



ORIGINAL
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An altitudinal comparison of caterpillar (Lepidoptera) assemblages on *Ficus* trees in Papua New Guinea

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ABSTRACT

Aim This analysis of caterpillar (Lepidoptera) beta-diversity between tropical lowlands and highlands attempts to separate the effects of between-site (1) turnover of herbivore species on particular host plants, (2) changes in host use by herbivores, and (3) turnover of plant species on changes in herbivore assemblages.

Location Two rain forest areas 130 km and 1700 altitudinal metres apart were studied in Papua New Guinea: one in the lowlands (100 m a.s.l.) on the northern coast of the island and one in the central New Guinean cordillera at 1800 m a.s.l.

Methods The analysis is based on caterpillar feeding records obtained by quantitative sampling and rearing of caterpillars from four *Ficus* species studied in the mountains and 21 *Ficus* species and 62 plant species from other genera and families studied in the lowlands, including three *Ficus* species studied in both areas.

Results Only 17% of species feeding on *Ficus* in the highlands also occurred in the lowlands. These species represented 1–46% of individuals in caterpillar assemblages on particular *Ficus* hosts. Widespread species included both *Ficus* specialists and generalists feeding on numerous plant families. Some of the *Ficus* specialists changed their preferred host species with altitude. High species turnover was not explained by changes in the species composition of host plants with altitude as lowland and montane assemblages feeding on the same *Ficus* species showed high turnover. Despite the rarity of widespread caterpillars, the lowland and montane *Ficus* assemblages were remarkably similar in their dominance structure, species richness, host specificity, generic composition and familial composition.

Main conclusions *Ficus*-feeding Lepidoptera assemblages between tropical lowlands and highlands are characterized by substantial species turnover not explained by altitudinal changes in the composition of the vegetation. Further, species-rich plant genera can support caterpillar assemblages with relatively low beta-diversity compared with species-poor genera as caterpillars can switch their host preferences from one congeneric host species to another along an altitudinal gradient. Closely related plant species can thus represent a broad, continuously distributed resource along such gradients.

Keywords

Beta diversity, cryptic species, elevation gradient, *Ficus*, host specificity, Lepidoptera, Malesia, rain forest, species diversity, species turnover.

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INTRODUCTION

Gradients in environmental variation can cause substantial species turnover with altitude and are thus among the most pervasive factors explaining species diversity on larger

geographical scales (Hebert, 1980; McCoy, 1990; Allison *et al.*, 1993; Fernandes & Lara, 1993; Olson, 1994; Brehm & Fiedler, 2003). For instance, global maxima of plant diversity, measured as the number of plant species per 10,000 km², are associated with altitudinal gradients in the tropics (Barthlott *et al.*, 1996).

We can only speculate that a similar pattern applies to insects, as broad patterns of insect diversity and distribution are difficult to study in the tropics. The integration of local studies into regional databases is often impossible as many specimens are classified as unnamed morphospecies, which cannot be cross-referenced geographically (Janzen, 1992; Kitching, 1993). Even with voucher specimens available for comparisons between geographical areas, it is often difficult to differentiate sibling species due to poor taxonomic knowledge and scarcity of collections. In New Guinea, for example, limited data are available for only a few of the better known taxa (Miller, 1996), such as cicadas (de Boer & Duffels, 1996), butterflies (Parsons, 1999), and aquatic Heteroptera (Polhemus & Polhemus, 1998).

Beta-diversity of herbivorous insects is a combination of between-site (1) turnover of herbivore species on particular host plants, (2) changes in host use by herbivores, and (3) turnover of plant species. The relative importance of these factors in the tropics is unknown as virtually all studies along altitudinal gradients analysed only overall patterns of insect beta-diversity on diverse vegetation, which also varied with altitude. The beta-diversity of plants can be separated from that of their insect herbivores by the analysis of herbivorous assemblages on a particular plant species at different altitudes. However, such studies are surprisingly scarce (Allison *et al.*, 1993).

Steep altitudinal gradients in environmental parameters including temperature, rainfall and predation (Givnish, 1999) lead to the expectation of high species turnover in insect herbivores apart from changes in plant composition, but this hypothesis has not been tested. There seems to be no altitudinal change in herbivore species richness per host plant species (cf. Basset, 1996; Novotny *et al.*, 2002a). The data on altitudinal trends in host specificity are not available as most studies have focused on tropical lowlands (Novotny & Basset, in press). Finally, there is no theoretical framework for predicting dominance structure in herbivore communities (Novotny *et al.*, 2002c).

Recent studies suggest that many herbivorous insects feed on multiple closely related plant species in tropical forests (Novotny *et al.*, 2002a,b). This result raises a possibility that the turnover of congeneric plant species with altitude may not necessarily lead to turnover in the assemblages of insect herbivores. The present study explores this possibility as it examines changes in species composition of caterpillars (Lepidoptera) feeding on the large plant genus *Ficus* (Moraceae) between montane (1800 m a.s.l.) and lowland (100 m a.s.l.) sites in Papua New Guinea. This altitudinal range thus encompasses a substantial floristic and structural change that occurs between 800 and 1200 m in tropical forests (Ashton, 2003).

METHODS

Study sites

Caterpillars were sampled in two study areas situated c. 130 km and 1700 altitudinal metres apart in elevation

spanning the northern coastal lowlands and the central New Guinean cordillera, dominated by the Mt Wilhelm massif (4509 m a.s.l.).

The lowland study area was located near Madang town, Madang Province. Fieldwork was concentrated in primary and secondary lowland forests within a 10 × 20 km area, near Baitabag, Ohu and Mis villages (145°41–47' E, 5°08–14' S, c. 0–200 m a.s.l.). The montane study area was situated near Kundiawa town, Chimbu Province. Fieldwork was concentrated in primary and secondary forests and the partially deforested landscape around Mu Village (145°02' E, 6°05' S, 1800 m a.s.l.).

