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"Devil's Gardens" in the Ecuadorian Amazon - Association of the allelopathic tree *Duroia hirsuta* (Rubiaceae) and its "gentle" ants

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Abstract: The relationship between the myrmecophytic tree *Duroia hirsuta* (Rubiaceae) and its associated, minute, non-aggressive *Myrmelachista* sp. (Formicinae) ants is poorly investigated, even though the small understory tree is surrounded by a conspicuos zone almost devoid of vegetation. As to the cause of these barely vegetated "Devil's Gardens", two alternative interpretations exist in the literature: the pruning activity of ants and allelopathy. We investigated the mutualistic *Duroia-Myrmelachista* system in the Ecuadorian Amazon, focusing on the phenomenon of the areas of reduced vegetation, as well as on the natural history of the associated ants. We conducted planting experiments and behavioral studies, including coccoids, the third partner in this mutualism. Because the well-studied *Triplaris americana* (Polygonaceae) possesses analogous vegetation free surroundings created by the assiduous mechanical pruning of its mutualistic ant partner (*Pseudomyrmex* sp.), parallel comparative investigations of this ant-plant association were conducted. The two systems are not equivalent; it was demonstrated that the remarkably inactive *Myrmelachista* ants are not responsible for the bare areas around *Duroia* plants. Instead, we regard allelopathy as the causative agent for the clear zones.

Key words: Allelopathy, ant-plant interaction, *Duroia hirsuta*, Ecuadorian Amazon, *Myrmelachista* sp., mutualism, myrmecophyte, scale insects.

Myrmecophytism, the close association between ants and plants encompasses a great diversity of interactions, occurring mostly in tropical forest ecosystems. With approximately 250 associations between myrmecophytes and ants (*e.g.* Bequaert 1922, Benson 1985), the Neotropics harbor the greatest richness of ant-plants (*e.g.* Davidson and McKey 1993a). In general, the benefits gained by ants associated with myrmecophytes are more obvious than vice versa. Advantages conferred by ants on plants vary among systems and are not always clear (Gaume *et al.* 1997). Many plant species provide food and/or nest sites for ants in exchange for protection from herbivores or to gain nutrients (Beattie 1985). A protective benefit for the plant mostly exists in systems involving large, aggressive ants; but it is also known in connection with smaller aggressive ants (Maschwitz and Fiala 1995).

There is some evidence that even minute and "timid" ants can act as protective agents of their host plant (Vasconcelos 1991). However, the protective role of small non-aggressive ants is often questioned. Risch *et al.* (1977) proposed that small ants might supply their host plants with detritus rather than protect them. In general, large colonies of active, aggressive ants occupy fast-growing, light-demanding pioneer trees of early succession, whereas small, timid ants inhabit slower-growing, shade-tolerant plants with trichomes on stem and domatia (Davidson and McKey 1993b).

Duroia hirsuta (Poeppig and Endlicher) K. Schumann (Rubiaceae) is one of these "hairy" plants with a broad distribution in central and western Amazonia (Gentry 1993, Williamson *et al.* 1998). It is a small, dioecious, understory tree without ant-feeding structures. *Duroia hirsuta* trees are characteristically surrounded by anomalously clear zones lacking dense undergrowth. Typically growing in clusters of small trees, many of these openings form so called "Devil's Gardens" devoid of other plants. *Duroia hirsuta* and the myrmecophilious *Triplaris* sp. (Polygonaceae), whose associated ants kill vegetation on and around host trees by pruning (Wheeler 1942), are often mentioned together in the literature. For comparative purposes and because of the frequent generalizations involving both *Duroia* and *Triplaris* (*e.g.* Morawetz *et al.* 1992), we included *T. americana* in our experiments.

Two frequently cited hypotheses are invoked to explain the "Devil's Garden" phenomenon. On one hand the bare areas could be created by the pruning of intruding vegetation by ants that inhabit the elongated swollen internodes of *Duroia*'s branches (Campbell *et al.* 1989, Schultes and Raffauf 1990, Williamson *et al.* 1998). Alternatively, the lack of dense vegetation may be attributed to *Duroia*'s allelopathic properties (Page *et al.* 1994, Jasen *et al.* 1995, Aquino *et al.* 1999).

