School of Doctoral Studies in Biological Sciences
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# Host specificity and species diversity in communities of frugivorous insect in lowland rain forest of Papua New Guinea

Ph.D. Thesis

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## Annotation

The thesis describes host specificity and species diversity in communities of frugivorous insect in lowland rain forest of Papua New Guinea. It focuses separately on weevils and Lepidoptera, as main groups of frugivores. Further, it focuses on fruit morphology and the structure of frugivorous communities.

## Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury. Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů, provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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## List of papers and authors' contributions

The thesis is based on the following papers:

1. Frugivorous weevils are too rare to cause Janzen-Connell effects in New Guinea lowland rain forest. Ctvrtecka R., Sam K., Brus E., Weiblen G., Novotny V. 2014. *Journal of Tropical Ecology* 30:521-535 (IF = 1.2222)

    [RČ conceived the study, led the fieldwork, led the analysis of specimens, analyzed the data with substantial contribution by KS, and wrote the manuscript with contribution by VN]

2. Low host specifity and abundance of frugivorous Lepidoptera in lowland rain forest of Papua New Guinea. Ctvrtecka R., Sam K., Miller E. S., Novotny V. (Manuscript)

    [RČ conceived the study, led the fieldwork, led the analysis of specimens with substantial contribution of SM, analyzed the data with substantial contribution by KS, and wrote the manuscript with contribution by VN]

3. Fruit morphology and the structure of frugivorous communities in a New Guinea lowland rain forest. Ctvrtecka R., Sam K., Novotny V. (Manuscript)

    [RČ conceived the study, led fieldwork, led the analysis of specimens, analyzed the data with substantial contribution by KS and wrote the manuscript with contributions by VN]

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Eric Brus [EB] - assistant based at New Guinea Research Center, Papua New Guinea, trained by RČ in insect rearings from the fruits, insect mounting and sorting

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**Co-author agreement:**

Vojtěch Novotný, the supervisor of Ph.D. thesis and co-author of all presented papers, fully acknowledges the contribution of Richard Čtvrtečka as the first author and her major contributions as stated above.

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Prof. RNDr. Vojtěch Novotný, CSc.

## CONTENT:

# Host specificity and species diversity in communities of frugivorous insect in lowland rain forest of Papua New Guinea

## INTRODUCTION

In the tropics, fleshy fruits are produced by more than 70% of rainforest plants (Willson *et al*. 1989). Fruits typically consist of seeds surrounded by fruit pulp that contains varying amounts of carbohydrates, proteins and lipids, often in higher concentrations than in most other plant parts (Cooper & Cooper 2004). Therefore fruits are an attractive target for a tremendous diversity of organisms. Frugivores attack the ultimate product towards which the existence of plants is geared, namely their propagules. Considering this, frugivores may have a more immediate impact on plants due to seed mortality than any other type of herbivore (Moore 2001). To understand the ecology of fruits and their frugivores, we must study the interactions between fruiting plants, their mutualists (vertebrate dispersers), and their predators and parasites, including insect herbivores (Herrera 1982, 2002; Jordano 2000; Levey *et al.* 2007). Frugivorous insects may attack the pulp and/or seeds of fruits. The most obvious negative effect to the parent plant of this behaviour is a possible reduction in the viability of the enclosed seeds (Janzen 1971, Herrera 1982). Moreover, damage to the pulp by invertebrates may open the way to subsequent attack by pathogens (Christensen 1972, Herrera 1982). However, seed predators may be the most important group for plant reproduction and abundance. Seed predators, which represent many insect species, may attack seeds in fruits when seeds are not completely developed, and thus not dispersed yet (Crawley 1992). This guild of pre-dispersal seed predators is usually different from post-dispersal guild that consumes seeds once they have been released from parent plants (Ramirez & Traveset 2010).

The main pre-dispersal seed predator groups include weevils (e.g. Janzen 1980; Lyal & Curran 2000, 2003; Nakagawa *et al.* 2003, Pinzon-Navarro *et al.* 2010), bruchids (e.g. Janzen 1980, Kergoat *et al.* 2005, Delobel & Delobel 2006) and moths (e.g. Nakagawa *et al.* 2003, Hoddle & Hoddle 2008, Adamski *et al.* 2014, Brown *et al.* 2014). Moreover, we can find seed predators among other insect orders such as wasps (Janzen 1979, Weiblen 2002), bugs (Slater 1972), and katydids (Tan 2011). Frugivorous insects which do not directly affect seed mortality as they feed on pulp (i.e. mesocarp) include flies, particularly tephritids (e.g. Novotny *et al.* 2005, Copeland *et al*. 2006, Raga *et al*. 2011), and moths (McQuate *et al.* 2000).

There are also many other post-dispersal insect species associated with fallen fruits. The most abundant groups, including drosophilid flies (Mitsui *et al*. 2010) and sap beetles (Grimbacher *et al.* 2013), usually feed on decaying mesocarp and participate in decomposition of the fleshy pulp. While some seed eaters, e.g. scolytids, attack the endocarp and may kill a substantial part of seed crop pre-dispersal (Moore 2001), others, such as some bruchids, attack seeds only once the pulp is rotten or removed by vertebrate frugivores (Moore 2001), earwigs (Lott *et al*. 1995), or ants (Mares & Rosenzweig 1978). There are also insect groups associated with fallen fruit, including carabid or staphylinid beetles, that are either omnivorous, or predators attacking frugivores on fruits (Borcherding *et al*. 2000, Grimbacher *et al*. 2013).

## **Plant protection against insect seed predators**

Plants have evolved various strategies to avoid seed predation:

(1) Secondary compounds

Secondary compounds are plant metabolites without a direct role in primary metabolism (i.e. growth and development). Although their role in defence against herbivores is widely assumed (Herms & Mattson 1992), they can also have non-defensive functions, such as protection from UV (Levey *et al.* 2007).

In terms of chemical composition there are three groups of secondary metabolites: (1) nitrogen compounds including alkaloids or cyanogenic glycosides, (2) terpenoids, and (3) phenols (Bennet & Wallsgrove 1994). Most studies focused on secondary compounds evaluate the effect of particular compounds on frugivores, i.e. alkaloids (Cipollini & Levey 1997), glycoalkaloids (Levey & Cipollini, 1998), glycosides (Bowers 1988), tannin (Coley 1986, Stanley & Lill 2001), or phenols (Cipollini & Stiles 1991, Numata *et al*. 1992, Kestring *et al*. 2009). However, these compounds may have multiple effects on multiple taxa over multiple time scales (Izhaki 2002, Levey *et al*. 2007). Before dispersal, when fruits and seeds are especially vulnerable to pathogens and predators as they occur in large numbers for a relatively long time in a predictable place, these chemicals deter frugivores (Levey *et al*. 2007) or decrease their fitness due to lower fruit palatability (Moore 2001). During fruit maturation most deterrent secondary metabolites decrease in concentration as the fruit ripens, because the fruit has to become attractive for vertebrate dispersers (Goldstein & Swan 1963, Cipollini & Levey 1997). There is thus a period of vulnerability after fruit maturation but before dispersal, during which pre-dispersal seed predation by invertebrates and microbes can destroy fruit (Hulme & Benkman 2002, Schaefer *et al*. 2003, Levay *et al.* 2007), since the widely used secondary compounds do not protect seeds completely. Their use has to achieve a compromise between predation avoidance and attraction of dispersers (Sallabanks & Courtney 1992).

Many secondary metabolites, such as some alkaloids (Janzen 1969), cyanogenic compounds (Nahrstedt 1985) or aminoacids (Rehr *et al*. 1973) are toxic and may protect fruit of particular plant species against all or most frugivore predators. However, many frugivores (coleopteran species especially) are able to break down toxic products and thereby overcome defences to become specialized fruit eaters, tolerant of, or even dependent on these toxics compounds (Janzen 1969, Rehr *et al.* 1973, Janzen *et al.* 1977, Bleiler *et al.* 1988, Bowers 1988, Ehrlen *et al*. 1993).

(2) Morphological traits

Pulp (i.e. both exocarp and mesocarp) or pods surrounding seeds may play an important role in physical protection of seeds against seed predators. In these cases pulp may be hard (Kuprewicz & Garcia-Robledo 2010) or contain undigestible fibers or other compounds as a quantitative defence against herbivores. Sometimes this role is fulfilled by a massive hard seed coat (i.e. endocarp; Grubb *et al.* 1998). Seed size may be another decisive factor for many seed predators. Some species may be able to feed on multiple small seeds, while others, such as bruchids (Coleoptera: Bruchinae) prefer seeds above a certain minimum threshold (Janzen 1969). Intra-specifically, seed shape is also an important trait that can be critical for the attack of particular seeds (Kestring *et al.* 2009).

(3) Temporal and spatial dynamics of populations.

Synchronized reproductive phenology of plants, resulting in a large abundance of fruits at a particular time, may affect the degree of escape from seed predators (Forget *et al*. 1999). In particular, the tremendous fruit overproduction found in e.g. many palm species may satiate predators and thus ensure a sufficient amount of seed survives for reproduction in spite of heavy seed predation (Moore 2001). Mast fruiting observed in the supra-annual and synchronized production of large fruit crops of many species may have a strong influence on the whole community structure of plants as well as seed predators (Kelly 1994, Norden *et al.* 2007, Wright *et al*. 2005, Hosaka *et al*. 2009). This pattern is the most important and best known from South-East Asia where insect seed predators are a major mortality factor for dipterocarp seeds and notably decrease the total seed crop. In consequence, the capacity of the community to satiate post-dispersal vertebrate predators is reduced (Nakagawa *et al.* 2005, Sun *et al*. 2007).

According to the leading predator-satiation hypothesis explaining the evolution of this spectacular reproduction phenology (Janzen 1974), irregular massive and synchronized seed production can supress, in particular, generalist seed predators during multi-year intervals between masting events. The remaining seed predators are satiated by sudden massive and synchronous seed production. The effectiveness of satiation increases with the length of the inter-masting period which is, moreover, highly variable, and the intensity of seed production during masting (Hosaka *et al.* 2011). However, many seed predators, weevil larvae especially, may survive periods between events in prolonged dormancy inside seeds or in capsules in the soil (Hanski 1988). Another strategy is to switch between confamilial host plants that do not usually follow a synchrony in flowering, if they co-occur there (Hosaka *et al*. 2009).

Although the detrimental effects of insect frugivores on plant fitness are unquestionable (Andersen 1988), their role in multitrophic systems is in many cases neutral or even beneficial. They accelerate germination by removing fruit pulp from seed (Drew 1988) or attract frugivores prefering pulps containing insect larvae (Drew 1987) .

## **The relationship between seed dispersers and predators**

Plants use the pulp surrounding seeds as an attractive and edible target for dispersers. This interaction between fleshy-fruited plants and the animals (birds and mammals in most cases) that ingest and disperse their seeds (i.e. endozoochory), has been the subject of many ecological studies (e.g. Estrada & Fleming 1986, Jordano 1992). However, the pulp may act as a protective layer of seeds excluding invertebrate fruit predators and pathogens (Janzen

1969, Mack 2000, Lewis & Gripenberg 2008) and it has been found that fleshy fruited species have lower seed predation rates than dry fruited species (Herrera 1989). Frugivorous insects, which may use pulp for larval development or just chew through towards the seeds inside, can be killed by dispersers during digestion. Therefore fruit-eating vertebrates may have a significant impact on the population sizes of insect fruit predators that remain inside the fruit after ripening (Drew 1987, Herrera 1989).

Fruit predators, for instance some nanophyid weevils, tephritid flies, pyralid moths, and bruchid beetles, may avoid mortality risks associated with ripening by feeding only on developing, unripe fruits, and leaving them just before ripening (Southgate 1979; Herrera 1984, 1989; Hosaka *et al.* 2009). These predators in early stages of seed development may not affect substantially the total number of mature seeds because usually only a small portion of the initial fruits can grow with sufficient resources provided by the mother tree in any circumstances, whether they were attacked or not (Momose *et al*. 1996, Hosaka *et al.* 2009). In this context, late predation has the greatest impact on ripe seed production (Nakagawa *et al.* 2005, Hosaka *et al.* 2009).

Insect and microbial frugivores may also change physical and chemical properties of the ripe fruits so as to make them unpalatable for the vertebrate frugivores (Janzen 1983, Manzur & Courtney 1984, Jordano 1987). Finally, some species of intervertebrate seed predators are able to survive passage through the digestive tract of dispersers using the seed coat for protection (Herrera 1984, Guix & Ruiz 2000).

## Plant–insect interactions at the community level

Seed predators are the most important group of frugivorous insect. They may play a crucial role in maintaining high plant diversity in tropics due to their impact on the population dynamics of individual plant species. Seed predators can substantially reduce populations of host plant species as long as the seed mortality they inflict is sufficiently large, distance-dependent and/or density-dependent. It means that locally rare plant species have an advantage because of lower predation pressure. Further, seeds dispersing large distances from the mother tree may also benefit from reduced predation. This mechanism is known as the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) which is a leading explanation for high plant diversity in tropics. Under this hypothesis, seed predators or other plant natural enemies, such as pathogens (Freckleton & Lewis 2006) have the greatest diversifying effects on vegetation if they are host-specific, because of their ability to respond to the density of their sole host species (Lewis & Gripenberg 2008). Host specific predators are well attuned to host plant phenology and its defending mechanisms, therefore may rapidly respond to the seed density (Janzen 1970). Although many recent studies confirm that the Janzen-Connell effect plays a key role in maintenance of high species diversity in tropics (Wills *et al.* 1997, Wills & Condit 1999, Harms *et al.* 2000), Janzen’s original assumption that seed predators may be important, remains poorly documented (Lewis & Gripenberg 2008). There is an obvious need for comprehensive data on the abundance and host specificity of frugivores in tropical forests (Janzen 1980, Nakagawa *et al.* 2003).

## **Aims of the thesis**

This thesis focuses on the community of frugivorous insects in a lowland rain forest in Papua New Guinea, particularly on the host specificity of the principal insect orders attacking fruits as a key factor for the operation of the Janzen-Connell mechanism maintaining plant diversity in tropical forests. Further, the thesis also documents species diversity in frugivorous communities and examines its principal drivers, particularly morphological characteristics of fruits, and the taxonomic position of host plant species. These attributes of frugivorous insect assemblages on host plants were studied previously but restricted to particular insect taxa (e.g. Janzen 1980, Lyal & Curran 2000, Pinzon-Navarro *et al.* 2010) or plant families (Nakagawa *et al.* 2003). A large frugivore rearing programme from Kenya represents one of a few comparable studies available (Copeland *et al.* 2009, Ramirez & Traveset 2010). The present thesis provides the first comprehensive data set including quantitative information on major frugivores from a large selection of plant species.

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# Chapter I

# Frugivorous weevils are too rare to cause Janzen–Connell effects in New Guinea lowland rain forest

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## ABSTRACT

A community of frugivorous weevils was studied by quantitative rearing of 57 weevil species represented by 10 485 individuals from 326 woody plant species in lowland rain forest in Papua New Guinea. Only fruits from 35% of plant species were attacked by weevils. On average, weevils were reared from only 1 in 33 fruits and 1 kg of fruit was attacked by 2.51 individuals. Weevil host specificity was relatively high: 42% of weevil species fed on a single plant genus, 19% on a single plant family and only 16% were reared from more than one family. However, monophagous specialists represented only 23% of all reared individuals. The average 1 kg of fruits was infested by 1.84 individuals of generalist weevils (feeding on allogeneric or allofamilial host species), 0.52 individual of specialists (feeding on a single or several congeneric species), and 0.15 individual of unknown host specificity. Large-seeded fruits with thin mesocarp tended to host specialist species whereas those with

thick, fleshy mesocarp were often infested with both specialists and generalists. Weevils tended to avoid small-seeded, fleshy fruits. The low incidence of seed damage (3% of seeds) suggests that weevils are unlikely to play a major role in regulating plant populations via density-dependent mortality processes outlined by the Janzen–Connell hypothesis.

The contribution of Richard Ctvrtecka as the first author: 60%

# Chapter II

# Low host specificity and abundance of frugivorous Lepidoptera in the lowland rain forests of Papua New Guinea. (manuscript)

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## ABSTRACT

A community of frugivorous Lepidoptera was studied through quantitative rearing of 118 Lepidoptera species represented by 1,710 individuals from 326 woody plant species found in the lowland rainforest of Papua New Guinea. Only fruits from 52% of the plant species sampled were attacked by Lepidoptera. On average, Lepidoptera were reared from 1 in 89 fruits and a kilogram of fruit was attacked by 1.01 individuals. Host specificity of Lepidoptera was notably low: 68% of Lepidoptera species attacked plants from >1 family, 6% fed on single family, 11% on single genus and 15% were monophagous. The average kilogram of fruits was infested by 0.81 individuals from generalist species (defined here as feeding on confamilial and allofamilial host species) and 0.07 from specialist species (feeding on a single host or congeneric hosts). Large-seeded fruits with thin mesocarp tended to host specialist species whereas those with thick, fleshy mesocarp were often infested with both specialist and generalist species. Lepidoptera preferred smaller fruits with both smaller mesocarp and seeds. The very low incidence of seed damage suggests that Lepidoptera

species do not play a major role in regulating plant populations via density-dependent mortality processes outlined by the Janzen-Connell hypothesis.

## INTRODUCTION

Lepidoptera represent an important component of the frugivorous insect guild, but have rarely been studied at a community level (Colepand 2009, Ramirez & Traveset 2010). Many studies (Adamski *et al*. 2010, Razowski & Brown 2012, Brown *et al*. 2014, Miller *et al*. 2014) are restricted to single lepidopteran families, and/or to a single plant family (Nakagawa 2003, Hosaka *et al*. 2009, 2011) or even a single plant species (Evans 1970, McQuate *et al.* 2000, Hoddle & Hoddle 2008, Gilligan *et al*. 2011).

