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Are orchid bees useful indicators of the impacts of human disturbance?

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Abstract

Biodiversity and ecosystem functions are threatened by human disturbance, and tropical forests are one the most vulnerable habitats. Monitoring the impacts of disturbance and the success of conservation projects is crucial, and to do this effectively it is important to identify suitable measures that are sensitive to ecosystem disturbance. Orchid bees (Euglossini) are a specialist group with mutualistic relationships with many plant species and can fly long distances, making them important pollinators of widely dispersed plant species. A loss of specialist pollinators such as these could have severe consequences for the plants that rely on their services. We therefore aimed to answer the following question: are orchid bees useful indicators of the impacts of human disturbance? If so, what measures of orchid bee diversity are most sensitive? And do orchid bees provide any indication of changes in pollination services along a disturbance gradient? Orchid bees were collected from 18 sites across a gradient of disturbance in a tropical forest region in southeast Peru. Alpha diversity across the gradient was compared using Hills numbers. Beta diversity was assessed using community composition, species contributions to beta diversity, beta diversity partitioning and novel measures of redundancy and representativeness. The potential pollination services available at each site were measured using artificial flowers and counts of pollinator visits. Alpha diversity of orchid bees showed low sensitivity to disturbance. Beta diversity measures were more informative, with disturbed sites found to be highly redundant in the ecosystem compared to the less disturbed sites. However, the most sensitive measure across the gradient was abundance – there was a significant decrease in the number of bees caught as disturbance increased, with likely consequences for pollination services. These results suggest that orchid bees may be useful indicators of the impacts of human disturbance, but alpha diversity is a poor metric for this purpose. In order to understand how human disturbance is affecting biodiversity, multiple diversity indices should be considered, and in the case of orchid bees, redundancy and abundance could be useful for detecting sensitive responses to forest disturbance.

Keywords

Biodiversity indices, indicator, Euglossini, disturbance, agriculture, rainforest.

1.1 Introduction

Covering only a small percentage of the world's surface, tropical forest harbours over 50% of terrestrial biodiversity. Yet this cover is decreasing globally, with forest being cut down for timber and conversion to agriculture (FAO, 2016), with severe consequences for biodiversity (Alroy, 2017; Gibson et al., 2011) and ecosystem functions (DeFries et al., 2004). It is therefore of the utmost importance that we have effective tools for detecting changes in biodiversity and ecosystem function in response to anthropogenic disturbance (Feest et al., 2010; Hill et al., 2016; Kremen, 2005; Pimm and Raven, 2000). Indicator groups have been widely used for this purpose (Cleary, 2004; Krug et al., 2017; Schulze et al., 2004), however choosing suitable indicator groups can be challenging (Broszeit et al., 2017; Fleishman and Murphy, 2009; Gao et al., 2015). Ideally they should be efficient to survey, show a predictable, sensitive response to environmental change, correlate well with overall biodiversity responses and play an important role in the ecosystem (Brown, 1997; Hilty and Merenlender, 2000).

Bees are the most important group of pollinators (Bawa, 1990) but have been declining globally (Allen-Wardell et al., 1998; Potts et al., 2010), with land conversion and habitat loss the leading causes (Winfree et al., 2009). Orchid bees (Hymenoptera: Apidae: Euglossini) are found throughout the Neotropics and are one of the best studied groups of bees in the region. They exhibit many of the recommended features that could make them suitable indicators of disturbance impacts (Brown 1997; Favila & Halffter 1997; Gardner et al. 2008a; Goodsell, Underwood & Chapman 2009), including being widespread, common, cost-effective, easy to sample using standardised methods (Pearson and Dressler, 1985) and having well developed taxonomic literature (eg. Dressler 1982a; Roubik 2004; Nemésio & Silveira 2007a). They have close associations with plant species and play important ecological roles as pollinators, able to access flowers that are unavailable to many other insects (Dressler, 1982a), due to their long tongues and also the large body size of some species. They can fly long distances, making them valuable long-distance pollinators (Janzen, 1971) for many widely-spaced plant species and many orchids are entirely dependent on orchid bees for their pollination (Dressler, 1982a). Another key feature of a good indicator is that they should display a clear, graded response to environmental change. There is some evidence that orchid bees display graded responses to human disturbance, but the results have been mixed and part of our motivation is to study this in greater detail. Orchid bees can persist in heavily degraded ecosystems in some cases, including forest fragments (Storck-Tonon et al., 2013) and farmland (Otero and Sandino, 2003; Sandino, 2004), although this may depend on the proximity to intact forest (Briggs et al., 2013). At the same time, there is concern that orchid bees are sensitive to forest loss (Roubik and Hanson, 2004) and some species are thought to be at risk of extinction (Nemesio, 2013), which would have major consequences for the plants they pollinate. The loss of old-growth forest and canopy disruption is likely to result in a loss of orchid bee resources (Hietz et al., 2006; Nöske et al., 2008), such as orchids, other epiphytes and specific tree saps (Dressler, 1982a; Roubik and Hanson, 2004), with probable negative consequences for the orchid bee species that depend on them. Together these features suggest that orchid bees could be an excellent candidate for use as an indicator of faunal and floral responses to tropical forest disturbance.

So far, studies on orchid bee responses to forest disturbance have primarily focused on the effects of forest fragmentation, with mixed patterns identified. The abundance and diversity of euglossine bees have been suggested to decline with decreased forest fragment size (Brosi, 2009; Brosi et al., 2008), but other studies found no effect of fragmentation on abundance or richness (Storck-Tonon et al., 2013). A few studies have compared agricultural land to intact forest but these have mostly been focused on less diverse Central American habitats and generally only compared two or three land uses. Briggs *et al.* (2013) found that polyculture could sustain orchid bee communities similar to forest habitats in composition, but abundance was higher in the polyculture than in either forest or monoculture, although abundance did decline with increasing distance from the forest. Abundance and richness of orchid bees have been found to decrease in some agricultural matrix habitats compared to forests (Aguiar et al., 2015), although others have been found to support similar communities to forest (Rosa et al., 2015) and some found higher capture rates in agricultural areas than in forest (Otero and Sandino, 2003; Sandino, 2004). However, studies of forest disturbance gradients are relatively uncommon, and none have covered the response of orchid bees across a continuous, multi-level gradient from monoculture agriculture to intact forest. There are several studies on the mutualistic relationships between orchid bees and orchids (Dressler 1967; Ackerman 1983), but again there is a lack of studies relating orchid bee diversity to overall pollination services available in the ecosystem.

As well as the challenge of selecting suitable indicator groups, another difficulty is deciding how to quantify biodiversity. There are many indices available to measure the alpha, beta and gamma components of diversity. Alpha diversity is usually the main focus of diversity studies, and species richness the most commonly used measure because it is intuitive, simple and often sensitive. However, species richness lends a lot of weight to rare species, while other indices such as Shannon and Simpson diversity place more weight on the more dominant species in the community. Recent discussions on diversity partitioning have concluded that diversity profiles (a set of multiple diversity measures that differ in the relative weight given to rare and common species, and are particularly powerful as a graphical tool) based on Hill numbers (Hill, 1973) could help avoid a narrow focus on a single result (Chao et al., 2012; Jost, 2006). Beta diversity is also often of interest in ecological studies but has an even wider array of indices to choose from than alpha diversity (Anderson et al., 2011; Tuomisto, 2010). Beta diversity measures differ in their approaches to quantifying similarity or dissimilarity between sites, and the importance of species abundance differences and the relative importance of species turnover or richness differences (Socolar et al., 2016). Beta diversity can also be placed into a unified framework for partitioning diversity effectively using diversity profiles (Reeve et al., 2016). The large number of diversity measures available have been developed to fit a broad range of questions and few perform consistently well under different conditions, which means that focusing on a single index may risk overlooking important ecological patterns (Santini et al., 2017). We are therefore proponents of using multiple measures of alpha and beta diversity to maximise our understanding of biodiversity responses to anthropogenic disturbance.

In this study, we investigated how orchid bee communities respond to habitat conversion across a gradient of human disturbance, from minimally disturbed tropical forest to banana plantations. We aimed to study how alpha and beta diversity changed across this disturbance gradient and aimed to investigate which measures were most sensitive for detecting orchid bee responses to disturbance. Identifying the aspects of the orchid bee community most sensitive to disturbance can inform which metrics to use when applying orchid bees as indicators of environmental change. Identifying which components of the community respond to disturbance may also help us better understand what they are responding to and pave the way for further investigation into the mechanisms involved.

We assessed alpha diversity using Hill numbers and used several approaches to quantify beta diversity, including two recently developed measures, redundancy and representativeness (Reeve et al., 2016). Finally, we studied the activity of general pollinators across the gradient using artificial flowers. We aimed to identify if there was any change in pollinator activity across the disturbance gradient, and if orchid bee diversity provided any indication of the potential general pollination services available in the ecosystem (Engel and Irwin, 2003). We conducted our study in the highly biodiverse Manu Biosphere Reserve, Peru, where there has been limited work on the orchid bee communities, and none to our knowledge on their responses to disturbance.

1.2 Materials and methods

1.2.1 Study area

This study was based around the Manu Learning Centre (-12.789882, -71.391753, 470 m above sea level), a research station run by the Crees Foundation, in the cultural zone of the Manu Biosphere Reserve in southeast Peru, a UNESCO World Heritage Site. This zone contains a mixture of protected areas of lowland tropical forest interspersed with areas of high human impact, including logging and agriculture, and is intended as a buffer for Manu National Park. Eighteen sites were chosen to represent a gradient of human disturbance from banana monoculture to minimally disturbed tropical forest. A stratified site selection approach ensured sampling was not dominated by a single disturbance history, with three sites chosen for each of the six of major land uses in the local area, covering a gradient of human disturbance (supplementary materials Figure S.1). These were ranked from highest to lowest disturbance intensity based on land use (Beck et al., 2002; Eggleton et al., 2002), with 1 being the most disturbed and 6 the least disturbed (details in Table 1). For each land use type, one of the replicates was named ‘A’, ‘B’ or ‘C’, semi-randomly, taking into consideration suitable site groupings for access and analysis. We sampled all ‘A’ sites in the first week, then the ‘B’ and ‘C’ sites in the following weeks, so that one of each habitat types would be sampled concurrently.

At each site, data were collected on the vegetation structure to assess how this changed across the disturbance gradient. Three vegetation points were randomly selected within each site, and a 25m^2 plot marked out at each. Within this plot, canopy cover was quantified using a quadrat held above the sampler’s head and the quadrat used to estimate the percentage of canopy cover at five points within the circle. Understory vegetation density was estimated at the four corners of the sampling plot using the modified Braun-Blanquet scale as described in Hurst and Allen (2007). We counted the number of trees with a diameter >5cm at breast height and measured the diameters of the three largest trees within each vegetation plot, and measured leaf litter depth at 16 random points within the plot. These followed the protocols for vegetation assessment used by Whitworth et al., (2016). Weather data were collected at the research station, with temperature, rainfall and humidity data collected daily at 7am, manually checking a thermometer, humidity meter and rain gauge at the weather station located at the research centre each morning. Elevation data for each site were obtained from Google Earth Pro 7.3.2.5491, and distance to the main river, the Alto Madre de Dios, was measured in QGIS 2.18.7 (QGIS Development Team, 2017), measuring the straight line distance from the centre of each site to the nearest edge of the river using the ‘measure line’ tool and manually comparing the distances to the edges of the river to find the shortest.

Table 1 - Disturbance gradient description

Disturbance Rank	Disturbance type	Description
1	Banana plantation	Primarily banana monocultures, but occasionally including a few other crops; generally open habitat with low vegetation.
2	Agroforestry	Banana plantations interspersed with native tree species, providing more shade and habitat complexity.
3	Disturbed secondary forest	Uncultivated but heavily disturbed forest lying in between plantations, with more canopy cover and thick understory vegetation.
4	Cleared regenerating forest	Forest once cleared for agriculture and grazing, now regenerating under protection for over 30 years to form a closed canopy with thick understory vegetation.
5	Mixed history forest	Selectively logged forest with small patches cleared for cultivation, regenerating under protection for over 30 years. The canopy is well defined and the understory less dense, but large trees are absent.
6	Minimally disturbed primary forest	Primary forest protected for over 30 years, with little evidence of previous disturbance. The canopy is high and well defined, large trees are present and the understory is more open.

Sites of the different disturbance types were interspersed in space as much as possible. The potentially confounding effects of large landscape and climatic differences were minimised by selecting sites within a small area (20 km^2), while ensuring sites of the same disturbance type were far enough apart (>500 m) to avoid sampling pseudo-replication (Ramage et al., 2013). To minimise spatial effects on the results we kept groups of sites of different disturbance levels as close together as possible given other constraints and the locations of these habitats. We used linear models to validate the results of our correlation tests and to check for any significant effect of these other environmental variables, including them as explanatory variables along with disturbance if they had any significant effect on the response.

This project was conducted in two parts, the primary study looking at changes in the orchid bee community along the gradient and then a second study exploring potential pollination services across the same sites. We cover the methods and results of the main study first, followed by the pollination study.

