



REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

www.rbentomologia.com



Biology, Ecology and Diversity

Distribution, habitat use and plant associations of *Moluchia brevipennis* (Saussure, 1864) (Blattodea: Ectobiidae): an endemic cockroach from Chilean Mediterranean Matorral biome



Constanza Schapheer^{a,*}, Margarita M. Lopez-Uribe^b, Alejandro Vera^c, Cristian A. Villagra^a

^a Universidad Metropolitana de Ciencias de la Educación, Facultad de Ciencias Básicas, Instituto de Entomología, Santiago, Chile

^b University Park, Pennsylvania State University, Department of Entomology, United States

^c Universidad Metropolitana de Ciencias de la Educación, Facultad de Ciencias Básicas, Departamento de Biología, Santiago, Chile

ARTICLE INFO

Article history:

Received 10 October 2016

Received in revised form 27 January 2017

Accepted 1 February 2017

Available online 17 February 2017

Associate Editor: Gustavo Gracioli

Keywords:

Larcenists

Habitat fragmentation

Ecological interactions

South American cockroaches

ABSTRACT

Wild cockroaches are often described as abundant and diverse insects from wet tropical zones; however, they can also be found in arid and semiarid areas. It is proposed that in these drier environments cockroach survival may depend on its tight association with native plant species. In this work, using bait trapping and active collection methods, we surveyed cockroach species along central Chile coastal scrubland; the southern limit of the semiarid Mediterranean Matorral biome in the Neotropical Region (32° S). Based on morphological and DNA barcoding methods we found that our collected cockroaches belonged to native species *Moluchia brevipennis* (Saussure, 1864) (Blattodea: Ectobiidae). Furthermore, thanks to field sampling, we noticed for the first time that *M. brevipennis* predominantly can be found in patches of native vegetation from Matorral biome, for instance, associated to endemic plant species from *Puya* (Bromeliaceae) genus, where we recorded these wild cockroaches feeding on flowers at dusk. Under the light of these findings, we discuss the relevance of the association between *M. brevipennis* and native plants for its survival in this semiarid habitat, its potential ecological function and the ongoing hazards for native insect species resulting from nearby urban sprawl in coastal central Chile.

© 2017 Sociedade Brasileira de Entomologia. Published by Elsevier Editora Ltda. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

Despite being popularly recognized as household pests, less than 1% of all described cockroach species are adapted to human-dominated habitats. Pest or domestic cockroaches are capable of colonizing human habitat and can become a health concern as well as an urban nuisance (Rivault et al., 1993; World Health Organization, 1999). By the contrary, the remaining known cockroach species are commonly not associated with urbanized environments, as they live in diverse natural ecosystems, where these insects play key ecological roles (Roth and Willis, 1960; Bell et al., 2007). For instance, besides of its contribution with nutrient cycling and organic matter turnover (Irmer and Furch, 1979; Geng and Côté, 2002; Tarli et al., 2014), wild cockroaches play important ecological roles as detritivores (Tarli et al., 2014; Mullins, 2015), florivores (Ball et al., 1942), xylophagous (Pellens et al., 2002),

and even pollinators (Nagamitsu and Inoue, 1997; Vlasáková et al., 2008).

The distribution of wild cockroaches is mainly restricted to natural areas in tropical regions of the globe. For instance, in South America most records for wild species are from Brazil (Albuquerque and Lopes, 1976; Pellens and Grandcolas, 2008) and Guiana Shield (Grandcolas, 1994a,b; Evangelista et al., 2015). Among the explanations for this constraint distribution is that cockroaches exhibit intolerance to low humidity and extreme temperatures, which also restricts the number of potential habitats for these insects to the equatorial regions (Bell et al., 2007). Despite this general pattern, there are formidable exceptions of wild cockroaches found in dry environments such as genus *Arenivaga* (Corydiidae) inhabiting sand dunes in California (Hawke and Farley, 1973), *Heterogamisca chopardi* Uvarov, 1936 (Corydiidae) (Grandcolas, 1995) and *Polyphaga aegyptiaca* (Corydiidae) from Saudi-Arabia desert (Grandcolas, 1996). Moreover, wild cockroaches can also inhabit temperate environments, as it is the case of *Epilampra hualpensis* (Blaberidae) (Urbe, 1977) and *Moluchia strigata* (Ectobiidae), endemic species from Mediterranean-type sclerophyllous forest in central Chile (Villagra and Schapheer, 2016). In these

* Corresponding author.

E-mail: cp.schapheer@gmail.com (C. Schapheer).

last-mentioned cases, roaches were found in association with endemic Bromeliad litter (Uribe, 1977; Villagra and Schapheer, 2016).

Considering these examples of habitat use by non-tropical species, it is possible to suggest that wild cockroaches' distribution and its ecological associations may be underrepresented in current literature; currently, we made a search for scientific articles in Google Scholar® using keywords; cockroach, Blattodea or Blattaria, between years 2000 and 2016 ($n = 500$ papers), and discovered that only 36% (178 papers) corresponded to studies on wild cockroaches. Furthermore, from that fraction no more than 7% (13 papers) were focused on the ecological associations or distribution of native species. Despite this scarcity of non-tropical cockroaches studied, these evidences may illustrate the colonization patterns of subtropical and temperate regions of the world by Blattodea. Thus, this kind of work is quite valuable and efforts concentrated in surveying for new species in non-tropical regions as well as disentangling its ecological interaction are paramount in order to understand the ecological and evolutionary dynamics of these insects (Caesar et al., 2015).

South America temperate regions such as central Chile are suitable candidate spots for these explorations, as these latitudes have been scarcely explored for native cockroach species. Regarding cockroaches in Chile, the most recent species description was made in the seventies (Uribe, 1977), and the latest revision on this order was published in the same decade (Moroni and Camousseight, 1976). To date, thirteen endemic and five introduced cockroach species have been reported for Chile (see Appendix A; Moroni and Camousseight, 1976; Artigas, 1994; Camousseight, 2008a,b).

With respect to its distribution, while pest species have been reported in urban centers and commercial ports in central Chile (Schapheer et al., 2016), Chilean wild cockroaches have been reported in areas with native plant communities along inner valleys of this region (Villagra and Schapheer, 2016). However, so far, these insects have never been surveyed along the coastline of the Mediterranean scrubland type biome (Matorral) in central Chile. This unique biome sustains a rich community of xeric and sclerophyllous autochthonous plant species, being considered among world biodiversity hotspot, even despite of human-derived habitat degradation (Mittermeier et al., 2004; Wilson et al., 2007; Underwood et al., 2009; Schulz et al., 2010; Armesto et al., 2010).

The aim of this work it is to study the distribution, habitat use and possible associations of a wild cockroach species, *Moluchia brevipennis* (Saussure, 1864) (Ectobiidae), with native vegetation at a transitional zone between desertic and temperate environments in Mediterranean Matorral of central Chile (Santibañez et al., 2008). We sampled cockroaches in natural habitats and urban areas through field surveys using two methods (onion baits and active collecting). Species identification was achieved using a combination of morphological and molecular data. We discuss our results in the context of cockroach's use of drier regions of the world as well as the potential ecological relationships for *M. brevipennis* and its tolerance to different degrees of urbanization.

