Host specialization and species richness of fruit flies (Diptera: Tephritidae) in a New Guinea rain forest

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Abstract: Frugivorous dacine fruit flies were studied in a lowland tropical rain forest in Papua New Guinea to determine their host specificity, abundance, and the number of species attacking various plant species. Plant species hosted 0–3 fruit fly species at median (1–3 quartile) densities of 1 (0–17) fruit flies per 100 fruits. Fruit flies were mostly specialized to a single plant family (83% species) and within each family to a single genus (88% species), while most of the species (66%) were able to feed on >1 congeneric plant species. Only 30 from the 53 studied plant species were colonized by fruit flies. The plant–fruit fly food web, including these 30 plant species and the total of 29 fruit fly species feeding on them, was divided into 14 compartments, each including 1–8 plant species hosting mutually disjunct assemblages of fruit flies. This structure minimizes indirect interactions among plant species via shared herbivores. The local species pool was estimated at 152 ± 32 ($\pm$ SE) fruit fly species. Forty per cent of all taxonomically described species known from Papua New Guinea were reared or trapped in our study area. Such a high proportion indicates low beta-diversity of fruit flies. Steiner traps were highly efficient in sampling the lure-responsive fruit fly species as they re-collected 84% of all species trapped in the same area 5 y before. Fruit fly monitoring by these traps is a cheap, simple and efficient method for the study of spatial and temporal changes in rain-forest communities.

Key Words: beta-diversity, fruits, herbivore communities, insect–plant interactions, Papua New Guinea, species richness, steiner traps

INTRODUCTION

Detailed plant–herbivore food webs are important for the analysis of direct and indirect interactions between plants and herbivores, but the number of such webs described for species-rich tropical communities is very limited (Godfray *et al.* 1999). Concealed larval feeders are particularly poorly known, probably because they often have to be collected by blind sampling, which includes indiscriminate collecting and processing of both infested and non-infested plant parts as herbivore infestation cannot be easily recognized. Such sampling and rearing of insects is very labour-intensive. It is therefore unsurprising that host specificity data based on extensive rearing of endophytic larvae are scarce (but see Janzen 1980, Tavakilian *et al.* 1997). This lack of data is in

contrast with the relative abundance of analogous studies targeting externally feeding herbivores, particularly leaf-chewers (Barone 1998, Basset 1996, 1999; Janzen 1988, Marquis 1991, Novotny *et al.* 2002a).

The present study focuses on dacine fruit flies (Diptera: Tephritidae: Dacinae) as an important component of the poorly known guild of concealed fruit feeders. While dacine fruit flies have been extensively studied in the tropics as agricultural pests (Clarke *et al.* 2001, Drew & Romig 1997, Leblanc *et al.* 2001, White & Elson-Harris 1994), quantitative studies based on the rearing of non-pest fruit flies in their rain-forest habitat are not available. A few studies on rain-forest species addressed their population ecology rather than community patterns of host plant use (Drew 1987, Drew & Hooper 1983, Drew *et al.* 1984, Raghu *et al.* 2000, Zalucki *et al.* 1984).

Dacine fruit flies (particularly the 500+ species of *Bactrocera* Macquart) are endemic to subtropical and tropical rain forests from the Indian subcontinent across

to Oceania (Drew 1989a). They reach their greatest diversity in Papua New Guinea (PNG) with 181 described species (Drew 1989b) and another at least 50 undescribed species (R. Drew, unpublished data). The larvae of nearly all dacine fruit flies feed on the soft fleshy fruit of rain-forest plants and speciation within the Dacinae may be associated with changing patterns in host use (Drew 1989b). Dacines are considered to play a role in rain-forest ecology by helping to scarify flesh from seeds, so enhancing germination, or by attracting frugivorous vertebrates which target infested fruit (Drew 1987). However, more studies are needed to assess the effect of fruit flies on plant fitness and thus their role as agents of either direct or indirect effects on plants. Fruit flies are the only specialist group of internal fruit-feeding insects in the region, but individual species of Lepidoptera, Coleoptera and other Diptera also use this resource.

Our study relied on the rearing of fruit flies from fruits of 53 species of woody plants including both closely and distantly related hosts from 38 genera and 27 families. It examined principal characteristics of plant–fruit fly food webs from a lowland rain forest, including the host specialization of fruit flies, their species richness and abundance on individual hosts and the compartmentalization of the plant–fruit fly food web. These are key characteristics for the analysis of ecological and phylogenetic determinants of host range in fruit flies, as well as for the assessment of potential for indirect interactions among plants via shared fruit fly species. Further, the host specificity data were also used in combination with data on fruit flies collected by baited traps to estimate the size of the local pool of rain-forest fruit fly species and its relationship to the regional fruit fly fauna.

METHODS

Fruit fly sampling and rearing

The study area was situated in the Madang Province of Papua New Guinea. It has a humid tropical climate with average annual rainfall of 3558 mm, a moderate dry season from July to September, and mean air temperature 26.5 °C (McAlpine *et al.* 1983). Fieldwork was concentrated in primary and secondary forests near Baitabag and Ohu Villages (145°41–8'E, 5°08–14'S, *c.* 0–200 m asl). A 1-ha plot in a primary rain forest in Baitabag contained 152 species with a diameter at breast height > 5 cm (Laidlaw *et al.*, in press).

Fruit samples were collected from an approximately 6-km^2 area of primary and secondary forest vegetation near Baitabag Village and from a similar area near Ohu Village. Samples from both areas were combined for the analysis as both areas are a part of a 10 × 20-km

continuous mosaic of primary and secondary forests of the same vegetation type (described in Laidlaw *et al.*, in press).