The Madang area has a lowland humid climate with mild drought from July to September, characterized by the rainfall seasonality index (the sum of mean monthly rainfalls for the three consecutive wettest months divided by the sum for the three consecutive driest months) of 2.6. The average annual rainfall is 3558 mm and the annual average temperature is 26.5 °C (McAlpine *et al.*, 1983).

The Kundiawa area has a lower montane humid climate with a mild dry season from June to August (rainfall seasonality index 2.6, average annual rainfall 2249 mm). Long-term records on temperature are not available. The temperature for the study area was therefore extrapolated, using regressions and data for nearby Mt Hagen (1630 m) and Wabag (1980 m) obtained from McAlpine *et al.* (1983). The annual average temperature was thus estimated at 17.5 °C.

Study plants

Ficus (Moraceae) is a large, pantropical genus with over 750 species, representing an important component of tropical floras (Berg, 1989; Basset *et al.*, 1997). New Guinea is a major centre of diversity in the region, with 150 described species (c. 20% of the world species count) from all subgenera and a high degree of endemism (53% of species; Corner, 1967). *Ficus* is an important component of rain forest vegetation, particularly in the lowlands. Our lowland and montane study areas hosted 51 and 19 sympatric *Ficus* species, respectively (Appendix 1).

Twenty-one locally common species of *Ficus*, including 19 forest and two seacoast species, were selected for the study of their caterpillar assemblages in the lowland study area. Four species were studied in the montane study area, including one species restricted to montane forest (*F. iodotricha*) and three widespread species (*Ficus copiosa*, *F. dammaropsis* and *F. wassa*) also studied in the lowlands (Appendix 1). These three species have a wide altitudinal range from 0 to 2300–2600 m. *Ficus wassa* and *F. copiosa* are predominately lowland species as the median (1–3 quartile) altitude of specimens from New Guinea deposited at Lae Herbarium was 100 (25–1186) m for *F. wassa* ($n = 202$ specimens) and 61 (20–489) m for *F. copiosa* ($n = 98$). In contrast, *F. dammaropsis* is of predominately montane distribution, characterized by median altitude 1500 (763–1830) m ($n = 41$) and is absent from some of the lowland areas.

Caterpillars

All externally feeding caterpillars, including leaf rollers and leaf tiers, were collected by hand from the foliage of target trees in both secondary and primary forests. At each sampling occasion, a collector spent 1 day walking throughout the study area and searching the foliage of the target tree species for caterpillars. The sampling included accessible branches from the forest canopy and understorey, which could be climbed or reached from the ground, and included most of the habitat for folivorous herbivores on the study trees. The approximate area of the foliage sampled was estimated visually and recorded.

The following data sets were assembled (see Appendix 1):

1. Twenty-one *Ficus* species including 19 forest and two seacoast species were sampled in the lowland study for 1 year between 1994 and 2000 with sampling effort 1500 m² of foliage per species. Two 1-year samples were obtained for *Ficus wassa*, one from 1994 to 1995 with sampling effort of 1500 m² of foliage and another from 1999 to 2000 with sampling effort 10,500 m² of foliage.
2. Four *Ficus* species sampled in the montane study area from June 2001 to July 2002. Sampling effort varied from 500 m² (*F. wassa* and *F. dammaropsis*) to 700 m² (*F. iodotricha*) and 1300 m² (*F. copiosa*) of foliage per species. The sampling effort was standardized to 500 m² for all species by random removal of individual samples for comparative analyses.
3. Sixty-two forest species from 51 genera and 25 families, each studied for a 1-year period between 1996 and 2002 with sampling effort 1500 m² of foliage per species. These data were presented elsewhere (Novotny *et al.*, 2002a,b,c) and are used for the analysis of host plant range of *Ficus* feeders.

In the laboratory, each caterpillar was provided with fresh leaves of the plant species from which it was collected and reared to an adult whenever possible. Only caterpillars that fed were considered in the analyses. Relying heavily on parataxonomists (Basset *et al.*, 2004), our sampling produced data on 12,389 caterpillars of 161 species feeding on *Ficus* hosts in the lowlands and 2314 caterpillars of 48 species in the montane area (Appendix 2). Further, 33,972 caterpillars feeding on non-*Ficus* hosts in the lowland study area were used to estimate host specificity and species overlap with the montane study area. Insect vouchers are deposited in the Smithsonian Institution (Washington), the National Agricultural Research Institute (Port Moresby) and Bishop Museum (Honolulu). Plant vouchers are deposited at herbaria including A, CANB, BISH, KEW, L, LAE, MIN and US.

Taxonomic and ecological analysis

All feeding caterpillars were assigned to morphospecies, which were verified and refined using the adults reared from them. The morphospecies were verified by specialist taxonomists and identified as far as possible. Taxonomic methods and classification used are detailed in Holloway *et al.* (2001) and Miller *et al.* (2003).

The study focused on the four montane assemblages from *Ficus* hosts and their overlap with lowland assemblages described elsewhere (Basset *et al.*, 1997; Basset & Novotny, 1999; Novotny *et al.*, 2002a,b,c). The presence of montane *Ficus*-feeding species in the lowlands could be analysed with some confidence, as our information on the lowland caterpillar fauna was extensive. However, the montane data, limited to four *Ficus* hosts, were insufficient for analogous estimates of the presence of lowland *Ficus*-feeding species in the montane area.

The lowland–montane comparisons contrasted caterpillar assemblages from the same host species (*F. copiosa*, *F. dammaropsis*, *F. wassa*), as well as compound assemblages from all 21 lowland and four montane species of *Ficus* studied. Some analyses excluded two coastal species of *Ficus* from the lowland sample. Unless stated otherwise, the analyses included samples from 1500 and 500 m² of foliage from each lowland and montane *Ficus* species, respectively. Species richness of caterpillar assemblages between the two areas was compared using the number of species encountered in a random sample of 100 caterpillars from the assemblage, calculated by rarefaction (e.g. Krebs, 1989). Each caterpillar assemblage was also characterized by dominance, i.e. the proportion of individuals in the assemblage from its most common species.

