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Host specialization and species richness of root-feeding chrysomelid larvae (Chrysomelidae, Coleoptera) in a New Guinea rain forest

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Abstract: The assemblages of root-feeding chrysomelid larvae from 21 locally common tree species were studied in a secondary tropical forest in New Guinea and compared with confamilial larvae and adults feeding on the foliage. Larval host plants were inferred from adults emerging from the soil containing the roots of known tree species. In total, 2495 chrysomelids from 100 species were reared from the roots. Almost 90% of adults in the forest canopy recruited from the species with root-feeding larvae, while species with leaf-feeding larvae represented 1% of individuals (the feeding guild for the remaining 9% was unknown). The root-feeding larvae were thus more important in tropical than temperate forests, possibly because of predation pressure by ants on tropical vegetation. The number of chrysomelids emerging annually from the soil in 1 ha of the forest was approximately 0.2 million. Root-feeding larvae were polyphagous as their modal host range included three or four from the six plant families studied. The lack of correlation between the phylogenetic distance of tree species and the similarity of their chrysomelid assemblages indicated that host choice was not constrained by plant phylogeny. The host range of larvae feeding on roots was as wide as that of the conspecific adults feeding on the foliage. The density and species composition of larval and adult assemblages on the studied trees were not correlated. These results suggest that even studies restricted to adult assemblages, which represent a majority of chrysomelid studies, can be informative, as the composition of adult assemblages is not necessarily constrained by larval host-plant selection.

Key Words: herbivore communities, insect–plant interactions, leaf beetles, Papua New Guinea, rhizophagy, species richness, underground herbivory

INTRODUCTION

Numerous studies have examined local species richness (Erwin & Scott 1980, Farrell & Erwin 1988, Ødegaard 2000a), beta diversity (Allison *et al.* 1993, Erwin 1983), habitat preference (Wagner 1997), stratification (Charles & Basset 2005), colonization dynamics (Floren & Linsenmair 1998) and host specificity (Basset & Samuelson 1996, Flowers & Janzen 1997, Novotny *et al.* 1999a, 2002a; Ødegaard 2003) of beetles, including chrysomelids, living on the foliage of tropical trees. Such studies have also played a prominent role in the assessment of global species richness for insects (Basset *et al.* 1996, Erwin 1982, Novotny *et al.* 2002b, Ødegaard 2000b).

Attention has focused almost exclusively on adult beetles, probably because their larvae are conspicuously missing from tropical foliage. Among chrysomelids, this scarcity of feeding larvae on the vegetation is due to the prevalence of species from the subfamilies Eumolpinae, Galerucinae and Alticinae in most tropical assemblages (Basset & Samuelson 1996, Charles & Basset 2005, Farrell & Erwin 1988, Novotny *et al.* 1999a, Ødegaard 2003, Stork 1987, Wagner 1997), many of which have subterranean, root-feeding larvae (Jolivet & Hawkeswood 1995). The focus on the study of adults is unfortunate as host-plant utilization by adults can be of marginal importance compared with their larvae. The composition of adult-dominated communities of chrysomelids in the canopy may be largely determined by host-plant requirements of their root-feeding larvae. Although there is anecdotal information on hosts of root-feeding chrysomelid larvae (reviewed by Jolivet & Hawkeswood 1995 and Jolivet 1988), quantitative community studies

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Table 1. Sampling protocol and chrysomelid community characteristics on the study plants. BA: the percentage share of the total basal area of 14.4 m^2 ha^{-1}; S1, S2, S3: the number of traps used in respectively Series 1, 2 and 3; N_L and S_L: the number of chrysomelid individuals and species that emerged from 2 m^2 of forest floor (i.e. two traps) in 6 mo; N_A and S_A: the number of chrysomelid individuals and species collected from 1500 m^2 of foliage by Novotny *et al.* (2002a); * Species that represented their respective genus and family in host specificity analyses.

Plant species	Family	BA	S1	S2	S3	N_L	S_L	N_A	S_A
Artocarpus camansi Blanco	Moraceae	0.1		4		14	7	258	13
Endospermum labios Schodde	Euphorbiaceae	3.1			2	23	5	9	5
Ficus hispidioides S. Moore	Moraceae	0.3		4		48	5	159	11
Ficus nodosa Teysm. & Binn.	Moraceae	0.2	2			4	2	344	24
Ficus pungens Reinw. ex Bl.*	Moraceae	2.3	2	4	6	93	26	230	19
Ficus variegata Bl.	Moraceae	1.5	2			75	18	488	20
Geunsia farinosa Blume	Verbenaceae	0.8			2	18	4		
Hibiscus tiliaceus L.	Malvaceae	3.9			2	16	2		
Homalanthus novoguineensis (Warb.) K. Schum.	Euphorbiaceae	0.1		4		66	17	342	19
Kleinhovia hospita L.	Malvaceae	3.1			2	33	6		
Leucosyke capitellata (Poir.) Wedd.	Urticaceae	0.3		4		85	22	143	14
Macaranga aleuritoides F. Muell.*	Euphorbiaceae	2.0	2	4	6	146	19	369	24
Macaranga brachytricha Airy Shaw	Euphorbiaceae	1.0			2	73	20	210	20
Macaranga densiflora Warb.	Euphorbiaceae	>0.1		4		17	8	289	20
Melanolepis multiglandulosa (Reinw. ex Bl.) Reichb.f. & Zoll.	Euphorbiaceae	4.7			2	23	6	100	18
Neuburgia corynocarpa (A. Gray) Leenh.	Loganiaceae	>0.1		4		49	18	7	4
Piper aduncum L.	Piperaceae	21.4			4	1	1		
Premna obtusifolia R.Br.*	Verbenaceae	3.1			2	25	3	77	10
Spathodea campanulata (L.) Kunth	Bignoniaceae	14.3			4	0	0		
Sterculia schumanniana (Lauterb.) Mildbr.*	Malvaceae	>0.1		4		38	18	169	21
Trichospermum pleiostigma (F. Muell.) Kostermans	Malvaceae	12.3			2	1	1		

