

EFFECTS OF DEFORESTATION ON THE DIVERSITY AND ACTIVITY OF  
FRUGIVORE SPECIES IN NORTHWESTERN ECUADOR

AN HONORS THESIS

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WITH HONORS IN ECOLOGY AND EVOLUTIONARY BIOLOGY

BY



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Annalisa Teleha

APPROVED:



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Jordan Karubian, Ph.D.

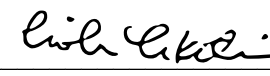
Director of Thesis



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Donata Henry, Ph.D.

Second Reader



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Nicole Katin, Ph.D.

Third Reader



Annalisa Teleha. Effects of Deforestation on the Diversity and Activity of Frugivore Species in Northwestern Ecuador.

(Dr. Jordan Karubian, Department of Ecology and Evolutionary Biology)

## **ABSTRACT**

Tropical forests are among the most diverse ecosystems in the world, yet anthropogenic land-use changes and habitat degradation have majorly impacted tropical ecosystem functioning and biodiversity. Seed dispersal by frugivorous vertebrates is an essential ecosystem function that aids in maintaining plant community diversity and is a tool for the passive regeneration of degraded and fragmented habitats. The research conducted for this thesis aims to deepen the understanding of how local habitat degradation, caused by habitat loss, fragmentation, and deforestation, impacts local species diversity and seed dispersal dynamics. This thesis aims to evaluate the hypothesis that habitat fragmentation and deforestation of the Ecuadorian Chocó rainforest negatively impact species diversity and seed dispersal activity but positively impact species evenness. This study collected data in three habitats using camera traps and four habitats using mist nets, although no camera and mist net locations overlapped. Through the application of diversity and interaction analyses to the camera trap data, the results of this study did not support this thesis' hypothesis. Instead, the pasture had the highest species diversity and interactions of all three habitat types. The mist net data was not used in any statistical tests, but analysis of the raw data revealed the early successional forest to have the highest species abundance and richness. These results provide context to the natural progression of succession and the life histories of the floral and faunal species characteristic of each habitat type. The findings of this study give insight into the impacts

of habitat degradation on species diversity in northwestern Ecuador and similar tropical rainforest ecosystems.

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## INTRODUCTION

### *The Tropics and Habitat Degradation*

Being one of the top ten most biodiverse-rich nations in the world, multiple national and international conservation organizations have, within the past 20 years, identified Ecuador as a biodiversity hotspot (Lopez *et al.*, 2010; Manchego *et al.*, 2017). Situated at the intersection of three major Neotropical geographical regions – the Chocó, Tumbesian, and Tropical Andes – northwestern Ecuador is of great conservation concern due to high rates of species endemism and biodiversity (Carrasco *et al.*, 2013). The biodiversity of this region provides ecosystem stability and resilience and increases the flow of ecosystem services between community members in this tropical forest environment (Brandon, 2014). Some of these ecosystem services, defined as the direct and indirect contributions of ecosystems to human well-being, include natural disaster mitigation, water quality improvement, climate regulation, and carbon sequestration (Braat *et al.*, 2012; Brandon, 2014). Tropical forests act as particularly effective carbon sinks as they sequester approximately 47% of the world's atmospheric carbon; however, current changes in land use patterns, particularly those which degrade forests, harm such ecosystem services essential to the maintenance of biodiversity (Brandon, 2014; Sedjo & Sohngen, 2012).

Habitat fragmentation and habitat loss are two leading causes of species decline worldwide today (Cook *et al.*, 2019). Habitat fragmentation, a landscape-scale process involving habitat loss and the breaking apart of habitats, is attributed to anthropogenic activities such as land conversion, habitat degradation, and deforestation (Fahrig, 2003). These phenomena are incredibly prevalent in tropical ecosystems, particularly in highly threatened regions such as western Ecuador, where 75% of all natural forests have already been degraded or cleared (Escobar *et al.*, 2020). Conservation of the Ecuadorian Chocó is of particular concern due to

increased logging activity in the past 20 years in response to increased local and national demands for timber (Lopez *et al.*, 2010). More recently, deforestation of the Chocó rainforest has accelerated due to intense land conversion for agricultural cash crops, such as cacao, coffee, and timber, as well as the maintenance of pasture animals, such as cattle (Durães *et al.*, 2013). Environmental degradation due to habitat fragmentation and loss continues to increase severely in the Ecuadorian Chocó, posing serious threats to the region's biodiversity and maintaining essential ecosystem services (Lopez *et al.*, 2010). Habitat loss has extensive adverse effects on biodiversity as it alters species interactions, predation rates, breeding success, genetic diversity, species richness, and species composition (Fahrig, 2003). The continuation of degrading activities resulting in habitat loss is leading to the rapid and widespread extinction of species, suggesting that such anthropogenic changes threaten the permanence of the Ecuadorian Chocó ecosystem and the biodiversity it supports, which is of particular significance considering its high levels of endemism (Durães *et al.*, 2013).

#### *Frugivores, Seed Dispersal, and Restoration*

As habitat disturbances alter the biodiversity and composition of tropical communities, the seed dispersal dynamics that shape these ecosystems are also negatively impacted (Escobar *et al.*, 2020). Seed dispersal, the movement of seeds away from parent plants, is a vital ecosystem function that generates and maintains plant diversity through the promotion of offspring survival, escape from density-dependent mortality factors, genetic connectivity between populations, and the colonization of new habitats (Escobar *et al.*, 2020; Mahoney *et al.*, 2017). Many tropical plants produce fleshy fruits adapted for dispersal by fruit-consuming birds and mammals called frugivores (Saavedra *et al.*, 2014). Frugivores consume the fruits of various tree species and distribute their seeds long and short distances through fruit or pulp consumption and subsequent

defecation or regurgitation (Wunderle, 1997). Such consumption and dispersal by frugivorous vertebrates further promote the probability of seed germination as the digestion in the disperser's gut breaks down the seed's coat (Wunderle, 1997). As a result of these interactions, seed dispersal by frugivores benefits ecosystem functioning through the promotion of seedling recruitment and the maintenance of tree species richness and diversity (Walter *et al.*, 2017). The maintenance and successful restoration of degraded tropical ecosystems depend on frugivores for their seed dispersal services that promote tree regeneration and increase diversity in forest fragments (Walter *et al.*, 2017). Habitat loss and fragmentation continue to alter animal seed dispersers' biodiversity and species composition, primarily due to local extinction and habitat loss, resulting in reduced seed removal rates and dispersal distances (Escobar *et al.*, 2020). Such limitations in seed dispersal activity severely impact the trajectory of Neotropical habitat restoration and plant regeneration that are responsible for maintaining tropical forest biodiversity and ecosystem functioning (Neuschulz *et al.*, 2016).

Ecological restoration works to reestablish ecosystem diversity, patterns, and processes previously destroyed by humans through the acceleration of natural succession (Howe & Miriti, 2004). Although ecological restoration commonly focuses on species conservation, growing evidence suggests that maintaining and reestablishing interaction networks in degraded ecosystems is key to preserving and restoring tropical biodiversity (Traveset *et al.*, 2014). Seed dispersal by frugivorous vertebrates is a fundamental process contributing to natural vegetation dynamics and forest succession in degraded tropical landscapes (Corlett & Hau, 2000). Therefore, reestablishing mutualistic animal-seed interactions in deforested habitats is one of the most critical strategies in restoration projects as it promotes the regeneration of plant populations (Traveset *et al.*, 2014). In tropical regions, animal dispersal is the predominant form of seed

distribution, facilitating ecological succession through the recolonization of native vegetation on degraded sites (Wunderle, 1997). However, degraded habitats are often dispersal-limited due to varying degrees of isolation from seed sources, the absence of animal seed dispersers, and large seed sizes (Wunderle, 1997). Researchers and conservationists should consider seed dispersal patterns and relationships when planning tropical restoration projects to reduce dispersal limitations and promote succession (Howe & Miriti, 2004). For example, reintroducing animal-dispersed tree species in highly fragmented landscapes aids forest restoration by attracting seed dispersers to highly dispersal-limited areas (Viani, *et al.*, 2015). Therefore, restoring animal-seed dispersal networks is essential to reforestation projects as it promotes succession, regeneration, and long-term stability of degraded ecosystems (Traveset *et al.*, 2014). As such, incomplete restoration of seed-dispersal networks and their essential ecosystem services may result in failing communities (Traveset *et al.*, 2014).

