

Incorporating intraspecific trait variation into functional diversity: Impacts of selective logging on birds in Borneo

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Summary

1. As conservation increasingly recognizes 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 find that incorporating ITV significantly alters 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, is largely unchanged by the inclusion of ITV. However, by accounting for ITV, we are 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.

Key-words: bootstrapping, conservation, functional ecology, functional trait, habitat degradation, individual variation, tropical rainforests

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, Mason & Mouillot 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, Middelhoff & Reuter 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 (Díaz & Cabido 2001; Albert *et al.* 2010a; Griffiths *et al.* 2016), which

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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.* (2013b). 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, Edwards & Hamer 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 Supporting Information Table S1 for variables and data sources). Our aim was not to examine the effects of logging on 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 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 Appendix S1).

Five commonly used functional diversity indices were calculated for each community using the 'FD' package (Laliberté, Legendre & Shipley

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, Mason & Moullot 2008 for further details of these two indices); functional dispersion (FDis, Laliberté & Legendre 2010); Rao's quadratic entropy (RaoQ, Rao 1982); and Petchey & 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, Petchey & Pomati 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 (600 individuals of 58 species in primary forest, 735 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. Petchey & Gaston 2002; Villéger, Mason & Moullot 2008). 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, Mason & Moullot 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, Mason & Moullot 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; Fig. 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:

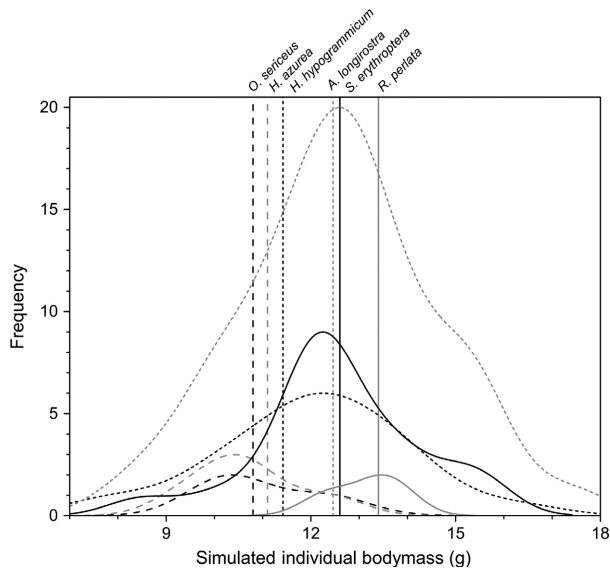


Fig. 1. Simulated variation in body mass for a representative selection of birds in the primary forest in northern Borneo. Vertical lines show mean body mass for each species (see Table S1 for data sources). Kernel densities represent the range of generated body mass values in our individual-based model, 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).

1. 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 $\pm 20\%$ of each species' mean, with symmetrical data bounded by 0% and 100%, the SD (calculated as $[95\% \text{ range}]/4$; Hozo *et al.* 2005) was then 10% of the mean in most cases (smaller for means close to 0% or 100%; see Appendix S1 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 mid-point

of each range, we then calculated SDs in each case using eqn (1) below (Formula 16 in Hozo *et al.* 2005; this estimate makes no assumptions about the distribution of the underlying data).

$$S^2 = \frac{1}{12} \left(\frac{((a - 2m + b)^2)}{4 + (b - a)^2} \right) \quad \text{eqn 1}$$

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

2. We used recorded and estimated means and SDs for each species to generate a Gaussian frequency distribution for each trait in each habitat (Fig. 1) and assigned trait values to each individual by drawing them at random from the frequency distribution for that species.
3. We used these 'virtual' individuals to calculate each of our five FD indices across all individuals in each habitat.
4. We repeated steps (2) and (3) 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.
5. We next calculated 95% CIs for the difference between primary and logged 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% CIs. 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.
6. We have provided R-code for this new bootstrapping procedure (steps 2–5 above), which we call *btFD* (see Data S1).

