BIODIVERSITY ANALYSIS USING CAMERA TRAPS BETWEEN SUB-HABITATS AND HUMAN DISTURBANCE WITHIN NEOTROPICAL MONTANE CLOUD FOREST

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Abstract – 329 words

Anthropogenic action and disturbance continue to impact terrestrial ecosystems, often affecting native fauna within these environments negatively, leading to biodiversity loss, population decline, and behavioural alteration. As conservationists aim to combat this, there is great interest in habitat regeneration, particularly reforestation and its role in recovering lost biodiversity. Stakeholders within the ecotourism industry also rely on natural habitats to attain an improved quality of life. One such habitat is the neotropical montane cloud forest, which is particularly vulnerable to climate change and human land use. Cloudbridge Nature Reserve, Costa Rica, is an example of restoration efforts for this biome, featuring a mosaic of sub-habitats grouped by forest age, from newly planted to old growth. Cloudbridge is an ecotourism destination, protecting the forest and showing visitors its unique wildlife. This research aimed to ascertain any differences between the biodiversity/abundance of different sub-habitats and assess the impact of visitors on the fauna. Corresponding hypotheses synthesised that (1) biodiversity and abundance would increase with forest maturity and (2) increased human disturbance would cause greater diel shifts in diurnal species to avoid peak human activity; nocturnal species would be unaffected. Sampling utilised on-trail camera traps within the reserve across the sub-habitat types to monitor mammalian and avian species. Results found that natural regrowth - the intermediate forest age - had the highest species total, but the old growth had the highest abundance. Overall, mammalian activity shifted away from peak human activity, whilst birds did not; however, both taxa showed species-specific responses. The discussion deliberates over the biodiversity/abundance results, with arguments from the literature suggesting that more mature forests support higher biodiversity, thus, the results may be due to methodological limitations. The conclusion highlights the ecological importance of habitats from all disturbance levels and their need for protection. The diversity and impact of behavioural changes are also discussed, emphasising that mitigation must consider both conservationists' and stakeholders' best interests. Deeper analysis of the studied variables exceeded the scope of this research, demanding further study.

Lay Summary – 327 words

Human action continues to impact land-based environments, often harming native wild animals. This leads to a decrease in the number of species, total populations, and alters their daily behaviour. As scientists aim to combat this, there is great interest in recreating lost habitats, particularly by replanting forests and how it can counteract localised animal extinctions. People employed in ecotourism, an especially nature-focused tourism industry, also rely on natural habitats to attain an improved quality of life. One such habitat is the neotropical montane cloud forest (NMCF), a misty, high-altitude rainforest, vulnerable to climate change and deforestation. Cloudbridge Nature Reserve, Costa Rica, is an example of restoration efforts for NMCF, featuring a mixture of forests at different ages, from newly planted to mature forest. Cloudbridge is an ecotourism destination, protecting the forest and showing visitors its unique wildlife. This research aimed to describe any differences between the diversity/sighting frequency of animals depending on the forests' age and assess the impact of visitors on the animals. It was predicted that (1) diversity and sighting frequency would increase with forest age, and (2) increased human presence would cause greater avoidance in species active during the day, avoiding peak human presence (nocturnal species would be unaffected). Motion-activated camera traps placed across forest ages were used within the reserve to monitor wildlife. Results found that the middle-aged forest had the highest species diversity, but older forests had the highest sightings. These results may come from limitations with this study's camera trapping, since some previous research suggests that older forests support more animal species. Overall, mammals avoided peak human presence times, whilst birds did not; however, all animals varied in response per species. It was concluded that all forest ages are important for wildlife and need protection. The diverse animal reactions to humans are also discussed, emphasising that actions to reduce their behavioural changes must consider both scientists' and the ecotourism industry's best interests. More research is recommended to fully understand these impacts.

SDGS

This research helps address three Sustainable Development Goals (SDGs): SDG 8 Decent Work and Economic Growth, SDG 15 Life on Land, and SDG 17 Partnership for the Goals. The results contribute to SDG 8 by informing stakeholders in ecotourism of the potential impacts of human disturbance, particularly on animal diel activity. The information provided can assist those employed within the sector to make informed decisions for controlling or mitigating these impacts. With this, they can ensure that their employment is more sustainable, which in turn improves the economic growth of communities and nations like Costa Rica as a whole. SDG 15 is addressed with the analysis of sub-habitat forest maturity and biodiversity/abundance. This details the effects of habitat restoration and recovery on a terrestrial ecosystem within a conservation context. It also highlights the important role of protected land, further backing support for 30 by 30 targets. For SDG 17, the informing and involvement of relevant stakeholders in both ecotourism and conservation helps contribute to this SDG. In doing this, greater partnership between these stakeholders can be fostered so that both people's livelihoods are protected, alongside protecting nature and wildlife.

Beneficiaries of research – 178 words

Two main stakeholders stand to benefit from the data of this research, the first of which is conservationists. The literature hotly debates whether the Earth is undergoing a sixth mass extinction event, prompted by the accelerated extinction of species due to anthropogenic activity (Cowie et al., 2025; Bocchi et al., 2025; Jarne, 2025). Regardless, global targets were set to conserve remaining ecosystems and restore lost habitats to combat extinction

(Convention on Biological Diversity, n.d.). The recovery modelling in Cloudbridge Nature Reserve could better inform conservationists on the efficacy of human-assisted reforestation, the expected resultant ecological changes and how it can help reach conservation targets. The other beneficiary stakeholder encompasses those in the ecotourism industry, especially in developing tropical countries. Ecotourism, when implemented responsibly, can be a sustainable economic and conservation framework that can improve the quality of life for locals employed in the sector (Miller et al., 2023; Hunt et al., 2015). A better understanding of how it can be managed more sustainably and ethically helps ensure its persistence for future generations, as well as conserving threatened species.

Introduction – 1298 words

Biodiversity and Ecological Recovery

Anthropogenic actions have generated significant repercussions on flora and fauna in terrestrial ecosystems. Prominent impacts include poaching (Mateo-Tomas et al., 2025), noise pollution (Kok et al., 2023), chemical pollution (Liu et al., 2025; Edo et al., 2024), invasive species introduction (Peller and Altermatt, 2024), and anthropogenically-accelerated climate change driven by greenhouse gas emissions from fossil fuels (Wu et al., 2025; Krueger et al., 2024). The most severe practice, however, concerns habitat destruction and degradation (Gonçalves-Souza et al., 2020; Heinrichs et al., 2016; Fischer and Lindenmayer, 2007). In tropical countries, natural forests are cleared primarily for agriculture and, to a lesser extent, urban development and infrastructure (Pendrill et al., 2022; Jones and Spadafora, 2017). These issues were prevalent in Costa Rica from the late 1800's, peaking between the 1950's-80's. This period saw agriculture, including bovine livestock, and crops such as bananas and coffee beans, as important contributing factors to the nation's economy (Obando, 2024). Consequently, many tropical forests were felled, making way for pastures (Obando, 2024). As the beef market imploded in the 1980s (Stan and Sanchez-Azofeifa, 2019), the country refocused its economy in the 1990s towards the growing tourism industry (Miller et al., 2023),

