

1 **Large avian frugivores in the Philippines show linear responses to**  
2 **improvements in forest quality**

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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.

43 **1. Introduction**

44 Frugivores, with their role as seed dispersers, are crucial to healthy ecosystem  
45 functioning through the formation and maintenance of biodiversity (Corlett 2009;  
46 Corlett and Hau 2000; Holbrook et al. 2002; Kitamura 2011). While a broad range of  
47 animals disperse seeds, birds (and especially larger-bodied species such as hornbills  
48 and pigeons) are notable for their dispersal not only at local but also at regional and  
49 even transcontinental scales (Green et al. 2002; Holbrook et al. 2002). In places  
50 where large frugivores are absent or scarce, forest regeneration capacity is  
51 compromised, sometimes with substantial loss of plant species richness and/or  
52 abundance (Babweteera and Brown 2010; Moran et al. 2009; Neuschulz et al.  
53 2011).

54 Philippine forests have a high proportion of zoochorous (animal-dispersed)  
55 trees, with late-successional species most specialized with respect to dispersal  
56 agents (Hamann and Curio 1999). Birds are particularly important seed dispersers  
57 on Luzon (Ingle 2003), but, with just 7% of its original primary forest remaining,  
58 this large Philippine island has seen such alarming declines in frugivore numbers  
59 that frugivore population collapse across most reserves appears inevitable without  
60 urgent conservation intervention (Española et al. 2013). Such a collapse will  
61 inevitably have negative consequences for the long-term structure and functioning  
62 of the forest reserves themselves. However, few studies have assessed long-term  
63 changes in tree population dynamics or community structure as a consequence of  
64 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).

81

## 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  $\pm$  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<sup>-1</sup>, 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.

178



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  $0.84 \pm 0.22$  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  $0.59 \pm 0.18$  SD) and mean tree girths (12  
192 species; mean Akaike weight =  $0.60 \pm 0.25$  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*

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.

306

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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
<i>Correlations with individual variables</i>			
Food crops	-0.33	+0.21	
Palms Arecaceae	+0.70		
Figs <i>Ficus</i> spp.	+0.25	+0.78	-0.35

Dipterocarps	+0.68		-0.47
Epiphytes	+0.59		+0.31
Leguminous tree <i>Parkia javanica</i>			
Pioneer trees		+0.64	-0.21
Dead standing trees	+0.31		
Banana <i>Musa</i> spp.		+0.49	
Guava <i>Psidium guajava</i>			
<i>Pandanus</i> 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.**

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

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

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

		0.31		0.36		0.39	0.77	0.51
Frugivore species richness		-		+		+	+	+
		<b>0.97</b>		<b>1.00</b>		0.39	0.61	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	<b>523.5</b>	676.3	525.5	<b>524.3</b>	676.2	526.3	525.7	<b>525.0</b>	527.7	525.7	<b>525.6</b>	527.7
Common emerald dove	563.3	633.9	<b>561.7</b>	<b>564.1</b>	635.1	566.0	563.8	<b>563.4</b>	565.8	<b>562.5</b>	564.0	564.5
Luzon bleeding-heart	504.0	540.9	<b>497.3</b>	<b>505.2</b>	540.6	507.2	<b>502.9</b>	503.2	504.7	505.6	<b>504.8</b>	507.6
White-eared brown-dove	<b>1169.0</b>	1312.0	1171.0	<b>1165.0</b>	1312.0	1167.0	1168.0	<b>1163.0</b>	1165.0	<b>1167.0</b>	1169.0	1169.0
Amethyst brown-dove	<b>922.2</b>	1039.0	924.2	<b>935.5</b>	1052.0	937.5	939.7	<b>937.8</b>	941.5	939.1	<b>936.9</b>	938.7
Flame-breasted fruit-dove	<b>261.7</b>	296.1	263.7	<b>262.1</b>	296.1	263.9	262.0	<b>260.7</b>	264.0	<b>261.0</b>	262.0	263.0
Cream-bellied fruit-dove	<b>443.0</b>	492.5	445.0	<b>452.2</b>	500.7	454.2	451.1	<b>450.3</b>	452.7	452.2	<b>452.0</b>	454.2
Yellow-breasted fruit-dove	<b>656.5</b>	767.0	658.5	<b>659.8</b>	766.8	661.8	660.8	<b>660.2</b>	662.7	<b>656.1</b>	661.9	657.8
Black-chinned fruit-dove	<b>413.0</b>	476.3	415.0	421.3	476.4	<b>418.0</b>	420.3	<b>415.8</b>	418.6	420.1	<b>419.9</b>	421.4
Green imperial-pigeon	<b>200.1</b>	255.0	202.1	202.0	254.8	<b>200.7</b>	<b>202.0</b>	202.5	204.0	202.5	<b>202.5</b>	204.5

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

