

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

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4 Chris Dahl^{1,2*}, Richard Ctvrticka², Sofia Gripenberg^{3,4}, Owen T. Lewis⁴, Simon T. Segar^{1,2,5}, Petr
5 Klimes², Katerina Sam^{1,2}, Dominic Rinan⁶, Jonah Filip⁶, Roll Lilip⁶, Pitoon Kongnoo⁷,
6 Montarika Panmeng⁷, Sutipun Putnau⁷, Manat Reungaew⁷, Marleny Rivera⁸, Hector Barrios⁸,
7 Stuart J. Davies⁹, Sarayudh Bunyavejchewin⁷, Joseph S. Wright¹⁰, George D. Weiblen¹¹, Vojtech
8 Novotny^{1,2}, and Yves Basset^{2,8,10}

9
10 ¹Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic;

11 ²Biology Center of the Czech Academy of Sciences, Institute of Entomology, Czech Republic;

12 ³School of Biological Sciences, University of Reading, UK; ⁴Department of Zoology, University
13 of Oxford, UK; ⁵Department of Crop and Environment Sciences, Harper Adams University, UK;

14 ⁶New Guinea Binatang Research Center, Madang, Papua New Guinea; ⁷ForestGEO Arthropod
15 Laboratory, Khao Chong Botanical Garden, Nayoung, Thailand; ⁸Maestria de Entomologia,

16 Universidad de Panama, Panama City, Panama; ⁹Center for Tropical Forest Science-Forest

17 Global Earth Observatory, Smithsonian Tropical Research Institute, Washington, DC, U.S.A.;

18 ¹⁰Smithsonian Tropical Research Institute, Apartado 0843–03092, Panama City, Republic of

19 Panama; ¹¹Bell Museum and Department of Plant Biology, University of Minnesota, U.S.A

20

21

22 *Correspondence: Chris Dahl, Faculty of Science, University of South Bohemia and Biology
23 Center of the Czech Academy of Sciences, Institute of Entomology, Czech Republic. Email:
24 cd.rokrok@gmail.com

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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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396 Barcoding Center (Kunming Institute of Zoology, Chinese Academy of Sciences) assisted with
397 DNA sequencing of insect specimens.

398

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.