including ecotourism (Jones and Spadafora, 2017). Costa Rica was a natural fit for ecotourism due to its rich biodiversity, boasting 4-5% of all known species (Jones and Spadafora, 2017). Being in Central America, the country provides stopover and wintering habitats for New World latitudinal migrants (Menacho-Odio et al., 2025; Wolfe et al., 2014), alongside resident flora and fauna, combining to an estimated total of 500,000 species (Pullaiah, 2018). They inhabit several contrasting biomes, from montane páramo (Quesada-Román and Pérez-Umaña, 2020) to lowland rainforest (Genereux and Jordan, 2006) in a relatively small area of 51,100km² (Instituto Geográfico Nacional del Registro Nacional, 2021). To safeguard them, over 25% of Costa Rica's land was legally protected (World Bank Open Data, 2024; Steed et al., 2003) in national parks such as Corcovado (SINAC n.d.) and Chirripó (SINAC n.d.). An additional 11.2% was covered by private ownership as of 2003 (Environmental Law Institute, 2003), one such being Cloudbridge Nature Reserve (Cloudbridge Nature Reserve n.d.). This area was once agricultural pasture (Cloudbridge Nature Reserve n.d.) but is being anthropogenically reforested (Cloudbridge Nature Reserve n.d.). Due to the reserve's high-altitude location, the reforested habitat consists of neotropical montane cloud forest (NMCF) (Powell et al., 2022), a unique habitat where low-lying clouds regularly contact the vegetation, with much flora specially adapted to exploit this atmospheric moisture (Ray, 2013). Reforestation efforts have facilitated the natural regrowth (NR) of the NMCF (Cloudbridge Nature Reserve n.d.), as a secondary plant succession, alongside the existing primary forest (old growth (OG)), bridging to neighbouring reserves, such as the Chirripó National Park (van der Sanden, 2017, Cloudbridge Nature Reserve n.d.). Consequently, Cloudbridge can be viewed as a complex mixture of different forest sub-habitats, defined by their age. This varies from planted woodland (P) (up to 15 years) to NR (9 to 50 years old), then mature OG (more than 70 years) (van der Sanden, 2017). This comparative mosaic could be viewed as snapshots into temporal change in floral communities over time through plant succession. From this, it is possible to infer how the previously disturbed ecosystem progressively rejuvenates, including the trophic changes as the forest matures (Chazdon et al., 2006). Trends discovered from this may inform conservationists on the impacts of human-assisted

reforestation. Fauna-centric ecological recovery in NMCF is understudied, so this study aims to build on previous work (Díaz-García et al., 2020; Díaz-García et al., 2020), in which Cloudbridge has featured (van de Walle, 2024; Modrok, 2023; Smith, 2021; Marrocoli, 2007). Some of these contributions suggest that the NR supported greater biodiversity than the OG, aligning with the Intermediate Disturbance Hypothesis (IDH), which postulates that medium disturbance levels promote the greatest biodiversity (Connell, 1978). This, however, challenges the current reforestation efforts, which encourage plant succession (Cloudbridge Nature Reserve n.d.). Disentangling the knowledge gap is imperative given the NMCF's scarcity, biodiversity and vulnerability to climate change (Karger et al., 2021), as well as the conservational efficacy of the reforestation. The first aim of this paper is to discern the differences, if any, between the biodiversity of each sub-habitat in this environment.

The Ecotourism Dilemma

When considering tourism, especially in Costa Rica, for which a sizable portion of the economy is supported (Monge-González, 2016), it is imperative that the ecological impact is minimal and promotes the sustainability of socio-economic benefits (Samal and Dash, 2024). In 2024 alone, 2,919,483 people visited the country (ICT, 2024), many of whom came to see the vast biodiversity it offers (ICT, 2024). These high visitor numbers are financially beneficial in maintaining protected areas, upholding vulnerable flora and fauna preservation (Whitelaw et al., 2014). Reserves also provide employment opportunities for locals (OECD, 2024), supporting their economy, alongside several socio-economic advantages, e.g. improved educational possibilities, higher disposable income and overall quality of life (Hunt et al., 2015). Contrastingly, they can be detrimental to resident wildlife due to increased human disturbance (Fonda et al., 2025; Taylor and Knight, 2003). This can be characterised as anthropogenic noise, path erosion, littering or simply human presence (Shannon et al., 2017; Pimentel and Kounang, 1998; Wallin and Harden, 1996). Disturbance can induce stress in animals and damage their habitats, which, among other factors, compounds pressure on the fauna, reducing their fitness (Shannon et al., 2017; Pimentel and Kounang, 1998). Human

disturbance can cause some animals to alter their temporal activity (Gaynor et al., 2018), decrease their abundance (Palacios et al., 2022; Dirzo et al., 2014), or, for more sensitive species, be locally extirpated (Wan et al., 2019). This outcome is antithetical to the original purpose of protected areas, greatly attenuating their efficacy. Consequently, research, especially in understudied areas like the NMCF, is required to fully understand the impact of human disturbance on natural ecosystems. Greater comprehension of this issue can inform adjustments to ecotourism strategies that are less detrimental to nature and thus more sustainable. Enacting appropriate measures, therefore, aids future livelihood security for local stakeholders and the wider national economy. Thus, the second aim of this research is to assess the impact of human disturbance on NMCF.

Hypotheses and Predictions

Given the aims of this study, two hypotheses were formulated.

> H1: Biodiversity (species richness) and bioabundance (individual detections) would increase with NMCF sub-habitat maturity.
>
> H2: Increased human disturbance would induce more severe temporal-avoidance behaviour in diurnal fauna.

The first hypothesis was synthesised from literature, which indicated that older forests harbour greater diversity (Meyer et al., 2015). Certain species also take longer to recolonise secondary habitats, depending on ecological requirements, and secondary forest fauna diversity increased with age (Dent and Joseph Wright, 2009). Additionally, OG forests were shown to facilitate specialist regionally-endemic species often absent in younger forests (Dent and Joseph Wright, 2009). Supporting evidence analysing woodland fragment size suggested that larger fragments could support greater biodiversity, particularly with sensitive species, as their protected status reduced anthropogenic stressors (Magioli et al., 2021). The second hypothesis was similarly devised. Many papers discuss how even recreational human presence (Taylor and Knight, 2003) was a factor influencing diel behaviour of fauna, especially

mammals (Fonda et al., 2025). Species have been shown to avoid human activity, sometimes increasing nocturnality to avoid it (Mirante et al., 2024). Several bird taxa show negative reactions to human disturbance (Price, 2008), with select species known to adjust singing times in response to noise pollution (de Framond and Brumm, 2022).

Following these hypotheses, coinciding predictions were made.

> P1: Species richness and bioabundance would be greatest in OG forest and least in P forest.
>
> P2: In areas of high human disturbance, diurnal species will become more crepuscular to avoid peak human activity, whilst nocturnal species will remain unaffected. In areas of low disturbance, changes will be attenuated.

Methodology – 754 words

Study Area

Data was collected in Cloudbridge Nature Reserve, situated within the Pacific slopes of the Talamanca mountain range in Costa Rica (1550m-2600m above sea level), featuring nearly 200 hectares of restored NMCF (Cloudbridge Nature Reserve, n.d.). As introduced previously, this features a mosaic of three forest sub-habitats of varying maturity (van der Sanden, 2017). Each sub-habitat was readily accessible for sampling via a public and private trail network, which also ensured human disturbance was measurable in the investigation. This made it an ideal study site for data collection.

