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DISTRIBUTION OF LEAFHOPPERS (AUCHENORRHYNCHA, HEMIPTERA) ON THEIR HOST PLANT *OXYSPORA PANICULATA* (MELASTOMATACEAE) IN THE UNDERSTORY OF A DIVERSE RAINFOREST

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Abstract. This study, using data on the distribution of leafhoppers (Auchenorrhyncha) among individuals of an understory shrub species, *Oxyspora paniculata* (D. Don) DC. (Melastomataceae), tests the hypothesis that low densities of herbivore populations in rainforest understory are caused by scarcity of their host plants. The study was conducted in an evergreen monsoon montane forest in northern Vietnam. Vegetation in the understory was extremely diverse, with 179 species found in three 16 x 16 m plots. The increase in species number with area followed roughly the power curve and gave the *z*-value 0.45, much higher than values for other communities. Also the differences between the three study plots were large; although they were very close to each other, the average similarity expressed by the Sorensen coefficient did not reach 0.5. Leafhopper community in the understory was also diverse (187 species in the sample of 2,500 sweeps), but low on density (20 individuals per 10 m^3 of vegetation). The increase in species number with the number of individuals in the sample, estimated by rarefaction method, followed the power curve and gave the *z*-value 0.86, an extremely high value. *Oxyspora paniculata* was an abundant understory shrub, found in 35 out of 60 sampling plots of 30 x 6 m, with average cover of 4.7%. Four leafhoppet species were found feeding on this species; at least three of them were not monophagous, being also abundant on other understory vegetation. Although each of the four species colonized a high proportion of available *Oxyspora paniculata* individuals (15–30%), their density on colonized shrubs remained very low (average 4, median 1, maximum 40 leafhoppers per shrub). Distribution among individual shrubs of the most abundant leafhopper species followed the Poisson distribution, i.e., their spatial pattern was very close to random. This pattern indicates that low population density of leafhoppers cannot be explained by their poor success in locating and colonizing host plants. Relatively high density of the host plant, and/or the polyphagy of the leafhopper species under study may explain these results. *Accepted 20 August 1997.*

Key words: *Auchenorrhyncha, diversity, montane rainforest, spatial pattern, Vietnam.*

INTRODUCTION

Communities of herbivorous insects associated with understory vegetation in rainforests typically consist of many species, most of them exhibiting low population density (Janzen & Schoener 1968, Elton 1975, Buskirk 1976, Hodkinson & Casson 1987, Wolda & Wong 1988, Basset *et al.* 1992, Kikkawa & Dwyer 1992). Although low density is a characteristic feature of these communities, little is known about factors limiting herbivore populations. Natural enemies (predators, parasites, pathogens), low quality of resources (host plants), and low abundance of resources combined with their high temporal and/or spatial heterogeneity have been suggested as determinants of herbivore population size and species diversity of (Janzen 1983, Brown & Ewel 1987, Dixon *et al.* 1987, Lawton & McNeill 1979, Dixon & Kindlmann 1990, Basset 1992a, Gauld & Gaston 1992, Kikkawa & Dwyer 1992). The importance of predators, namely ants, is indicated by a higher predator to herbivore ratio in rainforest than in temperate communities (Stork 1988). The effect of resource quality is indicated by a positive correlation between foliar nitrogen and the abundance of herbivores, namely phloem-feeders including leafhoppers, on rainforest vegetation (Basset 1991, 1992b). Vegetation in rainforest understory is typically composed of many plant species present at low population densities, and the productivity of the vegetation is also generally low. With this vegetation structure, resources are scattered and generally scarce for a specialized herbivore. High spatial variability and low density of resources have been invoked as an explanation not only of low population density (Dixon & Kindlmann 1990), but also of low species richness of certain specialist taxa (Dixon *et al.* 1987), low degree of host specificity (Jaenike 1990, Basset 1992a,), and high dispersal ability (Derr 1980) of herbivorous insects.

