

1 Relating beta-diversity to distance and disturbance in the
2 conversion of Borneo’s tropical forests to palm oil plantation

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5 **Abstract**

6 The tropical lowland forests of Borneo are increasingly threatened by logging and conversion
7 to palm oil plantation. Previous studies have concluded declines in alpha-diversity associated
8 with this form of land-use modification, but trends in other components of diversity have been
9 largely neglected. We applied Jost’s “true” diversity with a functionally-diverse group (beetles,
10 order: Coleoptera) to estimate the changes in gamma-, alpha- and beta-diversity associated with
11 disturbance. Using richness-based measures, both gamma- and beta-diversity decreased with
12 disturbance. Using proportion-based measures, only beta-diversity decreases. In all cases beta-
13 diversity is influenced by interactions between distance and disturbance, and gives a far more
14 useful insight into diversity change than the other two components. GDMs revealed that where
15 beta is based on richness, distance is by far the strongest predictor, whereas the opposite is true
16 when proportions of taxa are considered. We conclude that the changes in beta-diversity result
17 from a decline in habitat heterogeneity and the following competitive exclusion of specialist taxa.
18 This study highlights the risk that beta-diversity can change dramatically while alpha remains
19 constant. Conversion of Borneo’s natural forest leads to a significant decline in biodiversity, but
20 there is the potential that beta-diversity can be used to determine suitable spatial scales for the
21 efficient conservation of biodiversity in new protected areas.

22 **Keywords**— beta-diversity; deforestation; Coleoptera; habitat heterogeneity; oil palm

1 Introduction

Southeast Asia has suffered extensive deforestation over recent decades, losing around 12% of forest cover between 1990 and 2010. Approximately two-thirds of the forest cleared from the region between 2000 and 2010 was from insular Southeast Asia (Stibig et al., 2014). Malaysian Borneo has been particularly effected over recent decades. Just 22% of the land area here remained as pristine forest in 2009, and 45% as degraded forest (Bryan et al., 2013).

Selective logging for high-value timber typically leads to clearing, and by 2009 a further 22% of Malaysian Borneo had been replaced with monoculture (Bryan et al., 2013) consisting primarily of oil palm (*Elaeis guineensis*). The plant is native to West Africa and grows rapidly in the Malaysian climate of consistent high temperature and rainfall. Oil from the fruit is extracted and used in cooking, while oil from the seed is used in soaps and cleaning products. Production is highly efficient, with usable oil constituting around 10% of the plants total dry biomass (Basiron, 2007).

Export of timber and palm oil have been imperative in the development of Malaysia, but such extensive land-use modification has unavoidable impacts on the forest ecosystem. The Malaysian Palm Oil Council describes palm oil production as “sustainable” (Basiron, 2007), but conversion of natural landscapes for agriculture is often detrimental to biodiversity (Foley et al., 2005; Tilman et al., 2001). Comparisons of pristine forest with palm oil plantation have indeed concluded reduced diversity in a variety of taxa (Azhar et al., 2011; Faruk et al., 2013; Fayle et al., 2010; Hamer et al., 2003).

Diversity can be partitioned into several components which can each be measured by an array of indices. Often, only a single component is quantified for a taxonomic group that has limited relevance to ecosystem-level biodiversity. As such, there exists a considerable amount of confusion where broad conclusions are made regarding loss of diversity.

The majority of studies in this system employ taxa richness to examine counts a particular group (Azhar et al., 2011; Faruk et al., 2013; Gillespie et al., 2012). These basic measures of area diversity and point diversity, or gamma- and alpha-diversity respectively Whittaker, 1972, are useful in assessing the vulnerability of particular taxa, perhaps endemic or threatened species, but give little insight into community structure. Relative species abundance theory suggests that counts of taxa groups are rarely even (Hubbell, 2001) and as a result the proportions of each group provide an important insight into community composition. Few analyses of Borneo’s expanding oil palm plantations use proportion-based measures of diversity, and where this is the case the metrics applied are incomparable (Benedick et al., 2006; Gray et al., 2014).

Diversity between points (beta-diversity, Whittaker, 1972) is often totally neglected from these studies, yet imperative in examining spatial patterns in biodiversity. Where this component is considered, it is quantified in metrics that are either directly dependent on alpha or dissimilar in scale (Benedick et al., 2006; Pfeiffer et al., 2008). Sometimes alpha-diversity is calculated using proportion-based indices and presented alongside richness-based beta-diversity values (Gray et al., 2014; Lucey et al., 2014). This prohibits the comparison of alpha-diversity with beta-diversity and the calculation of beta over gradients in alpha. Jost (2007, 2010) has developed methods of quantifying each of the components of diversity in independent forms that allow meaningful comparison. These measures of “true” diversity present the potential to standardise evaluation of biodiversity, and allow comparisons that would have previously been invalid.

Spatial scale is a significant factor in ecological responses to land-use modification (Levin, 1992) but, to the authors’ knowledge, has yet to be considered in studies relating to the effects of plantation expansion on diversity. Calculating Jost’s beta-diversity across a range of distances would therefore provide new insights into the effects of this kind of disturbance on community structure.

