



# *The insect-focused classification of fruit syndromes in tropical rainforests: an inter-continental comparison*

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1 The insect-focused classification of fruit syndromes in tropical rainforests: an inter-continental  
2 comparison

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29

### 30 **ABSTRACT**

31 We propose a new classification of rainforest plants into eight fruit syndromes, based on fruit  
32 morphology and other traits relevant to fruit-feeding insects. This classification is compared with  
33 other systems based on plant morphology or traits relevant to vertebrate fruit dispersers. Our  
34 syndromes are based on fruits sampled from 1,192 plant species at three Forest Global Earth  
35 Observatory plots: Barro Colorado Island (Panama), Khao Chong (Thailand) and Wanang (Papua  
36 New Guinea). The three plots differed widely in fruit syndrome composition. Plant species with  
37 fleshy, indehiscent fruits containing multiple seeds were important at all three sites. However, in  
38 Panama a high proportion of species had dry fruits, while in New Guinea and Thailand, species  
39 with fleshy drupes and thin mesocarps were dominant. Species with dry, winged seeds that do  
40 not develop as capsules were important in Thailand, reflecting the local importance of  
41 Dipterocarpaceae. These differences can also determine differences among frugivorous insect  
42 communities. Fruit syndromes and colours were phylogenetically flexible traits at the scale  
43 studied, as only three of the eight seed syndromes, and one of the 10 colours, showed significant  
44 phylogenetic clustering at either genus or family levels. Plant phylogeny was, however, the most

45 important factor explaining differences in overall fruit syndrome composition among individual  
46 plant families or genera across the three study sites.

47

48 *Key words:* ForestGEO; fruit colour; plant traits; seed predation; seed dispersal; tropical insects

49

50 TROPICAL RAIN FORESTS ARE KNOWN FOR THEIR HIGH NUMBER OF TREE SPECIES IN COMPARISON TO  
51 TEMPERATE FORESTS. Seed dispersal and survival represent potentially important but poorly-  
52 documented processes maintaining the high tropical diversity of plants (Janzen 1970; Nathan &  
53 Muller-Landau, 2000). Fruit-feeding insects may influence plant demography because they can  
54 kill individual trees while they are still at the embryo stage (Ehrlen 1996). For example, seed  
55 predators in the beetle families Bruchinae and Scolytinae are responsible for high mortality of  
56 dry seeds of some rainforest trees (Janzen 1980, Peguero & Espelta 2013), while predation rates  
57 on seeds infleshy fruits appears to be much lower (Ctvrtecka *et al.* 2016, Sam *et al.* 2017, Basset  
58 *et al.* 2018). Tropical forest trees rely mostly on frugivorous birds and mammals for seed  
59 dispersal (Janson 1983, Gautier-Hion *et al.* 1985, Florchinger *et al.* 2010). This leads to high  
60 variability of tropical fruits and seeds in their morphology, colour, and size (Janson, 1983,  
61 Florchinger *et al.* 2010). Fruits with fleshy tissues surrounding seeds are a food resource for  
62 many animals such as ants (Altshuler 1999, Borges 2015), birds (Gautier-Hion *et al.* 1985,  
63 Herrera 1981, Mack 2000, Pizo & Vieira 2004, Erard *et al.* 2007), and mammals (Janson 1983,  
64 Cáceres *et al.* 1999), including bats (Shanahan *et al.* 2001, Kalka *et al.* 2008) and primates  
65 (Gautier-Hion *et al.* 1985). Mutualistic interactions between fruiting plants and frugivorous  
66 animals represent a significant component of interaction webs in tropical rain forests, with  
67 potential to influence rainforest ecosystem dynamics (Janzen 1980, Correa *et al.* 2015).

68 To help explain the diversity of fruits and seeds in an ecological context, both botanists  
69 and zoologists have proposed their own classification systems of fruit syndromes (Table 1).  
70 These systems focus on seed and fruit morphology from the perspective of either plants, or their  
71 vertebrate dispersers. For example, zoologists have based their classification on fruit  
72 morphology, size, mass, and colour relevant to animal visitation to fruiting trees (Janson 1983,  
73 Gautier-Hion *et al.* 1985, Table 1). However, current classification systems ignore seed predation  
74 and frugivory by insects. Furthermore, existing classification systems can allow individual plant  
75 species to be placed in multiple classes (Table 1), making comparative analyses among  
76 individual species and sites difficult. Here we define a new classification system of fruit  
77 syndromes relevant to insect predation which accounts for different modes of oviposition and  
78 larval and adult feeding by insects, and which allows individual plant taxa to be classified in a  
79 single class (see Table 1, Table S1). We relate and compare these fruit syndromes with those  
80 proposed on the basis of botanical and vertebrate studies.

81 Fruit and seed morphology can be described by multiple continuous (e.g., size), and  
82 categorical (e.g., colour) variables. These can be used to organize plant species into relatively  
83 homogeneous groups, for instance using multivariate analysis methods, and then look for  
84 ecological or phylogenetic interpretations of these groups. Alternatively, we can define suites of  
85 traits, i.e., syndromes, known to be relevant to a particular ecological process, such as dispersal  
86 or seed predation, and examine their importance in various ecosystems or geographic areas. Such  
87 syndromes can be useful as long as they are rigorously defined (Table 1) and combine traits that  
88 are functionally relevant. For instance, fruit fleshiness, number and size of seeds, and physical  
89 protection of seeds by a mesocarp all relate to vulnerability to seed predation by insects, so that  
90 the study of particular combinations of these traits can provide insights into the insect predation

91 pressure on plants. As for any categorical classification of continuous variability involving  
92 multiple traits, syndromes represent a simplification, but can help generate ecological  
93 hypotheses. For instance, the definition of discrete life-history syndromes has contributed to the  
94 development of ecological theory in the context of succession (Turner 2008) and plant responses  
95 to herbivory (Herms & Mattson 1992).

