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

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ABSTRACT

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

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

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

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

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

Fruit and seed morphology can be described by multiple continuous (e.g., size), and categorical (e.g., colour) variables. These can be used to organize plant species into relatively homogeneous groups, for instance using multivariate analysis methods, and then look for ecological or phylogenetic interpretations of these groups. Alternatively, we can define suites of traits, i.e., syndromes, known to be relevant to a particular ecological process, such as dispersal or seed predation, and examine their importance in various ecosystems or geographic areas. Such syndromes can be useful as long as they are rigorously defined (Table 1) and combine traits that are functionally relevant. For instance, fruit fleshiness, number and size of seeds, and physical protection of seeds by a mesocarp all relate to vulnerability to seed predation by insects, so that the study of particular combinations of these traits can provide insights into the insect predation pressure on plants. As for any categorical classification of continuous variability involving multiple traits, syndromes represent a simplification, but can help generate ecological hypotheses. For instance, the definition of discrete life-history syndromes has contributed to the development of ecological theory in the context of succession (Turner 2008) and plant responses to herbivory (Herms & Mattson 1992).

Tropical forest trees produce a wider variety of fruits ranging from fleshy to dry (e.g., achenes, Armesto *et al*. 2001). Most fleshy fruits are dispersed by animals while dry fruits are usually dispersed through other means (Howe & Smallwood 1982, Janson 1983, Gautier-Hion *et al*. 1985, Mack 1993, Du *et al*. 2009, Florchinger *et al*. 2010, Valido *et al*. 2011). Multiple factors have contributed to the evolution of the wide range of fruit and seed types observed in tropical forests. To assess the role of different factors in shaping the diversity of fruit traits, a helpful approach is to compare the relative frequencies of fruit syndromes across multiple forest sites. Inter-continental comparisons of ecological patterns are highly instructive, as they show the variance of these patterns in evolutionarily distinct species pools (Primack & Corlett 2005), but data for such comparisons are rarely available. Inter-continental comparisons can shed light on different patterns of seed distribution and mortality, shaped mostly by the evolution of flowering plants, and the selection of dispersal agents or seed predators (Janzen 1971, Lewis & Gripenberg 2008, Bolmgren & Eriksson 2010). Tropical rain forests vary in plant species composition and vegetation structure. These forests may also differ in seasonality, climate and fruiting periods, as well as the composition of frugivore faunas (Corlett & Primack 2006). For example, forests in the Neotropics are characterized by a high abundance of understory fruiting shrubs. In contrast, many forests in Southeast Asia are dominated by dipterocarps with seeds dispersed by wind during mass-fruiting events (Corlett & Primack 2006). Australasian rain forests have a high diversity of plant species that produce large, fleshy fruits (Chen *et al*. 2017). These differences in the production of fruits in rain forests may impact the way fruits and seeds are attacked by insects (Table S1). Therefore, it is important to document the distribution of fruit syndromes relevant to insects across rainforest locations in distinct biogeographical regions. Our insect-oriented classification of fruit syndromes is based on 1,192 plant species collected at three tropical forest sites in Panama, Thailand and Papua New Guinea. We quantified plant diversity and abundance represented by each syndrome in a phylogenetic context and across the three continents. We use this information to explore the resource base for fruit and seed eating insects in tropical rainforests.

