Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea

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Summary

1 The spatial distribution of 30 woody species (15 species each of Euphorbiaceae and Moraceae) and their associated leaf-chewing communities (Orthoptera, Phasmatodea, Coleoptera and Lepidoptera) were studied in coastal, riverine and rain forest habitats. A successional series, from abandoned gardens to primary forest, was examined. Host plant records for more than 27 000 insects, all verified by feeding experiments, and spatial distribution of almost 9000 plant specimens were evaluated.

2 Phylogenetic (taxonomic) relatedness of host plants explained 56% of the variability in the composition of their herbivore communities, while the ecological (distribution) similarity of plants explained only 4%.

3 The successional optimum of plant species was not an important determinant of the composition of their herbivore communities.

4 Neither plant successional optimum nor plant palatability to a generalist herbivore were correlated with the number of species, abundance or host specificity of its herbivores, nor was there a correlation between a plant's palatability to a generalist herbivore and its successional optimum.

5 Herbivore communities became dominated increasingly by a few abundant species in later stages of succession.

6 On average, *Ficus* species had lower palatability and supported more species of herbivores than species of Euphorbiaceae. The abundance of herbivores and their dominance index were not significantly different between the two plant families.

7 These results contradict several previous studies of successional trends in temperate regions. Many tropical successions, however, start with pioneer trees, rather than with annual herbs, and may present a permanent and predictable habitat for insects even at the earliest stages, with no advantage for polyphagous species. Numerous pioneer trees in the tropics possess anti-herbivore defences, resulting in their low palatability to generalists, increased host specificity of herbivores, and often idiosyncratic composition of herbivore communities. Even plant traits such as species richness of their herbivores or palatability may have a phylogenetic component which should not be ignored.

Key-words: Euphorbiaceae, host specificity, Moraceae, plant palatability, rain forest

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Introduction

Although host-plant selection has a phylogenetic component (e.g. Ackery 1991; Fiedler 1998), plant phylogeny is not necessarily the best explanatory variable for the species composition of herbivore communities (Basset *et al.* 1996; Becerra 1997). Often, herbivores colonize unrelated plants with convergent life history traits. For example, preference for latex (Farrell & Mitter 1993), or pioneer plants (Novotný 1995) can explain the composition of paraphyletic host-plant ranges. Host-plant choice by polyphagous species may be flexible, depending on the changing quality of plants and their environment (Brodbeck *et al.* 1990).

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Hosts in the same habitat may share more herbivore species than plants from different habitats because they: (1) share ecological traits, which are preferred by their herbivores and avoided by others; (2) occur in an environment preferred by their herbivores; or (3) grow in physical proximity, facilitating mutual colonization of plants by non-specific herbivores ('mass effect', Shmida & Wilson 1985). Each plant species is most abundant at a particular successional age (its successional optimum). Both species traits and microclimate change in a predictable way during succession so that it might be expected that species with similar successional optima share more herbivores than species differing in their successional optima.

Most of the information on the successional dynamics of insect communities refers to old-field successions in the temperate zone (e.g. Brown 1985; Hendrix *et al.* 1988). These studies revealed important changes in community structure and insect life histories along successional series (Brown 1982; Brown & Southwood 1983; Brown & Hyman 1986; Novotný 1995). Although secondary succession of plant communities in the tropics is fairly well known (Whitmore 1975; Ewel 1980; Denslow 1987; Richards 1996), studies of insects in tropical succession are few (Bowman *et al.* 1990; Spitzer *et al.* 1993). Herbivore damage and anti-herbivore secondary chemistry have been compared between early and late successional trees (Coley & Barone 1996), but studies of the composition of herbivore communities and of the life histories of constituent species on such plants are rare (Marquis & Braker 1993; Basset 1996). The limited data available are insufficient to enable robust generalizations to be made about successional trends in herbivore communities in the tropics.

The present study tests the extent to which the distribution of plant species in various habitat types determines the species composition, species richness, dominance structure and host specificity in the communities of their insect herbivores. Extensive data on leaf-chewing insects feeding on 30 species of trees and shrubs in a lowland rain forest in Papua New Guinea are used to study the pattern associated with secondary succession in this habitat.

Methods

STUDY AREA AND PLANTS

The study area was situated in the lowlands of the Madang Province in Papua New Guinea (hereafter PNG), extending from the coast to the slopes of the Adelbert Mountains and bounded by the Gogol and Sempi Rivers. Fieldwork was concentrated in primary and secondary lowland forests near Baitabag, Pau, Ohu and Mis villages, and in a coastal area near Riwo village (145°41–8′ E, 5°08–14′ S, ≈ 0–200 m). General descriptions of a similar, nearby forest site and of coastal areas can be found in Bowman *et al.* (1990) and Jebb & Lowry (1995), respectively. The average annual

rainfall in the Madang area is 3558 mm, with a moderately dry season from July to September; mean air temperature is 26.5 °C and varies little throughout the year (McAlpine *et al.* 1983).

Thirty locally abundant species of trees and shrubs – 15 species of *Ficus* (Moraceae), 6 species of *Macaranga* and 9 species from 9 other genera (total 15 species of Euphorbiaceae) (Table 1) – were selected for the study. Their distribution was recorded in a total of 124 quadrats, each 400 m², distributed across seven habitats: recently abandoned garden, young secondary forest, old secondary forest, primary forest, riverine, coastal ruderal, and sea-shore. The first four vegetation types form a typical successional series. The gardens, which ranged in area from 500 m² to one hectare, had been cleared, most often within an area of secondary forest, as a part of the swidden (slash-and-burn) agricultural cycle, cultivated for 1 to 3 years, and then abandoned up to 5 years before the study. The canopy at these sites was partially open. Young secondary forest was characterized by most trees being under 20 cm d.b.h. (diameter at breast height), whilst old secondary forest always had some trees above this size. Primary forest always contained numerous large trees (often d.b.h. ~100 cm), lianas and epiphytes. The riverine habitat occurred on rocky beds where the stream was wide enough to prevent canopy closure overhead. The coastal ruderal habitat consisted mainly of young re-growth in abandoned or occasionally weeded coconut plantations, and the sea-shore habitat was on raised coral up to 10 m from the tidal line.

In linear habitats (i.e. riverine and seashore) quadrats were 5×80 m, while 20×20 m quadrats were used in forest and coastal ruderal habitats. All individuals of each of the study species were recorded in each quadrat and d.b.h. was measured for individuals taller than 1.5 m. Smaller individuals were arbitrarily assigned a d.b.h. of 1 mm. The representation of each species in a plot was characterized by its basal area used to estimate species' successional optimum. In one quadrat per successional habitat type, the number of all woody, free standing species higher than 1.5 m and all woody climbers with d.b.h. > 5 mm were also recorded. All quadrats were surveyed in January and February 1997.

