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Incorporating intraspecific trait variation into functional diversity:

Impacts of selective logging on birds in Borneo

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Abstract

1. As conservation increasingly recognises the importance of species’ functional roles in ecosystem processes, studies are shifting away from measuring species richness towards measures that account for the functional differences between species in a community. These functional diversity (FD) indices have received much recent attention and refinement, but their greatest limitation remains their inability to incorporate information about intraspecific trait variation (ITV).

2. We use an individual-based model to account for ITV when calculating the functional diversity of two avian communities in Borneo; one in primary (unlogged) forest and one in selectively logged forest. We deal with the scarcity of trait data for individual species by developing a simulation approach, taking data from the literature where necessary. Using a bootstrapping procedure, we produce a range of ecologically feasible FD values taking account of ITV for five commonly-used FD indices, and we quantify the confidence that can be placed in these values using a newly-developed bootstrapping method: btFD.

3. We found that incorporating ITV significantly altered the FD values of all indices used in our models. The rank order of FD for the two communities, indicating whether diversity was higher in primary or selectively logged forest, was largely unchanged by the inclusion of ITV. However, by accounting for ITV, we were able to reveal previously unrecognized impacts of selective logging on avian functional diversity through a narrower dispersion of individuals in functional trait space in logged forest.

4. Our results highlight the importance of incorporating ITV into measures of functional diversity, whilst our simulation approach addresses the frequently encountered difficulty of working with sparse trait data and quantifies the confidence that should be placed in such findings.
Introduction

Change in land-use is a major global driver of ecosystem degradation (Brooks et al. 2002; Edwards et al. 2011; Barber et al. 2014) with a growing proportion of the world’s natural habitats being altered by anthropogenic activities (Morris 2010). The impacts of land-use change on biodiversity are often examined using measures of diversity, such as species richness, that take no account of differences in species’ life-history traits and ecological niches. Yet changes in environmental conditions following disturbance may well allow only a narrow spectrum of traits to persist (Hamer et al. 2003; Layman et al. 2007; Cardinale et al. 2012; Fauset et al. 2012). Consequently, such established diversity measures may underestimate the true extent of biodiversity loss following disturbance (Cardinale et al. 2012; Mouillot et al. 2013; Edwards et al. 2014).

One solution to this problem is to use measures of functional diversity (FD), which seek to quantify the range of functional (i.e. trait) differences among species in a community (Tilman et al. 1997; Petchey & Gaston 2002), thus bridging the gap between species diversity and composition. FD can be measured using a variety of different indices (Petchey & Gaston 2006; Villéger et al. 2008). However, a limitation of most FD studies to date is that they have largely ignored intraspecific trait variation (ITV) despite widespread recognition that ITV is critical to a range of ecological and evolutionary processes (Breckling et al. 2006; Albert et al. 2010a; Bolnick et al. 2011; Andersen et al. 2012; de Bello et al. 2013), and that by disregarding variation, this forces assumptions of rigid functional space occupancy (Al Haj Khaled et al. 2005). Despite this problem, few studies have addressed the issue of how to incorporate ITV into measures of FD, particularly for taxa other than plants (Diaz & Cabido 2001; Albert et al. 2010a; Griffiths et al. 2016), which potentially restricts the ability of FD indices to accurately represent real ecosystems (de Bello et al. 2011; Albert et al. 2012).

In this study, we explore the application of ITV and its consequences for the measurement of FD in primary (unlogged) and logged tropical forest in Sabah, Borneo. We use community data from a previous study (Edwards et al. 2013a) to calculate FD for bird communities in primary forest and in forest that had been subjected to repeated rounds of selective logging, following Edwards et al.
We incorporate ITV into well-established FD indices using a simulation approach based on ecologically realistic trait values from the literature (Cianciaruso et al. 2009; Flynn et al. 2009; Santini et al. 2016). This approach not only addresses the frequently occurring problem of sparse or low-resolution trait data in studies of conservation ecology but it also helps to elucidate the impact of ITV on the functional consequences of selective logging in this system. In addition, we develop a bootstrapping method to quantify the confidence that can be placed in the calculated differences in FD between communities, and to assign a probability that such differences could have occurred by chance.