of host selection by larvae in tropical forests are non-existent. The sampling and rearing of root-feeding larvae is difficult and time consuming. It is therefore unsurprising that they have been only used for studies on single plant species (Ferronatto 1999). Collecting chrysomelids emerging from the soil in the vicinity of particular tree species is a simpler but less reliable method for the identification of larval host plants. We are not aware of any studies of chrysomelid root-feeding assemblages in tropical forests using this methodology.

Studies from temperate areas suggest that root-feeding herbivores have important impacts on vegetation as well as on above-ground herbivores (Brown & Gange 1990). However, as noted by Blossey & Hunt-Joshi (2003), 'significant information gaps exist about the impact of root feeders on plant physiology and their importance in natural areas, particularly in the tropics'. The present study attempts to correct this lack of community data on root-feeding assemblages by studying chrysomelids from 21 locally abundant tree species in a secondary tropical forest in Papua New Guinea. It analyses the host specificity and species richness of root-feeding larvae and compares them with data on leaf-feeding larvae and adults from the same study site (Novotny *et al.* 1999a, 2002a, 2004a).

METHODS

Study site and trees

The study area was situated in the Madang Province of Papua New Guinea. It has a humid tropical climate with average annual rainfall of 3558 mm, a moderate dry season from July to September, and mean air temperature 26.5 °C (McAlpine *et al.* 1983). Fieldwork was performed in an approximately 6-km^2 mosaic of secondary and primary forest vegetation near Ohu Village (145°41′ E, 5°14′ S, 200 m asl).

The study was conducted in a 5–30-y-old succession forest (described in Novotny *et al.* 2004b) bordered by primary lowland hill forest (described in Laidlaw *et al.* in press). Succession typically starts in abandoned garden clearings after traditional swidden agriculture, but similar succession follows natural disturbance events such as tree falls and landslides (Johns 1986, Leps *et al.* 2001). Vegetation from a 1-ha area included 6848 stems taller than 1.5 m from 171 species, 120 genera and 54 families (Novotny *et al.* 2004b). Their total basal area (i.e. the area of stem cross-sections at 1.5 m above the ground) was 14.4 m^2. The three most abundant species, *Piper aduncum*, *Spathodea campanulata* and *Trichospermum pleiostigma* represented 47.9% of the total basal area (Table 1). The former two species are aliens that have only recently invaded the vegetation (Leps *et al.* 2002). The study was limited to secondary forest, as only there was it possible to find mature trees growing sufficiently far apart that their roots were not entangled with roots of other tree species.

Eighty mature trees, 2–12 per tree species, from 21 tree species were selected for the study (Table 1). This selection included the nine locally most abundant plant species and represented 76% of the total basal area in the forest. Further, the selection included both closely related

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congeneric species and more distantly related species from six different families as well as two alien species.

Sampling of chrysomelids

Vegetation within a 5-m radius around each target tree was cleared and a trap designed to collect insects emerging from the ground was placed within a 2-m radius of each target tree. The trap was a 1 × 1-m square, 15-cm-high wooden frame embedded 5 cm deep in the soil and covered with strong black cloth on top. Single transparent plastic containers partly filled with 70% ethanol were inserted in two opposite sides of the frame. Insects emerging from the 1-m^2 area of the soil within the trap were attracted by light to the containers where they were collected in ethanol. Traps were emptied at weekly intervals. All collected chrysomelids were mounted, sorted to morphospecies and identified as far as possible by Samuelson. Voucher specimens are deposited at the National Agriculture Research Institute in Port Moresby and Bishop Museum in Honolulu.

The traps were run in three consecutive series: the S1 series comprised eight traps run for 6 mo (1 May–31 October 2002), the S2 series comprised 36 traps run for 11 mo (21 November 2002 –21 October 2003), and the S3 series comprised 36 traps run for 6 mo (22 December 2003–22 June 2004) (Table 1). A different tree was used for each trap and series and the trees from different species were intermingled within the study area to avoid pseudoreplication.

