

# Impact of human activity on the distribution of native and non-native cockroach species (Dictyoptera) in La Réunion and Mayotte

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## Abstract

Establishment of non-native species and human-driven alteration of habitats are major causes of the decline of native faunas. Interference between native and non-native cockroach species was evaluated here by comparing their distribution areas in two oceanic islands: Mayotte and La Réunion. A factorial correspondence analysis showed that their presence is related to environmental parameters among which human activity, humidity and altitude are the three most important. Human activity and humidity favour establishment and development of non-native species, whereas altitude limits their presence. Non-native species form guilds (up to seven species). Their distribution areas overlap and illustrate their colonizing capacities. On the contrary, distribution areas of native species never overlap, although some co-occur with non-native species. Native species are more endangered when they are established in cultivated areas than when they are in protected natural areas.

**Keywords:** distribution area, native/non-native cockroaches, invasion pressure, La Réunion, Mayotte

## Introduction

The most important conservation problems concerning island insects are the continual introduction of non-native species of plants and animals (Howarth & Ramsay, 1991) and the alteration of habitats and communities resulting from human activities (Pyle *et al.*, 1981; New, 1984). Non-native species occur outside their natural ranges and dispersal potential, i.e. they have not previously occurred there, or their dispersal into the area has been mediated by humans (IUCN, 2000). Sizes of distribution areas and types of habitats occupied by non-native species illustrate their level of establishment in recently colonized environments and give an indication of their colonizing capacities in various types of habitats. The presence (arrival) of

most non-native species has only minor consequences (Williamson, 1996) and their effects may remain unnoticed in natural areas and in unmonitored habitats if not specifically sought (Samways, 1994). However, some species threaten the survival of local native species and become invasive in that they displace formerly established native species from their habitats (Reitz & Trumble, 2002). Competition between native and invasive species often leads to community disassembling and severe asymmetric competitive displacement of native species has been observed in ants (Human & Gordon, 1996; Holway *et al.*, 2001; Sanders *et al.*, 2003). The conservation of native species is threatened by changes in ecological parameters of their habitat and by the reduction of their distribution areas. The fact that more island species than continental species are listed as endangered species (Vitousek, 2002) indicates that islands are particularly vulnerable to invasions and more likely to suffer loss of biodiversity because geographical distribution of species is limited and their populations are reduced in size. The threat is more important on oceanic

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islands because their species evolved in isolation with low functional redundancy (Moller, 1996; Gillespie & Roderick, 2002; O'Dowd *et al.*, 2003).

Taxonomic and ecological information concerning many native and non-native insect species is lacking for two oceanic islands, La Réunion and Mayotte (DOM-TOM France), located in the Indian Ocean. The sub-order Blattaria (Dictyoptera) is particularly poorly known. This group includes at least 3000 species with some extreme examples of distributional ranges, from worldwide to endemic or locally distributed species. Cockroach studies have focused mainly on the 25 to 30 species that live in urban areas (Cornwell, 1968). Although inventories of cockroach species have been established for many parts of the world (Princis, 1951, 1963, 1964, 1969a,b; Roth, 1985, 1989, 1990, 1991a,b, 1996, 1998, 1999, 2000), very few precise descriptions of their natural habitats and their distribution areas exist.

The aim of this study was to map the distribution areas of all native and non-native cockroach species in Mayotte and La Réunion. As non-native cockroach species might be a threat for native species, special focus was given to species overlap. Numbers of non-native versus native species for each prospected site were evaluated in relation to human disturbance levels.

## Materials and methods

### *Study sites*

Two oceanic islands in the Indian Ocean, Mayotte and La Réunion (DOM-TOM, France) were surveyed. They have never been attached to a continent, but were formed by submarine volcanoes. Therefore, species present there have either immigrated or been introduced through maritime exchanges. Mayotte (13°S, 45°E) is one of the Comoro islands at the northern end of the Mozambican pass. La Réunion (21°06'S, 55°32'E) is part of the Mascarene archipelago. Mayotte, formed by two main islands, Petite Terre and Grande Terre, measures 374 km<sup>2</sup> and culminates at 600 m asl. La Réunion is larger (2512 km<sup>2</sup>) and is characterized by a more rugged surface that culminates at 3096 m asl. The climate of these two islands is tropical, with one hot wet season from November to April and one dry, cooler season from May to October. Average temperatures are higher in Mayotte (25.6°C) than in La Réunion (20°C). Annual rainfall reaches 1500 mm in Mayotte, whereas in La Réunion it varies from 525 mm in the west to 11000 mm in the east. Rainfall occurred mainly during a 3-month period (from December to February). Microclimates on these islands vary along an east-west axis and with altitude. These climatic variations are particularly important in La Réunion where a temperate zone can be found in altitude.

