

Impact of the Little Fire Ant, *Wasmannia auropunctata*, on Native Forest Ants in Gabon¹

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ABSTRACT

The Neotropical little fire ant, *Wasmannia auropunctata*, is notorious for its negative impacts on the native biota of tropical islands, such as the Galapagos and New Caledonia, where it has been introduced. Here, I evaluate the impact of exotic *W. auropunctata* populations on continental Africa. I surveyed ants at nine sites in Lopé National Park in Gabon, Central Africa, and found a highly significant correlation between ant diversity and length of infestation by *W. auropunctata*. I found many more native ant species present in areas not infested with *W. auropunctata* (39.0 ± 4.6) compared with areas infested by *W. auropunctata* for approximately 5–10 yr (7.0 ± 6.2 and 1.7 ± 1.2 , respectively). In infested areas, *W. auropunctata* made up the bulk of specimens collected in every plot. This study demonstrates that the threat posed by *W. auropunctata* to biodiversity is as serious in continental ecosystems as it is in the more fragile island ecosystems of previous studies. Introductions near waterways are particularly devastating: in Lopé, the infested territory is most extensive along waterways and occurs in a pattern that strongly suggests moving water facilitates colonization.

RÉSUMÉ

La petite fourmi rouge, *Wasmannia auropunctata*, est réputée pour ses impacts négatifs sur la biocénose indigène des îles tropicales où elle a été introduite, comme aux îles Galápagos et en Nouvelle-Calédonie. Cette étude évalue les conséquences des populations exotiques de *W. auropunctata* en Afrique continentale. En échantillonnant la myrmécofaune dans neuf sites au Parc National de la Lopé au Gabon, j'ai trouvé une forte corrélation entre la diversité de fourmis et la durée écoulée depuis l'arrivée de *W. auropunctata*. Les espèces de fourmi indigènes sont beaucoup plus nombreuses dans les zones encore vierges (39.0 ± 4.6) en comparant avec les sites envahis depuis environ 5 et 10 ans (7.0 ± 6.2 et 1.7 ± 1.2 , respectivement). Dans les sites envahis, *W. auropunctata* représentait la majorité des spécimens rencontrés dans chaque échantillonnage. Cette étude met en évidence la menace posée par *W. auropunctata* aux écosystèmes continentaux, tout comme l'ont montrées les études antérieures pour des écosystèmes insulaires plus fragiles. L'implantation près des cours d'eau est fulgurante: à la Lopé, l'essentiel du territoire envahi est situé le long des cours d'eau, suggérant un transport facilité par l'eau.

Key words: biodiversity; Congo basin; equatorial Africa; exotic ants; Gabon; invasive species; *Wasmannia auropunctata*.

THE CONGO BASIN RAIN FOREST REGION IS CRITICAL TO BIODIVERSITY CONSERVATION; it is the world's second largest and most intact tropical forest region and houses a remarkably diverse array of flora and fauna, particularly in terms of primates and large mammals (Besselin *et al.* 1998). While biodiversity conservation can often be difficult in developing tropical countries, such as those comprising the Congo basin, Gabon presents great potential for conservation due to the nation's low population density and newly established network of 13 national parks.

To realize this potential, assessment and control of factors that could diminish biodiversity in the region are essential. Research in the Congo Basin forests is often focused on high-profile, human-oriented activities such as logging and poaching. Although these activities are undoubtedly critical for conservation, other less-controversial issues, such as biological invasion, could rival these in ability to alter biodiversity, and thus deserve considerable attention as well.

Invasions by exotic species pose a serious threat to conservation of native flora and fauna because of their potential to reduce biodiversity and cause local extinctions. The little fire ant, *Wasmannia auropunctata*, is a well-known invader in the tropics. This tiny Neotropical ant is considered one of the world's worst invasive alien

species (Lowe *et al.* 2000) because of its devastating effect on the native fauna. While previous studies have established the capacity of exotic *W. auropunctata* populations to drastically reduce the diversity of ants and other arthropods (Clark *et al.* 1982, Lubin 1984, Guilbert *et al.* 1994, Jourdan 1997, Le Breton *et al.* 2003), all of these studies have concerned island ecosystems. This study is the first to assess quantitative impacts on diversity in continental forests.

Most known introductions of *W. auropunctata* occur on islands, where the higher vulnerability of native species to exotic invaders has long been recognized (Atkinson 1989, Loope & Mueller-Dombois 1989, Gillespie & Roderick 2002, Le Breton *et al.* 2005). Continental tropical forests, however, are considered less susceptible to bio-invasions due to their high species richness (Rejmánek 1996). Invasion by *W. auropunctata* might therefore be predicted to be less devastating to the native fauna in these forests than in the insular habitats. Observations in Florida, where *W. auropunctata* was introduced around 1924 (Wheeler 1929) support this theory. On the mainland, *W. auropunctata* tends to cohabit with the native ant assemblages and does not become overly abundant (Klotz *et al.* 1995, Deyrup *et al.* 2000). In the insular habitats of the Florida Keys, however, Fleming (in Wetterer & Porter 2003) found that *W. auropunctata* accounts for as much as 97.6 percent of all ants observed at baiting stations.