Past studies have predominantly compared diversity within discrete habitat types; usually including forest at various stages of degradation with oil palm plantation (Faruk et al., 2013; Fayle et al., 2010; Gillespie et al., 2012). This grouping is sufficient in highlighting the need to conserve natural habitat types but is unhelpful in linking habitat quality to complex ecological processes that will not respond in a categorical fashion. Using a scale of disturbance based on continuous vegetation

74 measurements allows identification of the ecological transitions accompanying land-use modification,
75 and also promotes direct comparison between studies.

76 This study aims to combine comparable, independent metrics with continuous measures of distance
77 and disturbance to estimate the impacts of tropical forest conversion on ecosystem diversity, paying
78 particular attention to the beta-component. It is hypothesised that, in line with previous studies,
79 overall diversity will decrease. Exactly how the predicted change in diversity might occur will be
80 assessed by examining each component of diversity through the entire transition from pristine forest
81 to oil palm plantation.

82 **2 Methods**

83 **2.1 Description of the experimental design**

84 The Sustainability of Altered Forest Ecosystems Project (Ewers et al., 2011) in Sabah, Malaysia was
85 an ideal study area for this investigation. The project utilises a novel experimental design to allow
86 investigation into the impacts of land-use modification on ecological processes (Marsh and Ewers,
87 2013).

88 An experimental area covers 7 200ha of forest that has been previously subjected to either one or
89 two rotations of selective logging. Within the area, clearing of the forest for oil palm began in 2012.
90 Through agreement with the Sabah Foundation, a Malaysian Government organisation promoting
91 education and development, 800ha of this forest will remain as fragments shaped according to the
92 SAFE Project. Six blocks of sample points exist here, each of which will eventually sample fragments
93 of 1ha, 10ha and 100ha in size as well as surrounding matrix.

94 Bordering the experimental area are areas of twice-logged forest and a protected area that has not
95 been logged (with exception to its edges). A linear transect extends into each from the border with
96 the eventual purpose of examining edge effects. Three control blocks also exist, sampling continuous
97 expanses of habitat. One is situated in plantation, another in twice-logged forest and the third within
98 the Maliau Basin Conservation Area which has been only partially logged at low intensity.

99 All blocks are based on fractal sampling designs, allowing study of ecological processes over
100 different spatial scales. Each design consists of four orders of points, with lower-order points clustered
101 in respective formation around higher-order points (Marsh and Ewers, 2013). In this report a
102 hypothetical fifth-order point is also used, which refers to the entire block.

103 **2.2 Justification for the study group**

104 Insects are ideal subjects for studying spatial ecology patterns because their high abundance grants
105 sufficient statistical power and a range of economical standardised methods are available for sampling
106 them. Beetles (order: Coleoptera) are especially suitable for their inherent diversity with a predicted
107 400 000 described species (Hammond, 1992). Their rapid evolution is catalysed by short generations
108 and large numbers of offspring. The continuing radiation of beetles into countless niche spaces,
109 facilitated through all manner of adaptations, has led to an order-level functional diversity suitable
110 for the majority of ecological investigations. Their proven sensitivity to environmental gradients
111 (Ewers and Didham, 2008; Heliola et al., 2001) renders them especially useful in quantifying impacts
112 of habitat modification.

113 As such, beetles have been used in the measurement of diversity in various study systems
114 (Fattorini, 2006; Garcia-Lopez et al., 2012; Weibull et al., 2003). Much of this work focuses on a
115 single group within the order and thus uses targeted trapping methods. This is suitable for assessing
116 the effects of change in a subset of environmental variables. However, any correlations detected are
117 unlikely to be applicable to the ecosystem as a whole. In order to successfully estimate diversity
118 within overall systems, it is necessary to sample taxa of multiple disparate niches. Beetle families
119 can be confined to broad functional clades in terms of feeding habits or preferred microhabitat, for
120 example leaf beetles (family: Chrysomelidae) and sap beetles (family: Nitidulidae). In Sabah a high

121 number of families are represented (Chung et al., 2000) and this taxonomic level is taken to represent
122 a suitable subset of total functional diversity. Diversity of beetle families is therefore used as a proxy
123 for diversity of available habitat types with the taxa that would hypothetically occupy them.

124 **2.3 Field methodology**

125 Since early 2011, biannual invertebrate trapping has been carried out across the SAFE Project study
126 area. Traps set at each of the 579 first-order points are assembled in the field and based on a design
127 combining pitfall, flight-interception and malaise trap. Flying insects are directed either upwards into
128 a “top” trap or downwards into a “bottom” trap, to target invertebrates of various morphology and
129 behaviour. Specimens are collected in plastic bottles filled partially with 70%-ethanol solution. The
130 pitfall-style bottom trap is dug flush into the ground, where the hole is preserved between trapping
131 periods to limit bias associated with soil and leaf litter disturbance (Digweed et al., 1995). Each trap
132 is left for three days before the samples are collected and the traps removed. While it is logistically
133 impossible to set all traps on the same day, they are set within a period of one month to control for
134 seasonality. On collection, malfunctioned traps are noted for exclusion in later analysis.

