1 **Large avian frugivores in the Philippines show linear responses to**

2 **improvements in forest quality**

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4 C. P. Española[a,b], N. J. Collar[c], N. A. D. Mallari[d] & S. J. Marsden[a*]

5 [a] School of Science & the Environment, Manchester Metropolitan University, Chester

6 Street, Manchester M1 5GD, UK

7 [b] Institute of Biology, College of Science, University of the Philippines, Diliman,

8 Quezon City 1101, Philippines

9 [c] BirdLife International, David Attenborough Building, Cambridge CB2 3QZ, UK.

10 [d] Center for Conservation Innovations Philippines, Foggy Heights, Tagaytay City,

11 Cavite 4120, Philippines

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13 [*] Corresponding author. Tel.: +441612476215; fax: +441612476318

14 *E-mail addresses:* cpespanola@up.edu.ph (C. Española), nigel.collar@birdlife.org (N.

15 Collar), aldrin.mallari@gmail.com (N. A. Mallari), s.marsden@mmu.ac.uk (S.

16 Marsden).

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18 threshold.

19

20   **ABSTRACT**

21   Large avian frugivores are important in ecosystem function, but are seriously

22   threatened across the tropics. To conserve them we must understand their habitat

23   needs and the effects of improved forest management on individual species and the

24   community as a whole. We recorded the presence/absence of 18 parrot, pigeon and

25   hornbill species along nearly 500 km of transects at 24 sites in Luzon, Philippines,

26   and used logistic GLMMs to identify bird-habitat associations based on

27   topographical, forest structure and floristic data taken at 1227 habitat plots. We

28   then searched for more complex relationships and thresholds in species responses

29   along forest quality/restoration gradients using GAMMs. Frugivore species richness

30   was highest in forest with large-girthed trees, although some small-scale

31   agricultural disturbance was tolerated or even favoured. Importantly, richness was

32   highest in forests on flat ground, areas which are usually the first to be converted to

33   agriculture. Individual species were positively associated with large trees but

34   responses to floristic gradients were more variable. Very few species had complex

35   relationships with forest quality; for the great majority, the probability of

36   occurrence increased linearly along the forest quality/restoration gradient. While

37   the precise benefits in terms of seed dispersal, and costs of management, at

38   different points along the quality/restoration gradient are likely to be themselves

39   complex, avian frugivores benefit proportionately from step improvements right

40   along the gradient. Thus, any actions to improve forest quality on Luzon, from

41   reforesting the most degraded lands to preventing degradation of relatively healthy

42   forests, are likely to benefit frugivores.

## 1. Introduction

Frugivores, with their role as seed dispersers, are crucial to healthy ecosystem functioning through the formation and maintenance of biodiversity (Corlett 2009; Corlett and Hau 2000; Holbrook et al. 2002; Kitamura 2011). While a broad range of animals disperse seeds, birds (and especially larger-bodied species such as hornbills and pigeons) are notable for their dispersal not only at local but also at regional and even transcontinental scales (Green et al. 2002; Holbrook et al. 2002). In places where large frugivores are absent or scarce, forest regeneration capacity is compromised, sometimes with substantial loss of plant species richness and/or abundance (Babweteera and Brown 2010; Moran et al. 2009; Neuschulz et al. 2011).

Philippine forests have a high proportion of zoochorous (animal-dispersed) trees, with late-successional species most specialized with respect to dispersal agents (Hamann and Curio 1999). Birds are particularly important seed dispersers on Luzon (Ingle 2003), but, with just 7% of its original primary forest remaining, this large Philippine island has seen such alarming declines in frugivore numbers that frugivore population collapse across most reserves appears inevitable without urgent conservation intervention (Española et al. 2013). Such a collapse will inevitably have negative consequences for the long-term structure and functioning of the forest reserves themselves. However, few studies have assessed long-term changes in tree population dynamics or community structure as a consequence of reduced seed dispersal (Terborgh et al. 2008; Harrison et al. 2013).

