

The Little Fire ant *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) as a Diversity Indicator of Ants in Tropical Dry Forest Fragments of Colombia

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ABSTRACT Ant richness within 14 Colombian dry forest fragments varies from at least 34–128 species. We have collected the little fire ant, *Wasmannia auropunctata* (Roger) in each of the fourteen forest fragments, by means of tuna baits, pitfall traps, sampling of logs, understory vegetation and forest litter sampling. A highly significant negative relation was found between the percentage of *W. auropunctata* samples per forest fragment and richness for the ant community. Additionally, a significant positive relationship was found between the abundance of *W. auropunctata* and the number of ant-plant associations in nine of the forest fragments. The displacement of other ants by *W. auropunctata* could be explained in terms of its competitive performance, natural history and ability to exploit disturbed sites. This opportunistic species displays high interspecific aggressiveness, recruiting workers massively to a variety of food resources. It also colonizes different substrates and forms unicolonial societies, which disperse broadly by detaching groups of workers along with multiple queens. The species can be easily monitored with tuna baits, which showed the same significant negative relation. We propose that the abundance of the little fire ant can be used as an indicator of low diversity ant communities in dry forest fragments of the Cauca river valley of Colombia.

KEY WORDS ants, bioindicator, Colombia, forest fragments, tropical dry forest, *Wasmannia auropunctata*

ACCORDING TO BROWN (1989) and Pearson (1994) an indicator species should be easy to detect, easy to evaluate and should provide valuable ecological information. Brown (1989) evaluated 15 outstanding insect taxa as ecological indicators by using 12 criteria including taxonomical, ecological, and behavioral aspects. Ants, along with a group of Lepidoptera, received the highest score of 21 over 24 possible points, suggesting that they make a good indicator species.

Ants (Hymenoptera: Formicidae) have been considered a special ecological group given their properties as indicators of biodiversity (Roth et al. 1994), disturbance (Burbidge et al. 1992, Majer 1992, Olson 1991, Brown 1989) and rehabilitation or successional stages in ecosystems (Majer 1983, 1985, Cabrera and Jaffe 1993, Roth et al. 1994). Further, it has been proposed that ant diversity may reflect the nature of vegetation, physical conditions and possibly the variety of other invertebrates that are present in a given area (Andersen and Majer 1991). Nevertheless, the role of ants as indicators of biodiversity of other groups is still a controversial subject (Alonso 2000). Roth et al. (1994) considered ants as potential indicators to

examine the conservation potential in a mosaic of differently disturbed habitats in Costa Rica. Burbidge et al. (1992) demonstrated in Australia how slight alterations in ecosystems have lead to changes in ant communities, with some ant species being especially sensitive (e.g., disappearing or reducing populations) to such alterations. For instance, the ant fauna has been described in humid forest fragments of Australia for future monitoring purposes (Andersen and Majer 1991).

During the last 5 yr in Colombia, several studies have sampled the ant fauna that is still present in small forest remnants along the geographic valley of Cauca river, located at the Southwest Andean region. Tropical dry forest in Colombia is one of the most endangered habitats in the country (IAvH 1998) because of the intensive habitat fragmentation that it has suffered in the last decades. Currently, more than two hundred ant species are known from the region (Armbrecht 1995, Chacón de Ulloa et al. 1996, Armbrecht and Ulloa-Chacón 1997, 1999), among which the Myrmicinae is the most abundant and species-rich group. From the Myrmicinae subfamily, *Wasmannia auropunctata* (Roger), commonly known as the little fire ant, is particularly common, easy to identify and to collect.