135 **2.4 Calculating diversity metrics**

136 Counts of beetle families were recorded from each first-order point for every trapping period within
137 the first two years. For each second-order points, counts from each of the respective first-order
138 points were used to calculate gamma-, alpha- and beta-diversity using the equations devised by Jost
139 (2007). This process was repeated grouping counts from first-order points to calculate diversities at
140 respective third- and fourth-order points as well as at block-level. For each point of the respective
141 order, calculations were weighted so that diversity values were not skewed by the ratios of first-order
142 points used.

143 Jost’s equations allow weighting with respect to proportions of taxa also. Using the standard
144 measure where $q = 1$, individuals have equal influence on diversity regardless of family. Gamma- and
145 alpha-diversities where $q = 1$ can be derived from the Shannon index. When $q = 0$, equal weighting
146 is instead given to present families. In this case, gamma-diversity becomes taxa richness and alpha
147 the mean number of groups per sample. When $q = 2$ gamma- and alpha-diversity are equivalent to
148 the reciprocal of Simpson’s index, and give greater weighting to abundant families. Each diversity
149 component was calculated using each values of q for every point in the SAFE design.

150 Using Jost’s equations, total counts of 0 are undefined in gamma- and alpha-diversity, yet
151 important in terms of community structure. For this reason, undefined values were assigned a
152 diversity of the relative minimum possible. This is 0 where $q = 0$ and 1 where $q \neq 0$. Where both
153 gamma- and alpha-diversity equal 0 (only possible when $q = 0$), beta-diversity is undefined, and so
154 these values were removed from analysis.

155 **2.5 Assessing habitat quality**

156 Disturbance was measured as above ground biomass estimates calculated from tree measurements
157 within 25m by 25m plots (Pfeifer et al., 2014) at each of the 193 second-order points. Biomass
158 values were extrapolated to higher-order points by taking means of respective second-order values.
159 Low levels of disturbance were characterised by high above ground biomass, with the greatest values
160 calculated within Maliau Basin and the lowest values from oil palm plantation.

161 **2.6 Modelling beta-diversity against environmental variables**

162 For each value of q , gamma- and alpha-diversity were plotted against above ground biomass and
163 significant linear correlations plotted. A regression was then fitted to the beta-component of diversity
164 with mean distance between grouped same-order points and biomass data. Preliminary models

165 included both linear and quadratic terms for distance and disturbance as well as their possible
166 interactions. Optimum models were selected through stepwise term deletion using Akaike Information
167 Criterion and visualised as a three-dimensional plane, allowing inspection of the summed model
168 terms.

169 In order to assess the relative influence of each variable over beta-diversity, generalised dissimilarity
170 models (GDMs) were fitted using a modified version of the software developed by Ferrier et al.
171 (2007). Pairwise comparisons are made between points within blocks, and so diversity, distance and
172 disturbance values were calculated as before but for each possible pair of same-order points within
173 groups. GDMs were originally developed for use with Bray-Curtis dissimilarity, but can be applied
174 to any fractional measure of dissimilarity (Ferrier et al., 2007). To fulfil this criterion, Jost beta-
175 diversity values were scaled to proportions of the maximum calculated for each q -value so that they
176 ranged from 0 to 1. In this way, the highest calculated beta-value was assumed to be the maximum
177 possible..

178 GDMs are parametrised by keeping the majority of variables constant while varying each in turn
179 to determine the leverage of every variable on the response. At quantiles across the range of variable
180 values, the leverage on the response is calculated as a function of that value. Monotonic curves are
181 fitted between these points and joined by splines. Linear predictors are then calculated for each
182 supplied response data point as the sum of the functions fitted to each variable. Including a greater
183 number of quantiles in the function-fitting process may improve the level of deviance explained by the
184 GDM, but introduces the risk of over-fitting (Ferrier et al., 2007). This is manifested in a distinctive
185 step-like series of function curves.

186 Both variables were \log_{10} -transformed to achieve normal distributions of frequencies suitable
187 for deriving evenly-distributed quantiles. The maximum number of quantiles before evidence of
188 model over-fitting became apparent was fitted to the transformed biomass data. Because of the
189 SAFE Project experimental design, transformed distance measures were still heavily skewed towards
190 lower-order points. To combat this, quantiles were placed at the minimum and maximum value of
191 lowest-order and highest-order distances respectively and at mean distances for each point order in
192 between. A total of four splines were used.

193 Preliminary GDMs were fitted for each value of q before model selection. For each of distance and
194 disturbance, values were sequentially taken from the dataset, shuffled and replaced, before a second
195 GDM was fitted (with the same quantiles). This was repeated 1 000 times, and the proportion of
196 random models explaining a greater level of deviance treated as a p -value. Variables were counted
197 as significant and included in the final model where $p < 0.05$. A function curve was plotted for each
198 significant variable and the linear predictor, or "predicted ecological distance" (Ferrier et al., 2007),
199 fitted against observed beta-values.

200 3 Results

201 After data cleaning, a total of 23 129 beetles were used in this analysis from 1 440 individual traps.
202 55 families were recorded and, as might be expected, total counts were unevenly distributed with a
203 median of just 18. Most abundant families caught were Staphylinidae ($N = 13\,721$), Curculionidae
204 ($N = 4\,048$) and Mycetophagidae ($N = 885$).

