BIODIVERSITY RESEARCH

Effect of propagule pressure on the establishment and spread of the little fire ant *Wasmannia auropunctata* in a Gabonese oilfield

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ABSTRACT

We studied the effect of propagule pressure on the establishment and subsequent spread of the invasive little fire ant *Wasmannia auropunctata* in a Gabonese oilfield in lowland rain forest. Oil well drilling, the major anthropogenic disturbance over the past 21 years in the area, was used as an indirect measure of propagule pressure. An analysis of 82 potential introductions at oil production platforms revealed that the probability of successful establishment significantly increased with the number of drilling events. Specifically, the shape of the dose–response establishment curve could be closely approximated by a Poisson process with a 34% chance of infestation per well drilled. Consistent with our knowledge of largely clonal reproduction by *W. auropunctata*, the shape of the establishment curve suggested that the ants were not substantially affected by Allee effects, probably greatly contributing to this species' success as an invader. By contrast, the extent to which *W. auropunctata* spread beyond the point of initial introduction, and thus the extent of its damage to diversity of other ant species, was independent of propagule pressure. These results suggest that while establishment success depends on propagule pressure, other ecological or genetic factors may limit the extent of further spread. Knowledge of the shape of the dose–response establishment curve should prove useful in modelling the future spread of *W. auropunctata* and perhaps the spread of other clonal organisms.

Keywords

Biological invasions, clonality, invasive species, rain forest, tropics, petroleum extraction.

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Human activities radically alter the structure and connectivity of landscapes. For some species, this means virtually limitless worldwide dispersal, travelling alongside human cargo. However, to successfully establish in a new habitat, a species must overcome several hurdles, including establishment and eventual range expansion. The vast majority of species arriving in a new habitat fail to sustain viable populations and become extirpated (Holdgate, 1986; Williamson, 1996). A few establish successfully, continuing to exist as minor components of the system. Others expand dramatically, sometimes displacing native species and even radically altering the habitats that receive them in the process (Williamson & Fitter, 1996; Sakai *et al.*, 2001). The study of factors that affect the successful establishment of a species, as well as those that determine the extent and impact of its later spread has been a major focus of ecological research (Richardson & Pysek, 2006).

Recent work has shown that the number of arriving invaders (propagule pressure) plays an important role in the establishment of invasive species (Cassey *et al.*, 2004; Lester, 2005; Lockwood *et al.*, 2005; Suarez *et al.*, 2005; Von Holle & Simberloff, 2005; Colautti *et al.*, 2006; Duggan *et al.*, 2006). First, this is due to the larger numbers of colonists offsetting the extinction risk that faces many small populations due to environmental or demographic factors. Second, repeated introductions may sustain initial populations below survival thresholds and also provide sources of additional genetic variability (Brown & Kodric-Brown, 1977; Kolbe *et al.*, 2004). Thus, propagule pressure allows invasives to overcome stochastic factors, which may doom the vast majority of incipient invasions (Williamson, 1996).

However, despite the importance of propagule pressure to the establishment of invasive species, it is one of the least understood facets of biological invasions. For example, due to the lack of quantitative data on propagule pressure, little is known about the shape of the 'dose–response' curve of biological invasions, i.e. the probability of establishment as a function of the size or number of arriving propagules (Lockwood *et al.*, 2005). The dose–response

curve may be a sigmoidal function, where a threshold must be crossed before a high likelihood of establishment, such as in the presence of strong Allee effects, which limit the growth of small populations (Allee, 1931; Stephens *et al.*, 1999). Alternatively, invasive species may consistently benefit from additional or larger propagule sizes (Leung *et al.*, 2004; Drake & Lodge, 2006). In order to quantitatively evaluate the effect of propagule pressure on establishment and also on the further spread of an invasive species, we studied colonization and invasion of lowland rain forest by the little fire ant *Wasmannia auropunctata* in a Gabonese oilfield.

Although native to the New World, *W. auropunctata* has spread widely over the past 100 years, colonizing numerous Pacific islands, Central Africa, and, most recently Papua New Guinea and Australia (Wetterer & Porter, 2003). Most of the new introductions appear to arise from other invasive populations, rather than from independent introductions from the native range (Mikheyev & Mueller, 2007). Introduced *W. auropunctata* often negatively impact the native ant fauna (Clark *et al.*, 1982; Lubin, 1984; Jourdan, 1997; Roque-Albelo *et al.*, 2000; Le Breton *et al.*, 2003; Walker, 2006). Additionally, some reports suggest that *W. auropunctata* attack native reptiles, birds, and mammals (Roque-Albelo & Causton, 1999; Wetterer *et al.*, 1999; Jourdan *et al.*, 2001; Walsh *et al.*, 2004). Given the ecological importance of this pest, the rapid rate of its spread through Central Africa, and continuing colonization of sensitive tropical habitats, it is important to understand the dynamics of its establishment. To this end, we used a combination of field surveys and historical records to reconstruct the invasion of numerous *W. auropunctata* invasions over the course of more than two decades. Specifically, we focused on estimating the relationship between propagule pressure and the successful establishment and further spread of *W. auropunctata*.