W. auropunctata, a widely distributed ant throughout South America (Kempf 1972), colonizes disturbed

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areas sometimes becoming an economic problem (Fowler et al. 1990). This species, which is both opportunistic and excellent competitor, is therefore able to displace the local myrmecofauna (e.g., Ulloa-Chacón and Cherix 1990). High populations of *W. auropunctata* have been related to marked reductions of other ant species, especially in regions where it has been introduced, such as the Galapagos islands (Clark et al. 1982, Lubin 1984, Ulloa-Chacón and Cherix 1994), and also in agricultural lands such as cocoa farms in Brazil (Delabie 1988, Majer et al. 1994). Nevertheless, *W. auropunctata* is common in humid forests of lowland tropical lands of Panamá and Costa Rica, where it does not dramatically affect other ant populations, and may coexist with other species (Levings and Franks 1982, Tennant 1994), though always showing a better ability to exploit food resources (Tennant 1994).

To explore the potential performance of *W. auropunctata* as an indicator of the diversity of other ants, we evaluated the ant community present in 14 tropical dry forest fragments distributed in the 210 km long valley of the Cauca river, Colombia. We examined the relationship between the abundance of *W. auropunctata* and community variables of the ant assemblage in this fragmented scenario.

Materials and Methods

We selected 14 secondary forest fragments distributed within the tropical dry forest life zone along the geographic valley of Cauca river, Southwest of Colombia which includes three Departments named Cauca, Valle, and Risaralda. This region, located between 2°98'N–5°05'N and 75°07'–76°30'W, is the third most important representative of the Colombian tropical dry forest life zone, covering ≈1,835 ha of secondary vegetation (IAvH 1998). The forests are located at altitudes between 950–1000 m, the average temperature is above 24°C and the average annual precipitation fluctuates between 1000–2000 mm (IAvH 1998). The locations of the forest fragments are as follows (three Departments ordered North-South, forest fragments ordered by decreasing area): at the Risaralda Department, Alejandría, Aguas Claras, Miralindo I, Miralindo II, La Carmelita, Córcega, and El Trapiche; at Valle Department, El Vínculo, El Medio, Las Pilas, Colínder, Las Chatas, and El Hatico; and at Cauca Department, San Julián. The matrices that surround the forest fragments are composed of sugar cane plantations (e.g., El Medio and San Julián), pasture lands shaded with scattered trees (Alejandría, El Hatico, El Vínculo), pineapple and pasture (El Trapiche), and unshaded pasture lands (Las Pilas). The forests are secondary with relatively well structured canopies of ≈25 m height dominated by tree species such as *Anacardium excelsum* (Ber. et Balb.) Skeels (Anacardiaceae), *Laetia americana* L. (Flacourtiaceae), *Xylopia ligustrifolia* Dunal (Annonaceae), and overstory vegetation as *Guadua angustifolia* Kunth (Gramineae) among others.

Forests were sampled between 1994–1999. Two to three linear transects were placed in each of the forest fragments in an attempt to traverse them completely from one end to the other. Equidistant sampling points (stations) were located every 10–20 m along each of the transects. Ants were sampled by using five methods per station: 1) pitfall traps: 24 h exposure (Olson 1991); 2) leaf litter sifting (a volume of 5 liters of leaf litter per station) followed by direct ant searches within 36 h after collection; bait sampling using tuna-oil placed in two strata; 3) on the forest floor; and 4) on a living tree trunk at 1.70 m height, and 5) 15 min of direct searching in all available substrates: inside decomposing logs, under rocks, epiphytes, understory vegetation, and foraging trails. A detailed description of each of the sampling methods can be found in Armbrrecht and Ulloa-Chacón (1999). To assess the problem of differential sampling effort in larger sites that smaller sites, we standardized for equal sampling area by randomly selecting twenty stations at each forest fragment. All results in this paper will refer to this standardized set of data unless otherwise stated. The collected material was identified to genus level by using keys from Hölldobler and Wilson (1990), Jaffé et al. (1993) and Bolton (1994). The ants were then identified to species (or sorted in morpho-species), and vouchers are deposited in the Entomology Museum of the Biology Department, Universidad del Valle, Cali (MEUV). A complete list of the ant genera and species is available directly from the authors and partially in Armbrrecht et al. (2001) and Ramírez et al. (2002).

