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Assessing the relative importance of isolated Ficus trees to insectivorous birds in an Indian human-modified tropical landscape

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1 Title: Assessing the relative importance of isolated *Ficus* trees to insectivorous birds
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23

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32 **Compliance with ethical standards**

33 This research was conducted with ethical approval from the University of Oxford
34 (Departmental CUREC reference number: SOGE C1A-99). Surveys were conducted
35 with permission from local landowners where necessary, and permission to conduct
36 this field work in India was granted by the High Commission of India, London, under
37 visa number 4246496. Field studies did not impact the welfare of the animals studied,
38 and the authors have no conflicts of interest to declare.

39

40

41 **Abstract**

42 The destruction of forest for agricultural expansion has created a vast estate of
43 human-modified land in tropical regions. One group of organisms that are particularly
44 vulnerable to the loss of forest habitat are insectivorous birds. Despite this, few
45 conservation strategies have been identified for this group in human-modified
46 landscapes. We survey the use of 104 isolated trees by insectivorous birds in rural
47 Assam, India. We used an information theoretic model comparison approach to
48 determine the important variables driving insectivorous bird diversity within these
49 isolated trees. Our work demonstrates that the conservation of large trees in human-
50 modified landscapes may play an important role in maintaining bird diversity and
51 ecological function beyond the forest edge. More specifically, we found that isolated
52 *Ficus* trees hold assemblages with particularly high insectivore abundance, richness
53 and functional diversity when compared to other isolated fruit and large trees. We
54 argue that, where present, *Ficus* trees should be actively conserved in human-
55 modified landscapes to maintain the composition of insectivore communities in a
56 “*Ficus* first” strategy.

57 **Keywords** Conservation beyond protected areas, birds, ecological function, *Ficus*,
58 India, insectivores, isolated trees, multimodel inference

59 **Introduction**

60 As agricultural expansion continues to fragment the world’s tropical forests and
61 occupy large areas of land (Phalan et al. 2013), it is increasingly important to devise
62 conservation strategies for human-modified landscapes (Chazdon et al. 2009; Gardner
63 et al. 2009; Melo et al. 2013). The conversion of forest has a range of impacts on
64 different taxa. Here our focus is on the largest avian feeding guild, insectivorous

65 birds, an ecological group that is considered particularly vulnerable to habitat loss
66 (Tschardt et al. 2008).

67 Several studies have demonstrated lower abundance and species richness of
68 insectivores in human-modified landscapes compared to intact forest habitats (Harvey
69 et al. 2006; Şekercioğlu 2012). Studies in habitat fragments have found similar
70 results; especially when there is limited tree cover surrounding fragments (Stouffer
71 and Bierregaard 1995). Not only does this cause deterioration in the conservation
72 status of insectivorous birds (Şekercioğlu et al. 2002), but it also diminishes their
73 beneficial pest control services (Van Bael et al. 2008; Karp and Daily 2013).

74 One possible strategy to mitigate the decline of insectivorous birds in human-
75 modified landscapes might be the conservation of isolated trees (Manning et al. 2006;
76 Cottee-Jones et al. 2015a). These trees can increase the abundance and richness of
77 insectivores by providing connectivity between forest remnants for forest-dependent
78 species (Harvey et al. 2006), along with feeding and nesting sites for matrix-tolerant
79 taxa (Şekercioğlu et al. 2007), thereby moderating the impact of habitat loss
80 (Şekercioğlu 2012). However, our understanding of conservation tools that are
81 appropriate in human-modified landscapes represents a critical frontier in tropical
82 conservation biology (Tschardt et al. 2008; Melo et al. 2013). Indeed, we have very
83 limited experimental evidence to help guide conservation practitioners working in the
84 2.5 billion ha of tropical land area that has been modified by humans (see Supporting
85 Information 1; Fischer et al. 2006; Melo et al. 2013).

86 *Ficus* trees have long been recognised as important food resources for frugivores
87 (Terborgh 1986; Cottee-Jones et al. 2015b), with almost 1,000 frugivorous bird
88 species recorded consuming *Ficus* fruit (Shanahan et al. 2001). They may also be
89 overlooked but important foraging sites for insectivores. Their co-evolved mutualism

90 with pollinating fig wasps (Hymenoptera, Agaonidae, Agaoninae) means that millions
91 of fig wasps (and non-pollinating fig wasps; Hymenoptera, Chalcidoidea) are found in
92 association with fruiting figs (Harrison 2003; Bain et al. 2013). As well as being a
93 food resource for insectivorous birds themselves, these fig wasps are also the prey of
94 other invertebrates that inhabit or visit *Ficus* trees (Schatz et al. 2008). Numerous
95 other insects, including heteropterans, nematodes, coleopterans, and fruit flies, also
96 exploit the extremely large fruit crop, which may number as many as one million
97 syconia per tree (Cushman et al. 1998). Indeed, notwithstanding chronic under-
98 sampling, there are published records of 1,875 species of arthropod feeding on *Ficus*,
99 including 742 species feeding on syconia, 481 feeding on sap, 369 leaf-chewers, and
100 283 wood borers (Basset et al. 1997). Ants (Hymenoptera: Formicidae) for example,
101 have been found to specialise in predating non-pollinating fig wasps in some dioecious
102 *Ficus* species, predate on fig dwelling herbivorous insects, consume partially eaten
103 ripe syconia, and nest in figs (Schatz et al. 2008; Harrison 2013). The complex trunk
104 morphology of many strangler *Ficus* trees provides further habitat for arthropods, all
105 of which suggests that *Ficus* trees may be attractive feeding sites for insectivorous
106 birds.

107 In this study, we sought to test whether isolated *Ficus* trees were particularly
108 important foraging sites for insectivorous birds in human-modified landscapes,
109 relative to other fruit-bearing and large non-fruit trees found in open habitats, as
110 indicated by higher levels of insectivore richness, abundance, and functional diversity.

111 **Materials and methods**

112 Study area

113 The study took place from April 2012 to June 2013 in the Golaghat District of Assam,
114 North-east India (see Fig. 1). The study site is a $\approx 250 \text{ km}^2$ area bounded by the
115 Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of
116 Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93
117 54.978. The elevation of the study area ranges between 30 and 100 m above sea level,
118 and the mean annual rainfall for the region is 1,500–2,500 mm, most of which falls in
119 the June to September monsoon (Shrivastava and Heinen 2007). The annual
120 temperature range varies from an average minimum of 5°C to an average maximum
121 of 35°C (Barua and Sharma 1999).

122 The original habitat of moist subtropical deciduous forest (Champion and Seth 1968)
123 was largely cleared following the local commercialisation of tea production in 1840
124 (Shrivastava and Heinen 2007). Remnants of the original forest remain in the 7.65
125 km^2 Panbari Forest Reserve on the edge of the Karbi Hills, and in the 430 km^2
126 Kaziranga National Park (Barua and Sharma 1999). Other small areas of forest
127 regrowth exist, but are typically less than 1 ha. Agriculture is the dominant land-use,
128 with a mixture of small-holder rice cultivation, village home gardens, and large
129 commercial tea estates.