Although we know that many frugivorous Lepidoptera have an effect on fruits of economically important plants (Brown 2006), their role in tropical forests is almost unknown because of the lack of life history information on rainforest Lepidoptera species. Fruits represent two very distinct, high-quality food resources: seeds and mesocarp (Short & Epps 1976, Mattson 1980) and can be therefore attacked by seed predators (Janzen 1980, Nakagawa *et al.* 2003, Hosaka *et al.* 2009) as well as frugivores attacking mesocarp (Gilligan *et al*. 2011) or the whole immature fruit content (Janzen 1981). In each of these cases Lepidoptera negatively affect fruit development and cause fruit abortion or early fruit fall, but the importance of this impact on fruit production and survival remains unknown. Moreover, some of Lepidoptera can be scavengers (Robinson 2009).

The most important herbivores affecting seed survival are seed predators which consume the seed contents, therefore decreasing plant reproductive potential (Steffan-Dewenter *et al*. 2001, Kolb *et al.* 2007). Lepidoptera, as well as other frugivorous insects, may play a role in such a mechanism by maintaining high species diversity in tropical forest due to seed mortality, particularly if mortality is positively dependent on plant density

(Janzen 1970, Connell 1971). Such density dependence is more likely in specialized herbivores than in generalist ones.

Our goals in this study are to examine the abundance, species richness and host specificity of frugivorous Lepidoptera on a phylogenetically diverse sample of plants in the lowland rain forest of Papua New Guinea, testing if they are (i) host specific, (ii) causing significant seed mortality, and (iii) potentially important density-dependent mortality factors in maintaining plant diversity. Further, we explore the effect of fruit and seed morphology on the diversity of frugivorous Lepidoptera.

## METHODS

### Study areas

The study was conducted between March 2008 and April 2009 in two areas approximately 100 km apart: (1) near the villages of Baitabag, Mis and Ohu within a 20 × 10-km area comprising a successional mosaic of disturbed and mature lowland rainforest ($5^o$08'-14'S, $145^o$7'-41'E, 50–200 m asl, Madang Province, Papua New Guinea), and (2) in relatively less disturbed forest near Wanang village ($5^o$14'S, $145^o$11'E, 100 m asl). Vegetation in these areas is similar in species composition and has been classified as mixed evergreen rain forest on Latosol (Laidlaw *et al.* 2007, Paijmans 1976, Whitfeld *et al.* 2012) with a humid climate (mean annual rainfall 3,600 mm), a mild dry season from July to September, and mean annual temperature of 26°C (McAlpine *et al*. 1983).

### Study design

Fruits were sampled by searching a 200–400-ha matrix of mature and early-successional forest at each site and by collecting all plant species encountered in the fruiting condition. Sampling effort amounted to 1,284 person-days of field work (312 person-days per site in

Baitabag, Mis, Ohu, and 348 person-days in Wanang). Mature or nearly mature fruits were collected from branches and the forest floor whereas decomposing fruits on the ground were avoided. A collection of fruits from an individual tree or liana on a particular day represented a single sample unit for analysis. Individual samples comprised 1 to 1500 individual fruits and weighed between 22 and 8311 g. We employed a functional definition of the individual fruit for the purpose of measurement to encompass aggregate fruits arising from the fusion of adjacent carpels (e.g. *Artocarpus* and *Ficus*). For a subset of plant species, basal area in a 50-ha forest dynamics plot at Wanang, where all trees individuals with dbh>1 cm were measured and identified (G. Weiblen unpubl. data), was used as a proxy for local abundance. We were able to calculate basal area for 218 species which were present in the plot out a total of 531 plant species from which fruits were sampled.

One or several ripe fruits from each sample were cut along both axes and photographed. Cross-sectional area of the fruit and the seed were estimated for 268 species from diameter measurements of the photographs using Adobe Photoshop and the volume of each was calculated as a volume of ellipsoid ($4/3 \times 3.14 \times A/2 \times B/2 \times C/2$, where A, B and C is the length, width and height of the fruit respectively). The volume of the fruit, the combined volume of seeds per fruit (in the case of many-seeded fruits), and fleshiness (% of fruit volume represented by mesocarp) were used as plant traits in an analysis of fruit suitability for Lepidoptera development.

Fruit-feeding Lepidoptera were reared from fruit samples placed in ventilated plastic boxes. Emerging adults were drawn to light through a drilled hole on the side of boxes and collected in vials that were monitored every 24 h. Rearing boxes were also opened and checked every 2 days to remove excessive moisture and any reared adults. Each fruit sample was reared for 10 weeks, which was deemed sufficient to rear most seed predators since the number of reared individuals decreased sharply afterwards. All specimens were assigned to morphospecies using a reference collection in The New Guinea Binatang Research Center (http://www.entu.cas.cz/png/parataxoweb.htm). Cytochrome c oxidase subunit I (COI) sequences (Willson 2012) of all morphospecies were analyzed at the University of Guelph (www.boldsystems.org; project FRUT) to verify our species concepts. Most of the confirmed morphospecies were identified to species by S. E. Miller and collaborators at the Smithsonian Institution in Washington, DC.

Insect vouchers were deposited at the Smithsonian Institution and at the Papua New Guinea Agriculture Research Institute in Port Moresby. Fruit and plant vouchers were deposited at the Papua New Guinea Forest Research Institute in Lae and at the University of Minnesota in St. Paul. Digital photographs and voucher information associated with fruit specimens were submitted to the New Guinea Atrium digital herbarium (http://ng.atrium-biodiversity.org/atrium).

### Data analysis

Only plant species with a total sample weight of ≥1 kg and >50 individual fruits were included in the analyses. These thresholds represent a compromise between maximizing the number of plant species analysed and the thorough sampling of Lepidoptera assemblages from every host plant species.

Species accumulation analyses were based on complete Lepidoptera records including rare species and singleton records. However, host specificity was analysed for only those Lepidoptera species represented by at least 10 individuals in our samples. Their host associations were considered only if supported by at least two observations of feeding. Host specificity was categorized as monophagous (M) for species feeding on a single plant species, congeneric (CG), confamilial (CF), and allofamilial (AF) for species feeding on either >1 congeneric species, >1 confamilial genus, or >1 family, respectively. Monophagous and congeneric host ranges are hereafter referred to as specialists and the remaining two categories as generalists. We did not assess seed mortality but rather we calculated the density of Lepidoptera per fruit and per unit mass of fruit.

The overlap between species reared from fruit and those feeding on plant foliage was estimated using our existing data on caterpillars feeding on the foliage sampled at our study areas (Novotny *et al*. 2002, http://www.entu.cas.cz/png/parataxoweb.htm).

Accumulation curves for herbivore species with increasing numbers of plant species and samples were implemented in EstimateS. The species richness of Lepidoptera was extrapolated for the local plant diversity using a power function fitted to the empirical data for N = 100–169 plant species (Novotny *et al.* 2010).

## RESULTS

In total, we collected 4,268 samples weighing 3,556.8 kg from 531 woody plant species representing 84 families. This included 326 plant species from 58 families sampled for at least 50 fruits and weighing at least 1 kg in aggregate per plant species for a total mass of 2,758.8 kg, which was further analysed. The total sample size per plant species thus varied from 1–65 kg and 50–7,166 fruits. The total weight and number of fruits collected per tree species was significantly correlated with the basal area, a proxy for local abundance (sample weight = 6,670 + 0.0565 × basal area, $R^2 = 0.22$, $P < 0.001$; number of fruits = 687 + 0.0072 × basal area, $R^2 = 0.37$, $P < 0.001$).

We reared 1,710 individual Lepidoptera representing 118 species from 169 plant species, i.e. 51.8% of all plant species sufficiently sampled. The proportion of plant species infested by Lepidoptera increased with the total weight of the fruit sample ($\chi^2_4 = 47.4$; $P < 0.001$; Figure 1a) and the number of fruits collected per species (Figure 1b).

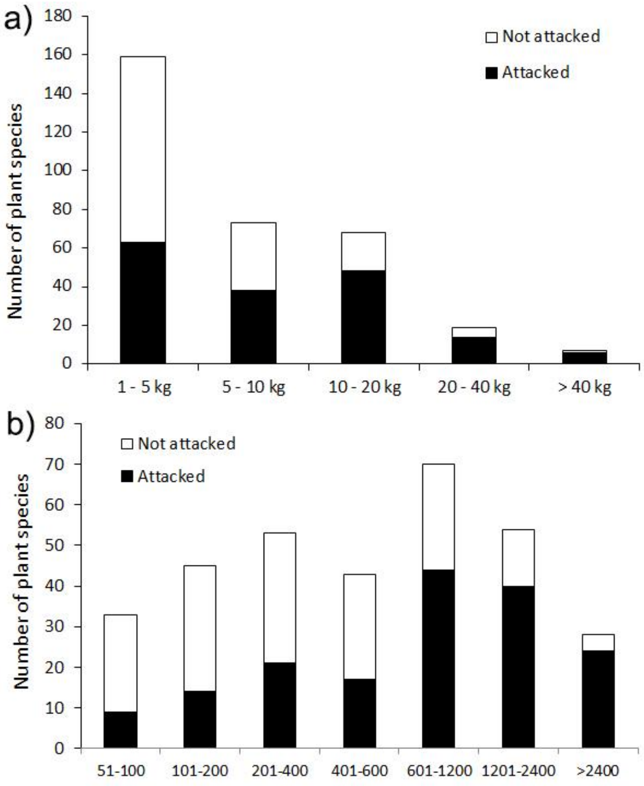

**Figure 1**. The number of plant species attacked (black bar) and not attacked (white bar) by frugivorous Lepidoptera in samples categorized by (a) fruit weight and (b) the number of fruits.

The frugivorous communities comprised 118 species from the following families: Arctiidae (1 sp.), Blastobasidae (2 spp.), Brachodidae (1 sp.), Cosmopterygidae (5 spp.), Crambidae (11 spp.), Gelechiidae (3 spp.), Gracillariidae (5 spp.), Heliodinidae (1 sp.), Immidae (1 sp.), Lecithoceridae (5 spp.), Lycaenidae (4 spp.), Noctuidae (1 sp.), Nolidae (5 spp.), Oecophoridae (6 spp.), Pterophoridae (1 sp.), Pyralidae (8 spp.), Tineidae (11 spp.) and Tortricidae (33 spp.). A further 12 species of Lepidoptera and 2 species of Microlepidoptera were not been identified to the family level (Appendix 1).

Host specificity was quantified for the 47 Lepidoptera species (represented by ≥10 individuals) reared from 169 plant species and 48 plant families. Thirty-two Lepidoptera species attacked plants from >1 family (allofamilial host range). This includes one species that was reclassified as allofamilial based on additional hosts that were not included in the analysis because of their low sample size (Lepidoptera sp6, see Appendix 1). Further, three species attacked plants from >1 genus within a single family (confamilial host range), five species attacked >1 congeneric plant species and seven were monophagous. Generalists were more abundant (mean ± SE = 0.81 ± 0.18 individuals $kg^{-1}$ fruits) than specialists (mean ± SE = 0.07 ± 0.02 individuals $kg^{-1}$ fruits) and also than the species for which we were not able to identify specialization (mean ± SE = 0.09 ± 0.02 individuals $kg^{-1}$ fruits).

Overall, 14 from the total of 118 species reared from fruit were also found feeding on leaves (Table 1). These include 3 species where we could estimate their host specificity on fruits, as they were reared from fruit as ≥10 individuals; they all were allofamilial.

Mesocarp and seed volumes were significantly correlated [mesocarp = -27763.38 + 3.314*seed ($mm^3$); $r^2 = 0.74$] across plant species, and plant species across the whole range of both mesocarp and seed sizes were infested (Figure 2).

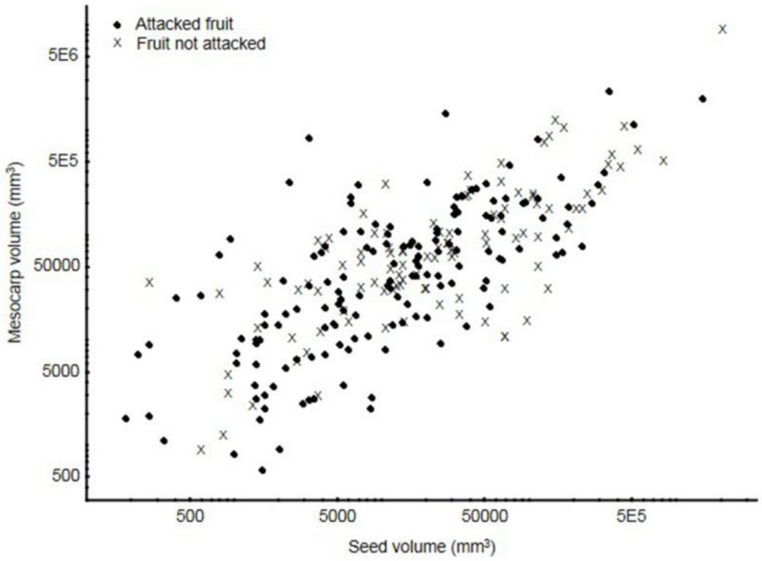

**Figure 2**. Relationship between seed and mesocarp volume for 268 plant species attacked and not attacked by Lepidoptera.

However, infested plant species had significantly smaller fruit size, as well seed and mesocarp volumes than non-infested species (fruit volume: $U_{106,151} = 5624$, $Z = 3.064$, $P = 0.002$; seeds volume: $U_{106,151} = 5346$, $Z = 3.574$, $P < 0.001$; mesocarp volume: $U_{106,151} = 5828$, $Z = 2.69$, $P = 0.007$), while fleshiness (i.e. proportion of mesocarp in whole fruit) did not have significant effect on infestation ($U_{106,151} = 6839$, $Z = 0.83$, $P = 0.401$) (Figure 3).

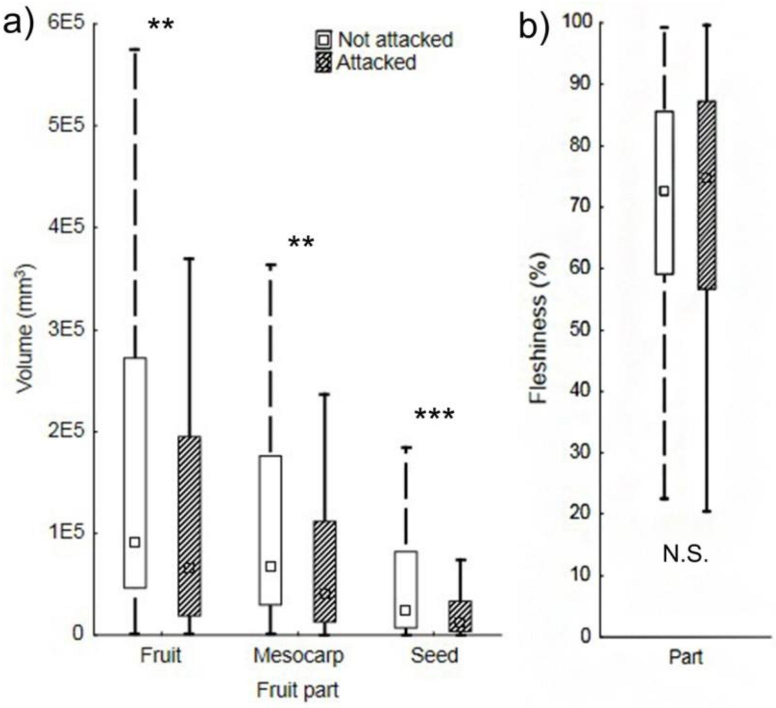

**Figure 3**. (a) Mean volume for whole fruit, mesocarp and seeds in plant species attacked and not attacked by Lepidoptera. The differences between attacked and non-attacked species are significant (whole fruit: $U_{106,151} = 5624$, $Z = 3.064$, $P = 0.002$; mesocarp: $U_{106,151} = 5828$, $Z = 2.69$, $P = 0.007$; seeds: $U_{106,151} = 5346$, $Z = 3.574$, $P < 0.0010$), (b) Fleshiness (i.e. proportion of mesocarp in whole fruit) did not have significant effect on infestation ($U_{106,151} = 6839$, $Z = 0.83$, $P = 0.401$).

None of the Lepidoptera superfamilies or clades (Apodytrisia, Dytrisia, Macrolepidoptera, Obtectomera) showed any preferences towards specific fruit characteristics, including the whole fruit volume, flesh volume, and seed volume (superfamilies: $H_{6,267} = 10.9 – 8.77$, $p = 0.09 – 0.51$; clades: $H_{3,229} = 6.07 – 3.91$, $p = 0.11 – 0.27$).

Magnoliids, eudicots and monocots were attacked with similar frequency. Within eudicots, Lepidoptera more frequently attacked asterids than rosids and core eudicots (Figure 4).

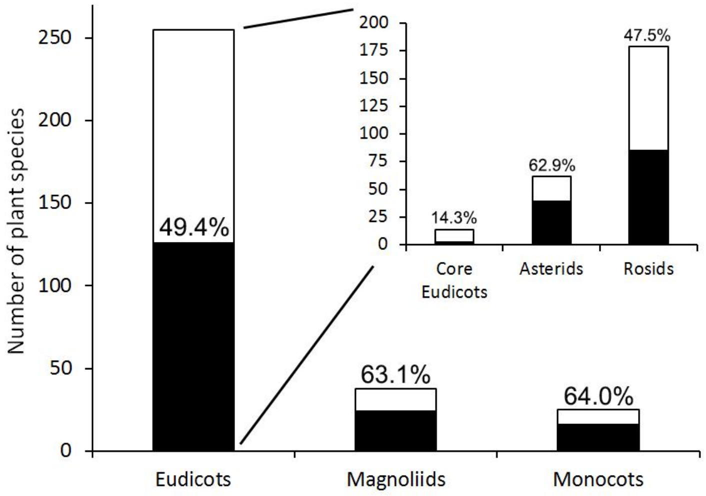

**Figure 4**. Numbers of Lepidoptera-infested plant species (black bars) relative to the total number of plant species sampled (white bars) for major flowering plant clades. The percentage of infested plant species is shown above the bars. The differences in attack rate between Magnoliids, eudicots and monocots were not significant. Within eudicots, Lepidoptera attacked more frequently asterids (63% of 62 species) than rosids (47% of 179 species, $\chi^2_1$= 3.8, P = 0.05), and core eudicots (14% of 14 species, $\chi^2_1$= 9, P = 0.002). Classification according to the Angiosperm Phylogeny Group (APG III 2009).