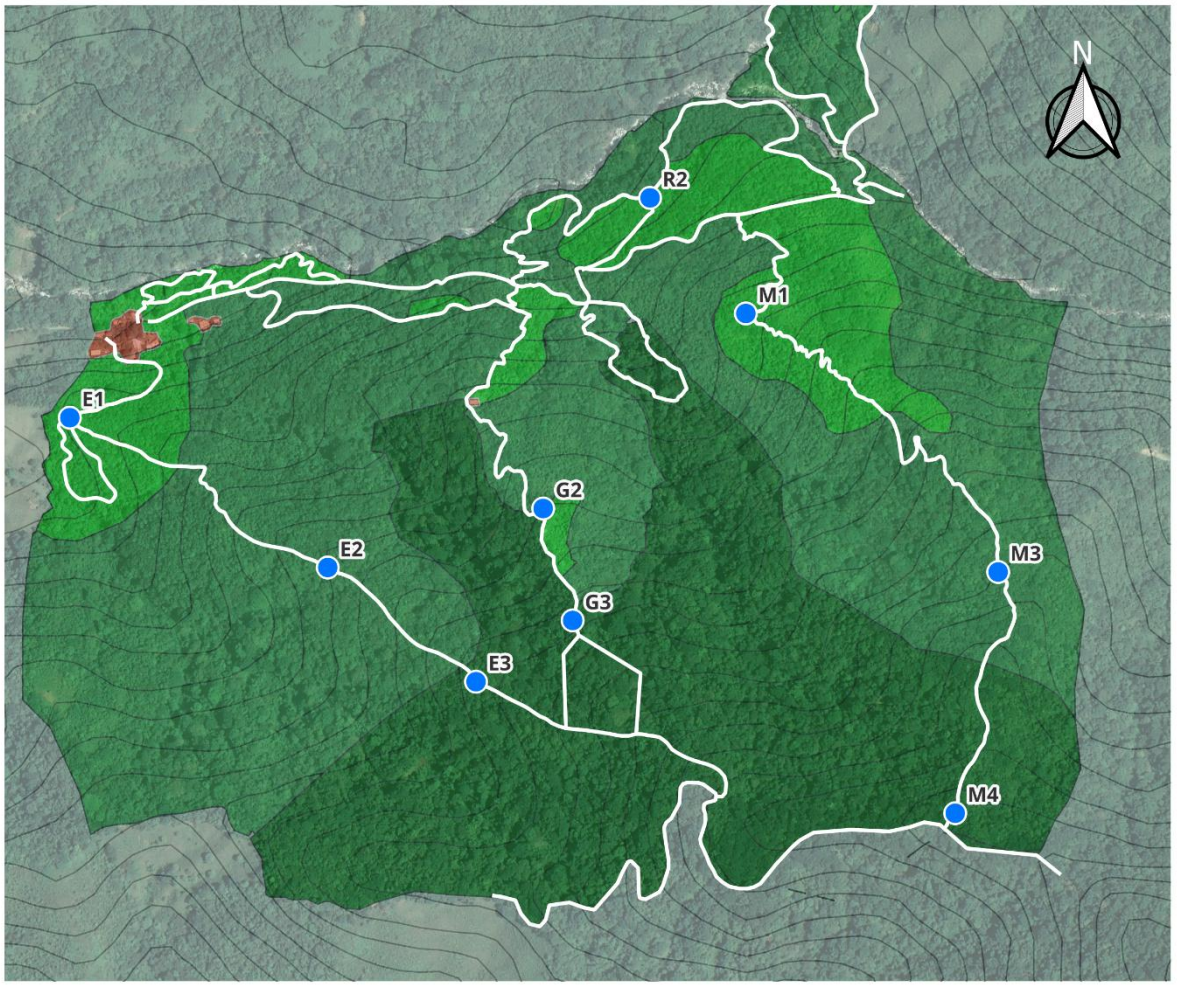
Camera Trapping

To record species reliably, a non-invasive technique was required to significantly reduce disturbance and attenuate the impact of observation, so camera traps were the chosen sampling method. The devices were attached to the bases of trees approximately 30 cm off the ground, facing into the cleared trails, typically allowing clear species identification and safe researcher access to replenish batteries and SD cards. Captured videos were standardised,

where possible, to 10 seconds long, with a minimum interval of 3 seconds at medium motion sensitivity. A small number of camera brands couldn't match these specifications exactly, so they were tuned as close as allowed. For social fauna, e.g., collared peccary (*Pecari tajacu*), subsequent videos of the same species were considered the same sample if the inter-video gap was below 5 minutes. For certain taxa, namely Chiroptera and Rodentia/Eulipotyphla, speciation was not possible from the footage. To compromise, they were classified as "bats" and "rodents or shrews" respectively. Every attempt was made to ensure that sampling days and geospatial distribution were even, as they were spread across the three forest sub-habitats present: P, NR and OG forest (Fig. 1). Location-labelled SD card and battery replacements were performed every 2 weeks to ensure continuous sampling coverage and ongoing data entry.

a)

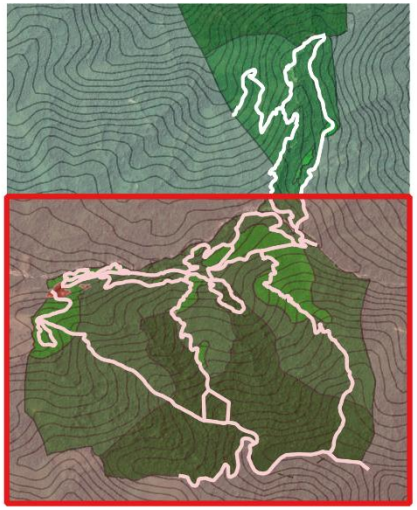
Camera Trap Locations - Cloudbridge South Section



Legend:

- Human Use
- Natural Regrowth
- Old Growth
- Planted
- Trails
- Camera Locations

Map Section:



b)

