

# The insect-focused classification of fruit syndromes in tropical rain forests: An inter-continental comparison

by Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Segar, S.T., Klimes, P., Sam, K., Rinan, D., Filip, J., Lilip, R. Kongnoo, P. *et al.*

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DOI: <https://doi.org/10.1111/btp.12622>



Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Segar, S.T., Klimes, P., Sam, K., Rinan, D., Filip, J., Lilip, R. Kongnoo, P. et al. 2019. The insect-focused classification of fruit syndromes in tropical rain forests: An inter-continental comparison. *Biotropical*.

28 January 2019

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

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26 Running title: Rainforest fruit syndromes

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28 Received \_\_\_\_\_; revision accepted \_\_\_\_\_. (*Biotropica* will fill in the dates.)

29

### 30 **ABSTRACT**

31 We put forward 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 that are based on plant morphology, or traits relevant to vertebrate fruit dispersers.

34 Our syndromes are based on fruits sampled from 1,192 plant species at three ForestGEO plots:  
35 Barro Colorado Island (Panama), Khao Chong (Thailand) and Wanang (Papua New Guinea). We  
36 found large differences in the fruit syndrome composition among the three forests. Plant species  
37 with fleshy indehiscent fruits containing multiple seeds were important at all three sites.

38 However, Panama had a higher proportion of species with dry fruits while in New Guinea and  
39 Thailand, species with fleshy drupes and thin mesocarps were dominant. Species with dry  
40 winged seeds that do not develop as capsules were important in Thailand, reflecting the local  
41 importance of Dipterocarpaceae. These differences can also determine differences among  
42 frugivorous insect communities. Fruit syndromes and colours were phylogenetically flexible  
43 traits at the scale studied, as only three of the eight seed syndromes, and one of the 10 colours,  
44 showed significant phylogenetic signal, viz. phylogenetic clustering at either genus or family  
45 levels. Plant phylogeny was however the most important factor when explaining differences in

46 overall fruit syndrome composition among individual plant families or genera across the three  
47 study sites.

48

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

50

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

68 forests, with a potential to determine rainforest ecosystem dynamics (Janzen 1980, Correa, *et al.*  
69 2015).

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

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

91 mechanical protection by mesocarp all define vulnerability to seed predation by insects so that  
92 the study of particular combinations of these traits can provide insights into the insect predation  
93 pressure on plants. As any categorical classification of continuous variability involving multiple  
94 traits, syndromes represent a simplification, but we find the concept useful for generating  
95 ecological hypotheses. For instance, the definition of discrete life-history syndromes has  
96 contributed to the development of ecological theory of succession (Turner 2008) or plant  
97 response to herbivory (Herms & Mattson 1992).

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

114 forests in Southeast Asia are dominated by dipterocarps with seeds dispersed by wind in massive  
115 fruiting events (Corlett & Primack 2006). Australasian rain forests have a high diversity of plant  
116 species that produce large fleshy fruits (Chen *et al.* 2017). These differences in the production of  
117 fruits in rain forests may impact the way fruits and seeds are attacked by insects (Table S1).  
118 Therefore, it is important to document the distribution of fruit syndromes relevant to insects  
119 across rainforest locations in distinct biogeographical regions. Our insect-oriented classification  
120 of fruit syndromes is based on 1,192 plant species collected across three tropical forest sites (in  
121 Panama, Thailand and Papua New Guinea). We quantified plant diversity and abundance  
122 represented by each syndrome in a phylogenetic context and across the three continents. We use  
123 this information to explore the resource base for fruit and seed eating insects in tropical  
124 rainforests.

125

## 126 **METHODS**

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

136 programs (Ctvrtecka *et al.* 2016, Basset *et al.* 2018) that became the basis for our fruit  
137 classification systems (Table 1).