Host specificity

Larval host plants were inferred indirectly, based on the adults that emerged from the soil that included predominately or exclusively roots of the putative host tree species. After completion of the insect sampling, smaller roots (< 5 cm in diameter) were removed from the top 50-cm layer of soil from within each trap, identified to species and weighed. Larger roots were excluded as they generally lacked surface rootlets that served as food resources for chrysomelid larvae, while numerous very small roots were often difficult to separate from soil. The estimates of root biomass are therefore approximate. The identification of roots to species was possible due to detailed knowledge of local farmers who practice swidden agriculture in the studied forests. The proportion of root biomass from the target tree species was used to evaluate the reliability of the host-plant associations obtained from each trap. The roots of the target tree represented 67–100% of the total root biomass in each trap, with the median (1–3 quartile) of 98% (92–100%).

Host specificity of chrysomelids was analysed using two data sets with the number of traps and the length of their exposure standardized for all tree species. The T9 data set included nine tree species sampled by the trap series S2, i.e. by four traps per tree species exposed for 11 mo. The T21 data included 21 target tree species, each sampled by two traps exposed for 6 mo. This data set was obtained by combining samples from the first 6 mo of sampling from the traps in S1–S3. The two traps with the highest proportion of root biomass from the target tree were included in the data set for each of the 21 tree species. The effect of sample size on the species richness and host specificity estimates was examined using data from *Ficus pungens* and *Macaranga aleuritoides*, each of them sampled by 12 traps exposed for 6 mo.

Host specificity was quantified as the percentage of individuals (P) feeding on a single, most preferred host-plant species from those studied. The species with $P \geq 90\%$ of individuals feeding on a single host were considered specialized to this host (Thomas 1990). Although arbitrary, we preferred this threshold to the strict definition, requiring that all individuals feed on a particular plant taxon as some of the reared individuals may have fed on roots other than those of the target tree species. The proportion of chrysomelid species specialized to a single plant species, genus and family was determined from data sets including potential alternative hosts from respectively the same genus, different confamilial genus, and different family. The following data sets were used: (1) four *Ficus* species, (2) three *Macaranga* species, and single representatives of (3) four Euphorbiaceae genera, (4), four Malvaceae genera, (5) two Moraceae genera, (6) two Verbenaceae genera and (7) six plant families. The species used to represent their respective genera and families are noted in Table 1.

Further, host specificity was also estimated as the number of host-plant families recorded for each species. The species collected as < 10 individuals and host-plant records based on single individuals (singletons) were excluded from the analyses. The effect of sample size on host specificity estimates was explored using subsets of species with the minimum total abundance from 1 to 10 individuals and subsets of host-plant records documented by the minimum of 1 to 10 individuals.

The chrysomelid density (D) on diverse vegetation was calculated as the average of chrysomelid densities (n_i, in individuals per m^2) from individual tree species i, weighted by host tree relative basal area (b_i where $\Sigma b_i = 1$) used as an index of tree abundance: $D = \Sigma b_i n_i$. The unweighted average of chrysomelid densities (n_i) across the study trees was denoted d.

Community similarity and species richness

The similarity between chrysomelid assemblages from different hosts was characterized by Sørensen and

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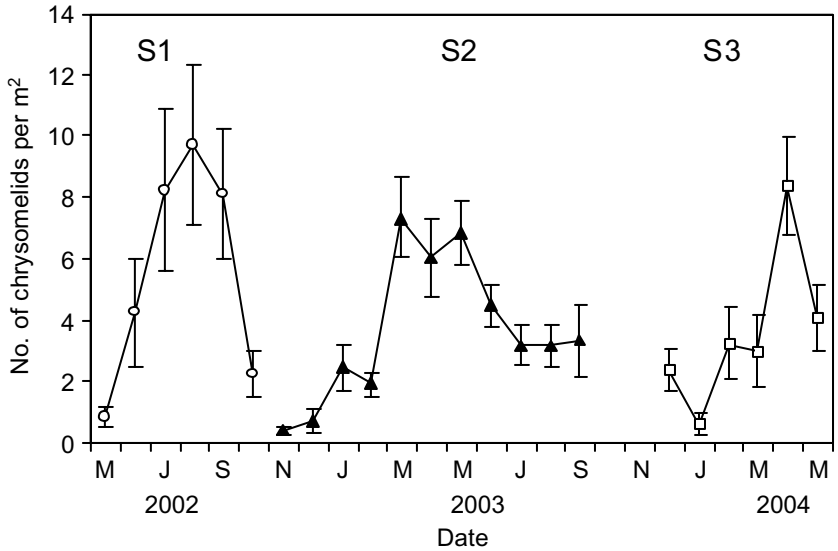

Figure 1. The number of chrysomelids (individuals m^{-2} mo^{-1}) emerging from the forest floor during the S1–S3 trapping series. Means with SE (error bars) were calculated from all traps, combining different tree species.