96         Tropical forest trees produce a wider variety of fruits ranging from fleshy to dry (e.g.,  
97 achenes, Armesto *et al.* 2001). Most fleshy fruits are dispersed by animals while dry fruits are  
98 usually dispersed through other means (Howe & Smallwood 1982, Janson 1983, Gautier-Hion *et al.*  
99 *al.* 1985, Mack 1993, Du *et al.* 2009, Florchinger *et al.* 2010, Valido *et al.* 2011). Multiple factors  
100 have contributed to the evolution of the wide range of fruit and seed types observed in tropical  
101 forests. To assess the role of different factors in shaping the diversity of fruit traits, a helpful  
102 approach is to compare the relative frequencies of fruit syndromes across multiple forest sites.  
103 Inter-continental comparisons of ecological patterns are highly instructive, as they show the  
104 variance of these patterns in evolutionarily distinct species pools (Primack & Corlett 2005), but  
105 data for such comparisons are rarely available. Inter-continental comparisons can shed light on  
106 different patterns of seed distribution and mortality, shaped mostly by the evolution of flowering  
107 plants, and the selection of dispersal agents or seed predators (Janzen 1971, Lewis & Gripenberg  
108 2008, Bolmgren & Eriksson 2010). Tropical rain forests vary in plant species composition and  
109 vegetation structure. These forests may also differ in seasonality, climate and fruiting periods, as  
110 well as the composition of frugivore faunas (Corlett & Primack 2006). For example, forests in  
111 the Neotropics are characterized by a high abundance of understory fruiting shrubs. In contrast,  
112 many forests in Southeast Asia are dominated by dipterocarps with seeds dispersed by wind  
113 during mass-fruiting events (Corlett & Primack 2006). Australasian rain forests have a high

114 diversity of plant species that produce large, fleshy fruits (Chen *et al.* 2017). These differences in  
115 the production of fruits in rain forests may impact the way fruits and seeds are attacked by  
116 insects (Table S1). Therefore, it is important to document the distribution of fruit syndromes  
117 relevant to insects across rainforest locations in distinct biogeographical regions. Our insect-  
118 oriented classification of fruit syndromes is based on 1,192 plant species collected at three  
119 tropical forest sites in Panama, Thailand and Papua New Guinea. We quantified plant diversity  
120 and abundance represented by each syndrome in a phylogenetic context and across the three  
121 continents. We use this information to explore the resource base for fruit and seed eating insects  
122 in tropical rainforests.

123

## 124 **METHODS**

125 **STUDY SITES.**—We sampled three Forest Global Earth Observatories (ForestGEO) plots in  
126 biogeographically distinct rainforest regions: Neotropical: Panama: Barro Colorado Island (BCI,  
127 50 ha plot); Oriental: Thailand: Khao Chong (KHC, 24 ha plot) and Australasian: Papua New  
128 Guinea: Wanang (WAN, 50 ha plot). ForestGEO (<http://www.forestgeo.si.edu/>) is a global  
129 network of permanent forest plots established to study long term forest ecosystem dynamics  
130 (Anderson-Teixeira *et al.* 2014). All three of our study sites are located in undisturbed lowland  
131 forests, either wet (KHC, WAN) or with a moderate dry season (BCI). Important characteristics  
132 of their vegetation are summarized in Table S2; see also Anderson-Teixeira *et al.* (2014) for  
133 details. We have obtained data on seed and fruit feeding insects at all three sites through  
134 extensive rearing programs (Ctvrtecka *et al.* 2016, Basset *et al.* 2018) that became the basis for  
135 our fruit classification systems (Table 1).

136



137 PLANT SURVEYS.—We sampled available fruits from all plant species within or near permanent  
138 forest plots. This protocol was initiated in 2010 at BCI and introduced at KHC and WAN in 2013  
139 (Basset *et al.* 2018). Sampling took place over three or four years at each site. During the first  
140 survey year at each site, we searched and sampled fruits and seeds haphazardly from all locally  
141 available trees, shrubs, lianas and (more rarely) epiphytes and herbs. In subsequent years we  
142 restricted our sampling to plant species found in 10 families that are commonly distributed in  
143 these forest regions. Eight of these families are well represented across three sites and two other  
144 families are only important locally, at a single site (Table S3). Data on plant abundance were  
145 taken from the most recent ForestGEO plot survey at each plot; these surveys record all stems  
146 with DBH>1cm every five years (Anderson-Teixeira *et al.* 2014).

147  
148 FRUIT CLASSIFICATION SYSTEMS.—Each plant species sampled was assigned to a category using  
149 our new entomocentric classification, and compared to the previous botany and zoology systems  
150 (Table 1). The botany system is based on plant morphology, while the zoology system was  
151 motivated largely with respect to plant dispersal by vertebrates. Our entomology system is  
152 concerned primarily with seed predation by insects. The first dichotomy in the botany system is  
153 whether the fruit is fleshy or dry. The former includes drupes, berries, and other fleshy fruits with  
154 multiple seeds. The dry fruits are classified as dehiscent, indehiscent and schizocarps (Hickey &  
155 King 1981, Zomlefer 1994, Table 1). The zoology system uses fruit traits such as size, colour,  
156 number of seeds and seed protection (Janson 1983, Gautier-Hion *et al.* 1985, Table 1). For our  
157 new entomology system, we selected 2-4 individual fruits per tree species, classified fruits by  
158 morphology, estimated their size (length and width to the nearest millimeter) and weight (to the  
159 nearest gram), and photographed them. We identified fruit colour using a colour scheme

160 developed for vertebrate dispersal assessment by Janson (1983) and Gautier-Hion *et al.* (1985).  
161 To control for colour choice biases, the Munsell Colour index system (Sturges & Whitfield 1995)  
162 was used to match colours to black, blue, brown, green, orange, purple, red, violet, white and  
163 yellow on the basis of pictures of ripened fruits.

164 Our previous analyses identified fleshiness as a critical trait for insect frugivores and seed  
165 predators (Ctvrtecka *et al.* 2014). The proposed entomology fruit classification system  
166 recognizes fleshiness as an important criterion, as does the botany system. Further, the number of  
167 seeds per fruit is included as an important variable for ovipositing insects (Table 1, Table S1).  
168 Finally, it takes into consideration the thickness and toughness of the mesocarp protecting seeds  
169 from insects (Table 1, Table S1). The individual categories correspond to “syndromes,” each  
170 used by a different suite of insect taxa (Table S1). These fruit syndromes could be used to assess  
171 the diversity of food resources for insects that attack seeds in rain forests (Armesto & Rozzi  
172 1989, Corlett & Primack 2006).