65        Knowledge of factors that determine species presence in a landscape

66 underpins many biodiversity management and conservation programmes (Collinge

67 1996; Guedes 2004; Stagoll et al. 2010; Suchant et al. 2003), by, for example,

68 predicting the impacts of land-use changes or habitat management on populations

69 (Brooks et al. 1997; Neuschulz et al. 2011; Swift and Hannon 2010). Bird-habitat

70 relationships are often complex (Meents et al. 1983), and the identification of

71 nonlinearities or thresholds in responses is important, as small changes in habitat

72 quality can affect the species disproportionately (Radford et al. 2005).

73        In this study, we aimed to associate the presence of large avian frugivores

74 with habitat and physical features at sites, and to determine the most important

75 drivers of frugivore presence across Luzon. To do this, we first developed linear

76 models to identify important habitat features for each species and for frugivore

77 species richness. Then we examined species-specific relationships more closely

78 using generalised additive models to search for nonlinearities and thresholds in

79 bird-habitat associations that may help develop forest management strategies to

80 conserve key species (Naidoo 2004).

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82 **2. Methods**

83 *2.1 Field methods: bird counts and vegetation measures*

84 Bird and habitat data were collected between December 2009 and September 2010

85 at 14 general areas comprising 24 specific sites across Luzon (Fig. 1; general areas

86 are described in Appendix A). The sites were at least 5 km apart (mean minimum

87     distance between sites = 31.0 km ± 28.6 SD), and belong to one of five

88     biogeographical regions in the island: Cordillera, Sierra Madre, western Luzon,

89     central Luzon, and southern Luzon. We included in our survey Luzon's two hornbill

90     species, its eight parrot species, and its 15 forest-based pigeon species.

91     Our sampling currency was the presence/absence of each species along 400 m

92     segments of the line transects. Transects were positioned along hunter trails (80%

93     of total transect length), old logging roads, farm access tracks and, occasionally,

94     motorable roads within forested reserves (9%), and specially cut trails (11%). All

95     individuals of each target species heard or seen along the transect were recorded,

96     regardless of their distance from the transect line, although the great majority of

97     bird records were within 50 m of the line. Ideally, detectability issues would have

98     been addressed using a method such as Distance Sampling (for site-based density

99     estimates for frugivores from this study see Española et al. 2013). However, this

100     was not seen as feasible for this analysis given the low number of encounters of

101     most species, and because we are examining the reaction of species to habitat at a

102     much finer resolution than a site level. Only perched individuals, or individuals

103     flushed by the recorders, were included in the analysis, as only these birds gave an

104     indication of their habitat choice along the transect. Transects were walked, once

105     only, at a standardized pace of 1 km h$^{-1}$, either between 05h30 and 11h00, or 15h00

106     to 18h00, i.e. when birds are most active (Robbins 1981). No surveys were

107     conducted in rain, wind or fog, as such conditions affect bird activity and

108     detectability (Bibby et al. 2000). Surveys were conducted by CPE along with two

109     experienced MSc students, and field assistants, all of whom underwent prior

110    training on bird call identification and habitat assessment. The field assistants were

111    indigenous hunters already familiar with bird vocalisations.

112         Habitat and altitudinal data were collected from 10x20 m habitat plots

113    located alternately to the left and right of the trail at the 200 m mark of each 400 m

114    transect segment. Path width along the transect was measured at the 0, 10 and 20 m

115    mark of each habitat plot. The girths at breast height (GBH) of the three largest-

116    boled trees in the habitat plot were measured. Canopy closure was estimated using

117    a concave forest canopy densitometer at three locations within the plot: one along

118    the transect at the 10 m mark of each habitat plot, and the other two at the opposite

119    corners of the plot. Slope was measured within each plot using a clinometer at the

120    same three locations. Mean canopy cover, slope, path width, altitude and tree girth

121    were computed for each plot. The presence or absence within each plot of a series of

122    key plant types was recorded. These were: planted crops, pioneer tree species,

123    banana *Musa* sp. and guava *Psidium guajava* (all indicators of current or recent

124    disturbance); the leguminous tree *Parkia javanica*, palms Arecaceae and figs *Ficus*

125    spp. (known food plants); tree ferns (known nesting substrate for the Colasisi);

126    epiphytes (indicators of high humidity); dipterocarps (indicators of primary forest);

127    pandans *Pandanus* sp. (potential food plant and nesting habitat); and dead standing

128    trees (Meijaard et al. 2005, Orwa et al. 2009, Zotz and Heitz 2001).