Materials and Methods

Our study site was the Yayasan Sabah logging concession, a 1-million hectare lowland rainforest in eastern Sabah, Malaysian Borneo. The concession includes the Danum Valley Conservation Area and Palum Tambun Watershed Reserve, comprising 45,200 ha of unlogged (primary) lowland Dipterocarp rainforest dominated by valuable timber species of the Dipterocarpaceae (Reynolds et al. 2011). This primary forest is contiguous with the 238,000 ha Ulu Segama-Malua Forest Reserve, which includes selectively logged forest that has undergone two rotations of timber extraction. Sampled locations in logged forest were first logged between 1987 and 1991 using a modified uniform system in which all commercial stems > 0.6 m diameter were removed, yielding an average of 120 m³ of timber per ha. They were then logged again between 2001 and 2007 employing the same logging techniques but with the minimum tree diameter reduced to 0.4 m (0.25 m in some cases), resulting in an additional 15–72 m³ of timber extracted per ha (Fisher et al. 2011; Reynolds et al. 2011). Compared to unlogged forests, logged forests have a greater cover of ground and understory vegetation, a lower density of trees and a more open canopy, as well as incursions by skid trails, roads and logging dumps (Berry et al. 2010; Ansell et al. 2011; Edwards et al. 2016).

Published data on avian species identity and abundance in primary (unlogged) and logged forest were obtained from the literature (Edwards et al. 2013a) as were data for 14 different
functional traits reflecting dietary composition, trophic position, foraging substrate and resource requirements (see Table S1 for variables and data sources). Our aim was not to examine the effects of logging on functional diversity (FD) per se, which have already been examined in detail in these forests for both birds (Edwards et al. 2013b) and dung beetles (Edwards et al. 2014), but to determine how incorporating intraspecific trait variation (ITV) affects different measures of FD and the conclusions drawn from them. Hence we did not include all possible functional traits, but instead focused mainly on those related to foraging and resource requirements (see Supporting Information).

Five commonly used functional diversity indices were calculated for each community using the ‘FD’ package [Laliberté et al. 2014] and the Xtree function [Schumacher, 2003] in R version 3.2.2 (R Development Core Team, 2016). These were: Functional Richness (FRic) and Functional Evenness (FEve; see Mason et al. 2005 and Villéger et al. 2008 for further details of these two indices); Functional Dispersion (FDis, Laliberté & Legendre 2010); Rao’s Quadratic Entropy (RaoQ, Rao 1982); and Petchey and Gaston’s (2002) FD index (FD_{PG}). At the species level, FRic measures the volume of functional trait space occupied by a community and reflects the richness of functional roles performed by species; FEve measures the evenness of species abundances and of distances among species in functional space; FDis and RaoQ both measure the dispersion of species in trait space. FDis weights species by their relative abundances and measures the mean distance of individual species to the weighted functional space centroid (Laliberté & Legendre 2010) whereas RaoQ is calculated as the mean distance between randomly-selected pairs of species in functional space (Botta-Dukát 2005). Finally, FD_{PG} sums the total branch length of a hierarchical functional dendrogram connecting all species in functional space, based on pairwise distances between species (Petchey & Gaston 2006). Two additional indices of individual-level trait diversity have recently been proposed (Fontana et al. 2016). However, the high dimensionality of our data made the calculation of these two indices computationally impossible, and so they were not considered further.
The five FD indices above were each calculated in three different ways, using recorded data on species richness and abundance in each habitat (594 individuals of 58 species in primary forest, 739 individuals of 63 species in logged forest; Appendix S3 in Edwards et al. 2013a) in each case.

First, we followed established methods that used species-level data and weighted each species by its abundance but took no account of ITV (e.g. Villéger et al. 2008; Petchey & Gaston 2002). In these methods, and in each of our three approaches to calculating functional diversity, traits act as coordinates in functional space, thus identifying a species’ functional niche (Villéger et al., 2008).

