



How many species of host-specific insects feed on a species of tropical tree?

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The assumptions on the host specificity of beetles that led Terry Erwin to suggest that there may be over 30 million arthropod species were tested for 10 species of trees and their insect associates at a rainforest site in Papua New Guinea. The data included 391 species and 4696 individuals of herbivorous beetles collected during a one year period using hand collecting, beating, branch clipping, intercept flight traps and pyrethrum knockdown. Insect host specificity was assessed by feeding trials in captivity. The data suggest that between 23 and 37 monophagous leaf-feeding species are most likely to be present in this system, whereas Erwin's method yields an estimate of 138 monophagous species. The major factors responsible for the discrepancy between our observations and Erwin's assumptions appears to be (a) the importance of transient species; (b) the insect fauna that is shared among tree species; (c) some generalist wood-eating species may inflate the apparent species richness of leaf-feeding beetles; and (d) the proportion of specialist species varies significantly among tree species. We conclude that studies reporting the proportion of specialist insect herbivores associated with particular tropical tree species will yield only a portion of the information needed to estimate global arthropod species richness, but may be useful for elucidating certain aspects of food-web ecology in tropical rain forests.

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ADDITIONAL KEY WORDS:— beetles – biodiversity – chewing insects – Coleoptera – host specificity – Papua New Guinea – species richness.

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INTRODUCTION

Nearly 15 years ago, in an ingenious and visionary paper, Erwin (1982) suggested that there may be as many as 30 million species of arthropods, instead of the previously estimated 1.5 million species. His conclusions were based on fogging 19 individuals of the tropical tree *Luehea seemannii* in Panama (Erwin & Scott, 1980). His assumptions and calculations are well-known and can be summarized as in Table 1.

Subsequently, Erwin (1988) admitted that he was surprised by the attention that his calculations received and the controversy they generated. He stressed that he had simply advanced a hypothesis that could be tested rigorously, and suggested that this "must begin by refining of our knowledge about host specificity of insects in tropical forests". Most of the attention in this controversy has focused on the likely number of tropical insect species in relation to the massive destruction of tropical forests. This is a different issue. As Erwin (1988) put it, "no matter what the number we are talking about, whether 1 million or 20 million (arthropod species), it is massive destruction of the biological richness of Earth."

The important scientific controversy surrounding Erwin's paper concerns the relative species richness of soil and canopy faunas (Step 10 in Table 1; e.g. Stork, 1988; Hammond, 1992; André, Lebrun & Noti, 1992) and the proportion of host-specific insect species associated with tropical trees (Step 3 in Table 1; e.g. Stork, 1988; May, 1988, 1990; Thomas, 1990; Hammond, 1992; and see Erwin, 1988). Several authors pointed out the sensitivity of Erwin's estimates to the proportion of

TABLE 1. Assumptions and calculations that led Erwin (1982) to suggest that there are as many as 30 million species of tropical arthropods

1. Number of beetle species collected from <i>L. seemannii</i> :	c. 1200
2. Number of beetle species is distributed among trophic categories as follows: herbivores = 682; predators = 296; fungivores = 69; scavengers = 96.	
3. Proportion of beetles host-specific to <i>L. seemannii</i> guessed among trophic categories as: herbivores = 20%; predators = 5%; fungivores = 10%; scavengers = 5%	
4. Number of beetle species host-specific to <i>L. seemannii</i> : $(682 \times 0.2) + (296 \times 0.05) + (69 \times 0.1) + (96 \times 0.05) =$	163
5. Average percentage of host-specific beetle species on <i>L. seemannii</i> : $(163 / 1200) \times 100 =$	13.5%
6. Number of species of tropical trees:	50 000
7. Number of beetle species supported by tropical trees: $163 \times 50\ 000 =$	8 150 000
8. Beetle species represent about 40% of all arthropod species	
9. Number of arthropod species supported by tropical trees: $8\ 150\ 000 \times 2.5 =$	20 375 000
10. Canopy fauna twice as rich as that of the forest floor	
11. Number of species of tropical arthropods: $20\ 375\ 000 \times 1.5 =$	c. 30 000 000

host-specific herbivores (20%, see Step 3 in Table 1; e.g. Stork, 1988; May, 1988, 1990). Thomas (1990) further contended that tropical plants do share certain insect species and that Erwin's estimates must be corrected accordingly.

Most authors commented on the actual value of the proportion of specialist insect species that depend on a particular tree species, but few addressed whether this proportion would vary significantly among tropical tree species and whether it was sound to use the same proportion for the 50 000 tree species in Erwin's calculations. In other words, how representative is *Luehea seemannii* of other tropical tree species? (See May, 1990; and Briggs, 1994 for a similar contention regarding estimates of species-richness in marine ecosystems). In reviewing the scarce information on the host specificity of free-living insect herbivores in rainforests, Basset (1992) suggested that insect faunas supported by particular tree species could range from highly specialist to highly generalist, depending on the characteristics of the host-tree and of the surrounding forest.