METHODS

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

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

FRUIT CLASSIFICATION SYSTEMS.—Each plant species sampled was assigned to a category using our new entomocentric classification, and compared to the previous botany and zoology systems (Table 1). The botany system is based on plant morphology, while the zoology system was motivated largely with respect to plant dispersal by vertebrates. Our entomology system is concerned primarily with seed predation by insects. The first dichotomy in the botany system is whether the fruit is fleshy or dry. The former includes drupes, berries, and other fleshy fruits with multiple seeds. The dry fruits are classified as dehiscent, indehiscent and schizocarps (Hickey & King 1981, Zomlefer 1994, Table 1). The zoology system uses fruit traits such as size, colour, number of seeds and seed protection (Janson 1983, Gautier-Hion *et al*. 1985, Table 1). For our new entomology system, we selected 2-4 individual fruits per tree species, classified fruits by morphology, estimated their size (length and width to the nearest millimeter) and weight (to the nearest gram), and photographed them. We identified fruit colour using a colour scheme developed for vertebrate dispersal assessment by Janson (1983) and Gautier-Hion *et al.* (1985). To control for colour choice biases, the Munsell Colour index system (Sturges & Whitfield 1995) was used to match colours to black, blue, brown, green, orange, purple, red, violet, white and yellow on the basis of pictures of ripened fruits.

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

DATA ANALYSIS.—Our analyses were based on all species sampled for fruits,both inside and outside the ForestGEO plots (1,192 species, Figs. 1a, 2a, 3 and 4), using number of species per category as a response variable. For tree species present within the ForestGEO plots (689 species), individual abundance and stem size data were available, and we used basal area and density of stems per species in combination with the “species” fruit syndrome to quantify the ecological significance of fruit syndromes (including life form) as resource for insects, and to make quantitative comparisons across sites (Fig. 1b, 2b, Table S1, Basset *et al*. 2018). We compared the proportion of species, basal area and stems represented by each fruit syndrome, life form and fruit colour among the study plots. At KHC, 14% of plant species (mostly unidentified lianas) were excluded from plant phylogeny analyses.

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

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

Often genera or families had multiple states (e.g., several syndromes) and we used the number of species within each genus or family to conduct abundance-weighted analyses using the R package “Picante” (Kembel *et al*. 2010). To evaluate simultaneous and separate effects of sites, fruit colours and plant phylogeny on the variance in fruit syndromes, we performed multivariate analysis with variation partitioning among three sets of these explanatory variables, using canonical correspondence analysis (CCA) in Canoco ver. 5.10 (ter Braak & Smilauer, 2012). The analysis was performed at two levels of taxonomic resolution of the plant communities, (1) plant families and (2) plant genera. We used the full datasets of all plant species, where fruit syndromes were measured, and retained all genera and families with available phylogenetic information. Each plant genus (or family) was regarded as a “sample” (i.e., individual rows in matrices), syndromes as a “species” (i.e., columns), and numeric values in the matrix were numbers of plant species (as dependent variable). The effect of phylogeny (at the genus or family level) was tested by including the phylogenetic principle co-ordinate axes (PCO axes) as co-variates. These axes were obtained from principle co-ordinates analysis of a distance matrix derived from the ultrametric phylogeny. We then used a forward selection (999 randomizations, variability adj., p-adj. <0.05) and selected the first 30 PCO axes as surrogates of the phylogenetic gradient.

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

RESULTS

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

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

Every fruit syndrome was represented at each study site. Approximately half of all species at each site had one-seeded drupe fruits (A and B syndromes). The flora was dominated by fleshy fruits (A1 and B1 syndromes) in WAN (72% of species) and KHC (68%), but only 44% species had fleshy fruits at BCI. The distribution of individual syndromes differed among individual plots (plant species: χ^2=229, df=14, p<0.001, basal area: χ^2=754.09, df=14, p<0.001, Fig. 1). The fleshy indehiscent fruits with multiple seeds (B1 syndrome) were important at all three sites. BCI had a higher proportion of dry fruits (C2 and C1) while at WAN and KHC, fleshy drupe with thin mesocarp fruits (A1.2) were important (Fig. 1).

