Community diversity of butterflies and their composition factors across three habitat types in a neotropical montane cloud forest

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ABSTRACT

While many forest ecosystems are at risk of fragmentation due to exploitation and land-use conversion, Costa Rica has prioritized the restoration of natural habitats like forests, where butterflies serve as useful indicators of habitat quality and insect diversity. To identify how various habitat types influence biodiversity assemblages, this rapid survey assessed butterfly diversity through two gradients of reforested habitat and primary forest, with fruit-feeding taxa sampled via baited traps and nectar-feeding taxa sampled via hand-net. Planted forest contained highest species richness and abundance of nectar-feeders, and the highest abundance of fruit-feeders. Species richness of fruit-feeders was highest within naturally regenerating forest. Primary forest contained the lowest abundance and richness of the forest types, and the hypothesis that all forest types contained equal diversity is rejected (p=5.99, x^2=22.29). Community similarity between habitat types was low, and lowest between primary and naturally regenerating forest. Diversity indices were highest in naturally regenerating forest, including Shannon and Simpson diversity and evenness measures. Planted forest, while high in richness and abundance, contained lowest diversity measures in frugivores while primary forest held lowest diversity measures of both guilds collectively. This survey represents a limited understanding of the butterfly community within Cloudbridge reserve, but if repeated could provide a means to assess longer-term diversity response following reforestation. Restoration of natural habitats is a crucial tool in mitigating consequences of the biodiversity and climate crises.

INTRODUCTION

The complexity of biological assemblages and factors influencing diversity within ecosystems are of primary interest in ecology. The operational structure of an ecosystem, and the more specific hierarchies therein, are determined by several interrelated and competing factors. While discriminate and incongruent in how they influence different communities, these factors indicate patterns of potential and realized biodiversity within an area. Biodiversity is closely linked to environmental resources, which form defining components of a habitat and are critical for all biological forms to carry out their life cycle. These resources include a diverse array of fundamental items including forage and nutritional sources, roosting/resting space, mating and nesting territory, and exploratory areas. A resource-based perception of habitat is useful for understanding species assemblages and their requirements, as resource quality and abundance determines productivity of environments and allows for greater species diversity (Dennis et al. 2003). Habitat heterogeneity is the variation of morphological structure and constitutes an important variable of the environment. Foundational vegetation provides more complex resources used by complementary life forms of comparatively high trophic levels, such as insects, who utilize the architectural landscape of habitat and heterogeneity therein. Heterogeneity implies increase in complexity of the microhabitat and microclimate, supporting niche specialization and taxonomic diversity. For example, heterogeneity would be greater in primary forest than silviculture plantations because inherently higher plant diversity and abundance results in more vegetational layers, developing smaller scales of habitat and climatic conditions which allow for greater faunal diversity and abundance (Ramesh 2010). Age also allows for plants of the primary forest, in this same example, to vegetate and develop increasing complexity and variability. Quantity of time environments have existed and been available for habitation is another causal factor of biodiversity. Time and stability allow species to adapt to environmental conditions and resources, and older habitats tend to contain more biodiversity than younger ones. Climate, another determinant of biodiversity, shapes patterns of conditions like heat and humidity within environments, influencing physiological requirements for flora and fauna while indirectly affecting resource and habitat qualities (Menéndez et al. 2007). These are strong determining forces for species' habitability of an area. Even microclimatic conditions like light penetration to forest floors can be a powerful force to more sensitive taxa like butterflies (Shulze et al. 2004; Bobo et al. 2006), which require floral resources and sunny conditions.

Add to this complexity of interacting variables the impact of mankind in affecting biotic and abiotic processes at various ecologic levels. The influence of artificial pressures is powerful and expansive, causing compositional and structural loss of biological communities globally. Destruction and modification of habitat, land-use change, pollution and chemical biocides, overharvesting and overcollection, isolation of habitat, and anthropogenic climate change have stressed ecosystems and caused significant landscape change in relatively short time spans. These impacts play a significant role on distributions of flora and fauna, transforming natural environments

while causing cascading effects across species assemblages. All species have unique requirements, resulting in differences in how natural and anthropogenic disturbances affect ecosystems and taxa therein (Ribeiro et al. 2012; Steffen-Dewenter & Tscharntke 2000). Insects are a taxon sensitive to environmental changes because they require a wide array of resources, which are altered during habitat modification (Lourenço et al. 2022). Land-use management changes drive destruction, fragmentation, and isolation of habitat while damaging resources, altering their availability and quality (Lourenço et al. 2022). Butterflies are especially connected to resources because of high dependence on foraging and nutritional sources (Ehrlich & Gilbert 1973; Singer 1974). Highly diverse plant communities often indicate more diverse butterfly communities (Sharp et al. 1974; DeVries 1992; Maharaj et al. 2019), and vegetation characteristics like distribution and abundance of foodplants are a primary element of habitat quality (Kalarus & Nowicki 2015; Maharaj et al. 2019; Ramesh 2010). Resources required for survival and reproduction (e.g. imago nutriment sources, larval host plants) provide important signals in habitat selection (Maharaj et al. 2019; Ramesh 2010), and butterfly assemblages respond to the local landscape structure of vegetation assemblage (Ribeiro et al. 2012; Sharp et al. 1974; DeVries et al. 1999). This landscape-level vegetation microstructure can be a stronger determinant than local plant phylogenetic diversity (Sharp et al. 1974), indicating habitat heterogeneity is more important than nutritional sources in certain situations and environments. Butterfly assemblages vary throughout spatial and temporal scales, due to changes in plant composition and resource abundance or quality often following disturbance or seasonal changes (DeVries & Walla 2001; DeVries et al. 2012; DeVries et al. 1999; Grøtan et al. 2014; Pozo et al. 2009). Furthermore, patterns of movement in butterflies are often based on host plant distribution, resource availability, and landscape structure (Lourenço et al. 2022). Describing these correlations and variables is essential to better understand butterfly diversity and habitat use for use in effective conservation practices (Lourenço et al. 2022)