### *Predictions*

This research evaluates the relationship between habitat degradation, tropical forest community composition, and network interactions. I hypothesize that habitat fragmentation and deforestation of the Ecuadorian Chocó rainforest negatively impact species diversity and seed dispersal activity but positively impact species evenness. (Dunn & Ralph, 2004; Wearn & Glover-Kapfer, 2019). This research asks how species diversity differs between habitats with different levels of disturbance and regeneration. Due to differences in vegetation, canopy cover, and resource availability, I predict the camera trap data will find species diversity to be lowest in the pasture but that species evenness will be high. Furthermore, I predict the camera trap data will reveal that the old-growth and secondary-growth forests have higher species diversity and lower species evenness than the pasture because of extensive vegetation cover and resource

availability. Comparing the old-growth and secondary-growth forests' camera trap data, I predict the old-growth will have greater species diversity and evenness than the secondary-growth forest due to more extensive and increased vegetation and resource presence.

Additionally, I predict the early successional forest and pasture sampled through mist netting will have the lowest species richness and abundance. On the other hand, I predict the secondary-growth to have the second highest and the old-growth to have the highest species richness and abundance. In terms of seed dispersal interactions, my research focused on the question of how habitat disturbance affects frugivorous disperser-fruit interactions. Using camera trap data, I predict less seed dispersal activity in the pasture due to low frugivore presence because disturbed habitats are often dispersal-limited (Wunderle, 1997). In contrast, I predict both the secondary-growth and old-growth forests to have more frugivore interactions than the pasture due to differences in vegetation, canopy cover, and resource availability.

## **METHODS**

### *Study Site*

This research was conducted at Fundación para la Conservación de los Andes Tropicales (FCAT), located in the Chocó rainforest of northwestern Ecuador. Data was collected by a team of seven undergraduate research assistants, including myself, and two Ph.D. for six weeks between mid-June and late-July, 2022. A total of four habitat types – old-growth forest, secondary-growth forest, pasture, and early successional forest – were used in data collection, and all plots differed in their degrees of disturbance and succession. The old-growth forest is a fragment of primary forest, characterized by tall trees with a dense canopy and smaller vegetation underneath, that has remained undisturbed for over 40 years. The secondary-growth forest, which corresponds to 20 years of regrowth, consists of a continuous secondary forest with

lots of understory vegetation and mature trees that compose a tall canopy, although less dense than the old-growth forest. The pasture is an abandoned cattle pasture that has been allowed to regenerate for between four and six years. This habitat has no canopy and is instead covered by short shrubs and trees, tall remnant palm trees, and various vine and weedy species. Lastly, the early successional forest, which has experienced one year of regrowth, also consists of no connected canopy. Instead, this habitat consists of barren land with short grass, tree, shrub species, and tree saplings planted as part of FCAT's current restoration project.

### *Camera Traps*

We set and left camera traps, motion-censored cameras used to collect video data, for five days in three habitats: old-growth forest, secondary-growth forest, and pasture. We placed all camera traps on either fruit growing on vegetation or fruits located on the ground to collect data on both primary and secondary seed interactions. After five days, we collected the cameras, downloaded data for analysis, and then replaced all 22 camera traps in the following habitat to be sampled. During video data analysis, for each species observed, I noted its class (Aves or Mammalia), common and scientific name, diet guild, habitat type, and type of seed activity. In addition, I categorized each activity as either an interaction (fruit removal, complete fruit consumption, or mesocarp consumption) or no interaction.

### *Mist Netting*

In addition to camera traps, we used mist nets, which are large mesh nets strung between two poles used to intersect and capture birds' mid-flight, to collect data on avian diversity and abundance. We mist netted in four habitats: old-growth forest, secondary-growth forest, pasture, and early successional forest. The camera trap and mist netting data were collected in three of the

same habitat types but in different locations. Eight mist nets were placed at each plot to collect data for two consecutive days, from 7 am to 12 pm. Mist nets were checked every 10 to 20 minutes depending on the time of day and weather conditions. For each bird captured, we took note of the species' age, sex, weight (g), fat, molt status, and parasite presence and count, and measured its wing cord (mm) using a wing rule as well as its beak length (mm), tail length (mm), and tarsus length (mm) using a caliper.

### *Statistical Analysis*

Following sampling, I pooled together the camera trap data and conducted statistical analyses to infer how diversity and seed interactions vary between the old-growth forest, secondary-growth forest, and pasture. The mist net data was not used in any statistical tests due to insufficient sample sizes. To analyze differences in species diversity among the three camera-trap habitats, I ran a one-way ANOVA test to compare the impact of habitat type on species richness. Because species richness is a poor index of diversity, I estimated and compared the Hill number diversities ( ${}^qD$ ) for the orders  $q = 0$  (Hill-species richness), 1 (Hill-Shannon diversity), and 2 (Hill-Simpson diversity) of all three habitats (Chao *et al.*, 2014). Furthermore, I compared the  ${}^qD$  values for the orders 0, 1, and 2 to infer the evenness of each habitat. Additionally, I analyzed seed dispersal activity and interactions by visualizing interaction networks for each habitat type.

## **RESULTS**

### *Camera Traps Species Diversity*

310 individuals of 58 species were observed in the old-growth forest, secondary -growth forest, and pasture through camera trap footage (Table 1). Of these 310 individuals, 152 were

identified as frugivores, 44 as insectivores, 112 as omnivores, and two as carnivores (Table 2).

Of these 58 species, there were 27 frugivores, 16 insectivores, 14 omnivores, and one carnivore.

Additionally, 28 species were found in the old-growth forest, 30 in the pasture, and 15 in the secondary-growth forest (Figure 1, Figure 2, Table 3).

**Table 1:** Species observed and abundances per habitat type from camera trap data.

Scientific Name	Common Name	Pasture	Old-Growth	Secondary-Growth
<i>Gymnopithys bicolor</i>	Bicolored Antbird	1	-	-
<i>Thamnophilus atrinucha</i>	Black-crowned Antshrike	-	-	1
<i>Formicarius nigricapillus</i>	Black-headed Antthrush	-	8	2
<i>Saltator atripennis</i>	Black-winged Saltator	5	-	-
<i>Lepidothrix coronata</i>	Blue Crowned Manakin	-	2	-
<i>Dacnis cayana</i>	Blue Dacnis	1	-	-
<i>Volatinia jacarina</i>	Blue-black Grassquit	1	-	-
<i>Thraupis episcopus</i>	Blue-gray Tanager	2	-	-
<i>Stelgidopteryx serripennis</i>	Blue-necked Tanager	3	-	-
<i>Myiothlypis fulvicauda</i>	Buff-rumped Warbler	-	5	-
<i>Saltator maximus</i>	Buff-throated Saltator	1	-	-
<i>Dasyprocta punctata</i>	Central American Agouti	-	25	9
<i>Caluromys derbianus</i>	Central American Woolly Opossum	-	1	-
<i>Poliocrania exsul</i>	Chestnut Backed Antbird	-	2	-
<i>Ramphastos brevis</i>	Choco Toucan	2	9	1
<i>Viverra nasua</i>	Coatimundi	-	31	-
<i>Pteroglossus torquatus</i>	Collared Aracari	1	-	-
<i>Nyctidromus albicollis</i>	Common Paraque	3	-	-
<i>Procyon cancrivorus</i>	Crab-eating Raccoon	-	1	-
<i>Ramphocelus flammigerus</i>	Flame-rumped Tanager	9	-	-
<i>Troglodytes aedon</i>	House Wren	7	-	-
<i>Sporophila crassirostris</i>	Large-Billed Seed Finch	1	-	-
<i>Dryocopus lineatus</i>	Lineated Woodpecker	-	-	1
<i>Crypturellus soui</i>	Little Tinamou	-	-	1
<i>Cuniculus paca</i>	Lowland Paca	-	2	4
<i>Murinae sp.</i>	Mouse	2	5	10
<i>Dasyprocta novemcinctus</i>	Nine-banded Armadillo	1	1	5
<i>Leopardus pardalis</i>	Ocelot	-	1	1
<i>Mionectes olivaceus</i>	Olive-striped Flycatcher	2	-	-
<i>Euphonia xanthogaster</i>	Orange-bellied Euphonia	4	-	-
<i>Myiobuteo ornatus</i>	Ornate Flycatcher	-	1	-
<i>Zenaidura macroura</i>	Purplish-backed Quail-Dove	-	9	-
<i>Murinae sp.</i>	Rat	1	9	9
<i>Certhia mentalis</i>	Red-capped Manakin	-	1	-
<i>Sciurus granatensis</i>	Red-tailed Squirrel	-	2	3
<i>Stelgidopteryx serripennis</i>	Rough-winged Swallow	1	-	-