HERBIVOROUS INSECTS

All ectophagous leaf-chewing insects (Orthoptera, Phasmatodea, Coleoptera and Lepidoptera) were collected individually by hand from the foliage of the plants studied. All 15 plant species within a family were sampled simultaneously, and surveys were spread over at least 1 year (*Ficus* spp. from July 1994 to March 1996 and Euphorbiaceae from August 1996 to August 1997). Five teams, usually including three people per team, collected insects and represented a total of approximately 950 days of fieldwork.

Collecting effort was recorded as the time spent searching the foliage of each plant species for insects, which was approximately proportional to the leaf area

Table 1 Plant species studied, their abbreviations and their habitat. For forest species, the successional optimum is given in brackets. The optimum is species score on the constrained axis in CCA of species composition of forest quadrats, with the successional stage being the explanatory variable. The values are on a relative scale, with negative values signifying the preference for the early successional stages, and positive values signifying preference for the late successional stages

Species group	Identification	Species name	Abbreviation	Habitat
Ficus	C.C.Berg	*F. bernaysii* King	Fbe	Forest (0.74)
Ficus	C.C.Berg	*F. botryocarpa* Miq.	Fbo	Forest (0.11)
Ficus	C.C.Berg	*F. conocephalifolia* Ridley	Fcon	Forest (0.49)
Ficus	C.C.Berg	*F. copiosa* Steud	Fcop	Forest (−0.28)
Ficus	C.C.Berg	*F. dammaropsis* Diels	Fda	Forest (−0.28)
Ficus	C.C.Berg	*F. hispidioides* S. Moore	Fhi	Forest (−0.62)
Ficus	C.C.Berg	*F. microcarpa* L.	Fmi	Sea-shore
Ficus	C.C.Berg	*F. nodosa* Teysm. & Binn	Fno	Forest (−0.20)
Ficus	C.C.Berg	*F. phaeosyce* Laut. & K. Schum.	Fph	Forest (0.61)
Ficus	C.C.Berg	*F. pungens* Reinw. ex Bl.	Fpu	Forest (−0.63)
Ficus	C.C.Berg	*F. septica* Burm.	Fse	Forest (−0.63)
Ficus	C.C.Berg	*F. tinctoria* Forst.	Fti	Sea-shore
Ficus	C.C.Berg	*F. trachypison* K. Schum.	Ftr	Forest (−0.05)
Ficus	C.C.Berg	*F. variegata* Bl.	Fva	Forest (−0.15)
Ficus	C.C.Berg	*F. wassa* Roxb.	Fwa	Forest (0.18)
Macaranga	T.C.Whitmore	*M. aleuritoides* F. Muell.	Mal	Forest (−0.51)
Macaranga	T.C.Whitmore	*M. bifoveata* J. J. Smith	Mbi	Forest (−0.55)
Macaranga	T.C.Whitmore	*M. brachytricha* A. Shaw	Mbr	Forest (−0.65)
Macaranga	T.C.Whitmore	*M. densiflora* Warb.	Mde	Forest (−0.84)
Macaranga	T.C.Whitmore	*M. novoguineensis* J. J. Smith	Mno	Forest (0.75)
Macaranga	T.C.Whitmore	*M. quadriglandulosa* Warb.	Mqu	Forest (−0.81)
Other Euphorbiacea	P van Welzen	*Breynia cernua* (Poir.) Muell. Arg.	Bce	Forest (−0.63)
Other Euphorbiacea	P van Welzen	*Codiaeum ludovicianum* Airy Shaw	Clu	Riverine
Other Euphorbiaceae	P. van Welzen	*Endospermum labios* Schodde	Ela	Forest (0.02)
Other Euphorbiaceae	P. van Welzen	*Excoecaria agallocha* L.	Eag	Sea-shore
Other Euphorbiaceae	P. van Welzen	*Homalanthus novoguineensis* (Warb.) K. Schum	Hno	Forest (−0.90)
Other Euphorbiaceae	P. van Welzen	*Mallotus mollissimus* (Geisel.) Airy Shaw	Mmo	Forest (−0.46)
Other Euphorbiaceae	P. van Welzen	*Melanolepis multiglandulosa* (Reinw. ex Bl.) Reichb.f. & Zoll.	Mmu	Forest (−0.45)
Other Euphorbiaceae	P. van Welzen	*Phyllanthus lamprophyllus* Muell. Arg.	Pla	Riverine
Other Euphorbiaceae	P. van Welzen	*Pimelodendron amboinicum* Hassk.	Pam	Forest (1.07)

examined. The number of trees inspected was also recorded. Collecting effort was identical for each plant species and amounted to 1500 m² foliage sampled and more than 1000 tree inspections per plant species.

All insects were kept in the laboratory with a fresh supply of foliage of the species from which they had been collected, until they fed or died. Only the specimens that fed were considered in the analyses, in order to exclude transient species from the samples. Larvae were reared to adults whenever possible. All insects were assigned to morphospecies, later verified and identified as far as possible by various taxonomists. Voucher specimens are deposited in the Bishop Museum, Hawaii. In total, 27 651 records of herbivores, each confirmed by a feeding test, were included in the analyses. Further information on study sites, plant species and taxonomic composition of insect samples is detailed in Basset & Novotný (1999), Miller *et al.* (2001) and Novotný *et al.* (1999).

PLANT PALATABILITY

Palatability of each plant species to generalist herbivores was quantified by feeding experiments, using a highly generalist weevil species (*Oribius* sp., species CURC012). Each weevil was starved for 24 h and then placed in a vial, fastened to a living leaf on a potted sapling and the feeding damage scored after 24 h. Each weevil was used for only one experiment. Both young and mature leaves on two to five saplings of each species were used for an average of 25 such experiments. An index of palatability was derived by recording the number of cases of extensive feeding divided by the number of cases tested. This procedure emphasized regular consumption in contrast to food probing. Palatability values for all studied plants are reported in Novotný *et al.* (1999).

DATA ANALYSIS

Plant distribution

The variability in plant distribution was analysed by methods of gradient analysis (constrained and unconstrained ordinations using the programme CANOCO, ter Braak & Šmilauer 1998). In those analyses, 'samples' were the quadrats, and the abundance of plant species was characterized by basal area after log (x + 1)

transformation. First, the overall variability of the whole data set was analysed by a method of unconstrained ordination, detrended correspondence analysis (DCA). The plant species scores on the first two DCA axes were used as the characteristics of their spatial distribution (the 'DCA1' and 'DCA2' variables). The species with similar spatial distribution (i.e. found in the same quadrats) are expected to have similar habitat preferences. They also have similar DCA scores, and consequently DCA scores can be used as a characteristic of habitat preferences, so that species with similar scores prefer similar habitats.