130 Focal tree sampling

131 To compare the insectivore assemblages visiting *Ficus* trees to other isolated trees in
132 this human-modified landscape, we surveyed three categories of focal tree: 1) isolated
133 *Ficus* trees, which we surveyed when in fruit; 2) isolated fruit trees that did not
134 belong to the *Ficus* genus, which we surveyed when in fruit; 3) isolated large, non-
135 fruiting trees (i.e. trees that did not produce fruit during the study). We surveyed a
136 total of 40 *Ficus* trees, 33 fruit trees, and 31 large non-fruiting trees in the study area
137 (Table 1). The selection of focal *Ficus* and other non-*Ficus* fruit trees (herein in “fruit

138 trees”) was determined by their fruiting cycle; only trees with crops of ripe fruit were
139 surveyed. Large non-fruiting trees (“large trees”) were selected from the largest trees
140 in the landscape, exclusive of the two previous groups, with a minimum
141 circumference at breast height of over 1 m, so that we had a dataset that was
142 comparable in tree stature to the *Ficus* trees.

143 For each tree, we measured the diameter at breast height (DBH), estimated the
144 maximum tree height with a clinometer, and estimated the canopy area by measuring
145 the canopy diameter at ground level along two axes, deriving canopy area using the
146 formula for an ellipse. To obtain a single estimate for tree size, a Principal
147 Components Analysis (PCA) with Kaiser stopping criterion extraction (eigenvalues
148 >1) and oblique rotation was conducted using DBH, maximum height, and canopy
149 area in IBM SPSS Statistics 22 (IBM 2013). The first axis of this PCA explained over
150 80% of the variance in the three variables and was significantly correlated with all
151 three tree size variables (Pearson's product-moment correlation coefficient greater
152 than 0.8 in each case). Thus, the first axis was used as our tree size variable. The
153 intensity of human land-use within a 100 m radius of each focal tree was recorded
154 using a three-point scale (where 0 is very little human land use; 1 is some human land
155 use, such as cultivation; and 2 is intense human land use, in cases where a road,
156 house, or paddy field were present).

157 We measured the distance to the nearest protected area with intact forest by marking
158 the focal trees with a GPSmap 62s device, and then overlaying the GPS markers on
159 Landsat 8 satellite images of the region in ArcGIS 10.2.1 (ESRI 2014). We digitised
160 the protected area borders through an on-screen visual interpretation, and then
161 measured the distance (in km) of each focal tree to the nearest protected area. In all
162 cases, protected areas held the only high-quality forest habitat left in the study

163 landscape. In addition to protected areas, small (≤ 1 ha), low-quality wooded areas
164 were located through consultation with local landholders and marked with a GPS
165 device. We then recorded a second distance measurement: the distance to the nearest
166 wooded area of any quality (whether a protected area or small wooded area).

167 *Insectivore surveys*

168 Each focal tree was surveyed once, for three hours, from first light. Surveys were only
169 conducted in fair weather conditions. During the survey, a single observer would
170 watch the tree from a concealed position with a good view, typically about 20 m from
171 the trunk. Each individual bird that landed in the tree was recorded, and birds that
172 made repeated visits to and from the tree were denoted with an asterisk to avoid
173 double counting. Trees in the *Ficus* and fruit categories were only surveyed when the
174 crop was ripe. Deforestation in the study area occurred over 150 years ago, and was
175 largely uniform in timing, so differential rates of matrix assemblage relaxation were
176 not considered to have an effect on bird communities in the study area. As all trees
177 were surveyed in the same Assamese season, the presence or absence of migratory
178 species was consistent across the three tree groups.

179 Each species was classified into primary dietary guilds (frugivore, nectivore,
180 insectivore, granivore, or carnivore; omnivores were classified according to their
181 main food type, and were not included in any further analyses on insectivorous birds
182 as they may have been attracted to *Ficus* and fruit trees by the fruit present) following
183 del Hoyo et al. (1992–2002; 2003–2011). Nomenclature also followed del Hoyo et al.
184 (1992–2002; 2003–2011).

185 *Ecomorphological data collection*

186 To calculate functional diversity scores, we preferred to use ecomorphological trait
187 data from the insectivores recorded in the surveys rather than guild classifications
188 extracted from the literature or assessed using our field experience. This is because
189 continuous traits have been argued to produce more accurate representations of
190 species' functional roles in ecosystems (McGill et al. 2006), and the use of continuous
191 trait data removes the need to arbitrarily assign species into different categories. We
192 defined a "trait" as a measurable aspect of an organism, which determines its
193 interaction with the environment (Flynn et al. 2009). Here we were interested in the
194 foraging and dispersal capacity of insectivorous birds, so we measured traits
195 associated with locomotive behaviour, dispersal ability, gape size, bill structure, and
196 body size (Derryberry et al. 2011; Claramunt et al. 2012). In order to obtain
197 ecomorphological trait data, each species recorded in the surveys was measured
198 following Edward Grey Institute protocols at the British Natural History Museum's
199 ornithological collections (Supporting information 2).

200 Functional diversity calculation

201 We follow the definition of functional diversity as the distribution of functional traits
202 within multidimensional niche space (Petchey and Gaston 2006), and used Laliberté
203 and Legendre's functional dispersion (FDis) index to measure functional diversity in
204 our dataset (Laliberté and Legendre 2010; please see Supporting information 3 for a
205 justification of the method selected). We calculated FDis for each of our focal trees
206 using "package FD" in Programme R (Laliberté and Shipley 2013; R Core Team
207 2014).

208 As our trait data were measured on a continuous scale, rather than classified into
209 nominal groups, a species-species uncorrected distance matrix was computed. A
210 Principal Co-ordinates Analysis (PCoA) was performed after the distance matrix was

211 corrected for negative eigenvalues. Each trait axis was standardised to have a mean of
212 zero and a standard deviation of one (Petchey and Gaston 2006). These corrected
213 PCoA trait axes were used to calculate the FDis scores for our focal trees. FDis could
214 not be computed for trees with no insectivore records, but these trees were included in
215 further analyses with index scores of 0. Similarly, trees with only one species of
216 insectivore were given a score of 0 following Laliberté and Shipley (2013). We
217 checked the functional relationships between the sampled insectivorous bird species
218 by constructing a dendrogram: we transformed the species–trait data into a distance
219 matrix (Euclidean distance), and applied the UPGMA clustering algorithm. The
220 resulting dendrogram was subsequently converted into a tree object and plotted (Fig.
221 2).

222 *Statistical analysis*

223 The effect of tree size, land-use intensity, distance to the nearest protected area and
224 nearest forest of any type, and tree type on insectivore abundance, richness, and FDis
225 (the three response variables) were examined using an information-theoretic approach
226 (Burnham and Anderson 2002). For each response variable, we fitted a full
227 generalized linear model (GLM), i.e. a model with all predictor variables included.
228 Abundance and richness are count data and thus for these response variables we used
229 GLMs with the Poisson family and a log link function. As the Poisson distribution
230 assumes that the mean is equal to the variance, a quasi-Poisson model was fitted with
231 each response variable to assess for over-dispersion. In both cases, the data were
232 found to be over-dispersed and thus quasi-AIC_c (QAIC_c; Richards 2008; Bolker 2016)
233 was used for subsequent model comparisons using models with these two response
234 variables. Functional diversity was found to be normally distributed following a log
235 transformation; as the logarithm of zero is not defined, a constant of 0.1 was added to

236 all FDis values. Thus, for models in which FDis was used as the response variable, we
237 fitted GLMs with the Gaussian family and identity link function.