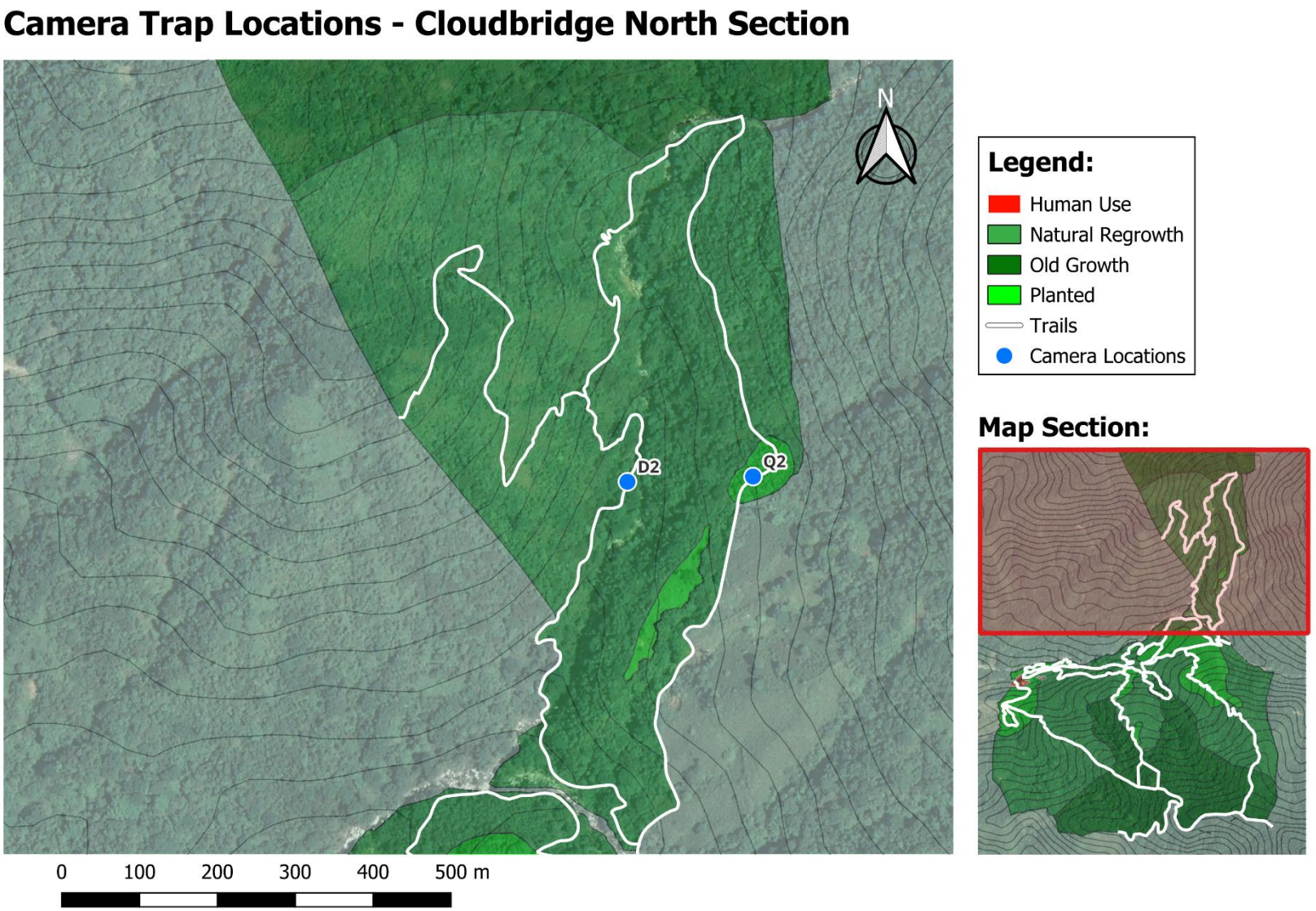


Figure 1: GIS maps detailing the study area's camera trap locations in (a) Cloudbridge South Section and (b) Cloudbridge North Section.

Collected footage was reviewed to determine the species and number of individuals per sample with the videos themselves reporting variables, including the date, time (HH:MM), temperature and moon phase. The latter two variables, alongside elevation (determined using GPS coordinates), were unused as they were beyond the study's scope. Camera location, coordinates and sub-habitat type were noted upon initial site deployment.

Statistics

Variables were analysed in RStudio (R Core Team, 2025) to assess statistical significance and to illustrate trends visually. Packages used included dplyr (Wickham et al., 2023), ggplot2 (Wickham, 2016), stringr (Wickham, 2025), purr (Wickham and Henry, 2025), tidyr (Wickham, Vaughan and Girlich, 2024), MASS (Venables and Ripley, 2002), emmeans (Lenth and Piaskowski, 2026), ggrepel (Slowikowski, 2026), vegan (Oksanen et al., 2026), lubridate (Grolemund and Wickham, 2011) and minpack.lm (Elzhov et al., 2023). To compare biodiversity, each sub-habitat had species accumulation curves (SAC) plotted. These SACs were fitted with a projected Clench model, producing asymptotic richness estimates that were bootstrap-resampled (500 iterations) for confidence intervals (CIs) and compared pairwise. For bioabundance, accumulated detected individuals were plotted per sub-habitat. Overdispersion was calculated with a Pearson χ^2 dispersion statistic, so was followed by a Negative Binomial Generalised Linear Model (NB GLM) on the daily detection rates per sub-habitat. This assessed the significance of the sub-habitat variable, complemented by a pairwise comparison to identify any significant differences between sub-habitats. To assess the impact of human disturbance, the total number of detected humans at each camera location was calculated. For each camera location, biodiversity, measured by Shannon's Diversity Index (SDI) (acknowledging species diversity and prevalence), and total detected individuals were calculated and analysed using linear regressions. The median for site-based human detections categorised the location's conditions; those above the median were considered high disturbance, and those below were considered low disturbance. To investigate behavioural alterations due to the disturbance levels, sample times were plotted

on activity curves. Separate curves were plotted for mammals and birds overall, as well as individual graphs per species. Only the overall graphs were statistically tested, as a per-species analysis exceeded the scope of this study. Activity curve analysis included hourly paired t-tests and visual comparison to an overall human activity curve.

Ethical statement

Camera trapping was chosen as a non-invasive methodology to sample fauna in the study area. Possible anthropogenic stress during sampling was mitigated through ethical practices, e.g., not approaching wild fauna. For human samples, which included private information, e.g. date and time, location, and identity, videos were discreetly analysed and promptly deleted afterwards. Environmental impact was minimal, save for soil erosion on trails, human disturbance from researchers and physical attachment of cameras to trees. There are no conflicts of interest to declare for this study, and it was conducted in cooperation with local communities.

Results – 487 words

Biodiversity and Bioabundance

Excluding humans, 28 species were observed (Table 1a): 20 mammals and 8 birds (Appendix 1a and b). Every identifiable non-human species was globally classified as least concern, except for *S. dicei* and *C. imitator*, both being vulnerable. Most trophic guilds observed were prey and mesopredators, with *P. concolor* as the only non-human top predator. Humans and *P. tajacu* were the most observed taxa in the study. Observed bird species were diurnal and predominantly ground-associated.

Table 1: Tables for camera trap data describing (a) species observation data, (b) sample size and sub-habitat context per camera location, and (c) sample size per sub-habitat, including overlapping days between camera locations.

a)

