

Functional diversity and community assembly patterns in ant (Hymenoptera: Formicidae) communities across a forest disturbance gradient in Sabah, Malaysia

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Abstract

1. A functional trait based approach to studying ecological communities provides a number of advantages over a purely taxonomic method. Functional diversity can be calculated and the processes of community assembly can be investigated. Both these aspects of communities will have an influence on ecosystem functions.
2. Here, patterns of functional diversity and community assembly processes are explored across a tropical forest disturbance gradient in Sabah, Malaysia for a dominant group of terrestrial insects, the ants, in order to characterise and understand the changes that may be occurring due to conversion of forest to agriculture.
3. Three functional diversity metrics (FRic, FEve and FDiv) were calculated based on five functional traits that were chosen to represent resource use for replicate leaf-litter and soil ant communities. Differences in these metrics across habitat types were analysed and community assembly processes revealed by comparison to null distributions.
4. It is found that FEve and FDiv change with habitat type but FRic and alpha species richness do not. Furthermore, a gradient of assembly processes is found across different levels of disturbance: old growth forest appears largely competitively structured whilst oil palm habitats are dominated by a mixture of stochastic and habitat filtering processes.
5. In addition, these changes across habitat type are tied to particular functional trait complexes. Notably, traits states that are linked to hypogaeic predators appear to be underrepresented in oil palm whilst those associated with both large and small omnivores may be missing from secondary forest.
6. The pattern of these results contradicts that already reported for tropical ants. Previous work suggests a linear increase in deterministic processes with disturbance. This study proposes a quadratic relationship: pristine and highly disturbed habitats tend toward determinism whilst habitats of intermediate disturbance appear largely stochastically assembled. This disagreement is likely due to the differences in the ant fauna sampled and the analytical methods used. These results suggest that functional traits are crucial to a complete understanding of changes in community level processes in complex systems such as the rainforest floor.

Introduction

Tropical forests form a major vegetation type on Earth and have a wide significance due to their rich biodiversity and interactions with numerous global cycles (Ghazoul and Sheil 2010). These forests, however, are facing increasing anthropogenic pressure in the form of habitat conversion and fragmentation which has detrimental effects on species and the processes which they mediate (Morris 2010). Such threats are particularly acute in Southeast Asia where they are primarily driven by the conversion of primary rainforest to oil palm plantations (Sodhi et al. 2004, Koh and Wilcove 2008). Such conversion has a largely negative effect on biodiversity, with oil palm habitats supporting far fewer species than primary forests (Fitzherbert et al. 2008, Foster et al. 2011). Understanding how and why communities respond to these changes is crucial if we are to mitigate or reverse the loss of biodiversity and the functions which it provides (Chapin et al. 2000). Here, these questions are addressed by investigating the patterns of functional diversity and community assembly processes across a tropical disturbance gradient for a successful and dominant taxon: the ants (Hymenoptera: Formicidae).

It is becoming increasingly apparent that a trait-based view of ecology can offer a number of advantages over traditional taxonomic approaches (McGill et al. 2006). By viewing a community of organisms as a distribution of measurable trait values rather than as a collection of discrete taxonomic units we are able to increase the ecological generality and predictability of our conclusions in both pure and applied research (Fukami et al. 2005, Cadotte et al. 2011, Simberloff 2004). Additionally, species traits allow us to look in greater detail at the functional attributes of communities and the processes that ultimately organise them. Both of these aspects of ecological communities are important for our understanding of biodiversity change across disturbance gradients yet have been relatively understudied.

In this vein, the study of functional diversity aims to link the species that are present in a community to the types and rates of ecological functions that are occurring by measuring the traits of species (Cadotte et al. 2011, Petchey and Gaston 2006). Functional diversity may be defined as a component of biodiversity which quantifies *“the value and range of those species and organismal traits that influence ecosystem functioning”* (Tilman 2001). This definition makes an explicit link between the measurable traits of an organism and the ecosystem processes which they ultimately mediate. There is increasing theoretical and empirical support for the use of functional diversity as a surrogate of actual ecosystem functioning (Cadotte et al. 2011, Diaz and Cabido 2001, Hooper et al. 2005). Consequently, functional diversity may offer us a greater insight into how ecosystems are changing than traditional species diversity indices.

A positive relationship between measures of functional diversity and rates of ecosystem functioning is expected. A popular reason for this is that high diversities of functional traits result in greater resource use efficiency in heterogeneous environments (Diaz and Cabido 2001). What is less clear, however, is the relationship between functional diversity and species diversity. This relationship can take on a range of forms that profoundly alter the way in which we interpret changes in biodiversity due to anthropogenic impacts (Mayfield et al. 2010). For example species diversity can increase or decrease following land use change but functional diversity may remain the same if no new functional types are added or removed from the community. It is also theoretically possible to have a decrease in functional diversity with an increased species diversity or an increase in functional diversity with a decreased species diversity (Mayfield et al. 2010).

Crucially, these different patterns of covariance between species diversity, functional diversity and ultimately ecosystem functions, are dictated by the rules and processes that assemble communities from the larger pool. Community assembly occurs as a sequence of filters leading from regional to local species pools and has long been of interest to ecologists (Diamond 1975, Weiher and Keddy 2001). These filters restrict which species are able to gain community membership and can broadly be categorised as either habitat filtering or competition. Habitat filtering excludes those species that have a physiology or anatomy that makes them ill adapted to a particular environment. This effect results in the underdispersion of trait values within a community (Weiher and Keddy 2001). On the other hand, competitive exclusion causes an overdispersion of trait values (Weiher and Keddy 2001). In this case, species are only able to coexist if they are different enough from each other to partition resources effectively. Competitive interactions will prevent a species from establishing in a community if its niche is already occupied. Both types of filters may act simultaneously on a community and can also operate on a number of spatial scales. Furthermore, both are likely to be influenced by land use change. For example, logging a forest may alter the importance of different habitat filters as microclimatic conditions change. Additionally, logging and eventually complete land conversion may increase the importance of competitive interactions as species compete for limited resources in a more homogenous environment (Mayfield et al. 2010).

Globally, and certainly within tropical forests, ants are ubiquitous on nearly all continents and play a dominant role in the functioning of ecosystems. Ants can make up to 30% of the total animal biomass in tropical systems (Fittkau and Klinge 1973) and mediate functions as diverse as seed dispersal, soil turnover and nutrient cycling (Hölldobler and Wilson 1990, Folgarait 1998). They may also be described as ecosystem engineers by virtue of the changes in physical structure which they may bring to an environment (Jones et al. 1994). Previous work has shown that ant biodiversity is

negatively affected by the conversion of primary rainforest to agriculture (Fayle et al. 2010, Bruhl and Eltz 2010, Philpott and Armbrrecht 2006). Consequently, changes in the functional diversity and assembly processes of ant communities may be particularly important for the biodiversity patterns of other invertebrate groups and the functioning of the forest system as a whole.

In order to investigate communities along a forest disturbance gradient a range of multivariate functional diversity metrics was chosen to represent the diversity of ant resource use. Diversity in resource use is expected to relate to the nutrient cycling role of ants through different predatory, scavenging and foraging behaviours and habitat preferences (Hölldobler and Wilson 1990). Multivariate measures of functional diversity aim to describe ecological communities as species plotted in T -dimensional space (Rosenfeld 2002, Villéger et al. 2008). T refers to the number of traits that have been quantified or, different multivariate axes that summarise trait information. Recorded trait values may be used as coordinates to position species in this multidimensional functional trait space. Functional diversity can then be interpreted as the distribution of species and their abundances in this trait space.

The orthogonal metrics of FRic, FEve and FDiv described by Villéger et al. (2008) were used to quantify the three primary components of functional diversity: richness, evenness and divergence (Mason et al. 2005). Richness measures the total volume of trait space that a community occupies, evenness quantifies the regularity of abundances distributed throughout the space and divergence encapsulates how abundance is spread throughout the range of traits (Villéger et al. 2008, Mason et al. 2005). All three metrics can also be used to infer what kinds of assembly processes are in operation by assessing if they are under or overdispersed compared to a random null distribution. Values higher than expected can be attributed to the predominance of competition in influencing assembly of communities (Mason et al. 2008) whilst values lower than expected reflect a predominance of habitat filtering (Cornwell et al. 2006, Mouchet et al. 2010).

