Imperial College London

Relating beta-diversity to distance and disturbance in Borneo's disturbed tropical forests

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September 2014

Declaration

Data used

Beetle specimens used in this thesis had been trapped and sorted to order-level by SAFE Project research assistants. With the exception of the family Staphylinidae (counted separately by research assistants because of their distinctive appearance), counts of each family were recorded by myself. I was present for a period of insect-catching in early 2014, but for logistical reasons this data could not be included. Habitat quality data was provided by Marion Pfeifer of SAFE Project, and referenced fully in the text. Coordinates for each sample point in the SAFE Project were also provided.

Data processing

As well as counting beetle families, I checked the order-level sorting for errors, particularly for mixing of true bugs (order: Hemiptera) with beetles and also misclassification of beetles with unusual morphology. A large number of errors were identified and corrected. Many Staphylinid counts were also corrected by myself from previous incomplete data entry.

Notes regarding unavoidable errors in field work were supplied by SAFE Project and used by myself to remove data from malfunctioned insect traps. These notes were also used to identify points that were sampled, but from which data or insect samples were missing.

Analysis tools used

The majority of statistical code was written by myself in R script executed from a master script including functions for cleaning data, collating data frames, manipulating habitat data, relating data to sample points in two-dimensional space, calculating diversity values, autonomous model building and selection and data plotting. The only R code which was not written by myself or included as a base package with R was Imap by John Wallace, which was downloaded through CRAN and used for calculating distances given latitude and longitude values, and the GDM package developed by Ferrier et al., downloaded from https://sites.google.com/site/gdmsoftware/. Ferrier's package for generalised dissimilarity modelling includes an R script defining functions which call a Windows dynamic link library (DLL). The DLL was used as-is in the fitting of models to inputs derived by myself, however R functions were rewritten to customise output plots and also to correct for errors which become apparent when non-default parameters are supplied. Use of this software was referenced fully in the text.

Input from supervisor

My supervisor, Dr. Robert Ewers, was extremely helpful in introducing me to Jost's measures of diversity and also suggesting modelling techniques that might expand on the regression models developed, as well as facilitating all field work and data collection at SAFE Project. A full acknowledgement is included in the text.

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September 5, 2014

Highlights

- Borneo's biodiversity is increasingly threatened by logging and palm oil expansion.

- Declines in diversity can be attributed to reduced habitat heterogeneity.

- Where beta-diversity is based on taxa richness, distance is its strongest predictor.

- Considering taxa proportions, disturbance becomes the strongest predictor of beta.

- Beta-diversity provides further insight into community composition than alpha alone.

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Abstract

The tropical lowland forests of Borneo are increasingly threatened by logging and conversion to palm oil plantation. Previous studies have demonstrated declines in alpha-diversity associated with this land-use modification, but trends in other components of diversity have been largely neglected. I applied Jost's "true" diversity measures with a functionally-diverse group (beetles, order: Coleoptera) to estimate ecosystem-level changes in gamma-, alpha- and beta-diversity associated with disturbance. Calculating diversity based on taxa richness, gamma- and beta-diversity decreased with disturbance. When proportions of taxa counts were considered, only beta-diversity decreased. In all cases beta-diversity is influenced by interactions between distance and disturbance, and provides a more descriptive insight into changing community structure than either other component. Generalised dissimilarity models revealed that where beta is based on richness, distance is by far its strongest predictor, whereas disturbance is stronger when proportions are included. Declines in beta-diversity likely result from reduced habitat heterogeneity and a switch from niche differentiation to habitat filtering. Studies in this field cannot continue to rely solely on alpha-diversity when beta can be the only component to respond to disturbance. Taxa proportions must be included in future diversity quantification to reveal the full impact of habitat quality on community composition. There is potential for beta-diversity to be used in determining suitable spatial scales for the efficient conservation of biodiversity in new protected areas.

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). Borneo, the third-largest island in the world, has been particularly effected since the start of industrial-scale forest exploitation in the earlier 1970's. Between 1973 and 2010, there was a 30.2% decline in forest area across Borneo, and a 39.5% decline within the Malaysian state of Sabah (Gaveau et al., 2014); the area most extensively modified. Just 22% of the land area of Borneo 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 2010 approximately 10% of Borneo had been converted to oil palm and timber plantation (Gaveau et al., 2014). The oil palm (*Elaeis guieensis*) 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 the manufacture of 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 fundamental to the development of Malaysia, but such extensive land-use modification has inevitable effect on ecosystems. 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 demonstrated 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

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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 within 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, such as 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 are relevant to 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 author's 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 novel insights into the effects of this form of disturbance on community

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104 structure.

