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**Article**

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1 # Are orchid bees useful indicators of the impacts of
2 # 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

## 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

75   greater detail. Orchid bees can persist in heavily degraded ecosystems in some cases,

76   including forest fragments (Storck-Tonon et al., 2013) and farmland (Otero and Sandino,

77   2003; Sandino, 2004), although this may depend on the proximity to intact forest (Briggs et

78   al., 2013). At the same time, there is concern that orchid bees are sensitive to forest loss

79   (Roubik and Hanson, 2004) and some species are thought to be at risk of extinction

80   (Nemesio, 2013), which would have major consequences for the plants they pollinate. The

81   loss of old-growth forest and canopy disruption is likely to result in a loss of orchid bee

82   resources (Hietz et al., 2006; Nöske et al., 2008), such as orchids, other epiphytes and

83   specific tree saps (Dressler, 1982a; Roubik and Hanson, 2004), with probable negative

84   consequences for the orchid bee species that depend on them. Together these features

85   suggest that orchid bees could be an excellent candidate for use as an indicator of faunal

86   and floral responses to tropical forest disturbance.

87   So far, studies on orchid bee responses to forest disturbance have primarily focused on the

88   effects of forest fragmentation, with mixed patterns identified. The abundance and

89   diversity of euglossine bees have been suggested to decline with decreased forest

90   fragment size (Brosi, 2009; Brosi et al., 2008), but other studies found no effect of

91   fragmentation on abundance or richness (Storck-Tonon et al., 2013). A few studies have

92   compared agricultural land to intact forest but these have mostly been focused on less

93   diverse Central American habitats and generally only compared two or three land uses.

94   Briggs *et al*. (2013) found that polyculture could sustain orchid bee communities similar to

95   forest habitats in composition, but abundance was higher in the polyculture than in either

96   forest or monoculture, although abundance did decline with increasing distance from the

97   forest. Abundance and richness of orchid bees have been found to decrease in some

98   agricultural matrix habitats compared to forests (Aguiar et al., 2015), although others

99   have been found to support similar communities to forest (Rosa et al., 2015) and some

100  found higher capture rates in agricultural areas than in forest (Otero and Sandino, 2003;

101  Sandino, 2004). However, studies of forest disturbance gradients are relatively uncommon,

102  and none have covered the response of orchid bees across a continuous, multi-level

103  gradient from monoculture agriculture to intact forest. There are several studies on the

104  mutualistic relationships between orchid bees and orchids (Dressler 1967; Ackerman 1983),

105  but again there is a lack of studies relating orchid bee diversity to overall pollination

106  services available in the ecosystem.

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

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

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

## 1.2 Materials and methods

### 1.2.1 Study area

150   This study was based around the Manu Learning Centre (-12.789882, -71.391753, 470 m
151   above sea level), a research station run by the Crees Foundation, in the cultural zone of
152   the Manu Biosphere Reserve in southeast Peru, a UNESCO World Heritage Site. This zone
153   contains a mixture of protected areas of lowland tropical forest interspersed with areas of
154   high human impact, including logging and agriculture, and is intended as a buffer for Manu
155   National Park. Eighteen sites were chosen to represent a gradient of human disturbance
156   from banana monoculture to minimally disturbed tropical forest. A stratified site selection
157   approach ensured sampling was not dominated by a single disturbance history, with three
158   sites chosen for each of the six of major land uses in the local area, covering a gradient of
159   human disturbance (supplementary materials Figure S.1). These were ranked from highest
160   to lowest disturbance intensity based on land use (Beck et al., 2002; Eggleton et al.,
161   2002), with 1 being the most disturbed and 6 the least disturbed (details in Table 1). For
162   each land use type, one of the replicates was named 'A', 'B' or 'C', semi-randomly, taking
163   into consideration suitable site groupings for access and analysis. We sampled all 'A' sites
164   in the first week, then the 'B' and 'C' sites in the following weeks, so that one of each
165   habitat types would be sampled concurrently.

166   At each site, data were collected on the vegetation structure to assess how this changed
167   across the disturbance gradient. Three vegetation points were randomly selected within
168   each site, and a 25m$^2$ plot marked out at each. Within this plot, canopy cover was

169    quantified using a quadrat held above the sampler's head and the quadrat used to

170    estimate the percentage of canopy cover at five points within the circle.  Understory

171    vegetation density was estimated at the four corners of the sampling plot using the

172    modified Braun-Blanquet scale as described in Hurst and Allen (2007). We counted the

173    number of trees with a diameter >5cm at breast height and measured the diameters of the

174    three largest trees within each vegetation plot, and measured leaf litter depth at 16

175    random points within the plot. These followed the protocols for vegetation assessment

176    used by Whitworth et al., (2016). Weather data were collected at the research station,

177    with temperature, rainfall and humidity data collected daily at 7am, manually checking a

178    thermometer, humidity meter and rain gauge at the weather station located at the

179    research centre each morning. Elevation data for each site were obtained from Google

180    Earth Pro 7.3.2.5491, and distance to the main river, the Alto Madre de Dios, was

181    measured in QGIS 2.18.7 (QGIS Development Team, 2017), measuring the straight line

182    distance from the centre of each site to the nearest edge of the river using the 'measure

183    line' tool and manually comparing the distances to the edges of the river to find the

184    shortest.

185

186 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. |

187

188 Sites of the different disturbance types were interspersed in space as much as possible.

189 The potentially confounding effects of large landscape and climatic differences were

190 minimised by selecting sites within a small area (20 km$^2$), while ensuring sites of the same

191 disturbance type were far enough apart (>500 m) to avoid sampling pseudo-replication

192 (Ramage et al., 2013). To minimise spatial effects on the results we kept groups of sites of

193 different disturbance levels as close together as possible given other constraints and the

194    locations of these habitats. We used linear models to validate the results of our
195    correlation tests and to check for any significant effect of these other environmental
196    variables, including them as explanatory variables along with disturbance if they had any
197    significant effect on the response.

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

202
203    **1.2.2 Orchid bee diversity**

204    **1.2.2.1  Data collection**

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

212    At each site, two sampling stations were set up 50 m apart to reduce any bias from a
213    single within-site location choice. At each of these stations, eight balls of cotton were
214    hung from branches at a height of 1.5 m, with 2 m between cotton balls. Each cotton ball
215    was baited with two drops of one of the following eight attractants: wintergreen oil,
216    methyl salicylate, eucalyptus oil, eucalyptol, vanillin (3 tsp vanillin dissolved in 50 ml 96%
217    ethanol), benzyl acetate, clove oil, eugenol. The bait stations were monitored over the
218    three-hour sampling period, and orchid bees attracted to the baits were caught using hand
219    nets then killed and preserved in 70% ethanol. Orchid bees attracted to the survey area
220    that did not settle at a specific bait but came within 1m of a bait and flitted between
221    baits, were also captured. Multiple researchers conducted the hand netting, three per site
222    each day. This included trained researchers experienced with capturing insects with nets,
223    and less experienced volunteers. To reduce biases from experience, we ensured that the

224 teams surveying the different sites were as balanced as possible, with less experienced
225 people paired with more experienced people and the teams rotated between the sites.
226 Some of the potential issues associated with capture rates are explored in the discussion.

227 Preserved orchid bees were identified in Cusco, using a stereo microscope, published keys,
228 checklists and descriptions (Bonilla-Gomez and Nates-Parra, 1992; Dressler, 1978, 1979,
229 1982b, 1982c, 1982d, 1984; Faria and Melo, 2007; Hinojosa-Díaz and Engel, 2011, 2012,
230 2014; Kimsey, 1979, 1982; Melo, 2014; Moure, 1965; Nemésio, 2011, 2009; Nemésio and
231 Silveira, 2007b; Niemack et al., 2012; Roubik, 2004; Roubik and Hanson, 2004). For as
232 many species as possible, identification was verified by consulting the collections at the
233 Department of Entomology at the Universidad de San Antonio Abad de Cusco, and at the
234 Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima. Reference
235 specimens were deposited in both these collections in September 2016.

