

Comparing composition and diversity of parasitoid wasps and plants in an Amazonian rain-forest mosaic

Ilari E. Sääksjärvi^{*1}, Kalle Ruokolainen^{*}, Hanna Tuomisto^{*}, Samuli Haataja^{*}, Paul V.A. Fine[†], Glenda Cárdenas[‡], Italo Mesones[‡] and Víctor Vargas[‡]

^{*} Department of Biology, University of Turku, FIN-20014 Turku, Finland

[†] Department of Biology, University of Utah, Salt Lake City, USA

[‡] Universidad Nacional de la Amazonía Peruana, Facultad de Biología, Iquitos, Peru
(Accepted 30 August 2005)

Abstract: Local species richness and between-site similarity in species composition of parasitoid wasps (Hymenoptera: Ichneumonidae; Pimplinae and Rhyssinae) were correlated with those of four plant groups (pteridophytes, Melastomataceae, Burseraceae and Arecaceae) in a western Amazonian lowland rain forest mosaic. The mosaic structure of the forest was related to variation in soils within the non-inundated terrain. Significant matrix correlation between patterns in parasitoid wasp species composition and plant species composition was found. Most of the overall correlation was due to idiobiont parasitoids of weakly concealed hosts, which attack host larvae and pupae in exposed situations, with two of the four ecologically defined parasitoid groups showing no correlation at all. A positive correlation between the number of plant species and the number of Pimplinae and Rhyssinae species at a site was found when the latter was corrected for collecting effort. Consequently, the degree of floristic difference between sites may be indicative of the difference in species composition of ichneumonids, and the species richness of plants may serve as a predictor of the species richness of parasitoid wasps. Although these results were obtained in a mosaic including structurally and floristically clearly different types of rain forest, the correlation coefficients were relatively low, and the present results lend only weak support to the idea of using plant distributions as indicators of animal distributions.

Key Words: environmental heterogeneity, faunistic composition, floristic composition, Ichneumonidae, lowland rain forest, parasitoid wasps, species richness

INTRODUCTION

What makes the family Ichneumonidae (Hymenoptera) interesting is its enormous size. Townes (1969) estimated that there are about 60 000 species of ichneumonids worldwide, and recently Gauld (2000) increased the estimate to over 100 000 species. Another aspect that has prompted a lot of interest is the anomalous latitudinal species richness gradient in this family; it has been reported to be more species rich in temperate areas than in the tropics (Owen & Owen 1974).

One of the least studied ichneumonid faunas occurs in the vast Amazonian lowland rain forest area, but during the last few years, the ichneumonid faunas of Peruvian and Colombian Amazonia have been inventoried by

Sääksjärvi *et al.* (2003, 2004a, b) and Edgard Palacio (pers. comm.). The results of these studies are in agreement with the findings of Gauld (1991) and Gaston & Gauld (1993): at least some ichneumonid subfamilies, e.g. Pimplinae and Rhyssinae, show high local species richness in the tropics (Sääksjärvi 2003, Sääksjärvi *et al.* 2004b).

Amazonian lowland rain forests are structurally rather homogeneous over wide areas, and only a few forest types have traditionally been distinguished (Encarnación 1985, Hueck & Seibert 1972, Prance 1989). Within the non-inundated areas (*tierra firme*), an important distinction is that between forests on nutrient-poor quartzitic white sand soils (Anderson 1981, Encarnación 1985), and forests on more fine-textured soils. The soils in the non-inundated areas now appear much more heterogeneous than was previously thought, largely due to the complex geological history of the area (e.g. Räsänen

¹ Corresponding author. Email: ilari.saaksjarvi@utu.fi

et al. 1987, Salo *et al.* 1986). The non-inundated areas consist of a mosaic of floristically differentiated forest types, where the floristic similarity patterns are highly correlated both between plant groups and with similarity patterns in local edaphic conditions at various spatial scales (Ruokolainen & Tuomisto 1998, Ruokolainen *et al.* 1997, Tuomisto & Ruokolainen 1994, Tuomisto *et al.* 1995, 2002, 2003a, b; Vormisto *et al.* 2000). Thus, specialization into different edaphic conditions contributes to the high total species richness of plants in Amazonia. An interesting question is whether such specialization is also observable among animals, because these represent higher trophic levels and are, therefore, not directly dependent on local soil conditions.

There are several ways in which the patchily distributed plant communities may affect the distribution of parasitoid wasps. Species richness and architectural complexity of the vegetation are expected to increase the number of available niches both for herbivores and their parasitoids (Hawkins 1988), and variation in these vegetation properties may affect the cues that parasitoids use for host location (Gauld 1991, Vinson 1976). There is some experimental evidence that the herbivore-induced volatiles of different plant species may attract different parasitoid species (Godfray 1994). In addition, many specialized herbivores sequester secondary chemicals from their food plants for protection against predators and parasitoids, which may force the parasitoids to specialize on hosts that feed only on a limited range of (patchily distributed) plant species (Gauld *et al.* 1992). Correlation between plant and parasitoid species richness and the patterns in their species compositions would support the idea that such niche differentiation is an important factor in explaining the high diversity of parasitoid wasps in Peruvian Amazonia.

In the present study, we are especially interested in how similar the patterns of species richness and species composition are between pimpline and rhyssine parasitoid wasps and plants that represent different growth forms. The plant groups included in the study are pteridophytes (terrestrial to low-epiphytic herbs), Melastomataceae (mostly shrubs, some vines and small trees), Burseraceae (small to large trees) and Arecaceae (palms). We concentrated the insect study effort on the subfamilies Pimplinae and Rhyssinae because these are relatively well known both biologically and taxonomically. The subfamily Pimplinae is also of particular interest because it is biologically very diverse (see below and Fitton *et al.* 1988, Gauld 1991, Gauld *et al.* 2002).