205 3.1 Trends in gamma- and alpha-diversity

206 Relatively little correlation was observed in gamma- and alpha-diversity. Mean distance was $53.0m$
207 (S.D. $0.472m$) in second-order points, $145m$ (S.D. $3.65m$) in third-order points, $447m$ (S.D. $11.5m$)
208 in fourth-order points and $1774m$ (S.D. $13.7m$) in fifth-order points. Gamma-diversity where $q = 0$
209 increased for third-order ($t = 2.20$, 195 d.f., $p < 0.05$) and fourth-order ($t = 2.43$, 79 d.f., $p < 0.05$)
210 points only. It is likely that no correlation was found for fifth-order points for insufficient statistical
211 power (8 d.f.). A linear regression confirmed this, fitting gamma-diversity as a function of distance
212 suggested an increase in gamma with distance ($t = 21.6$, 757 d.f., $p < 0.001$).

213 Alpha-diversity where $q = 0$ correlated positively at the second-order level ($t = 2.78$, 473 d.f.,
214 $p < 0.01$) but no higher. No correlation was observed where $q = 1$ or $q = 2$.

215 **3.2 Correlations in beta-diversity with distance and disturbance**

216 Regression models of beta-diversity suggested correlations with both distance, disturbance and their
217 interactions. The selected model fitted for each of $q = 0$ (fig. 2a, $F = 203$, 7 d.f., $p < 0.001$), $q = 1$
218 (fig. 2b, $F = 32.3$, 6 d.f., $p < 0.001$) and $q = 2$ (fig. 2c, $F = 7.32$, 6 d.f., $p < 0.001$) were highly
219 significant. In all cases, beta-diversity is lowest at the minimum distance value. Highest values of
220 beta are always observed at maximum above ground biomass, but ranges of beta-values decrease
221 with increased q . Whereas beta-diversity always increases with distance where $q = 1$ and $q = 2$, beta
222 where $q = 0$ peaks between approximately 1 200m and 1 400m depending on distance.

223 Estimated coefficients of distance were positive ($p < 0.001$) for each value of q , suggesting that
224 each beta-diversity measure increases with distance. However, negative correlations ($p < 0.001$) with
225 the quadratic function of distance were retained only where $q = 0$ and $q = 1$, indicating that increases
226 in beta associated with distances plateau for these values. The relationship of beta with disturbance
227 also varies with q . While all linear and quadratic terms of above ground biomass were retained for
228 presence of interaction effects, only the linear term where $q = 1$ was significant ($p < 0.01$). Each of
229 the linear terms are estimated with a negative coefficient. This is noticeable at high distances with
230 heavy disturbance, where a decrease in biomass can lead to a slight increase in beta-diversity for all
231 values of q . No such correlation exists where biomass is high. These findings indicate that the effects
232 of disturbance alone are overpowered by interaction terms with disturbance where disturbance is low.

233 **3.3 Relative influences of distance and disturbance in beta-diversity**

234 Linear predictors from GDMs correlated well with scaled beta-values for each value of q (fig. 3). The
235 amount of deviance explained in the difference between null hypothesis and model levels were 37.1%,
236 39.6% and 55.0% for $q = 0$, 1 and 2 respectively. Both distance and above ground biomass (modelled
237 with six splines) were confirmed to be significant in the prediction of beta-diversity ($p < 0.05$) for
238 $q = 1$ (fig. 3b) and $q = 2$ (fig. 3c), which were based on 1 980 pairwise comparisons. Distance alone
239 was a significant predictor of beta-diversity where $q = 0$ (fig. 3a), based on 1 888 comparisons.

240 Where $q = 0$, the function of distance reached a maximum of 0.831 (3 s.f.). Maximum functions
241 of transformed distance were lower at other values of q , at 0.229 when $q = 1$ and 0.176 (3 s.f.) when
242 $q = 2$. Function of transformed biomass reached 0.540 when $q = 1$ and 0.538 (3 s.f.) when $q = 2$.
243 These figures suggest that when proportions of family counts are irrelevant (ie, when $q = 0$), distance
244 is a far stronger predictor of beta-diversity than disturbance. Where proportions and their weighting
245 are included, disturbance becomes the more significant predictor. In both cases, the leverage of
246 transformed distance appears to increase relatively linearly with its value, which would indicate a
247 gradual decline in gradient for non-transformed distance. Leverage of above ground biomass plateaus
248 where included, indicating that values of biomass above a threshold have no further impact on beta-
249 diversity.

250 **4 Discussion**

251 The results indicate that the diversity of Borneo's tropical forests is influenced strongly by disturbance.
252 The underlying ecological processes associated with diversity must be considered in order to draw
253 conservation implications from the observed trends.