### *Types of habitat*

The prospected sites were chosen in order to characterize cockroach habitats in relation to human activity and were divided into three categories: natural areas, degraded forest and cultivated lands.

1. Three different types of natural areas with very low human influence were sampled:

- (i) Natural forests (mainly located in the centre of the islands) and replanted forests.

- (ii) Humid water edges, near ponds or rivers. This type of habitat was prospected only in La Réunion; borders of rivers and ponds were very dry in Mayotte during the survey.

- (iii) Decaying dead trees with loose zones under their bark. Decaying trees, located in natural forests, in degraded forests and in abandoned ylang-ylang fields were investigated only in Mayotte; none were found in La Réunion.

2. Very degraded forests that included a few tall trees, fallows with herbaceous and shrub zones used as pasture, were prospected in both islands. These habitats are characterized by frequent human presence disturbing habitat structure and resources.

3. Cultivated lands maintained by human activity were surveyed in both islands. Fields in Mayotte cover from 0.25 to 2 ha and form a mosaic with natural or degraded forest areas (Bacheré, 2001). The main cultivated crops are: ylang-ylang, manioc, pigeon pea, banana, and banana intermingled with manioc or pigeon pea. The main cultivated crop in La Réunion is sugarcane, and the mean surface of fields is 5.4 ha, although some fields can cover more than 50 ha (Martignac & Pariente, 2003).

### *Sampling method*

Surveys were conducted in March 2001 in La Réunion, and in June 2001 in Mayotte. Cockroaches were found in the leaf litter on the ground. Units of 1 m<sup>2</sup> were intensively sampled by examining and removing all leaf litter and by scratching the ground within the 1 m<sup>2</sup> unit. Trunks were sampled by taking off the bark and examining the loose zones inside the trunk. As sizes of tree trunks were homogenous, each trunk was considered as one unit. This non-destructive method allows evaluation of the specific richness of each site without removing animals from their habitat and without biasing estimates due to interspecific locomotor differences as with pitfalls (Andersen, 1991). All species present were recorded and counted for each surface unit. Ten units were surveyed at each site, 112 sites were surveyed in Mayotte, 61 in La Réunion (fig. 1a). Sites were chosen in order to cover the entire surface of the islands and to represent all types of habitats.

Each site was characterized by several environmental parameters classically measured and known to influence insect species distribution (Wolda, 1983). Sites were described in relation to the following.

1. A gradient of anthropization: from natural habitats to degraded habitats and to cultivated lands.

2. A gradient of altitude: from 0 to 100 m, from 100 to 250 m and above 250 m asl.

3. A gradient of humidity: irrigated fields and water edges were considered humid habitats, while all other sites were called dry habitats.

4. Depth of litter: sites with litter less than 10 cm deep were categorized as shallow litter sites, sites with litter more than 11 cm deep were categorized as deep litter sites.

5. Constancy of vegetation: manioc, sugarcane, and decaying trees were categorized as non-constant, all other types of vegetation were considered constant.