Idiobiont parasitoids incapacitate their hosts during oviposition whereas koinobionts permit their hosts to develop further after oviposition (Askew & Shaw 1986). The living conditions experienced by koinobiont parasitoid larvae are considered to be rather demanding because they have to resist the various defences (e.g.

immune system) of an active host. Therefore, koinobiontism is often associated with a higher degree of host specialization than idiobiontism (Askew & Shaw 1986, Gauld 1987, Hanson & Gauld 1995). The pimpline and rhyssine species can be allocated to four ecological categories as follows (Gauld 1991):

- (1) Idiobiont parasitoids of deeply concealed hosts (in our study area all rhyssine species and the pimpline genera of the tribe Ephialtini, *Anastelgis* and *Dolichomitus*). These are mainly generalist parasitoids which use their very long ovipositors to attack hosts living deep in dead wood.
- (2) Idiobiont parasitoids of weakly concealed hosts (*Neotheronia*, *Nomosphacia*, *Xanthopimpla* and *Pimpla* of the tribe Pimplini and the ephialtine genera *Clydonium*, *Zonopimpla* and *Amazopimpla*; Sääksjärvi *et al.* 2003). These are mainly generalist parasitoids with short ovipositors and attack host larvae and pupae in exposed locations.
- (3) Pseudoparasitoids that feed on egg sacs of spiders or on spiders guarding these (the genus *Zaglyptus*).
- (4) Koinobiont parasitoids of adult spiders (*Polysphincta*, *Hymenoepimecis*, *Acrotaphus*, *Ticapimpla*, *Eruqa* and *Zatyptota*).

The four different ecological categories of parasitoids are expected to vary in their dependence on the species composition and structure of vegetation. The idiobiont parasitoids of weakly concealed hosts may be expected to be most strongly associated with plant species composition, because their hosts consume living plant material that is rich in secondary compounds (leaves, shoots etc.). The other parasitoid groups attack hosts that live either on dead wood or are predators, so their association with plant species composition is expected to be weaker.

Because different groups of organisms have distinct evolutionary histories and ecological requirements, the ideal way to carry out biodiversity inventories would be to study all taxa. However, the high species richness of tropical rain forests makes this impossible. If some groups of organisms can be used as indicators to reveal general faunistic and floristic patterns, this would significantly speed up biodiversity studies and facilitate conservation planning. Our main objective in the present study was to find out if the studied plant groups are useful as indicators of changes in parasitoid species assemblages.

METHODS

Study area

Fieldwork was conducted in the recently established Allpahuayo–Mishana National Reserve in the northern

part of Peruvian Amazonia (near the city of Iquitos, between the River Nanay and the Iquitos–Nauta road). The climate in the study area is humid, with mean annual precipitation about 3000 mm, and hot, with average temperature of 26 °C (Marengo 1998). The environmental conditions of the study area, including geology, soils, climate and vegetation, have been recently described in Kalliola & Flores Paitán (1998).

The forests near Iquitos are famous for their habitat heterogeneity (Whitney & Alvarez Alonso 1998). Many different kinds of forests can be distinguished in the area, and these support endemic species (Gentry 1977, Whitney & Alvarez Alonso 1998), characteristic plant communities (Tuomisto & Ruokolainen 1994, Vormisto *et al.* 2000), and high numbers of species (Gentry 1988, Sääksjärvi *et al.* 2004b). In flat low-lying areas, soils are often derived from the marine or semi-marine Pebas formation, which yields soils that are clayey in texture, relatively rich in nutrients, and mainly brownish-grey in colour. The soils on hill tops are often composed of so-called white sand, which is of quartzitic mineralogy, very nutrient-poor, and grey to white in colour. Loamy soils of intermediate nutrient contents that are probably derived from old river terraces are also found in the area.

The different soil types support different kinds of forest, which differ in both physiognomy and floristic composition. Forests growing on clayey soils usually have a dense shrub layer and an abundance of large herbs and tree ferns. In contrast, forests growing on white sand soils are characterized by slender trees, less complex canopy structure, and a very sparse shrub layer (Tuomisto & Ruokolainen 1994). The white sand forests can be further divided into smaller units on the basis of characteristics such as canopy height, soil humidity and peat accumulation (Alvarez & Soini, pers. comm., Encarnación 1985, Ruokolainen & Tuomisto 1993).

Field work and species identification

The parasitoid wasps were sampled by Malaise trapping. Sampling of parasitoid wasps was conducted from January 2000 to January 2001 in three locations (at most within some kilometres from each other) which all included similar kinds of forest types. Each location was sampled with five Malaise traps placed in different forest types: two traps were in forests on either clayey or loamy soil, and three in forests on white sand soil with differing soil humidity and canopy height (Appendix 1). Unfortunately, some gathering chambers were stolen or destroyed during the study. In addition, one trap was stolen halfway through the study, and although two new traps were established at nearby locations, only data from the original trap are used in the present study. Total sample size for all 17 malaise traps was 141 trap months,

which makes the sample one of the largest ever collected in Amazonia.

Ichneumonids were separated from the samples and identified to subfamilies. All pimplines and rhyssines were identified to genus and sorted to morphospecies mainly on the basis of characters used in Gauld (1991). A small number of the morphospecies could be referred to named species, but even those that remained unnamed will hereafter be considered as species. The voucher specimens are deposited in the Zoological Museum, University of Turku, Finland. In the future, a part of the vouchers will be moved to the Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Peru.