Common Name	Scientific Name	IUCN Red List Status	Trophic Guild	# Detected Individuals	Average Group Size	# Detection Events
People	*Homo sapiens*	N/A	Top Predator	1326	2	626
Collared Peccary	*Pecari tajacu*	Least Concern	Prey	566	5	123
Spotted Wood-Quail	*Odontophorus guttatus*	Least Concern	Prey	132	3	43
White-Nosed Coati	*Nasua narica*	Least Concern	Mesopredator	109	2	47
Chiriqui Quail-Dove	*Zentrygon chiriquensis*	Least Concern	Prey	78	1	73
Red-tailed Squirrel	*Sciurus granatensis*	Least Concern	Prey	66	1	62
Dice's Cottontail	*Sylvilagus dicei*	Vulnerable	Prey	34	1	34
Paca	*Cuniculus paca*	Least Concern	Prey	28	1	27
Rodent or Shrew	*Unidentifiable*	N/A	Prey	28	1	27
Tayra	*Eira barbara*	Least Concern	Mesopredator	24	1	23
Black Guan	*Chamaepetes unicolor*	Least Concern	Prey	23	1	21
Variegated Squirrel	*Sciurus variegatoides*	Least Concern	Prey	21	1	21
Ocelot	*Leopardus pardalis*	Least Concern	Mesopredator	10	1	10
Coyote	*Canis latrans*	Least Concern	Mesopredator	9	2	6
Panamanian White-faced Capuchin	*Cebus imitator*	Vulnerable	Mesopredator	6	3	2
Puma	*Puma concolor*	Least Concern	Top Predator	4	1	3
Common Opossum	*Didelphis marsupialis*	Least Concern	Mesopredator	3	1	3
Bat	*Chiroptera sp.*	N/A	Various	2	1	2
Central American Agouti	*Dasyprocta punctata*	Least Concern	Prey	2	1	2
Emerald Toucanet	*Aulacorhynchus prasinus*	Least Concern	Prey	2	1	2
Lesson's Motmot	*Momotus lessonii*	Least Concern	Prey	2	1	2
Long-tailed Weasel	*Mustela frenata*	Least Concern	Mesopredator	2	1	2
Ruddy-Capped Nightingale-Thrush	*Catharus frantzii*	Least Concern	Prey	2	1	2
Collared Trogon	*Trogon collaris*	Least Concern	Prey	1	1	1
Grey Four-Eyed Opossum	*Philander opossum*	Least Concern	Mesopredator	1	1	1
Highland Tinamou	*Nothocercus bonapartei*	Least Concern	Prey	1	1	1
Northern Olingo*	*Bassaricyon gabbii*	Least Concern	Mesopredator	1	1	1
Mexican Mouse Opossum	*Marmosa mexicana*	Least Concern	Mesopredator	1	1	1
Nine-Banded Armadillo	*Dasypus novemcinctus*	Least Concern	Mesopredator	1	1	1
*Previously identified as kinkajou (*Potos flavus*), but reidentified as *B. gabbii* upon reinspection		**TOTAL**		**2485**		**1169**

b)

Camera Location	Sub-Habitat	No. of Days Recorded
E1	Planted	18
E2	Natural Regrowth	86
E3	Old Growth	12
G2	Natural Regrowth*	6
G3	Old Growth	73
M1	Planted	11
M3	Natural Regrowth	55
M4	Old Growth	12
Q2	Planted	50
R2	Planted	4
*G2 features a triple boundary between sub-habitats, but is predominantly natural regrowth		

c)

Sub-Habitat	No. of Days Recorded (Including Overlaps)
Planted	83
Natural Regrowth	147
Old Growth	97

To illustrate recorded biodiversity, the cumulative number of unique species was plotted per sub-habitat (Fig. 2a). NR had the highest number of unique species detected (20), followed by OG (18), then P (14). The asymptotic Clench model estimates followed the same order, with NR as the highest (22), then OG (20), and finally P (18.1). Bootstrapping for each sub-habitat produced non-overlapping CIs (NR=21.4-22.5, OG=19.5-20.6, P=17.6-18.8), inferring strong biodiversity differences between sub-habitats. When each sub-habitat's bootstrapped asymptotic richness was compared pairwise, they all exhibited complete separation, indicating that the hierarchy of sub-habitat richness remained consistent (Appendix 2a).

The cumulative number of detected individuals per sub-habitat was plotted to demonstrate bioabundance (Fig. 2b) with OG being the highest (647), followed by NR (354) and P (158). A Pearson χ^2 dispersion statistic indicated that the data were overdispersed (6.29), so an NB GLM was used. The difference between OG and NR was significant (p=0.0181), whereas NR and P was insignificant (p=0.352). The pairwise comparison reinforced the NB GLM's inferences (OG-NR: p=0.0476, df=inf)(NR-P: p=0.620, df=inf), whilst also confirming a significant difference between OG and P (p=0.0115, df=inf) (Appendix 2b).

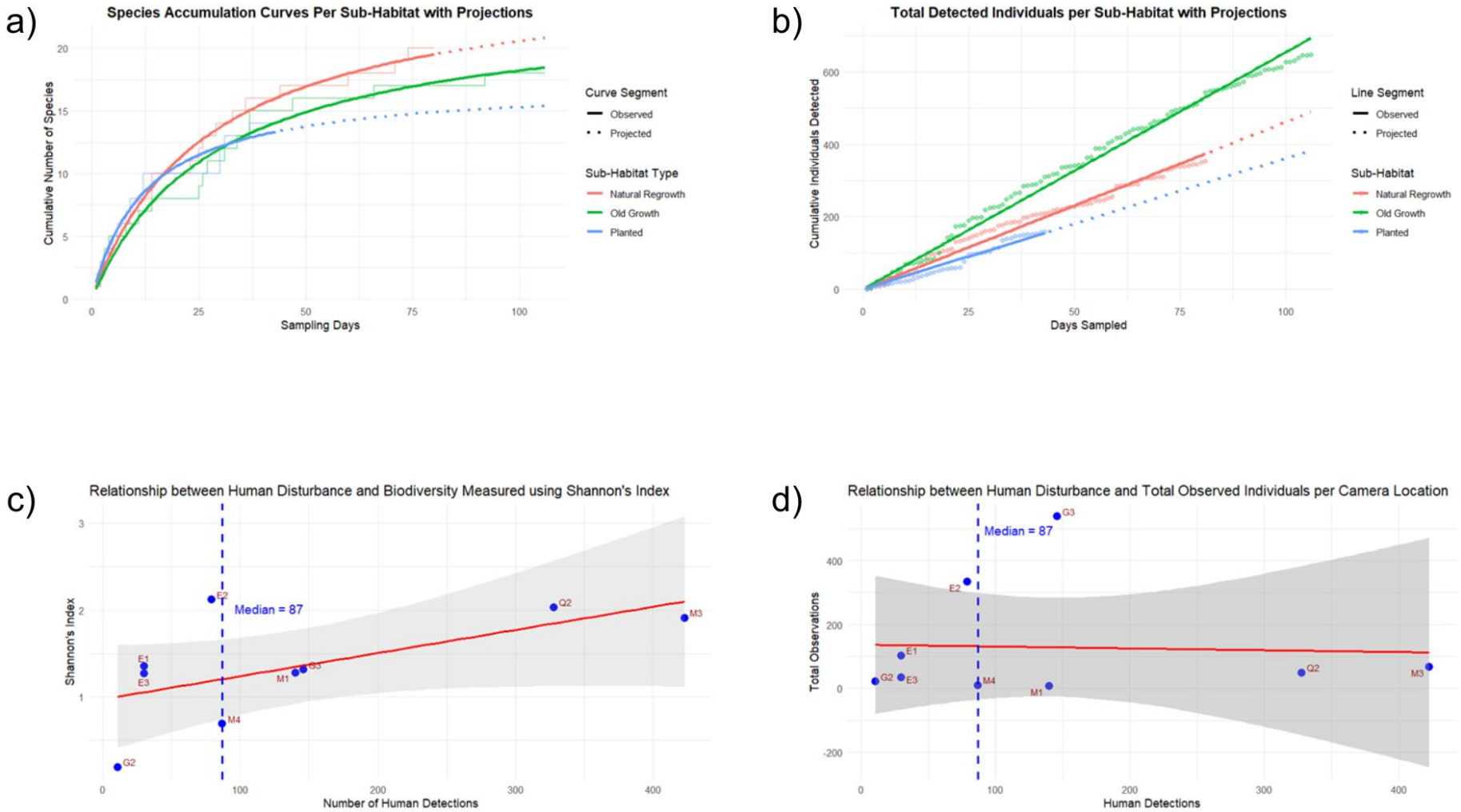


Figure 2: Graphs concerning the variables investigated relating to biodiversity and bioabundance including (a) total unique species accumulation per sub-habitat, (b) total accumulation of observed individuals per sub-habitat, (c) linear regression of total human observations per camera location with Shannon's Diversity Index and (d) linear regression of total human observations per camera location with total observed individuals.