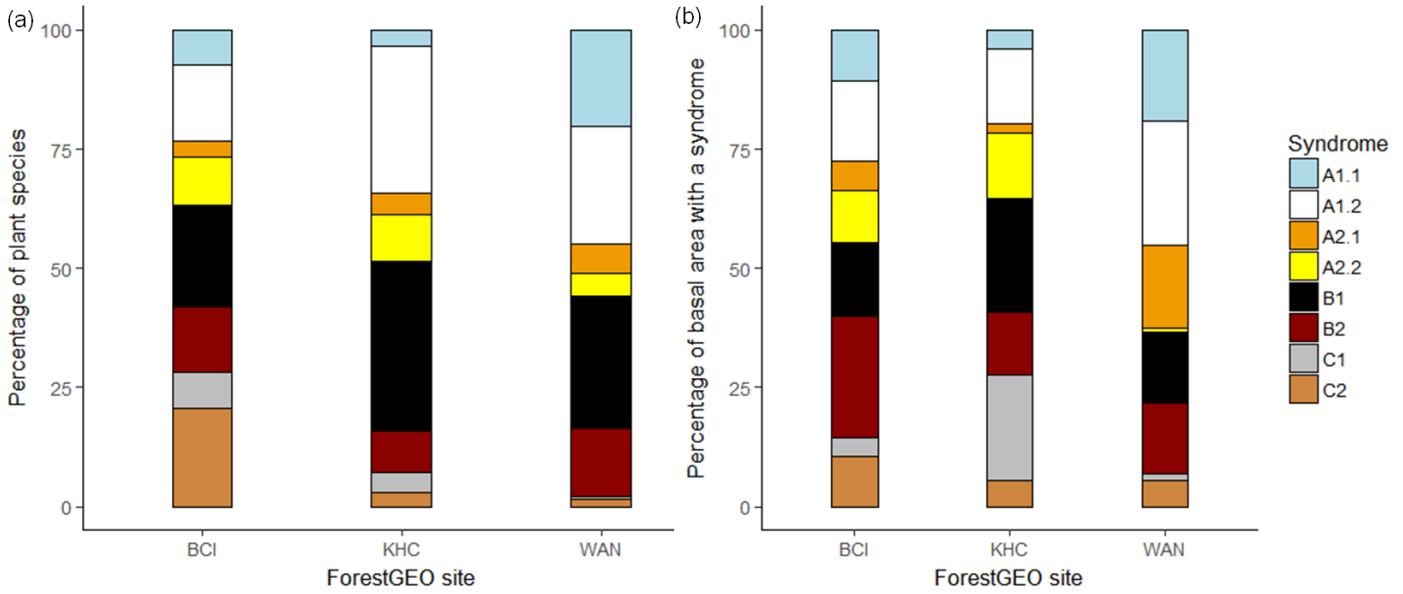
588 FIGURE 4. CCA ordination of fruit syndromes based on their distribution in plant genera, with
589 fruit colour, forest site (BCI, KHC, WAN) and plant phylogeny (represented by PCO vectors) as
590 explanatory variables (a) and Venn diagram visualizing the proportions of overall adjusted
591 variability 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-A. Succulent, fleshy fruit	Z-A. Colour	E-A. Drupe (one seed per fruit)
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	Z-B. Type of flesh	E-A1.2 Fleshy drupe with thin mesocarp (<5mm)
B-B. Dry fruit	Z-B1 Juicy soft	E-A2. Non-fleshy drupe
B-B1. Dehiscent fruit	Z-B2 Juicy fibrous	E-A2.1 Non fleshy with thick mesocarp (>5mm)
B-B1.1 Legume	Z-C. Protective coat	E-A2.2 Non-fleshy with thin mesocarp (<5mm)
B-B1.2 Follicle	Z-C1 Dehiscent coat	E-B. Fruit with multiple seeds
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-B2. Indehiscent fruit	Z-C4 Indehiscent coat - thick husk	E-C. Dry fruit/seed
B-B2.1 Samara	Z-D. Seed size	E-C1 Dry winged seed that do not develop in capsule
B-B2.2 Nut	Z-E. Number of seeds per fruit	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-B3. Schizocarpic fruit		
B-B3.1 Cremocarp		
B-B3.2 Double samara		

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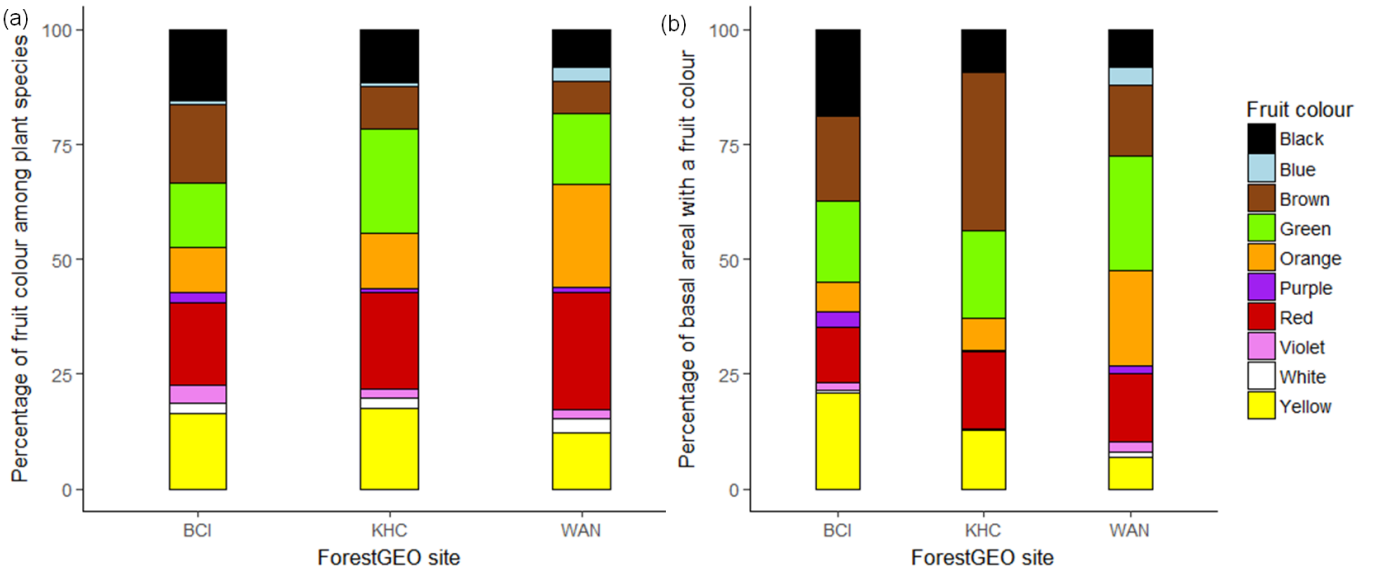
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598 FIGURE 1.