In this study, a sample or "occurrence" is any event in which an ant species (or morphospecies) is recorded in one of the sampling methods, regardless the number of workers or majors captured by such method. Thus, species abundance was determined as the number of occurrences and not by the number of workers collected (i.e., an ant species might be present in the five samples per station, although direct search may increase it if this ant was also found in the various substrates as twigs, vegetation, soil, wood, etc.). Pearson correlation coefficients and simple linear regressions (Zar 1996) between the percentage of samples of *W. auropunctata* and the ant richness each forest were both calculated by using STATISTIX for Windows. Shannon and Weaver diversity index ("Shannon": H') (Magurran 1988) was calculated with the program ESTIMATES 5.0.1 (Colwell 1997) for comparison purposes.

Results

A total of 3,594 ant samples were recorded in the 14 forests fragments with an average 256.7 ± 69.8 (SD) occurrences per forest. *W. auropunctata*'s abundance fluctuated widely among the forests (Table 1). The average richness of ant species per forest was 55.1 ± 13.6 with a minimum of 34 species in San Julián and a maximum of 71 species in La Carmelita and El Trapiche. For the total sampling (without standardizing), Alejandría was the richest forest fragment with

Table 1. Species richness, Shannon diversity index (H') and frequency of ant samples in fourteen Colombian dry forest fragments. Parenthesized abbreviations in the first column denote whether the forest is located North (n), center (c), or South (s) of the geographic valley of the Cauca river

Forest fragment	Size (ha)	N° of ant species	H'	Total samples	Samples with <i>W. auropunctata</i>
El Trapiche (n)	0.6	71	3.72	343	15
La Carmelita (n)	1.8	71	3.67	308	19
Alejandría (n)	13.4	69	3.80	201	11
Miralindo I (n)	7.8	68	3.70	218	37
El Hatico (c)	7.0	66	3.52	411	50
Córcega (n)	0.8	61	3.53	281	25
Miralindo II (n)	5.9	59	3.58	182	5
Aguas Claras (n)	9.2	59	3.26	235	77
El Medio (n)	12.7	50	3.48	174	26
Las Pilas (n)	12.2	47	3.33	172	8
El Vínculo (c)	15.0	41	2.59	238	94
Las Chatas (c)	8.7	38	2.87	318	93
Colínder (s)	12.3	37	2.57	257	75
San Julián (s)	6.0	34	1.96	256	154

128 species. A trend toward decreasing ant species richness along the geographic valley of Cauca river in a North-South direction was detected. The diversity indexes averaged 3.3 ± 0.5 and were the highest in the Northern-most forests (H' between 3.26 and 3.8), diminished in the forests located at the center of the valley (H' between 2.59 and 3.52) and were lowest in the Southern-most forest ($H' = 1.96$), San Julián.

From the total ant samples, 19.2% represented the little fire ant *W. auropunctata*, which was present in all 14 forests with an average number of samples of 49.2 ± 43.7 . Its relative proportion (samples of *W. auropunctata* per total samples) fluctuated between 2.74% (5/182) in Miralindo II, an ant-rich forest fragment (59 species) and 60.2% (154/256) in San Julián, the most species-poor fragment (34 species). The ant assemblage's richness was negative and significantly correlated with the percentage of samples of *W. auropunctata* both for the standardized data set ($R^2 = 0.53$; $F_{1, 12} = 13.44$; $P = 0.003$) (Fig. 1A) and for total samples in the study ($R^2 = 0.51$; $F_{1, 12} = 12.33$; $P = 0.004$).

The tuna baits at both strata soil and trees contributed to a high proportion of the samples (40.4%). From the baits in which *W. auropunctata* was attracted, the number of ant species per bait fluctuated between 1–5 and although 62.4% of the baits were occupied only by *W. auropunctata* workers, the remaining 37.6% captured this species together with mostly *Pheidole* or *Solenopsis* species. Further, data from only the tuna bait method showed the same negative trend described above (Fig. 1A): a strong negative relation was found between *W. auropunctata*'s abundance (percentage of baits attracting the species) and the number of ant morphospecies (attracted to tuna baits) in the forest fragments ($R^2 = 0.59$; $F_{1, 12} = 16.99$; $P = 0.001$) (Fig. 1B).