129    *2.2 Data analysis*

130    The twelve floristics variables (all presence-absence) were condensed into just

131    three floristics axes (Facs 1 to 3) using principal components analysis (PCA; Jolliffe

132    2011). PCA uses an orthogonal transformation to reduce a number of variables into

133     a smaller number of variability axes (Jongman et al. 1995). Table 1 shows PCA

134     results including correlations between factor scores and individual floristic

135     variables. The three retained axes accounted for 51.5% of overall variability. Sites

136     with high scores on Factor 1 (Fac 1, subsequently 'primary forest') are relatively

137     intact forest (no agriculture), rich in dipterocarps, epiphytes, tree-ferns and palms.

138     Fac 2 (subsequently 'agricultural disturbance') represents a gradient of forest

139     disturbance through agriculture (presence of banana *Musa* spp. and other

140     agroforestry crops, figs, pioneer tree species). High scores on Fac 3 ('higher

141     altitude') are characteristic of higher altitude mossy forest, associated with dense

142     tree-fern and epiphyte growth, as well as the absence of dipterocarps, fig and

143     pioneer tree species.

144        To identify problematic levels of multicollinearity among the environmental

145     variables (e.g. Grewal et al. 2004), Spearman's rank correlations were performed on

146     pairs of independent variables (Zuur et al. 2010). Since no strong correlations ($r_s >$

147     0.5) were recovered, we considered all eight variables (altitude, slope, path width,

148     tree girth, canopy cover and the three PCA floristic axes) in the analysis. To explore

149     the relationships between the presence/absence of frugivores and environmental

150     predictors, we used generalized linear mixed models (GLMMs; Bolker et al. 2009)

151     fitted by the Laplace approximation with a binomial error structure, a logit link

152     function, and site as a random factor. For species richness, we used the same

153     procedure but with Poisson error structure and a log link function. Analyses were

154     run using the package 'lme4' version 0.1-6 in R version 2.15.0 (R Development Core

155     Team 2013).

156     Models were built only for those two hornbill, six parrot and ten pigeon

157     species recorded on eight or more occasions on transects. Models were first

158     developed for each predictor individually, and entered both as linear and quadratic

159     terms. The five predictor variables with the lowest Akaike Information Criterion

160     (AIC) values were retained and used to build the GLMM models for each species

161     (Burnham et al. 2011). For amethyst brown-dove *Phapitreron amethystinus*,

162     however, the AIC values of the fifth to seventh most 'powerful' variables were the

163     same, so all seven variables instead of five were used in building the models. The

164     analyses involved a series of iterations using combinations of variables that yielded

165     a list of best models with the lowest AIC. Akaike weights were used to quantify the

166     strength of each model in the model set (Burnham and Anderson 2002;

167     Wagenmakers and Farrell 2004), and each contributing variable was then ranked

168     according to its strength by summing the Akaike weights of models where that

169     variable appeared.

170     Nonlinearities and thresholds in frugivore responses (individual species and

171     species richness) along the forest disturbance gradient were explored using

172     generalized additive mixed models (GAMMs) with package 'gamm4' in R version

173     2.15.0 (R Development Core Team 2013). Predictors considered were tree girth,

174     canopy cover and PCA Facs 1 and 2, because they are features that could

175     conceivably be manipulated by conservation managers. Predictors were considered

176     singularly, and number of splines for each variable selected through AIC

177     minimization.