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

149  
150 FRUIT CLASSIFICATION SYSTEMS.—Each plant species sampled was assigned to a specific  
151 category [using our new entomocentric classification](#) was compared to the [previous botany and](#)  
152 [zoology systems](#) (Table 1). The botany system is based on plant morphology, while the zoology  
153 system was created mostly with respect to plant dispersal by vertebrates. Our entomology system  
154 is concerned primarily with seed predation by insects. The first dichotomy in the botany system  
155 is whether the fruit is fleshy or dry. The former includes drupes, berries, and other fleshy fruits  
156 with multiple seeds. The dry fruits are classified as dehiscent, indehiscent and schizocarps  
157 (Hickey & King 1981, Zomlefer 1994, Table 1). The zoology system uses fruit traits such as size,  
158 colour, number of seeds and seed protection (Janson 1983, Gautier-Hion *et al.* 1985, Table 1).

159 For our new entomology system, we selected 2-4 individual fruits per tree species, classified  
160 fruits by morphology, estimated their size (length and width to the nearest millimeter) and weight  
161 (to the nearest gram), and photographed them. We identified fruit colour using a colour scheme  
162 developed for vertebrate dispersal assessment by Janson (1983) and Gautier-Hion *et al.* (1985).  
163 To control for colour choice biases, the Munsell Colour index system (Sturges & Whitfield 1995)  
164 was used to match colours to black, blue, brown, green, orange, purple, red, violet, white and  
165 yellow on the basis of pictures of ripened fruits.

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

175  
176 DATA ANALYSIS.—Our analyses were based on a complete plant species we sampled for fruits  
177 both inside and outside the ForestGEO plots, using number of species per category as response  
178 variable (1,192 species, Fig. 1a, 2a, 3 and 4). For each species which we had individual  
179 abundance and stem size (i.e., trees inside the ForestGEO plots, 689 species) we used basal area  
180 and density of stems per species in combination with the “species” fruit syndrome to quantify the  
181 ecological significance of fruit syndromes (including life form) as resource for insects and to

182 make quantitative comparisons across sites (Fig. 1b, 2b, Table S1, Basset *et al.* 2018). We  
183 compared the proportion of species, basal area and stems represented by each fruit syndrome, life  
184 form and fruit colour among the study plots. For plant phylogeny analyses, 14% of plant species  
185 with unknown plant families (mostly unidentified lianas) were excluded in our KHC data sets.

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

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

202 Often genera or families had multiple states (e.g. several syndromes) and we used the  
203 number of species within each genus or family to conduct abundance weighted analyses using  
204 the R package “Picante” (Kembel *et al.* 2010). To evaluate simultaneous and separate effects of

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

219 To assess the robustness of the PCO axes, we also ran a similar analysis with 100 axes  
220 (both approaches indicated the same results). To avoid overestimating phylogenetic effects, the  
221 final number of retained significant PCO axes was adjusted considering also the number of  
222 degrees of freedom and mean squares for the three sets of the variables compared (Table S4, S5).  
223 We then calculated the % of variance explained either by sites, colors, or phylogenetic axes, and  
224 both three groups together. The results were visualized using species-explanatory variables biplot  
225 of the first two CCA axes. In addition, Venn diagrams indicating the amount of variance in  
226 syndromes explained by each of the two analyses were drawn using package “vennerable” (Chen  
227 2018). The efficiency of the two axes was calculated compared to unconstrained multivariate

228 space (i.e., % of explanatory variance, Smilauer & Leps 2014). Our analyses were computed  
229 with the R package (Team R. 2011).

230

## 231 **RESULTS**

232 PLANT DIVERSITY, COMPOSITION AND FRUIT SYNDROMES.—A total of 1,192 plant species from  
233 548 genera and 107 families were scored for fruit morphology and colour, including 497 species  
234 from BCI, 360 from KHC and 335 from WAN (Table S3). We obtained fruit syndrome data for  
235 99% of species representing almost 100% of stems at BCI, 45% of species and 85% of stems in  
236 WAN and 45% of species and 66% of stems in KHC. Stem density representing certain fruit  
237 syndromes varied across study plots ( $\chi^2=137020$ ,  $df=14$ ,  $p<0.001$ , Fig. S1).