105 Past studies have predominantly compared diversity within discrete habitat
106 types; usually including forest at various stages of degradation and oil palm
107 plantation (Faruk et al., 2013; Fayle et al., 2010; Gillespie et al., 2012). This
108 broad grouping is sufficient in highlighting the need to conserve natural habitat
109 types but is unhelpful in linking habitat quality to complex ecological processes
110 that will not respond in a categorical fashion. Using a scale of disturbance based
111 on continuous vegetation measurements allows identification of the ecological
112 transitions accompanying land-use modification, and also promotes direct
113 comparison between studies.

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

121 ## 2. Methods

122 *2.1. Description of the experimental design*

123 The Stability of Altered Forest Ecosystems Project (Ewers et al., 2011) in Sabah
124 was an ideal location for this investigation. The project utilises a unique
125 experimental design to study the effects of land-use modification on ecological
126 processes at different spatial scales (Marsh and Ewers, 2013).

127 An experimental area covers $7\,200ha$ of forest that has been previously
128 subjected to either one or two rotations of selective logging. Within this area,
129 clearing of forest for oil palm began in 2012. Through agreement with the Sabah
130 Foundation, a Malaysian Government organisation promoting education and
131 development, $800ha$ of this forest will remain as fragments shaped according to
132 the SAFE Project. Six blocks of sample points exist here, each of which will

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₁₃₃ eventually sample fragments of $1ha$, $10ha$ and $100ha$ in size as well as

₁₃₄ surrounding matrix.

₁₃₅   Bordering the experimental area are areas of twice-logged forest and a

₁₃₆ protected area that has not been logged (with exception to its edges). A linear

₁₃₇ transect extends into each from the border with the eventual purpose of

₁₃₈ examining edge effects. Three control blocks also exist, sampling continuous

₁₃₉ expanses of habitat. One is situated in plantation, another in twice-logged forest

₁₄₀ and the third within the Maliau Basin Conservation Area. Approximately

₁₄₁ one-third of the block inside the protected area has been lightly logged while the

₁₄₂ remainder consists of pristine forest.

₁₄₃   All blocks are based on fractal sampling designs, allowing study of ecological

₁₄₄ processes at various distances. Each design consists of four orders of points,

₁₄₅ with lower-order points clustered in respective formation around higher-order

₁₄₆ points (Marsh and Ewers, 2013). In this report a hypothetical fifth-order point is

₁₄₇ also used, which refers to the entire block.

₁₄₈ *2.2.   Justification for the study group*

₁₄₉ Insects are ideal subjects for studying spatial ecology patterns because their

₁₅₀ high abundance grants sufficient statistical power and also a range of

₁₅₁ economical standardised methods are available for sampling them. Beetles

₁₅₂ (order: Coleoptera) are especially suitable for their inherent diversity with a

₁₅₃ predicted $400\,000$ described species (Hammond, 1992). Their rapid evolution is

₁₅₄ catalysed by short generations and large numbers of offspring. The continuing

₁₅₅ radiation of beetles into countless niche spaces, facilitated through all manner of

₁₅₆ adaptations, has led to an order-level functional diversity suitable for most

₁₅₇ ecological investigations. Their proven sensitivity to environmental gradients

₁₅₈ (Ewers and Didham, 2008; Heliola et al., 2001) renders them especially useful in

₁₅₉ quantifying impacts of habitat modification.

₁₆₀   As such, beetles have been used in the measurement of diversity in various

₁₆₁ study systems (Fattorini, 2006; Garcia-Lopez et al., 2012; Weibull et al., 2003).

₁₆₂ Much of this work focuses on a single group within the order, and thus uses

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targeted trapping methods. This is suitable for assessing the effects of change in a subset of environmental variables. However, any correlations detected are unlikely to be applicable to the ecosystem as a whole. In order to successfully estimate diversity within entire systems, it is necessary to sample taxa of multiple disparate niches. Beetle families can be confined to broad functional clades in terms of feeding habits or preferred microhabitat, for example leaf beetles (family: Chrysomelidae) and sap beetles (family: Nitidulidae). In Sabah a high number of families are represented (Chung et al., 2000) and this taxonomic level is taken to represent a representative subset of total functional diversity. Diversity of beetle families is therefore used as a proxy for diversity of available microhabitat types and all the taxa that would hypothetically persist in those microhabitats.

2.3. Field methodology

Since early 2011, biannual (with the exception of 2012) invertebrate trapping has been carried out across the SAFE Project study area. Traps set at each of the 579 first-order sample points are assembled in the field and based on a design combining pitfall, flight-interception and malaise traps. Flying insects are directed either upwards into a "top" trap or downwards into a "bottom" trap, to target invertebrates of various morphology and behaviour. Specimens are collected in plastic bottles filled partially with 70%-ethanol solution. The pitfall-style bottom trap is dug flush into the ground, where the hole is preserved between trapping periods to limit bias associated with soil and leaf litter disturbance (Digweed et al., 1995). Each trap is left for three days before the samples are collected and the traps removed. While it is logistically impossible to set all traps on the same day, they are set within a period of one month to control for seasonality. On collection, malfunctioned traps are noted for exclusion in later analysis.

