

Aphids and associated natural enemies on Ile Amsterdam and Ile Saint-Paul, Southern Indian Ocean

MAURICE HULLÉ¹, EVELYNE TURPEAU¹, SYLVIE HUDAVERDIAN¹, BERNARD CHAUBET¹,
YANNICK OUTREMAN¹ and MARC LÉBOUVIER²

¹UMR 1099 BiO3P, INRA, BP 35327, F35653 Le Rheu cedex, France

²UMR 6553 Ecobio, CNRS – Université de Rennes 1, Station Biologique, 35380 Paimpont, France

maurice.hulle@rennes.inra.fr

Abstract: Ile Amsterdam (37°50'S, 77°30'E, 55 km²) and Ile Saint-Paul (38°43'S, 77°31'E, 7 km²) are very isolated volcanic islands which were originally colonized by a few invertebrate fauna and flora. Invasive species richness has then increased along with human activity. A three-year monitoring programme (1997, 2000, 2001) and a summer campaign (2007) allowed species diversity, host plants, abundance and phenology of introduced aphids and natural enemies to be described. Seven cosmopolitan aphid species have been found on Ile Amsterdam (*Aulacorthum solani*, *A. circumflexum*, *Macrosiphum euphorbiae*, *Myzus ascalonicus*, *M. cymbalariae*, *M. ornatus* and *Rhopalosiphum padi*) and three on Ile Saint-Paul (*A. solani*, *M. cymbalariae* and *R. padi*). On Ile Amsterdam, these aphids were found on 28 host plants (out of 57 sampled plants), mainly introduced species. *Phytolacca arborea* was the only native plant much colonized by one aphid species, *A. circumflexum*. Aphids were mainly present on the base or in this vicinity. One Hymenopteran parasitoid, *Aphidius matricariae*, and two hyperparasites (*Dendrocerus aphidum* and *Phaenoglyphis villosa*), probably introduced along with their host, were collected. Aphid activity is very low during the autumn (March–May) and at a maximum in spring and summer. Their density and diversity decrease with distance from the research station. From these results, the possible impact of aphids on native plants is discussed.

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Introduction

Biological invasions have been widely recognized as one of the most important threats to native biodiversity of isolated islands (Frenot *et al.* 2005). Sub-Antarctic islands of both the cold-temperate and the warm-temperate zones (following the terminology of Stonehouse 1982) are among the more isolated islands. These islands have depauperate native floras and faunas reflecting isolation and severe climatic conditions (Chown *et al.* 1998). The terrestrial ecosystems of these islands depend mainly on the surrounding oceanic waters. Nutrients inputs are mostly marine in origin, due to the presence of numerous seabirds and seals coming ashore to moult and reproduce. Food webs are simplified, with a relatively high number of decomposers and very few herbivores or predators (Vernon *et al.* 1998). Many niches remained unfilled and many groups of plants and animals are absent (Whinam *et al.* 2004).

Due to their less diversified communities and simplified ecosystem functions, these islands are highly vulnerable to invasive species (Smith & Smith 1987, Convey *et al.* 2006). Except for a few known natural introductions due to long distance migration (Greenslade *et al.* 1999), the main source of introduction is passive transport by driftwood or by other organisms such as migrant bird and human voyagers. A strong correlation between the establishment of alien species and

human occupancy and activities has been clearly demonstrated (Chown *et al.* 1998, 2005, Frenot *et al.* 2001) both for deliberate introductions such as mammals and fishes but also for unintentional introductions of plants or invertebrates. On Iles Crozet and Kerguelen, the number of recorded plant species has been multiplied nearly by four and for invertebrates by three due to the establishment of non-native species since the end of the nineteenth century (Frenot *et al.* 2001, 2008, Lebouvier & Frenot 2007). The risk of alien species establishment is likely to increase with ameliorating climate (Bergstrom & Chown 1999).

Among recently introduced insects, aphids (Hemiptera, Aphididae) are now present on most of isolated Indian Ocean islands (Hullé *et al.* 2003b) and the Aphididae *Rhopalosiphum padi* L., is the most widely distributed alien insect along with *Psychoda parthenogenetica* (Diptera, Psychodidae) (Frenot *et al.* 2005). Except on the Falkland Islands where two endemic aphid species have been recorded (Brown 1987), all aphid species present in the sub-Antarctic islands are cosmopolitan and have a large range of host plants. These insects feed on plant sap, an ecological niche which remained nearly empty before their introduction to these islands. Aphids are important pests in the temperate regions they originate from (Tatchell 1989). When introduced on sub-Antarctic islands, they feed on both introduced and native plants (Hullé *et al.* 2003a, 2003b) and they are likely to damage both kinds of plants.