Because of the scale of habitat loss, the restoration and protection of natural ecosystems is necessary for the conservation of biodiversity and habitable living conditions for all species. Since there is considerable variation in butterfly assemblages based on vegetation composition and structure – and dependency of larval and imago fitness on specific plant resources – butterflies have a strong connection to their habitat, making them a valuable bioindicator for environmental monitoring (Mukherjee et al. 2019; Bobo et al. 2006). Furthermore, short generation times, well-described taxonomy, and ease of sampling, makes them a suitable indicator for environmental assessment (DeVries et al. 1997; Lourenço et al. 2022). While butterflies are viewed primarily as pollinators and nectivorous insects, there are two distinct feeding guilds (DeVries 1987). Nectar-feeders nearly exclusively visit flowers and obtain majority of their nutritional requirements from nectar. Fruit-feeding butterflies are typical of tropical latitudes, and represent 50-75% of all neotropical Nymphalids (comprised of Satyrinae, Charaxinae, Biblidinae, and some tribes of Nymphalinae) (Freitas et al. 2014; DeVries et al. 1997). These fruit feeders rarely visit flowers, instead obtaining nutrition primarily from rotting fruit, plant

sap, animal excrement, and decaying material (DeVries 1987; Freitas et al. 2014). As such, study of butterfly diversity and habitat across gradients of human land-use intensity can provide insight on status of health and biodiversity, and assist with development of appropriate conservation plans.

METHODS
Study Site

At Cloudbridge Nature Reserve (CNR), on the Pacific slope of Cerro Chirripó within the Cordillera de Talamanca, land formerly managed for agricultural use was purchased and subsequently established as a conservation area for the purpose of reforestation and research. In many areas of the reserve, the land was left to regenerate without human intervention. Where natural regrowth was slow, tree planting took place to supplement regeneration. In order to best replicate natural forest, planted species included natives that were dominant in the primary forest community including *Ulmus mexicana, Quercus rapurahuensis, Cedrela tonduzii, Alnus acuminata,* and *Inga oerstediana* (Redman 2019). The reserve reaches from 1500m to 2600m of elevation above sea level and includes 288 hectares (ha) of land, 28 ha of which is primary forest and 255 ha comprised of secondary forest of various ages, converted from plantation and pasture use. The land falls mostly within the delineation of a lower montane cloud forest zone, with higher altitude areas described as upper montane cloud forest (>2000m) (Bubb

et al. 2004; Redman 2019). Average annual rainfall is 2550mm, ranging from 2300-2900mm under typical conditions with about 90% falling in the wet season (Redman 2019). The longer wet season, or *invierano*, lasts from late April to early December – peaking in October. A pronounced dry season, spans from late December to early April. The defining quality of cloud forest is consistent cover of clouds and mist that moves at vegetation or ground level, immersing tree crowns in moisture and increasing ambient humidity (Ray 2013). Even during *verano* – or dry season – this phenomenon occurs regularly, facilitating condensation of cloud vapour onto vegetation surfaces as 'direct interception' of moisture. Many plants are specifically adapted to utilize this form of 'horizontal precipitation', and accounts for ~30% of total annual precipitation, often exceeding vertical rainfall in the dry season. This alternative mechanism of precipitation is additive to standard vertical rainfall, and not considered in the above rain measurements.
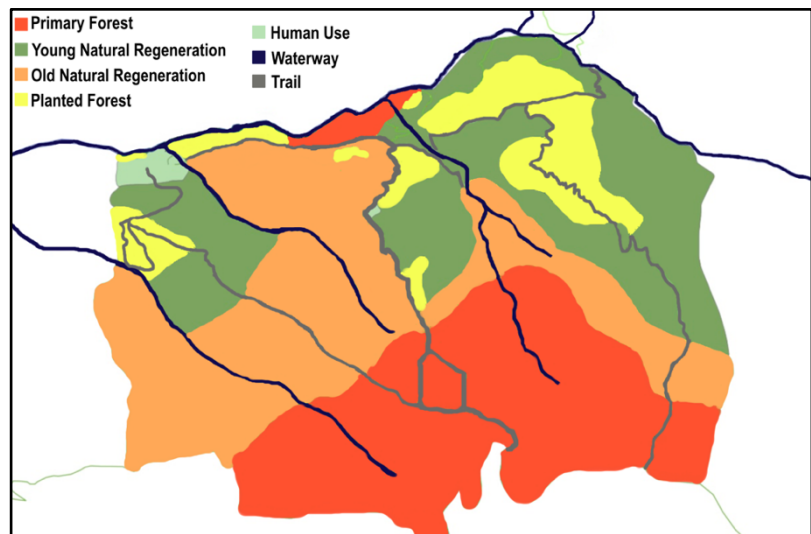

Figure 1: Map of forest types within Cloudbridge Nature Reserve. Note that 'old natural regeneration' was not used as a separate forest type for this project due to variations in time of last disturbance within the zone and especially compared to 'young natural regeneration'. Restoration of 'planted' forest and 'young natural regeneration' both commenced approximately 20–22 years ago.

