

Associations of Large Homoptera (Fulgoridae and Cicadidae) and Trees in a Tropical Forest

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ABSTRACT: To determine tree preferences of tropical homopterans, the lower trunks of all trees 20 cm dbh or greater were surveyed in 26.72 ha of semideciduous lowland forest in Panama during the wet season. Trees with adult Homoptera or nymphal exuviae were compared with trees available for choice. In the Cicadidae we found 243 adults and 81 exuviae of *Fidicina mannifera*, and in the Fulgoridae we found 63 *Enchophora longirostris*, 19 *Phrictus quinquepartitus*, 2 *Diareusa conspersa*, and 1 *Fulgora*. Disproportionate numbers of the cicadas (52%) were on 33 *Zanthoxylum belizense* (Rutaceae) and another 10% were on *Z. panamense*. The 81 exuviae were not associated with *Zanthoxylum*, and instead occurred on a diverse array of trees. Of the *Enchophora*, 71% were found on 26 *Simarouba amara* trees (Simaroubaceae). All but three of the 19 *Phrictus* rested in parallel arrays on two *Terminalia oblonga* (Combretaceae). The trees listed above are uncommon in the surveyed plot, ranging in rank order of abundance from 15th (1.95% of the trees) to 41st (0.45%). The results indicate, therefore, that Homoptera can be highly selective of tree species even in a diverse forest, where the low probability of encountering a given kind of tree might be thought to select against host tree specialization.

Although most investigators have found phytophagous insects to have narrow dietary niches (Strong et al., 1984), exceptions to stenophagy might be expected in tropical environments. Eastop (1972), for example, attributed the broader diet of tropical aphids compared to temperate aphids to the difficulty of finding a specific host in an environment of high plant diversity. Similarly, Rowell (1978) speculated that broad feeding niches might be found among insect herbivores in tropical wet forests because particular hosts would be rarer and harder to find. Another solution for tropical phytophages would be specificity to a plant species that is relatively common; according to Dethier (1970), food plants of monophagous insects are almost invariably very abundant.

In the present study we explored the question of diet breadth in tropical sap-feeding insects by surveying tree trunks in a large plot of tropical forest for associations between individual tree species and homopterans. We chose a site in Panama where the trees are identified and mapped, and where there is high biotic unpredictability in tree neighborhoods (Hubbell and Foster, 1985). Large Cicadidae and Fulgoridae were selected for the survey because these insects are conspicuous, and because data on host specificity of tropical homopterans is almost completely lacking (Wolda, 1982).

Materials and Methods

The survey was conducted on 26.72 hectares of a 50 hectare plot of semideciduous lowland forest on Barro Colorado Island, Panama (9°09'N, 79°51'W). The area surveyed consisted of one 480 × 500 m rectangle and a nearby irregular

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piece 2.72 ha in area. Using a map of the numbered trees identified by R.B.F., L.K.J. located all standing trunks ≥ 20 cm dbh and scanned each bole on all sides from ground level up to at least 3 m. The survey was conducted from early morning to mid-afternoon at a steady rate of about a hectare per day between July 20 and August 21, 1982, in the middle of the wet season.

When a large cicada or fulgorid or intact nymphal skin was found, the tree number was recorded. Trunks occupied and trunks available were compared using a computer printout of tree numbers, tree species, tree dbh's and mapped locations for all trees ≥ 20 cm dbh in the surveyed hectares. In order to meet the requirement of chi-square testing that the minimum expected values be at least equal to one (Snedecor and Cochran, 1967), tree species were sometimes lumped into orders and families as given by Cronquist (1981). Voucher samples of the insects were identified by J. P. Kramer, USDA, and deposited in the personal collection of L.K.J.

Results

On the 4203 tree trunks surveyed we found 243 *Fidicina mannifera* Fabricius (Cicadidae), 63 *Enchophora longirostris* Distant, 19 *Phrictus quinquepartitus* Distant, 2 *Diareusa conspersa* Schmidt and 1 *Fulgora* species (Fulgoridae). The *Fulgora* was on a trunk of *Eugenia oerstediana* (Myrtaceae), and the *Diareusa* were on *Poulsenia armata* and *Ficus tonduzii*, both in the Moraceae. The *Phrictus quinquepartitus* were aggregated: 9 occurred on one *Terminalia oblonga* (Combretaceae), 7 on another *T. oblonga* 63 m away, 2 on an *Anacardium excelsum* (Anacardiaceae), and 1 on an *Alchornea costaricensis* (Euphorbiaceae). The binomial probability that *T. oblonga*, rare in the surveyed area, would be chosen at least two out of four times by the *Phrictus* was $P = 0.0001$. The *Fulgora*, and all *Diareusa* and *Phrictus* were sitting quietly, heads pointing up the trunk, the *Phrictus* in parallel arrays (Fig. 1).