In their areas of origin, aphid populations are controlled by natural enemies such as entomopathogenic fungi, insect predators and parasitoids. Aphids attacked by Entomophthorales (Zygomycota) have been already observed on Kerguelen (Hullé & Dedryver, personal observation). One parasitoid species has been described from Marion Island, *Aphidius matricariae* (Hymenoptera, Braconidae) (Lee *et al.* 2007) and one from Gough Island, *A. colemani* which seems to have been introduced recently, between 2001 and 2003, by the vessel which supplies Marion Island from South Africa (Gaston *et al.* 2003). Apart from these few observations, the relationships between aphids and their natural enemies' in sub-Antarctic islands are poorly documented and with even less known of the possible role of natural enemies in aphid control.

This paper aims to complete the current knowledge of alien invertebrate fauna of the Southern Ocean islands by studying the aphid and associated natural enemies of two very isolated islands, Ile Amsterdam and Ile Saint-Paul, and discusses the possible impact of these insects on the native ecosystems of these islands.

Material and methods

Location and characteristics

Ile Amsterdam (37°50'S, 77°30'N) and Ile Saint-Paul (38°43'S, 77°31'E) are very isolated islands of the warm-temperate zone of the southern Indian Ocean (Stonehouse 1982). They are situated halfway between South Africa and Australia, around 3000 km from the nearest continent. Ile Amsterdam is about 55 km² in land area, entirely volcanic and forms a cone reaching a height of 881 m (Mont de la Dives). The coastline is surrounded by steep cliffs, commonly 30–60 m, rising up to 700 m in the western part (Entrecasteaux Cliffs). Ile Saint-Paul is 80 km south of Ile Amsterdam. It is a small crescent-shaped collapsed crater of 7 km² and 265 m high. A small scientific and meteorological station, Martin-de-Viviès, was established

on Ile Amsterdam in 1949 and has been permanently occupied while Ile Saint-Paul has been unoccupied since 1931 (the end of crayfish cannery) and now has limited access.

Due to their location north of the subtropical convergence, the climate of these islands is oceanic and mild. The mean air temperature is 14.0°C (11.2°C in August, 17.4°C in February) and strong westerly winds are frequent (Lebouvier & Frenot 2007).

The flora of Ile Amsterdam and Ile Saint-Paul includes 17 and 13 native vascular plants species and 71 and 14 introduced species respectively (Frenot *et al.* 2001, Lebouvier unpublished). On Ile Amsterdam there is one species of native tree, *Phyllica arborea* Thouars, also present on Tristan da Cunha which belongs to the same warm-temperate zone in the southern Atlantic Ocean. The introduced plant species have become dominant except in some sites (Frenot *et al.* 2001). A description of the ecological systems of Ile Amsterdam was given by Tréhen *et al.* (1990) and Frenot & Valleix (1990).

Insect study

Insect data came from a multi year monitoring programme on Ile Amsterdam (1990–2001) and a summer campaign on both Ile Amsterdam and Ile Saint-Paul (2007–08) funded by the French Polar Institute (IPEV, Institute Paul Emile Victor, Program Ecobio). Data from 1997, 2000 and 2001 with a complete and regular sampling all year round were selected from Ile Amsterdam monitoring programme to study the phenology of aphids and their natural enemies'. During these three years, five Barber traps (i.e. a catch unit) were placed twice a month for three days in three different sites, one inside the station (site 1) and two at 500 m (site 2) and 1000 m (site 3) southward. All insects collected were then stored in 70% alcohol. The total catches of the different species were compared between sites and years using Chi-square tests.

Table 1. Aphid and parasite species recorded on Ile Amsterdam and Ile Saint Paul, Southern Indian Ocean.

	Amsterdam	Saint-Paul	Southern Ocean island distribution	Worldwide distribution
Aphids				
<i>Aulacorthum (Neomyzus) circumflexum</i>	x		Pacific, Atlantic, Indian ¹	probably of East Asian origin, worldwide ⁵
<i>Aulacorthum solani</i>	x	x	Pacific, Indian ¹	probably of European origin, worldwide ⁵
<i>Macrosiphum euphorbiae</i>	x		Pacific, Indian ¹	probably of North American origin, almost worldwide ⁵
<i>Myzus ascalonicus</i>	x		Pacific, Indian ^{1,2}	origin unknown, worldwide ⁵
<i>Myzus cymbalariae</i>	x	x	New record	origin unknown, recent dispersion, worldwide ⁵
<i>Myzus ornatus</i>	x		Indian ¹	worldwide ⁵
<i>Rhopalosiphum padi</i>	x	x	Pacific, Atlantic, Indian ¹	possibly palaeartic in origin, worldwide ⁵
Parasitoids				
<i>Aphidius matricariae</i>	x	x	Indian (Marion Is) ³	west palaeartic in origin, worldwide ⁶
Hyperparasites				
<i>Dendrocerus aphidum</i>	x		New record	worldwide ⁷
<i>Phaenoglyphis villosa</i>	x	x	Atlantic (Gough Is) ⁴	worldwide ⁸