1.2.2 Orchid bee diversity

1.2.2.1 Data collection

Orchid bees were sampled in the morning between 09:00-12:00 and in the afternoon between 12:30-15:30 (± 15 mins). Each site was sampled for two morning and two afternoon sessions (a total of 12 hours per site) and these four sampling sessions were pooled to form a single sample for each site (a total of 18 samples). To reduce potential biases from weather or other potential temporal sampling biases, two sites were sampled simultaneously - one more disturbed (rank 1-3) and one less (rank 4-6), and on each day different disturbance types were sampled in the mornings and afternoons.

At each site, two sampling stations were set up 50 m apart to reduce any bias from a single within-site location choice. At each of these stations, eight balls of cotton were hung from branches at a height of 1.5 m, with 2 m between cotton balls. Each cotton ball was baited with two drops of one of the following eight attractants: wintergreen oil, methyl salicylate, eucalyptus oil, eucalyptol, vanillin (3 tsp vanillin dissolved in 50 ml 96% ethanol), benzyl acetate, clove oil, eugenol. The bait stations were monitored over the three-hour sampling period, and orchid bees attracted to the baits were caught using hand nets then killed and preserved in 70% ethanol. Orchid bees attracted to the survey area that did not settle at a specific bait but came within 1m of a bait and flitted between baits, were also captured. Multiple researchers conducted the hand netting, three per site each day. This included trained researchers experienced with capturing insects with nets, and less experienced volunteers. To reduce biases from experience, we ensured that the teams surveying the different sites were as balanced as possible, with less experienced people paired with more experienced people and the teams rotated between the sites. Some of the potential issues associated with capture rates are explored in the discussion.

Preserved orchid bees were identified in Cusco, using a stereo microscope, published keys, checklists and descriptions (Bonilla-Gomez and Nates-Parra, 1992; Dressler, 1978, 1979, 1982b, 1982c, 1982d, 1984; Faria and Melo, 2007; Hinojosa-Díaz and Engel, 2011, 2012, 2014; Kimsey, 1979, 1982; Melo, 2014; Moure, 1965; Nemésio, 2011, 2009; Nemésio and Silveira, 2007b; Niemack et al., 2012; Roubik, 2004; Roubik and Hanson, 2004). For as many species as possible, identification was verified by consulting the collections at the Department of Entomology at the Universidad de San Antonio Abad de Cusco, and at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima. Reference specimens were deposited in both these collections in September 2016.

1.2.2.2 Analysis

A principal component analysis (PCA) of the vegetation structure data across the gradient was performed using the vegan package v.2.4-6 in R (Oksanen et al., 2018), and we used a Spearman rank correlation test (Spearman, 1904) to check the correlation between disturbance rank and the first principal component of the vegetation PCA.

To test if alpha diversity varied with human disturbance, orchid bee alpha diversity was calculated for each site using Hill numbers, a family of diversity measures parameterised by a viewpoint parameter, q, with increasing emphasis on dominant species as the value of q increases (Hill, 1973; Reeve et al., 2016). We calculated diversity at $q = 0, 1, 2$ and ∞, as these correspond to the following commonly used diversity measures: species richness, Shannon entropy, Simpson diversity and Berger Parker diversity respectively, so our measures can be easily compared to previous studies.

All analyses were conducted using R version 3.3.2 (R Core Team, 2017) in RStudio version 1.0.136 (RStudio Team, 2016). Observed alpha diversity was calculated using the package rdiversity v.0.4.3 (Mitchell and Reeve, 2016). Estimates of species richness, Shannon entropy and Simpson diversity were calculated using the package iNEXT v.2.0.14 (Hsieh et al., 2016) to rarefy or extrapolate estimates to a standard sample size of 50 individuals at each site (Chao et al., 2014; Colwell et al., 2012). This sample size represented approximately double the smallest sample size, the maximum that can be reliably extrapolated at q = 0 with high confidence (Hsieh et al., 2016). This provided approximately 90% sample coverage for all sites (supplementary materials Figure S.3). The diversity estimates at each value of q were bootstrapped 1000 times using the iNEXT function in R, to calculate a confidence interval around our mean estimates. This allowed us to test for consistency in the direction of change in the diversity estimates while accounting for the uncertainty in the diversity estimates. We did this by extracting the 1000 raw estimates of the diversity of each site, and then calculating the proportion of times a less disturbed site was more diverse than a more disturbed site. All disturbance type pairs were compared, and a Spearman rank correlation test (Spearman, 1904) was used to test the correlation between the proportion of times that the less disturbed site was the more diverse of the pair and the difference in disturbance rank between the sites.

To understand how beta diversity was affected by human disturbance, we quantified the change between sites along the gradient using several methods, including community composition, beta diversity partitioning and two recently developed beta diversity measures, redundancy and representativeness (Reeve et al., 2016). The total beta diversity of the gradient, measured as the total variance of the community matrix, was calculated using the beta.div.comp function in the R package adespatial v.0.1-1 (Dray et al., 2018) along with the partitioning of the total beta diversity into nestedness and turnover. A Hellinger transformation of the species x site abundance matrix was used, as the Hellinger distance provides a good compromise between linearity and resolution and has been found to correlate better with ‘true’ distances in simulations than many alternatives (Legendre and Gallagher, 2001). Beta diversity decomposition was then calculated for this matrix using the quantitative form of Sorensen’s dissimilarity coefficient, in order to account for differences in relative abundances as well as species identity (Legendre and De Cáceres, 2013). A redundancy analysis (RDA) was used to examine the change in species composition across the gradient, applied to the Hellinger transformed community matrix and constrained by disturbance rank, elevation and distance to the river, using the vegan package in R (Oksanen et al., 2018). The use of this transformation overcomes many of the issues associated with raw Euclidean distances, including many zeros and large differences in abundances, which may lend disproportionate weight to rare species (Borcard et al., 2011; Legendre and Gallagher, 2001). Species contributions to beta diversity (SCBD index), which is the relative degree of variation in the abundance of individual species across the study gradient (Legendre and De Caceres, 2013), were calculated with the beta.div function in the adespatial package, using the Hellinger dissimilarity coefficient (Legendre and De Cáceres, 2013). The abundances of the species with the highest SCBD values were compared across the gradient, with some low SCDB species included for contrast.

The redundancy of the communities at each site was calculated using the redundancy (ρ) measure, available in the package rdiversity (Mitchell and Reeve, 2016). This is a measure of beta diversity that represents the extent to which the diversity of the overall metacommunity (the diversity of the whole gradient in this case) would be preserved if a single community or site was lost (Reeve et al., 2016). We also calculated the representativeness ($\bar{\rho}$) of the sites, which is a measure of how well a single site represents the overall metacommunity. Representativeness considers how much of the metacommunity diversity a site holds (i.e. the redundancy) relative to the size of the community at that site, providing a correction for the different sample sizes across the gradient. Both redundancy and representativeness were calculated at $q = 1$, as this provides an intermediate level of conservatism and is a key value of q due to its correspondence to many measures of beta diversity through relative entropy and K-L divergence (Reeve et al., 2016).

We used disturbance as a continuous explanatory variable since this allowed us to consider land-use on a continuous spectrum of disturbance intensity, with the possibility of other land-uses falling at intermediate intensities. We could have used an ordered discrete variable, which would have been better able to detect a signal in the presence of unevenness in disturbance differences, but this would have required more data to fit. Our simpler approach is supported by the strong correlation of our continuous disturbance rank with vegetation structure data. Nonetheless, because we could not be sure of the exact difference in disturbance between each level, where possible we used a Spearman rank correlation test to assess the patterns of diversity along this gradient. This approach makes no assumptions regarding the shape of the relationship between the variables, only that the pattern is monotonic along the gradient, and is a therefore a conservative approach for these analyses. Spearman rank correlation tests were used to test for correlations of disturbance rank with abundance, observed alpha diversity at q = 0, 1, 2 and ∞, estimated alpha diversity at q = 0, 1 and 2, and representativeness and redundancy at q = 1. In addition to checking each value of q independently, we tested if the overall pattern of alpha diversity change across the disturbance gradient was significant at $\alpha = 0.05$. To overcome the non-independence of the q values from one another, we used a permutation test to calculate the combined p value for the correlation between disturbance rank and observed alpha diversity at q = 0, 0.5, 1, 2 and ∞ and estimated alpha diversity at q = 0, 0.5, 1 and 2 (q = ∞ could not be included because the estimates all converged at 1, so there was no variation; we included q = 0.5 because q is on a logarithmic scale, so this prevents biased weighting of rare species when calculating the overall pattern of alpha diversity across multiple values of q). The permutation test involved randomly re-labelling the study sites, and then re-calculating the significance of the correlation between disturbance rank (now randomly re-assigned) and alpha diversity at each value of q (Good, 2000). These permuted p-values for each value of q were combined to determine the significance of the overall alpha diversity change across the gradient (Fisher, 1925). This was repeated for 10000 permutations, and the permuted p-values compared to those obtained with the original data, to determine the probability that the observed correlation of diversity could have occurred by chance. To check that the patterns of change in redundancy and representativeness across the gradient were not specific to our chosen value of q = 1, we also used a permutation test to obtain the combined p value for the correlation of disturbance rank with redundancy and representativeness calculated at q = 0, 0.5, 1, 2 and ∞.

As well as testing for the effect of disturbance on diversity and abundance, the potential effects of altitude, rainfall and distance to river were investigated using linear models, to confirm whether the effects of disturbance identified with the correlation tests remained significant when accounting for these variables. The diversity and abundance response variables were log-transformed and modelled with a gaussian distribution. The model summaries and residuals were inspected to evaluate model fit. None of the additional environmental variables resulted in a significant improvement compared the model that included only disturbance rank. Full details of the models tested can be found in Table S.2 of the supplementary materials. In the case of the relationship between abundance and disturbance rank, visual inspection of the data prompted us to also test a quadratic polynomial, but the AIC values indicated that a linear relationship was a better fit (ΔAIC = 1.42). Throughout the results section, the statistics reported are the results of the Spearman rank correlation test unless stated otherwise.

1.2.3 Pollination services

1.2.3.1 Data collection

The potential for the provision of pollination services (from any pollinators) across the gradient was tested using artificial flowers filled with sugar solution (Internicola et al., 2007; Real, 1981). The flowers were 5 cm in diameter and constructed from thin craft foam with a central well containing 1.5 ml of the sugar solution (1:1 sugar and water). Red, blue and yellow flowers were used, with five of each colour on an array that was suspended at a height of 1.3 m at the survey site. Two flower arrays (30 flowers in total) were used at each site, separated by approximately 30 m, and each monitored by a member of the research team. All insects (of any Order) that arrived at the flower array were counted as potential pollination events, apart from individuals that simply moved from one location on the array to another. The flowers were monitored for three periods of 45 minutes separated by 15-minute intervals during which the flowers were covered. This was repeated for four mornings, between 08:45 and 13:00, at each of the 18 sites.

1.2.3.2 Analysis

Spearman rank correlation tests were used to test the correlation between the number of potential pollination events (flower visits) with disturbance rank and with observed orchid bee species richness.

1.3 Results

1.3.1 Orchid bee diversity

1.3.1.1 Vegetation structure

The first component of the vegetation structure PCA (PC1) explained 33% of the variation in vegetation structure, with higher rankings (lower disturbance) correlated positively with canopy cover, tree count and diameter, and negatively with leaf litter depth and understory herb abundance (Figure S.2). There was a strong correlation between vegetation structure (PC1) and disturbance rank, supporting the disturbance ranking used to represent human disturbance intensity along the gradient ($p < 0.00001$, rho = 0.86; Figure 1). The results of all correlation tests are provided in Table S.1 in the supplementary materials.

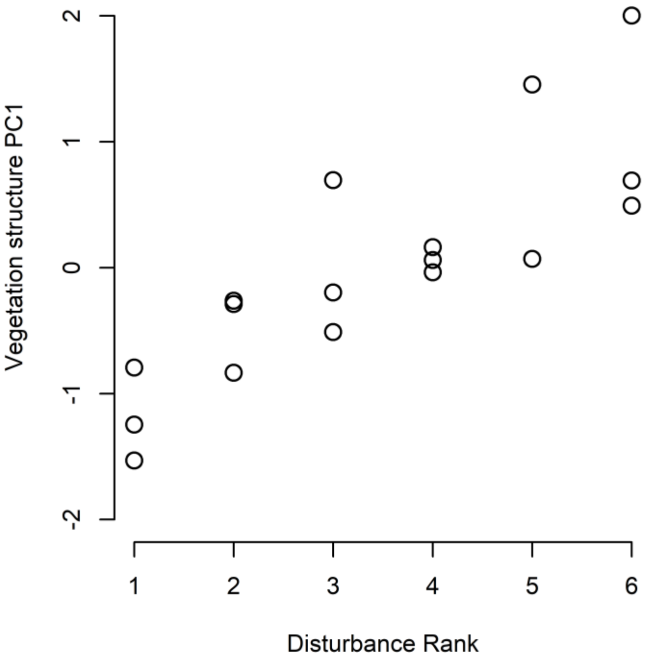

Figure 1 - Correlation between vegetation structure and disturbance rank ($p < 0.001$, rho = 0.86). Disturbance rank runs from the most disturbed (rank 1) to the least disturbed habitat (rank 6). The first axis of the principal component analysis of vegetation structure (PC1) was positively correlated with canopy cover, tree count and diameter, and negatively with leaf litter depth and understory herb abundance.

