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1 Incorporating intraspecific trait variation into functional diversity:

2 Impacts of selective logging on birds in Borneo

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22 published sources; SRP-JR, CH and WJEH wrote the code and produced the models and simulations;
23 SRP-JR, CH and WJEH analysed the data; SRP-JR led the writing of the manuscript. All authors
24 contributed critically to the drafts and gave final approval for publication.

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26 **Abstract**

- 27 1. As conservation increasingly recognises the importance of species' functional roles in
28 ecosystem processes, studies are shifting away from measuring species richness towards
29 measures that account for the functional differences between species in a community.
30 These functional diversity (FD) indices have received much recent attention and refinement,
31 but their greatest limitation remains their inability to incorporate information about
32 intraspecific trait variation (ITV).
- 33 2. We use an individual-based model to account for ITV when calculating the functional
34 diversity of two avian communities in Borneo; one in primary (unlogged) forest and one in
35 selectively logged forest. We deal with the scarcity of trait data for individual species by
36 developing a simulation approach, taking data from the literature where necessary. Using a
37 bootstrapping procedure, we produce a range of ecologically feasible FD values taking
38 account of ITV for five commonly-used FD indices, and we quantify the confidence that can
39 be placed in these values using a newly-developed bootstrapping method: *btFD*.
- 40 3. We found that incorporating ITV significantly altered the FD values of all indices used in our
41 models. The rank order of FD for the two communities, indicating whether diversity was
42 higher in primary or selectively logged forest, was largely unchanged by the inclusion of ITV.
43 However, by accounting for ITV, we were able to reveal previously unrecognized impacts of
44 selective logging on avian functional diversity through a narrower dispersion of individuals in
45 functional trait space in logged forest.
- 46 4. Our results highlight the importance of incorporating ITV into measures of functional
47 diversity, whilst our simulation approach addresses the frequently encountered difficulty of
48 working with sparse trait data and quantifies the confidence that should be placed in such
49 findings.

50

51 **Introduction**

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

61 One solution to this problem is to use measures of functional diversity (FD), which seek to
62 quantify the range of functional (i.e. trait) differences among species in a community (Tilman *et al.*
63 1997; Petchey & Gaston 2002), thus bridging the gap between species diversity and composition. FD
64 can be measured using a variety of different indices (Petchey & Gaston 2006; Villéger *et al.* 2008).
65 However, a limitation of most FD studies to date is that they have largely ignored intraspecific trait
66 variation (ITV) despite widespread recognition that ITV is critical to a range of ecological and
67 evolutionary processes (Breckling *et al.* 2006; Albert *et al.* 2010a; Bolnick *et al.* 2011; Andersen *et al.*
68 2012; de Bello *et al.* 2013), and that by disregarding variation, this forces assumptions of rigid
69 functional space occupancy (Al Haj Khaled *et al.* 2005). Despite this problem, few studies have
70 addressed the issue of how to incorporate ITV into measures of FD, particularly for taxa other than
71 plants (Diaz & Cabido 2001; Albert *et al.* 2010a; Griffiths *et al.* 2016), which potentially restricts the
72 ability of FD indices to accurately represent real ecosystems (de Bello *et al.* 2011; Albert *et al.* 2012).

73 In this study, we explore the application of ITV and its consequences for the measurement of
74 FD in primary (unlogged) and logged tropical forest in Sabah, Borneo. We use community data from
75 a previous study (Edwards *et al.* 2013a) to calculate FD for bird communities in primary forest and in
76 forest that had been subjected to repeated rounds of selective logging, following Edwards *et al.*

77 (2013b). We incorporate ITV into well-established FD indices using a simulation approach based on
78 ecologically realistic trait values from the literature (Cianciaruso *et al.* 2009; Flynn *et al.* 2009; Santini
79 *et al.* 2016). This approach not only addresses the frequently occurring problem of sparse or low-
80 resolution trait data in studies of conservation ecology but it also helps to elucidate the impact of
81 ITV on the functional consequences of selective logging in this system. In addition, we develop a
82 bootstrapping method to quantify the confidence that can be placed in the calculated differences in
83 FD between communities, and to assign a probability that such differences could have occurred by
84 chance.