238 Multicollinearity between the continuous predictor variables was assessed using
239 variance inflation factors using the 'car' R package (Fox and Weisberg 2011) and a
240 threshold of five. All continuous predictors had variance inflation factors of less than
241 five and so were included in the model comparisons. Outliers were assessed using
242 Cook's distance and a threshold of one. Two data points were removed prior to the
243 model comparisons based on this criterion. Continuous predictors were assessed for
244 normality: tree size and both distance measures were log transformed to induce
245 normality. A constant of 1.5 was added to tree size values as the raw values (PCA
246 axis values) contained negative numbers.

247 Model comparison was undertaken using an information theoretic approach. When
248 FDis was used as the response variable, we fitted a complete set of models
249 considering all predictor variables using the dredge function in the MuMIn R package
250 (Bartoń 2016). Models were ranked according to AIC_c values (Burnham and
251 Anderson 2002) and we also recorded the ΔAIC_c values and the AIC_c weights for
252 each model.

253 As the dispersion parameter in the Poisson GLM is taken to be one, and model fits
254 using abundance and richness were found to be over-dispersed, we compared models
255 with these two response variables using the quasi-Poisson family and $QAIC_c$
256 (Richards 2008). Thus, instead of using maximum likelihood estimation, we focused
257 on maximising the "quasi-likelihood." For each set of model comparisons, we
258 extracted the dispersion parameter from the full model (i.e. with all predictors) using
259 functions provided by Bolker (2016). We then, separately for each response variable
260 (i.e. abundance and richness), fitted a full set of models considering all predictors and

261 compared models based on their QAIC_c values; again, also storing the Δ QAIC_c values
262 and the QAIC_c weights. Thus, in total we had three model comparison tables, one for
263 each of the three response variables.

264 To evaluate the importance of individual variables, for each model comparison table
265 separately we calculated the weight of evidence (WoE) of each predictor by summing
266 the AIC_c weights (or QAIC_c weights) for each model in which a predictor variable
267 was included (Burnham and Anderson 2002; see also Giam and Olden 2016). As the
268 AIC_c and QAIC_c weights sum to one for a given model comparison, the WoE values
269 are constrained to be between 0 and 1. However, WoE values are not expected to be
270 zero even in cases where a predictor variable has no predictive value (see Burnham
271 and Anderson 2002, p. 345). Thus, we followed Burnham and Anderson (2002, p. 345
272 onwards) and used a bootstrap methodology to compute a baseline WoE value for
273 each predictor variable in each model comparison table. This worked by creating an
274 algorithm that took the i^{th} predictor and randomised the values whilst holding the
275 values of the other predictor variables constant. The model comparison was then
276 repeated and the WoE values calculated in the standard manner. The algorithm then
277 re-arranged the values in the i^{th} predictor back to their original order and moved onto
278 the $i+1^{\text{th}}$ predictor, and so on, until all predictor variables had been randomised. This
279 process was then repeated 500 times and the median value (the bootstrap distribution
280 of WoE values is occasionally skewed and thus the median is a preferable metric;
281 Burnham and Anderson 2002) taken. This approach was only undertaken for the
282 model comparison using FDis as the response variable, as it is straightforward to
283 implement in the context of Gaussian GLMs. In the model comparisons using
284 abundance and richness as the response variables, the models were fitted using the
285 Poisson/quasi-Poisson families and it was found that randomising the predictor values

286 frequently resulted in very high degrees of over-dispersion and the failure of models
287 to converge. Based on the bootstrap WoE results using FDis, we tentatively used a
288 baseline of 0.3 when analysing WoE results from model comparisons using
289 abundance and richness.

290 For each model comparison table, we took the full model and best model (i.e. lowest
291 AIC_c or QAIC_c value) and examined the residual plots (e.g. residuals against fitted
292 values, standardised residual values etc.) for any patterns. We also tested for spatial
293 autocorrelation in the residuals of the best model fits using the ‘spdep’ R package
294 (Bivand and Paris 2015), the nb2listw function and row standardised weights. When
295 FDis was used as the response variable, examination of the residuals revealed some
296 sort of pattern; potentially indicating that a variable was missing from the model
297 (Zuur et al. 2009). To account for this, we re-ran the model selection whilst including
298 an interaction term between tree size and tree type in the full model. This resulted in a
299 much more normal distribution of residuals in the best model fit. As such, we re-ran
300 the FDis model selection using the interaction as a fixed term within the ‘dredge’
301 function in MuMIn. As the interaction term is fixed, it means that the individual
302 variables ‘tree size’ and ‘tree type’ are also fixed. We also re-ran the abundance and
303 richness model selection analyses with this interaction term to assess whether the
304 interaction was important in regards to these response variables. As it was found to
305 improve the distributions of errors in the abundance and richness models, we also
306 fixed the interaction term in this model selection. Finally, for the FDis model
307 comparison we looked at the R² value of the best model, whilst for the abundance and
308 richness model comparisons we computed pseudo R² values for the best models using
309 the formula: 1 - (model deviance / null deviance).

310 **Results**

311 Over the 104 surveys, 33 species of insectivorous bird were recorded. The most
312 frequently recorded species were the Oriental white-eye (*Zosterops palpebrosus*) with
313 55 records, common tailorbird (*Orthotomus sutorius*) with 54, and the Oriental
314 magpie robin (*Copsychus saularis*) with 53. The Oriental white-eye was also the most
315 abundant species, with 146 individual records, followed by the great tit (*Parus major*)
316 with 86, and the Oriental magpie robin with 84.

317 *Ficus* trees had higher mean abundance (12.0, standard error = 0.96), richness (7.0,
318 SE = 0.38) and FDis (1.3, SE = 0.07) values compared to the other tree categories,
319 followed by large non-fruit trees (mean richness = 3.7, 2.5 and 0.8, respectively; SE =
320 0.74, 0.45 and 0.15) and then non-*Ficus* fruit trees (2.7, 1.9 and 0.6, SE = 0.37, 0.23
321 and 0.11; Fig. 3).

322 The results of the multimodel comparison analyses are described below for each of
323 the three response variables in turn.