1.3.1.2 Alpha diversity

We collected 1783 individuals of 31 species of orchid bee. Overall observed alpha diversity decreased across the disturbance gradient (permuted combined p value for $q = 0, 0.5, 1, 2$ and ∞: $p = 0.025$; Figure 2). This was mostly driven by the patterns of alpha diversity at low values of q, with observed species richness ($q = 0$) and observed Shannon diversity ($q = 1$) both decreasing with increased disturbance across the gradient (rho = 0.57, $p = 0.01$; rho = 0.51, $p = 0.03$). There was no significant change in alpha diversity across the gradient at higher values of q. However, when estimated diversity was examined, correcting for sample size (n = 50), there were no significant differences in estimated diversity across the disturbance gradient, either overall (permuted combined p value for q = 0, 0.5, 1 and 2: p = 0.330) or for any individual value of q, due to the wide confidence intervals around the mean estimates (Figure 3 and Figure S.4).

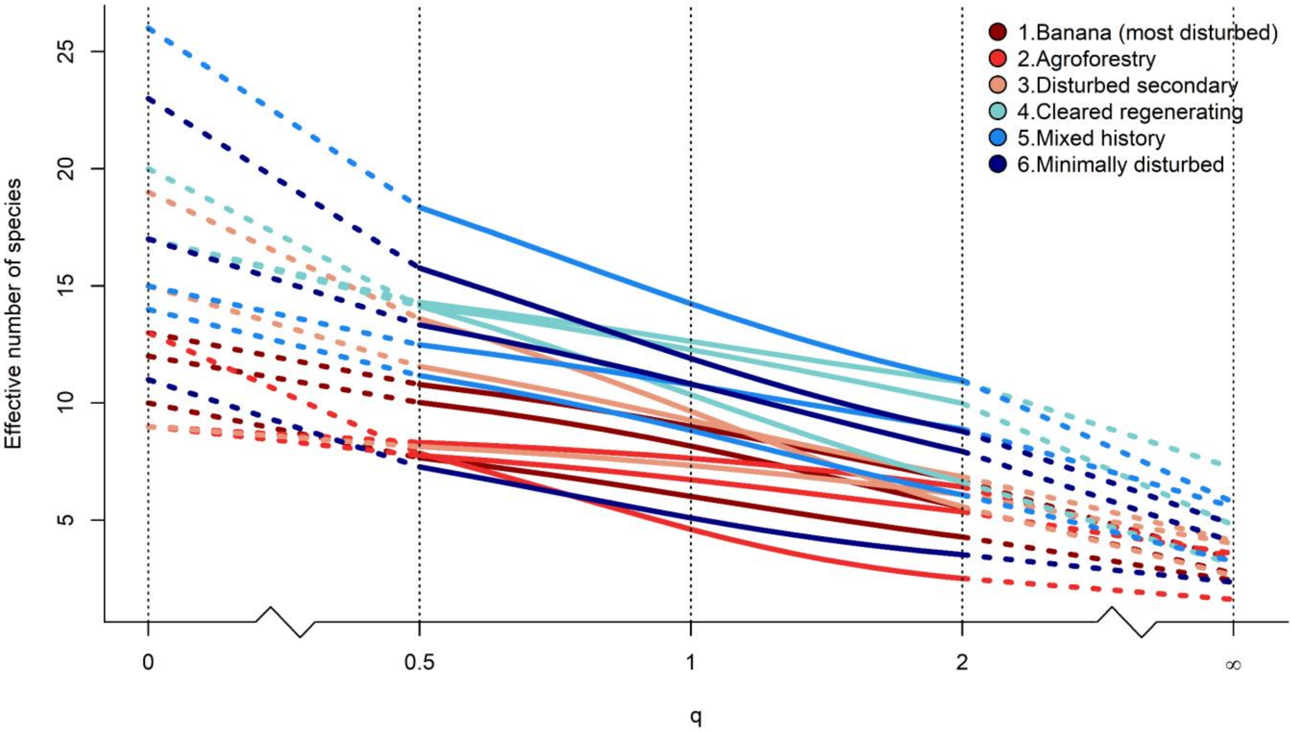

Figure 2 – Orchid bee observed alpha diversity across the disturbance gradient. Increasing values of q indicate increased emphasis on dominant species (q = 0 = species richness, 1 = Shannon diversity, 2 = Simpson diversity, ∞ = Berger Parker diversity). Disturbance rank is shown by a colour gradient, dark red for the most disturbed sites, dark blue for the least disturbed. Overall diversity was significantly higher in less disturbed sites (permuted combined p value = 0.025), and at q = 0 (rho = 0.57, p = 0.01) and q = 1 (rho = 0.51, p = 0.03), but not significantly different at or above q = 2 (rho = 0.45, p = 0.06) Because q is on a log scale, the broken axis and dashed lines indicate inferred values as diversity was calculated only for the values at either side of the break (0 and ∞); along the solid line, q was calculated at intervals of 0.1.

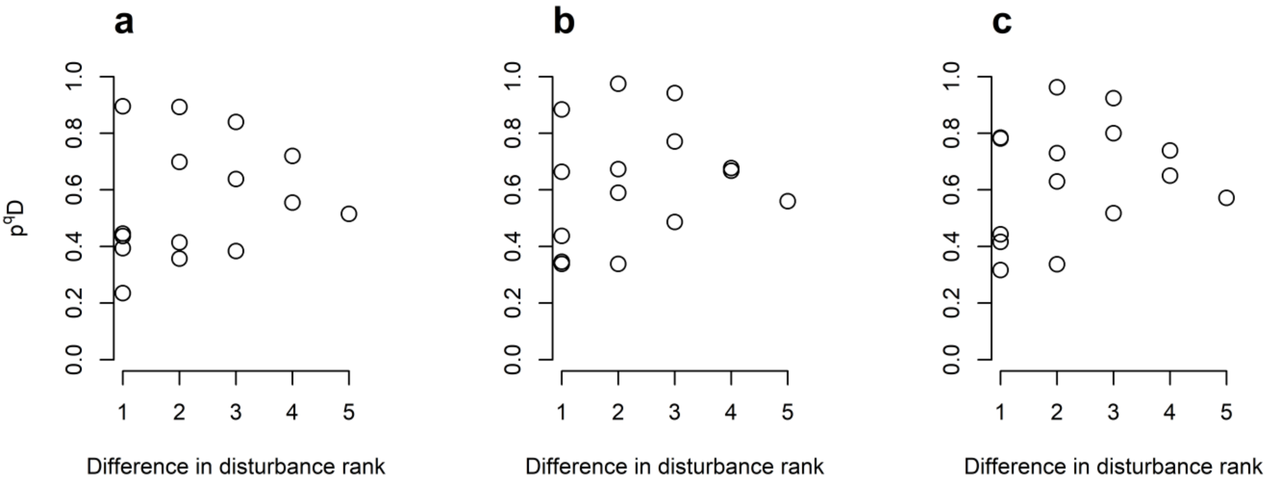

Figure 3 – The correlation between diversity estimates and disturbance ranking. Using the iNEXT package in R, we generated 1000 estimates for the diversity of each site. We then compared all possible habitat pairs to calculate the proportion of times that the less disturbed habitat was estimated to have a higher diversity than the more disturbed habitat, shown on the y axis ($p^{q}D$). This was calculated for diversity at a) $q = 0$ ($p = 0.33$; rho = 0.27), b) $q = 1$ ($p = 0.37$; rho = 0.25), and c) $q = 2$ ($p = 0.42$, rho = 0.22); $n = 50$. The difference in disturbance ranking between the sites is shown along the x-axis – high values mean the sites are further apart along the disturbance gradient.

1.3.1.3 Abundance

Abundance of orchid bees declined across the disturbance gradient (rho = 0.63, p = 0.005), with less than a quarter of the number of bees found in the most disturbed habitat compared to the best of the less disturbed forest sites (Figure 4).

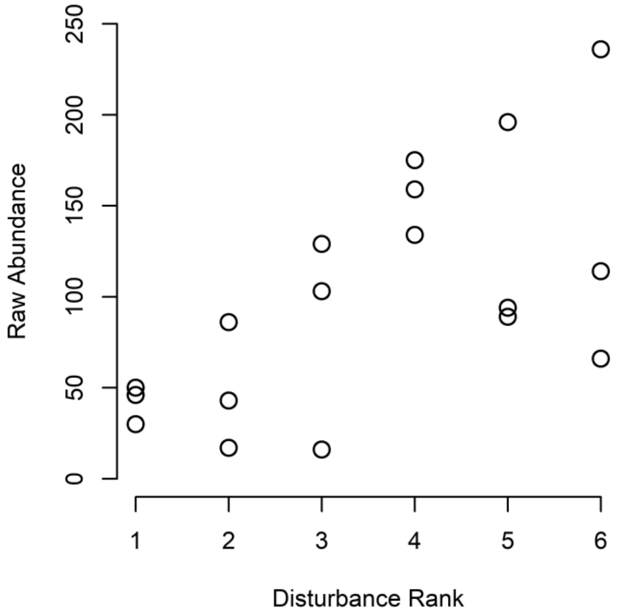

Figure 4 – Change in orchid bee abundance across the disturbance gradient. Abundance is the number of orchid bees captured at each site, plotted against the disturbance rank of the site (rho = 0.63, p = 0.005). Disturbance rank runs from 1 (most disturbed) to 6 (least disturbed).

1.3.1.4 Beta diversity

Although there was some change in the number of orchid bee species found across the disturbance gradient, beta diversity was driven primarily by a turnover of species, rather than a change in richness. The results of the beta diversity partitioning were a total beta diversity of 0.18 across the gradient (a total beta diversity of 1 would indicate that the sites had completely distinct communities; Legendre & De Cáceres 2013), with 77% of this due to species turnover and 22% due to differences in richness (nestedness).

The composition of the orchid bee community changed across the gradient, with different communities found in the more and less disturbed sites, as demonstrated by a separation along the RDA1 axis (Figure 5), which captured 37% of the variation in community composition. The Species Contributions to Beta Diversity (SCBD) index identified the species that changed most in abundance along the gradient (Figure 6). *Euglossa chalybeata* and *Euglossa orellana* appear to be forest specialists that are lost as forest disturbance increases, whereas *Euglossa despecta* appears to favour intermediate levels of disturbance.

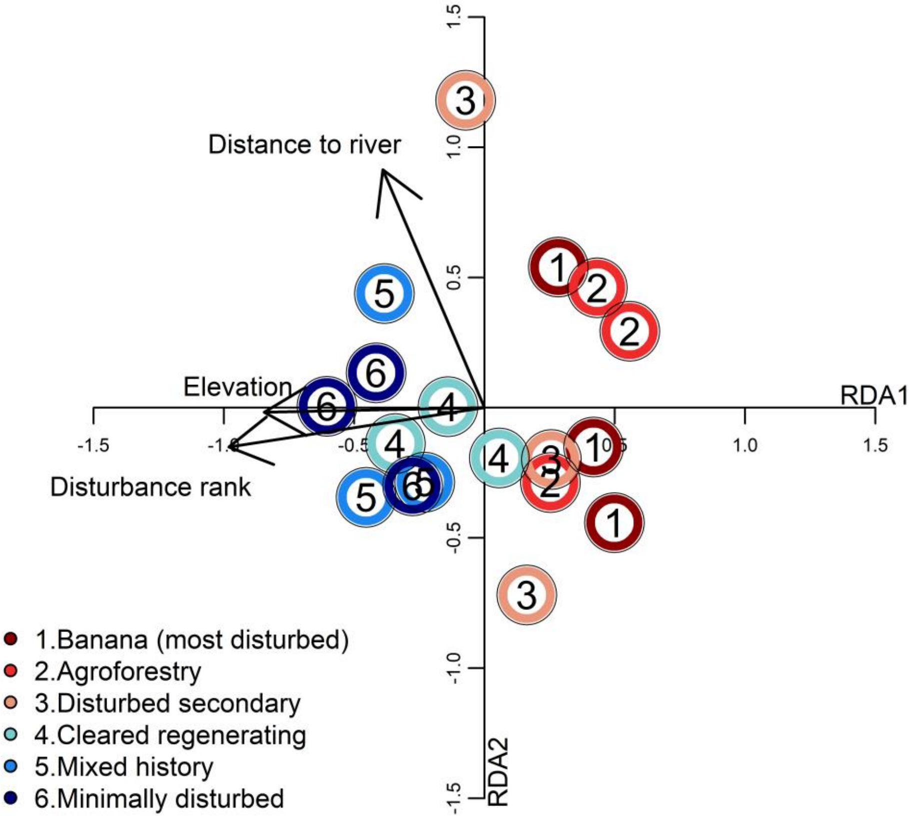

Figure 5 – RDA of orchid bee community composition across the disturbance gradient, constrained by disturbance rank, elevation and distance to the river. Disturbance rank is represented by a colour gradient from dark red (most disturbed) to dark blue (least disturbed), with the rank of each site also shown numerically.