Floristic data were collected at each Malaise trap locality using four 5-m-wide and 125-m-long line transects. The starting points of the transects were positioned at the four cardinal points around the edge of the Malaise trap, so that the transects formed a right-angled cross with the trap in the middle. All individuals of pteridophytes, Melastomataceae, Arecaceae and Burseraceae that exceeded a predefined minimum size limit in the transects were identified to species and counted. Burseraceae were counted only within the first 25 m of each transect, because this family was sampled as a part of a separate study and only later combined with the other data. Burseraceae were not inventoried at the site where the Malaise trap had been stolen. Pteridophytes were included if they had at least one leaf longer than 10 cm, Melastomataceae were included if they had at least one post-cotyledon leaf, all palms were included, and Burseraceae were included if their stem diameter exceeded 1 cm. Representative voucher specimens were collected for each species, and all individuals that could not be confidently referred to a species that was already represented by a voucher specimen were also collected. Duplicates of the voucher specimens are deposited in AMAZ, TUR and NY (herbarium acronyms according to Holmgren *et al.* 1990).

Numerical analyses

Distance matrices consisting of pair-wise comparisons of all the Malaise trap localities were constructed using the data on parasitoid wasps and plants separately.

To compute floristic distances between localities, we used the Bray–Curtis coefficient (Legendre & Legendre 1998), which uses abundance data and reflects differences in the absolute amounts of each plant species between localities. Separate distance matrices were computed for each of the four plant groups, and a fifth distance matrix was computed using all plant groups together to obtain a measure of the overall floristic differences between localities. Number of individuals was used as the measure of abundance.

Table 1. Matrix correlations between the faunistic and floristic distances. Idch = idiobiont parasitoids of deeply concealed hosts, Iwch = idiobiont parasitoids of weakly concealed hosts, Ps = pseudoparasitoids of spiders, Ks = koinobiont parasitoids of spiders. The parenthetical values are probabilities.

		All wasps	Iwch	Ps	Idch	Ks
Geographic distance		−0.13 (NS)	−0.15 (NS)	0.17 (NS)	0.03 (NS)	−0.17 (.076)
Plants	0.26 (.010)	0.21 (.034)	0.21 (.048)	0.35 (.050)	−0.05 (NS)	−0.13 (NS)

For parasitoid wasps, all data for the entire sampling year were pooled for each Malaise trap. To measure faunistic distances between Malaise traps, the Chord distance (Legendre & Legendre 1998) was used. This coefficient quantifies differences in the relative rather than absolute abundances of species, which was deemed appropriate for wasps because the absolute collecting efficiency of a trap can vary depending on how it is placed in the field. Separate distance matrices were computed for each of the four ecological wasp categories defined above, and a fifth distance matrix was computed using all wasp categories together.

A matrix of geographical distances between localities was computed using GPS coordinates that had been obtained in the field for each locality.

Correlations between floristic and faunistic distance matrices were tested using the Mantel test. To control for spatial autocorrelation, both the floristic and the faunistic distance matrices were first correlated with the geographical distance matrix, and if a significant correlation was detected, a partial Mantel test between the plant and wasp distance matrices was performed to see how much of the correlation between these remained after removing the effect of geographic distances.

Not all ecological categories of parasitoid wasps were found in all Malaise traps (Appendix 1), so when comparing the plant data with these ecological subgroups those study plots were excluded where no wasp specimens were found. Principal co-ordinates analysis (PCoA, Legendre & Legendre 1998) was used to illustrate floristic and faunistic similarities between the Malaise trap sites. A separate ordination was produced with each of the ten distance matrices.

The relationship between the number of plant species and the number of ichneumonid species at a site was studied using correlation analysis. For Ichneumonids (but not for plants) it was observed that the number of species found was strongly dependent on the number of individuals captured in a locality. Because the collection efficiency of Malaise traps varies with their exact position in the field (Gauld & Bolton 1988), we corrected the numbers of species recorded in each trap by regressing the number of species against the number of individuals, and using the residuals of the best regression model. These residuals indicate whether the number of species discovered in a given trap was higher or lower than expected, given the number of individuals caught.

RESULTS

The floristic inventory yielded 171 plant species and 24 803 plant individuals. All plant groups were well represented in the study area (Appendix 1).

The faunistic inventory yielded 76 parasitoid wasp species and 945 specimens. Idiobiont parasitoids of weakly concealed hosts and koinobiont parasitoids of spiders were the most common wasp groups, both in terms of species richness and in terms of the number of individuals in the sample. These groups were found in all Malaise traps. Idiobiont parasitoids of deeply concealed hosts were absent from three traps and pseudoparasitoids of spiders from five traps (Appendix 1).

There was a significant matrix correlation between the overall faunistic and floristic distances (Table 1). This correlation was mainly due to the behaviour of idiobiont parasitoids of weakly concealed hosts. When this group was correlated separately with the different plant groups, significant matrix correlations were found with Melastomataceae ($r = 0.31$, $P = 0.017$) and Arecaceae ($r = 0.26$, $P = 0.023$) but not with Burseraceae or pteridophytes. Distances in pseudoparasitoids of spiders also showed a near-significant correlation with floristic distances. Distances in the other two ecological wasp groups did not correlate significantly with floristic distances. Floristic distances between localities showed significant correlation with geographical distance, but distances of no ichneumonid group did. Therefore, it was not considered necessary to perform partial Mantel tests to remove the effect of geographic distances.

The five PCoA ordination diagrams based on floristic distances between the Malaise trap sites show approximately similar patterns, so only the one including all plant groups is shown in Figure 1c. Most of the sites with white sand soils are on the left side of the ordination, the sites with loamy soil are in the upper right corner, and the sites with clayey soils are at the bottom. However, the traps G1 and I1 are situated in the ordination among the loamy soil sites, even though they were meant to sample white sand forest. These sites are situated near the border of loamy soils, and even if the Malaise trap itself was on white sand, the floristic transects may have extended to loamy soil.