The number of lepidopteran species feeding on a particular plant species increased almost linearly with sample size, from 0.16 ± 0.06 (mean ± 95% CI) in 1-kg samples to 2.13 ± 0.64 in 20-kg samples (Figure 5a). This general trend conceals a diversity of species accumulation curves among individual plant species. We recognized four different patterns of species accumulation including: (1) an asymptote at a single Lepidoptera species per host species, (2) a linear increase in Lepidoptera species per plant species as a function of sample size, (3) an incomplete approach to an asymptote, and (4) an asymptote averaging more than one (specifically, 2 – 4) Lepidoptera species per host species (Figure 5b).

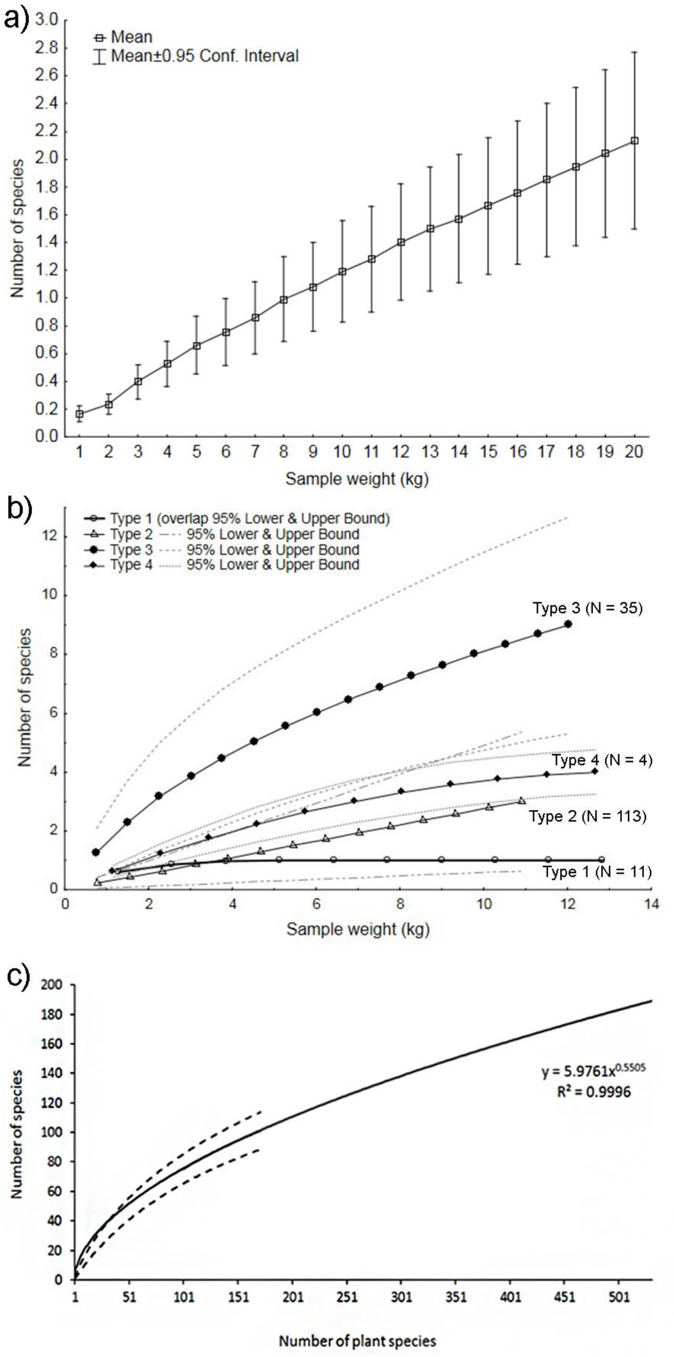

**Figure 5**. Species accumulation curves for Lepidoptera as functions of sample size. (a) Mean number of lepidopteran species as a function of fruit sample weight for a subset of 33 plant species with sufficiently large samples (1 to 20 kg). (b) Mean number of lepidopteran species per host plant species as a function of fruit sample weight. Confidence intervals (95%) are shown for each of four types of accumulation curve. The number of plant species (N) comprising each curve is also shown.

(c) Species richness of Lepidoptera as a function of plant species richness for 163 attacked plant species.

The number of Lepidoptera species increased with floristic diversity from 1.64 ± 0.55 (mean ± 95% CI) for a single plant species to 101 ± 12.64 (mean ± 95% CI) for the entire set of 169 plant species analysed, based on the analysis of 5 kg of fruits per species (Figure 5c). A power function extrapolation estimated there should be 189 ± 17 (mean ± 95% CI) Lepidoptera species feeding on the total number of 531 woody plant species sampled in the study (Figure 5c).

Most of the 326 plant species exhibited low densities of Lepidoptera, including both specialists and generalists (Figure 6). One kilogramme of fruits was attacked on average by 1.01 ± 0.18 (mean ± SE) Lepidoptera, and we reared one Lepidoptera individual per 89 individual fruits on average, including one generalist per 113 fruits, one specialist per 708 fruits, and one Lepidoptera where specialization could not be determined per 993 fruits.

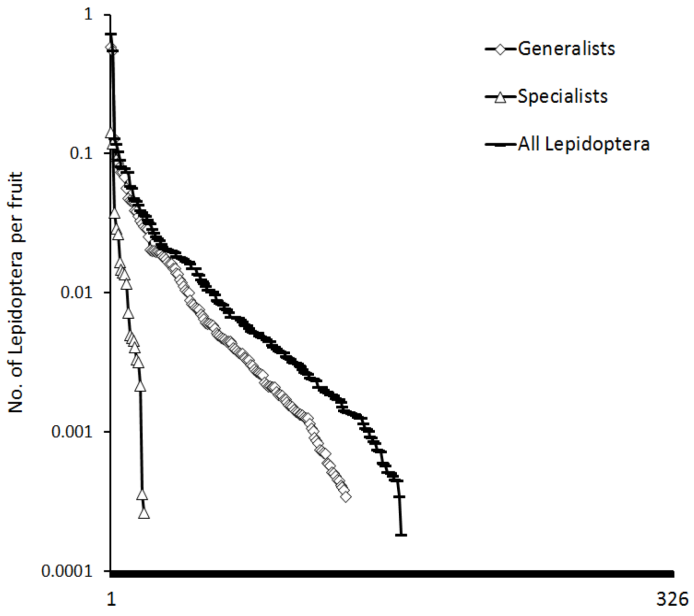

Figure 6. Density of all frugivorous Lepidoptera, and both specialist and generalists, per fruit. Host species are ranked from highest to lowest density for 326 plant species with samples of >1 kg and >50 fruits.

Only five out of 326 plant species hosted more than one Lepidoptera per 10 individual fruits (*Pterygota horsfieldii*, *Archidendron aruense*, *Maniltoa schefferi*, *Sterculia* *schumanniana*, *Xanthophyllum papuanum*; Figure 6), and 55 plant species hosted more than one Lepidoptera per 100 individual fruits. In contrast, 82% of plant species supported Lepidoptera densities of less than one Lepidoptera per 100 fruits, suggesting that <1% of fruits were typically attacked.

There was no correlation between lepidopteran density (log (n+1) transformed per 1 kg of fruit or one fruit) and basal area among 218 tree species (Pearson r = -0.007, P = 0.91; Pearson r = -0.02, P = 0.73 respectively). Restricting this analysis to only tree species attacked by Lepidoptera (N = 129) returned the same result (Pearson r = -0.07, P = 0.37; Pearson r = -0.07, P = 0.44 respectively).

## DISCUSSION

### *Species composition and host specificity*

The taxonomic composition of frugivorous Lepidoptera in our study is similar to that of frugivorous Lepidoptera communities from Kenya, except that Blastobasidae is a dominant family in Kenya, but represented by only several specimens from two species in our data (Miller pers. com.).

To our knowledge, our study is the first quantitative analysis of host specificity in frugivorous Lepidoptera for tropical forests, showing that their community is strongly dominated by generalist (allofamilial and confamilial) species (74%), whereas specialist are rare. Comparable data from other studies give inconsistent results. For example, all Lepidoptera species on Dipterocarpaceae in Borneo were confamilial, i.e. their specificity was low (Nakagawa *et al.* 2003). On the other hand, studies based on massive rearing of frugivorous insect in Kenya (Copeland *et al.* 2009) found high host specificity in particular families, but this conclusion may be influenced by the effect of sample size. For instance, 57 (58.8%) of the 97 tortricid species reared from fruits in Kenya (Brown *et al.* 2014) were recorded from a single plant species, but this number included also 30 species reared as singletons. When using the N=10 minimum abundance threshold for reared species, as in the present study, the number of monophages decreased to 12 (12.3%) species, similar to the proportion found in the present study where we recorded one (8.3%) monophagous species out of 12 reared tortricids (Appendix 1).

### *Attack rate*

The proportion of plant species attacked by Lepidoptera (51.8%) is similar to the 38.4% of attacked plant species found in Kenya (Copeland *et al*. 2009). This comparison is based on a similar sampling effort (4,268 of fruit samples in PNG vs 3,838 in Kenya), although the number of sampled plant species (531 vs 938) as well as biotopes was higher in Kenya. The attack rate by Lepidoptera was higher than the 32.5% attacked by weevils (Coleoptera: Curculionidae), obtained from the same data set (Ctvrtecka *et al*. 2014).

### *Overlap between frugivorous and folivorous guilds*

We found that even such different resources as fruits and leaves were jointly exploited by some Lepidoptera species (Tab 1). Although comparable studies analysing overlap between guilds among communities are not available, it has been documented for some Lepidoptera species that they can feed on more than one plant resource. For instance more species from family Gracillariidae feed on leaves, shoots as well as the fruit surface in avocado (Gilligan *et al*. 2011). Likewise, species of *Endothenia* spp. (Tortricidae) are borers in the stalks, roots, seeds and fruit of numerous families of flowering plants (Brown *et al.* 2011). *Heleanna physalodes* feed on both flower buds and fruits of different plant species (Clarke 1976) and may be either identical or closely related to the species we found in our study. We can distinguish three groups among the species feeding both on fruits and leaves: (1) leaf chewers rarely using fruits as a minority source of food; (2) species abundant in both guilds, usually also extremely polyphagous. They tend to attack mesocarp causing superficial damage or chewing holes (Gilligan *et al.* 2011), or they may use fruit accidentally (Brown *et al*. 2014). They may also include polyphagous pests or scavengers. (3) Notably, there were no abundant frugivorous species that used leaves only occasionally. (4) Species rare in both guilds where we can not specify their food preferences impact on fruit fitness.

| Family/species of Lepidoptera | Nf | Pf | S | Nl | Pl | Ns | Shared plant species |
|---|---|---|---|---|---|---|---|
| Cosmopterigidae/Labdia sp3 | 10 | 7 | AF | 1 | 1 | 0 | Ficus dammaropsis |
| Crambidae/Nacoleia octasema | 3 | 1 |  | 267 | 5 | 1 | Heliconia papuana |
| Crambidae/Pagyda salvalis | 3 | 2 |  | 142 | 3 | 1 | Vitex cofassus |
| Crambidae/Prophantis androstigmata | 4 | 3 |  | 1 | 1 | 1 | Randia decora |
| Crambidae/Prophantis cf eloria | 13 | 1 |  | 16 | ? | ? |  |
| Gracillariidae/Conopomorpha cramerella | 16 | 3 | AF | 1 | 1 | 1 | Caesaria erythrocarpa |
| Immidae/Moca congrualis | 1 | 1 |  | 3 | 1 | 0 |  |
| Lycaenidae/Deudorix epirus | 13 | 5 | AF | 7 | ?* | ? | Maniltoa |
| Nolidae/Etanna vittalis | 2 | 1 |  | 92 | 7 | 0 |  |
| Tortricidae/Isodemis nr stenotera | 1 | 1 |  | 30 | 9 | 0 |  |
| Tortricidae/Adoxophyes spn nr orana | 1 | 1 |  | 794** | 88 | 0 |  |
| Tortricidae/Adoxophyes sp1 | 1 | 1 |  | 794** | 88 | 0 |  |
| Tortricidae/Adoxophyes tripselia | 1 | 1 |  | 164 | 29 | 0 |  |
| Tortricidae/Heleanna nr physalodes | 1 | 1 |  | 92 | 7 | 1 | Pimelodendron amboinicum |

Table 1: Overlap of frugivorous and leaf-chewer guilds. Nf=number of individuals reared from fruits, Pf=number of host plant species used by frugivorous individuals, S=specificity (AF=allofamilial), Nl=number of individuals reared from leaves, Pl=number of host plant species used by folivorous individuals, Ns=number of shared plant species (Note: *incomplete plant id (genus), **one unidentified morphospecies).

Although we are not able to ascertain in most of cases whether our reared lepidopteran species feed on mesocarp or seeds, their impact on fruit fitness may be important in both cases. They may cause fruit loss or reduce seed viability (Herrera 1982) or, as well as other fruit predators, open the way to subsequent attack by pathogens (Christensen 1972) due to mining through the mesocarp or feeding on the surface. These pathogens may make the fruit unpalatable to dispersers through the production of toxins (Mirocha & Christensen 1974). However, there are also cases where fruit predators were beneficial to their hosts (Wilson *et al.* 2012) as frugivorous vertebrates preferred fruits infested by insects (Drew 1987). There are also predator/pollinator mutualisms of some moths that ensure efficient pollination while feeding on the resulting fruits (Pelmyr & Huth 1994, Marler 2010).

### *Species diversity and abundance*

Although Lepidoptera belong to the most studied herbivore orders in the tropics, this attention is heavily focused on folivorous species (Novotny & Basset 2005). Our studies from the same forests (Novotny *et al*. 2010, 2012, Butteril unpubl. data) found on average the following species diversities of Lepidoptera per plant species in different guilds: 1.8 (s.e. 0.25) miners, 15.3 (1.26) leaf-tiers and rollers, 9.5 (0.90) exposed leaf-chewers, 0.1 (0.04) gallers. This suggests that frugivores, with 6.0 (xxx) species, represent 18% of Lepidoptera diversity, except flower-, root- and wood-feeding species that have not been studied. However, this proportion will decrease with expanding the sampling universe from single plant species to diverse vegetation since frugivores appear to be the least host specific from all Lepidoptera guilds analysed here.

Lepidoptera is the most species rich order among frugivorous species, but their abundance (1.01 individuals per kg; one individual per 89 pieces on fruit) is much lower than in weevils, (2.51 individuals per kg; one individual per 33 pieces of fruit; Ctvrtecka *et al*. 2014). This low incidence of seed damage as well as very low portion of specialists make a major role of frugivorous Lepidoptera in maintaning of plant diversity due to density-dependent mortality promoting by specilized herbivores unlikely.

## Chapter II

## LITERATURE CITED

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**Appendix 1**: Frugivorous Lepidoptera and their host plant species. Ns=no. of reared individuals, Np = no. of host plant species, S = specifity (AF = allofamilial species, CF = confamilial species, CG = congeneric species, M = monophagous species; * in the case >5 host plant species only one most frequently plant species is shown).

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| Arctiidae | | | | | |
| Lithosiinae | | | | | |
| Chamaita sp1 | 1 | 1 | | Lamiaceae | Faradaya splendida |
| Blastobasidae | | | | | |
| Blastobasinae | | | | | |
| Blastobasis sp1 | 1 | 1 | | Annonaceae | Goniothalamus aruensis |
| Neoblastobasis sp1 | 10 | 3 | AF | Anacardiaceae | Semecarpus cassuvium |
| | | | | Euphorbiaceae | Macaranga aleuritoides |
| | | | | Rubiaceae | Versteegia cauliflora |
| Brachodidae | | | | | |
| Brachodinae | | | | | |
| Miscera basichrysa extensa | 4 | 2 | | Arecaceae | Calamus longipinna |
| | | | | Meliaceae | Dysoxylum arborescens |
| Cosmopterigidae | | | | | |
| Gn sp1 | 4 | 1 | | Araceae | Pothos rumphii |
| Cosmopteriginae | | | | | |
| Labdia sp1 | 17 | 3 | AF | Icacinaceae | Medusanthera laxiflora |
| | | | | Myristicaceae | Myristica buchneriana |
| | | | | Solanaceae | Solanum oliverianum |
| Labdia sp2 | 5 | 5 | | Arecaceae | Licuala beccariana |
| | | | | Fabaceae | Inocarpus fagifer |
| | | | | Meliaceae | Dysoxylum confertiflorum |
| | | | | Myristicaceae | Myristica buchneriana |
| | | | | Putranjivaceae | Drypetes longifolia |
| Labdia sp3 | 10 | 7 | AF | Euphorbiaceae | Cleistanthus myrianthus* |
| Pyroderces sp1 | 65 | 5 | AF | Araceae | Pothos rumphii |
| | | | | Arecaceae | Hydriastele macrospadix |
| | | | | Fabaceae | Millettia pinnata |
| | | | | Myristicaceae | Myristica buchneriana |
| | | | | Zingiberaceae | Pleuranthodium racemigerum |
| Crambidae | | | | | |
| Spilomelinae | | | | | |
| Cirrhochrista sp1 | 1 | 1 | | Moraceae | Ficus austrina |
| Conogethes pluto | 10 | 2 | AF | Fabaceae | Maniltoa megalocephala |
| | | | | Zingiberaceae | Pleuranthodium racemigerum |
| Conogethes semifascialis | 17 | 7 | AF | Malvaceae | Pterygota horsfieldii* |