The importance of resource distribution for the population dynamics of herbivores can be inferred indirectly from the spatial pattern of colonization of individual plants by a herbivore, which is a balance between the herbivore's efficiency in dispersal and plant location and the plant's abundance and distribution (Novotný 1994). When a herbivore is limited by its ability to locate host plants, it can be expected that a small proportion of plants will be colonized by high-density subpopulations of the herbivore while a majority of plants will not be colonized at all (Cates & Orians 1975). However, data on distribution of insect herbivores among individual host plants in rainforests are rather limited for technical reasons and many studies restrict sampling to only a few specimens of each host plant (Stork 1987, Ernest 1989, Basset 1992c, Aide 1993). This study quantifies species diversity of plants and leafhoppers (Auchenorrhyncha) in a rainforest understory and, using data on the distribution of leafhoppers among individuals of a shrub species, *Oxyspora paniculata* (D. Don) DC. (Melastomataceae), tests the hypothesis that populations of herbivores are limited by the scarcity of their host plant.

STUDY AREA

The study was conducted in a large (19,000 ha) evergreen monsoon montane forest in the Tam Dao Mountains in northern Vietnam (21°30'N, 105°40'E) at 900–1100 m. The forest is floristically very rich, with no apparent dominant trees. The closed forest (climax formation) is disturbed only by selective logging by native people. The gaps (natural or more often after logging) are quickly overgrown by bamboos and various shrubs. Emergent trees (incl. Dipterocarpaceae) are rare and were nearly eliminated in all accessible places. Canopy trees support many epiphytes. The forest understory is scattered (total cover about 50%, herbs about 10%). In general, the formation of the Tam Dao forest conforms in outline and characteristics to the Indochinese montane forest described by Vidal (1979). A more detailed description of plant and insect communities (leafhoppers, butterflies) in the Tam Dao Mts. has been published by Novotný (1992, 1993) and Spitzer *et al.* (1993). The weather in Northern Vietnam has a pronounced yearly periodicity, with the wet season from May to September and the dry season from October to April.

SAMPLING METHODS

Plants. Species-area relationship for understory plants was used as a quantitative description of habitat heterogeneity for insect herbivores. It was estimated from three quadrats of successively increasing size laid out in the forest understory; the quadrat size was 1, 4, 9, 16, 36, 64, 144 and 256 m^2 (the data are three independent collectors' curves *sensu* Pielou 1977). The plots were not more than 100 m apart. All understory species, i.e., species less than 2 m tall, were recorded. Consequently, the samples contained herbs, shrubs, and seedlings and saplings of trees. We were not able to identify all the species as many were neither flowering nor fertile; consequently, we assigned a number to each species and cross-referenced the numbers between the quadrats. When in doubt, we were rather conservative so the number of species might be a slight underestimate.

Distribution of *Oxyspora paniculata* was monitored along two belt transects, 1200 m and 600 m in length. The transects were divided into sections, each 30 x 6 m, and the *Oxyspora paniculata* cover was estimated in each section. *Oxyspora paniculata* is easy to identify so that both fertile and infertile specimens were recorded.

Leafhoppers. Leafhoppers (the term is used for all the Auchenorrhyncha) from *Oxyspora paniculata* were collected by an aspirator while thoroughly examining individual leaves and branches. Such sampling was made possible, without disturbing leafhoppers in the remaining parts of a shrub, by the structure of the shrubs, which were rather low (2–3 m) with sparse leaves spread in a single layer of foliage. A branch with a foliage area of approximately 9,000 cm^2, i.e., corresponding in size of 50 mature leaves represented one sample from an individual *Oxyspora paniculata* shrub. Although sample size is measured in terms of leaf area, the surface of leaves, branches, and flowers were examined. Only flowering shrubs were sampled (about 90% of shrubs were flowering during the sampling period). The minimum distance between any two sampled shrubs was 5 meters. Altogether 120 shrubs were sampled, with samples representing approximately 108 m^2 of foliage area. For 35 shrubs, the total number of leaves was counted and the number of leafhoppers per whole shrub calculated from the sample. This could be done as 50 leaves represented a substantial part of the whole shrub in most cases, with an average number of 250 leaves per shrub (median 100, range 20–1600, N = 35).