6. Habitat closure: banana fields, ylang-ylang plantations, humid water edges and most degraded forests

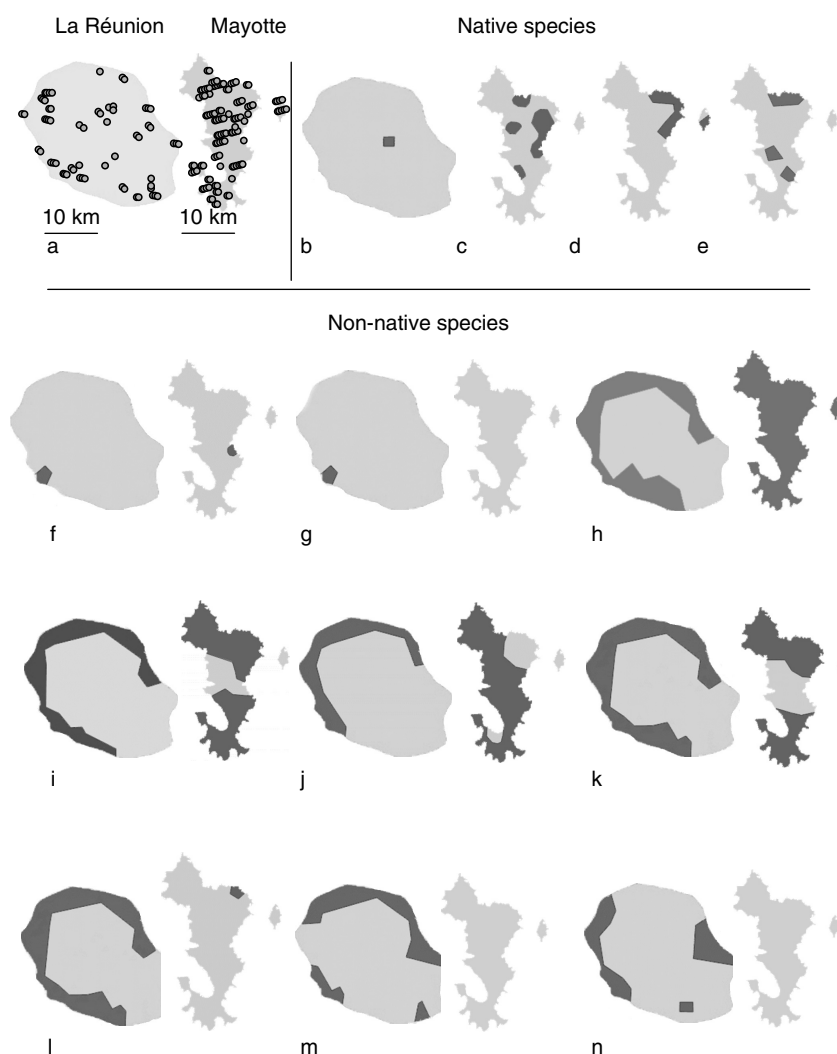


Fig. 1. Location of sites surveyed in La Réunion and in Mayotte and distribution areas of each species a, Survey sites (one dot = one site). b–e, Distribution areas of native species (■, presence; □, absence): b, *Chorisoblatta chopardi*; c, *Ylangella truncata*; d, *Mayottella dimorpha*; e, *Chorisoblatta denticulara*. f–n, Distribution areas of non-native species (■, presence; □, absence): f, *Symploce pallens*; g, *Neostylopyga rhombifolia*; h, *Lobopterella dimidiatipes*; i, *Blattella lituricollis*; j, *Pycnoscelus surinamensis*; k, *Balta longicercata*; l, *Blattella biligata*; m, *Margattea nimbata nimbata*; n, *Scalida latiusvittata*.

constitute open environments, whereas forests, sugarcane fields and decaying trees were considered closed environments.

A factorial correspondence analysis (FCA) computed species diversity in relation to environmental parameters at each site with ADE4 software (Thioulouse *et al.*, 1997). Kruskal-Wallis (KW) and Mann-Whitney (MW) tests were performed.

### Results

Thirteen different cockroach species were collected in both islands: Mayotte and La Réunion. Four of them were endemic (found nowhere else in the world): three were found in Mayotte: *Chorisoblatta denticulara* Roth, *Mayottella dimorpha* Roth and *Ylangella truncata* Roth (Roth & Rivault,

2002), and one in La Réunion: *Chorisoblatta chopardi* Princis (Chopard, 1957). Nine species were non-native: *Scalida latiusvittata* (Brunner), *Margattea nimbata nimbata* Shelford, *Neostylopyga rhombifolia* (Stoll), *Blattella lituricollis* (Walker), *Blattella biligata* (Walker), *Balta longicercata* (Bolivar), *Lobopterella dimidiatipes* (Bolivar), *Pycnoscelus surinamensis* (Linnaeus) and *Symploce pallens* (Stephen).