238 The floristic similarity of the three plots at genus level was expressed using the  
239 phylogenetic Chao-Sorensen index. The similarity values ranged from 0.52 for KHC-WAN  
240 through 0.34 for BCI-KHC to 0.39 for BCI-WAN comparisons. The distribution of plant species  
241 among life forms differed significantly between study plots ( $\chi^2=432.31$ ,  $df=14$ ,  $p<0.001$ , Figs.  
242 S2). Both KHC (87%) and WAN (80%) have a high proportion of trees, while only 40% of all  
243 plant species sampled were trees at BCI. In contrast, lianas (23%) and shrubs (28%) were  
244 relatively abundant at BCI in comparison to KHC (lianas 11.3%, shrubs 1.4%) and WAN (lianas  
245 1.5%, shrubs 1.8%) plots. Less than 5% of plant species represented other plant life forms across  
246 the three study plots (Figs. S2).

247 Every fruit syndrome was represented at each study site. Approximately half of all  
248 species at each site had one-seeded drupe fruits (A and B syndromes). The flora was dominated  
249 by fleshy fruits (A1 and B1 syndromes) in WAN (72% of species) and KHC (68%), but only  
250 44% species had fleshy fruits at BCI. The distribution of individual syndromes differed among

251 individual plots, (plant species:  $\chi^2=229$ ,  $df=14$ ,  $p<0.001$ , basal area:  $\chi^2=754.09$ ,  $df=14$ ,  $p<0.001$ ,  
252 Fig. 1). The fleshy indehiscent fruits with multiple seeds (B1 syndrome) were important at all  
253 three sites. BCI had a higher proportion of dry fruits (C2 and C1) while at WAN and KHC,  
254 fleshy drupe with thin mesocarp fruits (A1.2) were important (Fig. 1).

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

263

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

271 The number of genera represented by each colour ranged from 14 (purple) to 153 (green)  
272 while the number of families ranged from 11 (blue) to 60 (green). We tested phylogenetic  
273 clustering for all 10 fruit colours and only found the colour brown to be significantly clustered at

274 genus level (n=107, Z= -2.609, p=0.005) and marginally significant at the family level (n=38, Z=  
275 -1.326, p=0.035).

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

284

## 285 **DISCUSSION**

286 PLANT DIVERSITY, COMPOSITION AND FRUIT SYNDROMES.—Our study provides an entomocentric  
287 assessment of fruit classification systems based on fruit morphology, particularly fleshiness,  
288 mesocarp thickness and the number of seeds. As we expected, the three ForestGEO sites  
289 surveyed were distinct in their floral diversity as well as fruit syndromes and colours. The  
290 Neotropical BCI site was the most distinct in terms of plant species composition and fruit traits  
291 (fruit syndromes and colours) with KHC and WAN sites sharing both more phylogenetic and trait  
292 based similarity (Corlett & Primack 2006). Corlett and Primack (2006) stated that Southeast  
293 Asian forest plots are dominated mostly by canopy tree species whereas Neotropical plots are  
294 rich in understory shrub species. This distinction was confirmed by our study where we obtained  
295 fruits per plant species, then identified to its life form category (e.g., lianas, shrubs or trees). This  
296 major plant life form may explain dissimilarity among fruit syndromes and fruit colour and the

297 overall pattern of fruit-feeding insect assemblages observed at three rainforest regions (see  
298 Basset *et al.* 2018). For instance, BCI vegetation comprises a high proportion of shrub and liana  
299 species and has a high production of dry fruits. Lianas have a high proportion of dry fruits that  
300 were also often attacked by seed eaters, while fruits of shrubs are relatively smaller and rarely  
301 attacked by insects. In general, dry fruits are exposed to high insect damage compared to fleshy  
302 fruits at our study sites (Basset *et al.* 2018). Other studies from other tropical regions also found  
303 similar distinctions among plant life forms, fruit syndromes and fruit colours (see Chen *et al.*  
304 2004, Bolmgren & Eriksson 2010, Jara-Guerrero *et al.* 2011).

