Incorporating intraspecific trait variation into functional diversity:

Impacts of selective logging on birds in Borneo

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SRP-JR, CH and WJEH analysed the data; SRP-JR led the writing of the manuscript. All authors

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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

51 **Introduction**

52 Change in land-use is a major global driver of ecosystem degradation (Brooks *et al.* 2002; Edwards *et*

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*

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*

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 m^3 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 m^3 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

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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

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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 ± 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   $S^2 = 1/12 \, (((a-2m+b)^2)/4 + (b-a)^2)$ 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

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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).

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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

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

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

Index	Difference between Primary and Logged FD	Lower 95% CI of Difference	Upper 95% CI of Difference	P (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

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

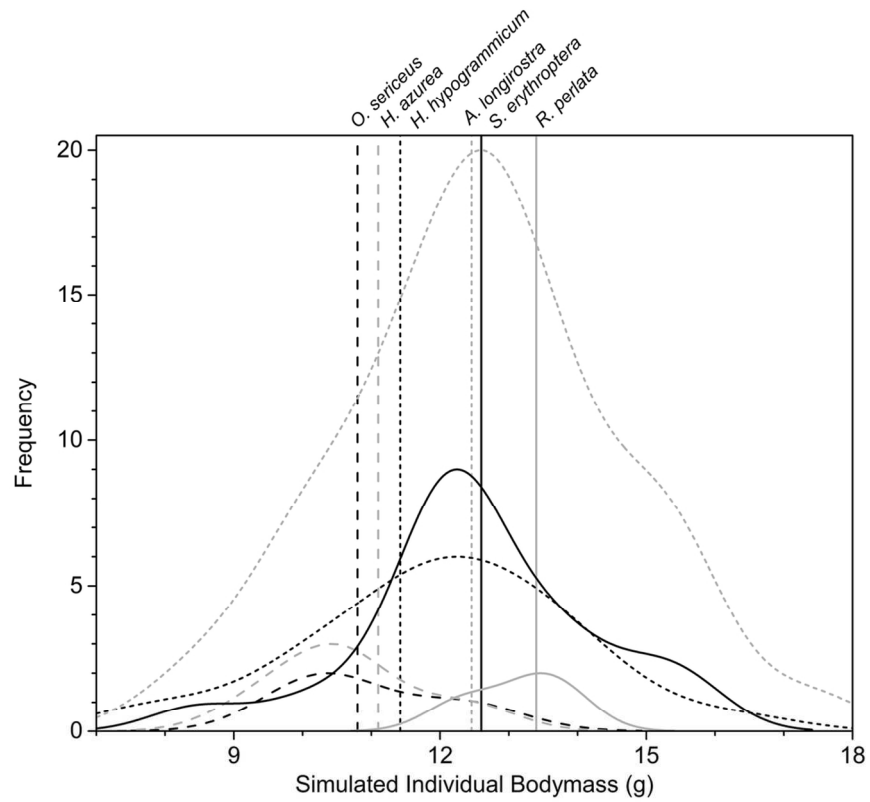463   between individual-level baselines and FD values when incorporating ITV.

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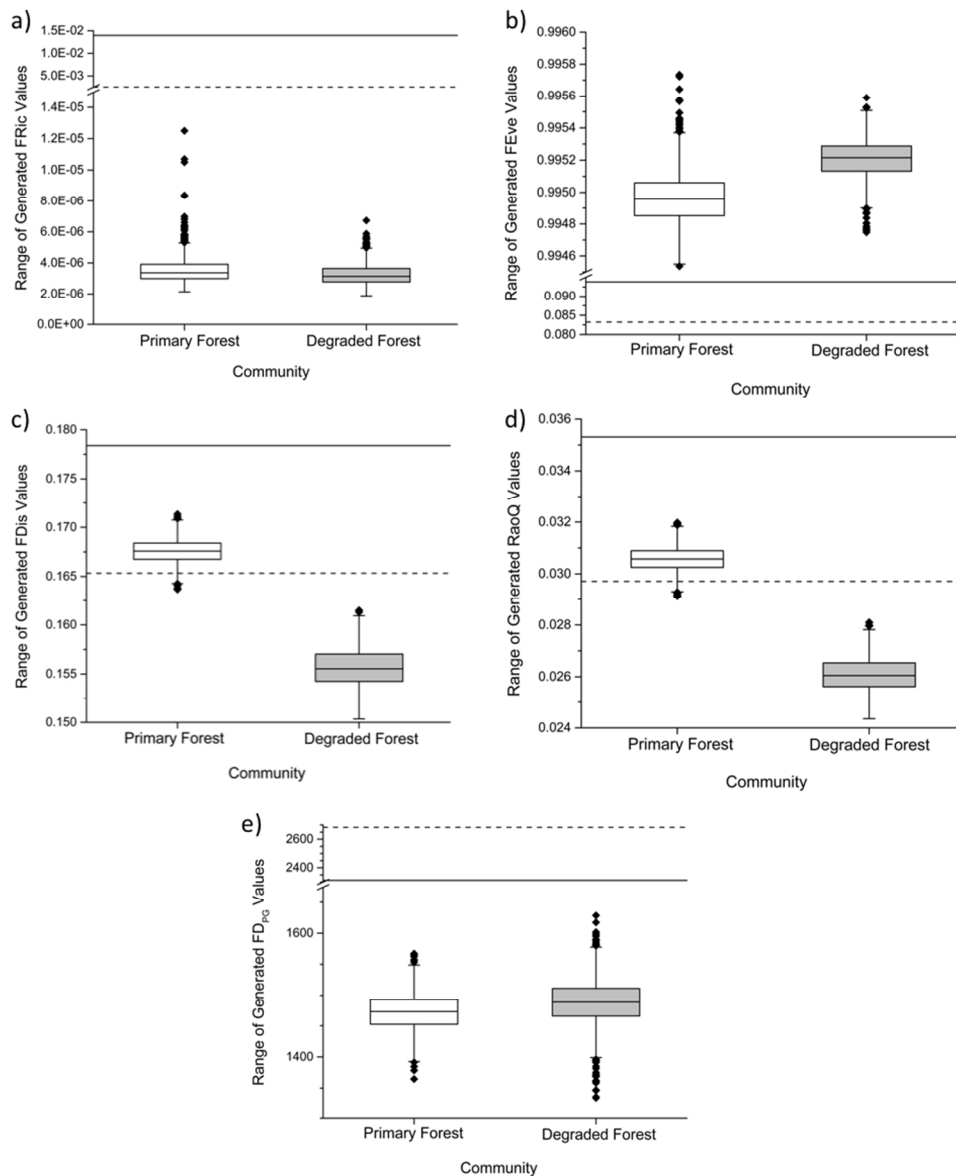
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Figure 2. Individual-based functional diversity (FD) of birds in primary and logged forest. Boxplots show bootstrapped means, SDs, 95% confidence intervals and values beyond this range for primary forest (white box) and logged forest (grey box), for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