Then, the four habitats forming a successional series were analysed separately in order to identify the successional optimum of each species. The ordinal explanatory variable (successional age) was constructed with the following values assigned to different habitats: garden = 1, young secondary forest = 2, old secondary forest = 3, and primary forest = 4. It was used as the only explanatory variable in a method of constrained ordination, canonical correspondence analysis (CCA). The species score on the first (i.e. constrained) CCA axis corresponded to the relative position of the species' maximum basal area along the successional series estimated by weighted averaging (ter Braak & Prentice 1988). This parameter, called successional optimum (Table 1), was used as an ecological characteristic of plant species in subsequent analyses.

The similarity of distribution between two plant species was quantified with Spearman's rank correlation coefficient (r_S) of their basal area values within the quadrats.

Herbivore community composition

The composition of herbivorous communities was also analysed by methods of unconstrained and constrained ordinations. For the analyses, the herbivore community of a plant species comprised all the insect individuals collected on that plant species during the whole year, and proven to feed on it. Thus, for those analyses the 'samples' are individual host species and species are insect species, with their abundances $\log(x + 1)$ transformed. Due to the collection of many rare species with very few individuals, the option 'downweighting of rare species' was used (see ter Braak & Šmilauer 1998 for technical details). DCA was used to obtain a general pattern describing the similarity of insect communities on different plant species. Subsequently, various partial CCAs were applied to separate the effect of the host-plant ecological similarity and of phylogenetic relatedness on the composition of the communities. A binary variable, plant family, separating Moraceae from Euphorbiaceae, accounted for plant relatedness. The ecological behaviour of plants was reflected by their distribution which, in turn, was characterized by their scores on the first two axes of DCA of plant distribution data (DCA1 and DCA2 variables, see above). The use of partial analyses (i.e. analyses with covariables) enabled the separation of the effects of various explanatory variables on the community composition: the effect of a covariable is first subtracted from the data and the analysis is then performed on the remaining variability. This approach is similar to using covariates in ANCOVA. The significance of relationships was evaluated by the Monte Carlo permutation test (499 permutations; see ter Braak & Šmilauer 1998 for details of permutation testing techniques).

The analyses performed are listed in Table 2. In analysis number 1, we tested how much of the variability in the composition of herbivore communities could be explained by differences between host-plant families, i.e. a null hypothesis that there is no difference in the composition between herbivore communities on *Ficus* and on Euphorbiaceae, once the effect of plant distribution (characterized by its DCA1 and DCA2 scores which were used as covariables) has been removed. In analysis number 2, covariables and explanatory variables were reversed to test the null hypothesis that there is no effect

Table 2 Results of CCA of herbivorous communities. Three different analyses were performed differing in explanatory variables and covariables used. (Analyses 1 and 2 for herbivorous communities from all the host plants, and analysis 3 for Euphorbiaceae only.) Each of the analyses was performed for all the herbivore species, and then for taxonomically defined subgroups: Coleoptera, Lepidoptera and Orthoptera

Analysis number		1			2			3		
Covariable(s)		DCA1 & DCA2			Plant family			None		
Explanatory variable(s)		Plant family			DCA1 & DCA2			Euphorbiaceae genus		
Insect group analysed	NSP	%	r	P	%	r	P	%	r	P
All species	606	16.3	0.992	0.002	10.3	0.858	0.004	13.5	0.950	0.004
Coleoptera	243	15.1	0.984	0.002	10.3	0.807	0.004	13.0	0.932	0.012
Lepidoptera	265	14.4	0.997	0.002	10.0	0.877	0.008	13.5	0.947	0.006
Orthoptera	98	16.3	0.979	0.002	9.6	0.865	0.016	13.4	0.933	0.012

Explanatory variables and covariables: Plant family = a binary variable, Moraceae or Euphorbiaceae; DCA1 and DCA2 = host plant species score on the first and second axes of DCA of plant distribution data (see Fig. 1); Euphorbiaceae genus = a binary variable, *Macaranga* spp. or other Euphorbiaceae genera; NSP = the number of herbivore species in analyses, % = the percentage of variability (after the effect of covariables had been removed) explained by all canonical axes, i.e. by all explanatory variables; r = species–environment correlation on the first axis; P = significance.

of plant species distribution on the composition of herbivore communities within confamilial plants. A third analysis, using data only from Euphorbiaceae, with a binary variable 'Euphorbiaceae genus' was used to separate *Macaranga* spp. from other genera.

Further CCA analyses were performed on the herbivore communities of 25 plant species found in forest succession (i.e. excluding the plants confined to seashore and riverine habitats, Table 1), using the plant's successional optimum as the explanatory variable (Table 2). These tested for a systematic change in the composition of herbivorous communities along the successional series. These analyses were performed for the whole set of 25 forest plant species, for species from each plant family separately, and for *Macaranga* species only.

Herbivore community similarity

The similarity between two herbivore communities (*x* and *y*) was quantified by a percentage similarity index,

$$PS = \sum_i \min(x_i, y_i),$$ where x_i and y_i is the relative abundance (N_i/N, $N = \sum N_i$) of the *i*-th species in the two communities compared. The percentage similarity of herbivore communities was correlated with the distribution similarity of their host plants, expressed as the Spearman's rank correlation coefficient of their basal area (r_S). Since the *PS* and r_S values in the similarity matrices were not mutually independent, a Mantel test was used to estimate the significance of their relationship (Sokal & Rohlf 1981).

In addition to their *PS* and r_S values, each pair of communities was assigned a categorical variable expressing the relatedness of their host plants: 1 = both plants belonged to the same genus; 2 = different genus from the same family; or 3 = different families. A general linear model analysis was then performed, using the similarity of herbivorous communities as the response (dependent variable), and the degree of taxonomic similarity (categorical variable) and ecological similarity of host plants as explanatory (independent) variables. Since the similarity values were not mutually independent, the error degrees of freedom in the *F*-test were highly inflated and, consequently, the *F*-tests could not be used as statistical tests of effects of the explanatory variables. However, the decomposition of the sum of squares was not influenced by the inflation of error degrees of freedom and gave a reasonable estimate of the relative portions of variability in the similarity of herbivorous communities, accounted for by taxonomic and ecological similarity of their host plants.

Herbivore community structure

The structure of the herbivore community on each host-plant species was described by two indices of dominance (Magurran 1988): the proportion of the most abundant species $D_1 = N_1/N$ (sometimes called

the Berger-Parker dominance index) and the Simpson's index of dominance, $SI = \sum_i \left(\frac{N_i}{N}\right)^2$ where N_i is number of individuals of *i*-th species, N_1 is number of individuals of the most abundant species and *N* is the total number of individuals in the community ($N = \sum N_i$).