METHODS

Study site

The Rabi-Kounga concession of Shell Gabon lies in lowland rain forest, close to the equator (1.91° S, 9.86° E). The concession has been selectively logged 17–20 years ago and has regrown as dense secondary forest. Other than past logging and current petroleum extraction, human activity is limited and strictly regulated by Shell Gabon. Company regulations isolate the production staff to a few camps and also prohibit forest access and hunting (Fig. 1). In addition, Shell maintains checkpoints, limiting access to the concession by external parties (Laurance *et al.*, 2006).

As much of the oil concession lies in a swamp on unstable sandy soils, laterite platforms (~100 × 100 m) are constructed prior to well drilling. The vegetation on the edges of these platforms is composed of woody pioneer species, chiefly *Harungana madagascarensis* and, to a lesser extent, azobé (*Lophira alata*). Due to the high cost of platform construction, new oil wells are drilled laterally from previously existing platforms whenever possible. Compared to the initial construction of the platform, subsequent drilling has relatively minor effects on the surrounding
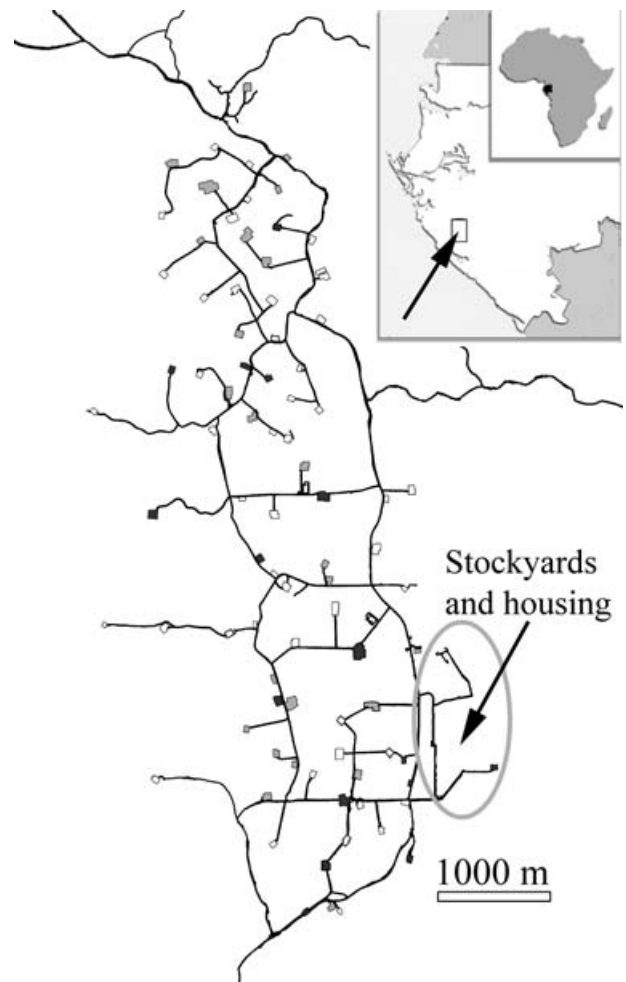

Figure 1 Distribution of *Wasmannia auropunctata* on production platforms in the Rabi-Kounga concession, Gabon. The diagram shows the distribution of platforms (polygons) and connecting roads (black lines). Uninfested platforms are shown as clear polygons, whereas partially and completely infested platforms are shown as light and dark grey, respectively. The scale bar represents 1000 m. Storage yards and personnel housing quarters are located in the south-east corner of the oilfield.

habitat, although the initial platform may be slightly enlarged. Each new well takes several weeks of continuous drilling, requiring the importation of many tonnes of supplies, the drilling rig, as well as temporary housing for the rig crew. The materials are brought in from a centralized storage yard, which at the time of field surveys for this study was heavily infested with *W. auropunctata*. No quarantine policies were in place at the time of this study, allowing unrestricted transport of materials among infested and un-infested sites during drilling. However, after a well is drilled, it generally undergoes only light maintenance and cleaning. Consequently, drilling is likely the principal mode of *W. auropunctata* introduction to a site and our chosen measure of propagule pressure. The number of drilling rig visits included both initial well drilling and, when applicable, later overhaul. The number of wells drilled per platform ranged from 1 to 8, with a mean of 2.5. Most wells

were drilled horizontally to oil deposits located several kilometres away. As the number of wells was dictated by the distribution of subterranean petroleum deposits at the oilfield, there is no reason to suspect that the number of wells drilled per platform may correlate with confounding environmental factors on the surface.