¹ review in Hullé *et al.* 2003b, ² Greenslade 2006, ³ Lee *et al.* 2007, ⁴ Gaston *et al.* 2003, ⁵ Blackman & Eastop 2000, ⁶ Starý 1974, ⁷ Fergusson 1980, ⁸ Pujade-Villar *et al.* 2007

Table II. Aphid host plant range recorded during the 2007 summer campaign on Ile Amsterdam: plants with no marks were found to host no aphids.

	<i>M. ornatus</i>	<i>M. cymbalariae</i>	<i>M. ascalonicus</i>	<i>M. euphorbiae</i>	<i>A. solani</i>	<i>A. circumflexum</i>	<i>R. padi</i>
Native							
Monocotyledons							
<i>Poa fuegiana</i>							
<i>Poa novarae</i>							
<i>Spartina arundinacea</i>							
<i>Trisetum insulare</i>							X
Dicotyledons							
<i>Acaena sanguisorbiae</i>	X				X	X	
<i>Phytolacca arborea</i>						X	
<i>Plantago pentasperma</i>							
<i>Plantago stauntoni</i>							
<i>Ranunculus biternatus</i>							
<i>Uncinia brevicaulis</i>							
<i>Uncinia compacta</i>							
Introduced							
Monocotyledons							
<i>Anthoxanthum odoratum</i>							X
<i>Dactylis glomerata</i>							
<i>Holcus lanatus</i>	X						X
<i>Lolium perenne</i>							X
<i>Poa annua</i>							
Dicotyledons							
<i>Agave americana</i>							
<i>Atriplex halimus</i>							
<i>Chrysanthemum</i> sp				X			
<i>Cirsium vulgare</i>							
<i>Conium maculatum</i>							
<i>Conyza canadense</i>							
<i>Coronopus didymus</i>				X			
<i>Cupressus macrocarpa</i>	X				X		
<i>Foeniculum vulgare</i>							
<i>Ficus carica</i>							
<i>Gladiolus</i> sp							
<i>Hydrangea macrophylla</i>							
<i>Lactuca sativa</i>			X	X	X		
<i>Leontodon taraxacoides</i>	X	X					
<i>Leucanthemum vulgare</i>	X						
<i>Lycopersicon esculentum</i>				X	X		
<i>Lycopodium trichatum</i>							
<i>Malva sylvestris</i>				X	X		
<i>Mentha pulegium</i>					X		
<i>Narosturtium officinale</i>			X	X	X		
<i>Pelargonium zonale</i>					X		
<i>Petroselinum crispum</i>							
<i>Pirus malus</i>						X	
<i>Plantago lanceolata</i>							
<i>Prunella vulgaris</i>	X						
<i>Rosa</i> sp							
<i>Rumex acetosella</i>							
<i>Rumex obtusifolius</i>	X			X	X		
<i>Sagina procumbens</i>							
<i>Scirpus nodosus</i>							
<i>Sinapis arvensis</i>		X		X	X		
<i>Solanum nigrum</i>							
<i>Sonchus asper</i>					X		
<i>Sonchus oleraceus</i>	X			X			
<i>Taraxacum officinale</i>							
<i>Trifolium dubium</i>	X			X	X	X	X
<i>Trifolium repens</i>		X			X		X
<i>Tropaeolum majus</i>				X	X		
<i>Vicia sativa</i>							
	9	3	2	11	14	4	6

From winter (July) to the mid-summer (December), the number of aphids per catch unit (total of aphid individuals found in the five Barber traps per site and per date) was analysed by a Generalized Linear Model with a quasipoisson error distribution (i.e. overdispersed data) using the temperature, the number of aphid parasitoids, the sampling year and the sampling site as independent variables. Each interaction between these variables was also considered. Models were then simplified to the minimal adequate model by stepwise removal of non-significant interactions followed by independent variables that were not included in any significant interaction. Data were analysed using the R software 2.10.0.

During the summer campaign (three days on Ile Saint-Paul and four weeks on Ile Amsterdam), aphid colonies were collected directly on plants in order to establish the host plant range of the different species. Mummies of parasitized aphids were also collected in the field and kept until hatching of parasitoid or hyperparasite imagoes.