2.4. Calculating diversity metrics

Counts of beetle families were recorded from each first-order point for every trapping period within the first two years. For each second-order point, counts

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from each of its respective first-order points were used to calculate gamma-,
alpha- and beta-diversity using the equations devised by Jost (2007). This
process was repeated by grouping counts from first-order points to calculate
diversities at respective third- and fourth-order points as well as at block-level.
For points of the respective order, valid comparisons were achieved by weighting
calculations to avoid potential skewing from unequal ratios of usable first-order
points.

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

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

2.5. Assessing habitat quality

Disturbance was quantified as above ground biomass and estimated from tree
measurements within $25m$ by $25m$, or $0.0625ha$, plots (Pfeifer et al., 2014) at
each of the 193 second-order points. Biomass values were extrapolated to
higher-order points by taking means of relevant second-order values. High levels
of disturbance were characterised by low above ground biomass, with the
greatest values calculated within Maliau Basin and the lowest values from oil

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palm plantation.

2.6. Modelling beta-diversity against environmental variables

For each value of q, gamma- and alpha-diversity were plotted against above ground biomass and significant linear correlations plotted. A regression was then fitted to the beta-component of diversity with mean distance between grouped same-order points and the biomass data. Preliminary models included both linear and quadratic terms for distance and disturbance as well as all their possible interactions. Optimum models were selected through stepwise term deletion using Akaike Information Criterion and visualised as a three-dimensional plane, allowing inspection of the summed model terms.

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

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

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Both variables were log$_{10}$-transformed to achieve normal distributions of

frequencies suitable for deriving evenly-distributed quantiles. The maximum

number of quantiles before evidence of model over-fitting became apparent was

fitted to the transformed biomass data at regular intervals in its distribution.

Because of the unequal numbers of points from each order in the SAFE Project

experimental design, quantiles could not be placed regularly in the distance

distribution. Quantiles were instead placed at the minimum and maximum value

of lowest-order and highest-order distances respectively, and at mean distances

for each point order in between; a total of four splines.

   Preliminary GDMs were fitted for each value of q before model selection. For

each of distance and disturbance, values were sequentially taken from the

dataset, shuffled and replaced, before a second GDM was fitted (with the same

quantiles). This was repeated $1\,000$ times, and the proportion of random models

explaining a greater level of deviance was treated as a p-value. Variables were

counted as significant and included in the final model where $p < 0.05$. A function

curve was plotted for each significant variable and the linear predictor, or

"predicted ecological distance" (Ferrier et al., 2007), fitted against observed

beta-values.

3.   Results

The first-order points were sampled on average 3 times each. After exclusion of

erroneous trap data, a total of $23\,129$ beetles were used from $1\,440$ combined

top-bottom samples. 55 families were recorded and, as might be expected, total

counts were unevenly distributed with a median of just 18. Most abundant

families caught were Staphylinidae ($N = 13\,721$), Curculionidae ($N = 4\,048$) and

Mycetophagidae ($N = 885$).

3.1.   Trends in gamma- and alpha-diversity

Relatively little correlation was observed in gamma- and alpha-diversity (Fig. 1).

Mean distance was $53.0m$ (S.D. $0.472m$) in second-order points, $145m$ (S.D.

$3.65m$) in third-order points, $447m$ (S.D. $11.5m$) in fourth-order points and $1774m$

281 (S.D. $13.7m$) in fifth-order points. Gamma-diversity where $q = 0$ increased for

282 third-order ($t = 2.20$, 195 d.f., $p < 0.05$) and fourth-order ($t = 2.43$, 79 d.f.,

283 $p < 0.05$) points only. It is likely that no correlation was found for fifth-order points

284 for insufficient statistical power (8 d.f.). A linear regression confirmed this. Fitting

285 gamma-diversity as a function of distance suggested an increase in gamma with

286 distance ($t = 21.6$, 757 d.f., $p < 0.001$). Alpha-diversity where $q = 0$ correlated

287 positively at the second-order level ($t = 2.78$, 473 d.f., $p < 0.01$) but no higher. No

288 correlation was observed where $q = 1$ or 2.

289 *3.2. Correlations in beta-diversity with distance and disturbance*

290 Regression models of beta-diversity suggested correlations with distance,

291 disturbance and their interactions. The selected model fitted for each of $q = 0$

292 (Fig. 2a, $F = 203$, 7 d.f., $p < 0.001$), $q = 1$ (Fig. 2b, $F = 32.3$, 6 d.f., $p < 0.001$) and

293 $q = 2$ (Fig. 2c, $F = 7.32$, 6 d.f., $p < 0.001$) were highly significant. In all cases,

294 beta-diversity is lowest at the minimum distance value. Highest values of beta

295 are always observed at maximum above ground biomass, but ranges of

296 beta-values decrease with increased q. Whereas beta-diversity always increases

297 with distance where $q = 1$ and $q = 2$, beta where $q = 0$ peaks between around

298 $1\,200m$ and $1\,400m$, depending on distance.