Investigating this question, which appears to be crucial in Erwin's estimates, is also an important step towards a better understanding of the ecology of tropical rainforest systems. In particular, it is of considerable interest to know, and perhaps even to be able to predict, to what extent insect species are shared between food-webs centered on particular tree species and whether these patterns are influenced by forest types, past history and geographical location.

However, since the publication of Erwin's paper, few data have appeared reporting the proportion of host-specific insect herbivores associated with different species of tropical trees (but see Marquis, 1991 for insects associated with *Piper* spp.). In this contribution, we present data on ten species of tropical trees and the proportion of host-specific insects associated with them. The aims of this paper are not to discuss global estimates of arthropod species richness (e.g. May, 1988, 1990; Stork, 1988, 1993; Erwin, 1991; Gaston, 1991; Hammond, 1992; Briggs, 1994), or the number of host-plants that insects use (e.g. May, 1990; Gaston, 1993) but to test empirically (a) whether the proportion of specialist insects varies markedly among tree species; (b) whether it is legitimate to use a common proportion derived from a particular tree species to estimate the number of host-specific species present in the system; and (c) whether other factors may complicate such estimates. The analyses emphasize leaf-chewing insects, since the association of these with their putative host-trees could be ascertained from feeding trials, and, secondly, beetles, because Erwin's calculations are derived from beetle data.

MATERIAL AND METHODS

Study site and insect collecting

The study was performed on the slopes of Mt Kaindi, near and within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7°24' S, 146°44' E). Altitude of collecting sites ranged from 1100–2362 m (summit), but was mostly confined around 1200–1400 m. Mt Kaindi has been locally cleared, leaving a mosaic of grasslands and forest patches dominated by secondary forest (Van Valkenburg & Ketner, 1994). Mean annual rainfall and temperature are 1900 mm and 22°C, respectively (Allison, Samuelson & Miller, 1993). The main forest formations encountered on the slopes include lower and mid-montane rain forest. The study

TABLE 2. Study trees, their successional status (Pi = pioneer, Pe = persistent) and average height when mature (H: S < 15 m, T > 15 m); their phenology of leaf production (Ph; C = continuous; I = intermittent; D = deciduous); the number of species of proven feeders (PR); the percentage ratio of specialist species for all chewing species (%CH) tested and for all non-beetle species tested (%NB, see text)

Hosts	Plant family	Status. H	Ph	PR	%CH	%NB
<i>Elmerrillia tsiampacca</i> (L.) Dandy	Magnoliaceae	Pe, T	C	20	36	33
<i>Cinnamomum</i> cf. <i>culilaban</i> (L.) Presl	Lauraceae	Pe, S	I	37	49	45
<i>Piper plagiophyllum</i> K. Sch. & Laut.	Piperaceae	Pi, S	C	18	38	13
<i>Ficus nodosa</i> Teys. & Binn.	Moraceae	Pi, T	D	61	63	69
<i>Pipturus argenteus</i> Wedd.	Urticaceae	Pi, S	C	52	60	61
<i>Castanopsis acuminatissima</i> A. DC.	Fagaceae	Pe, T	I	94	73	73
<i>Caldcluvia brassii</i> Hoogl.	Cunoniaceae	Pi, S	C	39	31	29
<i>Aleurites moluccana</i> Willd.	Euphorbiaceae	Pe, T	C	25	16	15
<i>Melicope denhamii</i> (Seem.) T. Hartley	Rutaceae	Pe, S	I	36	39	42
<i>Cordia dichotoma</i> Forst.	Boraginaceae	Pi, T	D	45	45	46

area is detailed further by Gressitt & Nadkarni (1978) and Van Valkenburg & Ketner (1994).

Insect herbivores were collected from ten common native species of forest trees and shrubs belonging to different plant families and of different successional status (Table 2). Hereafter, the hosts are designated by their generic names. Most of the chewing insects collected included: adults of Scarabaedidae (Melolonthinae), Lagriidae, Cerambycidae (species that chew leaves to mature), Chrysomelidae, Curculionoidea; Lepidoptera larvae; and adults and nymphs of Orthoptera and Phasmatoptera.