The frequency of occurrences of *W. auropunctata* in the different sampling methods (Fig. 2), reflects the wide distribution of the species at the interior of the forest, where it inhabits the various strata. Most of the ants (69%) were collected on the soil stratum, either through leaf litter search or soil tuna baits, followed

by pitfall traps and dissection of decomposing logs. The arboreal and herbaceous strata together comprise the rest of the samples (31%), obtained through recruitment of workers to tuna baits on tree trunks or by direct search on the forest understory vegetation. The relatively low number of occurrences in the pitfall method was probably a result of the short time of exposure of only 24 h.

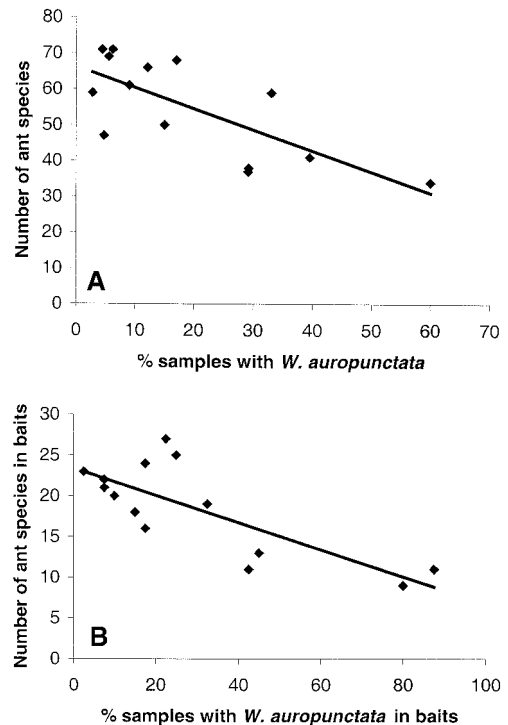


Fig. 1. Regression between the ant community richness and the percentage of occurrences of *W. auropunctata* in 14 dry forest fragments located Southwest in Colombia (Cauca river valley). (A) Data from all sampling methods ($y = -0.586x + 66.262$) and, (B) data only from baits ($y = -0.167x + 23.411$).

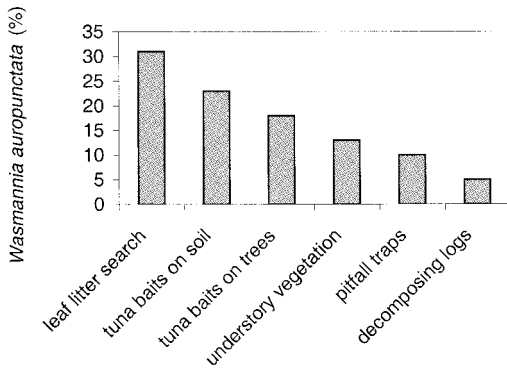


Fig. 2. Distribution of the percentage of samples with *W. auropunctata* using all capture methods and all the stations in the study. Total number of captures = 478.

Additional data demonstrated that the more dominant *W. auropunctata* was, the more plants it was present on. In a parallel and simultaneous study, the frequency of samples with *W. auropunctata* on the understory vegetation in nine of the same 14 forest fragments (same sampling points) was recorded. Ramírez et al. (2002) registered 67 ant species interacting with 91 plant species. In this study *W. auropunctata* was the most frequently observed species (17%). This ant species used 30 plant species for nests (e.g., *Heliconia* spp. and some epiphytes), fed on extrafloral nectaries (as for example *Passiflora* spp.) and homopteran honeydew, and also used plants for refuge or foraging place. We found a significant and positive correlation ($r = 0.90$, $df = 7$, $P < 0.001$) between the number of occurrences of *W. auropunctata* and the number of ant-plant associations in these nine forest fragments.