<i>Patagioenas subvinacea</i>	Ruddy Pigeon	-	7	-
<i>Baryphthengus martii</i>	Rufous Motmot	-	5	-
<i>Lipaugus unirufus</i>	Rufous Piha	-	1	-
<i>Odontophorus erythrops</i>	Rufous-fronted Wood-Quail	-	2	-
<i>Myiozetetes similis</i>	Rusty-margined Flycatcher	1	-	-
<i>Microcerculus marginatus</i>	Scaly-breasted Wren	-	1	-
<i>Synallaxis brachyura</i>	Slaty Spinetail	7	-	-
<i>Catharus fuscater</i>	Slaty-backed Nightingale-Thrush	-	1	-
<i>Crotophaga ani</i>	Smooth-billed Ani	13	-	-
<i>Tamandua tetradactyla</i>	Southern Tamandua	-	1	-
<i>Dysithamnus puncticeps</i>	Spot-crowned Antvireo	-	1	-
<i>Piaya cayana</i>	Squirrel Cuckoo	1	-	-
<i>Eira barbara</i>	Tayra	1	3	-
<i>Euphonia laniirostris</i>	Thick-billed Euphonia	12	-	-
<i>Sporophila funerea</i>	Thick-Billed Seed-finch	4	-	-
<i>Sporophila corvina</i>	Variable Seedeater	13	-	-
<i>Manacus manacus</i>	White-bearded Manakin	-	-	5
<i>Laterallus albigularis</i>	White-throated Crake	1	-	-
<i>Turdus assimilis</i>	White-throated Thrush	-	1	-
<i>Leptotila verreauxi</i>	White-tipped Dove	-	-	1
<i>Sporophila nigricollis</i>	Yellow-bellied Seedeater	13	-	-

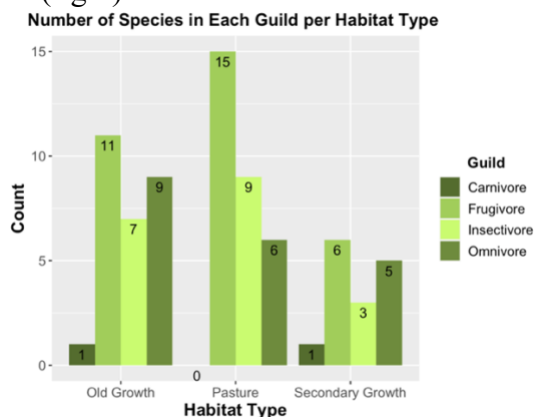
**Table 2:** Species abundance of each diet guild per habitat type from camera trap data. The four guilds include: carnivores (C), frugivores (F), insectivores (I), and omnivores (O).

	<b>C</b>	<b>F</b>	<b>I</b>	<b>O</b>	<b>Total</b>
<b>Old-Growth</b>	1	57	11	70	139
<b>Pasture</b>	0	72	26	19	117
<b>Secondary-Growth</b>	1	23	7	23	54

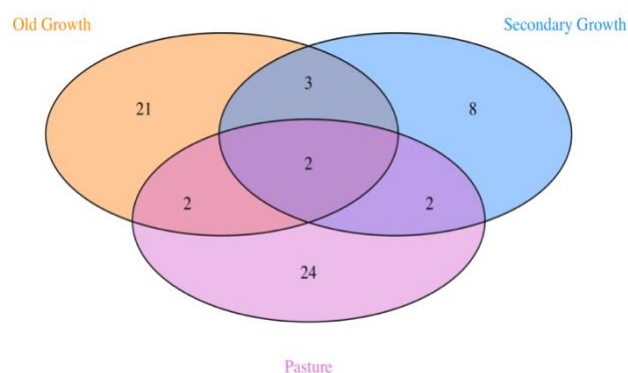
**Table 3:** Species richness of each diet guild per habitat type from camera trap data. The four guilds include: carnivores (C), frugivores (F), insectivores (I), and omnivores (O).

	<b>C</b>	<b>F</b>	<b>I</b>	<b>O</b>	<b>Total</b>
<b>Old-Growth</b>	1	11	7	9	139
<b>Pasture</b>	0	15	9	6	117
<b>Secondary-Growth</b>	1	6	3	5	54