Field Methods

Within Cloudbridge Nature Reserve, 36 sites were chosen and documented within representative areas of the three forest types, an equal number selected in each (12 sites per forest type). Selection was based on the correlating factors of forest age and habitat type, with the guide of a map (Figure 1), and positioned far as feasibly distanced with extra space especially considered between forest types. Cylindrical net-traps were rotated through sites, with 6 traps being setup and baited each time. Traps were checked daily when possible (>80% of the time), with no more than three days going between takedown and setup at the next 6 sites. Traps were stocked with a bait of fermenting bananas (locally obtained), mixed with raw sugar and yeast for at least 24 hours to enhance fermentation processes. The base of the traps were hoisted over a branch 2-3m above ground. Between the takedown of previous six traps and subsequent setup at another six sites, each forest type could be sampled in two days and all 36 sites could be sampled within 6 days – assuming daily maintenance. This protocol was executed from mid-February to mid-April, during peak dry season until conclusion of the dry season. As an addition to more systematic sampling of the frugivorous guild, butterflies were also captured via manual netting to gather information on the nectar-feeding guild not attracted to fruit baits, but remaining a visible and crucial part of the Lepidopteran community. From early March to mid-April, these nectivorous butterflies were caught opportunistically en route to and from baited sites, increasing data and learning value on both guilds of imago butterflies. When trapped (baited and hand-netted), specimens were extracted and placed into a petri dish for photographs prior to release, and site location was noted among other qualities. For the manually-netted nectar-feeders that were often trapped in open areas (e.g. main trail), if trap location did not fall into the strict limits of a forest type it was noted to be found in a forest edge.

Statistical Analyses

Community abundance data was analyzed by calculating various diversity indices for each forest type. Data were differentiated between counts at baited sites and counts of opportunistic manual trapping, and indices were calculated for each sample group (Table 1). The hypothesis that all forest types would contain equal diversity was assessed using a chi-square test, with expected values calculated as the average of the sum of all forest types species' richness. Total abundance (both guilds) was not assessed using statistical analyses because inequalities in sampling effort and technique
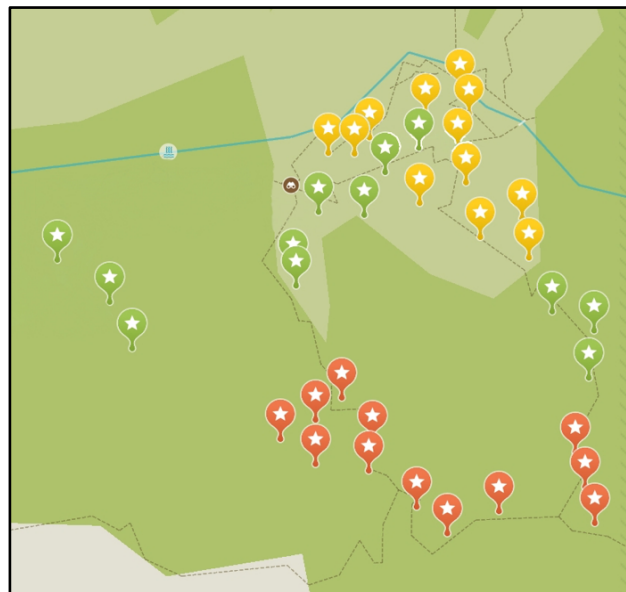

Figure 2: Relative locations of all 36 baited sites, six of which would be baited at any one time. Pins coloured yellow denotes sites within 'planted' forest, green denotes sites within 'naturally regenerating' forest, and orange denotes sites within 'primary' forest. 49 metres separated the sites of closest proximity not within the same forest type.

between would result in erroneous calculations not indicative of true diversity within the reserve. Beta-diversity (β-diversity) is often defined as the component of total diversity among community subdivisions, or the relative difference among divisions of the community (DeVries et al. 1999). Many formulas have been used to estimate β-diversity, the simplest of which is to calculate the total number of species unique to each of the subdivisions in a community. Morisita's index is a normalized calculation of community similarity, and the inverse of this index can be used as an estimation of β-diversity (1 – M). As this index encompasses two community partitions, a single value inherently represents the difference between these partitions. Abundances of both guilds and (exclusively) frugivorous butterflies were graphed (Figure 3), using fruit-feeders counts at baited sites and opportunistically trapped via hand net for the nectivorous guild. Species richness was also graphed (Figure 4), comparing frugivores to both

guilds of butterflies, using data from baited sites and opportunistic hand netting. This contrasts with the information in Table 1, where all calculations of the frugivorous sample therein used counts solely from baited sites. Richness counts included the 'forest edge' as a subdivision/habitat type in order to include more context of the greater diversity within the reserve.

RESULTS

A sum total of 277 adult butterflies were trapped, including 139 frugivorous butterflies at baited sites and another 138 individuals opportunistically with a hand net. *Satyrotaygetis satyrina* was the most abundant species, comprising over 48% of the individuals trapped at baited sites and over 28% of total trapped individuals. The next most abundant frugivores were *Cyllopsis argentella* and *Drucina leonata*, making up >10% and >9% of baited individuals and >8% and >6% of the total trapped sample, respectively. Of the frugivorous individuals caught at baited sites, five species were

Table 1: Biodiversity measures of exclusively frugivores and frugivores plus nectivores in each forest type. Nectivores were caught only by manual trapping, whereas frugivores were caught only by baited traps. These data do not consider fruit-feeders caught by manual trapping. A single Morisita similarity value represents species richness overlap between two habitat types.