254 **4.1 Relating to ecological response to habitat quality**

255 Explaining the correlations in diversity requires the consideration of habitat structure in terms
256 of complexity. Both temporal heterogeneity (Descamps-Julien and Gonzalez, 2005) and habitat

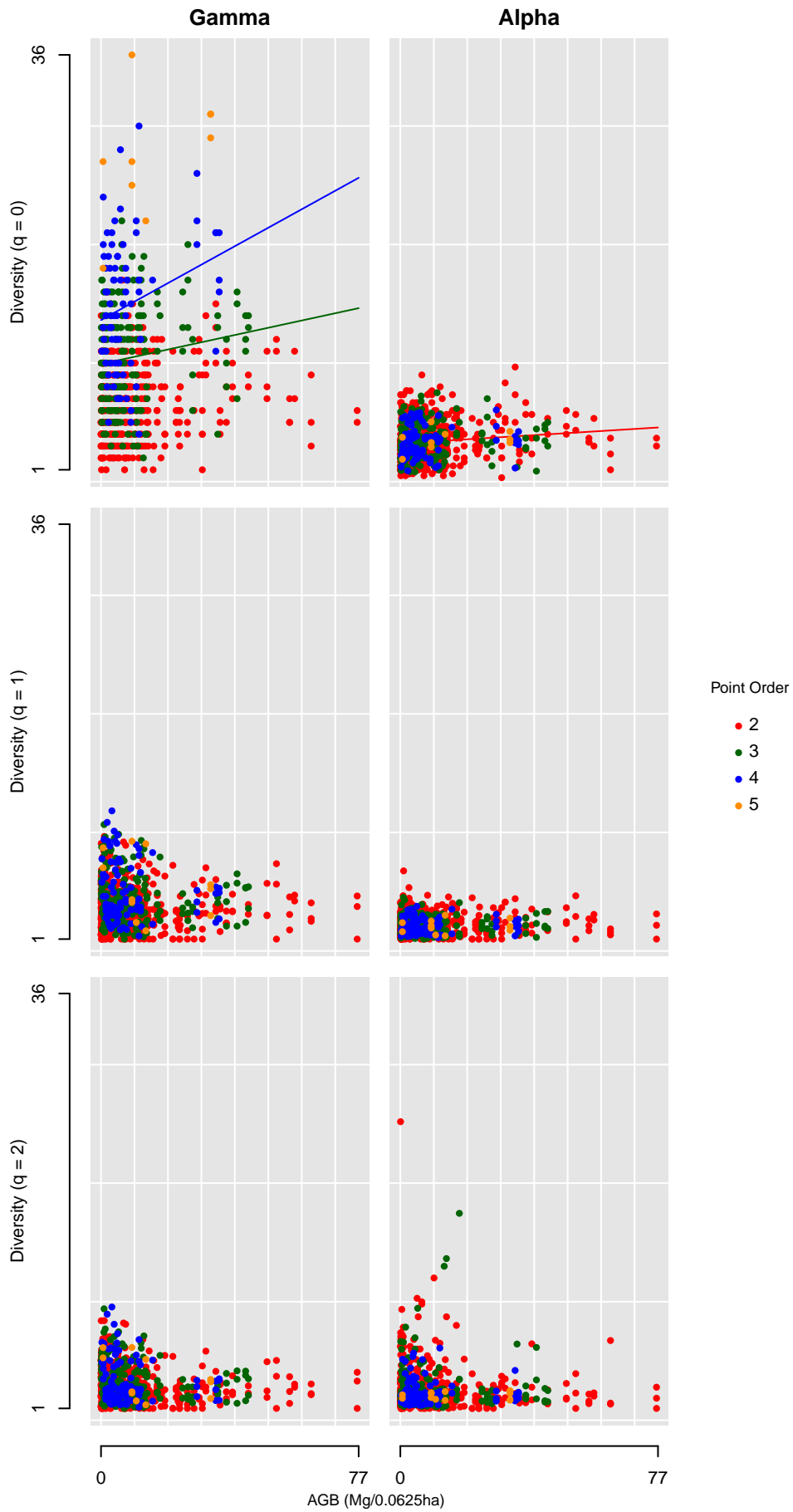


Figure 1: Scatter plots of gamma- and alpha-diversity for each value of q tested at each point with sufficient data for analysis.