The soil gradient is also visible in the ordination diagram that includes all parasitoid wasps (Figure 1a), although the sites with different kinds of soil are not

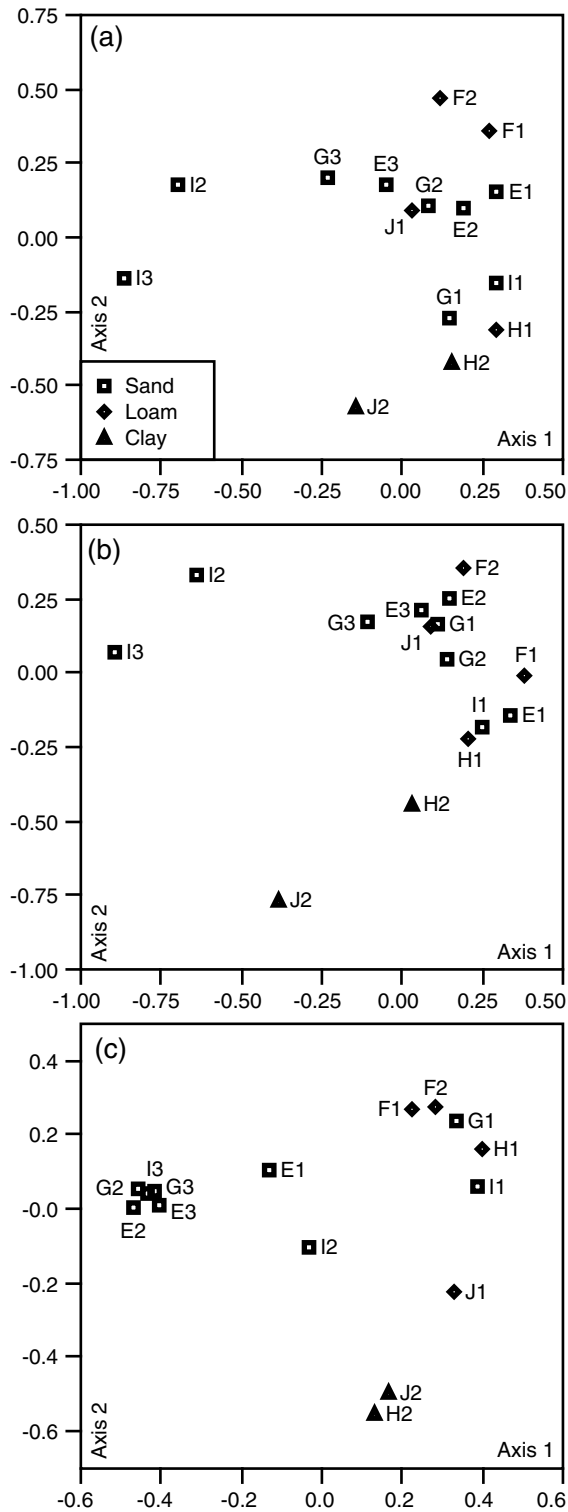


Figure 1. Ordination of Malaise trap sites in the Allpahuayo–Mishana National Reserve, north-eastern Peruvian Amazonia. Ordination based on the faunistic composition of all the studied parasitoid wasps together (a), idiobiont parasitoids of weakly concealed hosts only (b) and the floristic composition of all the studied plant groups together (c). Symbols indicate the soil type at each locality. The eigen values are (both axes): 36% (all parasitoid wasps), 43% (idiobiont parasitoids of weakly concealed hosts) and 51% (all plants).

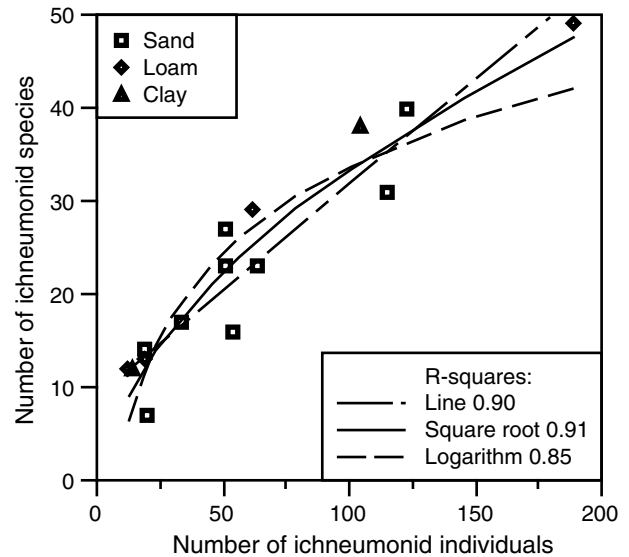


Figure 2. The relationship between the number of sampled ichneumonid individuals and the number of species discovered at a locality. The explanatory power of three regression models tested to account for the differences in sampling intensity are shown. Symbols indicate the soil type at each locality.

as clearly separated as in the ordination involving plants. Especially the relationships among the white sand sites are different compared to ordinations based on plants. These patterns are clearer in Figure 1b, which shows the ordination for idiobiont parasitoids of weakly concealed hosts. The ordinations based on the other ecologically defined parasitoid wasp groups show much less correspondence with the floristic ordination, which is in accordance with the results of the Mantel tests.

There was a clear positive relationship between the number of sampled pimpline and rhyssine individuals and the number of species discovered at a locality (Figure 2). This indicates that differences between localities in the number of species observed are to a great degree dependent on the sampling efficiency of the corresponding Malaise trap. However, it is also possible that some sites do, in fact, support more individuals and species than others. To account for differences in sampling intensity, three regression models of number of species on number of individuals were tested, and the square-root model was selected because it gave the best fit to the data (Figure 2). Corrected species richness values were then obtained by using the residuals of the square-root regression model.