Allelopathy concerns the production of specific biomolecules by a plant that can inhibit or benefit another plant. Several authors have speculated that ants in *Duroia* may have a weeding function, as is known for many other "plant-ants", thus characterizing the *Duroia* system as "ant-mediated" allelopathy (*e.g.* Renner and Ricklefs 1998). Paying equal attention to both hypotheses, our study investigated the causality of the "Devil's Garden" phenomenon and the role of the *Duroia*-*Myrmelachista* mutualism.

MATERIALS AND METHODS

The study was conducted from May to July 1999 at the Estación Científica Yasuní (ECY), located in the Parque Nacional Yasuní, Ecuador (00°40' S; 76°24' W). The study site is located in a region harboring pristine lowland rain forest. Annual precipitation is about 3200 mm (Pitman 2000).

The investigated myrmecophytes: We marked 18 trees of *D. hirsuta* (voucher Pfannes 1; WB) growing along a trail system in ten "Devil's Gardens" and seven trees of *T. americana*, recording tree height and diameter of crown. We calculated the area of each "Devil's Garden" by considering them to be elliptical. To compare the fate of plants growing on the bare areas under *T. americana* and *D. hirsuta* and to find out about a probable attenuation of the effect with increasing distance from the tree, two small individuals of the fern *Didymochlaena truncatula* (Dryopteridaceae) (height 16.9 ± 7.4 cm) and of the palm *Geonoma* sp. (Arecaceae) (height 22.1 ± 11.5 cm) were transplanted at a distance of 40 and 80 cm from each focal tree. *Didymochlaena truncatula* was chosen because it is one of the few small plants we found growing in "Devil's Gardens."

Additionally, the same palm and fern species potted in plastic bags were placed under ten of our experimental trees at a distance of 40 cm. Also, a climbing aroid (*Anthurium* sp., Araceae) (length 45.5 ± 16.8 cm) was attached to the stem at a height of 1.5 m. As a control, the same experiments were conducted just outside the gardens, and aroids were fixed on the stems of six trees of different genera. Plant condition was classified in six different categories (Table 1) and changes in plant condition were checked visually.

The investigated ants: We collected 30 ants from each *D. hirsuta* tree and identified them to genus level. In order to survey colony size, colony composition, distribution of inhabited domatia and generic composition, we wrapped all internodes of a single *Duroia* plant with film. Ants were killed by injection of insecticide into each internode. Data were recorded for number of domatia, number of ants per domatium and presence of coccoids. To observe ant behavior on *Duroia*, a scaffold was constructed next to one of our study trees.

TABLE 1

Condition of plantings around study trees and control trees (mean ± 1 SD)*

	Day	Ferns 40	Ferns 80	Palms 40	Palms 80	Aroids	Co. ferns	Co. palms
D. hirsuta ‡	6	1.0 ± 0	1.0 ± 0	1.0 ± 0	1.0 ± 0	2.3 ± 0.9	1.2 ± 0.4	1.4 ± 0.7
D. hirsuta ‡	57	1.8 ± 1.1	1.4 ± 0.6	3.7 ± 1.5	3.4 ± 1.5	5.7 ± 0.6	1.2 ± 0.5	1.5 ± 1.2
D. hirsuta Δ	6	1.2 ± 0.3	–	1.2 ± 0.3	–	–	1.2 ± 0.3	1.3 ± 0.4
D. hirsuta Δ	57	1.3 ± 0.4	–	1.3 ± 0.4	–	–	1.3 ± 0.6	1.4 ± 0.4
T. americana ‡	6	3.1 ± 1.5	1.4 ± 0.7	2.6 ± 1.5	2.1 ± 1.4	5.9 ± 0.3	1.3 ± 0.8	1.3 ± 0.8
Co. trees	6	–	–	–	–	1.6 ± 0.7	–	–
Co. trees	15	–	–	–	–	2.0 ± 0.6	–	–

* Conditions of plantings were classified in 6 categories: 1 = no visible damage; 2 = moderately wilted; 3 = wilted / moderately damaged; 4 = moderately dried / strongly damaged; 5 = strongly dried / substantially damaged; 6 = whole plant dead.
‡ = planted seedlings.
Δ = potted seedlings.
Day = day after starting the experiment.
Co. = control.
40 and 80 = distance of the seedlings from study tree in cm.