85

86 **Materials and Methods**

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

101 Published data on avian species identity and abundance in primary (unlogged) and logged
102 forest were obtained from the literature (Edwards *et al.* 2013a) as were data for 14 different

103 functional traits reflecting dietary composition, trophic position, foraging substrate and resource
104 requirements (see Table S1 for variables and data sources). Our aim was not to examine the effects
105 of logging on functional diversity (FD) *per se*, which have already been examined in detail in these
106 forests for both birds (Edwards *et al.* 2013b) and dung beetles (Edwards *et al.* 2014), but to
107 determine how incorporating intraspecific trait variation (ITV) affects different measures of FD and
108 the conclusions drawn from them. Hence we did not include all possible functional traits, but instead
109 focused mainly on those related to foraging and resource requirements (see Supporting
110 Information).

111 Five commonly used functional diversity indices were calculated for each community using
112 the 'FD' package [Laliberté *et al.* 2014] and the *Xtree* function [Schumacher, 2003] in R version 3.2.2
113 (R Development Core Team, 2016). These were: Functional Richness (FRic) and Functional Evenness
114 (FEve; see Mason *et al.* 2005 and Villéger *et al.* 2008 for further details of these two indices);
115 Functional Dispersion (FDis, Laliberté & Legendre 2010); Rao's Quadratic Entropy (RaoQ, Rao 1982);
116 and Petchey and Gaston's (2002) FD index (FD_{PG}). At the species level, FRic measures the volume of
117 functional trait space occupied by a community and reflects the richness of functional roles
118 performed by species; FEve measures the evenness of species abundances and of distances among
119 species in functional space; FDis and RaoQ both measure the dispersion of species in trait space. FDis
120 weights species by their relative abundances and measures the mean distance of individual species
121 to the weighted functional space centroid (Laliberté & Legendre 2010) whereas RaoQ is calculated as
122 the mean distance between randomly-selected pairs of species in functional space (Botta-Dukát
123 2005). Finally, FD_{PG} sums the total branch length of a hierarchical functional dendrogram connecting
124 all species in functional space, based on pairwise distances between species (Petchey & Gaston
125 2006). Two additional indices of individual-level trait diversity have recently been proposed (Fontana
126 *et al.* 2016). However, the high dimensionality of our data made the calculation of these two indices
127 computationally impossible, and so they were not considered further.

128 The five FD indices above were each calculated in three different ways, using recorded data
129 on species richness and abundance in each habitat (594 individuals of 58 species in primary forest,
130 739 individuals of 63 species in logged forest; Appendix S3 in Edwards *et al.* 2013a) in each case.
131 First, we followed established methods that used species-level data and weighted each species by its
132 abundance but took no account of ITV (e.g. Villéger *et al.* 2008; Petchey & Gaston 2002). In these
133 methods, and in each of our three approaches to calculating functional diversity, traits act as
134 coordinates in functional space, thus identifying a species' functional niche (Villéger *et al.*, 2008).
135 Species were weighted by their relative abundance and correlated traits were down-weighted, but
136 no further *a priori* assumption was made regarding the functional importance of any given trait. We
137 calculated a distance matrix based on functional trait dissimilarity between the traits of all species in
138 each community using the Gower distance measure, before running a principal coordinates analysis
139 (PCoA) to calculate a new trait matrix of transformed coordinates. PCoA axes were then used to
140 calculate the functional measures using a multidimensional convex hull to position species in
141 functional trait space (Petchey & Gaston 2002; Villéger *et al.*, 2008; Pavoine *et al.* 2009).

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

148 Third, we calculated each of our five functional diversity statistics once again, this time
149 incorporating ITV. In principle, we might have achieved this by using measured trait data from all
150 individuals sampled in each habitat. However, in most cases, including ours, such data are not
151 available for most traits but data are available on the average values and/or levels of variation
152 among individuals of each species. Hence we used these data to simulate virtual communities

153 comprising individuals drawn at random from within the frequency distribution of trait values
154 estimated for each species, following the steps below:

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

165

$$166 \quad S^2 = 1/12 (((a-2m+b)^2)/4 + (b-a)^2) \quad \text{Equation 1}$$

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

168

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

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

174 (iv) We repeated steps (ii) and (iii) above 1000 times to generate habitat-specific means for
175 each FD index. We also calculated 95% confidence intervals (CIs) as the 2.5th and 97.5th percentiles of
176 the distribution of simulated values for each index, and used single-sample t-tests to compare the
177 distribution of simulated values with the individual-level baseline value in each case.

178 (v) We next calculated 95% CIs for the difference between natural and degraded forest for
179 each FD index. We did this by generating a distribution of simulated differences between habitats
180 for each iteration, and taking the 2.5th percentile and 97.5th percentile as the 95% CI. We also
181 calculated the proportion of iterations in which primary forest had higher FD than logged forest and
182 considered a proportion >0.95 or <0.05 to indicate a significant difference between habitats.

