Logging Speeds Little Red Fire Ant Invasion of Africa

ABSTRACT
Here, we document the invasion of equatorial Africa by the little red fire ant (*Wasmannia auropunctata*). Commercial logging and other forms of natural resource extraction have catapulted *W. auropunctata* into the interior of Gabon at a rate 60 times faster than the unassisted rate we measured over 19 years at the Lope Reserve. We also present photographic evidence suggesting that *W. auropunctata* is negatively affecting the country’s exceptionally rich and intact large mammal fauna.

RESUMEN
Nous documentons l’invasion de l'Afrique Equatoriale par la fourmi eûlectrique (*Wasmannia auropunctata*). L’exploitation forestière et les autres formes d’extraction des ressources naturelles ont catapulté *Wasmannia auropunctata* à l’intérieur du Gabon à un rythme 60 fois plus rapide que la progression non assistée que nous avons mesurée sur 19 ans à la Réserve de la Lopé. Nous présentons également des photographies suggérant que *Wasmannia auropunctata* a un impact négatif sur la faune de grands mammifères exceptionnellement riche et intacte du pays.

Key words: equatorial Africa; invasive species; leopard; logging; *Wasmannia auropunctata*.

Western equatorial Africa (WEA) is a global biodiversity hotspot, holding some of the world’s largest blocks of intact tropical forest (Minnemeyer et al. 2002). The most pressing threat to the region’s biodiversity is mechanized logging, which fragments and destroys habitat (Laurance 1999) and facilitates a booming commercial hunting industry (Wilkie et al. 2000). Here, we identify another biodiversity impact of mechanized logging, the spread of a Neotropical invader, the little red fire ant (*Wasmannia auropunctata*). By displacing endemic ants and preying on or outcompeting a variety of other arthropods, *W. auropunctata* has earned a spot as one of the world’s top 100 invasive pests (ISSG 2002). Particularly hard-hit have been the Pacific islands, where *W. auropunctata* also affects lizards, tortoises, and domestic dogs (Lubin 1984; Wetterer 1997; Jourdan et al. 2001, 2002). Effects on wild mammals have not been widely reported, perhaps because mammals are rare in insular faunas. Here, we present the first material evidence of *W. auropunctata* impact on a large mammal in WEA, which holds one of the richest, most ecologically functional large mammal communities of any tropical forest region in the world (Mack 1993, Oates 1996, Barnes et al. 1998).

The first records of *W. auropunctata* infestation in Africa come from 1913 in the Gabonese capital Libreville (Santschi 1914). The next year, Albert Schweitzer noted that a small red stinging ant (probably *W. auropunctata*) was also present ca 145 km up the navigable Ogooué River at Lambaréné (Schweitzer 1931); however, movement overland was relatively slow, requiring another six decades before *W. auropunctata* was detected at the Lopé Reserve, 200 km inland from Lambaréné. *Wasmannia* presence at Lopé was first recorded in 1982, in the garage area of a recently abandoned logging camp, which later become the primary gorilla study area of the Station D’Etude des Gorilles et Chimpanzees (SEGC). Local villagers confirm that *W. auropunctata* was absent until logging roads were cut during the 1970s. Thus, it is likely that the ants that colonized Lopé were stowaways on a logging vehicle.

Between 1982 and 2001, five surveys in the SEGC study area have documented the expansion of *W. auropunctata* (Fig. 1a, b). These surveys suggest a two-phase expansion process in which *W. auropunctata* occasionally makes long-distance movements to colonize new areas, then expands locally around each colonization point. The resulting rate of radial spread at SEGC can be estimated by using the infestation “center of gravity” from the first survey year (1982) as an estimate of the original point of

---

1 Received 18 December 2003; revision accepted 4 June 2004.
colonization then, for each survey year, measuring the maximal distance of detected patches of infestations from this origin. For the most recent survey (2001), the patch farthest from the assumed origin was 1361 m farther than the farthest patch in the 1982 survey, implying a spread rate of 1361 m/19 yr or 71.6 m/yr. A linear regression using data on maximal distance from the assumed origin for all five survey years yields a very similar estimated spread rate of 72.9 m/yr ($R^2 = 0.99$, SE = 3.2 m/yr, $P = 0.0002$; Fig. 1a). Projecting this spread rate back in time implies an original infestation date of ca 1972, which is consistent with the logging history in the area.