Human Disturbance

A linear regression was performed for SDI per camera location against human observations (Fig. 2c) to discern potential impacts on biodiversity by disturbance. Whilst not statistically significant ($p=0.0857$, $adjR^2=0.273$, $df=7$) (Appendix 2c), the regression showed a positive correlation between human presence and biodiversity per site. This regression was repeated for bioabundance, using total individual observations (Fig. 2d), yielding an insignificant, uncorrelated result ($p=0.910$, $adjR^2=0\text{-}0.141$, $df=7$) (Appendix 2d).

The remaining results concerned the temporal activity of observed species in relation to human disturbance. Overall mammal activity (Fig. 3a) and per mammalian species activities (Fig. 3b) were plotted. A Shapiro-Wilk test confirmed that the overall mammalian data were normally distributed ($W=0.926$, $p=0.0779$), so an hourly paired t-test was performed between the disturbance levels, which was significant ($p=0.0168$, $t(23)=-2.58$) (Appendix 2e). Similarly, overall bird activity (Fig. 3c) and separate bird species activities (Fig. 3d) were plotted, and the overall data were normally distributed ($W=0.917$, $p=0.297$). The following hourly paired t-test, however, was insignificant ($p=0.188$, $t(10)=1.41$) (Appendix 2f). To better understand the visual trends of these graphs, the overall human activity was plotted separately to identify peak disturbance times (Fig. 3e). The mean number of detections occurred between 9:45 am (1^{st}Qu.) and 12:40 pm (3^{rd}Qu.), i.e. mid-morning to midday (Appendix 2g). Per species responses varied in both mammals and birds between disturbance levels; these graphs were compared visually but non-statistically.

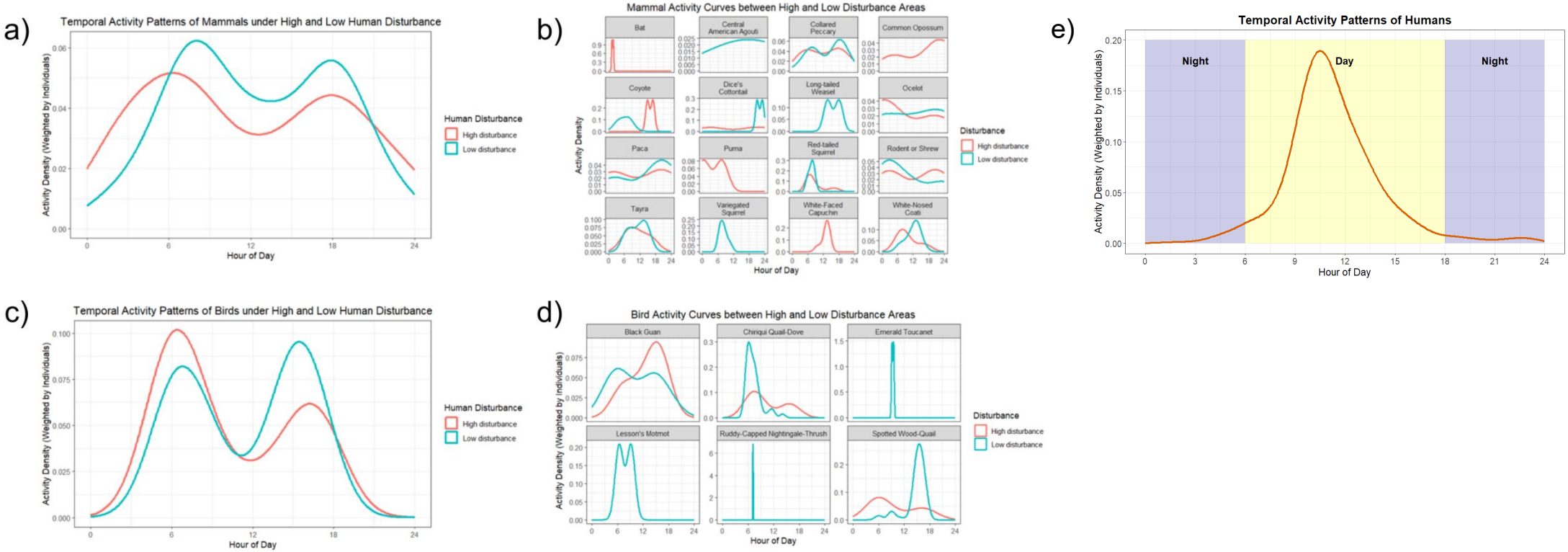


Figure 3: Activity curves showing the diel activity in high and low human disturbance areas for (a) mammals overall, (b) mammal species, (c) birds overall and (d) bird species, as well as (e) overall human activity.

Discussion – 1837 words

Sub-habitat Biodiversity and Bioabundance

As mentioned, NR had the highest species richness, whilst P had the least. The bootstrap-resampling analysis suggested strong separations, reinforcing the sub-habitat species richness hierarchy. The literature provides conflicting evidence for this trend. A supportive study by Schwegmann et al. (2025) found that intermediate *Capreolus capreolus* grazing increased the biodiversity of several taxa, e.g. spiders, birds, and hares. Additionally, Swart et al. (2019) demonstrated that medium-disturbances in South African forests increased arthropod diversity, since it opened the canopy, promoting generalist species colonisation. Theoretically, if plant diversity increases in medium-disturbance regions, due to mosaics of heliophilic pioneers alongside shade-tolerant species (Sheil and Burslem, 2003), more habitats, resources and ecological niches may be available, increasing faunal diversity (Del-Claro and Torezan-Silingardi, 2021). This may explain higher species richness in the NR. For biodiversity increases, the IDH alone has been criticised for being reductionist (Sheil and Burslem, 2003; Molino and Sabatier, 2001). Moreover, a global study on forest biomes reported that less disturbed or continuous forests yield more biodiverse mammalian communities (Ahumada et al., 2011), opposing the IDH. Owen et al. (2020) used acoustic sampling for birds, which could sample species unseen by camera traps. Their results reinforced arguments for positive correlations between faunal biodiversity and forest maturity. Furthermore, it suggests that this paper's results may be skewed due to an incomplete sampling methodology, rather than the IDH. Many of these papers support the idea that highly disturbed areas have the lowest biodiversity, aligning with this study's results; however, Mauffrey et al. (2007) reported that species richness of some small mammals increased, e.g. at human settlement boundaries. This is possibly due to the resources associated with settlements, e.g. refuge and food (Ebani, 2022); therefore, disturbance is not universally negative for all species.