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179    **3. Results**

180    *3.1 Frugivore-habitat associations*

181    Frugivore species richness was most likely to be (a) highest in areas on flatter

182    ground (negative coefficient for Slope) with large tree girths, but (b) higher in areas

183    with some agricultural disturbance (positive coefficient for Fac 2); Table 2; see

184    Appendix B for full confidence sets for all models. Unsurprisingly, altitude was the

185    strongest predictor of frugivore presence in models for twelve of the eighteen

186    species, with a mean Akaike weight across species of 0.84 ± 0.22 SD. Coefficients for

187    altitude were negative in seven species and, as expected, strongly positive in three

188    known high-altitude species (cream-bellied and flame-breasted fruit-doves

189    *Ptilinopus merrilli* and *P. marchei*, and Luzon racquet-tail *Prioniturus montanus*).

190    Among the other predictors, the primary forest axis (Fac 1; appearing in 15 species

191    models with mean Akaike weight of 0.59 ± 0.18 SD) and mean tree girths (12

192    species; mean Akaike weight = 0.60 ± 0.25 SD) were most powerful. All species had

193    linear positive relationships with increasing tree girths, but relationships with PCA

194    Fac 1 scores were variable, with the strongest relationships being quadratic. Canopy

195    cover and path width appeared in fewest likely models. While several predictors

196    generally acted in a linear way, relationships between frugivore presence and the

197    agricultural disturbance and higher altitude axes (Facs 2 and 3), and Slope were

198    quadratic in half or more species.

199    *3.2 Complexities in frugivore-habitat associations*

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200    Most relationships between species presence and the four predictors were either

201    linear (48 species/predictor cases) or quadratic (19 cases, all involving PCA Fac 1 or

202    Fac 2; Table 3). Only five more complex relationships were detected (Appendix C),

203    and in all cases, just three splines were selected. Two of these cases involved

204    ground-foraging pigeons (common emerald dove *Chalcophaps indica* and Luzon

205    bleeding-heart *Gallicolumba luzonica*) where the relationship was with tree girth.

206

207    **4. Discussion**

208    The key finding of this study is that the likelihood of the presence of individual

209    species, and frugivore richness in general, increased along the habitat quality

210    gradient in a straightforward and often linear way. Concomitantly, the probability of

211    occurrence of most large avian frugivores, and overall frugivore richness, was

212    highest in high-biomass (although not necessarily unmodified) forest on flatter

213    ground.

214       A preference in large frugivores for relatively intact over human-altered forests

215    occurs in response to various land-uses: selective logging (Gray et al. 2007);

216    agroforestry systems (Scales and Marsden 2008); and oil palm and rubber

217    plantations (Aratrakorn et al. 2006). It is noteworthy that species such as white-

218    eared brown-dove *Phapitreron leucotis*, generally thought to be tolerant of early

219    second-growth forest (e.g. Kennedy et al. 2000), was still more likely to occur in

220    primary forest. However, several frugivores showed quadratic or sometimes

221    positive associations with our axis describing forest encroachment by small-scale

222     agriculture. Crops such as bananas, pioneer trees re-growing in small cleared areas,

223     and figs were tolerated or even favoured, a pattern reported elsewhere in the

224     tropics (e.g. Marsden and Symes 2008; Cottee-Jones et al. 2015). That forests on flat

225     ground held the highest frugivore richness was another pattern mirrored

226     elsewhere, in this case by parrots in Papua New Guinea (Marsden and Symes 2006).

227     It is unclear why flat areas might be preferred, although it is possible that the

228     particularly high numbers of large trees found in flat areas (e.g. de Castilho et al.

229     2006) may be beneficial to frugivores in general, and cavity-nesting hornbills and

230     parrots in particular (e.g. Marsden and Pilgrim 2003). Moreover, and inevitably,

231     high biomass forests in flat, accessible areas are usually under the strongest

232     pressure for timber extraction (e.g. Shearman et al. 2009) and conversion to

233     agriculture. These conservation issues continue to affect all but the few small

234     frugivores, such as bulbuls, which can survive in open country (e.g. Fishpool and

235     Tobias 2005; Posa 2011).

236        There are clear advantages to being able to identify nonlinearities in animal-

237     habitat relationships, as a premise to finding areas where disproportionate benefits