Growth in the amount of habitat at SEGC infested by *W. auropunctata* was well described as an exponential process of the form $N_t = N_0 e^{bt}$, where $N_0$ is the surface area infested in 1982 and $t$ is the number of years since 1982. If this equation is rearranged to $\ln(N_t/N_0) = \beta t$, the value of $\beta$ can be estimated using linear regression (Fig. 1b). This produces an instantaneous growth rate $\beta$ of 0.168 ($R^2 = 0.46$, SE = 0.009 m/yr, $P = 0.0003$), which translates into an annual growth rate of $e^{0.168}$. In other words, the amount of habitat infested by *W. auropunctata* grew 18 percent each year on average. If exponential growth continues at this rate, a zone equivalent to the entire 25 km$^2$ SEGC gorilla study area will be infested by the year 2025.

Larger-scale observations also implicate logging in the spread of *W. auropunctata* into Gabon. The year 1987 saw the completion of a transnational railroad, built to allow export of timber and manganese from Gabon's interior. Since then, the penetration of *W. auropunctata* into Gabon's interior has greatly accelerated (Fig. 1c). In 1999, *W. auropunctata* was detected 320 km down the train line from Lopé in Franceville. In 2001, *W. auropunctata* was found in Makokou, 215 km by road northeast of Lopé, in a house previously occupied by building contractors and gold prospectors. Despite the shorter distance from Lopé, Makokou may have required longer to colonize because of the lack of rail access, which delayed the arrival of commercial timber exploitation until late 2001. The maximal straight-line distance covered from Lambaréné between 1914 and 2002 was 390 km, indicating that the average annual increase
in the radius of detected infestations in Gabon was 390 km/88 yr or 4.4 km/yr. Thus, logging and other natural resource extraction activities appear to have catapulted *Wasmannia auropunctata* into the interior of Gabon at a rate roughly 60 times greater than the local expansion rate observed at SEG.

Neighboring Republic of Congo is logged independently of Gabon and interviews with researchers and conservationists there suggest that *W. auropunctata* may not yet have invaded Congolese parks. *Wasmannia* has apparently not reached Odzala National Park, which lies in northwest Congo ca 185 km east of Makokou (F. Maisels, pers. comm.). *Wasmannia* also has not been observed in Conkouati National Park in southeast Congo (B. Braet, pers. comm.), even though it is common in the Mayumba region directly across from the border in Gabon (G. P. Sounget, pers. comm.). A cross-border difference in *W. auropunctata* presence also holds on the border with the Central African Republic (CAR), which is also logged independently of Congo. *Wasmannia* is absent from Nouabale-Ndoki National Park in Congo (P. Walsh, pers. obs.) but present directly across the border at Dzanga-Ndoki National Park in CAR (A. Todd and C. Chipolella, pers. comm.).

It seems unlikely that major *W. auropunctata* infestations in or around Congolese parks would have gone undetected if they were present. In Gabon, *W. auropunctata* tend to aggregate on leaves of the exceptionally thick understory vegetation. It is difficult to walk through a zone of heavy infestation without coming into direct body contact with *W. auropunctata* and, consequently, suffering numerous painful stings. Understory vegetation is equally thick in Congo, particularly in the previously logged areas where a great deal of research and conservation activity and infrastructure are concentrated. Furthermore, local villagers in at least one park in Congo (Nouabale-Ndoki) have no knowledge of *W. auropunctata* while villagers living around *W. auropunctata*-infested Gabonese parks (i.e., Petit Loango and Lope) are acutely aware of its presence and even have a specific local name for *W. auropunctata* (Wetterer *et al.* 1999).

Reports that *W. auropunctata* may be affecting wild mammals first came from the Petit Loango Reserve on the southwest coast, where forest elephants (*Loxodonta cyclotis*) and red river hogs (*Potamo-
cherus porcus) in zones of heavy *W. auropunctata* infestation behaved in a way suggesting unusually poor vision (Wetterer *et al.* 1999; S. Lahm, pers. obs.). Blindness is a useful indicator of *W. auropunctata* impact because vertebrate eyes are particularly vulnerable to *W. auropunctata* stings. For example, *W. auropunctata* stings are a common cause of blindness among domestic dogs in the Solomon Islands (Wetterer 1997) and cause blindness in reptiles on other Pacific islands (Lubin 1984; Jourdan *et al.* 2001, 2002). A study conducted in 2002 in the SEGC study area at Lopé suggested that leopards may also suffer from the sting of *W. auropunctata*. A leopard, photographed in the act of biting an automated camera trap, had milky corneas (Fig. 2c). Three other photographic “recaptures” of the same leopard showed that its home range contained several areas heavily infested with *W. auropunctata*. The leopard photograph was taken only a kilometer from the SEGC, where over the last decade a series of domestic cats have developed an eye ailment strikingly similar to that of the leopard (Fig. 2a, b). The building in which the cats lived is heavily infested by *W. auropunctata*, with a stream of ants perpetually eating from the cats’ food dish and ants regularly crawling on the cats’ fur. Domestic cats in Franceville and Makokou developed a similar ailment within two and six months after discovery of *W. auropunctata* in their respective houses.