Insects were collected by the first author from the foliage of the study trees by hand collecting, foliage beating, branch clipping, intercept flight traps and pyrethrum knockdown. The first four methods were used both during day and night, whereas pyrethrum knockdown was only performed early morning. Specimens collected alive with the first three methods were used in feeding trials (see next section). Hand collecting and foliage beating represented, for each tree species, about 50 hours of hand-collecting activity and 300 beating samples distributed among different individual trees. Branch clipping represented, for each tree species 55 samples of about 33 m² of leaf surface, obtained from different individuals. One intercept flight trap (Springate & Basset, 1966) was set up in the middle of the crown of one individual of each tree species. The trap collected insects continuously over 1 year and was surveyed approximately every 11 days. One individual of each tree species was sampled using pyrethrum knockdown (solution of 5% Pyranone[®] in kerosene), using from 12 to 20 trays (1 m² of surface each), depending on tree size (total 159 trays used for all tree species). The protocol of Allison *et al.* (1993) was followed with the only difference being that trees were fogged by climbing directly into them, instead of an adjacent tree.

Active sampling was performed from February to July 1992 and from November 1992 to April 1993; traps were run from April 1992 to April 1993. Thus, field data have been gathered over more than a year and take account of the seasonal variation in insect diversity and abundance at the Wau site. When the foliage could not be sampled from the ground, the single rope technique provided access to the crowns (Perry, 1978). Sampling effort was approximately the same for each tree species and all material thus derived has been considered for subsequent analyses.

Other parameters describing the study trees and their associated insects, particularly species accumulation curves and the representativeness of sampling, are presented elsewhere (Basset, 1996). Briefly, species accumulation curves showed that most leaf-feeding species associated with continuously-leaving tree species may have been collected, but that insect species-richness on intermittently flushing tree species may have been underestimated.

Morphospecies assignment and assessment of host-specificity

Insect herbivores were first assigned to morphospecies by Y.B. in Papua New Guinea on the basis of external characters. For Lepidoptera, only mature caterpillars were assigned to morphospecies. As far as possible, caterpillars were reared to obtain adults and to refine morphospecies assignments. Since knowledge of the ecology of most Papuan insects is fragmentary, specialization of adult insects had to be assessed from feeding trials in the laboratory. Insects were stored in plastic vials, at room temperature and near-saturated relative humidity. Fresh foliage of the tree from which they were collected was provided, until they died or accepted food. Those that fed were then tested in random order for 24 h periods on the foliage of the nine other plant species. Feeding damage was scored visually, relative to insect body size, on a logarithmic scale, as follows: 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding. This emphasized regular feeding as compared to food-probing. All Curculionoidea collected on the foliage (except Scolytinae and Platypodinae) were tested on leaves but some were later assigned to the wood-eater guild (see below). Insects were assigned to categories reflecting insect affinity with the 10 tree species studied on the basis of the feeding trials (see below).

Adults of insect herbivores were later dry mounted at the Bishop Museum, Honolulu. Morphospecies assignment, hereafter 'species' for sake of simplicity, was checked by the second and fourth authors (Coleoptera and Lepidoptera, respectively), and verified by specialists in many cases. The material has been deposited in the collections of the Bishop Museum.

Categories of host-insect affinity retained for the analyses

For sake of simplicity, we use the terms 'monophagous' as applying to herbivores feeding on a single host-plant (strict monophagy; equivalent to 'host-specific' in Erwin's assumptions); 'oligophagous' for herbivores feeding on a few hosts from the same plant family; and 'polyphagous' for herbivores feeding on hosts from unrelated plant families. Specialist and generalist feeders refer to monophagous and oligophagous species, and to polyphagous species, respectively.

Insects were initially assigned to five categories according to the results of the feeding tests on the nine other tree species:

- (a) 'specialists': insects tested on three or more plant species but which only fed extensively on the plant they were collected from (sum of feeding scores < 100);
- (b) 'generalists': insects tested on three or more plant species and which fed extensively on two or more plants belonging to different plant families (sum of feeding scores > 100);

(c) 'uncertains': insects which, because of death or pupation, could not be tested on more than two plant species;

(d) 'incidentals': insects which did not feed on any species in the trials (only beetle morphospecies were considered in this last assignment, in order to avoid including parasitized or molting caterpillars); and (e) 'additional': species collected dead (e.g. by intercept flight traps and pyrethrum knockdown) and which were not tested.

In general, there was a good correspondence between the food preferences as assessed in feeding trials and insect presence on a particular tree species. This is probably due to the emphasis of the experimental protocol being on recording possible feeding on hosts that belong to different plant families, rather than being on recording feeding on related hosts and the number of such hosts accepted (see further discussions in Basset, 1994; Basset & Samuelson, 1996).