In this study, the three Villéger et al. (2008) metrics will be used to ask whether functional diversity and the dominant community assembly processes change with disturbance. In addition, changes will be interpreted in terms of shifts in particular functional trait complexes. It is hypothesised that FRic will decline with increasing disturbance in tandem with decreasing species richness. Furthermore, it is expected that assembly processes will become increasingly deterministic with higher levels of disturbance. This is due to previous research on tropical arthropods and ants indicating that random processes may dominate in pristine forest but that highly competitive interactions may arise in simplified, disturbed habitats (Ellwood et al. 2009, Floren et al. 2001) and the *a priori* expectation that a harsher microclimate in disturbed forest will intensify filtering effects.

Methods

Study Site

Sampling took place during April and May 2010 in the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysia as part of a separate study (Luke 2010). SAFE is a large scale, long term project investigating the influence of tropical forest modification on species assemblages and ecosystem processes (Ewers et al. 2011). In this study, samples were collected at 46 points: nine oil palm, 32 secondary forest and eighteen old growth. The SAFE project survey points are arranged in a triangular fractal network distributed across the three habitat types. Four orders of survey points exist with higher orders forming the centre of equilateral triangles. The vertices of these triangles represent the survey points of the fractal order immediately below (Ewers et al. 2011). Samples were taken from 2nd order sites that were distributed as equilateral triangles with sides of 178m. Only two of the three triangle vertices were sampled at random. The sampled points were spread over five blocks of habitat: a single block of oil palm (OP3), two blocks of secondary forest (blocks F and C) and two blocks of old growth forest (OG2 and OG3). The old growth sites are located in the Maliau Basin Conservation Area whilst the secondary forest and oil palm sites are located at Benta Wawasan. Sites in the Maliau Basin are protected under Malaysian law and have never been commercially logged. Sites within block OG3 were lightly logged in the 1990s for the construction of the Maliau Basin Field Centre. However, the ecological structure and species composition of this block has not been profoundly influenced by this disturbance (Ewers et al. 2011). Secondary forest sites have experienced two rounds of logging. The oil palm sites are monocultures of *Elaeis guineensis* which were planted in 2000. Further details of the SAFE project design can be found in Ewers et al. 2011.

Ant Collection

At each 2nd order point a 4m x 4m quadrat was laid out. The 2nd order point itself was at the centre of this quadrat unless a path, fallen tree or vegetation too thick for collecting fell across the quadrat area. In these cases the quadrat was moved as close to the 2nd order point as possible whilst making sampling feasible. The Northern edge of the quadrat always ran East-West. Within each square metre of the plot a soil pit was dug measuring 12cm x 12cm wide and 10cm deep. Soil was removed from these pits and searched for ants for 10 person-minutes. Large dead wood inside the quadrat was also surveyed. One sample was taken per linear metre of dead wood (Davies et al. 2003). Additionally, bark was removed and holes in the wood were investigated. All ants found in dead wood in this manner were collected. All specimens were stored in 80% ethanol. This sampling

procedure gave a minimum of 16 samples (soil pits) per quadrat with a varying number of additional wood samples.

Identification and Measuring

Ants were identified to species level using published literature and online resources (Bihn and Verhaagh 2007, Heterick and Shattuck 2011, Brown 1980, Moffett 1986, Taylor 1990, Wilson 1964, Taylor 1985, Shattuck and Barnett 2007, Rigato 1994, Shattuck 2011, Fayle et al. In prep.-b, Bolton 1994, AntWeb 2012). For the vast majority of genera adequate keys were not available for the Bornean fauna and so specimens were assigned to morphospecies. Additionally, due to the inaccessibility of a reference collection for the hyperdiverse *Pheidole* and *Tetramorium* these genera were identified to morphospecies. Hereafter, all species and morphospecies are referred to as species. The abundance of species was recorded for use in analyses. Five quantitative morphological traits were measured that are expected to represent functional differences in resource usage within ant communities (Appendix). All relative measures were calculated by dividing by Weber's length:

- 1) **Weber's length.** This is defined as the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum (Sanders et al. 2007, Brown 1953, Weber 1946). This is generally the longest rigid section of the body and acts as a surrogate for body length which is thought to relate to many life history traits including individual prey selection (Traniello 1987) and thermal tolerance (Heinze et al. 1998). It is also correlated with other morphological features known to vary with resource selection (Kaspari 1996, Weiser and Kaspari 2006). Measuring Weber's length overcomes problems of measuring total body length which can be biased by variability in the length of the gaster due to specimen storage (Brown 1953).
- 2) **Relative hind leg length.** This is calculated as the sum of the hind femur and hind tibia length. The hind femur is measured as the chord distance from the insertion in the coxae, excluding the trochanter, to the tibia. Hind tibia is the chord length of the tibia from the attachment to the femur to the first tarsal segment. Variation in the size of legs is expected to allow ant species to occupy and access different size grains of the interstitial environment (Kaspari and Weiser 1999). Different leg sizes may also be an adaptation to carrying different sized loads of foraged items (Feener et al. 1988).
- 3) **Relative eye length.** Eye length is measured as the major axis of the eye with the head in profile. The size and presence of eyes is linked to a number of aspects of feeding ecology and habitat preference. Predatory specialists and cryptic subterranean species tend to have smaller eyes than omnivores and surface foragers (Weiser and Kaspari 2006, Gronenberg

and Hölldobler 1999). Conversely, larger eyes have been linked to navigating in more open environments (Hölldobler 1980) and attending a range of visual cues (Hölldobler and Wilson 1990). Thus, eye length variation is expected to capture variation in the type and location of resources that are foraged by ants in the environment.

- 4) **Relative mandible length.** Measured as the distance from the insertion of the mandible to its distal tip. Larger mandibles allow the predation of larger food items and may also indicate specialisation in a predatory role (Hölldobler and Wilson 1990, Gronenberg et al. 1997).
- 5) **Relative clypeus length.** Measured as the distance at the midpoint between the anterior and posterior margins of the clypeus in full-face view. The clypeus contains muscles used to perform a sucking action. Consequently, the presence of a well-developed clypeus is thought to relate to liquid feeding behaviour and the suite of ecological implications that this has (Davidson et al. 2004, Keller 2009).

Traits were measured to the nearest 0.01mm using an ocular micrometer attached to a Leica MS5 stereo-microscope (Leica Microsystems, Heerbrugg, Switzerland). Species without eyes were assigned a value of zero for eye length. For accuracy of measurement the highest possible magnification was used that allowed the entire structure of interest to be fitted within the range of the ocular micrometer. Reproductive forms and major castes were excluded from analyses and so were not measured. This is due to the unpredictability of collecting major castes using the sampling protocol and the non-foraging role of reproductive Formicidae (Hölldobler and Wilson 1990). In total, 836 individuals were measured from 260 species with an average of 2.78 individuals per species.

Analyses

All analyses were performed in R statistical software (R Development Core Team 2012). Plots of residuals were investigated to ensure normality of errors, homogeneity of variance and linearity where appropriate for the statistical tests.

Assessing independence of communities

For all analyses, 2nd order points from the same triangular groupings were pooled together to create independent communities. On average within habitat blocks these pairs were 520m apart. Each pair occupied the same area in each habitat. These paired communities will be referred to as replicate communities. In total, 23 replicate communities were analysed: three from oil palm, fourteen from secondary forest and six from old growth. Mantel tests were performed with 999 permutations using a Bray-Curtis dissimilarity index to test for spatial autocorrelation in community composition.

Calculation of dissimilarity indices and Mantel statistics were performed using the *vegan* package in R (Okansen et al. 2012).