324 Abundance

325 The inclusion of the interaction term resulted in a more normal distribution of errors
326 in the full and best models (for both the abundance and richness models), although
327 there was still a degree of spread towards the extreme tails of the distribution;
328 however, it is known that residuals in Poisson regression models are only
329 approximately normal, and there is expected to be a degree of spread towards the
330 extreme tails of the distribution. Thus, the model selections based on both the
331 abundance and richness (results presented below) response variables were run with
332 the interaction term included. When abundance was used as the response variable,
333 there was one model within 2 ΔQAIC_c values of the best model. The best model
334 contained tree size, tree type and the interaction between them (i.e. the fixed

335 parameters in the model selection) and the distance to the nearest protected area with
336 intact forest (Table 2a), and had a pseudo- R^2 value of 0.62. The distance to a
337 protected area variable also had a relatively high WoE value (0.59), which was larger
338 than the baseline of 0.3 that we employed for the quasi-Poisson model selections in
339 this study. The parameter estimates for the best model (using the quasi-Poisson
340 family) are included in Table S1 in Supporting information 4. Using the quasi-Poisson
341 family results in the same parameter estimates as the standard Poisson family. We did
342 not look at the significance of parameter estimates for the best model (including for
343 the best richness and FDis models, below), as this is not advised within information
344 theoretic model comparison approaches (Burnham and Anderson 2002). There was no
345 significant spatial autocorrelation in the residuals of the best model (Moran's $I = 0.03$;
346 $P = 0.31$). In regards to the tree type variable, the parameter estimates were negative
347 and relatively large (Table S1) and thus indicated that both fruit trees and large non-
348 fruiting trees supported lower abundance than *Ficus* trees. The effect of tree size was
349 positive, indicating abundance increased with the size of tree. Consideration of the
350 interaction term parameter estimates (Table S1) indicates that this is primarily driven
351 by the large non-fruiting tree category, i.e. the slope between abundance and tree size
352 is steeper for this tree category relative to the other two. Interestingly, the effect of
353 distance was positive, which implies that the abundance of insectivorous birds
354 increased with distance to the nearest protected area with intact forest. The WoE
355 values for the other distance variable and land use were both below the baseline value
356 (Table 2a), and thus these variables can be considered relatively unimportant in
357 determining abundance in this system.

358 Richness

359 When richness was used as the response variable, there were two models within 2
360 ΔQAIC_c values of the best model. The best model contained tree size, tree type and
361 the interaction between them (i.e. the fixed parameters in the model selection) (Table
362 2b), and had a pseudo- R^2 value of 0.60. The parameter estimates for the best model
363 (using the quasi-Poisson family) are included in Table S2 in Supporting information
364 4. In regards to the tree type variable, the parameter estimates were again negative
365 and relatively large (Table S2) and thus indicated that both fruit trees and large non-
366 fruiting trees supported lower richness than *Ficus* trees. As with the best model using
367 abundance, the effect of tree size was positive and the interaction term parameter
368 estimates (Table S2) indicate that this effect is primarily driven by the large non-
369 fruiting tree category. Whilst land use and the distance to the nearest protected area
370 with intact forest were included in the models within 2 ΔQAIC_c of the best model,
371 both variables had WoE values below the baseline of 0.3. The second distance
372 variable also had a WoE value below 0.3 (Table 2b). There was no significant spatial
373 autocorrelation in the residuals of the best model (Moran's $I = 0.03$; $P = 0.29$).

374 Functional Dispersion

375 When FDis was used as a response variable the best model had an adjusted R^2 value
376 of 0.29 (see Table S3 in Supporting information 4 for parameter estimates). There
377 were no additional models within 2 ΔAIC_c values of the best model (Table 3). As
378 described above, the FDis model selection analyses included an interaction term
379 between tree size and tree type as a fixed term in the model selection, to ensure a
380 more normal distribution of errors. Thus, tree type, tree size and the interaction term
381 were all included in the best model by default and the WoE values for these variables
382 are not interpretable (see Table S3). In regards to the tree type variable, the parameter
383 estimates were negative and relatively large (Table S3) and thus indicated that both

384 fruit trees and large non-fruiting trees supported lower FDis than *Ficus* trees. The
385 effect of tree size in the best model was small (-0.06) and negative, indicating that
386 FDis actually decreased with increasing tree size. However, closer inspection of the
387 best model's parameter estimates indicated that this was probably driven by the
388 interaction between tree type and tree size; the slope of the FDis – tree size
389 relationship was steeper for both fruit trees and large non-fruiting trees relative to
390 *Ficus* trees. Land use was also included in the best model and had a relatively high
391 WoE value, which was considerably larger than the bootstrapped baseline value.
392 Inspection of the best model's parameter estimates indicated that increasing land use
393 intensity resulted in a decrease in FDis. Neither of the distance variables were
394 included in the best model, and both had WoE values lower than the baseline values
395 (Table 3). There was no significant spatial autocorrelation in the residuals of the best
396 model (Moran's I = -0.02; $P = 0.46$).

397

398 **Discussion**

399 The conversion of tropical forest to agricultural production causes changes in
400 insectivorous species composition and functional diversity (Tschardt et al. 2008;
401 Azhar et al. 2013; Edwards et al. 2013). However, we found that isolated *Ficus* trees
402 provide important micro-site level habitat for insectivores in the human-modified
403 Assamese landscape. Compared to the other tree categories, *Ficus* trees had
404 consistently higher insectivore richness, abundance and functional diversity,
405 suggesting that these trees may be more valuable from a conservation perspective in
406 these modified landscapes than other isolated trees.

407 In addition to tree type, our model comparisons also indicated that tree size and the
408 interaction between tree size and tree type were important variables. Although these
409 variables were fixed in the model comparisons, the fact that they were needed to be
410 fixed to improve the error distribution indicates that they are important. In addition,
411 exploratory analysis indicated, once the assumptions of GLMs were temporarily
412 relaxed, that even when the model comparisons were run without fixing these
413 variables they consistently had high WoE values and were included in the best models
414 (results not shown). The interaction terms in the best models indicated that each of the
415 slopes between abundance, richness and FDis, and tree size were steeper in the large
416 non-fruit tree category relative to the other two categories. Figure 4 illustrates these
417 relationships for richness using scaled size (i.e. re-scaling each tree size such that the
418 data cover the same range for each tree type) for each of the three tree types. It can be
419 seen that for *Ficus* trees and the large non-fruit trees category, species richness
420 generally increases with tree size; although the relationship appears to flatten out at
421 large sizes for *Ficus* and the relationship is thus steeper for the large non-fruit tree
422 category. However, there does not appear to be any relationship between tree size and
423 richness for non-*Ficus* fruit trees. It should also be noted that if the tree sizes are
424 simply standardised by the largest tree in the dataset (i.e. not accounting for tree type)
425 the *Ficus* line still lies above the other two lines in Fig. 4 and thus, whilst the
426 relationship is steeper for large non-fruit trees, for any given tree size there is a higher
427 species richness in *Ficus* trees relative to the other tree types. The fact that the
428 relationship is steeper for large non-fruit trees relative to *Ficus* trees is likely due in
429 part to the fact the *Ficus* trees are generally larger than trees in the other two
430 categories and thus there are fewer small *Ficus* trees in our dataset, and in tropical
431 landscapes more generally (partly due to the “strangler” life history of many species).

432 Nonetheless, in regards to conservation actions and assuming that the retention of
433 ecological services such as pest control is a priority (and assuming that the birds
434 recorded in isolated trees are also foraging in agricultural crops), the conservation of
435 large trees *per se* may be the most effective strategy. In this case, isolated *Ficus* trees
436 would again be a conservation priority, as they were generally the largest trees in the
437 study area.

438 When abundance was used as the response variable, the model comparison results
439 indicated that abundance increased with increasing distance from a protected area
440 with intact forest. This is an interesting and counter-intuitive finding and is possibly
441 due to the effect of matrix specialist birds (Şekercioğlu 2012). Some of the species
442 with the highest number of recorded individuals were matrix specialist species, such
443 as great tit (*Parus major*), common iora (*Aegithina tiphia*), and crimson sunbird
444 (*Aethopyga siparaja*). These birds showed a distinct preference for non-forest
445 habitats, with increasing occurrence as the distance from the forest increased.