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

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

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

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

DISCUSSION

PLANT DIVERSITY, COMPOSITION AND FRUIT SYNDROMES.—Our study provides an entomocentric assessment of fruit classification systems based on fruit morphology, particularly fleshiness, mesocarp thickness and the number of seeds. As we expected, the three ForestGEO sites surveyed were distinct in their floral diversity as well as fruit syndromes and colours. The Neotropical BCI site was the most distinct in terms of plant species composition and fruit traits (fruit syndromes and colours), with KHC and WAN sites sharing both more phylogenetic and trait based similarity (Corlett & Primack 2006). Corlett and Primack (2006) stated that Southeast Asian forest plots are dominated mostly by canopy tree species whereas Neotropical plots are rich in understory shrub species. These differences in the representation of life form categories (e.g., lianas, shrubs or trees) may explain much of the observed dissimilarity in fruit syndromes and fruit colours, and the overall pattern of fruit-feeding insect assemblages observed at the three rainforest regions (see Basset *et al*. 2018). For instance, BCI vegetation comprises a high proportion of shrub and liana species and has a high production of dry fruits. Lianas have a high proportion of dry fruits that were also often attacked by seed eaters, while fruits of shrubs are smaller and are rarely attacked by insects. In general, dry fruits are exposed to high insect damage compared to fleshy fruits at our study sites (Basset *et al*. 2018). Other studies from other tropical regions also found similar distinctions among plant life forms, fruit syndromes and fruit colours (see Chen *et al*. 2004, Bolmgren & Eriksson 2010, Jara-Guerrero *et al.* 2011).

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

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

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

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

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

FRUIT SYNDROMES AND COLOUR IN APHYLOGENETIC CONTEXT.—Both floristic and fruit syndrome similarities can be explained by a more pronounced dry season at BCI compared to the other two sites, promoting the dominance of Fabaceae (Condit 1998, Chust *et al*. 2006). Fruit morphology can be shaped by mutualistic relationships with dispersers as well as antagonistic interactions with seed predators (Chen *et al*. 2004). Broadly speaking, BCI is the most phylogenetically distinctive site, yet many plant families and some genera have a pantropical distribution. The only syndromes aggregated on the plant phylogeny proved to be non-fleshy syndromes. Less surprisingly, fruit colour also proved generally unconstrained by phylogeny. Clearly the dry-fleshy continuum is at least partly explained by phylogeny, with colour retaining a smaller degree of phylogenetic predictability. The fruit syndromes as well as colours thus retain phylogenetic flexibility to respond to local species pools of insect pests and vertebrate dispersers, irrespective of taxonomic composition of the regional floras. However, our multivariate analyses revealed a subtler correlation between phylogeny and plant traits, with plant phylogeny explaining much of the variance in the overall "community" of syndromes across all sites.

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

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

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DATA AVAILABILITY

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TABLE LEGENDS

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

FIGURE LEGENDS

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

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

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

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

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 *et al.*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 ***		

