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Introduced Ants in Galápagos (Floreana Island): Importance of Competition, Coexistence and Aggressive Behaviors

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TABLE OF CONTENT

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Abstract

Invasive species represent with fragmentation of habitat the most serious threats to biodiversity in the world. Galápagos Archipelago, as most oceanic islands, suffers a high rate of introduced animals and plants that affect equilibrium and biodiversity of this unique biota. Ants rank among the most devastating invaders. Their social organization confer them a high ability to adapt and to spread in new environments forming rapidly populous communities. We studied the ant community of Floreana Island composed mainly of introduced species (at least 15). Introduction events occurred successively during last century. The last record is *Monomorium destructor* arrived in the eighties. Our aim is to investigate the modalities of interaction and coexistence of these introduced species.

We highlighted the competition hierarchy of the coexisting species using attractive food baits. Two species behave as competitively dominant by monopolizing an important part of resources. They are *M. destructor* restricted to a small area and the fire ant *Solenopsis geminata* widely distributed on the island.

Then we evaluated the relative importance of abiotic factors and interspecific competition in structuring the community. Ecological data were collected and presence and abundance of species were estimated using different methods in a wide range of habitats. Several species showed preferences either for arid or for humid areas. The little fire ant *Wasmannia auropunctata*, a well-known devastating species when introduced, was exclusively found in moist habitat in and around the agricultural area situated in the upper and central part of the island. It coexists with other species in several parts but in a restricted perimeter it excludes all other ants and worker's density on the ground is nearly 70 times higher than ant's density in similar habitats occupied by several species. But most opportunist tramp species establish everywhere without particular ecological requirement. Analyses of species co-occurrences at various levels didn't reveal any marked effect of competition in structuring ant's assemblages. We supposed that the lack of competition-derived structure has to be attributed to the dynamic of the system. Indeed, across the successive census of 1996, 2003, 2004 and 2005, species distributions and abundances appeared to be highly variables. In particular harsh conditions occurring in dry season in certain parts seem to be limiting to *S. geminata*. We suggest that huge variations in the local distribution of the dominant *S. geminata* disrupt the community organization.

Finally we conducted artificial ant confrontations to evaluate to what extend an aggressive behavior at the worker level may be linked to the ecological success of a species on the island. *S. geminata* was rather indifferent when confronted to a submissive species on food sources, suggesting that its competitive dominance is largely due to a numerical superiority. On the other hand *M. destructor* exhibits a strong agonistic behavior in similar confrontations. As soon as the presence of a competitor is detected, most workers were observed to abandon foraging and to take part in physical aggressions. Since it is still restricted nearby its introduction spot two decades after its arrival, we suggest that the energetic cost of such an aggressive behavior prevent it to spread on that island already highly colonized.

Dominant invasive species such as the fire ants *S. geminata* and *W. auropunctata* have negative impacts on Galápagos fauna, disturbing the hatching of land tortoises and birds. But very little is known about the impact of other exotic ants. Indeed, impact on arthropods and generally on ground-dwelling organisms is very difficult to evaluate.

As a consequence of the dynamic character of Floreana I. ant community it is difficult to build models or to make predictions on evolution of introduced ant fauna. But *Camponotus macilentus*, an abundant endemic species seems today to be little affected by introduced ant species thanks to its strong interference competition ability and its preference for arid and harsh environments.

Résumé

Les espèces envahissantes représentent, avec la fragmentation du paysage, la plus grande menace pour la biodiversité. L’archipel des Galápagos, comme la plupart des îles du Pacifique, compte un grand nombre d’espèces introduites qui menacent la biodiversité de ce milieu unique. Les fourmis sont parmi les envahisseurs les plus dévastateurs. Leur organisation sociale leur permet de s’adapter et de se propager pour devenir rapidement abondantes. Nous avons étudié la communauté de fourmis sur l’île de Floreana principalement composée d’espèces introduites (au moins 15). Les introductions se sont succédées au cours du siècle précédent. La dernière espèce recensée est *Monomorium destructor* introduite dans les années 80. Notre objectif est de mettre à jour les modalités des interactions et de la coexistence de ces espèces introduites.

Nous avons mis en évidence la hiérarchie de compétition des différentes espèces à l’aide d’appâts de nourriture. Deux espèces se comportent de façon dominante en monopolisant une part importante des ressources. Ce sont *M. destructor*, restreintes à un petit périmètre, et la fourmi de feu *Solenopsis geminata*, largement distribuée sur l’île.

Nous avons évalué l’importance relative des facteurs abiotiques et de la compétition interspécifique dans la structuration des peuplements. Des données écologiques ont été collectées et la présence et l’abondance des espèces ont été estimées à l’aide de trois méthode au sein d’une grande diversité d’habitats. Plusieurs espèces montrent des préférences soit pour les milieux humides, soit pour les milieux arides. La petite fourmi de feu *Wasmannia auropunctata*, une espèce connue pour être dévastatrice dans ses sites d’introduction, est présente exclusivement dans les habitats humides dans et à proximité de la zone agricole située dans la partie centrale de l’île. Elle coexiste en plusieurs points avec d’autres espèces mais au sein d’un périmètre restreint elle exclut toute autre fourmi et atteint des densités records au sol presque 70 fois supérieures aux densités de fourmis observées sur les sites voisins occupés par plusieurs espèces. Mais la plupart des espèces vagabondes opportunistes s’établissent partout sans exigences écologiques particulières. Des analyses de cooccurrence d’espèces à plusieurs niveaux n’ont pas révélé de rôle marqué de la compétition dans la structuration des communautés. Nous supposons que l’absence d’une telle structure doit être attribuée à la dynamique du système. En effet, au cours des différents recensements de 1996-1997, 2003, 2004 et 2005, la distribution et l’abondance des espèces était très variable. En particulier, les conditions rudes qui règnent dans la zone aride durant la saison sèche semblent affecter particulièrement *S. geminata*. Nous suggérons que de fortes variations dans la distribution de l’espèce dominante perturbent l’organisation des communautés.

Finalement nous avons effectué des confrontations artificielles pour évaluer dans quelle mesure un comportement agressif au niveau de l’ouvrière peut être lié au succès écologique d’une espèce sur l’île. *S. geminata* montre très peu de réaction face à une espèce subordonnée sur une même source de nourriture, ce qui laisse supposer que sa dominance est largement due à sa supériorité numérique. Par contre, dans des conditions similaires, *M. destructor* est fortement agressive. En présence d’un compétiteur, la plupart des ouvrières renoncent très vite à leur activité de fourragement pour agresser les individus de l’autre espèce. Puisque deux décennies après son introduction elle est toujours confinée à son point d’arrivée, nous supposons que le coût en énergie et en ouvrières de ce comportement très agressif est un obstacle à son expansion sur cette île déjà fortement colonisée.

Les espèces envahissantes dominantes comme les fourmis de feu *S. geminata* et *W. auropunctata s*ont connues pour leur impact négatif sur la faune des Galápagos, entre autre sur les jeunes des tortues terrestres et des oiseaux. Mais nous savons très peu de choses sur l’impact des autres espèces de fourmis introduites. En effet, l’impact sur les arthropodes, et plus généralement sur la faune du sol, est très difficile à évaluer.

En raison du caractère dynamique de la communauté de fourmi de Floreana, il est difficile de construire des modèles et de faire des prédictions sur l’évolution des peuplements de fourmis introduites. Mais *Camponotus macilentus*, une espèce endémique abondante, semble aujourd’hui peu affectée par les espèces introduites grâce à ses capacités de compétition par interférence et sa préférence pour les milieux arides.

Resumen

Las especies invasoras representan, junto con la fragmentación del paisaje, la mayor amenaza para la biodiversidad. El archipiélago de Galápagos, como la mayoría de las islas del Pacífico, cuenta con un gran número de especies introducidas que amenazan la biodiversidad de este lugar único. Las hormigas son uno de los invasores más devastadores. Su organización social les permite adaptarse y propagarse para ser rápidamente abundante. Estudiamos la comunidad de hormigas de la isla Floreana principalmente compuesta de especies introducidas (al menos 15). Las introducciones se sucedieron durante el siglo anterior. La última especie contabilizada es *Monomorium destructor* introducida en los años 80. Nuestro objetivo es poner al día las modalidades de las interacciones y de la coexistencia de estas especies introducidas.

Pusimos de relieve la jerarquía de competencia de las distintas especies con ayuda de cebos de comida. Dos especies se implican de manera dominante monopolizando una parte importante de los recursos. Son *M. destructor*, limitado a un pequeño perímetro, y la hormiga de fuego *Solenopsis geminata*, ampliamente distribuida por la isla.

Evaluamos la importancia relativa de los factores abióticos y de la competencia interespecífica en la estructuración de la communidad. Se recogieron algunos datos ecológicos y se consideraron la presencia y la abundancia de las especies con ayuda de tres métodos en una gran diversidad de hábitats. Varias especies muestran preferencias o por los medios húmedos, o por los medios áridos. La pequeña hormiga de fuego *Wasmannia auropunctata*, una especie conocida por ser devastadora en sus lugares de introducción, está presente exclusivamente en los hábitats húmedos y cerca de la zona agrícola situada en la parte central de la isla. Coexiste en varios puntos con otras especies pero en un perímetro limitado excluye a cualquier otra hormiga y alcanza densidades en el suelo casi 70 veces superiores a las densidades de hormigas observadas en los lugares vecinos ocupados por varias especies. Pero la mayoría de las especies vagabundas oportunistas se establecen por todas partes sin exigencias ecológicas particulares. Análisis de cooccurrencía de las especies a varios niveles no revelaron una grande importancía de la competencia en la estructuración de las comunidades. Suponemos que la ausencia de tal estructura debe ser por la dinámica del sistema. Efectivamente, durante los distintos censos de 1996-1997, 2003,.2004 y 2005, la distribución y la abundancia de las especies eran muy variables. En particular, las condiciones drásticas que reinan en la zona árida durante la temporada seca parecen afectar especialmente a *S. geminata*. Sugerimos que fuertes variaciones en la distribución de la especie dominante perturben la organización de las comunidades.

Finalmente efectuamos confrontaciones artificiales para evaluar hasta que punto un comportamiento agresivo a nivel de la obrera puede explicar el éxito ecológico de una especie en la isla. *S. geminata* muestra muy poca reacción ante una especie subordinada mientras comparten la misma comida, lo que deja suponer que su dominancia se debe a su superioridad numérica. Por el contrario, en condiciones similares, *M. destructor* es muy agresivo. En presencia de otra especie, la mayoría de las obreras renuncian muy rápidamente a alimentarse para atacar a los individuos de la otra especie. Puesto que dos décadas después de su introducción todavía se confina en su punto de llegada, suponemos que el coste en energía y en obreras de este comportamiento muy agresivo es un obstáculo a su extensión en esta isla ya muy colonizada.

Las especies invasoras dominantes como las hormigas de fuego *S. geminata* y *W. auropunctata* son conocidas por su impacto negativo en la fauna de Galápagos, entre otras cosas sobre los juveniles de las tortugas terrestres y pájaros. Pero sabemos muy poco sobre el impacto de las otras especies de hormigas introducidas. Efectivamente es muy difícil de evaluar el impacto en los artrópodos, y más generalmente en la fauna del suelo.

Debido al carácter dinámico de la comunidad de hormiga de Floreana, es difícil construir modelos y hacer predicciones sobre la evolución de las poblaciones de hormigas introducidas. Pero *Camponotus macilentus*, una especie endémica abundante, parece poco afectada hoy por las especies introducidas gracias a sus capacidades de competencia por interferencia y su preferencia por los medios áridos.

INTRODUCTION

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Invasive species

Invasive species are among the most significant threats to biodiversity in the world. They are the second cause of species rarefaction after habitat fragmentation (Mack et al. 2000) and a leading cause to animal extinction worldwide (Clavero and Garcia-Berthou 2005). They cause local extinctions and drastically alter ecosystem structures and functioning (Elton 1958, Lodges 1993, Pimentel et al. 2000). Colonization of new areas and extinction are both natural processes but they were strongly accelerated since the huge development of human trade during the 20th century. A lot of plant and animal species were released intentionally or not in new areas. Pimentel et al. (2000) estimated to 50’000 the number of introduced organisms in the United States and to 137 billion dollars per year the cost of it. Following the UICN definition, an invasive species is an alien species which has become established in natural or semi natural ecosystems or habitats, is an agent of change and threatens native biological diversity. All introduced species (also named alien or exotic) are not invasive. Most introduced species fail in trying to establish themselves and very few of them have a major impact on environment (Lodges 1993, Kareiva 1996, Williamson and Fitter 1996).

Since the publication of the book of Elton “The ecology of invasions by animals and plants” in 1958 we had to wait several decades to assist to the re-emergence of interest for the study of invasive organisms, as shown by the creation of the scientific journal “Biological Invasions” in 1999. Vermeij (1996) suggested that invasion biology should be considered as an important part of ecology and evolutionary biology.

Several attempts were done to characterize invasive species and invaded habitats. Using quantitative methods some succeeded in linking life history traits to invasion success in plants (Reichard & Hamilton 1997, Kolar & Lodge 2001). Principally these were the previous description of a species as invasive in other parts and vegetative reproduction. For Crawley (1986), establishment success of introduced insects is closely related to specie’s intrinsic rate of increase. Elton (1958) argues that the success of an invasion is inversely correlated with the ecological resistance of the recipient environment. He defines ecological resistance as the sum of negative effects due to competition, predation, parasitism and diseases. This is equivalent to the concept of niche opportunity (Shea & Chesson 2002).

Ants as invaders

Invasion success varies among taxonomic groups (Williamson & Fitter 1996) and introduced ant species are some of the most damaging invaders at both ecological and economical levels (Clark et. al 1982, Porter & Savignano 1990, OTA 1993). Several have negative impact on native ant fauna as well as on other invertebrates or vertebrates (see Table 1 for examples).

Table 1.- Studies highlighting the negative impact of invasive ant species on native ants, invertebrates and vertebrates (this table is not exhaustive)

species	island	continent	impact on…	locations & references
Wasmannia auropunctata (little fire ant)	x		ants	Galapagos (Clark et al 1982, Lubin 1994); New Caledonia (Le Breton et al. 2003)
	x		invertebrates	Galapagos (Clark et al 1982, Lubin 1994); New Caledonia (Jourdan et al. 2002)
	x		vertebrates	New Caledonia (Jourdan et al. 2001)
		x	vertebrates	Africa (Walsh et al. 2004)
Solenopsis invicta		x	ants	USA (Wojcik 1994)
(red imported fire ant)		x	invertebrates	USA (Porter & Savignano 1990, Morrison 2002)
		x	vertebrates	USA (Allen et al. 1997, Orrock & Danielson 2004)
Pheidole megacephala	x		ants	Bermuda (Haskins & Haskins 1965, Crowell 1968)
(big-headed ant)	x		invertebrates	Hawaii (Zimmerman 1970)
		x	ants	Australia (Vanderwoude et al. 2000)
		x	invertebrates	Australia (Hoffman et al. 1999)
Anoplolepis gracilipes	x		ants	Seychelles (Haines et al. 1994)
(crazy ant)	x		invertebrates	Seychelles (Hill et al. 2003)
Linepithema humile	x		invertebrates	Hawaii (Cole et al. 1992, Reimer 1994)
(Argentine ant)		x	ants	Portugal (Crowell 1968), USA (Holway 1999, Human & Gordon 1996, 1999, Suarez et al. 1998, Sanders et al. 2003); Japan (Miyake et al. 2002), Spain (Carpintero et al. 2005)
		x	invertebrates	USA (Human & Gordon 1997, Bolger et al. 2002)
		x	vertebrates	USA (Suarez et al. 2000, Fisher et al. 2002)

Their ability to invade new areas might be attributed to their small size facilitating their transport (Forys et al. 2002, Walsh et al. 2004, Ward et al. 2005) and their elaborate social behavior (Moller 1996, Holway et al. 2002). Not only is human being responsible for a multitude of unintentional introduction, but in the particular case of introduced ant species, it also contributes to their subsequent dispersion. This phenomena was highlighted at least for *Wasmannia auropunctata* (Walsh et al. 2004), *Solenopsis invicta* (Forys 2002) and *Linepithema humile* (Suarez et al. 2001, Ward et al. 2005).

In a review, Mc Glynn (1999) counted 147 ant species in the world that were found out of their native range, which represents 1.24 % of ant species (11’880 described species on April 2006, http//www.antbase.org). The 20-25 most widespread of them share the characteristics of tramp species described by Hölldobler & Wilson (1990) and Passera (1994). These particular traits are the small size and monomorphism of worker caste, the reproduction by budding, unicoloniality in introduced range (i.e. no intraspecific aggression), high interspecific aggression, polygyny, a great tendency to migrate and often a close relation to human environment. It is essential to distinguish between the concepts of tramp and invasive species. The definition of tramp species is functional, it considers biological traits as competitive and reproductive behavior of species. On the other hand the definition of invasive corresponds to a given impact on recipient biota and belongs more to the conservation biology vocabulary. Depending the authors (McGlynn 1999, Holway et al. 2002), between six and nine transferred ant species are considered as invasive. They are all tramp species excepted three fire ant species of the genus *Solenopsis* that present polymorphism of worker caste and nuptial flight. There are different views following the authors to determine which species is invasive and which is not. However, as noted by Holway et al. (2002), a great disparity exists with respect to how much is known about these species. The two best studied invasive ant species in the world are the fire ant *Solenopsis invicta* introduced in the United States in the early 20th century and around 1996 in Australia (Nattrass & Vanderwoude 2001) and the Argentine ant *Linepithema humile* that have colonized all six continents (Passera 1994; Majer 1994; Suarez et al. 2002). But that doesn't mean that other species are less invasive, most of the time in invasion biology, research interest is driven mainly by economical motivations.

Unicoloniality has been recognized as one of the most decisive attribute of the introduced populations of the Argentine ant *L. humile* (Holway et al. 1998, Tsutsui et al. 2003, Holway & Suarez 2004, Buczkowski et al. 2004) and of the little fire ant *W. auropunctata* (Ulloa-Chacon & Cherix 1990, Errard et al. 2005). Astruc et al. (2001) demonstrated for the tramp ant *Tetramorium bicarinatum* a total absence of intraspecific aggression at the world level that might be attributed to a particular structure of its cuticular hydrocarbons.

Galápagos Archipelago as a living laboratory

The impact of biological invasions is particularly important on island ecosystems (Elton 1958, Greimler et al. 2002). As mentioned by Elton (1958), islands species have often evolved within a relaxed competitive context. As a consequence, ant species invading oceanic islands with few or no native ants may exhibit different patterns of invasion than those observed in region with indigenous ants (Holway et al. 2002). The principle of niche opportunity predicts that the more species in a community, the lower the niche opportunity for a potential invader (Shea & Chesson 2002). Insect diversity per unit area in Galápagos is very low compared with continental South America (Peck 2001 *in* Causton 2006). Reimer (1994) suggests that the huge success of *Hypoponera opaciceps* and *Solenopsis papuana* in Hawaii is due to the absence of native ants.

Of volcanic origin and situated about 1'000 km from the Ecuadorian coast, the Galápagos Archipelago is composed of thirteen main islands and about 40 small islets or rocks for a total area of 8'000 km^2 (see Fig. 1). It was discovered in 1535 by Thomas de Berlanga. The current human population in Galápagos is of about 20'000 inhabitants. Since the beginning of human colonization, Galápagos suffered numerous intentional or non-intentional species introductions. Goats, donkeys, dogs, pigs and cats were carried to the islands with the first human settlers as well as agricultural and ornamental plants. But humans also brought accidentally to the island a high number of alien plants and animals. Causton et al. (2006) report that 463 alien insect species have been introduced, which represent 23% of Galápagos insect species. As for plants, Tye (2006) reports 544 alien species (the native flora includes some 560 species).

In 1959 Galápagos became a National Park and the Charles Darwin Research Station is funded in 1964. In 1980 it has been classified by the UNESCO as World Heritage.