Often weevils exhibit a wide range of food habits and are not restricted to leaf-feeding. Weevil species that were collected dead and not tested in feeding trials were assigned to the categories 'additional, chewing species' (i.e. feeding on living plant tissue) or 'additional, wood eater' (i.e. feeding on dead tissues) using the information provided by experienced weevil taxonomists (E. C. Zimmerman & R. S. Anderson, pers. comm.). The following nested beetle categories were retained for the analyses (listed in order of decreasing probability of strict association with the host):

- (1) *Specialists*. Category (a) in feeding trials. They include monophagous and oligophagous species.
- (2) *Proven feeders*. Categories (a), (b) and (c) in feeding trials. All of these species fed upon the study trees, but also include some polyphagous species.
- (3) *Likely associates*. This category included proven feeders plus other species likely to feed upon the study trees. In the incidental and additional categories, we selected species which were unlikely to be wood-eaters and for which four or more individuals were collected, irrespective of sampling methods. This threshold was chosen since a more detailed analysis of chrysomelid beetles (Basset & Samuelson, 1996) suggested that species for which fewer than four individuals were recorded in the samples were most likely to be transients present by chance and not associated with the tree species studied (see Janzen, 1977 for a thorough discussion of transient species). These selected species were added to the proven feeders category to obtain the 'likely' associates category. As such, the category include some leaf feeders that could not be tested in trials, as well as chewing insects likely to be associated with the seeds, flowers, buds, stems, etc. of the host, but not feeding on its leaves.
- (4) *Chewing species*. This category encompasses all species likely to feed on living plant tissues, including transient species (i.e. all species collected except those which are likely to be wood-eaters).
- (5) *'Herbivores'*. This category includes all chewing species plus some wood-eating Curculionoidea. It is close to the 'herbivores' category of Erwin (1982), which further included all Buprestidae, Cerambycidae, Scolytinae, etc.

Estimates of the number of monophagous species present in the system

We do not claim that sampling in our system has been thorough enough to identify with certainty all monophagous species present, as this would require additional

years of sampling on other hosts, as well as laboratory tests of all species collected. However, the scope of our data is such that it is possible to use them to calculate the lower and upper limits of an estimate of the number of monophagous species. It is even possible to distinguish between the 'most probable' and the 'least probable' estimates of the upper limit of such an estimate.

Our procedure can be summarized as follows: (1) to calculate the lower and upper limits of the estimate of the number of specialist species present in the system (including monophagous and oligophagous species); (2) to calculate the lower and upper limits of the estimate of the number of monophagous species; (3) to apply Erwin's assumptions to our data and to compare the estimate obtained with our results; and (4) to highlight some of the factors complicating Erwin's assumptions.

Firstly, we need to calculate the overall ratio of specialist species in the system, using 'pooled' numbers of species (i.e. numbers of species after insect species have been cross-referenced among tree species):

$$\text{Overall ratio of specialists} = \frac{\text{total no. of specialist spp.}}{\text{total no. of specialist spp.} + \text{total no. of generalist spp.}} \times (\text{Eq. 1})^{-1}$$

This ratio can also be calculated for the fauna of each tree species. Secondly, the lower limit of the number of specialist species in the system is straightforward: we assume that all specialist species have been collected and tested, and, therefore, use the number of species in the specialist category. Thirdly, we can estimate the most probable upper limit of the number of specialists by assuming that the ratio of specialist to generalist species in the likely associates which were not tested in the feeding trials, and in the 'uncertains', is similar to that found overall in the system:

$$\text{Most probable upper limit} = \text{Specialists} + (\text{Associates-Proven feeders}] + \text{Uncertains}) \times \text{Overall specialist ratio} \quad (\text{Eq. 2})$$

Similarly, assuming that the ratio of specialists to generalists in the 'herbivores' which were not tested and in the 'uncertains' is similar to that found overall in the system, we can easily calculate a least probable upper limit for the number of specialist species present in the system:

$$\text{Least probable upper limit} = \text{Specialists} + (\text{Herbivores-Proven feeders}] + \text{Uncertains}) \times \text{Overall specialist ratio} \quad (\text{Eq. 3})$$

Since each of the tree species studied belong to a different plant family, the feeding trials do not allow us to infer the number of monophagous species present in the system. This has to be estimated from local ratios of monophagous and oligophagous species in known tropical insect faunas. Unfortunately, data for tropical herbivorous beetles are few. The ratios of monophagous: (monophagous + oligophagous) species that we compiled from the literature are as follows: leaf-feeding weevils on *Piper* spp., La Selva, Costa Rica: 26% (Marquis, 1991); caterpillars in Santa Rosa, Costa Rica: about 56% (Janzen, 1988); Saturniidae and Sphingidae in Santa Rosa: 76% and 56%, respectively (Jansen, 1985); butterflies on the Wau Valley: 54% (Parsons, 1991); butterflies in La Selva: 81% (Marquis & Braker, 1993); and grasshoppers in La Selva: 50% (Marquis & Braker, 1993). We use the mean of these observations (57%), rather than that relevant to leaf-feeding weevils on *Piper*, as Marquis (1991) regarded this figure as exceptionally low.