173  
174 DATA ANALYSIS.—Our analyses were based on all species sampled for fruits, both inside and  
175 outside the ForestGEO plots (1,192 species, Figs. 1a, 2a, 3 and 4), using number of species per  
176 category as a response variable. For tree species present within the ForestGEO plots (689  
177 species), individual abundance and stem size data were available, and we used basal area and  
178 density of stems per species in combination with the “species” fruit syndrome to quantify the  
179 ecological significance of fruit syndromes (including life form) as resource for insects, and to  
180 make quantitative comparisons across sites (Fig. 1b, 2b, Table S1, Basset *et al.* 2018). We  
181 compared the proportion of species, basal area and stems represented by each fruit syndrome, life

182 form and fruit colour among the study plots. At KHC, 14% of plant species (mostly unidentified  
183 lianas) were excluded from plant phylogeny analyses.

184         Since there was little species-level overlap between study sites, differences between plant  
185 communities were assessed by comparing composition at the plant genus level using the  
186 phylogenetic Chao-Sorensen index, which calculates the proportion of shared branch lengths  
187 between sites. We estimated the phylogenetic relationships between genera and families using  
188 the online interface of Phylomatic v3 (Webb *et al.* 2008) and the APG III (Angiosperm  
189 Phylogeny Group 2009) phylogeny. We built ultrametric trees using the BladJ function in  
190 Phylocom (Webb *et al.* 2008) and dated nodes using the calibration points from Wickstrom *et al.*  
191 (2001).

192         To test for phylogenetic clustering or over-dispersion of fruit syndromes and colours  
193 (coded as categorical traits) across the global generic and familial phylogenies of plants from all  
194 three sites, we calculated the mean phylogenetic distance (MPD) occupied by taxa that belonged  
195 to each of the eight syndromes and 10 colours. All analyses were abundance-weighted using the  
196 number of species within each genus/family (columns) with a given syndrome or colour (rows).  
197 A genus or family could have multiple states. The significance of observed MPD was compared  
198 to null models generated through shuffling tip labels across 999 permutations (we tested for both  
199 clustering and overdispersion and therefore use a two tailed alpha of 0.025).

200         Often genera or families had multiple states (e.g., several syndromes) and we used the  
201 number of species within each genus or family to conduct abundance-weighted analyses using  
202 the R package “Picante” (Kembel *et al.* 2010). To evaluate simultaneous and separate effects of  
203 sites, fruit colours and plant phylogeny on the variance in fruit syndromes, we performed  
204 multivariate analysis with variation partitioning among three sets of these explanatory variables,

205 using canonical correspondence analysis (CCA) in Canoco ver. 5.10 (ter Braak & Smilauer,  
206 2012). The analysis was performed at two levels of taxonomic resolution of the plant  
207 communities, (1) plant families and (2) plant genera. We used the full datasets of all plant  
208 species, where fruit syndromes were measured, and retained all genera and families with  
209 available phylogenetic information. Each plant genus (or family) was regarded as a “sample”  
210 (i.e., individual rows in matrices), syndromes as a “species” (i.e., columns), and numeric values  
211 in the matrix were numbers of plant species (as dependent variable). The effect of phylogeny (at  
212 the genus or family level) was tested by including the phylogenetic principle co-ordinate axes  
213 (PCO axes) as co-variates. These axes were obtained from principle co-ordinates analysis of a  
214 distance matrix derived from the ultrametric phylogeny. We then used a forward selection (999  
215 randomizations, variability adj., p-adj. <0.05) and selected the first 30 PCO axes as surrogates of  
216 the phylogenetic gradient.

217 To assess the robustness of the PCO axes, we also ran a similar analysis with 100 axes,  
218 which generated similar results. To avoid overestimating phylogenetic effects, the final number  
219 of retained significant PCO axes was adjusted considering also the number of degrees of freedom  
220 and mean squares for the three sets of the variables compared (Table S4, S5). We then calculated  
221 the percentage variance explained either by sites, colours, or phylogenetic axes, and by the three  
222 groups together. The results were visualized with biplot, using species-explanatory variables in  
223 the first two CCA axes. In addition, Venn diagrams indicating the amount of variance in  
224 syndromes explained by each of the two analyses were drawn using the R package “venerable”  
225 (Chen 2018). The efficiency of the two axes was calculated compared to unconstrained  
226 multivariate space (i.e., % of explanatory variance, Smilauer & Leps 2014). Our analyses were  
227 computed with the R package (R Core Team 2014).

228 **RESULTS**

229 PLANT DIVERSITY, COMPOSITION AND FRUIT SYNDROMES.—A total of 1,192 plant species from  
230 548 genera and 107 families were scored for fruit morphology and colour, including 497 species  
231 from BCI, 360 from KHC and 335 from WAN (Table S3). We obtained fruit syndrome data for  
232 99% of species representing almost 100% of stems at BCI, 45% of species and 85% of stems in  
233 WAN and 45% of species and 66% of stems in KHC. Stem density representing particular fruit  
234 syndromes varied across study plots ( $\chi^2=137020$ ,  $df=14$ ,  $p<0.001$ , Fig. S1).

235 The floristic similarity of the three plots at genus level was expressed using the  
236 phylogenetic Chao-Sorensen index. The similarity values ranged from 0.52 for KHC-WAN  
237 through 0.34 for BCI-KHC to 0.39 for BCI-WAN comparisons. The distribution of plant species  
238 among life forms differed significantly between study plots ( $\chi^2=432.31$ ,  $df=14$ ,  $p<0.001$ , Figs.  
239 S2). Both KHC (87%) and WAN (80%) have a high proportion of trees, while only 40% of all  
240 plant species sampled at BCI were trees. In contrast, lianas (23%) and shrubs (28%) were  
241 relatively abundant at BCI in comparison to KHC (lianas 11.3%, shrubs 1.4%) and WAN (lianas  
242 1.5%, shrubs 1.8%) plots. Less than 5% of plant species represented other plant life forms across  
243 the three study plots (Figs. S2).

244 Every fruit syndrome was represented at each study site. Approximately half of all  
245 species at each site had one-seeded drupe fruits (A and B syndromes). The flora was dominated  
246 by fleshy fruits (A1 and B1 syndromes) in WAN (72% of species) and KHC (68%), but only  
247 44% species had fleshy fruits at BCI. The distribution of individual syndromes differed among  
248 individual plots (plant species:  $\chi^2=229$ ,  $df=14$ ,  $p<0.001$ , basal area:  $\chi^2=754.09$ ,  $df=14$ ,  $p<0.001$ ,  
249 Fig. 1). The fleshy indehiscent fruits with multiple seeds (B1 syndrome) were important at all

250 three sites. BCI had a higher proportion of dry fruits (C2 and C1) while at WAN and KHC,  
251 fleshy drupe with thin mesocarp fruits (A1.2) were important (Fig. 1).