Species were weighted by their relative abundance and correlated traits were down-weighted, but no further *a priori* assumption was made regarding the functional importance of any given trait. We calculated a distance matrix based on functional trait dissimilarity between the traits of all species in each community using the Gower distance measure, before running a principal coordinates analysis (PCoA) to calculate a new trait matrix of transformed coordinates. PCoA axes were then used to calculate the functional measures using a multidimensional convex hull to position species in functional trait space (Petchey & Gaston 2002; Villéger et al., 2008; Pavoine et al. 2009).

Second, we calculated ‘individual-level baseline’ indices by using the same methods and equations as above but treating every individual as a separate data point and giving all individuals of a species the same literature-based mean value for each trait (i.e. assuming identical individuals within each species). This approach yielded FD statistics that did not take account of individual trait variation but were more directly comparable with our individual-based models incorporating ITV (see below; Figure S1).

Third, we calculated each of our five functional diversity statistics once again, this time incorporating ITV. In principle, we might have achieved this by using measured trait data from all individuals sampled in each habitat. However, in most cases, including ours, such data are not available for most traits but data are available on the average values and/or levels of variation among individuals of each species. Hence we used these data to simulate virtual communities.
comprising individuals drawn at random from within the frequency distribution of trait values estimated for each species, following the steps below:

(i) We noted or estimated the mean and standard deviation (SD) of each trait for each species. Data on trophic positions were taken from Table S3 of Edwards et al. (2013a). Data on dietary composition and foraging substrates (from Wilman et al. 2014) were mean percentages of resources obtained from different categories. Assuming that 95% of individuals were within ± 20% of each species’ mean, with symmetrical data bounded by 0% and 100%, the SD (calculated as [95% range]/4; Hozo et al. 2005) was then 10% of the mean in most cases (smaller for means close to 0% or 100%; see Supporting Information and Table S1 for further information). Data on body mass and clutch size (see Table S1 for data sources) were overall ranges. Assuming the median was the midpoint of each range, we then calculated SDs in each case using Equation 1 below (Formula 16 in Hozo et al. 2005; this estimate makes no assumptions about the distribution of the underlying data).

\[ S^2 = \frac{1}{12} ((a-2m+b)^2)/4 + (b-a)^2 \]  
Equation 1

S = standard deviation, m = median, a = minimum value, b = maximum value.

(ii) We used recorded and estimated means and SDs for each species to generate a Gaussian frequency distribution for each trait in each habitat (Figure 1) and assigned trait values to each individual by drawing them at random from the frequency distribution for that species.

(iii) We used these ‘virtual’ individuals to calculate each of our five FD indices across all individuals in each habitat.

(iv) We repeated steps (ii) and (iii) above 1000 times to generate habitat-specific means for each FD index. We also calculated 95% confidence intervals (CIs) as the 2.5th and 97.5th percentiles of the distribution of simulated values for each index, and used single-sample t-tests to compare the distribution of simulated values with the individual-level baseline value in each case.
(v) We next calculated 95% CIs for the difference between natural and degraded forest for each FD index. We did this by generating a distribution of simulated differences between habitats for each iteration, and taking the 2.5th percentile and 97.5th percentile as the 95% CI. We also calculated the proportion of iterations in which primary forest had higher FD than logged forest and considered a proportion >0.95 or <0.05 to indicate a significant difference between habitats.

(vi) We have provided R-code for this new bootstrapping procedure (steps ii – v above), which we call btFD.

Results

Using established methods of calculation that took no account of ITV, three FD indices (FEve, FDis and RaoQ) were higher in primary forest than in logged forest whereas FD_{PG} was higher in logged forest (Table 1). Differences between habitats were, however, small and FRic was almost identical in primary and logged forest (Table 1). This overall pattern was not substantially altered by treating every individual as a separate data point and giving all individuals of a species the same mean value for each trait (individual-level baseline FD values; Table 1 and horizontal lines in Figure 2) although FRic was slightly higher in primary forest than in logged forest using this method.