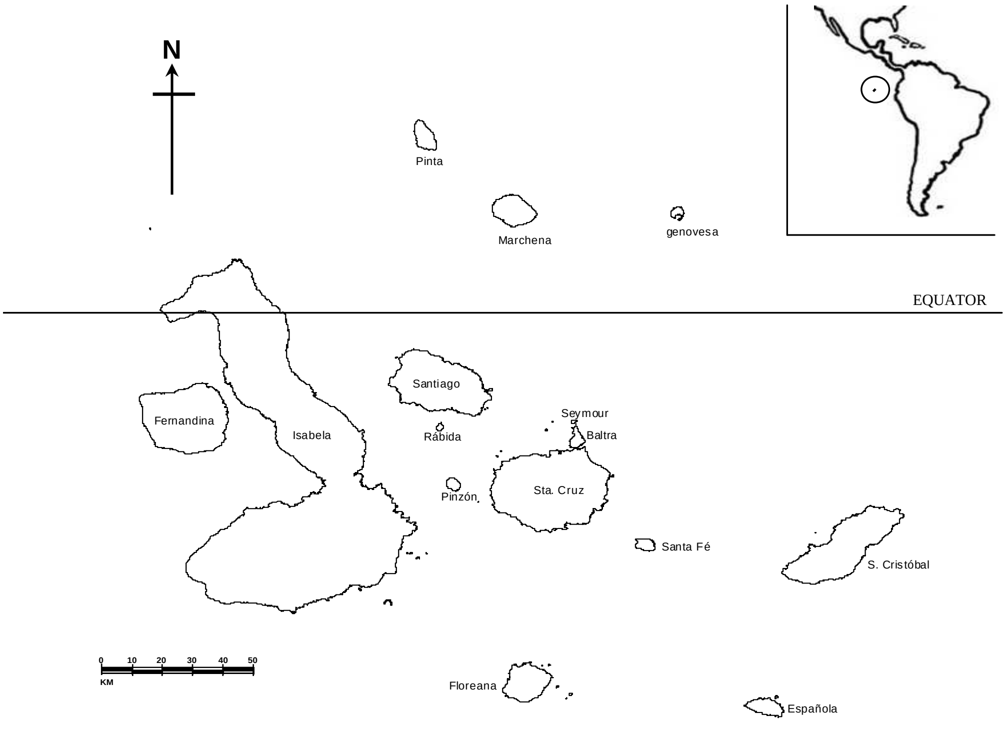

Fig 1.- Map of Galapagos Archipelago

Floreana Island where this study took place is situated on the southern part. It is a 173 km^2 island with a maximum elevation of 540 m. Of the four inhabited islands, Floreana is the smallest and the less populous with a unique village and a hundred inhabitants. A five kilometers long road leads from the village to the agricultural area of about 285 ha (1.6% of the island surface) situated in the upper humid part. The first permanent human settlers established on Floreana in 1832. But the presence of freshwater made of Floreana a very attractive spot for whalers and buccaneers well before. As a majority of Galápagos Islands, Floreana has a varying climate with arid conditions at lower altitude and a very humid zone on the upper part. During the dry season from June to December the top of most islands are rainy due to the establishment of a permanent fog causing a fine almost permanent rain called “garúa”.

Historical review of ants census in Galápagos

The first one to explore Galápagos with a naturalist interest was Charles Darwin during his trip with the H.M.S. Beagle in 1835. He was followed by numerous expeditions that visited the archipelago to collect samples of this unique ecosystem. But if Darwin and several others collected ants, very little attention was paid to these organisms. Some works were published at the end of the 19th and beginning of the 20th centuries on the identification of ants collected during several expeditions (Smith 1877, Emery 1893, Wheeler 1919, 1924, 1933, Stitz 1932).

Tab. 2.- List of collected species by Pezzatti et al. in 1996-97 on Floreana Island. Subfamilies abreviations are F=Formicinae, M=Myrmicinae, P=Ponerinae, D=Dolichoderinae. Functional group are given using the classification of Andersen (1997). Tramp and/or invasive status are given following McGlynn (1999).

Species (+ subfamily)		functional groups	Status	tramp/invasive	probable origin of introduced species
Camponotus macilentus	F	Subordinate Camponotini	endemic	-	
Camponotus planus	F	Subordinate Camponotini	endemic	-	
Cardiocondyla emeryi	M	Opportunist	recent intr.	T	Africa (1)
Cardiocondyla nuda	M	Opportunist	recent intr.	T	Africa (1)
Hypoponera sp. A *	P	Cryptic	?	-	
Hypoponera sp. B	P	Cryptic	?	-	
Monomorium destructor	M	Generalized Myrmicine	recent intr.	T	India (2), Africa (1)
Monomorium floricola	M	Generalized Myrmicine	old intr.	T	Tropical Asia (3)
Odontomachus bauri	P		possibly native	-	
Paratrechina longicornis	F	Opportunist	old intr.	T/I	Old World Tropics (1)
Paratrechina sp. **	F	Opportunist	?	(T)	
Pheidole sp. A ***	P	Generalized Myrmicine	?	-	
Pheidole sp. B	P	Generalized Myrmicine	?	-	
Solenopsis geminata	M	Hot Climate Specialist	possibly native	I	North to South America (4)
Solenopsis globularia pacifica	M		native	-	
Solenopsis sp.	M	Cryptic	?	-	
Strumigenys emmae	M	Cryptic	recent intr.	T	Afrotropical region (8)
Strumigenys louisianae	M	Cryptic	?	-	
Tapinoma melanocephalum	D	Opportunist	old intr.	T	Unknown (1), African or Oriantal origin (5)
Tetramorium bicarinatum	M	Opportunist	old intr.	T	South East Asia (7)
Tetramorium caldarium	M	Opportunist	old intr.	-	Africa (7)
Tetramorum lanuginosum	M	Opportunist	recent intr.	T	Asia (6)
Tetramorium simillimum	M	Opportunist	old intr.	T	Africa (7)
Wasmannia auropunctata	M	Cryptic	recent intr.	T/I	Tropical America (9)

(1) Wilson & Taylor (1967)
(2) Bolton (1987)
(3) Emeryi (1921) in Wilson & Taylor (1967)
(4) Trager (1991)
(5) Smith (1965)
(6) Bolton (1976)
(7) Bolton (1979)
(8) Bolton (1983)
(9) Ulloa-Chacon & Cherix (1990)

(Modified from Pezzatti et. al 1998)

* possibly *Hypoponera opaciceps* (tramp species)
** possibly Paratrechina vaga (tramp species)
*** possibly *Pheidole williamsi* (endemic of Galapagos)

The list published by Wheeler in 1919 represented 12 species, among which at least six were well-known tramp species. He went to Galápagos in 1923 and published in 1924 a list of 18 species, nine of which were considered as endemics. But most of the time old surveys are incomplete, due to the very short periods dedicated in the search of ants and the lack of systematic methods of sampling. One has to wait till the end of the last century to find publications of most extensive studies (Clark et al. 1982, Lubin 1984, Pezzati et al. 1998). Clark et al. (1982) recorded 17 species on Santa Cruz Island and considered four as endemics (*Cylindromyrmex williamsi*, *Pheidole williamsi*, *Camponotus macilentus* and *C. planus*). On Floreana Island, Pezzatti et al. (1998) found 24 ant species (see Table 2). Among them two species are endemic (*C. macilentus* and *C. planus*). It is often difficult with organisms so small and unnoticeable such as ants to know whether they were introduced by man or arrived by natural means. However for a majority of them that are commonly worldwide transferred species a human-mediated introduction is highly probable. On Floreana I., undoubtedly 15 ant species are aliens. Among them 12 are tramp species, belonging to the subfamilies Myrmicinae (10), Dolichoderinae (1) and Formicinae (2). Four of them are new records for Galápagos: *Monomorium destructor*, *Strumigenys emmae*, *Tetramorium caldarium* and *T. lanuginosum*

Our objectives

The interest of studying introduced ants in Galápagos is double. First, as many Pacific islands, Galápagos Archipelago suffered since its human colonization numerous introductions of alien species. Some ant species, as well as other plant or animal species, represent very serious threats to a variety of organisms, from arthropods to vertebrates (Causton et al. 2006). On the other hand, the coexistence of several introduced species is a unique opportunity to investigate competition behavior and coexistence patterns among them. Focusing on the ant community of Floreana, our aim was to investigate the competitive interactions of these species and the structure of this recent community.

In this study we focused on the ant community of Floreana Island. This island was chosen for the existence of previous detailed data (Pezzatti et al. 1998). Our first goal (Chapter 1) was to assess the evolution of ant community since this previous census by using a similar monitoring design. Ants were detected using attractive food baits. Since most ant species are introduced, some of them in the last decades, we wanted to evaluate the evolution and the dynamic of the system over the short period of seven years. In ecology, successive monitoring of a given area is something relatively rare. But it is an essential step in the understanding of many ecological processes, in particular in the context of a recently assembled community of mostly well-known introduced species. Moreover, we aimed to investigate the competition hierarchy in the community. The use of food baits is particularly adapted to the evaluation of exploitative and interference competition in ant communities (Hölldobler & Wilson 1990).

In Chapter 2, we conducted a wider sampling over 20 stations with the aim of determining factors responsible for the distribution and coexistence patterns of ant species. We collected data on environmental conditions and composition of local ant assemblages and we evaluated respective weights of interspecific competition and environmental factors in structuring communities. Indeed, it is commonly assumed that competition is an important factor governing ant community structure (Hölldobler & Wilson 1990, Andersen 1992, Davidson 1998). On the other hand Floreana, like a majority of Galápagos islands, offers a wide range of climatic conditions from lower arid area to upper humid zone. Thus ecological preference might also be decisive. Several authors showed a correlation between species richness and diversity or density of vegetation (Goldstein 1975, Majer et al. 1984, Perfecto & Snelling 1995, Morrison 1998, Ribas et al. 2003). To get reliable information on local species richness we applied conjointly various collection methods.

Finally, in Chapter 3 we examined in artificial conditions the behavior of ants when confronted to other species. We were wondering if the dominant status in Floreana ant community might be linked to a particularly aggressive behavior at the worker level. We conducted artificial confrontations, first on single workers and then on groups of foragers on food sources.

Compiling our different results on competition hierarchy, community structure and interspecific interactions allow us to formulate several assumptions on the modalities of coexistence and spread of introduced ants.

CHAPTER 1

INTRODUCED ANT SPECIES AND MECHANISMS OF COMPETITION ON FLOREANA ISLAND (GALÁPAGOS, ECUADOR)

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Abstract

Simultaneous presence of several tramp ant species of relatively recent introduction on a remote island is an excellent opportunity to study competition mechanisms that lead to the establishment of invasive species. Using attractive food baits we collected 14 ant species among which 10 are well-known tramp species. The most important change between 1996-97 and 2003 is the spread of the tropical fire ant *Solenopsis geminata* at the detriment of *Tetramorium simillimum*, suggesting that the colonization process on Floreana is still very dynamic. The follow-up of 400 food baits for 21 hours permitted to calculate for 11 species indices of competition abilities, revealing distinct strategies. The two small tramp species *Monomorium floricola* and *Tapinoma melanocephalum* are typically opportunists when large-sized *Odontomachus bauri* (possibly native species) and *Camponotus macilentus* (endemic species) are good interference competitors, oucompeting other species at food baits. Dominant species *S. geminata* and *Monomorium destructor* reach high scores for all indices due to their high abundance.

Introduction

Biology of invasions is an important new topic within the field of community ecology (Mooney and Drake 1986, Hengelveld 1989, Kareiva 1996). Invasions by alien species could represent a severe threat to biodiversity. Invasion success varies among taxonomic groups (Williamson & Fitter 1996) but most invading species fail in trying to establish themselves and very few of them have a major impact on environment (Lodges 1993, Kareiva 1996, Williamson and Fitter 1996). Introduced ant species are some of the most damaging invaders at both ecological and economical levels (Clark et. al 1982, Porter & Savignano 1990, OTA 1993). Invasive ants share typical characteristics of tramp species as unicoloniality, small size and monomorphism of worker caste, high polygyny, reproduction by budding and strong interspecific aggressivity (Passera 1994) that allow them to outcompete native species (Hölldobler & Wilson 1990, Lodge 1993, Passera 1994, Mc Glynn 1999).

Moreover, invasions by exotic species on isolated islands with high rates of endemic species represent a major ecological threat due to the low invasion resistance of such ecosystems. As mentioned by Mc Glynn (1999), Pacific Islands are the recipient of the most transferred ant species. Galápagos archipelago is not an exception with nearly half of its ant taxa belonging to tropical tramp species (Lubin 1984).

Many studies have been dedicated to describe the impact of particular invasive ant species on native ant's populations (Clark et. al 1982, Kennedy 1998, Holway 1999, Le Breton et. al 2003) or more generally on arthropod communities (Lubin 1984, Porter & Savignano 1990, Cole et. al 1992, Hoffmann et. al 1999, Human & Gordon 1997). But up to now little efforts have been performed to observe the establishment and evolution of several potentially invading ant species (i.e. tramp species) in a given community.

According to this problematic of coexisting invasive species, Floreana Island in the Galápagos archipelago is a very interesting place: it shelters a minimum of 14 cosmopolitan or pantropical well-known tramp species belonging to the following genera: *Cardiocondyla, Monomorium, Quadristruma, Solenopsis, Tetramorium, Wasmannia, Tapinoma* and *Paratrechina* (Pezzatti et al. 1998). Ants' inventories on Floreana have been conducted since the end of 19th century (Smith 1877, Emery 1893, Wheeler 1919, 1924,1933, Stitz 1932, unpublished data of Coulter, Alvarez and Lubin 1982-83, Pezzatti et. al 1998). Results of these collectors suggest that the different tramp species have been introduced gradually since the beginning of human presence on the island. Heger and Trepl (2003) described the invasion process in stages corresponding to "presence in a new area", "establishment" and finally "spread" of the introduced species. On Floreana we are in presence of invaders at different stages of their invasion with recent and old introductions. *Monomorium destructor* for example is the last known intruder and occupies an area nearby the harbour which is probably its arrival spot. On the other hand, species like *Solenopsis geminata* or *Wasmannia auropunctata* have clearly spread through a large part of the island. This makes of Floreana a very interesting place to investigate the biology of invasions.

In ant communities, competition for resources is one of the most important factor governing community structure (Davidson 1998, Wilson 1971). Coexisting species are using various competition strategies. Wilson (1971) described three categories of competitors: opportunists, insinuators and extirpators. Opportunists discover food quickly and exploit it with high efficiency. Extirpators dominate food aggressively while insinuators are discrete thieves inserting themselves inconspicuously. Fellers (1987), working with a community of woodland ants, distinguished exploitative competition and interference competition. Exploitative competition consists in being able to discover food very quickly and to exploit it before the arrival of other species by recruiting large foraging groups, it corresponds to Wilson's "opportunists". At the opposite interference competition consists in interfering directly with other species, using chemical repellents or direct aggression, in order to monopolize resources. They are Wilson's "extirpators". In an equilibrium case, each member of a community supposedly achieves a trade-off between theses two opposite strategies, with different degrees of specialization in one or another (Fellers 1987, Davidson 1998). But in the case of an invasion, the invader might be able to break down that trade-off. The reasons for its superiority are often either a numerical dominance probably due to the escapement from natural enemies (Davidson 1998) or the modification of genetic structure of populations as demonstrated for the Argentine ant *Linepithema humile* (Suarez et al. 1999, Tsutsui et al. 2000, Tsutsui & Case 2001). The previous equilibrium being broken it leads to regression or elimination of native species. This is the case of *L. humile* in California (Human & Gordon 1996) which is at the same time a good exploitative competitor and a good interference competitor because of its numerical dominance.

The aim of our study has two steps. The first one is to assess the modifications that occurred in ant fauna on Floreana Island during the last few years by comparing collection data from 1996-97 of Pezzatti et. al (1998) with the actual distribution. In order to get a significant comparison we applied the same sampling design. In a second part we focus on the dynamic of colonization at artificial food baits to evaluate competition strategies of the different species. It is essential to investigate the mechanisms of competition implicated in the direct confrontation on resources underlying the global mechanisms of spread of invasive specie.

Methods

1. Distribution pattern

We sampled the same points than Pezzatti et. al (1998) seven years before. Points were chosen to be representative of all types of habitat. The area occupied by the little fire ant *Wasmannia auropunctata* was intentionally ignored because of its lack of interest knowing that this species excludes all other ants (Pezzatti et. al 1998). Four points were chosen in man-impacted areas (A1-A4) and the other occurred in the natural area (N1-N4). The two series of points follow an altitudinal transect in order to consider the different vegetation zones of the island from the upper humid zone to the arid coastal zone (see fig. 1).

At each sampling point twenty-five attractive baits were laid on the ground. They were placed at two meters one of the other in an eight by eight meters square. Two type of food were used as attractive: honey and tuna in oil. This allowed us to avoid effect of eventual preferences of one species or another for sugar food or for protein food or even an eventual repellent propriety of oil. Between December 1996 and February 1997 each point were sampled twice with honey and twice with tuna baits. During May and June 2003 sampling points were tested once with each attractive substance.

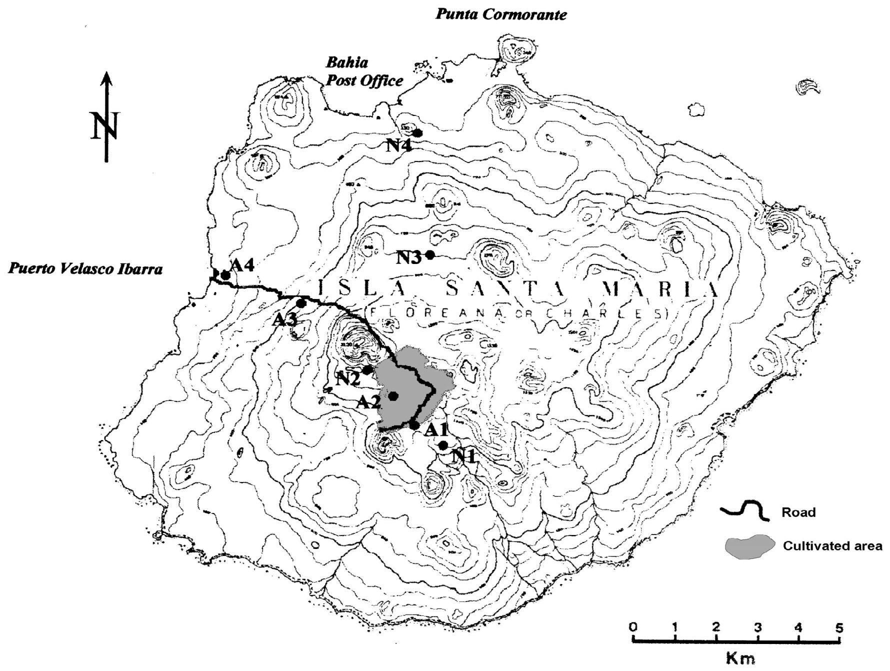

Fig 1.- Map of Floreana Island

Baits were put in place between midday and 4:00 p.m., checked two to four times at several hours intervals and collected the next morning. Ants were collected during controls in order to confirm species determinations and at the end of each experiment. A reference collection is deposited at the Charles Darwin Research Station, Galápagos, Ecuador and at the Museum of Zoology in Lausanne, Switzerland.

2. Dynamic of colonization at baits

The succession of observations at each bait from the beginning till the end of an experiment is considered as a sequence. The sequence is divided in five controls at precise intervals: 2h, 6h, 12h, 18h and 21h after beginning of experiment (2 p.m., 6 p.m., 12 p.m., 6 a.m. and 9 a.m.). We considered exclusively results from 2003 because data from 1996-97 lack regularity to be included in analysis. We conducted 16 experiments (8 sampling sites and two types of attractive food) of 25 baits which represents 400 sequences. They were pooled together for analyses. We evaluated the competitive ability of each species using the following parameters: frequency of large recruitment groups versus small groups, ability to quickly discover food, ability to monopolize baits, ability to persist a long time at baits and ability to win encounters with other species at food source in order to monopolize baits.

