

Original article

Habitat selection and coexistence of invasive cockroach species (Dictyoptera) in sugar-cane fields on Réunion island

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Abstract

Selection of habitat has a profound influence on interactions among species and the assembly of ecological communities. We investigated habitat preferences to understand how different cockroach species coexist in sugar-cane fields on Réunion island.

Cockroach populations belonging to a guild of seven species were surveyed during one annual cycle in eight sugar-cane fields that differed by several environmental factors, in order to investigate ecological features of cockroach species and their patterns of coexistence.

Structure variations of the cockroach communities were analyzed at the field scale, at the sample unit scale, and according to variations of environmental conditions related to the annual sugar-cane growth cycle. A canonical correspondence analysis (CCA) was used to elucidate relationships between species diversity, population abundance and environmental characteristics.

The examination of partitioning at different spatial and temporal scales evidenced that each species occupied a particular type of habitat. The main factors influencing spatial habitat selection were at the sample unit scale: presence of ants, edge effect, soil moisture and granulometry, at the field scale: irrigation, annual rainfall, altitude and age of the field. Although a pair of species shared the same type of habitat, annual population peaks of each species did not coincide in time. This suggests that resource partitioning is based both on ecological factors and interspecific competition.

Factors enhancing cockroach coexistence and factors favoring population outbursts are discussed as well as specific invasive capacities of these cockroaches and the role of the cockroach community in the sugar-cane trophic web.

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1. Introduction

How different species coexist in a given habitat is one of main questions in community ecology. Selection of habitat has a profound influence on interactions among species and the assembly of ecological communities (Morris, 2003). The process whereby individuals preferentially use, or occupy, a non-random set of available habitats may lead to resource partitioning between species that could be expressed as spatial or temporal segregation (Begon et al., 1986). Spatial segregation implies avoidance of competition and thus allows stable coexistence of species (Geervliet et al., 2000; Snyder and Chesson, 2003). Habitats can be partitioned either on a large scale, as illustrated by grassland ants (Albrecht and

Gotelli, 2001), or on a microhabitat scale, as illustrated by sympatric bark beetles (Ayers et al., 2001). Temporal segregation, by shifting population peaks and/or periods of activity also facilitates the coexistence of competing species through avoidance of direct confrontation or reduction of overlap of resource exploitation (Kronfeld-Schor and Dayan, 1999; Albrecht and Gotelli, 2001). The fact that several species may depend on the same resources led to the idea that interspecific competition plays an important role in shaping communities by determining which and how many species coexist (Hardin, 1960; MacArthur, 1972). As an example, the introduction of invasive insect species often disrupts the organization and functioning of many native communities and ecosystems (Sanders et al., 2003) and leads to displacement and sometimes to extinction of native species (Holway et al., 2002). Most introductions can be directly related to human transport (Gaston et al., 2002). Human activities also disrupt

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communities or population structures by changing biotic and physical environmental conditions, this is particularly true in arable lands that are subject to cyclic human disturbances (Samways, 1994). In tropical regions, reduction of forest and natural areas has induced many arthropods to invade cultivated environments where they may benefit from conditions favoring population outbreak (Samways, 1994). Furthermore, island faunas appear to be more sensitive to environmental changes and more prone to extinction than continental faunas (Simberloff, 1976; Vitousek, 1988). Thus, the impact of invasions is even more severe on oceanic islands, where the biota evolved in isolation (Gillespie and Roderick, 2002).

On Réunion island, seven cockroach species have invaded sugar-cane fields and become established there. They represent a high proportion of the arthropod biomass present in sugar-cane fields. Sugar-cane, which is currently the main cultivated crop, is itself an introduced species. Six of the cockroach species collected belong to the family Blattellidae: *Blattella lituricollis* (Walker), *Blattella biligata* (Walker), *Balta longicercata* (Bolivar), *Scalida latiusvittata* (Brunner), *Margattea nimbata nimbata* Shelford, and *Lobopterella dimidiatipes* (Bolivar). The seventh species: *Pycnoscelus surinamensis* (L.), is a blaberid. These cockroaches are widely distributed in Asia, in Oceania and on Pacific and Indian Ocean islands (Roth, 1985, 1989, 1990, 1991, 1996, 1999, 2000; Roth and Rivault, 2002). Our knowledge of these species is the result of systematic collections, but very little is known about their ecological and biological traits (Boyer and Rivault, 2004). The fact that these species coexist in sugar-cane fields where they share resources and predators, raised the question of habitat selection and species coexistence.

This research investigated the structure of cockroach communities in sugar-cane fields in relation to environmental features and aimed to understand how these species with the same habitat preferences coexist. The factors enhancing the stability of the system and the role of spatial and temporal resource partitioning in the coexistence of the species were investigated, as well as factors liable to favor establishment and population outbursts of cockroach species in sugar-cane fields.

2. Materials and methods

2.1. Study area and study sites

Réunion island is an oceanic island in the Indian Ocean, approximately 700 km east of Madagascar (21°06S, 55°36E). This mountainous island covers 2500 km² and has a tropical climate, with a hot wet season from November to April and a cooler dry season from May to October. Large climatic variations are recorded between the east and the west coasts and with altitude.

On Réunion island, sugar-cane is the main cultivated crop, covering 26,000 ha in 2001, thus representing approximately 10% of the whole surface of the island (AGRESTE, 2002). Sugar-cane fields are located at low altitudes all around the island. Only fields located in the drier western areas require continuous irrigation, except during the 2 months preceding harvest. Sugar-cane is harvested annually, between August and November, at the end of the dry season. Stalks are cut just above the ground. Dry leaves and apical parts of stalks are left on the ground, thus adding to the litter. Sugar-canes shoot up again after harvesting, each plant may produce for 8–10 years in the same field and crop rotation is not required (Fauconnier and Basserau, 1970). As this monoculture receives no insecticide treatments, large diversified arthropod communities develop there.