252 The proportion of plant species and basal area representing each fruit colour differed  
253 significantly among plots (plant species:  $\chi^2=108.44$ ,  $df=18$ ,  $p<0.001$ ; basal area:  $\chi^2=595.73$ ,  
254  $df=18$ ,  $p<0.001$ , Fig. 2). Blue, purple, violet, and white colours were always rare, together not  
255 exceeding 3.92% of species and 3.97% of basal area in any forest. The remaining colours  
256 (brown, black, red, green, orange and yellow) each represented from 7.2 to 25.6% of species in  
257 each of the forest communities (Fig. 2). Overall, there were more plant species with brown fruits  
258 on BCI and more species with orange fruits in WAN, but no colour dominated any of the studied  
259 communities.

260

261 FRUIT SYNDROMES AND COLOUR IN PHYLOGENETIC CONTEXT.—The number of genera represented  
262 by each syndrome ranged from 25 (C1) to 150 (B1) while the number of families ranged from 11  
263 (C2) to 58 (B1). All syndromes were broadly phylogenetically distributed. We tested all eight  
264 fruit syndromes for phylogenetic clustering in their distribution among both genera and families,  
265 and found only syndromes C1 ( $n=25$ ,  $Z=-2.655$ ,  $p=0.002$ ) and C2 ( $n=67$ ,  $Z=-3.778$ ,  $p=0.001$ )  
266 significantly clustered at the genus level, and syndromes B2 ( $n=28$ ,  $Z=-1.717$ ,  $p=0.009$ ) and C1  
267 ( $n=15$ ,  $Z=-1.731$ ,  $p=0.009$ ) clustered at the family level (Fig.3).

268 The number of genera represented by each colour ranged from 14 (purple) to 153 (green)  
269 while the number of families ranged from 11 (blue) to 60 (green). We tested phylogenetic  
270 clustering for all 10 fruit colours and found only the colour brown to be significantly clustered at  
271 genus level ( $n=107$ ,  $Z=-2.609$ ,  $p=0.005$ ) and marginally significant at the family level ( $n=38$ ,  $Z=-$   
272  $-1.326$ ,  $p=0.035$ ).

273           The CCA analysis explained 16.6% of variability in fruit syndromes at the genus level  
274 and 35.7% at the family level by the effects of sites, colours and plant phylogeny (Figs. 4, Figs.  
275 S3 and Tables S4, S5). The analysis separated fleshy from non-fleshy syndromes along the  
276 CCA1 axis, with red, orange and black colours in fleshy fruits, and green and brown colours in  
277 non-fleshy fruits. WAN and KHC were associated with fleshy syndromes and BCI to non-fleshy  
278 syndromes. However, the largest proportion of the overall variability across canonical axes was  
279 explained by plant phylogeny, both at the genus and family level, while the effect of forest site  
280 was low (Fig. 4, Fig. S3).

281

## 282 **DISCUSSION**

283 PLANT DIVERSITY, COMPOSITION AND FRUIT SYNDROMES.—Our study provides an entomocentric  
284 assessment of fruit classification systems based on fruit morphology, particularly fleshiness,  
285 mesocarp thickness and the number of seeds. As we expected, the three ForestGEO sites  
286 surveyed were distinct in their floral diversity as well as fruit syndromes and colours. The  
287 Neotropical BCI site was the most distinct in terms of plant species composition and fruit traits  
288 (fruit syndromes and colours), with KHC and WAN sites sharing both more phylogenetic and  
289 trait based similarity (Corlett & Primack 2006). Corlett and Primack (2006) stated that Southeast  
290 Asian forest plots are dominated mostly by canopy tree species whereas Neotropical plots are  
291 rich in understory shrub species. These differences in the representation of life form categories  
292 (e.g., lianas, shrubs or trees) may explain much of the observed dissimilarity in fruit syndromes  
293 and fruit colours, and the overall pattern of fruit-feeding insect assemblages observed at the three  
294 rainforest regions (see Basset *et al.* 2018). For instance, BCI vegetation comprises a high  
295 proportion of shrub and liana species and has a high production of dry fruits. Lianas have a high

296 proportion of dry fruits that were also often attacked by seed eaters, while fruits of shrubs are  
297 smaller and are rarely attacked by insects. In general, dry fruits are exposed to high insect  
298 damage compared to fleshy fruits at our study sites (Basset *et al.* 2018). Other studies from other  
299 tropical regions also found similar distinctions among plant life forms, fruit syndromes and fruit  
300 colours (see Chen *et al.* 2004, Bolmgren & Eriksson 2010, Jara-Guerrero *et al.* 2011).

301 Our fruit syndrome system represents a simple classification that emphasizes fruit traits  
302 relevant for insects (e.g., mesocarp thickness) rather than those important for vertebrates (e.g.,  
303 fruit colour). The present system offers a broad qualitative classification of fruits that could be  
304 further refined. For instance, Ctvrtecka *et al.* (2016) defined fleshiness as percentage of fruit  
305 volume represented by mesocarp and used a conditional inference tree to identify critical values  
306 of fleshiness and seed size of predictive value for frugivory by weevils. Basset *et al.* (2018)  
307 documented guild composition of frugivorous insects associated with individual syndromes in  
308 different geographical regions in the tropics.

309 The largest resource in the forests studied here is represented by fruits falling within the  
310 A1.2 and B1 syndromes. Interestingly, dry fruits are generally prevalent and are attacked by true  
311 seed-feeders at BCI, while pulp-feeders are common on fleshy fruits in KHC and WAN (Basset  
312 *et al.* 2018). The fruit syndromes therefore do not show inter-continental convergence in their  
313 frugivorous insect assemblages. The distribution of fruit syndromes reflected similarity in plant  
314 phylogenetic composition among the sites studied, with WAN and KHC being more similar to  
315 each other than to BCI.

316 We used stems per species abundance (as measured by basal area) to quantify the  
317 ecological dominance of each fruit syndrome, as overall resource availability is likely to be an  
318 important factor for predicting insect occurrence (Ctvrtecka *et al.* 2016, Basset *et al.* 2018).