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| cf Herpetogramma | 2 | 1 | | Zingiberaceae | Pleuranthodium racemigerum |
| Lipararchis sp1 | 3 | 1 | | Araceae | Epipremnum pinnatum |
| Nacoleia octasema | 3 | 1 | | Heliconiaceae | Heliconia papuana |
| Pagyda salvalis | 3 | 2 | | Lamiaceae | Vitex cofassus |
| | | | | Marantaceae | Donax canniformis |
| Piletocera nr aegimiusalis | 1 | 1 | | Sapindaceae | Lepidopetalum micans |
| Piletocera violascens | 1 | 1 | | Zingiberaceae | Pleuranthodium racemigerum |
| Prophantis androstigmata | 4 | 3 | | Elaeocarpaceae | Elaeocarpus amplifolius |
| | | | | Loganiaceae | Neuburgia corynocarpa |
| | | | | Rubiaceae | Randia decora |
| Prophantis cf "eloria" | 13 | 1 | M | Rubiaceae | Pavetta platyclada |
| Gelechiidae | | | | | |
| Gn sp1 | 13 | 1 | M | Sapindaceae | Tristiropsis acutangula |
| Dichomeridinae | | | | | |
| Dichomeris thryptica | 1 | 1 | | Sapotaceae | Chrysophyllum roxburghii |
| Gelechiinae | | | | | |
| Ardozyga sp1 | 1 | 1 | | Euphorbiaceae | Antidesma contractum |
| Gracillariidae | | | | | |
| Gn sp1 | 196 | 7 | AF | Fabaceae | Archidendron aruense* |
| Gn sp2 | 20 | 5 | AF | Arecaceae | Hydriastele microspadix |
| | | | | Asparagaceae | Cordyline terminalis |
| | | | | Asparagaceae | Dracaena angustifolia |
| | | | | Lamiaceae | Premna obtusifolia |
| | | | | Polygalaceae | Xanthophyllum papuanum |
| Gn sp3 | 14 | 3 | CF | Fabaceae | Archidendron aruense |
| | | | | Fabaceae | Archidendron glabrum |
| | | | | Fabaceae | Inocarpus fagifer |
| Gn sp4 | 10 | 6 | AF | Meliaceae | Dysoxylum confertiflorum* |
| Gracillariinae | | | | | |
| Conopomorpha cramerella | 16 | 3 | AF | Euphorbiaceae | Ryparosa javanica |
| | | | | Fabaceae | Maniltoa psilogyne |
| | | | | Sapindaceae | Pometia pinnata |
| Heliodinidae? | | | | | |
| Gn sp1 | 34 | 1 | M | Myrtaceae | Syzygium gonatanthum |
| Immidae | | | | | |
| Moca congrualis | 1 | 1 | | Burseraceae | Canarium vitiense |
| Lecithoceridae | | | | | |
| Gn sp1 | 14 | 5 | AF | Araceae | Epipremnum pinnatum |
| | | | | Euphorbiaceae | Macaranga aleuritoides |
| | | | | Euphorbiaceae | Macaranga bifoveata |

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| | | | | Meliaceae | Dysoxylum confertiflorum |
| | | | | Moraceae | Ficus pachyrrhachis |
| Gn sp2 | 10 | 2 | AF | Araliaceae | Osmoxylon novo-guineense |
| | | | | Monimiaceae | Steganthera hirsuta |
| Gn sp3 | 1 | 1 | | Lamiaceae | Clerodendrum tracyanum |
| Oditinae | | | | | |
| Lecithocera sp1 | 3 | 3 | | Annonaceae | Pseuduvaria mollis |
| | | | | Lamiaceae | Gmelina moluccana |
| | | | | Sapindaceae | Harpullia crustacea |
| Gn sp4 | 2 | 1 | | Menispermaceae | Pycnarrhena novoguineensis |
| Lycaenidae | | | | | |
| Polymmatinae | | | | | |
| Jamides cyta | 10 | 2 | CG | Myrtaceae | Syzygium amplum |
| | | | | Myrtaceae | Syzygium longipes |
| Theclinae | | | | | |
| Deudorix diovis | 11 | 4 | AF | Meliaceae | Chisocheton ceramicus |
| | | | | Sapindaceae | Cupaniopsis stenopetala |
| | | | | Sapindaceae | Harpullia crustacea |
| | | | | Sapindaceae | Lepidopetalum micans |
| Deudorix epirus | 13 | 5 | AF | Fabaceae | Maniltoa lenticellata |
| | | | | Fabaceae | Maniltoa psilogyne |
| | | | | Pandaceae | Galearia celebica |
| | | | | Sapindaceae | Harpullia longipetala |
| | | | | Thymelaeaceae | Phaleria macrocarpa |
| Deudorix littoralis | 4 | 2 | | Dipterocarpaceae | Vatica papuana |
| | | | | Pandaceae | Galearia celebica |
| Noctuidae | | | | | |
| Amphipyrinae | | | | | |
| Spodoptera pecten | 1 | 1 | | Arecaceae | Caryota rumphiana |
| Nolidae | | | | | |
| Chloephorinae | | | | | |
| Etanna vittalis | 2 | 1 | | Anacardiaceae | Spondias dulcis |
| Nolinae | | | | | |
| Nola sp1 | 1 | 1 | | Myristicaceae | Horsfieldia basifissa |
| Sarrothripinae | | | | | |
| Giaura nr leucophaea | 13 | 1 | M | Malvaceae | Pterygota horsfieldii |
| Gyrtothripa quadrifera | 27 | 3 | CG | Malvaceae | Sterculia shillinglawii |
| | | | | Malvaceae | Sterculia schumanniana |
| | | | | Malvaceae | Sterculia schumanniana |
| Gyrtothripa verecunda | 11 | 2 | CG | Malvaceae | Sterculia shillinglawii |
| | | | | Malvaceae | Sterculia schumanniana |

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| Oecophoridae | | | | | |
| Gn sp1 | 12 | 5 | AF | Meliaceae | Dysoxylum arborescens |
| | | | | Meliaceae | Dysoxylum confertiflorum |
| | | | | Meliaceae | Dysoxylum pettigrewianum |
| | | | | Myristicaceae | Myristica hollrungii |
| | | | | Phyllanthaceae | Bridelia macrocarpa |
| Stathmopodinae | | | | | |
| Gn sp2 | 3 | 2 | | Lauraceae | Litsea globosa |
| | | | | Lauraceae | Litsea timoriana |
| Stathmopoda nr periclina | 4 | 2 | | Lecythidaceae | Barringtonia calyptrocalyx |
| | | | | Myrtaceae | Syzygium malaccense |
| Stathmopoda nr tetrazyga | 1 | 1 | | Dipterocarpaceae | Vatica papuana |
| Stathmopoda sp1 | 6 | 1 | | Lauraceae | Litsea collina |
| Stathmopoda sp2 | 5 | 1 | | Arecaceae | Arenga microcarpa |
| Pterophoridae | | | | | |
| Pterophorinae | | | | | |
| Xyroptila nr peltastes | 1 | 1 | | Rubiaceae | Versteegia cauliflora |
| Pyralidae | | | | | |
| Galleriinae | | | | | |
| Lamoria adaptella complex | 13 | 4 | AF | Fabaceae | Intsia bijuga |
| | | | | Marantaceae | Phrynium macrocephalum |
| | | | | Marantaceae | Phrynium pedunculatum |
| | | | | Rubiaceae | Versteegia cauliflora |
| Microchlora sp.n. nr bileneella | 1 | 1 | | Myristicaceae | Horsfieldia sylvestris |
| Tirathaba pseudocomplana | 29 | 5 | CG | Arecaceae | Caryota rumphiana |
| | | | | Fabaceae | Inocarpus fagifer |
| | | | | Moraceae | Ficus congesta |
| | | | | Moraceae | Ficus hispidioides |
| | | | | Moraceae | Ficus pachyrrhachis |
| Tirathaba ruptilinea | 14 | 5 | AF | Araliaceae | Osmoxylon novo-guineense |
| | | | | Euphorbiaceae | Cleistanthus myrianthus |
| | | | | Moraceae | Ficus congesta |
| | | | | Moraceae | Ficus pachyrrhachis |
| | | | | Sapindaceae | Harpullia longipetala |
| Phycitinae | | | | | |
| Assara seminivale | 19 | 4 | AF | Dipterocarpaceae | Vatica papuana |
| | | | | Fabaceae | Inocarpus fagifer |
| | | | | Rubiaceae | Canthium cymigerum |
| | | | | Rubiaceae | Canthium longiflorum |
| Assara sp1 | 11 | 1 | M | Dipterocarpaceae | Vatica papuana |

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| Faveria nr dasyptera | 2 | 2 | | Dipterocarpaceae | Vatica papuana |
| | | | | Lauraceae | Cryptocarya caudata |
| Mussidia cf pectinicornella | 13 | 2 | CF | Fabaceae | Intsia bijuga |
| | | | | Fabaceae | Millettia pinnata |
| Tineidae | | | | | |
| Gn sp1 | 16 | 8 | AF | Lecythidaceae | Planchonia papuana* |
| Gn sp2 | 10 | 7 | AF | Fabaceae | Inocarpus fagifer* |
| Meessiinae | | | | | |
| Gn sp3 | 2 | 2 | | Araceae | Amorphophallus campanulatus |
| | | | | Icacinaceae | Gomphandra papuana |
| Erechtiinae | | | | | |
| Erechthias sp1 | 108 | 44 | AF | Lamiaceae | Premna obtusifolia* |
| Erechthias sp2 | 2 | 1 | | Polygalaceae | Xanthophyllum papuanum |
| Hapsiferinae | | | | | |
| Trachycentra chlorogramma | 7 | 4 | | Dipterocarpaceae | Vatica papuana |
| | | | | Lecythidaceae | Barringtonia calyptrocalyx |
| | | | | Marantaceae | Phrynium macrocephalum |
| | | | | Rubiaceae | Versteegia cauliflora |
| Hieroxestinae | | | | | |
| Opogona taochroa | 7 | 6 | | Arecaceae | Arenga microcarpa* |
| Opogona sp1 | 1 | 1 | | Meliaceae | Dysoxylum arborescens |
| Opogona sp2 | 22 | 2 | AF | Fabaceae | Archidendron glabrum |
| | | | | Heliconiaceae | Heliconia papuana |
| Gn sp4 | 8 | 3 | | Fabaceae | Maniltoa psilogyne |
| | | | | Meliaceae | Dysoxylum arborescens |
| | | | | Myrtaceae | Syzygium trivene |
| Tineinae | | | | | |
| Monopis pentadisca | 151 | 33 | AF | Gnetaceae | Gnetum gnemonoides* |
| Tortricidae | | | | | |
| Gn sp1 | 17 | 3 | AF | Proteaceae | Helicia latifolia |
| | | | | Sapindaceae | Harpullia crustacea |
| | | | | Sapindaceae | Tristiropsis acutangula |
| Gn sp2 | 2 | 1 | | Lauraceae | Cryptocarya massoy |
| Gn sp3 | 1 | 1 | | Sapindaceae | Cupaniopsis macropetala |
| Chlidanotinae | | | | | |
| Caenognosis incisa | 1 | 1 | | Sapotaceae | Chrysophyllum roxburghii |
| Polylopha sp1 | 3 | 1 | | Lauraceae | Litsea timoriana |
| Thaumatographa sp1 | 148 | 7 | AF | Loganiaceae | Strychnos minor* |
| Thaumatographa sp2 | 12 | 1 | M | Rubiaceae | Versteegia cauliflora |

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| Olethreutinae | | | | | |
| Andrioplecta nr leucodora | 72 | 13 | AF | Fabaceae | Kingiodendron alternifolium* |
| Cryptaspasma brachyptycha | 6 | 3 | | Lauraceae | Cryptocarya depressa |
| | | | | Lauraceae | Cryptocarya laevigata |
| | | | | Myrtaceae | Syzygium amplum |
| Cryptaspasma sp1 | 1 | 1 | | Lauraceae | Litsea collina |
| Cryptophlebia sp1 | 21 | 1 | M | Sapindaceae | Tristiropsis acutangula |
| Cryptophlebia sp2 | 1 | 1 | | Rubiaceae | Versteegia cauliflora |
| Cydia sp1 | 11 | 2 | CF | Fabaceae | Maniltoa psilogyne |
| | | | | Fabaceae | Millettia pinnata |
| Cydia sp2 | 2 | 1 | | Clusiaceae | Garcinia assugu |
| Demeijerella sp.n. | 19 | 4 | AF | Arecaceae | Hydriastele microspadix |
| | | | | Marantaceae | Donax canniformis |
| | | | | Rubiaceae | Psychotria leptothyrsa |
| | | | | Sapindaceae | Tristiropsis acutangula |
| Gnathmocerodes labidophora | 6 | 4 | | Fabaceae | Archidendron glabrum |
| | | | | Lecythidaceae | Barringtonia apiculata |
| | | | | Lecythidaceae | Barringtonia calyptrocalyx |
| | | | | Lecythidaceae | Planchonia papuana |
| Heleanna nr physalodes | 9 | 1 | | Euphorbiaceae | Pimelodendron amboinicum |
| Helictophanes nr scambodes | 20 | 3 | CG | Meliaceae | Dysoxylum arborescens |
| | | | | Meliaceae | Dysoxylum excelsum |
| | | | | Meliaceae | Dysoxylum pettigrewianum |
| Helictophanes prospera | 3 | 3 | | Malvaceae | Microcos argentata |
| | | | | Meliaceae | Dysoxylum arborescens |
| | | | | Meliaceae | Dysoxylum pettigrewianum |
| Helictophanes sp1 | 1 | 1 | | Meliaceae | Sandoricum koetjape |
| Lobesia sp1 | 2 | 2 | | Euphorbiaceae | Melanolepis multiglandulosa |
| | | | | Lamiaceae | Clerodendrum tracyanum |
| Thaumatotibia nr zophophanes | 155 | 22 | AF | Malvaceae | Pterygota horsfieldii* |
| Gn sp4 | 3 | 3 | | Burseraceae | Canarium vitiense |
| | | | | Fabaceae | Inocarpus fagifer |
| | | | | Polygalaceae | Xanthophyllum papuanum |
| Gn sp5 | 2 | 1 | | Lamiaceae | Vitex cofassus |
| Gn sp6 | 6 | 2 | | Marantaceae | Phrynium macrocephalum |
| | | | | Marantaceae | Phrynium pedunculatum |
| Gn sp7 | 4 | 1 | | Clusiaceae | Garcinia assugu |

| Taxon of Lepidoptera | Ns | Np | S | Plant family | Plant species |
|---|---|---|---|---|---|
| Tortricinae | | | | | |
| Adoxophyes sp.n. nr orana | 1 | 1 | | Euphorbiaceae | Cleistanthus myrianthus |
| Adoxophyes thoracica | 1 | 1 | | Elaeocarpaceae | Elaeocarpus amplifolius |
| Adoxophyes tripselia | 1 | 1 | | Araliaceae | Polyscias verticillata |
| Adoxophyes sp1 | 1 | 1 | | Oleaceae | Chionanthus sessiliflorus |
| Epitrichosma nr metreta | 11 | 5 | AF | Asparagaceae | Cordyline terminalis |
| | | | | Euphorbiaceae | Cleistanthus myrianthus |
| | | | | Fabaceae | Inocarpus fagifer |
| | | | | Lamiaceae | Clerodendrum tracyanum |
| | | | | Lamiaceae | Premna obtusifolia |
| Isodemis nr stenotera | 1 | 1 | | Lamiaceae | Clerodendrum tracyanum |
| Gn sp8 | 27 | 5 | AF | Araceae | Epipremnum pinnatum |
| | | | | Combretaceae | Terminalia complanata |
| | | | | Euphorbiaceae | Cleistanthus myrianthus |
| | | | | Icacinaceae | Gonocaryum litorale |
| | | | | Myristicaceae | Horsfieldia basifissa |
| Lepidoptera | | | | | |
| Gn sp1 | 3 | 2 | | Euphorbiaceae | Cleistanthus myrianthus |
| | | | | Lamiaceae | Clerodendrum tracyanum |
| Gn sp2 | 5 | 2 | | Malvaceae | Microcos argentata |
| | | | | Malvaceae | Microcos grandiflora |
| Gn sp3 | 26 | 3 | AF | Arecaceae | Arenga microcarpa |
| | | | | Burseraceae | Canarium vitiense |
| | | | | Sapindaceae | Cupaniopsis stenopetala |
| Gn sp4 | 2 | 1 | | Arecaceae | Hydriastele microspadix |
| Gn sp5 | 2 | 1 | | Arecaceae | Hydriastele microspadix |
| Gn sp6 | 19 | 1 | AF | Marantaceae | Phrynium macrocephalum |
| Gn sp7 | 1 | 1 | | Meliaceae | Dysoxylum microstachyum |
| Gn sp8 | 1 | 1 | | Phyllanthaceae | Aporosa papuana |
| Gn sp9 | 2 | 1 | | Arecaceae | Arenga microcarpa |
| Gn sp10 | 4 | 3 | | Burseraceae | Canarium vitiense |
| | | | | Lamiaceae | Vitex cofassus |
| | | | | Myristicaceae | Horsfieldia sylvestris |
| Gn sp11 | 1 | 1 | | Meliaceae | Aphanamixis polystachya |
| Gn sp12 | 1 | 1 | | Hypoxidaceae | Curculigo recurvata |
| Microlepidoptera | | | | | |
| Gn sp1 | 1 | 1 | | Myristicaceae | Endocomia macrocoma |
| Gn sp2 | 1 | 1 | | Euphorbiaceae | Macaranga aleuritoides |

# Chapter III

# Fruit morphology and the structure of frugivorous communities in a New Guinea lowland rain forest. (manuscript)

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## ABSTRACT

A community of frugivorous insects was studied by quantitative rearing of 21,941 individual insects representing three orders (Coleoptera, Diptera, and Lepidoptera) from 326 woody plant species in lowland rainforest in Papua New Guinea. Fruits from 21% of plant species were not attacked by any insects, 31% by a single insect order, 30% by two insect orders and 18% by all three orders. Plant species with fruits attacked by insects were not significantly more abundant in the forest than the species with non-attacked fruits. Fruits of most of the plant species exhibited low rates of attack and low densities of insects. One kilogram of fruits was attacked by the mean on 7.02 insect individuals, including 3.57 individuals from Coleoptera, 2.56 from Diptera, and 0.87 from Lepidoptera per kilogram of fruits. Thus, we reared on average one insect from 10 fruits, including one Coleoptera from 22 fruits, one Diptera from 25 fruits and one Lepidoptera from 100 fruits. Only 59 out of the 326 plant species hosted more than 1 insect per 10 individual fruits and only 6 species supported a density of >1 insect per fruit. Neither fruit weight, fruit volume, mesocarp volume, seed volume, or fleshiness had significant effect on the probability that a fruit would be attacked by

an insect frugivore. However, fruits attacked by Diptera were significantly larger and had larger volume of both mesocarp and seeds than fruits attacked by Coleoptera and Lepidoptera.