Field surveys

Each of the 86 platforms was visited at the beginning of the dry season in the first three weeks of May 2006. The platforms were re-visited in the wet season 5 to 6 months later to confirm the stability of the observed distributions. We noted the presence of *W. auropunctata* at each platform by visual inspection of leaf litter and vegetation, especially around the extra-floral nectaries of plants, such as the azobé. Surveys were conducted on dry days, in the mornings and in early afternoons, as *W. auropunctata* frequently ceased foraging in the heat or under rain and were hard to find. Each platform was surveyed for approximately one man-hour, although the search effort was increased slightly for larger platforms. Platforms were classified into three types, based on *W. auropunctata* presence and abundance: (1) absent, (2) part of platform colonized, and (3) platform perimeter fully colonized. Whenever a platform perimeter was fully colonized, the *W. auropunctata* population would inevitably extend for tens of metres into the surrounding forest.

In order to verify the adequacy of visual inspection for the detection of *W. auropunctata* in the field, we extracted ants from leaf litter using Winkler traps at 20 randomly selected platforms (10 where *W. auropunctata* was not detected by visual inspection and five each with partial and total platform colonization) (Agosti *et al.*, 2000). For each of the platforms, 1 m^2 of leaf litter was collected at eight sites uniformly spaced around the perimeter. Leaf litter was sifted and allowed to hang in a Winkler trap for 48 h. Finally, the number of *W. auropunctata* workers and the number of other ant morphospecies were counted. In addition to validating our sampling protocol, Winkler sifting also provided a measure of *W. auropunctata*'s impact on the native ant fauna at our site.

Statistical analysis

Dates of oil well drilling were obtained from Shell Gabon. In order to determine whether propagule pressure (the number of drilling rig visits), has an effect on the successful establishment of *W. auropunctata* at a platform, we conducted a binary logistic regression correlating the number of drilling rig visits (for both initial drilling and overhaul of existing wells) and platform age in years with the presence of *W. auropunctata*. We also conducted another binary logistic regression with the same predictors only on colonized platforms to determine the extent to which propagule pressure determines subsequent platform colonization.

The effect of *W. auropunctata* abundance across platforms on the morphospecies richness of other ants, estimated by Winkler extraction, was analysed using an ordinary least squares regression, with the dependent variable square-root-transformed to stabilize the variance. Statistical analyses were carried out in Minitab (version 11,

Minitab Inc., State College, PA, USA) and Matlab (version 7; The MathWorks, Inc., Natick, MA, USA). Coefficient estimates and means are given ±1 standard error.

We followed the methodology of Leung *et al.* (2004) for detecting the presence of Allee effects by fitting a Weibull distribution to the probability of *W. auropunctata* establishment as a function of the number of rig visits. Allee effects are present if the shape parameter of the fitted model is significantly greater than one, i.e. the dose–response establishment curve shows a disproportionately slower rate of establishment when fewer propagules are introduced. Curve-fitting was conducted in R (version 2.5).

RESULTS

Our analysis included 82 platforms, ranging in age from 1 to 21 years. The analysis included all platforms in the concession, except four that had uses other than oil production (e.g. housing, storage, drilling mud re-injection, etc.) and may have received additional *W. auropunctata* propagules. All such multiuse platforms were infested. Of the platforms used in the analysis 40 (49%) had no *W. auropunctata*, 26 (32%) had partial infestations, and 16 (20%) were completely infested. Winkler sifting gave results completely concordant with those obtained by visual inspection, with *W. auropunctata* being absent in all platforms where it was not detected by visual surveys. The extent of *W. auropunctata* infestation at a platform was negatively correlated with the species richness of other ants ($F_{1,18} = 11.7$, $P = 0.003$, Fig. 2).