|	Planted Forest		Naturally Regenerated		Primary Forest	
	Both Guilds	Frugivores	Both Guilds	Frugivores	Both Guilds	Frugivores
Total Abundance	109	67	82	50	34	22
Richness						
Species	22	11	21	12	12	9
Subfamilies	7	3	7	3	4	2
Diversity						
Shannon-W D	2.295	1.545	2.486	1.920	1.935	1.727
Simpson D	0.831	0.659	0.892	0.803	0.818	0.801
Evenness						
Shannon-W E	0.636	0.545	0.688	0.678	0.536	0.610
Simpson E	0.854	0.700	0.916	0.853	0.841	0.851
	between Planted-Naturally Regenerated		between Naturally Regenerated-Primary		between Primary-Planted Forest	
Morisita Similarity	0.152	0.352	0.146	0.244	0.193	0.348
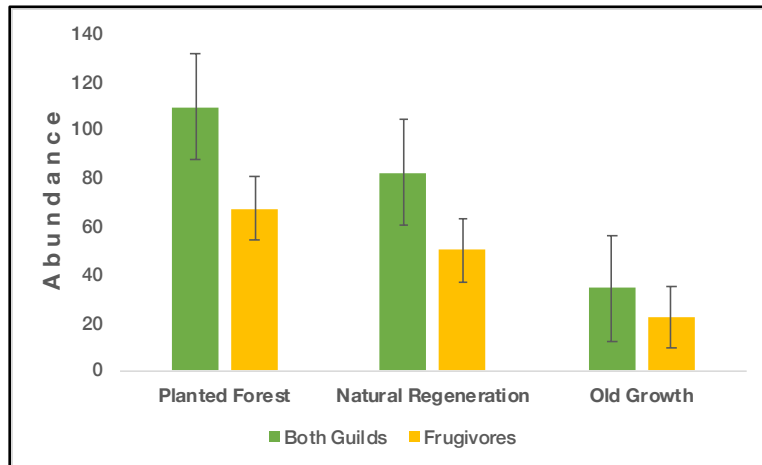
Figure 3: Abundances of exclusively frugivores and frugivores plus nectivores in each forest type +/- 1 standard error. Nectivores were caught only by manual trapping, whereas frugivores were caught only by baited traps. These data do not consider fruit-feeders caught by manual trapping. It is important to note these counts cannot be strictly compared due to inequalities in sampling effort and trapping method, however there is relevance to illustrating both together to deduce abundance relationships.

df=2, x^2=22.29). Morisita similarity between habitat types was broadly low, and lowest between primary and naturally regenerating forest (Table 1). All diversity indices were highest in naturally regenerating forest. Planted forest, while high in richness and abundance, contained the lowest diversity measures in frugivores, indicating this habitat type was dominated by relatively few fruit-feeding species. Primary forest contained lowest diversity measures of both guilds combined, indicating nectar-feeders were sparse here.

singletons (represented by a single individual captured), and three species were doubletons (represented by two individuals captured). Out of opportunistic manual captures, Ithomiini butterflies were most abundant. Planted forest had the highest abundance of individuals, with >48% of individuals trapped at baited sites and >39% of total trapped butterflies. Naturally regenerating areas contained >35% of individuals trapped at baited sites and >29% of total trapped individuals. Primary forest had the lowest abundance of all habitat types, containing >15% of baited captures and >12% of total trapped butterflies. The 'forest edge' habitat type, although sampled with less effort and differing method as other forest types, contained >18% of the total captured individuals. The hypothesis that all forest types would contain equal species richness is rejected (p=5.99,

DISCUSSION

High degrees of endemism are characteristic of tropical montane areas, including the Cordillera de Talamanca. In general, tropical forests often contain high species diversity
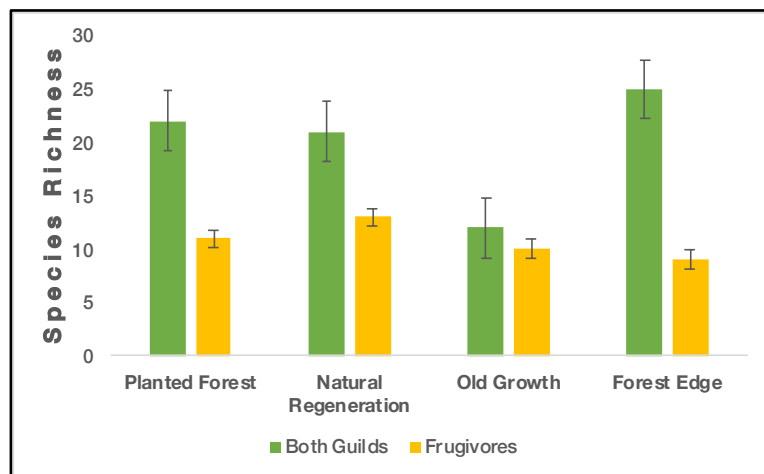

Figure 4: Species richness of exclusively frugivores and frugivores plus nectivores in each forest type +/- 1 standard error. Nectivores were caught only by manual trapping, whereas frugivores were caught by bait and manual trapping. The 'forest edge' type was added to illustrate the number of species caught by random manual trappings within open clearings, outside the delineation of three specified forest types. It is important to note these species counts cannot be strictly compared due to inequalities in sampling effort and trapping method, however there is relevance to illustrating both guilds together to deduce species richness relationships.

with relatively low abundances of species, but montane cloud forests are more extreme environments and typically less species-rich than lowland and mid-elevation rainforests. These qualities make the mountain range of unique interest in conservation biology, and surveying of its biodiversity is important and useful for ecological study. Promotion of conservation and habitat restoration, like at Cloudbridge Nature Reserve, has been prioritized throughout Costa Rica for decades (Montagnini & Finney 2011) and allowed fragmented habitat areas to develop into larger patches of forest and gradients of disturbed habitat. Studying and monitoring these landscapes can provide insight into changes taking place among ecosystem processes, and how habitat restoration can be optimized to efficiently improve biotic and abiotic conditions.

 Understanding ecology of butterflies and other insects is an effective and relatively easy way to assess the community of important players and draw conclusions about larger ecosystem dynamics. This survey has provided insight on the diversity of two guilds of butterflies and their distribution within variation of forest types and disturbance levels. Perhaps surprisingly, primary forest butterfly abundance and richness was lowest. This forest type seems to lend itself to less butterfly activity, having cooler ambient temperatures and less penetrating sunlight. These variable environmental conditions, resulting in reduced butterfly activity, may make trapping more difficult, especially during wet days and seasons (Murillo-Hiller et al. 2019). Being sensitive to changes in sunlight, it acts as an important activity determinant for butterflies (Brown & Hutchings 1997), and lack of penetration to the primary forest floor is due to increased cloud cover and canopy closure.