Comparison of functional diversity across habitat type

ANOVA was used to test for differences in the functional diversity metrics FRic, FEve, FDiv (Villéger et al. 2008) and alpha diversity across habitat types. Significant ANOVAs were followed up with Tukey's Honest Significant Differences to determine which habitat types differed. All three metrics are orthogonal to each other (Villéger et al. 2008). All metrics were calculated from the distribution of species abundances in a multivariate functional trait space following the methods described in Villéger et al. (2008). To prepare this multivariate space a Euclidean species distance matrix was first calculated from standardized trait values. Secondly, a principal coordinate analysis (PCoA) was performed on this matrix to summarise major axes of variation within the dataset. The resulting PCoA axes and the axis scores for each species were then used to plot communities in five dimensional functional trait spaces. FRic measures the functional richness of a community by calculating the volume of the minimum convex hull that is required to encompass all species present. The convex hull is calculated using the Quickhull algorithm (Barber et al. 1996). Relative abundance is not considered in the calculation of FRic and its value is not bounded (Villéger et al. 2008). FEve describes functional evenness by summing the branch lengths of the minimum spanning tree that is required to connect all species in a community. FDiv measures functional divergence as the species deviance from the mean distance to the centre of gravity of the convex hull. Both FEve and FDiv are weighted by the relative abundance of species and are constrained between zero and one, with values of zero representing low evenness or divergence and values of one representing high evenness or divergence (Villéger et al. 2008). Metrics were calculated for each community using the *FD* package in R (Laliberté and Shipley 2011).

Detecting community assembly processes

To detect the presence of non-random community assembly processes 1,000 null communities were generated for each replicate community. Null communities were constrained to have the same species richness and total abundance as the community for which they were acting as a null. Species were added to null communities at random from the regional pool weighted by their relative abundance across all samples. The functional diversity metrics of FRic, FEve and FDiv were then calculated for these null communities to give an expected frequency distribution of each metric for each community. Observed metrics were compared to these null frequency distributions. If observed

values fell outside the 2.5th or 97.5th quantiles of the null distribution they were judged to be significantly non-random ($p < 0.05$). Observed metrics greater than the 97.5th quantile were described as overdispersed whilst those smaller than the 2.5th quantile were described as underdispersed. Observations landing within this range were deemed not to be different from null expectation.

Interpretation of PCoA axes across communities and habitats

For each PCoA axis whose relative eigenvalues explained greater than 10% of total variation in multivariate trait space, relative associations (correlation coefficients) between the axis and each trait were investigated to determine which gradients of trait variation, hence functional trait complexes, were represented by each axis. Having interpreted the most important axes in this way, each set of species scores for each axis treated separately was then used to re-calculate functional diversity metrics for each community with respect to each axis in turn. Detection of assembly processes were performed on each axis using null communities in the same way as described above. Only FRic and FEve were calculated at this stage as FDiv requires at least two dimensions (Villéger et al. 2008). In addition, the mean weighted values of each axis for each observed community were calculated and investigated to determine where bias may lie in community composition. The mean weighted score of an axis for a given community is calculated as the average of the axis scores for each species in a community, weighted by their abundance. This gives a measure of the distribution of functional trait complexes represented by that axis for a community. Mean values of 0 indicate that equal numbers of the functional complexes represented by an axis are present in a community. Positive or negative values indicate a bias in that community toward a particular suite of functional traits.

Testing continuous change in assembly processes

The observed-expected value for each functional diversity metric for each replicate community was used as a surrogate for the position of that community along a continuum of variation in the prevailing assembly processes. The expected value was calculated as the mean of the metrics generated from the null communities. Positive values of $O-E$ are thought to indicate competitive processes whilst negative values indicate a tendency toward underdispersion and habitat filtering. Overdispersion is interpreted as signalling competition and occurs if the observed values are greater than those expected. Underdispersion represents habitat filtering and can be seen when the observed values are smaller than those expected. $O-E$ was then used as a community response variable and regressed against a forest quality index for each replicate community. This index was

collected in accordance with the SAFE projects' standardised scale of zero (oil palm) to five (primary forest) (Appendix). This continuous measure is used in order to capture and understand the variation in quality that is present within secondary forest. This approach does not comment on the significant departures from null expectation for individual communities but rather looks at whether a shift in relative predominance of underlying assembly processes can be detected across sites of differing forest quality.

Results

Assessing Independence of Communities

Replicate communities showed no spatial autocorrelation within any of the habitats. Mantel test were nonsignificant for oil palm ($p = 0.50$), secondary forest ($p = 0.23$) and old growth ($p = 0.31$). Each replicate community was therefore treated as spatially independent for subsequent analyses.

Comparison of functional diversity across habitat type

No significant differences were found for mean FRic or alpha species richness between habitat types ($p > 0.05$). Significant differences in the means of FEve ($F_{2,20} = 7.31$, $p < 0.01$, figure 1) and FDiv ($F_{2,20} = 6.64$, $p < 0.01$, figure 2) were found. For FEve, oil palm had significantly smaller values than secondary forest and old growth (Tukey HSD, $p < 0.05$), while secondary forest and old growth were not significantly different (Tukey HSD, $p > 0.05$). For FDiv, old growth had significantly higher values than secondary forest (Tukey HSD, $p < 0.05$). Oil palm was not significantly different from either old growth or secondary forest (Tukey HSD, $p > 0.05$). These results indicate that while all habitats retain equal levels of functional diversity and alpha species richness, oil palm has significantly lower functional evenness than the other habitats and that old growth has higher functional divergence than secondary forest. Oil palm has intermediate divergence.

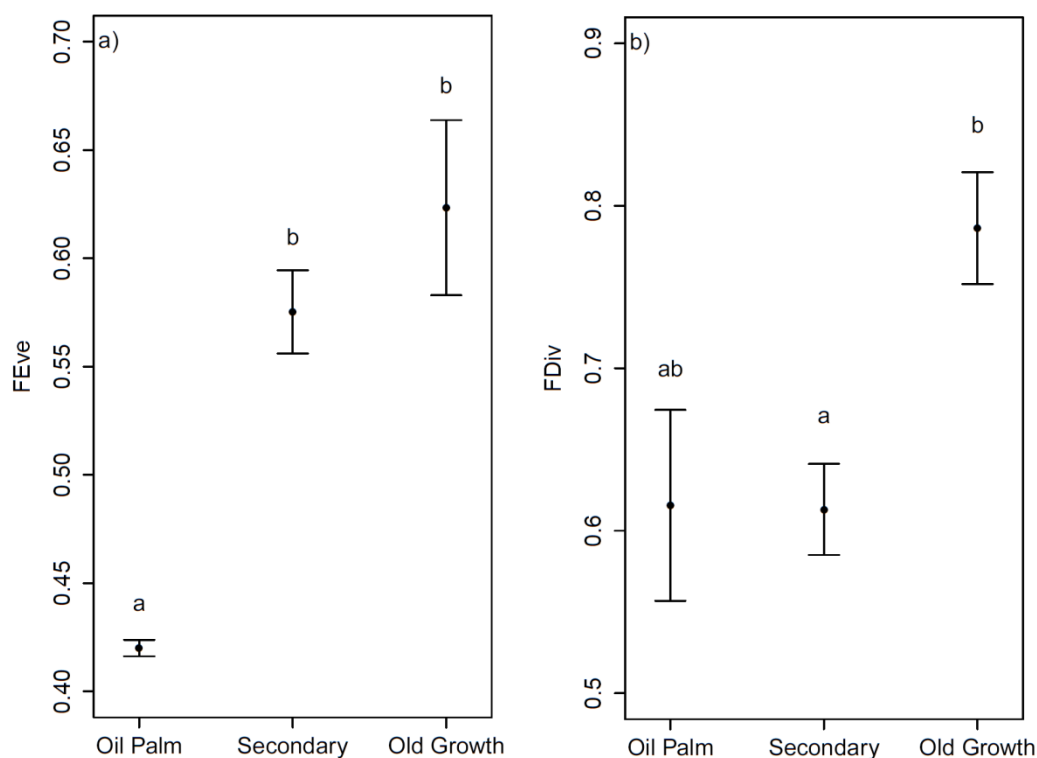


Figure 1. Mean ± 1 SE of a) FEve and b) FDiv across habitat types. Letters above means denote groups that are not significantly different according to Tukey's Honest Significant Differences.