Wasmannia auropunctata was introduced to Gabon's coasts sometime before 1914 (Santschi 1914) and has been further

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transported within the country, via both inadvertent and intentional transport by humans (Wetterer & Porter 2003). The Congo Basin contains the only documented sites outside of Florida where *W. auropunctata* is unquestionably non-native, yet well established, in a natural mainland habitat. Although some anecdotal observations have been published on the topic (Wetterer *et al.* 1999, Wetterer & Porter 2003, Walsh *et al.* 2004), no previous study has examined the impact of *W. auropunctata* on the native fauna of these habitats in an analytical, quantitative fashion.

The objective of this study was to evaluate the impact of *W. auropunctata* on native ant species in Gabon; a necessary step toward assessing what priority the control of this species should be given for conservation in equatorial Africa. A second objective was to map the distribution of *W. auropunctata* in a relatively recently invaded region in Gabon to better understand the rate and mechanism of local dispersion.

METHODS

STUDY SITE.—The study was conducted at the *Station d'Etude des Gorilles et Chimpanzés* (SEGC) research area in Lopé National Park, Gabon (0°10'–0°16'S, 11°33'–11°39'E). The forests in Lopé are part of the Congo Basin rain forest block and are vital to many large mammals, including forest elephants and buffalos, gorillas, chimpanzees, and the largest known mandrill populations in the world (Blom *et al.* 1992).

This location is not only ecologically important, but also provides an ideal situation to compare sites where *W. auropunctata* has existed for varying durations due to documentation of the origin and subsequent expansion of the infestation. The introduction of *W. auropunctata* in the Lopé area can be reliably pinpointed to around 1965, when the first logging camp was established in the area that is now the SEGC research site. European foresters in Gabon, in addition to locals that knew the forest well, recall the sudden appearance of these fire ants shortly after logging activities began (SEGC records; Wetterer *et al.* 1999). Since there had been no human settlements from the Ogooué River to the watershed of this area for at least 50 yr prior to 1965 (Pourtier 1989), these claims

are difficult to contest; they represent the only feasible explanation for the sudden appearance of exotic ants in this formerly remote location. Constant research activity in the area since 1983 provides records that document the subsequent spread of infestation in the area. Due to its slow rate of colonization when unassisted, *W. auropunctata* is not yet established throughout the entire SEGC research area, permitting comparison between infested and noninfested sites.

The ecological composition in Lopé is heterogeneous. I therefore examined ant assemblages in three different types of forest to assess whether the effect of *W. auropunctata* on local ants differs with forest composition. (*cf.* White & Abernethy 1996)

- (1) Marantaceae forest: Immature forest with a dense understory layer of herbaceous plants mostly belonging to the *Marantaceae* and *Zingiberaceae* families.
- (2) Open forest: Mature or otherwise closed-canopy forest, lacking dense understory layer of herbaceous plants.
- (3) Bosquet: Small forest patch surrounded by savannah, which acts in many ways as an islet for microfauna.

Within each forest type, I selected three sites according to age of infestation by *W. auropunctata* (Table 1). Age of infestation was divided into three categories: No presence of *W. auropunctata*, presence of approximately 5 yr, and presence dating more than 10 yr. Infestation categories were assigned to sites based on the field notes of doctoral researchers which document the presence of the fire ants later identified as *W. auropunctata* in the focal areas of this study in 1983, 1993, 1995, 1996, 2000, and 2003 (SEGC, pers. comm.). These categories represent broad limits, and should not be interpreted as attempts to assign exact moments of colonization to any specific location. "Presence of approximately 5 yr," for example, means that *W. auropunctata* was found in a given area in 2000, but not in 1996. "Presence dating more than 10 yr" means that the area was noted to be infested in 1993 or earlier.

Samples were collected during the wet season from March to June 2003. Because the forests in the area are heterogeneous, a two-level sampling design was used. Within each site of roughly 1 ha, eight 314 m² subsites were selected. Each subsite consisted of a circle with a 10 m radius. The center points of these circles were selected

TABLE 1. Site descriptions.