#### Species distribution areas and selected habitats

A factorial correspondence analysis (FCA) analysed the distribution of each cockroach species on relation to habitat parameters. The FCA diagram describes the distribution of the different species on each island in relation to environmental factors (fig. 2). The first three axes accounted for 76% of the total inertia. The factors that contributed the most to the first two axes were: anthropization and humidity,

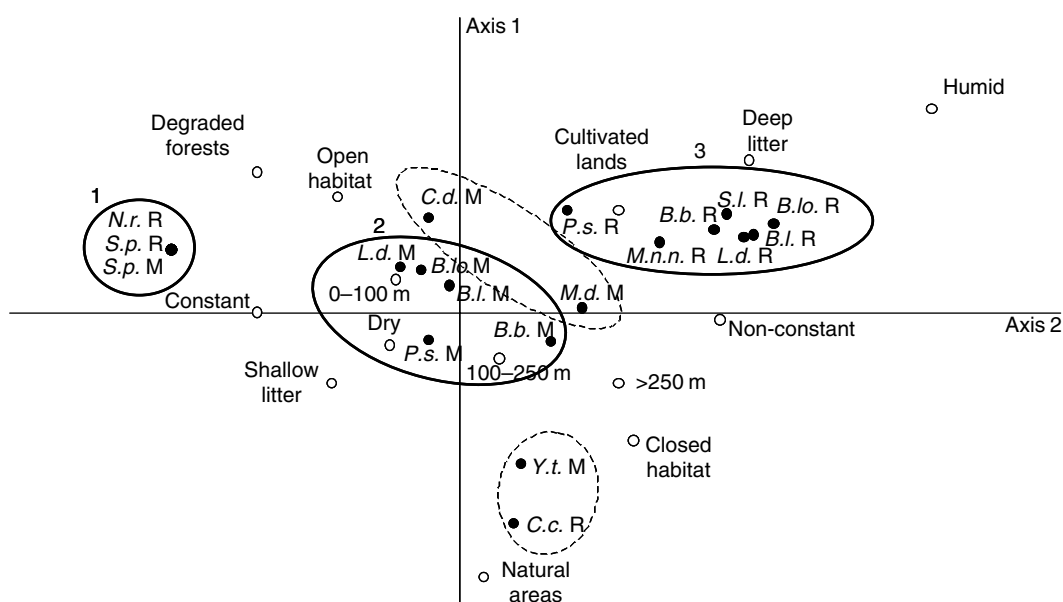


Fig. 2. Factorial correspondence analysis (FCA) diagram (axes 1 and 2) of the distribution of each species in relation to environmental parameters. ○, environmental variables; ●, cockroach species; *L.d.*, *Lobopterella dimidiatipes*; *B.b.*, *Blattella biligata*; *B.l.*, *Blattella lituricollis*; *B.lo.*, *Balta longicercata*; *S.l.*, *Scalida latiusvittata*; *M.n.n.*, *Margattea nimbata nimbata*; *P.s.*, *Pycnoscelus surinamensis*; *S.p.*, *Symploce pallens*; *N.r.*, *Neostylopyga rhombifolia*; *C.c.*, *Chorisoblatta chopardi*; *M.d.*, *Mayottella dimorpha*; *C.d.*, *Chorisoblatta denticulara*; *Y.t.*, *Ylangella truncata*. M (Mayotte) and R (La Réunion) following the species names refer to the island where they were collected. Groups of non-native species are enclosed by a solid line and groups of native species by a dashed line.

whereas altitude contributed the most to the formation of the third axis. Depth of litter, constancy of vegetation and habitat closure contributed less to the formation of the FCA diagram.

#### Native species

The FCA diagram (axes 1 and 2) separated the four native species into two groups (fig. 2). *Chorisoblatta chopardi* (La Réunion) and *Y. truncata* (Mayotte) were well isolated from all the other species. They are present only in natural areas. *Mayottella dimorpha* and *C. denticulara* (Mayotte) are found only in cultivated areas.

*Chorisoblatta chopardi* was the only native species collected in La Réunion. The distribution area of this species is limited to the humid high-altitude Bébour forest (fig. 1b; table 1). Its presence suggests that it is well adapted to high altitudes (1300 to 1500 masl) and low temperatures. Individuals occupy holes in tree trunks and stumps, indicating that it is a forest species. Its distribution area has changed since 1957 as it was initially identified in the Bélouve forest (Chopard, 1957), but none were found there during our survey (2001). No other cockroach species were collected in the Bébour forest.

*Ylangella truncata* is largely distributed over the central part of Grande Terre (Mayotte), but it is absent from Petite Terre (fig. 1c). This forest species lives in large decaying tree trunks (table 1) that form closed patchy microhabitats and is not specific to any particular tree species, but it depends on the level of decay of the trees. *Ylangella truncata* was found either alone, on half of the sites, or with *P. surinamensis*, on the other sites. When both species were found in the same tree, *Y. truncata* was always more

abundant and the two species were separated from each other in the tree trunk.