Leafhoppers were also sampled by sweeping with a standard circular-mouthed sweep net from the vegetation at 0 to 2 m above the ground. Bare ground patches were avoided. A sample consisting of 300 sweeps was taken from *Oxyspora paniculata*, and three samples, totalling 2,500 sweeps, were taken from other understory vegetation, avoiding all *Oxyspora paniculata* shrubs and their immediate surroundings.

The sampling of both leafhoppers and plants was carried out from 20 August through 4 September 1993, during the late wet season. At this time, abundance of leafhoppers is maximal, and most species are represented by adults (Novotný 1993). All adult leafhoppers were assigned to morphospecies, based on their external morphology and dissection of male genitalia. Voucher specimens are deposited at the Institute of Entomology (Czech Republic). Nymphs were ignored since it was impossible to match nymphal and adult morphospecies.

DATA ANALYSIS

Species-area relationship: plants. The power curve was used for the description of the species-area relationship: $S = cA^z$, where S is number of species, A is area and c and *z* are parameters. Estimations of c and *z* were made by linear regression after logarithmic transformation of the variables S and A. The power curve fitted better than the logarithmic curve, although the fit was not perfect, particularly for larger quadrats. Consequently, the values of parameters should be considered only for the quadrat sizes used in this study, and should not be extrapolated (for larger quadrats in particular the value of *z* would be lower). For each quadrat size, the heterogeneity of the plots was expressed as the average value of the Sørensen coefficient of similarity calculated between all pairs of the plots.

Species-area relationship: leafhoppers. As Auchenorrhyncha samples were not related to particular areas, we examined the relationship between number of individuals and number of species. Provided that the density of individuals is roughly constant, the *z*-values should be the same for the species-area and species-individual relationships. The expected number of species for a particular number of individuals was obtained by the rarefaction method (Ludwig & Reynolds 1988; we used an adaptation of their program). It is known that the number of species for small samples can be overestimated by this method (see Novotný 1992). Consequently, the value of *z* obtained by fitting the rarefaction curves could be an underestimate. The z-value was estimated by a regression of log(number of species) on log(number of individuals) through origin, as there can be only one species in a sample containing one individual.

Spatial pattern. Distribution of leafhoppers among *Oxyspora paniculata* shrubs (their degree of aggregation) was evaluated by fitting the numbers of individuals in sampling units, each taken from one shrub (see above), by Poisson, negative binomial and Neyman type A distributions. The negative binomial was fitted using both maximum likelihood (Bliss & Fisher 1953) and minimum Chi^2 criteria; the results were nearly identical so the maximum likelihood was used. The Neyman type A distribution was fitted using the minimum Chi^2 (Gurgland & Hinz 1971). The fit was then tested by Chi^2 goodness of fit, categories with expected frequencies smaller than 5 were pooled. In addition, the degree of aggregation was also expressed by the Lloyd's index (Pielou 1977). The values of Lloyd's index larger than 1 indicate aggregation, smaller than 1 a tendency toward regularity.

RESULTS

Species richness of vegetation in the understorey. There were 88, 97, and 99 plant species found within our three 16 x 16 m plots, and 179 species when all three plots were combined. The increase in species number with area roughly follows the power curve and gave very similar results in all the three plots. Although the relationship after the log-log transformation is not perfectly linear (Fig. 1), the fit is much better than that for the logarithmic curve. The estimate of the *z*-value is 0.45, much higher than values for other communities. Note that the relationship is not strictly linear and the slope of the line decreases (albeit slightly) with increasing area. When, for instance, plots smaller than 16 m^2 are excluded from the data then $z = 0.35$. Consequently, it is not possible to compare our values with those determined for much larger plots.