238     are accrued for limited costs, and especially in identifying thresholds beyond which

239     extinction probability is disproportionately great (Meents et al. 1983; Hill and

240     Curran 2003). Such nonlinearities have often been examined in the context of

241     habitat fragmentation and viability of populations across landscapes (e.g. Fahrig

242     2002; Cunningham et al. 2014), but the relationship between animal

243     distribution/abundance and measures of local habitat quality has been less well

244     studied. In our study, both the likelihood of the presence of individual species and

245 frugivore richness overall tended to increase linearly along the habitat quality

246 gradient. By extension, sensible restoration interventions at any point along the

247 habitat quality gradient will yield benefits for avian frugivores.

248       Our measures of frugivore richness and probability of occurrence may not be

249 as appropriate as, say, population density estimates, but we would argue that

250 habitats which have a high probability of holding good numbers of frugivores must,

251 in general, be good habitats for them. However, we recognize that, although some

252 species, especially cavity-nesters such as parrots and hornbills, feed freely in more

253 disturbed forests, they may breed at higher densities in primary forests (Marsden

254 and Pilgrim 2003). Areas of forest with higher levels of disturbance can act as sinks

255 for tropical forest species (e.g. Beck et al. 2004), while poor reproductive success

256 and increased hunting in degraded forests (e.g. Parry et al. 2009) may also be

257 serious issues. An important consideration is that direct exploitation of avian

258 frugivores is common in many of the forests surveyed (Española et al. 2013).

259 Therefore, what we report are the probabilities of occurrence for frugivores under

260 the influence of both habitat quality and concurrent hunting. Finally, we do not

261 know the relative economic or management costs of interventions at different

262 points along the disturbance gradient against which to balance the biological

263 benefits we found.

264       Protection and restoration of forests have already been identified as the two

265 key conservation imperatives for the Philippines (Sodhi *et al.* 2010). Our results

266 fully support this assertion by providing concrete evidence that forest fortification

267 through both protection and restoration will directly benefit Philippine biodiversity.

268    We thus recommend complementing the country's existing protection bias towards

269    more intact forests at mid- to high elevations with the rehabilitation and restoration

270    of degraded forests at low elevations. This could be achieved  by upgrading the

271    management status of areas of 'intermediate' quality areas from multiple-

272    use/buffer zone to protection zone or restoration zone. Outside of protected areas,

273    restoration of severely degraded lowland areas through assisted regeneration

274    techniques would be beneficial (see below; de la Pena-Domene et al. 2013). Avian

275    frugivores, being fairly conspicuous and well-known, could act as good indicators of

276    the health or quality of existing forests, or of the success of restoration schemes (e.g.

277    Seki et al. 2014). Two candidate species, if encounter rates were considered, are

278    White-eared brown-dove and Amethyst brown-dove as they were commonly

279    recorded, occurred right across the disturbance gradient, and showed linear

280    relationships with increasing canopy cover or tree sizes. For indicators of the high

281    quality forest with lower levels of hunting, simply the presence of *Ducula* pigeons

282    might be a useful indication for habitat managers.

283        Government and civil society reforestation programmes are already

284    underway (e.g. Espaldon and Smit 1997), and these have the potential to benefit

285    frugivores such as white-eared brown-dove and common emerald dove, species

286    which occur in young secondary forest, relatively quickly. Other frugivores such as

287    imperial pigeons *Ducula* spp. and fruit-doves *Ptilinopus* spp. will be longer-term

288    beneficiaries, especially if schemes target appropriate tree species (Martínez-Garza

289    and Howe 2003) and lands close to existing forests (e.g. Holl 2007) rather than in

290    abandoned/waste land with little prospect of connectivity to standing forest.

291   Reforestation schemes should be intelligent in terms of tree planting, with early-

292   successional tree species appropriate for 'open-field' plantations, and mid-

293   successional species for enrichment of existing, but degraded, wooded areas

294   (Hamman and Curio 1999). Implementation of projects using the performance-

295   based forest carbon finance incentive schemes, such as avoided destruction via

296   Reduction of Emissions from Deforestation and forest Degradation (REDD+), are

297   well underway in the Philippines (Lasco et al. 2013).