Detecting community assembly processes

The results of the comparison of observed functional diversity metrics to those expected under stochastic processes are summarised in table 1. FRic appears to be dominated by stochastic processes although there is a minor tendency for overdispersion in all habitats. FEve is also dominated by stochastic processes for all habitats. FDiv behaves stochastically in oil palm and secondary forest but displays clear overdispersion in old growth. This suggests that competitive interactions are the most influential force driving the assembly of old growth communities and that high abundances are concentrated at the extreme edges of morphological space.

Table 1. Percentage of communities per habitat that display underdispersion, overdispersion or met null expectation for each functional diversity metric. Dominant forces in each habitat are highlighted in bold. Number of replicate communities given in parentheses.

Functional diversity metric	Dispersion	Oil Palm (n=3)	Secondary Forest (n=14)	Old Growth (n=6)
FRic	Underdispersed	0.0%	0.0%	0.0%
	Stochastic	66.6%	71.4%	83.3%
	Overdispersed	33.3%	28.6%	16.7%
FEve	Underdispersed	33.3%	0.0%	0.0%
	Stochastic	66.6%	100.0%	100.0%
	Overdispersed	0.0%	0.0%	0.0%
FDiv	Underdispersed	0.0%	7.1%	0.0%
	Stochastic	100.0%	71.4%	16.6%
	Overdispersed	0.0%	21.4%	83.3%

Interpretation of PCoA axes across communities and habitats

Only the first three axes of the PCoA were investigated individually as these were the only axes that explained more than 10% of variation in functional trait space (39.75%, 26.8% and 16.35% respectively). Investigation of biplots suggested a continuum of ecological strategies represented by each PCoA axis. Axis 1 encompasses a gradient from epigaeic omnivores at low axis scores to hypogaeic predators at high axis scores (figure 2a). This gradient is interpreted due to the high relative leg, eye and clypeus lengths associated with low axis 1 scores. Axis 2 represents variation from small predators with low axis scores to large omnivores with high axis scores (figure 2a,b). This interpretation arises from low axis 2 scores having large relative mandible lengths but small Weber's lengths. Finally, axis 3 represents variation from large bodied predators at low axis scores to small bodied omnivores at high axis scores (figure 3b). For axis 3, relatively large mandibles, large Weber's lengths and relatively small eyes suggest that low scores represent large bodied predators. Figure 3 (a-c) is a graphical visualisation of species abundances and their convex hulls for the first two PCoA axes. A representative community from each habitat has been plotted to aid interpretation of multivariate metrics. Processes described in table 2 can be observed. Figure 3d illustrates the overlap of the convex hulls for the combined communities from each habitat.

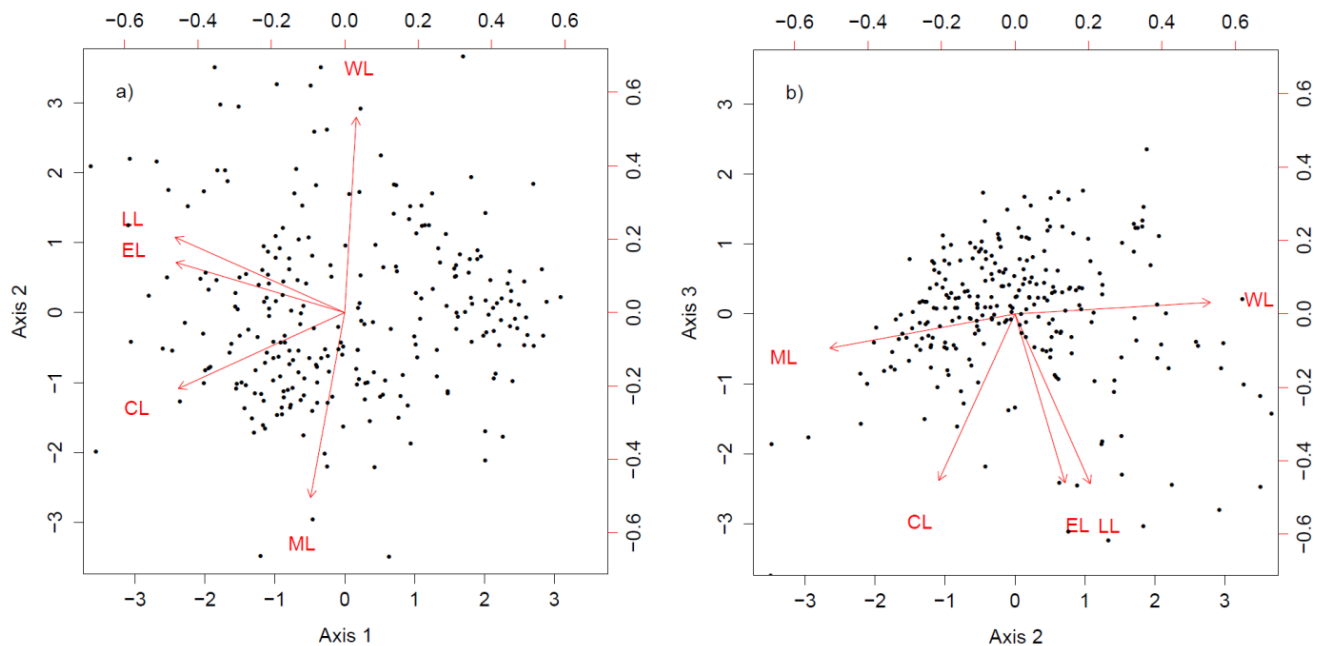


Figure 2. PCoA biplots for a) axes 1 and 2 and b) axes 2 and 3. Points represent species. Red arrows represent traits. WL = Weber's length, LL = relative leg length, EL = relative eye length, CL = relative clypeus length, ML = relative mandible length.