236 **1.2.2.2 Analysis**

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

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

248 All analyses were conducted using R version 3.3.2 (R Core Team, 2017) in RStudio version
249 1.0.136 (RStudio Team, 2016). Observed alpha diversity was calculated using the package
250 rdiversity v.0.4.3 (Mitchell and Reeve, 2016). Estimates of species richness, Shannon
251 entropy and Simpson diversity were calculated using the package iNEXT v.2.0.14 (Hsieh et
252 al., 2016) to rarefy or extrapolate estimates to a standard sample size of 50 individuals at

253 each site (Chao et al., 2014; Colwell et al., 2012). This sample size represented

254 approximately double the smallest sample size, the maximum that can be reliably

255 extrapolated at q = 0 with high confidence (Hsieh et al., 2016). This provided

256 approximately 90% sample coverage for all sites (supplementary materials Figure S.3). The

257 diversity estimates at each value of q were bootstrapped 1000 times using the iNEXT

258 function in R, to calculate a confidence interval around our mean estimates. This allowed

259 us to test for consistency in the direction of change in the diversity estimates while

260 accounting for the uncertainty in the diversity estimates. We did this by extracting the

261 1000 raw estimates of the diversity of each site, and then calculating the proportion of

262 times a less disturbed site was more diverse than a more disturbed site. All disturbance

263 type pairs were compared, and a Spearman rank correlation test (Spearman, 1904) was

264 used to test the correlation between the proportion of times that the less disturbed site

265 was the more diverse of the pair and the difference in disturbance rank between the sites.

266 To understand how beta diversity was affected by human disturbance, we quantified the

267 change between sites along the gradient using several methods, including community

268 composition, beta diversity partitioning and two recently developed beta diversity

269 measures, redundancy and representativeness (Reeve et al., 2016). The total beta

270 diversity of the gradient, measured as the total variance of the community matrix, was

271 calculated using the beta.div.comp function in the R package adespatial v.0.1-1 (Dray et

272 al., 2018) along with the partitioning of the total beta diversity into nestedness and

273 turnover. A Hellinger transformation of the species x site abundance matrix was used, as

274 the Hellinger distance provides a good compromise between linearity and resolution and

275 has been found to correlate better with 'true' distances in simulations than many

276 alternatives (Legendre and Gallagher, 2001). Beta diversity decomposition was then

277 calculated for this matrix using the quantitative form of Sorensen's dissimilarity

278 coefficient, in order to account for differences in relative abundances as well as species

279 identity (Legendre and De Cáceres, 2013). A redundancy analysis (RDA) was used to

280 examine the change in species composition across the gradient, applied to the Hellinger

281 transformed community matrix and constrained by disturbance rank, elevation and

282 distance to the river, using the vegan package in R (Oksanen et al., 2018).  The use of this

283 transformation overcomes many of the issues associated with raw Euclidean distances,

284 including many zeros and large differences in abundances, which may lend

285    disproportionate weight to rare species (Borcard et al., 2011; Legendre and Gallagher,

286    2001). Species contributions to beta diversity (SCBD index), which is the relative degree of

287    variation in the abundance of individual species across the study gradient (Legendre and

288    De Caceres, 2013), were calculated with the beta.div function in the adespatial package,

289    using the Hellinger dissimilarity coefficient (Legendre and De Cáceres, 2013). The

290    abundances of the species with the highest SCBD values were compared across the

291    gradient, with some low SCDB species included for contrast.

292    The redundancy of the communities at each site was calculated using the redundancy ($\rho$)

293    measure, available in the package rdiversity (Mitchell and Reeve, 2016). This is a measure

294    of beta diversity that represents the extent to which the diversity of the overall

295    metacommunity (the diversity of the whole gradient in this case) would be preserved if a

296    single community or site was lost (Reeve et al., 2016). We also calculated the

297    representativeness ($\bar{\rho}$) of the sites, which is a measure of how well a single site represents

298    the overall metacommunity. Representativeness considers how much of the

299    metacommunity diversity a site holds (i.e. the redundancy) relative to the size of the

300    community at that site, providing a correction for the different sample sizes across the

301    gradient. Both redundancy and representativeness were calculated at $q = 1$, as this

302    provides an intermediate level of conservatism and is a key value of q due to its

303    correspondence to many measures of beta diversity through relative entropy and K-L

304    divergence (Reeve et al., 2016).

305    We used disturbance as a continuous explanatory variable since this allowed us to consider

306    land-use on a continuous spectrum of disturbance intensity, with the possibility of other

307    land-uses falling at intermediate intensities. We could have used an ordered discrete

308    variable, which would have been better able to detect a signal in the presence of

309    unevenness in disturbance differences, but this would have required more data to fit. Our

310    simpler approach is supported by the strong correlation of our continuous disturbance rank

311    with vegetation structure data. Nonetheless, because we could not be sure of the exact

312    difference in disturbance between each level, where possible we used a Spearman rank

313    correlation test to assess the patterns of diversity along this gradient. This approach

314    makes no assumptions regarding the shape of the relationship between the variables, only

315    that the pattern is monotonic along the gradient, and is a therefore a conservative

316    approach for these analyses. Spearman rank correlation tests were used to test for

317    correlations of disturbance rank with abundance, observed alpha diversity at q = 0, 1, 2

318    and ∞, estimated alpha diversity at q = 0, 1 and 2, and representativeness and

319    redundancy at q = 1. In addition to checking each value of q independently, we tested if

320    the overall pattern of alpha diversity change across the disturbance gradient was

321    significant at α = 0.05. To overcome the non-independence of the q values from one

322    another, we used a permutation test to calculate the combined p value for the correlation

323    between disturbance rank and observed alpha diversity at q = 0, 0.5, 1, 2 and ∞ and

324    estimated alpha diversity at q = 0, 0.5, 1 and 2 (q = ∞ could not be included because the

325    estimates all converged at 1, so there was no variation; we included q = 0.5 because q is

326    on a logarithmic scale, so this prevents biased weighting of rare species when calculating

327    the overall pattern of alpha diversity across multiple values of q). The permutation test

328    involved randomly re-labelling the study sites, and then re-calculating the significance of

329    the correlation between disturbance rank (now randomly re-assigned) and alpha diversity

330    at each value of q (Good, 2000). These permuted p-values for each value of q were

331    combined to determine the significance of the overall alpha diversity change across the

332    gradient (Fisher, 1925). This was repeated for 10000 permutations, and the permuted p-

333    values compared to those obtained with the original data, to determine the probability

334    that the observed correlation of diversity could have occurred by chance. To check that

335    the patterns of change in redundancy and representativeness across the gradient were not

336    specific to our chosen value of q = 1, we also used a permutation test to obtain the

337    combined p value for the correlation of disturbance rank with redundancy and

338    representativeness calculated at q = 0, 0.5, 1, 2 and ∞.

339    As well as testing for the effect of disturbance on diversity and abundance, the potential

340    effects of altitude, rainfall and distance to river were investigated using linear models, to

341    confirm whether the effects of disturbance identified with the correlation tests remained

342    significant when accounting for these variables. The diversity and abundance response

343    variables were log-transformed and modelled with a gaussian distribution. The model

344    summaries and residuals were inspected to evaluate model fit. None of the additional

345    environmental variables resulted in a significant improvement compared the model that

346    included only disturbance rank. Full details of the models tested can be found in Table S.2

347    of the supplementary materials. In the case of the relationship between abundance and

348 disturbance rank, visual inspection of the data prompted us to also test a quadratic

349 polynomial, but the AIC values indicated that a linear relationship was a better fit ($\Delta$AIC =

350 1.42). Throughout the results section, the statistics reported are the results of the

351 Spearman rank correlation test unless stated otherwise.

### 1.2.3 Pollination services

#### 1.2.3.1 Data collection

354 The potential for the provision of pollination services (from any pollinators) across the

355 gradient was tested using artificial flowers filled with sugar solution (Internicola et al.,

356 2007; Real, 1981). The flowers were 5 cm in diameter and constructed from thin craft

357 foam with a central well containing 1.5 ml of the sugar solution (1:1 sugar and water).

