ARE SUCCESSFUL COLONIZERS NECESSARILY INVASIVE SPECIES? THE CASE OF THE SO-CALLED "INVADING PARTHENOGENETIC COCKROACH", *PYCNOSCELUS SURINAMENSIS*, IN THE BRAZILIAN ATLANTIC FOREST

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RÉSUMÉ

Les espèces colonisatrices sont potentiellement des espèces invasives. Même dans le cas où elles ne seraient pas encore devenues invasives à proprement parler, elles offrent l'occasion d'étudier des situations analogues aux étapes précédant ou amorçant l'invasion. Leur étude devrait permettre de mieux identifier les caractéristiques écologiques spécifiques qui conduisent à l'invasion biologique, en particulier par comparaison entre invasions réussies et invasions avortées. Ce type d'analyse doit nécessairement compléter la compilation habituelle des caractéristiques des espèces invasives. La « blatte parthénogénétique envahissante » (selon son appellation la plus commune), *Pycnoscelus surinamensis*, a été étudiée dans la région Atlantique du Brésil, afin de déterminer si elle est capable de se disperser des plantations colonisées aux fragments forestiers perturbés et adjacents. *P. surinamensis* a été observée extrêmement rarement dans les fragments forestiers et sa présence n'a pas pu être reliée à son abondance dans les plantations adjacentes mais plutôt à l'activité humaine à l'intérieur du fragment. Cette blatte n'est donc pas une espèce invasive localement mais seulement une espèce colonisatrice efficace. Des observations futures devront déterminer si la cause de cette absence d'invasion peut être recherchée dans une faible capacité de dispersion.

SUMMARY

Successful colonizers are potentially invasive species. They offer the opportunity to study the first steps toward invasions, even if these colonizing species failed until now to become invasive. They should allow the critical characteristics which first permit species to become invasive to be better understood, especially when comparing failed and successful invasions. This kind of analysis complements the listing of all characteristics of invasive species which are supposed to favor invasiveness. The so-called invasive parthenogenetic cockroach, *Pycnoscelus surinamensis*, has been studied in the Atlantic region of Brazil to assess if it is able to spread from colonized plantations to adjacent disturbed forest fragments. *P. surinamensis* is extremely rare in forest fragments and its presence cannot be related to its commonness in adjacent plantations but merely to man's activity inside the fragment. This

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cockroach is only a successful colonizer, not an invasive species. Pending on further observations, we hypothesize that its failure to invade is probably related to a low ability for dispersal.

INTRODUCTION

Biotic invasions are a threat to ecosystems but they also present an opportunity to better understand the way communities are organized and can be conserved (Carey *et al.*, 1996; Joly, 2000; Sol & Lefebvre, 2000). Many studies have attempted to understand how and why invasions occur and several traits supposedly related to invasiveness have been identified, which deal mainly with high population growth and the ability to deal with disturbed habitats and to take advantage of the decrease of enemy pressure (*e.g.*, Rejmánek, 1996; Williamson & Fitter, 1996a; Sax & Brown, 2000). Two interesting ideas have been repeatedly put forth but remain little studied, according to Morrison (2000) and Mack *et al.* (2000). First, invasions often occur after several failed attempts at colonization or introduction (Lodge, 1993; Williamson, 1996; Williamson & Fitter, 1996b). Even if they are very significant, these failures are rarely studied in contrast to successful invasions (Carey *et al.*, 1996). Second, many failed attempts can be related to the inability to invade in spite of successful local colonization (Pyšek, 1997). The same way that invasive species and their non-invasive relatives have been compared (Di Castri, 1990), comparing failed and successful attempts can permit how and why invasions occur to be better understood. In this context, colonization is a first and particular step prior to any invasion, meaning that only some colonies of the possibly invading species are established in a new area (Pyšek, 1997; Morrison, 2000; Mack *et al.*, 2000), as similarly stated in the case of parasitic diseases (Russo, 2000). Invasion occurs only if these colonies are able to produce enough individuals, being able to spread further and further and to establish themselves in the local communities (Williamson, 1996).