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

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

Type of forest	FD index	Established method	Individual-level baseline method	Mean ITV value	Lower 95% CI	Upper 95% CI
Primary (unlogged)	FRic	0.003	0.014	3.55×10^{-6}	2.41×10^{-6}	5.51×10^{-6}
	FEve	0.671	0.094	0.995	0.995	0.995
	FDis	0.178	0.178	0.168	0.165	0.170
	RaoQ	0.035	0.035	0.031	0.030	0.032
	FD_{PG}	2343.5	2312.1	1472.5	1413.8	1531.4
Logged	FRic	0.003	0.003	3.27×10^{-6}	2.29×10^{-6}	4.93×10^{-6}
	FEve	0.653	0.083	0.995	0.995	0.995
	FDis	0.165	0.165	0.156	0.152	0.160
	RaoQ	0.030	0.030	0.026	0.025	0.027
	FD_{PG}	2691.5	2682.7	1488.2	1410.4	1564.1

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.

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 Fig. 2) although FRic was slightly higher in primary forest than in logged forest using this method.

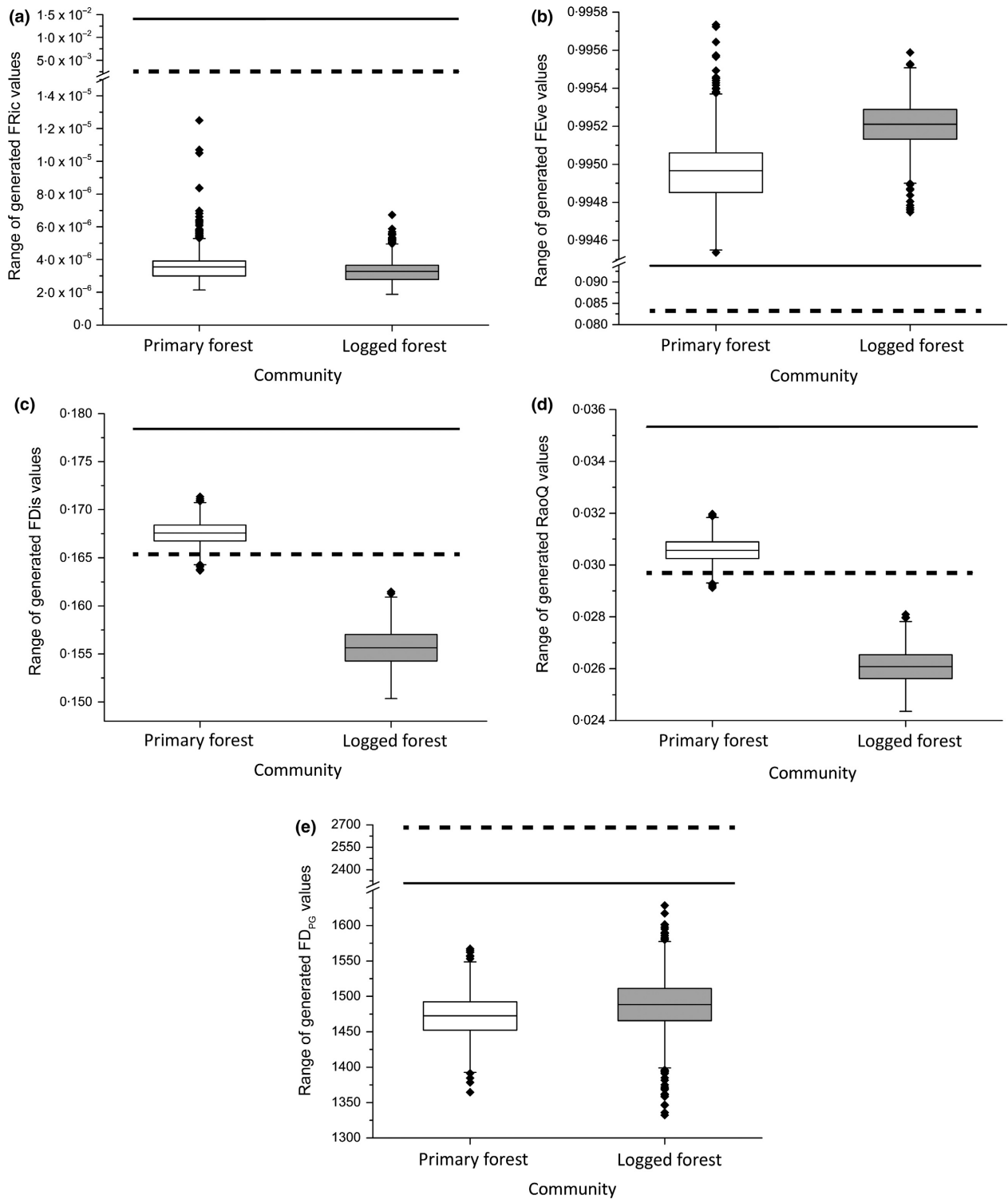


Fig. 2. Individual-based functional diversity (FD) of birds in primary and logged forest. Boxplots show bootstrapped means, SDs, 95% confidence intervals and values beyond this range for primary forest (white box) and logged forest (grey box), for (a) functional richness, (b) functional evenness, (c) 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.

Table 2. Statistical comparison of functional diversity (FD) measures for birds in primary and logged Bornean forests, based on trait data bootstrapped 1000 times

Index	Difference between Primary and Logged FD	Lower 95% CI of Difference	Upper 95% CI of Difference	<i>P</i> (Primary > Logged)
FRic	2.77×10^{-7}	-1.83×10^{-6}	2.61×10^{-6}	0.594
FEve	-2.44×10^{-4}	-6.16×10^{-4}	2.16×10^{-4}	0.125
FDis	0.012	0.007	0.016	1.000
RaoQ	0.004	0.003	0.006	1.000
FD _{PG}	-15.680	-111.100	85.700	0.368

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.

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 (Fig. 2; single sample *t*-tests = *P* < 0.0001 in all cases). Thus, 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 (Fig. S2).

Discussion

Our study addresses the growing recognition of the importance of incorporating ITV into measures of FD within and among communities (Cianciaruso *et al.* 2009; Albert *et al.* 2010b; Griffiths *et al.* 2016). We developed 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 (Figs 2 and 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, Petchey & Pomati 2016). Four indices (FRic, FDis, RaoQ and FD_{PG}) were significantly lower after accounting for ITV whereas FEve was higher, probably reflecting differences among indices in the weighting given to the overall range of trait values

