NOTTINGHAM TRENT UNIVERSITY

INVESTIGATING THE ANTHROPOGENIC IMPACTS ON HUMMINGBIRD DIVERSITY AND COMMUNITY STRUCTURE AT FEEDING SITES IN MONTANE CLOUD FOREST

by

FERGUS R. H. JACKSON

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Abstract

Diversity is a fundamental concept in ecosystem ecology that encompasses species richness, community composition, and species distribution. Ecological and environmental factors, including habitat type, resource availability, and climatic conditions, significantly influence species diversity both within and among communities, which are categorised as alpha (within-habitat), beta (between-habitat), and gamma (regional) diversity. Due to their sensitivity to habitat, elevation, and seasonal variations, hummingbird communities offer a valuable system for studying diversity, offering insights into mutualistic interactions and the development of effective conservation techniques.

Over a 6-month period, surveys were conducted daily to record hummingbird species at productive feeding sites at Cloudbridge nature reserve, Costa Rica. A treatment of habitat influence; human influenced and non-human influenced sites was used to discern how diversity and community structure is impacted by anthropogenic effects.

True diversity measures were used to assess alpha, beta, and gamma diversity of hummingbirds at their feeding sites, while environmental factors such as altitude and floral assemblages were noted for their influence.

Alpha diversity exhibited minimal discernible differences between human and non-human influenced sites, though significant variation was observed among individual sites within each treatment. Beta diversity analysis revealed a higher rate of species turnover in non-human influenced habitats across all diversity orders. Gamma diversity analysis indicated that the effective number of species varied between habitat types depending on the diversity order considered. Community structure and composition was investigated and found to be more consistent in non-human influenced feeding sites, while human influenced sites exhibited greater variability.

The combined pressures of diminishing cloud forest habitat and expanding urban and agricultural development suggest a future trend towards the generalisation of hummingbird communities and a subsequent decline in specialised ornithophilous plants and their pollinators. This predicts that due to anthropogenic effects, populations of generalist hummingbird species will increase, specialised hummingbird populations will decrease, and community structure will show less variance with reduced species turnover.

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Introduction

Species diversity has been shown as a critical component of ecosystem health and stability. Trends in population richness and abundance provide understanding of potential threats and advise conservation techniques for rare and vulnerable species (Jetz et. al., 2019). Monitoring and preserving optimal levels of diversity has also shown to be beneficial for human health (Methorst et. al., 2021). There is also strong evidence that greater levels of biodiversity provide valuable provisioning, regulating, cultural and supporting ecosystem services (Harrison et. al., 2014). It is widely thought that diversity is under significant pressure from current global changes such as habitat destruction (Shivanna, 2022; Weiskopf et. al., 2020), however, Sax and Gaines, (2003) predict that local populations may instead be increasing. High levels of biodiversity enhance ecosystem resilience by providing functional redundancy, which safeguards against the loss of vital ecosystem functions (Fetzer et. al., 2015). Diversity within communities is primarily influenced by ecological processes which are likely to be affected significantly by environmental change (Martínez-Roldán et. al., 2024; Simkin et. al., 2022).

Birds are an extensively studied taxonomic group with wide-ranging traits and behaviours, making them ideal indicators for biodiversity studies (Tobias et. al., 2022).

Tropical birds in particular have species specific requirements including unique nesting material and food sources (Lee and Marsden, 2008); therefore, diversity and community makeup reflect both habitat health and the effects of anthropogenic impacts.

Hummingbirds (Trochilidae) are recognized as one of the most remarkably adapted and unique families within the animal kingdom, renowned for their unmatched aerial prowess (Reddish and Attenborough, 2012). They have developed into a diverse assemblage of nectarivores, providing vital ecosystem services such as pollination of ~15% of plant species throughout the Americas and biological control of pests (McGuire, et. al., 2014). Pollination is achieved through unique morphological adaptations, co-evolved alongside many of the ornithophilous species they feed from. Kessler et al. (2019) estimate that hummingbirds have driven the evolutionary diversification of over 50% of known bromeliad species. They also play significant cultural roles, representing fertility, wellness and good luck (Prieto-Torres et. al., 2021).

Research conducted by Bleiweiss et. al., (1997) redefined the hummingbird family lineage; originally divided into 2 subfamilies, now divided into 6, with 9 monophyletic groups. Found throughout the Americas, these avian pollinators occur in tropical rainforest, temperate woodland, deserts and mountain meadows alike (Leimberger et. al., 2022). What's more, communities are often defined by floral availability (Maruyama et. al., 2019) due to their dependence on nectar to support an accelerated metabolism.

Unlike many avian species less than 10% of hummingbird species migrate, occurring during winter from both North and South America to the tropics in pursuit of warmer climates (López-Segoviano et. al., 2018). These migrations are achieved through metabolising endogenous lipids to sustain the high energy use for flight (Gershman et. al., 2023).

Social and hierarchical behaviours play a heavy role in community dynamics of hummingbirds. Smaller sized species are often excluded from feeding sites by larger species through feather display, vocalisation and aerial combat (Bribiesca et. al., 2019). Dominant species will control and defend territories which encompass feeding and nesting spaces (Márquez-Luna et. al., 2018). Hummingbird communities are often extremely diverse, despite the fact that species with similar morphological traits frequently compete for resources, making co-habitation challenging (Guevara et. al., 2023). This diversity is maintained through niche partitioning and resource specialisation.

Many species of hummingbird seasonally 'drift' to ensure nectar availability all year round. This may be movement to different territories within a habitat, meaning ever varying community structures (English et al., 2024).

Foraging roles can be categorised into distinct behaviours: territorial defence, where individuals monopolize nectar sources; trap-lining, involving sequential visits to feeding sites with varying rewards; territory parasitism, encompassing both filching (covert nectar theft) and marauding (exposed nectar theft); and generalist foraging, characterised by opportunistic feeding or undefined community roles (Márquez-Luna et. al., 2018).

Nectar provides the main energy source for hummingbird's high metabolism, however invertebrates also make up a large portion of diet (Spence et. al., 2021). Nectar collection is achieved though the ability to hover at any given angle and feed from producing flower cups. Hummingbirds achieve wing beats of over 200 per second through 180° wing rotations facilitated by their freely articulating shoulder joints (Kruyt et. al., 2014).

Furthermore, hummingbirds are equipped with specialized, elongated, partially cartilaginous tongues. These tongues, which extend to approximately twice the length of their bills, split into two curled, grooved structures that act as "scoops," efficiently collecting nectar and transporting captured insects. (Rico-Guevara, 2017).

Reddish and Attenborough (2012) describe how in colder climates, their endothermic nature allows hummingbirds to pollinate independently of solar warmth, giving them an advantage over insect pollinators. Ornithophilous plants have developed adaptations that ensure pollen adheres to hummingbirds' foreheads or bills, strategically placing it for transfer (Murcia and Feinsinger, 1995). The prevalence of red flowers with ultraviolet patterning in these plant species reflects the specialized visual ability of hummingbirds, which includes a sensory cone receptive to UV light, and the general inability of insects to detect red (Altshuler and Wylie, 2020). This, along with the remarkable foraging capacity of individual hummingbirds – visiting up to 2,000 flowers per day – makes them highly effective pollinators (Pyke, 1978).