In this framework, the colonizers, those species known to establish distant and local colonies frequently (*sensu* Richardson *et al.*, 2000), are especially worthwhile to study. They can be supposed to include many potentially invasive species and they can shed light on the reason why invasions occur or not. Parthenogenesis can be also a related concern in this respect since it is well known to provide organisms with an advantage for increasing their distribution area (Parker & Niklasson, 2000), similar in some aspects to vegetative reproduction in plants (Pyšek, 1997). The parthenogenetic so-called "invading" cockroach *Pycnoscelus surinamensis* is a valuable model for studying the transition between colonization and invasion. This parthenogenetic cockroach is well known as a worldwide but not ubiquitous peridomestic species, establishing itself mainly in small colonies in all places disturbed by man's activities in the tropics, also occurring in greenhouses in temperate areas (Rehn, 1945; Roth & Willis, 1960; Cornwell, 1968; Grandcolas, 1998). The clones were first characterized by Roth & Willis (1961) and Roth (1967, 1974) and their genotypes and fitness were further studied by Parker (1984), Niklasson & Parker (1994) and Parker & Niklasson (1995) who especially analyzed if some of these clones show genotypic characteristics which could explain their distribution wider than in the relative sexual species *P. indicus* originating from the Indo Malayan region. In addition, Grandcolas *et al.* (1996) recently used field data to question if *P. surinamensis* is actually able to spread from established colonies to invade wide areas and if the use of the terms "colonizing" and especially "invading" is appropriate.

This work is aimed at studying if *P. surinamensis* colonies are able to invade any forested area in the context of forest fragments of the Tableland Atlantic forest in Espírito Santo, Brazil. Forest fragments are known to be not only prone to species extinction but also predisposed to invasion by exotic species and by species from open areas, that can lead to dramatic effects for local fauna (Laurance *et al.,* 1997). Forest fragments are much more accessible to human penetration than larger continuous forested areas, and man's activities inside forest fragments can not only disturb natural communities but also transport some species that usually would not be able to reach these natural areas.

The data sets of previous studies indicated that *P. surinamensis* was widespread in planted areas surrounding forest remnants in this region and probably introduced in plantations with mould (Pellens & Garay, 1999a, 1999b). For the present study, we sampled adjacent forest remnants and planted areas to determine whether the presence of colonies of *P. surinamensis* in plantations is predicting the colonization of the adjacent forest remnants by *P. surinamensis.* Depending on the generality of this colonization, *P. surinamensis* could be considered as invasive or not. Since invasions often involve substitution or impact on the local fauna, an invasion of *P. surinamensis* in forest fragments could represent a risk for the fragment's fauna and should be thought as detrimental to the conservation of fragments biodiversity, in the already threatened Atlantic region where more than 90 % of the forest has already been destroyed (SOS Mata Atlântica/INPE/ISA, 1998).

MATERIALS AND METHODS

The present study was carried out between October 1999 and November 2000, in Linhares and Sooretama, Espírito Santo, Brazil. In these two municipalities are, respectively, the Natural Reserve of Companhia Vale do Rio Doce (NRCVRD), and the Biological Reserve of Sooretama (BRS), which taken together with some private properties linking them cover a territory of 47 563 ha of continuous forest, the biggest remnant of Atlantic forest of Espírito Santo (SOS Mata Atlântica/INPE/ISA, 1998). Although there are some other types of vegetation, the Tableland forest is the dominant physiognomy in the region (IBDF/FBCN, 1981; Jesus, 1987).

In addition to this large forest, five forest fragments of various sizes from less than 1ha to up to 100 ha were studied, mostly on private property. All these remnants, as well as the reserves, are imbedded in an agricultural landscape dominated by coffee plantations, notably *Coffea robusta*, but also with plantations of *Eucalyptus grandis*, *Hevea brasiliensis*, *Acacia mangium* as well as pasture. Most of these fragments are frequently visited and used by local populations in many ways. Hunting, trapping, wood extraction, specific plant extraction are commonly observed and weeds occasionally develop large populations in the understory. Their vegetation structure is also irregular, very disturbed with large gaps and discontinuous canopies.

P. surinamensis was studied in every site and in the plantations immediately adjacent to them (Table I). In the forest fragments, our observations were never done close to the edge in order to prevent any confusion between colonization/invasion and a possible edge effect.

TABLE I

Abundance and presence of P. surinamensis *in forest fragments and adjacent plantations, respectively. The abundance is estimated relative to the sampling effort in each place. In plantations,* P. *surinamensis is estimated either occasionally present (x) or abundant (+) (see Materials and methods). The characteristics of the fragments are given in the table of appendix 1.*

Study site	Total numbers of Cockroach specimens	*P. surinamensis* abundance in fragments	*P. surinamensis* presence in adjacent plantation
Natural Reserve of Linhares	836	0	×
Biological Reserve of Sooretama	1 609	0	+/×
Bioparque	758	0.0132	+
MEME	125	0	+
Fazenda Pasto Novo	356	0	+
Sítio São Pedro	1 003	0.0299	+
Juncado	4	0.25	0