## INTRODUCTION

In the tropical rainforest, fruit morphology may play an important role in shaping mutualistic relationships between plants and their predominantly vertebrate dispersers, as well as antagonistic relationships with intervertebrate fruit predators. However, it is not clear whether pulp has primarily evolved as a reward for dispersers (Mack 2000) or as mechanical protection of the seed (Herrera 1982). Previous analysis suggests that the fruit morphology of a species frequently is adapted, contributing to the general characteristics of the animals that eat it. The strong association between size, color, and morphology even among species within genera implies that natural selection has produced the divergence in fruit form associated with bird and mammal fruit-eating (Janson 1983). Alternatively, this may also be the result of defensive adaption against seed predators since fleshy fruited species have lower seed predation rates than dry fruited species (Janzen 1969, Herrera1987, Wright 1990). Pulp is important for instance in bruchid seed predators as they are not able to penetrate through the pulp. The fleshy-fruited species may therefore be colonized only after dehiscence (in case of dehiscent fruits) or when the pulp is damaged by vertebrate predators (Wright 1990) or decayed during the postdispersal phase. This example highlights the potential for three-way interactions among plants, vertebrate and invertebrate predators and dispersers.

Fruit and seed size and shape can also be important factors for dispersers as well as seed predators. Species with very large seeds are adapted primarily to dispersal by large animals rather than to protection against small predators (Grubb 1998), their nutrient resources being sufficient for successful germination even if they are partly consumed. However, large seeds also represent an extraordinarily attractive target for herbivores, unless they also contain high amounts of crude fibers (Ramirez & Traveset) or toxic compounds (Janzen *et al*. 1977, Nahrstedt 1985), that protect them from insects (Ramirez & Traveset). Small fruit, and seed size may on the other hand act as a limiting factor for frugivores, requiring certain minimum amount of recources for development (Center & Johnson 1974, Szentesi & Jermy 1995). For instance, many bruchid species are unable to colonise very flat seeds, in which the smallest dimension is smaller than the size of adult beetles (Center & Johnson 1974, Szentesi & Jermy 1995). As a result, host plant species of bruchids have significantly more spherical seeds than the non-host species. However many plant species with seeds of suitable sizes and shapes are not infested by bruchids, suggesting other factors, such as plant chemical defences, may be also important (Szentesi & Jermy 1995).

Frugivorous species, when they develop inside of one fruit, may suffer from interspecific competition. However, multiple frugivore species many avoid competition between larvae developing inside of the same fruit by (1) spatial separation, with different species limited to e.g. either pulp or seed (Janzen 1983), or (2) temporal separation, specializing to either pre- or post-dispersal phase (Perreira *et al*. 2014), or segregating even during the same phase of ripening (Janzen 1983), or (3) the ability to share resource (pulp especially) without competition when in abundance (Wilson *et al*. 2012).

Intraspecific competition between insect frugivores sharing the same fruit has also been documented, particularly when the host seed can support only one individual until maturity (Alves-Costa & Knogge 2005). A general scenario is that older larvae kill those that enter later (Janzen 1975). In some cases, potential for competition may lead to the selection of specific adaptive behaviour (Sanz & Gurrea 2000) and morphology, i.e. changes in the mandible morphology from the first instar, where mandibles make it possible to kill competitors, to second and following instars where the mandibles are adapted for feeding and boring through woody endocarp (Alves-Costa & Knogge 2005).

The effect of fruit morphology on the composition of frugivorous insects on the community level was partly studied only by Ramirez &Traveset (2010) with the main focus on fruit traits, but without detailed data on the composition of frugivorous insect groups. Other existing studies are focused either on insects feeding on a particular plant family (Nakagawa 2003, Hosaka 2009), or on a particular insect group (Janzen 1980, Pinzon-Navarro *et al*. 2010, Grimbacher *et al*. 2013). Our study offers quantitative data on all three principal frugivorous insect orders across a broad phylogenetically diverse selection of plants from entire local plant community, in a lowland rain forest. The aims of the study are (1) to quantify the abundance and taxonomic composition of frugivorous insects on individual plant species, (2) to analyse what plant species escape attack by frugivores altogether, and (3) to predict frugivore composition on an ordinal level from the morphological traits of fruits and/or phylogenic position of host plant species.

## METHODS

### Study areas

The study was conducted from March 2008 to April 2009 in two areas approximately 100 km apart: (1) near the villages of Baitabag, Mis and Ohu within a 20 × 10-km area comprising a successional mosaic of disturbed and mature lowland rainforest ($5^{o}$08'-14'S, $145^{o}$7'-41'E, 50–200 m asl, Madang Province, Papua New Guinea), and (2) in relatively less disturbed forest near Wanang village ($5^{o}$14'S, $145^{o}$11'E, 100 m asl). Vegetation in these areas is similar in species composition and has been classified as mixed evergreen rain forest on Latosol (Laidlaw *et al.* 2007, Paijmans 1976, Whitfeld *et al.* 2012) with a humid climate (mean annual rainfall 3600 mm), a mild dry season from July to September, and mean annual temperature of 26°C (McAlpine *et al*. 1983).

## Study design

Fruits were sampled by searching a 200–400-ha matrix of mature and early-successional forest at each site and by collecting all plant species encountered in the fruiting condition. Sampling effort amounted to 1284 person-days of field work (312 person-days per site in Baitabag, Mis, Ohu, and 348 person-days in Wanang). Mature or nearly mature fruits were collected from branches and the forest floor whereas decomposing fruits on the ground were avoided. A collection of fruits from an individual tree or liana on a particular day represented a single sample unit for analysis. Individual samples comprised from 1 to 1500 individual fruits and weighed between 22 and 8311 g. We employed a functional definition of individual fruit for the purpose of measurement to encompass aggregate fruits arising from the fusion of adjacent carpels (e.g. *Artocarpus* and *Ficus*). For a subset of plant species, basal area in a 50-ha forest dynamics plot at Wanang, where all trees individuals with dbh>1 cm were measured and identified (G. Weiblen unpubl. data), was used as a proxy for local abundance. We were able to calculate basal area for 218 species which were present in the plot out a total of 531 plant species from which fruits were sampled.

One or several ripe fruits from each sample were cut along both axes and photographed. Cross-sectional area of the fruit and the seed were estimated for 268 species from diameter measurements of the photographs using Adobe Photoshop and the volume of each was calculated as a volume of ellipsoid (4/3 × 3.14 ×A/2 x B/2 x C/2, where A, B and C is the length, width and height of the fruit respectively). The volume of the fruit, the combined volume of seeds per fruit (in the case of many-seeded fruits), and fleshiness (% of fruit volume represented by mesocarp) were used as plant traits in an analysis of fruit suitability for insect development.

Fruit-feeding insects were reared from fruit samples placed in ventilated plastic boxes. Emerging adults were drawn to light through a drilled hole on the side of boxes and collected in vials that were monitored every 24 h. Rearing boxes were also opened and checked every 2 days to remove excessive moisture and any reared adults. Each fruit sample was reared for 10 weeks, which was deemed sufficient to rear most seed predators since the number of reared individuals decreased sharply afterwards. All specimens were assigned to morphospecies with using a reference collection in The New Guinea Binatang Research Center (http://www.entu.cas.cz/png/parataxoweb.htm). Cytochrome c oxidase subunit I (COI) sequences (Willson 2012) of all morphospecies were analyzed at the University of Guelph (www.boldsystems.org; project FRUT) to verify our species concepts. Most confirmed morphospecies were identified to species by: A. Riedel & R. Thomson (Coleoptera, Curculionidae); R. Rozkosny (Diptera: Stratiomyidae); S. Kubik (Diptera: Chloropidae); M. Bartak (Diptera: Micropezidae, Syrphidae); S. E. Miller and collaborators at the Smithsonian Institution in Washington, DC (Lepidoptera).

Insect vouchers were deposited at the Smithsonian Institution and at the Papua New Guinea Agriculture Research Institute in Port Moresby. Fruit and plant vouchers were deposited at the Papua New Guinea Forest Research Institute in Lae and at the University of Minnesota in St. Paul. Digital photographs and voucher information associated with fruit specimens were submitted to the New Guinea Atrium digital herbarium (http://ng.atrium-biodiversity.org/atrium).

### Data analysis

Only plant species with a total sample weight of ≥1 kg and >50 individual fruits were included in the analyses. These thresholds represent a compromise between maximizing the number of plant species analysed and the thorough sampling of insect assemblages from every host plant species. We did not assess seed mortality but rather we calculated the density of weevils per fruit, per unit mass of fruit, and the proportion of infested plant species.We used variance test (Schluter 1984) and log-linear analysis of frequency tables to assess simultaneously whether insect groups are associated with plant species. Standard statistical tests were implemented in R.

## RESULTS

In total, we collected 4268 samples weighing 3556.8 kg from 531 woody plant species representing 84 families. This included 326 plant species from 58 families sampled by at least 50 fruits and weighing at least 1 kg in aggregate per plant species. These samples, representing a total mass of 2758.8 kg, were further analysed. The total sample size per plant species thus varied from 1–65 kg and 50 – 7166 fruits. The total weight and number of fruits collected per tree species was significantly correlated with basal area, a proxy for ecological dominance (sample weight = 6670 + 0.0565 × basal area, $R^2 = 0.22$, $P < 0.001$; number of fruits = 687 + 0.0072 × basal area, $R^2 = 0.37$, $P < 0.001$).

We reared 21,941 individual insects representing three orders (Coleoptera, Diptera, and Lepidoptera; Appendix 1) from 256 plant species, i.e. 48.2% of all species sampled (Appendix 1).The proportion of plant species infested by insects increased with the total weight of the fruit sample (Figure 1, but see sample size 1-5 kg) and the number of fruits collected per species. Overall, 70 from 326 plant species, (i.e., 21%) were not attacked by any insect. The attacked species included 31% of all plant species that were attacked by a single insect order, 30% attacked by two orders, and 18% that were attacked by all three studied orders: Coleoptera, Lepidoptera, and Diptera (Figure 2). The proportion of plants that escaped the insect attack entirely, as well as the proportion of plant species attacked by all three orders, were higher than expected if the attacks by individual insect orders were mutually independent events (Figure 2). Variance test (Schluter 1984) confirmed significant and positive ($P < 0.001$, variance ration 1.43, $w = 467$, $df = 326$) association between insect

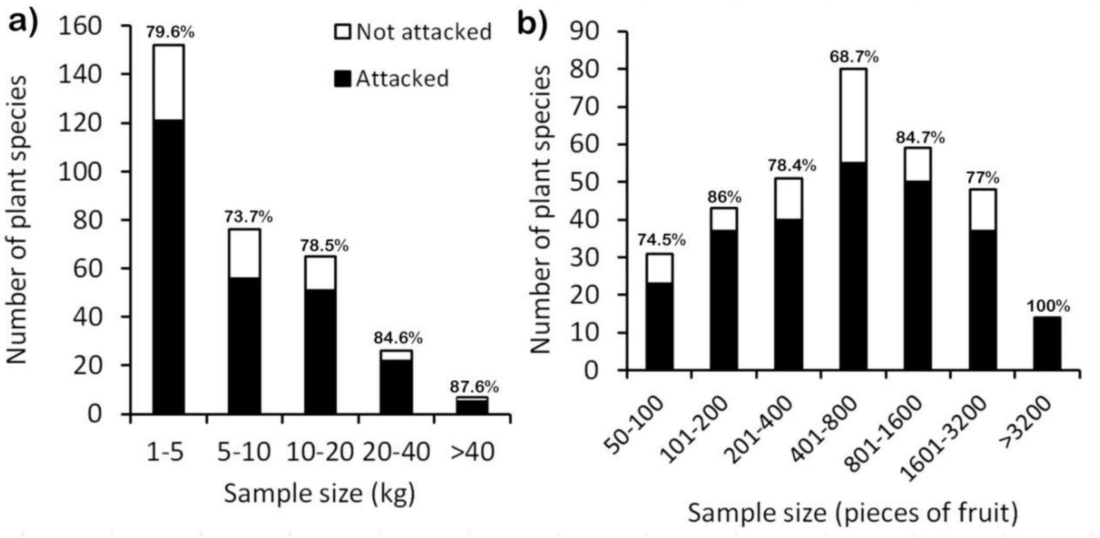

**Figure 1**. The number of plant species attacked and not attacked by frugivorous insects (Coleoptera, Diptera, Lepidoptera) in categories of fruit sample weight (a) and the number of fruits per sample (b) in Papua New Guinea. Percentages indicate the proportion of plant species in each category that were attacked by frugivorous insects.

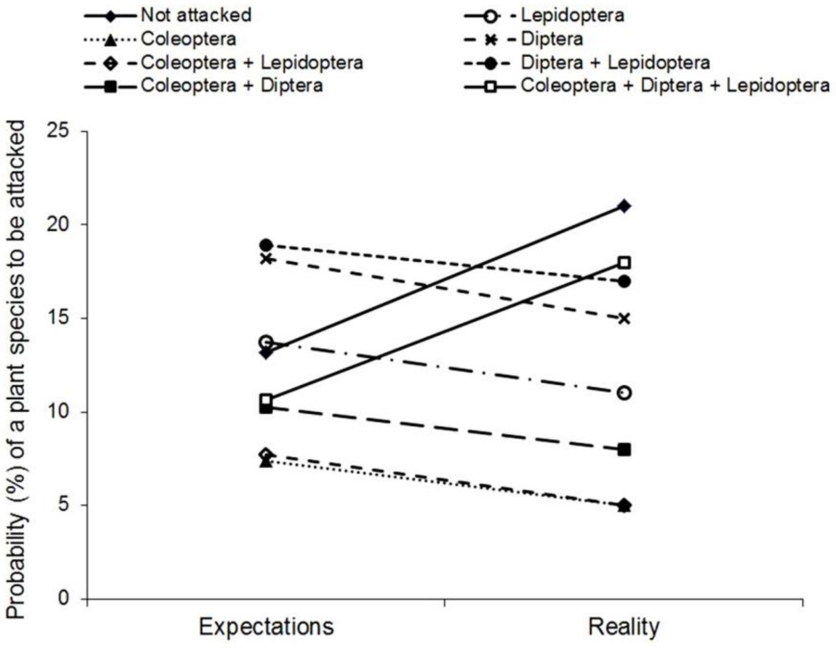

**Figure 2**. Expected and observed probability of a plant species to have fruits attacked by various combinations of insect orders, on the assumption that insect orders attack plant species independently from each other.

orders, and the positive association between Diptera + Coleoptera, and Diptera + Lepidoptera was selected as the best model.

On a taxonomically finer scale, most of the plant species were attacked by a limited number of insect families; 71% of species by 1-5 insect families (Figure 3). The distribution of plant family numbers per plant species was significantly different from Poisson distribution, with higher than expected number of plants escaping the attack.

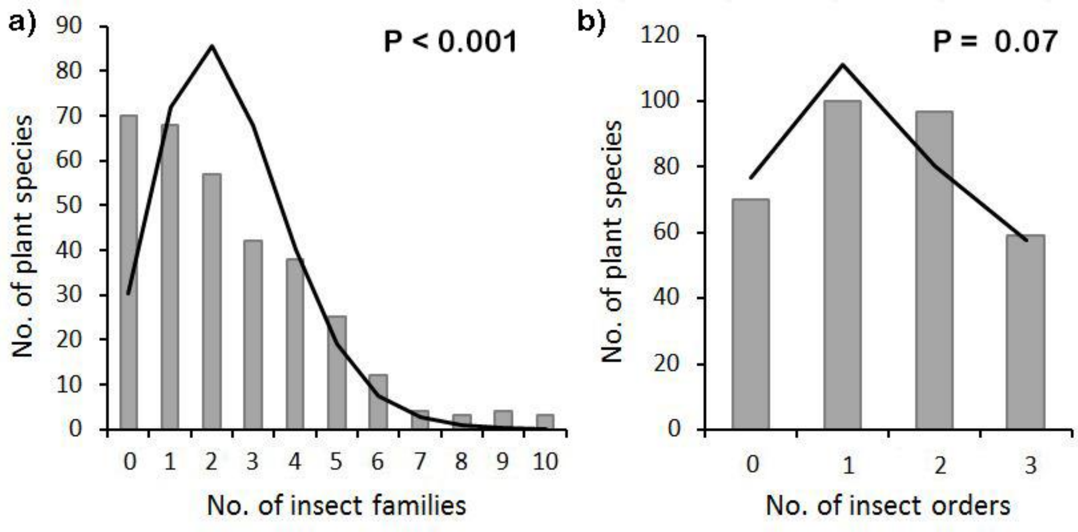

**Figure 3**. Distribution of the number of insect families (a) and insect orders (b) attacking individual plant species, with expected values for a Poisson distribution (line). The observed distribution is significantly different from Poisson distribution for the number of insect orders ($x^2$ tests, P value is reported).

Fruit weight, fruit volume, mesocarp volume, seed volume, and fleshiness did not have a significant effect on chance that a fruit would be attacked by insects (fruit weight: $F_{1,324} = 0.26$, $P = 0.61$; fruit volume: $F_{1,324} = 0.37$, $P = 0.54$; seed volume: $F_{1,324} = 0.68$, $P = 0.41$; mesocarp volume: $F_{1,324}= 0.26$, $p = 0.61$; fleshiness: $F_{1,324} = 0.01$, $p = 0.91$; Figure 4). However, the plant species with attacked fruits tend to have heavier (16.1 ± 4.1 vs. 18.5 ± 2 g) , and larger fruit (179.4 ± 83.9 vs. 237.1 ± 43.8 $cm^3$), with larger seed (48.46 ± 20.7 vs. 67.7 ± 10.8 $cm^3$), and mesocarp volume (130.9 ± 66.5 vs. 169.3 ± 37.8 $cm^3$) .