319 Basset *et al.* (2018) observed that seed eaters accumulate at a higher rate on plants with dry fruit  
320 syndromes relative to fleshy syndromes (BCI>KHC>WAN) across study plots.

321 Dry fruits tend to be abundant in dry tropical sites where fleshy fruits are less common  
322 (Willson & Whelan 1990, Ramirez & Traveset 2010). Most plant species producing black,  
323 orange, red, yellow or brown fruits are reported as being vertebrate dispersed (Gautier-Hion *et al.*  
324 1985). These fruit colours were prevalent in the fleshy fruit syndromes common at KHC and  
325 WAN but not at BCI. BCI retained mostly black/brown coloured fruits (>21% of basal area),  
326 largely associated with small trees and shrubs and lianas. Black fruits were common among  
327 understory shrubs/herbs and are more likely to be visible to frugivorous birds than insect seed  
328 predators in Neotropical rainforests (Wheelwright & Janson 1985). Furthermore, this may partly  
329 explain the low number of seed-feeding insects observed from fruit samples in BCI (Basset *et al.*  
330 2018) and other dry forests (Janzen 1980).

331  
332 FRUIT SYNDROMES AND COLOUR IN APHYLOGENETIC CONTEXT.—Both floristic and fruit syndrome  
333 similarities can be explained by a more pronounced dry season at BCI compared to the other two  
334 sites, promoting the dominance of Fabaceae (Condit 1998, Chust *et al.* 2006). Fruit morphology  
335 can be shaped by mutualistic relationships with dispersers as well as antagonistic interactions  
336 with seed predators (Chen *et al.* 2004). Broadly speaking, BCI is the most phylogenetically  
337 distinctive site, yet many plant families and some genera have a pantropical distribution. The  
338 only syndromes aggregated on the plant phylogeny proved to be non-fleshy syndromes. Less  
339 surprisingly, fruit colour also proved generally unconstrained by phylogeny. Clearly the dry-  
340 fleshy continuum is at least partly explained by phylogeny, with colour retaining a smaller  
341 degree of phylogenetic predictability. The fruit syndromes as well as colours thus retain

342 phylogenetic flexibility to respond to local species pools of insect pests and vertebrate dispersers,  
343 irrespective of taxonomic composition of the regional floras. However, our multivariate analyses  
344 revealed a subtler correlation between phylogeny and plant traits, with plant phylogeny  
345 explaining much of the variance in the overall “community” of syndromes across all sites.

346       Even though our seed syndrome system has entomocentric interest, our results generally  
347 confirm those of others (Willson & Irvine 1989, Forget *et al.* 2007, Chen *et al.* 2017). For  
348 example, fruiting trees bearing fleshy fruits coupled with an endozoochory relationship reliant on  
349 high local bird density are more prominent in tropical forest regions with high precipitation  
350 (Almeida-Neto *et al.* 2008). The high abundance of fruit flies reared from fleshy fruits from  
351 Papua New Guinean (Ctvrtecka *et al.* 2016) and Thai forest contrasts with lower numbers from  
352 Panamanian forest, with fewer fleshy fruits (Basset *et al.* 2018), suggesting our insect seed  
353 syndrome results reflect the endozoochory dichotomy pattern of fleshy vs. dry fruits present  
354 across rainforest regions (Chen *et al.* 2017). Further, birds and mammals that consume fleshy  
355 fruits have played a role in the evolutionary diversification of fruit morphology (Whitney, 2009,  
356 Valido *et al.* 2011). Typically, a given colour of fleshy fruits has a wide distribution among  
357 tropical plant communities (Willson & Whelan, 1990). We observed higher frequencies of  
358 preferred vertebrate colours (black, orange, red and green or brown; Janson 1983, Gautier-Hion  
359 *et al.* 1985, Willson & Whelan 1990, Duan *et al.* 2005).

360

361 CONCLUSION.—There are many studies on fruit and seed syndromes by botanists and vertebrate  
362 zoologists. However, studies on insect fruit syndromes across inter-continental rainforest regions  
363 are few (Basset *et al.* 2018). We have shown large inter-continental variability in the  
364 representation of fruit syndromes and colours, with likely consequences for seed predators and

365 dispersers. Plant species with fleshy and non-fleshy (dry) fruit syndromes may prefer different  
366 forest types and be attacked by different insect feeders (Basset *et al.* 2018), and fruits with  
367 different colours preferred by different vertebrate dispersers. The individual insect fruit  
368 syndromes and colours showed low levels of phylogenetic signal with only limited evidence of  
369 clustering across the plant phylogeny. However, in a multivariate context plant phylogeny is  
370 clearly an important driver of overall syndrome composition. Both fruit syndromes and colours  
371 are, to some extent, evolutionarily flexible traits at higher taxonomic levels and capable of  
372 responding to local species pools of seed predators and dispersers. We consider our insect fruit  
373 syndromes to be ecologically useful. They can be further refined when additional information on  
374 the mode of attack by various frugivorous taxa becomes available.

375

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384 DNA sequencing of insect specimens.

385

#### 386 DATA AVAILABILITY

387

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557

558 **TABLE LEGENDS**

559 TABLE 1. Three classification systems of fruits used in previous studies (botany and zoology  
560 systems) and in this study (a novel entomology system). Consistent shading across systems  
561 denotes similar or equivalent categories.

562

563 **FIGURE LEGENDS**

564 FIGURE 1. Percentage of plant species (a) and basal area (b) represented by individual fruit  
565 syndromes at each of the three ForestGEO sites. BCI=Barro Colorado Island, Panama;  
566 KHC=Khao Chong, Thailand; WAN=Wanang, Papua New Guinea.