This study was conducted in eight sugar-cane fields located around the island (Fig. 1). Five irrigated fields located on the west coast were chosen: four were near sea level: Pointe au Sel (Pas), Saint Louis (Lou), Savannah 1 (Sa1) and Savannah 2 (Sa2) and the fifth, Antenne 4 (An4), was 600 m a.s.l. Three non-irrigated fields located on the east coast were chosen: Saint Benoit (Ben) and Sainte Marie (Mar) were near sea level and the third one, Saint Joseph (Jos) was 300 m a.s.l. All these fields were located close to a meteorological station (Météo-France or CIRAD Réunion) (Fig. 1), which provided temperature and rainfall data (Table 1).

2.2. Sampling methods

Cockroach population censuses were taken within the eight fields over an annual cycle, from February 2001 to March 2002 (13 months). Each field was surveyed every 3 weeks, in the morning, from 08.00 to 12.00 h. Each field survey yielded

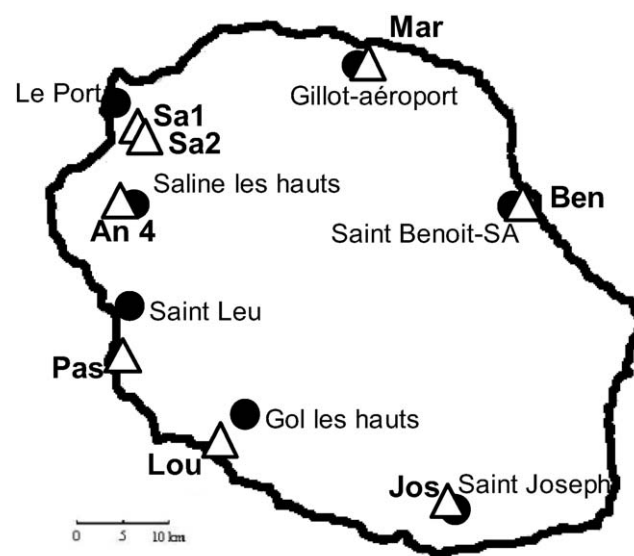


Fig. 1. Location of sugar-cane fields studied (Δ) and meteorological stations (\bullet) on Réunion island. Legend: Mar: Sainte Marie; Sa1: Savannah 1; Sa2: Savannah 2; Pas: Pointe au Sel; Lou: Saint Louis; Jos: Saint Joseph; Ben: Saint Benoit.

Table 1
Macro-environmental factors and total number of cockroaches recorded in each of the eight sugar-cane fields studied, for all the surveys

Locality	Savannah1	Savannah2	Pointe au Sel	Antenne 4	Saint Louis	Sainte Marie	Saint Benoit	Saint Joseph
Abbreviation	Sa1	Sa2	Pas	An4	Lou	Mar	Ben	Jos
Localization	West	West	West	West	West	East	East	East
Meteorological station	Le Port	Le Port	Saint Leu	Saline les Hauts	Gol les hauts	Gillot Aéroport	Saint Benoit SA	Saint Joseph
<i>Environmental variables</i>								
Temperature (°C)	25.97 ± 0.12	25.97 ± 0.12	24.20 ± 0.12	25.32 ± 0.13	22.08 ± 0.13	24.57 ± 0.09	23.67 ± 0.11	24.59 ± 0.11
Rainfall (mm year ⁻¹)	281.4	281.4	302.5	475.3	632.0	995.6	3453.6	1129.5
Irrigation	+	+	+	+	+	–	–	–
Altitude (m a.s.l.)	10	10	30	600	30	50	50	300
Age of field (years)	> 10	> 10	2	3	> 10	> 10	> 10	> 10
Ant species	<i>P.m.</i>	<i>P.m.</i>	<i>P.m.</i>	<i>P.m.</i>	<i>P.m.</i>	<i>P.m.</i>	<i>S.g.</i>	<i>S.g.</i>
<i>Total number of cockroaches recorded in all the surveys</i>								
<i>B. longicercata</i>	818	172	420	1032	354	240	234	43
<i>B. biligata</i>	50	23	33	383	328	40	15	0
<i>B. lituricollis</i>	323	988	0	0	367	0	25	0
<i>L. dimidiatipes</i>	643	161	423	21	203	802	176	45
<i>M. nimbata nimbata</i>	196	18	0	0	41	265	170	0
<i>P. surinamensis</i>	15	45	20	0	64	0	0	0
<i>S. latiusvittata</i>	329	86	0	0	128	5	9	5

Temperature: annual means (± S.E.) of daily maximum temperatures; rainfall: total of daily precipitations, in mm; irrigation: “+” = irrigated fields, “–” = non-irrigated fields; altitude; age of field: duration since cultivation of sugar-cane started in each field; ant species: *S.g.* = *S. geminata*, *P.m.* = *P. megacephala*. The two ant species are mutually exclusive, and one field harbors either one or the other species.

census data for cockroaches from 50 sample units. Sample units were chosen in the inter-rows of sugar-cane plants and distributed over approximately 1500 m². Distance between rows was 1.5 m. Ten inter-rows were selected for each survey, at five inter-row intervals (1–60). Between two successive surveys, censuses were shifted by two inter-rows, in order to avoid sampling the same sample unit too often as this could disturb the insects on that unit. The first survey included inter-rows 1, 6, 11, 16, 21, 26, 31, 36, 41, 46; the second 3, 8, 13, 18...; the third, 5, 10, 15, 20...; the fourth, 2, 7, 12, 17..., the fifth, 4, 9, 14, 19... The sixth survey was similar to the first. Five sample units, placed at 5 m intervals, from the edge of the field to 20 m inside the field, were surveyed in each selected inter-row.

During the survey, sample units were delimited by a metal cylinder that penetrated slightly into the ground and acted as a sort of trap. This cylinder was 60 cm in circumference (286 cm² surface area) and 20 cm high, and prevented cockroaches from escaping from the sample unit and thus avoided interspecific differences due to locomotor's capacities. Cockroaches were found by sorting out the leaf litter and by sifting the soil inside the cylinder. Individuals were identified and counted inside the cylinder, in the field. Data were expressed as the number of individuals per species per sample unit.