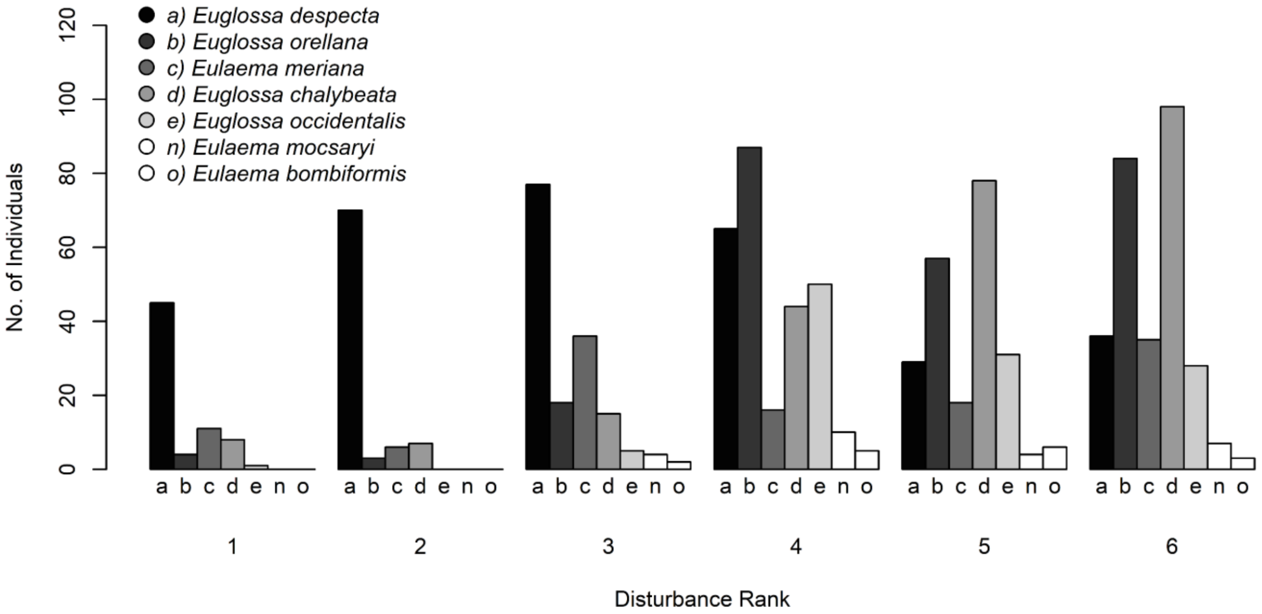

Figure 6 – Differences in abundance across the gradient of the species that contribute most to beta diversity. A total of 31 species were found. The grey bars (a-e) show the top five contributors to beta diversity, in order of contribution. Two examples of low contributors to beta diversity are shown in white (n and o) for comparison. Disturbance rank runs from 1-6, with 1 representing the most disturbed sites.

The less disturbed sites hold communities that are less redundant (Figure 7a; at $q = 1$: $p = 0.02$, rho = -0.55; permuted combined p value for $q = 0, 0.5, 1, 2$ and ∞: $p = 0.016$) and more representative of the overall metacommunity (Figure 7b; at $q = 1$: $p = 0.04$, rho = 0.4922; permuted combined p value for $q = 0, 0.5, 1, 2$ and ∞: $p = 0.024$) than the more disturbed sites. This suggests that the overall diversity of the region (all sites across the gradient) would suffer a greater loss should the community of one of the less disturbed sites be lost, than if the community of a highly disturbed site was lost.

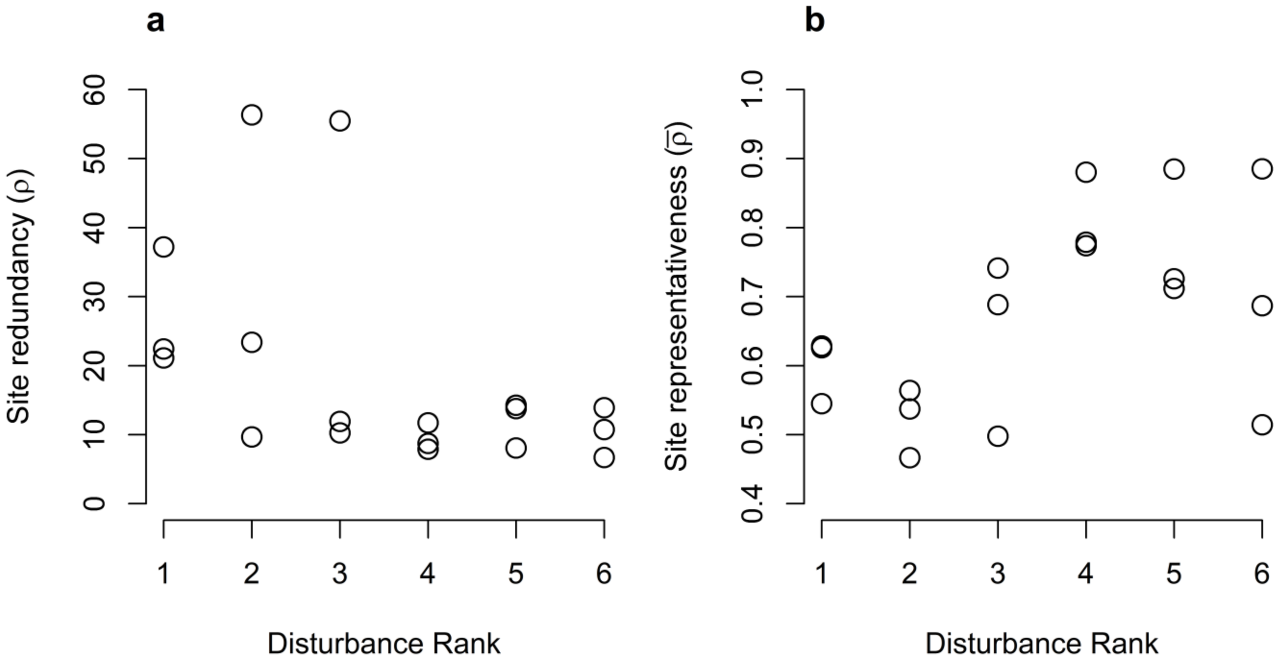

Figure 7 – Change in the a) redundancy (ρ) of sites ($p = 0.02$, $rho = -0.55$) and b) representativeness ($\bar{\rho}$) of sites ($p = 0.04$, $rho = 0.49$) across the disturbance gradient at $q = 1$. The disturbance rank runs from 1 (most disturbed) to 6 (least disturbed).

1.3.2 Pollination services

There was no relationship between the number of visits from potential pollinator insects and disturbance rank (Figure 8a; $rho = 0.1160$, $p = 0.6467$) or orchid bee diversity (Figure 8b; $rho = -0.19$, $p > 0.4$ at $q = 0$, 1 and 2). The artificial flowers received similar numbers of visits across the disturbance gradient, with slightly more visits occurring in lower disturbance sites but with a large amount of variance within each disturbance level. We found no evidence that orchid bee diversity (specialised pollinators) indicated any trend in the activity of pollinators in general.

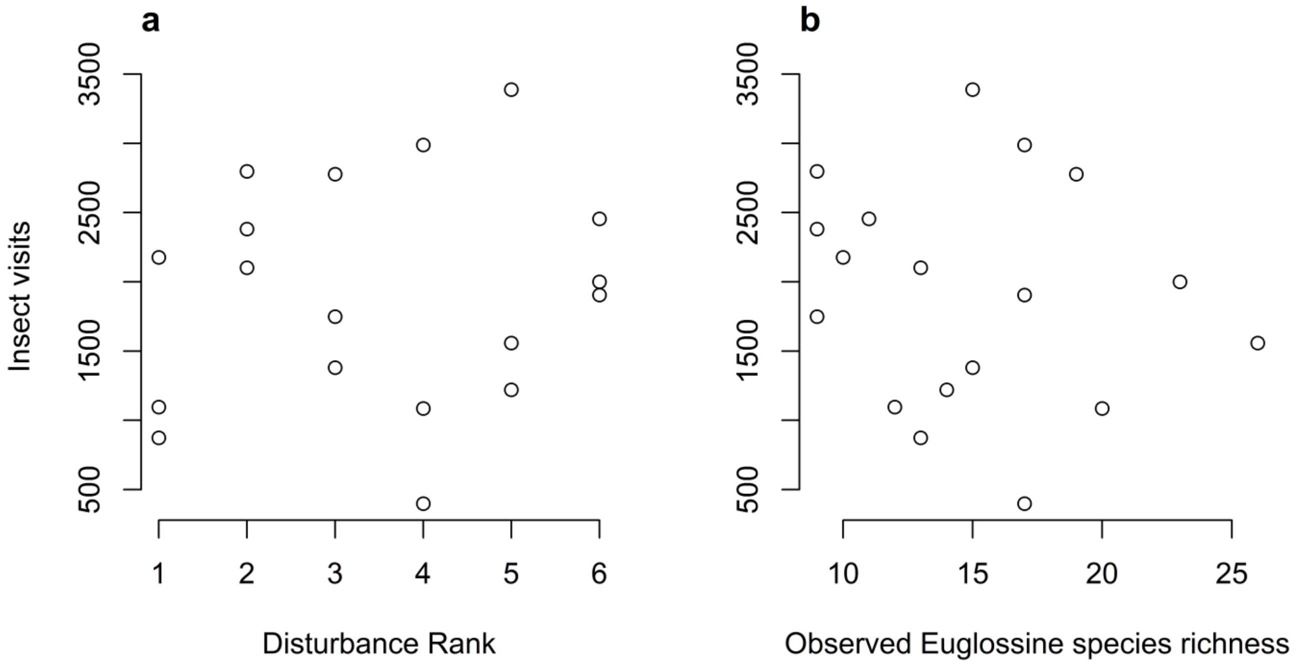

Figure 8 – Potential pollination events. Number of insect visits to artificial flower arrays correlated with (a) disturbance rank (rho = 0.12, p = 0.65) and (b) observed orchid bee species richness (q = 0; rho = -0.20, p = 0.44). Disturbance ranking runs from 1 (most disturbed) to 6 (least disturbed).

1.4 Discussion

Orchid bees declined in abundance as disturbance increased, and community composition changed across the gradient, suggesting that orchid bees can be useful as indicators of the impacts of human disturbance. Redundancy of the orchid bee community at a site increased with increased disturbance and representativeness of the sites decreased. No changes in species richness or higher order alpha diversity could be detected after controlling for sample sizes, suggesting that, unlike many other groups, alpha diversity of orchid bees is unlikely to be a strong indicator of human disturbance impacts. We found no change in pollinator visits in response to disturbance nor any correlation between pollinator visits and orchid bee species richness.

Previous studies that suggested orchid bees show little response to human disturbance focused on different disturbance types and fewer sites with less replication than covered in our study (Nemésio and Silveira, 2006; Rasmussen, 2009). The first of these studies sampled a similar number of bees as in our study over a longer period in only six sites, focusing on the effect of distance to the forest edge. They found no change in observed species richness, and erratic differences in abundance, uncorrelated with distance to edge, but they did find some change in community composition, though many species were shared across sites (Nemésio and Silveira, 2006). The second study considered alpha diversity at q = 0, 1 and 2 as well as abundance and community similarity between sites and found no significant relationship between any of these with disturbance level (Rasmussen, 2009). However, only three sites were compared, one of each disturbance type: primary forest, a reforested site and one heavily disturbed forest. Like these studies, we also found no significant change in alpha diversity after controlling for sample size. However, it should be noted that this lack of a significant response appeared to be because there were many more bees caught in the less disturbed sites, consistent with the marked decrease in orchid bee abundance with increased disturbance we detected. When comparing observed alpha diversity, without controlling for the number of bees caught, there was a decrease in species richness and Shannon diversity as disturbance increased. Since standardised sampling effort was used there is no reason to suspect the observed differences were caused by any bias in the sampling design, and so this difference should not be dismissed. That there are fewer bees in the disturbed sites means that the confidence interval around the estimated true number of species present is large, however if sampling time was extended to catch the same number of bees as found in the least disturbed sites, it would be unsurprising if there were still fewer species (supplementary materials Figure S.4). In any case, the fact that during a set time period, fewer individuals of fewer species are likely to visit plants in disturbed habitats is an ecologically meaningful result, as it is likely to impact plant pollination, even if similar total numbers of species could eventually be detected over a longer time.