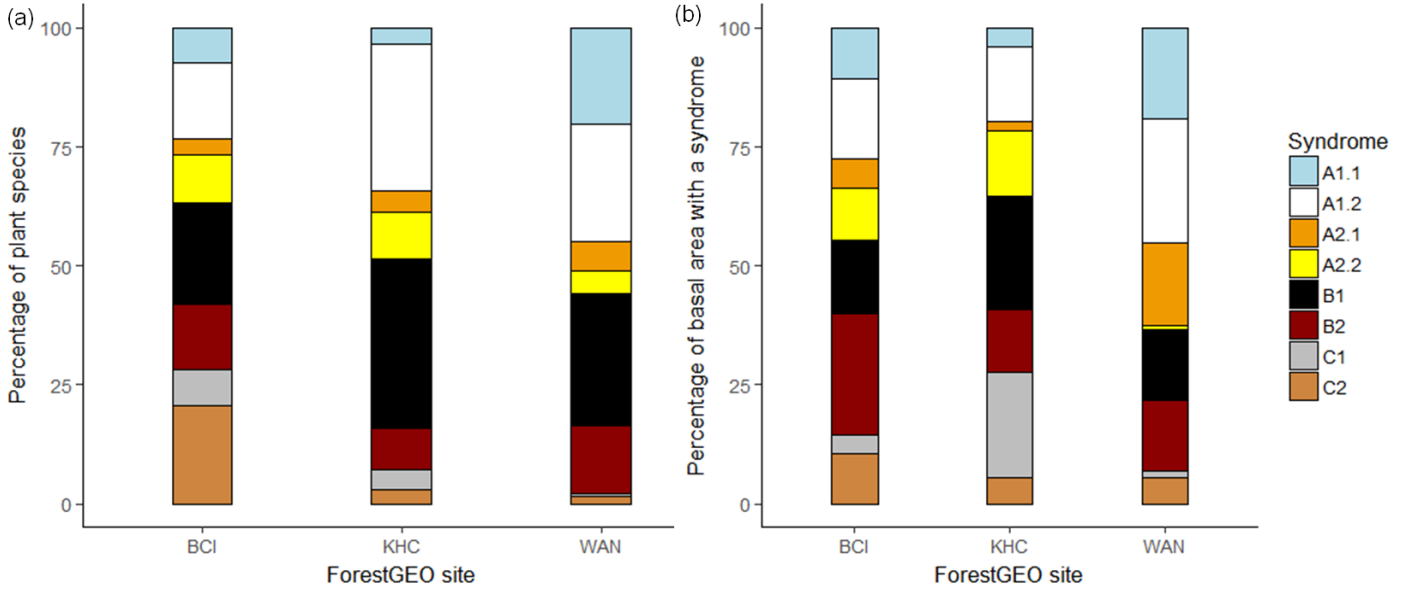
567 FIGURE 2. Percentage of fruit colour represented by plant species (a) and basal area (b) at each  
568 of the three ForestGEO sites. BCI=Barro Colorado Island, Panama; KHC=Khao Chong,  
569 Thailand; WAN=Wanang, Papua New Guinea.

570 FIGURE 3. The number of species in phylogenetically ordered plant genera (a) and families (b)  
571 possessing a particular fruit syndrome (C1, C2, B2) or fruit colour (brown), and the total number  
572 of species at each site. Only syndromes and colours showing significant phylogenetic clustering  
573 are shown.

574 FIGURE 4. CCA ordination of fruit syndromes based on their distribution in plant genera, with  
575 fruit colour, forest site (BCI, KHC, WAN) and plant phylogeny (represented by PCO vectors) as  
576 explanatory variables (a) and Venn diagram visualizing the proportions of overall adjusted  
577 variability explained by each set of variables and their combinations (b). Centroids of individual  
578 seed syndromes in (a) are represented by circles for dry fruits and squares for fleshy fruits.  
579 CCA used forward selection of the individual predictors (999 randomizations,  $p\text{-adj} < 0.05$ ) and  
580 variation partitioning among the three sets of variables (see Table S4 for details).

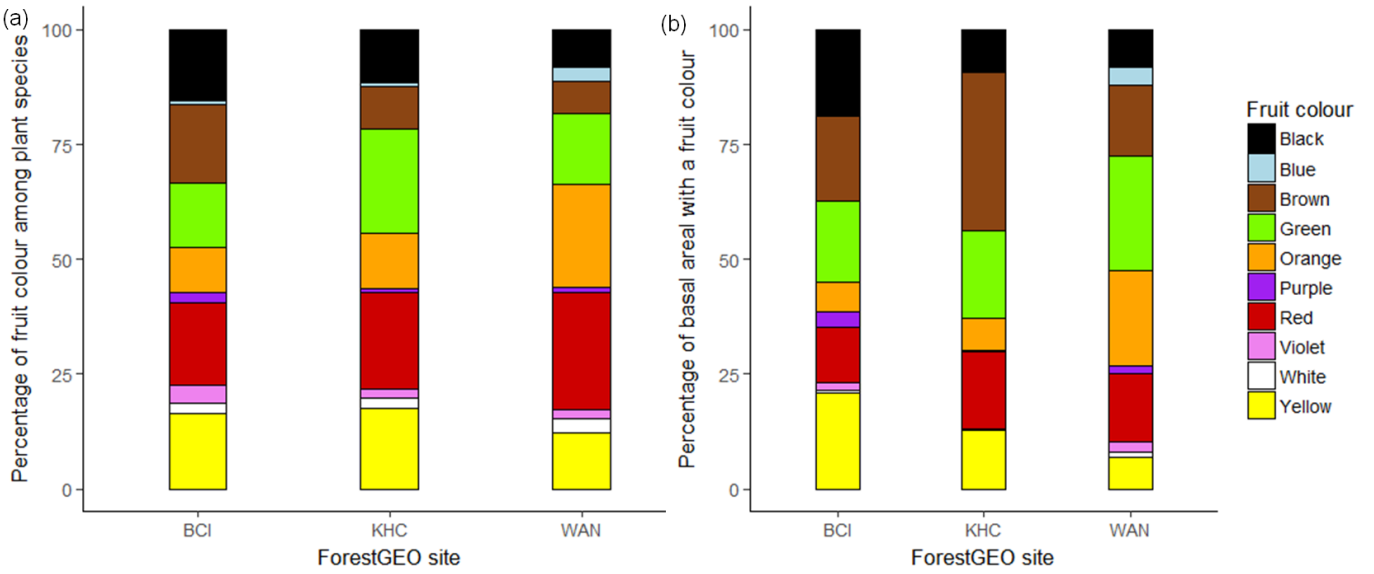
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BOTANY SYSTEM	ZOOLOGY SYSTEM	ENTOMOLOGY SYSTEM
<b>Related to plant morphology</b>	<b>Related to frugivory and seed dispersal</b>	<b>Related to seed predation</b>
Hickey & King, 1981, Zomlefer, 1994	Janson, 1983, Gautier-Hion <i>et al.</i> 1985	This study
Categories mutually exclusive	Categories not mutually exclusive	Categories in most cases mutually exclusive
Code (B-), Category	Code (Z-), Category	Code (E-), Category
<b>B-A. Succulent, fleshy fruit</b>	<b>Z-A. Colour</b>	<b>E-A. Drupe (one seed per fruit)</b>
B-A1 Drupe - a single seed ***	Z-A1 Colour either red, white, black, or mixed (mostly dry fruits)	A1. Fleshy drupe
B-A2 Berry - a single fruit with several seeds †††	Z-A2 Colour either orange, brown, yellow, green, purple (mostly fleshy fruits)	E-A1.1 Fleshy drupe with thick mesocarp (>5mm) ***
B-A3 Multiple fruit with several seeds †††	<b>Z-B. Type of flesh</b>	E-A1.2 Fleshy drupe with thin mesocarp (<5mm) ***
<b>B-B. Dry fruit</b>	Z-B1 Juicy soft	E-A2. Non-fleshy drupe ***
<b>B-B1. Dehiscent fruit</b>	Z-B2 Juicy fibrous	E-A2.1 Non-fleshy with thick mesocarp (>5mm) ***
B-B1.1 Legume ***	<b>Z-C. Protective coat</b>	E-A2.2 Non-fleshy with thin mesocarp (<5mm) ***
B-B1.2 Follicle ***	Z-C1 Dehiscent coat ***	<b>E-B. Fruit with multiple seeds</b>
B-B1.3 Capsule ***	Z-C2 With aril ***	E-B1 Fleshy indehiscent fruit with multiple seeds †††
B-B1.4 Others (silique, silicula, lomentum, etc.) ***	Z-C3 indehiscent coat - thin husk ***	E-B2 Non-fleshy dehiscent fruit with multiple seeds, (dehiscence typically across multiple axes) ***
	Z-C4 indehiscent coat - thick husk ***	<b>E-C. Dry fruit/seed</b>
<b>B-B2. indehiscent fruit</b>	<b>Z-D. Seed size</b>	E-C1 Dry winged seed that do not develop in capsule ***
B-B2.1 Samara ***		
B-B2.2 Nut ***	<b>Z-E. Number of seeds per fruit</b>	E-C2 Multiple dry seeds (with or without wings) that do develop in capsule (dehiscence typically across one single axis) ***
B-B2.3 Achene ***	Z-E1 Fruits with multiple seeds ***	
B-B2.4 Others (caryopsis, utricle, etc.) ***		
<b>B-B3. Schizocarpic fruit</b>		
B-B3.1 Cremocarp ***		
B-B3.2 Double samara ***		