Sampling was conducted through direct observation and captures by looking and digging in the litter and humus mainly at night (Schal & Bell, 1986; Grandcolas, 1994a,b), and complemented during the day. Visual night sampling effort represents 150 hours of search and averages 21 h 30 mn per site. The presence and abundance of *P. surinamensis* in the fragments was estimated relative to the entire sample of cockroaches for a given search period (Table I). *P. surinamensis* was considered as abundant in plantations when found in more than 5 different places distant from at least 10 meters in one hour of search and occasional only when found in less places. The precise locations where *P. surinamensis* was found in forest were characterized from the point of view of human activity on a all or nothing basis. It was verified that the *Pycnoscelus* cockroaches were female and reproduced without fecundation, showing that the local populations belonged to parthenogenetic clones (*P. surinamensis*, according to Roth, 1967; Parker *et al.*, 1977). Voucher specimens were deposited in the collections of Museu Nacional do Rio de Janeiro and in Muséum national d'Histoire naturelle de Paris. A laboratory culture issuing from these colonies is maintained to permit any future genetic studies.

RESULTS

P. surinamensis was very abundant in every but one planted area adjacent to the forest (Table 1). Its relative abundance in planted areas averaged 72 % of cockroach specimens, making it the first species in terms of abundance ranks. Except in the gardens of the reserves where its presence was occasional (one individual captured at each site), it occurred very commonly at the bases of planted trees and bushes, always beneath the leaf litter, half burrowed in the dusty substratum, rather sandy than clayey. Coffee bushes as well as *Acacia* or

Eucalyptus trees sheltered small colonies in the litter at their bases where several individuals were always found together. Only one coffee plantation was observed not to harbour colonies of *P. surinamensis* although it looked similar to every other visited plantation. The parts of coffee plantations with very young plants (lower than 0.30 m, without significant leaf litter at their bases) or cleared (with only bare ground) did not harbour colonies of *P. surinamensis.*

Among eight forest areas, only three were reported to harbour *P. surinamensis.* These three sites were very small to small fragments and in all cases *P. surinamensis* was recorded extremely rarely, each individual found was a unique and isolated specimen not representative of a colony (Table I), making it one of the last species in terms of abundance ranks. Only one of the fragments harbouring *P. surinamensis* ("Juncado", Table I) was surrounded by a coffee plantation that was not colonized.

The relative abundance of the cockroach is inversely related to the area of the fragment (Spearman correlation coefficient, $R = -0.906$, $P < 0.01$) which is itself highly correlated with perimeter length ($R = 1.000$, $P < 0.01$). The estimate of cockroach abundance is not biased by the sampling effort as shown by the lack of correlation between sample size and *P. surinamensis* abundance ($R = -0.206$, $P > 0.20$). Inside each concerned forest fragment, the cockroach was found in small areas with strong indications of man's activity, either present (permanent mammal trapping, cattle raising) or recent past (area of wood cutting and converting) (Table II).

DISCUSSION

The parthenogenetic *P. surinamensis* is very common and abundant throughout the plantations of the study area, namely coffee but also *Acacia* and *Eucalyptus* plantations. This is in agreement with previous knowledge about this cockroach, which was considered as a common, although not ubiquitous, peridomestic species in many different biota from savannas to forests, little or very disturbed, and also in man-made places like greenhouses (Roth & Willis, 1960; Grandcolas *et al.,* 1996). This commonness can be related to parthenogenesis, given that any isolated individual can found a colony if it is imported to a suitable site (Roth, 1967).

This situation highly contrasts with the rarity or absence of *P. surinamensis* in forests and forest fragments. Because the cockroach is not present in most fragments or forests surrounded by colonized plantations, this indicates that it does not spread actively to areas adjacent to its colonies. It cannot be confused with a mere low survival after spreading in forests. In this last case, we should have found at least numbers of individuals, if not even healthy colonies. The presence of this cockroach in smaller fragments can be interpreted in two ways. First, according to previous studies, smaller and elongated forest fragments are relatively more prone to colonizations/invasions because they are easier to penetrate, present relatively more edge, and are generally more disturbed (Laurance *et al.*, 1997). If *P. surinamensis* spreads by itself, it could be more common in fragments smaller or presenting more edge. Second, because smaller fragments are easier to penetrate, they are also more prone to introductions by man. This second interpretation seems more plausible in the present case, given the highest abundance of *P. surinamensis* in the smallest and very disturbed fragment which is also the only fragment

TABLE II

Characteristics of forest fragments studied in Espírito Santo, Brazil.