Due to this reliance on frequent feeding to maintain a high metabolism, starvation can onset rapidly and is a common cause of mortality (López-Calleja et. al., 1997). Spiders and insects such as mosquitos, mites and flies provide a vital protein source, while reducing the spread of diseases and crop pests (Peaker, 1989).

Hummingbirds are highly active and extremely responsive to environmental pressures (Martínez-Roldán et. al., 2024). Several studies investigating the impacts of hummingbird habitat fragmentation due to agricultural development show that while initial impacts are devastating for communities, given time and providing essential resources are still attainable, local populations will adapt (Mendiola-Islas et. al., 2023).

Hummingbirds are naturally predated on by snakes, spiders, mantises, owls and wildcats, (Miller and Gass, 1985) predation however does not contribute that significantly to mortality rates. While domestic cats have caused a recent increase in hummingbird mortality (Loss et. al., 2013), research by Choi et. al., (2023) has revealed that the most significant factor is unsanitary feeders and harmful artificial nectar – contributing to ~7000 deaths per year. Encroaching human presence into natural habitats is only likely to increase these mortality rates.

Closely related sympatric species can experience vastly different population changes in response to the same environmental shifts (English et al., 2024). This is evident in how different habitat types, such as continuous and fragmented forests, support distinct ecological communities (Huh et al., 2023). The significant impact of human-caused habitat modification on hummingbird populations further underscores this point (Greig et al., 2017). For example, the population decline of the rufous hummingbird *(Selasphorus rufus)* due to habitat loss (Jefferys et al., 2024) may be a sign of future declines in other species facing similar pressures. Climate change is projected to have a particularly detrimental impact on specialised species, which are often more vulnerable to environmental shifts due to limited habitat range (NAPPC, 2008). As climate change alters habitat suitability, species will redistribute, resulting in perpetually evolving community structures (Carranza-Quiceno et. al., 2024). One such habitat affected is tropical montane cloud forest, which supports the highest diversity of hummingbirds of any neotropical habitat (Rodríguez-Flores et. al., 2019).

Montane cloud forest is a diminishing habitat, restricted latitudinally and thus found only in the tropics (Toledo-Aceves et. al., 2011), with 41% of the worlds cloud forest found in central and south America (Karger et. al., 2021). A cloud forest develops when moisture-laden air currents from lower elevations are forced upwards by mountainous terrain, causing cooling and condensation into persistent fog or clouds at a specific altitude. This creates a humid environment where specialised vegetation thrives, often embodied by knotted trees laden in moss and epiphytes which collect moisture directly from the fog (Oliveira et. al., 2014). These habitats not only support a magnitude of endemic biodiversity but also play a vital role in hydrological and nutrient cycles (Martínez et. al., 2009). Cloud forests generally occur between 500 – 4000m above sea level (Kappelle, 2004). Due to this limited elevation range, all endemic floral and faunal species that rely on this environment are significantly threatened by extinction (Toledo-Aceves et. al., 2011). A multitude of pressures continuously threaten these forests, including logging, deforestation due to agricultural expansion, human settlement and changes in the global climate (Ponce-Reyes et. al., 2013). Recent research has revealed a spatially heterogeneous rise in average annual temperature over the past century (Cuervo-Robayo et. al., 2020). Moreover, this is changing hydrological and seasonal cycles, forcing cloud circulations into higher altitude ranges, where atmospheric conditions are still adequate (Helmer et. al., 2019; Bode, 2024) causing ever more frequent fragmentation. This poses a significant threat to hummingbird communities, as their species' have evolved adaptations for specific altitudinal ranges and may not be able to shift their distributions quickly enough to keep pace with inevitable habitat changes (Spence et. al., 2022). Hummingbirds are crucial for pollinating plant species that exhibit year-round (e.g., Blue porterweed - *Stachytarpheta frantzii*) or recurrent (e.g., Yellow jacobinia - *Justicia aurea*) flowering patterns (Kay and Grossenbacher, 2022). Minor climate fluctuations can lead to substantial changes in flowering seasonality, potentially breaking the co-evolved synchrony between hummingbird and plant lifecycles, and causing ecological disruption well before extinction events occur (Gonzalez and Wethington, 2014).

Anthropogenic pressures and changes to natural habitat are the biggest current threat to hummingbird populations (Medel et. al., 2022; Prieto-Torres et. al., 2021). However, species exhibit varying responses, for example while urbanisation appears to be decreasing survival rates for rufous hummingbirds, it's also thought to be a factor in the expanding range of Anna's hummingbirds (English et. al., 2024).
Urbanisation and encroachment of man-made structures and agricultural practices is causing increased habitat fragmentation, degradation and conversion on both global and local scales (Simkin et. al., 2022; Li et. al., (2022). These effects have already been quantified as one of the largest drivers of biodiversity loss, with ~50% of bird species affected (Santos et. al., 2024). Additionally, urbanisation alters floral communities, leading to a decline in pollinator diversity within a habitat (Ruas et. al., 2022). Furthermore, impacts from urbanisation not only cause changes in populations and species behaviours; Santos et. al., (2023) finds in highly urbanised areas, morphological shifts can also be observed.
Human-populated areas, through the loss of natural floral growth and the introduction of non-native plant species, are experiencing significant alterations in flower distributions. Urban landscapes often feature small, concentrated patches of flowers with minimal surrounding canopy (Theodorou, 2022). These changes are driving behavioural shifts in hummingbirds, leading to increased territoriality and aggression, potentially favouring individuals with brighter plumage and greater mass. Consequently, the diminished role of hummingbirds in pollinating non-native species can diminish the functional significance of certain morphological adaptations (Anselmo et. al., 2023). Hadley and Betts (2009) find that forest fragmentation causes changes in movements of generalist species, changing feeding patterns and therefore plant assemblages over time. Moreover, Greig et al. (2017) posit that anthropogenic disturbances are contributing to the homogenization of hummingbird

assemblages, favouring generalist species through diminishing the pressure of migration behaviours.

Encroachment of agricultural land accompanies the use of Neonicotinoid pesticides. Hummingbirds' high feeding rate can lead to potential ingestion of large quantities of contaminated nectar and pollen. Exposure can also occur through direct skin contact and consumption of poisoned invertebrates (English et. al., 2021; Bishop et. al., 2018). Their small body size and high metabolic rates may amplify the negative effects of toxicants like neonicotinoids along with migratory patterns also subject them to varying pesticide regulations across different regions (Bishop et. al., 2022).

Data from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (2024) reveal that 35 hummingbird species are at risk of extinction in the next century. Of these, eight are critically endangered, with an estimated 50% probability of extinction within the next decade. Moreover, two species have already gone extinct emphasizing the critical need for immediate conservation measures (IUCN, 2024).

Rationale

Exploring the true diversity of hummingbirds in montane tropical cloud forest can help to further understand their importance in both local and wider ecosystems. Incorporating anthropogenic effects and achieving quantifiable evidence of influence on diversity and community structure will provide strong indications for future threats to hummingbirds and predict how cloud forest ecosystems may be affected. Future conservation efforts may be informed for individual and communities of species along with habitat preservation and restoration.