This non-destructive method allows rapid evaluation (on average, 3 min observation for each sample unit) 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). Thus seasonal variation of population densities could be monitored.

2.3. Analysis of environmental factors

Data were analyzed at the field scale, at the sample unit scale and in relation to sugar-cane growth.

2.3.1. Macro-environmental factors at the field scale

The following factors were taken into account to characterize each field studied (Table 1):

- 1) mean annual temperature, calculated as the mean of daily maximal temperatures;
- 2) annual rainfall, given as the total of daily precipitations;
- 3) presence or absence of irrigation;
- 4) altitude: the fields were divided into two groups, those below 50 m a.s.l. and those between 300 and 600 m a.s.l.;
- 5) age of field, estimated by the number of years since cultivation of sugar-cane started there: old fields, where sugar-cane had been cultivated there for more than 10 years, were distinguished from young fields, where sugar-cane had been cultivated there for only 2 or 3 years;
- 6) ant species: two species of ants predominated in sugar-cane fields: *Solenopsis geminata* and *Pheidole megacephala*.

Each of these species exerts strong predation pressures on insect populations (Hoffmann et al., 1999; Lang et al., 1999; Vanderwoude et al., 2000). They were mutually exclusive in the sugar-cane fields studied. The presence/absence for each species was therefore redundant because the presence of one species implied the absence of the other. As the canonical correspondence analysis (CCA, see below) was unable to run with redundant factors, only the presence/absence of *S. geminata* was considered.

2.3.2. Micro-environmental factors at the sample unit scale

The following micro-environmental factors, liable to influence species distribution, were measured at each sample unit and for each survey:

- 1) Moisture of soil was divided into five categories: very dry (40–60% hygrometry); dry (61–70%); humid (71–80%); very humid (81–90%); damp (> 90%).
- 2) Soil granulometry was divided into four categories: compact, light, granular and stony.
- 3) Depth of leaf litter was divided into four categories: 0–5 cm; 6–10 cm; 11–15 cm; > 16 cm.
- 4) Edge effect was estimated by the distance between sample unit and border of the field. Ten of the 50 sample units located on the edge of the field were coded as having a minimum value.
- 5) Row effect was estimated by the distance between the sample unit and the first row. Five of the 50 sample units located on the first row were coded as having a minimum value.
- 6) Presence/absence of grass.
- 7) Presence/absence of spiders (mainly Lycosidae sp.).
- 8) Presence/absence of ants (*S. geminata* or *P. megacephala*).
- 9) Number of other invertebrate species (essentially woodlice, millipedes, large collembolan species, beetles, grasshoppers and earthworms).

2.3.3. Effect of sugar-cane growth

Seasonal variation of cockroach populations was evaluated in relation to the growth cycle of sugar-cane. Its growth presents an annual rhythm, synchronized by variations of daily maximum temperatures and variations of day length. The cycle was divided into four 3-month periods beginning after the harvest date of the field:

- 1) Sprouting: sugar-cane plants start growing again and form small groups of vegetation.
- 2) Growth: the space between rows remains open.
- 3) Inter-row closure: leaves of sugar-canes in adjacent rows touch one another and the space between rows closes completely.
- 4) Maturation: sugar-canes mature and many dry leaves intertwine over the inter-row space; in irrigated fields, irrigation is interrupted 2 months before harvest.

2.4. Statistical analyses

The study of species–environment relationships involved the analysis of two data sets: one set containing environmental data and one set containing the data for population composition and abundance. CCA is a multivariate method used to elucidate relationships between biological assemblages of species and known variations in their environment (Chessel et al., 1987; Lebreton et al., 1988; Mercier et al., 1992). It extracts synthetic environmental gradients from ecological data sets. These gradients are the basis for describing succinctly and for visualizing habitat preferences of species. This

method yields an ordination diagram where points represent species and sites, and vectors represent environmental factors. A species point is at the centroid (weighted average) of the site points where it occurs (Ter Braak, 1987; Ter Braak and Verdonschot, 1995). CCA selects the linear combinations of environmental factors that maximize the dispersion of species scores. Furthermore, CCA is not very sensitive to species-poor sites containing rare species (Ter Braak, 1987). The field and species points are interpreted as in a Factorial Correspondence Analysis (Greenacre, 1984). They display variation in species composition and abundance among sites. The length and the direction of a vector are proportional to the contribution of the corresponding environmental factor to axes 1 and 2. The arrow points in the direction of maximum change.

In order to compare observed pattern and null expectation model of species coexistence, CCA significance was tested using a Monte Carlo permutation test ($n = 10,000$ random permutations).

Based on the results of the CCA, an ascending hierarchical ranking (AHR) can be performed, using an UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster analysis with Euclidean distances. This ranking allows the clustering of species in relation to their abundance related to environmental factors (Rouanet and Le Roux, 1993).

On a CCA diagram, each vector representing an environmental factor determines an axis on the diagram. Based on this diagram, the species points can be projected onto these axes, and the order of the projection points corresponds approximately to the ranking of the species in relation to that environmental factor. Thus species can be ranked in relation to the influence of each factor (Ter Braak, 1987).

We conducted two CCA analyses. The first CCA analyzed the effects of macro-environmental factors on cockroach communities at the field scale. It was based on two data matrices. The first data matrix included the six macro-environmental factors for each of the eight fields and for each of the 16 surveys. The second data matrix included the total number of individuals of each of the seven species in each of the eight fields for each of the 16 surveys. Data were summed over the 50 sample units of one survey.

The second CCA analyzed the effects of micro-environmental factors at the sample unit scale. It was based on two data matrices. The first data matrix included the nine micro-environmental factors for each of the 50 sample units in each of the eight fields and for each of the 16 surveys. The second data matrix included the total number of individuals for each of the seven species, for each of the 50 sample units in each of the eight fields for each of the 16 surveys.