The number of species, number of individuals and dominance in herbivore communities were tested by general linear models, using the successional optimum and family of their host plants as explanatory variables. In addition to the complete leaf-chewing community, some analyses were also performed separately for Coleoptera, Lepidoptera and orthopteroids (i.e. Orthoptera and Phasmatodea). These major taxa coincided, to a large extent, with different feeding guilds. Almost all Coleoptera fed on the foliage only during their adult stage, while all Lepidoptera fed only as larvae, and all Orthoptera and Phasmatodea fed throughout their life cycles (Novotný & Basset 1999).

Herbivore host specificity

Host specificity of herbivores was inferred from their distribution among the plants studied, as for most of them, no other data on their host range were available. The host specificity was quantified as the variance of the species' distribution among the plant species. The host specificity parameter used was Lloyd's index, $L = \dfrac{S_X^2 - \overline{X}}{\overline{X}^2} + 1$, where S_X^2 and $\overline{X}$ are variance and mean, respectively, of abundance values. This index is considered to be the best way of standardization of variance with respect to the mean (Lepš 1993). Its value is minimum for an equitable distribution (i.e. indiscriminate polyphagy).

The choice of host plants could bias the estimates of *L*. For example, the host specificity of *Ficus*-feeding specialists is lower than those specializing on *Macaranga* or *Phyllanthus* when all 30 host species are included, but this is simply due to the different number of species from each genus in the analysis. To avoid this artefact, host specificity with respect to congeneric plants was analysed in *Ficus* communities, using Lloyd's index calculated from the distribution of insects among the 15 *Ficus* species. Similarly, host specificity with respect to confamilial genera was analysed in communities on Euphorbiaceae, where Lloyd's index was calculated from distribution among the 10 genera from this family (using a mean value for the six species studied to represent *Macaranga*). Only host specificity with respect to plant families could be analysed for the whole set of 30 communities, since Lloyd's index was calculated from distribution between Moraceae and Euphorbiaceae.

Many species were too rare to derive any meaningful estimates of their host specificity. Potentially spurious correlation of host specificity with species abundance (i.e. sample size) was eliminated when species
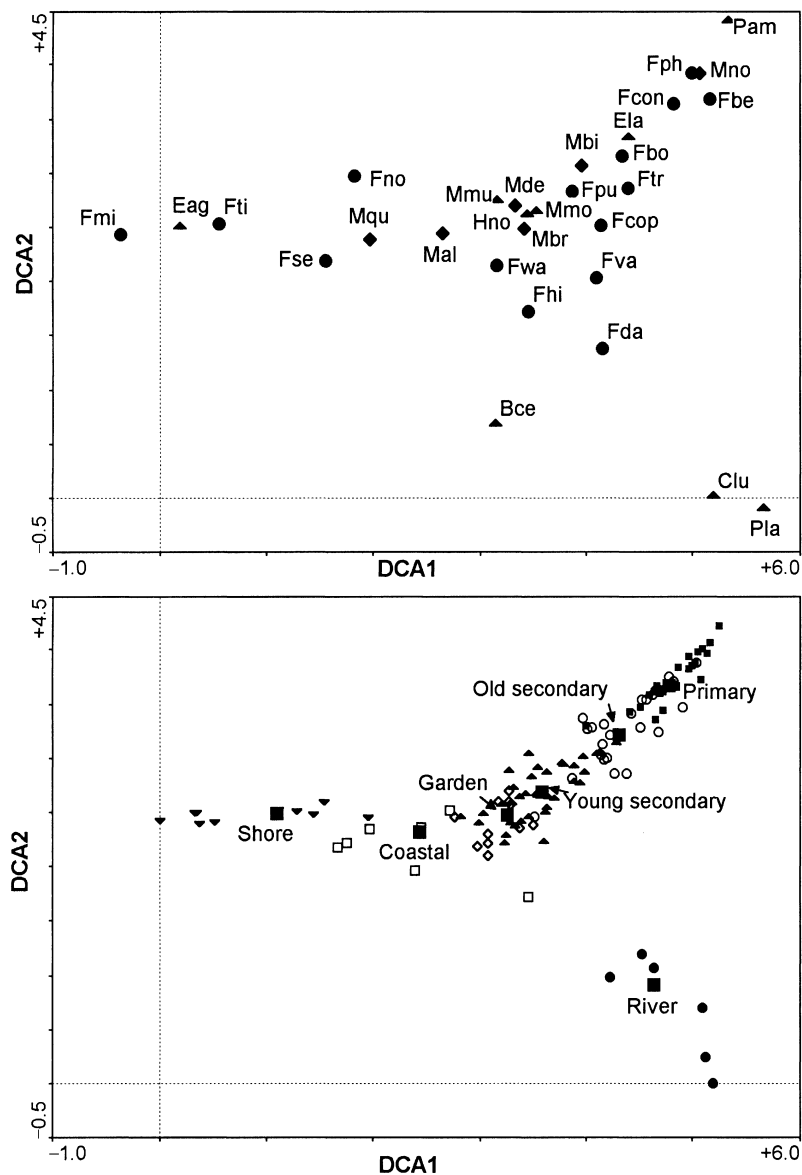
Fig. 1 Results of DCA of the distribution of 30 plant species among 124 quadrats. Above: ordination of species; symbols: ●, *Ficus* species; ◆, *Macaranga* species; ▲, other Euphorbiaceae. (See Table 1 for full names.) Below: ordination of plots; each habitat type displayed by a different symbol. Centroids of habitat types (■) were fitted *a posteriori* to the DCA ordination.

collected as less than 15 individuals for *Ficus*, less then 10 individuals for Euphorbiaceae genera and less than 6 individuals for plant families were excluded. Host specificity in each herbivore community was calculated as average *L* for all species above these thresholds.

Results

PLANT DISTRIBUTION

The DCA (Fig. 1) revealed considerable differences in habitat preferences of the plants studied, with sea-shore and riverine being the most distinct habitats. The first and the second axis accounted for 19.0% and 12.9%, respectively, of total variability in species composition, whereas the third and the fourth axis accounted for only 6.2% and 3.7%, respectively. This shows that the first two

axes, taken together, can be regarded as a reasonably good characterization of species spatial distribution. Three species, *Ficus microcarpa*, *F. tinctoria* and *Excoecaria*, were confined to sea-shore, and another two, *Codiaeum* and *Phyllanthus*, to riverine habitat (species other than *Ficus* and *Macaranga* are referred to by genus alone). The successional series after swidden agriculture forms a distinct, one-directional gradient in the ordination diagram, from garden through the secondary forest to primary forest. The coastal ruderal habitat is in-between garden and sea coast habitats, since it contained some of the early successional species, found also in gardens, as well as species sometimes able to enter the shoreline (e.g. *F. septica*); no species were confined to coastal ruderal habitat alone.