299   Estimated coefficients of distance were positive ($p < 0.001$) for every value of

300 q, suggesting that each beta-diversity measure increases with distance.

301 Negative correlations with the quadratic function of distance were also retained

302 for all values of q, indicating that the increases in beta associated with distances

303 always plateau.

304   Each of the linear above ground biomass terms are retained and estimated

305 with a negative coefficient. This is manifest at high distance and heavy

306 disturbance, where a decrease in biomass can lead to a slight increase in

307 beta-diversity for all values of q. No such correlation exists where biomass is

308 high. These findings indicate that the effects of disturbance alone are

309 overpowered by interaction terms with disturbance except for at high

310 disturbance.

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3.3. Relative influences of distance and disturbance in beta-diversity

312 Linear predictors from GDMs correlated well with scaled beta-values for each

313 value of q (Fig. 3). The amount of deviance explained in the difference between

314 null hypothesis and model levels were 37.1%, 39.6% and 55.1% for $q = 0$, 1 and 2

315 respectively. Both distance and above ground biomass (modelled with six

316 splines) were confirmed to be significant in the prediction of beta-diversity

317 ($p < 0.05$) for $q = 1$ (Fig. 3b) and $q = 2$ (Fig. 3c), which were based on $1\,980$

318 pairwise comparisons. Only distance was a significant predictor of beta-diversity

319 where $q = 0$ (Fig. 3a), based on $1\,888$ comparisons.

320   Where $q = 0$, the function of distance reached a maximum of 0.831 (3 s.f.).

321 Maximum functions of transformed distance were lower at other values of q, at

322 0.278 when $q = 1$ and 0.201 (3 s.f.) when $q = 2$. Function of transformed biomass

323 reached 0.457 when $q = 1$ and 0.465 (3 s.f.) when $q = 2$. These figures suggest

324 that when proportions of family counts are irrelevant (ie, when $q = 0$), distance is

325 a far stronger predictor of beta-diversity than disturbance. Where proportions are

326 included, disturbance becomes the more significant predictor. In both cases, the

327 leverage of transformed distance appears to increase relatively linearly with its

328 value, which would indicate a gradual decline in gradient for non-transformed

329 distance. Where significant, leverage of above ground biomass plateaus

330 indicating that values of biomass above a certain threshold have no further

331 impact on beta-diversity.

4. Discussion

333 The results show that the diversity of Borneo's tropical forests is affected

334 strongly by disturbance, and beta-diversity also by distance. The underlying

335 ecological processes associated with diversity must be considered in order to

336 draw meaningful conservation implications from the observed trends.

4.1. *Relating to ecological response to habitat quality*

Explaining the correlations in diversity requires the consideration of habitat structure in terms of complexity. Both temporal heterogeneity (Descamps-Julien and Gonzalez, 2005) and habitat heterogeneity (Vanbergen et al., 2007) have been proven to facilitate high diversity. Temporal heterogeneity can be greater in oil palm plantation than natural tropical forest (Luskin and Potts, 2011) where the open canopy facilitates high daytime ground temperatures and low humidity. However, habitat heterogeneity in the form of vegetation is unsurprisingly reduced in the replacement of natural forest with monoculture (Nakagawa et al., 2013). Because the results suggest declines in diversity with oil palm expansion, it could be concluded that in this particular system, habitat heterogeneity is a stronger influence of community composition than temporal heterogeneity. It is possible that temporal heterogeneity in oil palm plantation is sufficiently extreme that the majority of forest-adapted invertebrates are physiologically excluded through possible desiccation.

It would be expected that, by probability as well as through competition-driven processes (Connell, 1971; Janzen, 1970), above ground biomass correlates with plant diversity as well as related environmental factors such as leaf litter composition. The selective removal of particular timbers from forest (reducing biomass) also suggests a non-random decrease in plant diversity. If these assumption are made, then above ground biomass represents a gradient in habitat heterogeneity which can explain trends in diversity.

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

Using richness-based diversity indices ($q = 0$), gamma-diversity behaved as might be expected, increasing with both distance (point order) and above ground biomass. The relationship with distance is a simple function of the species-area curve (Preston, 1962). As the sample area is increased in a heterogeneous landscape, a greater number of different microhabitat types are covered and as a result the specialist taxa that are adapted to those various microhabitats are detected. Where above ground biomass is lower and the landscape is less

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heterogeneous, new microhabitat types are encountered less frequently, and gamma-diversity increases at a lesser rate. This theory is supported by the positive linear correlation of distance with beta-diversity. With increased distance between two points, habitat structure is more likely to differ significantly, and as a result the respective taxa pools could be expected to contain dissimilar groups.