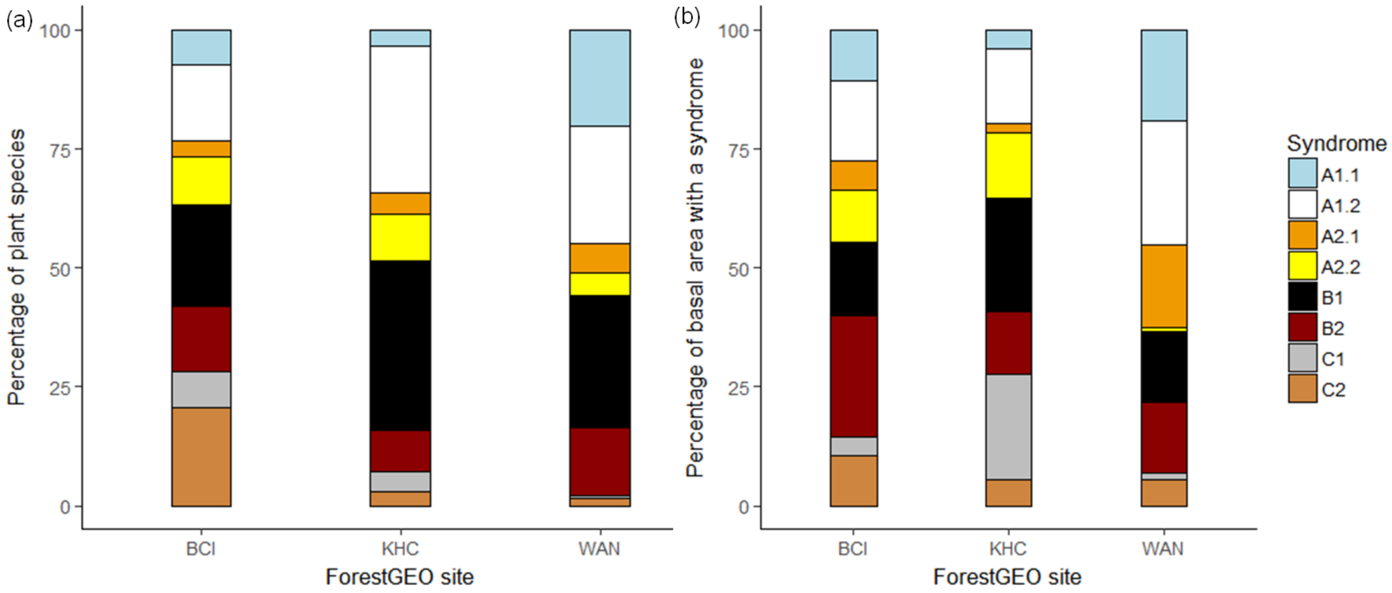

FIGURE 1.

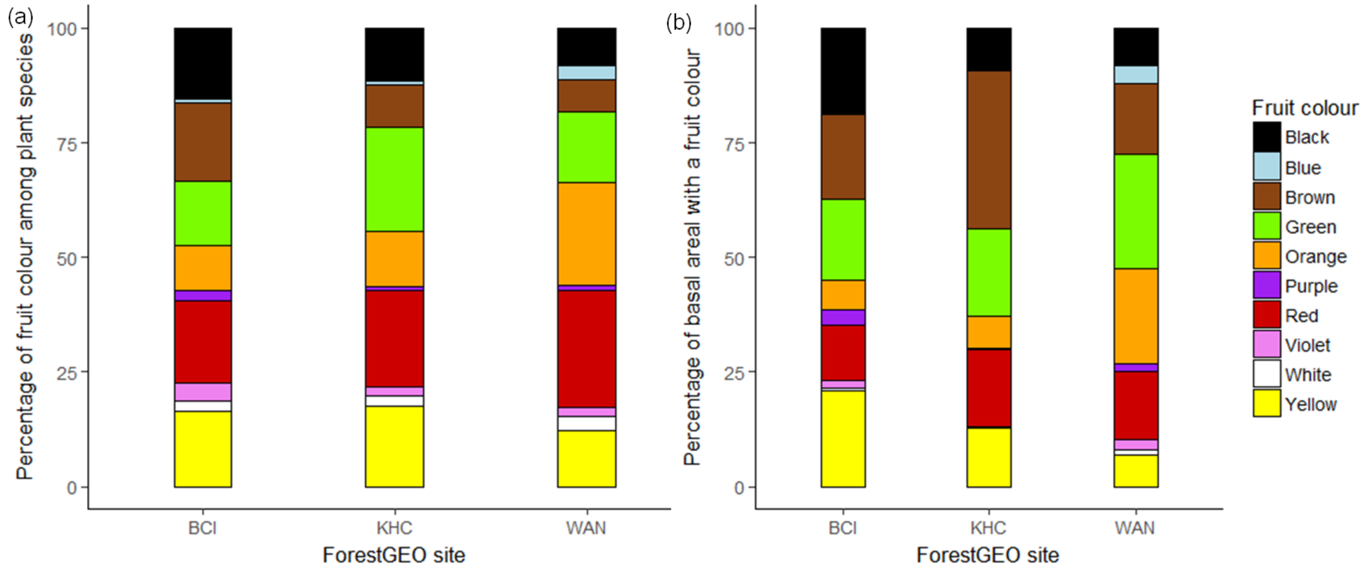

FIGURE 2.