The CCA analysis of the forest succession plots revealed a highly significant effect ($P < 0.01$) of successional

age, the only explanatory variable, which explained 19.5% of the species variability. The second axis (unconstrained, constructed to explain as much of the remaining variability as possible) accounted for only 10% of species variability.

The Euphorbiaceae species were concentrated mostly in early successional stages. Five common species, *Melanolepis*, *Homalanthus*, *Macaranga quadriglandulosa*, *M. brachytricha* and *M. aleuritoides* were confined to early successional plots, whilst only *Pimelodendron* and *M. novoguineensis* showed an optimum in the primary forest. *Endospermum* represented an intermediate situation since, numerically, it was concentrated in early successional stages, but some large trees persisted in the late stages.

Many *Ficus* species had their optimum in secondary forest, in the middle portion of the successional series. Three species, *F. hispidioides*, *F. septica* and *F. pungens*, were confined to early stages of succession, while *F. bernaysii*, *F. conocephalifolia* and *F. phaeosyce* were found predominately in late succession, although none of them was completely absent from the early stages. *F. nodosa* and *F. variegata* were found as numerous saplings in early successional stages, while their peak basal area was in later succession, due to large, mature trees found there. *F. wassa* had no marked optimum along the successional series. It was found in 90% of all forest succession quadrats, from garden to primary forest, both as small and mature trees.

The forest species studied here were slightly more concentrated in the earlier successional stages; in gardens, there were 12 ± 4.7 (mean ± standard deviation) species per quadrat, in young secondary forest 13.1 ± 3.1 species, in old secondary forest 7.5 ± 2.6 species, and in primary forest 5.9 ± 1.3 species. The highest variability in the number of species was found in abandoned gardens (the coefficient of variation was 39%). Some of this variability was caused by a recent invasion of an American species *Piper aduncum* L. (Piperaceae), which became dominant in some sites that were consequently species-poor. Conversely, the primary forest quadrats had the lowest coefficient of variation, 22%, and a remarkably stable species composition: *M. novoguineensis* and *Pimelodendron*, together with *F. bernaysii*, *F. phaeosyce* and *F. wassa* were found throughout the old secondary and primary forest quadrats. When only trees higher than 1.5 m were considered, all these five species were still present with a high frequency, from 47% (*F. bernaysii*) to 98% (*Pimelodendron*) of secondary old and primary forest quadrats.

The total number of all woody species (including climbers) present in quadrats increased during succession. There were 38, 39, 52 and 78 woody species per quadrat in garden, young secondary, old secondary and primary forest, respectively. A one-hectare area of primary forest at one of our sites, Baitabag, contained 152 woody species with d.b.h. > 5 cm (Laidlaw & Kitching, personal communication). Thus, the present selection of 25 forest species represented a progressively smaller fraction of the whole plant community from early to later successional stages.

Since the gardens were typically surrounded by more advanced successional stages, a probable source of seeds for re-colonization, the succession progressed rapidly. Frequent re-sprouting from stumps also contributed to forest regeneration. Saplings of some of the early successional trees were even present in the gardens as weeds during cultivation. For example, in a garden 3 months after establishment (i.e. in the early stages of cultivation), 13 of the 25 forest species studied were already present. Nine established themselves from seeds (*Melanolepis* being the most frequent, with density of 12 seedlings per 100 m^2) and four species established themselves by re-sprouting. Thus, a typical succession started with woody plants already present, so that no stage was dominated by herbaceous plants. The growth of trees was very fast, with the canopy of a *Macaranga*-dominated re-growth in one of the gardens reaching 3 m within 18 months. Sometimes, the course of succession may be deflected towards tall grasses, particularly when gardens are located far from the forest, but this succession is infrequent.

PLANT PALATABILITY

There was no correlation between a plant's palatability to a generalist weevil and its successional optimum. This was the case for the overall analysis, involving all 25 plant species, as well as for separate analyses of *Ficus* and Euphorbiaceae species ($P > 0.4$ in all cases). A general linear model analysis, using the palatability as a dependent variable and the family and successional optimum of host plants as independent variables, showed that the effect of successional optimum was not significant ($P > 0.7$), whilst there was a significant difference in palatability between the two families ($P < 0.05$; mean palatability 0.19 and 0.50 for *Ficus* and Euphorbiaceae, respectively). Likewise, a similar analysis, contrasting *Macaranga* and the remaining genera within Euphorbiaceae, revealed no effect of successional optimum ($P > 0.6$) and a significant ($P < 0.05$) difference between *Macaranga* spp. (mean palatability 0.7) and other Euphorbiaceae (mean 0.29). The palatability of *Macaranga* spp. was also significantly higher than that of *Ficus* spp. (*t*-test, $P < 0.001$).

HERBIVORE COMMUNITY COMPOSITION

The similarity of herbivorous communities reflected the taxonomy of their host plants. There was a clear division between communities from hosts in *Ficus* and Euphorbiaceae, whilst communities from congeneric hosts, both in *Ficus* and *Macaranga*, were similar to one another (Fig. 2). Within plant families, some effect of the habitat type was also detectable, in particular that each of the three seashore species, *Ficus tinctoria*, *F. microcarpa* and *Excoecaria*, were separated from the members of their family.
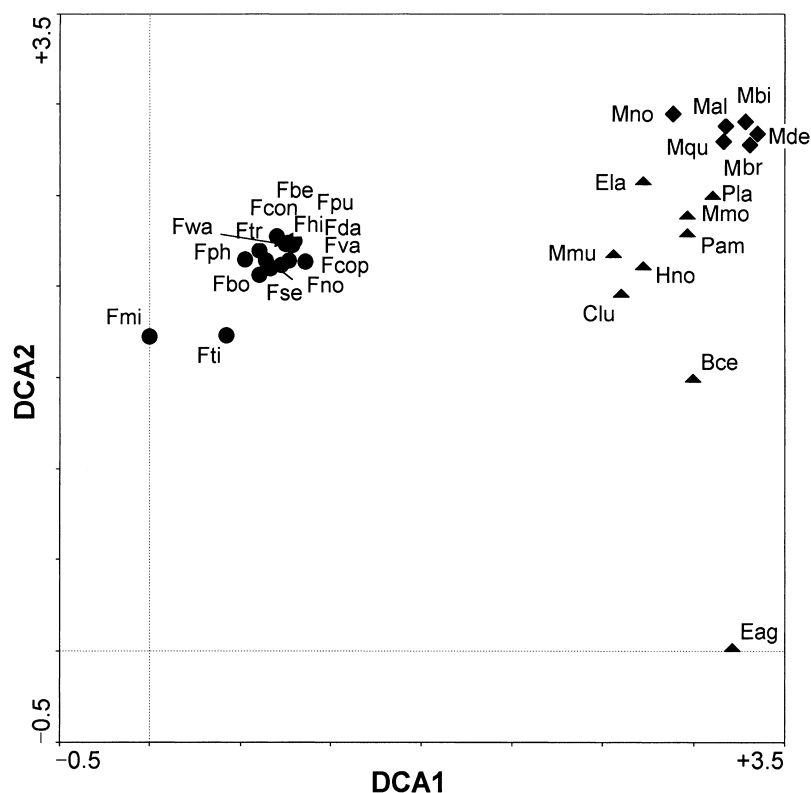
Fig. 2 Results of DCA of herbivorous communities from 30 host plant species. (See Table 1 for full names.) Symbols for host plants: ●, *Ficus* species; ◆, *Macaranga* species; ▲, other Euphorbiaceae.