Hypotheses

Proposed hypotheses: H1: Human influence of feeding sites causes hummingbird diversity to favour both dominant and generalist species. Natural, undisturbed feeding sites favour rare, specialist species. H2: Natural un-affected sites will show more consistent community structure across the region. H3: More species will be encountered at Natural un-disturbed sites, but more individuals will be encountered at disturbed sites.

Methods

Cloudbridge Nature reserve

An abundance of both naturally growing and planted species of nectar producing flowers allows for ideal conditions to investigate population dynamics, therefore Cloudbridge nature reserve provided an ideal location for this investigation.

Founded in 2002, Cloudbridge is located in the Talamanca Mountain range of Costa Rica. The tropical montane cloud forest present in the reserve can be found in varying stages of planted or natural regrowth (See figure 2) (Cloudbridge Nature Reserve, 2016) known to promote and conserve high levels of biodiversity (Santos et. al., 2024). The reserve is located at an altitude of 1500m, reaching to 1900m where it meets the Chirripó national park. Research and conservation projects are frequently conducted at Cloudbridge, including floral and faunal studies and ongoing reforestation. The reserve is supported by the U.S. based non-profit, Cloud Forest Conservation Alliance (CFCA) (Nature Reserve, 2016).

A species list completed for Cloudbridge Nature Reserve in November 2019 shows evidence of 27 species of hummingbird having been sighted and recorded (Powell et al., 2019). This provides a background of information on feeding sites, behaviours and diversity.

Moreover, multiple studies have been conducted in the past at Cloudbridge on how feeders can affect hummingbirds and feeding habits (Rabone & Staunton, 2015; Reessink, 2022; Cannon, 2017). Nonetheless, there were no artificial feeders present in the reserve during this survey period.

In the absence of other avian pollinators, various plant species found in cloud forest habitat have co-evolved alongside the *Phaethornis* genus. This hummingbird genus, commonly referred to as hermits, have long, curved bills capable of retrieving nectar from these ornithophilous plants (Feinsinger & Colwell, 1978). The Violet Sabrewing (*Campylopterus hemileucurus)* is one of the few species not found in the *Phaethornis* genera that, alongside the hermits, is also capable of feeding from the ornithophilous flora. The *Trochilinae* subfamily, of which *C. hemileucurus* is part of, typically have shorter, straighter bills and consist of many 'generalist' species, feeding from a wide variety of flowering plants, often less rich in nectar (Rico-Guevara et. al., 2021). These generalist species share pollination of these plants with bats and insects (Martén-Rodríguez et al., 2009).

Site selection

18 sites were selected to be surveyed over the course of six months, 8 of which are based in protected forest of the nature reserve where primarily natural influences will affect hummingbird behaviour, shown in figure 2. These areas without the impact of human influence are separated by natural breaks in food sources and a minimum of 100m (Jackson, 2024). The remaining 8 sites consisted of active feeding sites heavily influenced by human activity, as also seen in figure 2. These disturbed sites consist primarily of planted floral assemblages and are all found within 10m of buildings and other man-made structures. There was also at least one natural break or artificial barrier separating each of these sites.

The sites were chosen for suitability; each required to have an abundance of flowering plants to ensure it a viable feeding site for hummingbirds. In areas with limited flowering plants, the energy expended by hummingbirds in foraging likely outweighs the nectar reward, resulting in low bird attraction (Pyke, 1978).

After two months, all sites were reviewed for continuing suitability due to the varying cycles of bloom in feeding flora and cloud forest ecosystem dynamics. After eight weeks, Jilguero site 2 was no longer deemed a suitable location due to a distinct lack of nectar availability, therefore, a new site on Sentinel trail was selected.

Data collection

Each site observation was undertaken for one hour beginning at 7:00am, followed by a second site observation at a different location beginning at 9:00am. One human disturbed site and one undisturbed site were surveyed per day, four days a week, over a schedule of 2 weeks. To ensure all sites were visited equally, the starting time of each site changed every 2 weeks so all sites were surveyed at 7:00am and 9:00am equally (Jackson, 2024). Weather conditions and other potential impactful disturbances were made note of (e.g. landslides and tree falls). Data collection took place between 07/08/2023 - 08/12/2023 and species were identified using the Garrigues & Deans (2014) field guide and the Cornell lab Merlin bird ID app. Hawke frontier ED X 8x42 binoculars were used to aid identification. Data collection was facilitated by prior experience surveying bird communities in montane cloud forests and a comprehensive understanding of the species present within the reserve. Species, sex and displayed behaviours were recorded during observation the observation period.

Non-human influenced sites

***Table 1**: List of non-human influenced sites with altitude and primary species of feeding flora*

Site	Elevation	Primary feeding flora
Jilguero 1	1790m	*Justicia aurea, Costus wilsonil*
Jilguero 2 (07/08/2023 – 30/09/2023)	1730m	*Moussonia deppeana*
Rio 1	1660m	*Justicia aurea*
Rio 2	1630m	*Phaseolus vulgaris*
Gavilan 1	1830m	*Besleria solanoides*
Gavilan 2	1700m	*Palicourea padifolia*
Los quetzals 1	1820m	*Moussonia deppeana*
Los quetzals 2	1760m	*Besleria solanoides*
Sentinel (17/10/2023 – 08/12/2023)	1750m	*Phaseolus vulgaris*

Human influenced sites

***Table 2**: List of human influenced sites with altitude and primary species of feeding flora*

Site	Elevation	Primary feeding flora
Visitor car park	1540m	*Stachytarpheta frantzii*
Lab site	1560m	*Stachytarpheta frantzii, Heliconia wagneriana*
Classroom site	1560m	*Stachytarpheta frantzii, Heliconia wagneriana*
Memorial garden	1550m	*Fuchsia boliviana, Megaskepasma erythrochlamys*
Private trail	1550m	*Stachytarpheta frantzii*
Bird Café	1510m	*Stachytarpheta frantzii, Heliconia wagneriana*
Casita Gavilan 1	1790m	*Stachytarpheta frantzii*
Casita Gavilan 2	1790m	*Stachytarpheta frantzii, Hibiscus mutabilis*