**Figure 1:** Number of species observed per diet guild per habitat type from camera trap data (right).

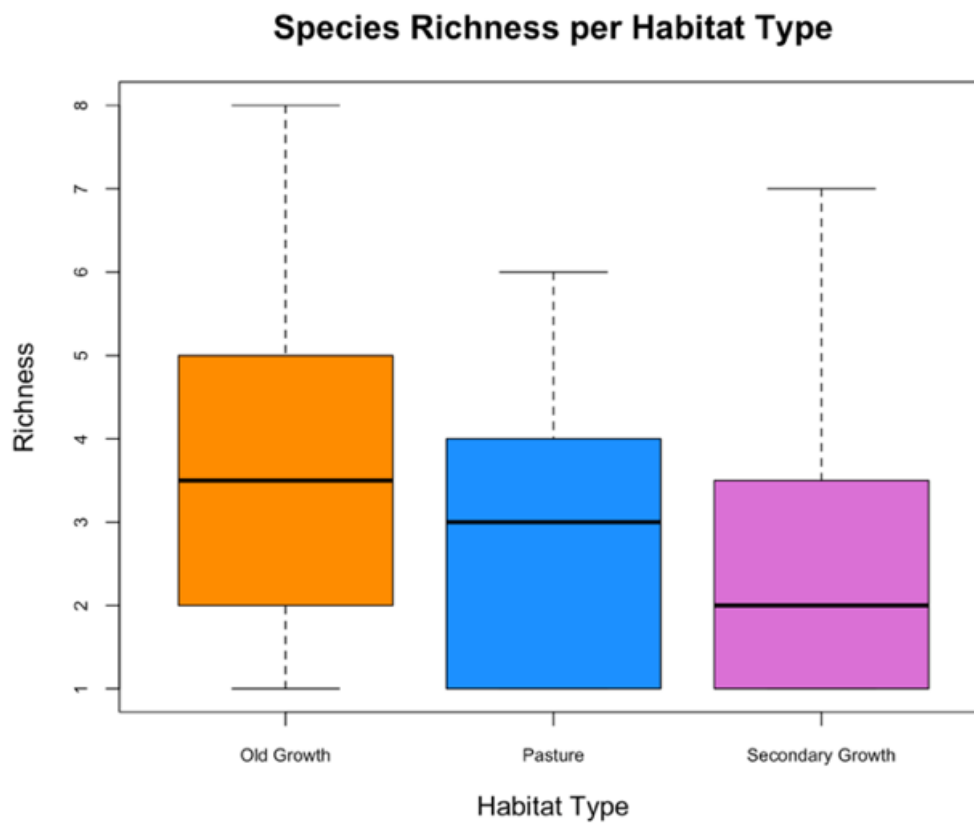


**Figure 2:** Venn diagram of the species observed in each habitat type from camera trap data (right).

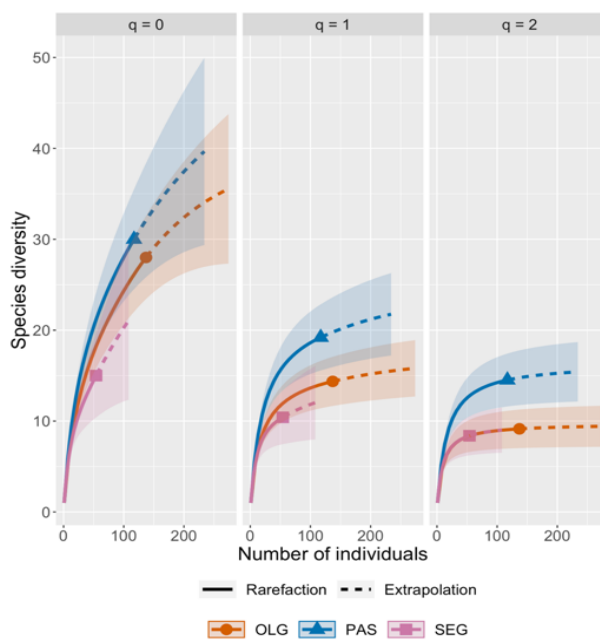


The one-way ANOVA found no significant difference between the mean species richness of any of the three habitat types ( $F(2, 41) = 0.801$ ;  $p = 0.456$ ) (Figure 3). The sample-size-based rarefaction and extrapolation of the three habitat types found that for Hill-species richness ( $q = 0$ ), the pasture had the highest Hill-species diversity, although insignificant (Figure 4). The pasture also had the highest Hill-Shannon diversity, although this difference significantly differed from the secondary-growth forest but not the old-growth forest (Figure 4). A significant difference was found between the pasture's Hill-Simpson diversity and the old- and secondary-growth forests (Figure 4). The sample-size-based sample-completeness curve revealed that for any sample size less than 54, the estimated completeness of the secondary-growth forest, although insignificant, is higher than those of both the old-growth forest and pasture (Figure 5). In sample sizes larger than 54, the estimated completeness of the old-growth forest, secondary-growth forest, and pasture barely differed (Figure 5). A comparison of the coverage-based diversities of all three habitat types for  $q = 0, 1, \text{ and } 2$  revealed that the pasture had the highest Hill-species diversity for all sample coverages (Figure 6). However, its significance varies (Figure 6).

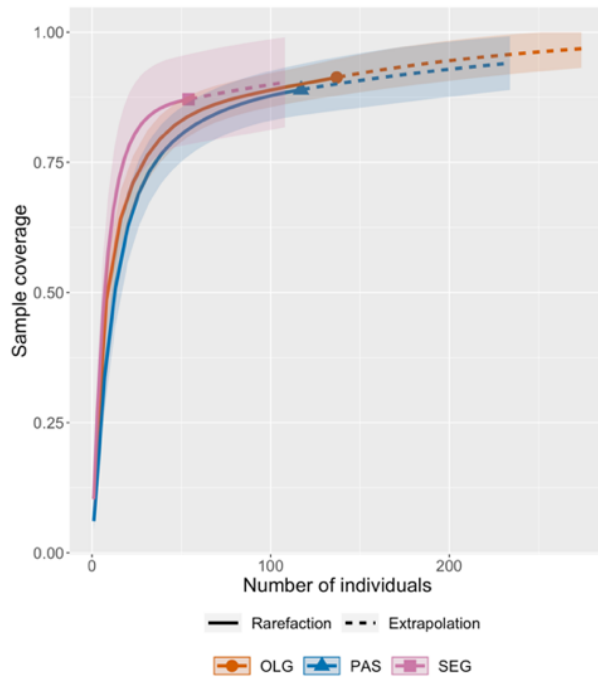
**Figure 3:** Boxplot of the species richness of each habitat type from camera trap data.



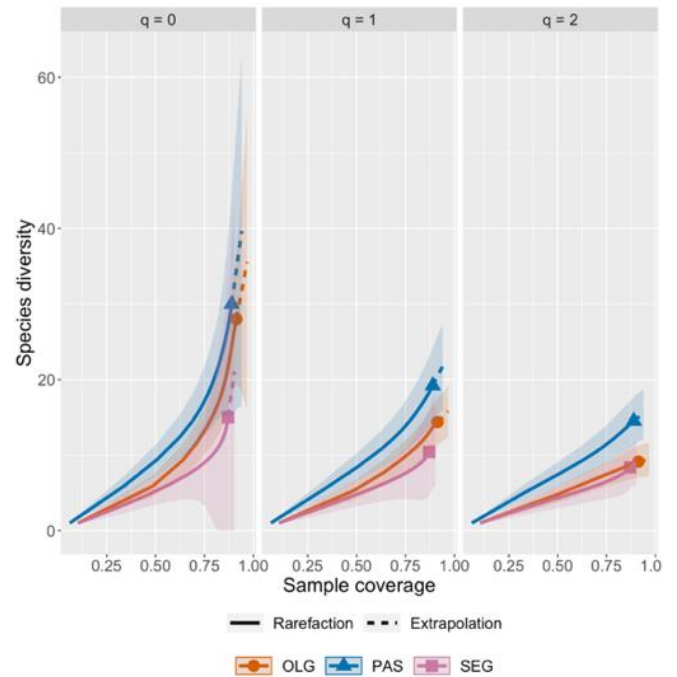
**Figure 4:** Species accumulation curve of each habitat for orders  $q = 0, 1, 2$  from camera trap data.



**Figure 5:** Sample completeness curve of all habitats for the order  $q = 0$  from camera trap data.

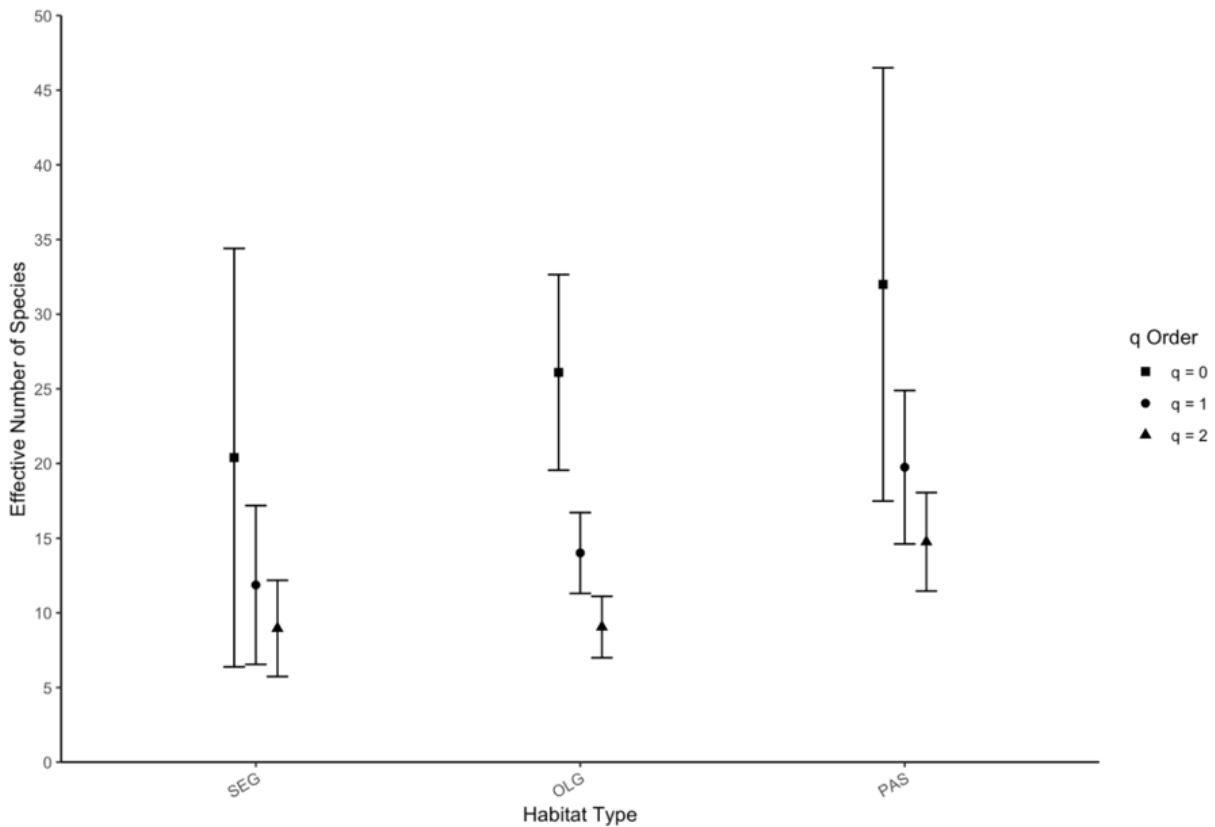


**Figure 6:** The coverage-based diversities of each habitat type for order  $q = 0, 1,$  and  $2$  from camera trap data.