Activity was recorded at 15-min intervals for a total of 95 hr (day and night observations). To record feeding preferences, baits (sugar, marmalade, bread and tuna fish) were offered to the ants on branches. To observe ant behavior in the presence of plant enemies and ant enemies/enemies' odor, individuals of *Atta* sp. (Myrmicinae) and *Dolichocherus* sp. (Dolichoderinae), respectively, were transferred to *Duroia* and their scent trail, fixed on paper, was attached to branches.

To examine if ants keep *Duroia* free from epiphyllae, we wrapped grease-smeared strips of fabric around three randomly chosen branches below young leaves. Ant-excluded leaves were checked 20 days for herbivore or other damage. Variations in leaf condition were recorded systematically.

The investigated Homoptera: We noted the existence of scale insects in each of the investigated *Duroia* plants by taking random samples of domatia.

Statistics were calculated using Mann-Whitney U-test. All results are given as mean ± 1 SD.

RESULTS

The investigated myrmecophytes: Tree height of *D. hirsuta* was 4.9 ± 1.9 m; crown diameter was 3.0 ± 1.0 m. The trees were distributed over ten bare areas with an extent of 71.8 ± 60.2 m^2, while the extent of the circular area around isolated *Duroia* trees (5.5 ± 1.4 m^2) was smaller than the corresponding extent of trees clustered in "Devil's Gardens" (33.2 ± 9.2 m^2). The size of the seven trees of *Triplaris* was 12.6 ± 6.5 m. The bare zone around each study tree was characterized by its circularity and by complete absence of vegetation. The extent of a clear area was 11.8 ± 3.8 m^2.

On average, seedlings around *Duroia* were in significantly better shape in comparison to those around *Triplaris*. The data for the mean conditions of all plantings are represented in Table 1. Compared to palms set around *Duroia*, controls were significantly less deteriorated (U-test, $p < 0.001$). The condition of aroids attached to stems of *Duroia* and *Triplaris* was significantly worse than control while aroids on *Triplaris* were worse than those on *Duroia* (U-test, $p < 0.01$). Ferns in "Devil's Gardens" were not significantly different from control; control plant condition did not change significantly at any site. Seedlings planted near to and farther from *Duroia* differed not significantly in condition. Around *Triplaris*, only ferns showed a significant deterioration depending on distance (U-test, $p \leq 0.5$). There were no differences between potted plants and controls.

Fig. 1. SEM micrograph of side view from *Myrmelachista* sp. worker (photo: K. Pfannes). *Myrmelachista* is an exclusively neotropical genus of the ant subfamily Formicinae (waist of 1 segment, the petiole). *Myrmelachista* is characterized by 9- or 10-segmented antennae. The apical and 1 or 2 preapical antennal segments are broader than the preceding segments and form a swollen and conspicuous club whose segments are strikingly differentiated from the funinculus (Bolton 1994).

Aroids attached to *Duroia* stems developed a necrotic leaf area leading of from the main nerve. Some palms around *Duroia* trees also showed brown spots at the base of the lamina. According to literature and personal observation, the aggressive ants of *Triplaris* destroy surrounding vegetation by chewing. They also seem to "inspect" thoroughly the small offspring of their host for herbivores or intruding vegetation.

The investigated ants: *Myrmelachista* (Formicinae) was the only genus found in investigated *D. hirsuta* (Figure 1). The ants occupying *T. americana* were identified as *Pseudomyrmex* (Pseudomyrmecinae). One *Duroia* tree of 2.4 m height offered 38 domatia to ants, of which 10 were uninhabited; the latter were most frequently located at the base of twigs and possessed thickened walls. The number of ants per internode amounted to 165 individuals (± 58.8; n = 28). Young domatia contained larger numbers of ants. The different stages of development of ants and coccoids were often lacking in young domatia. Thus, we observed a gradient of ant abundance, from low densities at the base of the tree toward higher densities at the apical twigs. Empty domatia were seldom occupied by coccoids (scale insects), whereas internodes inhabited by ants always sheltered coccids (soft scale insects) and, to a lesser extent, pseudococcids (mealybugs). Reproductive individuals and their developmental stages were not found in every internode. Domatia had a length of 5.3 cm (± 1.1; n = 38). These results match with other samples taken from various *Duroia* trees; therefore, we suggest that the results are transferable to other trees of this species.