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

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

320 We used stems per species abundance (as measured by basal area) to quantify the  
321 ecological dominance of each fruit syndrome as overall resource availability is likely to be an  
322 important factor for predicting insect occurrence (Ctvrtecka *et al.* 2016, Basset *et al.* 2018).  
323 Basset *et al.* (2018) observed that seed eaters accumulate at a higher rate on plants with dry fruit  
324 syndromes to fleshy syndromes (BCI>KHC>WAN) across study plots.

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

335

336 FRUIT SYNDROMES AND COLOUR IN A PHYLOGENETIC CONTEXT.—Both floristic and fruit  
337 syndrome similarities can be explained by a more pronounced dry season at BCI compared to the  
338 other two sites, promoting the dominance of Fabaceae (Condit 1998, Chust *et al.* 2006). Fruit  
339 morphology can be shaped by mutualistic relationships with dispersers as well as antagonistic  
340 interactions with seed predators (Chen *et al.* 2004). Broadly speaking BCI is the most  
341 phylogenetically distinctive site, yet many plant families and some genera have a pantropical  
342 distribution. The only syndromes aggregated on the plant phylogeny proved to be non-fleshy

343 syndromes, less surprisingly, fruit colour also proved generally unconstrained by phylogeny.  
344 Clearly the dry-fleshy continuum is at least partly explained by phylogenetic relationships, with  
345 colour retaining a smaller degree of phylogenetic predictability. The fruit syndromes as well as  
346 colours thus retain phylogenetic flexibility to respond to local species pools of insect pests and  
347 vertebrate dispersers irrespective of taxonomic composition of the regional floras. [However](#), our  
348 multivariate analyses revealed a subtler correlation between phylogeny and plant traits, with  
349 plant phylogeny explaining much of the variance in the overall “community” of syndromes  
350 [across all sites](#).

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

365

366 CONCLUSION.—There are many studies on fruit and seed syndromes by botanists and vertebrate  
367 zoologists. However, studies on insect fruit syndromes across inter-continental rainforest regions  
368 are few (Basset *et al.* 2018). We have shown large inter-continental variability in the  
369 representation of fruit syndromes and colours, with likely consequences for seed predators and  
370 dispersers. Plant species with fleshy and non-fleshy (dry) fruit syndromes may prefer different  
371 forest types and be attacked by different insect feeders (Basset *et al.* 2018), and fruits with  
372 different colours preferred by different vertebrate dispersers. The insect fruit syndromes and  
373 colours showed low levels of phylogenetic signal individually with only limited evidence of  
374 clustering across the plant phylogeny. Although in a multivariate context plant phylogeny is  
375 clearly an important driver of overall syndrome composition. Both fruit syndromes and colours  
376 are, to some extent, evolutionarily flexible traits at higher taxonomic levels and capable of  
377 responding to local species pools of seed predators and dispersers. We consider our insect fruit  
378 syndromes to be ecologically useful. They can be further refined when additional information on  
379 the mode of attack by various frugivorous taxa becomes available.

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389 ACKNOWLEDGMENTS

390 We are grateful to our colleagues of the Smithsonian Tropical Research Institute, (BCI, Panama),  
391 Khao Chong Botanical Garden (Thailand) and Binatang Research Centre and Wanang  
392 Conservation area (Papua New Guinea) for helping with this project which was funded by the  
393 Czech Science Foundation (GACR grant 16-20825S), the Center for Tropical Forest Science  
394 small grant scheme, the University of South Bohemia (grant GA JU 152/2016/P). The Canadian  
395 Centre for DNA Barcoding (Biodiversity Institute of Ontario) and Southern China DNA  
396 Barcoding Center (Kunming Institute of Zoology, Chinese Academy of Sciences) assisted with  
397 DNA sequencing of insect specimens.