For all orders of  $q$ , no significant difference was found between the species diversity of the old-growth and secondary-growth forests. When sample coverage was less than 62.5%, the pasture's species richness was significantly higher than that of the secondary-growth forest (Figure 6). Similarly, the pasture and secondary-growth forest's Hill-Shannon diversities significantly differed for sample coverages up to 62.5% (Figure 6). The pasture's Hill-Simpson diversity was significantly greater than those of the old- and secondary-growth forests for all sample coverages (Figure 6). By comparing the  ${}^qD$  values for orders 0, 1, and 2 of all three habitats at 90% sample coverage, the secondary-growth forest was found to have the greatest evenness, although no habitats were found to be perfectly even (Table 4, Figure 7).

**Figure 7:** Comparison of all orders of  $q$  for all three habitats from camera trap data. The habitats include the secondary-growth forest (SEG), old-growth forest (OLG), and pasture (PAS).



**Table 4:** Descriptive values for all orders  $q$  at 90% sample coverage for the habitat types sampled with camera traps. This information is reflected in the graph in Figure 7.

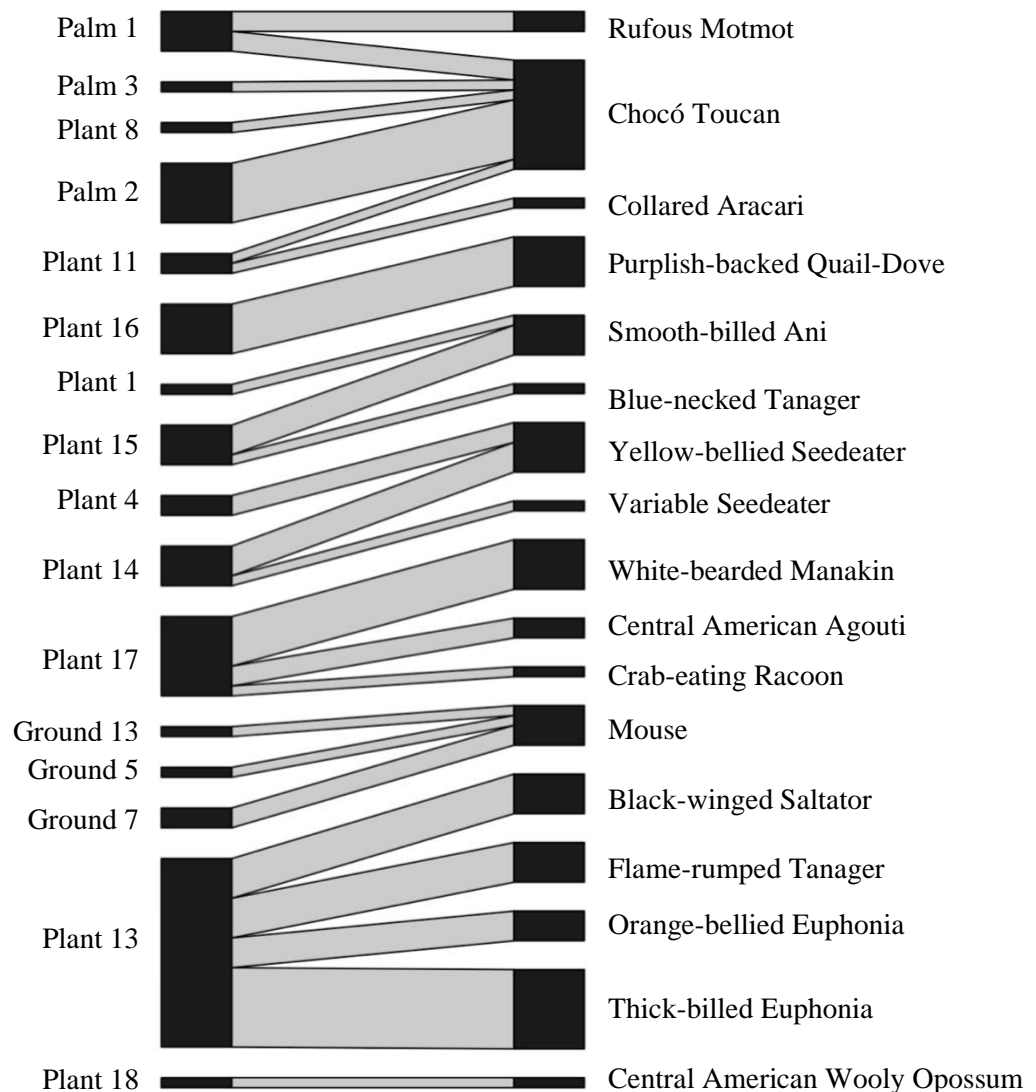
Habitat	Order $q$	$m$	Method	SC	$q^p$	$q^p$ LCL	$q^p$ UCL
Old-Growth	0	116.7846	Rarefaction	0.9	26.104	18.422	33.786
	1	116.7846	Rarefaction	0.9	14.009	11.738	16.279
	2	116.7846	Rarefaction	0.9	9.048	7.337	10.759
Pasture	0	135.9131	Extrapolation	0.9	31.994	18.874	45.115
	1	135.9131	Extrapolation	0.9	19.752	15.476	24.028
	2	135.9131	Extrapolation	0.9	14.756	11.895	17.616
Secondary-Growth	0	101.2690	Extrapolation	0.9	20.396	1.144	39.648
	1	101.2690	Extrapolation	0.9	11.867	6.366	17.367
	2	101.2690	Extrapolation	0.9	8.961	6.207	11.716

### Camera Trap Interactions

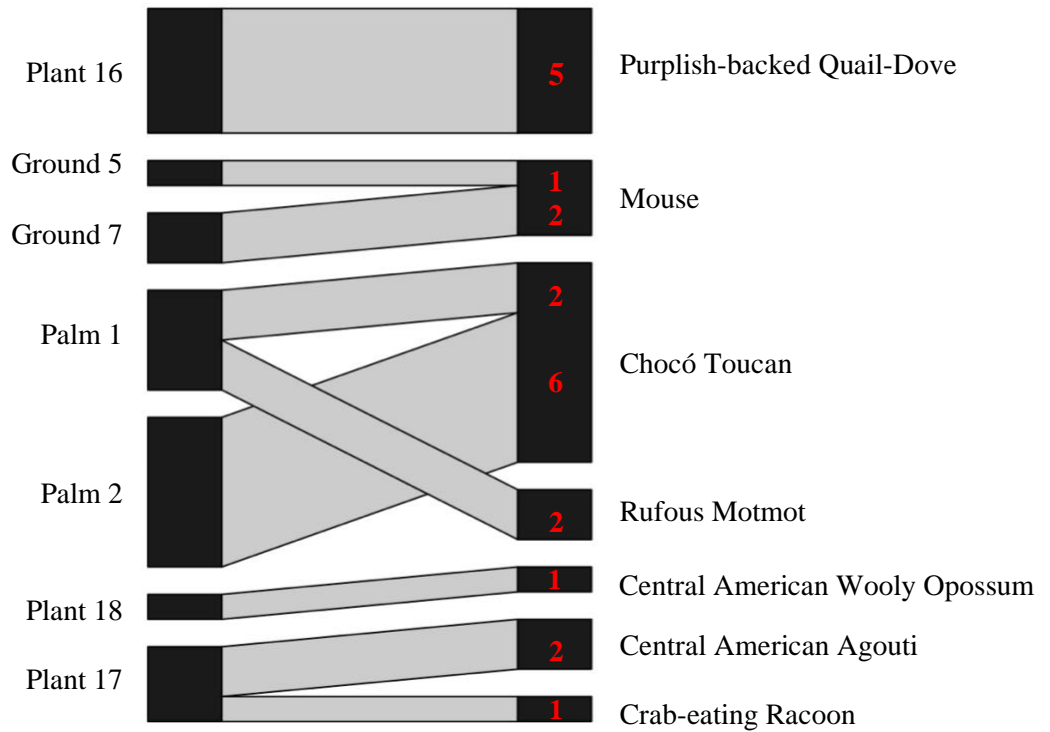
Of the 310 individuals observed, 62 interactions among all three habitat types, with 22 in the old-growth forest, 33 in the pasture, and 7 in the secondary-growth forest (Table 5). Of these

62 interactions, 21 were identified as unique pairwise interactions between frugivores and plant species (Table 5). The pasture had the highest number of interactions, while the secondary-growth forest was found to have the lowest (Table 5). Additionally, the pasture was also found to have the greatest number of pairwise interactions, although the old-growth forest did not differ by much (Table 5). Overall, the pasture had the greatest number of interactions and pairwise interactions compared to those of the old-growth and secondary-growth forests.