A high degree of variation in the original number of pimpline and rhyssine species was observed, but this was not related to plant species richness or vegetation type in any obvious way (Figure 3a). The variation in the residual number of parasitoid species, in contrast, revealed some interesting patterns (Figure 3b). In the localities on clayey and loamy soils, the variation in species richness could

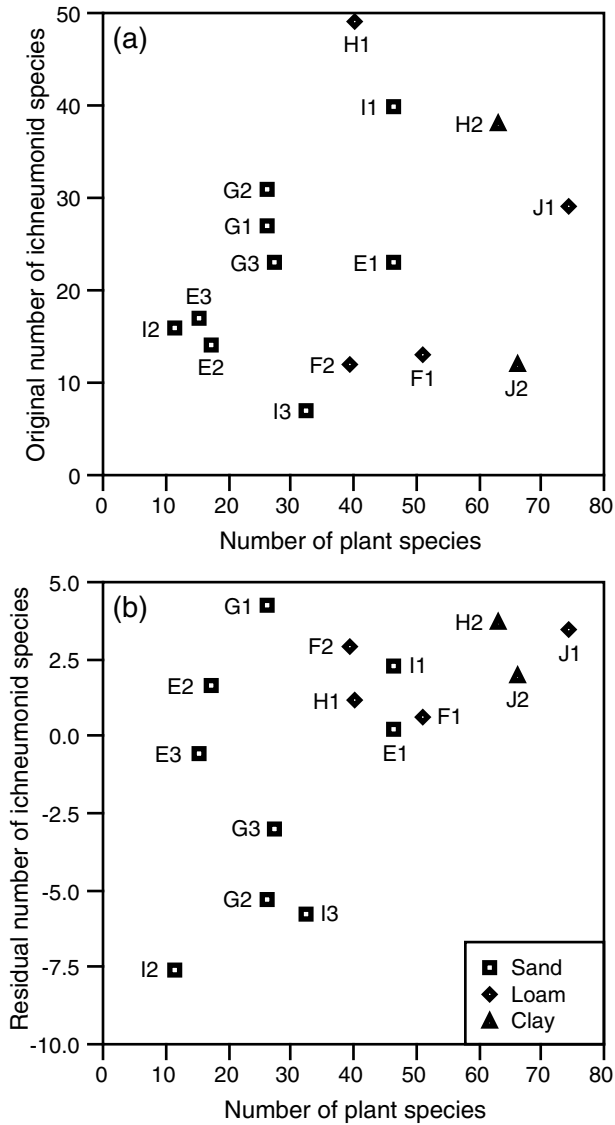


Figure 3. Relationship between plant species richness and ichneumonid species richness using the original ichneumonid species richness (a) and using ichneumonid species richness corrected for sampling intensity by using residuals of the square-root model from Figure 2 (b). Symbols indicate the soil type at each locality.

almost entirely be explained by sampling intensity, and the residual species richness was uniformly high. In the white sand forests, a high degree of variation in species richness remained after sampling efficiency had been accounted for.

Very different results on the correlation between plant species richness and pimpline and rhyssine species richness were obtained depending on whether the original species counts or the corrected ones were used in the analysis. When using the original species counts, there was no correlation between plant species richness and ichneumonid species richness (Pearson's $r = 0.24$, $P = 0.38$; Figure 3a). In contrast, there was a significant

positive correlation (Pearson's $r = 0.57$, $P = 0.03$; Figure 3b) when the corrected values for ichneumonid species richness were used.

DISCUSSION

Species richness and composition

The species richness of parasitoid wasps at a locality was positively associated with that of plants when sampling intensity was accounted for. The evidence that higher plant species richness would result in higher parasitoid species richness is weak, and it is possible that the positive association is actually caused by increased plant functional group richness and architectural complexity at locality (Haddad *et al.* 2001, Hawkins 1988, Siemann *et al.* 1998). Because such evidence is, however, obtained from experiments conducted in relatively simple communities in temperate region, we do not want to rule out the possibility that plant species richness directly is positively associated with parasitoid species richness.

Our study area in Peruvian Amazonia is famous for its diversity of both structurally and floristically clearly different lowland rain forest types and we anticipated that many pimpline and rhyssine species might be habitat specialists in the area.

However, the matrix correlations between floristic distances and distances in parasitoid wasp species composition were quite low, although some of them were statistically significant. The most obvious difference between the floristic and faunistic patterns, as judged from the ordination diagrams (Figure 1), was that the white sand sites seemed floristically relatively similar to each other, but were quite heterogeneous in parasitoid species composition. The number of parasitoid species sampled at a locality was also more heterogeneous on white sand sites than on loamy and clayey soil sites, especially after the data had been corrected for sampling intensity (Figure 3). These observations suggest that plant species composition does not affect the distribution of parasitoid wasp species very strongly.

Three sources of error, each of which might blur the relationship between plant and ichneumonid data, should be kept in mind here. That the sampling efficiency of Malaise traps may be strongly influenced by the precise positioning of the trap (Hammond 1992) has already been mentioned. Many species of pimplines and rhyssines are rare (Sääksjärvi *et al.* 2004b), so their presence or absence in a trap may be largely a coincidence. Furthermore, ichneumonids are strong fliers, so a Malaise trap may catch individuals that are just passing a forest patch without actually being resident there.

As expected on the basis of their biology, idiobiont parasitoids of weakly concealed hosts emerged as the

wasp group that showed the clearest relationship with the floristic patterns (Table 1, Figure 1). In the study area, this ecological group is by far the most abundant of all the pimelines and rhyssines, and comprises approximately half of the species and three quarters of the specimens collected (Appendix 1). Such high diversity of closely related genera and species within a single area may partly be maintained via niche differentiation to patchily distributed vegetation types. The result that this group correlated significantly only with Melastomataceae and Arecaceae but not with Burseraceae or pteridophytes remains unexplained. The small group of pseudoparasitoids of spiders was rather poorly represented in our data, but it also showed a near-significant matrix correlation with overall floristic similarity (Table 1). Gauld *et al.* (1998) observed in Costa Rica that the species of *Zaglyptus* are rarely collected, but may occur in quite large numbers in some localities. Thus, the pattern detected in our study, although based on a small sample, may be important (Appendix 1). However, it also needs to be taken into account that all spiders are predators. Herbivorous insects may be restricted to a certain habitat if they are specialized on a host plant that is specialized to that habitat. The distribution of spiders may be less affected by the distribution of plant species, because they are one trophic level further away from the defence chemicals of plants.