Discussion

The forests fragments with the highest dominance of the little fire ant had the lowest number of ant species in the study area, which covers a considerable proportion of the Colombian Western dry forest region. Although a direct cause-effect relationship between the two variables (richness of the ant community and abundance of *W. auropunctata*) is not demonstrated in this study, we cannot discard the possibility that the populations of *W. auropunctata* are increasingly responding to the perturbation levels at the interior of the forests. We could speculate that in the disturbed forest where abundant remains of twigs, leaf litter and logs are available on the ground, the accelerated increase of *W. auropunctata* could be favored, because it efficiently exploits this type of nesting substrate (Torres 1984, Ulloa-Chacón and Cherix 1990). Additionally, the Southern-most less diverse forests (e.g., San Julián, Colínder) which exhibited the highest abundance of *W. auropunctata*, did not have protective fence at the border of the forest, and showed more signs of human and cattle penetration in their interior, affecting the understory vegetation and

soil quality (unpublished data). It is noticeable that the less diverse forests are precisely those in which *W. auropunctata* (and not especially other ant species) was dominating. Although no direct evidence is available we speculate that this North-South trend of decreasing ant diversity might be related with a more intense management of the matrix surrounding de forests in the South, in which a transformation toward industrialized sugar cane monocultures is taking place.

The behavior of the species as a colonizer of disturbed areas can be compared with a certain extent with findings of other researchers in those habitats in which the species have been introduced resulting in the extermination of the local ant fauna (Clark et al. 1982; Lubin 1984, Vega 1994). This displacement of other ant species can be partly explained by the fact that *W. auropunctata* is extremely aggressive at the interspecific level, though not intraspecifically (i.e., within its colonies). This is one of the characteristics of "tramp species" (examples of tramp species: *W. auropunctata*, *Monomorium pharaonis* L., *Linepithema humile* Mayr), which can be of economic importance for human beings causing environmental damages to natural ecosystems and to agricultural systems (Passera 1994).

The way in which *W. auropunctata* nests and invades new areas illustrates the role that this ant plays in ant communities. *W. auropunctata* is considered to be unicolonial, or characterized by the absence of aggressive behavior between individuals from different nests in a given area. The colonies disperse widely through deployment of groups of workers accompanied by inseminated queens, which result in a great capacity of colony movement (Hölldobler and Wilson 1990). Polygyny with multiple queens is associated with nesting adaptation to "short-lived" substrates as decomposing wood. *W. auropunctata* is very opportunistic, occupies very small and unstable sites and is able to maintain big populations in an area (Hölldobler and Wilson 1990; Passera 1994). Further, the positive relation between ant-plant associations detected on the understory vegetation of the forests in this study reinforces the evidence of the high ability of *W. auropunctata* to exploit resources for food as extrafloral nectaries, refuges within the vegetation, homopterans as resource of honeydew and possibly displacing other ant species from these resources in the fragmented dry forests of Colombia. The negative relation found between *W. auropunctata* and the ant richness attracted to baits also reinforces findings about the high ability of this species to monopolize food resources (Clark et al. 1982, Meier 1985, Vega 1994) and suggests the usage of tuna baits as a simple and efficient method to easily evaluate its presence in these forest fragments.

Our results suggest that the monitoring of *W. auropunctata* as an indicator of low biodiversity of the ant community in the geographic valley of Cauca river, Colombia, could be very useful and relatively easy to implement because this species is extremely easy to detect and identify. This consideration agrees with Samways (1994), in that indicator species do not have

to be the rarest ones, and instead, abundant species could have a great value for species as easily located indicator. Although the data of one single species will never reflect the patterns of a whole community, the results of this research suggest tuna baits as a useful method when implementing easy and low expense monitoring programs to quickly compare forest fragments in this region of Colombia.