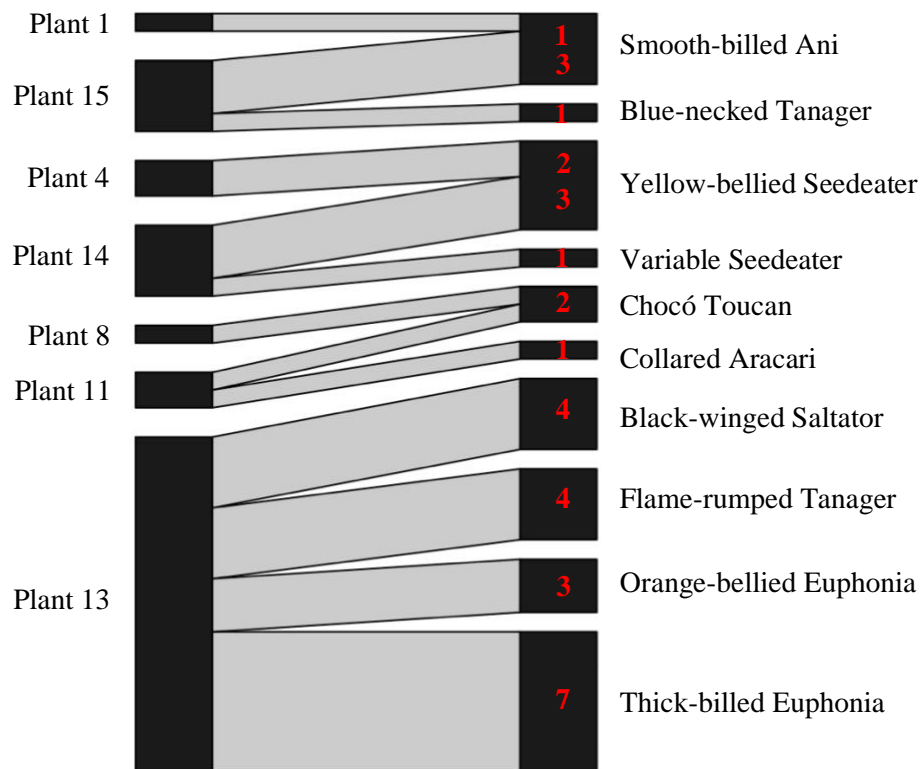
**Figure 8:** Interaction network between fruits and frugivores for all habitats from camera trap data.



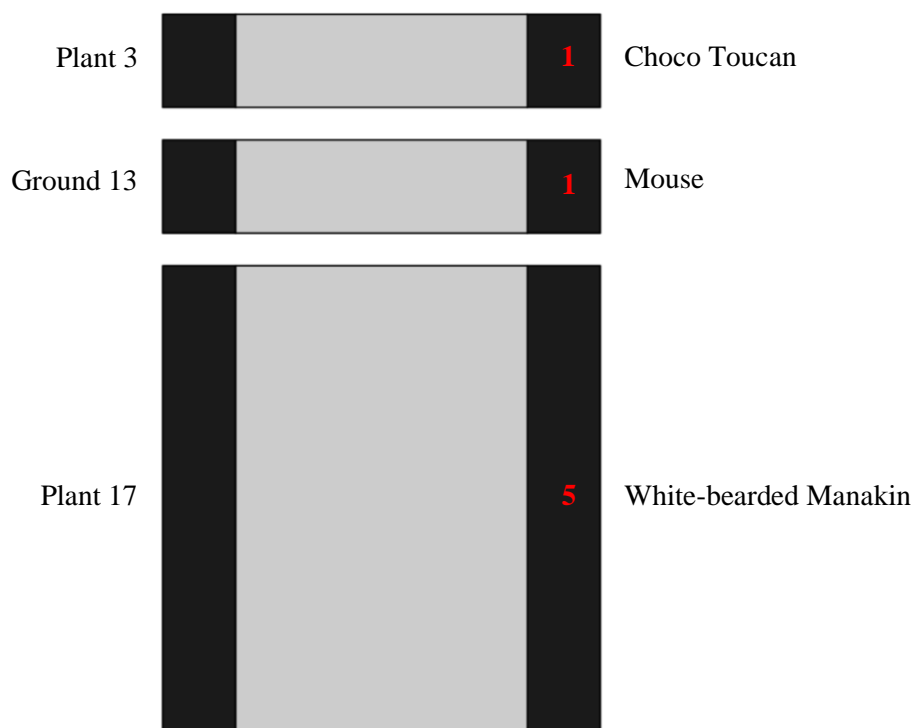
**Figure 9:** Interaction network between fruits and frugivores in the old-growth forest from camera trap data. The abundance of interactions with each plant per species is listed in red.



**Figure 10:** Interaction network between fruits and frugivores in the pasture from camera trap data. The abundance of interactions with each plant per species is listed in red.



**Figure 11:** Interaction network between fruits and frugivores in the secondary-growth forest from camera trap data. The abundance of interactions with each plant per species is listed in red.



**Table 5:** Total and pairwise interactions observed in each habitat type from camera trap data.

	<b>Interactions</b>	<b>Pairwise Interactions</b>
<b>Old-Growth</b>	22	9
<b>Pasture</b>	33	10
<b>Secondary-Growth</b>	7	3
<b>Total</b>	62	21

## DISCUSSION

### *Camera Trap Species Diversity and Evenness*

Centered on the impacts of habitat fragmentation and deforestation on the Ecuadorian Chocó rainforest, the results of this research did not support the hypothesis that habitat disturbance negatively impacts species diversity and seed dispersal activity but positively impacts species evenness. Neither the ANOVA test nor Hill number diversity analyses ran on the camera trap data found evidence for significant differences between the species diversity and evenness of the pasture, old-growth forest, and secondary-growth forest. Furthermore, the

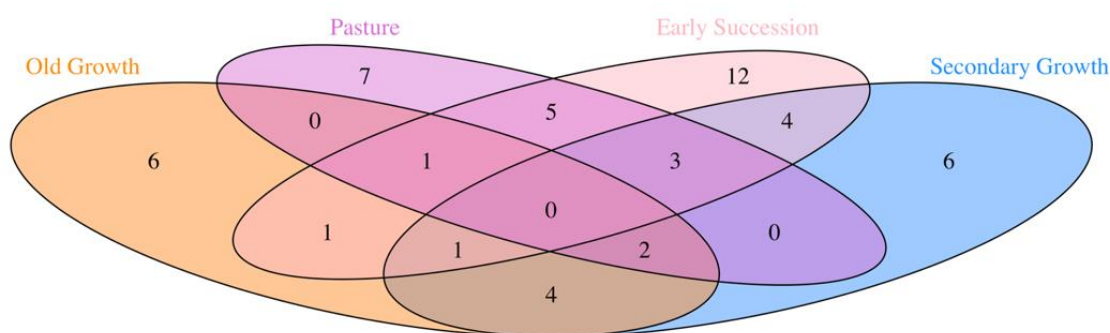
prediction of greater species diversity and evenness in the old-growth and secondary-growth forests was inaccurate as, although insignificant, the pasture had the highest Hill number diversity for all three orders of  $q$ . In comparison, the old-growth forest had the second lowest Hill number diversity, and the secondary-growth forest had the lowest Hill number diversity and highest evenness of all three habitats. Nevertheless, unrepresentative sample sizes may have skewed these findings. The secondary-growth forest's sample size (54) was much smaller than those of both the old-growth forest (139) and pasture (117), which may be a result of camera trap placement. Because the habitats sampled are vast and diverse, the camera traps may have, by chance, been placed in areas with low or high activity. Such camera placement would result in insufficient samples that fail to detect all species present, subsequently impacting the species richness and abundances used in diversity analyses.