The heterogeneity of the plots is very high (Fig. 1). Although the plots were close to each other

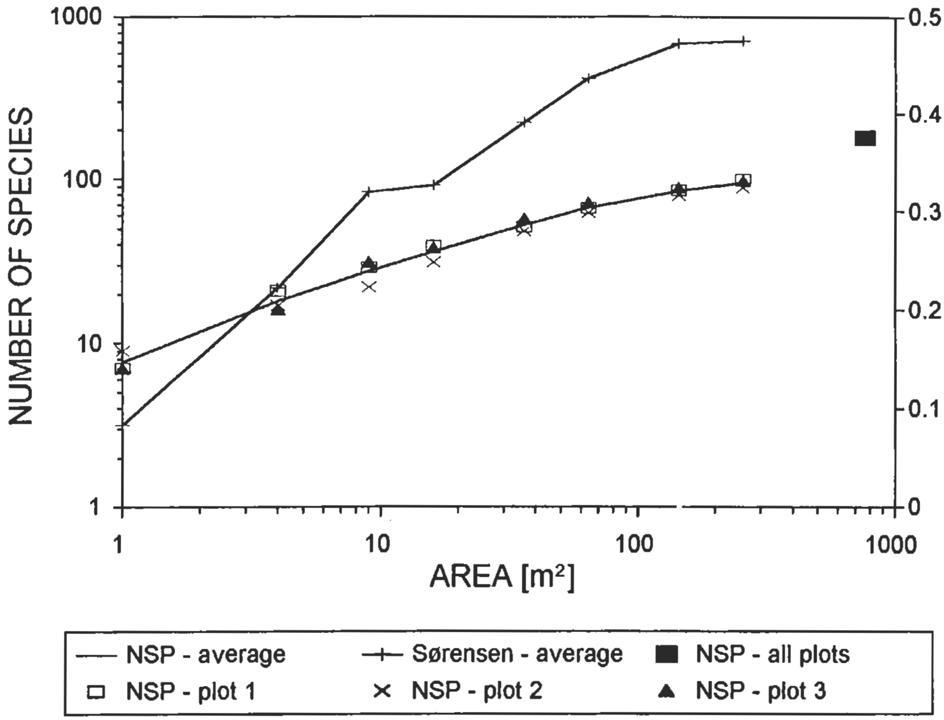

FIG. 1. Species-area and heterogeneity curves for forest understorey vegetation. Number of species (NSP) is plotted against area (A) for three plots; the average regression line is: log NSP = 0.966 + 0.453 log A. All the plots combined are depicted by a marker. Heterogeneity is expressed as average Sørensen coefficient for pair-wise comparisons among the three plots.

(less than 100 m), the average similarity expressed by the Sørensen coefficient did not reach 0.5, even when 256 m^2 plots were compared.

Species richness of leafhoppers in the understory. Leafhopper assemblage on the forest understory vegetation (excluding *Oxyspora paniculata*) was species-rich, with 187 species found in the sample of 2,500 sweeps. Even in such a relatively large sample, corresponding roughly to 350 m^3 volume of vegetation, 47% of species were represented by singletons, and only one species by more than 50 specimens. The increase in species number with sample size is very rapid; the estimate of the *z*-value is 0.86 when all three samples, giving very similar results, are averaged (Fig. 2).

Although *Oxyspora paniculata* shrubs were avoided when sampling forest understory vegetation, the issid sp. #1, *Carinata bifurcata*, and *Kutara* sp., ranked among the most abundant species in the

TABLE 1. Density of leafhoppers on *Oxyspora paniculata* and on other understory vegetation. N - number of specimens per 100 sweeps in the samples from forest understory vegetation (excluding *Oxyspora paniculata*), and from *Oxyspora paniculata*; % - percentage dominance of a species in the sample, rank - species' rank in the sample according to its abundance (from highest to lowest); Total - all leafhopper species; 2,500 sweeps was taken from the understory, and 300 sweeps from *Oxyspora paniculata*.