599  
600 FIGURE 1.

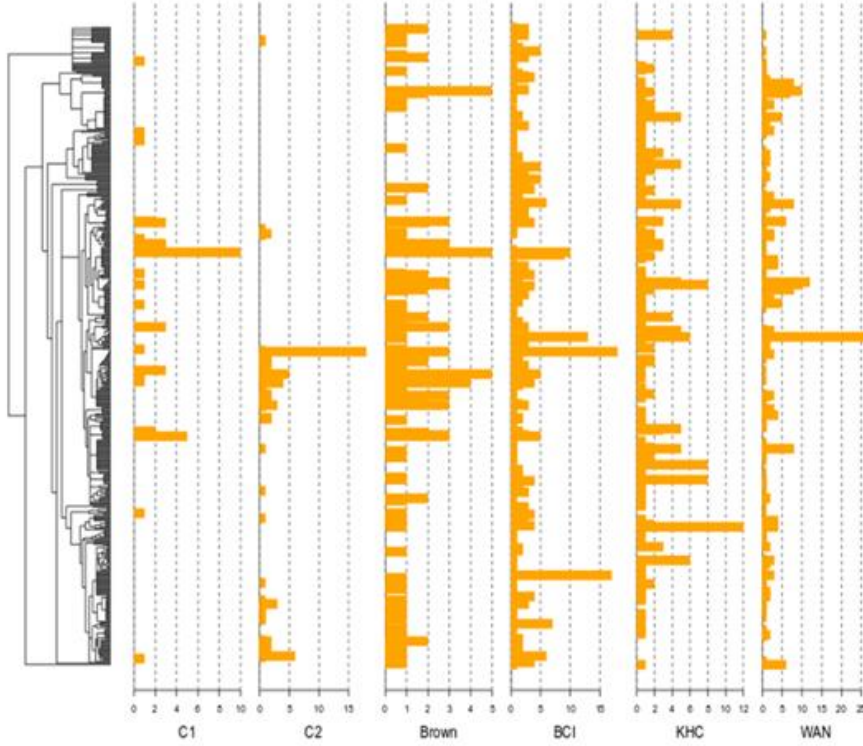
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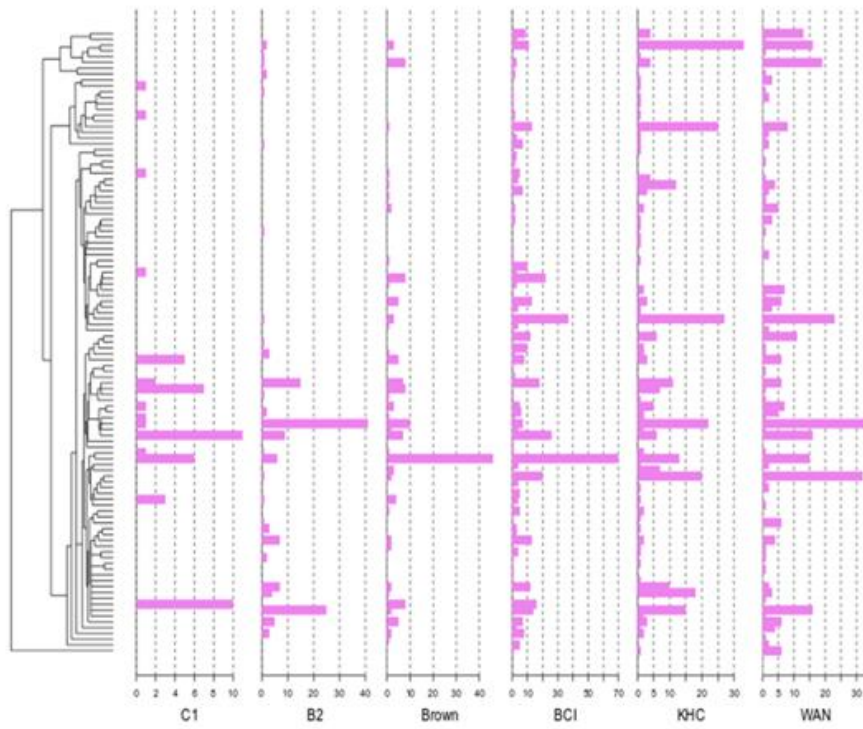
604  
605 FIGURE 2.