Results

Species diversity and distribution

Seven aphid species were recorded on Ile Amsterdam (Table I). Five species (*Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), *Myzus ascalonicus* Doncaster, *M. cymbalariae* Stroyan, and *Rhopalosiphum padi*) were present on the station and in its surroundings. *A. solani* and *M. euphorbiae* were especially abundant in the gardens which have been installed in lava open top tunnels and scarce everywhere else. *Myzus ascalonicus* was found only on the station. Six species, i.e. all except *M. ascalonicus*, were recorded on the slopes of the volcano, but only two were abundant there, *Myzus ornatus* Laing and *R. padi*. *Aulacorthum* (*Neomyzus*) *circumflexum* (Buckton) was found mainly on *Phyllica arborea* trees and on the plants below. The number of aphid species decreased with the distance from the base and only two species (*M. ornatus* and *R. padi*) were found at Del Cano (9 km away) and only one (*R. padi*) at the bottom of Entrecasteaux Cliffs (8 km away). In these remote

locations aphids were never abundant. Lastly, four species were recorded at high altitude in the vicinity of the caldera (750 m a.s.l., 6 km away): *Myzus ornatus* and *A. circumflexum* were the most frequent, whereas *R. padi* was moderately abundant and *A. solani* very rare.

Three aphid species (*A. solani*, *M. cymbalariae* and *R. padi*) were recorded on Ile Saint-Paul (Table I). They were all found close to the old cannery site within the crater. Only *R. padi* was also found outside the crater on the volcano slopes but only a few individuals at one site.

One aphid parasitoid, *Aphidius matricariae* Haliday (Braconidae, Aphidiinae), and two hyperparasites, the ectoparasite *Dendrocerus aphidum* (Rondani) (Megaspilidae) and the endoparasite *Phaenoglyphis villosa* (Hartig) (Figitidae), were recorded on both islands. On Ile Amsterdam, emergences of both hyperparasites were observed from mummies of *R. padi* and *M. ornatus*.

Aphids' host plants

Eleven native plants (out of 17) and 39 introduced plants (out of 56) were examined during the 2007 summer campaign on Ile Amsterdam in order to find breeding aphids. Four native plants and 29 introduced ones hosted aphids (Table II).

Myzus ascalonicus, *M. cymbalariae* and *M. euphorbiae* colonized only introduced plants. The scarce species *M. ascalonicus* was found mainly on *Lactuca sativa* in gardens. *Myzus cymbalariae* was common on three plants belonging to three different families (Asteraceae, Brassicaceae, Fabaceae), and principally on the very common *Trifolium repens*. *Macrosiphum euphorbiae* was found on eleven plant species and was very abundant on *Sonchus oleraceus*, on garden flowers such as *Chrysanthemum* sp., and on vegetables such as *Lactuca sativa* or *Nasturtium officinale*. *Myzus ornatus* colonized one native species, the austral Rosaceae, *Acaena sanguisorbiae*, and eight introduced plants. This species was particularly abundant on the Polygonaceae *Rumex obtusifolius*. *Aulacorthum solani* also colonized *A. sanguisorbiae* but was less abundant than *M. ornatus* on this plant. *Aulacorthum solani* was abundant on the Asteraceae (*Lactuca sativa*, *Leontodon*

Table III. Test of independence between the numbers of insects and the sites or the years.

Aphids	Site 1	Site 2	Site 3	Total		1997	2000	2001	Total
<i>R. padi</i>	349	263	18	630	<i>R. padi</i>	101	152	377	630
<i>M. cymbalariae</i>	806	1380	2314	4500	<i>M. cymbalariae</i>	1416	1080	2004	4500
<i>M. ornatus</i>	1	116	209	326	<i>M. ornatus</i>	321	4	1	326
Total	1156	1759	2541	5456	Total	1838	1236	2382	5456
			p(Chi ²)	<0.00				p(Chi ²)	<0.001
Parasitoids	Site 1	Site 2	Site 3	Total		1997	2000	2001	Total
<i>A. matricariae</i>	411	650	331	1392	<i>A. matricariae</i>	339	288	765	1392
<i>D. aphidum</i>	82	193	113	388	<i>D. aphidum</i>	278	46	64	388
<i>P. villosa</i>	5	21	18	44	<i>P. villosa</i>	16	15	13	44
Total	498	864	462	1824	Total	633	349	842	1824
			p(Chi ²)	<0.001				p(Chi ²)	<0.001