This kind of study is prone to problems with biases arising from study design and the assistance of volunteers. As well as training, and pairing experienced staff with inexperienced samplers, we randomised the location of the teams to avoid systematic biases. The high turnover of volunteers allowed us to keep this strategy constant over the sampling period. Capture success was high, and although there were some escapes, many of these individuals could be seen leaving and returning to the bait, allowing a second capture attempt. We did not record miss rates but there was no noticeable difference observed between genera or species identifiable in flight, although this would be valuable to investigate in future studies. Another known issue in studies like this is the potential for differences in the attractive radius of the baits between sites to affect capture rates, because differences in vegetation structure and shade between the sites could affect the evaporation rates and how much the baits might be carried on the wind. Further research is needed to fully address this (Nemésio, 2012), but we followed standard practice from previous studies in using standardised bait protocols across all sites, including regularly refreshing the bait to avoid evaporation issues. Since capture rate was higher in the less open forest, there was also no evidence for sampling issues related to scent dispersal being inhibited by vegetation. Due to this study region consisting of a matrix of different habitat types, it was unavoidable that some sampling sites would not be far from other disturbance types. We set up the bait stations near the middle of a habitat type to ensure that the majority of bees were likely to be attracted from within that site, with a minimum of 100m to the neighbouring habitat. It is plausible that some bees may have been attracted from neighbouring habitats, yet this should theoretically weaken our power to detect a correlation between the orchid bee community and habitat type, lending confidence to the patterns that we have detected, as discussed in Brosi (2009). Furthermore, for ecological purposes we care about the bees that visit a site to provide pollination services, so it is still relevant if some bees visit from neighbouring habitats, as we are interested in the disturbance impacts on orchid bees in the context of this matrix landscape.

Regarding the value of orchid bees as indicators, in this study we have shown that changes in the orchid bee population are strongly correlated with intensity of forest disturbance, and identified which measures are most useful for detecting these responses. The results of the vegetation surveys showed a loss of canopy cover and number of large trees as disturbance increased (Figure S.2). This may also result in a change in microclimate and a loss of epiphytes. A loss of resources such as nectar and nesting habitats may have contributed to the decline in orchid bee abundance, and a change in the plant species composition could have influenced the change in orchid bee species along the gradient. A more detailed exploration of the mechanisms behind the orchid bee responses are important in order to understand what exactly they are indicative of: is it a change in vegetation structure (shown to be closely correlated with disturbance in our study), a decline in overall biodiversity, a loss of important nesting habitats, a loss of epiphytes or particular flower species? These are important points for further investigation, as there is a general lack of information about the relationship between ecological indicators and indicandum (Gao et al., 2015). It would also be worth expanding on research assessing how far these disturbance effects penetrate into forest edges (Nemesio and Silveira, 2006), considering the different indices used in this study and comparing different land uses and regions. For basic assessments, orchid bee abundance is a simple measure that can be monitored by conservation managers without the need for much analytical expertise or even species identification. Although this should not be used in isolation, it could serve as a useful warning flag of negative impacts of disturbance. The Hill numbers diversity measures in the rdiversity package require more technical skills but allow efficient calculation of a broad suite of indices, including alpha and beta diversity (redundancy and representativeness) at multiple values of q, using a single input of the species x site data matrix and only simple code modifications to calculate multiple indices.

Species richness has been recognised as a poor index for detecting the effect of disturbance on some other taxonomic groups, and it has been suggested that community composition may be more sensitive (Stork et al., 2017). For example, Samejima *et al.* (2004) found that stingless bees (Meliponini) showed a change in community composition in response to human disturbance. We also found that community composition changed across the disturbance gradient, but community composition can be expected to change for many reasons, including non-disturbance related changes in vegetation and other habitat features. Due to the small spatial scale of this study and the history of the area, we expect that the habitats of the study sites would have been very similar prior to the anthropogenic disturbance; this assumption is less likely to hold true across larger spatial scales, making it harder to link changes in species composition to habitat disturbance across space. However, as a potential indicator, identifying shifts in orchid bee community composition could be useful for monitoring a site over time, to provide an indication of whether the site is being disturbed to a degree that is negatively impacting the ecosystem (Santini et al., 2017).

In ecological terms, reduced orchid bee abundance in highly disturbed habitats is of concern, as it is indicative of a potential cascade effect resulting from the loss of forest canopy, along with habitat complexity and epiphytic diversity (Barthlott et al., 2001). This could result in a loss of specialist pollinators that are crucial for the persistence of many plant species, which may reduce the resilience of the remaining degraded forest, as the ecological networks have been weakened. However, the services provided by orchid bees may be partially maintained by a well-connected patchwork of habitats including high quality forest, as the dispersal distances of this group (Janzen, 1971) enables them to make opportunistic visits to degraded habitats when resources are available. This way, they may be able to provide pollination services to habitats that possibly lack the resources to support viable orchid bee populations independently, but this will require a substantial area of intact forest to be maintained nearby.

We found that the redundancy (ρ) of the sites increased with increased disturbance. Redundancy is therefore likely to be a useful measure of disturbance impacts, because it considers both the species present and their abundance, so gives a more complete picture of how the sites differ. From these results, we can see that the impact of losing a minimally disturbed site would more severely impact the overall diversity of the region than the loss of a highly disturbed site. Similarly, when we considered the representativeness ($\bar{\rho}$) of the sites at $q = 1$, we found that in each of the less disturbed sites (ranks 4-6) about 80% of the overall biodiversity of the study area could be found, on average, whereas the more disturbed sites (ranks 1-3) only held an average of about 60%.

Pollination potential showed no correlation with orchid bee abundance or alpha diversity (Figure 8; supplementary materials Table S.1). This is probably because visitors to the flower arrays were mostly sweat bees (family Halictidae) and these visited the flowers in high abundance. Other visitors included flies, wasps, butterflies, a few orchid bees, and even a hummingbird on one occasion. An important caveat in interpreting this experiment was that we were only able to measure the potential opportunities for pollination (the number of visits the flower received), and were not able to account for the fact that insects differ widely in their effectiveness as pollinators (Ivey et al., 2003; King et al., 2013; Primack and Silander, 1975; Ramsey, 1988; Schemske and Horvitz, 1984). Turnover of species between sites also means that higher bee diversity than expected is likely to be required to deliver pollination services over large spatial scales (Winfree et al., 2018). Halictid bees are considered valuable pollinators and visit many different plant species (Lindsey, 1984), although they do not show such distinctive host adaptations as the orchid bees. Orchid bees do pollinate a wide range of plants; however, they are particularly important due to their many species-specific relationships and cannot be easily substituted by more generalist pollinators. Further research into the pollination networks of orchid bees and the plants they visit would be helpful to understand how a loss or change in the orchid bee community might impact the plant community. Exploring functional differences (e.g. tongue length and body size) between the orchid bee species affected by disturbance would also add valuable information on the contributions of specific orchid bee species as specialist pollinators.

1.5 Conclusion

Orchid bees show a clear negative response to human disturbance across a tropical forest-agricultural gradient. They are also efficient to sample and play a key role in pollination services. We therefore suggest they can be a useful addition to the indicator groups available for studying the impacts of forest loss on biodiversity and ecosystem functioning. In choosing whether to use orchid bees in future biodiversity studies it should be noted that it is important to consider more than one indicator group in any assessment (Hilty and Merenlender, 2000; Lawton et al., 1998). When orchid bees are selected as a suitable indicator group, our results show that abundance, redundancy (ρ) and representativeness ($\overline{\rho}$) provide the most sensitive measures for detecting the response of orchid bees to human disturbance. In order to understand the response of biodiversity to human disturbance, it is essential to consider the response measures carefully, as a measure that works well for one group may not always be the best for another, and often multiple indices are necessary.

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1.8 Competing interests

The authors have no competing interests to declare.

1.9 Figures

Figure 2 to be printed in colour.

1.10 Data Access

The data have been made publicly available and can be accessed from the University of Glasgow Enlighten repository: http://dx.doi.org/10.5525/gla.researchdata.589

1.11 References

Ackerman, J.D., 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. Biol. J. Linn. Soc. 20, 301–314.

Aguiar, W.M., Sofia, S.H., Melo, G., Gaglianone, M., 2015. Changes in Orchid Bee Communities Across Forest- Agroecosystem Boundaries in Brazilian Atlantic Forest Landscapes. Environ. Entomol. 1–7. doi:10.1093/ee/nvv130

Allen-Wardell, A.G., Bernhardt, P., Bitner, R., Burquez, A., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P., 1998. The Potential Consequences of Pollinator Declines on the Conservation of Biodiversity and Stability of Food Crop Yields. Conserv. Biol. 12, 8–17.

Alroy, J., 2017. Effects of habitat disturbance on tropical forest biodiversity. Proc. Natl. Acad. Sci. 114, 6056–6061. doi:10.1073/pnas.1611855114

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of beta diversity: A roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28. doi:10.1111/j.1461-0248.2010.01552.x

Barthlott, W., Schmit-Neuerbug, V., Nieder, J., Engwald, S., 2001. Diversity and Abundance of Vascular Epiphytes: A Comparison of Secondary Vegetation and Primary Montane Rain Forest in the Venezuelan Andes. Plant Ecol. 152, 145–156.

Bawa, K., 1990. Plant-Pollinator Interactions in Tropical Rain Forests. Annu. Rev. Ecol. Syst. 21, 399–422.

Beck, J., Schulze, C.H., Linsenmair, K.E., Fiedler, K., 2002. From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. J. Trop. Ecol. 18, 33–51. doi:10.1017/S026646740200202X

Bonilla-Gomez, M.A., Nates-Parra, G., 1992. Abejas Euglosinas de Colombia (Hymenoptera: Apidae) 1. Claves Ilustradas. Caldasia 17, 149–172.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer Science and Business Media, New York Dordrecht London Heidelberg. doi:10.1007/978-1-4419-7976-6

Briggs, A.H.M., Perfecto, I., Brosi, B.J., 2013. The Role of the Agricultural Matrix: Coffee Management and Euglossine Bee (Hymenoptera: Apidae: Euglossini) Communities in Southern Mexico. Environ. Entomol. 42, 1210–1217.

Brosi, B.J., 2009. The effects of forest fragmentation on Euglossine bee communities (Hymenoptera: Apidae: Euglossini). Biol. Conserv. 142, 414–423. doi:10.1016/j.biocon.2008.11.003

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., Durán, G., 2008. The effects of forest fragmentation on bee communities in tropical countryside. J. Appl. Ecol. 45, 773–783. doi:10.1111/j.1365-2664.2007.01412.x

Broszeit, S., Beaumont, N.J., Uyarra, M.C., Heiskanen, A.S., Frost, M., Somerfield, P.J., Rossberg, A.G., Teixeira, H., Austen, M.C., 2017. What can indicators of good environmental status tell us about ecosystem services?: Reducing efforts and increasing cost-effectiveness by reapplying biodiversity indicator data. Ecol. Indic. 81, 409–442. doi:10.1016/j.ecolind.2017.05.057

Brown, K.S., 1997. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. J. Insect Conserv. 1, 25–42.

Chao, A., Chiu, C., Hsieh, T.C., 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93, 2037–2051.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E., Colwell, R.K., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67.

Cleary, D.F.R., 2004. Assessing the use of butterflies as indicators of logging in Borneo at three taxonomic levels. J. Econ. Entomol. 97, 429–435. doi:10.1603/0022-0493-97.2.429

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J. Plant Ecol. 5, 3–21. doi:10.1093/jpe/rtr044

DeFries, R.S., Foley, J.A., Asner, G.P., 2004. Land-use choice: balancing human needs and ecosystem function. Front. Ecol. Environ. 2, 249–257. doi:10.1890/1540-9295(2004)002[0249:LCBHNA]2.0.CO;2

Dray, S., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., 2018. adespatial: Multivariate Multiscale Spatial Analysis.

Dressler, R.L., 1967. Why do euglossine bees visit orchid flowers? Atas do Simpósio sóbre a Biota Amaz. 5, 171–180.

Dressler, R.L., 1978. An infrageneric classification of Euglossa, with notes on some features of special taxonomic importance (Hymnoptera; Apidae). Rev. Biol. Trop. 26, 187–198.

Dressler, R.L., 1979. Eulaema bombiformis, E. meriana and Mullerian Mimicry in Related Species (Hymenoptera: Apidae). Biotropica 11, 144–151.

Dressler, R.L., 1982a. Biology of the Orchid Bees (Euglossini). Annu. Rev. Ecol. Syst. 13, 373–394. doi:10.1146/annurev.es.13.110182.002105

Dressler, R.L., 1982b. New species of Euglossa II (Hymenoptera: Apidae). Rev. Biol. Trop. 30, 121–129.

Dressler, R.L., 1982c. New species of Euglossa III. The bursigera species group. Rev. Biol. Trop. 30, 31–40.

Dressler, R.L., 1982d. New species of Euglossa IV. The cordata and purpurea species groups (Hymenoptera: Apidae). Rev. Biol. Trop. 30, 141–152.

Dressler, R.L., 1984. Euglossine Bees of the Tambopata Reserved Zone, Madre de Dios, Peru. Rev. Peru. Entomol. 27, 75–79.