Site code	SEGC name	Coordinates	Forest type	Age of infestation by <i>W. auropunctata</i>
B0	Centroplacus	0°12.0'S, 11°35.5'E	Bosquet	Absent
O0	Saline Three	0°12.7'S, 11°36.3'E	Open	Absent
M0	Cephus	0°12.4'S, 11°34.0'E	Marantaceae	Absent
B5	Klainedoxa	0°11.8'S, 11°36.1'E	Bosquet	~5 yr
O5	Azobe	0°12.4'S, 11°36.5'E	Open	~5 yr
M5	Kapok	0°12.0'S, 11°36.5'E	Marantaceae	~5 yr
B10	Camp Bosquet	0°12.0'S, 11°36.0'E	Bosquet	>10 yr
O10	Saline Zero	0°12.3'S, 11°36.2'E	Open	>10 yr
M10	Foret de l'aeroporte	0°11.4'S, 11°36.6'E	Marantaceae	>10 yr

nonrandomly to best represent the dominant forest composition of the site. Individual sampling units were then located within each subsite by randomly selecting from 100 possible combinations of azimuth and distance from the center point. This two-level design ensured sample sites of fairly equal size and habitat composition and allowed for analysis of spatial heterogeneity both within and between subsites.

INVENTORY TECHNIQUE.—The ant inventory technique included direct searches, soil samples, and sweep netting. Direct searches consisted of five 1 m² plots in each subsite (a total of 40 plots per site) that were searched thoroughly for ants by two people simultaneously for a period of 5 min. The soil samples consisted of one 0.5 m² plot in each subsite (a total of eight plots per site) in which the soil was removed to a depth of 3 cm, and collected along with its leaf litter. The samples were then sifted to remove any ants. One sweep-netting sample was also taken at each subsite, yielding eight sweep-net samples per site. A sample consisted of five short transects walked at a steady pace while completing ten full 180° sweeps with the net. The heavy net was vigorously swung through the vegetation at various heights to dislodge and catch ants (Fisher 2004). All inventory techniques were repeated for each combination of infestation category and forest type for a total of nine sites, 72 subsites, and 360, 72, and 72 sampling units for direct

search, soil samples, and sweep net transects, respectively. Each of the three methods was conducted on three different days in each site to balance possible climatic effects on ant activity. No collecting was done within 24 h after any rainfall.

To map the distribution of *W. auropunctata* (Fig. 1), I walked around the perimeter of the forests in the principal SEGC research area, stopping at regular intervals to search thoroughly for *W. auropunctata*. In areas where I found infestations along the border, I conducted sweeps toward the interior of the forest with one to five assistants at regularly spaced intervals to determine the interior limit of the infestation. I also followed all waterways in contact with infested areas in both directions until I could no longer find *W. auropunctata*. Points delineating infestation borders were recorded using GPS and mapped in ArcGIS. I then connected the data points to represent the most likely continuous extent and estimated the area of this infestation using a basic ArcGIS query. I extended the distribution map beyond the principal SEGC research area and to the town of Lopé by visiting points along the main rivers and borders of forested areas within 100 m of the main road leading to SEGC.

DATA ANALYSIS.—Only ant workers were counted, since presence of alates does not necessarily indicate colony establishment (Fisher 2002). Species presence, rather than individual occurrence, was recorded for each sample. Voucher specimens have been

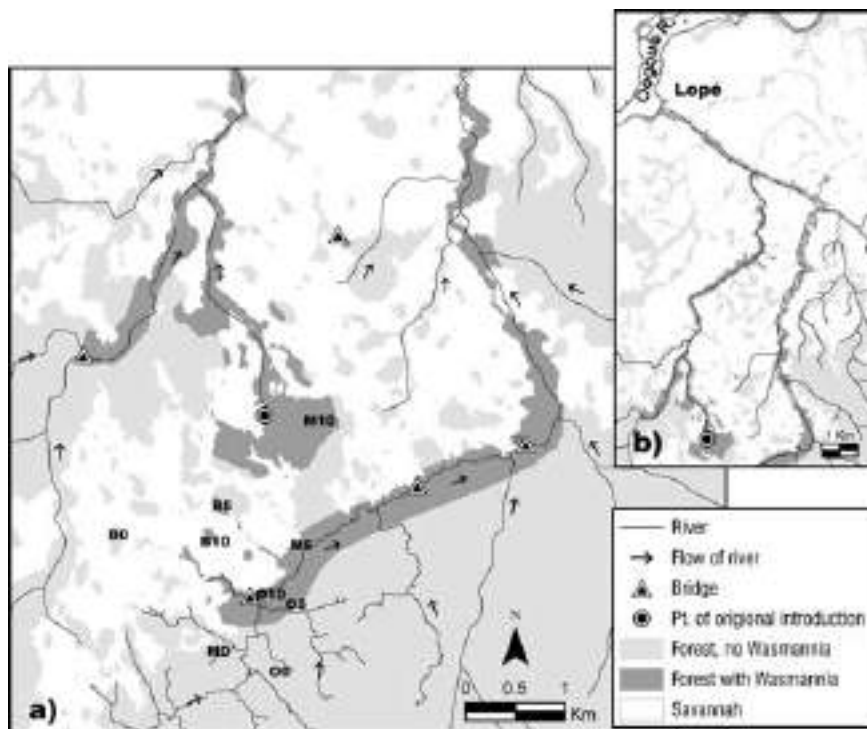


FIGURE 1. (a) Map of SEGC principal research area, showing study sites and extent of territory invaded by *W. auropunctata* in correlation with bridges and waterways. The assumed point of original infestation is determined by evidence from remains of the 1965 logging camp, as well as from SEGC records. (b) The infested area follows two small rivers through the northern border of the principal forest study area and continues several kilometers to the town of Lopé, where the smaller rivers meet up with the Oogoué, the largest river in Gabon.