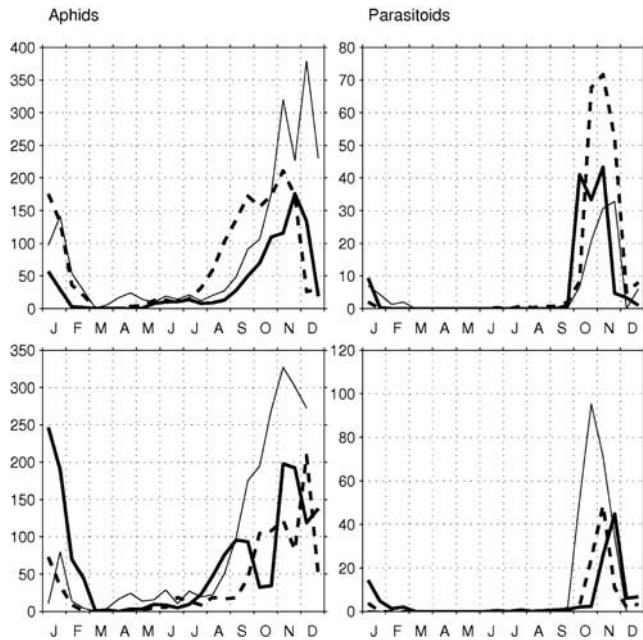


Fig. 1. Mean aphid and parasitoid catches on Ile Amsterdam per site (top section: thick line = site 1, dotted thick line = site 2, thin line = site 3) and per year (bottom section: thick line = 1997, dotted line = 2000, thin line = 2001).

taraxacoides and *Sonchus asper*) and on the Malvaceae *Malva sativa*. *Rhopalosiphum padi* was found mainly on the very common introduced Poaceae *Holcus lanatus*. *Aulacorthum circumflexum* was very common and abundant on the native tree *P. arborea*, and to a smaller extent on the native Rosaceae *A. sanguisorbiae* and the introduced Fabaceae *Trifolium dubium*. This was the only species really abundant on a native plant.

On Ile Saint-Paul, *M. cymbalariae* was found on the Apiaceae *Apium* sp. (possibly *A. graveolens*, unpublished data), *R. padi* on the endemic *Poa novarae* and the

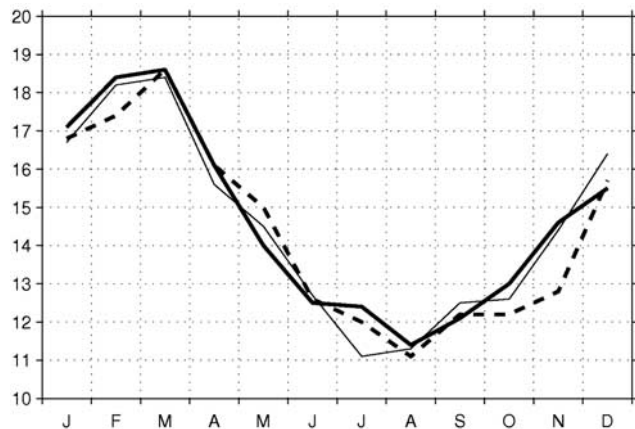


Fig. 2. Monthly mean air temperatures at the base of Ile Amsterdam during the years of operation (data Météo France) (thick line = 1997, dotted line = 2000, thin line = 2001).

introduced grass *H. lanatus* and *A. solani* on the introduced Asteraceae *S. oleraceus*.

Phenology of aphids and their natural enemies

A total of 5456 aphids and 1824 Hymenoptera parasites were identified during the three years of operation. Three aphid species out of the seven were caught in barber traps: *Myzus cymbalariae* (82%), *Rhopalosiphum padi* (12%) and *Myzus ornatus* (6%). Aphid species' composition was different between sites and between years (Table III and Fig. 1). *M. ornatus*, the less abundant species, was trapped essentially in 1997 and was absent on site 1. *M. cymbalariae* was very abundant in 2001 on site 3. *Rhopalosiphum padi* was the most abundant in 2001 and site 1. Aphids were active all year round but principally from July when temperatures were above 12°C (Fig. 2) to February with a peak in November (Fig. 1). All aphids were parthenogenetic viviparous females.

The three Hymenoptera were caught: the parasitoid *Aphidius matricariae* (79%) and the two hyperparasites *Dendrocerus aphidum* (19%) and *Phaenoglyphis villosa* (2%). Hymenoptera species' composition was different between sites and years mainly with a lack of hyperparasites in 2001 and site 1 (Table III and Fig. 1). Winter catches started in October, six weeks after aphids, and ended in December earlier than aphids.

From the winter (July) to midsummer (December), the number of aphids per catch unit increased with time. The temperature explained this rise of aphid density ($\chi^2 = 2670$, d.f. = 1, $P < 0.001$). Both spatial and temporal variations in the number of aphids were also found (site effect: $\chi^2 = 995$, d.f. = 2, $P < 0.001$; year effect: $\chi^2 = 913$, d.f. = 2, $P < 0.001$) and the spatial variation depended on the sampling year (interaction term: $\chi^2 = 945$, d.f. = 1, $P < 0.001$). Finally, the number of aphids was found to be positively linked to the number of parasitoids ($\chi^2 = 2430$, d.f. = 1, $P < 0.001$), suggesting synchronous temporal dynamics during this year period.