Using this average value, we can easily estimate the lower and upper limits of the number of monophagous species present in the system:

$$\text{Lower limit} = \text{lower limit of the specialist estimate} \times 0.57 \quad (\text{Eq. 4})$$

$$\text{Most probable upper limit} = \text{most probable upper limit of the specialist estimate} \times 0.57 \quad (\text{Eq. 5})$$

$$\text{Least probable upper limit} = \text{least probable upper limit of the specialist estimate} \times 0.57 \quad (\text{Eq. 6})$$

On the other hand, applying Erwin's assumptions to calculate the number of monophagous species present in the system results in considering 20% of species in our 'herbivore' category collected on each tree species as being monophagous. This is the same as considering 20% of the total of 'unpooled' species of 'herbivores' (i.e. species not cross-referenced among tree-species) as being monophagous:

$$\text{Erwin's assumption} = \text{Sum of unpooled herbivores} \times 0.2 \quad (\text{Eq. 7})$$

RESULTS

The number of beetle species present in the system

The analyses included 6130 individuals of chewing insects distributed in 704 species. Beetles dominated the samples with 4696 individuals and 391 species. The Appendix summarizes the results of feeding tests plus the ultimate assignments of beetle 'herbivores' into either chewing or wood-eating species. The number of chewing species collected per host (all insect taxa considered), and the percentage ratio of specialists, are detailed in Table 2; the data specific to the beetles are given in Table 3. For sake of completeness, we present separately data obtained with pyrethrum knockdown (since Erwin gathered his data with this method) and with all

TABLE 3. Number of species of beetle 'herbivores' collected by fogging (F) and by all collecting methods (AM), detailed for the following categories: specialists (with % of specialist species for the particular collecting method in brackets); proven feeders; associates; chewing species; and 'herbivores' (see text)

Host	Specialists		Pr. feeders		Associates		Chewing		Herbivores	
	F	AM	F	AM	F	AM	F	AM	F	AM
<i>Elmerrillia</i>	0 (0)	1 (33)	0	8	1	12	4	31	4	39
<i>Cinnamomum</i>	0 (0)	3 (75)	0	4	11	26	27	68	29	83
<i>Piper</i>	2 (100)	4 (50)	2	8	3	14	15	44	23	69
<i>Ficus</i>	4 (36)	8 (38)	11	22	12	29	21	55	26	82
<i>Pipturus</i>	4 (50)	10 (59)	9	22	14	32	16	52	20	73
<i>Castanopsis</i>	2 (50)	5 (71)	3	9	7	19	19	54	20	64
<i>Caldcuvia</i>	2 (40)	5 (33)	5	17	6	33	13	86	22	113
<i>Aleurites</i>	0 (0)	1 (17)	2	7	3	11	9	36	9	46
<i>Melicope</i>	0 (0)	2 (22)	1	9	7	17	13	65	14	76
<i>Conlia</i>	0 (0)	2 (40)	1	5	5	9	9	32	10	45
All (not pooled)	14 (41)	40 (43)	34	111	69	202	146	523	177	690
All (pooled)	14 (50)	40 (55)	28	86	53	118	106	300	130	391

sampling methods considered together. However, the results and discussion focus on the latter. The number of beetle species that fed upon or were collected from different tree species was considerable in our insect-plant system. In proven feeders, the pooled data showed that 40, 33 and 13 species of specialists, generalists and uncertain, respectively, were present in the system. The total number of species was reduced by 43% when pooling the results among tree species. For example, the category 'herbivores' was reduced from 690 to 391 species (Table 3). This decline was similar in the likely associates and chewing species categories (43 and 42% of reduction, respectively), but was much lower in the proven feeders category (23% by definition the decline is 0% in the specialist category). This suggests that the probability of a specialist (i.e. a species not shared among tree species) being recorded in either the likely associates, chewing species or 'herbivores' categories, and not in the proven feeders category, is rather low.

As seen from Table 3, the number of species collected in each category increases with a diminishing probability of being strictly associated with the host. The largest discrepancy is found between the likely associates and the chewing species categories (an increase from 118 to 300 species, data pooled, Table 3). Since the probability of discovering 'new' specialist species in the chewing species category is probably low, this should not affect confidence in the 'proven feeders' and 'likely associates' data. These trends were similar when we restricted the analysis to fogging data (Table 3).