An ANOVA analyzed the effect of sugar-cane growth on variations of the abundance of each species. Data for each species were summed for all fields in relation to time.

CCA, AHR and Monte Carlo permutation tests were computed with ADE-4 software (Thioulouse et al., 1984). The ANOVA was performed with Stat View 5.0 (1998).

3. Results

3.1. Macro-environmental factors: the field scale

Results of the first CCA, are given by an ordination diagram (Fig. 2a). The first two axes account for 85% of the

total inertia. The permutation test indicated that the distribution of the species differed significantly from the null expectation of random distribution (Monte Carlo permutation test, $P < 0.0001$), thus indicating niche segregation at the macro-environmental scale. The six macro-environmental factors studied and their contributions to the CCA are given in Table 2.

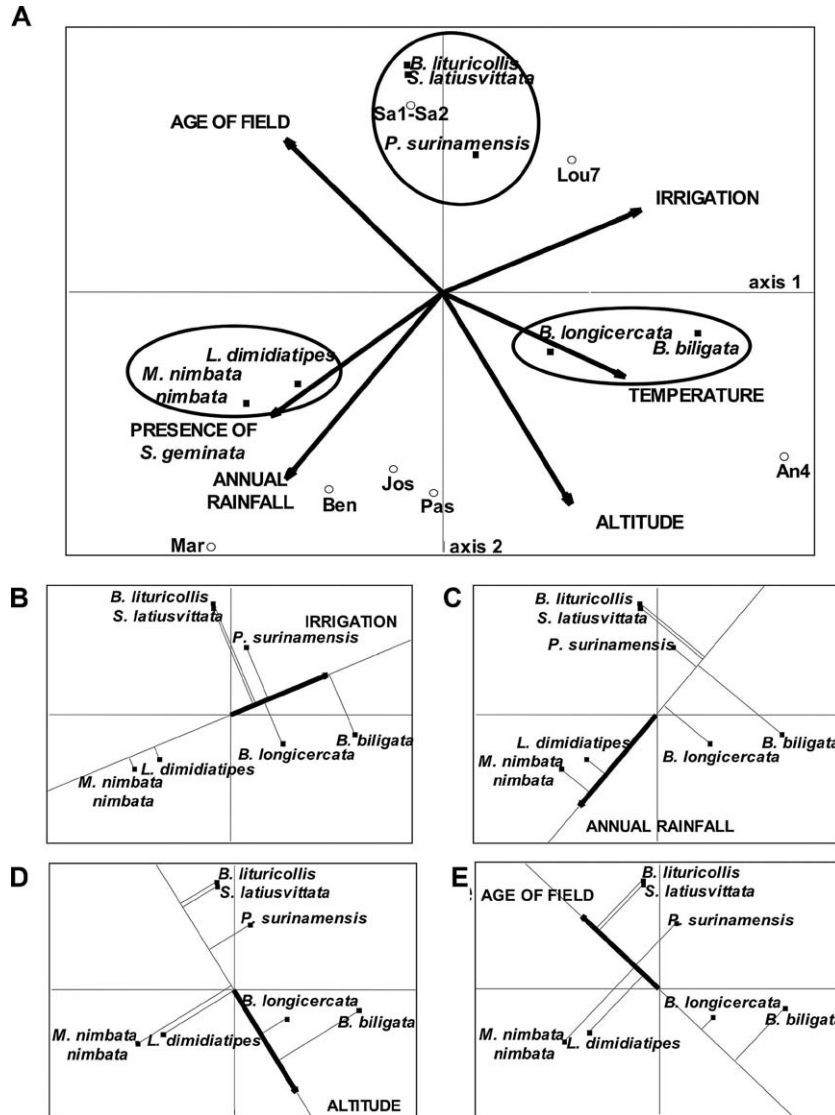


Fig. 2. Macro-environmental factors at the field scale.

a) CCA ordination diagram of the abundance of the seven cockroach species in relation to fields and in relation to the six macro-environmental factors studied. The first two axes of this diagram account for 85% of the total inertia.

Arrows: Macro-environmental factors (upper case); black squares: cockroach species points (in italics); white dots: field points (abbreviations, see Fig. 1); circles: species grouped by the AHR analysis.

b–e) Details of macro-environmental factors at the field scale. Projection of each cockroach species point on the axes of the four main environmental factors, b) irrigation, c) annual rainfall, d) altitude and e) age of the field. Arrows point in the direction of the highest values.

b: Projection on the irrigation axis ranked the species, from non-irrigated to irrigated fields, as follows: *M. nimbata nimbata*, *L. dimidiatipes*, *S. latiusvittata*, *B. lituricollis*, *B. longicercata*, *P. surinamensis* and *B. biligata*.

c: Projection on the annual rainfall axis ranked the species from fields with low annual rainfalls to fields with high annual rainfalls, as follows: *M. nimbata nimbata*, *L. dimidiatipes*, *B. longicercata*, *P. surinamensis*, *B. biligata*, *S. latiusvittata* and *B. lituricollis*.

d: Projection on the altitude axis ranked the species, from low altitude fields to fields located above 300 m a.s.l., as follows: *B. lituricollis*, *S. latiusvittata*, *P. surinamensis*, *M. nimbata nimbata*, *L. dimidiatipes*, *B. longicercata*, and *B. biligata*.

e: Projection on the age-of-field axis ranked the species, from old fields to young fields, as follows: *B. lituricollis*, *S. latiusvittata*, *P. surinamensis*, *M. nimbata nimbata*, *L. dimidiatipes*, *B. longicercata*, and *B. biligata*.