Discussion

The seven species found on Ile Amsterdam have a worldwide or almost worldwide distribution (Table I) which is the case for many alien species present in the Antarctic (Frenot *et al.* 2008). Six of them have been already recorded from other isolated sub-Antarctic islands (Hullé *et al.* 2003b) and one, *M. cymbalariae* was recorded for the first time. They were possibly introduced with their host plants via human occupancy. The number of introduced insects can be explained by environmental characteristics of each island such as temperature, available energy, total area, number of vascular plant species or by human occupancy and activities (Chown *et al.* 1998, 2005, Frenot *et al.* 2001, 2005). The number of aphid species found on Ile Amsterdam is comparable to that on Auckland Island (Palmer 1974), Campbell Island (Gressitt 1964,

Palmer 1974) in the New Zealand Province, and Gough Island (Gaston *et al.* 2003) in the South Atlantic Province. Campbell and Auckland islands are colder than Ile Amsterdam and should be less colonized (Hullé *et al.* 2003b) but they are much longer (113 km² and 626 km² respectively) than Ile Amsterdam (55 km²) and have a greater number of plant species which could compensate (Chown *et al.* 1998). Gough Island hosts eight aphid species (Gaston *et al.* 2003). The significant characteristics explaining the colonization of Gough Island by alien insects such as total area (57 km²), mean annual sea surface temperature (12.3°C) and number of occupants (38 per year) are comparable to those of Ile Amsterdam (Chown *et al.* 1998). Even if the numbers of plant species given by Chown *et al.* (1998) are not updated, the main differences between both islands lies in the species richness of introduced vascular plants which is more higher on Ile Amsterdam (81) than on Gough Island (24) and in the number of indigenous plants (57 vs 26 on Gough Island and Ile Amsterdam respectively) which should favour a higher number of introduced insects on Ile Amsterdam. Ile Amsterdam appears therefore to be less colonized than other islands compare to its biological, physical and anthropogenic characteristics.

Ile Saint-Paul was colonized by three aphid species which were all also present on Ile Amsterdam. Furthermore, both islands host *Myzus cymbalariae* which has not been reported from any other Southern Ocean island. This confers a distinctive characteristic to the Ile Amsterdam and Ile Saint-Paul group which is consistent with the prediction of colonization by highly dispersal taxa from nearby islands implying spatial autocorrelations in species richness (Selmi & Boulinier 2001).

In their reviews, Frenot *et al.* (2005, 2008) underlined that most alien established invertebrates belong to a limited number of higher taxonomic groups in particular Diptera, Hemiptera and Coleoptera, and many of them share the biological trait of parthenogenetic reproduction. For example, 28% of established insects on Gough Island are parthenogenetic (Jones *et al.* 2003 in Gaston *et al.* 2003). With seven species of aphids, one Delphacidae and one Reduviidae, the Hemiptera is one of the major insect groups of Ile Amsterdam. Sexual forms of aphids were found neither in trap samples over a 10-year period nor during the summer campaign investigation. This suggests that all aphid species which have colonized both Ile Amsterdam and Ile Saint-Paul have only an asexual mode of reproduction. Moreover, the seven species found on these islands are all described as being either strictly parthenogenetic or possibly entirely parthenogenetic when the climate is mild enough (Blackman & Eastop 2000) which is the case with Ile Amsterdam and Ile Saint-Paul. This unique asexual mode of reproduction of aphid species has already been reported from other islands such as Kerguelen, Crozet (Hullé *et al.* 2003a) and Macquarie

(Greenslade 2006). This mode of reproduction obviously reduces the barrier to establishment as, in theory, the arrival of a single female is sufficient to found colonies. Furthermore, all aphid species established on Ile Amsterdam and Ile Saint-Paul are polyphagous, a biological trait which enhances the chance of a successful establishment.

The complex of aphids' natural enemies on these two islands comprised three Hymenoptera species, one parasitoid *Aphidius matricariae* and two hyperparasites *Dendrocerus aphidum* and *Phaenoglyphis villosa*. All these parasites have a worldwide distribution (Table I). This is the first record of *D. aphidum* on a sub-Antarctic island. *Aphidius matricariae* was already known from Marion Island (Lee *et al.* 2007). Another *Aphidius* species, *A. colemani* and one hyperparasite, *P. villosa* were recorded on Gough Island (Gaston *et al.* 2003). *Dendrocerus* is the most economically important genus of the Ceraphronoidea as it contains most of the aphid hyperparasites known from this super family (Fergusson 1980). *Aphidius matricariae* is a generalist and common aphid parasitoid. Among the seven potential aphid hosts present on Ile Amsterdam and Ile Saint-Paul, *R. padi*, *M. cymbalariae*, *M. ornatus* and *A. solani* are already known as hosts (Mackauer & Starý 1967, Kavallieratos *et al.* 2004, Lee *et al.* 2007). In this study, we found mummies of *R. padi* and *M. ornatus*. Other species are likely to be parasitized. Aphids and their parasitoids presented synchronous temporal dynamics: the density of their populations increased from July to November with temperatures and then declined from November to February when temperatures were still going up. Parasitoids are suggested to exert a significant control of aphid populations (Dixon 1987) but present data did not allow this assumption to be clearly demonstrated. To determine the real impact of parasitoids on the populations of their aphid hosts, a continuous measure of the parasitism rate (i.e. the rate of the aphid populations containing parasitoid immatures) during the summer would be necessary. The observed decline on aphids from November to February may be due to abiotic factors such as elevated temperatures.