Sampling was performed at weekly intervals from April 2000 to November 2001, on 96 sampling days in Baitabag and 86 sampling days in Ohu. During each sampling day, two collectors walked through the study area and picked ripe fruits from the plants or collected them from the ground. Individual fruit samples belonged, as far as possible, to a single crop, weighed 0.01–1 kg and included 1–200 fruits. The number and size of samples from different plant species was determined primarily by the availability of fruits in the forest. Vouchers from the plants providing fruit samples were collected and later identified by Kipiro Damas and Paul Marai of the Forestry Research Institute in Lae, PNG, and are deposited in this institution.

Samples of fruit from individual trees were placed in plastic containers above a layer of sterilized sawdust and kept there for 2–3 wk, until fruit fly larvae left fruits and pupated. Puparia were then extracted from sawdust and kept in separate containers until they hatched. Adult fruit flies were kept alive for approximately 1 wk until they matured, then killed and mounted.

One pair of Steiner traps (Queensland modification; White & Elson-Harris 1994) baited with either cuelure or methyl eugenol was operated at each of the two study sites. These lures are known to attract males of 73% of the described fruit fly species in PNG (Drew 1989b). The traps were located in primary forest vegetation, in the centre of the vegetation survey plots used by Laidlaw *et al.* (in press). They were emptied at approximately weekly intervals from September 1999 to January 2001.

All fruit flies were identified by R. Drew. The specimens are deposited at Griffith University in Brisbane, Australia. The identity of undescribed species was not cross-referenced between the samples obtained by rearing so that comparative analyses between samples produced by these two methods are limited to the described species.

Data analysis

Analyses of fruit fly assemblages feeding on individual plant species were restricted to plant species with > 100 fruits that weigh > 1 kg. Host specificity was analysed only for fruit fly species reared as at least 10 individuals. These minimum sample size thresholds were set arbitrarily, as a compromise between conflicting demands for using large sample size for each plant and fruit fly species, while retaining as many plant and fruit fly species as possible in the analysis. The effect of these thresholds on the results is examined and discussed.

Fruit fly host specificity was analysed with respect to all sampled plants as well as congeneric plant species,

confamilial plant genera, and plant families, using the host specificity index H. We propose this index as an estimate of the proportion of available alternative hosts used by fruit fly species as

$$H = (S_F - 1)/(S_T - 1), \qquad \text{(Eqn 1)}$$

where S_F is the number of plant taxa fed upon by the fruit fly species and S_T is the total number of plant taxa analysed. H ranges from 0 for monophagy to 1 for complete polyphagy on all available plant taxa. It is not defined for $S_T = 1$ as it is impossible to evaluate host specificity in the absence of potential alternative hosts.

The H index relates the number of hosts to the locally available pool of potential hosts, combining thus an innate ability of a species to utilise hosts with an environmental component of the availability of these hosts. Another parameter, the proportion of fruit fly species feeding on a single host taxon (species, genus or family), focused on the absolute number of plant taxa used by the herbivore. The plant species represented by the largest sample size (fruit mass) was selected to represent each family and genus in analyses restricted to plant species from different families and confamilial genera, as fruit flies from these plants were considered to be better documented than those from other hosts (Appendix 1).

Plant–fruit fly food web was characterized by connectance (C), defined as the proportion of all possible plant–fruit fly combinations (i.e. the product of the number of plant species and the number of fruit fly species) observed in the samples (Lewis *et al.* 2002; note that this definition excludes the possibility of plant–plant and fruit fly–fruit fly interactions). Further, we determined the number of compartments (Lewis *et al.* 2002), i.e. sets of plant species with no fruit fly species shared with the rest of the plant species, present in the food web.

Local species richness of fruit flies was estimated using an approach analogous to capture–mark–recapture methods designed to estimate population size (Novotny & Missa 2000), based on the comparison of species richness data from a comprehensive but incomplete survey including an entire taxon (S_{large}) with those from complete census available for a limited subset of species (S_{small}). The species richness of the entire taxon (S_{total}) is calculated from the number of species known from the limited census 'recaptured' during the comprehensive taxon-wide survey ($S_{overlap}$) as

$$S_{total} = S_{large} S_{small}/S_{overlap} \qquad \text{(Eqn 2)}$$

The overlap in species composition between the incomplete data on species richness obtained by rearing fruit flies from fruits and a nearly complete survey of fruit fly species attracted by the baited traps was used for the calculation. As Equation 2 is analogous to the Lincoln index used to estimate population size from capture–mark–recapture data, the variance estimate for
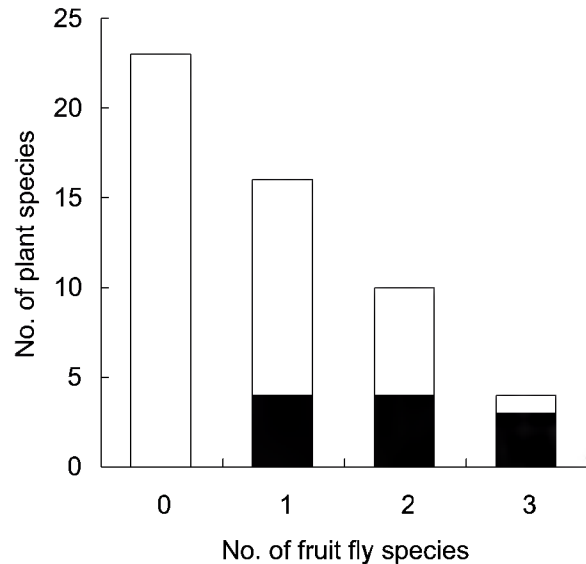

Figure 1. Species richness of fruit fly assemblages. The number of species in fruit fly assemblages from plant species sampled as > 10 kg of fruits (black bars) and 1–10 kg of fruits (white bars).

the Lincoln index (Poole 1974) can be used to calculate the variance of S_{total}:

$$\text{var}(S_{total}) = S_{large} S_{small}^2 (S_{large} - S_{overlap})/S_{overlap}^3 \qquad \text{(Eqn 3)}$$

RESULTS

Fruit fly density and species richness

In total, 2816 samples including 33 854 fruits and weighing 570.2 kg were collected from 168 plant species; samples including > 100 fruits and weighing > 1 kg were obtained from 53 plant species representing 38 genera and 27 families (Appendix 1). The samples yielded 7920 adults representing 38 species (Appendices 2 and 3), including 6349 fruit flies from 29 species from the 53 plant species used in quantitative analyses.