358 Red, blue and yellow flowers were used, with five of each colour on an array that was

359 suspended at a height of 1.3 m at the survey site. Two flower arrays (30 flowers in total)

360 were used at each site, separated by approximately 30 m, and each monitored by a

361 member of the research team. All insects (of any Order) that arrived at the flower array

362 were counted as potential pollination events, apart from individuals that simply moved

363 from one location on the array to another. The flowers were monitored for three periods

364 of 45 minutes separated by 15-minute intervals during which the flowers were covered.

365 This was repeated for four mornings, between 08:45 and 13:00, at each of the 18 sites.

#### 1.2.3.2 Analysis

367 Spearman rank correlation tests were used to test the correlation between the number of

368 potential pollination events (flower visits) with disturbance rank and with observed orchid

369 bee species richness.

## 1.3 Results

### 1.3.1 Orchid bee diversity

#### 1.3.1.1 Vegetation structure

373 The first component of the vegetation structure PCA (PC1) explained 33% of the variation

374 in vegetation structure, with higher rankings (lower disturbance) correlated positively with

375    canopy cover, tree count and diameter, and negatively with leaf litter depth and

376    understory herb abundance (Figure S.2). There was a strong correlation between

377    vegetation structure (PC1) and disturbance rank, supporting the disturbance ranking used

378    to represent human disturbance intensity along the gradient ($p < 0.00001$, rho = 0.86;

379    Figure 1). The results of all correlation tests are provided in Table S.1 in the

380    supplementary materials.
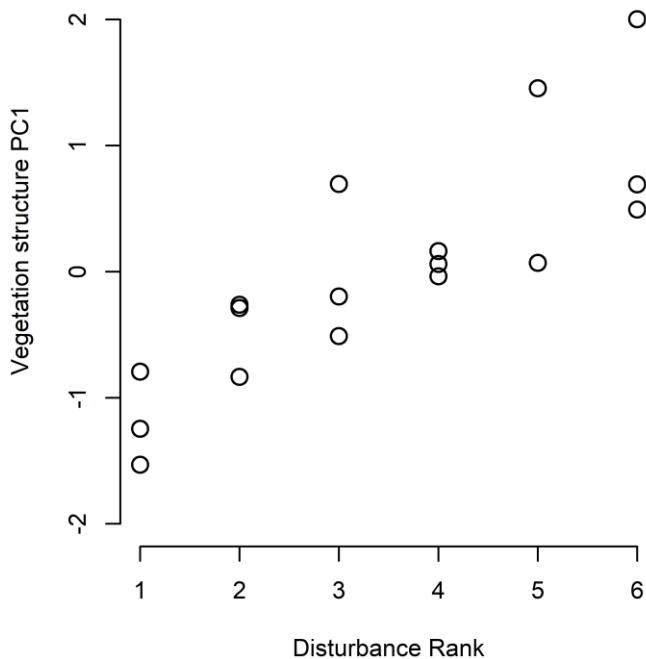


381

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

386    **1.3.1.2 Alpha diversity**

387    We collected 1783 individuals of 31 species of orchid bee. Overall observed alpha diversity

388    decreased across the disturbance gradient (permuted combined p value for $q = 0, 0.5, 1, 2$

389    and $\infty$: $p = 0.025$; Figure 2). This was mostly driven by the patterns of alpha diversity at

390    low values of q, with observed species richness ($q = 0$) and observed Shannon diversity ($q =$

391    1) both decreasing with increased disturbance across the gradient (rho = 0.57, $p = 0.01$;

392    rho = 0.51, $p = 0.03$). There was no significant change in alpha diversity across the

393    gradient at higher values of q. However, when estimated diversity was examined,

394    correcting for sample size (n = 50), there were no significant differences in estimated

395    diversity across the disturbance gradient, either overall (permuted combined p value for q

396    = 0, 0.5, 1 and 2: p = 0.330) or for any individual value of q, due to the wide confidence

397    intervals around the mean estimates (Figure 3 and Figure S.4).
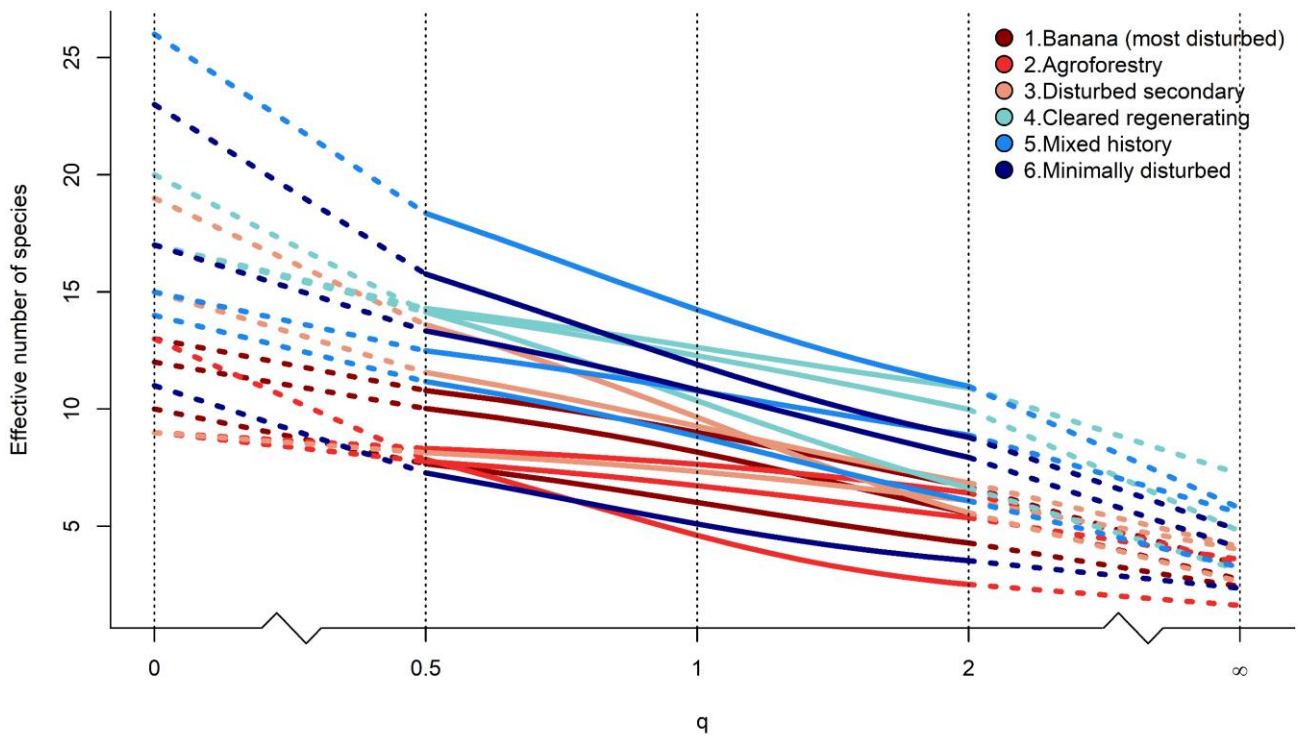