The impact of alien invertebrates on native fauna is well documented (Frenot *et al.* 2005) but their impact on native flora is poorly known. On Ile Amsterdam, with the exception of *A. circumflexum* which have notably colonized the native tree *Phyllica arborea*, aphids breed mainly on introduced plants. Furthermore, aphids were rare in the less disturbed ecosystems of the island, such as Entrecasteaux Cliffs or the Caldera, and some species were present principally or exclusively on or around the station, especially in the gardens. This limits the possible impact of these introduced damaging insects on native plants of Ile Amsterdam. The distribution of introduced insects restricted to the vicinity of settlements and without expanding has already been described in sub-Antarctic islands (Gaston *et al.* 2003, Hullé *et al.* 2003a). On Ile Amsterdam, the question of whether the gardens could act

as reservoir or source of introduced species which could later expand their distribution has to be considered. The fact that aphids have been found everywhere on Ile Amsterdam leave this question opened. However, our results did not clearly demonstrate this assumption, as species abundant in these gardens were scarce outside and anyway aphid populations could be easily controlled in these very limited locations.

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References

- BERGSTROM, D.M. & CHOWN, S.L. 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology and Evolution*, **14**, 472–477.
- BLACKMAN, R.L. & EASTOP, V.F. 2000. *Aphids on the world's crops: an identification and information guide*, 2nd ed. Chichester: John Wiley, 466 pp.
- BROWN, P.A.A. 1987. Key to the genus *Pentamyzus* Hille Ris Lambers (Homoptera, Aphididae), with a description of a new species from the Falkland Islands. *Systematic Entomology*, **12**, 1–6.
- CHOWN, S.L., GREMMEN, N.J.M. & GASTON, K.J. 1998. Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts and conservation. *American Naturalist*, **152**, 562–575.
- CHOWN, S.L., HULL, B. & GASTON, K.J. 2005. Human impacts, energy availability and invasion across Southern Ocean islands. *Global Ecology and Biogeography*, **14**, 521–528.
- CONVEY, P., FRENOT, Y., GREMMEN, N. & BERGSTROM, D.M. 2006. Biological invasions. In BERGSTROM, D.M., CONVEY, P. & HUISKES, A.H.L., eds. *Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator*. Dordrecht: Springer, 193–220.
- DIXON, A.F.G. 1987. Seasonal development in aphids. In MINKS, A.K. & HARREWIJN, P., eds. *Aphids, their biology, natural enemies and control*, vol. A. Amsterdam: Elsevier, 315–320.
- FERGUSON, N.D.M. 1980. A revision of the British species of *Dendrocerus* Ratzeburg (Hymenoptera: Ceraphronoidea) with a review of their biology as aphid hyperparasites. *Bulletin of the British Museum of Natural History (Entomology)*, **41**, 255–314.
- FRENOT, Y. & VALLEIX, T. 1990. Carte des sols de l'Ile Amsterdam (Terres Australes et Antarctiques Françaises). *CNFRA*, **59**, 1–48.
- FRENOT, Y., GLOAGUEN, J.C., MASSÉ, L. & LÉBOUVIER, M. 2001. Human activities, ecosystem disturbance and plant invasions in sub-Antarctic Crozet, Kerguelen and Amsterdam islands. *Biological Invasions*, **101**, 33–50.
- FRENOT, Y., CHOWN, S.L., WHINAM, J., SELKIRK, P.M., CONVEY, P., SKOTNICKI, M. & BERGSTROM, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, **80**, 45–72.
- FRENOT, Y., CONVEY, P., LÉBOUVIER, M., CHOWN, S.L., WHINAM, J., SELKIRK, P.M., SKOTNICKI, M. & BERGSTROM, D.M. 2008. Antarctic biological invasions: sources, extents, impacts and implications. In ROGAN-FINEMORE, M., ed. *Non-native species in the Antarctic: proceedings*. Christchurch: Gateway Antarctica, 53–96.