deposited at the California Academy of Sciences, San Francisco, California, U.S.A.

Statistical analyses were carried out using SPSS version 11. Nonparametric Kruskal–Wallis and Mann–Whitney U tests were used to determine differences in species richness between sites. Since species richness alone is not always the best measure of diversity, evenness was also analyzed using a Simpson index: $D = \sum n_i(n_i - 1)/N(N - 1)$, where n_i = the number of individuals of species i , and N = the total number of individuals (Smith & Wilson 1996).

To evaluate sampling efficiency, species accumulation curves were generated for each site in terms of new species found over total species encounters. The curves were generated based on the mean of 100 randomizations using Estimates 7.5 (Colwell 2005). The maximum likelihood asymptote of each curve was estimated using the Michaelis–Menten Means output (Raaijmakers 1987, Colwell & Coddington 1994, Colwell 2005), which characterizes the main body of the community and provides a reliable estimate of sampling efficiency (Magurran 2004). Whereas the Michaelis–Menten asymptote may also provide an adequate estimate of total species richness (Soberón & Llorente 1993), it tends to underestimate rare species (Magurran 2004). To estimate maximum species richness based on both common and rare species, the accumulation data were extrapolated using Incidence-based Coverage Estimator (ICE; Chao *et al.* 2000). Although such methods of estimating asymptotic richness via extrapolation of observed data show variable behavior and are still in a trial phase (Longino *et al.* 2002, Colwell *et al.* 2004), ICE has been shown to be a fairly robust species richness estimator across sites (Chazdon *et al.* 1998). ICE and Michaelis–Menten estimates are included here for their usefulness in visualizing and comparing the accumulation curves rather than to predict the exact species richness of each site. To accurately predict total species richness, more exhaustive sampling would be necessary (Longino *et al.* 2002).

Because the sample size for soil and sweep-net samples was small in comparison to that of direct search plots, the data collected from these former techniques were not included in statistical analysis, or in the generation of accumulation curves. For this reason, estimated species richness based on ICE and Michaelis–Menten only reflects ants found in direct search plots. Although excluded from statistical analysis, species observed in the soil and sweep-net samples are reported here as an indicator of species found in other strata of the forest. For an accurate assessment of diversity in these strata, more extensive sampling would be needed.

RESULTS

SPECIES RICHNESS.—With all sample methods, I collected a total of 79 ant species (20 genera) in all nine of the sites. A total of 75, 17, and 3 species were collected where *W. auropunctata* is not yet present, where it has been present for approximately 5 yr, and more than 10 yr, respectively. In the six invaded sites, *W. auropunctata* was found in every sample, using every sample method. In direct search plots, I found an average of 3.20, 0.45, and 0.14 other ant species per square meter for the above respective categories of *W. auropunctata* infestation.

A sharp decline in species richness accompanies infestation by *W. auropunctata* regardless of forest type (Fig. 2). Forest type did not significantly influence richness of ant species in the leaf litter (Kruskal–Wallis; $H = 4.98$; $df = 2$; $P = 0.083$). In contrast, the age of infestation by *W. auropunctata* had a highly significant impact on species richness (Kruskal–Wallis; $H = 51.06$; $df = 2$; $P < 0.001$). Posthoc tests indicate that the most significant impact arises from the presence or absence of *W. auropunctata* regardless of the duration of infestation (Mann–Whitney; $U = 0.0$; $P < 0.001$ for both). The difference in ant species richness between sites where *W. auropunctata* has been present for 5 yr and those where it has been present for more than 10 yr was also significant ($U = 194.5$; $P = 0.038$), but the principal effect depended simply on presence.

The high significance of the results using only eight samples (eight five-plot clusters) per site rendered it unnecessary to extend the sample size to 40 by analyzing each plot as an independent sample. Since it is, therefore, unnecessary to evaluate the independence of the plots using spatial analysis of ant species between and within subsites, such spatial analysis is irrelevant to the scope of this paper.