Fruit flies were reared from 30 (57%) of the 53 plant species, but this proportion increased with sample size to 100% for plant species sampled as > 10 kg of fruits per species (Figure 1). Fruit flies infested plant species at densities 0–110 fruit flies per kg fruit and 0–1430 fruit flies per 100 fruits. The median (1–3 quartile) was respectively 1 (0–12) fruit flies per kg fruit and 1 (0–17) fruit flies per 100 fruits.

Individual plant species hosted 0–3 fruit fly species (Figure 1). Extensively sampled hosts, including 11 plant species with 10–55 kg of fruits sampled, hosted 1–3 fruit fly species. Distribution of fruit fly species richness among host species approximately corresponds to a Poisson distribution (mean = 0.906, variance = 0.933, Kolmogorov–Smirnov test, d = 0.04, P > 0.05).
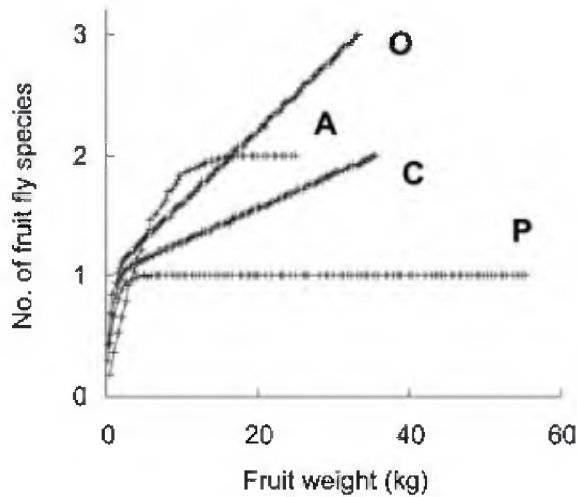
Figure 2. Randomized species accumulation curves for fruit fly assemblages on *Ochrosia oppositifolia* (O), *Artocarpus altilis* (A), *Cerbera manghas* (C) and *Pangium edule* (P). Samples from each plant species were amalgamated in random order and the number of fruit fly species calculated for each sample size; an average from 5000 random species accumulation curves is presented.

Figure 3. Number of fruit fly species specialized to a single plant taxon (family, genus or species) (black bars) and feeding on > 1 taxon (white bars) in the analysis of hosts from different families (Families), confamilial genera (Conf. G) and congeneric species (Cong. S).

The dependence of species richness on sample size was explored by randomized species accumulation curves (Colwell & Coddington 1994) for plant species with samples > 25 kg of fruits and at least 100 fruit flies per species (Figure 2). The fruit fly assemblage on *Cerbera manghas* included one common species and one species found only in one of the 130 samples studied. The probability of encountering this single sample increased linearly with increasing sample size and so did the species accumulation curve up to the final sample of 35 kg of fruits. A similar pattern was found on *Ochrosia oppositifolia*, which hosted one common species and two others, each found only in one of the 112 samples analysed. In contrast, the assemblage on *Pangium edule* included only one species infesting a large proportion of fruits. The species accumulation curve thus reached an asymptote at a low sample size of approximately 3 kg of fruits, with no subsequent increase up to the total sample of 55 kg of fruits. *Artocarpus altilis* had two moderately common fruit fly species. The species accumulation curve reached an asymptote at a medium sample size of 15 kg.

Fruit fly host specificity and food web compartmentalization

Eighteen fruit fly species were reared from one host only, eight species from two, one species from three, one species from four and one species from seven hosts. Fruit flies were mostly specialized to a single plant family (83% of species) and within each family to a single genus (88% species), while most of the species (66%) were able to feed on > 1 congeneric plant species (Appendix 4, Figure 3).
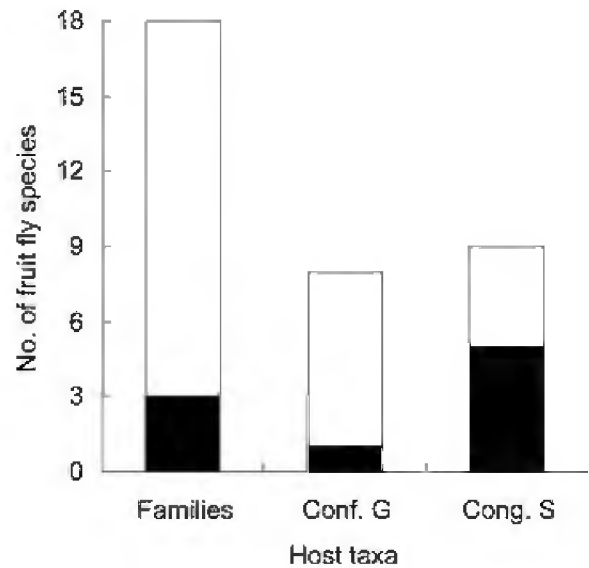
The host specificity was quantified for 21 fruit fly species reared as at least ten individuals from the 53 study plant species as the H value for these fruit fly species was not correlated with the number of reared individuals (Spearman $r = 0.352$, $P > 0.1$, $N = 21$). The average host specificity of fruit fly species with respect to all studied plants was $H_{avg} = 0.02$, i.e. a fruit fly species feeding on a particular host used an average of only 2% of other available plant species (Table 1).