OG had the highest individual observations, whereas P had the least. Moreover, pairwise comparisons of daily detection rates between OG and the other sub-habitats were statistically significant, implying that mature forests possess higher carrying capacities. Owen et al. (2020) supported this for avian abundance, similarly to their aforementioned diversity increases. A mammalian study in Borneo disagreed, as large and small mammals appeared more abundant in logged forests than in OG (Wearn et al., 2017), aligning with the IDH. Other results in the same study, however, showed that greater forest cover increased abundances across several mammal groups (Wearn et al., 2017). This may suggest that habitat distribution/continuity supersedes habitat maturity for influencing abundance, although more established habitats reduced invasive species abundance (Wearn et al., 2017), potentially attenuating related pressures (Sodhi and Ehrlich, 2010), protecting vulnerable species. Furthermore, the accumulations were biased by social species, e.g. *P. tajacu*, since unique individuals were indistinguishable, and likely recorded repeatedly. Nonetheless, the abundance results in isolation lend support towards H1.

Overall, whilst some evidence may support H1: “Biodiversity (species richness) and bioabundance (individual detections) would increase with NMCF sub-habitat maturity”, it cannot be accepted based on these results due to their inconclusive nature.

Human Disturbance

The SDI regression with human observations showed an unexpected positive correlation with increasing human presence. This is contrary to certain contributions to the literature, which suggest it impacts species richness negatively (Ouboter et al., 2021; Almeida Cunha, 2010; Price, 2008). Furthermore, bioabundance appeared to be unaffected by increasing human presence, again, opposing some of the literature (Ouboter et al., 2021; Almeida Cunha, 2010), although non-correlated responses to humans were described for many species in Blake et al. (2017). Hidinger (1996) reported that certain species, e.g. N. narica, increased in density near tourists, as they exploited associated benefits, e.g. food, predator avoidance. Species diversity in Pereira et al. (2023) also benefited from human settlements via reduced predator

presence. Both studies show how humans can unexpectedly boost species richness, although this may have negative long-term ecosystem cascades (Tossens et al., 2025). Visitors to Cloudbridge are interested in seeing wildlife, since it is an ecotourism destination. Consequently, they are likely to visit areas in the reserve with known higher biodiversity/bioabundance, encouraged by guided tours (Cloudbridge Nature Reserve 2016). This may explain the positive correlation, although visitor surveying could provide more evidence. Hunting was not considered an onsite factor, which can otherwise deplete fauna populations (Hoskins et al., 2020), further explaining non-negative correlations. For this study, human disturbance was rejected as an impacting factor on diversity/abundance.

The temporal analysis for mammals revealed an overall diel shift in detections away from midday hours in high human disturbance areas, with a statistically significant hourly difference. This implies a corresponding increase in their crepuscular/nocturnal activity to avoid peak human activity near midday. Previous research describes similar patterns, e.g. with jaguars (*Panthera onca*) in Ouboter et al. (2021), crested porcupine (*Hystrix cristata*) and roe deer (*C. capreolus*) in Mirante et al. (2024). These papers, whilst geographically distinct, share another common result with this study: responses differ on a species-by-species basis. Discussing every species (Fig. 3b and d) in detail was beyond the scope of this study; however, it highlighted the variability of behaviour within the ecosystem. Some species, like *B*. *gabbii*, had too few samples to plot activity curves, whereas others, like *C. imitator*, only had enough samples in one disturbance level. These gaps, alongside overall low sample sizes, reduced the comprehensive nature of the behavioural analysis. Brief overviews of species plots suggested behavioural alterations in nocturnal species, like *L. pardalis* and *C. paca*, showing variation between disturbances despite their absence at peak human activity. This possibly resulted from indirect interactions with humans, e.g. local reduction in top predator pressure (Ouboter et al., 2021), although trends may reflect skewing from low sample sizes. Consequently, nocturnal responses to H2 were inconclusive. No species showed an overt activity preference towards peak human activity in high disturbances, suggesting that species

were either indifferent or avoidant of human presence. This differed from Hidinger (1996) and Mirante et al. (2024), where certain species fared better under increased human disturbance. For mammals, H2: “Increased human disturbance would induce more severe temporal-avoidance behaviour in diurnal fauna”, cannot be accepted on a species-level basis, due to insufficient sampling and analysis, but can be accepted as a general response.

Overall, bird activity followed a crepuscular pattern regardless of disturbance level. Whilst hourly activity differences were insignificant, birds appeared more active in the evening with low disturbance. Crepuscularity was unsurprising given the ethological and ecological importance of the dawn and dusk choruses (Bustamante and Garitano-Zavala, 2024; Catchpole and Slater, 2008). Attenuated temporal shifts between disturbances may be explained by crepuscularity due to the limited overlap of avian activity with peak human activity. The responses of the most sampled species, *Z. chiriquensis* and *O. guttatus*, deviated from the overall pattern. In low disturbance, each species was highly active in the morning or evening, respectively, but when disturbance increased, their activity flattened out across the day. Since species often react to diurnal human presence as predator-associated stress (Harmange et al., 2021; Gaynor et al., 2018), and some mammalian predators of the ground-dwelling birds are nocturnal (Cepeda-Duque et al., 2021; Huck et al., 2017; de Villa Meza et al., 2009), spread-out diel activity may be preferable to simultaneously reduce stress and predation risk. To better ascertain the reason, more research is required. No nocturnal bird species were recorded in this study, so their response was unknown. Since diurnal birds did not shift overall (unlike mammals), and more research on species-specific dynamics is required, H2: “Increased human disturbance would induce more severe temporal-avoidance behaviour in diurnal fauna”, for birds is rejected.

Wider Implications

Whilst not all results were conclusive, they highlight the importance of mature forests for high individual carrying capacity and biodiversity. Additionally, it demonstrates that semi-disturbed or developing habitats still hold ecological value and should be protected. Ecotourism may not

be deleterious to species diversity/abundance in these results, but it is likely ethologically influential, unique to each species. For example, altered responses of diurnal prey may induce long-term ecological damage if diel overlaps with nocturnal/crepuscular predators increase (Patten et al., 2019). The results may encourage ecotourism stakeholders to employ mitigation methods, e.g. limiting visitor numbers; however, mindful consideration must be taken to balance this with economic factors, so as not to disadvantage stakeholders. Consequently, open collaboration to optimise sustainability, ecosystem health and financial benefits is recommended. Safeguarding habitats for ecosystem resilience against changing climates and land use should be prioritised by conservationists to protect threatened species and improve quality of life through sustainable ecosystem services (Wu et al., 2026).

Limitations and Further Study

Uneven sampling between sub-habitats and camera locations (Table 1b and c), due to technical difficulties, i.e. cameras malfunctioning, limited total cameras, etc., likely impacted this study's validity. Addressing this in future research would make each variable's analysis more robust. Increasing the camera total would allow more comprehensive sample point distribution, especially the OG section in Fig. 1b, which may support cryptic *P. onca* (Silver et al., 2004), otherwise unseen in this study. Consequently, this would better inform ecological differences between sub-habitats.