There is evidence that koinobiont parasitoids of spiders are specialized to attack mainly spiders of the families Araenidae and Tetragnathidae (Gauld 1991, 2000; Shaw 1994). The relationship between koinobiont parasitoids of spiders and their hosts is clearly very specialized (Shaw 1994), as it includes, for example, complex manipulation of host behaviour (Eberhard 2000). The most abundant Araenidae species in Manu National park in southern Peru are usually not restricted to specialized forest types (Silva & Coddington 1996), and therefore it seems that koinobiont parasitoids of spiders may find hosts from several different vegetation types. In addition, it is proposed that their host location is perhaps based mainly on cues emanating directly from the host's silk (Gauld 1991), and therefore the structure of the vegetation may play a smaller role in their host searching.

Idiobiont parasitoids of deeply concealed hosts did not show matrix correlation with floristic distance either (Table 1). This may indicate that these parasitoids are not very sensitive to variation in forest habitat, but it may also be due to their scarcity in our material in spite of the year-long sampling (Appendix 1).

Biodiversity inventories

From the rapid biodiversity assessment point of view, it would be very interesting if species richness patterns of

different groups of organisms would coincide. Unfortunately, most of the studies conducted so far have shown rather low congruence in species richness across different groups of organisms (e.g. Lawton *et al.* 1998). However, insect species richness has been reported to correlate with plant species richness at different spatial scales (Prendergast *et al.* 1993, Southwood *et al.* 1979), although this relationship might be much more complicated than has been thought (Hawkins & Porter 2003). Our results in an area with structurally and floristically clearly different rain-forest types were not unambiguous either. No correlation between ichneumonid and plant species richness was found with the original species count data, but when sampling effect was accounted for, a significant correlation emerged.

Studies comparing species composition patterns, rather than species richness, among different plant groups have given results consistent with the hypothesis of environmental heterogeneity driving species distribution patterns. In Amazonia, patterns in pteridophyte, tree, Melastomataceae and palm species compositions have been observed to be highly correlated and to reflect similarities in local edaphic conditions, even where the edaphic differences between sites are not as clear as in the present study (Ruokolainen & Tuomisto 1998, Ruokolainen *et al.* 1997, Tuomisto *et al.* 1995, 2002, 2003a, b; Vormisto *et al.* 2000). These studies imply that different plant groups can be used as indicators of general floristic patterns. The present study extends these results. Floristic patterns seem to be predictive of faunistic patterns for some animal groups (e.g. idiobiont parasitoids of weakly concealed hosts) but not for others (e.g. koinobiont parasitoids of spiders). However, even when present, these relationships were not nearly as strong as those that have been found among different plant groups. Consequently, the present results lend only weak support to the idea of extending the indicator species approach from plants to animals.

ACKNOWLEDGEMENTS

We thank the following persons and institutions for helping us in many ways during the study: José Alvarez, Mario Escobedo, Ian D. Gauld, Bradford A. Hawkins Reijo Jussila, Gerardo Lamas, Teotista Mafaldo, Andres Marmol Burgos, Petri Martikainen, Seppo Neuvonen, Mari Pohja, Manuel Reategui, Sandra Rios, Jukka Salo, Leif Schulman, Pekka Soini, Tauno Sääksjärvi, Anssi Teräs, Tuuli Toivonen, Ian Turner Varpu Vahtera, Marja Vieno and Sondra Ward, Universidad Nacional de la Amazonía Peruana, Instituto Nacional de Recursos Naturales (Peru), Instituto de Investigaciones de la Amazonía Peruana, Instituto Nacional de Investigación

Agraria (Peru), Universidad Nacional Mayor de San Marcos (Peru), The Natural History Museum, London (UK), and the Zoological Museum of the University of Turku (Finland). Financial support was obtained from the Academy of Finland, Ministry of Education, Finland, the Entomological Society of Finland and the EC-funded Bioresource-Programme (The Natural History Museum, London).