Methods

Study area

Our study covered coastal Mediterranean-type scrubland biome from the southern frontier of the IV Region, Choapa Province, to V Region, San Antonio Province Chile (see Table 1 and Fig. 1) central Chile (Luebert and Plissock, 2006). This area is characterized by consistent low temperatures year-round, with an annual average temperature of 14 °C, oscillating in summer between 15 °C and 27 °C and in the winter between 8 °C and 18 °C and 450 mm annual

Table 1
Large-scale distribution data of *Moluchia brevipennis*.

Site	Geographical coordinates	Data type	<i>M. brevipennis</i> presence
Cachagua	32°34'36.56" S 71°27'09.79" W	FC	Yes
Los Molles	32°14'09.92" S 71°31'30.55" W	FC	Yes
Zapallar	32°33'08.88" S 71°28'07.95" W	FC	Yes
Los Molles	32°14'07.39" S 71°30'40.85" W	FC	Yes
Los Molles	33°22'51.24" S 71°14'11.46" W	FC	Yes
Cuesta Zapata	32°08'01.57" S 71°32'01.48" W	FC	Yes
Pichidangui	32°30'16.00" S 71°28'08.73" W	FC	Yes
Cementerio Papudo	32°33'08.88" S 71°28'07.95" W	FC	Yes
Los Lilenes	33°22'03.10" S 71°40'17.60" W	FC	Yes
Papudo Centro	33°19'20.52" S 71°39'00.29" W	FC	Yes
Mirasol	33°26'23.56" S 71°39'05.23" W	FC	Yes
Punta Lobos	31°54'53" S 71°31'03" W	EC MCCN	Yes
Playa de Ñague	31°55' S 71°31' W	EC IEUMCE	Yes
Quintay	33°11'30.1" S 71°41'52.3" W	FC	Yes
Valparaíso	33°01'11.5" S 71°38'18.0" W	FC	No
Viña del Mar	33°00'14.7" S 71°33'00.3" W	FC	No
Concon	32°55'19.4" S 71°31'25.8" W	FC	No
Pullally	32°23'27.4" S 71°24'31.6" W	FC	No
Calera de Tango	33°38'10.3" S 70°46'16.7" W	FC	No
Pirque	33°40'56.7" S 70°34'44.7" W	FC	No
San Sebastián	33°31'35.7" S 71°36'07.4" W	FC	No
Santo Domingo	33°38'07.7" S 71°38'07.5" W	FC	No
Las Cruces	33°30'00.6" S 71°38'03.9" W	FC	No

Abbreviations: FC, field collect; EC, entomological collection; MCCN, Museo Nacional de Historia Natural; IEUMCE, Colección Entomológica Instituto de Entomología.

precipitation. Average humidity is consistently high around 75–80% due to sea mist, which maintains this humidity level throughout almost the whole year along the coastline (Di Castri and Hajek, 1976).

Sclerophyllous and xerophyllous vegetation such as trees, bushes and cacti dominate the landscape (Parsons, 1976). The most representative plants from this scrubland biome include *Bahia* spp., *Haplopappus* spp. (Asteraceae), *Fuchsia* spp. (Onagraceae), *Puya* spp. (Bromeliaceae) and *Pouteria* spp. (Sapotaceae) (Villagrán et al., 2007) among other native and endemic plant species (Zizka et al., 2009).

Large spatial scale: distribution

James Rehn reported *Moluchia brevipennis* in 1933, only labeling its collection locality as "Valparaiso" (fifth region of Chilean territory) without given any further detail of collecting site of the specimen. We first studied collection specimens of native cockroaches in order to determine the geographic distribution

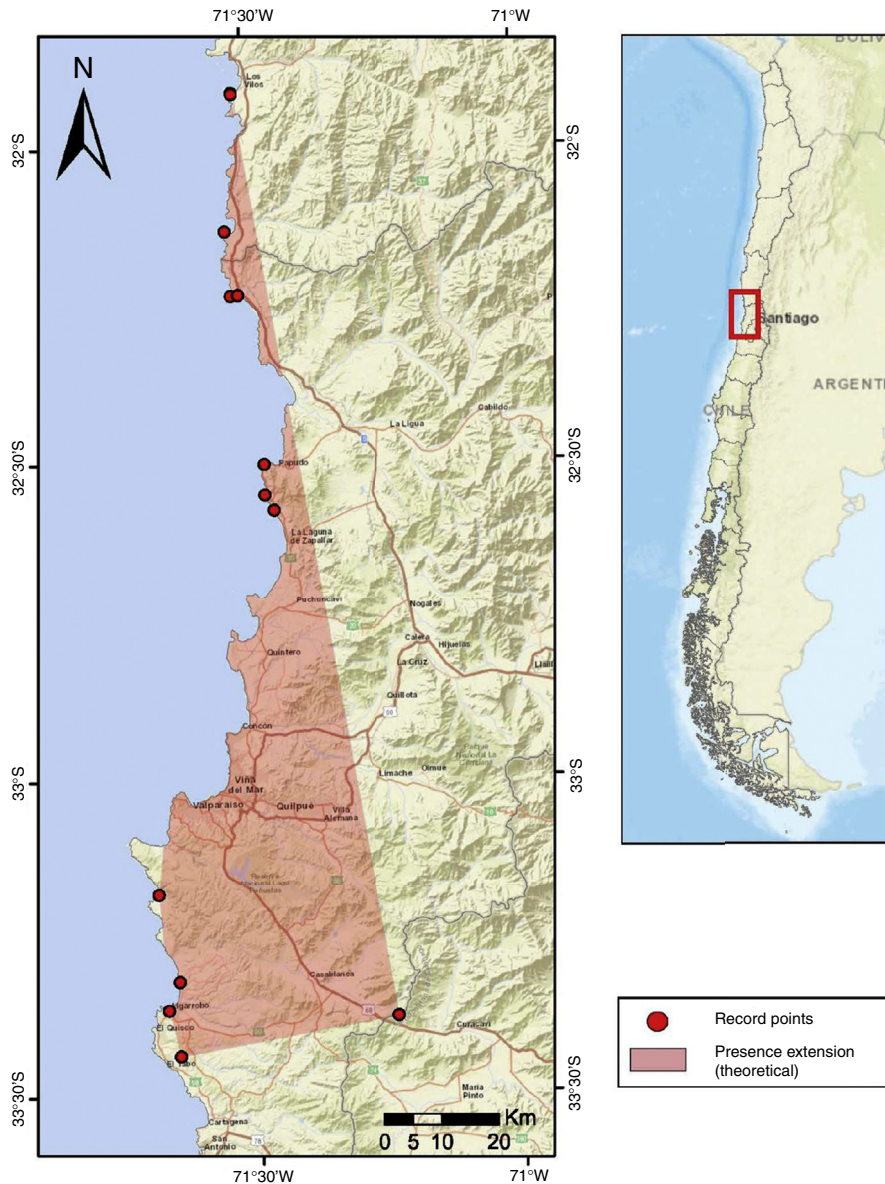
Moluchia brevipennis (Saussure, 1864)