During our observations we recorded no ant behavior that could be construed as aggressive or protective. Ants remained in the domatia most of the time. They were never observed outside the internodes during rain or at night, and even when the sun was shining, we recorded little ant activity. Maximum activity was observed on dry, sunny days from late morning until afternoon.

The most frequently observed behavior was an uncoordinated rapid patrolling along stem, branches, buds and young leaves. In this situation an erect gaster was frequently noted. No feeding or food gathering was observed. We never saw ants patrolling on planted seedlings and only a few crawling on aroids. While few ants were recorded at the baits and neither recruitment nor food gathering could be observed, no food preferences were detected. There was no obvious reaction of *Myrmelachista* to direct presentation of *Atta* or *Dolichoderus* ants. Apart from this experiment, we observed few attacks on foreign ants and no aggression against flying insects. A very small proportion of ants bit into scented paper, losing interest after a short time.

No changes in state of condition were visible on leaves devoid of patrolling ants and plant cover on leaf surfaces did not increase.

The investigated Homoptera: Taking random samples during the whole experimental time, we found coccoids inside most domatia –not only coccids but also pseudococcids. However, after several days of incessant rainfall we registered the exclusive occurrence of pseudococcids.

DISCUSSION

Our results suggest that the small *Myrmelachista* ants on *Duroia* do not prune surrounding vegetation, as do the larger *Pseudomyrmex* ants on *Triplaris*. The aggressive, rapid and distance-dependent destruction of seedlings around *Triplaris* by the *Pseudomyrmex* ants contrasts starkly with the much slower decay of palms and aroids but not of ferns around *Duroia*. The lack of observed lingering of *Myrmelachista* ants on seedlings and the indifferent behavior toward the presence of the transplants as well as the ants' low activity and aggressiveness support our statement. Therefore, we hypothesize that allelopathy is the more likely causative agent of the "Devil's Garden" phenomenon.

Nevertheless, the appearance of necrotic leaf areas could easily lead to the supposition that ants inject herbicide into the plants' vascular bundles. This explanation for the "Devil's Garden" was suggested by Morawetz *et al.* (1992) and Renner and Ricklefs (1998), who considered *Duroia* to be similar to the melastomes *Tococa guianensis* and *Clidemia heterophylla*, all of which are *Myrmelachista* inhabited trichome myrmecophytes forming vegetation free-zones. Despite some noteworthy similarities between those plants and *Duroia*, their interactions with ants cannot simply be assumed to be equivalent.

The genus *Myrmelachista* is believed to have undergone major evolutionary specialization in response to weak competitive taxa (Davidson and McKey 1993b). It possesses a wide variety of behavioral patterns, ranging from non-pruning in some *Ocotea* (Lauraceae) plants in Central America, to the extreme case of killing intruding vegetation by the use of highly effective chemicals (Morawetz *et al.* 1992, Renner and Ricklefs 1998). Therefore it is not surprising that *Myrmelachista* ants in *Duroia* neither showed aggressive behavior against transplanted saplings nor attacked potential enemies, in contrast to *Myrmelachista* spp. associated with other trees. An additional difference between *Duroia* and the various melastomes is in the survival time of the exposed plants. While not a single individual survived longer than five days near *T. guianensis* and most transplants in the *Tococa-Clidemia* patches were dead after three weeks, the decay of the transplanted saplings around *Duroia* occurred much more slowly. Nevertheless, we cannot totally exclude that the slow decay is due to our choice of plant species. We suggest therefore that future research repeat the experiment using woody dicots as experimental plants.

Campbell *et al.* (1989) similarly observed a characteristic pattern of plant death, emerging from the leaf base over the center vein to the leaf margin, suggesting that an allelopathic agent may be absorbed by the roots. Further support comes from a study by Chu-Chou (1978) who reports on plants showing identical necrotic responses after absorbing allelopathic compounds dissolved in water.