- GASTON, K.J., JONES, A.G., HÄNEL, C. & CHOWN, S.L. 2003. Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London*, **B270**, 1091–1098.
- GREENSLADE, P. 2006. *The invertebrates of Macquarie Island*. Kingston: Australian Antarctic Division, 344 pp.
- GREENSLADE, P., FARROW, R.A. & SMITH, J.M.B. 1999. Long distance migration of insects to a subantarctic island. *Journal of Biogeography*, **26**, 1161–1167.
- GRESSITT, J.L. 1964. Insects of Campbell Island. *Pacific Insects Monograph*, **7**, 531–600.
- HULLÉ, M., PANNETIER, D., SIMON, J.C., VERNON, P. & FRENOT, Y. 2003a. Aphids (Hemiptera: Aphididae) of subantarctic Iles Crozet and Kerguelen: species diversity, host range and spatial distribution. *Antarctic Science*, **15**, 203–209.
- HULLÉ, M., MAURICE, D., COURMONT, L., CHAILLON, C., CHAILLON, P.E., SACCONI, P., HEBERT, C., GRACIA, M., BUFFIN, J., SIMON, J.C. & FRENOT, Y. 2003b. Aphids from Kerguelen and Crozet islands. In HUISKES, A.H.L., GIESKES, W.W.C., ROZEMA, J., SCHORNO, R.M.L., VAN DER VIES, S.M. & WOLF, W.J., eds. *Antarctic biology in a global context*. Leiden: Backhuys, 308–312.
- KAVALLIARATOS, G., TOMANOVIC, Z., STARÝ, P., ATHANASSIOU, C.G., SARLIS, G.P., PETROVIC, O., NIKETIC, M. & VERONIKI, M.A. 2004. A survey of aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) of south-eastern Europe and their aphid-plant associations. *Applied Entomology and Zoology*, **39**, 527–563.
- LÉBOUVIER, M. & FRENOT, Y. 2007. Conservation and management in the French sub-Antarctic islands and surrounding seas. *Papers and Proceedings of the Royal Society of Tasmania*, **141**, 23–28.
- LEE, J.E., SLABBER, B., JANSEN VAN VUUREN, B.J., VAN NOORT, S. & CHOWN, S.L. 2007. Colonisation of sub-Antarctic Marion Island by a non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae). *Polar Biology*, **30**, 1195–1201.
- MACKAUER, M. & STARÝ, P. 1967. *World Aphidiidae Hym. Ichneumonoidea*. Paris: Le Francois, 195 pp.
- PALMER, J.M. 1974. Arthropoda of the Subantarctic islands of New Zealand (2). Hemiptera: Aphidiidae. *Journal of the Royal Society of New Zealand*, **4**, 303–306.
- PUJADE-VILLAR, J., PARETAS-MARTINEZ, J., SELFA, J., SECO-FERNADEZ, M.-V., FÜLÖP, D. & MELIKA, G. 2007. *Phaeonoglyphis villosa* (Hartig 1841) (Hymenoptera: Figitidae: Charipinae): a complex of species or a single but very variable species? *Annales de la Société Entomologique de France*, **43**, 169–179.
- SELMI, S. & BOULINIER, T. 2001. Ecological biogeography of Southern Ocean Islands: the importance of considering spatial issues. *The American Naturalist*, **158**, 426–437.
- SMITH, V.R. & SMITH, R.I.L. 1987. The biota and conservation status of sub-Antarctic islands. *Environment International*, **13**, 95–104.
- STARÝ, P. 1974. Parasite spectrum (Hym., Aphidiidae) of the green peach aphid, *Myzus persicae* (Sulz.) (Hom., Aphididae). *Bollettino del Laboratorio di entomologia agraria di Portici*, **31**, 61–156.
- STONEHOUSE, B. 1982. La zonation écologique sous les hautes latitudes australes. *CNFRA*, **51**, 531–537.
- TATCHELL, G.M. 1989. An estimate of the potential economic losses to some crops due to aphids in Britain. *Crop Protection*, **8**, 25–29.
- TRÉHEN, P., FRENOT, Y., LÉBOUVIER, M. & VERNON, P. 1990. Invertebrate fauna and their role in the degradation of cattle dung at Amsterdam Island. In KERRY, K.R. & HEMPEL, G., eds. *Antarctic ecosystems: ecological change and conservation*. Berlin: Springer, 337–346.
- VERNON, P., VANNIER, G. & TRÉHEN, P. 1998. A comparative approach to the entomological diversity of polar regions. *Acta Oecologica*, **19**, 303–308.
- WHINAM, J., CHILCOTT, N. & BERGSTROM, D.M. 2004. Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation*, **121**, 207–219.