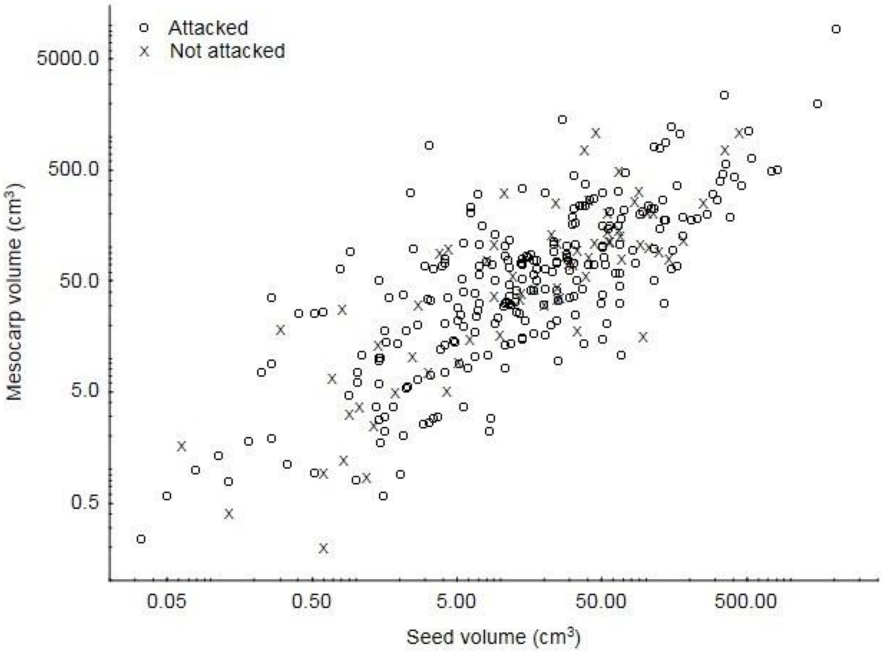

**Figure 4**. Correlation ($R^2 = 0.63$, $P < 0.001$) between seed and mesocarp volume for 327 plant species where fruits were or were not attacked by frugivorous insects in Papua New Guinea. Neither mesocarp volume ($F_{1,324}$= 0.26, p = 0.61) nor seed volume ($F_{1,324}$ = 0.68, P = 0.41) had a significant effect on the probability that a fruit will be attacked.

Fruits attacked by Diptera were significantly larger (KW-$H_{(2,469)}$ = 9.13, p = 0.01; mean ± SE = 284.9 ± 65.6 $cm^3$ ) than fruits attacked by Coleoptera and Lepidoptera (139.4 ± 17 $cm^3$and 169.9± 30.3 $cm^3$ respectively). Similarly, fruits attacked by Diptera had larger seeds (KW-$H_{(2,469)}$ = 8.63, p = 0.013; mean ± SE = 82.2 ± 11.9 $cm^3$) than fruits attacked by Coleoptera and Lepidoptera (41.4 ± 15.2 $cm^3$and 46.1± 12.6 $cm^3$ respectively), and larger volume of mesocarp (KW-$H_{(2,469)}$ = 8.54, p = 0.014; Coleoptera: 97.5 ± 45.3 cm3; Diptera: 202.6 ± 35.5 $cm^3$; Lepidoptera: 123.8 ± 37.6 $cm^3$; Figure 5)

Individual insect families followed similar trend, with Diptera and Coleoptera families showing preferences towards larger (Figure 6) and heavier fruits with larger seed and mesocarp volume. Note that all above mentioned characteristics closely correlated (fruit size and fruit weight: r = 0.90, P < 0.001; fruit volume and mesocarp volume: r = 0.98, P < 0.001;

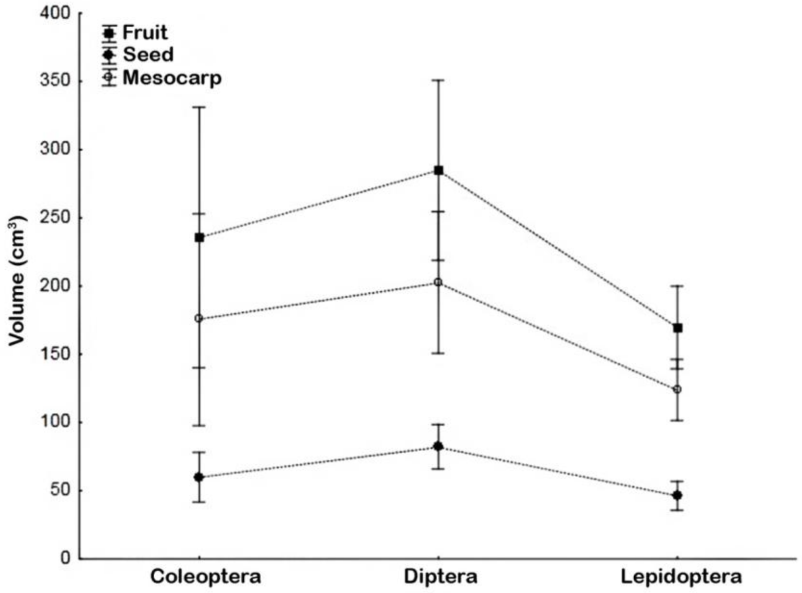

**Figure 5**. Mean volume comprised by whole fruit, mesocarp, or seed in fruits in Papua New Guinea attacked by frugivorous insects from different orders. Means (± SE) are shown for plant species attacked by Coleoptera (N = 132), Diptera (N = 347) and Lepidoptera (N = 296). Note that values for plant species with fruits attacked by more than one insect order appear more times in the graph.

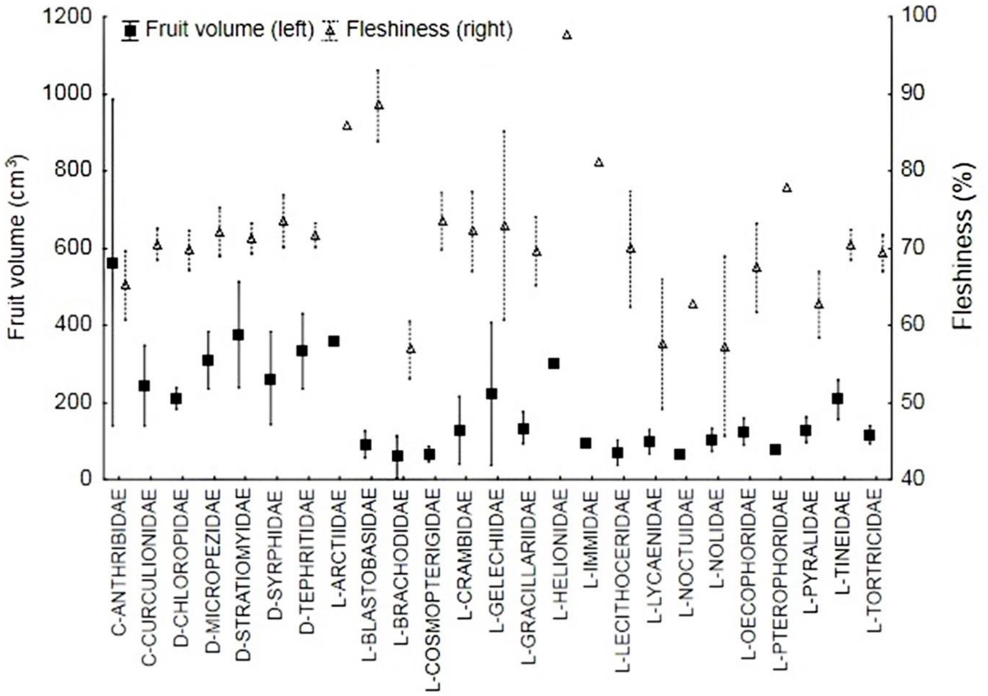

**Figure 6**. Mean fruit volume and fleshiness (percentage of total volume comprised by mesocarp) in fruits in Papua New Guinea attacked by insects. Means (± SE) are shown for plant species attacked by different insect families.  Letters in front of family names denote insect order: C = Coleoptera, D = Diptera, L = Lepidoptera.

fruit volume and seed volume: r = 0.87, $P < 0.001$). Individual insect families did not show any significant preferences toward fruit fleshiness (Figure 6).

There were no significant differences among major plant lineages in the proportion of attacked species. In particular, eudicots, magnoliids and monocots suffered similar rates of attack, as was the case for core eudicors, rosids and asterids within eudicots (Figure 7).

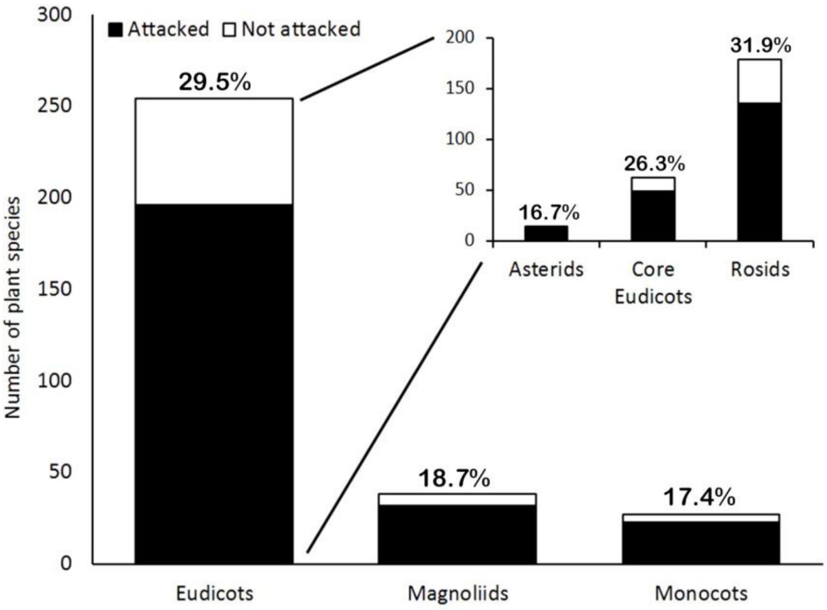

**Figure 7**. Fruit attack rate on plant species within individual plant taxa. Main figure: $X^2 = 1.72$, P = 0.42, inserted figure: $X^2 = 0.88$, P = 0.64.

Plant species with fruits attacked by insect were not significantly more abundant in the forest than plants that escaped the attack (ANOVA; $F_{(1,210)} = 1.38$, p = 0.241, mean ± SE number of stems of attacked plant species in 50 ha plot: 753.5 ± 86.1, number of stems of not attacked plant species: 519.1 ± 1279.6). However, plant species attacked by insects representing two or three insect orders were significantly more abundant in the forest ($F_{(2, 169)} = 3.38$, P = 0.05) than plant species attacked by insect representing one order only. There was no relationship between density of insects reared from a plant species and its abundance in forest.

Most of the 326 plant species exhibited low densities of frugivorous insects (Figure 8). One kilogram of fruits was attacked by 7.02 ± 1.01(mean ± SE) insects, including 3.57 ± 0.93Coleoptera, 2.56 ± 0.38 Diptera, and 0.87 ± 0.18 Lepidoptera. Thus, we reared on average one insect from 10 fruits, including one Coleoptera from 22 fruits, one Diptera from 25 fruits and one Lepidoptera from 100 fruits. Only 59 from the total of 326 plant species hosted more than 1 insect per 10 individual fruits and only six species supported a density of >1 insect per fruit (*Leucaena leucocephala*, *Maniltoa schefferi*, *Pandanus kaernbachii*, *Pouteria maclayana*, *Kingiodendron alternifolium*, and *K. novoguineense*; Figure 8). In contrast, 43% of plant species supported weevil densities of less than 1 weevil per 100 fruits.

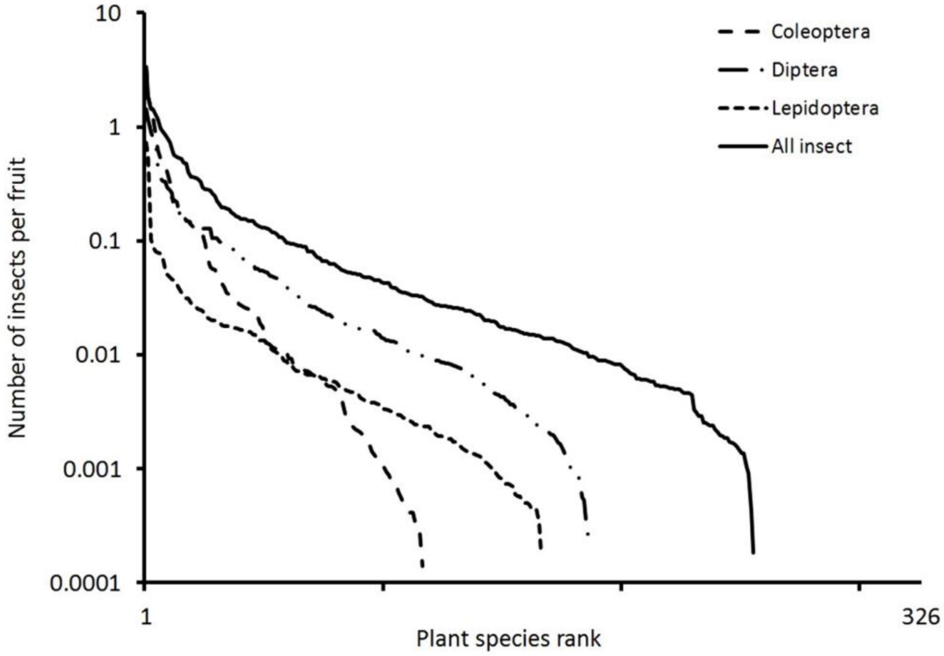

**Figure 8**. Density of all frugivorous insects, and individual insect orders in Papua New Guinea. Host species are ranked from highest to lowest insect density for 326 plant species with samples of >1 kg and >50 fruits.

## DISCUSSION

In total, 48,2% of plant species sampled were attacked by insect frugivores. This is the almost the same portion as in Venezuelan Central Plain with 187 sampled, and 47.6% attacked, plant species (Ramirez & Traveset 2010), or 42.9–46.4% plant species attacked in shrublands and 44.2% in secondary forest (Venezuela; Raimundez 2000). However findings from Kenya suggest a greater proportion of species are attacked (910 species sampled, 57.5% attacked; Copeland *et al*. 2009). Results from Venezuela are based on rearings from five different habitats (including forest, gallery forest, forest-savanna transition, savanna and secondary growth), in 250-ha study area, and thus represent a more heterogenous, yet local data set. In Kenya, fruits were sampled from forests and costal vegetation in multiple geographic regions and from 1 to 3077 m asl, so that the results represent regional species pool rather than a community (Brown *et al*. 2014). This may explain higher portion of attacked plant species in Kenya.

Rather surprisingly, morphological fruit traits that we tested failed to explain differential fruit predation by insect orders. This is however in accordance with the only comparable study on the community level (Ramirez & Traveset 2010) where the incidence of attack by predispersal predators was also generally independent of fruit and seed dimensions.

However, heavier and larger fruits with larger seeds tended to be more often attacked in our study, whereas non-predated plant species in a comparable study had significantly heavier seeds and heavier, although non-significantly, whole fruits (Ramirez & Traveset 2010). Results of few smaller studies are mixed. Some bruchid predispersal seed predators were shown to preferentially oviposit on larger seeds (Moegenburg 1996), while a negative relationship between seed mass and predispersal predation was found for five species of Piper by Greig (1993). Likewise Janzen (1969) showed that smaller seeds were attacked more by bruchids than larger seeds.

Fruits attacked by Diptera were significantly larger than fruits attacked by Coleoptera and Lepidoptera. The host range of most Diptera species (except Tephritidae which were not identified to species and Drosophilidae which were not sampled) was extremely wide across plant lineages (Table 1, Appendix 1).We suggest that this preference may be due to the extreme polyphagy of many Diptera species, where numerous large fruit species, typically avoided by beetles, were included in the diet of Diptera (Ctvrtecka *et al*. 2014). Similar polyphagy, where larvae are predominantly pulp feeders and develop in almost ripe and ripe fruits when seeds are mature, has been reported for particular tephritid species (Webber & Woodrow 2004,Wilson *et al*. 2012). This feeding mode may have no direct impact on seed survival, but may affect fruit dispersers, positively or negatively (Clarke *et al*. 2005, Wilson *et al*. 2012).

The most attacked plant species with density of >1 insect per fruit include three species from the family Fabacee (*Maniltoa schefferi, Kingiodendron alternifolium,* and *K. novoguineense*) with big seeds and thin non-fleshy mesocarp. They were attacked by 4-5 internal seed eating weevil species with one dominant species on each plant species. The fourth most attacked plant species, *Leucaena leucocephala*, was also from family Fabaceae. This species, with ca 15-20 seeds in long pods,was attacked by external seed eating anthribids. A further two species, *Pouteria maclayana,* with big sized fruits and massive fleshy mesocarp, and *Pandanus kaernbachii*, with fibrous fleshy mesocarp and small seeds, were attacked by flies from three different families, but particularly stratiomyids. In summary, fruit morphology may have idiosyncratic effect on the composition of particular frugivorous communities, but there are no general rules as how to become particularly attractive for frugivorous predators – as illustrated by the top 10 plant species with a variety of fruit and seed morphology, each attacked by different insect taxa. However, our results suggest that there may be plant species that are universally unpalatable, and others exceptionally suitable, for all three insect orders.

The combined assessment of attack on fruits and seeds by all three principal insect orders confirmed the conclusion based on the study of individual orders, that the infestation rates of fruits are generally too low for frugivores to act as important density-dependent mortality factors in New Guinea lowland rainforest, as proposed by the Janzen-Connell hypothesis (Janzen 1970, Connell 1971).