Table 3 Results of CCA of herbivorous communities on plants from the forest successional series. In all analyses, the species' successional optimum (Success. optimum) was the sole explanatory variable. Each of the analyses was performed for all the herbivore species, and for taxonomically defined subgroups: Coleoptera, Lepidoptera and Orthoptera

Analysis number	1			2			3			3		
Covariable	Plant family			None			None			None		
Explanatory variable	Success. optimum			Success. optimum			Success. optimum			Success. optimum		
Herbivore community	All plants			*Ficus*			*Macaranga*			Euphorbiaceae		
	%	r	P	%	r	P	%	r	P	%	r	P
All species	4.5	0.926	0.410	9.2	0.966	0.140	23.3	0.996	0.090	16.4	0.996	0.540
Coleoptera	3.6	0.935	0.880	9.5	0.983	0.084	24.0	0.995	0.070	13.3	0.972	0.870
Lepidoptera	5.0	0.848	0.302	9.8	0.863	0.146	19.3	0.990	0.452	16.8	0.994	0.448
Orthoptera	4.4	0.912	0.386	7.3	0.923	0.792	26.7	0.992	0.050	18.4	0.936	0.284

Herbivor community = herbivore communities included in the analysis: All plants = all forest plant species, *Ficus* = only 15 *Ficus* species; *Macaranga* = only 6 *Macaranga* species; Euphorbiaceae = only 10 Euphorbiaceae species, each from a different genus (*Macaranga* was represented by *M. quadriglandulosa*); % = the percentage of variability (after the effect of covariables had been removed) explained by plant successional optimum; r = species-environment correlation on the first axis, P = significance.

Variability in herbivore community composition was more attributable to host-plant family (16.3%) than it was to the ecological distribution of the host plant (10.3%). In fact, the difference is even more pronounced than this suggests, since the family was characterized by only one binary variable, whereas the ecology is represented by two quantitative variables. Further, herbivorous communities on *Macaranga* spp. proved to be significantly different from those on the other genera of Euphorbiaceae. Similar results were obtained also for separate analyses of Coleoptera, Lepidoptera and orthopteroids (Table 2).

Despite its smaller magnitude, the effect of ecological behaviour of plants on their herbivorous communities was still significant. The majority of this effect was caused by the seashore species since both their distribution and herbivores differed from those of all other plants. Analyses performed only on forest species (not shown here) did not reveal any significant effect of plant distribution on their herbivorous communities.

The successional optimum of the host plant was not an important determinant of the species composition of their herbivorous communities (Table 3). In most analyses, the successional optimum was not a significant
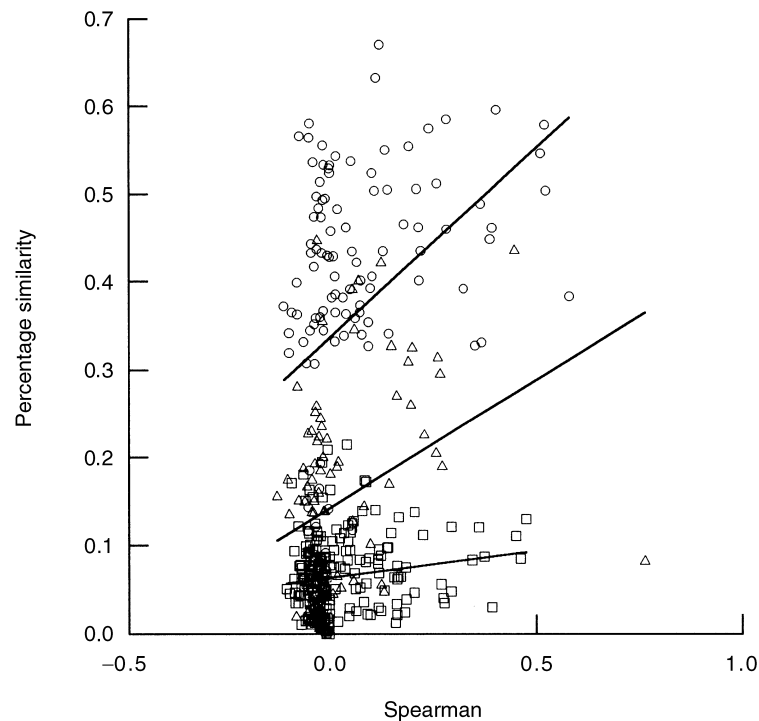
Fig. 3 Relationship between ecological similarity of plant species and similarity in the composition of their herbivorous communities. Spearman = ecological similarity of plants, expressed as Spearman rank correlation coefficient of their basal areas; percentage similarity = per cent similarity of herbivorous communities; three separate regression lines are fitted: comparisons between plants from the same genus (○), of different genera within Euphorbiaceae (△) and between families (□); a linear regression was fitted for each type separately.

explanatory variable, although its effect was close to significant (or marginally significant) when the variation within the same genus was considered (for *Macaranga* species, $P < 0.10$ in three out of four analyses, and for *Ficus* spp., $P < 0.15$ in three out of four analyses; Table 3). No effect of successional optimum was detected when analysing different genera of Euphorbiaceae (*Macaranga* was represented by a single species, *M. quadriglandulosa*, in this analysis; $P > 0.25$ in all four analyses) or the complete set of 25 plants ($P > 0.3$ in all four analyses; Table 3).

The ecological (distributional) similarity of pairs of trees was correlated positively with the similarity of their insect communities ($r = 0.290$, $P < 0.002$, Mantel test, 500 permutations). This positive correlation was again caused mainly by shoreline species: both their distribution and their herbivores were very different from the rest of the plant species. However, the major determinant of the similarity of herbivorous communities was the taxonomic similarity of their hosts. The highest similarity in herbivorous communities was found between species of *Macaranga* (median value 45%) and *Ficus* (median 40%). Similarities between species from different genera of Euphorbiaceae (median 15%) were much lower than the intrageneric similarities and the lowest were similarities between species from different families (median 6%).