398
399    Figure 2 – Orchid bee observed alpha diversity across the disturbance gradient. Increasing values of q indicate
400    increased emphasis on dominant species (q = 0 = species richness, 1 = Shannon diversity, 2 = Simpson
401    diversity, ∞ = Berger Parker diversity). Disturbance rank is shown by a colour gradient, dark red for the most
402    disturbed sites, dark blue for the least disturbed. Overall diversity was significantly higher in less disturbed sites
403    (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
404    not significantly different at or above q = 2 (rho = 0.45, p = 0.06)  Because q is on a log scale, the broken axis
405    and dashed lines indicate inferred values as diversity was calculated only for the values at either side of the
406    break (0 and ∞); along the solid line, q was calculated at intervals of 0.1.
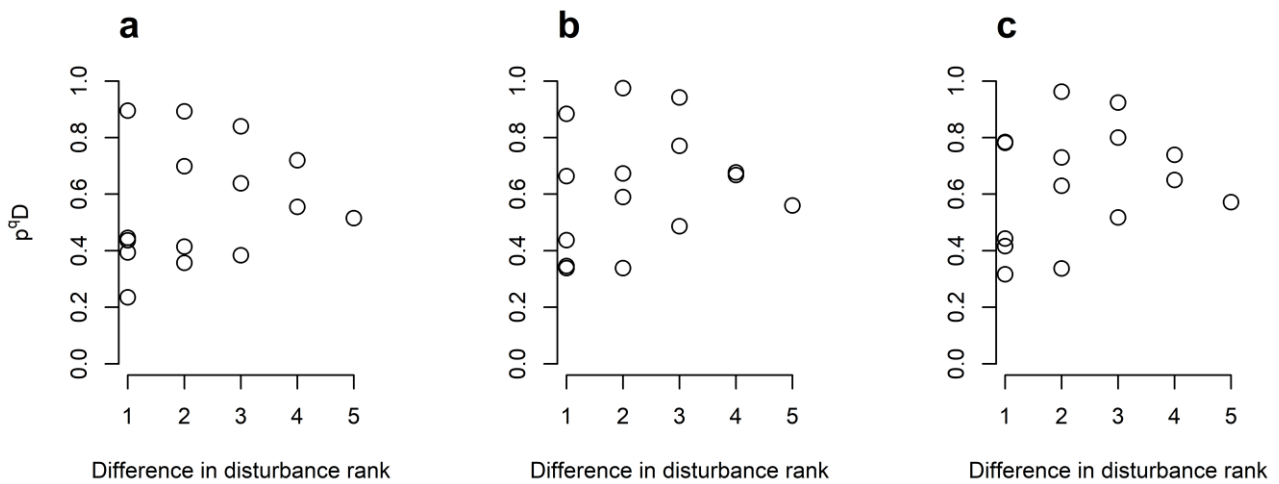
Figure 3 – The correlation between diversity estimates and disturbance ranking. Using the iNEXT package in R, we generated 1000 estimates for the diversity of each site. We then compared all possible habitat pairs to calculate the proportion of times that the less disturbed habitat was estimated to have a higher diversity than the more disturbed habitat, shown on the y axis ($p^qD$). 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).
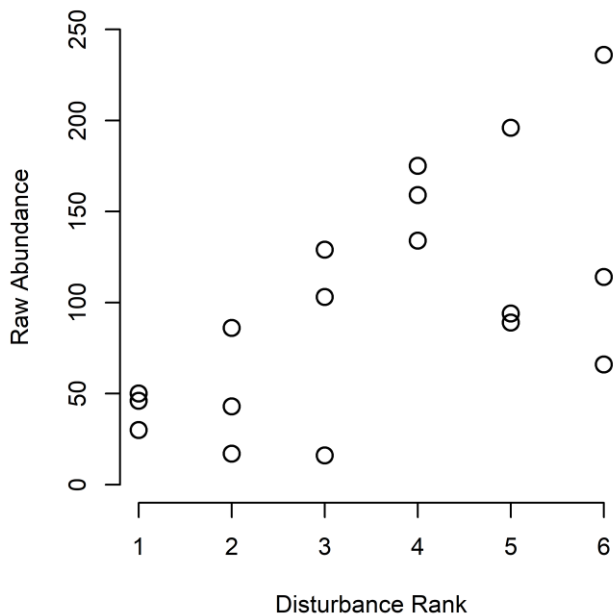


Figure 4 – Change in orchid bee abundance across the disturbance gradient. Abundance is the number of orchid bees captured at each site, plotted against the disturbance rank of the site (rho = 0.63, p = 0.005). Disturbance rank runs from 1 (most disturbed) to 6 (least disturbed).
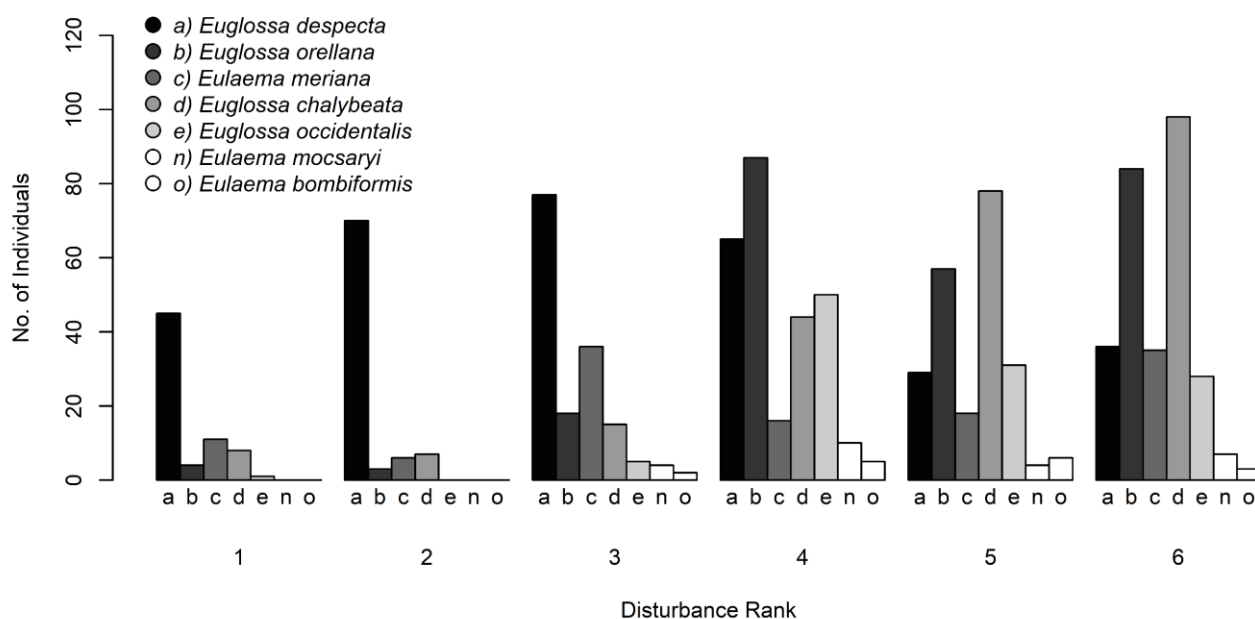
### 1.3.1.4 Beta diversity

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
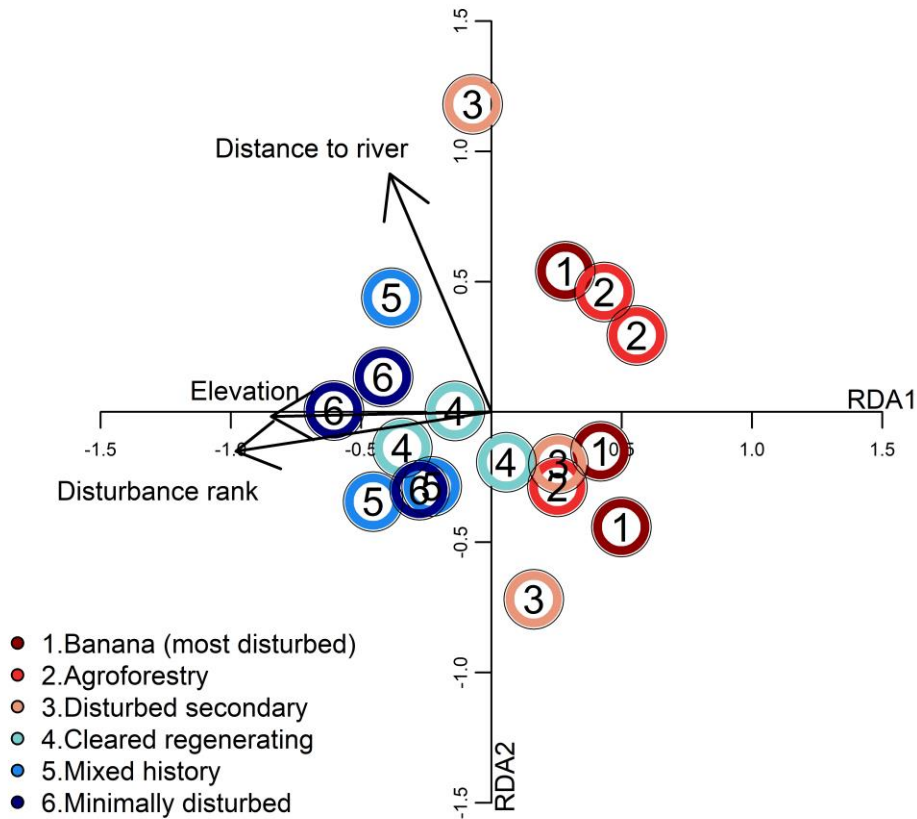
disturbance.