**Table 1.** Host range and abundance of reared Diptera species excluding Tephritidae and Drosophilidae (Nd=no. of reared specimens, Np=no. of attacked plant species, Nf=number of attacked plant families)

| Family | Species | Nd | Np | Nf |
|---|---|---|---|---|
| Chloropidae | | | | |
| | Aphanotrigonum sp.1 | 52 | 13 | 13 |
| | Arcuator sp.n.1 | 380 | 33 | 21 |
| | Cadrema sp.n.2 | 929 | 51 | 29 |
| | Cadrema sp.n.3 | 15 | 2 | 2 |
| | Cadrema sp.n.4 | 11 | 1 | 1 |
| | Conioscinella sp.2 | 10 | 4 | 3 |
| | Rhodesiella sp.1 | 10 | 2 | 2 |
| Micropezidae | | | | |
| | Rhoptrum annulipes | 529 | 40 | 26 |
| Stratiomyidae | | | | |
| | Camtopteromyia fractipennis | 59 | 4 | 4 |
| | Evaza inflata | 76 | 4 | 4 |
| | Gabaza argentea | 10 | 3 | 3 |
| | Glochinomyia nigriseta | 244 | 24 | 17 |
| | Graptomyza flavicolis | 40 | 7 | 7 |
| | Graptomyza punctata | 206 | 17 | 13 |
| | Hermetia illucens | 324 | 14 | 11 |
| | Lophosceles fascipennis | 22 | 3 | 3 |
| | Ptecticus danielsi | 16 | 4 | 2 |
| | Ptecticus ferrugineus | 12 | 4 | 4 |
| | Ptecticus longipes | 15 | 5 | 5 |
| | Ptecticus rogans | 386 | 43 | 27 |
| | Saldubella hardyi | 16 | 4 | 4 |
| | Saldubella margaritifera | 18 | 6 | 6 |

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**Appendix 1**: Abundance (N, number of individuals) of frugivorous Coleoptera (COL), Lepidoptera (LEP) and Diptera (DIP) on particular plant species, organized by plant families. Names of plant species follow www.ipni.org .

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| Anacardiaceae | | | | |
| | Campnosperma brevipetiolata Volkens | 0 | 0 | 0 |
| | Dracontomelon dao (Blanco) Merr. & Rolfe | 0 | 1 | 51 |
| | Dracontomelon mangiferum Blume | 0 | 0 | 0 |
| | Euroschinus papuanus Merr. & L.M.Perry | 0 | 0 | 0 |
| | Mangifera minor Blume | 0 | 0 | 0 |
| | Rhus taitensis Guill. | 0 | 0 | 0 |
| | Semecarpus australiensis Engl. | 10 | 0 | 4 |
| | Semecarpus cassuviumRoxb. | 2 | 6 | 0 |
| | Semecarpus forstenii Blume | 0 | 0 | 0 |
| | Semecarpus magnifica K. Schum. | 9 | 0 | 0 |
| | Semecarpus schlechteri Lauterb | 10 | 0 | 0 |
| | Spondias dulcis G.Forst. | 2 | 4 | 92 |
| Annonaceae | | | | |
| | Cananga odorata (Lam.) Hook.f. & Thomson | 0 | 0 | 0 |
| | Cyathocalyx polycarpa C.T.White&W.D.Francis | 25 | 0 | 12 |
| | Goniothalamus aruensis Scheff. | 8 | 2 | 1 |
| | Goniothalamus grandiflorus Boerl. | 3 | 1 | 17 |
| | Haplostichanthus longirostris (Scheff.) Heusden | 0 | 0 | 0 |
| | Polyalthia glauca Boerl. | 20 | 2 | 7 |
| | Popowia pisocarpa Endl. | 5 | 0 | 0 |
| | Pseuduvaria mollis (Warb.) J.Sinclair | 5 | 1 | 21 |
| | Uvaria rosenbergiana Scheff. | 0 | 1 | 0 |
| Apocynaceae | | | | |
| | Alyxia rostrata (Markgr.) Markgr. | 0 | 0 | 25 |
| | Cerbera floribunda K.Schum. | 1 | 0 | 166 |
| | Lepiniopsis ternatensis Valeton | 0 | 0 | 70 |
| | Neisosperma citrodora (Lauterb. & K.Schum.) Fosberg & Sachet | 0 | 0 | 0 |
| | Tabernaemontana aurantiaca Gaudich. | 1 | 1 | 0 |
| | Tabernaemontana orientalis R.Br. | 0 | 1 | 9 |
| | Voacanga grandifolia Rolfe | 0 | 1 | 10 |
| Araceae | | | | |
| | Amorphophallus campanulatus Decne. | 0 | 2 | 0 |
| | Epipremnum pinnatum Engl. | 0 | 5 | 218 |
| | Pothos rumphii Schott | 0 | 17 | 43 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| Araliaceae | | | | |
| | Osmoxylon novoguineense Becc. | 0 | 10 | 5 |
| | Polyscias verticillata B.C.Stone | 0 | 1 | 0 |
| Arecaceae | | | | |
| | Actinorhytis calapparia H.Wendl. & Drude | 0 | 0 | 3 |
| | Areca catechu L. | 0 | 0 | 0 |
| | Arenga microcarpa Becc. | 0 | 19 | 0 |
| | Brassiophoenix schumannii (Becc.) Essig | 1 | 0 | 0 |
| | Calamus longipinna K.Schum. & Lauterb. | 0 | 9 | 0 |
| | Calyptrocalyx albertisianus Becc. | 0 | 0 | 0 |
| | Caryota rumphiana Mart. | 0 | 2 | 17 |
| | Hydriastele macrospadix (Burret) W.J.Baker & Loo | 0 | 1 | 0 |
| | Hydriastele microspadix (Becc.) Burret | 0 | 4 | 0 |
| | Licuala beccariana Furtado | 0 | 1 | 0 |
| | Orania lauterbachiana Becc. | 0 | 0 | 1 |
| | Ptychococcus paradoxus (Scheff.) Becc. | 10 | 0 | 0 |
| | Ptychosperma pullenii Essig | 0 | 0 | 0 |
| Aristolochiaceae | | | | |
| | Aristolochia schlechteri Lauterb. | 0 | 0 | 0 |
| Asparagaceae | | | | |
| | Cordyline terminalis Kunth | 0 | 8 | 0 |
| | Dracaena angustifolia Roxb. | 2 | 3 | 203 |
| Burseraceae | | | | |
| | Canarium acutifolium Merr. | 10 | 7 | 7 |
| | Canarium indicum L. | 8 | 2 | 203 |
| | Canarium oleosum (Lam.) Engl. | 0 | 0 | 0 |
| | Canarium vitiense A.Gray | 5 | 5 | 0 |
| Cannabaceae | | | | |
| | Celtis philippensis Blanco | 0 | 0 | 29 |
| Celastraceae | | | | |
| | Siphonodon celastrineus Griff. | 7 | 11 | 53 |
| Clusiaceae | | | | |
| | Calophyllum soulattri "Burm." ex F.Mull. | 0 | 0 | 0 |
| | Garcinia assugu Lauterb. | 11 | 10 | 32 |
| | Garcinia hollrungii Lauterb. | 1 | 0 | 36 |
| | Garcinia hunsteinii Lauterb. | 0 | 0 | 0 |
| | Garcinia latissima Miq. | 0 | 0 | 3 |
| | Garcinia ledermannii Lauterb. | 0 | 0 | 25 |
| | Tripetalum cymosum K.Schum. | 0 | 0 | 0 |
| Combretaceae | | | | |
| | Terminalia catappa L. | 0 | 0 | 19 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| | Terminalia complanata K.Schum. | 62 | 2 | 11 |
| | Terminalia copelandii Elmer | 0 | 0 | 0 |
| | Terminalia eddowesii Coode | 10 | 0 | 10 |
| | Terminalia impediens Coode | 0 | 0 | 6 |
| | Terminalia kaernbachii Warb. | 0 | 0 | 88 |
| | Terminalia macrocarpa Steud. | 38 | 0 | 0 |
| | Terminalia microcarpa F.Muell. | 0 | 0 | 3 |
| | Terminalia sepicana Diels | 62 | 0 | 19 |
| Cycadaceae | | | | |
| | Cycas circinalis L. | 0 | 0 | 0 |
| | Cycas scratchleyana F.Muell. | 0 | 0 | 0 |
| | Cycas schumanniana Lauterb. | 0 | 1 | 7 |
| Dilleniaceae | | | | |
| | Dillenia castaneifolia Martelli | 0 | 0 | 0 |
| Dipterocarpaceae | | | | |
| | Vatica papuana Dyer | 2 | 28 | 64 |
| Ebenaceae | | | | |
| | Diospyros discolor Willd. | 0 | 0 | 2 |
| | Diospyros hebecarpa Benth. | 0 | 0 | 0 |
| | Diospyros papuana Valeton | 0 | 0 | 5 |
| Elaeocarpaceae | | | | |
| | Aceratium ledermannii Schltr. | 24 | 2 | 0 |
| | Aceratium oppositifolium DC. | 16 | 1 | 5 |
| | Elaeocarpus amplifolius Schltr. | 8 | 2 | 0 |
| | Elaeocarpus kaniensis Schltr. | 0 | 0 | 4 |
| | Elaeocarpus sphaericus K.Schum. | 0 | 0 | 0 |
| | Elaeocarpus tariensis Weibel | 0 | 0 | 0 |
| | Antidesma contractum J.J.Sm. | 0 | 1 | 0 |
| | Antidesma olivaceum K.Schum. | 0 | 0 | 10 |
| | Cleistanthus myrianthus Kurz | 0 | 9 | 0 |
| | Endospermum labios Schodde | 0 | 1 | 41 |
| | Macaranga albescens L.M.Perry | 0 | 0 | 0 |
| | Macaranga aleuritoides F.Muell. | 13 | 4 | 0 |
| | Macaranga bifoveata J.J.Sm. | 0 | 6 | 8 |
| | Macaranga punctata K.Schum. | 0 | 0 | 0 |
| | Mallotus floribundus Müll.Arg. | 0 | 0 | 0 |
| | Melanolepis multiglandulosa Rchb. & Zoll. | 0 | 14 | 3 |
| | Omphalea papuana Pax & K.Hoffm. | 0 | 0 | 17 |
| | Phyllanthus clamboides (F.Muell.) Diels | 0 | 1 | 0 |
| | Pimelodendron amboinicum Hassk. | 0 | 14 | 44 |
| | Ryparosa javanica Koord. & Valeton | 0 | 5 | 32 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| Fabaceae | | | | |
| | Archidendron aruense (Warb.) de Wit | 0 | 126 | 4 |
| | Archidendron glabrum (K.Schum.) Lauterb. & K.Schum. | 1 | 43 | 41 |
| | Archidendron lucyi F.Muell. | 0 | 25 | 7 |
| | Entada phaseoloides Merr. | 146 | 0 | 2 |
| | Gigasiphon schlechteri (Harms) de Wit | 0 | 2 | 0 |
| | Inocarpus fagifer(Parkinson) Fosberg | 223 | 26 | 80 |
| | Intsia bijuga Kuntze | 392 | 13 | 0 |
| | Kingiodendron alternifolium Merr.& Rolfe | 3051 | 15 | 0 |
| | Kingiodendron novoguineense Verdc. | 708 | 18 | 2 |
| | Leucaena leucocephala (Lam.) de Wit | 252 | 0 | 0 |
| | Maniltoa lenticellata C.T.White | 75 | 3 | 1 |
| | Maniltoa megalocephala Harms | 183 | 15 | 0 |
| | Maniltoa psilogyne Harms | 2468 | 32 | 1 |
| | Maniltoa schefferi K.Schum. | 567 | 5 | 0 |
| | Millettia pinnata (L.) Panigrahi | 3 | 12 | 100 |
| | Mucuna bennettii F.Muell. | 170 | 0 | 0 |
| | Mucuna nova-guineensis Scheff. | 1029 | 0 | 0 |
| | Strongylodon siderospermum Cordem. | 0 | 0 | 0 |
| Gnetaceae | | | | |
| | Gnetum costatum K.Schum. | 0 | 0 | 6 |
| | Gnetum gnemon L. | 1 | 0 | 34 |
| | Gnetum gnemonoides Brongn. | 1 | 20 | 183 |
| | Gnetum latifolium Blume | 0 | 0 | 11 |
| Hypoxidaceae | | | | |
| | Curculigo recurvata W.T.Aiton | 0 | 0 | 0 |
| Icacinaceae | | | | |
| | Gomphandra papuana (Becc.) Sleumer | 0 | 1 | 15 |
| | Gonocaryum litorale (Blume) Sleumer | 469 | 23 | 10 |
| | Medusanthera laxiflora (Miers) R.A.Howard | 0 | 2 | 4 |
| | Merrilliodendron megacarpum (Hemsl.) Sleumer | 0 | 5 | 66 |
| | Polyporandra scandens Becc. | 0 | 1 | 5 |
| Lamiaceae | | | | |
| | Callicarpa pentandra Roxb. | 0 | 1 | 0 |
| | Clerodendrum lindawianum Lauterb. | 0 | 0 | 0 |
| | Clerodendrum tracyanum F.Muell. ex Benth. | 0 | 5 | 93 |
| | Faradaya splendida F.Muell. | 0 | 10 | 700 |
| | Gmelina moluccana Backer ex K.Heyne | 0 | 2 | 26 |
| | Premna obtusifolia R.Br. | 0 | 30 | 0 |
| | Teijsmanniodendron bogoriense Koord. | 0 | 0 | 0 |
| | Vitex cofassus Reinw. ex Blume | 0 | 4 | 0 |
| | Vitex quinata F.N.Williams | 0 | 8 | 0 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| Lauraceae | | | | |
| | Cryptocarya ainikinii Kosterm. | 3 | 0 | 0 |
| | Cryptocarya caudata Meisn. | 3 | 1 | 0 |
| | Cryptocarya densiflora Blume | 105 | 3 | 2 |
| | Cryptocarya depressa Warb. | 4 | 2 | 0 |
| | Cryptocarya laevigata Blume | 0 | 1 | 0 |
| | Cryptocarya massoy (Oken) Kosterm. | 18 | 2 | 2 |
| | Cryptocarya weinlandii K.Schum. | 3 | 0 | 0 |
| | Litsea collina S.Moore | 5 | 11 | 1 |
| | Litsea globosa Kosterm. | 5 | 5 | 1 |
| | Litsea timoriana Span. | 2 | 6 | 0 |
| Lecythidaceae | | | | |
| | Barringtonia apiculata Lauterb. | 0 | 2 | 20 |
| | Barringtonia calyptrocalyx K.Schum. | 0 | 3 | 198 |
| | Planchonia papuana R.Knuth | 0 | 16 | 185 |
| Loganiaceae | | | | |
| | Neuburgia corynocarpa (A.Gray) Leenh. | 0 | 1 | 240 |
| | Strychnos minor Benth. | 1 | 118 | 22 |
| Malvaceae | | | | |
| | Microcos argentata Burret | 5 | 3 | 24 |
| | Microcos grandiflora Burret | 0 | 9 | 21 |
| | Microcos tetrasperma Merr. & L.M.Perry | 0 | 0 | 0 |
| | Pterygota horsfieldii (R.Br.) Kosterm. | 0 | 66 | 0 |
| | Sterculia ampla Baker f. | 0 | 5 | 4 |
| | Sterculia shillinglawii F.Muell. | 0 | 9 | 3 |
| | Sterculia schumanniana (Lauterb.) Mildbr. | 0 | 26 | 23 |
| Marantaceae | | | | |
| | Donax canniformis K.Schum. | 0 | 16 | 0 |
| | Phrynium macrocephalum K.Schum. | 0 | 18 | 5 |
| | Phrynium pedunculatum Warb. ex K.Schum. | 0 | 3 | 0 |
| Meliaceae | | | | |
| | Aglaia argentea Blume | 5 | 1 | 40 |
| | Aglaia brassii Merr. & L.M.Perry | 0 | 0 | 0 |
| | Aglaia cucullata (Roxb.) Pellegr. | 0 | 0 | 29 |
| | Aglaia goebeliana Warb. | 0 | 0 | 0 |
| | Aglaia lepiorrhachis Harms | 0 | 0 | 0 |
| | Aglaia rimosa Merr. | 0 | 0 | 0 |
| | Aglaia sapindina Harms | 0 | 0 | 0 |
| | Aglaia subcuprea Merr. & L.M.Perry | 0 | 0 | 60 |
| | Aglaia tomentosa Teijsm. & Binn. | 16 | 0 | 0 |
| | Aphanamixis macrocalyx Harms | 0 | 0 | 0 |
| | Aphanamixis polystachya (Wall.) R.Parker | 2 | 9 | 45 |
| | Dysoxylum alatum Harms | 0 | 1 | 13 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| | Dysoxylum alliaceum Seem. | 0 | 0 | 0 |
| | Dysoxylum arborescens (Blume) Miq. | 1 | 16 | 62 |
| | Dysoxylum confertiflorum Merr. &L.M.Perry | 12 | 16 | 35 |
| | Dysoxylum excelsum Blume | 0 | 3 | 0 |
| | Dysoxylum gaudichaudianum Miq. | 0 | 0 | 1 |
| | Dysoxylum micranthum Merr. & L.M.Perry | 3 | 0 | 8 |
| | Dysoxylum microstachyum Harms | 0 | 18 | 3 |
| | Dysoxylum parasiticum (Osbeck) Kosterm. | 0 | 0 | 1 |
| | Dysoxylum pettigrewianum F.M.Bailey | 0 | 16 | 2 |
| | Chisocheton ceramicus Miq. | 0 | 0 | 27 |
| | Chisocheton cumingianus Harms | 0 | 0 | 10 |
| | Chisocheton lasiocarpus (Miq.) Valeton | 5 | 0 | 0 |
| | Chisocheton longistipitatus (F.M.Bailey) L.S.Sm. | 0 | 0 | 0 |
| | Chisocheton trichocladus Harms | 0 | 8 | 12 |
| | Chisocheton weinlandii Harms | 0 | 0 | 0 |
| | Sandoricum koetjape Merr. | 19 | 1 | 4 |
| Menispermaceae | | | | |
| | Arcangelisia flava Merr. | 0 | 0 | 30 |
| | Arcangelisia tympanopoda Diels | 14 | 0 | 57 |
| | Chlaenandra ovata Miq. | 0 | 0 | 99 |
| | Macrococculus pomiferus Becc. | 10 | 0 | 248 |
| | Pycnarrhena novoguineensis Miq. | 1 | 5 | 32 |
| | Tinospora dissitiflora Diels | 1 | 0 | 52 |
| | Tinospora peekelii Diels | 0 | 0 | 6 |
| Monimiaceae | | | | |
| | Steganthera hirsuta Perkins | 0 | 3 | 0 |
| | Steganthera salomonensis (Hemsl.) Philipson | 0 | 0 | 0 |
| Moraceae | | | | |
| | Artocarpus communis J.R.Forst. & G.Forst. | 14 | 0 | 12 |
| | Artocarpus vriesianus Miq. | 0 | 0 | 0 |
| | Ficus arfakensis King | 0 | 0 | 3 |
| | Ficus austrina Corner | 0 | 1 | 0 |
| | Ficus bernaysii King | 0 | 0 | 0 |
| | Ficus botryocarpa Miq. | 0 | 0 | 0 |
| | Ficus congesta Roxb. | 0 | 13 | 0 |
| | Ficus copiosa Steud. | 0 | 0 | 13 |
| | Ficus edelfeltii King | 0 | 0 | 0 |
| | Ficus erythrosperma Miq. | 0 | 0 | 0 |
| | Ficus hispidioides L.f. | 0 | 4 | 12 |
| | Ficus hombroniana Corner | 0 | 0 | 0 |
| | Ficus morobensis C.C.Berg | 0 | 0 | 0 |
| | Ficus nodosa Teijsm. & Binn. | 0 | 0 | 0 |
| | Ficus odoardi King | 0 | 0 | 9 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| | Ficus pachyrrhachis K.Schum. & Lauterb. | 1 | 12 | 6 |
| | Ficus polyantha Warb. | 1 | 0 | 0 |
| | Ficus primaria Corner | 0 | 0 | 0 |
| | Ficus robusta Corner | 0 | 0 | 0 |
| | Ficus semivestita Corner | 0 | 0 | 1 |
| | Ficus septica Hook. ex Miq. | 0 | 0 | 1 |
| | Ficus subcuneata Miq. | 0 | 0 | |
| | Ficus variegata Blume | 0 | 0 | |
| | Ficus wassa Roxb. | 1 | 0 | 2 |
| | Prainea papuana Becc. | 0 | 0 | 17 |
| Musaceae | | | | |
| | Musa peekelii Lauterb. | 0 | 0 | 32 |
| Myristicaceae | | | | |
| | Endocomia macrocoma (Miq.) W.J.de Wilde | 0 | 0 | 2 |
| | Gymnacranthera paniculata Warb. | 0 | 1 | 5 |
| | Heliconia papuana W.J.Kress | 0 | 25 | 30 |
| | Horsfieldia basifissa W.J.de Wilde | 0 | 3 | 0 |
| | Horsfieldia hellwigii Warb. | 189 | 0 | 8 |
| | Horsfieldia irya (Gaertn.) Warb. | 78 | 1 | 0 |
| | Horsfieldia subtilis Warb. | 0 | 1 | 1 |
| | Horsfieldia sylvestris Warb. | 267 | 5 | 24 |
| | Myristica buchneriana Warb. | 8 | 16 | 28 |
| | Myristica crassipes Warb. | 2 | 0 | 3 |
| | Myristica fatua Blume | 0 | 1 | 31 |
| | Myristica filipes W.J.de Wilde | 0 | 0 | 0 |
| | Myristica globosa Warb. | 0 | 0 | 7 |
| | Myristica hollrungii Warb. | 2 | 3 | 37 |
| | Myristica schleinitzii Engl. | 0 | 3 | 0 |
| | Myristica uncinata J.Sinclair | 0 | 0 | 0 |
| Myrsinaceae | | | | |
| | Conandrium polyanthum Mez | 0 | 1 | 0 |
| Myrtaceae | | | | |
| | Eugenia javanica Lam. | 97 | 0 | 48 |
| | Eupomatia laurina Hook. | 0 | 0 | 0 |
| | Syzygium amplum T.G.Hartley & L.M.Perry | 82 | 8 | 47 |
| | Syzygium aqueum Alston | 12 | 0 | 8 |
| | Syzygium gonatanthum (Diels) Merr. & L.M.Perry | 30 | 56 | 172 |
| | Syzygium hylochare (Diels) Merr. & L.M.Perry | 88 | 0 | 16 |
| | Syzygium hylophilum (Lauterb. & K.Schum.) Merr. & L.M.Perry | 10 | 0 | 0 |
| | Syzygium javanicum Miq. | 66 | 0 | 5 |
| | Syzygium longipes (Warb.) Merr. & L.M.Perry | 99 | 6 | 2 |
| | Syzygium malaccense (L.) Merr. & L.M.Perry | 159 | 5 | 40 |
| | Syzygium nemorale Merr. & L.M.Perry | 10 | 0 | 1 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| | Syzygium pteropodum (Lauterb. & K.Schum.) Merr. & L.M.Perry | 2 | 0 | 0 |
| | Syzygium trachyanthum (Diels) Merr. & L.M.Perry | 0 | 0 | 2 |
| | Syzygium trivene (Ridl.) Merr. & L.M.Perry | 65 | 1 | 13 |
| | Syzygium variabile T.G.Hartley & L.M.Perry | 0 | 0 | 2 |
| Oleaceae | | | | |
| | Chionanthus brassii (Kobuski) Kiew | 1 | 1 | 15 |
| | Chionanthus ramiflora Roxb. | 0 | 0 | 3 |
| | Chionanthus sessiliflorus (Hemsl.) Kiew | 4 | 1 | 43 |
| | Jasminum bifarium Wall. | 0 | 0 | 9 |
| Opiliaceae | | | | |
| | Gjellerupia papuana Lauterb. | 1 | 11 | 6 |
| | Opilia amentacea Wall. | 0 | 0 | 0 |
| Pandaceae | | | | |
| | Galearia celebica Koord. | 4 | 31 | 92 |
| Pandanaceae | | | | |
| | Pandanus kaernbachii Warb. | 0 | 0 | 88 |
| Passifloraceae | | | | |
| | Adenia heterophylla (Blume) Koord. | 0 | 0 | 0 |
| Pentaphylacaceae | | | | |
| | Ternstroemia cherryi (F.M.Bailey) Merr. ex J.F.Bailey & C.T.White | 0 | 3 | 17 |
| Phyllanthaceae | | | | |
| | Aporosa papuana Pax & K.Hoffm. | 1 | 2 | 0 |
| | Bridelia macrocarpa Airy Shaw | 32 | 8 | 4 |
| | Bridelia penangiana Hook.f. | 9 | 1 | 4 |
| Pittosporaceae | | | | |
| | Pittosporum sinuatum Blume | 1 | 0 | 3 |
| Polygalaceae | | | | |
| | Xanthophyllum papuanum Whitmore ex Meijden | 0 | 17 | 133 |
| Proteaceae | | | | |
| | Helicia latifolia C.T.White | 187 | 12 | 27 |
| Putranjivaceae | | | | |
| | Drypetes lasiogynoides Pax & K.Hoffm. | 1 | 1 | 10 |
| | Drypetes longifolia Pax & K.Hoffm. | 0 | 1 | 8 |
| Rhamnaceae | | | | |
| | Ziziphus angustifolia (Miq.) Hatus. ex Steenis | 0 | 1 | 0 |
| Rubiaceae | | | | |
| | Canthium barbatum Seem. | 0 | 0 | 0 |
| | Canthium cymigerum (Valeton) B.L.Burtt | 0 | 9 | 0 |
| | Canthium longiflorum (Valeton) Merr. & L.M.Perry | 0 | 1 | 0 |
| | Gardenia hansemannii K.Schum. | 0 | 1 | 0 |
| | Gardenia papuana F.M.Bailey | 1 | 7 | 2 |
| | Mastixiodendron pachyclados Melch. | 45 | 0 | 2 |
| | Morinda bracteata Roxb. | 0 | 0 | 0 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| | Mussaenda cylindrocarpa F.Aresch. | 0 | 0 | 2 |
| | Nauclea coadunata Sm. | 0 | 0 | 0 |
| | Pavetta platyclada K.Schum. & Lauterb. | 0 | 13 | 11 |
| | Psychotria leptothyrsa Miq. | 0 | 1 | 9 |
| | Randia decora Valeton | 0 | 2 | 10 |
| | Randia schumanniana Merr. & L.M.Perry | 0 | 0 | 9 |
| | Sarcocephalus coadunatus (Sm.) Druce | 0 | 0 | 9 |
| | Timonius densiflorus Valeton | 0 | 0 | 4 |
| | Timonius rufescens (Miq.) Boerl. | 0 | 0 | 0 |
| | Versteegia cauliflora Valeton | 0 | 54 | 5 |
| Rutaceae | | | | |
| | Micromelum minutum (G.Forst.) Wight & Arn. | 0 | 0 | 0 |
| Salicaceae | | | | |
| | Casearia clutiaefolia Blume | 70 | 3 | 0 |
| | Erythrospermum candidum Becc. | 10 | 2 | 8 |
| | Pangium edule Reinw. | 0 | 1 | 15 |
| | Trichadenia philippinensis Merr. | 1 | 1 | 33 |
| Sapindaceae | | | | |
| | Alectryon ferrugineum Radlk. | 0 | 2 | 0 |
| | Cupaniopsis acuticarpa Adema | 180 | 1 | 3 |
| | Cupaniopsis macropetala Radlk. | 1 | 16 | 1 |
| | Cupaniopsis stenopetala Radlk. | 0 | 6 | 0 |
| | Harpullia crustacea Radlk. | 0 | 4 | 6 |
| | Harpullia longipetala Leenh. | 0 | 10 | 0 |
| | Lepidopetalum micans K.Schum. & Lauterb. | 0 | 15 | 8 |
| | Pometia pinnata J.R.Forst. & G.Forst. | 0 | 7 | 158 |
| | Tristiropsis acutangula Radlk. | 29 | 49 | 929 |
| | Tristiropsis subangula K.Schum. | 0 | 0 | 12 |
| Sapotaceae | | | | |
| | Chrysophyllum roxburghii G.Don | 41 | 5 | 72 |
| | Palaquium morobense P.Royen | 0 | 0 | 0 |
| | Pouteria firma (Miq.) Baehni | 0 | 1 | 0 |
| | Pouteria maclayana (Pierre) Baehni | 0 | 2 | 173 |
| | Pouteria obovoidea (H.J.Lam) Baehni | 0 | 1 | 1 |
| | Pouteria thyrsoidea (C.T.White) T.D.Penn. | 2 | 1 | 0 |
| Solanaceae | | | | |
| | Solanum oliverianum K.Schum. & Lauterb. | 0 | 13 | 9 |
| | Solanum torvum Sw. | 0 | 0 | 10 |
| Thymelaeaceae | | | | |
| | Phaleria coccinea F.Muell. | 0 | 0 | 6 |
| | Phaleria macrocarpa Boerl. | 3 | 9 | 560 |
| | Phaleria perrottetiana Fern.-Vill. | 28 | 0 | 14 |