Species	Understory			*O. paniculata*		
	N	%	rank	N	%	rank
Issid #1	2.4	8.4	1	13.0	26.5	1
Carinata bifurcata	1.2	4.2	2	5.3	10.8	3
Onukia emarginata	0.4	1.3	18	10.7	21.8	2
Kutara sp.	0.8	2.7	6	4.0	8.2	4
Other spp.	23.8	83.4		16.0	32.7	
Total	28.6	100		49.0	100	

understorey community (Table 1). The densities of all three species were higher on *Oxyspora paniculata* than those on other understorey vegetation.

Leafhoppers associated with Oxyspora paniculata. *Oxyspora paniculata* was one of most abundant shrubs in the understorey. It was found in 35 out of 60 transect sections. Its cover within the sections varied from 0 through 32%, with an average of 4.7 % (S.E. 0.9), and median 1.1%. Altogether, 192 leafhoppers belonging to 33 species were recorded in the leaf samples from 120 *Oxyspora paniculata* shrubs. Four species, namely an unidentified issid sp. #1 (Issidae), *Carinata bifurcata* Li & Novotný 1997 (Cicadellinae, Cicadellidae), *Onukia emarginata* Li et Wang (Cicadellinae, Cicadellidae), and *Kutara* sp. (Selenocephalinae, Cicadellidae) occurred on 15–32 % of *Oxyspora paniculata* shrubs, and were represented by 22–52 specimens in the samples (Table 2), whereas none of the remaining 29 species occurred on more than 5% of the shrubs and was represented in the samples by more than 6 individuals. Apparently, the four most abundant species are associated with *Oxyspora paniculata* (in the issid #1 and *Carinata bifurcata* feeding on the plant was directly observed), whereas no conclusion can be drawn on other species.

Although each of the four species colonized a high proportion (15–30%) of available *Oxyspora paniculata*, their density on colonized shrubs remained very low. Total leafhopper density ranged from 0 to 8 specimens (average 1.6, median 1) per sample (Table 3). This corresponds to a maximum of 50 specimens on a whole shrub (average 5.8, median 2; Table 3). Distribution among *Oxyspora paniculata* shrubs of the most abundant species (issid #1) and of all leafhoppers together (i.e., sum of all individuals present) were tested for randomness. In neither case could the Poisson distribution be rejected. Although for the issid #1 the fit of Poisson distribution was reasonably good (Chi^2 = 4.08 with 2 df, P = 0.14; Fig. 3), when fitting the negative binomial the Chi^2 goodness of fit test value had decreased significantly; decrease in Chi^2 is 3.91 with 1 df, suggesting that the improvement of the fit was statistically significant. The improvement for the Neyman A distribution was not significant (note that both negative binomial and Neyman A are generalized Poisson distributions). Nevertheless, the estimated value of negative binomial k was large (k = 1.45), suggesting that the population is very loosely aggregated (Lloyd's index of patchiness is 1.71). When fitting the data for individuals of all the species together, the Poisson distribution fits very well (Chi^2 = 4.08 with 4 df, P = 0.39) and neither negative binomial nor Neyman distribution improved the fit considerably. Accordingly, the estimated value of k was 4.76 and Lloyd's index was 1.26, and we can conclude that the spatial pattern of the individuals is very close to random.

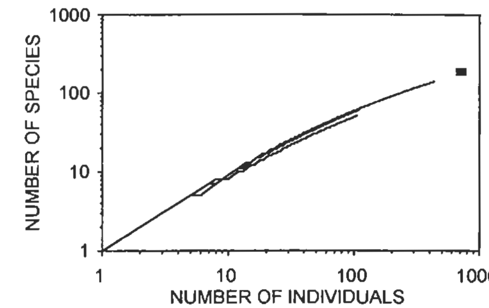

FIG. 2. Rarefaction curves for leafhoppers in the forest understory. Number of species (NSP) is plotted against number of individuals (NID) for three sweep net samples; regression line for the largest sample is: log NSP = 0.846 log NID. All the samples combined are depicted by a marker.