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.

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

449 The less disturbed sites hold communities that are less redundant (Figure 7a; at q = 1: p =

450 0.02, rho = -0.55; permuted combined p value for q = 0, 0.5, 1, 2 and ∞: p = 0.016) and

451 more representative of the overall metacommunity (Figure 7b; at q = 1: p = 0.04, rho =

452 0.4922; permuted combined p value for q = 0, 0.5, 1, 2 and ∞: p = 0.024) than the more

453 disturbed sites. This suggests that the overall diversity of the region (all sites across the

454 gradient) would suffer a greater loss should the community of one of the less disturbed

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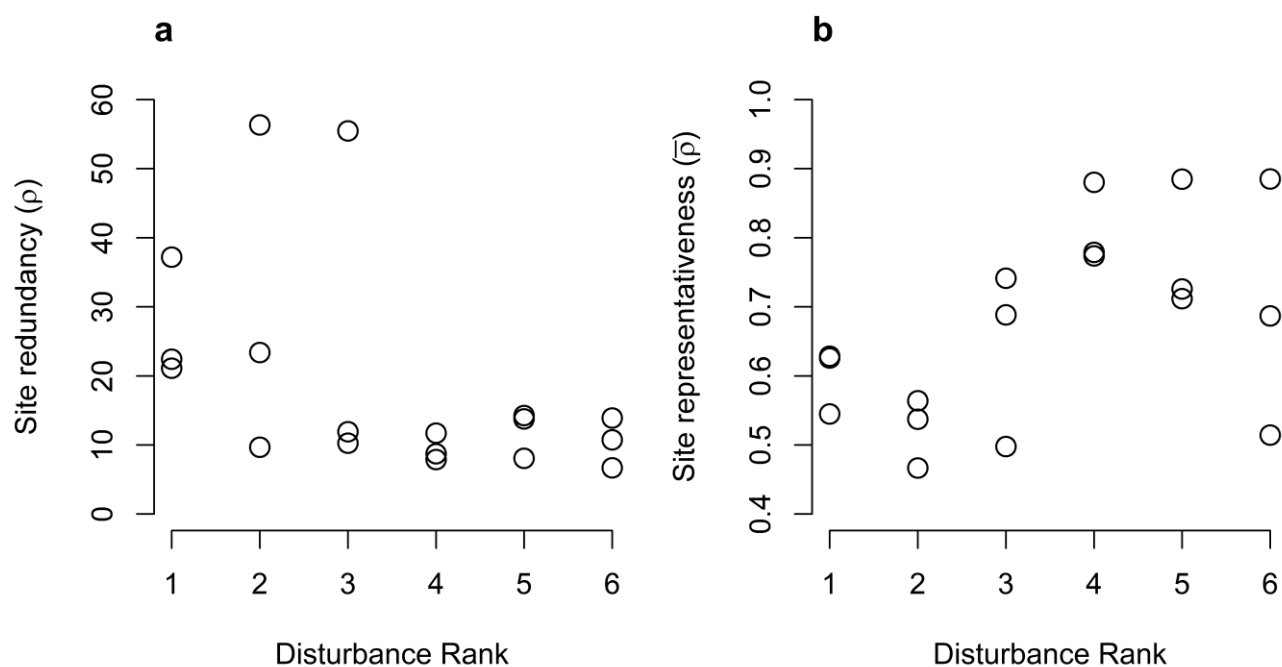
Figure 7 – Change in the a) redundancy (ρ) of sites (p = 0.02, rho = -0.55) and b) representativeness $(\overline{\rho})$ of sites (p = 0.04, rho = 0.49) across the disturbance gradient at q = 1. The disturbance rank runs from 1 (most disturbed) to 6 (least disturbed).

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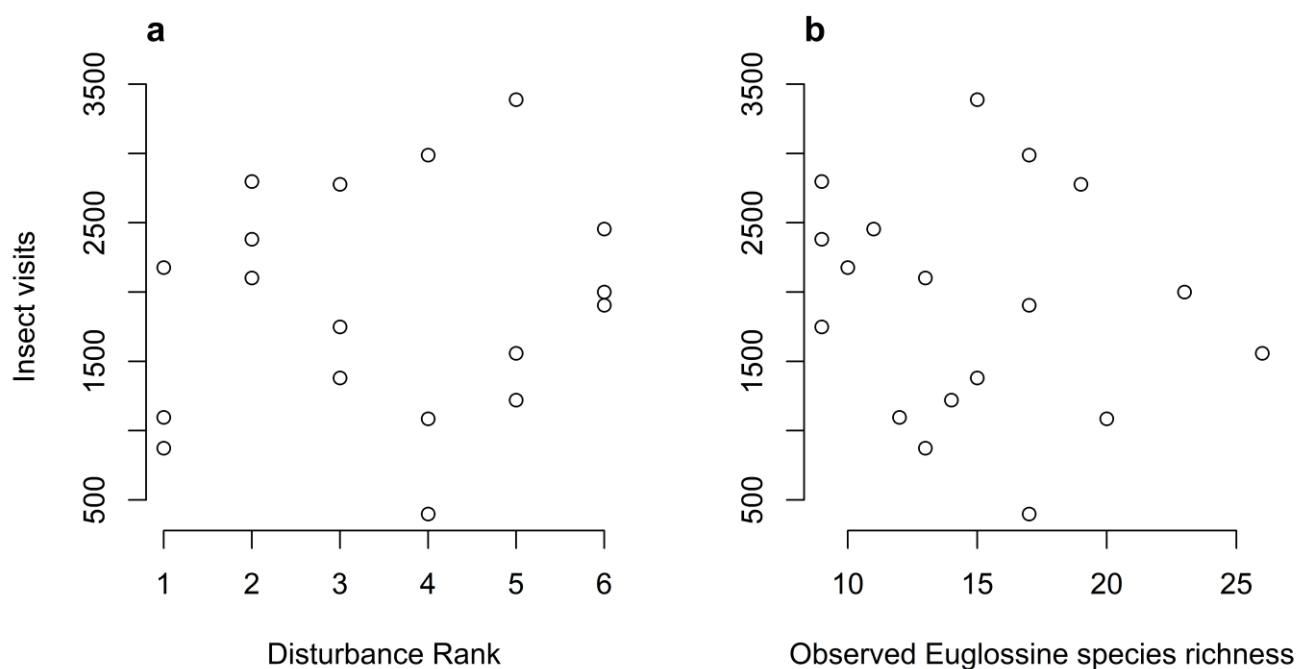
Figure 8 – Potential pollination events. Number of insect visits to artificial flower arrays correlated with (a) disturbance rank (rho = 0.12, p = 0.65) and (b) observed orchid bee species richness (q = 0; rho = -0.20, p = 0.44). Disturbance ranking runs from 1 (most disturbed) to 6 (least disturbed).

## 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

489    shared across sites (Nemésio and Silveira, 2006). The second study considered alpha

490    diversity at q = 0, 1 and 2 as well as abundance and community similarity between sites

491    and found no significant relationship between any of these with disturbance level

492    (Rasmussen, 2009). However, only three sites were compared, one of each disturbance

493    type: primary forest, a reforested site and one heavily disturbed forest. Like these studies,

494    we also found no significant change in alpha diversity after controlling for sample size.

495    However, it should be noted that this lack of a significant response appeared to be

496    because there were many more bees caught in the less disturbed sites, consistent with the

497    marked decrease in orchid bee abundance with increased disturbance we detected. When

498    comparing observed alpha diversity, without controlling for the number of bees caught,

499    there was a decrease in species richness and Shannon diversity as disturbance increased.