Fig. 1. Registration points and theoretical presence extension of *M. brevipennis*.

of this species. We used specimens from the following Chilean entomological collections: *Instituto de Entomología Universidad Metropolitana de Ciencias de la Educación* (IE-UMCE), *Museo Nacional de Historia Natural* (MNNC), *Museo de Zoología de la Universidad de Concepción* (MZUC-UCCC) and *Colección Entomológica Servicio Agrícola Ganadero* (CE-SAG). Additionally, as a supplementary source of distribution information, from September to April of 2014–2016 (spring to autumn in Southern Hemisphere), we actively field collected cockroaches in 21 consecutive sites separated approximately by 15 km. Our sampling was comprised in the Mediterranean Matorral biome area in central Chile covering approximately 3000 km² in total (see Table 1). Moreover, considering our previous work on Chilean wild cockroaches showing crepuscular foraging for these insect (Villagra and Schapheer, 2016), we actively-collected these insects from dusk to midnight (18:00–24:00 h) through five walking transects (at each site) along the east–west axis of the area, covering 2 km² in each row (e.g. Table 1). We preserved all collected specimens

in 95% ethanol and deposited samples in the Entomological Collection of *Instituto de Entomología* (IEUMCE) and *Museo Nacional de Historia Natural*, Santiago, Chile (MCCN).

Finally, using entomological collection records and our own field data, we developed a theoretical distribution map using minimum convex polygon method (Mohr, 1947), a technique that allow to estimate species use of a given area based on site of collecting information (De Almeida et al., 2010).

Local spatial scale: habitat use

During October 2013 to March 2015, we sampled crawling insects using active collecting (above mentioned) and bait trapping (using slices of fresh onion) from 40 collection points (9 m² each one) at Los Molles headland (32° 14' 22" S 71° 30' 54" W). This site is characterized as a coastal strip comprising sclerophyllous scrubland plant formation, a community dominated by plant species adapted to xeric environments from Mediterranean-type

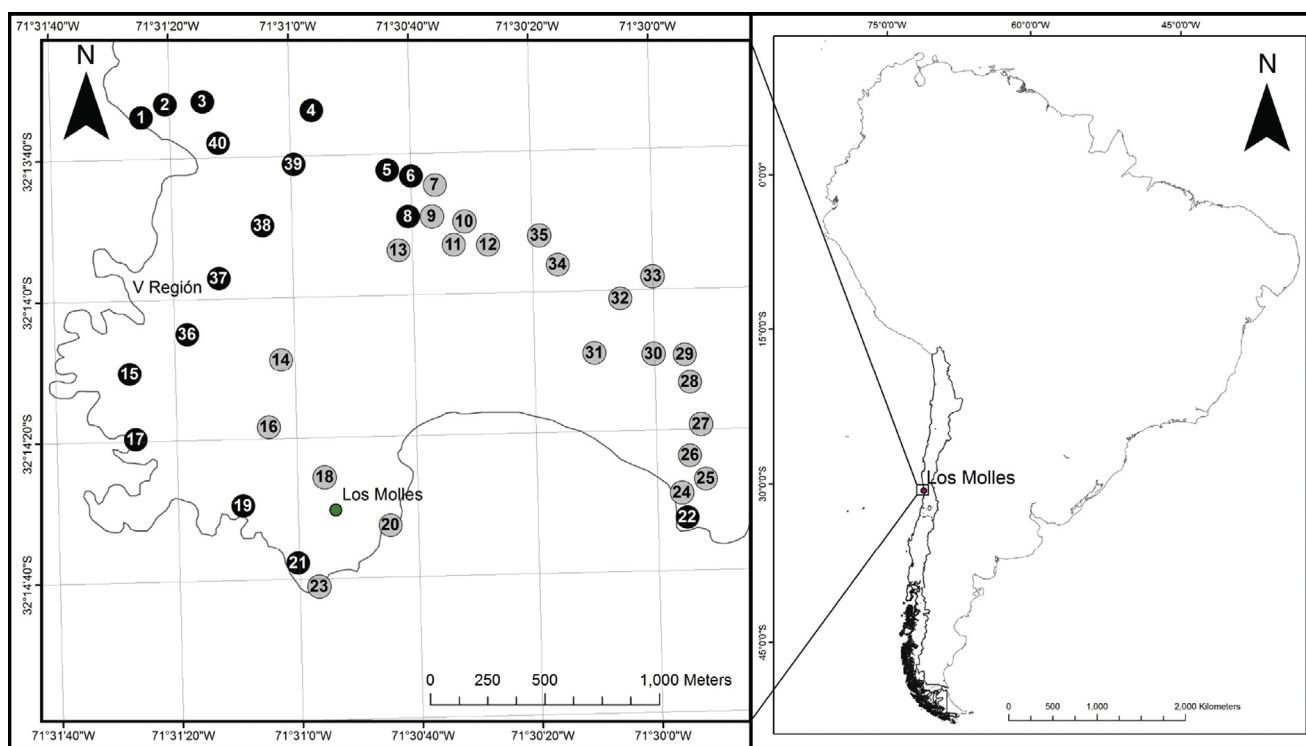


Fig. 2. Distribution of sampled sites at Los Molles. Right panel show South America map highlighting central Los Molles locality in Chile's Mediterranean Matorral area. Left panel correspond to a detailed map of Los Molles showing sampling details. Black dots correspond to active collecting and gray dots to trapping, see Table 1 for more details.

climate (Luebert and Plissock, 2006). This location is one of the best preserved patches for this native habitat, now heavily impacted by increasing urbanization, which drives native plant species loss (CONAF, 1989; Ormazabal, 1993; Rundel et al., 1998), and increasing habitat homogenization (Andrade and Hidalgo, 1996; Underwood et al., 2009).

Sampling at Los Molles covered approximately 6.6 km² in total (Fig. 2). We classified sampling points in two categories: “Matorral” for sites with native vegetation and “No Matorral” for sites without native plant formation (typically bare land or urbanized areas). In order to compare the presence of native cockroaches in “Matorral” and “No Matorral” sites we used Chi-square comparisons (Zar, 1999). For active collecting method (17 sampled sites), beside of plant formation classification, we recorded whether cockroaches were found in or nearby any plant (native or introduced) or if it was found in other substrates, such as naked soil or nearby rocks (Table 2). For plant identification, we followed Villagrán et al. (2007).

Taxonomic identification

In order to obtain a proper identification, first we discarded the presence of introduced cockroach species by using a general key for cosmopolitan and pest cockroaches present in Chile (extracted and modified from Ragge, 1973 by Camousseight, 2008b). Following this, we used the specific key for native cockroach from genus *Moluchia*, described for the V Region, Chile (Rehn, 1933). This latter key uses diagnostic characters only found in adult from this genus such as the number of tergal specializations (“TeS” in Fig. 3). Therefore, we based our taxonomic identification on *M. brevipennis* adult male characters. To corroborate morphological identification for nymph and female specimens, we sequenced the cytochrome oxidase I (COI) barcode region from three *M. brevipennis* individuals (1 male, 1 female and 1 nymph) and two adults of introduced species: *Blattella germanica* (Ectobiidae) and *Blatta orientalis*

(Blattidae). We extracted DNA using the DNAeasy QIAGEN kit, and we used the LepF1 (5'-ATTCAACCAATCATAAAGATAT-3') and LepR1 (5'-TAAACTTCTGGATGTCCAAAAA-3') primers to amplify the mitochondrial COI barcode region using standardized PCR conditions. Based on this, we performed a maximum likelihood phylogenetic reconstruction within Blattodea family, excluding Termitidae. By this procedure, we aim to confirm our morphological classification for immature and female specimens, which are not considered in Rehn's keys (1933) because it only focuses on male roach adult traits.