The number of rig visits correlated with the likelihood of successful *W. auropunctata* establishment, an effect independent of platform age (Table 1). Moreover, the probability of *W. auropunctata* establishment increased with the number of rig visits (Fig. 3). We were unable to detect the presence of Allee effects, since the shape parameter of the Weibull distribution was not significantly different from unity (95% confidence interval included [0, 1.2]). Furthermore, the data were statistically indistinguishable from those predicted by a Poisson process of *W. auropunctata* introductions, which explained 31% of the variance ($\lambda = 0.34$, 95% CI [0.23, 0.50]; Kolmogorov–Smirnov statistic = 0, $P = 0.19$, Fig. 3). However,
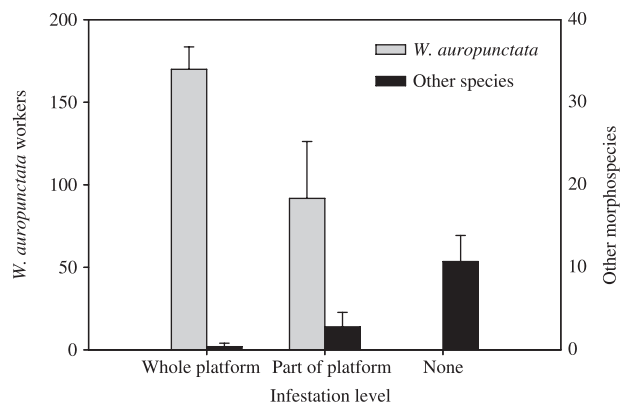
Figure 2 Abundances of *Wasmannia auropunctata* workers and species richness of native ants per m^2 leaf litter on oil production platforms with varying degrees of platform infestation.

Effect of propagule pressure and platform age on the likelihood of *Wasmannia auropunctata* establishment, as determined by binary logistic regression.

	Coefficient	Z	P	Odds ratio (low, high)
Constant	0.58 ± 0.89	0.66	0.51	
Rig visits	0.34 ± 0.14	2.35	*0.019*	1.40 (1.06, 1.85)
Platform age	-0.089 ± 0.056	1.59	0.11	0.91 (0.82, 1.02)

neither the number of rig visits nor the amount of time since platform construction had an effect on whether *W. auropunctata* fully colonized a platform after establishment ($G = 2.0$, d.f. = 2, $P = 0.37$). Since *W. auropunctata* may have been introduced during the drilling of any well after the initial construction of the platform, age of platform construction may not accurately reflect the amount of time *W. auropunctata* has been established. However, restricting the analysis to the 12 platforms where a single well had been drilled, time of construction still had no effect on the success of spread ($G = 2.6$, d.f. = 1, $P = 0.11$; coefficient = -0.20 ± 0.14).

DISCUSSION

The highly managed nature of construction in the Rabi concession allows for a precise description and quantification of human impacts on the rain forest. Thus, we were able to examine the consequences of replicated *W. auropunctata* introductions through well drilling without the confounding factors accompanying many historical studies of biological invasions, such as increased urbanization. As all platforms are constructed out of laterite, which is brought in from the same nearby quarry, they have essentially the same soil and undergo very similar successional dynamics. Thus, the construction and development of each production platform provides a nearly ideal experimental setup with highly standardized treatments (drilling rig visits) between replicates
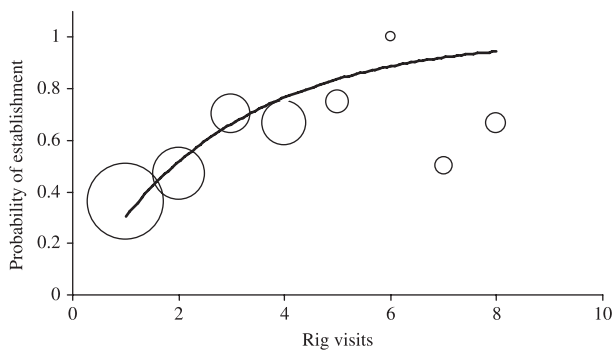

Figure 3 Probability of *Wasmannia auropunctata* establishment as a function of rig visits. The circle areas are proportional to the number of observations (from 1 to 33), and, thus, the accuracy of the estimate. Values predicted by modelling the establishment probability as a Poisson process are shown by the solid line ($1-e^{-\lambda*r}$, where λ is the probability of establishment at a platform with a single well and r is the number of rig visits).

(oil production platforms). Thus, variation in the number of wells drilled at a platform should correspond to differences in propagule pressure.

Our data show that well drilling is the likely culprit of *W. auropunctata* introductions to the production platforms (Fig. 3). The number of rig visits is not a perfect measure of propagule pressure, as it potentially confounds the probability of transport with the probability of establishment at a site. However, given (1) the large amount of material transferred to a drilling site, (2) the heavy infestation of material storage sites, and (3) the lack of quarantine protocols regulating the transfer of equipment between infested and non-infested sites, the probability of *W. auropunctata* transport with each drilling event is likely quite high.