Study site	Size (ha)/ Perimeter (km)	Geographical Coordinates	Kind of disturbance in the *P. surinamensis* spot	Adjacent plantation
Natural Reserve of Linhares	21.787/133.74[a]	S, 19° 08' 16.5" W 40° 03' 37"	—	Garden and fruiting trees
Biological Reserve of Sooretama	26.000/[b]	S, 19° 03' 20.7" W 40° 08' 49.0"	—	*Coffea robusta*/Garden
Bioparque	32.7/4.1[b]	S, 19° 11' 20.2" W 40° 06' 54.3"	Wood cutting and converting	*Eucalyptus grandis*/Garden
MEME	30/4.5[a]	S, 19° 08' 15.8" W 40° 05' 04.4"	—	mixed (*Acacia mangium, Eucalyptus grandis, Hevea brasiliensis, Coffea robusta*)
Fazenda Pasto Novo	66,7/4.9[b]	S, 19° 05' 04.2" W 40° 10' 39.8"	—	*Coffea robusta*
Sítio São Pedro	2,4/0.7[b]	S, 19° 09' 14.9" W 40° 11' 34.3"	Mammal trapping	*Coffea robusta*
Juncado	0.25/0.1	S, 19° 07' 48.8" W 40° 09' 19.1"	Cattle hosting	*Coffea robusta*

[a] unpublished data from Fernando Vieira Agarez, UFRJ; [b] data provided by Renato de Jesus, from NRCVRD.

surrounded by a non-colonized coffee plantation ("Juncado", Table I). In addition, the few individuals of *P. surinamensis* sampled in the forest fragments were all found in small areas with strong indications of human activity, suggesting that they have been brought there with human visits. They were always captured as isolated individuals, showing that they did not establish colonies.

All this evidence shows that *P. surinamensis* is unable to spread very efficiently by itself, from colonies in plantations to disturbed forest fragments or large forests but is very plausibly introduced by man in some places very often used and disturbed. In the same way, the commonness of *P. surinamensis* in plantations may be explained by the general introduction by man with the mould dressing of plants. Coffee and other plantations are regularly totally planted again after being cleared, leaving the bare ground exposed and remaining totally inappropriate for any cockroach survival during months. Both repeated introductions and parthenogenesis can explain commonness in plantations without hypothesizing *ad hoc* repeated dispersal events.

Another possibility could be that *P. surinamensis* actually spreads but is eliminated by interactions with local forest species. This last scenario is however less probable since it implies that we should have found some individuals of *P. surinamensis* especially in vulnerable fragments rather than none or extremely rare individuals. In addition, the few individuals found in forest fragments have never been found together with another insect or cockroach species sharing the same habitat or with potential predators.

According to preliminary studies in several sites in Africa, America and Oceania, we previously stated that sites colonized by *P. surinamensis* were never widely colonized areas but only small, isolated and man-disturbed areas (Grandcolas *et al.,* 1996). The present observations in the Atlantic region of Espírito Santo in Brazil corroborate this statement. Even if *P. surinamensis* is present in many colonies surrounding a disturbed site, it does not further colonize this site by itself, thus strongly implying a low dispersal ability and a history of repeated introductions, as suggested by Niklasson & Parker (1996).

The story of *P. surinamensis* is not one of successful invasion, in spite of its worldwide peridomestic presence. This parthenogenetic cockroach is obviously able to colonize many places where it is introduced, a first pre-requisite for invasion (Morrison, 2000), but it is clearly unable to spread by itself from a colonized to an empty site. The existing colonies of this cockroach are thus not able either to disperse, to grow, or even to establish themselves in some local communities. In this respect, *P. surinamensis* could be said "naturalized", according to the term recommended for plants by Richardson *et al.* (2000). Additional field studies should document which limitation(s) *P. surinamensis* actually have. As a matter of conjecture, a lack of dispersal ability is a possible explanation because the two other limitations seems less plausible. First, the parthenogenetic colonies should have very high growth rates, given the remarkable intrinsic characteristics of every clone in terms of development kinetics and resistance to physical stress (Roth, 1974; Niklasson & Parker, 1994). Second, establishing itself in local communities is a step occurring in plantations as well as in forest fragments and so far it does not entirely explain so much differential success between plantations and forests. The cockroach communities in both cases do not include species having the same habitat and life habits.

These results stress how much species must have peculiar characteristics to be truly invasive. They do need not only to be good at surviving, growing (Rejmánek, 2000; Sol & Lefebvre, 2000; Sax & Brown, 2000), and competing (Lubin, 1984; Lodge, 1993; Callaway & Aschehoug, 2000), but also at dispersing themselves over long distances (Wilson & Lee, 1989; Mack *et al.*, 2000). As suggested by recent demographic and dispersal models, this is the "long-distance component [of dispersal] that governs the invasion speed" (Neubert & Caswell, 2000). The case of *P. surinamensis* could suggest that this "long-distance component" cannot be replaced only by repeated introductions by man. This should be the matter of further observations in the field.

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