Beta-diversity where $q = 0$ does, however, differ to gamma in its response to distance because it can decrease. At a certain range the majority of microhabitat types in the matrix would have been sampled, and at this point fewer new types will be sampled. Following this logic, encounter of new taxa becomes rarer, and beta-diversity may fall. This process was described by the interaction terms derived from regression modelling. Although the influence of above ground biomass was determined to be insignificant via GDM, it has a significant effect on beta-diversity through these interactions. The magnitude of the peak in beta-diversity as well as the distance at which it occurs is determined by disturbance.

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

This explains trends in beta-diversity where $q = 1$, but fails to account for the correlation of environmental heterogeneity with diversity measures that are weighted towards common taxa. Sample points are often dominated by a single group, either because of some environmental condition or an artefact of life

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history (such as mass eclosion in insects within a small area). High beta-diversity where $q = 2$ results when points may be monopolised by a small number of taxa, but compared points are not dominated by the same taxa. In this study system, beetle family counts from points in oil palm plantation are frequently dominated by weevils (subfamily: Scolytinae) and sap beetles (family: Nitidulidae). This does not infer high beta-diversity as, unlike in natural forest, the most prolific groups are often the same.

The small increase in beta at high distance with high disturbance exists for all values of q, and can therefore not be explained in terms of weighting and proportions. It can instead be interpreted by considering the specialisation of taxa. In highly heterogeneous habitat, such as natural forest, specialist taxa that are better adapted to present microhabitat types may outcompete generalists that are lesser adapted to those particular types (Manor and Saltz, 2008). Where these habitats are removed, the corresponding specialists are themselves likely to become replaced by generalist taxa (Gillespie et al., 2012; Hinsley et al., 2009). Research on vertebrates has previously concluded that the generalist taxa associated strongly with Borneo oil palm are of far lesser conservation concern than the taxa adapted to natural forest (Faruk et al., 2013). In this study, it is possible that the minimum value of beta at high distances represents the transition from niche differentiation to habitat filtering processes in line with community assembly theory (Poff, 1997), and that the increase in beta-diversity is a results of competitive release of generalists in a homogeneous habitat.

4.3. Implications to other taxa and studies

All of the applied diversity measures suggest a significant decline in diversity of beetle families in the conversion of tropical lowland forest, however these conclusions present broader implications. Because of the functional diversity of the order Coleoptera, it is justifiable to relate these trends to entire ecosystem diversity. While it is obviously impossible to extrapolate estimates of particular values to different taxa, general ecological patterns are unlikely to differ. High habitat heterogeneity infers increasing gamma- and beta-diversity in

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richness-based indices, and the conversion of forest to oil palm plantation decreases diversity values. Using proportion-based indices, this form of land-use modification does not impact gamma- or alpha-diversity, but does affect beta-diversity where distance is considered. Overall decreases in diversity can be attributed to a transition from niche differentiation to habitat filtering in community assembly theory.

These findings can be related to an increase in dispersion with disturbance, where the recurring habitat-filtered taxa present in oil palm plantation are not limited by spatial variation in microhabitat. Conversely, the specialist taxa of natural forest are confined to their respective microhabitats by environmental barriers and therefore have relatively little dispersive ability. This idea is supported by the calculated regression coefficients for beta-diversity, where there is little interaction between distance and above ground biomass at high disturbance levels.

Including distance in beta-diversity analysis adds great value in relating conservation problems to ecosystem process. With further investigation, it could also suggest suitable sizes for protected areas by identifying the spatial scales at which these processes operate. This is especially important considering the failure of current fragment-orientated attempts at protecting Borneo's biodiversity from oil palm expansion (Edwards et al., 2010).

This study also exposes the risk of missing important correlations in biodiversity with land-use modification when using unsuitable metrics. Future work cannot continue to rely on alpha-diversity alone when beta-diversity can be the sole component of diversity to vary with disturbance. Similarly, proportion-based measures must be employed either instead of or alongside richness-based measures as they better represent the impact of habitat quality on community composition.

4.4. Limitations in the methodology

The most obvious limitations of this study surround the chosen taxonomic group. While beetles cover at least the majority of available broad niche categories

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(Chung et al., 2000), their ecology cannot be considered equal to that of all other taxa. This is especially true for the large mammals of Borneo's tropical forests, which are of highest conservation concern. It is logistically impossible to sample and identify sparsely-related taxa, but beetles are one of the most suitable single groups for such an analysis.