Results

1. *Distribution pattern*

Using attractive food baits 17 species were collected in 1996-97 and 14 species in 2003 (Tab. 1). *Hypoponera sp.* and *Solenopsis sp.* are totally absent of 2003 collection; in 1996-97 only one specimen of *Hypoponera sp.* was collected at a honey bait, this data may then be considered as anecdotal. *Tetramorium caldarium* was found in 2003 exclusively by visual search. Considering the work of Pezzatti et al. (1998) in which pitfall traps, visual search and

Tab. 1.- List of collected species at food baits in 1996-97 and 2003. Species with an asterisk (*) were found at baits only in 1996-97 survey.

Species	Status	tramp	probable origin of tramps
Camponotus macilentus	endemic	No	
Camponotus planus	endemic	No	
Cardiocondyla emeryi	recent intr.	Yes, pantropical	Africa (1)
Cardiocondyla nuda	recent intr.	Yes, pantropical	Africa (1)
Hypoponera sp. A	?	No	
Hypoponera sp. B			
Monomorium destructor	recent intr.	Yes, pantropical	India (2), Africa (1)
Monomorium floricola	old intr.	Yes, pantropical	Tropical Asia (3)
Odontomachus bauri	possibly native	No	
Paratrechina longicornis	old intr.	Yes, pantropical	Old World Tropics (1)
Paratrechina sp.	?		
Pheidole sp. A			
Pheidole sp. B			
Solenopsis geminata	possibly native	Yes, cosmopolitan	North to South America (4)
Solenopsis globularia pacifica	native	No	
Solenopsis sp. *	?		
Strumigenys emmae			
Strumigenys louisianae			
Tapinoma melanocephalum	old intr.	Yes, pantropical	Unknown (1), African or Oriantal origin (5)
Tetramorium bicarinatum	old intr.	Yes, cosmopolitan	South East Asia (7)
Tetramorium caldarium *	old intr.	Yes, cosmopolitan	Africa (7)
Tetramorum lanuginosum			Asia (6)
Tetramorium simillimum	old intr.	Yes, cosmopolitan	Africa (7)
Wasmannia auropunctata			

(Partially reproduced from Pezzatti et. al 1998)

(1) Wilson & Taylor (1967)
(2) Bolton (1987)
(3) Emeryi (1921) in Wilson & Taylor (1967)
(4) Trager (1991)
(5) Smith (1965)
(6) Bolton (1976)
(7) Bolton (1979)

attractive baits were used jointly, we missed underground foraging ants like *Quadristruma emmae*, *Strumigenys louisianae* and two *Pheidole spp* that were collected in 1996-97.

Among the ant fauna of Floreana there are two endemic species (*Camponotus macilentus* and *C. planus*), one native species (*Solenopsis globularia pacifica*), two possibly natives (*S. geminata* and *O. bauri*) and nine species of either old or recent introductions (Pezzatti et al. 1998). Species recorded by early collectors (Smith 1877; Emery 1893; Wheeler 1919, 1924, 1933; Stitz 1932) are considered as old introductions, while species mentioned for the first time in recent census (unpublished data from M. Coulter and M. Alvarez 1982 and Y. Lubin and M. Alvarez 1983; Pezzatti et al. 1998) represent recent introductions.

In table 2 we compare the number of occurrences of species during our 2003 baiting experiments depending on food type, sites location (in the natural area or in the man-impacted area) and climate (upper sites A1, A2, N1 and N2 are considered as humid when sites A3, A4, N3, N4 are located in the arid zone).

Tab. 2.- Number of occurrences for all species on food type (tuna/honey), on both site categories (N = natural / A = man-impacted) and in humid versus arid zona (2003).

		Tuna	**Honey**	**sites N**	**sites A**	**Humid**	**Arid**
	rate of bait occupation	75.4%	71.3%	74.9%	71.9%	73.3%	73.5%
species	*Camponotus macilentus*	15	2	15	2	-	17
	Camponotus planus	1	-	1	-	-	1
	Cardiocondyla emeryi	4	11	15	-	-	15
	Cardiocondyla nuda	12	42	3	51	1	53
	Monomorium destructor	75	59	-	134	-	134
	Monomorium floriocola	63	31	20	74	53	41
	Odontaumachus bauri	18	23	17	24	41	-
	Paratrechina longicornis	1	-	1	-	-	1
	Paratrechina sp.	16	10	1	25	25	1
	Solenopsis geminata	490	458	617	331	446	502
	Solenopsis globularia	1	4	-	5	-	5
	Tapinoma melanocephalum	31	62	13	80	73	20
	Tetramorium bicarinatum	18	18	1	35	36	-
	Tetramorium simillimum	31	40	65	6	69	2
	Total	**776**	**760**	**769**	**767**	**744**	**792**
	Nb species	**14**	**12**	**12**	**11**	**8**	**12**

Excluding the two anecdotal captures of *C. planus* and *P. longicornis* at tuna baits, both types of food attracted all species. The number of species captured in natural and man-impacted area was similar. More species were found at baits in the lower arid zone then in the upper humid area. *C. macilentus* and *C. emeryi* are strictly found in lower arid zone when *T. bicarinatum* is captured exclusively in the upper humid area. *O. bauri* and *T. simillimum* are more abundant at baits in the upper part but visual search reveals their presence in almost all sampling points. If here *M. destructor* is present exclusively in arid area and man-impacted site, it is due to its very restricted range of expansion confined to one sampling point in the village.

Table 3 pools all species observations at baits at the eight study sites during sampling efforts of 1996-1997 and 2003. Values represent percentage of occupation of baits (0 - 100%). These data do not include abundance per bait. Dots represent occurrence of species collected only by visual search (1996-97 and 2003) and/or in pitfall traps (1996-97).

Tab. 3.- Species collected during two samplings efforts (Dec1996 - Feb 1997 and May -June 2003) on four natural sites (N1-N4) and four man-impacted sites (A1-A4) using attractive food baits (tuna and honey alternatively). Occurrences of species are presented as percentage of occupied baits.
• = species observed at sampling sites but not present in baits
* = no more than one or two specimens collected at baits

Sampling points

	N1		**N2**		**N3**		**N4**		**A1**		**A2**		**A3**		**A4**		**General**	
Species collected	97	03	97	03	97	03	97	03	97	03	97	03	97	03	97	03	97	03
Camponotus macilentus	-	-	-	-	16.3	•	6.7	6.0	-	-	-	-	•	0.4	0.7	0.4	2.96	0.85
Camponotus planus	-	-	-	-	-	-	6.7	0.4*	-	-	-	-	-	-	-	-	0.83	0.05
Cardiocondyla emeryi	-	-	-	-	2.5	1.6	13.3	4.8	-	-	-	-	20.0	-	2.2	-	4.75	0.75
Cardiocondyla nuda	-	-	•	-	-	1.2	-	-	12.8	0.4*	-	-	1.2*	20.0	-	-	1.75	2.7
Hypoponera sp.	•	-	•	-	-	-	-	-	0.5*	-	•	-	-	-	-	-	0.07	-
Monomorium destructor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	45.5	53.6	5.68	6.7
Monomorium floricola	-	-	1.8	2.8	6.2	2.0	0.3*	3.2	-	14.4	5.1	4.0	3.2	10.8	0.7	0.4*	2.17	4.7
Odontomachus bauri	•	2.4	6.2	4.4	5.2	•	-	•	-	6.0	1.5	3.6	0.8	•	•	•	1.71	2.05
Paratrechina longicornis	-	-	0.4	-	-	-	-	0.4*	-	-	-	-	-	-	4.7	-	0.64	0.05
Paratrechina sp.	-	-	2.2	-	-	-	-	0.4	-	-	17.5	10.0	-	-	-	-	2.45	1.3
Solenopsis geminata	26.8	38.8	4.4	77.6	-	81.6	-	48.8	12.0	17.6	2.9	44.4	14.4	56.0	30.5	14.4	11.4	47.4
Solenopsis globularia	-	-	-	-	29.2	-	50.0	-	-	-	-	-	-	2.0	6.5	-	10.7	0.25
Solenopsis sp.	-	-	-	-	-	-	-	-	11.5	-	0.7	-	-	-	-	-	1.52	-
Tapinoma melanocephalum	-	-	-	0.4	3.4	•	0.3	4.8	2.7	27.6	1.5	1.2	3.2	2.8	0.4	0.4	1.43	4.65
Tetramorium bicarinatum	-	-	•	0.4*	-	-	-	-	-	0.8*	17.8	13.2	-	-	-	-	2.23	1.8
Tetramorium caldarium	-	-	5.5	-	2.5	-	-	•	-	-	-	-	10.4	-	0.4	-	2.33	•
Tetramorium simillimum	59.4	19.6	64.4	6.4	9.2	•	1.3	-	17.6	1.2	34.9	0.4*	40.0	0.8	-	-	28.4	3.55
Number of species at baits	**2**	**3**	**7**	**6**	**8**	**4**	**7**	**8**	**6**	**7**	**8**	**7**	**8**	**7**	**9**	**5**	**17**	**14**

The most important observed change between 1996-97 and 2003 is the progression of the fire ant *Solenopsis geminata* that extended its range to remote sites N3 and N4. At the same time it is more dominant at every sampling site excepted in the village (A4) where it is confronted to *Monomorium destructor*. It is present in 47.4% of baits in 2003, compared to 11.4% in 1996-97. While the presence of *S. geminata* grew considerably, occurrences of *Tetramorium simillimum* decreased significantly from 1996-97 (28.4% of baits occupied) to 2003 (3.6%). *T. simillimum* is the dominant species at baits in 1996-97 and it is now supplanted by *S. geminata* (see fig. 2). There is an important decrease in the number of species collected at baits at sites N3 and A4. This is probably due for site N3 to the abundance of *S. geminata* that recently colonized the area. *Cardiocondyla emeryi*, in spite of its abundance in 1996-97 survey, is not collected in this study at site A3. On the other hand, its congeneric species *C.*

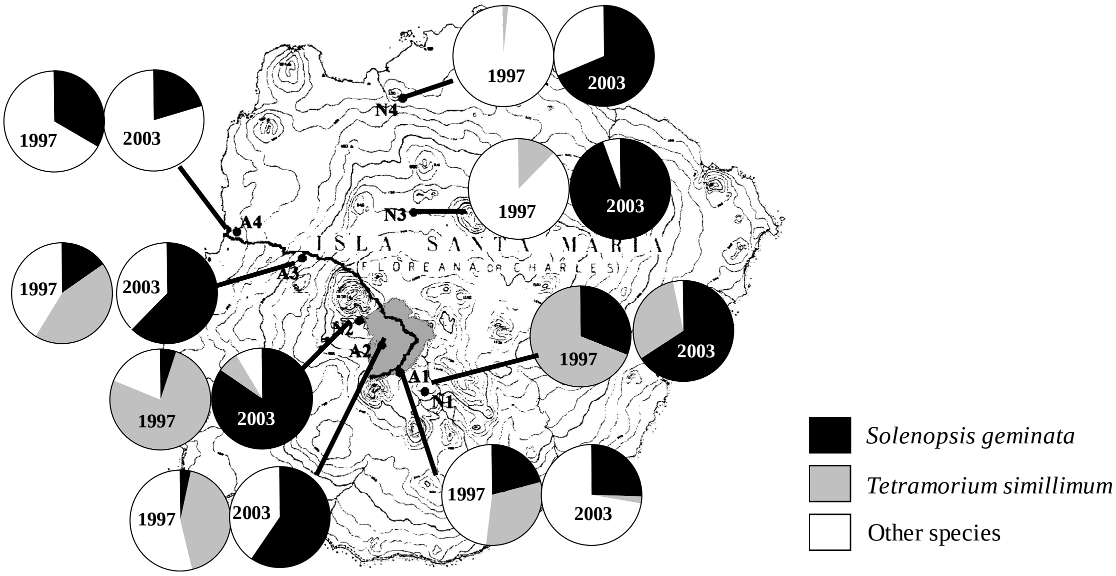

Fig. 2 - Evolution of presence rates of *Tetramorium simillimum* and *Solenopsis geminata* between 1996-97 and 2003 surveys. Graphics represent precentages of observations of both species compared with total number of ants sobservations.

nuda became much abundant. *Monomorium floricola* is much more abundant in 2003 survey. It strongly increased its bait occupancy at A3 and is newly recorded at A1.

2. *Dynamics of colonization at baits*

The number of observations of a given species during controls gives an idea on its rate of activity at different periods of the day. Dynamics of this rate of activity is presented in Fig 3. *M. floricola*, *T. melanocephalum*, *T. simillimum*, *C. emeryi* and *C. nuda* present a diminution of their foraging activity during the night when other species like *C. macilentus* and *O. bauri* are active principally at night. *S. geminata* and *M. destructor*, which are dominant when present, show a more continuous pattern of activity. The global rate of occupation of baits during first control (2 p.m.) is of 46% when occupation rate during following controls at 2 p.m., 12 p.m., 6 a.m., and 9 a.m. reach respectively 91%, 82%, 85% and 80%. This is probably due to a combination of two factors: the short period of time since the beginning of the experiment (two hours) and the sunny location of a majority of baits at that time.

Using data of presence and relative abundance of species during controls, we calculated several indices of competitive ability of the eleven most abundant species. They are classified in two groups presented in Table 4. A first index (a) is the frequency of large foraging groups at bait (more than 20 workers) compared with the total number of observed individuals of the species. The second index (b) is measuring the ability to discover food sources. We consider a "discovering event" the presence of a species at first control (2 p.m.). We calculate the ratio between total number of occurrence of the species (several observations of a species at the same bait during consecutive controls is considered here as one occurrence) and the number of occurrence at 2 p.m.. We consider these two indices as estimators of *exploitative competition* abilities. Index (c) corresponds to the percentage of solitary occurrences of a species among all observations. The "persistence" index (d) is the percentage of occurrences for which a species is present during at least three consecutive controls at the same bait. The last index (e) is the percentage of successful win-loss events. If Species A is the only present species at a bait and Species B occupies solitarily that bait during the following consecutive control, Species B is considered to have won encounter against Species A. Indices (c), (d) and (e) describe typical traits of *interference competition* specialists. For a better visibility in Tab. 4 the five best scores for each index are indicated in bold characters.

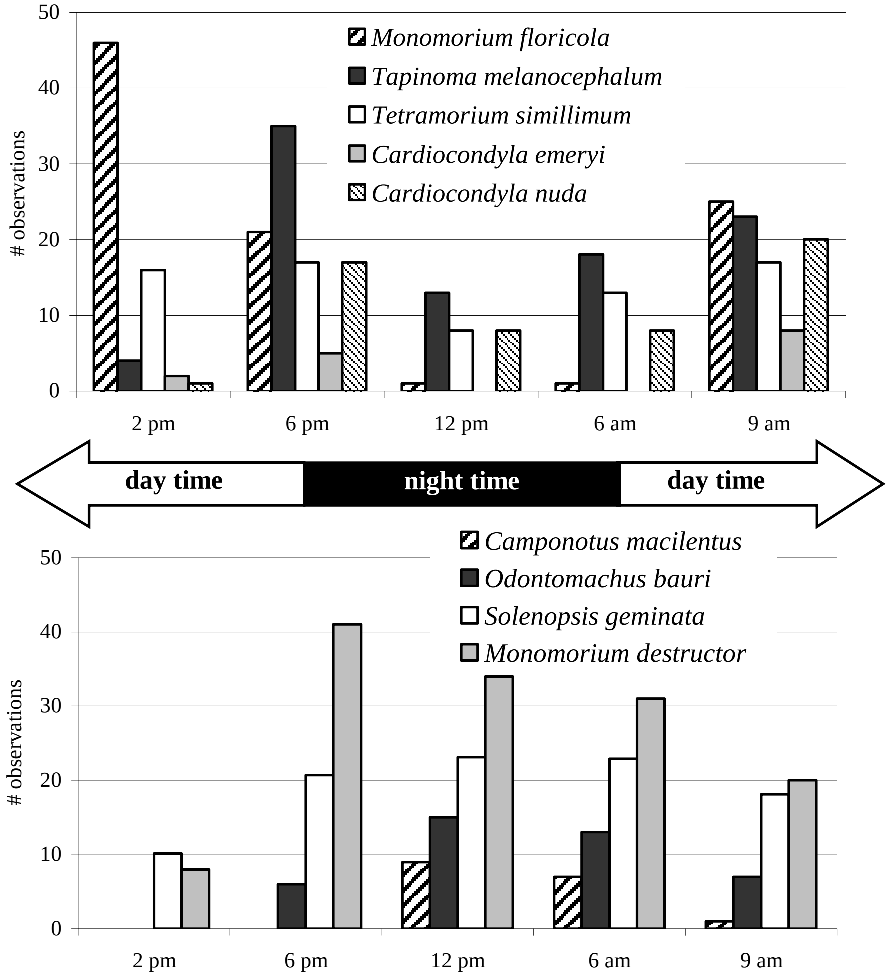

Fig. 3.- Pattern of activity of the different species at different times (controls). The activity is expressed by the number of observations pooled for all experiments. For *S. geminata* values are divided by ten due to its high abundance.

Considering index scores of Table 4, it appears that both *S. geminata* and *M. destructor* produced high scores in a majority of indices. They exhibit the higher percentages of large recruitment groups and higher rates of solitary occurrences and large sequences. *C. macilentus, C. nuda* and *O. bauri* are never present in large groups. These same species are scarecely observed during the first control. At the opposite *M. floricola* shows the best score at food discovery, followed by *T. simillimum*. The two species of *Cariocondyla* genus get the lowest scores at solitary occurrences and at win-loss records. *C. emeryi* and *T. bicarinatum* have a null persistence index, which means that they are never observed at baits during two consecutive controls. *O. bauri*, *C. macilentus* and *S. geminata* have good win-loss scores compared to other species.

Tab. 4.- Indices of competitive ability

		Exploitative competition		**Interference competition**		
		(a)	(b)	(c)	(d)	(e)
	Number of occurrences	% of large groups (>= 20 ind)	% food discovery	% solitary occurrences	% of large sequences (>=3 controls)	% of win / losse
Camponotus macilentus	17	0	0	**94**	10	**71**
Cardiocondyla emeryi	15	7	15	47	0	0
Cardiocondyla nuda	52	0	3	37	**18**	22
Monomorium destructor	134	**66**	**42**	**97**	**67**	42
Monomorium floriocola	94	**44**	**68**	80	1	23
Odontaumachus bauri	45	0	0	**91**	**19**	**65**
Paratrechina sp	22	19	**31**	77	6	**57**
Solenopsis geminata	951	**77**	**37**	**95**	**64**	**72**
Tapinoma melanocephalum	92	**41**	9	88	**15**	48
Tetramorium simillimum	69	1	**44**	**90**	13	31
Tetramoruim bicarinatum	35	**31**	8	83	0	**57**

Discussion

Among the fourteen species collected, a minimum of ten are considered as cosmopolitan or pantropical tramp species. This means that they share several characteristics like unicoloniality, strong interspecific aggressiveness, high polygyny, reproduction by budding (with intranidal mating), small size, monomorphism of worker caste (excepted for the case of *S. geminata* as we discuss later) and worker sterility (see Passera 1994). Their origins, sometimes uncertain, are of all around the world. The ant community of Floreana is a recently assembled one. The presence of so many species reflects a low invasion resistance from the previous community. Shea & Chesson (2002) regroup factors of availability of resources, presence or not of natural enemies and characteristics of physical environment in the "niche opportunity" concept. Le Breton et. al (2005) show in a New Caledonian rainforest that the little fire ant *Wasmannia auropunctata*, due to the absence of dominant species, benefited of a high niche opportunity to establish and to spread.

The 1996-97 census occurs during the warm and rainy season when the 2003 survey takes place at the beginning of the cool dry "garúa" season. But weather in the Galápagos is always humid and temperatures are relatively constant all around the year (ranging from 19-26°C in August-September to 24-31°C in March). So we may consider that the season doesn't have a great effect on ant collection.

Even if some species remind discrete, their wide distribution on the island proves that they got the opportunity to spread and to establish. We are in presence of several tramp species among which *S. geminata* is dominant while others species either maintain their population to constant levels or apparently regress, like *Tetramorium simillimum*. Even if tramp species share typical characteristics favoring invasive behavior they present a variety of differences in their competition strategies.