Effects of incorporating ITV on FD values

Regardless of habitat, bootstrapping to account for ITV produced values that were significantly lower than individual-level baselines for FRic, FDis, RaoQ and FD_{PG} but higher than these baselines for FEve (Figure 2; single sample t-tests = P<0.0001 in all cases). Hence accounting for ITV resulted in a lower divergence but a more even distribution of individuals in functional trait space within each habitat. When accounting for ITV, two indices (FDis and RaoQ) were significantly higher in primary forest, with no significant difference between habitats for the other three indices (see 95% CIs of differences between habitats and associated probability values in Table 2). Hence, accounting for ITV
revealed previously unrecognized impacts of selective logging on FD through a reduction in the dispersion of individuals in functional trait space in logged forest (Figure S2).

Discussion

Our study addresses the growing recognition of the importance of incorporating intraspecific trait variation (ITV) into measures of Functional Diversity (FD) within and among communities (Cianciaruso et al. 2009; Albert et al. 2010b; Griffiths et al. 2016). We develop a method for incorporating ITV when trait data are unavailable at the individual level. Using this method, we found that estimates of FD incorporating ITV produced quantitatively different results to those based on species’ mean trait values, which are used most commonly in studies of FD. The rank order of FD for the two communities we examined, indicating whether diversity was higher in primary or logged forest, was largely unchanged by the inclusion of ITV. However, by accounting for ITV, we were able to reveal previously unrecognized impacts of selective logging on FD through a lower dispersion of individuals in functional trait space in logged forest (Figure 2,S2).

We found that incorporation of ITV significantly altered all indices of FD compared to individual-level baseline values (Table 1), highlighting the importance of accounting for within-species variation in functional traits (Fontana et al. 2016). Four indices (FRic, FDis, RaoQ and FD\textsubscript{PG}) were significantly lower after accounting for ITV whereas FEve was significantly higher, probably reflecting differences among indices in the weighting given to the overall range of trait values present versus the distribution of traits within the overall range (Albert et al. 2010a; Fontana et al. 2016). For instance, FRic measures the volume of trait space occupied by individuals within each habitat as a proportion of that across both habitats combined (Villéger et al. 2008). For any trait, the maximum difference between any two individuals of different species cannot be smaller than that between average individuals and will always tend to be larger (e.g. the difference between the lightest bird of the lightest species and the heaviest bird of the heaviest species is greater than that between the average weight of the lightest and heaviest species). However, this effect was greater...
across both habitats combined than within either primary or logged forest, due to a greater range of
species, and hence trait values, present across both habitats combined. Consequently, there were
lower values for FRic (and for the other three distance-based measures: FDis, RaoQ and FD\textsubscript{PG}) in both
habitats after accounting for ITV.

In contrast, FEve is related to how individuals are distributed within the overall volume of
functional trait space occupied. In this case, attributing the same (mean) trait values to all individuals
of a species resulted in a more clumped distribution of individuals in trait space and hence lower
values than those obtained after accounting for ITV. It should be stressed, however, that
incorporating ITV had little effect on the rank order of FD for the two communities we examined,
suggesting that ignoring ITV did not introduce any systematic biases into the comparison between
habitats. Further work is now needed to establish the degree to which intraspecific trait variation
influences assessments of ecosystem dynamics, redundancy and stability (Bolnick \textit{et al.} 2011;