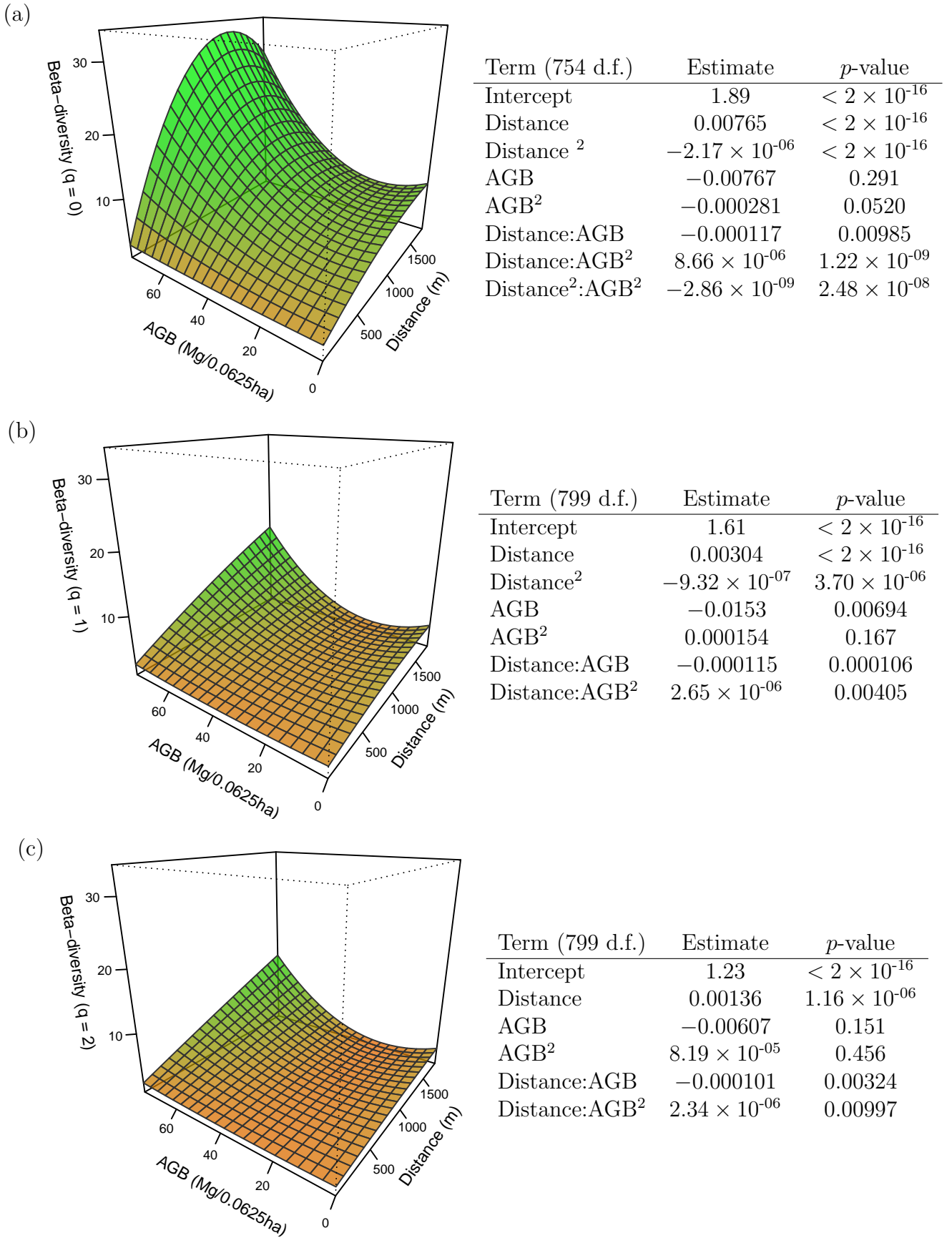


Figure 2: Regression surfaces showing relation between beta-diversity, distance and disturbance when (a) $q = 0$, (b) $q = 1$ and (c) $q = 2$ with accompanying coefficient statistics (3 s.f.). Colons represent interaction effects.

