (Fig. 6). The mean diameter and height at DM were 0.64 cm and 37.22 cm. At SG, mean diameter and height were 1.86 cm and 265.18 cm, respectfully. Welch two-sample, one tailed t-tests were conducted, with insignificant results for both diameter (t-test = 1.3, n = 12, p = 0.46) and height (t-test = 1.74, n = 12, p = 0.41).

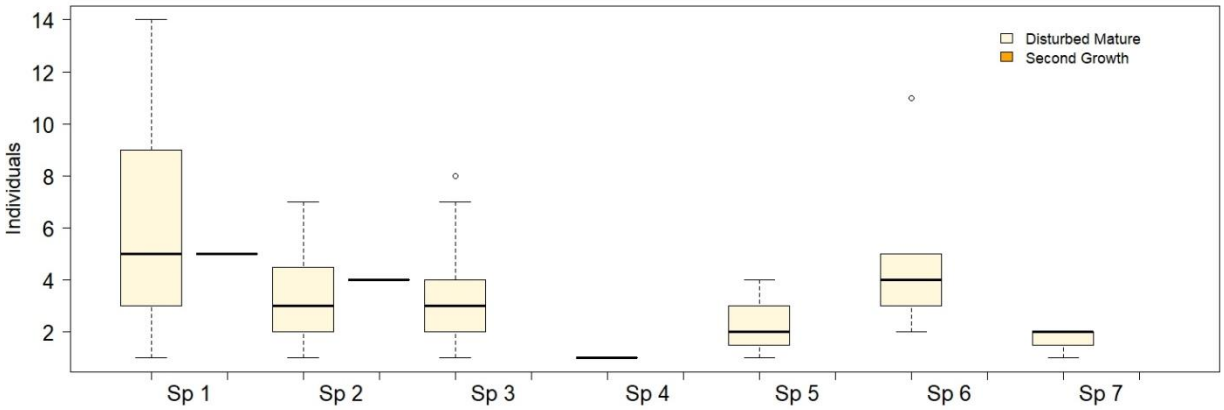

Figure 4. Box plot of the relative abundance per morphospecies across both disturbed mature and regenerating second growth habitats (R Core Team, 2021). See Table 1 for morphospecies descriptions.

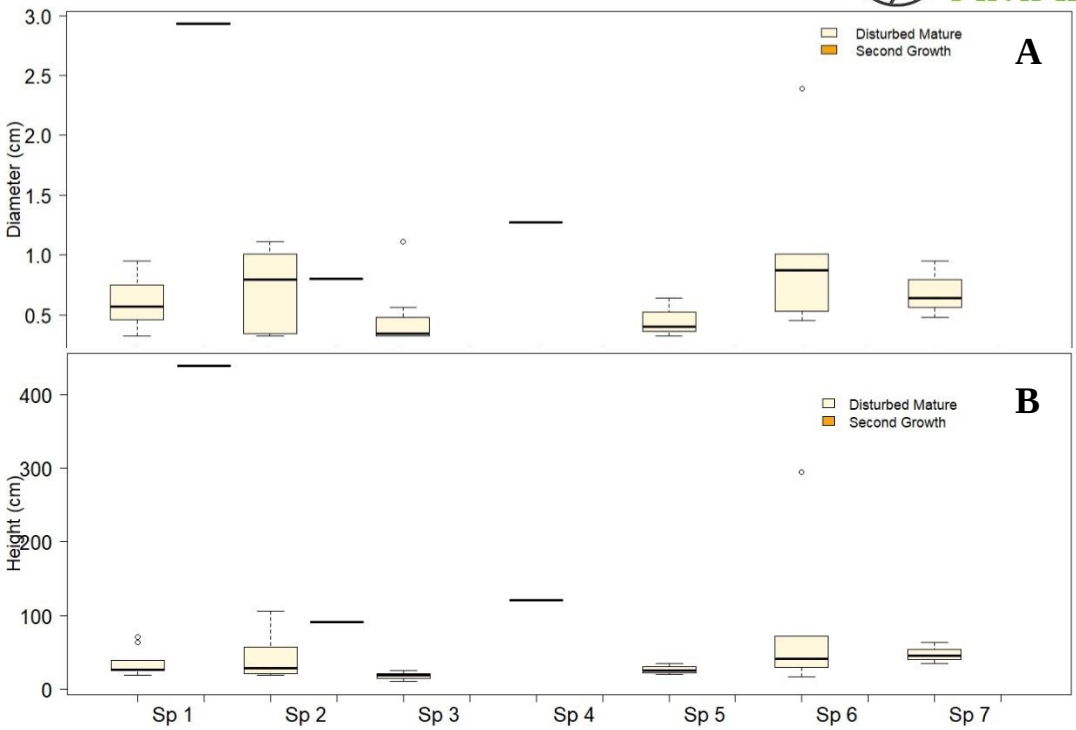

Figure 5. Box plot distributions of (A) diameter at 7 cm and (B) height per morphospecies (R Core Team, 2021). See Table 1 for morphospecies descriptions.