The 63 *Enchophora longirostris* were found on 40 tree trunks, where they tended to run about, rather than sit quietly. The trunks occupied were not a random selection from among the 34 available tree orders ($\chi^2_4 = 58.51$, $P < 0.001$). Only four orders, the Magnoliales, Sapindales, Gentianales, and Malvales, were selected. Eight of the trunks (20%) were *Quararibea asterolepis* (Bombacaceae); these had 9 (14%) of the fulgorids. *Q. asterolepis* was occupied significantly more than expected compared to its relative abundance in the surveyed area ($\chi^2_1 = 20.90$, $P < 0.001$), but it was not chosen disproportionately over other trees in the Malvales ($\chi^2_1 = 2.05$, NS).

Most (71%) of the *Enchophora* were found on 26 *Simarouba amara* trees (Simaroubaceae), a strikingly non-random arrangement (Fig. 2). A chi-square test of the null hypothesis of no discrimination among trees was done on the 1187 trees in the Sapindales. According to the test, the fulgorids significantly preferred *S. amara* over other Sapindales ($\chi^2_1 = 334.54$, $P < 0.001$). There was no difference in the mean diameter of *S. amara* occupied versus unoccupied by *Enchophora* (*F*-test, equal variances; *t*-test, NS).

The fulgorids were aggregated on the *S. amara* trunks. In all, 45 *Enchophora* occupied 26 of the 82 *S. amara* trees, giving a mean density of 0.55 insects per tree. The frequencies of 0, 1, 2, and 3 or more *Enchophora* per trunk were significantly different from those expected according to a Poisson distribution

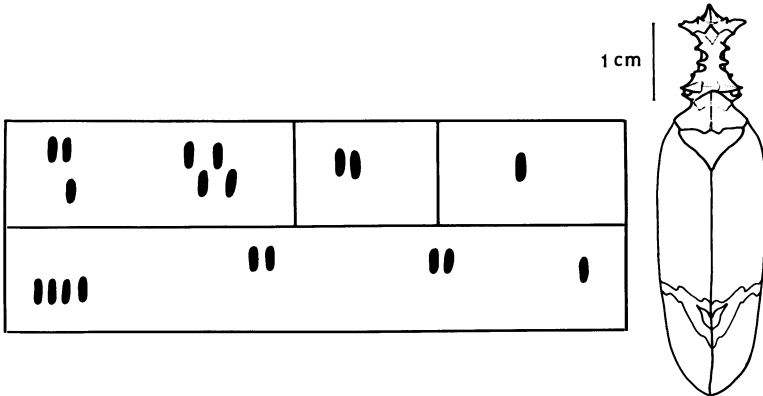


Fig. 1. The spatial arrangement of the fulgorids, *Phrictus quinquepartitus*, on the four trunks on which they were found. Within each box is the arrangement on one trunk. Distortion because of trunk curvature is minimal, for the trunks were wide, ranging from 44–103 cm dbh. All *Phrictus* were oriented head up. A dorsal view of the insect depicts the bizarre ornamentation of the head.

($\chi^2_3 = 14.52$, $P < 0.005$); there were too many trunks with none, and too many trunks with 3 or more.

The adult *Fidicina mannifera* were most often found sitting quietly on the trunk, head pointing up, but on three occasions they were singing or chorusing as they were censused. The 243 adults were found on 89 trunks of 19 species in 15 families in 11 orders. They occurred disproportionately, however, on the genus *Zanthoxylum* (Rutaceae) ($\chi^2_1 = 1138.01$, $P < 0.001$) (Fig. 3), where they were seen to feed in the early morning. Of 44 *Z. belizense* trunks in the surveyed area, 33 had cicadas; of 19 *Z. panamense* trunks, 8 had cicadas. Of all the cicada individuals, 52% were found on *Z. belizense* and 10% on *Z. panamense*. No cicadas were found on the 3 trunks of *Z. procerum*. Among the three species of *Zanthoxylum*, no preference was detected ($\chi^2_2 = 4.26$, NS). Trunks of *Z. panamense* and *Z. belizense* occupied by cicadas were no different in diameter than the unoccupied ones (F -tests, equal variances; t -tests, NS).