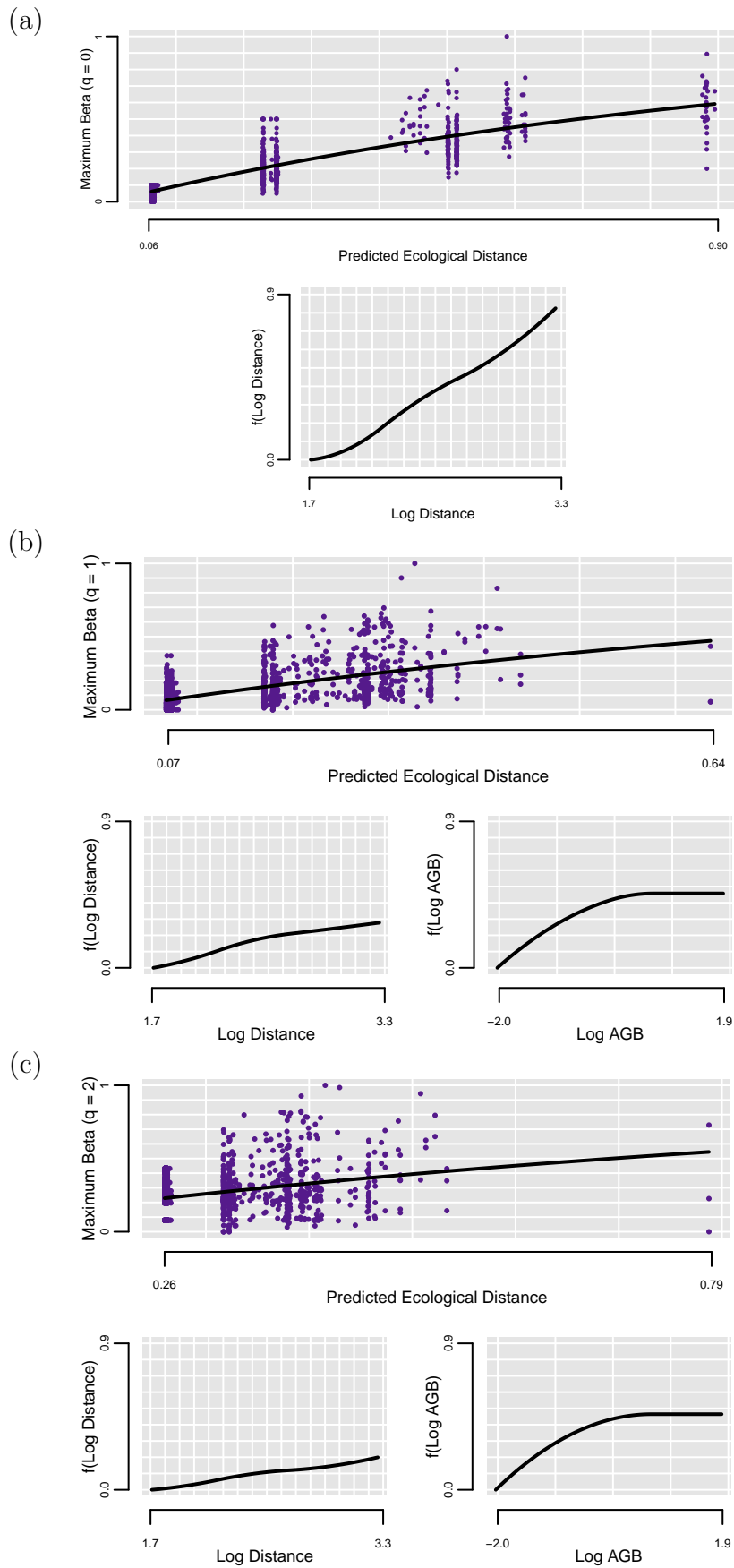


Figure 3: Summaries of generalised dissimilarity models fitted where (a) $q = 0$, (b) $q = 1$ and (c) $q = 2$. For each, first row shows correlation between scaled beta-values and the calculated linear predictor, while second row shows leverage functions of each variable tested.

257 heterogeneity (Vanbergen et al., 2007) have been proven to facilitate high diversity. Temporal
258 heterogeneity can be greater in oil palm plantation than natural tropical forest (Luskin and Potts,
259 2011), where the open canopy results in high daytime ground temperatures and low humidity.
260 However, habitat heterogeneity in the form of vegetation is obviously reduced in the replacement
261 of natural forest with monoculture (Nakagawa et al., 2013). Because the results suggest declines
262 in diversity with oil palm expansion, it could be concluded that in this particular system, habitat
263 heterogeneity is a stronger influence of community composition than temporal heterogeneity. It is
264 possible that temporal heterogeneity in plantation is so extreme that the majority of forest-adapted
265 invertebrates are physiologically excluded through possible desiccation.

266 It would be expected that, by probability as well as through competition-driven processes (Connell,
267 1971; Janzen, 1970), above ground biomass correlates with plant diversity as well as the associated
268 variation in other environmental factors. If this assumption is made, then above ground biomass
269 represents a gradient in habitat heterogeneity which can explain trends in diversity. Community
270 assembly theory suggests that reduced habitat heterogeneity increases habitat filtering (Poff, 1997)
271 and taxa not sufficiently adapted to the preserved habitat type will be competitively excluded.

272 4.2 Explaining Jost's beta-diversity with varying taxa-weighting

273 Using richness-based diversity indices ($q = 0$), gamma-diversity behaved as might be expected,
274 increasing with both distance and above ground biomass. The relationship with distance is a simple
275 function of the species-area curve (Preston, 1962). As the sample area is increased in a heterogeneous
276 landscape, a greater number of different microhabitat types are covered and as a result the specialist
277 taxa that are adapted to those various microhabitats are detected. This theory is supported by
278 the positive linear correlation of distance with beta-diversity. With increased distance between two
279 points, habitat structure is more likely to differ significantly, and as a result the respective taxa pools
280 could be expected to contain dissimilar groups.

281 Beta-diversity where $q = 0$ does, however, differ in its response to distance in that it cannot
282 reach a plateau stage as gamma might. At a certain range the majority of microhabitat types in
283 the matrix would have already been sampled, and at this point fewer new types will be sampled.
284 Following this logic, encounter of new taxa becomes rarer, and beta-diversity will decrease. This
285 process was described by the interaction terms derived from regression modelling. Although the
286 influence of above ground biomass was determined to be insignificant via GDM, it has a notable
287 effect on beta-diversity through these interactions. The magnitude of the peak in beta-diversity as
288 well as the distance at which it occurs is governed by disturbance. Where above ground biomass is
289 at its highest, the peak value of beta is over four times greater than at it is lowest, and occurs at
290 slightly shorter distances.

291 Using diversity indices weighted for individuals instead of whole groups, the species-area relationship
292 cannot fully explain trends in diversity. While sampling of new taxa still leads to an increase in these
293 beta-measures, the proportions in which which groups are represented is of far higher significance
294 to the value calculated. It is local environmental heterogeneity which accounts for the proportions
295 of various taxa. If sample points are positioned within a relatively heterogeneous environment, they
296 are not only likely to sample a greater number of groups (as confirmed by alpha-diversity of second-
297 order points where $q = 0$), but also a more even representation of various groups. In environments
298 dominated by a particular habitat type, the groups best adapted to that corresponding niche will
299 contribute a far greater proportion of occurrences than groups better adapted elsewhere, which would
300 reduced the value of beta.