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399 DATA AVAILABILITY

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572 **TABLE LEGENDS**

573 TABLE 1. Three classification systems of fruits used in previous studies (botany and zoology  
574 systems) and in this study (a novel entomology system). Same colour across systems denotes  
575 similar or equivalent categories.

576

577 **FIGURE LEGENDS**

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

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

584 FIGURE 3. The number of species in phylogenetically ordered plant genera (a) and families (b)  
585 possessing a particular fruit syndrome (C1, C2, B2) or fruit color (brown), and the total number  
586 of species at each site. Only syndromes and colors showing significant phylogenetic clustering  
587 are shown.

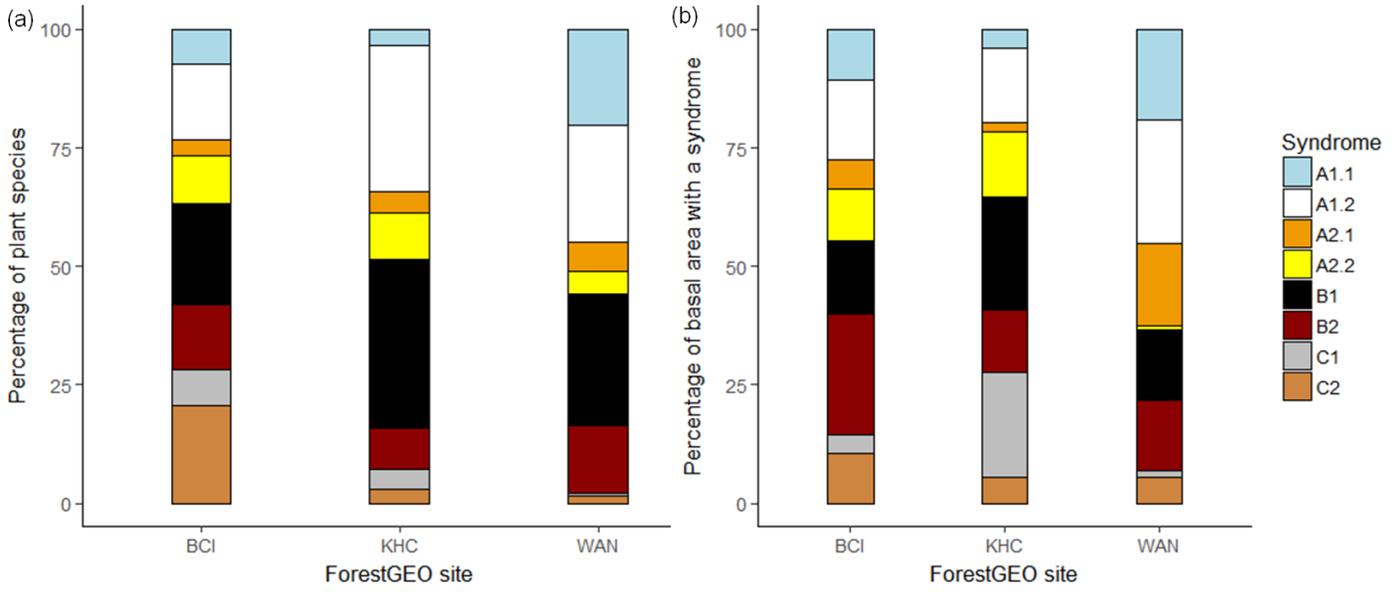
588 FIGURE 4. CCA ordination of fruit syndromes based on their distribution in plant genera, with  
589 fruit colour, forest site (BCI, KHC, WAN) and plant phylogeny (represented by PCO vectors) as  
590 explanatory variables (a) and Venn diagram visualizing the proportions of overall adjusted  
591 variability explained by each set of variables and their combinations (b). Centroids of individual  
592 seed syndromes in (a) are represented by circles for dry fruits and squares for fleshy fruits.