Eggleton, P., Bignell, D.E., Hauser, S., Dibog, L., Norgrove, L., Madong, B., 2002. Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. Agric. Ecosyst. Environ. 90, 189–202. doi:10.1016/S0167-8809(01)00206-7

Engel, E.C., Irwin, R.E., 2003. Linking pollinator visitation rate and pollen receipt. Am. J. Bot. 90, 1612–1618. doi:10.3732/ajb.90.11.1612

Faria, L., Melo, G., 2007. Species of Euglossa (Glossura) in the Brazilian Atlantic forest, with taxonomic notes on Euglossa stellfeldi Moure (Hymenoptera, Apidae, Euglossina). Rev. Bras. Entomol. 51, 275–284. doi:10.1590/S0085-56262007000300004

Favila, M. and Halffter, G., 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. Acta Zool. Mex. 72, 1-25.

Feest, A., Aldred, T.D., Jedamzik, K., 2010. Biodiversity quality: A paradigm for biodiversity. Ecol. Indic. 10, 1077–1082. doi:10.1016/j.ecolind.2010.04.002

Fisher, R., 1925. Statistical methods for research workers, Biological monographs and manuals. doi:10.1056/NEJMc061160

Fleishman, E., Murphy, D.D., 2009. A realistic assessment of the indicator potential of butterflies and other charismatic taxonomic groups. Conserv. Biol. 23, 1109–1116. doi:10.1111/j.1523-1739.2009.01246.x

Food and Agriculture Organisation of the United Nations, 2016. Global Forest Resources Assessment 2015. 2nd Edition, Rome (available at: http://www.fao.org/3/a-i4793e.pdf)

Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol. Indic. 57, 420–434. doi:10.1016/j.ecolind.2015.05.028

Gardner, T., Barlow, J., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A., Costa, J., Esposito, M.C., Ferreira, L. V, Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L. a M., Miranda-Santos, R., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C. A, 2008. The cost-effectiveness of biodiversity surveys in tropical forests. Ecol. Lett. 11, 139–50. doi:10.1111/j.1461-0248.2007.01133.x

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C. A, Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–81. doi:10.1038/nature10425

Good, P., 2000. Permutation tests: a practical guide to resampling methods for testing hypotheses, 2nd edition. Springer Series in Statistics. Springer Science and Business Media., New York.

Goodsell, P.J., Underwood, A.J., Chapman, M.G., 2009. Evidence necessary for taxa to be reliable indicators of environmental conditions or impacts. Mar. Pollut. Bull. 58, 323-331. doi:10.1016/j.marpolbul.2008.10.011

Hietz, P., Buchberger, G., Winkler, M., 2006. Effect of forest disturbance on abundance and distribution of epiphytic bromeliads and orchids. Ecotropica 12, 103–112.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Hill, S.L.L., Harfoot, M., Purvis, A., Purves, D.W., Collen, B., Newbold, T., Burgess, N.D., Mace, G.M., 2016. Reconciling Biodiversity Indicators to Guide Understanding and Action. Conserv. Lett. 9, 405–412. doi:10.1111/conl.12291

Hilty, J., Merenlender, A., 2000. Faunal indicator taxa selection for monitoring ecosystem health. Biol. Conserv. 92, 185–197. doi:10.1016/S0006-3207(99)00052-X

Hinojosa-Díaz, I. A., Engel, M.S., 2011. Revision of the orchid bee subgenus Euglossella (Hymenoptera, Apidae), Part I, the decorata species group. Zookeys 140, 27–69. doi:10.3897/zookeys.140.1923

Hinojosa-Díaz, I.A., Engel, M.S., 2012. Alloglossura, a new subgenus of the orchid bee genus Euglossa (Hymenoptera: Apidae), with a review of the included species. Sci. Pap. Nat. Hist. Museum, Univ. Kansas 45, 1–37.

Hinojosa-Díaz, I.A., Engel, M.S., 2014. Revision of the orchid bee subgenus Euglossella (Hymenoptera: Apidae), Part II: The viridis and mandibularis species groups. J. Melitollogy 36.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. doi:10.1111/2041-210X.12613

Hurst, J.M., Allen, R.B., 2007. A permanent plot method for monitoring indigenous forests. Landcare Research New Zealand, Canterbury.

Internicola, A.I., Page, P.A., Bernasconi, G., Gigord, L.D.B., 2007. Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: an experimental test of the effects of floral colour similarity and spatial mingling. Funct. Ecol. 21, 864–872. doi:10.1111/j.1365-2435.2007.01303.x

Ivey, C.T., Martinez, P., Wyatt, R., 2003. Variation in pollinator effectiveness in swamp milkweed, Asclepias incarnata (Apocynaceae). Am. J. Bot. 90, 214–225. doi:10.3732/ajb.90.2.214

Janzen, D.H., 1971. Euglossine Bees as Long-Distance Pollinators of Tropical Plants. Science 171, 203–205.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. doi:10.1111/j.2006.0030-1299.14714.x

Kimsey, L., 1979. An Illustrated Key to the Genus Exaerete with Descriptions of Male Genitalia and Biology (Hymenoptera: Euglossini, Apidae). J. Kansas Entomol. Soc. 52, 735–746.

Kimsey, L.S., 1982. Systematics of Bees of the Genus Eufriesea. University of California Press, Berkeley and Los Angeles.

King, C., Ballantyne, G., Willmer, P.G., 2013. Why flower visitation is a poor proxy for pollination: Measuring single-visit pollen deposition, with implications for pollination networks and conservation. Methods Ecol. Evol. 4, 811–818. doi:10.1111/2041-210X.12074

Kremen, C., 2005. Managing ecosystem services: What do we need to know about their ecology? Ecol. Lett. 8, 468–479. doi:10.1111/j.1461-0248.2005.00751.x

Krug, C.B., Schaepman, M.E., Shannon, L.J., Cavender-Bares, J., Cheung, W., McIntyre, P.B., Metzger, J.P., Niinemets, Ü., Obura, D.O., Schmid, B., Strassburg, B.B., Van Teeffelen, A.J., Weyl, O.L., Yasuhara, M., Leadley, P.W., 2017. Observations, indicators and scenarios of biodiversity and ecosystem services change — a framework to support policy and decision-making. Curr. Opin. Environ. Sustain. 29, 198–206. doi:10.1016/j.cosust.2018.04.001

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N. A, Stork, N.E., Srivastava, D.S., Watt, A. D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391, 72–76. doi:10.1038/34166

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. doi:10.1111/ele.12141

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. doi:10.1007/s004420100716

Lindsey, A.H., 1984. Reproductive Biology of Apiacea. I. Floral Vistors to Thaspium and Zizia and Their Importance in Pollination. Am. J. Bot. 71, 375–387.

Melo, G.A.R., 2014. Notes on the systematics of the orchid-bee genus Eulaema (Hymenoptera, Apidae). Rev. Bras. Entomol. 58, 235–240.

Mitchell, S., Reeve, R., 2016. rdiversity: Measurement and Partitioning of Similarity-Sensitive Biodiversity.

Moure, J.S., 1965. Some New Species of Euglossine Bees (Hymenoptera: Apidae). J. Kansas Entomol. Soc. 38, 266–277.

Nemésio, A., 2009. Taxonomic notes on Euglossa (Glossuropoda) with a key to the known species (Hymenoptera: Apidae: Euglossina). Zootaxa 56, 45–56.

Nemésio, A., 2011. The orchid-bee fauna (Hymenoptera: Apidae) of a forest remnant in southern Bahia, Brazil, with new geographic records and an identification key to the known species of the area 54, 47–54.

Nemésio, A., 2012. Methodological Concerns and Challenges in Ecological Studies with Orchid Bees (Hymenoptera: Apidae: Euglossina). Bioscience 26, 2012.

Nemésio, A., 2013. Are orchid bees at risk? First comparative survey suggests declining populations of forest-dependent species. Brazilian J. Biol. 73, 367–374.

Nemésio, A., Silveira, F. A, 2007a. Diversity and distribution of orchid bees (Hymenoptera: Apidae) with a revised checklist of species. Neotrop. Entomol. 36, 874–888. doi:10.1590/S1519-566X2007000600008

Nemésio, A., Silveira, F. A, 2007b. Orchid bee fauna (Hymenoptera: Apidae: Euglossina) of Atlantic Forest fragments inside an urban area in southeastern Brazil. Neotrop. Entomol. 36, 186–191.

Nemésio, A., Silveira, F. A, 2006. Edge effects on the orchid-bee fauna (Hymenoptera: Apidae) at a large remnant of Atlantic Rain Forest in southeastern Brazil. Neotrop. Entomol. 35, 313–323. doi:10.1590/S1519-566X2006000300004

Niemack, R.S., Bennett, D.J., Hinojosa-Diaz, I., Chaboo, C.S., 2012. A contribution to the knowledge of the orchid bee fauna of the Los Amigos Biological Station, Madre de Dios, Peru (Hymenoptera: Apidae: Euglossini). Check List 8, 215–217.

Nöske, N.M., Hilt, N., Werner, F.A., Brehm, G., Fiedler, K., Sipman, H.J.M., Gradstein, S.R., 2008. Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. Basic Appl. Ecol. 9, 4–12. doi:10.1016/j.baae.2007.06.014

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package.

Otero, J.T., Sandino, J.C., 2003. Capture Rates of Male Euglossine Bees across a Human Intervention Gradient, Chocó Region, Colombia. Biotropica 35, 520–529. doi:10.1111/j.1744-7429.2003.tb00608.x

Pearson, D.L., Dressler, R.L., 1985. Two-year study of male orchid bee (Hymenoptera: Apidae: Euglossini) attraction to chemical baits in lowland south-eastern Perú. J. Trop. Ecol. 1, 37. doi:10.1017/S0266467400000067

Pimm, S.L., Raven, P., 2000. Extinction by numbers. Nature 403, 843–845. doi:10.1038/35002708

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. doi:10.1016/j.tree.2010.01.007

Primack, R.B., Silander, J.A., 1975. Measuring the relative importance of different pollinators to plants. Nature 255, 143–144. doi:10.1038/255143a0

QGIS Development Team, 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team, 2017. R: A language and environment for statistical computing.

Ramage, B.S., Sheil, D., Salim, H.M.W., Fletcher, C., Mustafa, N.Z.A, Luruthusamay, J.C., Harrison, R.D., Butod, E., Dzulkiply, A.D., Kassim, A.R., Potts, M.D., 2013. Pseudoreplication in Tropical Forests and the Resulting Effects on Biodiversity Conservation. Conserv. Biol. 27, 364–372. doi:10.1111/cobi.12004

Ramsey, M.W., 1988. Differences in pollinator effectiveness of birds and insects visiting Banksia menziesii (Proteaceae). Oecologia 76, 119–124. doi:10.1007/BF00379609

Rasmussen, C., 2009. Diversity and abundance of orchid bees (Hymenoptera: Apidae, Euglossini) in a tropical rainforest succession. Neotrop. Entomol. 38, 812–9.

Real, L.A., 1981. Uncertainty and Pollinator-Plant Interactions: The Foraging Behavior of Bees and Wasps on Artificial Flowers. Ecology 62, 20–26.

Reeve, R., Leinster, T., Cobbold, C.A., Thompson, J., Brummitt, N., Mitchell, S.N., Matthews, L., 2016. How to partition diversity. arXiv 1404.6520, 1–9.

Rosa, J.F., Ramalho, M., Monteiro, D., Silva, M.D., 2015. Permeability of matrices of agricultural crops to Euglossina bees (Hymenoptera, Apidae) in the Atlantic Rain Forest. Apidologie 46, 691–702. doi:10.1007/s13592-015-0359-9

Roubik, D., Hanson, P., 2004. Orchid bees of tropical America: Biology and Field Guide. InBio Press, Heredia, Costa Rica.

Roubik, D.W., 2004. Sibling Species of Glossura and Glossuropoda in the Amazon Region (Hymenoptera: Apidae: Euglossini). J. Kansas Entomol. Soc. 77, 235–253. doi:10.2317/0308.20.1

RStudio Team, 2016. RStudio.

Samejima, H., Marzuki, M., Nagamitsu, T., Nakasizuka, T., 2004. The effects of human disturbance on a stingless bee community in a tropical rainforest. Biol. Conserv. 120, 577–587. doi:10.1016/j.biocon.2004.03.030

Sandino, J.C., 2004. Are there any agricultural effects on the capture rates of male euglossine bees (Apidae: Euglossini)? Rev. Biol. Trop. 52, 115–118.