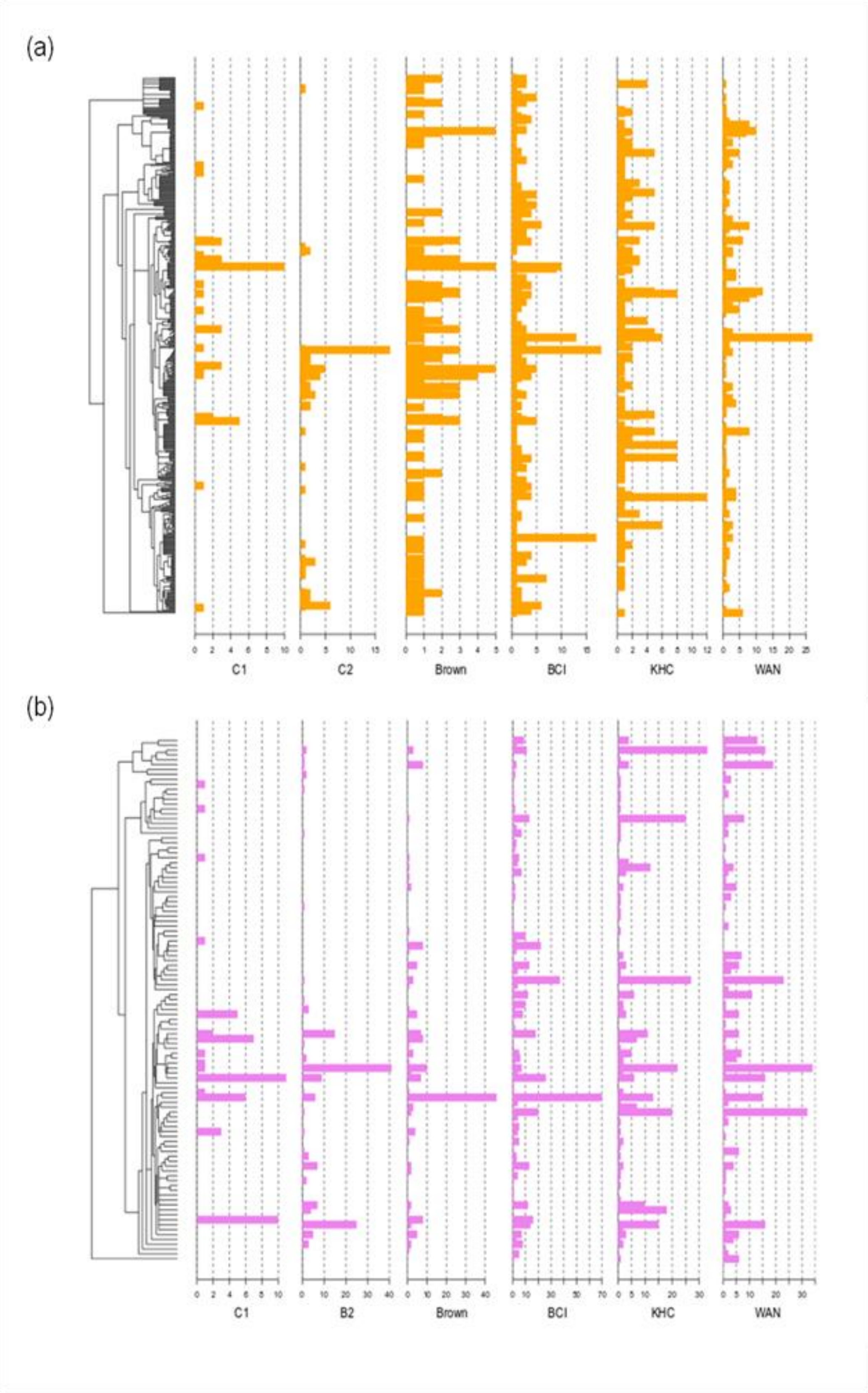
(a)
0 2 4 6 8 10
C1
0 5 10 15
C2
0 1 2 3 4 5
Brown
0 5 10 15
BCI
0 2 4 6 8 10 12
KHC
0 5 10 15 20 25
WAN
(b)
0 2 4 6 8 10
C1
0 10 20 30 40
B2
0 10 20 30 40
Brown
0 10 30 50 70
BCI
0 5 10 20 30
KHC
0 5 10 20 30
WAN