593 CCA used forward selection of the individual predictors (999 randomizations,  $p\text{-adj} < 0.05$ ) and  
594 variation partitioning among the three sets of variables (see Table S4 for details).

595 TABLE 1.

BOTANY SYSTEM	ZOOLOGY SYSTEM	ENTOMOLOGY SYSTEM
Related to plant morphology	Related to frugivory and seed dispersal	Related to seed predation
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)
<b>B-B2. Indehiscent fruit</b>	Z-C4 Indehiscent coat - thick husk	<b>E-C. Dry fruit/seed</b>
B-B2.1 Samara	<b>Z-D. Seed size</b>	E-C1 Dry winged seed that do not develop in capsule
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		

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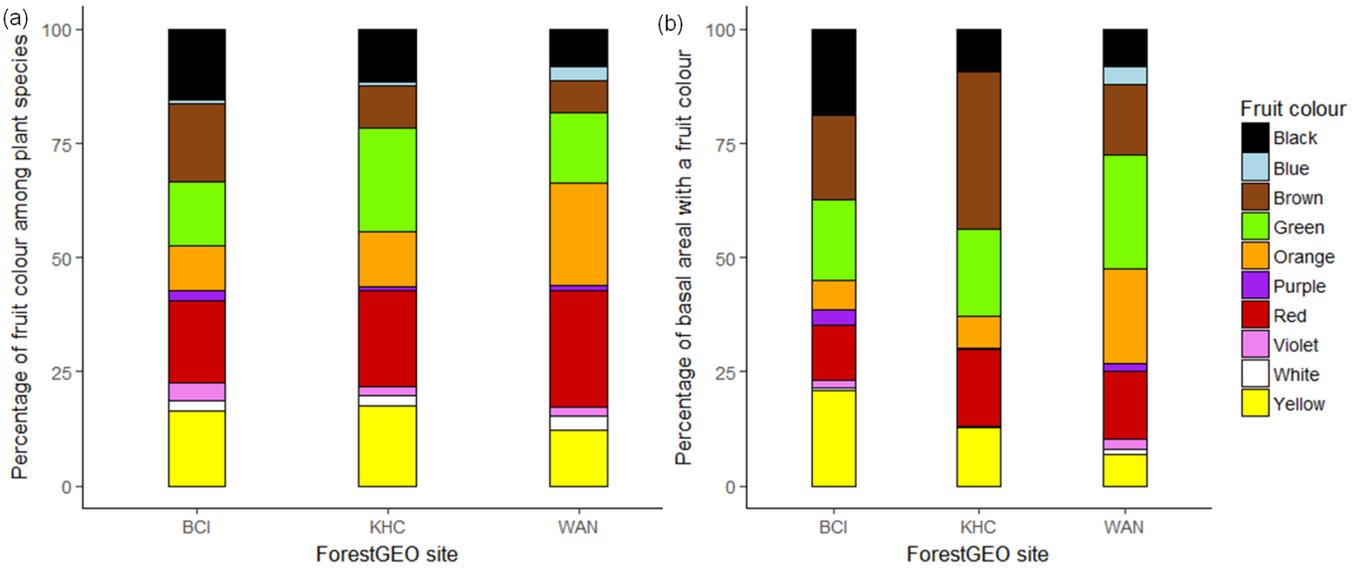
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598 FIGURE 1.