Evidence of impact on large mammals in WEA is still anecdotal. We do not yet have quantitative data on the incidence of *W. auropunctata*-induced blindness in wild mammals or even on the background level of similar symptoms that may be induced by causes other than *W. auropunctata* stings. Data on the impact of *W. auropunctata* on other fauna are also lacking. But, given the pervasive effects of *W. auropunctata* in other regions, the implications of *W. auropunctata* infestation are chilling. This tiny ant may eventually threaten WEA’s biological riches to an extent equal to the more tangible threats posed by commercial hunting and habitat destruction. Research on the impact of *W. auropunctata* on the fauna of WEA and potential management options is urgently needed.

---

**References**


ISSG. 2002. 100 of the world’s worst alien invasive species. Invasive Species Specialist Group, Auckland, New Zealand.


---

Peter D. Walsh
Department of Ecology and Evolutionary Biology,
Princeton University,
Princeton, New Jersey 08540, U.S.A.

Phillipp Henschel
Wildlife Conservation Society,
Bronx, New York 10460-1099, U.S.A.

Kate A. Abernethy
Department of Biological and Molecular Sciences,
The Azteca–Cecropia Association: Are Ants Always Necessary for Their Host Plants?1

ABSTRACT

We assessed the effects of Azteca alfari presence on herbivory and growth of saplings for two Amazonian Cecropia species. For both species, rates of herbivory were low and did not differ between ant-removed and ant-maintained plants. Plant growth, measured over six months, was also similar among treatments. This is the first experiment to show that in its native mainland habitat, Cecropia may suffer low incidence of attack by insect herbivores in the absence of associated ants.

RESUMO

Nós testamos os efeitos da presença de Azteca alfari sobre a herbivoria e crescimento em arvoretas de duas espécies de Cecropia, na Amazônia. Para ambas espécies, as taxas de herbivoria foram baixas e não diferiram entre plantas que tiveram as formigas removidas ou mantidas. O crescimento das plantas, medido após seis meses, também foi similar entre os tratamentos. Este é o primeiro experimento que mostra que em seu hábitat natural, Cecropia pode sofrer baixa incidência de ataque por herbívoros na ausência das formigas associadas.

Key words: ants; ant–plant interactions; herbivory; mutualisms; myrmecophytes.

One of the most conspicuous ant–plant associations in the Neotropics is that between Azteca and Cecropia. Most members of the plant genus Cecropia are myrmecophytic and display obvious adaptations to house ants, including large hollow internodes, thin spots in the internode wall via which ants gain access, and a modified petiole base (trichilium) from which food bodies are continuously produced and harvested by associated ants (Bailey 1922, Wheeler 1942, Rickson 1971, Berg 1978). Cecropia trees, in turn, may benefit from their Azteca in several ways. Azteca often chews and kills the shoot tips and tendrils of vines that attempt to climb Cecropia trunks, thus acting as an allelopathic agent of the plant (Janzen 1969, Schupp 1986). In addition, these ants may provide supplemental nutrients to Cecropia trees (Sagers et al. 2000, cf. Putz & Holbrook 1988). There has been a lack of consensus, however, on

1 Received 10 February 2004; revision accepted 10 June 2004.
whether or not _Azteca_ effectively protect their _Cecropia_ host plants against herbivores. One study in Ecuador showed that damage by Coleoptera, but not homoptera (Hemiptera) and cecidomyiid gall flies, was lower on ant-occupied plants (Schupp 1986). Ant-occupied _Cecropia_ were also found to suffer fewer attacks from leaf-cutter ants than unoccupied plants (Jolivet 1990, Vasconcelos & Casimiro 1997); however, contrasting results have been found (see counter examples by Wheeler 1942 and Andrade & Carauta 1982), and as Janzen (1969) has pointed out, “it is commonplace to encounter occupied _Cecropia_ with foliage heavily eaten by insects, and healthy unoccupied _Cecropia_ are apparently not rare in some habitats.”