present vs. the distribution of traits within the overall range (Albert *et al.* 2010a; Fontana, Petchey & Pomati 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, Mason & Mouillot 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_{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 ITV influences assessments of ecosystem dynamics, redundancy and stability (Bolnick *et al.* 2011; Donohue *et al.* 2016; Ricotta *et al.* 2016).

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 *et al.* 2013a; Hamer *et al.* 2015). In this system for example, Edwards *et al.* (2013a) and Hamer *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 *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 *et al.* 2011, 2013b). That said, in keeping with previous studies of FD (see table 1 in Edwards *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 particular 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 ITV 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 ITV 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).

Authors' contributions

S.R.P.-J.R. and K.C.H. conceived the ideas and all authors designed the methodology; F.A.E., D.P.E. and K.C.H. collected the field data; S.R.P.-J.R. collated the data from different published sources; S.R.P.-J.R., C.H. and W.J.E.H. wrote the code and produced the models and simulations; S.R.P.-J.R., C.H. and W.J.E.H. analysed the data; S.R.P.-J.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Uploaded as supporting information is a pdf-file which provides full details on the primary sources used for gathering functional trait data. Data on avian community composition for primary and logged forest communities is available from the original supplementary information of Edwards *et al.* (2013a) doi: 10.1111/cobi.12059, but has also been archived in association with this paper; data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.5vr09> (Ross *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Appendix S1 includes: **1** Descriptions of functional trait data, justification behind their use, and the primary sources used during their collection (Table S1). **2** Comparisons between established functional diversity indices and our modified individual-level baseline functional diversity values, including Figure S1. **3** A conceptual figure (S2) illustrating our main findings, as referenced in the main text.

Data S1. *btFD* R script. R script demonstrating methods for calculating 95% confidence intervals for ranges of produced functional diversity values, for generating the proportion of functional diversity values that were in a given direction and hence how much confidence should be placed in results (*btFD*), and for calculating 95% confidence intervals for the difference between functional diversity values of the focal communities.