Table 1. Fruit fly host specificity with respect to congeneric species, confamilial genera, different families, and all studied species of plants. Plant taxa – number of congeneric species, confamilial genera, families and all plant species analysed; Fly spp. – number of fruit fly species collected as at least 10 individuals on the plant taxa analysed; PF – number of documented plant–fruit fly interactions; H_{avg} – average host specificity index of fruit fly species feeding on the particular plant taxa (see Equation 1 in Methods).

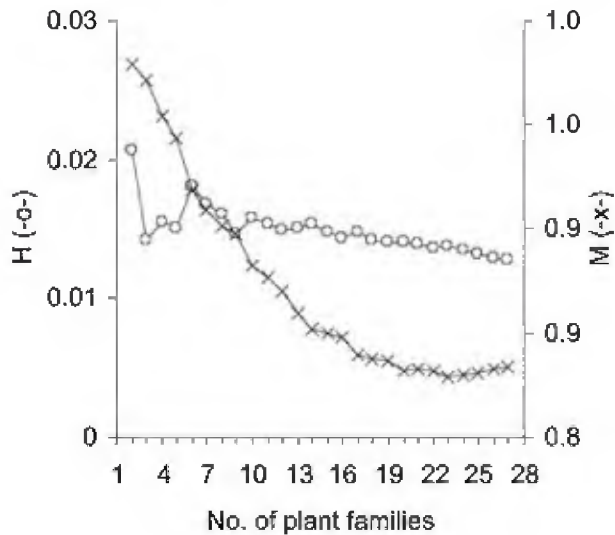|	Plant taxa	Fly spp.	PF	H_{avg}
Congeneric species				
Ochrosia	2	3	3	0
Garcinia	2	2	3	0.50
Syzygium	4	2	6	0.66
Gnetum	2	2	4	1.00
Average				0.54
Confamilial genera				
Anacardiaceae	2	1	1	0
Apocynaceae	2	3	4	0.33
Myristicaceae	2	1	1	0
Rubiaceae	5	3	3	0
Average				0.08
Different families	27	18	24	0.01
All hosts	53	21	40	0.02

Figure 4. Relationship between the host specificity estimates for fruit fly assemblages on the number of plant families included in the study. H_{avg} – average value of the host specificity index H (see Equation 1 in Methods), M – the proportion of fruit fly species recorded from only one plant family. Samples from plant species, each from a different family, were amalgamated in random order; an average from 1000 random replicates is presented.

Figure 5. Number of plant species hosting only unique fruit flies not shared with any other hosts (black bars), fruit flies at least partially shared with other hosts (white bars) and not hosting any fruit flies (hatched bars) in data sets including all studied plant species (All S), and plant species from different families (Families), confamilial genera (Conf. G) and congeneric species (Cong. S).

The host specificity with respect to different plant families was $H_{avg} = 0.01$ as *Bactrocera frauenfeldi* was sampled from four families, *B. trivialis* from three families, *Bactrocera* sp. from two families and the remaining 15 species each from a single family (Appendix 4). The average H value for the entire fruit fly assemblage was only weakly dependent on the number of plant families studied, as long as the samples included at least ten families; it decreased only slightly from $H_{avg} = 0.016$ for ten families to $H_{avg} = 0.013$ for the total data set including 27 families (Figure 4). Similarly narrow host specificity was found with respect to confamilial genera ($H_{avg} = 0.08$), but not congeneric species ($H_{avg} = 0.54$).

The total matrix of 53 plant and 29 fruit fly species was characterized by connectance $C = 0.03$, while the matrix of 27 plant species from different families by $C = 0.05$. Plant–fruit fly food web was highly compartmentalized (Figure 5). Only 34 (8%) from the 435 pairs of plant species which could be generated from the 30 plant species hosting fruit flies shared at least one fruit fly species. The 30 plant species were divided into 14 compartments with mutually disjunct fruit fly assemblages, including eight represented by single plant species and six composed from 2–8 plant species. Likewise, fruit fly assemblages from 19 plant species representing different families were divided into 14 compartments, including 12 represented by single plant species.
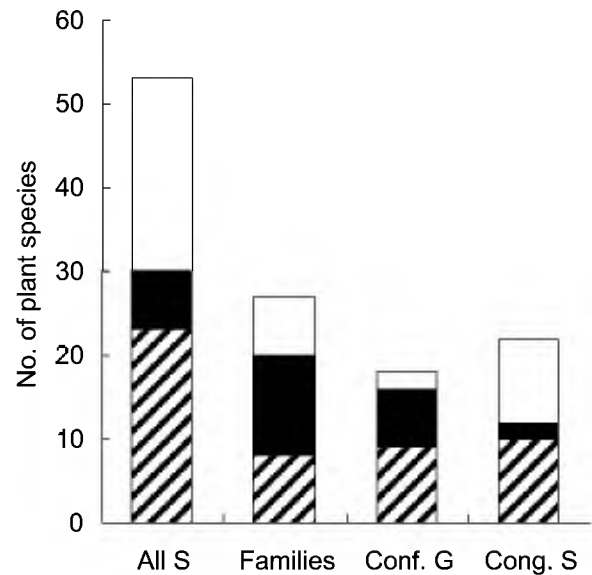
Local pool of fruit fly species

The baited traps in Baitabag and Ohu produced 20 927 fruit flies. They included 56 taxonomically described species (Appendix 5), 13 undescribed species and 21 species of uncertain status; most of them are probably also valid undescribed species, but further taxonomic work is required for clarification.

The species accumulation curve for the subset of taxonomically described species indicates that their local diversity was almost completely sampled as it was approaching an asymptote (Figure 6). Fourteen of the 56 described species collected by the traps were also among the 38 species reared from the fruit samples. This overlap was used to estimate the local species richness of fruit flies from the Equations 2 and 3 as $S_{total} = 38 \times 56/14 = 152$ (SE = 32) species.