500    Since standardised sampling effort was used there is no reason to suspect the observed

501    differences were caused by any bias in the sampling design, and so this difference should

502    not be dismissed. That there are fewer bees in the disturbed sites means that the

503    confidence interval around the estimated true number of species present is large, however

504    if sampling time was extended to catch the same number of bees as found in the least

505    disturbed sites, it would be unsurprising if there were still fewer species (supplementary

506    materials Figure S.4). In any case, the fact that during a set time period, fewer individuals

507    of fewer species are likely to visit plants in disturbed habitats is an ecologically

508    meaningful result, as it is likely to impact plant pollination, even if similar total numbers

509    of species could eventually be detected over a longer time.

510    This kind of study is prone to problems with biases arising from study design and the

511    assistance of volunteers. As well as training, and pairing experienced staff with

512    inexperienced samplers, we randomised the location of the teams to avoid systematic

513    biases. The high turnover of volunteers allowed us to keep this strategy constant over the

514    sampling period. Capture success was high, and although there were some escapes, many

515    of these individuals could be seen leaving and returning to the bait, allowing a second

516    capture attempt. We did not record miss rates but there was no noticeable difference

517    observed between genera or species identifiable in flight, although this would be valuable

518    to investigate in future studies. Another known issue in studies like this is the potential for

519    differences in the attractive radius of the baits between sites to affect capture rates,

520    because differences in vegetation structure and shade between the sites could affect the

521    evaporation rates and how much the baits might be carried on the wind. Further research

522    is needed to fully address this (Nemésio, 2012), but we followed standard practice from

523    previous studies in using standardised bait protocols across all sites, including regularly

524    refreshing the bait to avoid evaporation issues. Since capture rate was higher in the less

525    open forest, there was also no evidence for sampling issues related to scent dispersal

526    being inhibited by vegetation.  Due to this study region consisting of a matrix of different

527    habitat types, it was unavoidable that some sampling sites would not be far from other

528    disturbance types. We set up the bait stations near the middle of a habitat type to ensure

529    that the majority of bees were likely to be attracted from within that site, with a

530    minimum of 100m to the neighbouring habitat. It is plausible that some bees may have

531    been attracted from neighbouring habitats, yet this should theoretically weaken our power

532    to detect a correlation between the orchid bee community and habitat type, lending

533    confidence to the patterns that we have detected, as discussed in Brosi (2009).

534    Furthermore, for ecological purposes we care about the bees that visit a site to provide

535    pollination services, so it is still relevant if some bees visit from neighbouring habitats, as

536    we are interested in the disturbance impacts on orchid bees in the context of this matrix

537    landscape.

538    Regarding the value of orchid bees as indicators, in this study we have shown that changes

539    in the orchid bee population are strongly correlated with intensity of forest disturbance,

540    and identified which measures are most useful for detecting these responses. The results

541    of the vegetation surveys showed a loss of canopy cover and number of large trees as

542    disturbance increased (Figure S.2). This may also result in a change in microclimate and a

543    loss of epiphytes. A loss of resources such as nectar and nesting habitats may have

544    contributed to the decline in orchid bee abundance, and a change in the plant species

545    composition could have influenced the change in orchid bee species along the gradient. A

546    more detailed exploration of the mechanisms behind the orchid bee responses are

547    important in order to understand what exactly they are indicative of: is it a change in

548    vegetation structure (shown to be closely correlated with disturbance in our study), a

549    decline in overall biodiversity, a loss of important nesting habitats, a loss of epiphytes or

550    particular flower species? These are important points for further investigation, as there is

551    a general lack of information about the relationship between ecological indicators and

552    indicandum (Gao et al., 2015). It would also be worth expanding on research assessing how

553 far these disturbance effects penetrate into forest edges (Nemesio and Silveira, 2006),
554 considering the different indices used in this study and comparing different land uses and
555 regions. For basic assessments, orchid bee abundance is a simple measure that can be
556 monitored by conservation managers without the need for much analytical expertise or
557 even species identification. Although this should not be used in isolation, it could serve as
558 a useful warning flag of negative impacts of disturbance. The Hill numbers diversity
559 measures in the rdiversity package require more technical skills but allow efficient
560 calculation of a broad suite of indices, including alpha and beta diversity (redundancy and
561 representativeness) at multiple values of q, using a single input of the species x site data
562 matrix and only simple code modifications to calculate multiple indices.

563 Species richness has been recognised as a poor index for detecting the effect of
564 disturbance on some other taxonomic groups, and it has been suggested that community
565 composition may be more sensitive (Stork et al., 2017). For example, Samejima *et al*.
566 (2004) found that stingless bees (Meliponini) showed a change in community composition in
567 response to human disturbance. We also found that community composition changed
568 across the disturbance gradient, but community composition can be expected to change
569 for many reasons, including non-disturbance related changes in vegetation and other
570 habitat features. Due to the small spatial scale of this study and the history of the area,
571 we expect that the habitats of the study sites would have been very similar prior to the
572 anthropogenic disturbance; this assumption is less likely to hold true across larger spatial
573 scales, making it harder to link changes in species composition to habitat disturbance
574 across space. However, as a potential indicator, identifying shifts in orchid bee community
575 composition could be useful for monitoring a site over time, to provide an indication of
576 whether the site is being disturbed to a degree that is negatively impacting the ecosystem
577 (Santini et al., 2017).

578 In ecological terms, reduced orchid bee abundance in highly disturbed habitats is of
579 concern, as it is indicative of a potential cascade effect resulting from the loss of forest
580 canopy, along with habitat complexity and epiphytic diversity (Barthlott et al., 2001). This
581 could result in a loss of specialist pollinators that are crucial for the persistence of many
582 plant species, which may reduce the resilience of the remaining degraded forest, as the
583 ecological networks have been weakened. However, the services provided by orchid bees
584 may be partially maintained by a well-connected patchwork of habitats including high

585    quality forest, as the dispersal distances of this group (Janzen, 1971) enables them to

586    make opportunistic visits to degraded habitats when resources are available. This way,

587    they may be able to provide pollination services to habitats that possibly lack the

588    resources to support viable orchid bee populations independently, but this will require a

589    substantial area of intact forest to be maintained nearby.

590    We found that the redundancy ($\rho$) of the sites increased with increased disturbance.

591    Redundancy is therefore likely to be a useful measure of disturbance impacts, because it

592    considers both the species present and their abundance, so gives a more complete picture

593    of how the sites differ. From these results, we can see that the impact of losing a

594    minimally disturbed site would more severely impact the overall diversity of the region

595    than the loss of a highly disturbed site. Similarly, when we considered the

596    representativeness ($\bar{\rho}$) of the sites at q = 1, we found that in each of the less disturbed

597    sites (ranks 4-6) about 80% of the overall biodiversity of the study area could be found, on

598    average, whereas the more disturbed sites (ranks 1-3) only held an average of about 60%.

599    Pollination potential showed no correlation with orchid bee abundance or alpha diversity

600    (Figure 8; supplementary materials Table S.1). This is probably because visitors to the

601    flower arrays were mostly sweat bees (family Halictidae) and these visited the flowers in

602    high abundance. Other visitors included flies, wasps, butterflies, a few orchid bees, and

603    even a hummingbird on one occasion. An important caveat in interpreting this experiment

604    was that we were only able to measure the potential opportunities for pollination (the

605    number of visits the flower received), and were not able to account for the fact that

606    insects differ widely in their effectiveness as pollinators (Ivey et al., 2003; King et al.,

607    2013; Primack and Silander, 1975; Ramsey, 1988; Schemske and Horvitz, 1984). Turnover

608    of species between sites also means that higher bee diversity than expected is likely to be

609    required to deliver pollination services over large spatial scales (Winfree et al., 2018).

610    Halictid bees are considered valuable pollinators and visit many different plant species

611    (Lindsey, 1984), although they do not show such distinctive host adaptations as the orchid

612    bees. Orchid bees do pollinate a wide range of plants; however, they are particularly

613    important due to their many species-specific relationships and cannot be easily substituted

614    by more generalist pollinators. Further research into the pollination networks of orchid

615    bees and the plants they visit would be helpful to understand how a loss or change in the

616  orchid bee community might impact the plant community. Exploring functional differences

617  (e.g. tongue length and body size) between the orchid bee species affected by disturbance

618  would also add valuable information on the contributions of specific orchid bee species as

619  specialist pollinators.