Results

We identified male individuals from our samplings as the native species *M. brevipennis* (*sensu* Rehn, 1933). Likewise, we were capable to differentiate *M. brevipennis* nymphs from cosmopolitan introduced species, such as *B. orientalis*, based on 10th abdominal tergite morphological differences; *M. brevipennis* individuals have one tip in the supranal plate whereas *B. orientalis* has two tips protruding from that terminal structure (Fig. 3). We corroborated that females collected corresponded to *M. brevipennis* based on careful comparisons of morphological traits not associated with the genitalia. This was also supported by barcode COI region of the three specimens we sequenced. The phylogenetic reconstruction placed *M. brevipennis* within the family the family Ectobiidae, which comprises major pest species such as *B. germanica* (Fig. 4). Sequences from *M. brevipennis* were deposited in GenBank (Accession Nos. KT957948–KT957950).

The distribution of *M. brevipennis* extends between the 31°54'53" S and 33°26'23.56" S South Latitude, with most of their records next to the coastline of the continent (93%). All these localities share a similar habitat corresponding to the Mediterranean Matorral biome of the coastline in Valparaíso region. Estimated distribution area covers a minimum convex polygon of 2.546 km² (Mohr, 1947). However, this range includes also large areas

Table 2
Cockroach sampled by trapping and active collect in Matorral and No-Matorral sites.

No.	Sampling type	Site category	Site description	Date	Developmental stage
1	A	M	<i>Carpobrotus chilensis</i> flowers and <i>Nolana sediflora</i> leaves	March 15	Ny
2	A	M	<i>Puya chilensis</i> scape and leaf flowers	November 14	Ad
3	A	M	Around <i>Haplopappus platylepis</i>	December 14	Ny
4	A	M	Under stones	March 15	Ny
5	A	M	<i>Haplopappus foliosus</i> flowers and leaves	November 14	Ad
6	A	M	<i>Haplopappus foliosus</i> flowers and leaves	October 13	Adult
7	T	NM	Debris dump	November 14	Ad
8	A	NM	On stones	November 14	Ad
9	T	NM	Rubbish dump	November 14	Nc
10	T	NM	Public Square	November 14	Nc
11	T	NM	Empty place	November 14	Nc
12	T	NM	Occupied house	November 14	Nc
13	T	NM	Gate in empty place	November 14	Nc
14	T	NM	House garden	November 14	Nc
15	A	M	<i>Oenothera acaulis</i> flowers	October 13	Ad
16	T	NM	Abandoned house foundations with <i>Oenothera acaulis</i>	November 14	Ad
17	A	M	Coastline <i>Puya venusta</i> leaves	October 14	Ny
18	T	M	Square	November 14	Nc
19	A	M	<i>Haplopappus chrysantemifolius</i> flowers	October 13	Ny
20	T	M	Coastline <i>Carpobrotus chilensis</i> leaves	November 14	Ad
21	A	M	<i>Carpobrotus chilensis</i> flowers	October 13	Ad
22	A	M	<i>Nolana sediflora</i> leaves	November 14	Ad
23	T	NM	Ornamental bush	November 14	Ad
24	T	M	<i>Carpobrotus chilensis</i> flowers	December 15	Ad/Ny
25	T	M	Below <i>Puya chilensis</i>	December 15	Ad
26	T	M	<i>Lithrea caustica</i> leaves	December 15	Ad
27	T	M	Below <i>Fuchsia</i> sp.	December 15	Nc
28	T	NM	Next to a house fence	December 15	Nc
29	T	NM	In front of a house	December 15	Nc
30	T	NM	Near a lamp post	December 15	Nc
31	T	NM	Rubbish dump	December 15	Nc
32	T	NM	Entrance gate of a house	December 15	Nc
33	T	NM	Under a water tank	December 15	Ad
34	T	NM	Country road	December 15	Nc
35	T	NM	Country road	December 15	Nc
36	A	M	Below <i>Pouteria splendens</i> litter	October 15	Ad
37	A	M	Below <i>Pouteria splendens</i> litter	October 15	Ad
38	A	M	Below <i>Pouteria splendens</i> litter	October 15	Ad
39	A	M	Below <i>Pouteria splendens</i> litter	October 15	Ad
40	A	M	Below <i>Puya chilensis</i>	October 15	Ad

Abbreviations: A, active; T, trapping; M, Matorral; NM, No Matorral; Ny, nymph; Ad, Adult; Nc, no cockroaches.

modified by human activities such as urban areas, industry lots, ports and agriculture lands, among others. So, it is likely that *M. brevipennis*' populations may be highly fragmented inside this theoretical distribution (Fig. 1).

We exclusively found this wild cockroach species in well-preserved native vegetation of the Matorral biome. Moreover, these endemic reaches were absent from bare land and urbanized areas (Figs. 2 and 5 and Table 2). We found an association between presence of *M. brevipennis* and native plant species, with 80% of collected specimens from this wild cockroach found with the native vegetation (Chi-square: $q = 6.026$; $p < 0.05$; Table 2).

Both at large and local spatial scales we observed *M. brevipennis* feeding on floral resources (nectar and pollen). We identified these cockroaches as crepuscular floral visitors of various native plant species, such as *Carpobrotus chilensis* (Aizoaceae), *Nolana sedifolia* (Nolanaceae), *Haplopappus foliosus* and *Haplopappus chrysantemifolius* (Asteraceae), *Oenothera acaulis* (Onagraceae), as well as *Puya venusta* and *P. chilensis* (Bromeliaceae) (Fig. 5 and Table 2). We also found *M. brevipennis* individuals on leaves of plants that did not have any flowers, particularly *Lithrea caustica* (Anacardiaceae). Furthermore, occasionally, we also recorded the following insects: *Heteromallus* sp. (Orthoptera: Rhaphidophoridae), *Falcipectes divisus* Rentz & Gurney, 1985 (Orthoptera: Tettigoniidae) and *Anisophya* sp. (Orthoptera: Tettigoniidae) (Rentz and Gurney, 1985), as well as unknown Oniscidea (Isopoda). However, during our observations, we found *M. brevipennis* individuals are abundant

at flowers of native plants than any other nocturnal flower-visiting arthropod (Orthoptera, Coleoptera, Dermaptera and Isopoda).

Discussion

Here we report for the first time the distribution, habitat preference and plant associations for the endemic cockroach species *M. brevipennis* (Blattodea: Ectobiidae) at the coastal range of Mediterranean Matorral of central Chile. To date, this may correspond to the most southern record for wild Blattodea species from a semiarid biome in the Neotropical Region.