DISCUSSION

Fruit fly density and species richness

The estimate of the proportion of plant species colonized by fruit flies varied from 57–100%, depending on sample size. The lower estimate may be too low as it is based on samples of limited size. The higher estimate may be too high as the large samples used for the calculation were available only from locally common tree species, which may
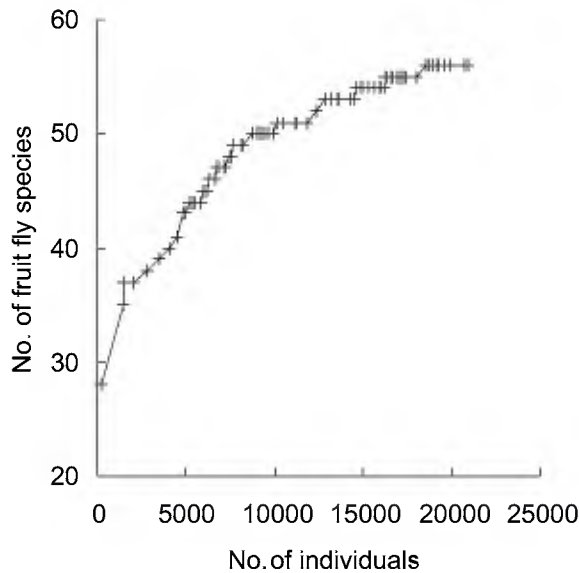
Figure 6. Species accumulation curve for fruit flies collected by baited traps. Samples were amalgamated in the sequence that they were collected in. Only taxonomically described species are included.

have unusually rich herbivore assemblages (Gilbert & Smiley 1978, Marquis 1991, Moran *et al.* 1994). Despite these uncertainties, it is likely that more than half of plant species with fleshy fruit are colonized by fruit flies.

The infestation rate and abundance of fruit flies was low in most of the plant species. The low densities can limit the impact of fruit flies on their host plants. Further, fruit fly assemblages from individual rain-forest hosts were also species poor, as they included up to three species. This conclusion is supported by a large-scale survey of fruit flies in South-East Asia by Allwood *et al.* (1999), which reared fruit flies from 428 plant species. Although the number of species varied from 1–13 per host species, as many as 89% of plant species harboured only 1–3 species. Notably, 34 of the 43 plants hosting more than three fruit fly species were cultivated species.

The distribution of fruit fly species richness among host species approaching the Poisson distribution is consistent with the model of host colonization where all plants have the same probability of being colonized by a new fruit fly, independent of the number of fruit fly species they already support.

Fruit fly host specificity and food web compartmentalization

The set of 53 studied plants represented those with the highest amount of available fruits in the forest. The low H value found for fruit flies from these plants therefore indicates that fruit flies have narrow host ranges with respect to the most abundant potential hosts in the forest, including only 2% of potential hosts. This host specificity

estimate is however influenced by taxonomic composition of the vegetation. Host range estimates, reported either as H values or simple counts of host species, genera or families, can be misleading, unless they are related to the distribution of studied plants among genera and families. For instance, there were 31 genera and 17 families represented by a single species among the 53 plant species studied. This taxonomic structure can artificially constrain host ranges to a single species or genus even for less-specialized species. We therefore also advocate a complementary approach including host specificity estimates for congeneric species, confamilial genera and different families of plants.

Although quantitative studies of fruit fly assemblages from tropical forests are non-existent, fruit fly host specificity can be inferred from qualitative surveys, particularly those from South-East Asia (Allwood *et al.* 1999) and Australia (Hancock *et al.* 2000). Both surveys report a high proportion of fruit flies confined to a single host family (75% of species in SE Asia and 71% in Australia), which is in agreement with our estimate of 83% of species feeding on a single plant family in our data.

Host specificity H could be calculated for extensive data obtained by sampling 1162 plant species from 127 families in South-East Asia by Allwood *et al.* (1999; Table 2). The narrow host specificity with respect to plant families ($H_{avg} = 0.02$) was in agreement with our results, but relatively narrow specificity was found also with respect to congeneric hosts ($H_{avg} = 0.14$), in contrast with our data ($H_{avg} = 0.54$). This difference has to be interpreted with caution as community studies and regional host plant lists each have their own sets of biases (Ward 1988). Host specificity may be overestimated in regional lists as they often collate plant and fruit fly species, which never coexist at any site within the study area.

Fruit fly host specificity parameters from our study can be compared with those derived from data on larvae from other herbivore taxa in tropical forests (Table 2). The comparable data sets include externally feeding folivorous caterpillars (Lepidoptera) from our study sites (Novotny *et al.* 2002a, b, c), and data on beetle seed-predators (Bruchidae, Curculionidae and Cerambycidae) from Costa Rica (Janzen 1980). The caterpillars exhibited similar host specificity patterns as fruit flies, viz. low host specificity with respect to congeneric plant species and much higher, and similar, host specificity with respect to both confamilial genera and different families. Further, fruit flies appear to be more specialized on all three taxonomic levels of analysis than caterpillars. Host specificity with respect to congeneric species ranged from 0.12 to 0.69 among taxa from different herbivore guilds. Beetle seed-predators were the most specialized guild, followed by fruit flies and leaf-chewing caterpillars. These patterns are similar to those reported from temperate ecosystems,

Table 2. Host specificity of herbivorous insect larvae in tropical forests. Herbivore taxa are listed with the plant part they use; taxonomic rank – the taxonomic level of hosts specificity analysis, including respectively congeneric species (Cg. spp.), confamilial genera (Cf. gen.), and different families of plants; data – the number of independent data sets (e.g. different genera in the analysis of congeneric species, different families in the analysis of confamilial genera), Plant S – the total number of target plant taxa (species, genera, or families) analysed; Herb. S and N – the number of herbivorous species and individuals analysed; H_{avg} – the average host specificity index (see Equation 1 in Methods); Ref. – data source: 1 – this study, 2 – Allwood *et al.* 1999, 3 – Novotny *et al.* 2002a and unpublished, 4 – Janzen 1980.