DISCUSSION

Species richness of vegetation and leafhoppers in the understory. Vegetation in the forest understorey is extremely diverse, as indicated by the number of species recorded in our plots as well as by the exceptionally high *z*-value (0.45). Within a similar area

TABLE 2. Frequency and abundance of leafhoppers found on *Oxyspora paniculata*. F - proportion (in %) of samples containing species; N - total number of specimens in the samples; n = 120 samples, each from a different *O. paniculata* shrub; a sample = leafhoppers from 50 mature leaves (9,000 cm^2 foliage area).

Species	F	N
Issid #1	30	48
Carinata bifurcata	19	29
Onukia emarginata	18	32
Kutara sp.	15	22
Remaining 29 spp.	–	57

range, Lepš & Stursa (1989) found maximum values of z in early successional communities and periodically disturbed communities to be about 0.34. Generally, for the majority of communities, the values lie between 0.15 and 0.35 (Wilson 1992); this range was apparently obtained using various ranges of area size. However, the z-value we were able to estimate from the data of Paijmans (1976) for large trees in Papua New Guinea rainforest was even higher, 0.68. These results indicate that the species richness of plants in tropical forest in general and in our study area in particular is enormous; no plant species forms continuous cover and consequently most plant species could be difficult for insects to locate.

Abundance of homopteran herbivores in rainforest understory is generally very low (Janzen & Schoener 1968: 1.3–3.2 specimens per 100 sweeps; Buskirk & Buskirk 1976: 3–20 specimens per 100 sweeps; Wolda & Wong 1988: maximum 10 specimens per 100 sweeps; Novotný 1992, 1993, and this study: 16–29 specimens per 100 sweeps; Basset *et al.* 1992: 0.3 specimens per m^2 of foliage; Elton 1975: 0.2 specimens per m^3 of space; see also Hodkinson & Casson 1987). Homopterans are by no means exceptional in this respect as the abundance of tropical herbivores as a whole is typically rather low (Janzen & Schoener 1968, Elton 1975, Boinski & Fowler 1989, Kikkawa & Dwyer 1992).

Two extensive samplings of leafhoppers from the forest understory within the same 5 x 5 km area of a rain forest preceded this study (Novotný 1992, 1993). When all these samples are combined, local leafhopper species diversity amounts to 397 species.

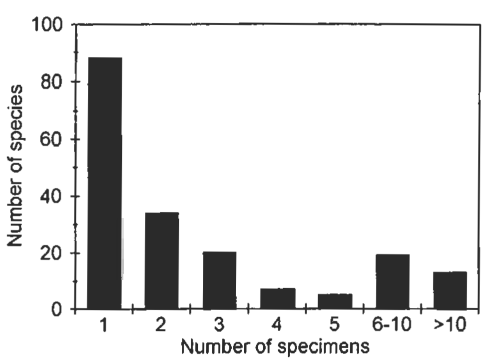

FIG. 3. Distribution of the issid #1 species among samples from individual *Oxyspora paniculata* shrubs. Number of individuals per sample is given on x axis.

TABLE 3. Distribution of leafhoppers among individual *Oxyspora paniculata* shrubs. N1 - number of leafhoppers per sample (50 leaves); N2 - number of leafhoppers on a whole shrub (as calculated from N1); N3 - number of specimens of most abundant leafhopper species on a whole shrub (as calculated from N1); n - total number of samples (each sample was taken from a different plant).