The adult *Fidicina* were aggregated on the *Zanthoxylum* trunks ($\chi^2_5 = 47.52$, $P < 0.001$, comparison with Poisson). There were more trunks than expected with 0 and with 5–9 cicadas. The mean number of cicadas per occupied *Zanthoxylum* trunk was 3.7.

On the 4203 trunks we also found 81 intact nymphal exuviae of *Fidicina mannifera*, which are shed above ground at eclosion. Young (1983) thought that the association of nymphal exuviae of *F. mannifera* with certain individual trees might reflect feeding sites of nymphs, which suck xylem from rootlets (White and Strehl, 1978). Accordingly, we analyzed the distribution of nymphal skins for indications of possible host preferences. The 81 skins occurred on 71 trunks of 31 tree species in 20 families and 14 orders. A chi-square test suggests that orders were chosen according to availability ($\chi^2_7 = 11.19$, NS). The Fabales, an order with possible hosts of *F. mannifera* (Young, 1980, 1983), did not have more skins than expected based on its relative abundance ($\chi^2_1 = 2.10$, NS). There was, however, evidence of non-random association with three species: *Prioria copaisera*

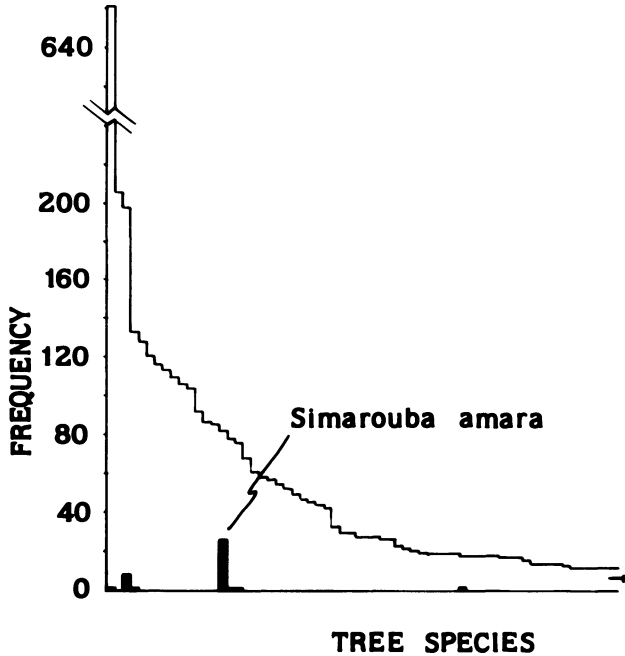


Fig. 2. Frequency distributions by species of all trunks surveyed (white bars) and those trunks on which *Enchophora longirostris* were found (black bars). The trunks most frequently occupied were *Simarouba amara* (26), *Quararibea asterolepis* (8), and *Hampea appendiculata* (2).

(Caesalpinaceae; 8 skins on 6 trunks), *Dendropanax stenodontus* (Araliaceae; 7 skins on 5 trunks), and *Apeiba membranacea* (Tiliaceae; 5 skins on 5 trunks) ($\chi^2_{19} = 32.07$, $P < 0.05$). Even so, the distribution of nymphal casts of *F. mannifera* was much closer to random than was the distribution of adults (Fig. 3).

We also thought that trees with exuviae might be near trees with adult *F. mannifera* based on Young's (1972) suggestion that distributions of adult cicadas are determined largely by the distribution of previous oviposition sites and nymphs in the soil. We ran a chi-square test on the observed nearest neighbor distances between trees with adults and trees with exuviae in the 480 × 500 m rectangle, using 1000 randomly chosen trees to generate predicted nearest neighbor values. However, trees with adults were not closer to trees with skins than expected by chance ($\chi^2_{11} = 7.88$, NS).