The number of *Ficus* host species recorded for a particular caterpillar species increased steadily with sample size even in large samples (Novotny *et al.*, 2002a). We limited our host specificity analysis to the set of species with an arbitrary minimum abundance of 10 individuals. Similarity relationships between caterpillar assemblages were explored by detrended correspondence (DCA, detrending by segments) and canonical correspondence (CCA) analysis, using square-root transformed abundance data and no down-weighting of rare species options in Canoco software (ter Braak & Smilauer, 2003).

RESULTS

Composition and structure of caterpillar assemblages

The assemblages on *Ficus* hosts both in the lowland and montane areas were dominated by caterpillars from the family Choreutidae, followed by Crambidae and Noctuidae (Fig. 1a). Two other families, Tortricidae and Lymantriidae, were species-rich but quantitatively unimportant (Fig. 1b); they both include mainly generalist species. Nymphalidae was the only relatively important family (represented by 4.5% of all caterpillars feeding on *Ficus* in the lowlands) which was present in only one of the two study areas. The lowland and the montane assemblages also had similar generic composition, as almost all speciose genera from one study area were also recorded in the other area (Table 1). *Cirrhochrista* (Crambidae) is an example of a genus limited to the montane area in our study (Table 2), and illustrates the importance of a strong taxonomic foundation for beta-diversity studies. Initial field observations suggested four

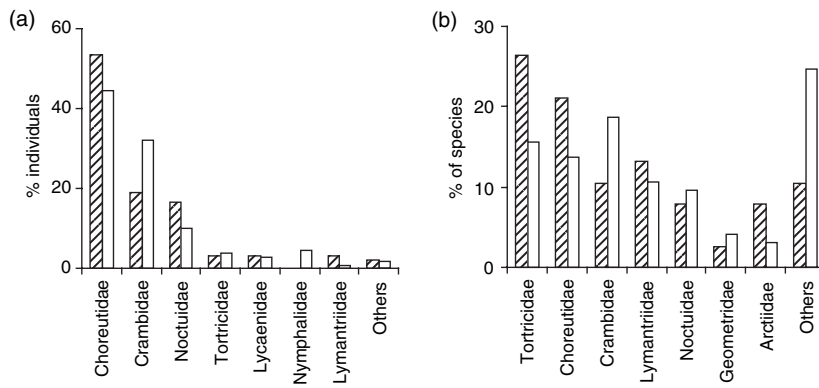


Figure 1 Taxonomic composition of caterpillar assemblages on *Ficus* hosts. The percentages of individuals (a) and species (b) from the most common families are reported for the compound assemblages on four *Ficus* species in the montane study area (hatched bars) and 21 *Ficus* species in the lowland study area (white bars).

Table 1 Species richness of the most important genera (i.e. genera represented by > 1 species) on 21 lowland and four montane species of *Ficus* hosts

Genus	Family	Lowland	Montane	Total
<i>Choreutis</i>	Choreutidae	7	7	14
<i>Adoxophyes</i>	Tortricidae	7	1	7
<i>Brenthia</i>	Choreutidae	6	1	7
<i>Asota</i>	Noctuidae	5	2	5
<i>Talanga</i>	Crambidae	4	2	5
<i>Glyphodes</i>	Crambidae	4	0	4
<i>Homona</i>	Tortricidae	3	1	3
<i>Pycnarmon</i>	Crambidae	3	0	3
<i>Euploea</i>	Nymphalidae	2	0	2
<i>Herpetogramma</i>	Crambidae	2	0	2
<i>Orvasca</i>	Lymantriidae	2	0	2
<i>Saphta</i>	Choreutidae	2	0	2
<i>Somena</i>	Lymantriidae	2	1	2
<i>Cirrhochrista</i>	Crambidae	0	2	2

Table 2 Dominance (D) and number of locally recorded *Ficus* hosts (H_{fc}) for the most abundant species in caterpillar assemblages on *F. copiosa* (COP), *F. dammaropsis* (DAM), and *F. wassa* (WAS) in the montane and the lowland study areas. WAS-1: sample from 1994 to 1995, WAS-2: sample from 1999 to 2000

<i>Ficus</i>	Area	Dominant species	Family	D	H_{fc}
COP	Montane	<i>Talanga exquisitalis</i>	Crambidae	0.32	3
DAM	Montane	<i>Choreutis niphocrypta</i>	Choreutidae	0.52	1
WAS	Montane	<i>Talanga exquisitalis</i>	Crambidae	0.48	3
COP	Lowland	<i>Talanga excelsalis moresbyensis</i>	Crambidae	0.41	14
DAM	Lowland	<i>Choreutis</i> sp. cf. <i>anthorma</i>	Choreutidae	0.33	18
WAS-1	Lowland	<i>Euploea leucosticos</i>	Nymphalidae	0.25	9
WAS-2	Lowland	<i>Talanga excelsalis moresbyensis</i>	Crambidae	0.28	14

species of *Cirrhochrista*, but subsequent analysis of genital morphology confirmed only two species with considerable variability in wing pattern (Fig. 2).

The number of caterpillar species found in a sample of 500 m² of *Ficus* foliage varied from 7 to 26 for *Ficus* in the montane area. Species richness standardized per 100 caterpillars increased with altitude on *F. copiosa* but decreased for *F. wassa* and *F. dammaropsis* (Fig. 3). The local species richness was not completely sampled for any *Ficus* host except probably for *F. wassa*, as indicated by increasing species accumulation curves (not shown).