620  ## 1.5 Conclusion

621  Orchid bees show a clear negative response to human disturbance across a tropical forest-

622  agricultural gradient. They are also efficient to sample and play a key role in pollination

623  services. We therefore suggest they can be a useful addition to the indicator groups

624  available for studying the impacts of forest loss on biodiversity and ecosystem functioning.

625  In choosing whether to use orchid bees in future biodiversity studies it should be noted

626  that it is important to consider more than one indicator group in any assessment  (Hilty

627  and Merenlender, 2000; Lawton et al., 1998). When orchid bees are selected as a suitable

628  indicator group, our results show that abundance, redundancy ($\rho$) and representativeness

629  ($\overline{\rho}$) provide the most sensitive measures for detecting the response of orchid bees to

630  human disturbance. In order to understand the response of biodiversity to human

631  disturbance, it is essential to consider the response measures carefully, as a measure that

632  works well for one group may not always be the best for another, and often multiple

633  indices are necessary.

634

## 1.6 Acknowledgements

## 1.7 Funding

## 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

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952
953 ## **1.12    Supplementary materials**



954
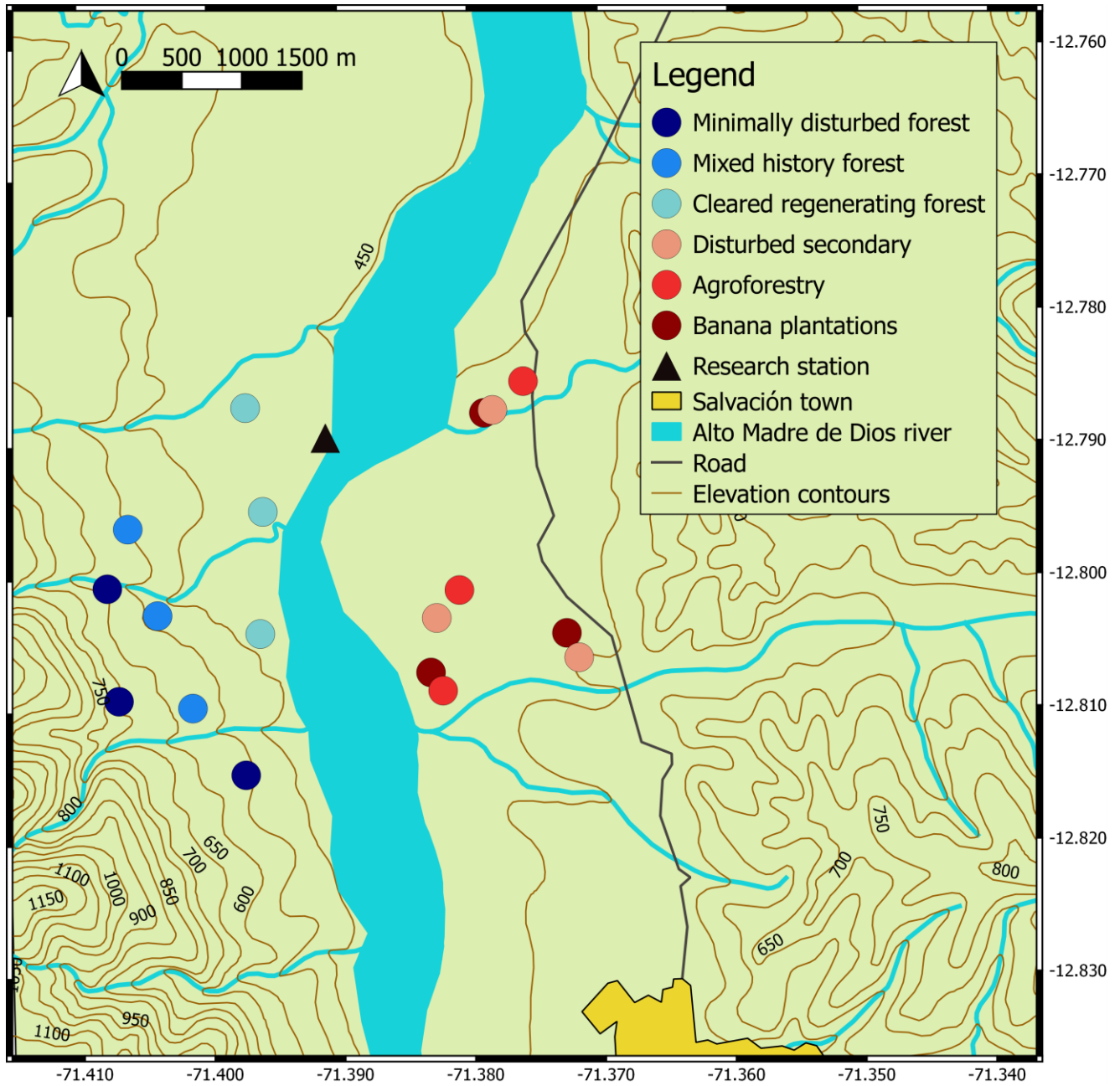
955 Figure S.1 – Map of our study sites in Manu, Peru. Colours represent disturbance gradient, dark red = 1. Most
956 disturbed, dark blue = 6. Least disturbed. The map also shows: elevation contour lines; the Manu Learning
957 Centre research station; the nearest local town, Salvación; the local road; the main river, Alto Madre de Dios,
958 and its tributaries.