Discussion

Based solely on the number of morphospecies found between mature and second growth forests (seven and two), the mature forest contains a much richer array of *Inga* species per 1000 m^2, and therefore has higher biodiversity. Results from the chi-squared test ($df = 1$, $\chi^2 = 4.14$, $0.025 < p < 0.05$) also confirms this as the occurrence of the number of *Inga* morphospecies in the different forest types differs significantly. This is further supported by the significantly larger average species richness values (Fig. 2) between DM (4) and SG (0.2) forests. Under this calculation, it can be assumed that the mature forest also contains a higher richness of other N_2-fixing species per a given area of land. This also could have the potential implication that a low soil-nitrogen level does not serve as a favourable characteristic for the growth of many N_2-fixing organisms despite their ability to undergo BNF.

Similarly, the measure of relative abundance of individuals were higher at mature forests than regenerating ones (16.1 at DM compared to 0.9 at SG). Their calculated p-value ($1.06E^{-5}$) indicates a significant difference between the two forest habitats. An important distinction between these values of the abundance of individuals and those of the Shannon-Wiener indices is that these base abundance on 100 m^2 plots – per transect – instead of per species. Given this, it can be concluded that the number of individuals, regardless of species, in each area are analytically higher at mature forests.

Calculations of the species richness index suggest opposite conclusions on *Inga*

biodiversity across mature and regenerating forests. Higher values of the index indicate larger richness. Therefore, based on the calculated results, SG forests are richer in *Inga* species (0.67 at SG compared to 0.55 at DM). An important difference between these index values and the simple richness counts is that the species richness index takes into consideration sample size. Only nine samples were collected in SG forests, while there were 161 *Inga* from the DM forest, resulting in a larger species count to sample size ratio in the regenerating forest. Using these indices, biodiversity at the regenerating forest would instead be greater than that of mature ones, and therefore it would also suggest the favourability of N_2-fixer growth in nutrient depleted soils.

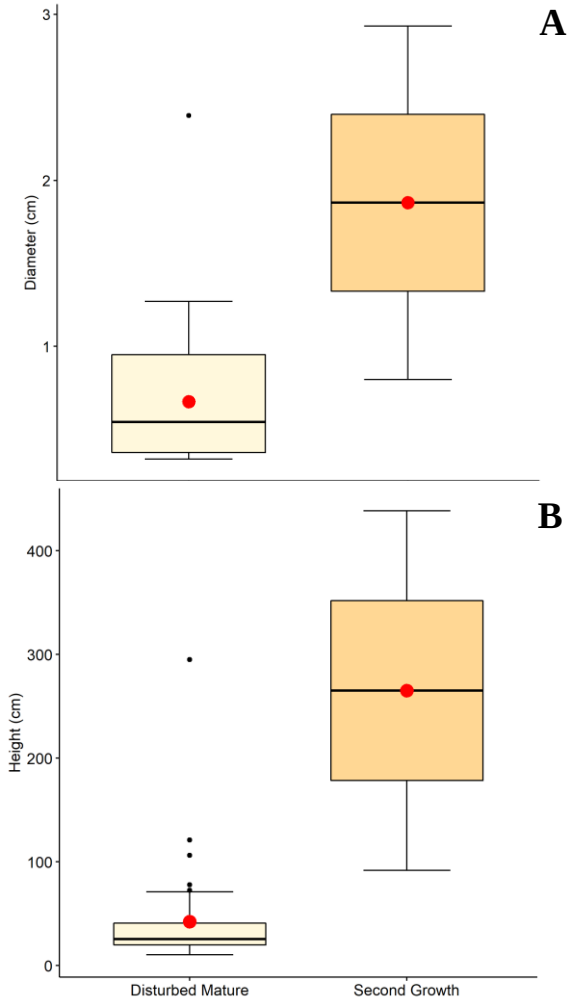

Figure 6. Comparison of all *Inga* from mature and second growth forests in terms of their measured (A) average diameter at 7 cm and (B) height (R Core Team, 2021).