Additionally, in the reserve, primary forest exists only above 1900m of elevation, besides one small fragment bordering the Río Chirripó Pacifico (Redman 2019). As such, this forest type is a more specialized environment and biotic organisms must be adapted for such conditions. Butterflies best adapted to conditions within a mature montane forest interior, will not make up the most of taxonomic diversity within an area (like the reserve), as most species will likely be generalists or less exclusive towards specific conditions and vegetation structures. Decreases in plant diversity will also generally result in decrease of butterfly diversity, especially if those taxa are larval host plants.

A surprise of this survey was the variability of results between naturally regenerating forest areas and planted areas. Morisita value of both guilds was lowest between forest types, meaning β-diversity was highest. More information on these habitat types provides appropriate context, and common forestry measurements can add insight as to how forest regimes differ in the reserve. In a study at CNR, Redman (2019) found that planted plots were further developed – with tree height, canopy closure, litter fall, and basal area greater than naturally regenerating plots of similar age. Yet, tree density in planted plots was notably less relative to naturally regenerating areas, owing at least in part to varying processes of forest regeneration between planted plots and naturally regenerating areas. Planted plots were largely 'problem' areas where natural regrowth was slow or nonexistent, and planted species included many climax species that would be atypical of a regenerating pioneer community. While planted species also included fast-growing flora, especially *Cecropia obtusifolia,* these plots had

substantially higher richness of climax species than a pioneer community (DeLyser 2015). Of 259 identified species of planted plots, 69 were climax compared to unplanted communities with only nine climax species out 223 (DeLyser 2015). Climax species, such as *Quercus rapurahuensis* and *Ulmus mexicanus*, are typically much larger specimens than fast growing, light-needy vegetation. These species also need more space to grow, and planted plots were less densely planted than plots of natural regeneration. These differences in reforestation processes have a clear impact on plant phylogenetic diversity and a resulting impact on diversity of vegetation structure within forest types.

Naturally regenerated and primary forest butterfly communities also contained more variation than expected. While notable differences exist between their environments, they are closer in proximity and elevation relative to planted areas. Additionally, naturally regenerating forest had higher tree density and more standing dead wood and tree mortality (Barz 2016), demonstrating natural processes of old-growth forest. However, similarity measures were lowest out of the other two compared areas for the frugivorous guild and both guilds. This is likely due, at least partially, to the aforementioned variability of reforestation processes. Naturally regenerating forest areas are developing by natural succession following severe disturbance and have significantly fewer large climax species than the primary and planted forest areas (DeLyser 2015). By natural succession it will likely take upwards of 100-200 years to replicate old-growth phylogenetic and structural complexity of vegetation. These differences have a profound impact on butterfly and other faunal diversity. Availability and quality of various resources are strong determinants for association and usage of habitat (Dennis et al. 2003), and are inherently unique between environments with significant variation in phylogenetic diversity and ambient climatic conditions. This heterogeneity in large and micro scales promote formation of animal communities, especially insects that rely on stable ambient conditions and complex array of resources (Brown & Hutchings 1997). Also of note in determining faunal diversity within environments is randomness, or stochasticity, which can produce low predictability of community composition and sampling results. While difficult to assess at any one time, high environmental and demographic stochasticity of faunal assemblages makes sampling of these groups difficult, especially in more complex environments and more fragmented environments (Brown & Hutchings 1997; Habel et al. 2016). While primary forests have had millennia to stabilize and develop intricacy, this is not the case for naturally regenerating areas that will continue to successively mature taxonomically and morphologically, more so than planted areas that already have a baseline of climax species. These factors likely play substantial roles in the dissimilarity of butterfly community composition within the primary and naturally regenerating forest types. Additionally, measurements of diversity are not always equally comparable between different study areas. The values they yield reflect species within the sampled community, and not all species are equal in conservation value. Endemic species and specialists, likely more relatively abundant in primary forest, are critical for the functioning of primary plant communities and more valuable to conservation biology (Bonebrake

et al. 2010; Hamer et al. 2003; Steffen-Dewenter & Teshanke 2000). Measures calculated from an intact old-growth community will likely represent the diversity of more specialized biota with narrow niches, and measures from a disturbed, human land-use regime will reflect a different set of species with broader niches and geographical ranges (Vu 2009). Thus, even if species richness, abundance, evenness, diversity, and similar measurements are close in number, results cannot be equated and the old-growth community sample will represent a more valuable and healthy ecosystem relative to an anthropogenically disturbed community irrespective of measurement number.

This survey is characterized by a high relative abundance of subfamily Satyrinae, a highly diverse and common woodland taxon. Some authors argue that high abundances of Satyrines are a sign of a healthy and typical neotropical forest community (Brown & Hutchings 1997), however others have noted that high abundances of Satyrines often indicate a disturbed forest environment (Ribeiro et al. 2012). Daily & Ehrlich (1995) posit that especially Charaxinae and Nymphalinae are probably better indicators of forest interior conditions than Satyrines, and within the subfamily tribes Brassolini and Morphini are better than Satyrini. Many Satyrines depend on monocotyledonous plants like grasses, palms, and bamboo as larval hosts, and for this reason they often thrive in disturbed areas or forest edges and clearings where these florae exist, especially Brassolini (Ribeiro et al. 2012; Araujo et al. 2020). For Satyrini and Brassolini, microhabitat heterogeneity is especially decisive in determining community composition and usage of an area (Ribeiro et al. 2012). Like many tropical insect communities, butterfly taxon exhibit