Host specificity of caterpillar species with respect to these three *Ficus* species did not differ between montane and lowland areas. Caterpillar species tended to have broad host plant ranges as the median and modal number of hosts was three in both study areas (Fig. 4; difference between the areas is not significant, Mann–Whitney test, $P > 0.4$). There were two specialists (defined as species with $\geq 90\%$ of individuals feeding on a single host species) among the 15 caterpillar species analysed in the lowland forest and four specialists among the 15 species analysed in the montane forest.

The dominance structure of montane and lowland assemblages was also similar. The median (1–3 quartile) dominance of the most abundant species in the assemblages from the 21 lowland *Ficus* species was 0.33 (0.23–0.54) while the dominance in the assemblages on the four montane *Ficus* species ranged from 0.32 to 0.52 (Table 2). The montane assemblages on *Ficus wassa* and *F. copiosa* shared the same most abundant species, *Talanga exquisitalis* (Kenrick) (Crambidae), while *F. dammaropsis* was dominated by *Choreutis niphocrypta* Meyrick (Choreutidae) (Table 2). The most abundant species in the lowland caterpillar assemblage on *F. wassa* was *Euploea leucosticos* Gmelin (Nymphalidae) during our first sampling period and *Talanga excelsalis moresbyensis* (Strand) (Crambidae) in the second sampling period. The latter was also the most abundant species on *F. copiosa*, while the dominant species on *F. dammaropsis* was *Choreutis* sp. cf. *anthorma* (Meyrick) (Choreutidae).

Overlap between montane and lowland assemblages

Caterpillar assemblages feeding on *Ficus* hosts cluster according to their altitude. They are also clearly separated from assemblages feeding on non-*Ficus* hosts in the lowlands. The closest pair of montane–lowland assemblages includes *Ficus*

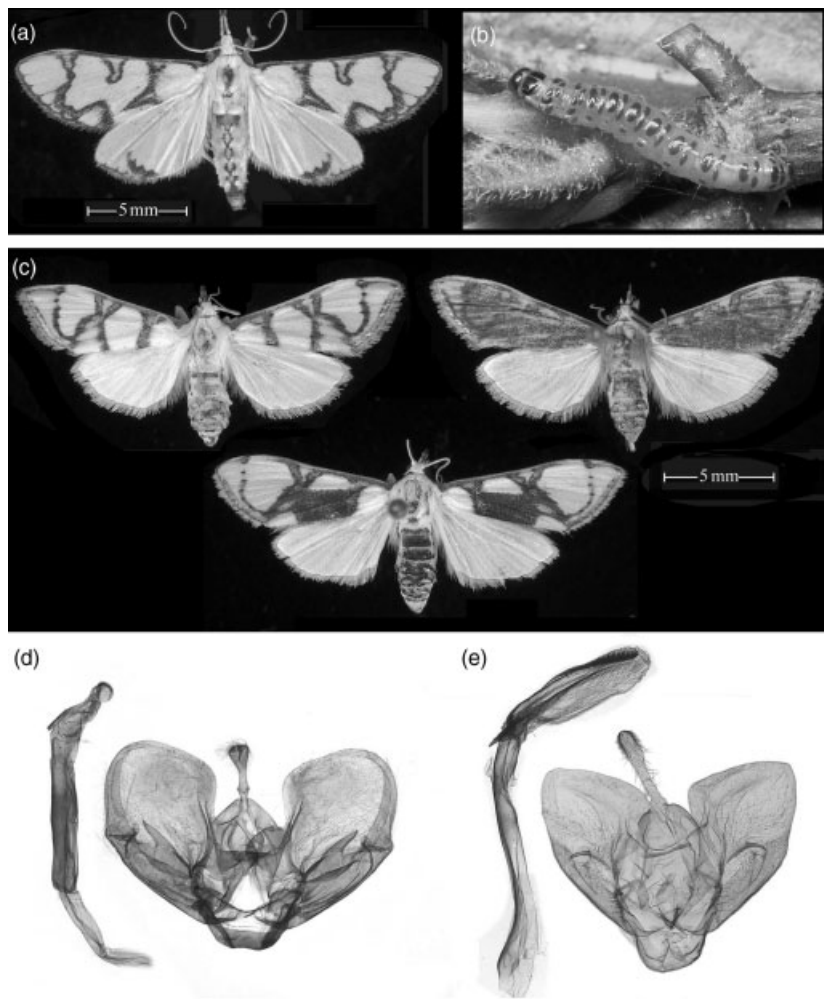
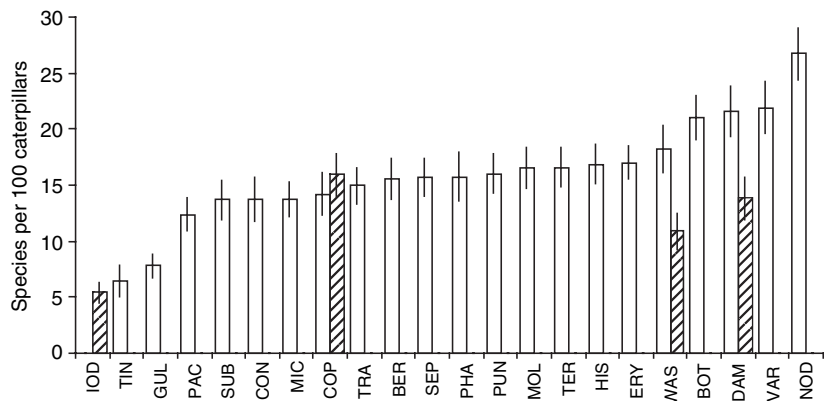


Figure 2 Two species of *Cirrhochrsta* (Lepidoptera: Crambidae) from the montane site, illustrated here for the first time: *C. xanthographis* Hampson, (a) adult female, (b) live larva, and (d) male genitalia. *C. primula* Hampson, (c) adult females exhibiting variations in wing pattern, and (e) male genitalia. Note that male and female wing colour and patterns do not differ.