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(a)

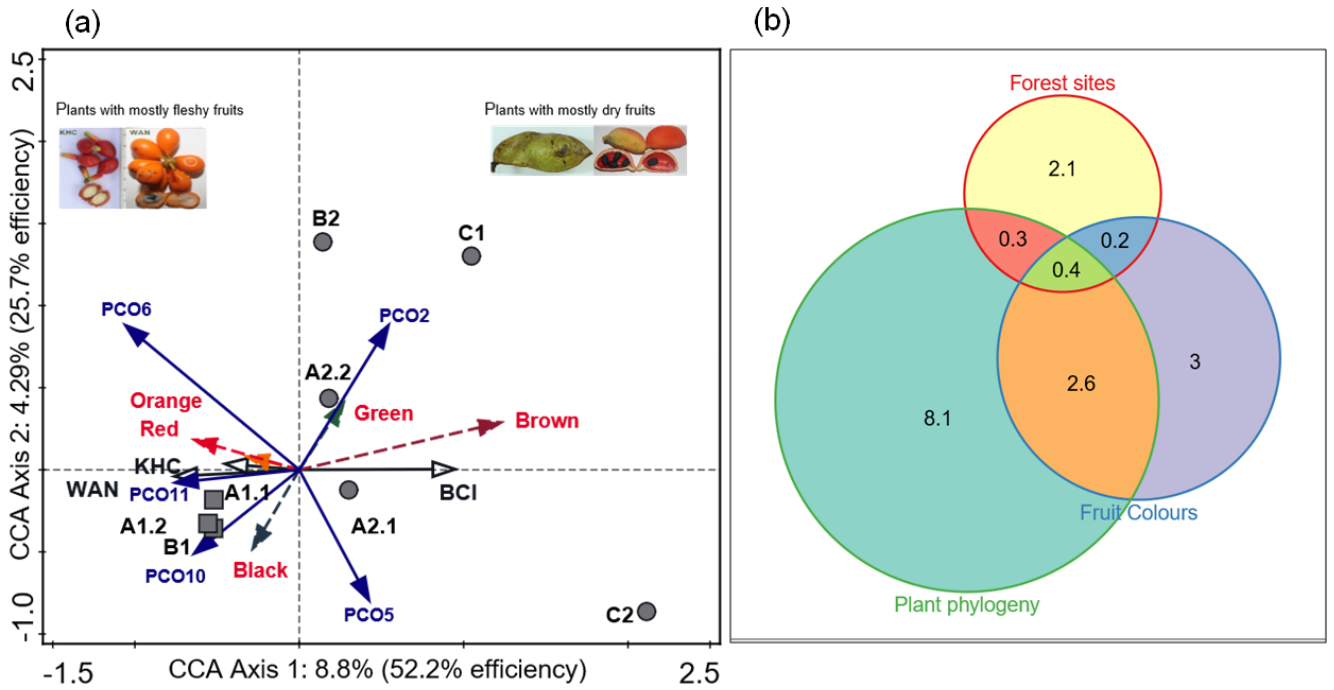


(b)



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608 FIGURE 3.



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610 FIGURE 4.

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613 **SUPPLEMENTARY INFORMATION**

614 Additional supporting information can be found in the online version of this article.

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624 **SUPPLEMENTARY TABLES**

625 TABLE S1. Syndrome categories for the entomology system. Codes refer to Table 1. Data are  
626 based on the rearing of ca 56,000 insects from seeds originating from Panama, Thailand and  
627 Papua New Guinea.

628 TABLE S2. Salient characteristics of study sites, and plant, seed and insect variables measured  
629 across sites. Means are reported with se in brackets and p values refer to Kruskal-Wallis tests.  
630 Plot data are from Anderson-Teixeira *et al.* (2014) and Basset *et al.* (2018).

631 TABLE S3. Plant families surveyed at the three study sites. \*\*Denotes eight focal plant families  
632 with wide distributions and \*\*\*indicates two plant families present only at a single site.

633 TABLE S4. Test of significance of the predictors in CCA affecting the seed syndromes, using  
634 plant genera as samples and forward selection of variables. For a diagram showing the first two  
635 canonical axes see Fig. 4. P(adj) was used with  $\alpha < 0.05$  for tests of significance. In the case  
636 of PCO phylogenetic axes, only the five most significant axes were retained (of 18 that were  
637 significant) to balance the variation partitioning analysis and avoid overestimating the effects of  
638 phylogeny and deep nodes (i.e. we retained a number of PCO that generated a similar DF and  
639 mean square to that for significant colours).

640 TABLE S5. Test of significance of the predictors in CCA affecting the seed syndromes using  
641 plant families as samples and forward selection. For a diagram of the first two canonical axes see  
642 Fig. S3. P(adj) was used with  $\alpha < 0.05$  for tests of significance.

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647 **SUPPLEMENTARY FIGURES**

648 FIGURE S1. Percentage of stems represented by individual fruit syndromes at each of the three  
649 ForestGEO sites. BCI=Barro Colorado Island, Panama; KHC=Khao Chong, Thailand;  
650 WAN=Wanang, Papua New Guinea.

651 FIGURE S2. Percentage of plant species from each plant life form at the three ForestGEO study  
652 sites. BCI=Barro Colorado Island, Panama; KHC=Khao Chong, Thailand; WAN=Wanang, Papua  
653 New Guinea.

654 FIGURE S3. CCA ordination of fruit syndrome distribution based on plant families, fruit colour,  
655 forest site (BCI, KHC, WAN) and plant phylogeny (represented by PCO vectors) as explanatory  
656 variables (a), and Venn diagram visualizing the proportions of overall adjusted variability  
657 explained by each set of variables and their combinations (b). Centroids of individual seed  
658 syndromes (a) are represented by circles for the dry fruits and squares for the fleshy fruits. CCA  
659 used forward selection of the individual predictors (999 randomizations,  $p\text{-adj} < 0.05$ ) and  
660 variation partitioning among the three sets of variables (see Table S5 for details).

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