446 Interestingly, the effect of land use was only important in the model comparisons
447 based on FDis. It was found that increasing land use intensity resulted in a decrease in
448 FDis. This is to be expected and several previous studies have shown that land use
449 change and intensification lead to a reduction in functional diversity (e.g. Schweiger
450 et al. 2007; Flynn et al. 2009; Laliberté et al. 2010). The reason why land use was not
451 an important variable in the abundance and richness model comparisons is unknown.
452 However, again, it may be due to the presence of matrix specialists in the landscape.
453 The inclusion of matrix specialist bird species in analyses such as those in this study
454 have sometimes been found to mask the effects of land use change on abundance and
455 richness (Matthews et al. 2014). If these matrix specialist species are relatively
456 immune to land use change and increase in abundance and richness in more disturbed

457 environments, but also possess similar trait values to one another, they may
458 compensate the loss of forest specialist abundance and richness with increasing land
459 use intensity whilst simultaneously resulting in a reduction in FDis, as we observed. It
460 is also possible that our coarse three-level ordinal land use scale did not contain
461 enough information to uncover relationships between abundance and richness, and
462 land use.

463 Several studies have argued for the need to conserve isolated trees in human-modified
464 habitat (Manning et al. 2006; Şekercioğlu et al. 2007; Fischer et al. 2010). Our results
465 build upon these arguments, adding that isolated trees can be important resources for
466 insectivores as well as frugivores (Luck and Daily 2003), and tree-hole nesters
467 (Manning et al. 2004). We consider this a valuable finding, as there are few
468 conservation strategies focused on this vulnerable group in modified landscapes. We
469 also add that *Ficus* trees may be particularly important for insectivorous birds in
470 human-modified landscapes. In our study area at least, this implies that conserving
471 *Ficus* trees ahead of other tree types may be a more effective conservation strategy
472 than conserving isolated trees at random. If *Ficus* trees are found to be similarly
473 important to insectivorous birds in modified landscapes on a wider spatial scale, a
474 “*Ficus* first” approach to isolated tree conservation may be effective across the tropics
475 (see Cottee-Jones & Whittaker 2015; Cottee-Jones et al. 2016). Although additional
476 studies on *Ficus* trees and insectivores are lacking, *Ficus* have been found to support
477 rich and abundant insect communities wherever they have been studied (Basset and
478 Novotny 1999; Pereira et al. 2000; Bain et al. 2013).

479 The conservation of isolated trees in modified landscapes presents significant
480 challenges, however. It requires a long-term vision with extensive commitment from
481 landowners (Manning et al. 2004), and can incur substantial costs if natural

482 regeneration is insufficient (Fischer et al. 2010). The regeneration of *Ficus* trees may
483 be particularly challenging, as many species are epiphytic in their early life stages,
484 and so depend upon the presence of large host trees (Leighton and Leighton 1983).
485 Fortunately, evidence from the study area indicates that, in this region at least, *Ficus*
486 trees are regenerating faster in modified habitats than are isolated trees in other parts
487 of the world (Gibbons et al. 2008; Cottee-Jones et al. 2016). If the conservation of
488 isolated *Ficus* trees was adopted in legislation, there is scope for future work to focus
489 on thresholds for the tree size required to qualify for protection, and the size of buffer
490 zones around isolated trees where land-use practices may be restricted.

491

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647

648 **Tables**

649 **Table 1:** Characteristics of the three isolated tree groups surveyed in Assam, India.
 650 DBH is diameter at breast height. Values for DBH, height, and canopy area are mean
 651 \pm standard error. The five most surveyed species are listed in order of decreasing
 652 number of surveys. Fruit refers to large fruit-trees other than *Ficus* and Large to the
 653 category of large trees that did not bear fruit during the study.

Characteristic	<i>Ficus</i>	Fruit	Large
Total no. of individuals surveyed	40	33	31
Total no. of species surveyed	6	12	15
DBH (m)	1.51 \pm 0.13	0.45 \pm 0.02	0.61 \pm 0.05
Height (m)	27.29 \pm 1.40	18.86 \pm 1.03	20.91 \pm 0.89
Canopy area (m ²)	489.32 \pm 67.29	74.01 \pm 7.16	130.11 \pm 21.43
Five most surveyed species (in order of decreasing abundance)	<i>F. religiosa</i> , <i>F. benghalensis</i> , <i>F. rumphii</i> , <i>F. microcarpa</i> , <i>F. benjamina</i>	<i>Artocarpus heterophyllus</i> , <i>Tectona grandis</i> , <i>Artocarpus lakoocha</i> , <i>Syzygium cumini</i> , <i>Toona ciliata</i>	<i>Syzygium cumini</i> (non-fruiting), <i>Albizia lucidor</i> , <i>Albizia procera</i> , <i>Mangifera indica</i> (non-fruiting), <i>Neolamarckia cadamba</i>

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655

656 **Table 2** Model selection results for a set of the most parsimonious generalized linear
657 models (quasi-Poisson family), modelling the (a) abundance and (b) richness of
658 insectivorous birds in 102 isolated trees, in Assam. The predictor variables included
659 the land use surrounding the trees, tree type, tree size, the distance to the nearest
660 protected area with intact forest (Dist1) and the distance to any forest (Dist2). An
661 interaction between tree type and tree size (Int.) was also included as a term in the
662 model selection as a fixed term. The best model (i.e. lowest QAIC_c) and all models
663 within Δ QAIC_c of < 2 of the best model are given for both (a) and (b). The weight of
664 evidence of each variable, calculated by summing the quasi-Akaike weights of all the
665 models in which a variable was included is also given. + indicates a significant effect
666 of a categorical variable. A blank space indicates that a variable was not included in a
667 model. (L) indicates predictor variables that were log transformed. The Δ QAIC_c
668 (Δ QAIC_c) and QAIC_c weights (wQAIC_c) for each model selection are also presented.
669 *these variables were fixed in the model selection procedure and thus the WoE values
670 are constrained.

671

672 a) Abundance

673

Model Number	Land use	Tree type	Tree size (L)	Dist1 (L)	Dist2 (L)	Int.	Δ QAIC _c	wQAIC _c
1		+	0.39	0.33		+	0	0.38
2		+	0.36			+	0.9	0.24
Weight of evidence	0.18	1*	1*	0.59	0.23	1*		

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675

676 b) Richness

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Model Number	Land use	Tree type	Tree size (L)	Dist1 (L)	Dist2 (L)	Int.	Δ QAIC _c	wQAIC _c
1		+	0.32			+	0	0.39
2		+	0.34	0.13		+	1.83	0.16
3	+	+	0.17			+	1.84	0.16
Weight of evidence	0.27	1*	1*	0.28	0.24	1*		

678

679 **Table 3** Model selection results for a set of the most parsimonious linear models,
680 modelling the functional dispersion of insectivorous birds in 102 isolated trees, in
681 Assam. The predictor variables included the land use surrounding the trees, tree type,
682 tree size, the distance to the nearest protected area with intact forest (Dist1) and the
683 distance to any forest (Dist2). An interaction between tree type and tree size (Int.) was
684 also included as a term in the model selection as a fixed term. The best model (i.e.
685 lowest AIC_c) and all models within ΔAIC_c of < 2 of the best model are given. The
686 weight of evidence of each variable, calculated by summing the Akaike weights of all
687 the models in which a variable was included, and a bootstrapped baseline (see
688 Materials and methods) with which to compare these values to are also given. +
689 indicates a significant effect of a categorical variable. A blank space indicates that a
690 variable was not included in a model. (L) indicates predictor variables that were log
691 transformed. The ΔAIC_c (ΔAIC_c) and AIC_c weights ($wAIC_c$) for each model selection
692 are also presented. *these variables were fixed in the model selection procedure and
693 thus the WoE values are constrained.