We suggest that *D. hirsuta* has a double-barreled defense at its disposal. Though we consider allelopathy to be the main defense against intruding vegetation, the ants could also provide a benefit for the plant, even if it is not immediately apparent. However, considering the ants low activity, lack of aggression against herbivores as well as plantings, plus the small dispersal radius around the host tree, we conclude that whatever beneficial effect they do exert on the plant, it has to be small. Respiratory carbon dioxide released by inhabitants into hollow stems may be used in photosynthesis (Billings and Godfrey 1967). Additionally, ammonia produced by the ants nesting in domatia from decaying frass and body parts (Risch *et al.* 1977, Letourneau 1983) could be assimilated by the host plant. By this mechanism, *Myrmelachista* probably contributes to the plant's food supply by providing nourishment that plants can metabolize to produce new domatia.

Ant colony dispersal requires the availability of additional swollen internodes. Younger domatia are preferably colonized. Related to the observed presence of ant-attended scale insects inside the domatia of *Duroia*, there would be need also for a new home for them when the walls of older internodes are thicker; presumably coccoids cannot easily reach phloem leading to an insufficient availability of coccoids' honeydew for the ants. Supplying ants with products of coccoids is an important part of the mutualism because the presence of coccoids increases costs for the host tree, which may be compensated by the benefits ants confer to their host plants.

Coccids and pseudococcids were detected in this study. While Gullan (1997) reported unidentified coccids attended by *Myrmelachista* inhabiting *Duroia*, the presence of pseudococcids in *Duroia* was not mentioned before in the literature. The exclusive presence of pseudococcids after long periods of rain when ants had not left the domatia for extended periods suggests that in times of food shortage ants feed on coccids. Direct harvesting of coccoids has been reported for certain ant-plants (Gullan 1997) and seems to occur especially in dependent relationships (Carroll and Janzen 1973). According to Gaume *et al.*'s (1998) hypothesis coccids require more care from workers than pseudococcids because more coccids are necessary to obtain an equivalent benefit for ants. Also, ants derive more proteins or amino acids from coccids than from pseudococcids because their honeydew may contain more nitrogenous substances (Davidson and Patrell-Kim 1996) and because ants may harvest more coccids directly. The investigated ants may take full advantage of nutrients in *Duroia* while mostly feeding on coccoids' honeydew and falling back on coccids directly during scarcity of food. Lack of food gathering and the tendency of ants to remain in the domatia indicate that in the *Duroia*-system coccoids are *Myrmelachista*'s main source of food. Perhaps for this reason the ants paid little attention to offered food items.

The *Tachigali-Pseudomyrmex* system (Fonseca 1993) could be similar to the *Duroia-Myrmelachista* system because the ants tend coccids, never forage outside the host plant and do not attack herbivores, but do clean the host plant. The ants' cleaning, which would manifest itself in increased photosynthetic rates, could be a possible benefit for *Duroia*. According to Mooney (1972) increased leaf longevity is a result of workers removing epiphyllae and debris from leaf surfaces.

Even if many ant removal studies have demonstrated that ants protect plants against herbivory and competing plants (*e.g.* Janzen 1969), lack of epiphyllae growing on *Duroia*'s leaves could also be prevented by an allelopathic compound. The fact that we registered uninhabited *Duroia* trees partly covered by epiphyllae, but also occupied trees with epiphyllae and groundcover, is ambiguous. The existence of this plant cover could be because plants of the same species may vary in their allelopathic effects, possibly due to differences in microhabitats and/or stress conditions (Rice 1984). If ants provide nutrients for host trees, their absence could be a stress factor. Our barrier experiment could not clarify these circumstances because lacking of epiphyllae on ant-excluded leaves could also be due to the short experimental time.