Santini, L., Belmaker, J., Costello, M.J., Pereira, H.M., Rossberg, A.G., Schipper, A.M., Ceaușu, S., Dornelas, M., Hilbers, J.P., Hortal, J., Huijbregts, M.A.J., Navarro, L.M., Schiffers, K.H., Visconti, P., Rondinini, C., 2017. Assessing the suitability of diversity metrics to detect biodiversity change. Biol. Conserv. 213, 341–350. doi:10.1016/j.biocon.2016.08.024

Schemske, D., Horvitz, C., 1984. Variation Among Floral Visitors in Pollination Ability: A Precondition for Mutualism Specialization. Science 225, 519–521. doi:10.1126/science.225.4661.519

Schulze, C.H., Waltert, M., Kessler, P.J.A, Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I., Tscharntke, T., 2004. Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. Ecol. Appl. 14, 1321–1333. doi:10.1890/02-5409

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How Should Beta-Diversity Inform Biodiversity Conservation? Trends Ecol. Evol. 31, 67–80. doi:10.1016/j.tree.2015.11.005

Spearman, C., 1904. The Proof and Measurement of Association between Two Things. Am. J. Psychol. 15, 72–101. doi:10.1093/pan/mpj017

Storck-Tonon, D., Morato, E., Melo, A., Oliveira, M., 2013. Orchid Bees of forest fragments in Southwestern Amazonia. Biota Neotrop. 13, 133–141. doi:10.1590/S1676-06032013000100015

Stork, N.E., Srivastava, D.S., Eggleton, P., Hodda, M., Lawson, G., Leakey, R.R.B., Watt, A.D., 2017. Consistency of effects of tropical-forest disturbance on species composition and richness relative to use of indicator taxa. Conserv. Biol. 00, 1–10. doi:10.1111/cobi.12883

Tuomisto, H., 2010. A diversity of beta diversities: Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33, 23–45. doi:10.1111/j.1600-0587.2009.06148.x

Whitworth, A., Villacampa, J., Brown, A., Huarcaya, R.P., Downie, R., MacLeod, R., 2016. Past human disturbance effects upon biodiversity are greatest in the canopy; A case study on rainforest butterflies. PLoS One 11. doi:10.1371/journal.pone.0150520

Winfree, R., Aguilar, R., Vázquez, D., LeBuhn, G., Aizen, M., 2009. A Meta-Analysis of Bees' Responses to Anthropogenic Disturbance. Ecology 8, 2068–2076.

Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.W., Gibbs, J., 2018. Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 793, In press. doi:10.1126/SCIENCE.AAO2117

1.12 Supplementary materials

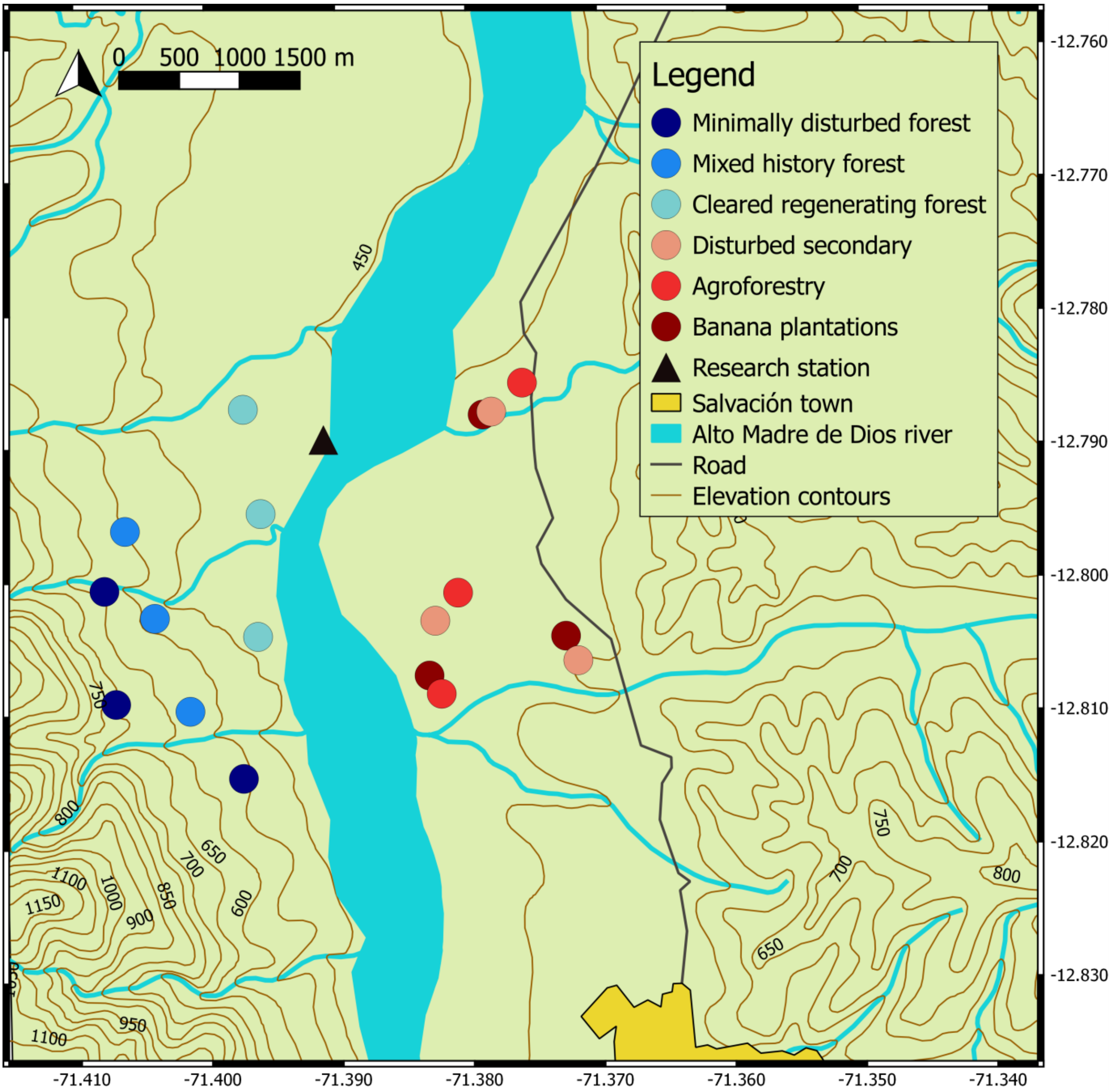

Figure S.1 – Map of our study sites in Manu, Peru. Colours represent disturbance gradient, dark red = 1. Most disturbed, dark blue = 6. Least disturbed. The map also shows: elevation contour lines; the Manu Learning Centre research station; the nearest local town, Salvación; the local road; the main river, Alto Madre de Dios, and its tributaries.

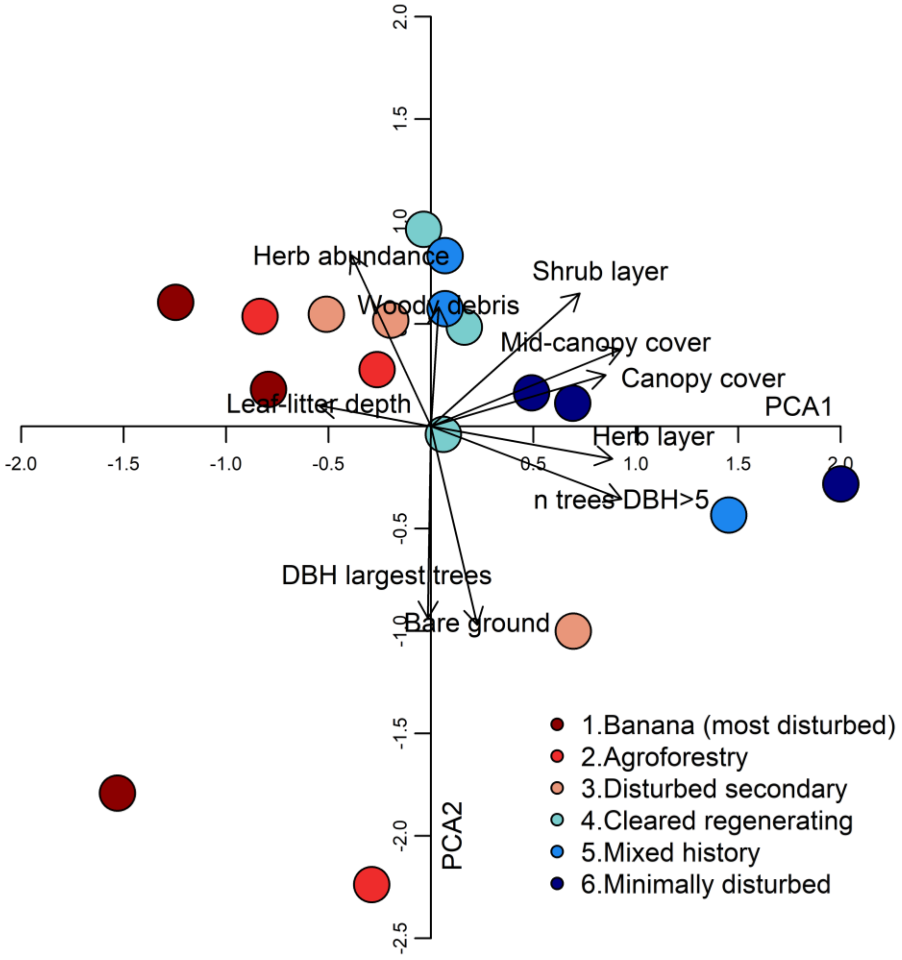

Figure S.2 – PCA of vegetation structure across the gradient, with sites colour coded by their disturbance level (dark blue least disturbed – dark red most disturbed).

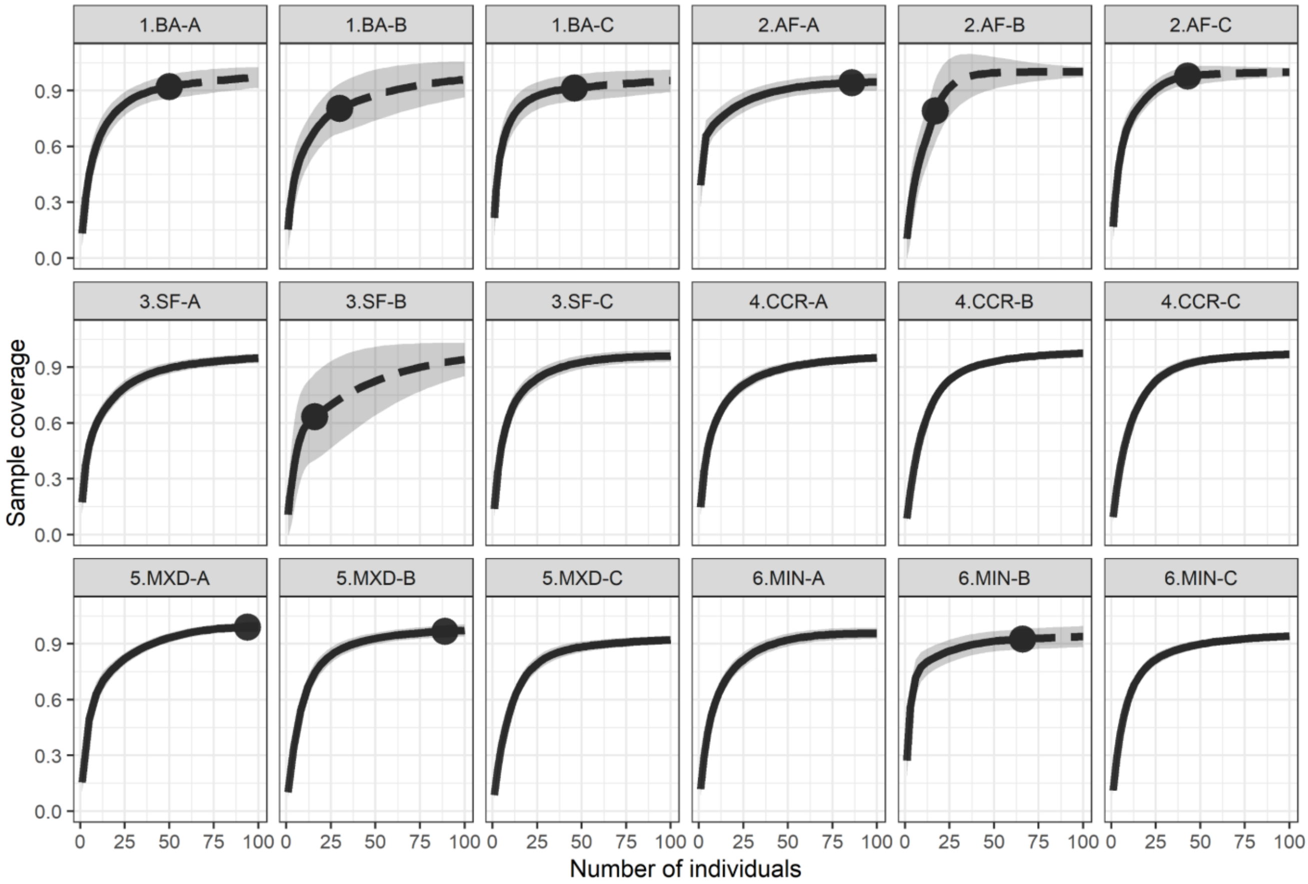

Figure S.3 – Sample completeness at q = 0. The sample completeness for each site is shown in a separate panel. The labels above each panel describe the disturbance rank (1-6, 1 is most disturbed) and habitat type of each site (BA: Banana, AF: Agroforestry, SF: Disturbed secondary forest, CCR: Cleared regenerating forest, MXD: Mixed history regenerating forest and MIN: minimally disturbed primary forest), as well as which of the replicates it was (A, B or C). The solid black line shows the rarefied estimate of sample coverage, and the dashed line is the extrapolated estimate, with the circle indicating the sample size collected. The grey shading indicates the 95% confidence interval around the coverage estimate. Coverage is shown up to 100 individuals for easy comparison between sites, but some sites did exceed this number; estimated diversity was compared at n = 50.