The proportion of specialist species on each tree species

The proportion of specialists associated with the tree species studied, measured either as beetle species, non-beetle species or all chewing species, tended to be very similar (compare Tables 2 and 3, all collecting methods considered). In particular, there was no significant difference between the proportion of specialists as expressed by beetles and non-beetle species (Mann-Whitney $U = 52.0$, $P = 0.88$). This suggests that in most cases the proportion of specialists within all chewing species can be inferred from that within beetles. However, in the proven feeders category, there was little correlation between the number of beetle and non-beetle species recorded ($r_s = 0.09$, $P > 0.50$). For example, *Castanopsis*, *Cordia* and *Cinnamomum* overall supported many species of chewing insects but the contribution that beetle species made to this richness was relatively low.

Overall the percentage of specialists within the system was 55% (Table 3, second column, data pooled for all tree species). The proportion of specialist beetle species did not vary significantly among tree species (range from 17 to 75%; G-test with the number of specialist and generalist species recorded, $G = 10.4$, $P = 0.32$). However, this result is certainly obscured by the low sample size and is statistically difficult to interpret. Indeed, the proportion of non-beetle specialist species and of all chewing specialist species differed significantly among study trees ($G = 38.0$, $P < 0.001$ and $G = 39.9$, $P < 0.001$, respectively).

The number of monophagous species present in the system

Using the data in Table 3, we can estimate a likely range for the number of specialist and monophagous species present in the system. First the lower limit of the

number of specialist species is 40 (Table 3, second column; data pooled). The most probable upper limit of the estimate is (Eq. 2):

$$40 + ((118 - 86) + 13) \times 0.55 = 65 \text{ specialist species}$$

Similarly, the least probable upper limit of the estimate is (Eq. 3):

$$40 + ((391 - 86) + 13) \times 0.55 = 215 \text{ specialist species}$$

Using 57% as a basis to extrapolate the number of monophagous species from the number of specialist species, the estimates of the number of monophagous chewing insects in the system now are (Eq. 4 to 6):

$$\text{Lower limit} = 40 \times 0.57 = 23 \text{ monophagous species}$$

$$\text{Most probable upper limit} = 65 \times 0.57 = 37 \text{ monophagous species}$$

$$\text{Least probable upper limit} = 215 \times 0.57 = 123 \text{ monophagous species}$$

Thus, our data suggest that it is most likely that between 23 and 37 monophagous species are present in the system. These estimates may be compared with those obtained using Erwin's assumptions (Eq. 7):

$$690 \times 0.2 = 138 \text{ monophagous species}$$

This estimate is 4.6 times greater than the mid-value of our most likely estimate (30 monophagous species).

Putative factors complicating Erwin's assumptions

Our data also provide the opportunity to examine particular caveats of Erwin's assumptions. First, the fauna shared between tree species must be accounted for in the calculations. If this was the only problem with Erwin's assumptions, we could calculate the number of monophagous species in the system as:

$$\text{Pooled no. of herbivore species (from Table 3, last column)} \times 0.2 = 391 \times 0.2 = 78 \text{ monophagous species.}$$

Despite this correction, the result is still rather higher than our most probable estimate. Second, the proportion of 20% monophagous insect-species per tree species suggested by Erwin (1982) may be too high. If we keep our assumption of 57% for the ratio of monophagous to oligophagous species, this 20% monophagous species should translate to 35% of specialist species overall [$0.2 \times (1/0.57) = 0.35$]. Since our unpooled data suggest a specialist ratio of 43% (Table 3 second column, unpooled data), there appears to be little problem with Erwin's estimate.

However, a related and more serious problem may be the inclusion in the calculations of many species that are not leaf-feeders but wood-eaters and, therefore, less host-specific (see Discussion). Accounting for the fauna shared between tree species and discounting weevil species most likely to be wood-eaters yielded an estimate closer to our observations:

$$\text{Pooled no. of chewing species (Table 3, 8th column)} \times 0.2 = 300 \times 0.20 = 60 \text{ monophagous species}$$

Third, Erwin's calculations overlook the problem of transient species that are dispersing from tree species not under study (see discussions in Janzen, 1977; Stork,

1993). Accounting for the fauna shared between tree species and retaining species only with a good probability of association yields an estimate within the range of our observations:

$$\text{Likely associates} \times 0.20 = 118 \times 0.20 = 24 \text{ monophagous species}$$