Other limitations were artefacts of the SAFE Project experimental design. While the point-order system allows distance comparisons that would be otherwise impossible, the difference in number of points of each order leads to unequal count variance and therefore statistical power. This can be countered through maximum experimental replication (in this case, using data from as many trapping periods as possible). Although this approach was largely effective in drawing conclusions, there remained one case in which 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 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 alters the spatial ecology of the landscape, resulting in reduced overall biodiversity. The reduction in habitat heterogeneity accompanying this form of disturbance likely affects diversity through a switch from niche differentiation to habitat filtering processes. Relating changes in each component of diversity to land-use modification is essential in assessing the full impact of deforestation on community composition. 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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Identifying the spatial scales at which assembly processes operate through use of beta-diversity could potentially suggest optimum fragment sizes suitable for the conservation of biodiversity in Borneo. This is of highest priority when just 8% and 3% of the land areas of the two Malaysian states on the island are currently protected (Bryan et al., 2013).

Acknowledgements

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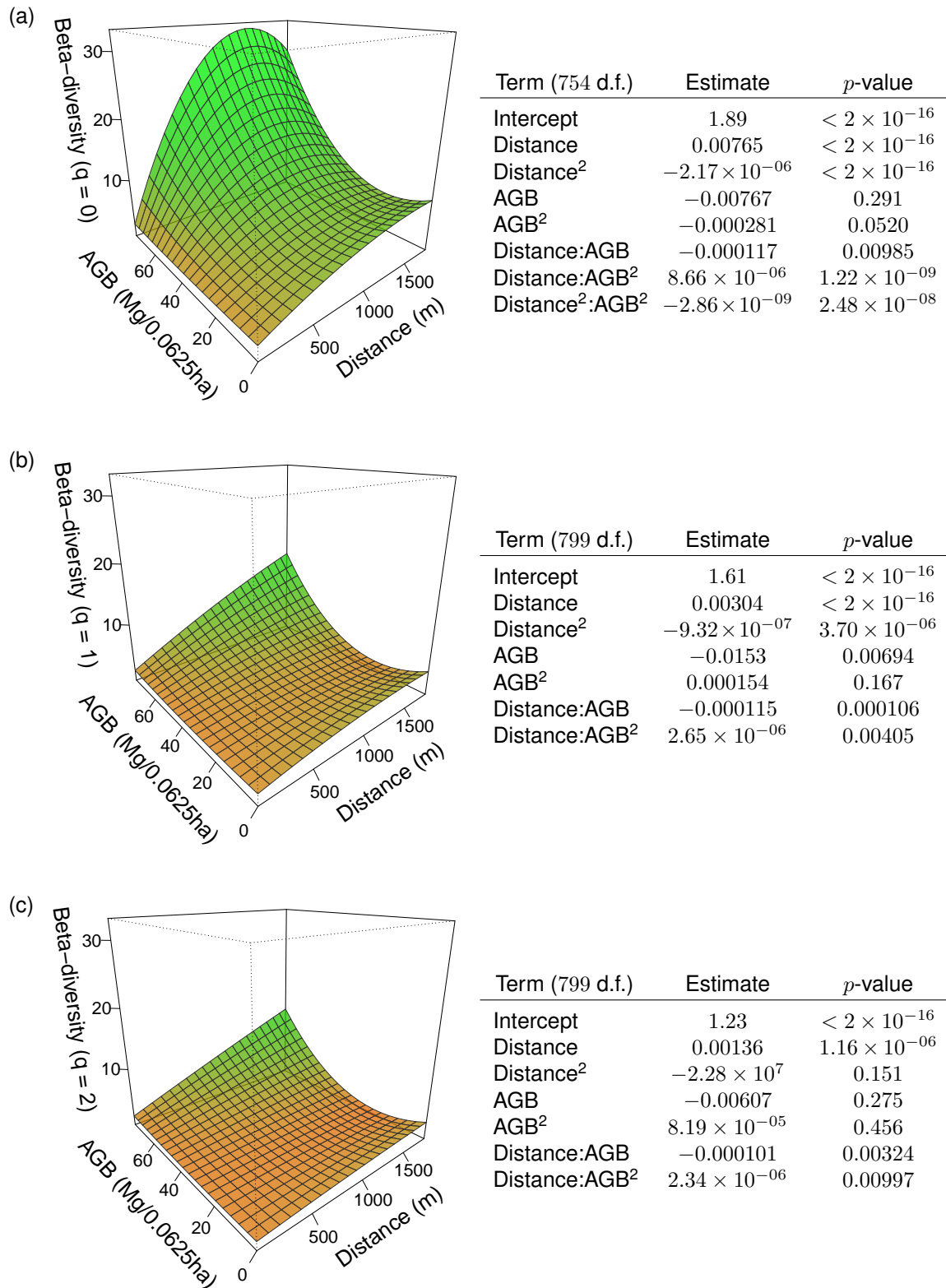595 73(6):1943–1967.