SAMPLING EFFICIENCY AND PROJECTED SPECIES RICHNESS.—The species accumulation curves (Fig. 3) for all three sites not yet colonized by *W. auropunctata* were still rising at the end of the sampling period. The Michaelis–Menten asymptote estimation and the ICE estimation of minimum total species richness both considerably exceed the observed species for these sites (Table 2). In most of the sites infested by *W. auropunctata*, however, the accumulation curves flatten out with additional sampling effort, and the Michaelis–Menten asymptote estimation is equal to the number of species observed. The one exception is B5, for which the accumulation curve is still climbing with sampling effort.

EVENNESS.—The results generated by the Simpson index, which weights the abundance, or dominance, of each species in a site, are similar to those for pure species richness (Table 2). The sites that *W. auropunctata* has not yet colonized have considerably smaller Simpson values than those where *W. auropunctata* is present. These values reflect the probability of any two individuals drawn at random from the community belonging to the same species (Simpson 1949); values closer to zero represent more even assemblages with higher β diversity.

DISTRIBUTION.—*Wasmannia auropunctata* infestations were found to cover approximately 6 km² of forest habitat through the principal SEGC research area to the town of Lopé (Fig. 1). Colonization across dry land appears to be relatively slow. The widest patch of continuous infested territory away from waterways measured approximately 800 m across. If *W. auropunctata* colonized this area linearly from the point assumed to be the origin of introduction in 1965 (the site of the former logging camp), it would have advanced an average of about 21 m per year away from the river. If the precise origin of the infestation were not actually at this assumed point, this estimate of advancement rate would be reduced. In contrast, where moving water was present, the infestation extended much farther; *W. auropunctata* continued all the way down the rivers to

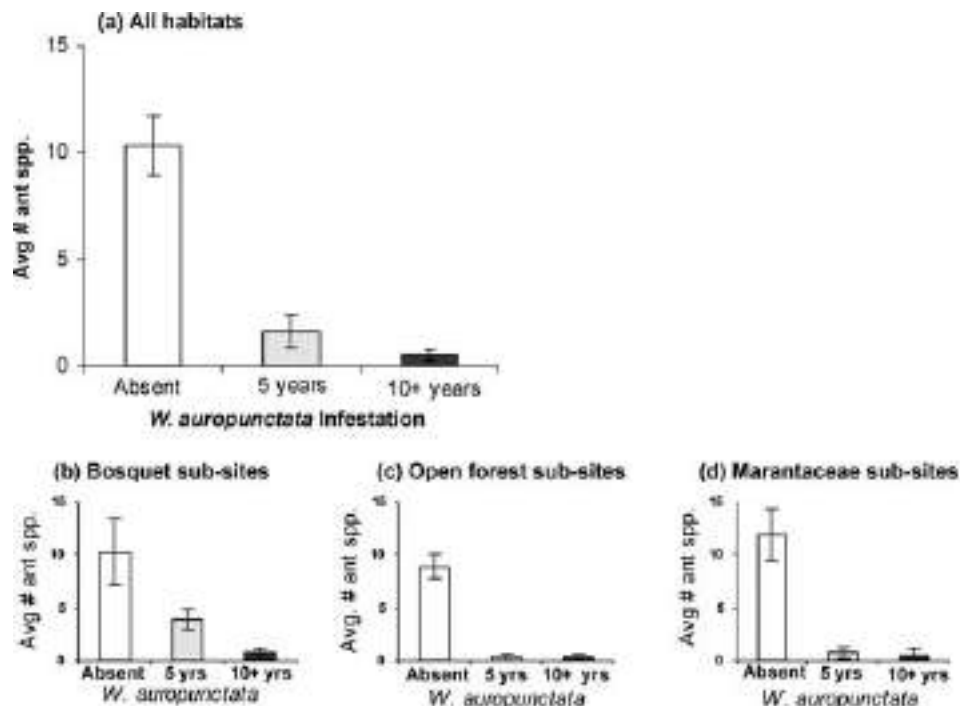


FIGURE 2. Average number of ant species found via direct search methods in subsites in (a) all habitats combined ($N = 24$ in each category), (b) bosquet subsites alone ($N = 8$ in each category), (c) open forest subsites alone ($N = 8$ in each category), and (d) marantaceae forest subsites alone ($N = 8$ in each category). See text for description of habitats. *Wasmannia auropunctata* is not included in the calculations of ant species.

the town of Lopé, nearly 12 km away. *Wasmannia auropunctata* was frequently observed only within a narrow strip along the banks of these rivers, and was often absent in locations more than 20–30 m beyond these banks. Where infested areas crossed rivers, I found the upstream limit of *W. auropunctata* occurrence to lie almost exactly on the line connecting the two infestation boundary markers 20 m away from the river on each side. Downstream, however, infested areas projected past this line and always tend to follow the waterway.

The distribution of *W. auropunctata* in relation to bridges is striking. The vegetation in the direct vicinity of all the five bridges in the area was found to be infested. Infestations continued in the downstream direction from bridges, but hardly in the upstream direction unless there was another bridge upstream. One bridge stood within an isolated patch of *W. auropunctata*.