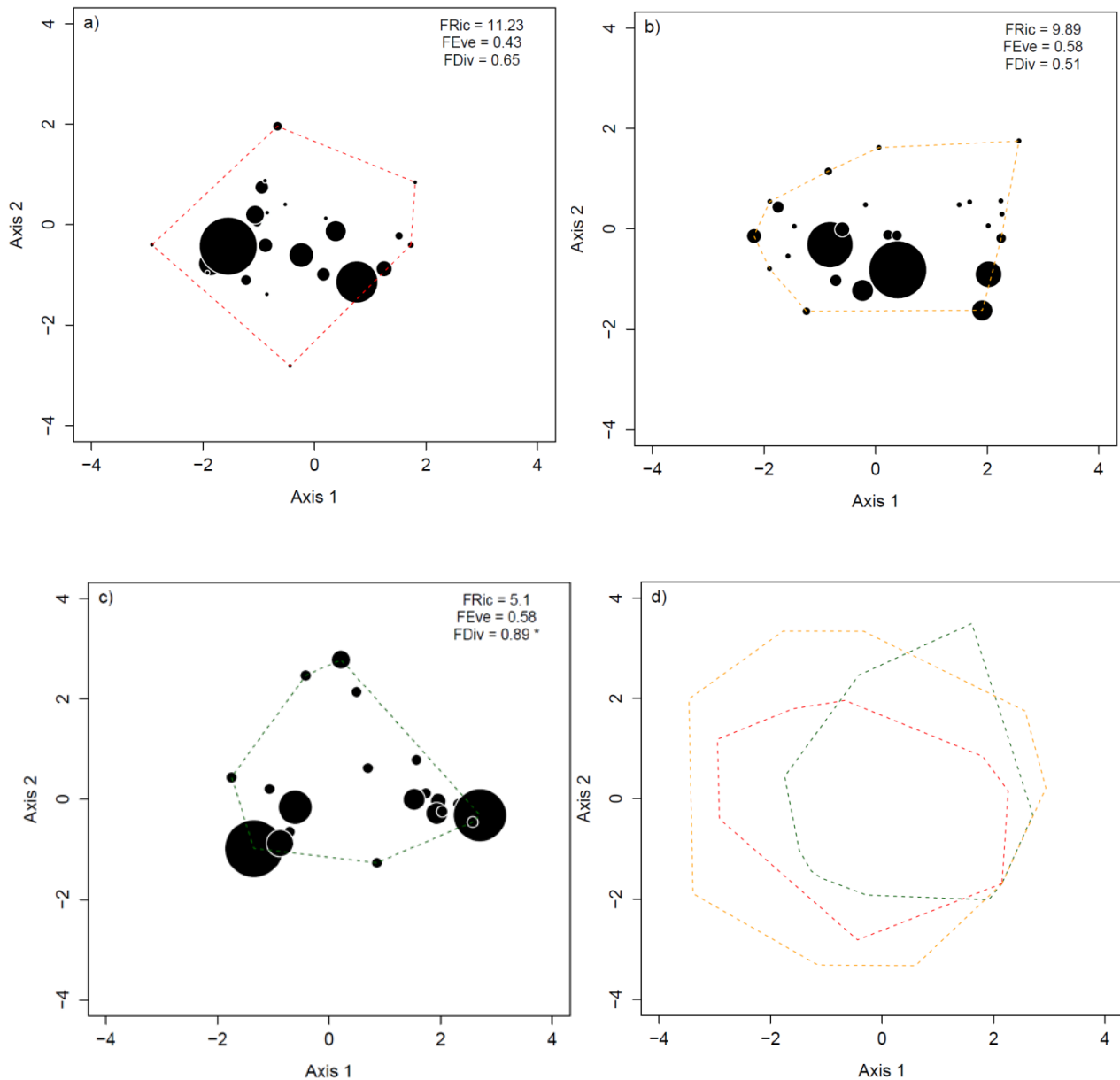


Figure 3. Visualisation of the structure of a single, representative community from a) oil palm, b) secondary forest and c) old growth in functional trait space. Points represent species in functional trait space and their size is indicative of relative abundance. Dashed lines indicate the convex hull (FRic) of the community. Some species appear to “escape” the convex hull: this effect is simply a visual artefact of plotting both the hull and species abundances. Annotations supply FRic, FEve and FDiv values for each community. Asterisks indicate significant deviations in metrics from null expectation (see text). Plot d) illustrates the total overlap of the three habitats in trait space. Red dashed lines are oil palm, orange are secondary forest and green are old growth.

Table 2 displays the results of the investigation of assembly processes using PCoA axes 1, 2 and 3. FRic is dominated by stochastic processes in each habitat for each axis. Oil palm appears to be underdispersed for FEve on axis 1 and 2 but conforms to stochasticity for this metric on axis 3. Secondary forest has no dominant pattern for FEve on axis 1 but tends toward underdispersion. On axis 2 and 3 FEve is underdispersed for secondary forest. Old growth appears stochastic for FEve on axis 1 but tends toward underdispersion on axis 2 and is clearly underdispersed for this metric on axis 3. These results highlight the tendency for oil palm communities to be underdispersed compared to null expectation for the PCoA axes that explain the most variation. In addition, secondary forest and old growth appear to behave in a largely stochastic manner for the axes that explain most variation and have greater amounts of underdispersion for less important axes.

Table 2. Percentage of communities per habitat that display underdispersion, overdispersion or met null expectation for each functional diversity metrics for individual PCoA axes. Dominant forces in each habitat are highlighted in bold. Number of replicate communities given in parentheses.

Functional diversity metric	PCoA Axis	Dispersion	Oil Palm (n=3)	Secondary Forest (n=14)	Old Growth (n=6)
FRic	Axis 1	Underdispersed	0.0%	7.1%	0.0%
		Stochastic	100.0%	85.7%	100.0%
		Overdispersed	0.0%	7.1%	0.0%
	Axis 2	Underdispersed	0.0%	7.1%	0.0%
		Stochastic	66.6%	85.7%	100.0%
		Overdispersed	33.3%	7.1%	0.0%
	Axis 3	Underdispersed	0.0%	7.1%	0.0%
		Stochastic	100.0%	85.7%	100.0%
		Overdispersed	0.0%	7.1%	0.0%
FEve	Axis 1	Underdispersed	66.6%	50.0%	16.7%
		Stochastic	33.3%	50.0%	66.7%
		Overdispersed	0.0%	0.0%	16.7%
	Axis 2	Underdispersed	100.0%	71.4%	50.0%
		Stochastic	0.0%	28.6%	50.0%
		Overdispersed	0.0%	0.0%	0.0%
	Axis 3	Underdispersed	33.3%	71.4%	83.3%
		Stochastic	66.6%	28.6%	16.7%
		Overdispersed	0.0%	0.0%	0.0%

Based on the conclusions from table 2, mean weighted scores of axis 1 indicate that underdispersion in oil palm is due to a relative lack of hypogaeic predators. No mean weighted axis 1 scores are above 0 for oil palm (figure 4a). For axis 2, both oil palm and secondary forest have a relative lack of large omnivores (figure 4b). No oil palm or secondary forest communities have positive mean scores for axis 2. On axis 3, only secondary forest and old growth display underdispersion (table 2). For both habitats, the location of this underdispersion is mixed (figure 4c). In old growth there is a tendency to be missing small omnivores, whilst in secondary forest, communities are more variable and display either a lack of large predators or small omnivores.