Human-induced habitat degradation can lead to systematic changes in some traits within a
species, through a combination of phenotypic plasticity and the selective disappearance of
individuals with particular phenotypes (Edwards \textit{et al.} 2013a; Hamer \textit{et al.} 2015). In this system for
example, Edwards \textit{et al.} (2013a) and Hamer \textit{et al.} (2015) found that understory bird species that
were present in both primary and logged forest had higher trophic positions in the latter, suggesting
a shift towards feeding on more predatory arthropods and/or less fruit. Edwards \textit{et al.} (2013a) also
found a decline in specialist frugivorous and insectivorous birds following two rounds of logging.
Thus, although logged forests retained similar levels of functional diversity to primary forest when
disregarding intraspecific variation, the composition of species in logged forest was significantly
altered, with functionally unique, endemic or endangered birds often being replaced with more
generalist species of lower conservation concern (Edwards \textit{et al.} 2011; Edwards \textit{et al.} 2013b). That
said, in keeping with previous studies of FD (see Table 1 in Edwards \textit{et al.} 2014), we do not consider
such effects, which would cloud the question of how within-habitat ITV affects measures of FD.
As the resolution of global trait databases increases (e.g. Wilman et al. 2014), the ease with which studies of FD can simulate realistic ITV improves. However, these trait databases must be based on large enough sample sizes to accurately account for the degree of ITV for any given species (Griffiths et al. 2016). Our simulation approach, which bootstraps literature-based trait values to produce a range of virtual communities, calculates the range of values that FD could take when measured at the individual level. We can then use our new btFD bootstrapping procedure to determine the probability that a given FD index is higher in a given community when accounting for ITV. Hence our bootstrapping analysis should be useful for determining the confidence that can be placed in conclusions based on simulation approaches. Whilst bootstrapping procedures are well established, we believe that the adoption of these methods for investigating the impacts of ITV on functional diversity has potential to provide continuing insight, particularly considering the sparsity of reliable data on intraspecific variation of functional traits for most species.

In conclusion, we support a much greater emphasis on intraspecific trait variation in studies of functional ecology, including relationships between functional diversity and ecosystem processes and stability (Solé & Montoya 2001; Ricotta et al. 2016). Additionally, because ITV is a fundamental component of evolutionary processes, increasing incorporation of ITV into eco-evolutionary models should prove interesting. Regardless of whether empirical or simulation-based approaches to quantifying intraspecific trait variation are taken, we support a shift towards studies of functional diversity that consider information at the critical scale: that of the individual (Bolnick et al. 2003; Clark et al. 2011).

Acknowledgements

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Trust for Ornithology. This work was supported by a research grant from the Leverhulme Trust, who played no part in the design of the study, the collection, analysis or interpretation of data, the writing of the paper or the decision to submit the paper for publication. We thank Thomas Cornulier for helpful discussion around simulating virtual individuals in our model and the handling of sparse data. SRP-JR was supported by the University of Leeds. CH was supported by a Marie Curie International Incoming Fellowship within the 7th European Community Framework Programme.

Data Accessibility

Community composition data: available from Edwards et al. (2013a) supplementary information (doi: 10.1111/cobi.12059)

Functional trait data: Sources listed in supporting information.

btFD R script: Uploaded as online supporting information.

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Table 1. Functional diversity (FD) of birds in primary and logged forests in northern Borneo, calculated using three different methods for five FD indices.

Established methods use species-level data. Individual-level baselines treat every individual as a separate data point and give all individuals of a species the same literature-based mean value for each trait. Mean Intraspecific Trait Variation (ITV) values and 95% Confidence Intervals (CIs) are from 1000 bootstrapped iterations of trait data, incorporating intraspecific trait variation. See text for further explanation of indices and methods.