Figure 1*: Location of Cloudbridge nature reserve and surrounding region*

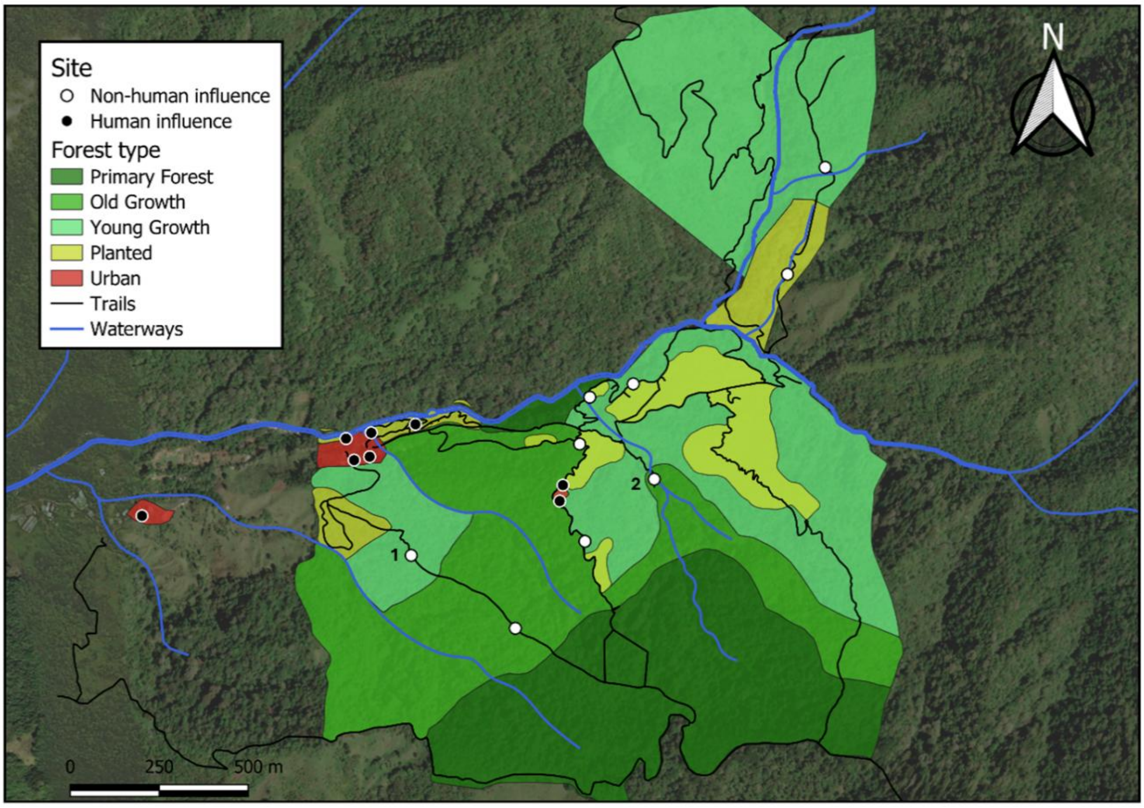

Figure 2*: Cloudbridge nature reserve area map showing main trails, waterways and forest types present. Non-human influenced survey sites are indicated by each white point, while human influenced sites are indicated by each black point. 1= Jilguero site 2; only visited for first half of survey period. 2 = Sentinel; only visited for second half of survey period*

Data analysis

Diversity indices are quantitative measures indicating the amount of species found in a community (Roswell et. al., 2021).

Alpha diversity, or species richness, measures the number of species in a local biological community, in the case of this investigation per site. Gamma diversity represents the total species richness across a larger regional scale, incorporating multiple communities. Beta diversity then describes the rate of species turnover, or compositional change, between alpha and gamma communities (Morris et. al., 2014).

Hill numbers were used to combine species richness and relative abundance thus producing the effective number of species in a community (Ricotta and Enrico, 2024). Hill numbers are applied to each order of diversity to understand true diversity. These are shown as: Q0 - representing richness and favouring rare species, Q1 – representing common species calculated by -Exponential of Shannon-Weiner Index, Q2 – representing dominant species using the inverse of Gini-Simpson index (Figure 3). These values were calculated for all orders of diversity using R studios (v.4.4.2, 2024.10.31 - R core team, 2024) software and represented graphically using ggplot (Wickham, 2016).

A non-metric two-dimensional scaling plot was used to visually represent the degree of dissimilarity between different samples based on their community composition.

$$q=0,\ D_0 = \sum_{i=1}^{S} Pi^{0} = S$$

$$q=1,\ D_1 = \exp\left(-\sum_{i=1}^{S} Pi \ln Pi \right)$$

$$q=2,\ D_2 = 1 / \sum_{i=1}^{S} Pi^{2}$$

***Figure 3**: Hill diversity equations for Q0, Q1 and Q2. S = number of sampled species, Pi = proportion of biomass occupied by species (i) (Yan et. al., 2023).*

Results

Alpha diversity

No significant differences were apparent in the average number of effective species when calculated for Q0, Q1 and Q2 for alpha diversity, as shown in figure 4. Non-human influenced sites showed a greater variation in values, with Los Quetzales 1 showing the highest Q0 value of 14, displaying particularly high diversity. Conversely Gavilan 1 shows the lowest Q0 value, demonstrating that only 4 species were encountered at this site.

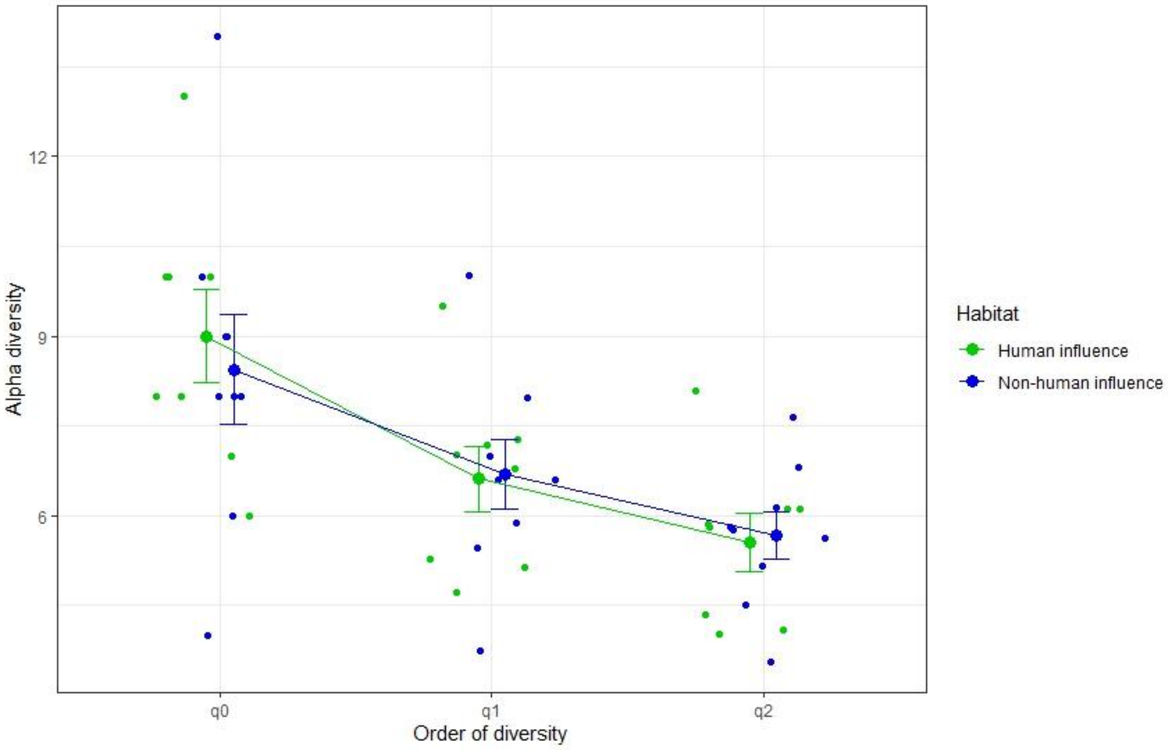

***Figure 4**: Visualisation of alpha diversity index values for each Q number order. Data table – Appendix 2*

Beta diversity

The index values for q0 for both habitat sites show little difference, with non-human influence habitat being marginally higher (figure 5). Non-human influence habitat q0 = 2.25, Human influence habitat q0 = 2.22.