Male specimens collected match morphological couplets available in keys for native cockroaches (Rehn, 1933) and do not fit morphological description for any introduced species reported for Chile (Camousseight, 2008a). Moreover, preliminary phylogenetic placement of our collected specimens based on mitochondrial barcode COI region separated them in a consistent cluster inside Ectobiidae; differentiated from cosmopolitan cockroach species currently recorded for Chile (Fig. 5). Therefore, our results suggest that previous reports of *B. orientalis* associated with native flora patches at Los Molles by Vergara et al. (2011) may correspond to a misidentification of specimens collected. This is very likely, considering that nymphal instar of *M. brevipennis* is slightly similar to the introduced species *B. orientalis* morphologically (Fig. 3). In synthesis, our results suggest that only native cockroaches are associated

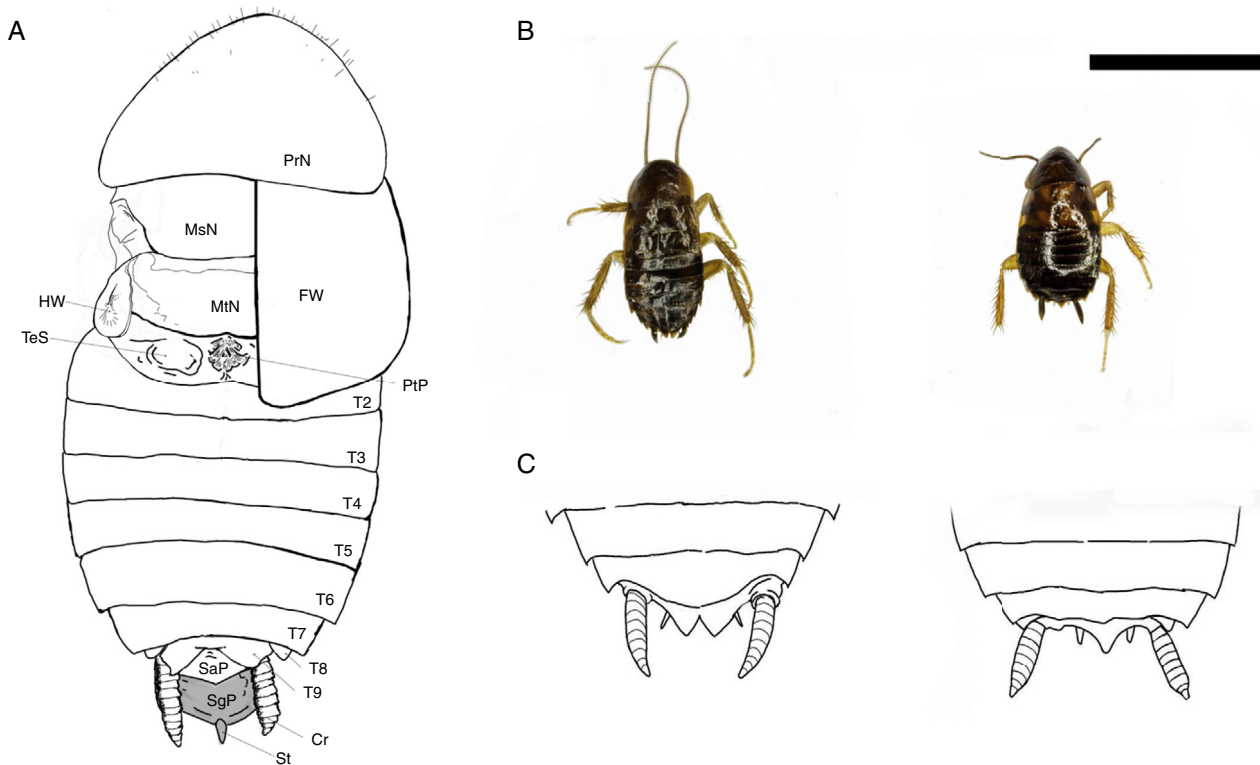


Fig. 3. (A) Diagram of male *M. brevipennis* without left forewing, dorsal view. Abbreviations: PrN, Pronotum; MsN, Mesonotum; MtN, Metanotum; HW, Hind Wing; FW, Fore Wing; TeS, Tergal specialization; PtP, Proximal tergal pubescence; T2–T9, Tergites; SaP, Supra-anal plate; Cr, Cercus; SgP, Subgenital plate; St, Style. (B) Nymphs photographs; *Blatta orientalis* (left side) and *Moluchia brevipennis* (right side), scale bar correspond 1 cm. (C) Schematic drawing of nymphs tenth tergite left side drawing correspond to *B. orientalis* meanwhile right side to *M. brevipennis*.

with native plant species along the coastal Mediterranean Matorral biome of central Chile.

Traditionally, wild cockroaches are associated with tropical environments and their importance in Mediterranean environments has been underestimated (but see Caesar et al., 2015). Besides of its intolerance to anthropized habitats, it is proposed that these insects may face physiological restrictions to relatively dry environments (Mullins, 2015). In the case of non-tropical species, it is also possible that wild cockroach distribution may depend on the availability of favorable conditions both at large and local scales. For *M. brevipennis*, large-scale distribution map shows a coastline-restricted distribution in the northernmost area of its theoretical distribution. However, as the sampling goes further south, this distribution goes widened (Fig. 1). This pattern is consistent with the limits for Chile's arid region, mapped in latitude 32° S. Therefore, it is plausible to hypothesize that the longitudinal expansion of *M. brevipennis* to the south may be supported by increase in humidity from inner valleys in this Mediterranean zone such as Curacaví locality (32°08'01,57" S, 71°32'01,48" W). Further research it is needed in order to evaluate ecophysiological restrictions on the southern distribution of this wild cockroach lineage.

This may also be the case of our study species *M. brevipennis*, where we found a trophic interaction with native plant species. Our observations indicate that *M. brevipennis* are floral visitors on a variety of native plant species (Table 2). For example, we observed *M. brevipennis* congregating around flowers such of evening primrose *O. acaulis*, *Haplopappus* shrubs, and the endemic bromeliad “chagualiyo” species *Puya venusta* and *P. chilensis*. For instance, we registered *M. brevipennis* eating pollen of *O. acaulis*, and even attempting to access to nectar resources from its flowers (Fig. 5). To the best of our knowledge the cases of pollen-feeding cockroaches are scarce (but see Lepschi, 1989; Rentz, 2014; Nagamitsu and Inoue, 1997). Thus *M. brevipennis*' pollen-feeding relationship

with native flora may be associated with the reproductive phenology of these cockroaches. This could explain why during peak adult emergence, we only found cockroaches near places where floral resources from native plant species were available (Table 2).