694

Model Number	Land use	Tree type	Tree size (L)	Dist1 (L)	Dist2 (L)	Int.	ΔAIC_c	$wAIC_c$
1	+	+	-0.06			+	0	0.5
Weight of evidence	0.87	1*	1*	0.26	0.24	1*		
Weight of evidence baseline	0.16	0.23	0.36	0.29	0.29	NA		

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703 **Figure legends**

704 **Figure 1:** A map highlighting the study site location. The inlay shows India and the
705 location of the study landscape within Assam.

706 **Figure 2:** The functional dendrogram converted into a tree object, for 33
707 insectivorous bird species sampled in isolated trees in Assam, India. The dendrogram
708 was constructed by first transforming the species – trait data into a distance matrix
709 (Euclidean distance), and then using the UPGMA clustering algorithm.

710 **Figure 3:** Mean insectivore abundance, richness, and FDis (functional dispersion)
711 recorded in isolated tree assemblages in Golaghat District, Assam, India. For *Ficus*
712 trees: n=40; fruit: n=33; and large: n=31. Error bars are standard error.

713 **Figure 4:** The relationship between tree size and insectivorous bird species richness
714 for 104 isolated trees in Assam. The data have been split according to the three tree
715 types analysed in the study: fig trees (type 1; red line), non-fig fruiting trees (type 2;
716 green line) and non-fruiting trees (type 3; blue line). The tree size data have been
717 scaled in order for each tree type to cover the same range of tree size; this was
718 achieved by first adding a constant (1.5) to each tree size value (PCA axis; see
719 Methods and material) and then dividing each tree size value by the maximum tree
720 size within that tree type. As the data are not normally distributed we simply fitted
721 loess best fit lines for each of the three tree types, in order to get a rough idea of the
722 patterns.