Percentual Similarity coefficients. Sørensen coefficient $SØ = 2S_c/(S_a + S_b + 2S_c)$, where S_a and S_b is respectively the number of species unique to the sample A and B and S_c is the number of species shared by the two samples. Percentual similarity $PS = \Sigma\min(A_i, B_i)$, where A_i, B_i are dominance values of species i (i.e. number of individuals of species i divided by the total number of individuals in a sample) in samples A and B. PS is an extension of the Sørensen coefficient for quantitative data (Ludwig & Reynolds 1988). Both coefficients range from 0 to 1.

The similarity of chrysomelid assemblages, quantified by the Sørensen and PS indices, was correlated with the phylogenetic distance of their hosts, estimated as the number of nodes in the phylogeny between these plant species. The fully resolved phylogenetic relationships of the study tree species have been obtained by combining the published information on familial relationships (Savolainen *et al.* 2000) with molecular and morphological analysis targeting most of the studied tree species (Novotny *et al.* 2002b, G. Weiblen unpublished). The chrysomelid similarity and phylogenetic distance for all pair-wise combinations of the study tree species were correlated by Pearson coefficient and tested by a Mantel test.

The relationship between various characteristics of chrysomelid communities from different tree species, such as the number of species reared from roots compared to that collected from the foliage, was explored using the independent contrasts method implemented in Compare 4.4 (Indiana University, USA) software. This approach takes into account the non-independence of plant species due to their phylogenetic relationships.

Larval–adult comparisons

The data obtained by capturing insects emerging from the soil were compared with data on chrysomelids feeding on the foliage of 59 tree species (Novotny *et al.* 2004a), including 15 species studied here (listed in Table 1). Each tree species was sampled in secondary and primary forests in Ohu and two nearby sites for 1 y between 1994 and 2000. The sampling effort was constant for all species at 1500 m^2 of foliage sampled per species. All adult and larval chrysomelids were collected from the foliage and tested in the laboratory for feeding on the plant species from which they were collected. Only individuals that fed were considered in the analyses. The data obtained by this study are summarized in Novotny *et al.* (1999a, 2002a, 2004a).

RESULTS

Abundance and species richness of chrysomelids

In total, 2495 chrysomelids emerged from the 80 traps. The emergence rate was low at the beginning of each rearing series, peaked during the fourth or fifth month at 7.4–9.8 chrysomelids m^{-2} mo^{-1} and then started to decline (Figure 1). The assemblages from *Macaranga aleuritoides* and *Ficus pungens* were characterized by the highest density of individuals. The lowest density was found for the two alien tree species (*Piper aduncum* and *Spathodea campanulata*) as well as for the most abundant native species in the secondary vegetation, *Trichospermum pleiostigma* (Table 1).

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Table 2. Larval host specificity of the most abundant root-feeding species. d: the number of individuals that emerged per m^2 over 6 mo, averaged across all study tree species; Hs and Hf: the number of host tree species and families (singleton host-plant records were excluded); Main host; the most preferred host species (see Table 1 for full plant names); P: the percentage of individuals feeding on the most preferred host species. Only species with $d \geq 0.25$ are included; the remaining 84 reared species of chrysomelids are listed in Appendix 1.

Species	Subfamily	d	Hs	Hf	Main host	P
Rhyparidella sobrina (Bryant) group	Eumolpinae	5.37	15	6	*F. pungens*	14
Rhyparida fruhstorferi Jacoby	Eumolpinae	1.53	9	4	*A. camansi*	44
Rhyparida coriacea Jacoby	Eumolpinae	1.37	8	5	*L. capitellata*	24
Rhyparida fasciata Baly	Eumolpinae	1.28	10	5	*L. capitellata*	20
Stethotes lateralis Baly	Eumolpinae	1.18	9	5	*F. variegata*	30
Sutrea sp.	Alticinae	0.81	3	2	*P. obtusifolia*	68
Unidentified sp. 1	Galerucinae	0.67	3	2	*F. hispidioides*	74
Aulacophora indica (Gmelin)	Galerucinae	0.58	8	5	*F. pungens*	18
Nisotra sp.	Alticinae	0.56	6	5	*N. corynocarpa*	30
Aulacophora sp.	Galerucinae	0.45	8	5	*M. brachytricha*	21
Xenidea sp.	Alticinae	0.41	5	3	*M. brachytricha*	41
Unidentified sp. 2	Eumolpinae	0.40	6	5	*K. hospita*	24
Aulacophora sp. nr. *pallidifasciata* Jacoby	Galerucinae	0.32	6	4	*M. brachytricha*	38
Unidentified sp. 3	Galerucinae	0.31	3	2	*M. brachytricha*	62
Rhyparida huona Gressitt	Eumolpinae	0.29	5	2	*H. novoguineensis*	33
Thyrasia? sp.	Eumolpinae	0.25	3	2	*M. brachytricha*	39

The combined chrysomelid density on the 19 native tree species was $D = 15.9$ individuals emerging from 1 m^2 in 6 mo of collecting, while the combined density for the two alien species was $D = 0.3$. The combined density for the entire vegetation was estimated at $D = 10.3$ individuals as the alien trees represented 36% of the basal area while the native trees represented the remaining 64%. This estimate assumes that the chrysomelid density for the 19 studied native trees was representative of the remaining native tree species.