Table 2

Relative contributions on the first three axes of the CCA analyses. Contributions of the six macro-environmental factors studied at the field scale in the first CCA. Contributions of the nine micro-environmental factors studied at the sample unit scale in the second CCA

	Axis 1	Axis 2	Axis 3
<i>Environmental factors</i>			
Irrigation	0.6121	0.1017	0.0304
Annual rainfall	0.5159	0.1048	0.3663
Altitude	0.2549	0.6671	0.0018
Age of field	0.3756	0.5115	0.0421
Temperature	0.3793	0.3464	0.1199
Presence of <i>S. geminata</i>	0.4521	0.2258	0.0793
<i>Micro-climatic factors</i>			
Moisture of the soil	0.4453	0.0103	0.0055
Granulometry	0.3750	0.0626	0.0112
Presence of ants	0.0172	0.3698	0.1304
Edge effect	0.0001	0.3096	0.0501
Row effect	0.0293	0.2387	0.0690
Presence of spiders	0.2660	0.0994	0.0567
Number of invertebrate species	0.2428	0.1405	0.1916
Depth of the litter	0.0892	0.0167	0.2243
Presence of grass	0.0826	0.0003	0.1635

The main factors that contributed to their formation are: irrigation and annual rainfall on axis 1, altitude and age of field on axis 2. Mean annual temperature and presence of *S. geminata* contributed less.

The distribution of species and field points reveals the influence of macro-environmental factors (Fig. 2a) (Table 1). Sa1 and Sa2, which were near each other, presented the same macro-environmental conditions and thus were projected on the same point on the CCA diagram.

AHR revealed three groups of species, indicated on the CCA diagram: *B. longicercata* and *B. biligata*; *B. lituricollis*, *S. latiusvittata* and *P. surinamensis*; *M. nimbata* and *L. dimidiatipes* (Fig. 2a).

Species were ranked by the projection of their centroids on the axes of each of the main macro-environmental variables, indicating the influence of each factor on each cockroach species. Irrigation and rainfall are represented by two opposite axes on the CCA diagram (Fig. 2a). Long periods of water deficit were observed in non-irrigated fields although annual rainfall ranged from 995 to 3454 mm (Table 1). In irrigated fields, the quasi-continuous water deficit is compensated by irrigation because annual rainfall was insufficient, ranging from 281 to 632 mm year⁻¹ (Table 1). Therefore, soil moisture is more important in irrigated fields than in non-irrigated fields.

Except for *B. longicercata*, which is found in irrigated as well as in non-irrigated fields, the species in the first and the second groups (*B. biligata*, *B. lituricollis*, *S. latiusvittata* and *P. surinamensis*) are more abundant in irrigated fields than in non-irrigated fields (Fig. 2b–c). The species in the third group (*L. dimidiatipes* and *M. nimbata*) are more abundant on sites receiving only natural rainfall. Furthermore, these two species co-occur with *S. geminata* ants.

Altitude and age of field are opposed in the CCA diagram (Fig. 2a). This is because the fields where sugar-cane has been

cultivated for more than 10 years are located mainly at low altitudes, whereas fields more recently cultivated are situated at higher altitudes. The first cockroach group (*B. longicercata* and *B. biligata*) is frequent in young fields situated between 300 and 600 m a.s.l. (Fig. 2d–e). The second group (*P. surinamensis*, *S. latiusvittata* and *B. lituricollis*) is present only in old low-altitude fields and the third group (*L. dimidiatipes* and *M. nimbata*) does not appear to be influenced by these two variables.

We can summarize the species characteristics as follows: the group *B. lituricollis*, *S. latiusvittata*, and to a lesser extent, *P. surinamensis* were more abundant in old, low-altitude, irrigated fields with *P. megacephala* ants. The group *B. longicercata* and *B. biligata* was found mainly in irrigated fields, at relatively higher altitudes, where mean annual temperatures were higher and *P. megacephala* ants were present. Finally, the group *M. nimbata* and *L. dimidiatipes* was found in non-irrigated fields with high rainfalls; these species co-occurred with *S. geminata* ants.

3.2. Micro-environmental factors: the sample unit scale

Results of the second CCA, are given by an ordination diagram (Fig. 3a). The first two axes of this diagram account for 79% of the total inertia. The permutation test indicated that the distribution of the species differed significantly from the null expectation of random distribution (Monte Carlo permutation test, $P < 0.0001$), thus indicating niche segregation at the micro-environmental scale. The nine micro-environmental factors studied and their contributions to the CCA are given in Table 2. Soil granulometry and moisture of soil were the main factors that contributed to the formation of axis 1. Presence of spiders and number of invertebrate species contributed to a lesser extent. Presence of ants, edge effect and row effect contributed to the formation of axis 2. Depth of leaf litter and presence of grass contributed very little to the formation of the first two axes, however, they contributed more to axis 3. The distribution of species points reveals the influence of the micro-environmental factors. AHR revealed three groups of species indicated on the CCA diagram: 1) *B. longicercata* and *B. biligata*; 2) *B. lituricollis* and *P. surinamensis*; 3) *M. nimbata*, *L. dimidiatipes* and *S. latiusvittata* (Fig. 3a).

Species were ranked by the projection of their centroids on the axis of each of the main micro-environmental variables indicating the influence of each factor on each cockroach species. The CCA opposed the moisture of soil and granulometry axes (Fig. 3a). Species in the first and the second groups (*B. lituricollis*, *B. biligata*, *P. surinamensis* and *B. longicercata*) were mainly present on dry, granular soils. Species in the third group (*L. dimidiatipes*, *M. nimbata* and *S. latiusvittata*) were present on moist, fine soils (Fig. 3b, c).