FIGURE 3.

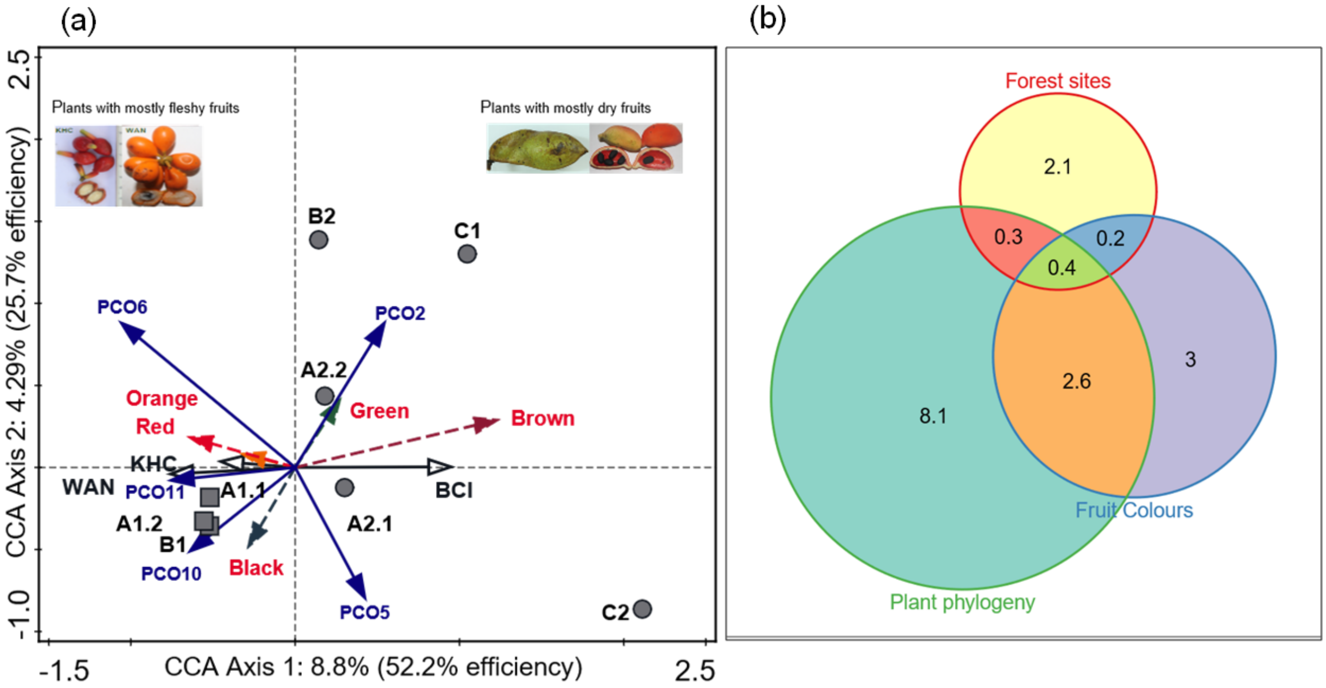

FIGURE 4.

SUPPLEMENTARY INFORMATION

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

SUPPLEMENTARY TABLES

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

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

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

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

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

SUPPLEMENTARY FIGURES

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

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

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