The density of reared larvae per m^2 of the forest floor was not correlated with the density of their conspecific adults per m^2 of the leaf area. This was tested using larval and adult densities for 114 chrysomelid species averaged across the 15 tree species studied both for larvae and adults (Spearman $r = -0.08$, $P > 0.4$). However, both larval and adult assemblages were dominated by *Rhyparidella sobrina* species complex that represented respectively 19 and 17% of all individuals.

A total of 184 chrysomelid species was recorded in the study area, including 61 species recorded as both larvae from roots and adults feeding on foliage, 39 species reared only from roots, 8 species feeding as both larvae and adults on foliage, and 76 species only recorded feeding as adults on foliage (Table 2, Appendix 1). Eumolpinae, Galerucinae and Alticinae were dominant in the samples, representing 89% of species and 97% of individuals reared from roots and 83% of species and 96% of individuals sampled from foliage.

Chrysomelid species with root-feeding larvae dominated the foliage-feeding assemblages of 15 tree species (43% of species, 81% of individuals). An additional 22% of species representing 9% of individuals were not reared from roots but as they belonged to Eumolpinae, it was assumed that they were rhizophagous as larvae. Species and individuals with leaf-feeding larvae were few, respectively 2 and 1% (Figure 2). The larval feeding mode of the remaining species and individuals remained unknown.

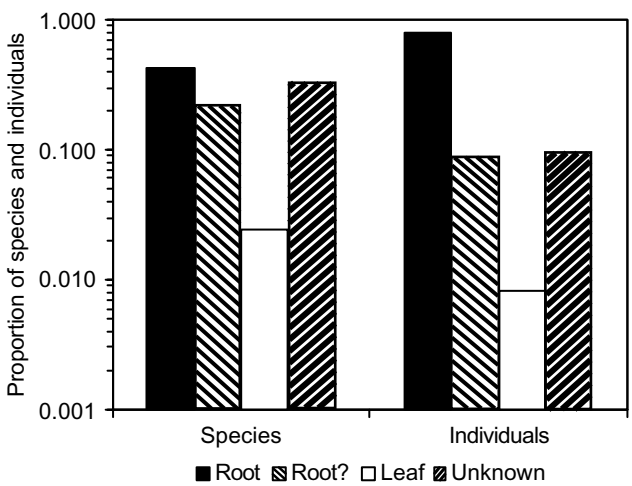

Figure 2. The importance of species with root- and leaf-feeding larvae in the assemblage of adult chrysomelids feeding on the foliage. The proportion of species (from the total of 82) and individuals (from the total of 3429) with larvae from different guilds is given for the combined sample of adult chrysomelids from the foliage of the 15 tree species studied for both root- and foliage-feeding guilds (listed in Table 1). Root: species reared from roots in the present study; Root?: Eumolpinae species that were not reared in this study; Leaf: species collected as folivorous larvae; Unknown: species collected only as adults whose subfamily affiliation is not informative on their larval feeding guild.

The number of chrysomelid species reared from particular tree species ranged from 0 to 26 per two traps and could be predicted from the number of reared

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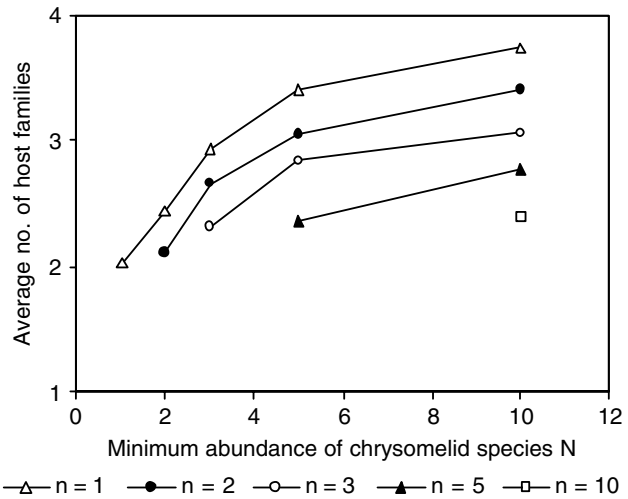

Figure 3. The effect of data filtering on host plant range estimates in a chrysomelid assemblage. The average number of host-plant families per chrysomelid species was calculated for the chrysomelid assemblage from the nine studied tree species (T9 data), using different thresholds for the minimum total abundance of each chrysomelid species across all hosts (N) and the minimum number of individuals supporting each particular host plant record (n). The complete community data are characterized by N = n = 1.