On the CCA ordination diagram, presence of ants and edge effect are strongly correlated illustrating the absence of ants on the edges of fields (Fig. 3a). The species points of *B. litu-*

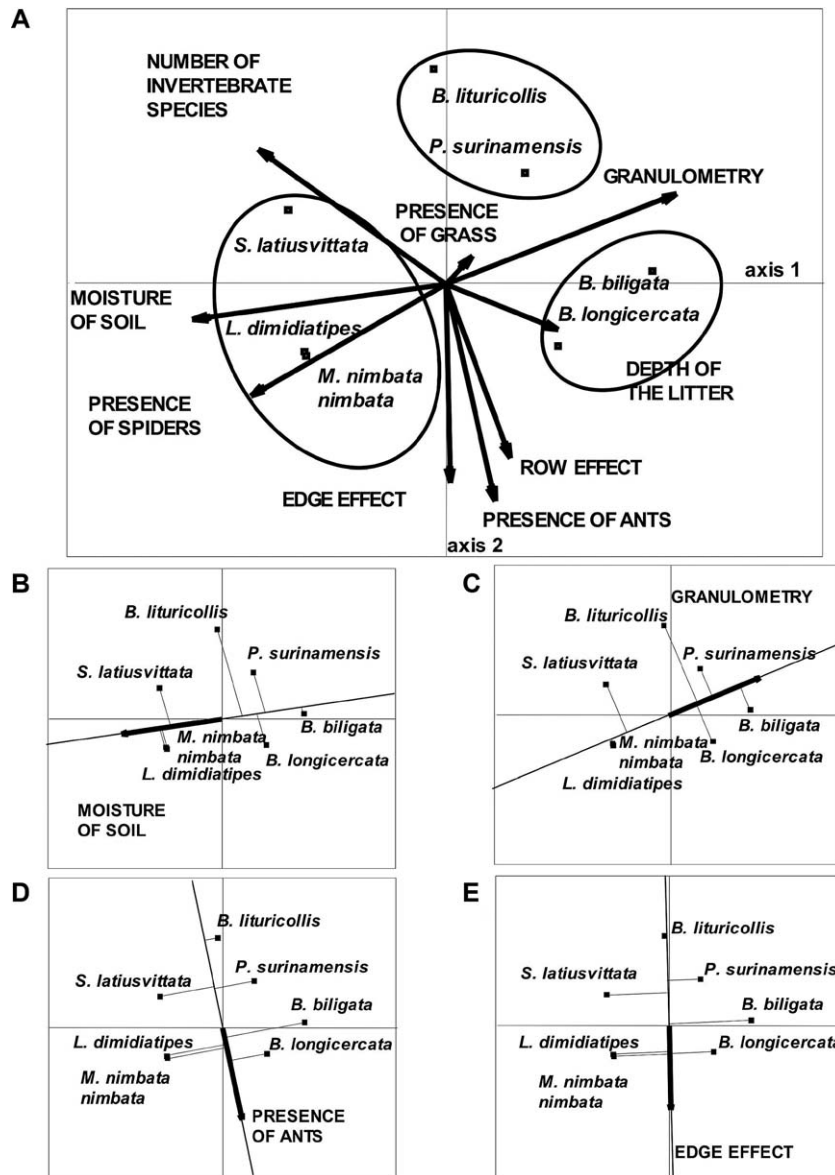


Fig. 3. Micro-environmental factors at the sample unit scale.

a) CCA ordination diagram of the abundance of the seven cockroach species in relation to the nine micro-environmental factors studied. The first two axes of this diagram account for 79% of the total inertia. Sample units were too numerous (6150) to be represented on the diagram.

Arrows: micro-environmental factors (upper case); black squares: cockroach species points (in italics); circles: species grouped by the AHR analysis.

b–e) Details of micro-environmental factors at the sample unit scale. Projection of each cockroach species point on the axes of the four main micro-environmental factors: b) moisture of soil, c) granulometry, d) presence of ants and e) edge effect. Arrows point in the direction of the highest values.

b: Projection on the moisture of soil axis ranked the species, from very dry sample units to damp sample units, as follows: *B. biligata*, *P. surinamensis*, *B. longicercata*, *B. lituricollis*, *S. latiusvittata*, *M. nimbata nimbata* and *L. dimidiatipes*.

c: Projection on the granulometry axis ranked the species, from stony soil sample units to fine soil sample units, as follows: *B. biligata*, *P. surinamensis*, *B. lituricollis*, *B. longicercata*, *S. latiusvittata*, *M. nimbata nimbata* and *L. dimidiatipes*.

d: Projection on the presence of ants axis ranked the species, from sample units without ants to sample units with ants, as follows: *B. lituricollis*, *S. latiusvittata*, *P. surinamensis*, *B. biligata*, *L. dimidiatipes*, *M. nimbata nimbata* and *B. longicercata*.

e: Projection on the edge effect axis ranked the species, from sample units located at the field-border to sample units located inside the field, as follows: *B. lituricollis*, *P. surinamensis*, *S. latiusvittata*, *B. biligata*, *L. dimidiatipes*, *B. longicercata* and *M. nimbata nimbata*.

ricollis and, to a lesser extent, of *P. surinamensis* and of *S. latiusvittata* are projected on the low values of these two parameters (Fig. 3d, e). These three species are located near the field borders. The other cockroach species points are near the central part of axis 2, which means that their distribution is less influenced by the presence of ants and edge effect. Edge effect and row effect are close to each other on the dia-

gram because they both estimated the position of sample units in the field. The factors presence of ants and numbers of other invertebrate species are opposed on the CCA diagram, which suggests that the predation pressure of ants on the entire invertebrate fauna is important. Spiders were located mainly in humid microhabitats, as indicated by the direction of the arrows on the CCA diagram.

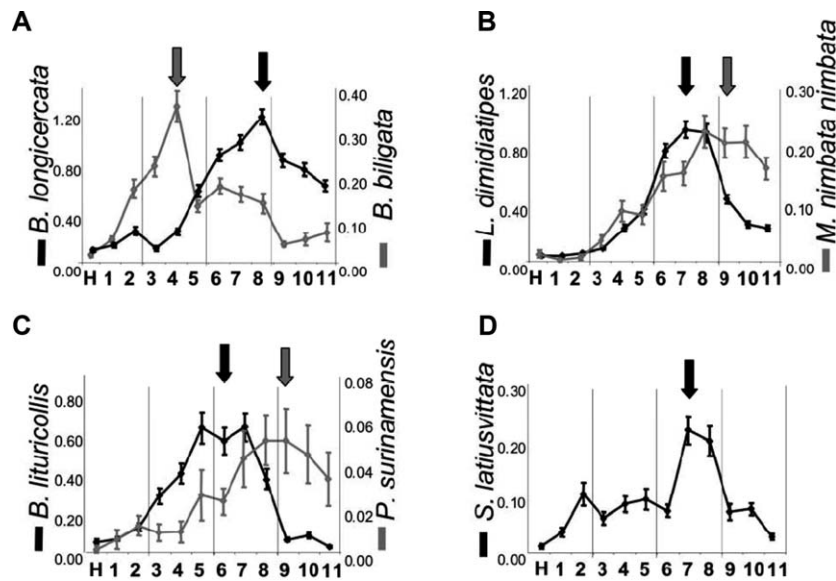


Fig. 4. Number of individuals of each species in relation to sugar-cane growth.