We observed *M. brevipennis* feeding mostly on floral resources from bromeliads *P. chilensis* and *P. venusta*; a plant genus belonging to tropical bromeliad origins (Zizka et al., 2009). Besides, we have found *M. brevipennis*' ootecae on the leaf joints of *P. venusta*. These observations suggest that, as it was discovered by Grandcolas (1995) for Sahara Desert cockroaches, *M. brevipennis* not only feed from many native plant species, but also use at least one native plant genus (*Puya*) to lay eggs in a microhabitat composed by the vegetation matrix that may protect its offspring from environmental stress and potential predators (Schapheer and Villagra, 2016, unpublished data). Based on all these evidences we suggest that the interaction of *M. brevipennis* with native plants may be essential for their survival in this non-tropical biome, allowing explaining the presence of these non-tropical wild cockroaches in the relatively dryer environment of Mediterranean Matorral in central Chile.

Our results allow us to hypothesize that the distribution of *M. brevipennis* extends to a theoretical polygon of 2.546 km² (Fig. 1). However, we are aware that this may correspond to an overestimation of the actual distribution of this species. The Chilean coastal area is currently suffering extensive human-driven modifications, including extensive fragmentation of native plant communities coupled with the replacement of wild vegetation with exotic plant species in central Chile (Armesto et al., 2010). Furthermore, we discovered that *M. brevipennis* it is only found in association with endemic flora at well-preserved patches of coastal Mediterranean Matorral biome in central Chile (such as Bioparque Puquén, at Los Molles), therefore, *M. brevipennis*' potential habitat specialization may also relate to a restricted distribution in central Chile. Known *Moluchia* species, due to its non-functional wing morphology

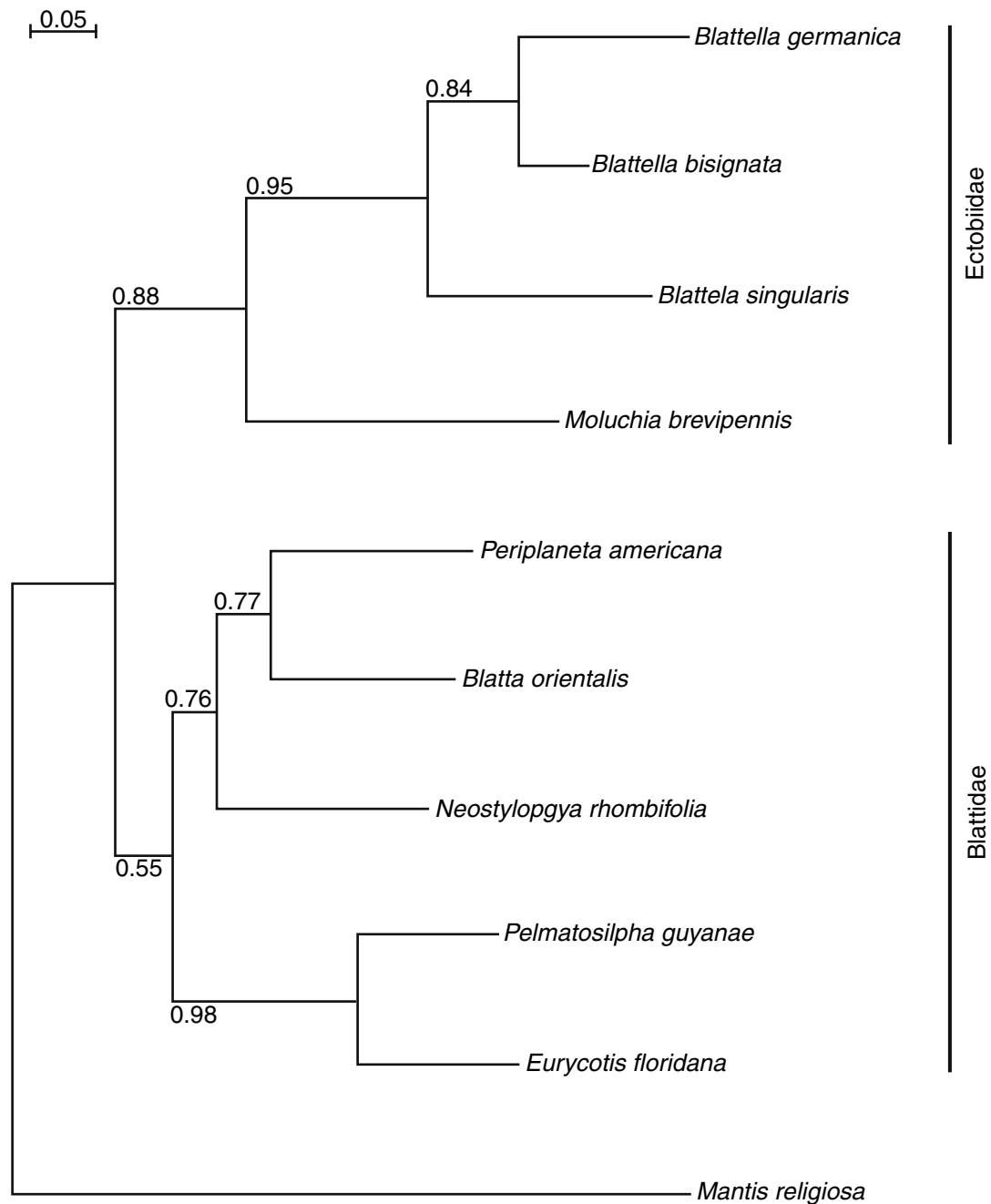


Fig. 4. Maximum likelihood genera phylogenetic reconstruction within Blattodea family, excluding Termitidae, based on the mitochondrial gene cytochrome oxidase I (COI). Numbers indicate branch support based on 1000 bootstrap replicates.

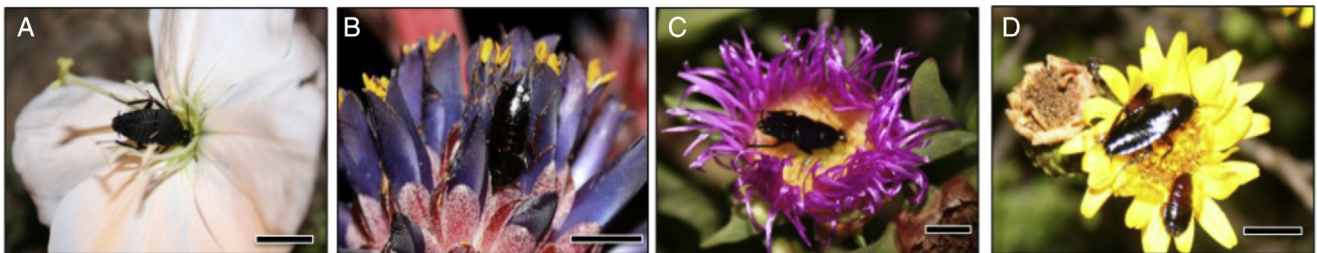


Fig. 5. Native plant hosting *M. brevipennis* cockroaches at our study site. (A) Cockroaches feeding pollen from *Oenothera acaulis* (Onagraceae) flowers, (B) *Puya venusta* (Bromeliaceae) inflorescences with cockroaches reaching nectar sources, (C) *Carpobrotus chilensis* (Aizoaceae) with cockroach inside inflorescence and climbing branch, (D) *Haplopappus chrysantemifolius* (Asteraceae) with adult and nymphs feeding on florets from floral head, black bar indicates a 1 cm scale.