The endemic species *Camponotus macilentus* and the probably native one *Odontomachus bauri* show very high scores in solitary occurrences (respectively 94% and 91%) and at win/loss scores (71% and 65%). Both forage at night. On the other hand they have very low persistence scores and were never observed in large foraging groups. Thus, they can be classified in "interference competition specialists" or following Wilson (1971) in "extirpators". Their large sizes compared to other species allow them to exclude competitors from baits.

At the opposite, the behavior of *Monomorium floricola* that presents high scores in large foraging groups and strong ability in discovering food is a good example of exploitative competition. It occurs at every sampling site excepted N1 and it is a new record for point A1 comparing to precedent survey. Globally it colonizes more attractive baits in 2003, though relatively discrete. *M. floricola* is totally absent at night (see Fig. 3). Meier (1994) describes the same diurnal pattern of activity for *M. floricola* on cacti on Santa Cruz Island (Galápagos). This could be due to the presence of other more aggressive species during the night. On the other hand its scores in interference competition ability such as percentage of solitary occurrence, persistence and win/loss scores are low. This suggests that *M. floricola* is not a good competitor in direct interspecific interactions.

Tapinoma melanocephalum is a worldwide distributed tramp species known to establish in human buildings under temperate climates (Steinbrink 1987, Dorn et. al 1997, Hugel et. al 2003) or to spread in natural environment like in Galápagos, but it has never been described as replacing native species. In Floreana Island, it is largely distributed over sampling sites but rarely monopolizing many baits. Likewise, we collected only few specimens of the crazy ant *Paratrechina longicornis* but its simultaneous presence at sites A2 and N4 and nearby site A4 in the village suggests that it spreads and establishes over large distances on the island. These two species don't possess stings to defend themselves or to attack other ants, then they probably have a strong interest in remaining discrete. They correspond to "opportunists" in Wilson (1971) classification. *T. melanocephalum* is very efficient at territory exploration and food exploitation, recruiting in a very short time large groups of workers (von Aesch & Cherix 2001). This behavior allows it to share the habitat of more aggressive species by exploiting resources before arrival of others. Fig. 2 shows that these two species decrease their rate of activity at night, probably due to competition pressures.

In 2003 the fire ant *Solenopsis geminata* is clearly the dominant species everywhere, excepted in A4 where baits are monopolized by *Monomorium destructor*. Both species show high activity rate all along experiments and present high scores for all competition ability indices (Table 5). Their numerical superiority probably allows them to break the discovery-dominance trade-off supposed to structure communities. As suggested by Davidson (1998), this could be due to the escapement to natural enemies these species have to face in their native range. Feener and Brown (1992) report that in presence of parasitic phorid flies *S. geminata* decrease strongly its foraging activity. Orr et. al (1995) show that activity of the strongly invasive red fire ant *Solenopsis invicta* present in the United States is restraint in its native range by a parasitoid fly (Diptera, Phoridea). Likewise, absence of natural enemies might explain the success of Argentine ant *Linepithema humile* in North America (Orr & Seike 1998).

S. geminata was already collected at the end of 19th century in Galápagos Archipelago on San Cristobal Island (Emery 1893, Wheeler 1919). But we don't have any precise idea of its time of arrival on Floreana Island. It is not a tramp species *sensu stricto*. Its workers are polymorphic (divided in major and minor workers). Like the red fire ant *S. invicta*, it presents both monogyne and polygyne social forms (Banks et al. 1973, Adams et. al 1976). At least the monogyne form possesses a nuptial flight (McInnes & Tschinkel 1995). But the locally highly dense population of Floreana, is probably polygyne, then one may ask if it disperse by flying queens or not. Reproduction by budding can hardly explain rapid colonization of natural sites N3 and N4. An other possibility is a new recent introduction of *S. geminata* at the highly visited Post Office bay, which is less than one-mile form site N4. Its behavior at food baits is very similar to that of *Wasmannia auropunctata* described by Clark et. al (1982) on Santa Cruz Island: largest foraging groups, high win/loss scores, strong persistence and continuous activity. According to Lubin (1984) *S. geminata* may be the only successful competitor of *Wasmannia* in Galápagos ant fauna.

The little tramp species *Monomorium destructor* is a very interesting case. It was first recorded in 1996 (Pezzatti et al. 1998) on Floreana and it is its first and still unique record in Galápagos archipelago. Originating from Africa (Wilson & Taylor 1967) or India (Bolton 1987), it is a well-known house-infesting pest and has been already introduced in Madagascar, Hawaii, Australia, North, Central and South America and Caribbean Islands (Mc Glynn 1999). Like in 1996-97 survey, it doesn't appear in sampling points outside of the village (point A4). However, using attractive baits at A4 permitted the capture of nine species in 1996-97 for only 5 species in 2003. This doesn't mean that other species are absent of the area, for example *Paratrechina longicornis* has been observed visually inside the village. But it suggests that *M. destructor* reinforced its presents and by the way its competitive pressure on other species. *M. destructor* is probably at the "establishment stage" of invasion described by Heger (2003).

Wilson (1971) classifies *Cardiocondyla* species and *Tetramorium simillimum* in the "insinuators": discrete thieves inserting themselves inconspicuously. Due to their small size and small foraging groups, they can reach food without eliciting aggressive behavior from other species. *Cardiocondyla* species recruit by tandem: a scout that discovers food recruits only one nestmate at a time. This is confirmed by our results: they were never observed in large foraging groups. *T. simillimum* dominates the majority of baits in 1996-97 survey. But even then number of workers at food sources is always lower than for *Solenopsis geminata* which practice mass recruitment. We have to admit that these species don’t seem to have expanding populations.

The question is to know if the system will reach an equilibrium stage or not. The case of invasion of Bermuda successively by *Pheidole megacephala* and then by the Argentine ant *Linepithema humile* shows that a certain mosaic equilibrium can be established between two invasive ants (Haskins & Haskins 1965, 1988). The observed simultaneous progression of *S. geminata* and regression of *T. simillimum* on the very short period of seven years indicates that the actual invasion process on Floreana is still very dynamic. The actual success of *S. geminata* may be ephemeral, and who knows which species will be the next dominant one? Brandaõ & Paiva (1994) suggest that on oceanic islands cyclic invasions may be the rule.

Globally, it appears that all successful introduced species exhibit strongly opportunist behavior practicing exploitative competition. But they are of two categories. *T. melanocephalum* and *M. floricola* may be qualified of discrete opportunists. They have no ability for interference competition on food sources. On the other hand the two dominant species *S. geminata* and *M. destructor* are also very opportunistic species. But at the same time, large-sized species like *O. bauri* and *C. macilentus* that where present before invasions seem to resist to the invaders through their high interference competition abilities. *O. bauri* for example is the only species observed in *Wasmannia auropunctata* highly infested area in the upper part of Floreana Island (pers. obs.), indicating a really strong resistance to invaders.

We know little about the evolution of invasive species population in a long term after introduction. Porter & Savignano (1990) described an invasion by the imported fire ant *Solenopsis invicta* in Texas. Their study reveals the reduction of 50% of ant diversity and a strong negative effect on arthropods community. Morrison (2002) showed that twelve years later *S. invicta* is not as abundant as during initial phase of invasion and the arthropod community recovered its previous diversity. This suggests that impact of invasive species may be more important at the beginning. These authors hypothesized that the observed regression could be due to an overexploitation of resources during the phase of invasion or to the apparition of natural enemies. Concerning *S. geminata*, it is interesting to know that it appeared in huge numbers in some Caribbean islands during first Spanish settlements before to become an actual moderately abundant species in these places (Wilson 1971).

In the future, it will be of great interest to follow the evolution of *M. destructor* population on this island and to analyze at a more detailed scale competition behavior of the different species in order to establish prediction schemes of invasion success.

CHAPTER 2

WHAT IS STRUCTURING A COMMUNITY OF INTRODUCED ANT SPECIES?

WHAT IS STRUCTURING A COMMUNITY OF INTRODUCED ANT SPECIES?

This chapter is in preparation for publication.

Abstract

Floreana Island shelter a community of 24 ant species, most of which are introduced. Here we evaluated separately the importance of environmental factors and interspecific competition in structuring species assemblages and distributions. Multivariate analysis and generalized linear models highlighted the preferences of a set of species for particular ecological conditions. But opportunist tramp species seem to escape this rule and were found without any preferences in most habitats. The attempt to explain species assemblages with competition using co-occurrence analyses failed. We attributed the lack of competition-derived structure to the dynamic of the system. Indeed climatic conditions in Galápagos are highly variables depending on the seasons. We supposed that regular and important variations in the distribution of the principal dominant species *Solenopsis geminata* particularly sensitive to harsh conditions may disrupt community structure. Our hypothesis of a dynamic system with regular migrations is supported by the observation of similarities among nearby sampling stations in ant composition.

Introduction

The introduction of alien species at large scale around the world is a recent phenomenon strongly linked to the huge development of human trade (Jenkins 1996; Work et al. 2005). If most introduced species failed to establish, some of them have a major impact on environment (Elton 1958, Mooney & Drake 1986, OTA 1993, Pimentel et al. 2000). This is especially true for oceanic islands with a particular fauna and flora that confer them a low ecological resistance and makes them very vulnerable ecosystems (Elton 1958; Anderson 1997; Le Breton et al. 2005). As a consequence a majority of them shelters a large amount of alien species. Ants are among the most successful invaders (Williamson & Fitter 1996). They outcompete easily the local fauna causing important damages on native ants diversity and abundance (Haskins & Haskins 1965; Haines et al. 1994; Clark et al. 1982; Le Breton et al. 2003) and more generally on invertebrates (Zimmerman 1970; Clark et al. 1982; Reimer 1994; Jourdan et al. 2002).

In Galápagos Archipelago, the current total of introduced insects stands at 463 species among which 22 are ant species (Causton 2006). Early detection of organisms as insects is particularly difficult due to their small size. Concerning ants, their social organization confer them a high ability to adapt themselves to new environments and once established it is often very difficult to eradicate them since they form rapidly very populous communities. Most of the introduced ants are tramp species. This group of easily transferred ant species share several characteristics as unicoloniality, small size and monomorphism of worker caste, polygyny, reproduction by budding and a strong tendency to migrate (Passera 1994). Another particularity of introduced species is their opportunistic behavior as well as for nesting sites as for food preferences. Then, the coexistence of exotic species implies inevitably some competition among them.

In this study we focus on the ant community of Floreana Island in the Galápagos Archipelago. It is a 173 km2 island with, as most of Galápagos Island, important climatic variations between lower arid and upper humid parts. Its ant fauna is composed of 24 species, among them two or three are endemics and at least 15 are introduced. We tested two hypothesis. The first one is that environmental conditions are good predictors to explain ant species distribution. Many studies highlighted the correlation between species richness and diversity of vegetation (Goldstein 1975; Greenslade & Greenslade 1977; Majer et al. 1984; Morrison 1998; Ribas et al. 2003). Our second hypothesis is that competition is a structuring factor of the ant community. Many authors have postulated that competition structures ant communities (Savolainen & Vespäläinen 1988; Hölldobler & Wilson 1990; Vespäläinen & Savolainen 1990; Andersen 1992; Davidson 1998; Mody & Linsenmair 2003). Several argues that ant communities follow mosaic patterns, in particular when several dominant species coexist (Room 1971; Majer et al. 1994; Morrison 1996; Vanderwoude et al. 2000; Ambrecht et al. 2001; Folgarait et al. 2004). In particular Fluker & Bearsley (1970) describe in Hawaii, an island with exclusively introduced ants, the competitive exclusion of three dominant species: *Pheidole megacephala*, *Linepithema humile* and *Anoplolepis longipes*. However if many authors have tried to explain community structure via several structuring factors, some others claim that stochasticity may explain a majority of observed patterns (Torres 1984; Floren & Lindsenmair 2000; Ribas & Shoereder 2002). Hubbell in his book “The unified neutral theory of biodiversity and biogeography” (2001) opposes the niche-assembly perspective and the dispersal-assembly perspective. In the first one presence and absence of species can be deduced from assembly rules based on the ecological niches or functional role of each species. In the second one communities are open nonequilibrum assemblages of species largely thrown together by chance, history and random dispersal.

In order to prospect in a wide spectrum of climatic conditions we selected a variety of stations in arid and humid zones, situated either in man-impacted or in natural areas (see Fig 1). We measured diverse environmental variables and presence and abundance of species.

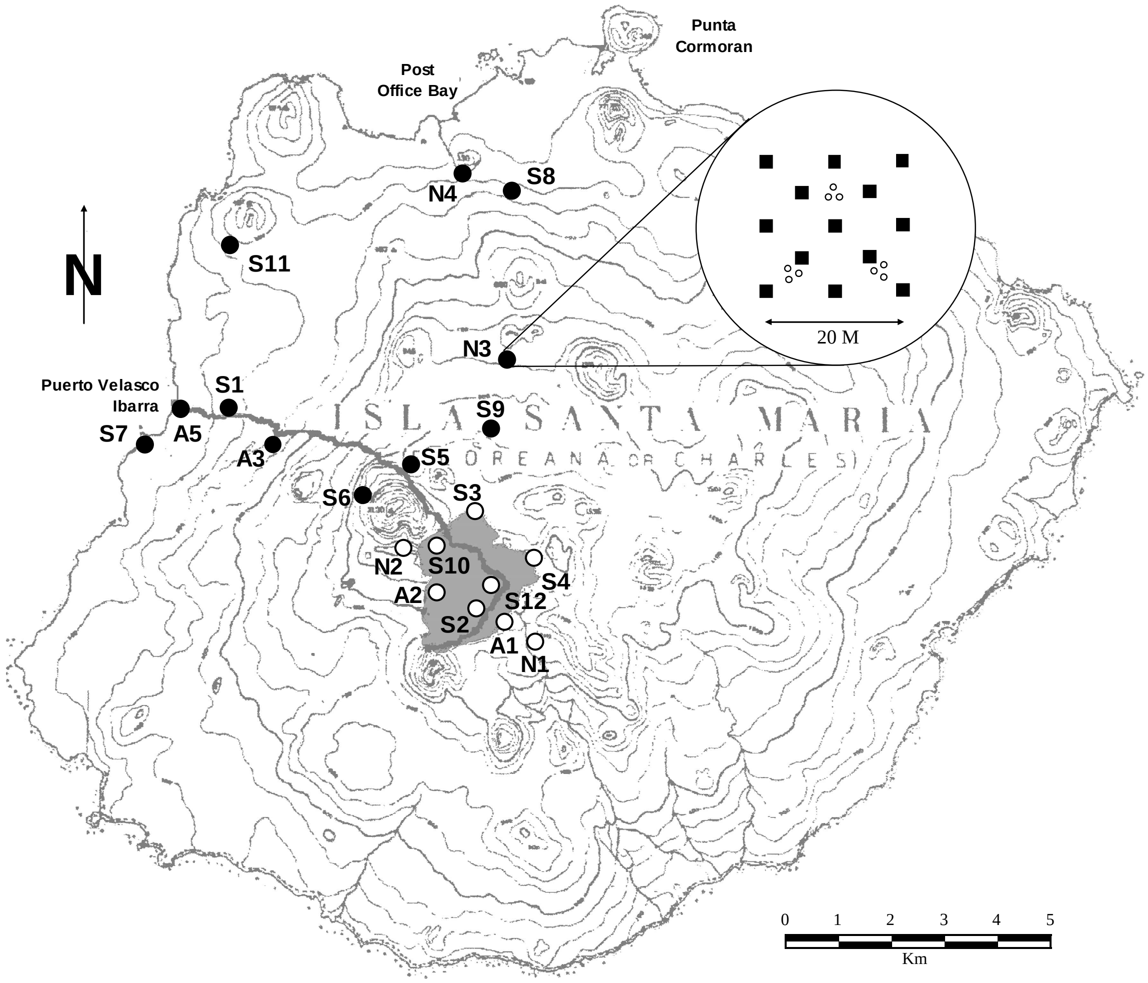

Fig 1.- Map of Floreana Island with the 20 sampling stations. Black dots are stations situated in the arid area and white dots are in the humid one. The thick line is the road leading from the village (sampling station A5) to the cultivated zone (grey area). The enlarged circle shows the disposition of the 13 points of measurment (■) and of the nine pitfall traps within each sampling stations (∴).

Material & Methods

Field work took place on Floreana Island (Galápagos Archipelago, Ecuador) during November – December 2005. In total 20 stations were selected. Nine are located in the upper humid zone and 11 in the lower arid area. Eight stations were considered as disturbed (five humid and three arid) and 12 as natural (four humid and eight arid). Each station was divided in 13 points of measure disposed in a regular grid in a 20 x 20 meters square (see Fig 1). Collected data and the type of measurements are summarized in Table 1.

Environmental factors

We used a camera with fisheye lens to measure the amount of daily solar radiation reaching the soil at each 13 points. Pictures were analyzed with GLA 2.0 (Frazer et al. 1999). On each point we measured the soil porosity as the time for a water column of four cm diameter and seven cm height to penetrate in the ground. The results were log^{-1} transformed. The soil was also characterized visually at each point on a 50 x 50 cm square. We estimated the abundance of grass cover, litter cover and bare soil using the following categories 0 = absent, 1 ≤ 5% of ground surface, 2 = 5-50%, 3 = 50-95% and 4 ≥ 95%. Our index permits a correct description of under-represented types of soil, adapted to the observed patterns. At the station level we calculated a heterogeneity factor as the standard deviation of solar radiation on the 13 points. To measure daily temperature variation we used iButtons® (http://www.maxim-ic.com) recording temperature every hour for at least six days. We estimated for each station the shortest distance to one of the four potential introduction spots: the village (Puerto Velasco Ibarra, at A5), the garbage dump (near S1), the agricultural area (grey area on Fig 1) and a highly visited tourist spot (Post Office Bay, 1km north of N4).

Table 1.- Recapitulation of collected data and level of measure.

Collection of data …

	… at the 20 stations	**… at the 13 points per station (n = 247)**
environmental variables	→ heterogenity (standard deviation of daily solar radiations at the 13 points)	→ daily solar radiation → soil porosity
	→ daily temperature variation	→ index of grass cover
	→ distance to an introduction spot	→ index of litter cover
		→ index of bare soil
faunistic data	→ pitfall trapping (7 days, 9 pitfalls)	→ attractive baiting (at sunrise and sunset)
		→ visual observations (at sunrise and sunset)

Presence and abundance of ants

Presence and abundance of ants were estimated using three different methods. Nine non-attractive pitfall traps were laid for seven days on each station. They were grouped by three and placed in a triangle each 50 cm from the others. Each group was itself distant from the other two groups by 12 meters (see Fig. 1). Pitfall traps were five cm diameter containers filled with 30 ml of ethylene glycol at 66%. At each of the 13 points, we used two methods to inventory ants. Attractive food baits of honey and tuna were used simultaneously for two hours, at sunrise (6:00-8:00 am) and at sunset (6:00-8:00 pm). Finally two persons performed visual observation of ant’s activity on the ground for five minutes at sunrise and at sunset on each point. Visual observations and attractive baiting were performed on different days. Abundance of individuals per species was estimated.

Due to time and access limitations, ants were sampled only by intensive visual search and two over-night food baiting at station S9. Environmental factors were measured as on other sites but only on five points instead of 13.

Statistical analyses

1. Multivariate analyses

Using R free statistical software (http://www.r-project.org, R development Core Team 2006), we performed a Canonical Correspondence Analysis (Ter Braak 1986) on the 20 sampling stations with presence-absence data of species as dependant variables and the eight environmental factors as explanatory variables. To test the possible correlation between geographical distances of sampling stations and similarity of ant fauna composition we performed a Mantel test based on 1’000 replicates. It compares similarity between a matrix of geographical distances and a matrix of distances issued from a Factorial Correspondence Analysis (FCA) on presence-absence of species. We tested also the correlation of geographical distances and ecological similarities issued of a Principal Component Analysis (PCA) for interpretation of the results.