When considering relative abundance as a measure of biodiversity, the results of the Shannon-Wiener index were tested to be significant (t_{exp} = 2.12, t = 8.98, df = 16). This is indicative of an observable difference between the number of individuals per species between the two habitats. Furthermore, it implies that mature forests have comparatively higher relative abundance than regenerating forests, where a given *Inga* species would have on average more individuals in mature forests than regenerating ones. Applying the same concept to all N_2-fixing organisms would imply that mature forests contain higher counts of individuals per species than in second growth forests.

Morphospecies *1* and *4* are the highest and lowest in abundance, respectfully, across both sampled plots. The lack of differences in relative abundance of these morphospecies between the two habitats could potentially be an indicator of more species-specific characteristics, such as that morphospecies *1* is more suited for terra firme environments than morphospecies *4*, rather than it being a response to soil nitrogen levels. Alternatively, this trend could be potentially explained by the patterns of *Inga* seed dispersal and the distribution of the sampled secondary forests in relation to mature ones. The secondary forests were observed to grow in arguably near proximity to mature forests, providing reasonable distance for *Inga* seed dispersing animals like parrots, tamarins, and rodents (Galetti, 1993; Knogge & Heymann, 2003;

Gorchov, 2004) to cross and deposit their seed-filled droppings into the regenerating forest. The high abundance of morphospecies *1* in the mature forest could therefore translate into higher abundances of the same morphospecies in regenerating forests due to an increased probability of animal visitation for that morphospecies. To confirm this, however, further studies would be needed.

The locations of individual *Inga* samples were recorded, and presumably they showed evidence of clustering. This could possibly be a marker for local above-average vegetation biomass (Gehring et al., 2005). However, because only observational data was recorded regarding physical distribution, and because distribution was measured in arguably large increments (50 cm), the significance of such data and would need to be looked at in more detail in future research endeavours.

Morphospecies *1* sampled to both have the largest average diameter and height in secondary forests, while in mature forests, the largest of both variables was morphospecies *4*. Because two separate species ranged highest for both diameter and height for each separate forest plot, potential species-specific characteristics could be implied to assist in growth within either secondary or mature forests. Under the assumption that mature forest soils have greater nutrient input and that second growth forests are nutrient depleted, morphospecies *4* could therefore be implied to grow most effectively in nutrient richer soils – which may possibly explain their absence in second growth forests – and morphospecies *1* more suited for soils leached of nutrients. Confirmation of this would require additional research diving into correlations between long term growth and soil quality.

However, focusing on these variables of diameter and height as a collective of each habitat yields to no significant statistical differences (diameter $p = 0.46$, height $p = 0.41$). This may suggest that the biomass buildup of certain *Inga spp.* is not correlated with forest habitat types, therefore nor is it correlated with differing soil nutrient levels. Other variables such as light availability or clustering could also influence the growth of nitrogen fixing flora, and their correlations with *Inga* diameter and height would need to be studied in more depth in future studies.

Conclusion

Analyses on different measures of biodiversity have led to varied conclusions regarding the richness and relative abundance of nitrogen fixing *Inga spp.* across disturbed mature and regenerating secondary forests. Simple measures of species richness along with relative abundance opposed the hypothesis of a higher *Inga* biodiversity within regenerating forests. Results from these studies instead were in support of increased *Inga* biodiversity in mature forests. Nonetheless, measures of species richness through the species richness index (Jayaraman, 1999) suggest a lack of differentiation of *Inga* biodiversity between the two forest types.

At face-value, *Inga spp.* presumably showed evidence of clustering across both mature and regenerating forests, implying locally increased vegetation biomass. Furthermore, larger diameter and height averages of morphospecies *1* in secondary forests are associated with potential species-

specific characteristics suited for nutrient depleted soils. Morphospecies *4*, due to its larger diameter and height averages in mature forests, is likely to grow most effectively in nutrient rich soils. However, considering all morphospecies, diameter and height averages did not yield significant differences between mature and regenerating forests. This indicates that N_2-fixer growth does not change with forest habitat or soil nutrient levels.

Acknowledgments

I would like to thank Alliance for a Sustainable Amazon's academic programs coordinator, Consuelo Alarcón for her assistance in data analysis and mentorship throughout this research project. I would also like to thank PhD student Riley Fortier for his help in plant identification, as well as Johana Reyes and Geoff Gallice for allowing this research opportunity at Alliance for a Sustainable Amazon.