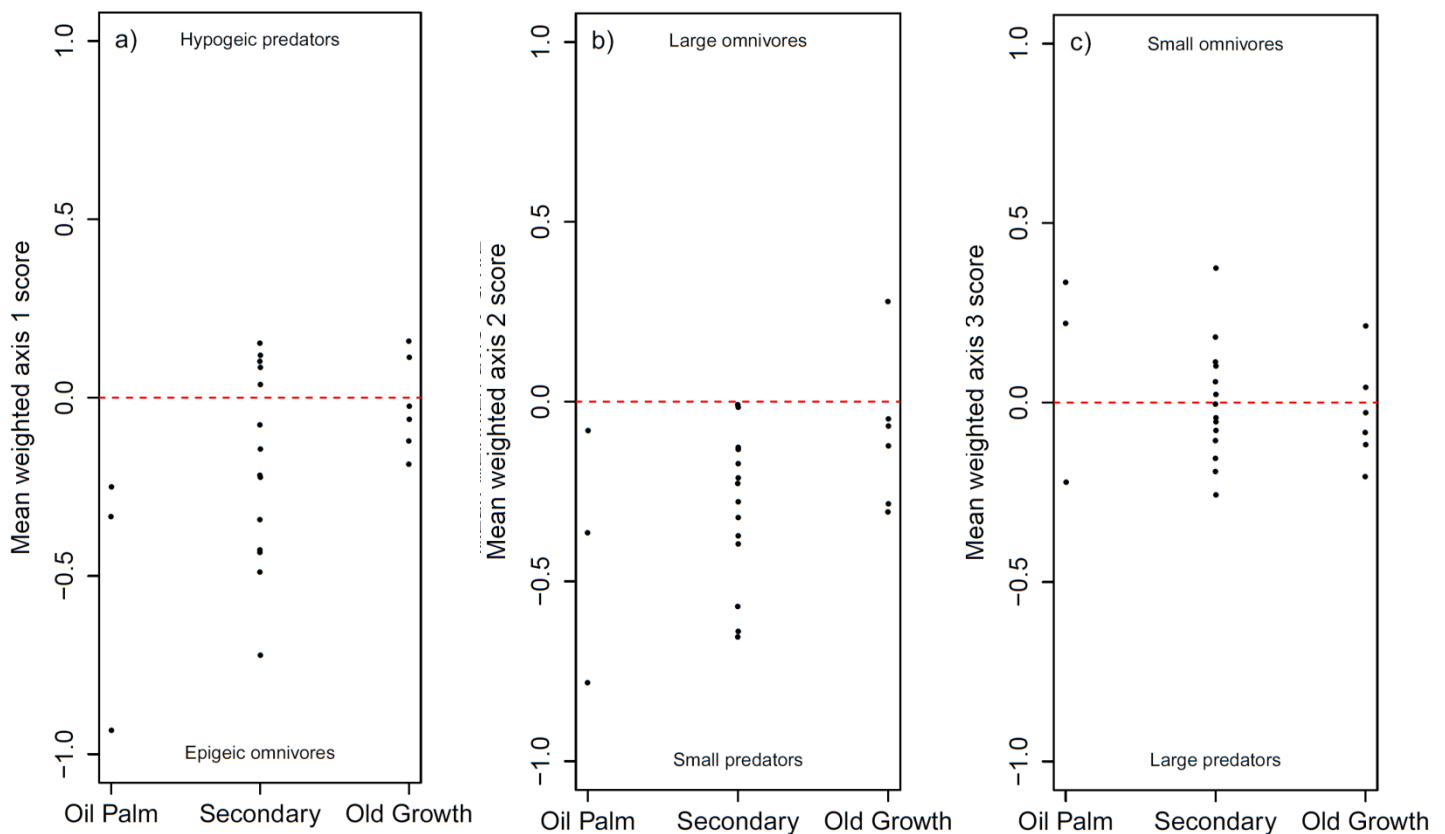


Figure 4. Mean weighted axes scores per habitat type for a) axis 1, b) axis 2 and c) axis 3. Descriptions at the top and bottom of plots indicate the functional complexes represented by high or low axis scores. Red dashed line indicates 0, where means fall if this is no bias in their community composition.

Testing continuous change in assembly processes

No significant relationship was found between $O-E$ of FRic and forest quality ($p > 0.05$). The relationship between the $O-E$ of FEve and forest quality was significant ($b = 0.03$, $df = 21$, $R^2 = 0.3$, $t = 3.21$, $p < 0.01$, figure 5) as was that between the $O-E$ of FDiv and forest quality ($b = 0.03$, $df = 21$, $R^2 = 0.14$, $t = 2.12$, $p < 0.05$, figure 6). Both of these results show that there is a tendency for overdispersion and competitive processes (high $O-E$ scores) to dominate in pristine habitat, with a slide toward underdispersion and habitat filtering processes in increasingly disturbed habitat (low $O-E$ scores).

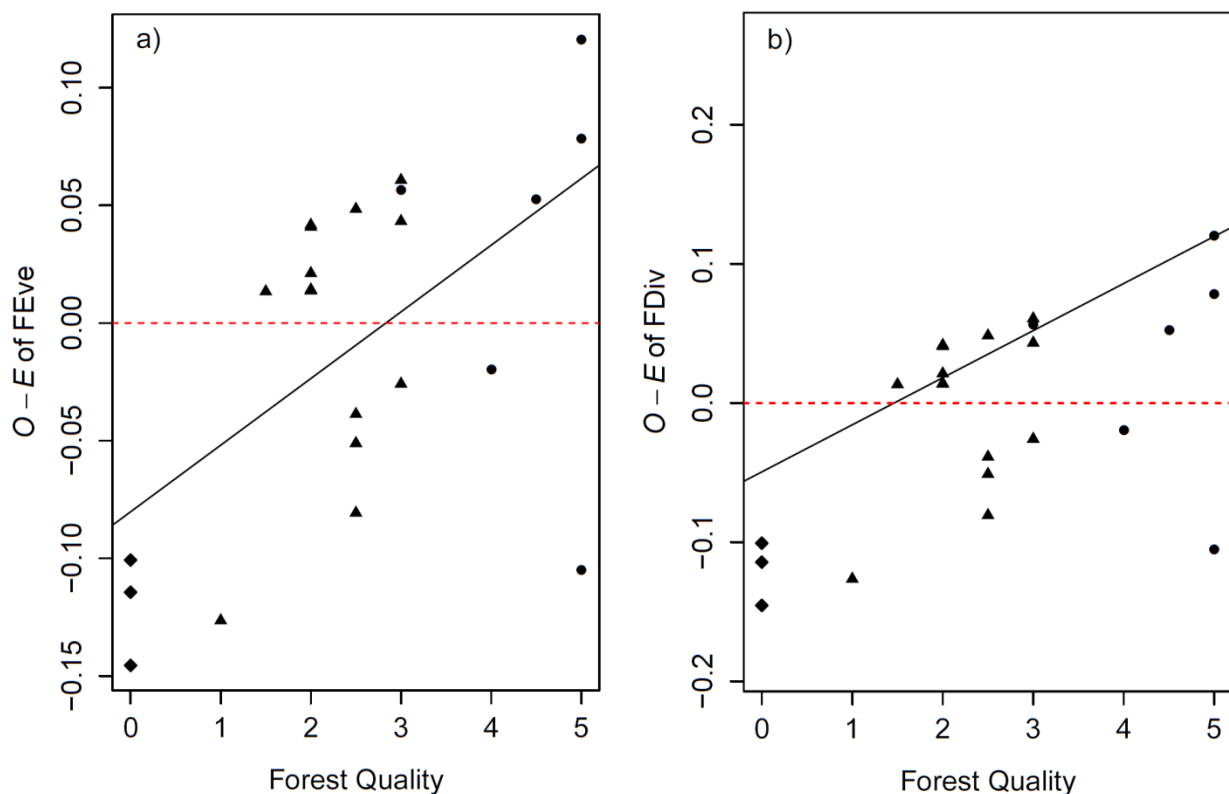


Figure 5. $O-E$ of a) FEve ($O-E \text{ FEve} = -0.08 + 0.02 * \text{Forest Quality}$) and b) FDiv as a function of forest quality ($O-E \text{ FDiv} = -0.05 + 0.03 * \text{Forest Quality}$). Black line represents significant least squares line. Red line indicates an $O-E$ of zero. • = old growth, ▲ = secondary forest, ♦ = oil palm. Positive $O-E$ scores represent competitive assembly whilst negative scores indicate habitat filtering. Scores of 0 denote that a community assembles stochastically.

Discussion

The results clearly illustrate that functional diversity and community assembly processes change as a result of forest disturbance and conversion to oil palm. It also appears that particular groups of functional trait values are relatively under-represented in certain habitats. Finally, a relationship between the quality of the forest and different assembly processes is established which suggests that broad scale changes in the community assembly dynamics of tropical forests may arise following disturbance. These changes in assembly patterns have not previously been reported for ants and their detection is likely due to the greater resolution of the functional trait based approach.

Firstly, neither functional richness, FRic, nor alpha species richness differed over the disturbance gradient. This combination of nonsignificant results is not surprising given that functional richness is known correlates closely with species richness (Appendix). Species richness is typically recorded to change across tropical forest disturbance gradients (Fayle et al. 2010, Floren and Linsenmair 2005, Bruhl and Eltz 2010). However, the current result does not necessarily contradict the established literature. Firstly, this study is not entirely unique in finding little difference in alpha or point level species richness in areas of different disturbance (Klimes et al. 2012, Fayle et al. 2011). Secondly, beta diversity within habitats is likely to change with disturbance by virtue of the larger species pools predicted in secondary forest and old growth (Appendix). The fact that functional and species richness are not affected by disturbance instead highlights that the changes in community functional structure in this system are concerned with either shifts in the relative abundances of species and functional traits, compositional changes, or both. All three habitats display changes of this nature.