| Plant family | Plant species | COL (N) | LEP (N) | DIP (N) |
|---|---|---|---|---|
| Vitaceae | | | | |
| | Cayratia geniculata Gagnep. | 0 | 0 | 0 |
| | Cayratia schumanniana (Gilg) Suess. | 0 | 0 | 0 |
| | Cissus trifolia K.Schum. | 0 | 0 | 0 |
| | Leea indica Merr. | 0 | 0 | 0 |
| | Tetrastigma maluense Lauterb. | 0 | 0 | 0 |
| Zingiberaceae | | | | |
| | Alpinia peekelii Valeton | 3 | 2 | 4 |
| | Amomum aculeatum Roxb. | 4 | 0 | 11 |
| | Pleuranthodium racemigerum (F.Muell.) R.M.Sm. | 0 | 47 | 8 |

# CONCLUSIONS

This thesis explored community structure of frugivorous insects in lowland rain forest in Papua New Guinea. Although it has been widely assumed that specialized insect seed predators may be important as density-dependent mortality agents in plant communities, promoting high species diversity in tropical forests, they have been poorly studied on the quantitative, community level. This thesis reports results of research aiming to analyse the impact of frugivores from all major insect orders on plants and to characterize the community of frugivorous insects on a broad range of plant species in terms of their species richness, abundance and host specificity. The results are based on extensive sampling and rearing of insects across all major lineages of angiosperm plants from a lowland rainforest ecosystem, allowing quantitative analysis excluding both insufficiently sampled plant and insect species. The extensive data set made it possible to explore the ecological determinants of frugivorous communities, including plant abundance and fruit morphology.

Host specificity (measured here as a proportion of monophages and genus specialists from the total number of species) was variable among insect orders, decreasing in the sequence: Coleoptera (65%) > Lepidoptera (26%) > Diptera (5%). This comparison is unfortunately biased by uneven taxonomic coverage, since, for technical reasons, we excluded anthribids (Coleoptera) and tephritids (Diptera) from the analysis. While the species diversity and abundance of anthribids were low and therefore probably did not bias the Coleoptera estimates significantly, tephritids, on the other hand, are an important component of Diptera, comprising also some specialists (Novotny *et al.* 2005). However, Diptera would probably retain their position as the least specialized order even with tephritids included.

Weevils represent the only important family with a notable portion of specialized species (Tab 1). Even there, true monophagy was rare, but many species were limited in their host ranges to a single plant genus. We argue that it is important to explore congeneric species for adequate description of host ranges. The differences in the range of potential host plant species reported by various studies may be one of several important factors shaping their host range estimates, with broader host ranges found when congeneric plants were studied (Lyal & Curran 2000, Nakagawa *et al*. 2003, Ctvrtecka *et al*. 2014; but see Janzen 1980).

Species diversity of frugivores decreased in the sequence Lepidoptera (118 spp.) > Coleoptera (57 spp.) > Diptera (38 spp.), although Diptera, with fruitflies included, would probably exceed the diversity of Coleoptera as Novotny *et al.* (2005) reared 38 tephritid species from 168 plant species from our study area. Frugivory guild is rather species poor overall as it represents only a small proportion of the total species pool for each of the three insect orders concerned. For instance, Missa (1999) documented 1168 species of weevils from local forest communities close to our study area. The low number of species per plant species in frugivores is in line with similar patterns found for other relatively specialized guilds, that tend to be also species poor (Novotny *et al.* 2010). Further, we have documented higher host specificity in seed than pulp feeders, as has been reported in other studies.

There are notable regional differences is a taxonomic composition of frugivores on sub-ordinal level. In Coleoptera, our study is dominated by weevils with a minor proportion of anthribids. Similarly, in closed canopy forest of Venezuela, weevils also dominated, but there bruchids were second most abundant. However, the habitats with herbaceous vegetation were dominated by bruchids, followed by weevils (Ramirez & Traveset 2010). Bruchids appear to be the main group of seed predators in the Neotropics (Janzen 1980) and Africa (Kergoat *et al.* 2005), while they were almost absent from our samples. This was somewhat expected since bruchids are rare in the Australian region (Basset 1991, Borowiec 1987), but their absence was notable as we reared just a single bruchid individual. Lepidoptera was dominated by Tortricidae as the most diverse family, in contrast to Kenya, where frugivorous communities were dominated by Blastobasidae. This family was present in our PNG samples, but only as a few specimens in two species.

Insect frugivores attacked 48% of the plant species we sampled. This proportion is similar to other studies (Ramirez & Traveset 2010, Copeland *et al*. 2009). We found out that there were no significant differences among major plant lineages in the proportion of attacked species. In particular, eudicots, magnoliids and monocots suffered similar rates of attack, as was the case for core eudicots, rosids and asterids within eudicots. Further, most of morphological fruit traits such as fruit weight, mesocarp volume, seed volume and fleshiness failed to explain differential fruit predation by insect orders. However, fruits attacked by Diptera were significantly larger than fruits attacked by Coleoptera and Lepidoptera. We suggest that this preference may be due to extreme polyphagy of many Diptera species. These Diptera often included numerous large fruited species in their diet, which were otherwise avoided by beetles or Lepidoptera. Fruit morphology may have a certain effect on the composition of particular frugivorous communities, but there are no general rules for becoming particularly (un)attractive for frugivorous predators.

Fruits of a large majority of plant species exhibited low rates of attack and low densities of frugivorous insects. One kilogram of fruits was attacked by the mean on 7.02 insect individuals, including 3.57 individuals from Coleoptera, 2.56 from Diptera, and 0.87 from Lepidoptera per kilogram of fruits. Further, we reared on average one insect from 10 fruits, including one Coleoptera from 22 fruits, one Diptera from 25 fruits and one Lepidoptera from 100 fruits. These densities include many pulp feeders, especially in Diptera, that develop in almost ripe and ripe fruits with no direct impact on seed survival (Webber & Woodrow 2004, Wilson *et al*. 2012). We can thus conclude that for most tropical tree species in our study system, the density of frugivorous insects is too low to play an important role in promoting high species diversity of vegetation by regulating plant populations via density-dependent mortality of seeds.

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**Table 1:** Community structure of frugivorous insects. Letters in front of family names denote insect order: C = Coleoptera, D = Diptera, L = Lepidoptera. Host specificity = No. of specialists/No of evaluated species.

| Family | Abundance | Species diversity | Host specificity |
|---|---|---|---|
| C-CURCULIONIDAE | 10485 | 57 | 20/31 |
| C-ANTHRIBIDAE | 1830 | | |
| D-CHLOROPIDAE | 1418 | 13 | 1/7 |
| D-MICROPEZIDAE | 530 | 2 | 0/1 |
| D-STRATIOMYIDAE | 1204 | 14 | 0/14 |
| D-SYRPHIDAE | 246 | 2 | 0/2 |
| D-TEPHRITIDAE | 4587 | | |
| L-ARCTIIDAE | 1 | 1 | |
| L-BLASTOBASIDAE | 11 | 2 | 0/1 |
| L-BRACHODIDAE | 4 | 1 | |
| L-COSMOPTERIGIDAE | 101 | 5 | 0/3 |
| L-CRAMBIDAE | 58 | 11 | 1/3 |
| L-GELECHIIDAE | 15 | 3 | 1/1 |
| L-GRACILLARIIDAE | 256 | 5 | 0/5 |
| L-HELIONIDAE | 34 | 1 | 1/1 |
| L-IMMIDAE | 1 | 1 | |
| L-LECITHOCERIDAE | 28 | 5 | 1/1 |
| L-LYCAENIDAE | 38 | 4 | 1/3 |
| L-NOCTUIDAE | 1 | 1 | |
| L-NOLIDAE | 54 | 5 | 3/3 |
| L-OECOPHORIDAE | 31 | 6 | 0/1 |
| L-PTEROPHORIDAE | 1 | 1 | |
| L-PYRALIDAE | 102 | 8 | 2/6 |
| L-TINEIDAE | 334 | 11 | 0/5 |
| L-TORTRICIDAE | 571 | 33 | 1/11 |