The distribution area of *M. dimorpha* is limited to a few sites, exclusively on cultivated lands in the north east of Grande Terre and in Petite Terre (fig. 1d). It was recorded only in a few pigeon pea and manioc cultivated fields (table 1). Individuals were found in the leaf litter near plant stalks. Cultivated areas with shallow litter seem to form a favourable habitat for this species. At these sites, *M. dimorpha* was always associated with five non-native species: *L. dimidiatipes*, *B. longicercata*, *B. lituricollis*, *B. biligata* and/ or *P. surinamensis*.

*Chorisoblatta denticulara* was found in three separated zones: one in the north and two in the centre of Grande Terre (fig. 1e). It was absent from Petite Terre. This species was exclusively recorded in banana and mixed banana fields (table 1). Individuals hide between the leaves and the trunk of banana plants. *Chorisoblatta denticulara* was always collected on sites where three non-native species, *L. dimidiatipes*, *B. longicercata* and *B. lituricollis* were present.

#### Non-native species

The FCA diagram (axes 1 and 2) separated the non-native species into three groups (fig. 2). Species (*N. rhombifolia* and *S. pallens*) in group 1 were well separated from all the other species. They were present mainly in degraded areas. Species in the second and third groups were present in cultivated areas. The main environmental parameters that separated these last two groups were humidity and depth of litter (group 2, dry and shallow litter; group 3, humid and deep litter). Group 2 species were present in Mayotte and

Table 1. Numbers of sites occupied by each species in relation to type of habitat in La Réunion and in Mayotte.

	Sugarcane	Banana	Pigeon pea	Mixed banana	Manioc	Ylang- ylang	Degraded forest	Water edges	Forest	Decaying trees
La Réunion										
<i>Lobopterella dimidiatipes</i>	18	0					0	0	0	
<i>Blattella biligata</i>	17	0					2	0	0	
<i>Blattella lituricollis</i>	11	0					0	1	0	
<i>Balta longicercata</i>	18	0					0	1	0	
<i>Scalida latiusvittata</i>	7	0					1	2	0	
<i>Margattea nimbata nimbata</i>	11	1					1	1	0	
<i>Pycnoscelus surinamensis</i>	6	0					4	1	0	
<i>Symploce pallens</i>	0	0					1	0	0	
<i>Chorisoblatia chopardi</i>	0	0					0	0	1	
<i>Neostylopyga rhombifolia</i>	0	0					4	0	0	
Total	29	2					12	3	15	
Mayotte										
<i>Lobopterella dimidiatipes</i>		14	3	7	13	2	13		2	0
<i>Blattella biligata</i>		0	0	0	1	0	0		0	0
<i>Blattella lituricollis</i>		5	3	3	8	1	6		0	0
<i>Balta longicercata</i>		2	0	2	5	1	2		0	0
<i>Pycnoscelus surinamensis</i>		4	1	1	0	1	3			9
<i>Symploce pallens</i>		0	0	0	0	0	1		0	0
<i>Mayottella dimorpha</i>		0	1	0	5	0	0		0	0
<i>Chorisoblatia denticulara</i>		2	0	2	4	0	0		0	0
<i>Ylangella truncata</i>		0	0	0	0	0	0		0	8
Total		18	4	10	19	3	23		17	18

Total: total numbers of sites prospected for each type of habitat, in La Réunion and in Mayotte.

group 3 species were present in La Réunion. The fact that some species belong to the two groups means that these species are able to settle in habitats with different environmental parameters (fig. 2).

*Symploce pallens* (group 1) was collected only once in Mayotte and in La Réunion, in degraded forests (table 1; fig. 1f). Its establishment seemed to be related to human activity.

*Neostylopyga rhombifolia* (group 1) was found only once in degraded forests in La Réunion (table 1; fig. 1g). The presence of this peridomestic species in degraded forests (found in dumps near habitations) seemed to be related to human presence. The species was already present in urban areas in 1957 (Chopard, 1957).

*Lobopterella dimidiatipes*, *B. lituricollis*, *P. surinamensis* and *B. longicercata*, belonging to groups 2 and 3, are widely distributed and well established in both islands (fig. 1h–k). In La Réunion, they followed the distribution of sugarcane fields that cover the low altitude border of the island. These species are present in cultivated fields and in degraded forests in Mayotte. *Pycnoscelus surinamensis* is also present in decaying trees. The fact that these four species belong to both groups 2 and 3 of the FCA diagram, can be explained by their large distribution areas in both islands and their wide tolerance to environmental parameters.