variation in usage of habitat factors like phylogenetic diversity, structural complexity, and abiotic conditions, thus segregating into spatial and temporal dimensions (DeVries et al. 1999; DeVries et al. 1997; Voltanen et al. 2013; Grøtan et al. 2014). Seasonal fluctuations like precipitation and temperature changes can act as cues of resource availability, prompting behaviours such as foraging, reproduction, and dispersion of butterflies and other insects (Lourenço et al. 2022). Segregations increase complexity of trapping and study of neotropical butterfly community composition, and are a variable that should be taken into account to portray accurate conclusions (DeVries & Walla 2001; DeVries et al. 2012; Bonebrake et al. 2010). Due to time constraints, this survey was unable account for these various dimensions, implying results deliver only a limited picture of butterfly composition at CNR. Spatial and especially temporal variables like seasonality are highly complex, and require many years of systematic sampling to understand the extent of variation within community composition or species population dynamics (DeVries & Walla 2001). Satyrine abundance in this survey is likely a result of the limited scope of time and methods. While many Charaxinae, Nymphalinae and Biblidinae preferentially fly in the canopy, Satyrinae is mostly associated with understorey vegetation (DeVries & Walla 2001; DeVries et al. 2012; DeVries et al. 1997; DeVries et al. 1999), although canopy species have been reported to descend in forest clearings/edges (Daily & Ehrlich 1995; Vu 2009). An extensive survey with protocols allowing for factors of seasonality and vertical variation, although canopy trapping may be difficult or

impossible in areas of the reserve lacking taller vegetation, especially large trees. The most abundant and species rich nectivorous taxon was Ithomiini, which are often associated with specific microhabitats based on abiotic conditions like sunlight and humidity (Bonebrake et al. 2010). Ithomiini are a diverse tribe of Danianae notoriously difficult identifying to the species level without electron microscopy in part due to lack of wing pigment and detail. They are relatively poor fliers, relying on unpalatability to avian predators in consequence to their sequestration of alkaloid compounds obtained from certain plants often growing in forest clearings (DeVries 1987; Beccaloni & Gaston 1995). This perhaps explains their high abundance within open forest edges in this survey, outside of strict forest types. In addition, Ithomiini often contract their range, congregating into high concentration 'pockets', such as leks, during dry seasons (Freitas et al. 1996). This is similar, yet more intense than many other migratory butterfly species, which often move into more humid forest interiors during *verano* (Kricher 2011; Murillo-Hiller et al. 2019). In this survey, it was predictably difficult to identify the most common taxon down to species level. The author suspects there are two or more glasswing species in this survey that were among the most abundant nectivorous taxon, but due to identification difficulties these were amalgamated into a single species for the purpose of data analysis (believed to be *Pteronymia simplex* or *Episcada salvinia*). Another abundant Ithomiini taxon with more wing detail was treated as a single species (potentially *Greta morgane* or *G. andromica*). Of the frugivorous guild, small Satyrines of *Cyllopsis* sp. also presented identification challenges and was allotted

two species in data analysis (*Cyllopsis argentella* and *C. philodice*), but there was likely one or two more species from this genus trapped during fieldwork that has been confirmed within CNR in prior surveys (e.g. *C. rogersi*) (Powell & Champion 2019). Because of these identification issues and resulting treatment of combined taxa as a single species, this survey underestimates species richness within CNR. Specimens representative of *Oxeoschistus cothonides,* trapped once within the 'planted' forest type in this survey, have historically been treated as a separate species (Warren et al. 2016). Following genetic and morphological analysis by Pyrcz et al. (2020), these specimens were found to be a female form not presenting sufficient physiological differences from *O. cothon* to impede copulation and species recognition, thus making reproduction between forms likely and not warranting separate species status. As such, the single trapping of this form was treated as a count of *O. cothon*.

The survey of Powell & Champion (2019) at CNR tested various baits and their usefulness for trapping butterflies, however all four baits tested were attractive only to frugivores. A study in Borneo by Beck et al. (1999) demonstrated several unique bait types to be effective in attracting nectivorous butterflies, foremostly sodium chloride and albumin (egg protein) solutions. During this survey, two bait types were trialed besides the standard banana mixture, including an albumin solution and salt-saturated beer – both of which yielded very little effectiveness. A solution capable of attracting both feeding guilds in order to sample all butterfly taxa simultaneously would certainly be of interest to bait-trapping studies, but this may not be possible considering the

segregated nature of both feeding guilds in the neotropics.

Results of this assessment are highly limited by short sampling period, seasonal and spatial constraints, and simple statistical analyses. The nature of research at CNR of intermittent, brief, small-scale surveys performed by undergraduate students limits the power of analysis and results, however with further study a more robust and detailed dataset could be established. It is the hope of the author that butterfly surveys with similar methods continue to be executed at CNR to develop a more comprehensive understanding of butterfly community composition in the Talamanca range and potential effects of various disturbance regimes. These short-term surveys become valuable for conservation knowledge and planning only after systematic, replicate, and consistent sampling cycles (DeVries et al. 1999).