In a general linear model using plant relatedness of each pair of host plants (categorized as congeneric,

confamilial but not congeneric, or heterofamilial) and their ecological (distribution) similarity as explanatory variables, the plant relatedness explained 56.2% of the variability in the composition of herbivore communities (measured by the proportion of respective sum of squares), whilst the ecological similarity explained only 3.8% (40% remained unexplained). Nevertheless, the within-group correlations were always positive (Fig. 3).

HERBIVORE COMMUNITY STRUCTURE

Plants from the forest succession series hosted a significantly higher number of herbivore species (average 77) than from the riverine (average 29 species) and seashore plants (average 31 species; ANOVA, $P < 0.001$), whereas no difference in the abundance of herbivores was found. Herbivorous communities on the five plants restricted to habitats other than the forest succession series were each dominated by one or a few species. Thus, they were characterized by higher values of Simpson's index than communities on plants from the forest succession (mean 0.264 and 0.113, respectively, $P < 0.01$), as well as higher values of the D_1 dominance index (mean 0.397 and 0.240, respectively, $P = 0.054$).

The number of herbivore species was poorly correlated with the successional optimum of host plants ($P > 0.4$), but the difference between families in species richness of herbivores was significant (average 88 species
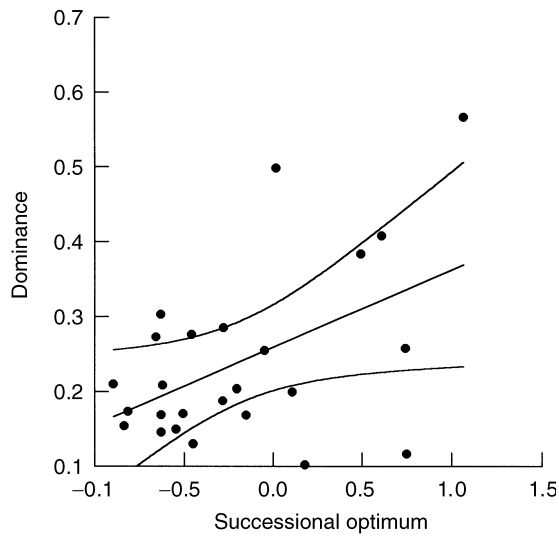
Fig. 4 Relationship between successional optimum of host plants and the dominance structure of their herbivorous communities. Successional optimum = plant successional optimum expressed as a score on the first canonical axis of CCA with successional stage being the only explanatory variable (higher values denote older successional stages); dominance = the proportion of individuals in the herbivorous community belonging to the most abundant species; linear regression line with 95% confidence interval is shown, $r = 0.493$, $P = 0.012$.

per *Ficus* and 72 species per Euphorbiaceae host; ANOVA, $P < 0.05$). There was no significant correlation between the number of herbivore individuals and successional optimum of the host plant ($P > 0.6$ for both Moraceae and Euphorbiaceae hosts). However, herbivorous communities were dominated increasingly by a single or a few abundant species in later stages of succession. This was reflected by a significant correlation between the D_1 dominance and successional optimum ($r = 0.493$, $P = 0.012$, Fig. 4) and between Simpson's indexes and successional optimum ($r = 0.509$, $P = 0.009$). The highest dominance, 57%, was achieved by *Oenospila* sp. (Lepidoptera: Geometridae) on a primary forest host, *Pimelodendron*. In *Ficus* species, a *Choreutis* sp. (Lepidoptera: Choreutidae) represented over 30% of individuals on two primary forest plants, *F. conocephalifolia* and *F. phaeosyce*. It was also the most abundant species (26% of individuals) on *F. bernaysii*, another primary forest species. The most marked exceptions from the overall trend of increasing dominance in late succession was *M. novoguineensis*, a primary forest species with N_1/N only 12%, and *Endospermum*, a secondary forest species containing a community dominated by a single species, *Lyssa macleayi* (Lepidoptera: Uraniidae), which accounted for 50% of all its herbivores.

HERBIVORE HOST SPECIFICITY

The average Lloyd's index, characterizing species' distribution between the two families was negatively correlated with successional optimum of host plant ($r = -0.390$, $P = 0.054$, $n = 25$ trees). This correlation indicated a possible tendency of late successional communities to be dominated by less specialized herbivores than communities on early successional plants. In herbivorous communities on *Ficus* spp., there was no correlation between the average host specificity with respect to congeneric plants and the successional optimum of the host plant ($P > 0.8$). Similarly, no correlation was found between the average host specificity with respect to confamilial genera and the successional optimum within Euphorbiaceae ($P > 0.8$).

Discussion

PLANT DISTRIBUTION AND SUCCESSION

Succession was a major determinant of plant distribution within this data set. Early succession was dominated by pioneer woody species, as is typical for forest regeneration in large gaps, both natural and those created by swidden agriculture (Whitmore 1975; Denslow 1987). Post-cultivation succession is similar to successions on alluvium and landslides, but is much faster (Richards 1996). In the area of the study, landslides might have been a major habitat of pioneer species in the pre-agricultural times (Garwood *et al.* 1979; Johns 1986).

The successional series described here appears to be typical for and widespread over a larger area in the Madang province (cf. Bowman *et al.* 1990). Whitmore (1975) noted that '*Macaranga* is the genus *par excellence* of pioneer trees'. All species of *Homalanthus*, as well as *Melanolepis multiglandulosa* and some *Mallotus* spp. are also pioneers (Whitmore 1975; Fontaine *et al.* 1978; Primack & Lee 1991). *M. mollissimus* behaves as a gap opportunist in Australia (Hopkins & Graham 1983) and *Macaranga* and *Homalanthus* are prominent in early stages of secondary succession also in montane forests in PNG (van Valkenburg & Ketner 1994). *Endospermum medullosum* was characterized as a long-lived pioneer by Whitmore (1975). Apparently, *E. labios* belongs to the same category, since mature trees persisted in older forests. *Ficus* spp. are reported as having their optimum predominately in secondary forests (Janzen 1979; Berg 1989), which was also the case in the present study.

PLANT PALATABILITY

Rapidly growing plants are thought to be less defended against, and more palatable to, generalist herbivores (Coley 1988; Price 1991; Herms & Mattson 1992; but see Fenner *et al.* 1999). In temperate ecosystems, some studies found that early successional, herbaceous plants were more palatable to generalist invertebrate herbivores than late successional herbaceous and woody species (Cates & Orians 1975; Dirzo 1980; Reader & Southwood 1981), whilst others did not (Otte 1975; Maiorana 1978;

Rathcke 1985). However, only Rathcke's study included a comparison between early and late successional woody species.