*Blattella biligata* also belongs to both group 2 and group 3, and is well established in sugarcane fields in La Réunion, but was collected only once in Mayotte (table 1, fig. 1l). We assume that its tolerance to environmental parameters is similar to that of the previous four species.

*Margattea nimbata nimbata* and *S. latiusvittata*, present only in group 3, have a narrower tolerance to environmental parameters. Well established in sugarcane fields, they are present only in La Réunion (table 1, fig. 3m–n). Their

preference for humid habitats might explain their absence from Mayotte where cultivated areas are not irrigated and undergo important dry periods.

#### Invasion pressure

The success of non-native cockroach species was studied in relation to the three most important parameters: anthropization, humidity and altitude.

#### Human activity

Cultivated lands appear to be more exposed to invasion by cockroach species than less disturbed environments (fig. 3a). The mean number of non-native cockroach species present at a site varied in relation to type of habitat. On cultivated lands, the number of species was significantly higher than for other types of habitat, both in Mayotte (KW,  $P < 0.0001$ ) and in La Réunion (KW,  $P < 0.0001$ ). The most suitable habitats for non-native species in La Réunion were sugarcane fields ( $3 \pm 0.5$  species per site) and water edges ( $2 \pm 0.6$  species per site). In Mayotte, cultivated lands (manioc, banana, mixed banana, pigeon pea and ylang-ylang) have the highest invasion pressure (about 1.5 species per site). Invasion pressure was intermediate in degraded forests and was similar in the two islands (about 1.1 species per site). In decaying trees in Mayotte, only 0.5 non-native species were recorded per site. The habitats the least exposed to cockroach invasions were natural forests: 0.12 species per site were recorded in Mayotte and 0 species per site in La Réunion (KW,  $P < 0.0001$ ).

The number of non-native species per site was significantly higher in La Réunion ( $1.75 \pm 0.28$ ) than in Mayotte ( $1.15 \pm 0.13$ ) (KW,  $P < 0.0001$ ). This difference is due in particular to the types of cultivated lands that seem to be