However, there is a more considerable difference in values for q1 and q2. Non-human influence habitat displays higher Beta diversity index value, indicating a greater degree of variance in species composition. This is shown in the non-human influence habitat q1 value = 1.61, compared to the human influence habitat q1= 1.36. A similar difference in values is apparent for Q2.

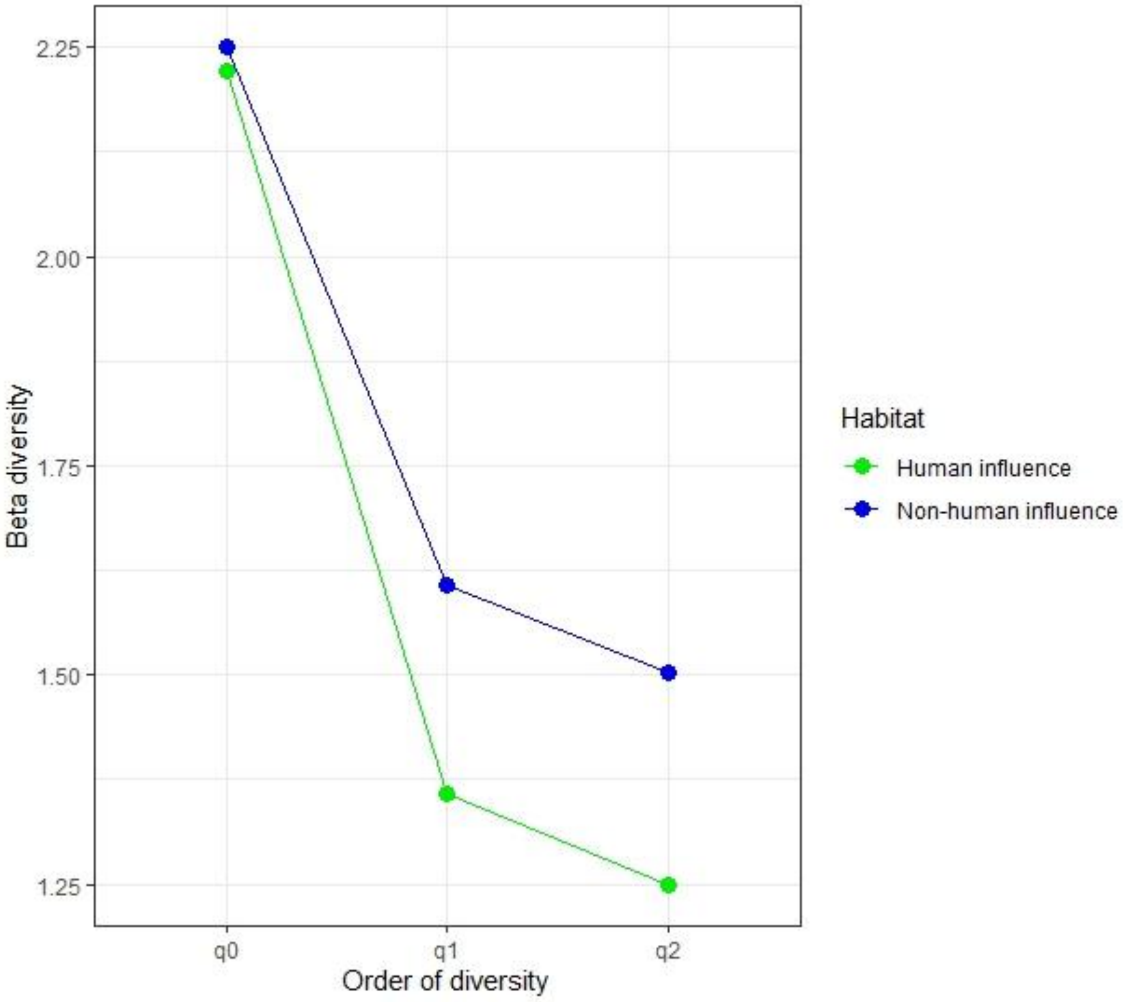

***Figure 5**: Beta diversity index values for each order of diversity for both human and non-human influenced habitats.*

Gamma diversity

Species richness of the surveyed ecosystem, represented by q0 shows a marginally higher value for sites with human influence than that produced for non-human influence. (Human influence habitat q0 = 20, non-human influence habitat q0 = 19) (figure 6).

The non-human influenced sites show a larger number of effective common species (non-human influence habitat q1 = 10.42, human influence habitat q1 = 8.78).

The effective number of dominant species is represented by q2, of which human influenced feeding sites show the lowest value, q2 = 6.59. Non-human influenced sites show a greater value of 8.14 effective species for the whole surveyed area.

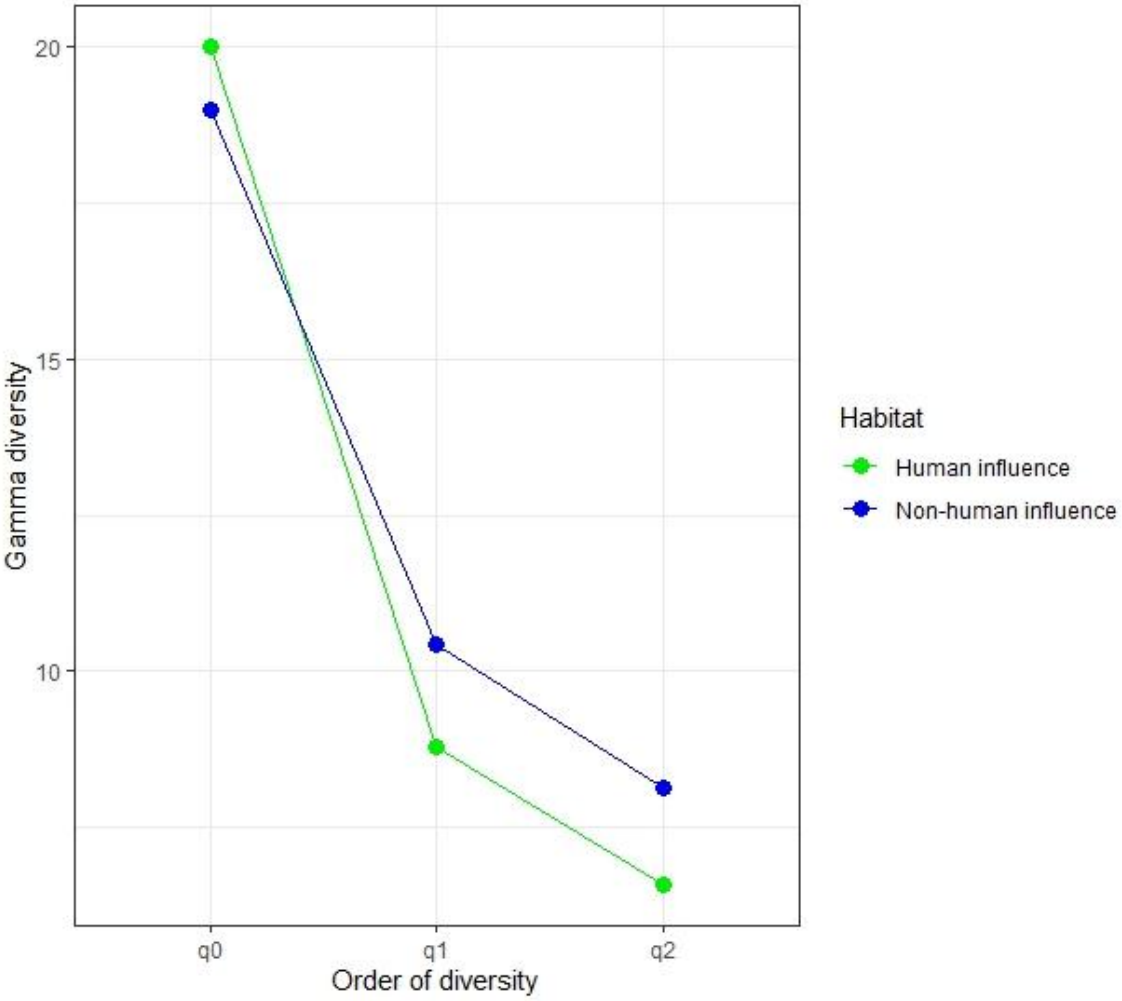

Figure 6*: Effective number of species calculated through gamma diversity using q0, q1, q2 for both human and non-human influenced habitats.*