Herbivore, Plant part	Taxon. rank	Data	Plant S	Herb. S	Herb. N	H_{avg}	Geogr. area	Ref.
Tephritidae, fruits	Cg. spp.	4	10	9	2367	0.54	PNG	1
Tephritidae, fruits	Cf. gen.	4	11	8	1805	0.08	PNG	1
Tephritidae, fruits	Families	1	27	18	4741	0.01	PNG	1
Tephritidae, fruits	Cg. spp.	70	484	90		0.14	SE Asia	2
Tephritidae, fruits	Cf. gen.	46	387	90		0.07	SE Asia	2
Tephritidae, fruits	Families	1	127	90		0.02	SE Asia	2
Lepidoptera, leaves	Cg. spp.	4	24	81	11 722	0.69	PNG	3
Lepidoptera, leaves	Cf. gen.	2	22	164	23 617	0.12	PNG	3
Lepidoptera, leaves	Families	1	23	117	11 760	0.10	PNG	3
Coleoptera, seeds	Cg. spp.	19	119	72		0.12	Costa Rica	4

viz. that concealed herbivores are more specialized that externally feeding ones (Gaston 1992, Mattson *et al.* 1988).

Low species richness and high host specificity of fruit flies produced a highly compartmentalized structure of plant–fruit fly web, composed from numerous sets of plants hosting completely disjunct assemblages of fruit flies. This is in contrast with assemblages of tropical parasitoids of leaf-miners (Lewis *et al.* 2002) or externally feeding caterpillars (Novotny *et al.* 2002a, V. Novotny *et al.*, unpublished data). This food web structure minimizes indirect interactions among plant species via shared herbivores, as well as interactions among fruit fly species.

Local pool of fruit fly species

Reliable estimates of local species richness for herbivorous insects in tropical forests are notoriously difficult (Novotny & Missa 2000). Our estimate of local species richness calculated from the overlap between fruit fly samples obtained by trapping and rearing is based on three assumptions: (1) taxonomically described species were trapped and reared at the same rate as undescribed species, (2) rearing success was equal for the species responding and not-responding to lures, and (3) trapping of lure-responding species was complete.

Assumption (1) was necessary as only described species were fully analysed in the trap samples and could be compared with Fletcher (1998). It is not generally valid since one of the reasons why species remain undescribed is that they are more difficult to find than the described ones. However, it is not unrealistic in the present study as the described and undescribed species reared from fruits did not differ in their abundance (median 26 and 87 individuals per described and undescribed species

respectively, Mann–Whitney U-test, $U = 318$, $n = 38$ species, $P > 0.10$).

The role of lures in the biology of fruit flies is most likely related to sexual recognition (Shelly & Dewire 1994): there is no evidence that it is associated with any character which may influence rearing success (Raghu *et al.* 2002).

The species accumulation curve suggests that the trapping of fruit flies was indeed nearly complete. Fletcher (1998) collected fruit flies at one of our study sites (Baitabag) over 4 mo in 1996, using the same baited traps as in the present study. He collected 52 species, 37 of them taxonomically described (Appendices 5–6); the latter included only six species not recollected by our study. Their inclusion in the calculation of local species richness leads to a revised estimate of the local pool of 168 ± 36, rather than 152 ± 32 fruit fly species. This species pool is small compared with local plant species diversity, including 152 species with a diameter at breast height > 5 cm found in 1 ha of the forest (Laidlaw *et al.*, in press), or at least 200 species with fleshy fruits suitable for fruit flies in the study area (V. Novotny *et al.*, unpublished information).

Local and regional diversity of fruit flies

Fruit fly rearing and trapping by the present study and by Fletcher (1998) documented 72 identified species (Appendices 2–3 and 5–6), i.e. 40% of the 181 taxonomically described species known from Papua New Guinea and 56% of the 129 described species known from the northern lowlands of PNG (Madang, Morobe, East Sepik and West Sepik Provinces; Drew 1989b and unpublished data of the PNG Fruit Fly Project). Such a high local-to-regional species ratio has to be viewed with caution as it does not take into account numerous undescribed species present in New Guinea, which can

exhibit a higher beta-diversity than described species (Novotny & Missa 2000). Despite this potential bias, the result is notable in the light of the exceptional topographic, habitat and vegetation diversity of New Guinea (McAlpine *et al.* 1983, Paijmans 1976) as well as its complex geological history. Several tectonic blocks that now compose the island of New Guinea remain distinct centres of endemism (de Boer & Duffels 1996, Polhemus 1996).

The high local-to-regional species ratio is in good agreement with several studies from other tropical regions, which reported similarly high ratios for both plants (Kochummen *et al.* 1992) and insects. For instance, Orr & Haeuser (1996) found one-third of the Bornean fauna of butterflies at a single locality while Robbins & Opler (1997) reported six studies, recording 600–1300 species of butterflies locally, in comparison with 7500 species for the Neotropical region. Similarly, de Vries (1994) reports on a high overlap, of ~50% of species, between butterfly faunas from three sites in Costa Rica and one in Panama. In contrast, Novotny & Missa (2000) estimated that local species richness of Cercopoidea (Hemiptera) in our study area represented only 4% of the New Guinean total. More data on the magnitude of species turnover from local to regional spatial scales are essential for understanding the overall distribution of species richness in tropical forests, particularly across large lowland areas.

Sampling issues

The extreme rarity of some fruit fly species on certain hosts makes complete survey of species richness in fruit fly assemblages by rearing very difficult. Our results have to be interpreted as preliminary as they are based on limited samples of 570 kg of fruits. This amount corresponds very approximately to annual fruit crop from only 1 ha of a lowland rain forest (Lugo & Frangi 1993).