It may be expected, given the attention received within conservation biology, that old growth and primary forests harbours highest biodiversity relative to younger and more disturbed forests. However, it is well documented that lower to intermediate levels of disturbance often increase diversity, including within insect groups (Mackie & Currie 2001; Shultze et al. 2004). Theoretically, with zero disturbance over evolutionary time, extreme stability could stagnate speciation as niche partitioning reaches equilibrium and colonization from unique species cannot be supported without sufficient opportunity. Ecological succession culminates, phylogenetic development is suspended, and environmental conditions remain stable. Without disturbance or competition, species ranges and niche requirements remain divided and securely independent, barring highly beneficial genetic mutations. Maximum stability can be reached in communities containing a specialized, efficient diet and niche where high species richness occurs (MacArthur 1955). Following a disruption, diversification and establishment of unique species can resume. Species with unique requirements, previously unable to colonize due to exclusivity of the perfectly stable environment, can utilize novel conditions and opened niche windows. The disruption allows previously separate niche partitions to overlap and thus develop competition between species that were segregated prior to disturbance of old-growth dynamics (Davis et al. 2001; Shultze et al. 2004). While this theoretical zero disturbance scenario may seem impossible given the complexity and chaos of ecosystems – especially in the modern epoch – insubstantial disturbance events could well deter development of biodiversity, especially in a secluded montane cloud forest. This trend may help explain how small-scale disturbance can assist in proliferation of diversity, and in this survey, how a reduction of richness and abundance occurs within primary forest.

Greater biodiversity within disturbed and secondary habitat types may be implied to mean these habitats are more important for and deserving of conservation than old growth and primary forests, however this is oversimplistic and a misunderstanding of ecosystem value (DeVries et al. 1997). If all old growth habitat was converted into secondary habitat, specialists would be more unlikely to persist with increasing separation from their ideal conditions (Shultze et al. 2004), allowing over-proliferation of generalists and reducing overall diversity and evenness (DeVries et al. 1997). Vegetation architecture and diversity is destructed,

losing the microhabitat, and replaced over time by comparatively small and simple vegetation structure that exists to exploit the novel ambient conditions. Meanwhile, environmental dynamics like biogeochemical cycles, soil conditions, and climatic regulation are altered. Such processes that involve complex contributing factors like microscopic fungal and bacterial associations, for example, are modified and potentially cannot wholly re-establish for extensive evolutionary time periods following severe disturbance. Several cycles of growth and decay of large climax species occur in order to create conditions and networks of functioning primary forest processes. Habitat conversion and fragmentation pressures promote dispersion, and butterflies must respond by altering behaviour within human land-use systems compared to natural forests (Scriven et al. 2017; Fermon et al. 2003; Lourenço et al. 2022). These pressures and resulting behavioural changes have clear relevance for study and conservation of insects in a highly disturbed and fragmented landscape. In tropical montane cloud forests, in addition to loss of phylogenetic diversity and its habitat-providing structural complexity, deforestation for land-use conversion modifies water provisioning services and deteriorates climatic regulation and stability (Redman 2019). Soil organic matter and infiltration rates, important qualities for provisioning of water to humans and other biota, are also compromised (Redman 2019). Vulnerable ecosystems like TMCFs are increasingly at risk from disturbance and climate change consequences, as cloud formation processes depend on evapotranspiration and orographically lifted vapour masses (Ray 2013; Smith 2001). Disruption to these processes has already

occurred following lowland deforestation, resulting in changes of moisture deposition on crown trees and epiphytes, for example (Ray 2013). This process is critical for cloud forest functioning and will alter vegetation productivity, nutrient uptake, soil composition, climate patterns, short-term weather conditions and extremes in a drought-sensitive plant community (Ray 2013; Smith 2001). In a similar highland forest in Monteverde, Costa Rica, increases in air temperature have been observed, in addition to shifts in communities of birds, reptiles and amphibians (Pounds et al. 1999). Within primary and old-growth communities, natural disturbances are often minor and usually beneficial for overall biodiversity. Natural disturbance and damage following storms, for example, forces trees to heal and allows opportunity for growth and expansion of new species in the altered environment. For resilient organisms like *Sequoia sempervirens* with strong capability to adapt and heal, tree injury and decay allows for proliferation of biodiversity within small pockets of organic material and water accumulated over time, becoming a thriving substrate for invertebrates and other fauna high above the forest floor (Sillett & Van Pelt 2007). The slow decay of crown woody material promotes accumulation of biodiversity beyond the scope of exclusively timber-based management perspective (Sillet et al. 2022). A similar process, while more dramatic, occurs following treefalls where canopy area opens and abundance of sunlight promotes plant growth and increases microhabitat variability, often resulting in rapid accumulation of diversity, including butterflies (Brown & Hutchings 1997). This low to mid-level disturbance modifies habitat and conditions such that unique organisms can establish and utilize these resources of

the novel environment, and may be important for maintaining diversity in ecosystems (Brown & Hutchings 1997). Arboreal biodiversity is often closely associated with increased structural complexity in the form of reiterated trunks, and expansion of limbs, which are absent or highly reduced in secondary forests (Sillet & Van Pelt 2007). Strong correlations occur between development of vegetation structure and epiphyte abundance, where a low number of large trees serve as biodiversity hotspots for mosses, ferns, bromeliads, orchids and fauna frequenting these plant structures (Sillet & Van Pelt 2007). In fire-frequent areas, disturbance can be a necessary ecologic phenomenon. Certain species and forest types are dependent on wildfire, for example, to reproduce and function in the case of *Pinus banksiana*. While this is not typically a climax species, it is an important species of boreal forests using a common disturbance to its benefit and adapting to conditions detrimental to competing species, although these benefits can be compromised by more frequent extreme-severity wildfires. While severe disturbance can function to destroy habitat; natural, minor disturbance regimes often serve to promote development of forest biomass and diversity. Like many environmental phenomena, diversity-disturbance relationships are complicated and based on numerous competing factors, thus it cannot be assumed that all systems will result in consistent diversity peaks at intermediate severity and frequency (Mackie & Currie 2001). However, while multidimensional and convoluted interrelationships of environmental factors mean disturbance events do not consistently lead to dramatic biodiversity loss, it seems impractical to argue that large scale