Community structure

Overall, 25 species of hummingbird were recorded during this study with multiple effective functioning communities throughout all surveyed sites.

Community composition in human influenced habitat is shown to have a greater degree of dissimilarity between sites (figure 7). The feeding sites of non-human influence show less variance in values (MDS1 and MDS2), therefore are more likely to have similar species and social or behavioural dynamics.

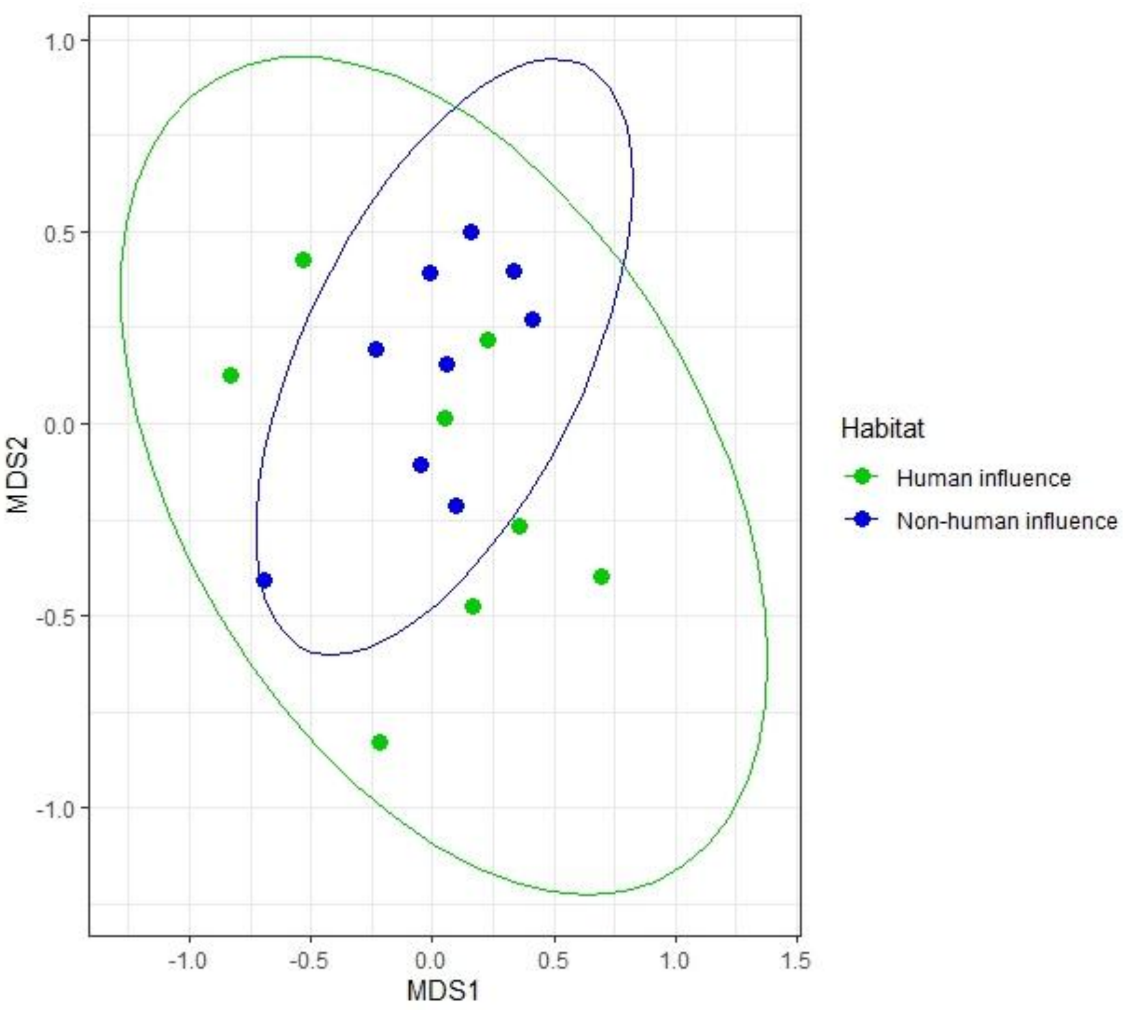

***Figure 7**: Non-metric two-dimensional scaling (MDS1 and MDS2) ordination plot showing community composition*

Discussion

Alpha diversity

Species richness between human-influenced and non-human-influenced sites showed minimal variation, indicating that habitat influence had little discernible impact when combined for all sites. However, extreme variation within these habitat types was shown.

The largest variation in species richness was exhibited in non-human influenced habitat which may be due to several factors such as bloom cycles and site selection. As aforementioned, Los Quetzales 1 (non-human influence) showed the highest richness of all sites with 14 recorded species and located the farthest away from human disturbance. Maruyama et. al., (2024) finds that hummingbird-plant communities were increasingly variated and diverse over spatial gradients travelling away from urban environments due to climatic changes. A wide range of seasonal flowering species were found at Los Quetzales 1, with bloom cycles taking place throughout the survey period. For example, the disappearance of *Moussonia deppeana* flowers coincided with the absence of Lesser violetears (*Colibri cyanotus)*, suggesting a critical link between the two species. Rappole and Schuchmann (2003) find similar patterns of local and seasonal migration behaviours following bloom cycles. However, these migrations lacked consistency, suggesting potential influences from climate variability and the ongoing adaptive responses of hummingbirds to environmental shifts.

Gavilan site 1 however exhibited the lowest hummingbird species richness throughout the whole survey period. This site featured specialized floral species, such as *Besleria solanoides*. Its small, tubular flowers limited access to only smaller hummingbird species, resulting in low overall richness, with the Scintillant hummingbird (*Selasphorus scintilla),* Costa Rica's smallest, being the most commonly encountered (Jackson, 2024). This particular site was also frequented by large mammals for passage through the reserve, particularly collared peccary (*Pecari tajacu*) which due to foraging and rooting behaviours, heavily impact vegetation structure (Herminio et. al., 2024).