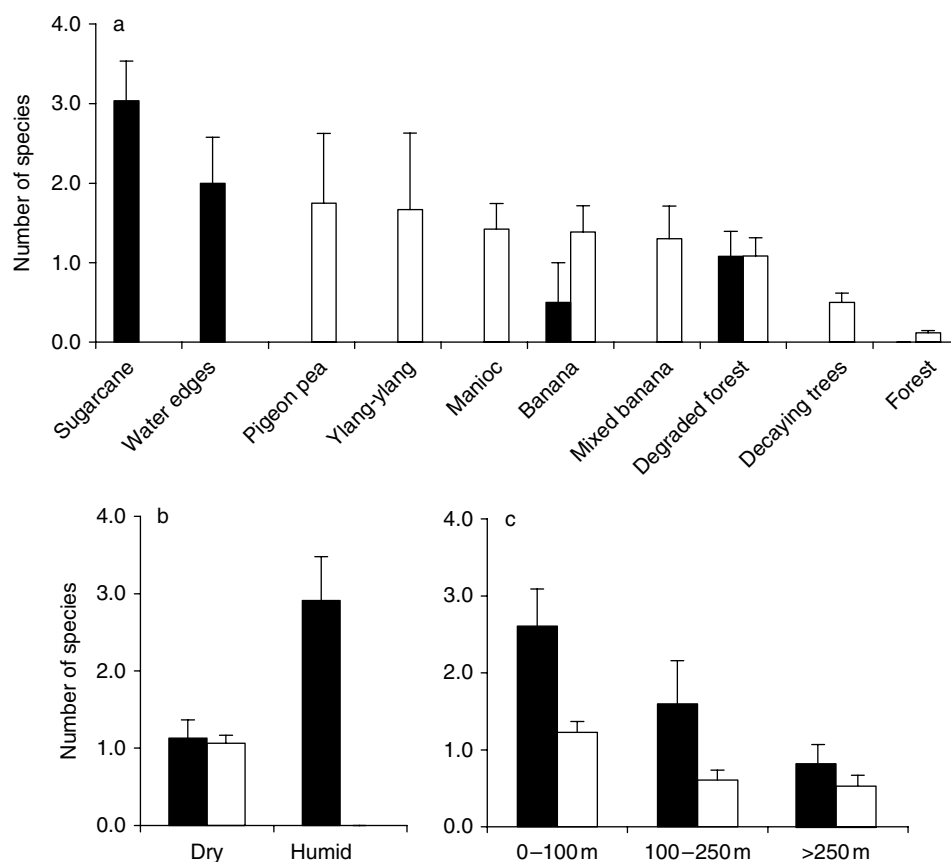


Fig. 3. Number of non-native species per site (mean  $\pm$  SE) in La Réunion (black bars) and in Mayotte (white bars) in relation to type of environment (a), humidity (b) and altitude (c).

more favourable for non-native cockroaches in La Réunion than in Mayotte.

#### Humidity

Humid sites were more exposed to invasion than dry sites (fig. 3b). The mean numbers of non-native species per site were  $2.9 \pm 0.6$  for humid sites, but only  $1.2 \pm 0.1$  for dry sites (MW,  $P=0.022$ ). No differences were evidenced between the numbers of non-native species in irrigated fields and on humid water edges (MW,  $P=0.33$ ).

#### Altitude

Sites at high altitude were less exposed to invasion than sites located near sea level (fig. 3c). The mean numbers of non-native species per site declined significantly when altitude increased both in Mayotte (KW,  $P<0.0001$ ) and in La Réunion (KW,  $P=0.018$ ). Between 0 and 100 m asl, the mean numbers of non-native species recorded per site were 2.6 in La Réunion and 1.2 in Mayotte, whereas above 250 m only 0.8 non-native species per site were recorded in La Réunion and 0.53 in Mayotte. *Balta longicercata* and *L. dimidiatipes* were the only species that were found up to 900 m asl in sugarcane fields in La Réunion. Non-native species were mainly located at very low altitudes, below 100 m asl (fig. 3c).

#### Distribution overlap between native and non-native species

The mean numbers of co-occurring non-native species and of co-occurring native species per site were calculated for each species in La Réunion and in Mayotte (table 2). No overlaps among native species were observed. The presence of one native species excluded the presence of another native species. Although *Mayottella dimorpha* and *C. denticulara* were both established in cultivated lands, they were never found together on the same site. Nevertheless, *M. dimorpha* was present with, on average, 2.3 non-native species, and *C. denticulara* with 1.6 non-native species. *Ylangella truncata* co-occurred with on average 0.5 non-native species and *C. chopardi* was always alone.

Non-native cockroach species form multi-species assemblages or guilds particularly on cultivated lands. In La Réunion, mean numbers of non-native species per site were high and species were rarely found alone (table 2). The seven species found the most frequently have similar co-occurrence rates (KW,  $P=0.64$ ) (table 2). Co-occurrence among the four species found the most frequently in Mayotte varied with species (KW,  $P<0.001$ ). Two species (*B. longicercata* and *B. lituricollis*) had high rates of co-occurrence, whereas the two others (*L. dimidiatipes* and *P. surinamensis*) had low co-occurrence rates, as they were often found alone.

Table 2. Co-occurrence of native and non-native cockroach species in La Réunion and Mayotte. Numbers of co-occurring non-native species per site and numbers of co-occurring native species per site (mean  $\pm$  SE) for each species, in both islands.

	Non-native	Native	N
<b>La Réunion</b>			
<i>Chorisoblatla chopardi</i>	0	0	1
<i>Blattella biligata</i>	3.11 $\pm$ 0.49	0	19
<i>Balta longicercata</i>	2.89 $\pm$ 0.52	0	19
<i>Lobopterella dimidiatipes</i>	3.33 $\pm$ 0.48	0	18
<i>Margattea nimbata nimbata</i>	3.46 $\pm$ 0.68	0	14
<i>Blattella lituricollis</i>	4.25 $\pm$ 0.51	0	12
<i>Pycnoscelus surinamensis</i>	3.73 $\pm$ 0.75	0	11
<i>Scalida latiuscittata</i>	4.00 $\pm$ 0.77	0	10
<i>Neostylopyga rhombifolia</i>	1.25 $\pm$ 0.48	0	4
<i>Symploce pallens</i>	1.00 $\pm$ 1.00	0	1
Mean	1.80 $\pm$ 0.27	0.02 $\pm$ 0.02	61
<b>Mayotte</b>			
<i>Ylangella truncata</i>	0.50 $\pm$ 0.19	0	8
<i>Mayotella dimorpha</i>	2.33 $\pm$ 0.50	0	6
<i>Chorisoblatla denticulara</i>	1.60 $\pm$ 0.40	0	5
<i>Lobopterella dimidiatipes</i>	1.06 $\pm$ 0.14	0.20 $\pm$ 0.06	54
<i>Blattella lituricollis</i>	1.54 $\pm$ 0.17	0.23 $\pm$ 0.08	26
<i>Pycnoscelus surinamensis</i>	1.00 $\pm$ 0.28	0.26 $\pm$ 0.11	19
<i>Balta longicercata</i>	2.00 $\pm$ 0.25	0.25 $\pm$ 0.13	12
<i>Blattella biligata</i>	3.00 $\pm$ 3.00	1.00 $\pm$ 1.00	1
<i>Symploce pallens</i>	0	0	1
Mean	1.01 $\pm$ 0.10	0.45 $\pm$ 0.17	112