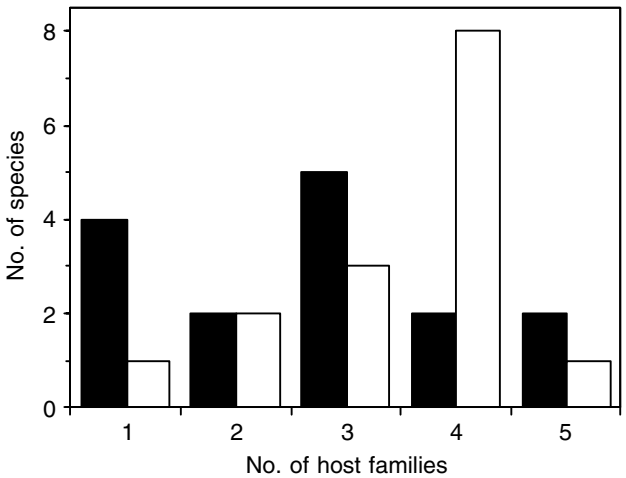

Figure 4. The number of host families recorded for chrysomelids reared from roots. Solid bars: tree species from five different families (T9 data, Table 1); empty bars: tree species from six different families (T21 data, Table 1). Only chrysomelid species collected as ≥ 10 individuals and host plant records based on >1 individual were included; each family was represented by one tree species (listed in Table 1).

individuals (Table 1; Species = 2.89 + 0.180 Individuals, r = 0.817, P < 0.001, N = 19; only native trees were included in the regression). This relationship persisted also after the effect of plant phylogeny had been removed by independent contrasts analysis (r = 0.840, P < 0.001). The number of reared chrysomelid species per tree species increased steadily with sample size from an average of 14.3 species per single trap to 59 species for the total of 12 traps in *Ficus pungens*, and from 9.2 to 42 species in *Macaranga aleuritoides*.

Host specificity of chrysomelids

The average number of host-plant families per chrysomelid species ranged from 2.0 for the entire data set to 3.7 for the subset of species collected as at least 10 individuals (Figure 3). In this data subset, the average number of host families further varied from 3.7 when all host-plant records supported by at least one individual were considered to 2.4 for host records supported by at least 10 individuals. The average host specificity in chrysomelid assemblage was thus dependent on the exact protocol used for the data filtering, i.e. the thresholds set for the minimum total abundance of each chrysomelid species in the samples and the minimum number of individuals that support each particular host-plant record.

The analysis of extensive samples from *Ficus pungens* and *Macaranga aleuritoides* demonstrated that host range also depended on sample size. The percentage of chrysomelid species found feeding on both tree species increased from 16% in the samples from one trap per tree species to 41% in the samples from 12 traps per tree species.

The modal host plant range of chrysomelid species included 3–4 families, depending on the analysis (Figure 4). None of the abundant species was specialised to a single plant family (Table 2). Further, there were three specialists with ≥ 90% of individuals feeding on a single host from the 14 chrysomelid species studied on multiple congeneric hosts (four *Ficus* and three *Macaranga* species). Likewise, five from the 14 species were limited to a single from several confamilial genera studied and five from the 15 species to a single plant family.

The abundance of chrysomelid species was a good predictor for the number of its host plant species. The number of hosts = 6.33 + 7.88 log (Density) (r = 0.886, P < 0.001, N = 20) where density was the number of individuals that emerged per m^2 during 6 mo, averaged across the 21 studied species. The number of hosts was excluding singleton records and N = 20 species collected as ≥ 10 individuals. Host-plant selection was not constrained by plant phylogeny as the Sørensen and PS similarity between pairs of chrysomelid assemblages from the 21 tree species did not decrease with increasing phylogenetic distance of their host tree species (r < 0.1, P > 0.1, Mantel test).

The host range of larvae feeding on roots was as wide as that of the conspecific adults feeding on the foliage. On average, a chrysomelid species fed on 5.8 hosts as a larva and 6.6 hosts as an adult from the 15 tree species sampled

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Table 3. Host specificity of root-feeding larvae and leaf feeding adults. N_L: the number of individuals reared from the 15 study tree species sampled both for larvae and adults (Table 1); N_A: the number of individuals collected from the foliage from the same 15 tree species; H_L: the number of hosts recorded by rearing larvae from roots; H_A: the number of hosts recorded by sampling adults from the foliage; H_Lr and H_Ar: the number of hosts expected in the samples reduced by rarefaction to the smaller of the N_L and N_A values; P_L: percentage of individuals collected by traps from the most preferred host species; P_A: percentage of individuals collected from the foliage of the most preferred host species; P: the significance of paired t-test between the parameters for larvae and adults. Only chrysomelid species with N_L and $N_A \geq 10$ and only host records supported by > 1 individual were included.