#### *Mist Netting Species Diversity and Abundance*

Our mist net data from the old-growth forest, secondary-growth forest, pasture, and early successional forest provided additional support for higher species diversity in young secondary forests. In the four plots sampled, we captured 172 individuals from 52 species (Table 6). However, the prediction of low species abundance and richness in the early successional habitat was not supported as it instead was found to have the highest number of individual captures (81), species captured (20), and species unique to it out of all habitat types (Table 6, Figure 12). In contrast, the pasture had the lowest number of individuals (30) and the second lowest number of species (18) captured, providing support for the prediction of low species diversity and abundance in the pasture (Table 7). However, the number of individuals and species captured in the pasture is similar to those of the old-growth (35, 15) and secondary-growth (32, 20) forests (Table 6).

Additionally, the early successional forest had the highest frugivore species diversity and abundance out of the four habitats (Table 7, Table 8). These differences in diversity between the pasture and early successional habitats, which are close in successional age, may be attributed to potential sampling bias caused by mist net location. Eight mist nets were set in each plot, yet the net location was selected based on personal judgment. Therefore, they may have been placed in areas with activity unrepresentative of the habitat sampled. Examining the natural progression of secondary succession and the life histories of the floral species present rationalizes the patterns of species diversity observed in habitats of different successional ages.

**Figure 12:** Venn diagram of the species observed in each habitat type from mist net data.



**Table 6:** Species captured in each habitat type and their abundances from mist net data.

Scientific Name	Common Name	Pasture	Old-Growth	Secondary-Growth	Early Succession
<i>Amazilia amazilia</i>	Amazilia Hummingbird	1	-	-	-
<i>Coereba flaveola</i>	Bananaquit	1	-	-	4
<i>Threnetes ruckeri</i>	Band-tailed Barbthroat	-	1	3	2
<i>Claravis pretiosa</i>	Blue Ground Dove	-	-	-	1
<i>Notiochelidon cyanoleuca</i>	Blue and White Swallow	-	1	1	-
<i>Volatinia jacarina</i>	Blue-black Grassquit	-	-	-	1
<i>Amazilia amabilis</i>	Blue-chested Hummingbird	-	-	1	1
<i>Myiothlypis fulvicauda</i>	Buff-rumped Warbler	-	2	-	-
<i>Epinecrophylla fulviventris</i>	Checker-throated Stipple Throat	-	-	-	-

<i>Poliocrania exsul</i>	Chestnut Backed Antbird	-	-	1	-
<i>Vireo chivi</i>	Chivi Viero	2	-	-	-
<i>Zimmerius albigularis</i>	Choco Tyrannulet	5	-	-	-
<i>Todirostrum cinereum</i>	Common Tody Flycatcher	2	-	-	2
<i>Thalurania colombica</i>	Crowned Woodnymph	1	-	-	-
<i>Tiaris obscurus</i>	Dull-colored Grassquit	-	-	-	4
<i>Patagioenas goodsoni</i>	Dusky Pigeon	-	1	-	-
<i>Ramphocelus flammigerus</i>	Flamed-rumped Tanager	-	-	-	3
<i>Myiothlypis chrysogaster</i>	Golden Bellied Warbler	-	-	1	2
<i>Tangara larvata</i>	Golden-hooded Tanager	-	-	1	2
<i>Colaptes rubiginosus</i>	Golden-olive Woodpecker	-	-	1	-
<i>Progne chalybea</i>	Gray-breasted Martin	-	-	-	-
<i>Chlorophanes spiza</i>	Green Honeycreeper	1	-	-	-
<i>Cryptopipo holochlora</i>	Green Manakin	-	2	-	-
<i>Troglodytes aedon</i>	House Wren	2	-	-	-
<i>Schiffornis veraepaci</i>	Northern Schiffornis	-	1	-	-
<i>Mionectes oleagineus</i>	Ochre-bellied Flycatcher	1	1	-	-
<i>Mionectes olivaceus</i>	Olive-striped Flycatcher	-	5	1	-
<i>Euphonia xanthogaster</i>	Orange-bellied Euphonia	2	1	-	-
<i>Myiotriccus ornatus</i>	Ornate Flycatcher	-	2	1	-
<i>Myrmotherula pacifica</i>	Pacific Antwren	1	-	-	-
<i>Thraupis palmarum</i>	Palm Tanager	1	-	-	-
<i>Sternoclyta cyanopectus</i>	Purple-chested Hummingbird	2	-	-	-
<i>Malurus coronatus</i>	Purple-crowned Fairy	-	-	-	-
<i>Ceratopipra mentalis</i>	Red-capped Manakin	-	1	-	-
<i>Cranioleuca erythroptus</i>	Red-faced Spinetail	-	-	-	-
<i>Stelgidopteryx serripennis</i>	Rough-winged Swallow	-	-	-	-
<i>Amazilia tzacatl</i>	Rufous-tailed Hummingbird	2	-	-	-
<i>Microcerculus marginatus</i>	Scaly-breasted Wren	-	-	1	-
<i>Tangara icterocephala</i>	Silver-throated Tanager	-	-	-	-
<i>Myrmotherula schisticolor</i>	Slaty Antwren	-	-	-	-
<i>Synallaxis brachyura</i>	Slaty Spinetail	1	-	-	-
<i>Camptostoma obsoletum</i>	Southern Beardless Tryanulette	-	-	-	-
<i>Mionectes olivaceus</i>	Striped Flycatcher	-	5	1	-

<i>Myiobius sulphureipygius</i>	Sulphur-rumped Flycatcher	-	1	-	-
<i>Sporophila funerea</i>	Thick-billed Seed-finch	2	-	-	-
<i>Euphonia lanirostris</i>	Thick-billed Euphonia	1	-	2	-
<i>Sporophila corvina</i>	Variable Seedeater	-	-	-	-
<i>Damophila julie</i>	Violet-bellied Hummingbird	-	-	1	-
<i>Glyphorynchus spirurus</i>	Wedge-billed Woodcreeper	-	1	-	-
<i>Eutoxeres aquila</i>	White-tipped Sicklebill	-	-	1	-
<i>Phaethornis yaruqui</i>	White-whiskered Hermit	2	10	4	-
<i>Sporophila nigricollis</i>	Yellow-bellied Seedeater	-	-	-	-
<b>Total Number of Individuals Caught</b>		30	35	32	81
<b>Total Number of Species Caught</b>		18	15	20	27

**Table 7:** Species abundance of each diet guild per habitat type from mist net data. The four guilds include: frugivores (F), insectivores (I), omnivores (O), and nectarivores (N).

	F	I	O	N	Total
<b>Old-Growth</b>	11	7	6	11	35
<b>Pasture</b>	7	13	1	9	30
<b>Secondary - Growth</b>	8	8	3	13	32
<b>Early Successional</b>	50	20	0	11	81

**Table 8:** Species richness of each diet guild per habitat type from mist net data. The four guilds include: frugivores (F), insectivores (I), omnivores (O), and nectarivores (N).

	F	I	O	N	Total
<b>Old-Growth</b>	6	5	2	2	15
<b>Pasture</b>	5	6	1	6	18
<b>Secondary-Growth</b>	5	8	1	6	20
<b>Early Successional</b>	12	9	0	6	27

### *Succession and r- vs. K-selected Species*

Secondary succession is the successional process following significant habitat disturbances and resulting in changes in species community composition as functional species groups are replaced by others with different life history traits (Breugel *et al.*, 2007; Chazdon, 2017). Removal of the canopy of old-growth forests produces disturbed habitats with dramatically different microclimates than the original forest due to shifts in environmental metrics such as increased light, temperatures, and wind velocity (Swanson *et al.*, 2011). As

succession progresses through these altered habitats, forest successional theory predicts that light-demanding species with high resource acquisition and growth will eventually be replaced by shade-tolerant species with high resource conservation and persistence (Poorter *et al.*, 2021). This species trait shift reflects the trade-off between productivity and efficiency in r- and K-selected species during succession, as K-selected species replace the first colonizing r-selected species in later succession (Opler *et al.*, 1980; Pinotti, *et al.*, 2015). Proposed as one of the first predictive models for life history evolution, the r- and K- selection theory characterizes K-selected species as having high efficiency, low reproduction, high competition, and high resource maximization when present (Opler *et al.*, 1980; Reznick *et al.*, 2002). On the other hand, r-selected species are those with high productivity, rapid colonization, high reproductive capacity, and highly cyclic life cycles (Opler *et al.*, 1980; Reznick *et al.*, 2002). As early succession favors r-strategists while later succession and mature forests favor K-strategists, the colonization-competition trade-off in r- and K-selected species significantly influences the progression of successional change (Opler *et al.*, 1980).