LITERATURE CITED

- ANDERSON, A. B. 1981. White-sand vegetation of Brazilian Amazonia. *Biotropica* 13:199–210.
- ASKEW, R. R. & SHAW, M. R. 1986. Parasitoid communities: their size, structure and development. Pp. 225–229 in Waage, J. & Greathead, D. (eds.). *Insect parasitoids*. Academic Press, London.
- EBERHARD, W. G. 2000. Spider manipulation by a wasp larva. *Nature* 406:255–256.
- ENCARNACIÓN, F. 1985. Introducción a la flora y vegetación de la Amazonia peruana: estado actual de los estudios, medio natural y ensayo de una clave de determinación de las formaciones vegetales en la llanura amazónica. *Candollea* 40:237–252.
- FITTON, M. G., SHAW, M. R. & GAULD, I. D. 1988. Pimpline ichneumonflies Hymenoptera: Ichneumonidae (Pimplinae). *Handbooks for the Identification of British Insects* 7:1–110.
- GASTON, K. J. & GAULD, I. D. 1993. How many species of pimplines (Hymenoptera: Ichneumonidae) are there in Costa Rica? *Journal of Tropical Entomology* 9:491–499.
- GAULD, I. D. 1987. Some factors affecting the composition of tropical ichneumonid faunas. *Biological Journal of the Linnean Society* 30:299–312.
- GAULD, I. D. 1991. The Ichneumonidae of Costa Rica, 1. *Memoirs of the American Entomological Institute* 47:1–589.
- GAULD, I. D. 2000. The re-definition of Pimplinae genus *Hymenopimecis* (Hymenoptera: Ichneumonidae) with a description of a plesiomorphic new Costa Rican species. *Journal of Hymenoptera Research* 9:213–219.
- GAULD, I. D. & BOLTON, B. 1988. *The Hymenoptera*. British Museum (Natural History) and Oxford University Press, Oxford.
- GAULD, I. D., GASTON, K. J. & JANZEN, D. H. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the 'nasty' host hypothesis. *Oikos* 65:353–357.
- GAULD, I. D., HANSON, P. & UGALDE GÓMEZ, J. A. 1998. Guía de los Pimplinae de Costa Rica (Hymenoptera: Ichneumonidae). *Revista de Biología Tropical* 46:1–189.
- GAULD, I. D., WAHL, D. B. & BROAD, G. 2002. The suprageneric groups of the Pimplinae (Hymenoptera: Ichneumonidae): a cladistic re-evaluation and evolutionary biological study. *Zoological Journal of the Linnean Society* 136:421–485.
- GENTRY, A. 1977. Endemic plant species and habitats of Ecuador and Amazonian Peru. Pp. 136–149 in Prance, G. T. & Elias, T. (eds.). *Extinction is forever*. New York Botanical Garden, New York.
- GENTRY, A. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of USA* 85:156–159.
- GODFRAY, H. C. J. 1994. *Parasitoids: behavioural and evolutionary ecology*. Princeton University Press, Princeton. 473 pp.
- HADDAD, N. M., TILMAN, D., HAARSTAD, J., RITCHIE, M. & KNOPS, J. 2001. Contrasting effects of plant species richness and composition on insect communities: a field experiment. *The American Naturalist* 158:17–35.
- HAMMOND, P. M. 1992. Species inventory. Pp. 17–39 in Groombridge, B. (ed.). *Global biodiversity. Status of the Earth's living resources*. Chapman & Hall, London.
- HANSON, P. E. & GAULD, I. D. (eds.) 1995. *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford. 893 pp.
- HAWKINS, B. A. 1998. Species diversity in the third and fourth trophic levels: patterns and mechanisms. *Journal of Animal Ecology* 57:137–162.
- HAWKINS, B. A. & PORTER, E. E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist* 161:40–49.
- HOLMGREN, P. K., HOLMGREN, N. H. & BARNETT, L. C. 1990. *Index Herbariorum. Part I: The Herbaria of the World*. (Eight edition). New York Botanical Garden, New York.
- HUECK, K. & SEIBERT, P. 1972. *Vegetation map of South America*. Gustav Fischer Verlag, Stuttgart.
- KALLIOLA, R. & FLORES PAITÁN, S. (eds.) 1998. Geocología y Desarrollo Amazónico. *Annales Universitatis Turkuensis Ser A II*. University of Turku, Turku. 544 pp.
- LAWTON, J. H., BIGNELL, D. E., BOLTON, B., BLOEMERS, G. F., EGGLETON, P., HAMMOND, P. M., HODDA, M., HOLT, R. D., LARSEN, T. B., MAWDSLEY, N. A., STORK, N. E., SRIVASTAVA, D. S. & WATT, A. D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forests. *Nature* 391:72–76.
- LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical ecology*. (Second edition). Developments in environmental modelling 20. Elsevier scientific publishing company, Amsterdam. 853 pp.
- MARENGO, J. 1998. Climatología de la zona de Iquitos, Perú. Pp. 35–57 in Kalliola, R. & Flores Paitán, S. (eds.). *Geocología y Desarrollo Amazónico*. *Annales Universitatis Turkuensis Ser A II* 114. University of Turku, Turku.
- OWEN, D. H. & OWEN, J. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249:583–584.
- PRANCE, G. 1989. American tropical forests. Pp. 99–132 in Leith, H. & Werger, M. J. A. (eds.). *Ecosystems of the world 14B. Tropical rain forest ecosystems: Biogeographical and ecological studies*. Elsevier, Amsterdam.
- PRENDERGAST, J. R., QUINN, R. M., LAWTON, J. H., EVERSHAM, B. C. & GIBBONS, D. W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335–337.
- RÄSÄNEN, M. E., SALO, J. S. & KALLIOLA, R. J. 1987. Fluvial perturbation in the Western Amazon basin: regulation by long-term sub-Andean tectonics. *Science* 238:1398–1401.
- RUOKOLAINEN, K. & TUOMISTO, H. 1993. La vegetación de terrenos no inundables (tierra firme) en la selva baja de la Amazonia peruana. Pp. 139–153 in Kalliola, R., Puhakka, M. & Danjoy, W. (eds.). *Amazonía peruana. Vegetación húmeda tropical en el llano subandino*. PAUT y ONERN, Jyväskylä.