In oil palm, functional evenness, FEve, is significantly lower (figure 1a). This trend suggests that oil palm may be underdispersed and experiencing habitat filtering as trait values are aggregated in functional trait space. Despite this, no dominant patterns of underdispersion were detected when utilising all trait data (table 1). When investigating single axes of trait variation, however, high levels of underdispersion in functional evenness are found (table 2). This underdispersion manifests itself on axis 1 as a relatively reduced abundance of hypogaeic predatory species (figure 4a). On axis 2, a lack of large omnivorous species can be seen (figure 4b). These patterns of unevenness within oil palm imply that a habitat filter is in place that excludes certain soil dwelling predators and large omnivorous species. It is likely that the soil structure itself is the abiotic filter causing the reduced abundance of hypogaeic predators in oil palm. The soil is more compacted in this environment than in natural systems and could behave as a filter directly by preventing species from nesting or indirectly by reducing the abundance of hypogaeic prey species (Foster et al. 2011, Mohd Suffian et al. 2010, Zuraidah et al. 2010). Reasons for the filtering of large omnivorous species are less clear but

may be a combination of the loss of suitable nesting sites due to the simplification of the habitat or intolerance of the highly variable microclimatic conditions of oil palm (Foster et al. 2011). Indeed, nest temperature has been shown to be an important factor for niche partitioning in Bornean leaf-litter ants (Mezger and Pfeiffer 2010). This niche requirement may be interacting with the oil palm microclimate to filter species that require cool or highly stable nest temperatures.

Secondary forest appears to be dominated by stochastic processes when using all trait data but underdispersion is revealed when single axes of variation are investigated. Secondary forest shows underdispersion for functional evenness on axes 2 and 3 (table 2). This implies a relative lack of large omnivores (figure 4b) and a mix of small omnivores and large predators depending on the community (figure 4c). The actual attributes of the environment causing the filtering of these functional trait complexes are again unknown, but as most communities show a lack of omnivorous groups it may be that the selective logging of the secondary forest has reduced the availability of liquid food in the form of hemipteran trophobionts or plant extrafloral nectaries close to ground level. Explanations concerning nest temperature could also be valid here. Like oil palm, secondary forest appears to be assembled by both stochastic and deterministic processes.

Old growth is the only habitat that shows any strong signal of competitive structuring. The functional divergence in old growth is greater than that in secondary forest (figure 1b). Additionally, the majority of old growth communities show significant overdispersion for FDiv (table 1). This overdispersion may be explained as a result of competition. Over ecological timescales, those species at the isolated margins of functional trait space will become more abundant as they experience less competition due to their divergent and unique morphology. Individual axes are unable to detect which trait complexes are overdispersed, however. This is likely due to the fact that overdispersion was originally detected in FDiv which cannot be calculated when only a single dimension is available. High functional divergence implies that common species are located close to the edge of functional trait space (Villéger et al. 2008) - if this pattern of abundance distribution is the primary outcome of competitive interactions in old growth then it will not be detected by either FRic or FEve. Alternatively, this result could indicate that overdispersion is a general feature of the fauna in old growth and cannot be tied to any particular complexes of functional traits. In addition to competition, underdispersion of functional evenness is found within old growth for axis 3 (table 2). This relates to a relatively low abundance of small omnivores (figure 4c). Similar to the explanation for secondary forest, this may be a result of access to liquid feeding sources although the validity of this suggestion is currently unexplored. It must be remembered, however, that axis 3 accounts for

only 15.6% of the variation in the traits dataset. On the whole, it appears that old growth is dominated by competitive interactions (table 1).

The pattern of these results is reflected in the regressions of *O-E* and forest quality (figure 5a-b). In this case, the *O-E* values directly quantify the degree of under or overdispersion in relation to environmental variation without regard to the statistical significance of each of these replicate departures from null expectation. This is a novel finding for the community assembly patterns of tropical ants and is similar to patterns revealed for tropical forest plants (Ding et al. 2012). Different gradients of community structuring processes have previously been reported for tropical ants. For example, it has been suggested that ant communities in primary rainforests are stochastically structured and secondary forest communities are more deterministic (Floren et al. 2001, Floren and Linsenmair 2001). The ultimate in deterministic, competitively assembled communities can then be found in highly disturbed agroecosystems and plantations in the form of the “ant-mosaic” (Bluthgen and Stork 2007). The results presented here disagree with this sequence of processes along a forest disturbance gradient. In terms of a deterministic/stochastic gradient, the results here describe a quadratic function where forests of very high and very low quality are deterministically assembled and forests of intermediate quality display assembly that is indistinguishable from a stochastic process (figure 5a-b).

This disagreement is likely due to two reasons. Firstly, previous work has focussed on arboreal ants and the difference in conclusions may be due to fundamental differences in ecology. The canopy fauna can be quite different from that found on the ground and there are certainly expected to be broad scale phylogenetic and dietary differences between the two (Davidson et al. 2003, Wilson and Hölldobler 2005). Indeed, differences in responses of simple biodiversity measures to disturbance have already been recorded between these faunas (Fayle et al. 2010). Furthermore, there may be greater limitation of nest sites in the canopy (Dejean et al. 2007). This could generate an inherently stochastic process of community assembly as the lottery of species recruitment dictates co-occurrence patterns (Andersen 2008). Such nest site limitation may not be as strong an effect on the ground where there appears to be an abundance of leaf litter and soil matter in which to establish a nest. Further work should include considerations of environmental variables representative of nest site availability to test ideas concerning recruitment limitation. Secondly, the approaches of previous work and the current research are different. Previous studies on canopy ants typically utilise a taxonomic approach often with only presence/absence data. This study uses five different species traits and relative abundance data in order to investigate the distribution of functional diversity within and across communities. The current approach is more likely to pick up trends in assembly

processes and community structure as species identities may vary independently of the traits that are actually found within a community. Such variation cannot be detected by strictly taxonomic analyses. Additionally, the use of species abundances is likely to increase the sensitivity of analyses to non-random processes if they exist (Ulrich and Gotelli 2010, Lester et al. 2009).

The analytical differences between the current and previous studies are likely to be more than conjecture. Work on Borneo using a species co-occurrence analysis without trait data found random community structuring in leaf-litter for both rainforest and oil palm habitats (Fayle et al. In prep.-a). The data presented here largely agree with this interpretation following preliminary re-analysis using a co-occurrence C-score approach (Appendix). These two threads indicate that the inclusion of functional trait data is a key factor in our ability to detect non-random community assembly patterns.

In summary, functional diversity has been recorded to change in clear, but subtle, ways across a tropical forest disturbance gradient. Oil palm exhibits lower functional evenness whilst old growth has higher levels of functional divergence. These differences ultimately manifest themselves as changes in the prevailing community assembly processes. A transition can be seen from overdispersed, competitively assembled communities in old growth to stochastic and underdispersed, habitat filtered communities in oil palm. This result boosts our knowledge of how tropical leaf litter ant communities assemble themselves in space and also highlights which species groups and environmental variables we should investigate further if we are to understand the consequences of habitat conversion for ecosystem function in this system. Finally, the fact that the results here contradict existing studies concerning tropical ant communities highlights the influential role that trait data may have in studies of community assembly.