N: total number of sites where each species was recorded; mean: mean numbers of native species and of non-native species per site in La Réunion and in Mayotte.

## Discussion

Although the non-native cockroach species present in La Réunion and Mayotte are widely distributed in Oceania, in Asia and on Pacific islands (Roth, 1990, 1991a,b, 1996, 1998), they were almost exclusively present in cultivated areas. Species that have self-sustaining populations are considered as well established on islands (Williamson, 1996). Guilds included more species in La Réunion than in Mayotte. In the present study, no exclusion between particular pairs of species was found. Most species had already colonized all suitable habitats and their distribution areas overlapped in La Réunion, whereas in Mayotte some species had not yet colonized all habitats. The present data suggest that colonization of non-native cockroach species occurred earlier in La Réunion than in Mayotte. For instance, *L. dimidiatipes*, largely distributed on both islands, was often found alone in Mayotte and always co-occurred with other species in La Réunion. *Lobopterella dimidiatipes* either arrived earlier than the other species or had colonized new sites more rapidly and could be considered as a pioneer species (Perfecto, 1991). Two species (*B. biligata* and *S. pallens*) were found only once although they tolerate a broad range of environmental parameters and have important reproduction capacities (Lee *et al.*, 2000; Boyer & Rivault, 2004). Thus they are probably on their way to becoming established on these islands.

Establishment of non-native species in La Réunion might have occurred after 1957 because none of the species that we collected there were in Chopard's list, except *P. surinamensis*. Consequently, the rapid expansion of non-native species

over these two islands stresses their important colonizing capacities. Their establishment is restricted by altitude, whereas it is favoured by humidity and human activity (Boyer & Rivault, 2003). In Mayotte, a high proportion of the island was colonized because altitudes are low, whereas in La Réunion, cockroach distribution is limited to a low altitude peripheral ring. A similar decrease in cockroach species richness related to altitude was reported in Panama (Wolda, 1983). Irrigation of cultivated sites may favour their development. In Mayotte, fragmentation of habitats with small cultivated fields intermingled with natural forest areas reduced insect migrations between suitable sites and impairs colonization (Samways, 1994).

The four native species on both islands occupy restricted distributions areas. No overlap of native species distribution areas was observed. Nevertheless, three of them co-occurred with non-native species. When their distribution is restricted to natural areas, their survival is related to the maintenance of these areas, which are currently included in natural reserves (Barré *et al.*, 1996; Louette, 1999). *Ylangella truncata* is linked to the presence of decaying dead trees that are the outcome of the forest's natural ageing processes and *C. chopardi* is linked to the Bébou primary forest. Furthermore, the fact that these habitats are located at high altitude limits the establishment of non-native cockroach species. The original habitats of *M. dimorpha* and *C. denticulara*, found only in cultivated areas, will probably remain unknown. Among the factors that could threaten these two species, predation by invasive ants and use of insecticides in agricultural practices might be more important than competition with non-native cockroach species. Their presence in a restricted number of sites and their low population levels stress their endangered situation. *Brachynauphoeta mayottensis* Bruijning, described as endemic from Mayotte (Bruijning, 1945), and *Themnopteryx abbreviata* (Saussure), described as endemic from La Réunion (Chopard, 1957), were not found during our study. Although their original habitat was never described, their absence could be the result of habitat disturbances.

The modification of habitats and food web structure due to human activity enhances the establishment and development of non-native species and weakening of native species (Byers, 2002).

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