Also, it appears that the levels of *W. auropunctata* infestation at the storage sites have been comparably high throughout the history of the oilfield. First, the age of platform construction was not a significant predictor of colonization, indicating that the likelihood of *W. auropunctata* transfer per drilling event was comparable during the early stages of oilfield development. Second, sites that were used for initial housing of personnel and equipment storage, which were abandoned over a decade ago, were also heavily infested (A.S.M., unpublished data). The regular presence of *W. auropunctata* in the storage sites, together with comparable amounts of material being moved from the storage sites to the drilling rigs, suggests fairly similar introduction levels per well drilled.

Given the largely clonal reproduction of *W. auropunctata* elsewhere in the world (Fournier *et al.*, 2005a; Foucaud *et al.*, 2006) and our data indicating the presence of clonality at the Rabi-Kounga oilfield (A.S.M. and S. Bresson, unpublished data), one would not expect density-dependent effects on population establishment and growth (Allee effects). Accordingly, the probability of establishment can be accurately approximated by a Poisson distribution where each drilling event is associated with a 34% chance of successful establishment (Fig. 2). Consequently, single introduction events are sufficient to initiate invasions, such as appears to have happened in New Caledonia, where an infestation was initiated by the introduction of a single mated female (Foucaud *et al.*, 2006).

In addition to establishing a viable population, a successful colonizer also needs to spread beyond the point of initial introduction. In principle, a greater number of propagules may increase the genetic diversity of the founding population and facilitate adaptation to the new environment (Lockwood *et al.*, 2005). Multiple introductions from different sources may create a higher diversity in the invasive range, compared to even the native range and possibly facilitating invasion, such as has been documented for a Cuban lizard (Kolar & Lodge, 2001). This does not appear to play a major role in the spread of *W. auropunctata*, whose expansion beyond the point of introduction was independent of propagule pressure. A lack of correlation between propagule pressure and postintroduction spread is not surprising, since repeated introductions from the same centralized storage system at Rabi-Kounga should not provide substantially higher genetic variation. This is especially true in the case of asexually reproducing organisms such as *W. auropunctata*, where many of the queens

are genetically identical (Fournier *et al.*, 2005a,b). However, these results underscore the need to study factors other than propagule pressure, particularly ecological factors, underlying the spread of *W. auropunctata* from the point of introduction.

Potentially, some of the platforms may have become infested with *W. auropunctata* by dispersal from other nearby platforms either through the flight of winged reproductive castes or by the incremental expansion of a neighbouring invasion, rather than through drilling. Indeed, although this may have happened in some cases, as a rule *W. auropunctata* infestation fronts advance slowly, only on the scale of tens of metres per year (Walsh *et al.*, 2004; A.S.M., unpublished; Walker, 2006). The fact that older platforms, which have had a longer time to receive dispersing *W. auropunctata*, do not show higher levels of infestation also argues against high levels of interplatform dispersal. Ruling out *W. auropunctata* introductions by foresters, who logged the petroleum extraction concession at the time of its establishment as a petroleum extraction concession, is more difficult. However, most of the logging tracks and storage platforms dating to the time of the timber extraction are generally free of *W. auropunctata* and, in many cases, infestations centre around production platforms (A.S.M., unpublished data). Furthermore, logging history should have no effect on the link between the number of wells drilled and *W. auropunctata* establishment.

Our results support the ubiquitous influence of propagule pressure in the establishment of invasive species (Colautti *et al.*, 2006). Recently, Drake & Lodge (2006) have highlighted the need to understand the shape of the dose–response establishment curves for invasive species of special concern in order to generate realistic risk analysis models. Our results make progress towards the generation of such risk analysis models for *W. auropunctata* by justifying and parameterizing a simple Poisson model of establishment. It seems likely that a Poisson process may be used to model the spread of other asexual invasives.

However, propagule pressure does not explain the observed variation in the ability of some but not of other *W. auropunctata* populations to initiate a full-scale invasion of the surrounding habitat. This result is consistent with data from other studies, which have found that propagule pressure, although important, fails to explain variance in invasion success, especially at finer-scale levels (Foxcroft *et al.*, 2004). Given the clonal reproduction of *W. auropunctata* and the fact that most of the introductions arose from a common source, it seems unlikely that genetic factors govern the observed differences in postintroduction spread. It seems more likely, that the postintroduction success of *W. auropunctata* depends on local variation in ecological factors, such as the availability of microsites or competition, which limit the establishment of other invasive species (Eriksson & Ehrlén, 1992; Jongejans *et al.*, 2007). Future studies integrating *W. auropunctata* genetics and ecological variation between sites are necessary to explain the differences in postintroduction variability.

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