The absence of tree canopies in early successional habitats allows r-selected species to flourish, further promoting the high productivity, complex food webs, large nutrient fluxes, and high complexity characteristic of early successional stages (Swanson *et al.*, 2011). Due to their high productivity, young successional habitats, such as the pasture and early successional forest, provide an abundance of food and nesting habitats for a variety of faunal species, and such resource availability may, in part, explain the pasture's high diversity observed through the camera trap data of this study (Swanson *et al.*, 2011). Similarly, young successional habitats' high food and habitat availability may explain the high number of individuals and species captured through mist netting in the early successional forest. Furthermore, remnant trees and

vegetation in young succession ecosystems provide further reasoning for the relationship between early successional habitats and increased species diversity. Frugivores are likely to only venture into habitats that provide adequate resources for foraging or perching (Chazdon, 2017). Isolated remnant trees in early successional habitats may provide abundant food and perching resources, attracting frugivorous species and increasing seed dispersal (Chazdon, 2017). Because such remnant trees characterize the pasture habitat in which we collected camera trap data, the connection between remnant trees and frugivores provides further evidence for a relationship between increased species diversity and early successional habitats.

#### *Camera Trap Network Interactions*

The results of the interaction network analysis from the camera trap data found the pasture to have the highest number of interactions and unique pairwise interactions, although the old-growth forest did not differ by much (Table 5). Such results disprove the prediction that more interactions would be observed in the old-growth and secondary-growth forests than in the pasture. Additionally, the pasture had the greatest number of plants with multiple species interactions. The pasture had the highest number of productive frugivorous species – those with three or more interactions – which included: smooth-billed ani (*Crotophaga ani*), yellow-bellied seedeater (*Sporophila nigricollis*), black-winged saltator (*Saltator atripennis*), orange-bellied euphonia (*Euphonia xanthogaster*), thick-billed euphonia (*Euphonia laniirostris*) (Figure 10). In contrast, the old-growth forest had only three productive frugivorous species, which included the Chocó toucan (*Ramphastos brevis*), the purplish-backed quail-dove (*Zentrygon lawrencii*), and a mouse species (*Murinae sp.*) (Figure 9). Of all three habitats, the secondary-growth forest had the smallest number of interactions and unique pairwise interactions and only had one productive frugivorous species, the white-bearded manakin (*Manacus manacus*) (Figure 11). These results

may be due to abundant fruit and other resources in each habitat type. For example, an overabundance of fruit would provide visiting dispersers with many fruits for consumption, so the visitation rate at individual camera traps might be low. In turn, such low rates of interactions with the fruits camera traps were placed on may not be representative of the actual interaction networks of this habitat as active dispersers could simply be visiting other fruits nearby instead of the fruits our cameras faced. Future researchers should replicate all modes of data collection in each habitat type multiple times to avoid the potential sources of bias mentioned here and previously throughout this discussion. Because the habitats sampled are so large and diverse, future studies should also increase the number of camera traps used in each plot to obtain more representative data.

### *Generalists and Specialists*

The increased interactions observed in the pasture habitat are attributable to the wide range of foraging and habitat resources provided by early successional forests and the frugivore species they attract (Chazdon, 2017). As secondary succession progresses, the regeneration process significantly changes these habitat's plant and animal communities. The vast diversity of plant species present in early successional forests provides abundant resources, including grasses, nectar, seeds, and shrub-borne fruit, thus supporting a highly complex food web system (Swanson *et al.*, 2011). Just as secondary succession alters plant communities, so are animal communities, as early successional stages tend to be dominated by forest generalists and later succession and old-growth forests by forest specialists (Pinotti *et al.*, 2015). In network ecology, generalists are species that interact indiscriminately with many plants, while specialists interact with a few plants that are different from those of generalists (Dehling *et al.*, 2021). As secondary succession progresses, the regeneration process results in major changes to the plant and animal

communities of these habitats (Pinotti *et al.*, 2015). On the other hand, habitat generalists are typically unaffected or positively affected by habitat degradation and forest fragmentation (Pinotti *et al.*, 2015).

Early successional forests favor r-selected plant species with traits that increase their survival and reproductive ability, such as small and abundant seeds, rapid growth, and shade tolerance (Pinotti *et al.*, 2015). The fruits of such species are commonly consumed by small-bodied forest generalists that disperse small- to mid-sized fruits and are typically found in deforested and fragmented forest areas (Silva *et al.*, 2020; Pinotti *et al.*, 2015). This pattern is reflected in this study's results, as the pasture had the largest number of productive small-bodied species – *C. ani*, *S. nigricollis*, *S. atripennis*, *E. xanthogaster*, *E. laniirostris*) – interact with one or multiple plant species and may be categorized as forest generalists. R-selected species prosper in the micro-climate conditions of early successional forests as their abundance of small fruits attracts a wide variety of generalist species. The selection for r-selected species in early successional forests is also reflected in these results as the pasture had the plant species with the highest number of interactions and species interacting with it. Previous research has found that generalists prefer habitats with abundant food resources, such as the pasture in our study (Pinotti *et al.*, 2015). As succession progresses, the net primary productivity of habitats decreases due to increased canopy coverage, reduced light availability, and changes to other micro-climate conditions (Pinotti *et al.*, 2015). This reduction in primary productivity is reflected in the resources available in later successional and old-growth forests as fruit availability and arthropod abundance decrease during the recovery of tropical landscapes (Pinotti *et al.*, 2015). As such, the high number of interactions observed in the pasture's camera trap data is understood through the tradeoff between productivity and efficiency in plant species that subsequently determines

resource availability during succession. Therefore, the high number of interactions, species, and plants with multiple dispersers observed in the pasture's camera trap data may be attributed to the presence of r-selected plant species and forest generalist's characteristic of early successional habitats.

### *Future Directions*

The maintenance and prosperity of the Chocó rainforest, which is under continuous threat, depends on the seed dispersal services provided by frugivores and the biodiversity found in the region. Tropical forest ecosystems are essential to global carbon and water cycles and provide hope for conserving our planet's biodiversity (Poorter *et al.*, 2021). However, today these tropical landscapes are converted to barren lands at alarming rates as deforestation has reduced the area of tropical forests around the world from 12 percent to less than 5 percent of the Earth's total surface (Brandon, 2014; Poorter *et al.*, 2021). Most ecological and conservation literature has failed to acknowledge the potential of successional forests to facilitate passive landscape restoration and faunal community recovery (Bowen *et al.*, 2007). Yet, the conservation of the biodiversity and services of these ecosystems depends on the complete restoration of these habitats through natural secondary succession and the persistence of old-growth forest fragments (Martinez-Ramos *et al.*, 2016). To plan and conduct successful site-specific restoration projects, researchers and conservationists need to identify and utilize plants with traits attractive to frugivorous species (Viani, *et al.*, 2015). Planting animal-dispersed tree species with desirable traits is a common restoration practice that may promote forest regeneration by restoring soil properties and attracting seed dispersers (Abelleira Martínez *et al.*, 2015). Therefore, using seed dispersal dynamics is a potential agent in the restoration of

biodiversity in degraded habitats as it promotes quick and passive regeneration and is low in cost compared to other restoration strategies (Traveset *et al.*, 2014; Wunderlee, 1997).

In addition, studies of seed dispersal networks provide a holistic approach to ecosystem restoration that has shown to be helpful in both the planning and monitoring stages for forest regeneration projects (Traveset *et al.*, 2014). Understanding which frugivore species are present and active in heavily deforested habitats is essential for reforestation efforts. Species diversity and interaction network data infer what species contribute the most to passive reforestation and which natural seed-dispersal dynamics are most important to consider when maintaining and regenerating degraded habitats. This study, and others like it, allows for the analysis of differences between the frugivore communities of different habitats, which provides ecologists and restoration planners to infer the impacts of deforestation on frugivore diversity and seed dispersal activity. As such, the knowledge attained through this research and similar studies is essential to future reforestation project planning and implementation and should be used to infer which species contribute the most to tropical reforestation to utilize natural seed-dispersal dynamics. Future research should aim to replicate this study to achieve results that are more representative of the habitats studies and to investigate how the results of diversity and seed dispersal network analyses can be used as tools in reforestation projects to restore ecosystem diversity and networks in degraded and deforested tropical habitats.

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