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

185

186 **Results**

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

194

195 *Effects of incorporating ITV on FD values*

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

203 revealed previously unrecognized impacts of selective logging on FD through a reduction in the
204 dispersion of individuals in functional trait space in logged forest (Figure S2).

205

206 **Discussion**

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

217 We found that incorporation of ITV significantly altered all indices of FD compared to
218 individual-level baseline values (Table 1), highlighting the importance of accounting for within-
219 species variation in functional traits (Fontana *et al.* 2016). Four indices (FRic, FDis, RaoQ and FD_{PG})
220 were significantly lower after accounting for ITV whereas FEve was significantly higher, probably
221 reflecting differences among indices in the weighting given to the overall range of trait values
222 present versus the distribution of traits within the overall range (Albert *et al.* 2010a; Fontana *et al.*
223 2016). For instance, FRic measures the volume of trait space occupied by individuals within each
224 habitat as a proportion of that across both habitats combined (Villéger *et al.* 2008). For any trait, the
225 maximum difference between any two individuals of different species cannot be smaller than that
226 between average individuals and will always tend to be larger (e.g. the difference between the
227 lightest bird of the lightest species and the heaviest bird of the heaviest species is greater than that
228 between the average weight of the lightest and heaviest species). However, this effect was greater

229 across both habitats combined than within either primary or logged forest, due to a greater range of
230 species, and hence trait values, present across both habitats combined. Consequently, there were
231 lower values for FRic (and for the other three distance-based measures: FDis, RaoQ and FD_{PG}) in both
232 habitats after accounting for ITV.

233 In contrast, FEve is related to how individuals are distributed within the overall volume of
234 functional trait space occupied. In this case, attributing the same (mean) trait values to all individuals
235 of a species resulted in a more clumped distribution of individuals in trait space and hence lower
236 values than those obtained after accounting for ITV. It should be stressed, however, that
237 incorporating ITV had little effect on the rank order of FD for the two communities we examined,
238 suggesting that ignoring ITV did not introduce any systematic biases into the comparison between
239 habitats. Further work is now needed to establish the degree to which intraspecific trait variation
240 influences assessments of ecosystem dynamics, redundancy and stability (Bolnick *et al.* 2011;
241 Donohue *et al.* 2016; Ricotta *et al.* 2016).

242 Human-induced habitat degradation can lead to systematic changes in some traits within a
243 species, through a combination of phenotypic plasticity and the selective disappearance of
244 individuals with particular phenotypes (Edwards *et al.* 2013a; Hamer *et al.* 2015). In this system for
245 example, Edwards *et al.* (2013a) and Hamer *et al.* (2015) found that understory bird species that
246 were present in both primary and logged forest had higher trophic positions in the latter, suggesting
247 a shift towards feeding on more predatory arthropods and/or less fruit. Edwards *et al.* (2013a) also
248 found a decline in specialist frugivorous and insectivorous birds following two rounds of logging.
249 Thus, although logged forests retained similar levels of functional diversity to primary forest when
250 disregarding intraspecific variation, the composition of species in logged forest was significantly
251 altered, with functionally unique, endemic or endangered birds often being replaced with more
252 generalist species of lower conservation concern (Edwards *et al.* 2011; Edwards *et al.* 2013b). That
253 said, in keeping with previous studies of FD (see Table 1 in Edwards *et al.* 2014), we do not consider
254 such effects, which would cloud the question of how within-habitat ITV affects measures of FD.

255 As the resolution of global trait databases increases (e.g. Wilman *et al.* 2014), the ease with
256 which studies of FD can simulate realistic ITV improves. However, these trait databases must be
257 based on large enough sample sizes to accurately account for the degree of ITV for any given species
258 (Griffiths *et al.* 2016). Our simulation approach, which bootstraps literature-based trait values to
259 produce a range of virtual communities, calculates the range of values that FD *could* take when
260 measured at the individual level. We can then use our new *btFD* bootstrapping procedure to
261 determine the probability that a given FD index is higher in a given community when accounting for
262 ITV. Hence our bootstrapping analysis should be useful for determining the confidence that can be
263 placed in conclusions based on simulation approaches. Whilst bootstrapping procedures are well
264 established, we believe that the adoption of these methods for investigating the impacts of ITV on
265 functional diversity has potential to provide continuing insight, particularly considering the sparsity
266 of reliable data on intraspecific variation of functional traits for most species.