2. Co-occurrence analyses

To test non-random structure of ant assemblages, we used ECOSIM 7.0 software (Gotelli & Entsminger 2002). We analyzed presence-absence at global level (one matrix, presence-absence at the 20 stations) and within stations (19 matrices, presence-absence at the 13 points within each station). The original matrix is randomized here 10’000 times. Each randomized matrix generate a co-occurrence index and the index of the original matrix is compared to its frequency distribution from generated matrices. We used the Stone & Robert’s C-score co-occurrence index (1990). The C-score is the average number of checkerboard units for each unique species pair. An observed C-score higher than expected by chance means that species co-occur less often than by chance. EcoSim offers different rows and column constrains, their total can be “equiprobable”, “fixed” or “proportional”. We used fixed row total algorithms which is the best way to avoid Type I error of statistically significant pattern for a random matrix (Gotelli 2000). This means that the number of presence for each species is constant.

For the global analysis of presence-absence of species at the 20 sampling stations, we ran EcoSim with the “proportional” column option. So the probability of a species to be found in a given station is proportional to the specific richness of the station. We used the fixed-equiprobable algorithm to analyze within-station matrices since the 13 points are very close. An equiprobable total of columns means that species are distributed randomly on the different stations, which is the most realistic approach in this case.

To test for potential associations between pairs of species we applied two different methods. Firstly we used the Cohen’s Kappa co-occurrence index varying between -1 and 1. Using 10’000 bootstraps we estimated for each species pair the limits of the confidence interval at 95% (program developed by A. Hirzel on R). If both limits are positive the pair of species is considered to be significantly more associated than by chance. On the contrary if both limits are lower than zero, the species pair presents an exclusion pattern. The second method consisted in analyzing probability of non-random co-occurrences between pairs of species using output of prior null model analyses of co-occurrence in EcoSim (COOC software, Sfenthourakis et al. 2005). It estimates the probability of a species pair to co-occur more or less in an observed matrix than in the 10’000 randomly simulated ones. The two methods were applied at both levels: between stations and within stations.

3. Generalized Linear Models

In an attempt to link species distribution to environmental factors, we performed Generalized Linear Models on presence-absence of species at the 19 x 13 = 247 sampling points. It represents pooled data of visual observations and attractive baiting. We selected the eight species that were observed at least at 10% (9% for *Wasmannia auropunctata*) of the 247 sampling points. Using R statistical software, the models were selected running a stepwise both direction procedure. Explanatory variables were linear terms of the eight environmental variables and squared terms of three of them: soil porosity, solar radiation and heterogeneity. The best models are fitted following the measure of AIC (Akaike Information Criterion). We calculated an adjusted D^2 for GLM (Guisan & Zimmermann 2000). With the same set of species we tested the eventual effect of competition by running GLMs with presence-absence data of the other species. All species which appear to have a positive effect on the response species were removed from the analysis in order to keep exclusively negatively correlated species. We performed also a GLM to determine the ecological factors affecting species richness over the 20 sampling stations.

Results

Presence and abundance of ants

We collected in total 19 species belonging to four subfamilies and eleven genera. We counted 49’479 specimens, of which about 30’000 have to be attributed to the huge amount of the little fire ant *Wasmannia auropunctata* collected in pitfall traps on station S4. Four species that were collected by Pezzatti et al. (1998) were absent of our data: *Hypoponera* sp B, *Pheidole* sp A and B and *Strumigenys emmae*. Actually they found only one specimen of *Pheidole* sp A and *S. emmae*. *Hypoponera* sp B and *Pheidole* sp B were both found by visual search outside of our sampling site.

Table 2.- List of collected species with comparison of three different methods of ant collection on 20 sampling stations. ● = pitfall trapping; o = visual observations; x = attractive baiting (tuna and honey baits). Food baiting and visual observations were performed on the same 13 points per station. Pitfall baiting consisted in 3 x 3 pitfall traps on each sampling station.

	sampling stations																			
	disturbed & humid					disturbed & arid			natural & humid				natural & arid							
species	A1	A2	S2	S10	S12	A3	A5	S1	N1	N2	S3	S4	N3	N4	S5	S6	S7	S8	S9	S11
Camponotus macilentus		o		● o x		● o x	● o	● o x		o x	● o		● o x	● o x	● o x	● o x	o x	● o x	o x	● x
Camponotus planus														o x			o	● o x		
Cardiocondyla emeryi				●	o		o	● x						● o				● o		
Cardiocondyla nuda	● x	x	●	●	●	● o		●		●	●				● o x	● o x			x	
Hypoponera sp $^{(1)}$			●		o						●									
Monomorium destructor							● o x	● o x												
Monomorium floricola	● o	●	●	●	●	●				●	● o		●	●	● o x	● x	● o x	● x	x	x
Odontomachus bauri	● o	● o x	● x	● o x	● o x		●		o	● o x	● o x		o	o	● o x	o		● o	o x	
Paratrechina longicornis			●		● o					●	● o				● o x	● x	●	● o x	no pitfall trapping at this station	
Paratrechina sp $^{(2)}$		●	x	● o x	● o		● o x			x				● o x				o x		x
Solenopsis geminata	● o x	● o x	● o x	● o x	● o x	o x		x	● o x	● o x	● o x			● o x	● o x		● o x	o x		● o x
Solenopsis globularia								● o x									● o x			● o x
Solenopsis sp $^{(3)}$	x	●	● x	●						●										
Strumigenys louisianae			● o		● o					o										
Tapinoma melanocephalum	● o	● o	● o	● o	●	● o x	●	● x		● x			● o x	● o x	● o x	● o x	● o x	o x	o	
Tetramorium bicarinatum	● o x	x		● o x	x					o							● o x			
Tetramorium caldarium				● o x		● o x	o						● o x							
Tetramorium simillimum	● o x	● o x	o	● o x		● o			● o x	● o x	● o x		o x		● o x	● o x	● o x		o x	
Wasmannia auropunctata		● o x	● o x		● o x							● o x								
# species	7 6 5	8 6 6	# 5 5	# 6 7	9 8 4	6 6 4	5 5 2	6 3 6	2 3 2	8 6 6	8 6 3	1 1 1	4 5 4	6 7 5	8 8 8	5 5 6	7 8 7	6 8 7	- 4 5	3 2 4
	8	**11**	**12**	**12**	**12**	**7**	**7**	**7**	**3**	**12**	**8**	**1**	**6**	**8**	**8**	**7**	**9**	**9**	**6**	**5**

Notes: (1) possibly *Hypoponera opaciceps* ; (2) possibly *Paratrechina vaga* ; (3) subgenera *Diplorhoptrum*

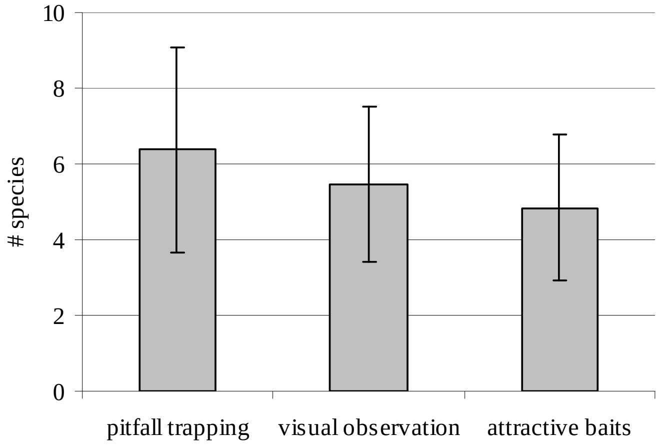

Fig 2- Mean number of species collected per sampling station using three different sampling methods. N=19.

Species collected at each sites and methods of collect are presented in Table 2. The two passive ways of collecting that are pitfalls and visual observations matched most of the time the higher diversity (Fig 2). Pitfalls trapped in average 49.4 ant individuals in humid zone and 24.7 in arid one. Table 3 presents number of individuals listed per species following the three sampling methods. Species have been categorized into functional groups based on Andersen North American ants classification (Andersen 1997) and competition hierarchy observed of Floreana ant community (von Aesch & Cherix 2005; see Chap.1) The two endemic *Camponotus* species and *Odontomachus bauri* are "large-sized" ants. They are never seen in large foraging groups and forage preferentially at night (exclusively at night for *Camponotus* spp). They are interference competition specialists (von Aesch & Cherix 2005). *Monomorium destructor*, *Solenopsis geminata* and *Wasmannia auropunctata* are "dominant" species. This means that at least on a particular area of Floreana, they monopolize the majority of food sources in baiting experiments. *Hypoponera* sp, *Solenopsis* sp and *Strumigenys louisianae* are "cryptic" species. None of them were caught by all three sampling methods. The ten remaining species belong all to the "opportunist" category. With the exception of *Solenopsis*

Table 3.- Number of individuals counted for each species following the three collection methods. Species are attributed to a functional group corresponding to their status in Floreana Island ant community. When *T. simillimum* and *T. caldarium* coexists on the same station, it is not possible to distinguish them during visual observations (last line).

Species	**functional group**	**∑ pitfalls**	**∑ baits**	**∑ obs**	**∑ TOTAL**
Camponotus macilentus	large-sized	334	450	152	936
Camponotus planus	large-sized	9	4	14	27
Odontomachus bauri	large-sized	34	28	52	114
Monomorium destructor	dominant	602	1147	15	1764
Solenopsis geminata	dominant	764	4617	1008	6389
Wasmannia auropunctata	dominant	30959	763	666	32388
Hypoponera sp	cryptic	2	0	1	3
Solenopsis sp	cryptic	8	47	0	55
Strumigenys louisianae	cryptic	17	0	4	21
Cardiocondyla emeryi	opportunist	16	2	24	42
Cardiocondyla nuda	opportunist	255	9	14	278
Monomorium floricola	opportunist	770	217	32	1019
Paratrechina longicornis	opportunist	256	18	7	281
Paratrechina sp	opportunist	171	548	131	850
Solenopsis globularia	opportunist	59	266	10	335
Tapinoma melanocephalum	opportunist	225	777	181	1183
Tetramorium bicarinatum	opportunist	35	140	75	250
Tetramorium caldarium	opportunist	334	68	9	411
Tetramorium simillimum	opportunist	931	1437	439	2807
Tetramorium cald or *sim*	opportunist	0	0	326	326
		35781	**10538**	**3160**	**49479**

globularia which is not known as a common transferred species, all of them are tramp species.

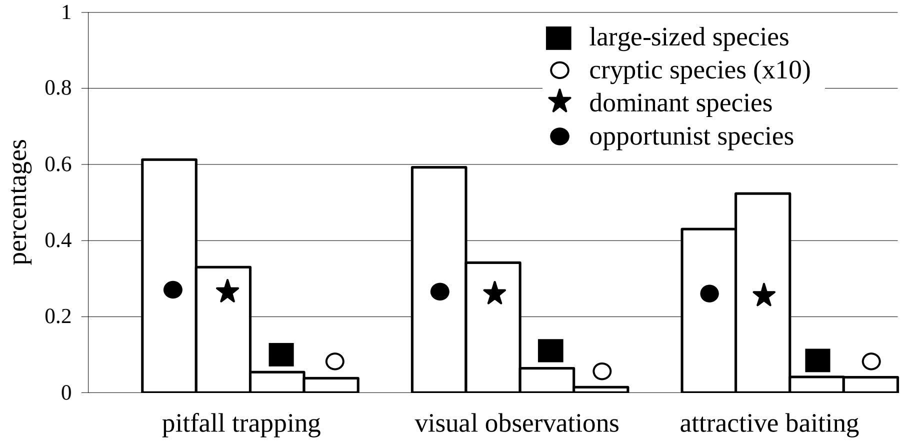

Fig 3.- Evaluation of sampling methods following the functional groups of species.

In Fig 3, proportions of ants belonging to the different functional groups were plotted following the sampling method. Both passive collection methods, i.e. pitfall trapping and visual observation, give appreciably the same results. On the other hand dominant species were collected in huge numbers at food baits as a logical consequence of their mass recruitment strategy and their high competitive ability. The very few amount of cryptic species detected at visual observations is probably due to the fact that they are very small and discrete and could have remained undetected by the observers.

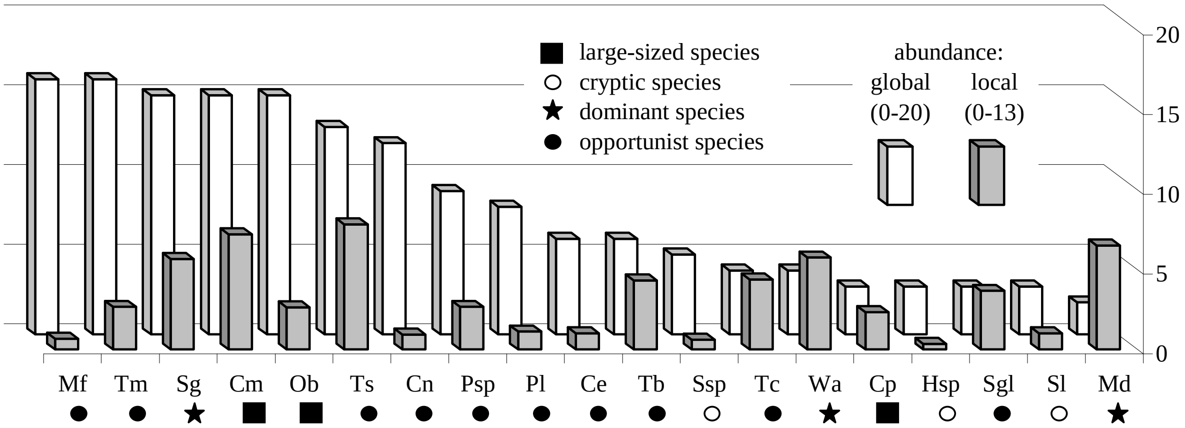

Fig 4.- Sampling profile of each species. White bars repersent the number of sampling stations were they are present; grey bars are the mean abundances at stations (number of points out of 13) when present.
Cm = *Camponotus macilentus*; Cp = *C. planus*; Ce = *Cardiocondyla emeryi*, Cn = *C. nuda*; Hsp = *Hypoponera* sp; Md = *Monomorium destructor*; Mf = *M. floricola*; Ob = *Odontomachus bauri*; Pl = *Paratrechina longicornis*; Psp = *Paratechina* sp; Sg = *Solenopsis geminata*; Sgl = *S. globularia*; Ssp = *Solenopsis* sp; Sl = *Strumigenys louisianae*; Tm = *Tapinoma melanocephalum*; Tb = *Tetramorium bicarinatum*; Tc = *T. caldarium*; Ts = *T. simillimum*; Wa = *Wasmannia auropunctata*.

Fig. 4 describes the global and local abundance of species. The first one (rear line) is the number of stations out of 20 where a species have been recorded; local abundance (front line) is the mean number of points of presence out of 13 within each station (considering exclusively stations where it is present). Only five species exceed in average five points of presence per station. They are the three dominants, the opportunist *Tetramorium simillimum* and the endemic *Camponotus macilentus*. Of the three dominant species, *S. geminata* is the only one to be widely distributed over sampling area. *T. simillimum* not only is present at large scale on the island but it is also the most "surface abundant" at local scale. Data of local abundance of *C. macilentus* have to be carefully analyzed. Local abundance of large-sized species might have been over-estimated due to the very fast moving of their workers. Two observation points distant by 10 meters might generate observations that are less independent than for other species. *Tapinoma melanocephalum* and *Monomorium floricola,* both typical and very common tramp species, are the most widespread species over our survey. *M. floricola* shows the highest contrast between global and local abundance.

Environmental factors

Environmental characteristic of sampling stations are summarized in Table 4. For station S9, as index of soil type were measured only on five points instead of 13, obtained values were corrected using a $^{13}/_{5}$ factor.

Table 4.- Environmental characteristics of the twenty sampling stations. Distance to an introduction spot and daily temperature variations are measured once for each station. Heterogeneity is the standard deviation of solar radiations measures over 13 points on each station (5 points for S9). Soil porosity and solar radiations are measure on 13 points per stations (5 on S9) and the mean values and standard deviation are presented here. Indices of soil categories correspond to the number of occurrences of each of them on the 13 points of observation.

station	station type	distance to a potential introduction spot [km]	daily temperature variations [°C]	hetero-geneity (SD of solar rad)	soil porosity [(log s)$^{-1}$]	solar radiation [Mols m^{-2} d^{-1}]	index of bare soil	index of grass cover	index of litter cover
A1	disturbed & humid	0	2.65	5.10	0.78 ± 0.18	13.70 ± 5.10	2	9	2
A2	disturbed & humid	0	2.32	3.77	0.86 ± 0.18	16.00 ± 3.77	0	13	0
S2	disturbed & humid	0	3.50	5.02	0.51 ± 0.08	14.61 ± 5.02	0	7	6
S10	disturbed & humid	0	3.90	4.70	1.02 ± 0.20	15.18 ± 4.70	0	5	8
S12	disturbed & humid	0	4.45	4.00	0.66 ± 0.23	10.82 ± 4.00	4	2	7
A3	disturbed & arid	0	10.18	1.25	1.08 ± 0.73	17.73 ± 1.25	11	0	2
A5	disturbed & arid	0	7.07	2.35	0.48 ± 0.11	18.43 ± 2.35	13	0	0
S1	disturbed & arid	0	11.88	2.85	0.48 ± 0.13	17.67 ± 2.85	7	0	6
N1	natural & humid	0.8	2.58	1.91	0.66 ± 0.17	6.80 ± 1.91	1	10	2
N2	natural & humid	0.4	6.27	2.95	0.89 ± 0.76	12.33 ± 2.95	0	0	13
S3	natural & humid	0.1	4.16	1.86	0.79 ± 0.18	12.08 ± 1.86	1	3	9
S4	natural & humid	0.1	5.44	1.38	1.17 ± 0.34	9.21 ± 1.38	2	6	5
N3	natural & arid	2.7	5.44	2.93	0.53 ± 0.19	16.11 ± 2.93	9	0	4
N4	natural & arid	0.8	7.91	2.44	0.42 ± 0.08	17.69 ± 2.44	6	0	7
S5	natural & arid	1.2	7.53	3.01	0.87 ± 0.75	15.27 ± 3.01	8	0	5
S6	natural & arid	1.8	5.51	2.05	0.82 ± 0.58	16.63 ± 2.05	4	0	9
S7	natural & arid	0.7	8.08	2.73	0.56 ± 0.15	16.60 ± 2.73	2	0	11
S8	natural & arid	1.4	7.00	2.48	0.65 ± 0.82	18.18 ± 2.48	8	0	5
S9	natural & arid	1.2	2.27	2.40	0.49 ± 0.05	17.53 ± 2.40	10.4	0	2.6
S11	natural & arid	1.8	11.79	1.98	0.46 ± 0.10	17.88 ± 1.98	3	0	10

Statistical analyses

1. Multivariate analysis

Results of the Canonical Correspondence Analysis (CCA) are presented in Fig 5. Stations and species have been projected following the two first CCA axis that explain respectively 23.7% and 13.8% of total variance. Dots are position of sampling stations predicted by their species composition and arrows indicate their position predicted by the model built on environmental factors. There is a clear discrepancy between humid and arid stations following the first CCA axis. On Fig 5c., it appears that excepted for litter cover index, all original explanatory variable discriminates graphically humid and arid stations. In particular, bare soil, strong solar radiations and important daily temperature variation are typical of arid area and at the opposite an important grass cover and a high heterogeneity of the environment are good descriptors of humid zone. Compared to humid stations, arid ones are situated in a wider geographical range and also a wider ecological conditions range. So their segregation in the CCA plan is better. The very bad prediction of the model concerning S4 is due to the exclusive presence of *Wasmannia auropunctata* at this point. Also station N1 fits poorly the