301 This explains trends in beta-diversity where $q = 1$, but fails to account for the correlation
302 of environmental heterogeneity with diversity measures that are weighted towards common taxa.
303 Sample points are often dominated by a single group, whether this is because of some environmental
304 condition or an artifact of life history (such as mass eclosion in insects within a small area). High
305 beta-diversity where $q = 2$ results when points may be monopolised by a small number of taxa, but
306 compared points are not dominated by the same taxa. In this system, beetle family counts from

307 points in oil palm plantation are frequently dominated by weevils (subfamily: Scolytinae) and sap
308 beetles (family: Nitidulidae). This does not infer high beta-diversity as, unlike in natural forest, the
309 most prolific groups are often the same.

310 The small increase in beta at high distance with high disturbance exists for all values of q , and
311 can therefore not be explained in terms of weighting and proportions. It can instead be interpreted
312 by considering the specialisation of taxa. In highly heterogeneous habitat, such as natural forest,
313 specialist taxa that are better adapted to present microhabitats may outcompete generalists that
314 are lesser adapted to those particular types (Manor and Saltz, 2008). Where these habitats are
315 removed, either purposefully (for example through selective logging) or otherwise, the corresponding
316 specialists are themselves likely to become replaced by generalist taxa (Gillespie et al., 2012; Hinsley
317 et al., 2009). Research on vertebrates has previously concluded that the generalist taxa associated
318 strongly with Borneo oil palm are of far lesser conservation concern than the taxa adapted to natural
319 forest (Faruk et al., 2013). In this study, it is possible that the minimum value of beta at high
320 distances represents the transition from a specialist-rich community to a generalist-rich one, and
321 that the increase in beta-diversity is a results of competitive release of generalists.

322 4.3 Implications to other taxa and studies

323 All of the applied diversity measures suggest a significant decline in diversity of beetle families
324 in the conversion of tropical lowland forest, however these conclusions have broader implications.
325 Because of the functional diversity of the order Coleoptera, it is justifiable to relate these trends to
326 entire ecosystem diversity. While it is obviously impossible to extrapolate estimates of particular
327 values to different taxa, general ecological patterns remain valid. High habitat heterogeneity infers
328 increasing gamma- and beta-diversity in richness-based indices, and the conversion of tropical forest
329 to oil palm plantation decreases these values. Using proportion-based indices, this form of land-
330 use modification does not impact gamma- or alpha-diversity, but does reduce beta-diversity where
331 distance is considered.

332 These findings can be related to an increase in dispersion with disturbance, where the recurring
333 likely-generalist taxa present in oil palm plantation are not limited by spatial variation in microhabitat.
334 Conversely, the specialist taxa of natural forest are confined to their respective microhabitats by
335 various environmental barriers and therefore have relatively little dispersive ability. For the present
336 taxa at the respective stage of disturbance, barriers to dispersal are removed with logging and eventual
337 clearing of natural forest.

338 Including distance in beta-diversity analysis adds great value in relating conservation problems
339 to ecosystem process. With further investigation, it could also suggest suitable sizes for protected
340 areas by identifying the spatial scales at which these processes operate. This is especially important
341 considering the failure of current fragment-orientated attempts at protecting Borneo's biodiversity
342 from oil palm expansion (Edwards et al., 2010). This study also exposes the risk of missing important
343 correlations in diversity when examining only a subset of its components (most often alpha-diversity).

344 4.4 Limitations in the methodology

345 The most obvious limitations of this study surround the study taxa. While beetles cover at least the
346 majority of available broad niche categories (Chung et al., 2000), their ecology cannot be considered
347 equal to that of all other taxa. This is especially true for the large mammals of Borneo's tropical
348 forests, which are of highest conservation concern. It is logistically impossible to sample and identify
349 sparsely-related taxa, but beetles are one of the most suitable single groups for such an analysis in
350 terms of both statistical power and functional diversity.

351 Other limitations were artefacts of the SAFE Project experimental design. While the point-order
352 system allows distance comparisons that would be otherwise impossible, the difference in number of
353 points of each order leads to unequal count variance and therefore statistical power across orders.
354 This can be countered through maximum experimental replication (in this study, including as many

trapping periods as possible). Although this approach appeared to be largely effective in drawing conclusions, there remained instances where data (number of diversity calculations) was insufficient at highest order points.

As with all models, the subject matter has been simplified. Here, deforestation in Borneo is treated as a continuous, direction-less process without ecotones or habitat boundaries. It is obviously unrealistic to ignore the purposeful expansion of plantations into forest, as well as the fragmentation that commonly occurs before clearing. It is also important to consider interactions between habitat quality and biotic impacts, such as invasive ant species (Fayle et al., 2010; Pfeiffer et al., 2008), on diversity. Evaluating the relationships between these factors and beta-diversity is therefore a much-needed topic of future work.

5 Conclusions

Conversion of tropical lowland forest to oil palm plantation in Malaysian Borneo affects the spatial ecology of the landscape, resulting in reduced overall biodiversity. Relating changes in each component of diversity to land-use modification is essential in assessing the full impact of deforestation on community composition. Identifying the spatial scales at which beta-diversity varies could potentially provide insight into optimum fragment sizes suitable for the conservation of biodiversity in Borneo; an important consideration when just 8% and 3% of the land areas of the two Malaysian states on the island are currently protected (Bryan et al., 2013). Diversity studies cannot continue to rely solely on alpha-diversity if the true extent of biodiversity loss in Borneo is to be realised.

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