Various host specificity indices characterizing fruit fly communities are inevitably dependent on sample size, although to a different degree. The expansion of sampling to new plant species can decrease host specificity estimates by discovering additional hosts of fruit fly species, as well as increase these estimates by discovering additional fruit fly species with restricted host ranges. The response of a particular host specificity index has to be therefore tested for each data set. In the present study, the host specificity H was only weakly dependent on sample size, unlike the proportion of monophagous species that stabilized only for large samples including > 20 plant families.

In contrast to rearing, baited traps appear to be highly efficient in monitoring lure-responding species of fruit flies in tropical forests. The 84% of species collected by baited traps by Fletcher (1998) were re-collected after 5 y by the present study. This is a remarkably high proportion for an insect taxon in a rain-forest ecosystem, particularly since the traps were not placed in exactly the same locations during both sampling periods and one of the sampling periods lasted only 4 mo. Approximately 73% of Papua New Guinean species respond to the lures (Drew 1989b) while 14 (60%) from the 24 identified species reared from fruits were trapped in this study.

Although the lure-responding species represent a phylogenetically poorly defined group (Drew 1989b), they can be useful in monitoring temporal and spatial changes in tropical forests. There are few other groups of herbivorous insects that can be sampled so easily and comprehensively in tropical forest habitats as the lure-responsive fruit flies. Steiner traps are simple, cheap, easy to service and they provide clean samples which are almost entirely restricted to fruit flies (Hooper & Drew 1978, Steiner 1957, White & Elson-Harris 1994). These characteristics make them particularly suitable for studies in tropical forests. Further, fruit flies have other characteristics desired of target taxa for ecological monitoring (Miller & Rogo 2002); they are moderately species rich, most of the species can be relatively easily identified as their taxonomy is relatively well known, and there are convenient keys for many of them (e.g. White & Hancock 1997).

CONCLUSIONS

Our study, being a descriptive inventory of plant–fruit fly relationships, represents only a first step in the analysis of ecological and phylogenetic processes determining the composition of fruit fly assemblages and their impact on rain-forest vegetation. Results obtained here already point to several important characteristics of fruit fly communities worth further study. Fruit flies were rare and species poor on rain-forest plants and at least some of the apparently suitable hosts were not colonized at all. The highly compartmentalized plant–fruit fly food web also indicates that indirect interactions among plant species via shared herbivores were probably rare. The low host specificity with regard to congeneric plant species replicated the pattern found in externally chewing caterpillars (Novotny *et al.* 2002a) and may be therefore widespread among herbivores, at least in New Guinea. This result is important given a prominent role of large genera in rain-forest vegetation (Novotny *et al.* 2002b). Not unexpectedly, the host specificity of fruit flies, which are concealed feeders, was higher than that of externally feeding caterpillars, but a broader comparative analysis is required to explore differences between herbivore guilds. Finally, the high proportion of all taxonomically known species from Papua New Guinea found in the study area supports the notion of low beta-diversity of rain-forest

insects in the tropics. However, more data sets are needed before any conclusions, which can be of consequence for the conservation of biodiversity, could be made (Bartlett *et al.* 1999).

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Appendix 1. Plant species studied. Species used as representatives of their genus in analyses of confamilial genera are marked by[G], species used as representatives of their family in analyses restricted to different families by[F].

Agavaceae: (1) *Dracaena angustifolia* Roxb., Anacardiaceae: (2) *Dracontomelon dao* (Blanco) Merr. & Rolfe, (3) *Spondias cytherea* Sonnerat,[F] Annonaceae: (4) *Uvaria* sp., Apocynaceae: (5) *Cerbera manghas* L.,[F] (6) *Ochrosia coccinea* (Teysm. & Binn.) Miq., (7) *O. oppositifolia* (Lam.) K. Sch., Arecaceae: (8) *Arenga* cf. *microcarpa* Becc., (9) *Brassophoenix schumannii* Burret, (10) *Caryota rumphiana* Mart.,[F] Barringtoniaceae: (11) *Barringtonia calyptrocalyx* K. Sch., Burseraceae: (12) *Canarium* sp., Clusiaceae: (13) *Garcinia* cf. *hollrungii* Laut.,[F] (14) *G. ledermannii* Laut., Combretaceae: (15) *Terminalia* sp., Elaeocarpaceae: (16) *Aceratium ledermannii* Schlechter, Euphorbiaceae: (17) *Pimelodendron amboinicum* Hassk., Flacourtiaceae: (18) *Pangium edule* Reinw., Gnetaceae: (19) *Gnetum costatum* K. Sch.,[F] (20) *G. gnemon* L., Icacinaceae: (21) *Medusanthera laxiflora* (Miers) Howard, Lauraceae: (22) *Litsea* sp., Leeaceae: (23) *Leea indica* (Burm. f.) Merr., Loganiaceae: (24) *Neuburgia corynocarpa* (A. Gray) Leenh., Meliaceae: (25) *Chisocheton* cf. *cumingianus* (D. DC.) Harms,[F] (26) *Dysoxylum molle* Miq.,[G] (27) *Dysoxylum* sp., Moraceae: (28) *Artocarpus vriesianus* Miq., (29) *Ficus bernaysii* King, (30) *F. botryocarpa* Miq., (31) *F. conocephalifolia* Ridley, (32) *F. copiosa* Steud., (33) *F. hispidioides* S. Moore,[GF] (34) *F. septica* Burm., (35) *F. variegata* Blume, (36) *F. wassa* Roxb., Myristicaceae: (37) *Horsfieldia spicata* (Roxb.) Sincl., (38) *Myristica* sp.,[F] Myrtaceae: (39) *Syzygium* cf. *pachycladum* (Laut. & K. Sch.) Merr. & Perry,[F] (40) *S.* cf. *samarangense* (Bl.) Merr. & Perry, (41) *S. longipes* (Warb.) Merr. & Perry, (42) *Syzygium* sp., Pandaceae: (43) *Galearia celebica* Koord., Rubiaceae: (44) *Morinda bracteata* Roxb.[F] (45) *Nauclea orientalis* (L.) L., (46) *Psychotria leptothyrsa* Miquel, (47) *Psychotria* sp.,[G] (48) *Randia dryadum* (S. Moore) Merr. & Perry, (49) *Versteegia cauliflora* (K. Schum. & Laut.), Sapindaceae: (50) *Pometia pinnata* Forster, Thymelaeaceae: (51) *Phaleria macrocarpa* (Scheff.) Boerl., Tiliaceae: (52) *Microcos* sp., Verbenaceae: (53) *Gmelina moluccana* (Bl.) Backer.