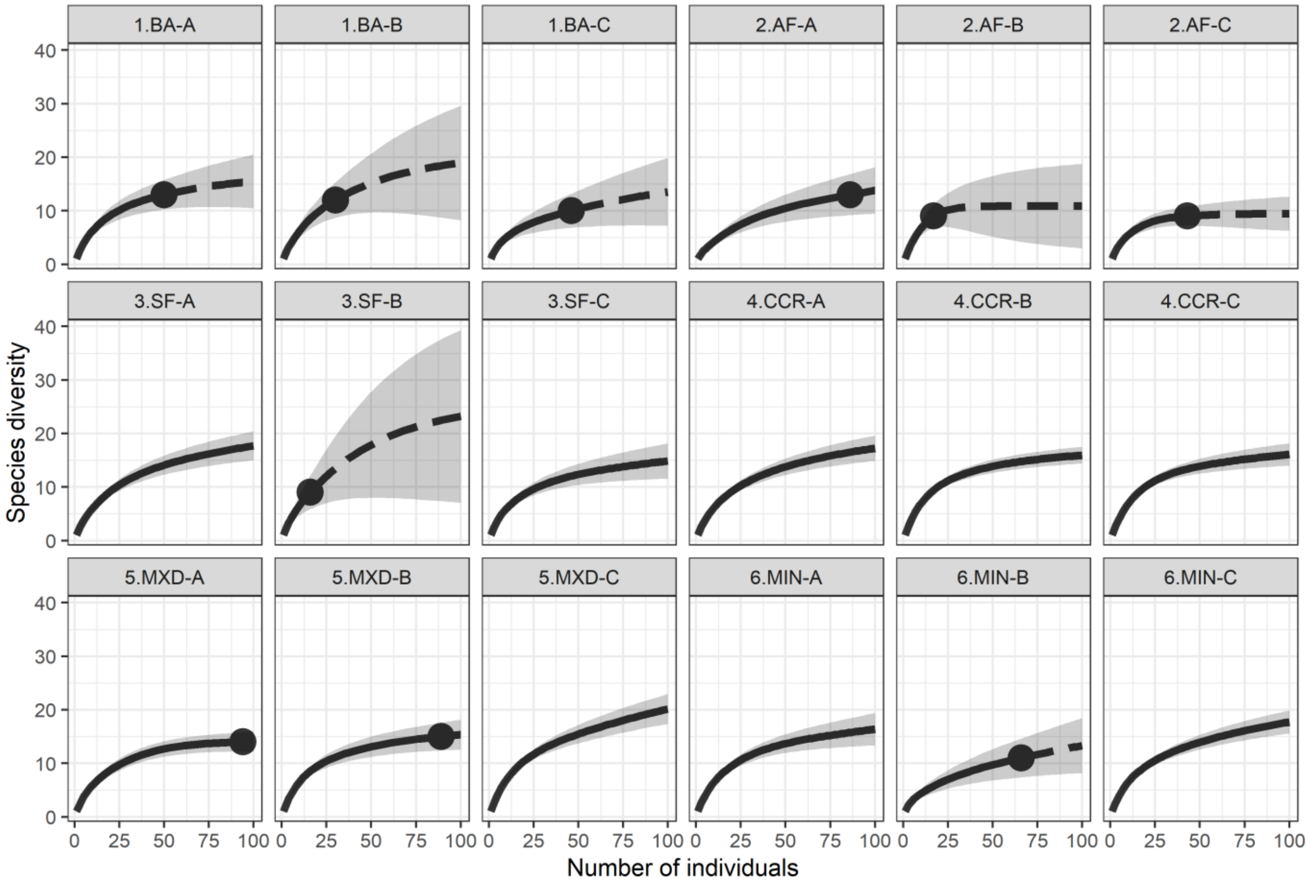

Figure S.4 – Estimated richness at each site extrapolated to a sample size of 250 individuals. Solid line shows rarefied estimate, dashed line shows extrapolation, and filled circle indicates the collected sample size. Shaded area indicates 95% confidence interval with 1000 bootstraps.

Table S.1 – Results of the Spearman rank correlation tests.
The p and rho values of the results of correlations between variables 1 and 2 are shown for all tests, along with the 95% confidence interval for the rho values.

Variable 1	**Variable 2**	**p**	**rho**	**rho 95% CI**
Abundance	Disturbance rank	0.0051	0.6301	0.2534 - 0.8303
Observed diversity q = 0	Disturbance rank	0.0141	0.5672	0.1538 - 0.808
Observed diversity q = 1	Disturbance rank	0.0302	0.5110	0.0105 - 0.8576
Observed diversity q = 2	Disturbance rank	0.0581	0.4546	-0.0517 - 0.817
Observed diversity q = ∞	Disturbance rank	0.0801	0.4232	-0.0701 - 0.7895
Vegetation structure PC1	Disturbance rank	0.0000	0.8621	0.6124 - 0.9679
Estimated diversity q = 0 (mean)	Disturbance rank	0.4472	0.1912	-0.3512 - 0.6686
Estimated diversity q = 1 (mean)	Disturbance rank	0.3747	0.2226	-0.2824 - 0.622
Estimated diversity q = 2 (mean)	Disturbance rank	0.2300	0.2978	-0.1826 - 0.6794
q = 0 raw iNEXT diversity estimates (x1000)	Difference in disturbance rank	0.3318	0.2693	-0.2551 - 0.6685
q = 1 raw iNEXT diversity estimates (x1000)	Difference in disturbance rank	0.3782	0.2453	-0.295 - 0.6639
q = 2 raw iNEXT diversity estimates (x1000)	Difference in disturbance rank	0.4201	0.2250	-0.3067 - 0.6463
Redundancy (ρ) q = 1	Disturbance rank	0.0168	-0.5549	-0.7938 - -0.1434
Representativeness (ρ) q = 1	Disturbance rank	0.0380	0.4922	0.0075 - 0.8126
Pollinator visits	Disturbance rank	0.6467	0.1160	-0.3499 - 0.5397
Pollinator visits	Observed diversity q = 0	0.4380	-0.1950	-0.5965 - 0.2459
Pollinator visits	Observed diversity q = 1	0.4331	-0.1971	-0.6293 - 0.3067
Pollinator visits	Observed diversity q = 2	0.4429	-0.1930	-0.6426 - 0.3347

Table S.2 – Model selection.
Where the correlations tested in Table S.1 were significant, linear models were used to control for the effect of other environmental variables. The log likelihoods and degrees of freedom for all models tested are presented here.

Model	**Log Likelihood (Max. Likelihood)**	**Degrees of freedom**
log(Abundance)~ Disturbance rank	-16.6356	3
log(Abundance)~ Disturbance rank + Elevation	-16.2785	4
log(Abundance)~ Disturbance rank + Distance to river	-14.0386	5
log(Obs. Diversity q = 0) ~ Disturbance rank	-1.1849	3
log(Obs. Diversity q = 0) ~ Disturbance rank + Elevation	-1.0606	4
log(Obs. Diversity q = 0) ~ Disturbance rank + Distance to river	0.4615	4
log(Obs. Diversity q = 1) ~ Disturbance rank	-2.3260	3
log(Obs. Diversity q = 1) ~ Disturbance rank + Elevation	-2.1954	4
log(Obs. Diversity q = 1) ~ Disturbance rank + Distance to river	-1.3630	4
log(Obs. Diversity q = 2)~ Disturbance rank	-6.2357	3
log(Obs. Diversity q = 2) ~ Disturbance rank + Elevation	-5.9173	4
log(Obs. Diversity q = 2) ~ Disturbance rank + Distance to river	-5.6520	4
log(Obs. Diversity q = ∞) ~ Disturbance rank	-5.0875	3
log(Obs. Diversity q = ∞) ~ Disturbance rank + Elevation	-4.6954	4
log(Obs. Diversity q = ∞) ~ Disturbance rank + Distance to river	-4.8372	4
Vegetation structure PC1 ~ Disturbance rank	-6.4559	3
Vegetation structure PC1 ~ Disturbance rank + Elevation	-6.2303	4
Vegetation structure PC1 ~ Disturbance rank + Distance to river	-5.7609	4
log(Est. diversity q = 0) ~ Disturbance rank	6.70	3
log(Est. diversity q = 0) ~ Disturbance rank + Elevation	6.82	4
log(Est. diversity q = 0) ~ Disturbance rank + Distance to river	6.83	4
log(Est. diversity q = 1) ~ Disturbance rank	-2.15	3
log(Est. diversity q = 1) ~ Disturbance rank + Elevation	-1.86	4
log(Est. diversity q = 1) ~ Disturbance rank + Distance to river	-2.10	4
log(Est. diversity q = 2) ~ Disturbance rank	-5.87	3
log(Est. diversity q = 2) ~ Disturbance rank + Elevation	-5.50	4

Model	**Log Likelihood (Max. Likelihood)**	**Degrees of freedom**
log(Est. diversity q = 2) ~ Disturbance rank + Distance to river	-5.70	4
log(ρ Redundancy q = 1) ~ Disturbance rank	-13.3025	3
log(ρ Redundancy q = 1) ~ Disturbance rank + Elevation	-12.7122	4
log(ρ Redundancy q = 1) ~ Disturbance rank + Distance to river	-11.5194	4
log(ρ Representativeness q = 1) ~ Disturbance rank	6.1746	3
log(ρ Representativeness q = 1) ~ Disturbance rank + Elevation	6.1913	4
log(ρ Representativeness q = 1) ~ Disturbance rank + Distance to river	9.1013	4

Table S.3 – Results of the best fitting models.
The estimated coefficients and significance are presented for the explanatory variables found to produce the best fitting models identified in Table S.2.

Model	**Variable**	**Est. coefficient**	**SE**	**t**	**p**
log(Abundance) ~ Disturbance rank + Distance to River	Rank	0.317	0.082	3.871	0.002
	Distance to river	-0.001	0.000	-2.240	0.041
log(Obs. Diversity q = 0) ~ Disturbance rank	Rank	0.103	0.038	2.724	0.015
log(Obs. Diversity q = 1) ~ Disturbance rank	Rank	0.077	0.040	1.914	0.074
log(Obs. Diversity q = 2) ~ Disturbance rank	Rank	0.087	0.050	1.730	0.103
log(Obs. Diversity q = ∞) ~ Disturbance rank	Rank	0.091	0.047	1.946	0.069
Vegetation structure PC1 ~ Disturbance rank	Rank	0.492	0.051	9.703	0.000
log(Est. diversity q = 0) ~ Disturbance rank	Rank	0.020	0.024	0.813	0.428
log(Est. diversity q = 1) ~ Disturbance rank	Rank	0.031	0.040	0.772	0.451
log(Est. diversity q = 2) ~ Disturbance rank	Rank	0.055	0.049	1.112	0.282
log(ρ Redundancy q = 1) ~ Disturbance rank	Rank	-0.217	0.074	-2.920	0.010
log($\bar{\rho}$ Representativeness q = 1) ~ Disturbance rank + Distance to river	Rank	0.0711	0.0227	3.136	0.0068
	Distance to river	-0.0002	<0.0001	-2.401	0.0298

Table S.4 – Moran's I
Results of the tests for spatial autocorrelation performed on the residuals of the best fitting models (Table S.3), for all models where a significant correlation was found.

Model	Observed	Expected	SD	p	Observed - Expected
log(Abundance) ~ Disturbance rank + Distance to river	-0.1074	-0.0588	0.0916	0.5950	-0.0487
log(Obs. Diversity q = 0) ~ Disturbance rank	-0.1237	-0.0588	0.0940	0.4901	-0.0649
log(Obs. Diversity q = 1) ~ Disturbance rank	-0.1346	-0.0588	0.0879	0.3883	-0.0757
log(Obs. Diversity q = 2) ~ Disturbance rank	-0.0950	-0.0588	0.0879	0.6806	-0.0362
log(Obs. Diversity q = ∞) ~ Disturbance rank	-0.0788	-0.0588	0.0912	0.8270	-0.0199
Vegetation structure PC1 ~ Disturbance rank	-0.0176	-0.0588	0.0958	0.6669	0.0412
log(Est. diversity q = 0) ~ Disturbance rank	-0.0403	-0.0588	0.0920	0.8401	0.0186
log(Est. diversity q = 1) ~ Disturbance rank	-0.0492	-0.0588	0.0889	0.9140	0.0096
log(Est. diversity q = 2) ~ Disturbance rank	-0.0648	-0.0588	0.0883	0.9464	-0.0059
log(ρ Redundancy q = 1) ~ Disturbance rank	0.00095	-0.0588	0.0914	0.5130	0.0598
log(ρ Representativeness q = 1) ~ Disturbance rank	-0.1439	-0.0588	0.0924	0.3570	-0.0851