(Rehn, 1933; Villagra and Schapheer, 2016; see Fig. 3 Panel A), may be highly susceptible to habitat fragmentation effect. This was found in the Brazilian cockroach species *Monastria biguttata* (Thunberg, 1826) (Blattodea: Blaberidae), which lacks functional wings and shows negative effect of fragmentation on the dispersal of individuals (Pellens et al., 2010; Pellens and Grandcolas, 2007). Our findings raise concerns about threats to native cockroaches and their interactions with native plants. It is possible that these associations may be susceptible to the replacement of native flora with introduced plant species. This introduction of ornamental or agriculturally relevant plant species is happening at an accelerated rate with the urbanization projects in coastal central Chile. Additional work is necessary to evaluate this environmental problem.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

We thank Christian Muñoz for his assistance with distribution map. Moreover, we thank Dr. Pablo Guerrero, Universidad de Concepción, Mario Elgueta, MNNC for their help with entomological collections, Dr. Derek Artz for valuable suggestions on our manuscript and Marco Baeza for fieldwork assistance. This research was funded by “Proyecto de Iniciación” FONDECYT No. 11100109 and DIUMCE FIBE 0812 granted to Cristian Villagra, RSG to Rufford Foundation Nos. 18114-1 and 21286-2 granted to Constanza Schapheer.

Appendix A. Cockroaches species present in Chile

The extreme right column refers to its “Category” regarding if the insect is “Endemic”, a species so far only reported only for Chile. “Domestic” category refers if this is an introduced species currently spreading in the main urban centers and finally “Exotic” represents introduced species that were trapped in ports or border posts, but have not yet established or reported in the country. Information obtained from Camousseight (2008a,b).

Species	Family	Category
<i>Eurycotis brevipes</i> (Philippi, 1863)	Blattidae	Endemic
<i>Phidon araucanus</i> Rehn, 1933	Ectobiidae	Endemic
<i>P. bullocki</i> Rehn, 1933	Ectobiidae	Endemic
<i>P. dubius</i> Princis, 1952	Ectobiidae	Endemic
<i>P. reticularis</i> (Blanchard, 1851)	Ectobiidae	Endemic
<i>Epilampra hualpensis</i> Uribe, 1978	Blaberidae	Endemic
<i>Ischnoptera brattstroemi</i> Princis, 1952	Ectobiidae	Endemic
<i>Moluchia brevipennis</i> (Saussure, 1854)	Ectobiidae	Endemic
<i>M. castanea</i> (Blanchard, 1851)	Ectobiidae	Endemic
<i>M. dahli</i> Princis, 1952	Ectobiidae	Endemic
<i>M. nana</i> Rehn, 1933	Ectobiidae	Endemic
<i>M. strigata</i> (Blanchard, 1851)	Ectobiidae	Endemic
<i>Parasphaeria ovata</i> (Blanchard, 1851)	Blaberidae	Endemic
<i>Periplaneta australasiae</i> (Fabricius, 1775)	Blattidae	Domestic
<i>P. americana</i> (Linnaeus, 1758)	Blattidae	Domestic
<i>P. brunnea</i> Burmeister, 1838	Blattidae	Domestic
<i>Blatta orientalis</i> (Linnaeus, 1758)	Blattidae	Domestic
<i>Blatella germanica</i> (Linnaeus, 1767)	Ectobiidae	Domestic
<i>Melanozosteria soror</i> (Brunner Von Wattenwyl, 1865)	Blattidae	Exotic
<i>Lupparia subnotulata</i> (Princis, 1950)	Ectobiidae	Exotic
<i>Blaberus atropos</i> (Stoll, 1813)	Blaberidae	Exotic
<i>Diploptera punctata</i> (Eschscholtz, 1822)	Blaberidae	Exotic
<i>Pycnoscelus surinamensis</i> (Linnaeus, 1758)	Blaberidae	Exotic

References

Albuquerque, I.R.S., Lopes, S.M.R., 1976. *Blattaria de bromelia* (Dictyoptera). Rev. Bras. Biol. 36, 873–901.