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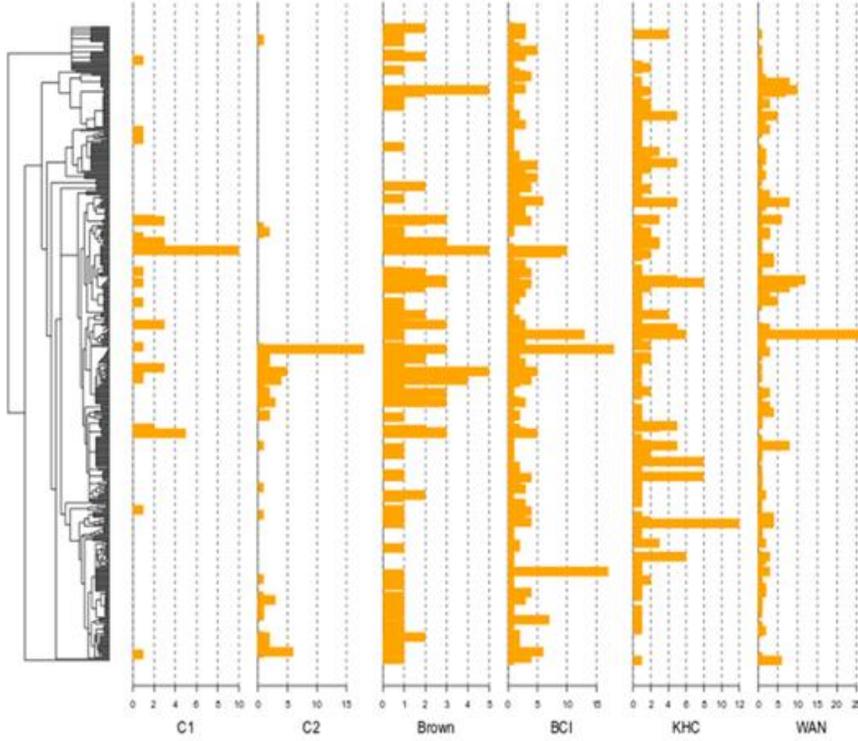


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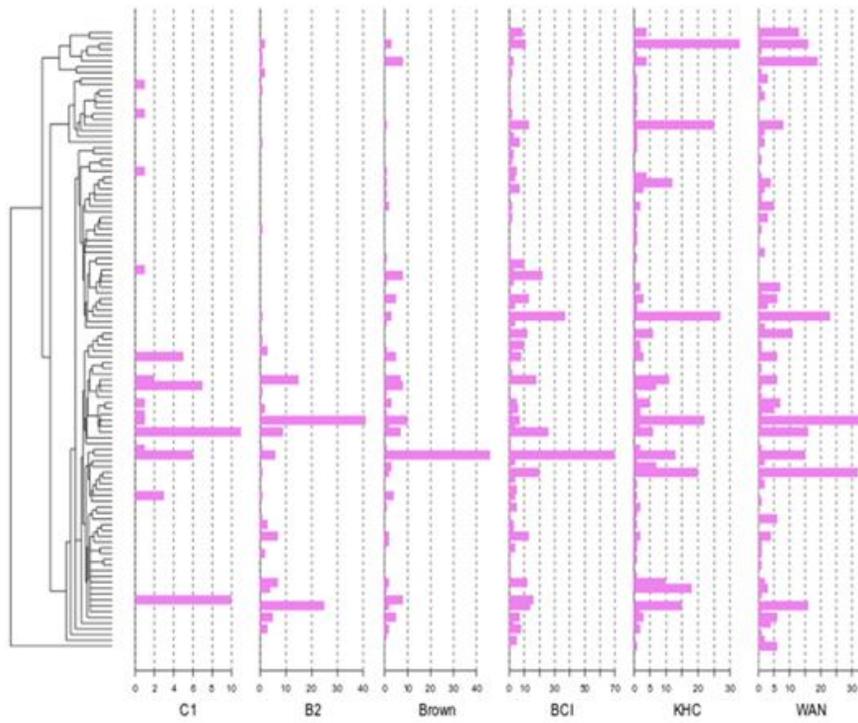
603 FIGURE 2.