DISCUSSION

Wasmannia auropunctata reduces native ant diversity both radically and rapidly. Even with the limited sampling of this study, it is evident that native ant diversity is high in areas where this exotic ant is not present, and drops severely following infestations. The capability of *W. auropunctata* to eliminate almost all native ant species in the continental forests of Lopé presents a serious threat to the conservation of biodiversity in the Congo Basin region. The threat to ant diversity alone is substantial; nearby forests of the Monts Doudou area contain the highest ant richness known in

Africa (Fisher 2004). The threats extend beyond ants, however. Other studies have found that *W. auropunctata* can have indirect effects on lizard diversity (Jourdan *et al.* 2001), as well as direct effect on tortoises, birds (Lowe *et al.* 2000, Wetterer & Porter 2003), and perhaps domestic dogs and cats (Wetterer *et al.* 1999) and their wild relatives (Walsh *et al.* 2004).

While *W. auropunctata* reportedly occupied an area of just over 60 ha at the SEGC study zone in Lopé in 2001 (Walsh *et al.* 2004), I found that the infestations covered more than 10 times that area in 2004. This enormous increase in infested territory is not likely due to an increase in colonization rate in the past 3 yr: Differences in study area definition and survey methods are the more probable cause. Previous reports were based almost exclusively on researchers' records. Such records may provide reliable data for areas where researchers work often, but they tend to result in an underestimation of the total extent of the infestation because they provide little data for areas where research is rarely conducted.

Regardless of the rate at which these areas are being colonized, the extent of the infested territory in Lopé is alarming. Even more alarming is the relationship between infested areas and waterways. Whereas Walsh *et al.* (2004) call attention to the important role that logging activities play in the transport of *W. auropunctata*, they fail to recognize the significant role of rivers and streams in transporting the invaders. While rates of unassisted colonization away from rivers appear to be fairly slow, probably because *Wasmannia* alates do not fly very far (Lubin 1984), my results suggest that rates of

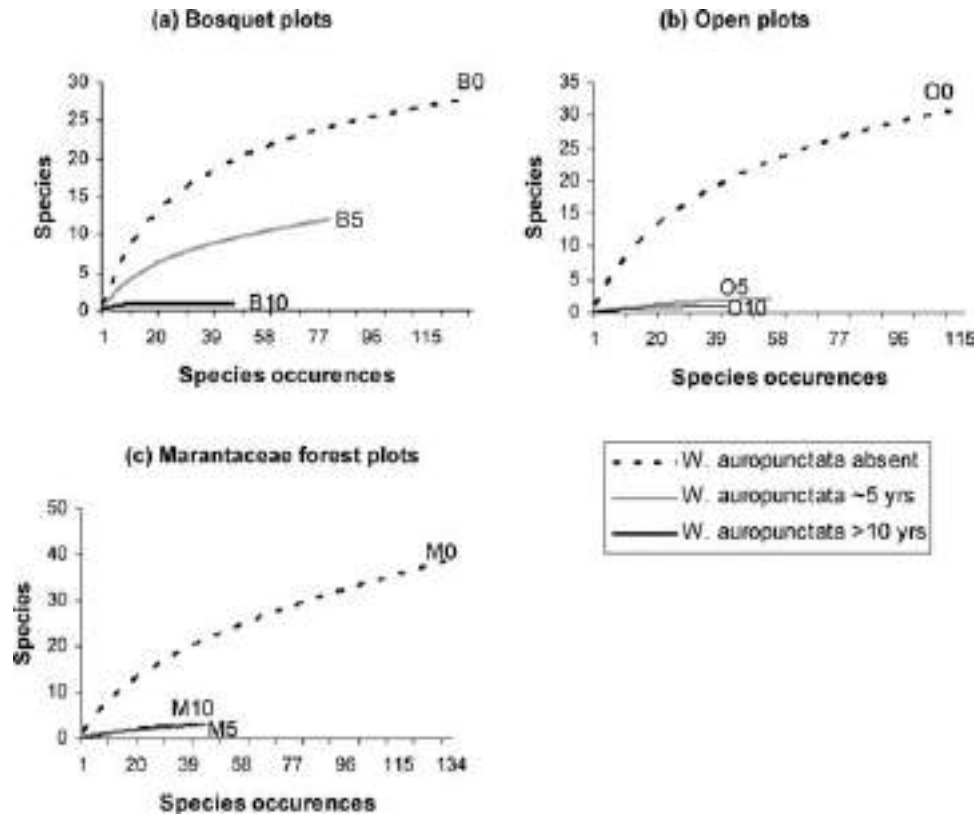


FIGURE 3. Assessment of effectiveness of direct search sampling ($N = 40$ samples) in (a) bosquet sites, (b) open forest sites, and (c) marantaceae forest sites. The species accumulation curves in each graph plot the number of species observed as a function of species occurrences. Curves are plotted from the means of 100 randomizations of accumulation order. Asymptote and total species richness estimates based on these curves are summarized in Table 2.

colonization are greatly accelerated when moving water is present. This relation to waterways is strikingly similar to patterns observed for other invasive ants, such as *Linepithema humile* (Holway 1998, Wild 2004).