Figure 3 Species richness in the montane and lowland assemblages of caterpillars on *Ficus* hosts. The mean (SE) number of species in a sample of 100 caterpillars was calculated by rarefaction for *Ficus* species from the montane (hatched bars) and lowland (white bars) study areas. See Appendix 1 for *Ficus* species names.



iodotricha and *F. pachyrrhachis*, rather than any of the pairs sharing the same *Ficus* host in both areas (Fig. 5). The altitude, entered as a categorical variable in the CCA analysis of all *Ficus* hosts, was highly significant ($P < 0.01$, Monte Carlo test), confirming the robustness of the clustering pattern observed in the DCA analysis.

We recorded 48 caterpillar species feeding on the four montane *Ficus* species, including eight species (17%) which

also occurred in the lowlands. The shared species included five species feeding in the lowlands on the shared *Ficus* hosts (*F. copiosa*, *F. dammaropsis* or *F. wassa*) as well as on other *Ficus* species, two species feeding only on other *Ficus* species, and one species found only on non-*Ficus* hosts (Tables 3 and 4). There were an additional 612 caterpillar species feeding exclusively on *Ficus* hosts and

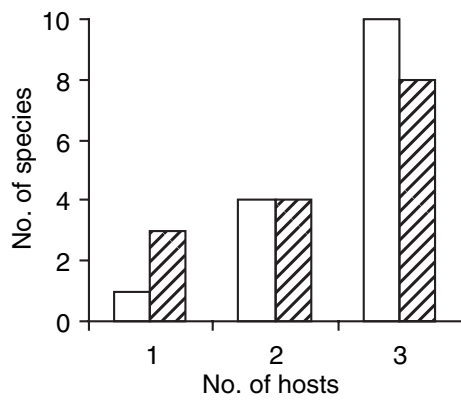


Figure 4 Host specificity in the montane and lowland assemblages of caterpillars on *Ficus* hosts. The number of host species from *Ficus copiosa*, *F. dammaropsis* and *F. wassa* is reported for all species collected as ≥ 10 individuals from the montane (hatched bars) and lowland (white bars) study areas.

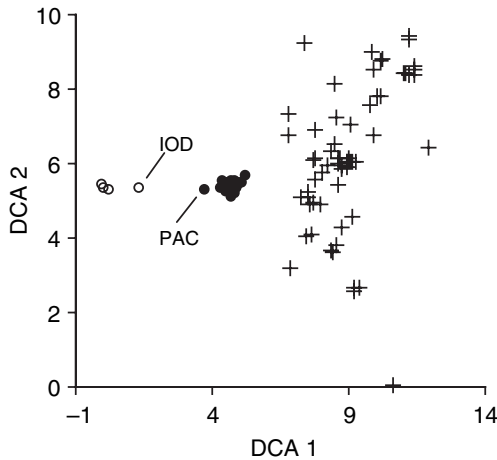


Figure 5 Detrended correspondence analysis (DCA) of caterpillar assemblages from montane *Ficus* (circles), lowland *Ficus* (dots) and lowland non-*Ficus* (crosses) hosts. IOD – *Ficus iodotricha*, PAC – *Ficus pachyrrhachis*.

51 partially, which were not found on *Ficus* in the montane area.

The proportion of shared species between a caterpillar assemblage on an individual *Ficus* species and the entire sample from the 83 plant species available from the lowlands ranged from 5% to 19% for the four *Ficus* species studied in the montane area (Table 5). However, only zero to two shared species were discovered when comparing only montane and lowland assemblages from the same *Ficus* host.

The species found in both the montane and lowland study areas can be classified into the following categories (Tables 3 and 4):

1. *Ficus*-specialists retaining the same preferred host species along the altitudinal gradient (*Talanga excelsalis moresbyensis* (Strand) on *F. copiosa*).
2. *Ficus*-specialists (*Asota plana* Walker and *A. versicolor* F.) that switched from a host limited to the lowlands (*F. pachyrrhachis*) to a montane endemic (*F. iodotricha*).
3. *Ficus*-specialists [*Philiris moira* (Grose-Smith)] that changed their preferred hosts (from *F. pachyrrhachis* in the lowlands to *F. dammaropsis* in the montane area) despite the fact that one host was available in both areas.
4. Generalists found on *Ficus* hosts in both areas and on several plant families in the lowlands, where they attain the highest densities on a non-*Ficus* host (*Adoxophyes nebrodes* Diakonoff and *Homona trachyptera* Diakonoff).
5. Probable generalists (*Somena alba* (Bethune-Baker)) found on *Ficus* in the montane area, but only on non-*Ficus* hosts in the lowlands. The limited host plant range of these species in the lowlands is probably due to insufficient sampling.

The only shared species common in both study areas were *Asota plana* and *A. versicolor*, responsible for high dominance of shared species in the assemblage on montane *F. iodotricha* (31%) and lowland *F. pachyrrhachis* (49%). These two *Ficus* hosts therefore exhibit the highest similarity between montane and lowland assemblages in our samples (Fig. 5).