	N_L	N_A	H_L	H_A	H_Lr	H_Ar	P_L	P_A
Rhyparidella sobrina gr.	149	596	10	11	10	9.1	0.19	0.33
Rhyparida coriacea	50	487	6	13	6	9.4	0.32	0.43
Rhyparida huona	19	354	4	7	4	4.2	0.42	0.54
Stethotes lateralis	53	305	7	11	7	7.8	0.28	0.35
Rhyparida cacaovora	15	122	3	9	3	6.3	0.73	0.25
Aulacophora sp.	26	89	5	3	5	2.5	0.50	0.87
Thyrasia? sp.	12	68	3	4	3	3.2	0.42	0.62
Nisotra sp.	21	44	4	1	4	1	0.52	0.98
Rhyparida fasciata	54	39	9	5	8.8	5	0.24	0.33
Rhyparida fruhstorferi	33	28	7	5	7	5	0.42	0.29
Aulacophora indica	25	28	6	4	7	4	0.28	0.43
Mean			5.8	6.6	5.9	5.2	0.39	0.49
P			>0.4		>0.3		>0.2	

for both larvae and adults (Table 3). Another analysis that corrected for unequal sample size between conspecific larvae and adults by rarefaction also did not reveal any differences between larvae and adults. Likewise, when the host specificity was expressed as the percentage of individuals feeding on the most preferred host species (*P*), the host specificity exhibited by larvae (average $P = 39\%$) was comparable to that of the adults ($P = 49\%$).

The composition of larval and adult assemblages was uncorrelated between different host tree species. The matrix of Sørensen similarities between all pair-wise comparisons of larval assemblages involving the 15 tree species studied both for larvae and adults was not correlated with analogous matrix for adult assemblages ($r = -0.05$, $P > 0.2$, Mantel test). The same result was obtained using the Percentual similarity ($r = 0.08$, $P > 0.1$).

DISCUSSION

Species richness and abundance of chrysomelids

The present study supports the widespread assumption that the assemblages of adult chrysomelids in the canopy of tropical forests derive largely from root-feeding larvae, as was the case for at least 90% of adult chrysomelids studied here. The prevalence of root-feeding larvae results from the dominance of universally root-feeding Eumolpinae and partially root-feeding Galerucinae and Alticinae. Similar composition is typical for chrysomelid assemblages from other tropical forests, including montane New Guinea (Basset & Samuelson 1996), Borneo (Stork 1987), tropical America (Charles & Basset 2005, Erwin 1983, Farrell & Erwin 1988, Ødegaard 2003) and Africa (Wagner 1997), where root-feeding species are also likely to dominate. This conclusion however depends on the widely accepted assumption that all or nearly all Eumolpinae are root-feeders, based however on larval hosts known for only a limited number of species (Jolivet & Hawkeswood 1985).

The temporal dynamics of chrysomelid emergence is difficult to explain. We expected emergence to be highest at the onset of trapping, steadily declining over time as the larvae in the soil continued to emerge while ovipositing females were excluded by the trap. The initial period of low emergence in each trapping series is therefore puzzling. The clearing of vegetation and associated disturbance before trap placement might cause some mortality but only selective mortality of pupae and possibly older larvae explains the observed pattern of emergence. Alternatively, higher soil temperatures presumably caused by the trap could have accelerated development, creating a peak in emergence. Given these uncertainties, the total numbers of individuals that emerged over 6 mo is probably the best estimate of natural rates available. They translate to 0.2 million chrysomelids emerging annually from 1 ha of the forest. This estimate is biased due to the traps excluding ovipositing females during the study period, but also by non-random placement of the traps close to mature trees. Despite the uncertainty of this estimate, it is clear that the number of chrysomelids emerging from the forest soil was large. Recent transformation of native secondary forests by invading *Piper aduncum* and *Spathodea campanulata* (Leps *et al.* 2002, Novotny *et al.* 2004b) however would reduce the abundance of chrysomelids to only 65% of the value estimated for native vegetation as the invasive plants were devoid of chrysomelids.

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There were only eight chrysomelid species with leaf-feeding larvae among the 145 species sampled as adults from the foliage of 59 forest tree species (Novotny *et al.* 2002 and unpublished data). By contrast, incomplete sampling of only 21 tree species has documented 100 species with root-feeding larvae. The absence of larvae from tropical foliage contrasts with temperate communities. For instance, species with leaf-feeding larvae represented 57% of species and 49% of individuals in European assemblages of chrysomelids on willows (*Salix*) (Topp *et al.* 2002), compared to 2% of species and 1% of individuals in our study. The simplest explanation is different taxonomic composition between the two areas. In particular, root-feeding Eumolpinae are common in the tropics while leaf-feeding Chrysomelinae dominate in temperate areas (Kimoto 1988). This difference in distribution of subfamilies may have historical or ecological causes unrelated to the feeding habit of their larvae, but it is also possible that leaf-feeding larvae are a more viable life history in temperate forests. Intense predation by ants may be responsible for the low abundance of leaf-feeding larvae on tropical vegetation as there is a latitudinal gradient in intensity of predation by ants (Jeanne 1979) and the predation risk in tropical lowland forests is high (Novotny *et al.* 1999b). Many externally feeding chrysomelid larvae are chemically well-defended (Blum 1999, Vencl *et al.* 1999), and chemical defence has been shown to be important as a protection against ant predation (Dyer 1995).