959
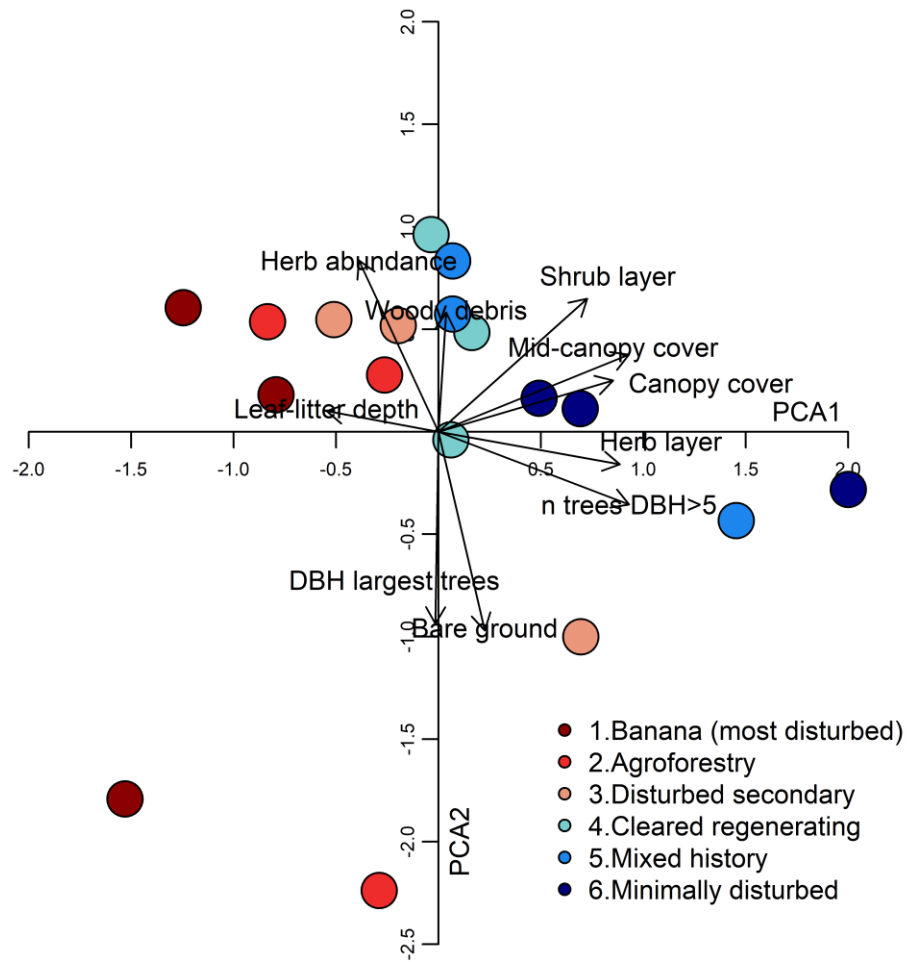


960

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

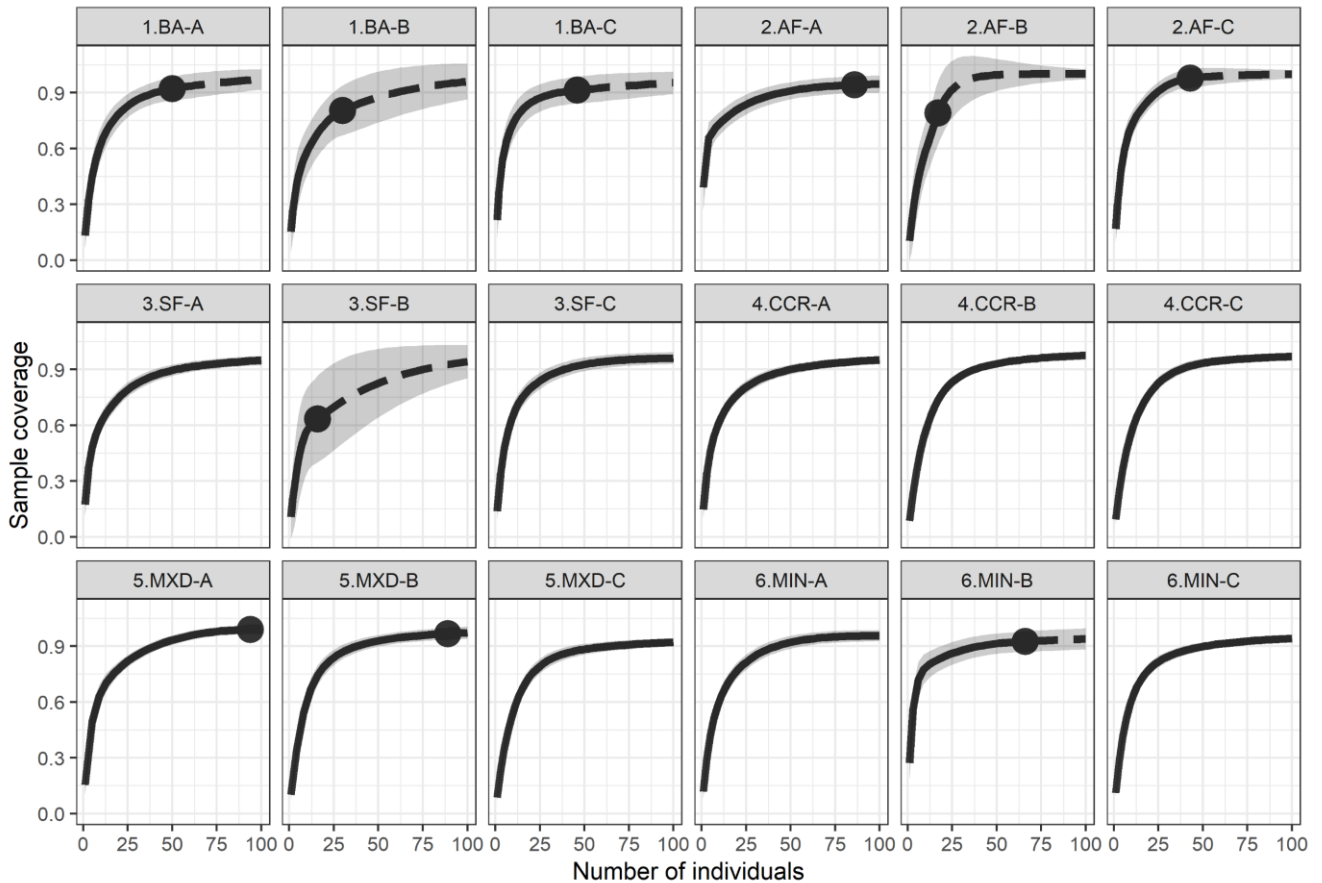Figure S.3 – Sample completeness at q = 0. The sample completeness for each site is shown in a separate panel. The labels above each panel describe the disturbance rank (1-6, 1 is most disturbed) and habitat type of each site (BA: Banana, AF: Agroforestry, SF: Disturbed secondary forest, CCR:  Cleared 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.
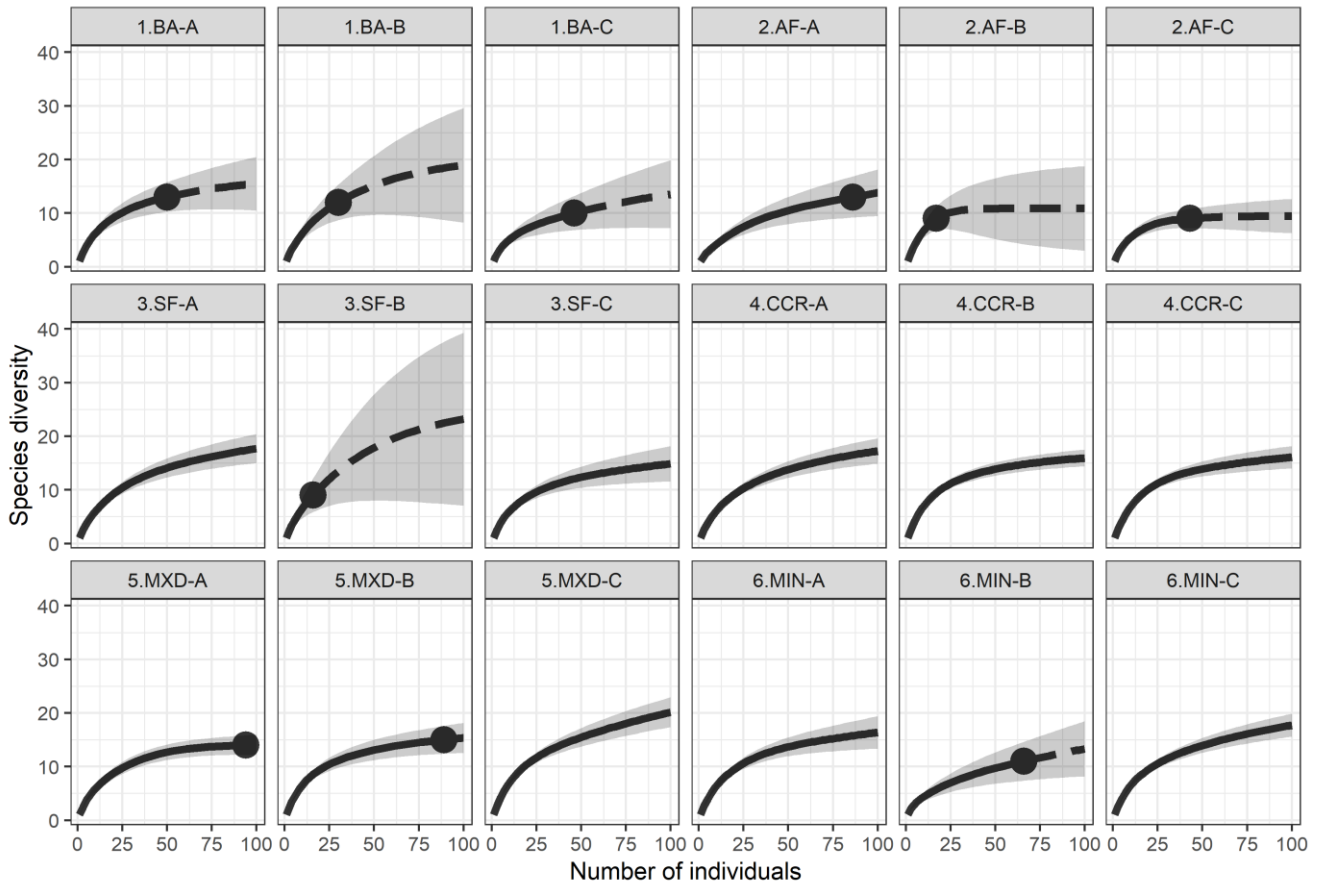
Figure S.4 – Estimated richness at each site extrapolated to a sample size of 250 individuals. Solid line shows rarefied estimate, dashed line shows extrapolation, and filled circle indicates the collected sample size. Shaded area indicates 95% confidence interval with 1000 bootstraps.

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($\rho$ 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 |