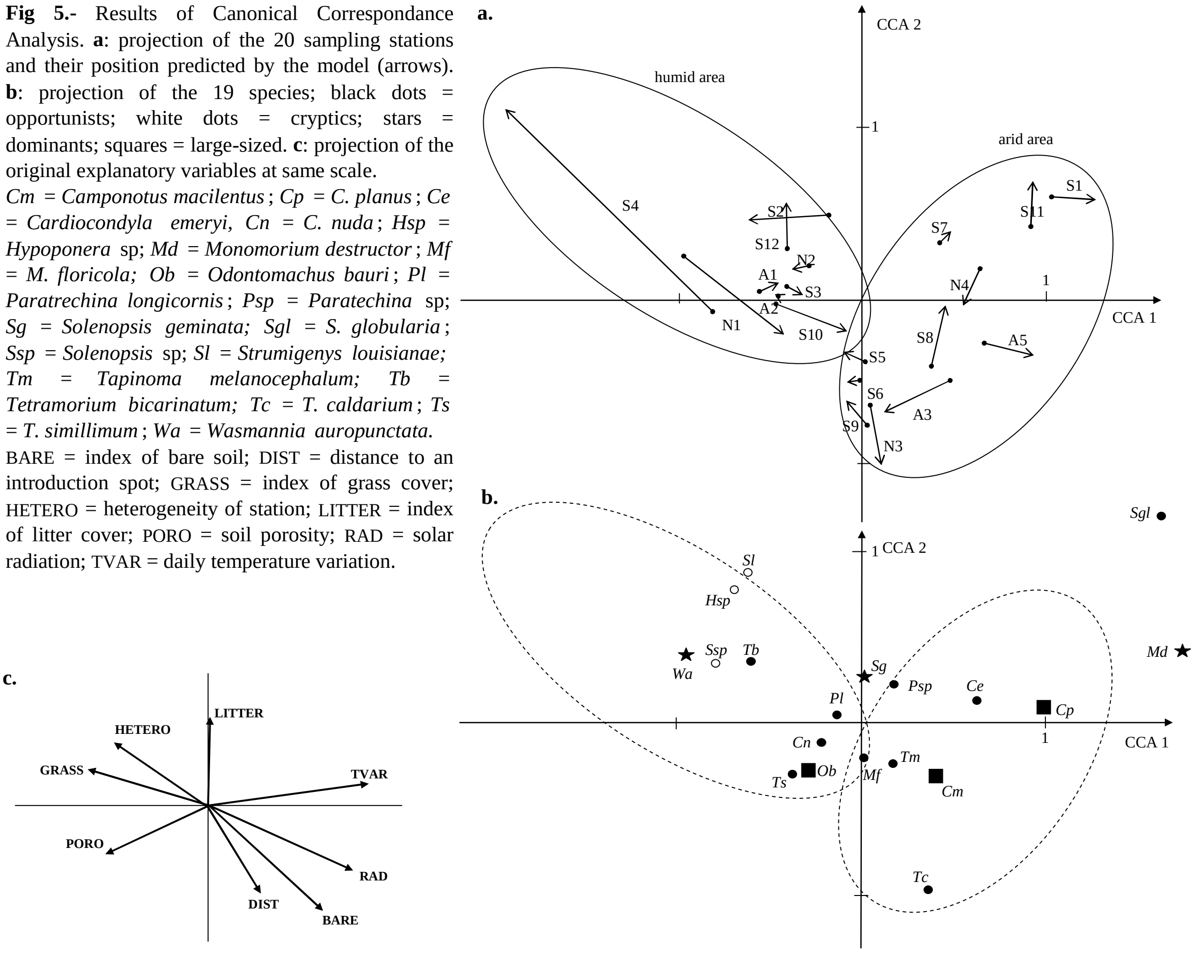

Fig 5.- Results of Canonical Correspondance Analysis. **a**: projection of the 20 sampling stations and their position predicted by the model (arrows). **b**: projection of the 19 species; black dots = opportunists; white dots = cryptics; stars = dominants; squares = large-sized. **c**: projection of the original explanatory variables at same scale. *Cm* = *Camponotus macilentus*; *Cp* = *C. planus*; *Ce* = *Cardiocondyla emeryi*, *Cn* = *C. nuda*; *Hsp* = *Hypoponera* sp; *Md* = *Monomorium destructor*; *Mf* = *M. floricola; Ob* = *Odontomachus bauri*; *Pl* = *Paratrechina longicornis*; *Psp* = *Paratechina* sp; *Sg* = *Solenopsis geminata; Sgl* = *S. globularia*; *Ssp* = *Solenopsis* sp; *Sl* = *Strumigenys louisianae; Tm* = *Tapinoma melanocephalum; Tb* = *Tetramorium bicarinatum; Tc* = *T. caldarium*; *Ts* = *T. simillimum*; *Wa* = *Wasmannia auropunctata.* BARE = index of bare soil; DIST = distance to an introduction spot; GRASS = index of grass cover; HETERO = heterogeneity of station; LITTER = index of litter cover; PORO = soil porosity; RAD = solar radiation; TVAR = daily temperature variation.

model. It shelters only three species compared to an average of 8.8 species per site in the humid area. On the upper left part of Fig 5b we found a group composed of the three cryptic species, the opportunist *Tetramorium bicarinatum* and the dominant *W. auropunctata*. This patchy assemblage indicates similar climatic preferences, typical of humid environments. *T. bicarinatum* is the only one that has been found on an arid spot, at S7. A group of species composed of most of the opportunist species found in our survey is situated close to the origin of axes as well as the dominant *S. geminata*. The two endemic *Camponotus* species are mostly found in arid part. Fig. 6 indicates for each of the 19 species the percentage of explained variability. It appears immediately that most of the opportunist species are grouped on the right side meaning that environmental variables affect less their distribution. The extreme position in the CCA projection for some species has to be attributed to some artifact effects principally due to their low frequency over sampling area. For example *Monomorium destructor* which is the last known introduced species is found only at two arid stations nearby the village. This species seems to be far from its realized niche on Floreana, being probably more restricted by historical and competition constraints than by ecological conditions (see Chapter 3).

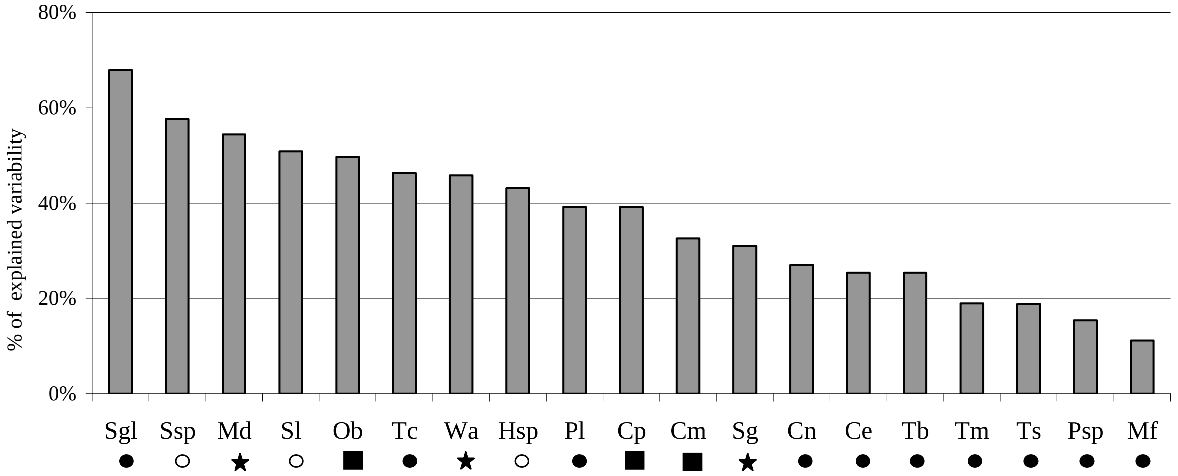

Fig 6.- Percentage of explained variability for each species by the Canonical Correspondance Analysis. Functional groups are indicated by symbols: black dots are opportunist species, white dots are cryptic species, squares are large-sizes species and stars are dominant species. For species names abbreviations refer to legend of fig 5.

Results of Mantel test (Table 5) show a significant negative correlation between geographical inter-station distances and species composition similarities ($p < 0.0001$). But the CCA reveals a marked disparity between stations from the arid and from the humid area. Thus, as the humid area is relatively small compared to our global sampling area, we were wondering if the pattern revealed by the Mantel test is only due to this proximity between ecologically

Table 5.- Results of distance Mantel tests.

Mantel test of correlation with geographical distances on:	FCA distances between stations (similarity of ant fauna)	PCA distances between stations (similarity of environmental conditions)
all stations (mean distance = 4.05 km)	r = 0.4873 **p < 0.0001 *****	r = 0.3879 **p < 0.001 *****
arid stations (mean distance = 4.06 km)	r = 0.2624 **p = 0.034 ***	r = -0.0172 p = 0.551
humid stations (mean distance = 1.39 km)	r = 0.1449 p = 0.263	r = 0.276 p = 0.160

similar stations. This is confirmed by the Mantel test on geographical distances *vs* ecological similarities (PCA distances). When conducted on all stations it reveals a strong correlation between geographical distance and ecological similarities ($p < 0.001$) but when performed exclusively on the arid or humid subgroups, the test shows no correlation of ecological similarities with the distance. Therefore we performed Mantel tests separately on arid and humid stations. In the latter, as expected, we found no effect of distance ($p = 0.263$). On the other hand the effect was significant for the set of eleven arid stations.

2. Co-occurrence analysis

Table 6 presents results of the test of non-random co-occurrence hypothesis using EcoSim. A p-value of observed C-score higher than expected signifies that species coexist less often than by chance. In the between-station analysis (global matrix) there is neither significant positive nor negative co-occurrence. This is also true for most of the within-stations analyses excepted for A2 and A5. The positive co-occurrence of species at A5 may be easily explained. This station located in the village is principally composed of bare soil with almost no vegetal cover. Thus ants were systematically observed on the same shady points. Here the positive co-occurrence is due to harsh conditions. In A2 however climatic conditions are more suitable (100% grass cover) and it appears that species at the 13 sampling points of that station are distributed following a competitive exclusion pattern.

Table 6.- C-score indices for the observed and random matrices for the island (Global) and for each station. The mean value and standard deviation for 10'000 randomized matrices are presented together with the observed index and the P-values for acceptation or rejection of the null hypothesis. An observed C-score higher than expected indicates that co-ocurrence in observed matrix is lower than by chance.

	model		**C-scores**			
data	**rows**	**colums**	**observed**	**simulated**	**obs<exp**	**obs>exp**
Global	fixed	proportional	10.6199	10.8369 ± 0.8350	0.3953	0.6076
A1	fixed	equiprobable	3.5257	4.2639 ± 0.4386	0.1436	0.8663
A2	fixed	equiprobable	3.5357	2.5449 ± 0.3391	0.9631	**0.0432**
A3	fixed	equiprobable	2.5000	2.8283 ± 0.9037	0.4106	0.6402
A5	fixed	equiprobable	0.9000	3.2727 ± 0.5137	**0.0024**	0.9992
N1	fixed	equiprobable	2.0000	1.6836 ± 0.5327	1.0000	0.8418
N2	fixed	equiprobable	3.8571	3.9984 ± 0.4172	0.4174	0.6069
N3	fixed	equiprobable	1.8333	2.3889 ± 1.5139	0.4948	0.7750
N4	fixed	equiprobable	4.8095	4.8866 ± 0.7937	0.4563	0.5637
S1	fixed	equiprobable	5.4000	5.0864 ± 0.9944	0.6203	0.4049
S2	fixed	equiprobable	3.8929	3.3296 ± 0.3113	0.8482	0.1681
S3	fixed	equiprobable	3.6000	3.1089 ± 0.5605	0.7471	0.2900
S5	fixed	equiprobable	5.0000	6.5315 ± 0.8301	0.0600	0.9443
S6	fixed	equiprobable	3.4762	2.5142 ± 0.4887	0.9241	0.0856
S7	fixed	equiprobable	5.7619	6.8050 ± 1.1023	0.1664	0.8454
S8	fixed	equiprobable	1.7778	2.6784 ± 0.1599	0.2916	0.7240
S10	fixed	equiprobable	4.7143	5.2154 ± 0.8713	0.2873	0.7278
S11	fixed	equiprobable	2.6000	2.8285 ± 0.4132	0.3775	0.6969
S12	fixed	equiprobable	2.4444	2.9249 ± 0.1755	0.1362	0.8778

Then positive or negative associations were analyzed at the species pairs level. Results of the Cohen’s Kappa method and COOC software are presented in Table 7. The most common association between pairs is the co-occurrence pattern. This should probably be interpreted as a consequence of similar ecological preferences (Morrison 1996). When pooling results of both methods, at the global level only 5 pairs of species appear to suffer exclusive competition, which represents less than 1.5% of all tested species pairs. When analyzing co-occurrence pattern at the within-station scale, one pair out of 726 tested shows an exclusion pattern. The little fire ant *Wasmannia auropunctata* is implicated in half of the observed exclusion patterns. There is only one concordant result between COOC and Kappa estimation of species pairs association: the significant co-occurrence of *Tetramorium bicarinatum* and *Solenopsis globularia* at S7.

Table 7.- Association of pair of species evaluated using two methods: the Cohen's Kappa confidence interval (on 10'000 bootstraps) and the COOC software using EcoSim output of prior model analysis of coocurrence (10'000 simulated matrices). Observed and simulated values on the right are: K = Coehn's Kappa on observed matrix; N = number of sites of co-occurrence observed for the species pair.

Data	species pair	association	test	obs. values	sim. values
Global	*Paratrechina sp* x *Cardiocondyla emeryi*	co-occurrence	Cohen's Kappa	K = 0.479	K = 0.466
Global	*Solenopsis sp* x *Cardiocondyla nuda*	co-occurrence	Cohen's Kappa	K = 0.429	K = 0.424
Global	*Solenopsis sp* x *Monomorium floricola*	co-occurrence	Cohen's Kappa	K = 0.200	K = 0.203
Global	*Solenopsis sp* x *Odontomachus bauri*	co-occurrence	Cohen's Kappa	K = 0.250	K = 0.250
Global	*Solenopsis sp* x *Solenopsis geminata*	co-occurrence	Cohen's Kappa	K = 0.200	K = 0.203
Global	*Solenopsis sp* x *Tapinoma melanocephalum*	co-occurrence	Cohen's Kappa	K = 0.200	K = 0.200
Global	*Solenopsis sp* x *Tetramorium simillimum*	co-occurrence	Cohen's Kappa	K = 0.364	K = 0.358
Global	*Tetramorium bicarinatum* x *Monomorium floricola*	co-occurrence	Cohen's Kappa	K = 0.250	K = 0.250
Global	*Tetramorium bicarinatum* x *Solenopsis geminata*	co-occurrence	Cohen's Kappa	K = 0.250	K = 0.251
Global	*Tetramorium bicarinatum* x *Tapinoma melanocephalum*	co-occurrence	Cohen's Kappa	K = 0.250	K = 0.250
Global	*Tetramorium caldarium* x *Camponotus macilentus*	co-occurrence	Cohen's Kappa	K = 0.194	K = 0.193
Global	*Tetramorium simillimum* x *Cardiocondila nuda*	co-occurrence	Cohen's Kappa	K = 0.490	K = 0.476
Global	*Tetramorium caldarium* x *Paratrechina longicornis*	competition	Cohen's Kappa	K = -0.364	K = -0.337
Global	*Wasmannia auropunctata* x *Camponotus macilentus*	competition	Cohen's Kappa	K = -0.417	K = -0.399
Global	*Wasmannia auropunctata* x *Tetramorium caldarium*	competition	Cohen's Kappa	K = -0.286	K = -0.255
Global	*Cardiocondyla emeryi* x *Tetramorium simillimum*	competition	COOC software	N = 1/20	N = 3.26/20
Global	*Odontomachus bauri* x *Solenopsis globularia*	competition	COOC software	N = 0/20	N = 1.87/20
A5	*Tetramorium sp* x *Cardiocondyla emeryi*	co-occurrence	Cohen's Kappa	K = 1	K = 1.000
S5	*Tapinoma melanocephalum* x *Camponotus macilentus*	co-occurrence	Cohen's Kappa	K = 0.435	K = 0.430
S7	*Tetramorium bicarinatum* x *Solenopsis globularia*	co-occurrence	Cohen's Kappa	K = 0.562	K = 0.553
S12	*Wasmannia auropunctata* x *Solenopsis geminata*	co-occurrence	Cohen's Kappa	K = 0.552	K = 0.539
S2	*Wasmannia auropunctata* x *Tetramorium simillimum*	competition	Cohen's Kappa	K = -0.519	K = -0.458
A1	*Odontomachus bauri* x *Tetramorium simillimum*	co-occurrence	COOC software	N = 3/13	N = 0.85/13
N2	*Camponotus macilentus* x *Paratrechina sp*	co-occurrence	COOC software	N = 2/13	N = 0.30/13
S7	*Tetramorium bicarinatum* x *Solenopsis globularia*	co-occurrence	COOC software	N = 4/13	N = 1.89/13

3. Generalized Linear Models

Results of GLM for the distribution of the eight most frequent species at the 247 sampling points are presented in Table 8.

GLMs on environmental variables permitted to explain between 3.5% and 31.1% of the distribution of the tested species. The less linkable distribution to environmental factors where those of the opportunist species *Tapinoma melanocephalum* and *Paratrechina* sp. The best models are obtained for the endemic *Camponotus macilentus* and the dominant *Wasmannia aurpunctata*. Only a very small rate of distribution patterns is explained by the presence of potential competitors. For three species we were even not able to fit a model. At least one of the dominant *Solenopsis geminata* and *W. auropunctata* has a significant effect on *Tetramorium simillimum/caldarium*, *Camponotus macilentus* and *T. melanocephalum*. It is interesting to notice that these models permit to put in evidence three apparently competitive pairs of species: *C. macilentus – W. auropunctata*; *C. macilentus – S. geminata* and *T. simillimum/caldarium – W. auropunctata*. Indeed, it seems logical that if a species A is negatively correlated to a species B, the contrary is similar. This implies that we cannot, from the exclusive results of these GLMs, decide which species is responsible for the exclusion

Table 8.- Coefficients of generalized linear models based on the presence-absence of the eight most abundant species on the visual observations data set (247 points). Adj D2 represent the total deviance explained by the models corrected by the number of predictors to the number of observations. Explanatory variables: **(a)** dist = distance to a potential introduction site; tvar = daily temperature variation; poro = soil porosity; hetero = heterogeneity of sampling station regard to vegetal cover; bare = index of bare soil; grass = index of grass cover; lit = index of litter. **(b)** presence - absence of potential competitors

(a) Species	nb of presence (n=247)	intercept	DIST	TVAR	PORO	PORO^2	RAD	RAD^2	HETERO	HETERO^2	BARE	GRASS	LITTER	adj D^2
Ts+Tc	102		3.09	-4.69	2.12		-2.48	-2.85					2.4	0.116
Cm	101		3.96				-3.44				1.96	-2.69		0.292
Sg	95								2.42	-2.06	-2.28	3.3		0.140
Tm	40	-9.16	2.86	3.2			-2.74		2.06					0.068
Ob	37	-2.9					-2.42	-2.5	2.54	-3.76		4.48		0.230
Tb	26	-6.17						-2.08	3.26		-2.75	-1.97		0.256
Psp	24	-9.78							2.38			-1.83		0.035
Wa	23	-6.39							-3.55	2.88		3.77	2.89	0.311

(b)		Ts+Tc	Cm	Sg	Tm	Ob	Tb	Psp	Wa	
Ts+Tc									-2.81	0.051
Cm				-3.56					-2.89	0.086
Sg			-3.37							0.032
Tm	-6.75			-2.21						0.021
Ob			*it was not possible to fit a GLM for this species*							
Tb			*it was not possible to fit a GLM for this species*							
Psp			*it was not possible to fit a GLM for this species*							
Wa	-4.84	-2.74	-2.72							0.220

Note: *Ts+Tc* = *Tetramorium simillimum* and *T. caldarium*; *Sg* = *Solenopsis geminata*; *Cm* = *Camponotus macilentus*; *Ob* = *Odontomachus bauri*; *Tm* = *Tapinoma melanocephalum*; *Tb* = *Tetramorium bicarinatum*; *Wa* = *Wasmnannia auropunctata; Psp* = *Paratrechina* sp (possibly *P. vaga*).

competition. But each pair comprises a species that is known for behaving as dominant on Floreana. Thus, we can suppose that they are responsible for the observed pattern.