298        However, while these findings make potentially encouraging news for

299   management efforts to help large avian frugivores, populations of most frugivores in

300   most areas are so small that their ability to survive long term in all but the largest

301   reserves must be in doubt (Española *et al*. 2013). Therefore the measures

302   recommended above need to be implemented with great urgency, resolve and

303   strategic foresight if the recovery of frugivore numbers is to be effective throughout

304   the island of Luzon and if, as a consequence, the forests themselves are eventually to

305   recover their full diversity.

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481 **Table 1. Principal components analysis (PCA) of environmental variables. Eigenvalues and**

482 **percentage variation explained by each factor, and correlations between factor scores and**

483 **individual variables. Correlation coefficients lower than 0.2 are not shown.**

|  | Fac 1 | Fac 2 | Fac 3 |
|---|---|---|---|
| Eigenvalue | 0.39 | 0.35 | 0.23 |
| % variation explained | 20.9 | 18.4 | 12.1 |
| *Correlations with individual variables* |  |  |  |
| Food crops | −0.33 | +0.21 |  |
| Palms Arecaceae | +0.70 |  |  |
| Figs *Ficus* spp. | +0.25 | +0.78 | −0.35 |

| Dipterocarps | +0.68 | | −0.47 |
| Epiphytes | +0.59 | | +0.31 |
| Leguminous tree *Parkia javanica* | | | |
| Pioneer trees | | +0.64 | −0.21 |
| Dead standing trees | +0.31 | | |
| Banana *Musa* spp. | | +0.49 | |
| Guava *Psidium guajava* | | | |
| *Pandanus* spp. | +0.29 | −0.35 | |
| Tree-ferns | +0.45 | +0.47 | +0.66 |

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**Table 2. Habitat association models for frugivore species in Luzon with corresponding Akaike variable weights. Figures in bold are significant contributions for that predictor. n = number of transect segments in which the species was recorded. NT = Near Threatened; VU = Vulnerable. Symbols represent the shape of the relationship between species presence and the habitat variable: + positive linear; − negative linear; ∩ quadratic.**

|  | AvAlt | AvSlope | AvPath | AvGirth | CCover | Fac 1 | Fac 2 | Fac 3 |
|---|---|---|---|---|---|---|---|---|
| **Species with n>50** | | | | | | | | |
| Philippine cuckoo-dove *Macropygia tenuirostris* (n=128) | +<br>**0.99** | ∩<br>0.73 | −<br>0.50 | +<br>0.55 | | | | ∩<br>0.34 |
| Common emerald dove *Chalcophaps indica* (n=119) | −<br>0.62 | | −<br>0.39 | | +<br>0.37 | ∩<br>0.47 | −<br>0.43 | |
| Luzon bleeding-heart *Gallicolumba luzonica* (NT) (n=87) | | | −<br>0.34 | +<br>0.71 | +<br>0.34 | +<br>**0.73** | | ∩<br>**0.80** |
| White-eared brown-dove *Phapitreron leucotis* (n=630) | −<br>**1.00** | | −<br>0.30 | +<br>0.58 | +<br>**1.00** | ∩<br>**0.89** | | |

| Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Amethyst brown-dove *Phapitreron amethystinus* (n=286) | | − 0.25 | − 0.30 | + 0.97 | − 0.31 | ∩ **0.68** | ∩ 0.42 | ∩ **0.73** |
| Cream-bellied fruit-dove *Ptilinopus merrilli* (NT) (n=79) | + **0.92** | ∩ 0.38 | | + 0.91 | | ∩ 0.38 | | ∩ 0.38 |
| Yellow-breasted fruit-dove *Ptilinopus occipitalis* (n=157) | | | + 0.47 | + 0.49 | | + 0.35 | + **0.92** | ∩ 0.34 |
| Black-chinned fruit-dove *Ptilinopus leclancheri* (n=75) | − **0.98** | ∩ 0.50 | | + **0.96** | | ∩ **0.82** | ∩ 0.36 | |
| Guaiabero *Bolbopsittacus lunulatus* (n=243) | | | | + 0.25 | + 0.30 | + **0.85** | ∩ **0.90** | + 0.31 |
| Colasisi *Loriculus philippensis* (n=137) | | − **0.95** | | + 0.27 | | + 0.67 | ∩ 0.28 | ∩ 0.40 |
| Rufous hornbill *Buceros hydrocorax* (NT) (n=199) | + 0.39 | | | + 0.45 | | − 0.41 | − 0.43 | ∩ 0.64 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Luzon hornbill *Penelopides manillae* (n-165) | **−** **0.99** | **−** **0.70** | − 0.62 | | | | + 0.36 | ∩ 0.53 |
| **Species with n<50** | | | | | | | | |
| Flame-breasted fruit-dove *Ptilinopus marchei* (VU) (n=36) | **+** **1.00** | ∩ 0.76 | − 0.52 | | | ∩ 0.55 | | ∩ 0.28 |
| Green imperial-pigeon *Ducula aenea* (n=30) | − 0.48 | − 0.74 | − 0.37 | + 0.69 | + 0.42 | | | |
| Green racquet-tail *Prioniturus luconensis* (VU) (n=14) | − 0.95 | + 0.30 | | | − 0.43 | + 0.53 | − 0.37 | |
| Blue-crowned racquet-tail *Prioniturus discurus* (n=9) | − 0.77 | | + 0.69 | | − 0.34 | − 0.58 | − 0.47 | |
| Luzon racquet-tail *Prioniturus montanus* (NT) (n=11) | **+** **1.00** | | − 0.81 | | | ∩ 0.57 | ∩ 0.33 | ∩ 0.76 |
| Blue-naped parrot *Tanygnathus lucionensis* (VU) (n=11) | | ∩ | | + | | − | ∩ | − |

|  |  | 0.31 |  | 0.36 |  | 0.39 | 0.77 | 0.51 |
|---|---|---|---|---|---|---|---|---|
| Frugivore species richness |  | −<br><br>0.97 |  | +<br><br>1.00 |  | +<br><br>0.39 | +<br><br>0.61 | +<br><br>0.29 |

**Table 3. AIC scores for GAMM model analyses of frugivore-habitat associations. Figures in bold are the models with the lowest AIC values. Quad = quadratic. k=3 refers to the maximum number of kernels in the GAMM analyses.**