The Bird Café site, while occurring at the lowest elevation (1510m) also showed a high richness of 13 species. The low elevation of this human influenced site resulted in the presence of several species not found elsewhere such as the Brown violetear *(Colibri delphinae)* and White-crested coquette *(Lophornis adorabilis)*, as it represents the upper limit of their range (Ebird, 2025). The presence of a substantial population of Blue porterweed (*Stachytarpheta frantzii*), a species exhibiting continuous anthesis (Liew and Yong, 2016) and accessible to a broad range of hummingbird species, ensures a continuing food supply at this site. The attraction of artificial feeders within 100 metres of the site may also have affected abundance and social dynamics.

Despite selecting sites with specific distances and both natural and artificial breaks for separation, species overlap between human and non-human influenced areas likely occurred due to the presence of habitat corridors.

Beta Diversity

Greater variation in species turnover was demonstrated in non-human influenced habitats across all surveyed sites was observed (figure 5). This is primarily due to the diverse plant-hummingbird assemblages found in these areas. Wolowski et. al., (2016) finds that variation in flower traits promotes specialization in plant-hummingbird interactions, resulting in more distinct ecological communities. Non-human influenced sites were observed to contain a wide range of native seasonal floral species, inducing ever changing species presence and dominance throughout the survey period. Cotton (2006) observes that resource availability very closely correlated with fluctuations in hummingbird species richness and abundance. Conversely, human-influenced sites exhibited lower rates of compositional change due to being dominated by a few abundant floral species that favour generalist hummingbird species. This abundance of perennial flora in human-influenced areas caused standardisation of hummingbird species, consequently reducing variance in community structure and annual change and species turnover. Because these areas offer consistent floral resources, there is a lessened need for hummingbirds to migrate between locations to track bloom cycles, this results in more stable and permanent community dynamics. According to Pyke's (1978) application of optimal foraging theory, hummingbirds make foraging decisions based on the energetic return, choosing to visit and compete for sites only when the available resources are sufficient to offset the energy invested.

Non-human influenced sites were more prone to natural disturbance events, for example, Los Quetzales 2 was drastically altered due to a landslide, effecting both the landscape and present floral species. This did not cause any observed drop in hummingbird presence at this site, however species interactions were influenced due to increased competition for resources.

Although species richness exhibited minimal variation between human and non-human influenced sites, encounter frequency was significantly lower in the latter. This discrepancy may arise from hummingbirds becoming habituated to human presence in anthropogenically disturbed sites, while the presence of surveyors at natural feeding sites could deter them from exhibiting their typical foraging behaviours.

Gamma diversity

A greater Q0 value for species richness of all the anthropogenic areas surveyed may perhaps be due to lower elevation sites causing increased potential for habitat crossover with lowland species. The reduced canopy cover in human-influenced sites, resulting in more open space and increased sunlight for flower growth, may have led to an observation bias, potentially explaining the higher number of species recorded in these areas due to increased visibility and ease of identification. Additionally, *S. frantzii* exhibited high relative abundance, representing a primary nectar resource for the majority of hummingbird species within anthropogenic habitats. Furthermore, Giant Lobster claw (*Heliconia wagneriana*) was often observed, providing a significant nectar resource for hermit hummingbird species at these sites, suggesting potential resource partitioning and resulting in a high species richness across all human-influenced areas.

Hadley et. al., 2017 finds that the number of species of hummingbird encountered is directly proportional to habitat patch size, particularly in forest. Human-influenced feeding sites, characterised by their open and fragmented characteristics, exhibit considerably lower connectivity to nesting sites and water sources than non-human influenced sites. This supports the findings for Q1 and Q2, which demonstrated higher values for natural feeding sites due to the facilitated movement of hummingbirds between connected habitat.

While both primary and secondary (old growth) cloud forests support thriving hummingbird populations, species richness is shown to recover from disturbances quicker than community composition (Kortmann et al., 2025). This suggests that species composition is in a state of continuous adaptation to environmental and habitat changes, as evidenced by comparisons between the species abundance recorded in this survey and previous research conducted at Cloudbridge. For example, Elliot et. al., (2021) recorded only two encounters of *Amazilla edward*, which was one of the most prevalent species documented in this investigation. A consistent finding across multiple studies however, is that hummingbird functional diversity is substantially higher in forest ecosystems than in plantation or agricultural landscapes (Chapman et. al., 2018; Edwards et. al., 2013; Prescott et. al., 2016). As shown in figure 2, Cloudbridge has a rich matrix of forest types in varying stages of regrowth and succession, presenting ideal habitat for rich assemblages of hummingbirds.

Community structure

Anthropogenic changes can be shown to affect community structure in hummingbirds as illustrated in figure 7. Homogenisation of feeding flora, combined with increased induced competition from habitat modification causes a greater range of disparity between human influenced site communities. Induced changes such as reduced canopy cover, increasing visibility and sunlight penetration, encourage plumage displays for both mating and territorial defence (Venable et. al., 2022). For example, species with vibrant coloration may thrive in human-modified habitats due to enhanced ability to communicate and interact with competitors and potential mates. This trend was also observed during surveys, as sighting frequency and overall hummingbird activity were significantly higher in human-influenced sites.

Seasonal flower assemblages will inevitably cause variations in community structure throughout the year. However, Elliott et. al., (2021) observed frugivory displayed by 4 species of hummingbird, feeding from the *Saurauia montana* (Actinidiaceae) tree on the mucilaginous pulp at Cloudbridge nature reserve, a behaviour with little to no past documentation. This suggests a potential for nutritional adaptation in response to limited nectar availability, although the long-term sustainability of this behaviour remains unclear.

Considering that 75% of the human influenced sites were at a lower elevation than any of the non-human influenced sites may suggest a reason for the greater degree of dissimilarity in community structures. Graham et al. (2009) observed generalist species inhabiting lower altitudinal zones exhibit lower phylogenetic affinity, whereas specialised species, restricted to less common higher altitudinal habitats, display greater phylogenetic clustering. Due to their specialised metabolism and flight mechanics, hummingbirds exhibit limited capacity to thrive outside their evolved altitudinal range (Altshuler et. al., 2004), thus the pressure of changing hydrological cycles, pushing cloud forest habitat into higher altitudes will further endanger these birds, particularly those already at high altitude habitats.

Eloranta et al. (2015) emphasises that competitive dynamics within a community significantly manipulate a species' response to environmental change. Therefore, the way a species reacts to human disturbance at feeding sites will likely vary depending on the local community structure.

White-throated Mountain-gem

The White-throated Mountain-gem (*Lampornis castaneoventris)* has a very limited range, found only in the highlands of southern Costa Rica and northern Panama, specifically between 1,500 meters and the timberline in oak dominated forests (Ebird, 2025). Despite being smaller than many species it cohabits with, *L. castaneoventris* has been observed as extremely territorial in nature, monopolising many of the most fruitful feeding sites. This ubiquity was demonstrated during observations as *L. castaneoventris* was the sole species encountered at every site (Jackson, 2024). Borgella et. al., (2001) finds this species to be frequently located in fragmented habitats and favouring high-elevation areas characterised by increased annual rainfall and cloud formation.

While *L. castaneoventris* was observed at all non-human influenced sites, its sighting frequency was significantly lower compared to human-influenced areas. Additionally, human-influenced areas showed a strong bias towards male encounters, whereas non-human influenced areas exhibited a higher frequency of female sightings. Males of this species are notably more aggressive, vocal, and dominant in their behaviour, suggesting a greater influence on the local community. Therefore, the community structure of sites may be heavily defined by this species in the current study region.