We ran also a GLM to determine which abiotic factors affect species diversity over the 20 sampling stations. The only environmental factor with a significant effect is the heterogeneity of the environment. Therefore we made a linear regression between diversity and heterogeneity, and we got an adjusted R^2 of 45.0%.

Discussion

Results and principal contributions from the different statistical approaches are summarized in Table 9.

Our data demonstrate that environmental factors are partly structuring ant community on Floreana Island. Actually, this was not so surprising given the huge variations in observed abiotic conditions over our sampling area. However, both multivariate analysis and generalized linear models reveal that opportunist species are clearly less dependent on

Table 9.- Recapitulation of observed trends in analyses of the respective role of environmental factors and competition in structuring ant communities on Floreana Island.

Statistical analyses	Role of environmental factors	Role of competition
Multivariate approach: Canonical Correspondence Analysis	a general discrimination in ant composition between humid and arid areas a preference of a group of species (in particular the 3 cryptic ones) for humid conditions the comparatively low explained variance for tramp species found in every type of habitats highlights their opportunistic behavior	
Co-occurrence analysis		
A. globally (EcoSim)		no general pattern, one observed negative co-occurrence trend was observed for station A2
B. pairs by pairs (Kappa and COOC)		1% of tested pairs show a positive co-occurrence (probably due to ecological affinities) and only 0.3% a negative one; *W. auropunctata* is implicated in half of the six pairs highlighted as "exclusives"
Generalized Linear Models	between 3.5% and 31 % of explained deviance for the eight tested species; higher scores were matched by the endemic *Camponotus macilentus* and the dominant *W. auropunctata*; models for the opportunists *Paratrechina* sp, *Tapinoma melanocephalum* and *Tetramorium simillimum/caldarium* explain very little deviance	the higher explained deviance (8%) was obtained for *C. macilentus*; in general explained deviance is smaller than in models on environmental factors
	→ ecological conditions seem to affect principally species issued from dominants, large-sized and cryptic functional groups; opportunist species are less or not affected	**→ competition is not a structuring factor**

environmental factors than others. They are able to establish in every type of ecological environment present in our study, whatever the ecological conditions. This is particularly true for *Monomorium floricola* and *Tapinoma melanocephalum* that are the two most widespread species on Floreana. Heterogeneity expressed as the variability in the amount of solar radiation reaching the soil over a sampling station is the only factor correlated, positively, with the local abundance of species. Heterogeneity on Floreana is principally due to human impact in the agricultural area. Goldstein (1975) has shown on an insular system that diversity of exposition to the sun is the best predictor of species number on an island. More generally, a huge diversity of vegetation is often linked with a higher diversity of ant species (Greenslade & Greenslade 1977; Majer et al. 1984; Perfecto & Snelling 1995; Morrison 1998; Ribas et al. 2003).

On the other hand, the role of competition in governing ant distribution is not evident here. In the co-occurrence analyses, exclusion patterns were observed for five species pairs. But a considerable part of these patterns should probably be attributed to distinct ecological preferences. It could be that Floreana Island ecosystem is still not saturated and resources are sufficiently abundant to allow the coexistence of many species, particularly opportunist ones with a broad ecological niche. But we lack information to support this assumption. Actually interspecific competition in ant communities is a fact largely admitted (Hölldobler & Wilson 1990), especially among worldwide transferred species that are highly opportunistic and thus share potentially similar resources preferences. Then we may wonder why the importance of competition seems to be so negligible here. Moreover, interspecific competition for food has been highlighted in previous chapter (von Aesch & Cherix 2005) and by other authors studying ant communities in Galápagos (Clark et al. 1982, Lubin 1984, Meier 1994). Maybe that consequences of competition are not expressed as a geographical segregation but rather as a functional segregation in ant communities. It has been demonstrated that competing species might coexist thanks to the discovery-dominance trade-off which consists in applying different foraging strategies (Davidson 1998). We have shown (von Aesch & Cherix 2005; see Chap. 1) that opportunist species are good at exploitative competition which consists in exploring efficiently the territory and exploit resources as soon as discovered using mass recruitment, but they are bad at defending resources when confronted to competitors. Inversely, the three large-sized species are poor explorers but good at defending resources once they discover it. Then, in a community of several coexisting species, every one is characterized by a feeding behavior situated between the two extremes that are exploitation and interference specialists. Torres (1984) demonstrates in a forest of Puerto Rico that species sharing the same kind of resources differ in their use of litter depth, daily activity and microhabitat.

An other hypothesis to explain the lack of competitive structure is to consider the system as too dynamic to allow the establishment of a competition modeled community. In Galápagos climatic variations occur at two different levels. First seasonal variations are relatively important with most annual precipitations occurring between January and May and a dry season from June to December. Secondly, Galápagos suffer regularly extreme periods of heavy rains lasting several months due to the El Niño phenomenon occurring once or twice in a decade. Last El Niño events occurred in 1982-83, 1986-87, 1991-92, 1994-95 and 1997-98. The 1982-83 and 1997-98 events were the strongest of last century. Some species of arthropods might have benefited on temporary water streams to disperse on long distances. This is probably the way *Wasmannia auropunctata* spread on Santa Cruz Island (Silberglied 1982; Lubin 1985). Indeed presence and abundance of species has been observed to be highly variable across the different census of 1996-1997, 2003, 2004 and 2005. This is particularly true concerning the dominant species *Solenopsis geminata* that seems to be sensitive to harsh conditions during dry season. It was totally absent of arid natural area in 1996-97 census, highly abundant in 2003 (100% of food bait occupancy at N3) and rare again in 2004 and 2005 (not detected at N3 in last census). *S. geminata* differs from other introduced species in that it can disperse by nuptial flight (see McInnes and Tschinkel 1995 for references on reproductive strategy of *S. geminata*). A combination of dispersion ability by budding and by nuptial flight may compensate its limited climatic tolerance and allow it to colonize areas as soon as conditions are suitable. Then we might logically suggest that important variations in presence and abundance of the most widespread dominant species on Floreana have a strong impact on variability of other species. Sanders et al. (2003) demonstrate in California that ant community loses its segregated structure after the invasion by the Argentine ant *Linepithema humile*. So it appears that the presence of a highly invasive species disrupt communities. Our hypothesis of a dynamic system with species displacements is supported by results of Mantel test: they demonstrate at least for arid station, a negative correlation between geographical distances and ant fauna similarities.

What about a potential mosaic pattern for dominant species? This kind of distribution structure is commonly observed between dominant species (Fluker & Beardsley 1970; Room 1971; Majer & Camer-Pesci 1991; Majer et al. 1994; Morrison 1996; Vanderwoude 2000; Ambrecht et al. 2001; Folgaraits et al. 2004). *S. geminata* occurs together in the village area with *Monomorium destructor* and in the agricultural area with the little fire ant *W. auropunctata*. In the first case, it is difficult to know whether both species overlap or if it is just a contact area since the range of *M. destructor* is rather small. Concerning *W. auropunctata*, it presents a particular form of dominance rather different from other “classical” dominant species. There is a clear threshold between places where it seems to coexist with several other species as a relatively discrete one and areas where it reaches very high density excluding all other ant species (Lubin 1994; Pezzatti et al. 1998). This pattern is observed on station S4 where its abundance estimated via pitfalls scores was 67 times higher than total abundance of ants in other humid stations! Then, excepted for areas occupied by dense population of the little fire ant, there is no evidence for a mosaic pattern on Floreana.

Globally, apart from some ecological preferences among a given set of species, we were not able to highlight clear factors structuring the ant community of Floreana Island. Our conclusions match the ones of Cerda et al. (1998) working on a Mediterranean community where they conclude that abiotic factors have sometimes more impact than competition on community organization. Following Ribas & Schoereder (2004), the use of a unique hypothesis to explain the distribution of species is an over-simplification, they argue that preferences of dominant species, competitive interactions, as well as stochastic processes are important. Floren & Linsemair (2000) searching for assembly rules in a pristine forest in Asia conclude that the community organization seems to be the product of very complex dynamic processes. Ribas & Shoereder (2002) analyzed 14 presence/absence matrices of published ant community structures and conclude that six of them have a structure not different from random.

From a practical point of view, our results suggest that the simultaneous use of a variety of collection methods is essential to get a reliable picture of ant composition. The use of attractive baits is well adapted to the study of interspecific competition (Hölldobler & Wilson 1990). However, for the monitoring of new potential ant introductions it will be highly recommended to prioritize the use of passive methods. In a general way, pitfall trapping was the most efficient method in terms of species detection. Working with ground ant community Wang et al. (2001) admits that pitfalls are better than baits to estimate diversity. Melbourne (1999) warns about the use of pitfalls, claiming that observed differences in abundance might be exclusively due to environment. However for Steiner (2005) the use of pitfalls gives repeatable pictures provided that a sufficient number of traps is used. Generally speaking, passive collection methods are more efficient than attractive baiting. It is logical since a bait already occupied by one or several species is less susceptible to be colonized by other ones. In our case five minutes of visual search on a 50 x 50 cm square repeated on 13 points permitted the detection of 5.4 species per station when simultaneous tuna and honey baits on the same points matched only 4.8 species per station.

From a conservation point of view we might conclude that the lack of clear mechanisms ruling the ant community makes the management of introduced ant species very complex. We may hopefully hypothesize that the two endemic *Camponotus* species are little affected by introduced ants. Results from Chapter 1 clearly demonstrate, at least for *C. macilentus*, that their interference competitive ability allows them to outcompete most tramp species and the present work highlights the poor capacity of dominant species to invade permanently arid area where these species are the most abundant. *M. destructor* is the last introduced potentially invasive species in Floreana. Since its introduction 20 years ago and in spite of locally very high abundance, it is still restricted in the village and around the garbage dump one km above.

But its anecdotal detection in 2000 in the agricultural (P. Licango, pers. comm.) indicates that the system, once more, is too dynamic to allow predictions.

CHAPTER 3

AGGRESSIVE BEHAVIOR OF INTRODUCED ANT SPECIES: A KEY CHARACTERISTIC FOR ESTABLISHMENT?

AGGRESSIVE BEHAVIOR OF INTRODUCED ANT SPECIES: A KEY CHARACTERISTIC FOR ESTABLISHMENT?

This chapter is in preparation for publication.

Abstract

When exotic ant species coexist in an area several behavioral traits might regulate competition among them. The importance of direct aggressive behavior as a component of interspecific competition was assessed. We conducted one-to-one and group confrontations on five and three introduced ant species respectively, occurring on Floreana Island in the Galápagos Archipelago. *Wasmannia auropunctata* appears to be the most aggressive, attacking other ants in half of the one-to-one encounters. The invasive *Solenopsis geminata* and the tramp *Tetramorium simillimum* were the less aggressive in the same conditions. The two dominant species *S. geminata* and *Monomorium destructor* exhibit very different behavior when confronted in small groups with the submissive *T. simillimum*. *S. geminata* workers maintain foraging activity and display little aggression toward *T. simillimum* whereas *M. destructor*’s behavior is highly agonistic. Confrontation behaviors and hierarchical status of species in the ant community are discussed. It appears that aggressive behavior is not a good predictor neither for the success of invasion nor for acquiring a dominant position in a recently assembled community.

Introduction

There is a growing interest in the processes of biological invasions and recently studies have been conducted on the traits of invasive species (Kolar and Lodge 2001; Passera 1994), characteristics of invaded areas (Lonsdale 1999; Davis et al. 2000; Le Breton et al. 2005) and the impact on the recipient ecosystems (Mooney and Drake 1986; Allen et al. 2004). Several species of ants rank among the most successful invaders (Williamson and Fitter 1996), probably due to the advantages accrued from their social organization (Moller 1996). Ant species that have principally spread throughout the world human trade are called tramp species. They share several characteristics as unicoloniality resulting in an absence of intraspecific aggression, polygyny (multiple queens nests), high interspecific aggression and the small size of workers (Passera 1994).

The impact of invasive ants on native fauna is well documented (Clark et al. 1982; Lubin 1984; Porter and Savignano 1990; Cole et al. 1992; Human and Gordon 1997; Kennedy 1998; Hoffmann et al. 1999; Holway 1999; Le Breton et al. 2003) but little is known about the underlying mechanisms responsible for these impacts (Holway et al. 2002; Holway and Suarez 1999). It is commonly assumed that one of the principal keys to the success of invasive ant species is high interspecific aggression (Hölldobler and Wilson 1990; Lodge 1993; Passera 1994; McGlynn 1999). Interspecific interactions at the worker or small group level might be an important component of interference competition ability and its exploration may help to understand behavior at colony level and community level. Rentana and Cerda (1995) suggest that an understanding of the factors affecting interspecific behavioral interactions of coexisting species is an important starting point for a deeper analysis of the success of each species and the dominance hierarchy in ant communities. However, though several authors report direct physical aggression in anecdotal observations, there are few detailed studies on its importance as a competition tool. The Argentine ant *Linepithema humile* in California shows a greater intimidation and aggressive behavior at food baits compared to eight native species (Human and Gordon 1999). Even if there was no significant relation between aggressive interaction frequency and outcome of competition, in one-to-one interspecific encounters at food baits the ant that initiates encounter is most likely to stay while the other leaves. Thus, we can expect an advantage for a species that systematically exhibits a strong aggressive behavior.

Morrison (2000) noted that dominant species usually have exclusive territories and large populations, and suggests that interference competition ability at worker level would not be a good predictor of invasion success. However in the case of multiple invasions by several potentially dominant species, we might expect that interference interactions play an important role at the establishment stage of a species. For Wilson (1971), aggression behavior is mostly linked to invasion contexts and/or highly simplified environments. But he argues that a competition for resource can establish without aggression. Floreana Island in the Galápagos Archipelago (Ecuador), along with the majority of Pacific islands, has suffered the introduction of several exotic ant species. Twelve of the 24 species sampled in 1996-1997 by Pezzatti et al. (1998) are cosmopolitan or pantropical tramp species. The process of invasion is still very dynamic due to some recent introductions and coexistence is probably regulated by strong interspecific competition. In this context, the nature of the interactions of the different protagonists may be crucial for their successful establishment and spread.

In this paper we examine worker-level and group-level interactions between introduced species. We tested worker-level interactions by confronting pairs of single workers from five species. All of them are widely distributed ant species in the tropics, however an earlier study of colonization dynamics at artificial food baits revealed that they have different competition strategies and abilities (von Aesch and Cherix 2005, see Chap. 1). We made the assumption that there is an analogy between the attitude of a given species during interspecific interactions and its ecological status in a community. According to our previous data, we expected a higher level of aggression in the dominants *Wasmannia auropunctata*, *Solenopsis geminata* and *Monomorium destructor*. In the second half of the study we performed group-level confrontations at food sources with pairs of three species in order to investigate the behavior of foragers when competing for food. We confronted the two dominant species *Solenopsis geminata* and *Monomorium destructor* and the submissive *Tetramorium simillimum*. *Wasmannia auropunctata* was not included in this design since it is already known to exclude other ant species by using a strong aggressive attitude (Clark et al. 1982; Lubin 1984; Ulloa-Chacon and Cherix,1994).

Material and Methods

Experiments took place on Floreana Island (Galápagos, Ecuador) during April-May 2004. Ants were collected using artificial food baits and stored with conspecifics in plastic vials. Confrontation tests were performed the day of collection.

Worker-level confrontation

Ten experimental pairs were tested with all combinations of the five following species: *Monomorium destructor*, *Wasmannia auropunctata*, *Solenopsis geminata*, *Tapinoma melanocephalum* and *Tetramorium simillimum*. Individuals were collected from two sites 300 m to 5 km from each other in order to avoid any local effects. Workers were used only once. We performed twenty replicates of all combinations and twenty intraspecific encounters per species as controls. Half of the controls used worker pairs collected at the same place and half were conducted with ants from the two distinct collecting locations.

In total each species was tested in 80 interspecific encounters (4 challenging species x 20 replicates). Ants were tested in pairs in a circular experimental arena of 1.5 cm diameter with sides coated with Fluon® to prevent escape. They were introduced simultaneously and the behavior of both individuals were recorded for five minutes. Confrontations were considered as “aggressive” if at least one ant aggressed the other physically by biting or stinging. We recorded which species initiated the aggressive behavior. When both individuals ignored each other or when they presented intimidating behavior such as lunging or opening their mandibles, the encounter was scored as “not aggressive”. *Tapinoma melanocephalum* does not possess a functional sting, but instead directs its gaster upwards or towards other ants similar to the behavior of the Argentine ant, another Dolichoderinae (Lieberburg et al. 1975; Holway 1999; Human and Gordon 1999). This behavior often results in an aggressive or fleeing response from the other ant and because of this, this behavior was considered as aggressive. We performed a binomial test within each pair of species to evaluate if one species initiated more often aggressive encounter than the other. Considering the 80 encounters performed for one given species, we used a binomial test to compare the number of aggressive encounters initiated by the focal species and number of encounters initiated by the challenging one

Group-level confrontations

We tested the following species in pairs: *Monomorium destructor*, *Solenopsis geminata* and *Tetramorium simillimum*. Groups of 150 workers were placed in artificial nests with water and complete darkness. Artificial nests were connected via plastic tubes to a common foraging arena of 12 x 17 cm with a food supply (peanut butter) located at the center (see Fig 1). The experimental arena was divided in half (12 x 8.5 cm) via a separation wall, preventing each species from coming into contact. Once a clear recruitment and food retrieval behavior was established on both sides, the separation wall was removed and the total number of workers found in the experimental arena, number of feeding workers and number of fights was recorded every 3 minutes for 30 minutes. Eight trials were conducted for each pair of species. Four intraspecific confrontations were also conducted for each species as a control.

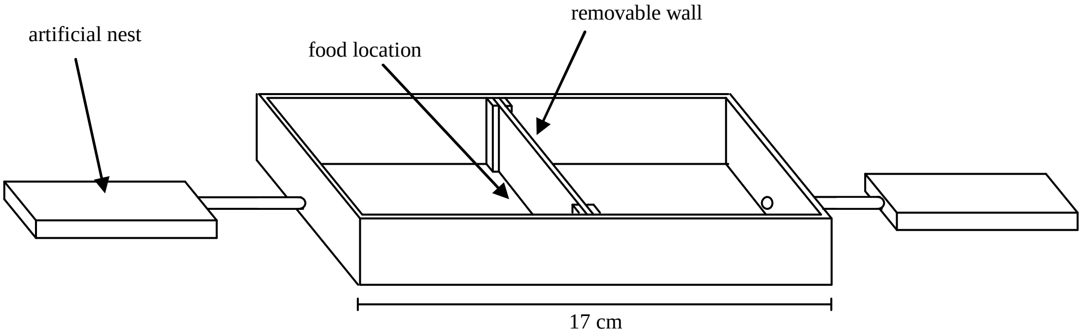

Fig.-1 Experimental set-up for confrontation of workers groups. Ants have access to the foraging arena via a plastic tube. The central wall is removed once both groups present a clear recruitment and feeding behavior.

For each species we used a two-tailed paired t-test to compare its outcomes when confronted to one or the other challenging species at beginning of confrontation and after three, 15 and 30 minutes.

Results

Worker-level confrontations

Of the 200 interspecific one-to-one encounters, we recorded 83 aggressive interactions representing 41.5% of the total (see Table 1). We observed a wide range of levels of aggression among pairs. The most aggressive pairing was *W. auropunctata – S. geminata* with 90% of aggressive encounters, all of which were initiated by *W. auropunctata* except one. At the other end of the spectrum we found that the *T. melanocephalum – T. simillium* pairings produced only one aggressive encounter out of twenty confrontations. Intraspecific confrontations showed an absence of aggression except for one pair of *S. geminata* and one of *T. melanocephalum*. In both cases workers were collected from distinct sites.

Tab 1.- Number of encounters with aggressive issue out of 20 for each tested pair in one-to-one confrontations, with indication on the right of number of aggression initiated by one or the other species. Results of binomial tests are indicated for each pair of species (* p<0.05 and ** p<0.01).