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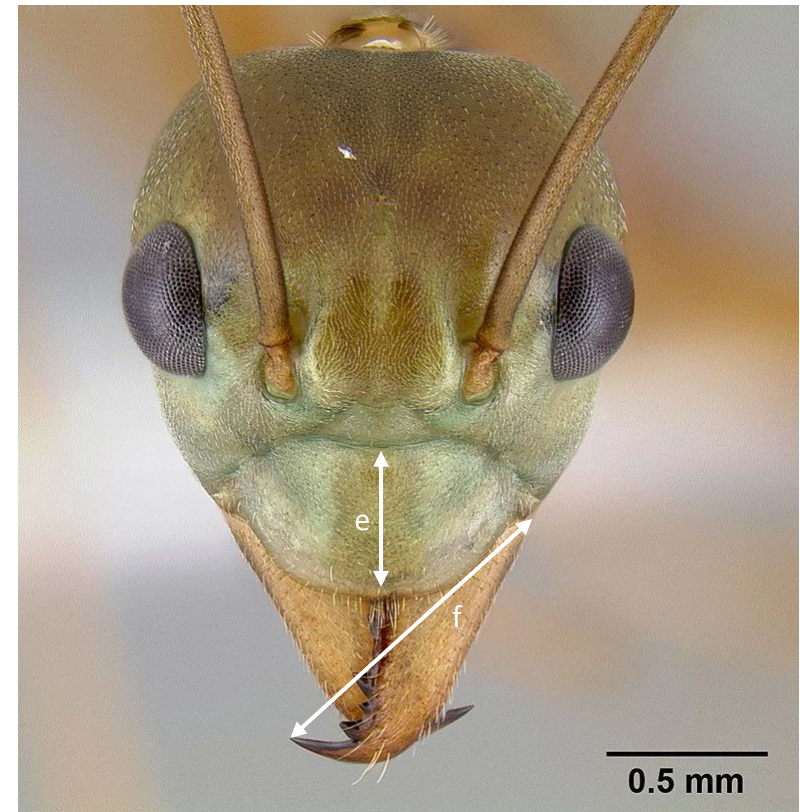
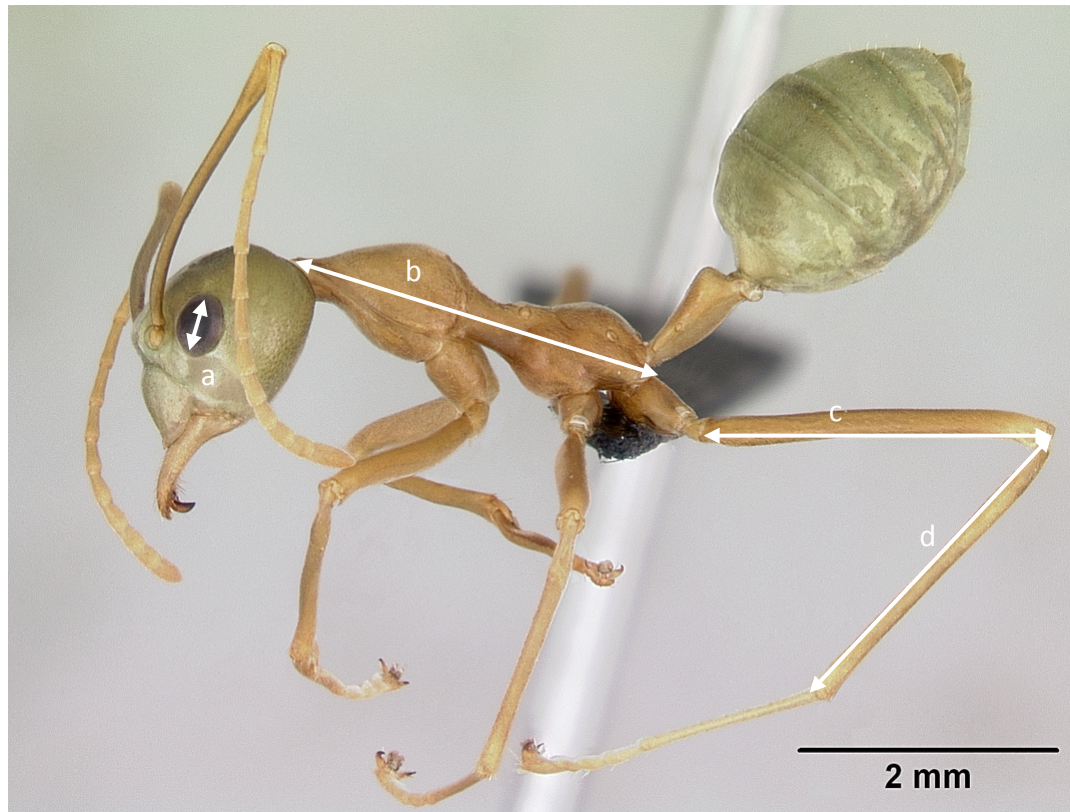
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Appendix



Appendix Figure 1. Location of measured traits on ant morphology. a = eye length, b = Weber's length, c = hind femur, d = hind tibia, e = clypeus length, f = mandible length. Image ©AntWeb

Forest Quality Index

Appendix Table 1. Description of SAFE Project standardised forest quality scores

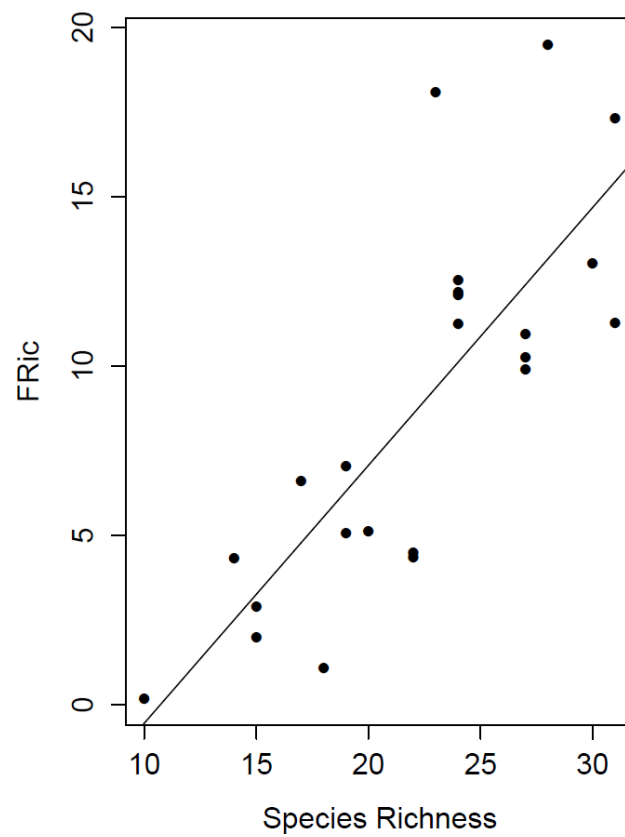
Score	Forest quality	Forest description
0	Palm oil	Palm oil
1	Very poor	No trees - open canopy with ginger/vines or low scrub
2	Poor	Open with occasional small trees over ginger/vine layer
3	OK	Small trees fairly abundant/canopy at least partially closed
4	Good	Lots of trees, some large, canopy closed
5	Very good	No evidence of logging at all, closed canopy with large trees

Species Pool Estimates per Habitat

Appendix Table 2. Estimated species richness \pm SE where appropriate for each habitat

Habitat	Number of communities	Observed		First Order Jackknife	Second Order Jackknife	Bootstrap
		Species Richness	Chao			
Oil Palm	3	44	126.57 \pm 43.11	66.67 \pm 16.18	76.83	54.33 \pm 7.37
Secondary Forest	14	189	377.16 \pm 48.43	298.57 \pm 33.87	370.44	235.79 \pm 15.23
Old Growth	6	83	154.27 \pm 25.79	129.67 \pm 21.30	155.27	103.73 \pm 9.74

Relationship between Functional Richness and Species Richness



Appendix Figure 2. Relationship between functional richness and species richness in this study is significant and positive ($b = 0.76$, $df = 21$, $R^2 = 0.64$, $t = 6.08$, $p < 0.01$). $FRic = -8.17 + 0.76 * \text{Species Richness}$.

Preliminary C-Score Analysis

A C-score analysis was carried out using the same abundance data that was used for the main analysis. The C-score is a metric of community wide species co-occurrence. High C-scores indicate segregation of species co-occurrences. Low significant scores indicate significant clustering of species co-occurrences. Significance is assessed in a similar way to the main analysis. Comparison to a null distribution of scores is made and values greater than 97.5% of lower than 2.5% of the null distribution are considered significant. Null distributions were generated on 30,000 simulations following a burn in of 30,000 simulations (as per Fayle et al. In prep.-a). The following results for each habitat block indicate that ground dwelling ant communities generally appear to be stochastically assembled and structured when using only co-occurrence data. The only significant result is for OG3 which shows the opposite result than that reported for old growth in the main analysis. Here, it displays significant clustering of species.

Appendix Table 3. Observed C-scores, test statistics and p-values for each habitat block.

Habitat	Block	Observed	Statistic	2.5%	97.5%	p
OP	OP3	0.02	524	523	550	0.18
OG	OG2	0.03	900	879	914	0.47
OG	OG3	0.04	1387	1388	1433	0.045
SF	SFC	0.18	6174	6047	6224	0.28
SF	SFF	0.1	3315	3244	3372	0.5761