Further research into this species could provide valuable insights into hummingbird social hierarchies and their ecological implications within the surrounding ecosystem.

Anthropogenic habitat fragmentation and reduction can lead to decreased species turnover and eventually extinction. However, Kuussaari et. al., (2009) highlight the phenomenon of time-delayed extinction, which provides a window of opportunity for species relocation or the implementation of conservation strategies. Urban flora is frequently selected for its functional attributes, such as hedge creation, and its capacity to attract a diverse range of pollinators. In situations where habitat destruction is unavoidable, the inclusion of a diverse array of nectar-producing plants, including ornithophilous species, is a recommended strategy for minimising impacts on affected hummingbird species and communities.

Limitations

This study took place between August and December 2023, which encompassed the transition from tropical dry into wet season. Therefore, to gain a more in depth understanding of true diversity of hummingbirds in the area along with community composition, a year-round survey encompassing all floral feeding bloom cycles would be appropriate.

Due to the purely observational nature of the surveys, species crossover between sites was not quantified. Implementing mist-netting at the sites would have enabled a more robust estimation of population trends, intra-ecosystem movement and migration periods (Maglianesi et. al., 2015; Dunn and Ralph, 2002). This would also enhance species identification, which is often constrained by factors such as ambient light levels and the rapid flight of hummingbirds during observational surveys.

While sites were selected based on perceived feeding suitability, the absence of prior knowledge regarding natural feeding sites resulted in a selection process heavily influenced by bloom cycles present during the survey design period. This resulted in one site being changed mid-survey, which, for the sake of consistency should have been applied to all sites or none. Additionally, even with extensive research, information of floral species and bloom cycles present at Cloudrbidge is limited.

Natural environmental conditions, specifically heavy precipitation, posed multiple challenges to the surveys. Rain not only deterred hummingbird foraging but also affected terrain conditions, requiring the cancellation and rescheduling of certain surveys due to landslides.

Implication for conservation

Investigating further into both individually dominant species, and those with specific habitat requirements could influence future conservation techniques, while providing an understanding of how humans can more effectively accommodate for all hummingbird species. Behavioural changes can serve as indicators of how community structure and dynamics respond to varying environmental and anthropogenic pressures. Consequently, behavioural studies, both at the individual and population levels, can offer valuable insights into the intricate social and ecological interactions exhibited by hummingbirds (Abrahamczyk and Kessler, 2014).

Replicating this investigation in diverse hummingbird habitats, including tropical lowland forests, plantations, and urban areas, could offer valuable comparative insights into the differential impacts of anthropogenic encroachment on various hummingbird communities. These findings could then inform the development of targeted conservation strategies and enhance our understanding of community dynamics and annual movement patterns (Martínez-Roldán et. al., 2024). In addition to traditional conservation strategies, such as habitat restoration and impact mitigation, simpler techniques may be equally effective in promoting hummingbird survival within urban environments. These techniques include limiting artificial feeder use and the availability of toxic energy sources, implementing window and structural modifications to prevent collisions, and establishing species-rich hedgerows and native floral assemblages (English et al., 2024).

Conclusion

The results of this investigation show that anthropogenic effects and influence of feeding sites had a quantifiable influence on hummingbird populations and communities.

These results underscore the importance of maintaining natural habitat connectivity for the preservation of hummingbird biodiversity. The observed homogenisation of community structure in human-modified sites highlights the potential for reduced ecological resilience and the loss of specialised species. Understanding these impacts is crucial for developing effective conservation strategies in rapidly changing landscapes.

The ecological consequences of environmental change disproportionately impact specialist species with specific adaptations, while generalist species exhibiting more defined social behaviours often demonstrate increased resilience. This shows potential projections for future trends in population composition and may lead to greater divide in community structure between habitat types.

Overall, the findings confirmed hypotheses 1, as human influence of feeding sites favoured both dominant and generalist species while natural, undisturbed feeding sites favoured rare, specialist species. H2 was also confirmed due non-human influence sites showing more consistent community structure, while exhibiting a higher level of complexity. However, hypothesis 3 was not supported, as human-influenced sites exhibited a higher species richness and greater encounter rates of individuals.

Ultimately, these findings emphasise the need for integrated conservation strategies that address both habitat preservation and the mitigation of anthropogenic pressures on hummingbird communities. The conservation of these populations requires a comprehensive understanding of the complex interactions between habitat, anthropogenic pressures, and species behaviour. Continuing to investigate these dynamics, will ensure the long-term persistence of these vital pollinators and the ecosystems they inhabit.

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Appendices

Appendix 1

***Table 3**: All species encountered with species codes used*

BVE = Brown violetear *(Colibri delphinae)*
BVH = Blue-vented hummingbird (*Saucerottia hoffmanni)*
FTH = Fiery-throated hummingbird *(Panterpe insignis)*
GCB = Green crowned brilliant *(Heliodoxa jacula)*
GE = Garden emerald (*Chlorostilbon assimilis)*
GFL = Green-fronted lancebill *(Doryfera ludovicae)*
GH = Green hermit *(Phaethornis guy)*
LBST = Long-billed star-throat *(Heliomaster longirostris)*
LV = Lesser violetear (*Colibri cyanotus)*
MTW = Magenta-throated woodstar (*Calliphlox bryantae)*
PCF = Purple crowned fairy *(Heliothryx barroti)*
RT = Rufous-tailed hummingbird *(Amazilia tzacatl*)
SB = Snowy bellied hummingbird *(Amazilia edward*)
SC = Scintillant hummingbird (*Selasphorus scintilla)*
SCB = Scaly-breasted hummingbird *(Phaeochroa cuvierii*)
ST = Stripe tailed hummingbird (*Eupherusa eximia)*
STH = Stripe-throated hermit (*Phaethornis striigularis)*
TH = Talamanca hummingbird *(Eugenes spectabilis*)
VH = Violet headed hummingbird *(Klais guimeti)*
VO = Volcano hummingbird *(Selasphorus flammula)*
VS = Violet sabrewing (*Campylopterus hemileucurus)*
WCQ = White-crested coquette *(Lophornis adorabilis)*
WTE = White tailed emerald *(Elvira chionura)*
WTMG = White throated mountain gem (*Lampornis castaneoventris*).

Appendix 2

***Table 4**: Raw data used for alpha diversity displayed in figure 4.*

	q0.Communities	q1.Communities	q2.Communities
Bird Café	13	9.494132	8.084175
Casita Gavilan 1	8	5.280531	4.027624
Casita Gavilan 2	6	4.727991	4.090909
Classroom	10	7.009329	5.850746
Gavilan 1	4	3.742410	3.567901
Gavilan 2	8	6.589316	5.761905
Jilguero 1	9	6.983045	5.630631
Jilguero 2	8	7.000000	6.125000
Lab	7	5.144380	4.343669
Los Quetzales 1	14	10.008208	7.643216
Los Quetzales 2	9	5.889805	4.500000
Memorial garden	10	7.271337	6.121019
Private trail	8	6.790106	6.111111
Rio 1	6	5.454328	5.148936
Rio 2	10	7.975515	6.810945
Sentinel	8	6.593026	5.800000
Visitor carpark	10	7.186346	5.802632