DISCUSSION

Limitations of the data

A summary of the differences between Erwin's study and ours and of the potential problems associated with both studies is necessary before discussing the results. The present sampling scheme aimed at collecting leaf-chewing insects, and, therefore, insects associated with flowers and seeds were rarely collected, and are likely under-represented in the samples. Therefore, the present data and discussion emphasizes leaf-feeding beetles. Our sampling scheme also included several complementary sampling methods, most of them being used during day- and night-time. In contrast, Erwin's samples were obtained solely from fogging performed early in the morning. Thus, our sampling effort is at least as high as that of Erwin's (see discussion of Hammond, 1990, for the usefulness of using complementary sampling methods). Erwin & Scott (1980) collected 2906 individuals of leaf-feeding beetles representing 215 species (excluding weevils), whereas the present samples consisted of 2612 individuals and 183 species (excluding weevils). Further, Erwin & Scott (1980) included many wood-eaters in their 'herbivore' category, such as some Buprestidae, Cerambycidae and Curculionidae. Assigning most of the species belonging to the above families to the 'scavenging fauna' guild (wood-eaters, fungal feeders and scavengers) appears more appropriate (Moran & Southwood, 1982), unless adults chew leaves regularly or for maturation feeding.

Further, both data sets are based on adult beetles. In our system, most of the larvae of the species collected do not live as free leaf-feeders, but rather as root-feeders and concealed feeders (Basset, Springate & Samuelson, 1994). Unfortunately, the larval ecology of most species collected is unknown, so that it is impossible to know whether our conclusions would have been different were they based on larval ecology alone.

Finally, the interpretation of our data concerns mainly beetles, as we wanted to test Erwin's assumptions, developed with beetle data. Our data suggest that the proportion of specialist insect species on each of the tree species studied and that of specialist beetle species may be similar. However, if Erwin would have applied his assumptions to insects less vagile than beetles, such as Lepidoptera larvae, it is not known whether his estimates of global arthropod richness would have been different. One complicating factor in using Lepidoptera larvae is that their taxonomy and morphospecies assignment is more difficult than that of adult beetles.

Factors complicating Erwin's assumptions

It is probable that the discrepancy between an estimate using Erwin's assumptions (138 leaf-feeding monophagous species predicted for the system) and ours (23–37

monophagous species) results from several factors. First, as already noted by several authors (e.g. May, 1990; Thomas, 1990), the fauna shared between tree species must be accounted for in the calculations. Despite this correction, Erwin's method still yields a high estimate (78 monophagous species). Thus, generalist species are but one problem for these estimates of species richness. May (1990) (see Stork, 1993) attempted to address this problem theoretically by using a function representing "the proportion of beetle species which are effectively specialised". However, these theoretical considerations do not solve the three other problems discussed below and, in particular, May's contribution does not solve the problem of transient species except in the unlikely situation that *all* plant species in the study area are sampled.

Second, several authors have suggested (e.g. Stork, 1988; May, 1990) that the proportion of 20% monophagous insect-species per tree species suggested by Erwin (1982) may be too high. The assumption that we applied to our data do not clearly negate this. Note that the proportion for the pooled data (55%; Table 3, second column, pooled data) suggests that slightly fewer than half the species within the system are generalist (polyphagous) as adults, a high proportion indeed.

Inclusion in the calculations of many species that are not leaf-feeders but wood-eaters may be a more serious problem, as our data suggest. Usually, wood-eaters rarely feed on living tissues and are therefore often much less host-specific in the tropics than leaf-feeders (e.g. Schedl, 1958; Basset, 1992).

Our data also suggest that Erwin's calculations overlook the problem of transient species that are dispersing from tree species not under study (see discussions in Janzen, 1977; Stork, 1993). For example, besides their normal hosts, specialist species may be collected on other tree species. With greater diversity of plant species within the study site, more transient species are likely to be collected on the foliage of study trees (further discussion in Basset).

Finally, the ratio of specialists may be very different among tree species and study sites and this may complicate the calculations. Our data support the suggestion of Basset (1992) that tropical tree species may support very different loads of specialist species according to host and forest characteristics (and see Basset, in press a). Further, certain of the tree species that we studied supported a relatively rich beetle fauna, whereas others did not. However, despite these important differences, in the end, the overall proportion of specialist beetle species was reasonably close to Erwin's estimate (Erwin, 1982), as previously emphasized. The problem lies elsewhere. If the proportion of specialist species varies significantly among tree species, it may also vary significantly between forest types and geographic locations. For example, chrysomelid samples obtained from *Luehea* on Panama (Erwin & Scott, 1980) and from different tree species in the Peruvian Amazon (Farrell & Erwin, 1988) were dominated by Alticinae, whereas our chrysomelid samples in Papua New Guinea (Basset & Samuelson, 1996) and those of Stork (1991) in Borneo were dominated by Eumolpinae. Since Alticinae are often more specific than Eumolpinae (e.g. Jolivet, 1988), the overall proportions of specialists on particular tree species in Panama or Peru may be higher than these in Papua New Guinea or Borneo. These considerations are not limited to herbivore groups. Another striking example of the difference between Erwin's samples in Panama and ours is the almost complete absence of Carabidae in New Guinea canopy samples, whereas these insects represented about 14% of all beetle individuals on *Luehea*.