| | TREE GIRTH | | | CANOPY COVER | | | FAC 1 | | | FAC 2 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Linear | Quad | k=3 | Linear | Quad | k=3 | Linear | Quad | k=3 | Linear | Quad | k=3 |
| Philippine cuckoo-dove | **523.5** | 676.3 | 525.5 | **524.3** | 676.2 | 526.3 | 525.7 | **525.0** | 527.7 | 525.7 | **525.6** | 527.7 |
| Common emerald dove | 563.3 | 633.9 | **561.7** | **564.1** | 635.1 | 566.0 | 563.8 | **563.4** | 565.8 | **562.5** | 564.0 | 564.5 |
| Luzon bleeding-heart | 504.0 | 540.9 | **497.3** | **505.2** | 540.6 | 507.2 | **502.9** | 503.2 | 504.7 | 505.6 | **504.8** | 507.6 |
| White-eared brown-dove | **1169.0** | 1312.0 | 1171.0 | **1165.0** | 1312.0 | 1167.0 | 1168.0 | **1163.0** | 1165.0 | **1167.0** | 1169.0 | 1169.0 |
| Amethyst brown-dove | **922.2** | 1039.0 | 924.2 | **935.5** | 1052.0 | 937.5 | 939.7 | **937.8** | 941.5 | 939.1 | **936.9** | 938.7 |
| Flame-breasted fruit-dove | **261.7** | 296.1 | 263.7 | **262.1** | 296.1 | 263.9 | 262.0 | **260.7** | 264.0 | **261.0** | 262.0 | 263.0 |
| Cream-bellied fruit-dove | **443.0** | 492.5 | 445.0 | **452.2** | 500.7 | 454.2 | 451.1 | **450.3** | 452.7 | 452.2 | **452.0** | 454.2 |
| Yellow-breasted fruit-dove | **656.5** | 767.0 | 658.5 | **659.8** | 766.8 | 661.8 | 660.8 | **660.2** | 662.7 | **656.1** | 661.9 | 657.8 |
| Black-chinned fruit-dove | **413.0** | 476.3 | 415.0 | 421.3 | 476.4 | **418.0** | 420.3 | **415.8** | 418.6 | 420.1 | **419.9** | 421.4 |
| Green imperial-pigeon | **200.1** | 255.0 | 202.1 | 202.0 | 254.8 | **200.7** | **202.0** | 202.5 | 204.0 | 202.5 | **202.5** | 204.5 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Colasisi | **697.7** | 713.6 | 699.7 | **697.3** | 713.3 | 699.3 | **694.7** | 697.4 | 696.7 | **695.7** | 697.4 | 697.7 |
| Green racquet-tail | 114.8 | 142.6 | **113.9** | **114.1** | 142.5 | 116.1 | **114.0** | 114.6 | 116.0 | **114.4** | 114.9 | 116.4 |
| Blue-crowned racquet-tail | **52.22** | 87.50 | 54.22 | **51.96** | 86.85 | 53.10 | **46.98** | 51.09 | 48.98 | 51.05 | **47.43** | 49.97 |
| Luzon racquet-tail | **105.5** | 117.4 | 107.5 | **105.5** | 117.0 | 107.5 | 105.5 | **104.0** | 107.4 | 105.4 | **105.0** | 107.4 |
| Blue-naped parrot | **83.68** | 124.0 | 85.68 | **83.67** | 123.9 | 85.67 | **83.25** | 83.79 | 85.25 | 83.96 | **80.38** | 84.74 |
| Guaiabero | **903.8** | 1013.0 | 905.8 | **904.5** | 1015.0 | 906.50 | **901.5** | 902.6 | 903.4 | 904.2 | **900.7** | 905.5 |
| Luzon hornbill | **727.9** | 757.8 | 729.9 | **734.8** | 795.9 | 736.8 | **734.8** | 734.8 | 736.8 | **732.8** | 734.8 | 734.8 |
| Rufous hornbill | **821.4** | 888.6 | 823.4 | **821.1** | 888.6 | 822.9 | **820.1** | 823.1 | 822.1 | **823.0** | 823.1 | 825.0 |
| *Species richness* | **1264.0** | 1278.0 | 1266.0 | **1282.0** | 1295.0 | 1284.0 | 1282.0 | **1281.0** | 1284.0 | **1280.0** | 1281.0 | 1281.0 |

**Figure 1.** Frugivore general sampling areas in Luzon. Water bodies are coloured grey. a

Calanasan, Apayao (Cordillera); b Balbalasang-Balbalan National Park, Kalinga (Cordillera); c Mt

Polis, Cambulo and Pula, Cordillera Administrative Region (Cordillera); d Mt Cetaceo,

Peñablanca, Cagayan (Sierra Madre); e Divilacan, Maconacon and San Pablo, Isabela (Sierra

Madre); f Baler, San Luis, Dilasag, Casiguran and Dinalungan, Aurora (Sierra Madre); g Mt

Tapulao, Zambales (West Luzon); h Subic Watershed Forest Reserve and Bataan National Park,

Bataan (West Luzon); i Burdeos, Polillo Island, Quezon (Central Luzon); j Mounts Banahaw-San

Cristobal Protected Landscape, Quezon (Central Luzon); k Quezon Protected Landscape, Quezon

(Central Luzon); l Mt Isarog National Park, Naga, Camarines Sur (South Luzon); m Caramoan

National Park, Camarines Sur (South Luzon); n Mt Malinao, Diaro, Camarines Sur (South Luzon).