The genus _Cecropia_ ranges from Mexico to southern Brazil, where it occupies almost every terrestrial habitat (Berg 1978). In spite of the ubiquitous nature and diversity of _Cecropia_ in the Neotropical region, surprisingly few studies have used an experimental approach to investigate the relationship between these plants and their associated ants. Here, we present the results of an experiment designed to determine the influence of _Azteca alfari_ on herbivory and growth of two Central Amazonian _Cecropia_ species: _Cecropia concolor_ and _C. purpurascens_.

Observations and experiments were performed in an abandoned pasture area located ca 80 km north of Manaus, in Brazilian Amazonia (2°25’S, 59°50’W). This area was used as pasture for cattle grazing for about ten years, and during this period it was burned every two to three years. At the time of our study (about nine years after pasture abandonment), many pioneer trees had established, forming an uneven and broken canopy up to 10 m high. The vegetation was dominated by _Vismia_ spp. (Clusiaceae) and _Cecropia_ spp. (Cecropiaceae; Williamson et al. 1998). The average temperature in Manaus is 26.7°C and the mean annual precipitation is 2100 mm, with a distinct drier season between June and October. The soils are classified as Yellow Latosols, which typically have a high clay content and are poor in nutrients (Chauvel 1983). For further information about the study site, see Bierregaard and Gascon (2001).

Forty individuals of _C. concolor_ and 37 of _C. purpurascens_ were located and marked in January 1999. Most of these were found along the margins of a dirt road. Given the inherent difficulties of working with taller plants, only saplings between 1 and 2.5 m tall were selected. All marked plants were inhabited by _A. alfari_. Ant occupation was determined by vigorously shaking the plant stem. In occupied plants, ants swarmed out of the plant stem. Ants were experimentally removed from about half of the plants ( _C. concolor_ = 21 plants; _C. purpurascens_ = 17 plants), whereas the remaining plants served as controls (ant-maintained). Assignment of marked plants into the control and experimental categories was made randomly. To remove ants, we used a syringe to apply a few milliliters of a contact insecticide (Dimmy®, Serv-San, Cajamar, SP, Brazil) into every plant internode that was colonized by ants (i.e., those having an open prostoma). We checked the plants at regular intervals, and in case of recolonization, insecticide was applied again. The contact insecticide used here has a very short residual time and thus does not affect the colonization of herbivores in ant-removed plants, as has been already shown in previous ant-removal experiments (Vasconcelos 1991, Izzo & Vasconcelos 2002).

For a period of six consecutive months (February–July 1999), we monitored all plants at 15-day intervals. On each observation, we measured the height of each plant (height being measured as the length of the trunk, from the ground to the apex of the terminal internode), individually marked all new leaves produced, and recorded which, if any, of the previously marked leaves abscised. For each plant individual, the rate of leaf emergence and leaf mortality were calculated, respectively, as the number of leaves produced or lost over the course of the experiment. Leaf turnover rates were calculated as: (mortality rate + emergence rate)/2 (Phillips & Gentry 1994).

At 15-day intervals, we measured the total area and the area damaged of all leaves emerging after the beginning of the experiment. Many of these leaves (ca 50%) were already fully or almost fully expanded when first marked and measured, given the rapid leaf expansion rates of _Cecropia_ leaves (less than two weeks for some pioneer species; Folgarait & Davidson 1994). The remaining leaves experienced a growth increment of up to 1500 percent. For these latter, we were unable to discriminate between missing tissue resulting directly from herbivore consumption and loss due to leaf expansion around damaged areas; however, as pointed out earlier (Schupp 1986), this distinction is unnecessary since the measurements show that the total loss of potential photosynthetic surface was ultimately due to herbivore feeding.

Herbivory rates were calculated as the difference in the percentage of damage between the initial leaf measurement and the final measurement, divided by the time interval (in days) between these measure-
ments. For determination of the damaged area, we used a transparent plastic grid (precision of 1 cm²).

For determination of the total leaf area, we used the following equations, derived after measuring the maximum leaf width, maximum leaf length, and total area of 25 randomly collected C. concolor leaves and 21 C. purpurascens leaves, which included both young, developing leaves, as well as fully developed leaves. For C. concolor, leaf area = −95.84 + 0.728∗(leaf width∗leaf length) (\( R^2 = 0.984, N = 25, P < 0.001 \)), whereas for C. purpurascens, leaf area = 6.26 + 0.609∗(leaf width∗leaf length) (\( R^2 = 0.993, N = 21, P < 0.001 \)).