Host specificity

The host-plant data obtained here are based only on indirect evidence. Some of the host plant records are probably false due to larvae feeding on roots other than those of the target tree species. Further, several individuals from Hispinae, Chrysomelinae and Cassidinae (Appendix 1), i.e. taxa that are not root-feeding, appeared in the samples. The source of this contamination is unclear but these species were invariably rare and did not enter the analyses based on the minimum abundance of 10 individuals per species.

Our study was restricted to secondary forest and would be difficult to replicate in primary forests where areas overwhelmingly dominated by roots of a single tree species are rare. However, assemblages of adult chrysomelids overlap between secondary and primary forest (Novotny *et al.* 1999b, 2002a) so that the present results may also be indicative of host specificity and other characteristics of chrysomelid assemblages in primary forests.

Despite these problems, the overall pattern of low host specificity is robust and well documented. Larvae typically fed on hosts from several plant families. Further, host-plant choice was not constrained by plant phylogeny as demonstrated by the lack of correlation between the similarity of chrysomelid assemblages and the phylogenetic distance of their hosts. The low host specificity of root-feeding larvae agrees with existing, largely anecdotal data. For instance, Jolivet (1988) concluded that root-feeding larvae of Eumolpinae are totally polyphagous.

The continuous increase in the number of host-plant records with increasing sample size indicates that the present estimates of host-plant ranges are conservative. Our results also demonstrate the impact of data filtering on estimates of host specificity. The use of a complete chrysomelid – host-plant matrix for the calculation of the average host specificity is clearly inappropriate because numerous singleton species, present in virtually all samples from tropical insect communities (Novotny & Basset 2000), bias the estimate towards higher host specificity. It is often impossible to decide on the minimum abundance of herbivore species sufficient for host range estimation, particularly when there is a positive correlation between the abundance of species and the number of recorded hosts across the entire abundance range, as in this and other studies (Belshaw 1994, Memmott *et al.* 1994). This correlation may reflect a biological pattern rather than a sampling artefact: viz. the abundant species having wider host ranges than rare species.

Root-feeding larvae were no more specialized than conspecific leaf-feeding adults. This is contrary to the usual trend of broadening host ranges from larval to adult stages in insect herbivores. Although conspecific larvae and adults feed on the same local vegetation, their preferences for particular hosts may not be identical, as suggested by the poor correlation between similarity matrices describing the composition of larval and adult assemblages on different tree species. Further, the densities of conspecific larvae and adults on the studied vegetation were not correlated. These results suggest that although ideally, larvae and adults should be studied in parallel, even isolated studies of adult assemblages can be informative, as the composition of adult assemblages is probably not constrained by larval host ranges.

Underground herbivory, through its impact on host-plant condition, affects the composition of above-ground herbivore communities, as well as that of the vegetation (Blossey & Hunt-Joshi 2003, Brown & Gange 1990). Root-feeding chrysomelids can be pests of tropical crops (Ferronatto 1999) or control agents of invasive plant populations (Blossey & Hunt-Joshi 2003). However, their impact on tropical forest vegetation is completely unknown. Blossey & Hunt-Joshi (2003) noted that less than 10% of studies on root-feeding insects concerned tropical ecosystems, all of them agricultural. They speculated whether this simply reflected lack of research

in the tropics or whether root-feeding insects were more important in temperate ecosystems. We suggest that root herbivory may actually be more important in tropical than temperate forests as predation pressure from tropical ants could have forced herbivorous larvae underground.

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APPENDIX 1

Additional chrysomelid species to these listed in Table 2 reared during the study. Alticinae: *Nisotra* Cassidinae: *Aspidimorpha australasiae* Boisduval, *Meroscalsis selecta?* Spaeth, 2 *Meroscalsis* spp.; Chrysomelinae: *Promechus bimaculatus* (Weise), 1 indet. sp.; Criocerinae: *Lema staudingeri* Jacoby, 2 indet. spp., Cryptocephalinae: 1 indet. sp.; Eumolpinae: *Cleorina* sp., 5 *Deretrichia* spp., *Rhyparida basalis* Baly, *R. cacaovora* Gressitt, *R. calami* Gressitt, *R. lineolata* Gressitt, *R. normalis* Gressitt, *R. picticollis* Gressitt, *R. sinuata* Gressitt, 8 *Rhyparida* spp., *Rhyparidella sewana* Gressitt group, 2 *Rhyparidella* spp., *Stethodes integra Neodrana*, *Stethotes nigritula*? Baly?, *Thyrasia*? sp., 10 indet. spp.; Galerucinae: *Aulacophora propinqua* Baly, *Aulacophora* sp. nr. *pallidifasciata* Jacoby, 1 *Aulacophora* sp., *Cassena* sp., *Lomirana* sp., 11 indet. spp.; *Microlepta* sp., *Monolepta* sp., *Neodrana* sp., *Prasyptera* sp. nr. *ornata* Baly, *Sastra limbata* Baly, 3 *Sastra* spp., 14 indet. spp.; Hispinae: *Hispellinus albertisi* Gestro.

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