- RUOKOLAINEN, K. & TUOMISTO, H. 1998. Vegetación natural de la zona de Iquitos. Pp. 253–344 in Kalliola, R. & Flores Paitán, S. (eds.). *Geoecología y Desarrollo Amazónico*. Annales Universitatis Turkuensis Ser A II 114. University of Turku, Turku. 544 pp.
- RUOKOLAINEN, K., LINNA, A. & TUOMISTO, H. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographic patterns in Amazonian rain forests. *Journal of Tropical Ecology* 13:243–256.
- SÄÄKSJÄRVI, I. E. 2003. Diversity of parasitoid wasps (Hymenoptera: Ichneumonidae) in a lowland rain forest mosaic in Peruvian Amazonia. *Annales Universitatis Turkuensis Ser. A II* 169. University of Turku, Turku. Ph.D. thesis. 124 pp.
- SÄÄKSJÄRVI, I. E., PALACIO, E., GAULD, I. D., JUSSILA, R. & SALO, J. 2003. A new genus and six new species of the tropical *Camptotypus* genus-group (Hymenoptera: Ichneumonidae; Pimplinae) from northern South America. *Zootaxa* 197:1–18.
- SÄÄKSJÄRVI, I. E., GAULD, I. D. & SALO, J. 2004a. Phylogenetic evaluation of the tropical *Camptotypus* genus-group, with a key to the world genera. *Journal of Natural History* 38:2759–2778.
- SÄÄKSJÄRVI, I. E., HAATAJA, S., NEUVONEN, S., GAULD, I. D., JUSSILA, R., SALO, J. & MARMOL BURGOS, A. 2004b. High local species richness of parasitoid wasps (Hymenoptera: Ichneumonidae; Pimplinae and Rhyssinae) from the lowland rain forests of Peruvian Amazonia. *Ecological Entomology* 29:735–743.
- SALO, J., KALLIOLA, R., HÄKKINEN, I., MÄKINEN, Y., NIEMELÄ, P., PUHAKKA, M. & COLEY, P. D. 1986. River dynamics and the diversity of Amazon lowland forest. *Nature* 322:254–258.
- SHAW, M. R. 1994. Parasitoid host ranges. Pp. 111–144 in Hawkins, B. A. & Sheehan, W. (eds.). *Parasitoid community ecology*. Oxford University Press, Oxford.
- SIEMANN, E., TILMAN, D., HAARSTAD, J. & RITCHIE, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist* 152:738–750.
- SILVA, D. & CODDINGTON, J. 1996. Spiders of Pakitza (Madre de Dios, Peru): species richness and notes on community structure. Pp. 253–313 in Wilson, D. E. & Sandoval, A. (eds.). *Manu – The biodiversity of southeastern Peru*. Smithsonian Institution and Editorial Horizonte, Peru.
- SOUTHWOOD, T. R. E., BROWN, V. K. & READER, P. M. 1979. The relationship of plant and insect diversities in succession. *Biological Journal of the Linnean Society* 12:327–348.
- TOWNES, H. 1969. The genera of Ichneumonidae, part 1. *Memoirs of the American Entomological Institute* 11:1–300.
- TUOMISTO, H. & RUOKOLAINEN, K. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in Amazonian rain forest. *Journal of Vegetation Science* 5:25–34.
- TUOMISTO, H., RUOKOLAINEN, K., KALLIOLA, R., LINNA, A., DANJOY, W. & RODRIQUEZ, Z. 1995. Dissecting Amazonian biodiversity. *Science* 269:63–66.
- TUOMISTO, H., RUOKOLAINEN, K., POULSEN, A. D., MORAN, R. C., QUINTANA, C., CAÑAS, G. & CELI, J. 2002. Distribution and diversity of Pteridophytes and Melastomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. *Biotropica* 34:516–533.
- TUOMISTO, H., POULSEN, A. D., RUOKOLAINEN, K., MORAN, R. C., QUINTANA, C., CELI, J. & CAÑAS, G. 2003a. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications* 13:352–371.
- TUOMISTO, H., RUOKOLAINEN, K. & YLI-HALLA, M. 2003b. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299:241–244.
- VINSON, S. B. 1976. Host selection by insect parasitoids. *Annual Review of Entomology* 21:109–133.
- VORMISTO, J., PHILLIPS, O. L., RUOKOLAINEN, K., TUOMISTO, H. & VÁSQUEZ MARTÍNEZ, R. 2000. A comparison of fine scale distribution patterns of four plant groups in an Amazonian rain forest. *Ecography* 23:349–359.
- WHITNEY, B. M. & ALVAREZ ALONSO, J. 1998. A new *Herpsilochmus* antwren (Aves: Thamnophilidae) from northern Amazonian Peru and adjacent Ecuador: the role of edaphic heterogeneity of *tierra firme* forest. *Auk* 115:559–576.

Appendix 1. Numbers of species and individuals collected from Allpahuayo-Mishana National Reserve. Arec = Palms. Burs = Burseraceae. Mela = Melastomataceae. Pter = pteridophytes. Idch = idiobiont parasitoids of deeply concealed hosts. Iwch = idiobiont parasitoids of weakly concealed hosts. Ps = pseudoparasitoids of spiders. Ks = koinobiont parasitoids of spiders. sp = number of species. i = number of individuals.

Trap	Soil type	Arec		Burs		Mela		Pter		Idch		Iwch		Ps		Ks	
		sp	i	sp	i	sp	i	sp	i	sp	i	sp	i	sp	i	sp	i
E1	sand	12	404	1	33	11	82	23	1285	4	8	14	38	1	2	4	4
E2	sand	3	1730	3	9	2	135	10	609	0	0	8	12	1	2	5	6
E3	sand	5	1962	1	7	2	195	8	322	1	1	9	22	0	0	7	11
F1	loam	8	445	9	40	11	278	24	338	4	4	8	14	0	0	1	2
F2	loam	8	402	5	47	10	182	17	227	3	3	7	8	1	1	1	1
G1	sand	10	251	1	1	6	65	10	171	1	1	14	26	2	3	10	22
G2	sand	7	328	2	2	4	163	14	1756	3	6	18	93	1	1	9	16
G3	sand	8	366	2	20	3	240	15	3878	0	0	20	62	0	0	3	3
H1	loam	10	462	8	21	8	103	15	143	9	20	24	96	2	7	14	67
H2	clay	14	230	6	29	13	99	31	577	10	19	16	62	1	1	11	23
I1	sand	14	519	5	21	11	81	17	149	4	6	22	72	2	13	12	33
I2	sand	2	79	1	5	2	38	7	958	3	3	11	50	1	1	1	1
I3	sand	7	222	0	0	7	472	19	3063	0	0	4	17	1	1	2	3
J1	loam	18	472	17	70	13	158	27	249	6	13	15	34	0	0	8	16
J2	clay	17	108	13	56	15	199	22	247	3	3	3	6	0	0	6	6
Total		32	7980	27	361	31	2490	81	13972	15	87	38	612	3	32	20	214