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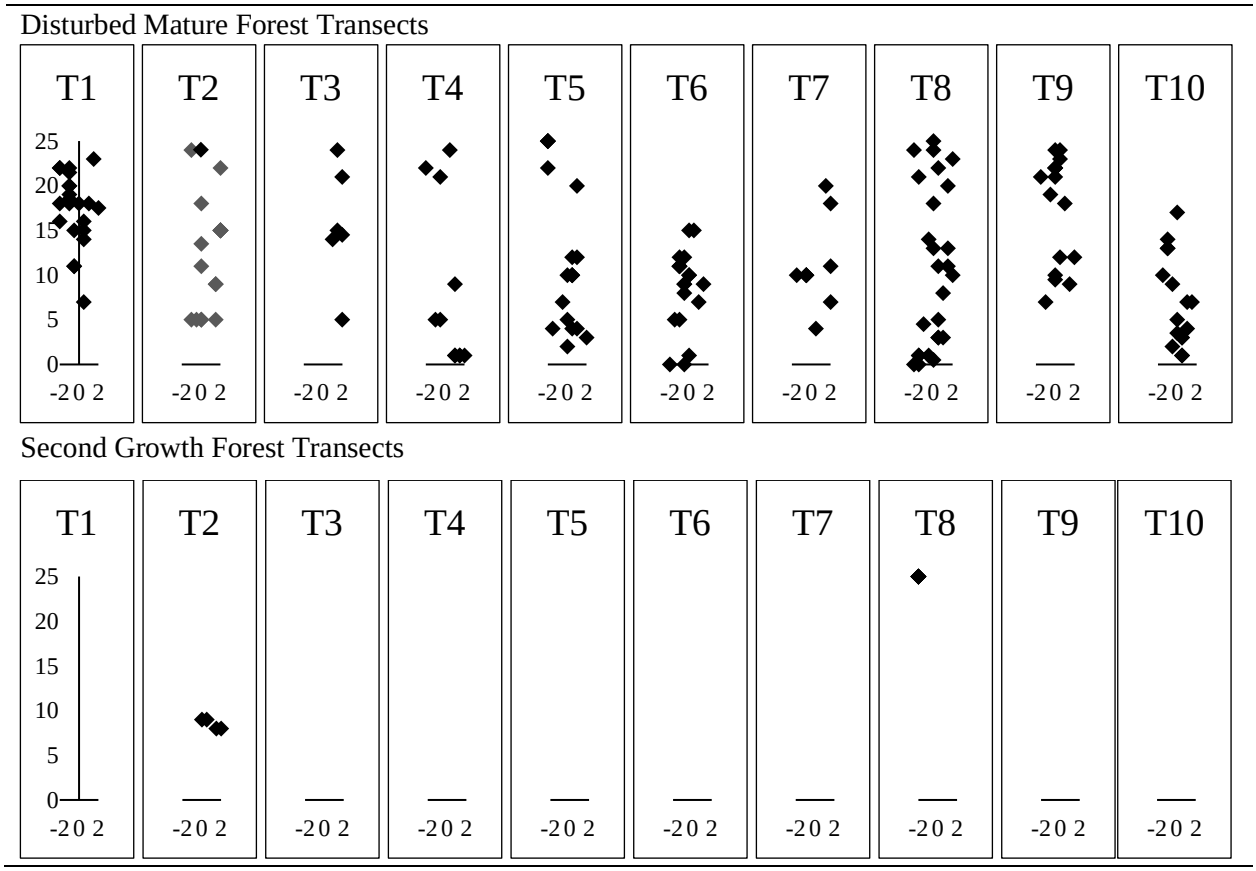
Supplementary Material

Appendix I: *Clustering observations of Inga morphospecies in the field, where individuals found ≤1 m away from another individual of the same morphospecies are labeled as clustered.*

Clustering Observation	Count per Observation
Clustered	**105**
DM	96
SG	9
Lone	**65**
DM	65
SG	0
Grand Total	179

Supplementary Material

Appendix II: *Distribution visualisation of sampled Inga per transect. All morphospecies are represented as black points.*



Supplementary Material

Appendix III: *Average diameter of Inga per transect and per forest type at a height of 7 cm, as well as average height of Inga per transect and forest type.*

Forest Type & Transects	Total Count	Average Diameter (cm)	Average Height (cm)
DM	**161**	**0.64**	**37.22**
T1	22	0.49	34.09
T2	18	0.37	19.28
T3	6	0.64	28.50
T4	11	0.69	31.36
T5	18	0.97	68.06
T6	19	0.84	57.89
T7	9	0.74	40.78
T8	26	0.62	33.42
T9	16	0.48	21.31
T10	16	0.64	29.88
SG	**9**	**0.99**	**284.44**
T1		0.00	
T2	4	0.80	91.75
T3		0.00	
T4		0.00	
T5		0.00	
T6		0.00	
T7		0.00	
T8	5	2.93	438.60
T9		0.00	
T10		0.00	
Grand Total	170	0.68	50.31