The combination of logging and waterways can be an especially deadly mix for ant biodiversity. If *W. auropunctata* is introduced to a location near a waterway, it can expand its territory much more rapidly than on dry land, rendering early eradication nearly

TABLE 2. Diversity of ant assemblages found at each site, as determined by: the total number of ant species observed per site by all sampling methods and by direct search only, the mean number of ant species per subsite ($N = 8$), the mean number of ant species per plot ($N = 40$), the Michaelis–Menten projected asymptote (MMM), the ICE estimate of total species richness, and the Simpson diversity index. *Wasmannia auropunctata* is not included in any figures.

Site	Forest type	Age of infestation	Total spp. observed		Mean spp. observed		MMM	ICE	Simpson
					/subsite	/ m ² plot			
			All	Direct search only					
B0	Bosquet	absent	35	27	10.25	3.53	33	33	0.06
O0	Open	absent	38	33	8.88	2.80	44	48	0.06
M0	Marantaceae	absent	44	39	11.88	3.17	52	75	0.07
B5	Bosquet	≈5 yr	14	12	3.88	1.08	16	18	0.26
O5	Open	≈5 yr	2	1	0.25	0.05	4	2*	0.95
M5	Marantaceae	≈5 yr	5	3	0.75	0.23	4	7	0.70
B10	Bosquet	>10 yr	1	1	0.75	0.18	1	1*	0.75
O10	Open	>10 yr	1	1	0.25	0.05	2	1*	0.91
M10	Marantaceae	>10 yr	3	3	0.50	0.20	6	4	0.79

*Stable for at least last five individuals added.

impossible. The pattern of the distribution of *W. auropunctata* in relation to bridges in Lopé, along with the witness of locals and researchers in the area, strongly suggests that bridges are a primary means of secondary introduction. It is essential that special caution should be taken to prevent further spread of *W. auropunctata* when constructing bridges or transporting materials via such waterways.

Although bridges and waterways are particularly worrisome, transport of materials to remote areas for any reason and via any medium presents opportunity for invasions. If the control of *W. auropunctata* is not a priority, Gabon's national parks could easily facilitate, rather than prevent, the spread of this ant into pristine habitats, due to the extensive transport of materials required to develop and maintain these parks.

Conservationists and ecotourism operators should take all possible measures to avoid spreading *W. auropunctata* to noninfested areas. All materials transported into Gabon's national parks should be carefully inspected for *W. auropunctata*, and any new introduction should be immediately and completely eradicated before it becomes too extensive to control effectively. It is easy to overlook a tiny ant when facing more dramatic issues such as logging and poaching, but this tiny ant may be capable of taxing the forest's biodiversity to a similar extent.