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References Cited

- Andersen, A. N., and J. D. Majer. 1991. The structure and biogeography of rainforest ant communities in the Kimberley region of northwestern Australia, pp. 333-346. *In* N. L. McKenzie, R. B. Johnston, and P. G. Kendrick [eds.], Kimberley rainforests. Suerrey Beatty & Sons Pty Limited, Chipping Norton.
- Alonso, L. E. 2000. Ants as indicators of Diversity. Chapter 6, pp. 80-88. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Shultz [eds.], Ants: standard methods for measuring and monitoring Biodiversity. Smithsonian Institution, Washington, DC.
- Armbrecht, I. 1995. Comparación de la mirmecofauna en fragmentos boscosos del valle geográfico del río Cauca, Colombia. *Bol. Mus. Entomol. Univ. Valle*. 3(2): 1-10.
- Armbrecht, I., and P. Chacón de Ulloa. 1997. Composición y diversidad de hormigas en bosques secos relictuales y sus alrededores, en el Valle del Cauca, Colombia. *Rev. Col. Entomol.* 23: 45-50.
- Armbrecht, I., and Ulloa-Chacón, P. 1999. Rareza y diversidad de hormigas en fragmentos de bosque seco colombianos y sus matrices. *Biotropica* 31: 646-653.
- Armbrecht, I., P. Ulloa-Chacón, and I. Tischer. 2001. Nested subsets and partition patterns in ant assemblages (Hymenoptera, Formicidae) of Colombian dry forest fragments. *Pan-Pacific Entomologist* 77(3): 127-143.
- Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Massachusetts.
- Brown, K. Jr. 1989. The conservation of Neotropical environments. Insects as indicators, pp. 354-404. *In* N. M. Collins and J. A. Thomas [eds.], The conservation of insects and their habitats. Fifteenth Symposium of Royal Entomological Society of London. Academic Hartcourt Brace Jovanovich Pubs, London.
- Burbidge, A. H., K. Leicester, S. McDavitt, and J. D. Majer. 1992. Ants as indicators of disturbance at Yanchep National Park, Western Australia. *J. R. Soc. W. A.* 75: 89-95.
- Cabrera, M., and K. Jaffé. 1993. Hormigas como bioindicadoras de la velocidad de recuperación de ecosistemas, pp. 204. *In* Sociedad Venezolana de Entomología [eds.], Resúmenes V Congreso Latinoamericano y XIII Congreso Venezolano de Entomología, Paríamar, Venezuela.
- Chacón de Ulloa, P., M. Baena, J. Bustos, R. Aldana, R. Gamboa, and J. Aldana. 1996. Fauna de hormigas del departamento del Valle del Cauca, pp. 413-451. *In* F. Fernández, G. Amat, and G. Andrade [eds.], Insectos de Colombia: estudios escogidos. Universidad Javeriana Qgy Academia de Ciencias, Santafé de Bogotá, Colombia.
- Clark, D. B., C. Guayasamin, O. Mazamio, C. Donoso, and Y. Paez de Villacis. 1982. The tramp ant *Wasmannia auropunctata*: autoecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos. *Biotropica* 14: 196-207.
- Colwell, R. K. 1997. <http://viceroy.eeb.uconn.edu/estimates>.
- Delabie, J.H.C. 1988. Ocorrença de *Wasmannia auropunctata* (Roger, 1863) (Hymenoptera, Formicidae, Myrmicinae) em cacauais na Bahia, Brasil. *Rev. Theobroma*. 18: 29-37.
- Fowler, H. G., J.V.E. Bernardi, J. C. Delabie, L. C. Forti, and V. Pereira-da-Silva. 1990. Major ant problems of South America, pp. 3-14. *In* R. K. Vander Meer, K. Jaffee, and A. Cedeño [eds.], Applied myrmecology: a world perspective. Westview Press, Boulder, CO.
- Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, MA.
- (IavH) Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt. 1998. Informe Nacional sobre el estado de la biodiversidad 1997-Colombia. 1998. Bosque seco tropical, pp. 56-71, *In* Chávez, M. E. and N. Arango [eds.], Tomo I: Diversidad Biológica. Instituto Humboldt, PNUMA, Ministerio del Medio Ambiente, vol. 3. Santafé de Bogotá, Colombia.
- Jaffé, K., J. Latkic, and E. Pérez. 1993. El mundo de las hormigas. Equinooccio Ediciones. Universidad Simón Bolívar, Venezuela.
- Kempf, W. W. 1972. Catálogo abreviado das formigas da Região Neotropical (Hymenoptera: Formicidae). *Studia Entomol.* 15: 3-344.
- Levings, S. C., and N. R. Franks. 1982. Patterns of nest dispersion in a tropical ground ant community. *Ecology* 63: 338-344.
- Lubin, Y. D. 1984. Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant *Wasmannia auropunctata*. *Biol. J. Linn. Soc.* 21: 229-242.
- Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology. Wiley, New York, 336 p.
- Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, New Jersey.
- Majer, J. D. 1983. Ants: bio-indicators of mine-site rehabilitation, land use and land conservation. *Environ. Manage.* 7(4): 375-383.
- Majer, J. D. 1985. Recolonisation by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. *Aust. J. Ecol.* 10: 31-48.
- Majer, J. D. 1992. Ant recolonization of rehabilitated bauxite mines of Pocos de Caldas, Brazil. *J. Trop. Ecol.* 8: 97-108.
- Majer, J. D., J.H.C. Delabie, and M.R.B. Smith. 1994. Arbo-real ant community patterns in Brazilian cocoa farms. *Biotropica* 26(1): 73-83.
- Meier, R. E. 1985. Interference behavior of two tramp ants (Hymenoptera: Formicidae) at protein baits on the Galapagos Islands, Ecuador (abstr.). *Experientia* 41: 1228.
- Olson, D. 1991. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenop-