Ordinates (right and left) = mean number of individuals (\pm S.E.) of each species of a couple that selected the same type of habitat; mean number of individuals observed in sample units made during the same month in the eight different fields; abscise = months following the harvest of the sugar-cane. H = sugar-cane harvest. Arrows: population peaks. Vertical lines: separation of the four 3-month periods of sugar-cane growth, from left to right: sprouting, growth, inter-row closure and maturation.

Thus, cockroach species are characterized as follows: species in the first group (*B. longicercata* and *B. biligata*) were found on sample units characterized by very dry or dry, granular or stony soils, with abundant leaf litter and few invertebrate species. Species in the second group (*B. lituricollis* and *P. surinamensis*) were present on dry sample units located near field borders, with medium-sized soil elements and without ants. Species in the third group (*S. latiusvittata*, *L. dimidiatipes* and *M. nimbata*) were present on moist sample units with fine soil elements and with many other invertebrate species and spiders.

Comparisons between the analyses at the field scale and at the sample unit scale revealed three pairs of cockroach species. Within each pair, one of the species was more abundant than the other (Table 1) and each species of a pair have similar preferences concerning macro- and micro-environmental factors. As *B. longicercata* and *B. biligata* were found in the same fields and on the same sample units, they have the same spatial niche preferences. The same can be said for the pairs of species *M. nimbata*–*L. dimidiatipes* and the pair *B. lituricollis*–*P. surinamensis*. Only *S. latiusvittata* changed groups with scale. *S. latiusvittata* was found on the same type of sample units as *L. dimidiatipes* and *M. nimbata*, but they were rarely found in the same fields. Thus *S. latiusvittata* occupies a particular niche that isolates it more or less from the other species.

3.3. Effect of sugar-cane growth

The analysis of the abundance of each species in each field revealed an effect of sugar-cane growth on the development of cockroach populations. The population size plot for each species presented an annual cycle characterized by one peak

(Fig. 4). However, population peaks of the species did not all occur at the same period in relation to sugar-cane growth. (ANOVA, date effect: $df = 11$, $P < 0.0001$; species effect: $df = 6$, $P < 0.0001$; interaction date \times species: $df = 66$, $P < 0.0001$).

Analyses at the field scale and at the sample unit scale evidenced three pairs of cockroach species occupying the same types of habitats (see Sections 1 and 2). Comparisons of the growth plots of the populations of each species within a pair revealed that population peaks of paired species do not coincide in time (Fig. 4). *B. biligata* populations peaked 4 months before *B. longicercata* populations did. *B. lituricollis* populations peaked 3 months before *P. surinamensis* populations did. *L. dimidiatipes* populations peaked 2 months before *M. nimbata* populations did. *L. dimidiatipes* populations dropped dramatically during the sugar-cane maturation period while *M. nimbata* populations appeared to remain abundant, their decrease being induced by the following harvest.

4. Discussion

The seven cockroach species collected in sugar-cane fields on Réunion island are invasive species, largely distributed in Oceania, Asia and Pacific islands (Roth, 1985, 1989, 1990, 1991, 1996, 1999, 2000; Roth and Rivault, 2002). Their native ranges will probably remain unknown. The only previous survey of cockroach species on Réunion island was made by Chopard (1957). Among the seven species we studied, *P. surinamensis* was the only species he mentioned. Therefore we could assume that the six other species became established on Réunion island after 1957. Since then, all these species

have colonized Réunion island successfully and have become established all around the island (Boyer and Rivault, 2003), as indicated by the presence of self-sustaining populations (Williamson, 1996).

Our results:

- 1) characterized habitat preferences for each species and revealed spatio-temporal segregation among the seven cockroach species;
- 2) evidenced some differences in their invading capacities;
- 3) and revealed environmental parameters favoring the development of cockroach populations.

Niche partitioning between cockroach species involves three selection scales related to the macro-environmental factors of each field, to the micro-environmental factors inside a field and to the annual rhythm of sugar-cane growth. Species need to find a suitable microhabitat within a suitable macrohabitat. Microhabitats provide suitable resources; macrohabitats provide conditions for the species to survive. Thus, even if microclimatic conditions can, in some circumstances, mitigate macroclimate conditions, the scale of climatic factors and the scale of micro-environmental factors are both crucial to define habitat selection for each species. The two CCAs give different results of habitat selection, at two different scales. Distribution of species is not homogenous within a field, because micro-environmental parameters vary among sample units.

Analyses at the field scale and at the sample unit scale evidenced three pairs of cockroach species. Each pair occupied particular types of habitat and the seventh species occupied another habitat.

The fact that these species are recent invaders with different tolerance levels to environmental factors could suggest that their initial habitats were separated. As nothing is known about their natural habitats (Roth, 1985, 1989, 1990, 1991, 1996, 1999, 2000; Roth and Rivault, 2002), more investigations of invasion events and life history traits of these species would be necessary. In sugar-cane cockroach guilds, habitat selection seems to be a consequence of non-competitive diversification of traits that leads to niche differentiation of pairs of species (Genner et al., 1999).