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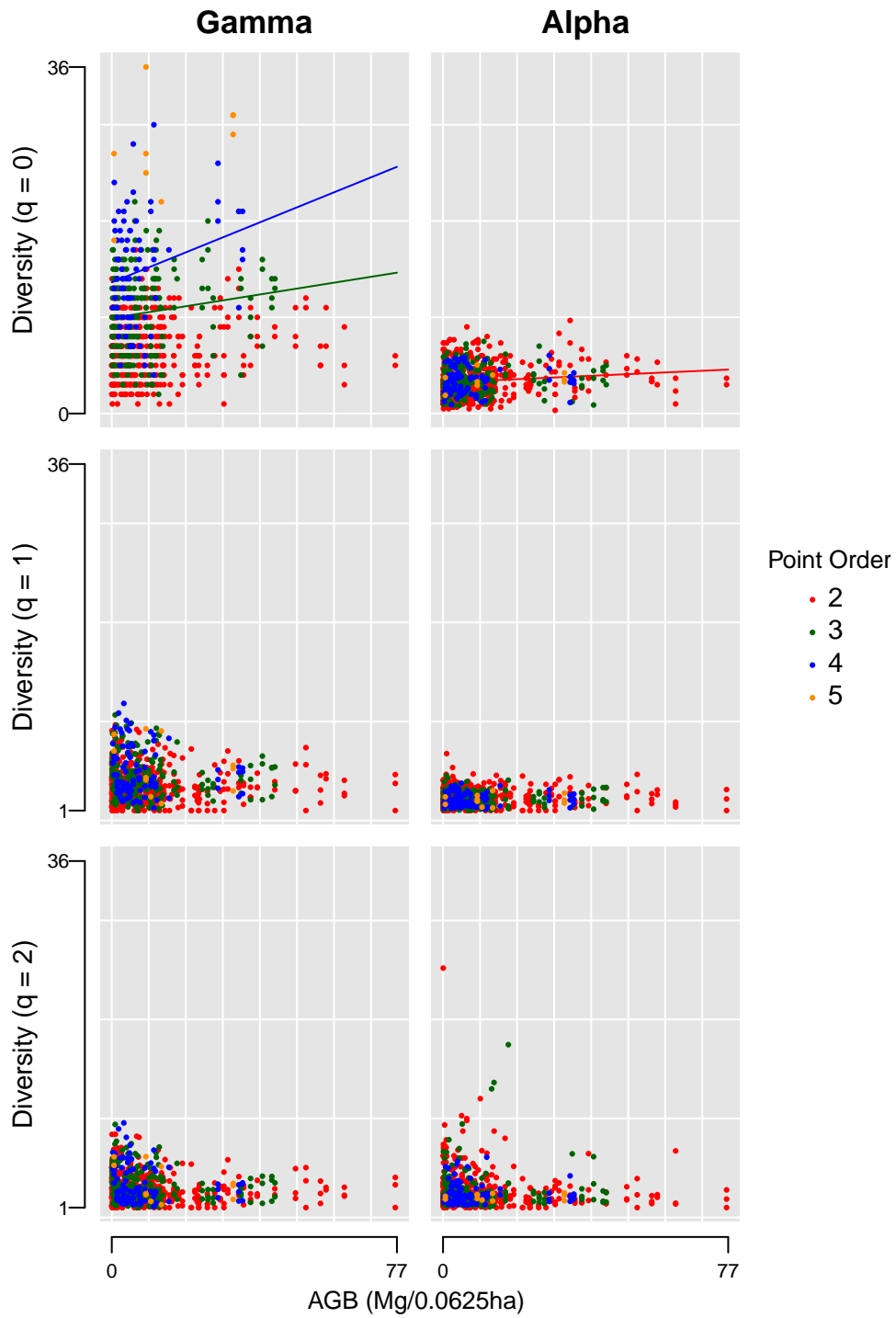
Fig. 1. Scatter plots of gamma- and alpha-diversity for each value of q tested at each point with sufficient data for analysis.