Data on tropical woody plants are also limited. Basset (1996) found no difference in palatability between five pioneer and five late successional trees in Papua New Guinea, whilst Hartshorn (1980) cited unpublished data of Waltz on the higher palatability of pioneer than late successional rain forest trees. Ewel (1980) cited the same pattern, but gave no supporting evidence. A higher level of damage by herbivores, sustained by pioneer species in comparison with those of primary forest (Coley 1982; Marquis & Braker 1993; Coley & Barone 1996) can reflect their higher palatability.

In the present study, differences in palatability were not correlated with the successional optimum, but congeneric plants had similar palatability. Notably, *Macaranga* spp., including the late successional *Macaranga novoguineensis*, were more palatable than *Ficus* spp. These results indicate that the phylogenetic component, not studied in any of the above mentioned studies (but see Maiorana 1978), may be as important as plant ecology.

HERBIVORE COMMUNITY COMPOSITION

Both the taxonomic and ecological dissimilarity of plants affected the similarity of their insect communities. Plants with similar habitat requirements had dissimilar herbivore communities if they were unrelated, and related plants shared fewer herbivores if they were confined to different habitats. Overall, plant taxonomy appeared to be more important, at least for the range of taxonomic and ecological variability of plants covered by this study.

The contrast between high similarity among herbivore communities from congeneric plants and low similarity among the communities from confamilial plants belonging to different genera indicates the importance of plant phylogeny. However, analogous differences in herbivore similarity may not be associated with other levels of phylogenetic (taxonomic) relatedness of plants. In particular, the pattern of similarity among herbivorous communities on the 15 species of *Ficus* did not follow their phylogenetic relationships (Weiblen 1999) and the same was true for herbivore communities on 10 trees from different families from New Guinea (Basset *et al.* 1996).

The distinctiveness of herbivore communities on *F. microcarpa*, *F. tinctoria* and *Excoecaria* could be attributed to their different habitat, rather than phylogeny, since the latter two species are closely related to some of the forest species included in the study (Webster 1994; Esser & van Welzen 1997; Weiblen 1999). A similar effect of plant habitat preference was not detected within the successional series, since there was no gradient in the composition of herbivore communities, which reflected the successional optimum of their hosts. There was only some indication that such a gradient might exist within a set of congeneric plants. Conceivably, host selection within a genus may be responsive to ecological factors (Basset & Novotný 1999), in contrast to more phylogenetically constrained host choice among plant genera and families.

The vegetation in both seashore and riverine habitats was species poor, which could reduce the species diversity of herbivores on any particular plant species by limiting the availability of alternative hosts as sources of colonists. Unlike the seashore plants, those in the riverine habitat could be colonized easily by herbivores from surrounding, diverse forest. However, the riverine plants were often (several times a year) submerged by flash floods after torrential rains. This unpredictable disturbance may explain the low number of herbivore species feeding on them.

Similarly to the present study, there was no difference in species richness of herbivores between pioneer and climax trees in a montane rain forest in New Guinea (Basset 1996), nor between gap and understorey species of *Piper* in Costa Rica (Marquis 1991). These results indicate that an increase in the species richness of herbivores from early successional to mature vegetation in the tropics may be driven by changes in the plant species richness rather than by an increase in herbivore richness on individual plant species. In tropical succession, the maximum plant diversity is invariably reached in mature forest (Richards 1996). The number of pioneer species in regional floras, as well as in communities, is small and they are represented by a limited number of plant families (Whitmore 1984).

High dominance in the communities from seashore and riverine habitats can be caused by, respectively, low diversity of surrounding vegetation and high disturbance in these habitats. However, it is not clear why dominance increased during the course of the succession, while the diversity of vegetation followed the opposite trend. In a similar study on rainforest herbivores (Basset 1997), dominance structure in their communities could not be predicted by any of several ecological traits of their host trees.

HERBIVORE HOST SPECIFICITY

Host specificity of insect herbivores increases in the course of secondary succession on temperate vegetation (Cates 1981; Brown & Southwood 1983; Jaenike 1990; Novotný 1994). This trend has been attributed to temporal unpredictability of pioneer, mostly annual, plants (Southwood *et al.* 1983; Jaenike 1990; Ward 1992). Tropical succession in abandoned gardens is however, often dominated by woody plants from its onset (Stromgaard 1986; Bowman *et al.* 1990; Walker *et al.* 1996) and even short-lived pioneer trees, with a life span of 15 or more years (Whitmore 1975), represent a relatively permanent resource for insect herbivores. High colonization rate by herbivores of isolated plants (Thomas 1990) and high levels of damage by herbivores

to pioneer trees (Coley 1982, 1983) indicate that even rare and short-living woody plants can be found and colonized easily by herbivores in rain forest.

The conventional view (Herms & Mattson 1992) that early successional species invest comparatively more resources in growth at the expense of investment in defence, may not hold for tropical species. Many of the fast growing pioneers in the tropics are unpalatable and well defended against herbivores. For example, *F. septica* is one of a few fig species containing alkaloids (Hartley *et al.* 1973), *Homalanthus* has poisonous latex (Beutler *et al.* 1996; Esser 1997) and *Endospermum* is protected by symbiotic ants (Letourneau *et al.* 1993). In general, Euphorbiaceae is a family with numerous early successional species (Airy Shaw 1980) and a high diversity of secondary metabolites (Rizk 1987). Protection by ants is common among other pioneer trees in the tropics, such as *Macaranga* (Fiala 1996) or *Cecropia* (Janzen 1968).

The lack of any tendency towards greater polyphagy in early successional communities is, therefore, unsurprising. Similarly, Basset (1996) found no difference in the proportion of specialists in communities of pioneer and late successional trees in a montane rain forest in New Guinea and there was no difference in the average number of host plants per species of Curculionidae and Geometridae between primary and secondary forest species of *Piper* in Costa Rica (analysis of data from Marquis 1991). In contrast, Loye (1992) found lower specificity in sap-sucking herbivores (Membracidae) feeding on fast growing than on slow growing plant species in a rain forest in Panama.

Conclusions

Patterns commonly found in temperate successional series may not apply for tropical succession, which starts with woody pioneers rather than annual herbs. In particular, host specificity of herbivores may not be dependent on the successional optimum of their hosts, and the structure of herbivore communities on early successional plants is similar to that on late successional ones. Early and late successional plants, although possessing distinct life histories (Whitmore 1975), thus may not appear as distinct categories to herbivorous insects. In consequence, plant phylogeny, rather than ecology, is the main determinant of the composition of herbivore communities along successional series. This is in marked contrast with temperate successions, where both life histories and community composition of herbivores vary according to the successional optimum of their host plants, which is often a more important factor in structuring herbivore communities than plant phylogeny (Novotný 1995). However, the generality of these tentative conclusions has yet to be established since detailed analysis is limited by the lack of data, particularly those from succession series dominated by woody plants in the temperate zone and tropical successions starting with herbaceous species.

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