- tera: Formicidae) in a tropical wet forest, Costa Rica. *Biotropica*. 23(2): 166–172.
- Passera, L. 1994. Characteristics of tramp species, pp. 23–43. In D. F. Williams [ed.], *Exotic ants*. Westview Press, Boulder, CO.
- Pearson, D. 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. *Phil. Trans. R. Soc. Lond. B*. 345: 75–79.
- Ramírez, M., P. Chacón de Ulloa, I. Armbrrecht, and Z. Calle. 2002. Contribución al conocimiento de las interacciones entre plantas, hormigas y homópteros en bosques secos de Colombia. *Caldasia (Colombia)*. 23(2): 523–536.
- Roth, D. S., I. Perfecto, and B. Rathcke. 1994. The effects of management systems on ground foraging ant diversity in Costa Rica. *Ecol. Appl.* 4(3): 423–436.
- Samways, M. J. 1994. Insects, the landscape and evaluating, pp. 235–276. In M. J. Samways [ed.], *Insect conservation biology*. Chapman & Hall, London.
- Tennant, L. E. 1994. The ecology of *Wasmannia auropunctata* in primary tropical rainforest in Costa Rica and Panamá, pp. 80–90. In D. F. Williams [ed.], *Exotic ants*. Westview Press, Boulder, CO.
- Torres, J. A. 1984. Niches and coexistence of ant communities in Puerto Rico repeated patterns. *Biotropica* 16: 284–295.
- Ulloa-Chacón, P., and D. Cherix. 1990. The little fire ant *Wasmannia auropunctata* R. (Hymenoptera: Formicidae), pp. 281–289. In R. K. Vander Meer, K. Jaffee, and A. Cedeño [eds.], *Applied myrmecology: a world perspective*. Westview Press, Boulder, CO.
- Ulloa-Chacón, P., and D. Cherix. 1994. Perspectives on Control of the little fire ant (*Wasmannia auropunctata*) on the Galapagos Islands, pp. 63–72. In D. F. Williams [ed.], *Exotic Ants*. Westview Press, Boulder, CO.
- Vega, I. 1994. Food searching behavior and competition between *Wasmannia auropunctata* and native ants on Santa Cruz and Isabella, Galapagos Islands, pp. 73–79. In D. F. Williams [ed.], *Exotic Ants*. Westview Press, Boulder, CO.
- Zar, J. H. 1996. *Biostatistical analysis*. Prentice Hall, New Jersey.

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