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

275

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287

288 **Data Accessibility**

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

291 *Functional trait data*: Sources listed in supporting information.

292 *btFD R script*: Uploaded as online supporting information.

293

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435 **Table 1.** Functional diversity (FD) of birds in primary and logged forests in northern Borneo, calculated using three different methods for five FD indices.
 436 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
 437 same literature-based mean value for each trait. Mean Intraspecific Trait Variation (ITV) values and 95% Confidence Intervals (CIs) are from 1000
 438 bootstrapped iterations of trait data, incorporating intraspecific trait variation. See text for further explanation of indices and methods.
 439

<i>Type of forest</i>	<i>FD Index</i>	<i>Established method</i>	<i>Individual-level baseline method</i>	<i>Mean ITV value</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>
<i>Primary (unlogged)</i>	FRic	0.003	0.014	3.55x10 ⁻⁶	2.41x10 ⁻⁶	5.51x10 ⁻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
<i>Logged</i>	FD _{PG}	2343.5	2312.1	1472.5	1413.8	1531.4
	FRic	0.003	0.003	3.27x10 ⁻⁶	2.29x10 ⁻⁶	4.93x10 ⁻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

440

441 **Table 2.** Statistical comparison of Functional Diversity (FD) measures for birds in primary and logged
 442 Bornean forests, based on trait data bootstrapped 1000 times. Mean differences in FD between
 443 primary and logged forest were calculated for each index, together with 95% Confidence Intervals
 444 (CIs). For each index, P (Primary > Logged) is the proportion of 1000 bootstrapped iterations of trait
 445 data that gave a higher value in primary forest.

446

447

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

448 **Figure 1.** Simulated variation in body mass for a representative selection of birds in primary forest in
449 northern Borneo. Vertical lines show mean body mass for each species (see Table S1 for data
450 sources). Kernel densities represent the range of generated body mass values in our individual-based
451 model, for six species of different abundance (data from Appendix S3 in Edwards et al. 2013a). Grey
452 dotted lines, *Arachnothera longirostra* (N=79); black dotted lines, *Hypogramma hypogrammicum*
453 (N=24); black solid lines, *Stachyris erythroptera* (N=21); grey dashed lines, *Hypothymis azurea* (N=5);
454 Black dashed lines, *Orthotomus sericeus* (N=3); grey solid lines, *Rhipidura perlata* (N=3).

455

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

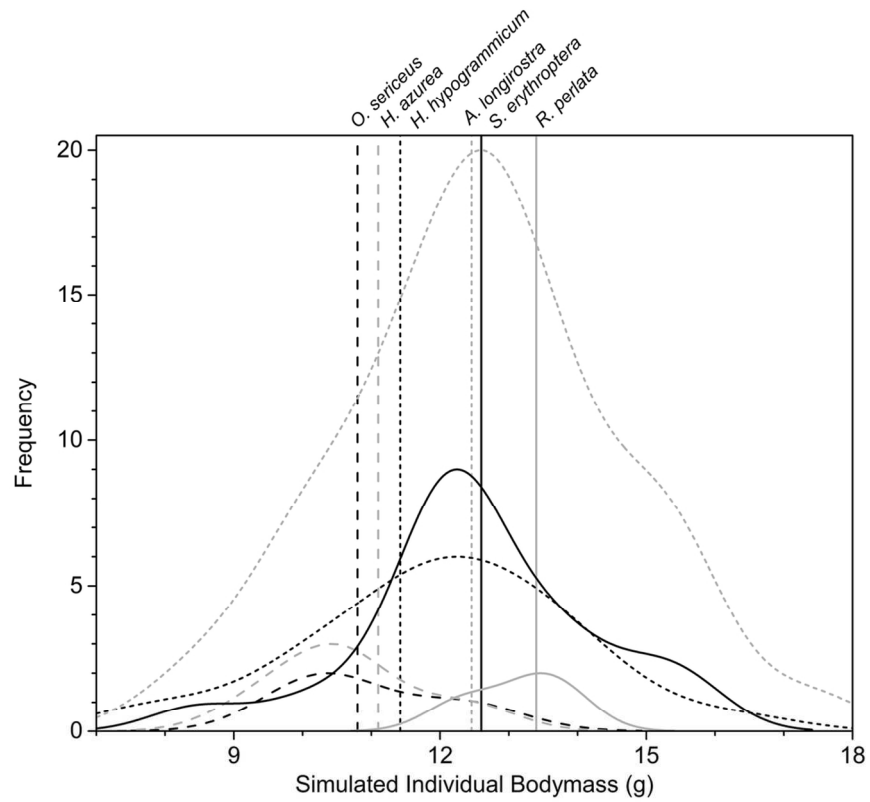


Figure 1. Simulated variation in body mass for a representative selection of birds in primary forest in northern Borneo. Vertical lines show mean body mass for each species (see Table S1 for data sources). Kernel densities represent the range of generated body mass values in our individual-based model,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