Aside from differences in taxonomic composition of the overall fauna, regional differences in overall tropical diversity cannot be ignored if one is interested in estimating global species richness. Although data on regional diversity are too poor for comparisons among most beetle taxa, there is a marked difference in regional butterfly faunas. Within equal-sized areas, species richness of butterflies in the Oriental region is about half that in the Neotropical region (Robbins, 1993). Similarly, regional differences in species richness have also been noted for trees, which are more speciose in the neotropics than in Southeast Asia (Gentry, 1988). Further, the geographical and geological isolation of New Guinea may prevent insect diversity from reaching the high levels found in large continental areas, such as South America.

The applicability of Erwin's assumptions to estimate global species richness

In our system, Erwin's method must be scaled down by a factor of 4.6 to yield estimates close to those we judge to be most probable. In other words, only about 4.3% of the total number of unpooled species of beetle 'herbivores' collected were likely to be monophagous in our system, instead of the 20% estimated by Erwin. Scaling down Erwin's estimate of 163 host-specific species on *Luehea* by a factor 4.6 (= 35 species; assuming that some of the problems that we uncovered with herbivorous beetles also apply similarly to beetle species belonging to other feeding guilds), following his chain of calculations and setting aside other potential problems, yields a global estimate of 6.6 million arthropod species. Is it legitimate to use this correcting factor, obtained from a site in Papua New Guinea, for data gathered in Panama? We do not believe so, since we showed that the proportion of specialist species varies significantly among tree species, and, therefore and most likely, also among study sites as well. In other terms, since tree species are so different, we are reluctant to use our Wau data to calculate total insect species richness in New Guinea or in the entire World. We see this as a major impediment to estimating global arthropod species-richness, unless, as suggested by Erwin (1991), most biodiversity occurs in certain restricted localities, such as the Amazon. On the other hand, if Erwin's estimates can be corrected by an appropriate factor, dependent on local characteristics (note that this may include scaling down or up, depending on the system studied; for the latter see Majer, Recher & Postle, 1994), they could be useful for predicting local species-richness, and, perhaps even regional species-richness, providing that local correcting factors do not differ markedly from each other. The ratios of monophagous to oligophagous species may also vary among geographic locations and, for insects associated with a limited number of hosts, may further covary with the taxonomic isolation of the hosts.

We conclude, as others have suggested previously but for different reasons (e.g. May, 1990; Hodkinson & Casson, 1991; Gaston, 1991; Hammond, 1992), that studies reporting the proportion of specialist insect herbivores associated with particular tropical tree species are unlikely to yield precise estimates of global arthropod species richness. However, such studies are useful in estimating local species richness, and elucidating certain aspects of food-web ecology in tropical rain forests.

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APPENDIX

Number of species of beetle 'herbivores' feeding, not feeding and not tested in feeding trials, along with the assignment of species to either the chewing or wood-eating categories (na = not available)

Taxa	Feeding	Not feeding	Not tested	Chewing	Wood-eaters
Scarabaeidae					
Melolonthinae	0	0	15	15	0
Buprestidae	0	2	na	0	na
Elateridae	1	na	na	1	na
Lagriidae	4	2	1	7	0
Cerambycidae					
Cerambycinae	1	na	na	1	na
Lamiinae	14	na	na	14	na
Chrysomelidae					
Alticinae	3	8	11	22	0
Cassidinae	0	3	0	3	0
Chrysomelinae	0	0	2	2	0
Cryptocephalinae	1	0	8	9	0
Eumolpinae	23	9	10	42	0
Galerucinae	9	21	28	58	0
Anthribidae	0	8	na	0	na
Belidae	0	0	1	0	1
Attelabidae					
Attelabinae	0	5	1	6	0
Rhynchitinae	1	0	2	3	0
Brentidae	0	2	na	0	na
Curculionidae					
Alcidoninae	0	1	0	0	1
Apioninae	0	5	3	8	0
Baridinae	2	4	9	15	0
Brachyderinae	1	0	0	1	0
Cossoninae	0	3	36	0	39
Cryptorhynchinae	6	22	26	6	48
Curculioninae	1	2	5	8	0
Eugnominae	0	3	3	6	0
Leptopiinae	5	0	0	5	0
Molytinae	1	1	13	2	13
Otiorhynchinae	12	3	1	16	0
Platypodinae	na	na	na	0	na
Rhynchaeninae	0	0	2	2	0
Scolytinae	na	na	na	0	na
Tychiinae	1	4	17	22	0
Zygopinae	0	2	8	0	10
Unknown	1	1	8	10	0