(a)

Term (754 d.f.)	Estimate	p-value
Intercept	1.89	$< 2 \times 10^{-16}$
Distance	0.00765	$< 2 \times 10^{-16}$
Distance^2	-2.17×10^{-06}	$< 2 \times 10^{-16}$
AGB	-0.00767	0.291
AGB^2	-0.000281	0.0520
Distance:AGB	-0.000117	0.00985
Distance:AGB^2	8.66×10^{-06}	1.22×10^{-09}
Distance^2:AGB^2	-2.86×10^{-09}	2.48×10^{-08}

(b)

Term (799 d.f.)	Estimate	p-value
Intercept	1.61	$< 2 \times 10^{-16}$
Distance	0.00304	$< 2 \times 10^{-16}$
Distance^2	-9.32×10^{-07}	3.70×10^{-06}
AGB	-0.0153	0.00694
AGB^2	0.000154	0.167
Distance:AGB	-0.000115	0.000106
Distance:AGB^2	2.65×10^{-06}	0.00405

(c)

Term (799 d.f.)	Estimate	p-value
Intercept	1.23	$< 2 \times 10^{-16}$
Distance	0.00136	1.16×10^{-06}
Distance^2	-2.28×10^{7}	0.151
AGB	-0.00607	0.275
AGB^2	8.19×10^{-05}	0.456
Distance:AGB	-0.000101	0.00324
Distance:AGB^2	2.34×10^{-06}	0.00997

Fig. 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.
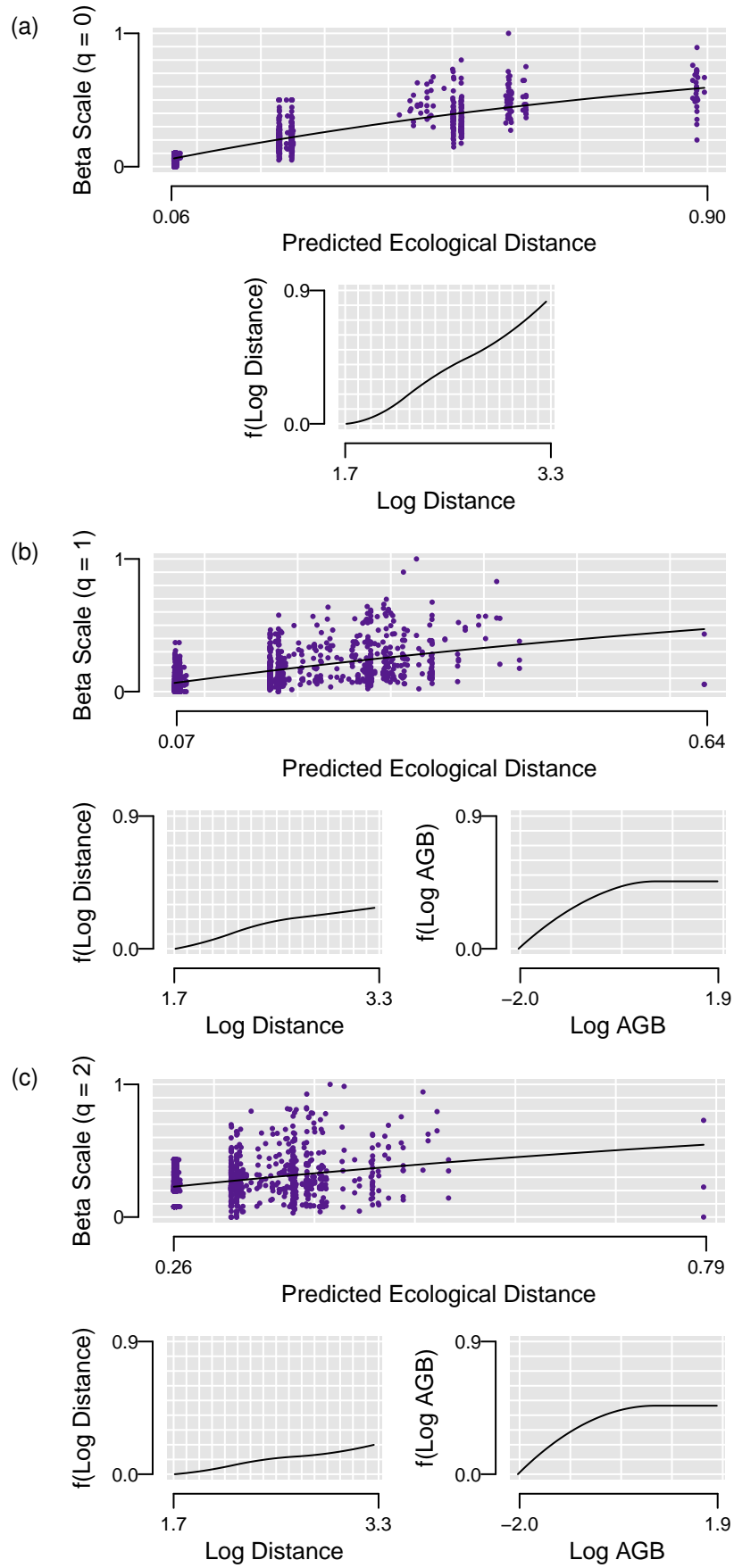
Fig. 3. Summaries of GDMs fitted where (a) $q = 0$, (b) 1 and (c) 2. First row compares scaled beta-values and the calculated linear predictor, while second row shows leverage functions of variables.