Further, *Talanga excelsalis moresbyensis* was common on *F. copiosa* in the lowland area, but found only as a singleton on this species in the montane area. This difference produced asymmetrical dominance of shared species between assemblages on *F. copiosa* in the lowland (43%) and montane (2%)

Species	Family	Montane				Lowland			
		COP	DAM	WAS	IOD	COP	DAM	WAS-1	WAS-2
<i>Talanga sexpunctalis</i>	Crambidae	0	0	1	0	49	30	57	65
<i>Talanga excelsalis moresbyensis</i>	Crambidae	1	0	0	0	239	6	32	135
<i>Asota plana</i>	Noctuidae	1	0	0	77	0	0	0	0
<i>Asota versicolor</i>	Noctuidae	0	0	0	130	0	0	0	0
<i>Philiris moira</i>	Lycaenidae	0	42	0	0	1	0	0	0
<i>Adoxophyes nebrodes</i>	Tortricidae	1	0	0	0	7	7	2	0
<i>Homona trachyptera</i>	Tortricidae	0	0	1	0	1	0	0	0
<i>Somena alba</i>	Lymantriidae	1	0	0	0	0	0	0	0

Table 3 The number of caterpillars from species occupying both lowland and montane study areas and feeding on *F. copiosa* (COP), *F. dammaropsis* (DAM), *F. wassa* (WAS) and *F. iodotricha* (IOD). WAS-1: sample from 1994 to 1995, WAS-2: sample from 1999 to 2000

Table 4 The abundance of species shared between lowland and montane study areas in standardized samples from 18 lowland *Ficus* hosts and 62 lowland non-*Ficus* hosts, the number of their lowland *Ficus* hosts (H_{fic}) and lowland host plant families (H_{fam}), their most preferred lowland host species (Major host), and the number of host families reported in the literature (Lit)

Species	<i>Ficus</i>	Non- <i>Ficus</i>	H_{fic}	H_{fam}	Major host	Lit*
<i>Talanga sexpunctalis</i>	368	0	16	1	<i>Ficus wassa</i>	0
<i>Talanga excelsalis moresbyensis</i>	248	0	14	1	<i>Ficus copiosa</i>	0
<i>Asota plana</i>	104	0	2	1	<i>Ficus pachyrrhachis</i>	1
<i>Asota versicolor</i>	231	0	8	1	<i>Ficus pachyrrhachis</i>	0
<i>Philiris moira</i>	217	0	10	1	<i>Ficus pachyrrhachis</i>	1
<i>Adoxophyes nebrodes</i> †	54	229	11	15	<i>Piper aduncum</i>	0
<i>Homona trachyptera</i>	1	49	2	13	<i>Kleinhovia hospita</i>	6
<i>Somena alba</i>	0	2	0	1	<i>Pometia pinnata</i>	0

*The number of host families world wide as reported by Robinson *et al.* (2003); the results including Moraceae are in bold.

†Matches Diakonoff (1952) figure of female *A. nebrodes*, but the association with males is not clear.

Table 5 The number and abundance of shared and endemic caterpillar species feeding on *F. copiosa* (COP), *F. dammaropsis* (DAM), *F. wassa* (WAS) and *F. iodotricha* (IOD) in the lowland and montane study areas. WAS-1: sample from 1994 to 1995, WAS-2: sample from 1999 to 2000

Study area	Host <i>Ficus</i> species							
	Montane				Lowland			
	COP	DAM	WAS	IOD	COP	DAM	WAS-1	WAS-2
Shared species	4	1	2	2	5	3	3	2
Endemic species	22	18	15	5	25	31	30	20
Individuals from shared species	4	42	2	207	297	43	91	194
Individuals from endemic species	402	258	234	247	280	220	284	275
% Shared species	15	5	12	19	17	9	9	9
% Individuals from shared species	1	14	1	46	52	16	24	41
Sample size (m ² foliage)	500	500	500	500	1500	1500	1500	1500

areas. Similar asymmetry in abundance was exhibited by *Philiris moira*, rare and restricted to *F. dammaropsis* in the highlands while common on *F. pachyrrhachis*, *F. mollior* and *F. hispidioides* in the lowlands.

The combined dominance of caterpillars from all species shared with the lowlands ranged from 1% to 5% in the montane and from 16% to 52% in the lowland assemblages on the three shared *Ficus* species, while it reached 46% in the montane *F. iodotricha* (Table 5). The shared species often reached low abundance on the montane hosts; four of the seven shared species were singletons, while there were only 12 singletons among the 43 species limited to the montane area.

DISCUSSION

Overlap between montane and lowland assemblages

Our results showed that only a minority (17%) of montane species feeding on *Ficus* occurred also in the lowlands. Further, these species were often rare. They together represented 1–46% of individuals in caterpillar assemblages on particular *Ficus* hosts in the montane forest. This low overlap cannot be explained by changes in the species composition of host plants with altitude as it was found also between lowland and montane assemblages feeding on the same *Ficus* species. It is possible that at least some of the shared species were rare

because they were approaching the limits of their altitudinal distribution, but this suggestion has to be tested when more information on their distribution becomes available.

The shared species did not represent a uniform group as they included both *Ficus* specialists and generalists feeding on numerous plant families. Some of the *Ficus* specialists changed their preferred host species with altitude. In some cases, caterpillar species switched from a host species restricted to the montane area to another species restricted to the lowlands (*Asota plana* and *A. versicolor*). Interestingly, some changes in host preference took place even when there was no change in the availability of host plants between the study areas (*Philiris moira*).

We can only speculate about the factors generating the rapid turnover of caterpillar species with altitude, but the *c.* 10 °C lower temperature encountered by montane caterpillars throughout the year may be an important factor (Alonso, 1999; Brehm *et al.*, 2003a). Developmental responses by insects to temperature, quantified by the lower developmental threshold and the sum of effective temperatures, change with latitude (Honek, 1996), but information on analogous changes from tropical lowlands to montane areas is insufficient (Chen *et al.*, 1990; Nedved, 2000). Biotic factors, such as predation, may be also important. In particular, there is a high predation pressure from ants in the lowland rain forests, including our study site (Novotny *et al.*, 1999), but it is much lower in the

montane areas, where ants become progressively less abundant with elevation and are already very rare at 1800 m a.s.l. (Janzen *et al.*, 1976; Koptur, 1985; McCoy, 1990; Samson, 1997). The quality of foliage as a resource for insect herbivores can also change with altitude even in the same plant species (Erelli *et al.*, 1998). Although it is not clear what environmental factors limit the distribution of montane species in the lowlands and vice versa, they clearly do not represent serious evolutionary constraints as numerous genera include both lowland and montane species feeding on *Ficus*.