Appendix 2. Fruit fly species reared from the studied plants (species collected also by baited traps are in bold).

(A) *Adrama selecta* Walker, (B) **Bactrocera bancroftii (Tryon)**, (C) B. *bullata* Drew, (D) **B. cheesmanae (Perkins)**, (E) B. *diaphana* (Hering), (F) **B. enochra (Drew)**, (G) **B. frauenfeldi (Schiner)**, (H) B. *hastigerina* (Hardy), (I) **B. lineata (Perkins)**, (J) **B. neocheesmanae Drew**, (K) **B. paramusae Drew**, (L) B. *penefurva* Drew, (M) **B. tinomiscii Drew**, (N) **B. trivialis (Drew)**, (O1–O11) 11 undescribed *Bactrocera* spp., (P) *Euphranta marginata* Hardy, (Q) *E. perkinsi* Hardy, (R) *E. quatei* Hardy, (S) *E. sp.*

Appendix 3. Additional fruit fly species reared from additional, marginally sampled hosts (species collected also by baited traps are in bold).

Bactrocera curvifera **(Walker)** – *Artocarpus altilis* (Park.) Fosb., *B. exima* Drew – indet. plant sp. A, **B. musae (Tryon)** – *Musa* sp., **B. recurrens (Hering)** – indet. plant sp. B, **B. thistletoni Drew** – *Elattostachys tetrappondra* Radlkofer, **B. umbrosa (F.)** – *Artocarpus altilis* (Park.) Fosb., *Callistomyia flavilabris* Hering – *Wenzelia dolichophylla* Tanaka, undescribed *Bactrocera* sp. 1 – *Timonius timon* (Spreng.) Merr., undescribed *Bactrocera* sp. 2 – 2 indet plant spp.

Appendix 4. Plant–fruit fly trophic links supported by reared fruit flies. Each link is reported in the format X–Y:Z where X is fruit fly species A–S (listed in Appendix 2), Y is plant species 1–53 (listed in Appendix 1) and Z is the number of reared fruit flies.

A-11:4, B-17:13, C-51:429, D-13:27, E-17:3, F-21:3, G-39:71, G-11:11, G-40:2, G-51:1, H-3:50, I-50:31, I-31:6, J-13:402, J-48:58, J-14:9, K-3:1, L-15:41, O1-7:917, O2-18:2116, O2-5:3, O3-17:9, O4-50:8, O5-4:37, O6-45:154, O7-5:522, O7-7:6, O8-19:66, O8-20:6, O9-20:68, O9-19:42, O10-7:10, O10-33:5, O11-3:4, M-49:3, N-39:379, N-11:100, N-40:9, N-41:8, N-43:2, N-15:1, N-42:1, P-24:258, Q-44:68, Q-6:1, R-53:14, S-6:350, S-38:20.

Appendix 5. Fruit fly species collected from rain forest by baited traps (only taxonomically described species are included; species collected also by Fletcher (1998) are in bold).

B. abdonigella (Drew), **B. abdopallescens (Drew)**, B. *aemula* Drew, B. *alyxiae* (May), B. *anfracta* Drew, **B. assita Drew**, **B. aurantiaca (Drew & Hancock)**, B. *bancroftii* (Tryon), B. *biarcuata* (Walker), B. *brachus* (Drew), B. *brevistriata* (Drew), **B. bryoniae (Tryon)**, B. *cheesmanae* (Perkins), B. *circamusae* Drew, **B. curreyi Drew**, **B. curvifera (Walker)**, B. *dapsiles* Drew, **B. endiandrae (Perkins & May)**, B. *enochra* (Drew), **B. frauenfeldi (Schiner)**, B. *fuliginus* (Drew & Hancock), **B. fulvicauda (Perkins)**, **B. furvilineata Drew**, B. *inconstans* Drew, **B. latissima Drew**, **B. lineata (Perkins)**, **B. macrovittata Drew**, B. *mimulus* Drew, **B. moluccensis Perkins**, **B. morobiensis Drew**, **B. musae (Tryon)**, **B. neocheesmanae Drew**, B. *neopallescentis* Drew, B. *oblineata* Drew, B. *papayae* Drew & Hancock, **B. paramusae Drew**, **B. phaea (Drew)**, **B. recurrens (Hering)**, B. *redunca* (Drew), **B. repanda Drew**, **B. resima (Drew)**, **B. sandaracina Drew**, **B. segnyi (Hering)**, **B. strigifinis (Walker)**, **B. thistletoni Drew**, **B. tinomiscii Drew**, B. *trichota* (May), **B. trivialis (Drew)**, **B. umbrosa (F.)**, B. *unistriata* (Drew), B. *ustulata* Drew, **B. vulgaris (Drew)**, *Dacus axanus* (Hering), *D. dissimilis* Drew, *D. impar* Drew, *D. mayi* (Drew).

Appendix 6. Additional fruit fly species collected by baited traps by Fletcher (1998) (only taxonomically described species are included).

Bactrocera consectorata Drew, *B. contigua* Drew, *B. propedistincta* Drew, *B. rhabdota* Drew, *B. breviaculeus* (Hardy), *B. trifaria* (Drew).