Treatment differences in herbivory rate, leaf emergence, mortality, and turnover were assessed using the Mann–Whitney U-test, as the data did not meet the assumption of normality. For analysis of differences in relative height increment (calculated as the difference between initial and final height, divided by the initial height), we used a t-test. All analyses were performed using Systat 8.0 (Wilkinson 1998).

Of a total 77 Cecropia saplings, only 49 were alive at the end of the experiment. Most (20 out of 28) of the dead saplings died due to attack by tapirs (Tapirus terrestris). Azteca alfari is ineffective against these animals because tapirs knock down the plant to eat its young leaves and buds. There was no difference in plant mortality among treatments (C. concolor, nine treatment and ten control plants dead; C. purpurascens, five and four plants, respectively).

Herbivory rates were low and did not differ between control and experimental plants either for C. concolor (\( U = 135, P = 0.40 \)) or C. purpurascens (\( U = 105, P = 0.19 \); Table 1). Since many Cecropia leaves did experience little or no growth over the course of the experiment—and therefore were presumably less dependent on ants for their defense—we further analyzed our data considering only leaves with a growth increment of over 20 percent. Here again, no treatment differences were detected either for C. concolor (\( U = 87, P = 0.08 \)) or C. purpurascens (\( U = 105, P = 0.28 \)).

Removal of ants also did not affect the increment in height of Cecropia saplings (C. concolor, \( t = 1.80, P = 0.097 \); C. purpurascens, \( t = 0.17, P = 0.86 \); Table 1). Finally, we did not detect a significant effect of the ant removal treatment on any parameter of leaf dynamics analyzed, including leaf emergence rates, mortality, and turnover (Mann–Whitney U-test, \( P > 0.05 \) in all cases; Table 1).

In spite of our negative results, it is premature to conclude that A. alfari does not defend its host plants against herbivores. If, in fact, C. concolor and C. purpurascens relied on ants for their defense, and A. alfari was ineffective in protecting them, one would have expected to find high levels of herbivore damage on both ant-removed and ant-maintained plants; however, that was not the case. Estimated rates of herbivory for C. concolor were 0.065 %/day, and for C. purpurascens, 0.053 %/day (data combining both control and treatment plants). These rates are two to ten times lower than those reported for C. insignis and C. obtusifolia in Panama (Coley 1983). In absolute values, herbivory rates in both C. concolor and C. purpurascens averaged 0.001 cm²/day, while Del Val and Dirzo (2003) reported values ranging between 0.18 and 0.26 cm²/day for C. pelata in Mexico. Our observed rates of herbivory in C. concolor and C. purpurascens are more similar to those found in plants that either (1) have a great amount of secondary compounds in their leaves (e.g. mature leaves of persistent trees in tropical forests having an estimated herbivory rate of 0.03–0.05 %/day; Coley 1983), (2) have strong biotic defenses (e.g., young leaves of ant-occupied Hirtella mirmecophyla; herbivory rates of 0.039 %/day; Izco & Vasconcelos 2002), or (3) presumably have no defenses but grow in areas in which specialist herbivores are absent (e.g., introduced C. pelata in Malaysia; herbivory rates of 0.046 %/day; Putz & Holbrook 1988).