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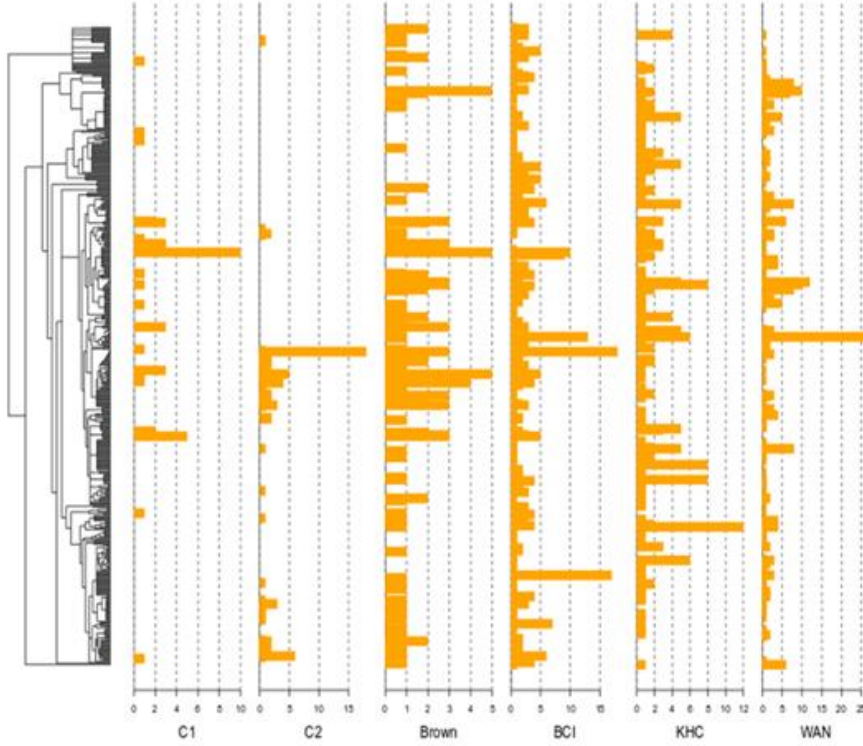


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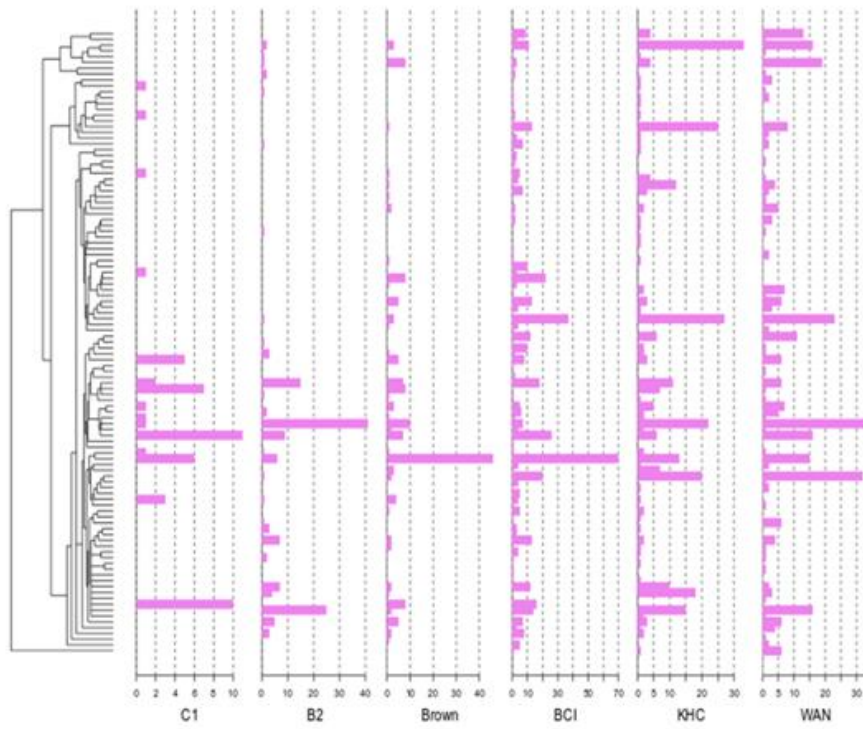
603 FIGURE 2.