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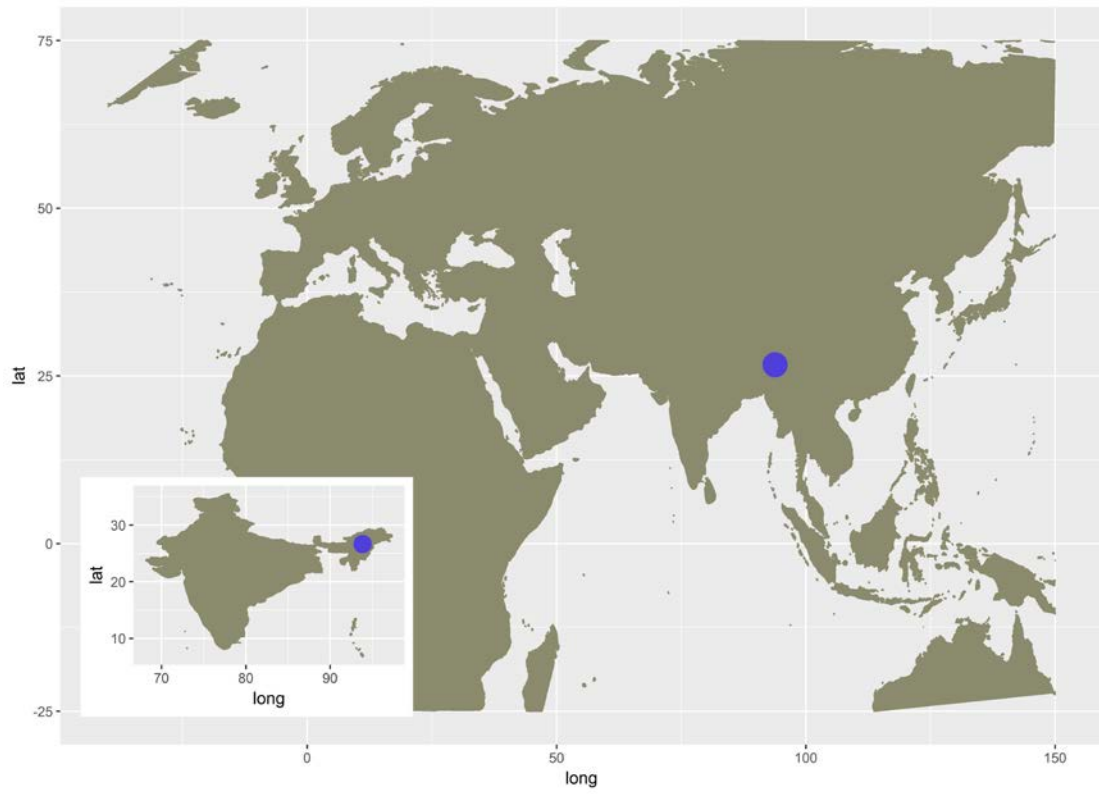
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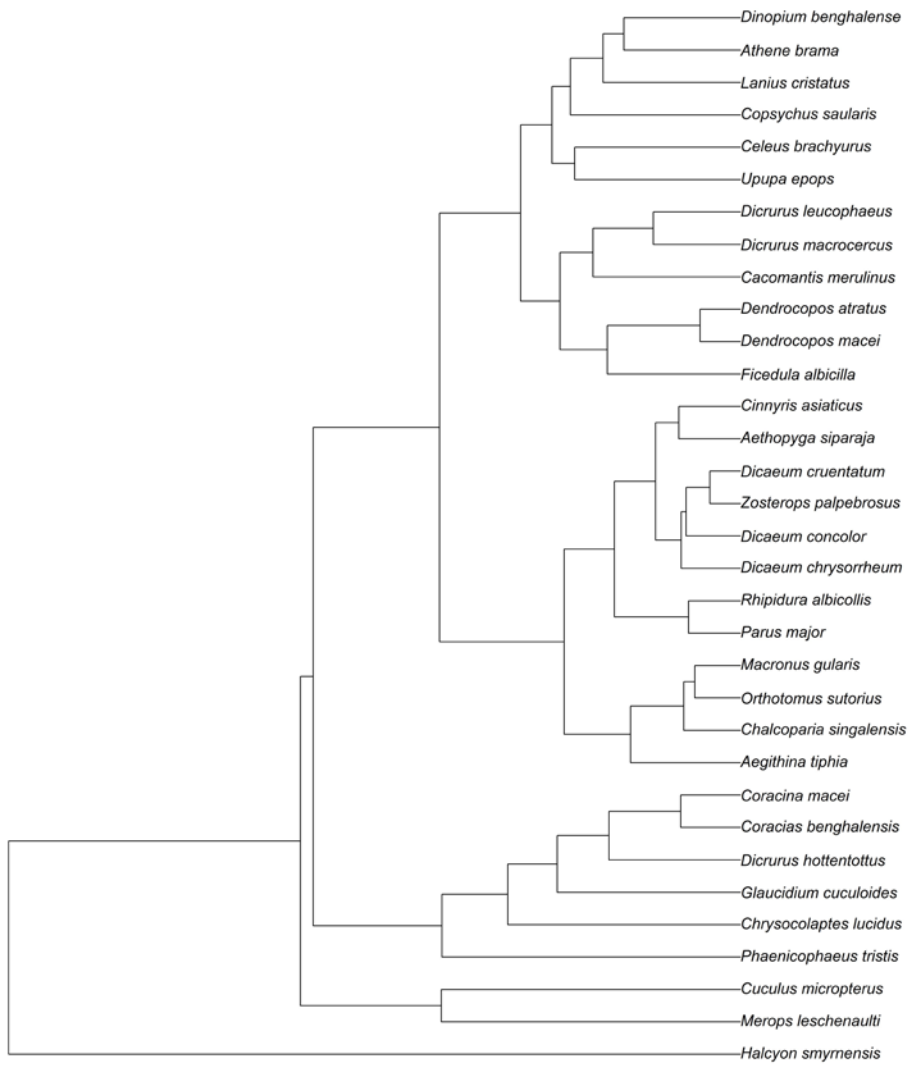
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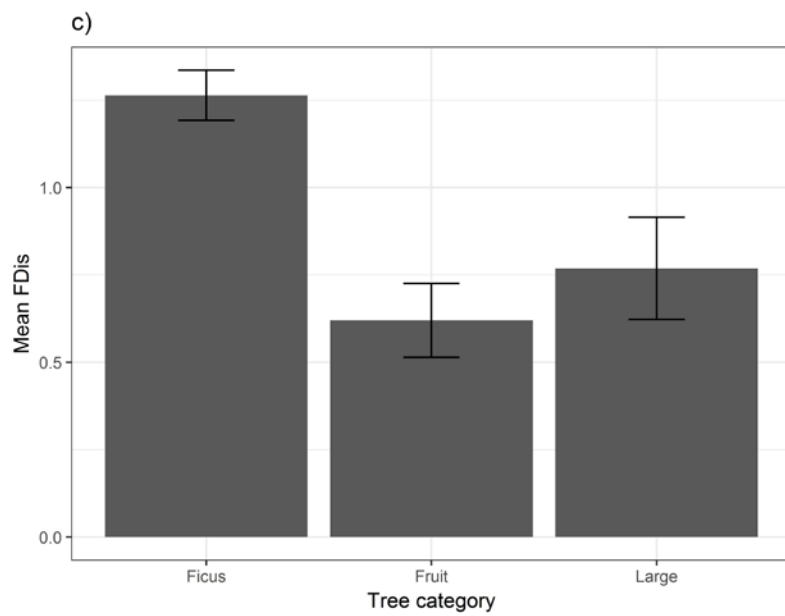
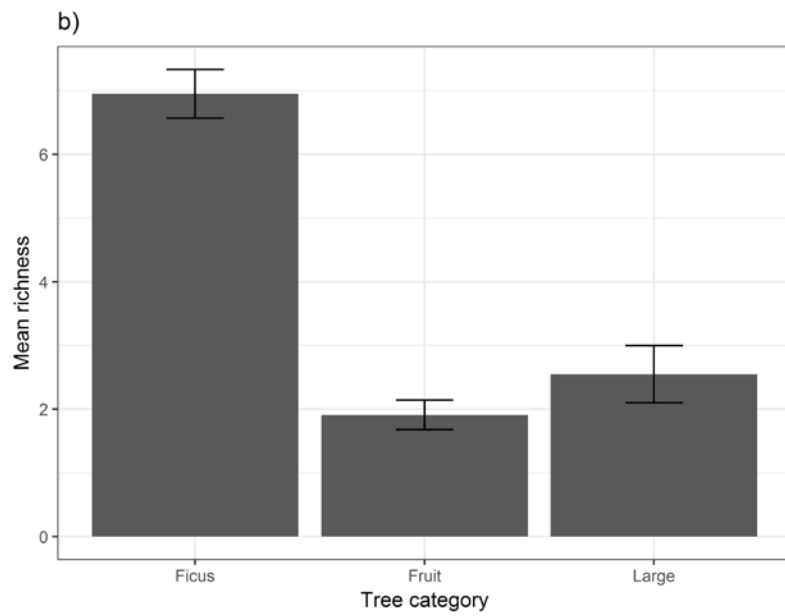
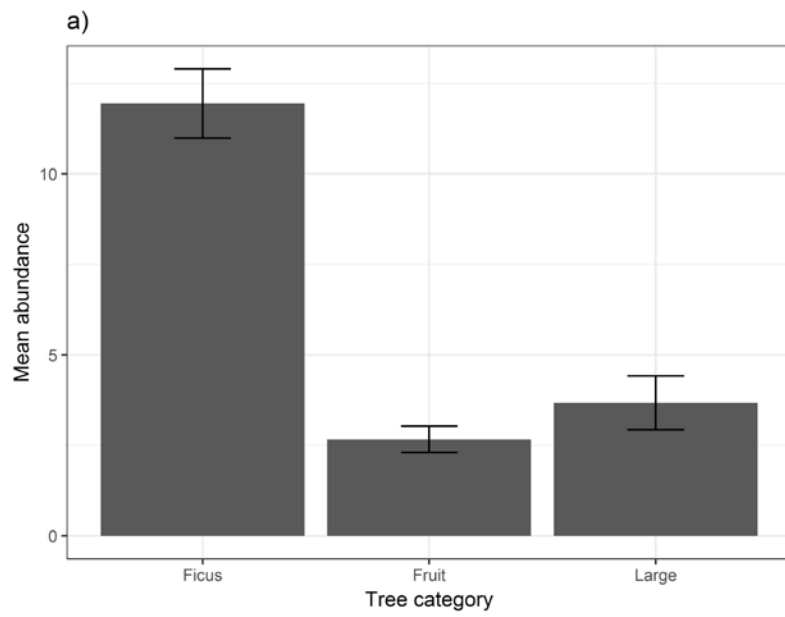
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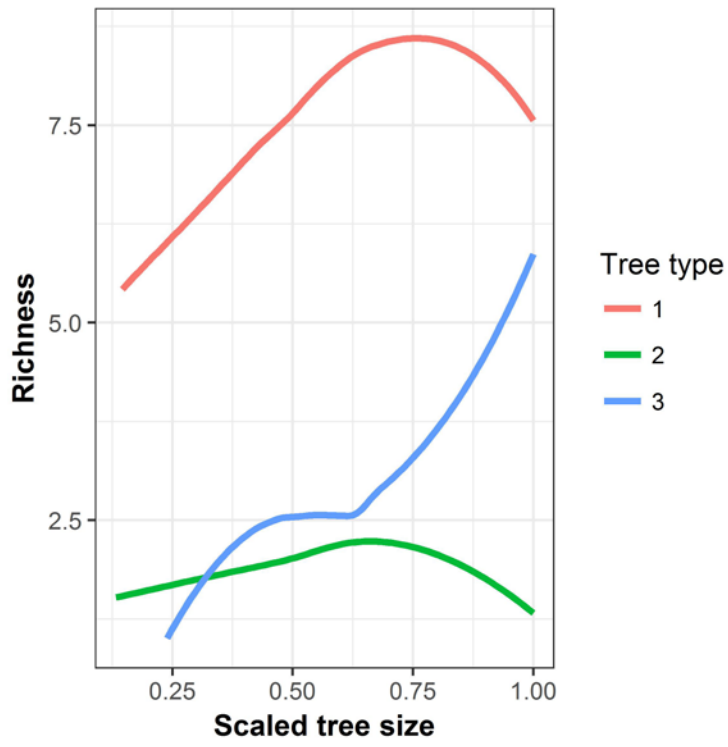
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747 **Assessing the relative importance of isolated *Ficus* trees to insectivorous birds in**
748 **an Indian human-modified tropical landscape – Supporting information**