Analysing unaccounted variables, e.g. floral compositions and soil compositions, may explain sub-habitat preferences more comprehensively beyond forest maturity. Variables like weather, temperature, and day-length were relatively consistent, with sampling almost exclusive to the dry season. Sampling in the wet season, when they change (Guswa et al., 2007), could compare faunal responses. Terrestrial camera trapping was restrictive, as fauna such as small and arboreal mammals, arboreal birds, herpetofauna, and invertebrates were unidentified or undersampled. For example, Central American spider monkeys (*Ateles geoffroyi*), an arboreal mammal, were spotted several times during field data collection, but not on video. The primate prefers more mature forests (Shedden et al., 2022), so inclusive sampling may impact

conclusions concerning sub-habitat biodiversity/abundance. Outstanding species are therefore a priority for subsequent research via arboreal camera traps, passive acoustic bird surveys, etc. (Knight et al., 2026; Moore et al., 2021) (Appendix 3). Other forms of anthropogenic disturbance, e.g., path erosion, noise, etc., could be investigated to compare their individual and cumulative impacts on wildlife. For abundance, fauna could be tagged, tracking actual numbers and sub-habitat movements, although this may decrease tagged animals' fitness (Lennox et al., 2023). Observations could be measured using relative abundance indices (RAI) per species to attenuate social species biases. RAIs are, however, vulnerable to their own bias, as they assume consistent detection ability between independent variables (Sollmann et al., 2013), so they must be utilised carefully. Finally, off-trail habitat was unsampled; this environment may include more reclusive species, such as Central American red brocket deer (*Mazama temama*) (Gallina-Tessaro et al., 2025), previously recorded in Cloudbridge (Cloudbridge Nature Reserve, 2024).

Conclusion

This study's results initially indicated that semi-disturbed forests may support greater biodiversity and bioabundance than undisturbed counterparts, but this is inconclusive due to limited sampling efforts and techniques used. Each sub-habitat was emphasised as ecologically important, so reforestation-protection efforts should continue. Ecotourism is a realistic model to achieve this sustainably; however, regulations are recommended to reduce the impact of anthropogenic disturbance on animal behaviour. Regulations must involve stakeholder investment to encourage sustainable ecotourism, national economic development, and avoid colonial conservation (Baker-Médard, 2022; Moola and Roth, 2019).

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Appendix 1 – Captures of each (a) Mammalian and (b) Avian Species in the Study

a)

Bat
Chiroptera sp.

Dice's Cottontail
(*Sylvilagus dicei*)

Panamanian White-Faced Capuchin
(*Cebus imitator*)

Mexican Mouse Opossum
(*Marmosa mexicana*)

Lowland Paca
(*Cuniculus paca*)

Puma
(*Puma concolor*)

Grey Four-Eyed Opossum
(*Philander opossum*)

Long-Tailed Weasel
(*Neogale frenata*)

Common Opossum
(*Didelphis marsupialis*)

Red-Tailed Squirrel
(*Sciurus granatensis*)

Rodent or Shrew
Rodentia/Eulipotyphla sp.

Tayra
(*Eira barbara*)

Collared Peccary
(*Pecari tajacu*)

Ocelot
(*Leopardus pardalis*)

Northern Olingo
(*Bassaricyon gabbii*)

Variegated Squirrel
(*Sciurus variegatoides*)

White-Nosed Coati
(*Nasua narica*)

Coyote
(*Canis latrans*)

Central American Agouti
(*Dasyprocta punctata*)

Nine-Banded Armadillo
(*Dasypus novemcinctus*)

b)

Highland Tinamou
(*Nothocercus bonapartei*)

Chiriqui Quail-Dove
(*Zentrygon chiriquensis*)

Collared Trogon
(*Trogon collaris*)

Ruddy-Capped Nightingale Thrush
(*Catharus frantzii*)

Northern Emerald Toucanet
(*Aulacorhynchus prasinus*)

Black Guan
(*Chamaepetes unicolor*)

Lesson's Motmot
(*Momotus lessonii*)

Spotted Wood Quail
(*Odontophorus guttatus*)

Appendix 2 – Complete Statistics for Analysis Tests

a)

Clench Model for Species Richness			
Habitat.Type	Asym_mean	Asym_lower	Asym_upper
Natural Regrowth	22	21.5	22.4
Old Growth	20	19.5	20.6
Planted	18.1	17.5	18.8

Bootstrap Pairwise Comparison			
	Natural Regrowth	Old Growth	Planted
Natural Regrowth	N/A	0	0
Old Growth	1	N/A	0
Planted	1	1	N/A

b)

Daily Detected Individuals per Sub-Habitat (NB GLM)				
Pearson χ^2 dispersion	6.288			
Coefficients	Estimate	Standard Error	Z value	Pr(>|z|)
Intercept	1.47	0.108	13.6	<0.001
Habitat.TypeOld Growth	0.334	0.141	2.36	0.0181
Habitat.TypePlanted	-0.174	0.186	-0.931	0.352

Tukey-adjusted Pairwise Comparisons of Estimated Marginal Means						
Emmeans						
Habitat.Type	Response	SE	df	Asymp.LCL	Asymp.UCL	
Natural Regrowth	4.37	0.472	Inf	3.54	5.4	
Old Growth	6.1	0.556	Inf	5.11	7.3	
Planted	3.67	0.557	Inf	2.73	4.95	
Contrasts						
Contrast	Ratio	SE	df	Null	z.ratio	p.value
Natural Regrowth / Old Growth	0.716	0.101	Inf	1	-2.36	0.0476
Natural Regrowth / Planted	1.19	0.222	Inf	1	0.931	0.62
Old Growth / Planted	1.66	0.294	Inf	1	2.87	0.0115

c)

Shannon's Diversity Index Regression

	Min	1Q	Median	3Q	Max
Residuals	-0.812	-0.188	-0.0496	0.215	0.937

Coefficients	Estimate	Standard Error	t value	Pr(>|z|)
Intercept	0.974	0.26	3.75	0.00719
Human.Count	0.00266	0.00133	2	0.0857

Residual standard error	0.537 (7 DF)
Multiple R-squared	0.363
Adjusted R-squared	0.273
F-statistic	3.997 on 1 and 7 DF
P-value	0.0857

d)

Bioabundance Regression

	Min	1Q	Median	3Q	Max
Residuals	-123	-115	-70.1	-32.2	410

Coefficients	Estimate	Standard Error	t value	Pr(>|z|)
Intercept	137	95.1	1.44	0.193
Human.Count	-0.0573	0.487	-0.118	0.91

Residual standard error	197 (7 DF)
Multiple R-squared	0.00197
Adjusted R-squared	-0.141
F-statistic	0.0138 on 1 and 7 DF
P-value	0.91

e)

Overall Mammals Hourly t-test

	W	P-value
Shapiro-Wilk normality test	0.926	0.0779

t	-2.58
DF	23
p-value	0.0168
95 percent confidence interval	-6.09 -0.667
Mean difference	-3.38

f)

Overall Birds Hourly t-test

	W	P-value
Shapiro-Wilk normality test	0.917	0.297

t	1.41
DF	10
p-value	0.188
95 percent confidence interval	-1.73 7.73
Mean difference	3

g)

Human Activity Curve

Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
1.433	9.758	10.883	11.374	12.679	23.383

Appendix 3 – Representatives of Under/Unsampled Taxa Sighted during Data Collection Period

Central American spider monkey (Ateles geoffroyi) – arboreal mammal

Blotched Eyelash-Pitviper (Bothriechis supraciliaris) - herpetofauna

Silk Moth (Rothschildia sp.) - invertebrate

Resplendent Quetzal (Pharomachrus mocinno) – arboreal bird