Discussion

The survey of lower trunks uncovered several strong associations between homopterans and tree species. The fulgorid *Phrictus quinquepartitus* was associated with *Terminalia oblonga*, the fulgorid *Enchophora longirostris* was associated with *Simarouba amara*, and the cicada *Fidicina mannifera* was associated with and seen feeding on *Zanthoxylum belizense* and *Z. panamense*. All these tree species are relatively thin-barked and fast-growing, with a presumably highly active flow of sugar in the phloem. In the case of the fulgorids we cannot assume the trees represent food plants, since feeding behaviors were not surveyed. However, we

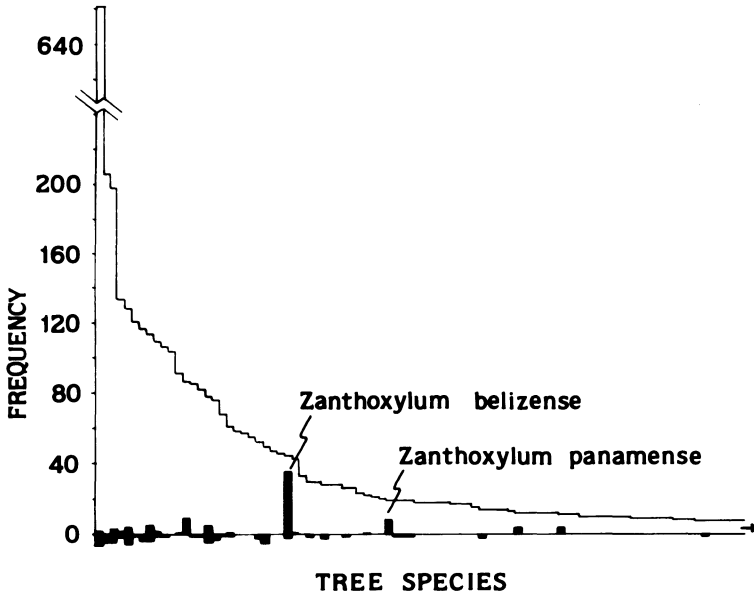


Fig. 3. Frequency distributions by species of all trunks surveyed (white bars), trunks on which adults of *Fidicina mannifera* were found (black bars above x-axis), and trunks on which nymphal exuviae of *F. mannifera* were found (black bars below x-axis). The trunks most frequently occupied by the adult cicadas were *Zanthoxylum belizense* (33), *Beilschmiedia pendula* (9), and *Z. panamense* (8).

can be sure the associations are real, for we objectively surveyed over a large area all examples of an unambiguous kind of microhabitat, namely trunks of trees ≥ 20 cm dbh. The possible biological meaning of the relationships between the tree species and the homopterans is discussed separately for the fulgorids and the cicadas.

FULGORIDS: Up to 5 *Enchophora longirostris* were seen on one *Simarouba amara* trunk, where they may have been feeding or engaging in reproductive behavior. There are few reports of the reproductive behavior of fulgorids, but oviposition, at least, is thought to take place away from the trunk, in branches or twigs. Adult fulgorids feed on phloem (Woodward et al., 1970), which in *S. amara* lies just below the smooth, thin outer bark. Thus, trunks of *S. amara* represent a potential site of feeding.

Simarouba amara also possesses a possible phagostimulant for its herbivores, a bitter principle in the bark called simarolide. Simarolide is a quassinoid, a class of compounds confined to the Simaroubaceae, and related to the limonoids, which occur only in the plant families Rutaceae and Meliaceae, also of the Sapindales (Connolly et al., 1970; Polonsky, 1973). Therefore, if *S. amara* turns out to be a host plant of *Enchophora*, we hypothesize that simarolide or other quassinoids are token stimuli. This hypothesis could be tested by sampling to determine if *Enchophora* also occur on other tree species in the Simaroubaceae.

In light of the chemical similarities of the Rutaceae, Meliaceae, and Simaroubaceae, it is interesting that *Fulgora* spp. are reported to sit preferentially on

trunks of *Simarouba* and *Simaba* (Simaroubaceae) and *Zanthoxylum* (Rutaceae) in various localities in South America (Poulton, 1932; Hogue, 1984; R. Foster, pers. obs.). More records of hosts and potential hosts of tropical fulgorids are to be encouraged. It may be that there is an association between the family Fulgoridae and certain taxa of flowering plants, as Hodkinson (1984) found for families of jumping plant lice (Homoptera: Psylloidea) and orders or families of host angiosperms.