54x44mm (600 x 600 DPI)



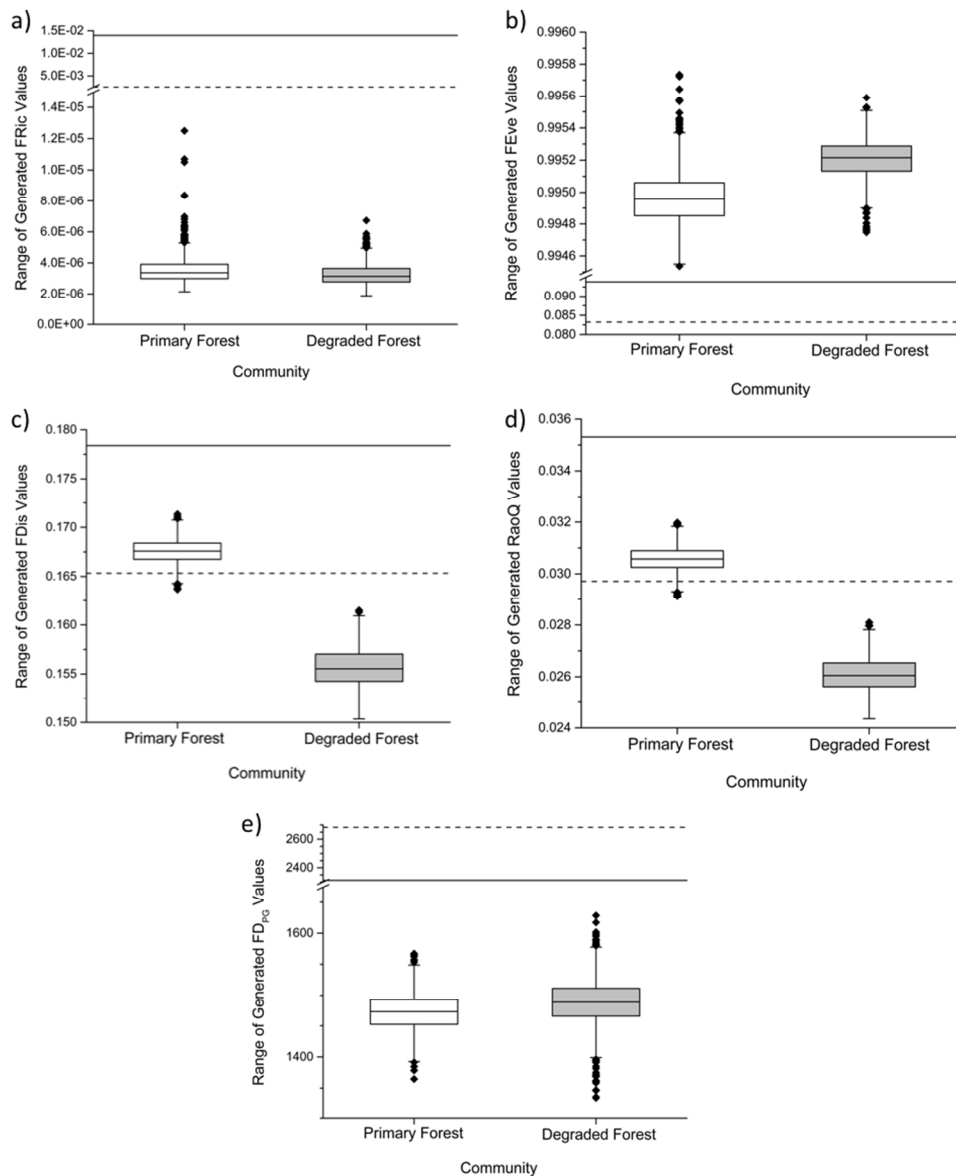


Figure 2. Individual-based functional diversity (FD) of birds in primary and logged forest. Boxplots show bootstrapped means, SDs, 95% confidence intervals and values beyond this range for primary forest (white box) and logged forest (grey box), for (a) functional richness, (b) functional evenness, (c)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