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LITERATURE CITED

- ATKINSON, I. 1989. Introduced animals and extinctions. In D. Western and M. C. Pearl (Eds.). *Conservation for the twenty first century*, pp. 54–75. Oxford University Press, New York, New York.
- BESSELINK, C., W. FERWERDA, AND P. SIPS, Eds. 1998. *The Congo Basin: Human and natural resources*, pp. 214. Netherlands Committee for IUCN, Amsterdam, Netherlands.
- BLOM, A., M. P. T. ALERS, A. T. C. FEISTNER, R. F. W. BARNES, AND K. L. BARNES. 1992. Primates in Gabon—Current status and distribution. *Oryx* 24: 223–234.
- CHAO, A., W. H. HWANG, Y. C. CHEN, AND C. Y. KUO. 2000. Estimating the number of shared species in two communities. *Statistica sinica* 10: 227–246.
- CHAZDON, R. L., R. K. COLWELL, J. S. DENSLow, AND M. R. GUARIGUATA. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rainforests of NE Costa Rica. In F. Dallmeier and J. A. Comiskey (Eds.). *Forest biodiversity research, monitoring and modeling: Conceptual background of Old World case studies*, pp. 285–309. Parthenon Publishing, Paris, France.
- CLARK, D. B., C. GUAYASAMIN, O. PAZMINO, C. DONOSO, AND Y. P. DEVILLACIS. 1982. The tramp ant *Wasmannia auropunctata*: autecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos. *Biotropica* 14: 196–207.
- COLWELL, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- , AND J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. (Series B)* 345: 101–118.
- , C. X. MAO, AND J. CHANG. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85: 2712–2727.
- DEYRUP, M., L. DAVIS, AND S. COVER. 2000. Exotic ants in Florida. *Trans. Am. Entomol. Soc.* 126: 293–326.
- FISHER, B. L. 2002. Ant diversity patterns along an elevational gradient in the Reserve Speciale de Manongarivo, Madagascar. *Boissiera* 59: 311–328.
- , Ed. 2004. *Monts Doudou, Gabon: A floral and faunal inventory with reference to elevational variation*, pp. 295. California Academy of Sciences, San Francisco, California.
- GILLESPIE, R. G., AND G. K. RODERICK. 2002. Arthropods on islands: Colonization, speciation, and conservation. *Annu. Rev. Entomol.* 47: 595–632.
- GUILBERT, E., J. CHAZEAU, AND L. BONNET DE LARBOGNE. 1994. Canopy arthropod diversity of New Caledonian forests sampled by fogging: Preliminary results. *Mem. Queensl. Mus.* 36: 77–85.
- HOLWAY, D. A. 1998. Factors governing rate of invasion: A natural experiment using Argentine ants. *Oecologia* 115: 206–212.
- JOURDAN, H. 1997. Threats on Pacific islands: The spread of the tramp ant, *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Pac. Conserv. Biol.* 3: 61–64.
- , R. A. SALLIER, AND A. M. BAUER. 2001. Little fire ant invasion (*Wasmannia auropunctata*) as a threat to New Caledonia lizards: Evidences from a sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology* 38: 283–302.
- KLOTZ, J. H., J. R. MANGOLD, K. M. VAIL, L. R. DAVIS, AND R. S. PATTERSON. 1995. A survey of the urban pest ants (Hymenoptera, Formicidae) of peninsular Florida. *Fla. Entomol.* 78: 109–118.
- LE BRETON, J., J. CHAZEAU, AND H. JOURDAN. 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Aust. Ecol.* 28: 204–209.
- , H. JOURDAN, J. CHAZEAU, J. ORIVEL, AND A. DEJEAN. 2005. Niche opportunity and ant invasion: The case of *Wasmannia auropunctata* in a New Caledonian rain forest. *J. Trop. Ecol.* 21: 93–98.
- LONGINO, J. T., J. A. CODDINGTON, AND R. K. COLWELL. 2002. The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology* 83: 689–702.
- LOOPE, L. L., AND D. MUELLER-DOMBOIS. 1989. Characteristics of invaded islands. In H. Mooney (Ed.). *Ecology of biological invasions: A global synthesis*, pp. 257–280. John Wiley & Sons, Chichester, England.
- LOWE, S., M. BROWNE, AND S. BOUDJELAS. 2000. 100 of the world's worst invasive alien species. *Aliens* 12: S1–S12.
- 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.
- MAGURRAN, A. E. 2004. *Measuring biological diversity*. Blackwell, Oxford, England.
- POURTIER, R. 1989. *Le Gabon: Etat et developpement*. l'Harmattan, Paris, France.
- RAAIJMAKERS, J. G. W. 1987. Statistical analysis of the Michaelis–Menten equation. *Biometrics* 43: 793–803.
- REJMÁNEK. 1996. Species richness and resistance to invasion. In G. H. Orians, R. Dirzo, and J. H. Cushman (Eds.). *Biodiversity and ecosystem processes in tropical forests*, pp. 153–172. Springer-Verlag, New York, New York.
- SANTSCHI, F. 1914. Formicides de l'Afrique occidentale et australe du voyage de M. le Professeur F. Silvestri. *Bollettino del Laboratorio di Zoologia general e agraria (Portici, Italia)* 8: 309–385.

- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163: 688.
- SMITH, B., AND J. B. WILSON. 1996. A consumer's guide to evenness measures. *Oikos* 76: 70–82.
- SOBERÓN, M., AND B. LLORENTE. 1993. The use of species accumulation functions for the prediction of species richness. *Conserv. Biol.* 7: 480.
- WALSH, P. D., P. HENSCHL, AND K. A. ABERNETHY. 2004. Logging speeds little red fire ant invasion of Africa. *Biotropica* 36: 637–640.
- WETTERER, J. K., AND S. D. PORTER. 2003. The little fire ant, *Wasmannia auropunctata*: distribution, impact, and control. *Sociobiology* 42: 1–41.
- , P. D. WALSH, AND L. J. T. WHITE. 1999. *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae), a destructive tramp-ant, in wildlife refuges of Gabon. *Afr. Entomol.* 7: 292–294.
- WHEELER, W. M. 1929. Two Neotropical ants established in the United States. *Psyche* 36: 89–90.
- WHITE, L. J. T., AND K. A. ABERNETHY. 1996. Vegetation Guide of the Lopé Reserve. ECOFAC, Libreville, Gabon.
- WILD, A. L. 2004. Taxonomy and distribution of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 97: 1204–1215.