Focusing on the "Devil's Garden" phenomenon, we suggest that most plant competition in the vicinity of *Duroia* is suppressed by the tree itself, with *Myrmelachista* ants exercising a more indirect effect. The experiment with potted plants, where a possible allelopathic effect was ruled out, produced no deterioration of plant condition. *Duroia*'s allelopathic properties have been known for a long time, particularly Indians took advantage of the trees' compounds in a variety of uses (Schultes and Raffauf 1990). Unequivocal evidence of allelopathy as the causative agent of *D. hirsuta* gardens exists (Campbell *et al.* 1989). Additionally, Page *et al.* (1994) report on the lactone plumericin, a potent inhibitor of plant growth, isolated from *D. hirsuta*'s roots and from leaves. Allelopathic terpenoides of *Duroia*'s bark have been identified by Jasen *et al.* (1995), and recently, the lactone duroin, two methyl-ethers and a flavonol, that are all confirmed to inhibit growth of other plants in *Duroia*'s habitat, were detected (Aquino *et al.* 1999). However, the isolation of various allelopathic compounds out of plant tissues *per se*, cannot simply be regarded as identical to the circumstances *in situ* because many plant compounds have allelopathic effects that are concentration sensitive and dependent on the affected plant. Nevertheless, these laboratory results offer compelling support that allelopathy causes the "Devil's Gardens."

Allelopathy is also implicated by the observation that several "resistant" plants, particularly ferns, grow in "Devil's Gardens," such as *D. truncatula*, *Lindsaea divaricata*, *Asplundia alata*, *Psychotria polyphlebia* and *Cordia nodosa*. Interestingly, we found two individuals of *C. nodosa*, growing at the edge one of *Duroia*'s "Devil's Gardens", to be also inhabited by *Myrmelachista* sp. Although the vegetation cover was reduced beneath them, there was more cover than beneath *Duroia*; the presence of the ants and the less pronounced development of the "Devil's Gardens" supports the interpretation of allelopathy as the major cause. The experimental conclusions remain equivocal because they could not exclude one of the hypotheses. It is also likely, that both hypotheses may operate. Circumstantial evidence, however, suggests that here allelopathy is the more likely cause of the "Devil's Gardens". To decide the issue we propose further studies examine the *Cordia-Myrmelachista* system.

Viewing the *Duroia-Myrmelachista* system from an evolutionary point of view, colonies of small, timid *Myrmelachista* (being old specialist plant-ants with restricted ecological distribution; Gaume *et al.* 1997) could not have withstood competition for plants offering greater resources due to the arrival of a new wave of dominant aggressive ants in former times. As a result, comparatively dominant ant species may have driven weakly competitive taxa to increasing evolutionary specialization and host specificity. Therefore, non-aggressive *Myrmelachista* might have been pushed back to plants providing less direct nutritional benefits to their ants or/and possessing hairs that may function to exclude larger ants (Davidson and McKey 1993b). Davidson *et al.* (1988) suggest that pruning of vegetation surrounding host trees of *Triplaris* limits potential invasion by foreign ants. Because this can be regarded primarily as a response to natural enemies rather than a means of stimulating productivity of the host plant, *Myrmelachista* would not need to prune because their host trees' trichomes inhibit invasion by larger-bodied ants. On the other hand, the plant did not need to evolve ant-attracting food resources such as extrafloral nectaries or food bodies because of its allelopathic defense system. The provision of domatia with only coccids as a food source has relieved the host plant of genetic and metabolic costs of nectaries (Huxley 1986).

In summary, the interaction between *D. hirsuta* and *Myrmelachista* sp. can be considered a facultative mutualism. Unfortunately, the genus *Myrmelachista* is largely uninvestigated. It would be interesting to clarify its phylogeny in order to get an insight into the possible coevolution of these ants and its various host plants.

RESUMEN

La relación entre el árbol *Duroia hirsuta* y su hormiga asociada, *Myrmelachista* sp., ha sido pobremente estudiada. Con el fin de investigar el grado del mutualismo que existe en este sistema y las causas de las zonas con poca vegetación alrededor de *Duroia*, realizamos experimentos de transplante de plantas y registros etológicos de las hormigas e insectos escama, los cuales son el tercer componente del mutualismo, en la selva Amazónica de Ecuador. Se comparó con la planta mirmecofita *Triplaris americana*, la cual poseé un área libre de vegetación a su alrededor creada por la hormiga *Pseudomyrmex* sp. Los dos sistemas mostraron no ser equivalentes ya que las hormigas no causan la zona libre de vegetación alrededor de *D. hirsuta*. La alelopatía es la causa probable de esa zona libre.

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