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(a)

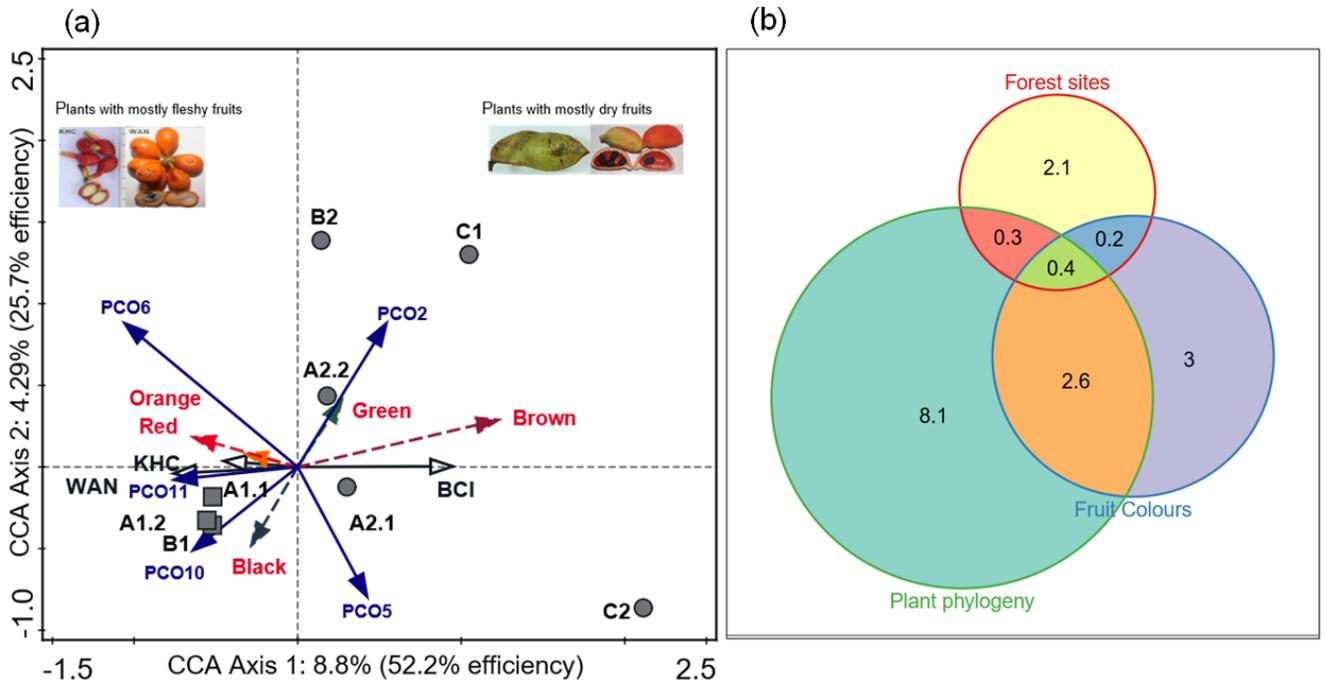


(b)



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606 FIGURE 3.



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608 FIGURE 4.

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611 **SUPPLEMENTARY INFORMATION**

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

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622 **SUPPLEMENTARY TABLES**

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

626 TABLE S2. Salient characteristics of study sites, and plant, seed and insect variables measured  
627 across sites. Means are reported with se in brackets and p values refer to Kruskal-Wallis tests.  
628 Plot data are from Anderson-Teixeira *et al.* (2014) and Basset *et al.* (2013).

629 TABLE S3. Plant families surveyed at the three study sites. Denotes (\*\*) eight focal plant  
630 families with wide distribution and (\*\*\*) two plant families are locally available at a single.

631 TABLE S4. Test of significance of the predictors in CCA affecting the seed syndromes using  
632 plant genera as samples and forward selection of variables. For diagram of first two canonical  
633 axes see Fig. 4. P(adj) was used with  $\alpha < 0.05$  for tests of significance. In case of PCO  
634 phylogenetic axes, only the first five top significant were retained of 18 being significant to  
635 balance the variation partitioning analysis and not overestimate the effects of phylogeny and its  
636 deep nodes (i.e. kept the same number of PCO as number of significant colours that resulted to a  
637 similar DF and mean square).

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

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645 **SUPPLEMENTARY FIGURES**

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

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

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

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