Leafhopper Distribution	N1	N2	N3
min	0	0	0
max	8	50	40
med	1	2	1
avg	1.6	5.8	4
var	2.3	109.4	55.14
n	120	35	35

High species richness of leafhoppers is a general pattern in rainforests, but that found in our study area belongs among the highest found in this habitat type (Novotný 1993). We are not aware of any comparable data on z values for rainforest entomocoenoses.

High species diversity in the understorey is probably in part an artefact caused by a constant influx of transient species from the canopy. As shown by Sutton & Hudson (1980), Rees (1983), Basset *et al.* (1992) and Kitching *et al.* (1993), abundance and flight activity of herbivores, including leafhoppers, is concentrated mainly in the canopy, and decreases from upper canopy through lower canopy to understory.

Leafhoppers associated with Oxyspora paniculata. Four leafhopper species found to be associated with *Oxyspora paniculata*, namely the issid sp. #1, *Carinata bifurcata*, *Onukia emarginata*, and *Kutara* sp., represent probably only a fraction of the leafhopper fauna of this shrub, as only relatively abundant species during a limited part of the season were examined. Taxonomic knowledge on Asian rainforest leafhoppers is fragmentary (Hodkinson & Casson 1991); not surprisingly, three out of the four species associated with *Oxyspora paniculata* are new to science, *Kutara* sp. is an undescribed species (Dr. M. Webb, pers. comm.), and *Carinata bifurcata* was described as a result of this study (Li & Novotný 1997). Similarly, data on their bionomy are patchy. There is no species from the family of Melastomataceae reported as a host species of any fulgoroid (Fulgoromorpha) leafhopper (Wilson *et al.* 1994); we are also not aware of any such record for a cicadelloid (Cicadellomorpha) species, but a review of host plants of this group is lacking.

Leafhoppers in temperate forest ecosystems are rather host-specific, although widely polyphagous species do occur (Claridge & Wilson 1981, Wilson *et al.* 1994). There are sound theoretical grounds for the prediction of herbivores being host-specific as well as polyphagous in floristically diverse rain forests (Basset 1992a), but the knowledge on the pattern actually prevailing is so far very incomplete (Gaston 1993). High density of the issid sp. #1, *Carinata bifurcata*, and *Kutara* sp. on other understory vegetation than *Oxyspora paniculata* indicates that these species do not specialize exclusively on this plant. However, the extent of the host range of these leafhoppers remains to be determined. It may still be quite limited as there were several orher species of the family Melastomataceae in the understory, some of them relatively common (especially *Blastus* cf. *cochinchinensis* Lour. and *B. borneensis* Cogn., but also *Melastoma malabuthricum* L., *Phyllagathis* sp., and *Sonerila* sp.).

Distribution of all four leafhopper species found to be associated wirh *Oxyspora paniculata* among individual shrubs exhibits two features: the proportion of shrubs colonized by each leafhopper species is high, and the density of leafhoppers on each of these colonized shrubs remains low. A hypothesis on random distribution of leafhoppers as a whole and of the issid sp. #1 cannot be rejected ($P > 0.05$). This pattern indicates that the hypothesis postulating that low densities of herbivore populations in rainforest understory are caused by a scarcity of their host plants can be rejected for these leafhopper species feeding on *Oxyspora paniculata*. However, it should be noted that an opposite pattern of herbivore distribution among individual plants, namely the clumped one, with some plants heavily infested bur others mostly not colonized at all, would not in itself represent strong support for the scarcity hypothesis as the absence of herbivores on some plants may be due to causes other than the herbivores' poor colonization success. Rowell (1978) reports such a distribution pattern for rainforest acridiids, exhibiting high host-specificity, low dispersal ability, and, subsequently, colonizing a small proportion of available host plants by high-density populations. In this case, population limitation by resource scarcity and heterogeneity was likely. Two factors may enhance the colonization of *Oxyspora paniculata* by the leafhoppers and hence explain different pattern found in our study, namely the plant's relatively high density, and the leafhoppers' polyphagy.

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