749 Biodiversity and Conservation

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757 ***Supporting information 1:***

758 To calculate the area of land under agricultural production in the world's tropics, we
759 followed the methodology of Phalan et al. 2013. We defined tropical countries as
760 those that have at least one-third of their land area between the Tropics of Cancer and
761 Capricorn, producing a list of 129 countries. We downloaded data on the extent of
762 total agricultural area in each of these countries from FAO STAT (2014) for the most
763 recent year (2011). We summed these figures to produce an estimate of the total land
764 area under agricultural production in tropical countries (2,455,649,900 ha, rounded to
765 2.5 billion ha).

766 ***Supporting information 2:***

767 To compute functional diversity scores, we first collected ecomorphological trait data
768 on the 34 insectivore species recorded in the study. We measured traits associated
769 with locomotive behaviour (tarsus length, wing chord, and tail length), dispersal

770 ability (Kipp's distance, hand-wing index), gape size (gape width), bill structure
771 (culmen length, bill length from nares, bill width, bill depth), and body size (via a
772 Principal Components Analysis, PCA).

773 Specifically, we measured four specimens of the local population for each species
774 recorded. In almost all cases we were able to measure specimens collected within 150
775 km of the study area. Two adult males and two adult females of each species were
776 measured with 150 mm outside diameter dial callipers (accurate to 0.1 mm), wing
777 rulers, and tail rulers (accurate to 0.5 mm). The measurements taken were: culmen
778 length (from the base of the skull to the tip of the bill), bill length from nares (from
779 the anterior edge of the nares to the tip of the bill), bill width (the width of the bill at
780 the anterior of the nares), bill depth (the depth of the bill at the anterior of the nares),
781 gape width, tarsus length (the length from the inner bend of the tibiotarsal articulation
782 to the base of the toes, where the scalation pattern changes), wing chord (from the
783 bend in the wing to the unflattened longest primary), Kipp's distance (the distance
784 from the longest primary to the first secondary), and tail length (to the tip of the
785 longest retriex).

786 As weight data for birds are often variable (Clark 1979), we preferred to measure
787 body size through a PCA. We initially conducted a pair of PCA analyses, one for
788 locomotive ability (with input measurements of tail length, wing chord, and tarsus
789 length) and one for bill shape (with bill depth, width, and length from nares) using
790 oblique rotation with Kaiser stopping criterion extraction (eigenvalues >1). Each of
791 these PCAs produced two components. In both cases, the first related to size, while
792 the second components were taken as indices for locomotive ability and bill shape,
793 respectively. To produce one index for body size, we ran an additional PCA using the
794 first components from the original analyses (Trisos et al. *in press*). To create an index

795 for dispersal ability that standardizes for bird size, we calculated the hand-wing index
796 (Claramunt et al. 2012), which is a surrogate for flight performance, migratory
797 behaviour, and natal dispersion in birds.

798 ***Supporting information 3:***

799 We used Laliberté and Legendre's functional dispersion (FDis) index to measure
800 functional diversity in our dataset (Laliberté & Legendre 2010). This represents the
801 spread of the species in quantitative trait space by calculating a multidimensional
802 index of the mean distance of an individual species to the centroid of all species in the
803 community (Laliberté & Legendre 2010). A major advantage of FDis over other
804 measures, such as FRic, FEve, and FDiv (Villéger et al. 2008; Mouchet et al. 2010) is
805 that it can be calculated for communities composed of only two species, rather than a
806 minimum of three, which was important for the species-poor insectivore assemblages
807 in the isolated trees. It is also independent of species richness, and can be weighted by
808 abundance, both of which were important considerations for our study.

809 ***Supporting information 4:***

810 **Table S1:** Parameter estimates and standard errors for all terms within the best model,
811 modelling the abundance of insectivorous birds in 102 isolated trees, in Assam. The
812 best model was selected based on comparing QAIC_c values of a complete set of
813 models after fixing the interaction term between tree type and tree size. The predictors
814 included in the best model are tree type (a categorical variable with three levels:
815 1=*Ficus* trees, 2=non-*Ficus* fruit trees and 3=large non-fruiting trees; see Materials
816 and methods), distance between the tree and the nearest protected area with intact
817 forest (Distance), tree size (the first axis of a PCA using three tree size variables;
818 measured on a log scale) and an interaction between tree size and tree type.

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Model term	Estimate	Std. error
Intercept	1.20	0.58
Distance	0.33	0.19
Tree type 2	-0.48	0.47
Tree type 3	-0.20	0.45
Tree size	0.39	0.14
Tree type 2 * tree size	-0.37	0.35
Tree type 3 * tree size	0.75	0.39

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826 **Table S2:** Parameter estimates and standard errors for all terms within the best model,
827 modelling the richness of insectivorous birds in 102 isolated trees, in Assam. The best
828 model was selected based on comparing QAIC_c values of a complete set of models
829 after fixing the interaction term between tree type and tree size. The predictors
830 included in the best model are tree type (a categorical variable with three levels:
831 1=*Ficus* trees, 2=non-*Ficus* fruit trees and 3=large non-fruiting trees; see Materials
832 and methods), tree size (the first axis of a PCA using three tree size variables;
833 measured on a log scale) and an interaction between tree size and tree type.

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Model term	Estimate	Std. error
Intercept	1.72	0.12
Tree type 2	-1.00	0.21
Tree type 3	-0.79	0.17
Tree size	0.32	0.14
Tree type 2 * tree size	-0.13	0.32

Tree type 3 * tree size	0.65	0.35
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839 **Table S3:** Parameter estimates and standard errors for all terms within the best model,
840 modelling the functional dispersion of insectivorous birds in 102 isolated trees, in
841 Assam. The best model was selected based on comparing AIC_c values of a complete
842 set of models after fixing the interaction term between tree type and tree size. The
843 predictors included in the best model are land use (on an ordinal scale: 1=low,
844 2=medium and 3=high land use intensity), tree type (a categorical variable with three
845 levels: 1=*Ficus* trees, 2=non-*Ficus* fruit trees and 3=large non-fruiting trees; see
846 Materials and methods), tree size (the first axis of a PCA using three tree size
847 variables; measured on a log scale) and an interaction between tree size and tree type.

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Model term	Estimate	Std. error
Intercept	1.17	0.49
Land use 2	-0.64	0.34
Land use 3	-1.18	0.41
Tree type 2	-1.43	0.38
Tree type 3	-1.27	0.38
Tree size	-0.06	0.36
Tree type 2 * tree size	0.08	0.49
Tree type 3 * tree size	1.42	0.6

849 **References**

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