Analysis in relation to sugar-cane growth indicated that all species exhibited an annual cycle characterized by a population peak. We hypothesized that if two species that share the same type of habitat had population peaks at the same time, they would compete for resources. Thus, the two species of each pair shared the same type of habitats but flourished at different periods of sugar-cane growth. Within a pair, the species with the higher population level (*L. dimidiatipes*, *B. longicercata* and *B. lituricollis*) (Table 1) presented a population peak during the sugar-cane inter-row closure period. The species with the lower population level (Table 1) presented a population peak either before (*B. longicercata*) or after (*M. nimbata* and *P. surinamensis*) the inter-row closure period. *S. latiusvittata*, which had rather low population levels, peaked during the inter-row closure period like the three most abundant species. This could be explained by the fact

that *S. latiusvittata* is spatially isolated and does not have the same habitat preferences as the other species. Therefore, the most favorable period for cockroach outbursts appears to be the inter-row closure period. These temporal differences in population peaks between paired species sharing the same spatial environment enable them to minimize population overlap and could be interpreted as temporal shifts by species with the lower population levels.

The duration of the biological cycle of these species (Boyer and Rivault, 2004) allows adults to reproduce several times during the year, and several generations are present simultaneously. When two species select the same habitat, their population peaks do not coincide in time. We cannot exclude that the observed temporal differences of cockroach population peaks could be the result of differential demographic traits or different physiological tolerances of each species to seasonal changes in environmental conditions. Nevertheless, we assume that the temporal differences are rather the consequences of the negative influence of a superior competitor that forced the inferior species to develop under less favorable conditions as stated by Genner et al. (1999). This temporal segregation could reduce the intensity of interspecific competition and thus enhance the stability of the system.

Differences in colonizing capacities among species are revealed by the presence of cockroaches in recently cultivated fields and/or isolated fields. These species were almost exclusively collected in sugar-cane fields (Boyer and Rivault, 2003). The increase of their distribution areas on the island is most probably related to the development of sugar-cane cultivation, which started on the east coast of Réunion island, under naturally favorable conditions and later reached the west coast due to the increase of irrigation. The species were largely distributed all around the island. Currently, sugar-cane fields are almost contiguous and cover nearly all the low altitude periphery of the island. This situation allows active migration of cockroaches between fields. Our results indicate that just a few individuals are able to populate a field and no local extinctions were observed during our survey.

The number of species in a field is related to altitude and age of the field. Old fields harbor more species than young ones. Comparisons between old and young fields highlighted a sequence of establishment of the different species in relation to the age of the field. *B. longicercata* and *B. biligata* are the first to colonize newly cultivated fields, probably due to better flying capacities (Boyer and Rivault, 2004). Then come *M. nimbata* and *L. dimidiatipes* and finally *B. lituricollis*, *S. latiusvittata* and *P. surinamensis*. Fields in altitude may present large daily temperature variations to which some species can be sensitive. Furthermore, these fields are relatively isolated one from the other and this could impair population exchanges between fields. *B. longicercata* and *B. biligata* are able to colonize isolated fields located above 300 m a.s.l. These two species may possess physiological adaptations that allow them to survive at altitudes where other species cannot. The fact that they have better flying capacities and wider ecological niches than the other species could result in better invading efficiency (Tilman, 1982; Sakai et al., 2001).

Cultivated lands constitute a favorable environment for the establishment of large cockroach populations and on Réunion island they are almost exclusively found in sugar-cane fields (Boyer and Rivault, 2003). As the size of cockroach populations in irrigated fields is larger than in non-irrigated fields, presence of water facilitates development and outbursts of cockroach populations. Five of seven species are present predominantly in irrigated fields, whereas the other two species, which are present mostly in non-irrigated fields, select microhabitats with high humidity. Cockroach population outbursts are limited by predation by ants (*S. geminata* and *P. megacephala*) and by spiders (Lycosidae), which are generalist predators (Perfecto, 1991; Wagner and Wise, 1997). Their predation pressure is important in cultivated areas where they are able to limit insect populations (Hoffmann et al., 1999; Lang et al., 1999; Vanderwoude et al., 2000). The presence of such predators, which do not have a particular preference for any species of a guild, enhances the stability of a system with several cohabiting species (Gouteux and Jarry, 1998). However, *P. surinamensis* might be less predated than the other cockroach species because it may avoid predation by spiders, which are ambush predators, by spending most of its time buried in the soil. Furthermore, *P. surinamensis* can live in nests of several ant species, including *P. megacephala* (Deleporte et al., 2002). *B. lituricollis* might be less predated on by ants as this species is located mainly near the borders of fields, whereas ants are present more inside fields. Predation pressure of ants and spiders on the five other cockroach species is presumed to be similar. As cockroaches are omnivorous and mainly detritivorous, eating decaying vegetation and animal remains (Bell, 1990), their presence does not affect sugar-cane production. However, when there is a cockroach population outburst, predation pressure of ants may decrease on the other invertebrate species in the field. The stem borer, *Chilo sacchariphagus*, which causes damage to sugar-cane on Réunion island (Goebel et al., 1999), is mainly predated by ants (Goebel et al., 1999) and thus could take advantage of cockroach outbursts. The presence of cockroaches could favor the development of either invading ants or sugar-cane pests and the cockroach guild would thus play a key role in the sugar-cane trophic web.

Our results characterized the ecological niches of several cockroach species, stressing a spatio-temporal segregation of the species that facilitates their coexistence in this recently invaded sugar-cane system. Thus, interspecific competition is avoided by spatial and temporal shifts of resource use. This cockroach guild illustrates the concept of niche complementarity (Pyke, 1982), and raises the problem of diffuse competition between the species (MacArthur, 1972), although the species might still be adapting to their habitat and to the presence of closely related species. As their establishment on the island has occurred since 1957, their coexistence patterns might still be dynamic. As the sugar-cane harvest induces a drastic decrease of resources for all cockroach species, the previous differences between population densities are erased and populations start again from similar low levels. The annual

cycle of harvest may allow short-term competition and prevent the monopolization of habitats by superior competitors (Begon et al., 1986). If sugar-cane was not harvested, the dominant species would probably become more and more abundant and could threaten inferior competitors. Consequently, human disturbance not only tends to facilitate establishment of several invasive species, but also enhances their coexistence in the longer run.

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