<table>
<thead>
<tr>
<th>Type of forest</th>
<th>FD Index</th>
<th>Established method</th>
<th>Individual-level baseline method</th>
<th>Mean ITV value</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary (unlogged)</td>
<td>FRic</td>
<td>0.003</td>
<td>0.014</td>
<td>3.55x10^{-6}</td>
<td>2.41x10^{-6}</td>
<td>5.51x10^{-6}</td>
</tr>
<tr>
<td></td>
<td>FEve</td>
<td>0.671</td>
<td>0.094</td>
<td>0.995</td>
<td>0.995</td>
<td>0.995</td>
</tr>
<tr>
<td></td>
<td>FDis</td>
<td>0.178</td>
<td>0.178</td>
<td>0.168</td>
<td>0.165</td>
<td>0.170</td>
</tr>
<tr>
<td></td>
<td>RaoQ</td>
<td>0.035</td>
<td>0.035</td>
<td>0.031</td>
<td>0.030</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>FD&lt;sub&gt;PG&lt;/sub&gt;</td>
<td>2343.5</td>
<td>2312.1</td>
<td>1472.5</td>
<td>1413.8</td>
<td>1531.4</td>
</tr>
<tr>
<td></td>
<td>FRic</td>
<td>0.003</td>
<td>0.003</td>
<td>3.27x10^{-6}</td>
<td>2.29x10^{-6}</td>
<td>4.93x10^{-6}</td>
</tr>
<tr>
<td></td>
<td>FEve</td>
<td>0.653</td>
<td>0.083</td>
<td>0.995</td>
<td>0.995</td>
<td>0.995</td>
</tr>
<tr>
<td></td>
<td>FDis</td>
<td>0.165</td>
<td>0.165</td>
<td>0.156</td>
<td>0.152</td>
<td>0.160</td>
</tr>
<tr>
<td></td>
<td>RaoQ</td>
<td>0.030</td>
<td>0.030</td>
<td>0.026</td>
<td>0.025</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>FD&lt;sub&gt;PG&lt;/sub&gt;</td>
<td>2691.5</td>
<td>2682.7</td>
<td>1488.2</td>
<td>1410.4</td>
<td>1564.1</td>
</tr>
</tbody>
</table>
Table 2. Statistical comparison of Functional Diversity (FD) measures for birds in primary and logged Bornean forests, based on trait data bootstrapped 1000 times. Mean differences in FD between primary and logged forest were calculated for each index, together with 95% Confidence Intervals (CIs). For each index, \( P \) (Primary > Logged) is the proportion of 1000 bootstrapped iterations of trait data that gave a higher value in primary forest.

<table>
<thead>
<tr>
<th>Index</th>
<th>Difference between Primary and Logged FD</th>
<th>Lower 95% CI of Difference</th>
<th>Upper 95% CI of Difference</th>
<th>( P ) (Primary &gt; Logged)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( FRic )</td>
<td>2.77x10^{-7}</td>
<td>-1.83x10^{-6}</td>
<td>2.61x10^{-6}</td>
<td>0.594</td>
</tr>
<tr>
<td>( FEve )</td>
<td>-2.44x10^{-4}</td>
<td>-6.16x10^{-4}</td>
<td>2.16x10^{-4}</td>
<td>0.125</td>
</tr>
<tr>
<td>( FDis )</td>
<td>0.012</td>
<td>0.007</td>
<td>0.016</td>
<td>1.000</td>
</tr>
<tr>
<td>( RaoQ )</td>
<td>0.004</td>
<td>0.003</td>
<td>0.006</td>
<td>1.000</td>
</tr>
<tr>
<td>( FD_{PG} )</td>
<td>-15.680</td>
<td>-111.100</td>
<td>85.700</td>
<td>0.368</td>
</tr>
</tbody>
</table>
Figure 1. Simulated variation in body mass for a representative selection of birds in primary forest in northern Borneo. Vertical lines show mean body mass for each species (see Table S1 for data sources). Kernel densities represent the range of generated body mass values in our individual-based model, for six species of different abundance (data from Appendix S3 in Edwards et al. 2013a). Grey dotted lines, *Arachnothera longirostra* (N=79); black dotted lines, *Hypogramma hypogrammicum* (N=24); black solid lines, *Stachyris erythroptera* (N=21); grey dashed lines, *Hypothymis azurea* (N=5); Black dashed lines, *Orthotomus sericeus* (N=3); grey solid lines, *Rhipidura perlata* (N=3).

Figure 2. Individual-based functional diversity (FD) of birds in primary and logged forest. Boxplots show bootstrapped means, SDs, 95% confidence intervals and values beyond this range for primary forest (white box) and logged forest (grey box), for (a) functional richness, (b) functional evenness, (c) functional dispersion, (d) Rao’s quadratic entropy and (e) Petchey and Gaston’s FD$_{PG}$. Each index took account of intraspecific trait variation (ITV). Horizontal lines are individual-level baseline FD values, calculated using identical individuals and mean trait values for primary forest (solid line) and logged forest (dashed line). Y axes are broken in (a), (b) and (e) to account for large differences between individual-level baselines and FD values when incorporating ITV.
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