- Armesto, J.J., Manuscovich, D., Mora, A., Smith-Ramirez, C., Rozzi, R., Abarzúa, A.M., Marquet, P.A., 2010. From the Holocene to the Anthropocene: a historical framework for land cover change in southwestern South America in the past 15,000 years. *Land Use Policy* 27, 148–160.
- De Almeida, M.C., Cortes, L.G., De Marco Junior, J., 2010. New records and a niche model for the distribution of two neotropical damselflies: *Schistobolus boliviensis* and *Tuberculosia inversa* (Odonata: Coenagrionidae). *Insect. Conserv. Divers.* 3, 252–256.
- Andrade, B., Hidalgo, R., 1996. La zona costera y los instrumentos de planificación territorial: Litoral de la Provincia de Petorca. *Rev. Geogr. Chile Terra Australis* 41, 111–120.
- Artigas, J.N., 1994. *Entomología económica insectos de interés agrícola, forestal, médico y veterinario*, vol. 1. Ediciones Universidad de Concepción, Concepción.
- Ball, E., Tinkham, E., Flock, R., Vorhies, C., 1942. The Grasshoppers and Other Orthoptera of Arizona. Technical Bulletin (University of Arizona, Agricultural Experiment Station).
- Bell, W.J., Roth, L.M., Nalepa, C.A., 2007. *Cockroaches: Ecology, Behavior, and Natural History*. JHU Press, Baltimore.
- Caesar, M., Roy, R., Legendre, F., Grandcolas, P., Pellens, R., 2015. Catalogue of dictyoptera from Syria and neighbouring countries (Lebanon, Turkey, Iraq and Jordan). *Zootaxa* 3948, 71–92.
- Camousseight, A., 2008a. Orden Blattodea (baratas, cucarachas). Biodiversidad de Chile, Patrimonio y Desafíos, 2nd ed. Comisión Nacional del Medio Ambiente, Santiago de Chile.
- Camousseight, A., 2008b. Baratas o cucarachas. *Zoología médica II: Invertebrados*, 1st ed. Editorial Universitaria, Santiago de Chile.
- CONAF, 1989. In: Benoit, L. (Ed.), Libro rojo de la flora terrestre de Chile (primera parte). CONAF, Santiago de Chile.
- Di Castri, F., Hajek, E.R., 1976. *Bioclimatografía de Chile*. Ediciones Universidad Católica de Chile, Santiago de Chile.
- Evangelista, D.A., Chan, K., Kaplan, K.L., Wilson, M.M., Ware, J.L., 2015. The Blattodea s.s. (Insecta, Dictyoptera) of the Guiana Shield. *ZooKeys* 475, 37–87.
- Geng, Y., Côté, R.P., 2002. Scavengers and decomposers in an eco-industrial park. *Int. J. Sustain. Dev. World Ecol.* 9, 333–340.
- Grandcolas, P., 1994a. Les Blattes de la forêt tropicale de Guyane Française: structure du peuplement (Insecta, Dictyoptera, Blattaria). *Bull. Soc. Zool. Fr.* 119, 59–67.
- Grandcolas, P., 1994b. La richesse spécifique des communautés de Blattes du sous-bois en forêt tropicale de Guyane Française. *Rev. Ecol. (Terre Vie)* 49, 139–150.
- Grandcolas, P., 1995. Bionomics of a desert cockroach, *Heterogamisa chopardi* Uvarov, 1936 after the spring rainfalls in Saudi Arabia (Insecta, Blattaria, Polyphaginae). *J. Arid Environ.* 31, 325–334.
- Grandcolas, P., 1996. Habitat and population structure of *Polyphaga aegyptiaca* (Blattaria Polyphagidae) in Asir, Saudi Arabia. *Ann. Soc. Entomol. Fr.* 32, 201–205.
- Hawke, S.D., Farley, R., 1973. Ecology and behavior of the desert burrowing cockroach, *Arenivaga* sp. (Dictyoptera, Polyphagidae). *Oecologia* 11, 263–279.
- Irmer, U., Furch, K., 1979. Production, energy and nutrient turnover of the cockroach *Epilampra irmieri* Rocha e Silva and Aguilar in a Central-Amazonian inundation forest. *Amazoniana* 6, 497–520.
- Lepschi, B., 1989. A preliminary note on the food of *Imblattella orchidae* Ashahina (Blattodea: Blattellidae). *Aust. Ent. Mag.* 16, 41–42.
- Mittermeier, R.A., Myers, N., Mittermeier, C.G., Robles-Gil, P., 2004. Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. CEMEX, SA, Agrupación Sierra Madre, SC.
- Mohr, C.O., 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37, 223–249.
- Moroni, J., Camousseight, A., 1976. Aporte al estudio de las baratas de Chile. *Bol. Soc. Biol. Concepción* 1, 43–51.
- Mullins, D.E., 2015. Physiology of environmental adaptations and resource acquisition in cockroaches. *Annu. Rev. Entomol.* 60, 473–492.
- Nagamitsu, T., Inoue, T., 1997. Cockroach pollination and breeding system *Uvaria elmeri* (Annonaceae) in a lowland mixed-dipterocarp forest in Sarawak. *Am. J. Bot.* 84, 208–213.
- Luebert, F., Plissock, P., 2006. Sinopsis bioclimática y vegetal de Chile. Editorial Universitaria, Santiago de Chile.
- Ormazabal, C.S., 1993. The conservation of biodiversity in Chile. *Rev. Chil. Hist. Nat.* 66, 383–402.
- Parsons, D.J., 1976. Vegetation structure in the Mediterranean scrub communities of California and Chile. *J. Ecol.* 64, 435–447.
- Pellens, R., Garay, I., Grandcolas, P., 2010. Biodiversity Conservation and Management in the Brazilian Atlantic Forest: Every Fragment Must Be Considered. *Biodiversity Hotspots*. New York, Nova Publishers.
- Pellens, R., Grandcolas, P., 2007. The conservation refugium value of small and disturbed Brazilian Atlantic forest fragments for the endemic ovoviviparous cockroach *Monastria biguttata* (Insecta, Dictyoptera, Blaberidae, Blaberinae). *Zool. Sci.* 24, 11–19.
- Pellens, R., Grandcolas, P., 2008. Catalogue of Blattaria (Insecta) from Brazil. *Zootaxa* 1709, 1–109.
- Pellens, R., Grandcolas, P., Silva-Neto, I.D., 2002. A new and independently evolved case of xylophagy and presence of intestinal flagellates in cockroaches: *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of Brazilian Atlantic Forest. *Can. J. Zool.* 80, 350–359.
- Rundel, P.W., Montenegro, G., Jaksic, F.M., 1998. *Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems* (Ecological). Berlin, Springer.
- Rehn, J., 1933. On the Dermaptera and Orthoptera of Chile. *Part One. Trans. Am. Entomol. Soc.* 59, 159–190.

- Rentz, D., 2014. *A Guide to the Cockroaches of Australia*, 1st ed. CSIRO Publishing, Collingwood.
- Rivault, C., Cloarec, A., Le Guyader, A., 1993. Bacterial load of cockroaches in relation to urban environment. *Epidemiol. Infect.* 110, 317–325.
- Roth, L.M., Willis, E.R., 1960. The biotic associations of cockroaches. *Smithson. Misc. Collect.* 141, 1–439.
- Santibañez, F., Roa, P., Santibañez, P., 2008. *El medio físico. Biodiversidad de Chile, patrimonio y desafíos*, 2nd ed. Comisión Nacional del Medio Ambiente, Santiago de Chile.
- Schapheer, C., Vera, A., Villagra, C.A., 2016. Native versus pest cockroaches in Chile, are they using the same habitat? In: VIII Southern Connection Congress. Punta Arenas, Chile.
- Schulz, J.J., Cayuela, L., Echeverría, C., Salas, J., Rey Benayas, J.M., 2010. Monitoring land cover change of the dry land forest landscape of Central Chile (1975–2008). *Appl. Geogr.* 30, 436–447.
- Tarli, V., Pequeno, P., Franklin, E., Morais, J., Souza, J., Oliveira, A., Guiherme, D., 2014. Multiple environmental controls on cockroach assemblage structure in a Tropical Rain Forest. *Biotropica* 46, 598–607.
- Uribe, L., 1977. *Epilampra huelpensis*, Nueva especie de blabero chileno (Insecta Dictyoptera, Blattaria). *Bol. Soc. Biol. Concepción* 51, 269–275.
- Vergara, R.C., Torres-Araneda, A., Villagra, D.A., Raguso, R.A., Arroyo, M.T.K., Villagra, C.A., 2011. Are eavesdroppers multimodal? Sensory exploitation of floral signals by a non-native cockroach *Blatta orientalis*. *Curr. Zool.* 57, 162–174.
- Villagra, C.A., Schapheer, C., 2016. New records of *Moluchia strigata* (Blanchard, 1851) (Blattodea: Ecttobiidae) in Mediterranean Matorral, Central Chile. *Gayana* 80, 137–140.
- Villagrán, C., Marticorena, C., Armesto, J.J., 2007. *Flora de las plantas vasculares de Zapallar. Revisión ilustrada y ampliada de la obra de Federico Johow*. Fondo Editorial UMCE, Santiago, Chile.
- Vlasáková, B., Kalinová, B., Gustafsson, M.H.G., Teichert, H., 2008. Cockroaches as pollinators of *Clusia aff. sellowiana* (Clusiaceae) on inselbergs in French Guiana. *Ann. Bot.* 102, 295–304.
- Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Pressey, R.L., 2007. Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biol.* 5 (9), e223.
- World Health Organization, 1999. In: Cochran, D.G. (Ed.), *Cockroaches: Their Biology, Distribution and Control*. 1st ed. World Health Organization.
- Zar, J., 1999. *Biostatistical Analysis*, 4th ed. Pearson Education India.
- Zizka, G., Schmidt, M., Schulte, K., Novoa, P., Pinto, R., König, K., 2009. Chilean Bromeliaceae: diversity, distribution and evaluation of conservation status. *Biodivers. Conserv.* 18, 2449–2471.
- Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the Mediterranean biome. *Divers. Distrib.* 15, 188–197.