In contrast, it is unlikely that species turnover is caused by geographical isolation. There are no obvious migration barriers separating the two study areas as they are connected by a 130 km long continuum of secondary and primary forests. *Ficus copiosa*, *F. wassa* and *F. dammaropsis* were common in both studied areas and are common and widespread in many other areas of New Guinea. They are also present at all altitudes intermediate between 0 and 1800 m a.s.l. (unpublished data based on specimens at Lae Herbarium). It is therefore probable that herbivorous insects can track the spatial distribution of their hosts, particularly as they typically have > 1 generation annually so that their generation times are 1–2 orders of magnitude shorter than those of their woody hosts. Likewise, our unpublished data on *Ficus*-feeding caterpillars from multiple lowland sites suggest that 130-km distance between two study sites alone does not generate large turnover in species composition of caterpillar assemblages.

Species turnover along an altitudinal gradient has some interesting parallels with species turnover along a vertical gradient from forest understorey to canopy. The vertical gradients can be also characterized by rapid change in environmental factors, including predation pressure and host plant quality (Basset *et al.*, 2003). Despite the absence of migration barriers, they are characterized by rapid species turnover even in herbivore assemblages feeding on the same plant species (Basset, 2001).

This study demonstrates the important role of species turnover along an altitudinal gradient in generating regional species diversity of tropical insect herbivores quite apart from changes in the composition of the vegetation along such gradients. Further, our study suggests that beta-diversity of Lepidoptera could be lower on large than on small plant genera as caterpillar species can switch their host preferences from one congeneric host species to another along the altitudinal gradient. Large genera can conceivably represent a large and continuously distributed resource in tropical forests for many caterpillar species. Our results also stress the need for research on beta-diversity of insect herbivores studied in multiple habitats and at multiple sites. Ideally, plants from other genera and families should be also included as they can be principal hosts for many species that are rare, marginal feeders on a target plant genus (Novotny & Basset, 2000).

Our conclusions are obviously tentative as only a small fraction of the plant community was surveyed for caterpillars in each study area and sampling from each particular plant was also incomplete. Larger sampling effort can discover new

species and find new records for known species such that any species overlap index may change in either direction with increased sampling effort. In addition, species concepts affect inferences of turnover in important ways. The taxonomic impediment in poorly described tropical communities may be overcome through a combination of careful morphological comparison and DNA barcoding for species-level identifications (Hebert *et al.*, 2003a,b).

Composition and structure of caterpillar assemblages

Despite the low number and numerical importance of shared species, the lowland and montane *Ficus* assemblages are remarkably similar in their dominance structure, species richness, host specificity and taxonomic composition on generic and familial levels.

The familial composition of lowland caterpillar assemblages on *Ficus* (Basset *et al.*, 1997, 1999; Basset & Novotny, 1999; Novotny *et al.*, 2002a) was similar to that in the highlands. In particular, the assemblages were again dominated by Choreutidae, which otherwise colonize only a limited number of other plant genera and families, together with more widespread Crambidae and Noctuidae. Further, the Geometridae, another prominent family in caterpillar assemblages, was marked by its low importance on *Ficus* in both study areas. These patterns were found also in Lepidoptera feeding on Moraceae elsewhere (Holloway *et al.*, 2001; Robinson *et al.*, 2003). The most important difference in taxonomic composition at the family level between the two areas was the absence of Nymphalidae from the montane area. This family was represented by two *Euploea* species and by *Cyrestis acilia* Godart in the lowlands. While no species of *Euploea* in New Guinea occur regularly above 1200 m, *C. acilia* is reported from 0 to 2000 m (Parsons, 1999) and its absence could have been due to inadequate sampling.

There were close parallels between the montane and lowland assemblages also in the taxonomic composition of their dominant species. The most abundant species in each assemblage recruited from the same genera both in the montane and the lowland areas (*Talanga*, *Choreutis*). Further, *Ficus copiosa* and *F. wassa* shared the dominant species within each study area, viz. *Talanga excelsalis moresbyensis* in the lowlands and *Talanga exquisitalis* in the montane study area.

The montane and lowland assemblages exhibited broadly parallel patterns in dominance, species richness and host specificity. We have reported on predictability of these parameters in caterpillar assemblages from various hosts in the lowlands (Novotny *et al.*, 2002c). Clearly, similar constancy exists also along an altitudinal gradient. However, these community structural constants remain difficult to explain. For instance, we still do not know why certain species achieve high dominance in a particular caterpillar assemblage while others remain rare or why caterpillar assemblages are so strongly dominated by a single or a few species, given high numbers of other species also present in the assemblage.

Extraordinary attention has been paid to altitudinal variation in species richness in various taxa, including insects (McCoy, 1990; Allison *et al.*, 1993; Lees *et al.*, 1999; Brehm *et al.*, 2003b). At the same time, species richness is probably the most difficult parameter to estimate in tropical assemblages of insect herbivores, characterized by numerous rare species (Longino *et al.*, 2002; Novotny *et al.*, 2002a). Perhaps unsurprisingly, data on altitudinal trends in the species richness of Lepidoptera, often estimated from light trap samples, are often inconclusive as they exhibit large variance even within the same altitude (Holloway, 1987). Although studies of caterpillar assemblages from particular hosts may help to reduce this variability, they are still unlikely to contribute reliable data on species richness, as indicated by ever-increasing species accumulation curves in the present study (shown in Novotny *et al.*, 2004).