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(a)

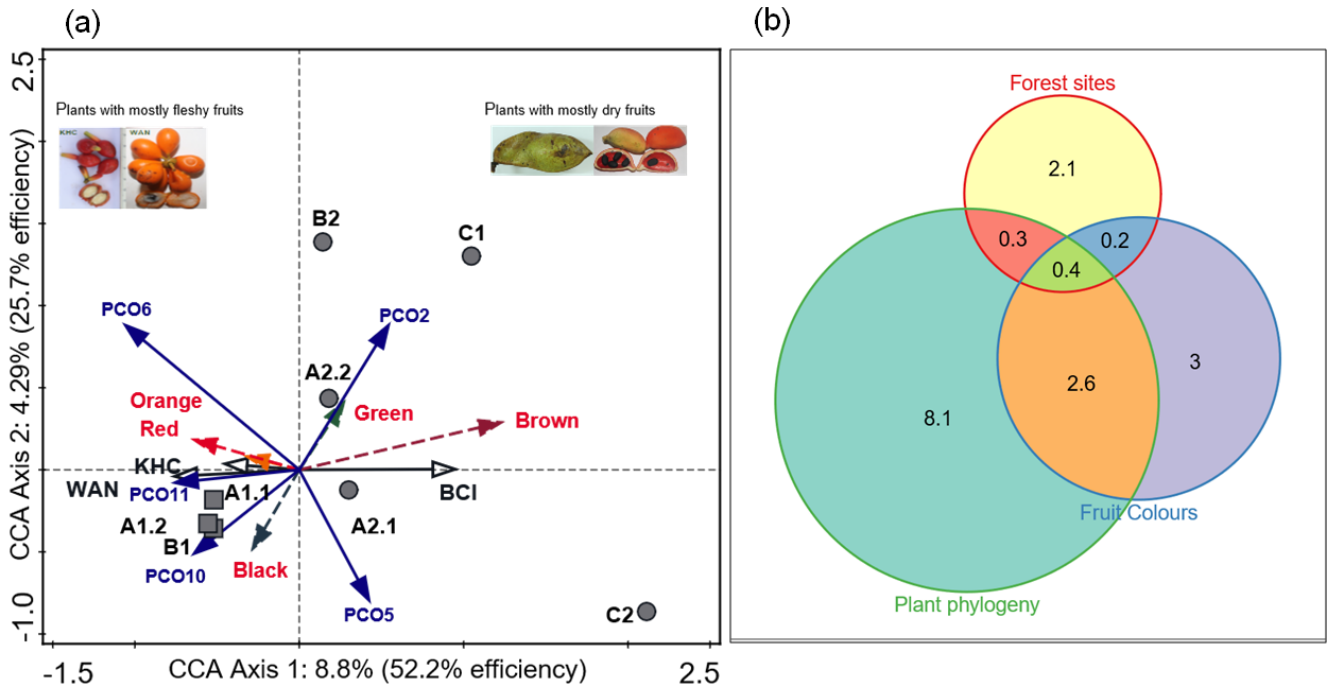


(b)



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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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