Since we removed all possible biotic defenses (ants) from our treatment plants, only two alternatives remain to explain why herbivory was so low in C. concolor and C. purpurascens. One possibility is that herbivore abundance was also low. In fact, a seedling-transplant experiment in our study area indicated that herbivore abundance in disturbed habitats, such as those where our Cecropia were located, was much lower than in nearby primary forest (Benitez-Malvido 1995). Alternatively or in addition, it is possible that Cecropia saplings were investing in chemical defenses and therefore were avoided by herbivores. Tannins are probably the major class of secondary compounds in Cecropia, and large variation exists in the amount of tannins produced by a given Cecropia individual (Coley 1986) as well as among Cecropia species (Folgarait & Davidson 1994). Tannin concentrations are also affected by light and are usually much greater in plants growing in full sun than in forest gaps or in the forest understory (Newbery & de Foresta 1985, Nichols-Orians 1991, Folgarait & Davidson 1994). Since most Cecropia individuals studied were in full sun, it is likely that their leaves had a greater concentration of tannins (Folgarait &
TABLE 1. Effects of ant removal on herbivory, growth, and leaf dynamics for two Amazonian Cecropia species. There was no significant effect of the ant-removal treatment for any of the variables measured in these two plant species.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Treatment</th>
<th>Cecropia concolor</th>
<th></th>
<th>Cecropia purpurascens</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( \bar{x} )</td>
<td>Median</td>
<td>Range</td>
<td>( \bar{x} )</td>
</tr>
<tr>
<td>Average leaf damage (%/d)</td>
<td>With ants</td>
<td>0.05</td>
<td>0.04</td>
<td>0.01–0.11</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Without ants</td>
<td>0.08</td>
<td>0.05</td>
<td>0.01–0.31</td>
<td>19</td>
</tr>
<tr>
<td>Relative height increment (%)</td>
<td>With ants</td>
<td>15.6</td>
<td>13.8</td>
<td>5–29.1</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Without ants</td>
<td>9.5</td>
<td>9.3</td>
<td>3.4–21.4</td>
<td>12</td>
</tr>
<tr>
<td>Rate of leaf emergence (leaves/d)</td>
<td>With ants</td>
<td>0.056</td>
<td>0.057</td>
<td>0.04–0.07</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Without ants</td>
<td>0.047</td>
<td>0.045</td>
<td>0.03–0.06</td>
<td>12</td>
</tr>
<tr>
<td>Rate of leaf mortality (leaves/d)</td>
<td>With ants</td>
<td>0.024</td>
<td>0.021</td>
<td>0.01–0.04</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Without ants</td>
<td>0.026</td>
<td>0.027</td>
<td>0–0.05</td>
<td>12</td>
</tr>
<tr>
<td>Leaf turnover</td>
<td>With ants</td>
<td>2.6</td>
<td>2.4</td>
<td>1.7–4.5</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Without ants</td>
<td>1.9</td>
<td>1.8</td>
<td>1.1–3.7</td>
<td>12</td>
</tr>
</tbody>
</table>
Davidson 1994) and therefore were less palatable to herbivores than, for example, individuals growing in forest gaps.

Whether or not the relationship between Azteca and Cecropia is a mutualistic one has been a matter of debate, because some investigators have found evidence in favor of a protective role for Azteca (Janzen 1969, Schupp 1986, Vasconcelos & Casimiro 1997) while others did not (Wheeler 1942, Andrade & Carauta 1982). Longino (1997) has recently proposed that the question should be rephrased to when and where herbivores and/or vines abound but not in sites in which these organisms are rare and/or at sites in which Cecropia invest more heavily in chemical defenses. In fact, the survival of Cecropia where associated Azteca ants do not occur, such as in the Caribbean islands and Malaysia (where C. peltata was introduced), has been attributed to the presumably low abundance of Cecropia herbivores at these sites (Janzen 1973, Putz & Holbrook 1988).

The results of our experiment strongly suggest that at least in parts of its native mainland habitat, Cecropia also suffers low incidence of attack by insect herbivores and therefore is able to survive in the absence of defensive ants. It must be stressed, however, that the habitat in which our experiments were performed (a large anthropogenic clearing) is a relatively novel habitat, very distinct from the ones in which the Cecropia-Azteca association probably evolved (forest gaps and river margins). Nevertheless, even though anthropogenic habitats are not a part of the evolutionary history of the Cecropia-Azteca association, they are now an important component of its contemporary ecology. If in these novel habitats, as shown here, Azteca is of little importance for its Cecropia, selection against the production of myrmecophytic traits may occur because production of these structures and associated food bodies is costly (Rickson 1977, Folgarait & Davidson 1994). Loss of myrmecophytic traits has been observed in introduced populations of C. peltata in Malaysia (Putz & Holbrook 1988), and the same could occur in large anthropogenic disturbances within the native range of Cecropia.

We thank A. Cardoso for his help with the fieldwork, and A. Andrade, S. Oliveira, E. Bruna, J. T. Longino, J. Fornoni, E. Mendoza, and two anonymous referees for commenting on the manuscript. Financial support was provided by CAPES, CNPq, and the INPA/Smithsonian Biological Dynamics of Forest Fragments Project (BDFFP). This represents publication 426 in the BDFFP Technical Series.


Sarita B. Fáveri and Heraldo L. Vasconcelos

2 Biological Dynamics of Forest Fragments Project, National Institute for Research in the Amazon (INPA), C.P. 478, 69011–970, Manaus, AM, Brazil; e-mail: sarita@inpa.gov.br

3 Institute of Biology, Federal University of Uberlândia (UFU), C.P. 593, 38400–902, Uberlândia, MG, Brazil