The *Phrictus quinquepartitus* were sitting side by side, mostly on *Terminalia*, oriented vertically up the trunk. The vertical posture was also assumed by the two solitary *Diareusa*, as well as by *Fulgora* spp. (Hogue, 1984). The vertical position may be a conservative characteristic of the family Fulgoridae. One could imagine, for example, that the Fulgoridae possess a nervous system specialized for certain kinds of postural adjustments relative to gravity or the analysis of stimuli coming from certain expected directions. It is perhaps premature to speculate why the *Phrictus* park themselves near one another; the proximity may have to do with mutual defense or be a by-product of the attractiveness of reproductive adults. Nor is it clear why the insects rest on *Terminalia*, for they are not particularly cryptic against the bark. We suspect that feeding or mating activities, perhaps nocturnal, provide the reason for the selection of *Terminalia*.

CICADAS: The cicadas were significantly aggregated on trunks of *Zanthoxylum*; of the trunks that were occupied, there was a mean of almost 4 and a range of 1–9 cicadas per trunk. On three trunks they were singing or chorusing as they were approached for census; other cicadas could be heard singing intermittently in the forest. Young (1983) has likewise found *Fidicina mannifera* in Costa Rica sitting on the lower trunks of large trees, singing sporadically by day.

Adult cicadas feed on sap by inserting the proboscis in xylem vessels (Cheung and Marshall, 1973). One of us (R.B.F.) has found *F. mannifera* feeding on *Zanthoxylum*, at least in the early morning, 7:00 to 7:30. When handled or disturbed while feeding, they eject urine in a jet through the anus (Cheung and Marshall, 1973; T. E. Moore, pers. comm.). Later in the day the association with *Zanthoxylum* appears to loosen as disturbed individuals fly to neighboring trees or, possibly, as males space themselves out, as Doolan (1981) has found for *Cystosoma saundersii*.

Nothing in our data suggests that *Zanthoxylum* serves as a host for the subterranean nymphs. In cicadas, the nymphs drop to the ground after hatching, burrow, probe the xylem vessels of roots, and re-emerge to eclose (Woodward et al., 1970; White and Strehl, 1978). *Fidicina mannifera* oviposits at the base of large trees (Young, 1972), but since we did not observe oviposition we cannot say if *Zanthoxylum* is chosen as a site. The exuviae, however, were not associated to any extent with *Zanthoxylum* (Fig. 3).

Young (1984) has claimed that nymphal skins are found under legume species in different parts of the range of *F. mannifera*, sometimes on the trunk of the legume (Young, 1972), and sometimes on vegetation under the canopy (Young, 1983). The characteristic proximity of emergence to legumes led him to assert that nymphs feed on the root crowns of legume trees. Here in Panama we did not find the exuviae to be associated with trunks in the Fabales (legumes), and six times as many of the skins were associated with non-legume trees as were with legume trees. We did find a significant association between the nymphal skins

and *Prioria copaiifera* (Caesalpiniaceae), the fifth most common tree, but the association was stronger with *Apeiba* and *Dendropanax*, non-legumes. It should be noted, however, that the root crown of a large legume is extensive, and the trunk nearest to an outer portion of the root crown may well be that of another tree.

We also note that there is an important procedural difference between our study and Young's studies. In order to cover a wide area in a short time, using a search method easy to explain and replicate, we did not look for exuviae anywhere except on the trunks of large trees. This meant we missed an unknown number of exuviae, for *F. mannifera* on Barro Colorado Island does sometimes eclose on little stems and fallen branches. Although there is little in our data to support a claim of a generalized host-insect relationship between the neotropical Cicadidae and legume trees (Young, 1984), the question clearly deserves further research.

Our main finding is that all big trees are not equivalent for the homopterans; the adults of three species are highly tree-specific. We expect that these trees are dietary host plants, for there are few recorded cases of phytophagous insects carrying out their different life functions on an array of function-specific plant species. If *Simarouba*, *Terminalia*, and *Zanthoxylum* are the main food plants, the idea that tropical sap-feeding insects ought to be polyphagous (Eastop, 1972), or monophagous on common plants (Dethier, 1970), is not supported.

In any event, whatever the diet breadth of these homopterans, we have shown that these insects can locate specific, rare trees in a diverse forest. In terms of search behavior, monophagy is within their capabilities. We expect that *Enchophora*, *Phrictus*, and *Fidicina* are highly mobile, and able to recognize their preferred trees at a distance, as predicted for host-specific insects in tropical forests (Rowell, 1978).

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