Information on the large-scale distribution of insect diversity is still lacking for any larger geographical area in the tropics (Bartlett *et al.*, 1999), despite its obvious importance for conservation decisions as well as for understanding the origin and maintenance of tropical diversity. A herbivorous assemblage hosted locally by a particular plant species can represent a suitable basic unit for building such a biodiversity map, as it can be accurately defined, is amenable to study and represents an ecologically and evolutionarily meaningful entity. An efficient strategy for building the biodiversity map can be to combine data on assemblages from numerous coexisting, phylogenetically diverse plant species at a limited number of sites with those from a few plant species at numerous sites representing various habitats types, elevations, and geographical areas. Large, widely distributed, and ecologically diverse plant genera, such as *Ficus*, *Psychotria*, *Macaranga* or *Piper*, and their herbivorous assemblages, can be suitable models for such broadly based studies of diversity patterns (e.g. Dyer & Palmer, 2004). In particular, *Ficus* is pantropical, species-rich (Berg, 1989), important in the ecology of tropical forests (Lambert & Marshall, 1991) and supports characteristic assemblages of herbivorous insects (Basset *et al.*, 1997; Miller *et al.*, 2000; Weiblen, 2002).

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APPENDIX 1

Ficus species recorded in the two study areas. Coastal and cultivated species are marked as such; others are native primary or secondary forest species. Asterisks mark species present in both lowland and highland areas. Species sampled for caterpillars are in bold. Note: *Ficus* species sampled for caterpillars are abbreviated in the text by the first three letters of their species name.

Lowland study area: *F. adelpha* Laut. et K. Schum., *F. adenosperma* Miq., *F. ampelas* Burm. f.*, *F. arbuscula* Laut. et K. Schum., *F. arfakensis* King, *F. baeuerlenii* King, *F. benjamina* L. (cultivated), ***F. bernaysii* King**, ***F. botryocarpa* Miq.**, *F. congesta* Roxb.*, *F. conocephalifolia* Ridley, *F. copiosa* Steud.*, *F. crassiramea* Miq., ***F. dammaropsis* Diels***, *F. drupacea* Thunb., *F. edelfeltii* King (cultivated), *F. elastica* Roxb., ***F. erythrosperma* Miq.**, ***F. gul* Laut. et K. Schum.**, *F. hesperidiiformis* King, ***F. hispidioides* S. Moore**, *F. itoana* Diels, *F. jimienensis* C.C. Berg, *F. macrorrhyncha* Laut et K. Schum., *F. melinocarpa* Bl., ***F. microcarpa* L.*(seacoast)**, ***F. mollior* Benth.***, *F. morobensis* C.C. Berg, ***F. nodosa* Teysm. et Binn.**, *F. novoguineensis* Corner, *F. odoardi* King, ***F. pachyrrhachis* Laut. et K. Schum.**, ***F. phaeosyce* Laut. et K. Schum.**, *F. polyantha* Warb., *F. prasinicarpa* Elm. (seacoast), *F. primaria* Corner, ***F. pungens* Reinw. ex Bl.***, *F. robusta* Corner, *F. semivestita* Corner, ***F. septica* Burm. F. ***, *F. subcuneata* Miq., ***F. subtrinervia* Laut. et K. Schum.**, *F. subulata* Bl.*, ***F. cf. ternatana* Miq.**, ***F. tinctoria* Forst. f (seacoast)**, ***F. trachypison* K. Schum.**, ***F. variegata* Bl.**, *F. virens* Alt.*, *F. virgata* Reinw. ex Bl., ***F. wassa* Roxb.**, *F. xylosyca* Diels.

Montane study area: *F. amblysyce* Corner, *F. ampelas* Burm. f.*, *F. comitis* King, *F. congesta* Roxb.*, ***F. copiosa* Steud.***,

F. dammaropsis* Diels, *F. distichoidea* Diels., *F. endochaete* Summerh., ***F. iodotricha* Diels**, *F. mafuluensis* Diels, *F. megalophylla* Diels, *F. microcarpa* L.*, *F. mollior* Benth.*, *F. pungens* Rein. ex Bl.*, *F. septica* Burm. f.*, *F. subulata* Blume, *F. trichocerasa* Diels, *F. virens* Alt.*, ***F. wassa* Roxb.***.

APPENDIX 2

Species of Lepidoptera reared from *Ficus* in the montane study area:

Arctiidae: '*Diacrisia*' *persimilis* Rothschild, *Lemyra* probably *punctatostrigata* (Bethune-Baker), '*Eilema*' probably *aurora* Rothschild, *Gymnasura* sp. nr. *saginaea* (Turner), unidentified sp. (unique female); Bombycidae: *Elachyophthalma* probably *kebeae* Bethune-Baker, *Elachyophthalma* sp.; Choreutidae: *Brenthia* sp., *Choreutis* probably *lutescens* (Felder & Rogenhofer), *Choreutis niphocrypta* Meyrick or near, *Choreutis* nr. but not *basalis* Felder, *Choreutis* spp. 1–3; Crambidae: *Cirrhochrista xanthographis* Hampson, *Cirrhochrista primulina* Hampson, *Talanga exquisitalis* (Kenrick), *Talanga excelsalis moresbyensis* (Strand), *Talanga sexpunctalis* (Moore), '*Udea*' probably *gigantea* (Hampson); Drepanidae: *Teldenia celidographia*? Wilkinson; Geometridae: *Cyclophora* probably *subrosea* Warren; Lycaenidae: *Philiris moira* Grose-Smith; Lymantriidae: *Olene* sp., *Somena alba* (Bethune-Baker), unidentified genus, *Teia* sp. nr. but not *dewara* Riotte; Noctuidae: *Acrapex pacifica* Holloway, *Asota versicolor* F., *Asota plana* Walker, *Tiracola aureata* Holloway; Pyralidae: *Cryptoblades* sp.; Tortricidae: *Adoxophyes nebrodes* meyrick, *Homona trachyptera* Diakonoff, *Isotenes* sp., *Isotenes* or *Neocalyptis* spp. 1–4, *Battalia* (= *Parachorista*) sp., *Rhabdotenes* probably *operosa* (Diakonoff) and eight unidentified species not reared to adults.

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