disturbance including removal of habitat and/or substantial change of phylogenetic diversity in an area will have an insignificant effect on biodiversity of an area. Especially when anthropogenic disturbance surpasses natural disturbance in severity, scale, and/or quality, it could lead to irreversible regional restructuring of ecosystem processes (Brown & Hutchings 1997). It is relatively clear that intensive anthropogenic disturbance like land use conversion, climate change, clear-cutting, and extensive species endangerment and extinction has negative effects on diversity and structure of communities (Maharaj et al. 2019; DeVries et al. 1997), thus land must be managed to prevent disturbance from exceeding beyond intermediate levels to preserve and enhance biodiversity. Yet intact natural ecosystems should be the focus of conservation management, especially primary and old-growth communities which are increasingly valuable amidst crises of climate and biodiversity (Shultze et al. 2004; Sillet et al. 2022). Natural forests shelter species with narrow geographical and ecological ranges that tend to be more vulnerable to impacts of habitat loss, such as specialists and endemics which are inherently more valuable to conservation (Bonebrake et al. 2010; DeVries et al. 1997; Hamer et al. 2003; Steffen-Dewenter & Teshanke 2000). Where primary ecosystems have already been converted to intensive human land-use areas, natural processes can be at least partially restored by promoting diversity of plant community so economic objectives can be balanced with ecological and holistic well-being (Sillett et al. 2022). When land-use management is optimized for equitable approach of human interests like economic prosperity and food security while promoting ecological health and earth system function, multiple benefits

can be realized. Within agricultural, silvicultural, and urban systems a modification of practices is needed to balance these goals, including incorporating more diverse plant regimes. High biodiversity within human land use systems will allow more natural ecosystem dynamics to flourish. While still suboptimal compared to old-growth habitat, more naturalized human-use areas could potentially be utilized as corridors and stopover sites of acceptable habitat for dispersing and migrating fauna like insects and birds (Rice & Greenburg 2000). Acting as a buffer, naturalized areas promote stability of populations and trophic networks instead of adding to the matrix of mostly unusable land area. In Costa Rica, 'rustic' plantations with native tree species offer natural shade of food and/or money crops such as cacao (Rice & Greenburg 2000). By retaining native vegetation, these systems incorporating relatively high diversity of trees and plants can retain coevolutionary relationships like natural pest control and pollinators, groups essential for functioning of ecological systems and global food security. These polyculture systems harbour numerous economically relevant plant cultivars grown with various floral species, including natives. Such systems can be increasingly manipulated to promote small-scale development of biodiversity (Rice & Greenburg 2000; Sillet et al. 2022), supporting a more species-rich and abundant community of predators and parasites of herbivorous insects relative to intensive monoculture. Understanding differences of ecological communities among various habitats and their responses to disturbance allows for development of knowledge, not only about individual taxon, but generally for the purpose of conservation and sustainable natural habitat management (Robinson et al.

2012). While this discussion has explored that complexity of insect community composition is substantial, simply providing resources that plants and animals need to complete their life cycles represents a starting point for the restoration of biodiversity and ecosystem health. The more precisely we understand determining factors of biodiversity in various systems, the clearer it will become how they respond to changes in their environment (Dennis et al. 2003), and how we should respond on a management level. With this knowledge, humans can play a more constructive role in conservation of ecosystems. While conceptively simple, holistic land system management will require a robust shift in perspectives and priorities, and a mobilization of action to restore natural environments and ecosystem services.

CONCLUSION
Butterflies are relatively well studied, and many insights have been explored regarding dynamics of community composition. Clearly, variability and complexity of vegetational structure – heterogeneity – is central to these dynamics of butterfly diversity and abundance, especially in small scales (Ribeiro et al. 2012). Spatial and temporal dimensions are also important influences of diversity as many species exhibit strong correlations to variation in spatial scales – like understorey and canopy stratification (DeVries & Walla 2001; DeVries et al. 2012) and temporal scales – like seasonal population and reproduction cycles (Grøtan et al. 2014; Voltanen et al. 2013). Physiological parameters of environmental conditions are also a strong determinant of assemblages due to sensitivity to climatic (and micro-climatic) conditions such as sunlight, humidity,

precipitation, and temperature. Availability and quality of life-history resources like host plants, roosting sites, and courtship sites were not strictly assessed in this survey, but also act as important features for butterfly habitat use and distribution (Kalarus & Nowicki 2015). Interspecific interactions like mutualism and predation also influence activity, evolution, and composition of butterfly species (DeVries et. al. 1997; Ramesh 2010). All these interacting factors may differ in degree of importance at any time or place, or for various taxon, based on competing environmental forces, adding to a complex, chaotic dynamism of butterfly community composition. These intricacies are considered a primary cause of biodiversity in the tropics, and the complexity of these associations can help explain the staggering diversity of butterflies in the neotropics (Bonebrake et al. 2010; de Sousa et al. 2019). Reforestation efforts at Cloudbridge have shown it is possible to re-establish biodiversity and ecosystem function following severe disturbance and anthropogenic land use. By replanting large tree species essential to the climax community in the Talamanca de Cordillera, CNR has aided in the restoration of a montane cloud forest and accelerated succession within the reserve, imitating old growth biotic and abiotic processes. These changes have likely played a role in the community composition of fruit-feeding and nectar-feeding butterflies. Where complete reforestation is not feasible, a reintroduction of diversity, especially focusing on native flora, is possible within confines of a human land use area like agriculture or silviculture. The integration of diverse plant forms within anthropogenic areas can promote proliferation of animal diversity, environmental stability, and ecosystem

services. Allowing human-use areas to be used as acceptable corridors or stopover sites, if not suitable habitat for entire life cycles, will permit proper ecosystem function – helping mitigate pressures caused by climate and biodiversity crises. These changes, though challenging to undergo, will allow humans to develop ability to live harmoniously with the rest of the natural world, and realize the benefits of holistic health for all species.

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