	Monomorium destructor	*Tetramorium simillimum*	*Solenopsis geminata*	*Wasmannia auropunctata*	*Tapinoma melanocephalum*
Monomorium destructor	0/20	5/20 ↗ 2 *Ts* ↘ 3 *Md* **ns**	10/20 ↗ 5 *Sg* ↘ 5 *Md* **ns**	11/20 ↗ **9 *Wa*** ↘ 2 *Md* *****	15/20 ↗ 3 *Tm* ↘ **12 *Md*** *****
Tetramorium simillimum		0/20	5/20 ↗ 3 *Sg* ↘ 2 *Ts* **ns**	13/20 ↗ **11 *Wa*** ↘ 2 *Ts* ******	1/20 ↗ 1 *Tm* ↘ 0 *Ts* **ns**
Solenopsis geminata			1/20	18/20 ↗ **17 *Wa*** ↘ 1 *Sg* ******	6/20 ↗ **6 *Tm*** ↘ 0 *Sg* *****
Wasmannia auropunctata				0/20	5/20 ↗ 1 *Tm* ↘ 4 *Wa* **ns**
Tapinoma melanocephalum					1/20

Rates of aggressive encounters are presented for each species separately in Figure 2. *Wasmannia auropunctata* is clearly the most aggressive species initiating an aggressive interaction in 39 of 80 cases (49%).

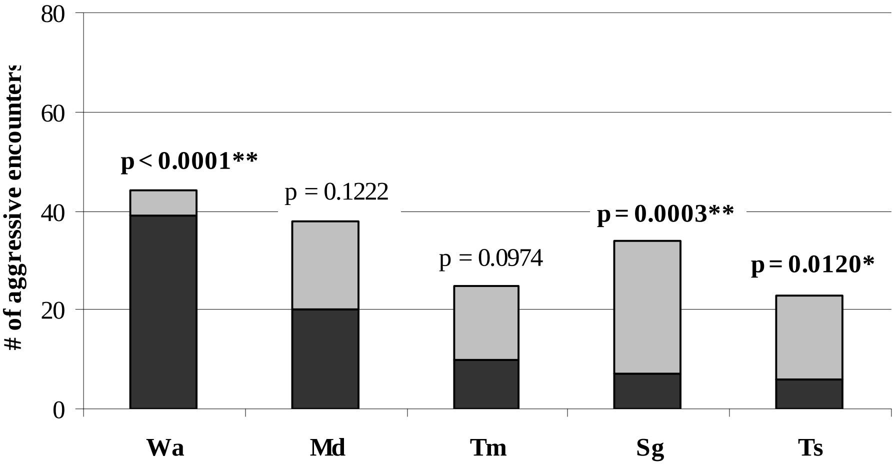

Fig. 2- Number of encounters where agression is initiated by the indicated species (*black*) or by the challenging species (*grey*). Wa = *Wasmannia auropunctata*, Md = *Monomorium destructor*, Tm = *Tapinoma melanocephalum*, Sg = *Solenopsis geminata*, Ts = *Tetramorium simillimum*

Above: p-values of the binomial test comparing black and grey areas.

Monomorium destructor and *Tapinoma melanocephalum* are statistically neither less nor more aggressive than the four others tested species in one-to-one interactions. *Solenopsis geminata* and *Tetramorium simillimum* are the less aggressive species with a low rate of initiated aggression (21% and 26% respectively).

Group-level confrontations

For each species the total number of ants in the arena, number of feeding workers and number of fighting ants at zero, three, 15 and 30 minutes following exposure to heterospecifics are presented in Table 2. For a given species there was no significant difference between the total number of workers and number of feeding workers at t = 0, so that the initial conditions might

Tab 2.- Results of group confrontations: total number of ants, number of feeding ants and number of fighting ants at beginning of experiments (t = 0), after 3, 15 and 30 minutes. For each species, number of workers involved in particular task is compared when confronted to the two other species using a two-tailes paired t-test (* p<0.05 and ** p<0.01).

		S. geminata paired with …			***M. destructor*** paired with …			***T. simillimum*** paired with …		
		… ***Md*** (n=8)	… ***Ts*** (n=8)		… ***Sg*** (n=8)	… ***Ts*** (n=8)		… ***Sg*** (n=8)	… ***Md*** (n=8)	
# ants	t = 0	46.1 ± 21.4	39.3 ± 13.8	**ns**	40.6 ± 16.6	47.1 ± 19.4	**ns**	44.8 ± 21.3	51.6 ± 15.0	**ns**
	t = 3	32.1 ± 17.5	33.4 ± 19.5	**ns**	46.3 ± 24.7	31.3 ± 23.5	**ns**	41.3 ± 19.7	44.9 ± 11.7	**ns**
	t = 15	28.5 ± 12.4	33.0 ± 18.7	**ns**	39.5 ± 20.8	46.9 ± 14.5	**ns**	33.0 ± 19.6	42.8 ± 6.8	**ns**
	t = 30	28.1 ± 15.6	28.9 ± 17.3	**ns**	25.9 ± 12.2	55.9 ± 28.4	**	26.5 ± 13.7	35.8 ± 10.4	**ns**
# feeding ants	t = 0	16.6 ± 12.8	22.9 ± 12.2	**ns**	11.0 ± 9.3	18.9 ± 15.7	**ns**	13.0 ± 3.9	17.1 ± 6.3	**ns**
	t = 3	7.5 ± 12.4	17.8 ± 17.4	**ns**	0.3 ± 0.7	3.5 ± 4.8	*	2.5 ± 2.2	9.5 ± 5.8	**
	t = 15	2.0 ± 3.7	16.6 ± 14.5	**	0.0 ± 0.0	5.6 ± 6.3	*	0.0 ± 0.0	1.6 ± 3.5	**ns**
	t = 30	2.6 ± 4.3	13.0 ± 12.1	*	0.1 ± 0.4	8.0 ± 9.6	*	0.1 ± 0.4	0.5 ± 0.9	**ns**
# fighting ants	t = 0	-	-		-	-		-	-	
	t = 3	17.1 ± 11.7	2.5 ± 1.1	**	17.1 ± 11.7	12.8 ± 9.1	**ns**	2.5 ± 1.1	12.8 ± 9.1	**
	t = 15	24.3 ± 13.6	2.9 ± 2.7	**	24.3 ± 13.6	23.3 ± 7.9	**ns**	2.9 ± 2.7	23.3 ± 7.9	**
	t = 30	20.6 ± 10.4	1.9 ± 2.0	**	20.6 ± 10.4	24.0 ± 8.3	**ns**	1.9 ± 2.0	24.0 ± 8.3	**

be considered the same for the different sets of experiments. For a better visibility, the levels of aggression expressed as the number of fights within each pair are presented in Fig. 3.

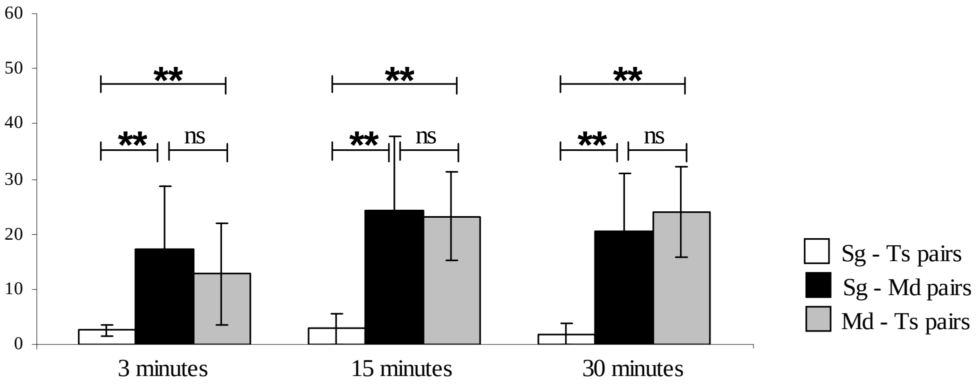

Fig 3.- Number of fights in the three combinaisons of *Solenopsis geminata*, *Monomorium destructor* and *Tetramorium simillimum* 3, 15 and 30 minutes after beginning of confrontations (n = 8). Results of t-tests with 1% confidence interval are presented above.

The complete dynamics of all interspecific pairing are plotted in Fig 4. Aggression was low between *S. geminata* and *T. simillimum* and high for both species when they were coupled with *M. destructor*. When suddenly confronted with a competitor at a food source, both *M. destructor* and *T. simillimum* reacted by drastically reducing their foraging activity. *S. geminata* was the only species that maintained a normal feeding activity, but only when confronted with the submissive *T. simillimum*. When confronted with *M. destructor* the majority of *S. geminata* workers were involved in fights, reducing the number of workers available for foraging. In intraspecific controls we observed aggressive behavior in the two

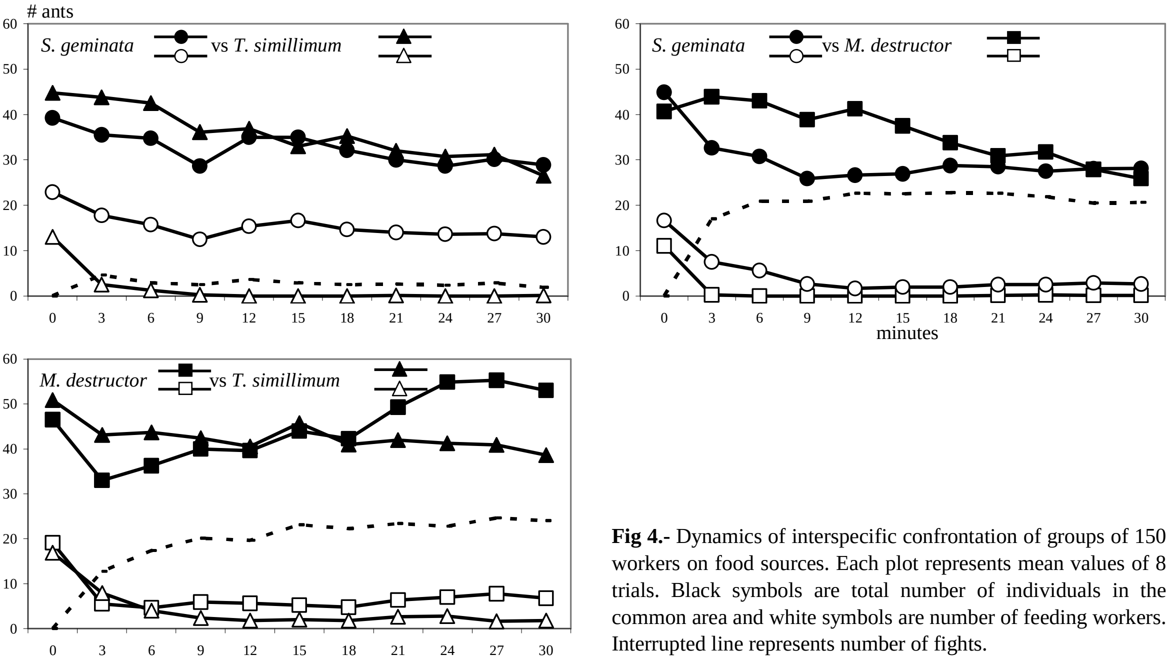

Fig 4.- Dynamics of interspecific confrontation of groups of 150 workers on food sources. Each plot represents mean values of 8 trials. Black symbols are total number of individuals in the common area and white symbols are number of feeding workers. Interrupted line represents number of fights.

experiments involving *S. geminata* workers collected from different sites and in one pair of *T. simillimum*, but only after 20 minutes. We never observed any aggressive behavior when groups of foragers where collected from the same location and ants showed a normal and constant foraging behavior after removal of the separation wall.

When paired with *T. simillimum*, a large number of *M. destructor* workers left the artificial nest to enter the common arena. On the contrary, the number of workers decreased in the presence of *S. geminata*. The number of feeding workers of *S. geminata* was clearly higher at t = 15 and t = 30 minutes when it was exposed to *T. simillimum* compared to when it was exposed to *M. destructor*. Both *S. geminata* and *T. simillimum* have higher numbers of fighting workers at any time of the experiment when confronted with *M. destructor*. On the other hand, the number of fighting *M. destructor* workers was constant whichever was the competing species.

Discussion

One-to-one confrontation issues show that the five species have the potential to be aggressive regardless of their dominance status in the competitive hierarchy of the community and their success as invaders on Floreana Island. However, levels of aggression are diverse. Three species might be considered as behaviorally dominant on this island: *Solenopsis geminata*, *Monomorium destructor* and *Wasmannia auropunctata*. A dominant status implies that at least in a given area the species monopolize most food resources. It is interesting to note that these three species matched the highest absolute number of aggressive encounters (43% to 55%), but there were important differences in which species initiated the attack. *Wasmannia auropunctata* is clearly the most aggressive of the set. Its workers attacked other ants in half of the confrontations. In places where it has been introduced *W. auropunctata* is commonly known to reach very high densities and to exclude all other ant species (Clark et al. 1982; Lubin 1984; Wetterer & Porter 2003). It has been observed attacking and killing all *Anoplolepis gracilipes* found at food baits in Vanuatu archipelago (southwest Pacific) where both species were introduced (Jourdan et al. 2002). It has also been observed at the entrance of a *Pheidole* nest in Brazil, biting workers and robbing food (Brandaõ & Paiva 1994). Therefore physical aggression might be an important component of the competitive ability of this highly invasive small ant. The fire ant *Solenopsis geminata* have a dense and widespread population on Floreana Island whereas the more recently introduced *Monomorium destructor* is restricted to the village area. It has been introduced on Floreana about 20 years ago and following our observations it is still confined nearby its probable introduction point. Observations of succession at food baits revealed that both species are dominant and show high competitive abilities in resource acquisition (von Aesch and Cherix 2005, see Chap. 1). However, behavior of individuals appears to be quite different. Our studies showed that *M. destructor* workers are more aggressive toward other ants. The relatively low level of aggression of *S. geminata* workers indicates that its numerical dominance rather than the strong aggressive behavior at worker level may be one of the main factors contributing to its success. In other *Solenopsis* species, authors have demonstrated that numerical superiority rather than aggressive behavior is the cause of dominance (Bhatkar 1972 for *S. invicta*, Gibbons & Simberloff 2005 for *S. invicta* x *richteri*). Holway (1999) showed for the introduced population of Argentine ant in California a large discrepancy between the interference competition ability at worker level and at colony level, suggesting that the key to the success of *Linepithema humile* is its high density. Holway and Case (2001) later demonstrated the importance of colony size on competitive ability under standardized laboratory conditions.

Tapinoma melanocephalum and *Tetramorium simillimum* present typical characteristics of discreet and opportunist tramp species (Andersen 1997). Both of them showed low interference competition scores in analyses of competition at food baits (von Aesch and Cherix 2005, see Chap. 1). But in one-to-one encounters *T. melanocephalum* is more aggressive than expected for a subordinate species indicating that the opportunistic status does not exclude some aggressive behavior. The low level of aggression of *T. simillimum* can be explained by its foraging behavior: this species, although widespread, is rarely observed in large foraging groups. The direct aggression of competitors would probably be too risky for a small group of foragers. This species is classified by Wilson (1971) in “insinuators”, discreet thieves inserting themselves inconspicuously.

Competition for food resources is one of the main aspects of interspecific interactions (Davidson 1998, Wilson 1971). Our second experimental design allowed us to evaluate agonistic behavior in a competition context. The most important result is the fundamental difference in the behavior of the two dominants *S. geminata* and *M. destructor* when confronted with the submissive *Tetramorium simillimum*. In both combinations *T. simillimum* was submissive, abandoning food very quickly. This is not surprising for an “insinuator” species. However, the response of its two competitors was radically different. *S. geminata* seemed to ignore the presence of *T. simillimum* and maintained a normal foraging activity. This non-aggressive coexistence of that pair at food sources has been observed *in situ* on artificial food baits (pers obs). These observations are consistent with one-to-one confrontation results where these two species were the least aggressive species. On the contrary, most of the *M. destructor*'s workers present in the common arena invested immediately in agonistic behavior towards *T. simillimum*. The cost of such an aggressive behavior is probably high because the more workers that are implicated in fights the less food is retrieved and taken to the nest. Since it is still confined to a restricted area nearby its probable arrival point, we might hypothesize that there is no ecological niche for this species on Floreana, except in the inhabited area since it is very common in houses. Czechowski (1985) observed competition between *Lasius niger* and *Myrmica laevinodis* and reports that even if *Lasius* is much more aggressive on baits it is slowly replaced by *Myrmica* in the studied area. Then *M. destructor,* as *L. niger*, might be much more a pioneer species adapting easily to disturbed habitats but unable to compete with other species. Moreover, Eow et al. (2004) show in laboratory conditions that colonial growth of *M. destructor* is much weaker than those of its congenerics *M. pharaonis* and *M. floricola*, both widespread in Galápagos Archipelago.

To conclude *Solenopsis geminata* behavior proves that a dominant species is not necessarily physically aggressive toward competitors and in many cases ecological success might be due to numerical dominance. *Monomorium destructor* seems not to be a potential invasive species on Floreana Island. It appears that its strong aggressive behavior is not a factor of success.

GENERAL DISCUSSION

GENERAL DISCUSSION

Initial questions and results

This research was motivated by the arising problematic of introduced species in Galápagos Islands. Focusing on ant species, we were interested in understanding the rules governing ant communities where most species are introduced, having reached the islands at distinct times during the last century. In this respect, Floreana Island was interesting because of the existence of previous detailed data on ant fauna of Pezzatti et al. (1998). Our aim was to evaluate up to what point it is possible to predict future expansion of species and evolution in time of local ant assemblages. We analyzed species distribution, competitive hierarchy and aggression behaviors in order to elucidate some aspects of interspecific competition, spread ability and coexistence patterns of the different protagonists.

A first very incomplete census conducted by Wheeler (1919) revealed the presence of seven ant species on Floreana. Pezzatti et al. (1998) counted 24 ant species by performing an intensive sampling in 1996-1997. Two species, the carpenter ants *Camponotus macilentus* and *C. planus*, are endemic of Galápagos. At least 15 are introduced species among which 12 are well-known tramp species and two are invasive: the fire ant *Solenopsis geminata*, widespread on Floreana, and the little fire ant *Wasmannia auropunctata*, restricted to the humid upper part of the island. Pezzatti et al. (1998) were the first to report the presence of the tramp ant *Monomorium destructor*, which was a new record for Galápagos. It arrived on Floreana probably during the eighties and is restricted nearby its probable introduction point in the village where it is very abundant.

In Chapter 1, we compared the species distribution between 1996-1997 census and ours (2003). *M. destructor* appeared to be still restricted to human environment in the village and *S. geminata* was newly recorded in the natural arid zone in huge densities. By a follow-up of foragers at attractive baits in time, we highlighted the competitive hierarchy of Floreana ant community. Commonly, coexistence of several ant species sharing the same resources is explained via a discovery-dominance trade-off (Schoener 1983; Fellers 1987, Davidson 1998). It implies that some species are exploitative specialists able to localize and retrieve food rapidly when others are interference specialists that defend successefully resources once encountered. On Floreana, small tramp species are good at exploitation and large-sized species, in particular the endemic *C. macilentus*, are better at interference competition. But two species, namely *M. destructor* and *S. geminata*, behaved as both exploitation and interference competitors, breaking the competition trade-off. This is typical of introduced invasive species in many habitats and is often associated to a numerical superiority (Holway et al. 1997). But the status of *M. destructor* still confined into a small range has to be elucidated.

In the second chapter we evaluated separately the importance of environmental factors and interspecific competition in structuring species assemblages and distributions. A multivariate analysis revealed a clear discrimination in species composition between stations sampled either in the arid or in the humid areas. This was especially true for dominant, cryptic and large-sized species. Opportunist tramp species seem to escape this rule and were found without any preferences in most habitats over sampling stations. The attempt to explain observed species assemblages with competition failed. Co-occurrence analyses revealed a negligible part of competitive exclusion. But since the existence of interspecific competition for resources has not to be proven in ant communities (Hölldobler & Wilson 1990), we attributed the lack of competition-derived structure to the dynamic of the system. Indeed, the successive census of species distribution conducted in 1996-1997, 2003, 2004 and 2005 revealed a strong variability in species abundances and distributions. In particular we attributed the sparse observations of the dominant fire ant *S. geminata* in arid areas during the dry season (1996-1997, 2005) to its sensitivity to dry harsh conditions. We supposed that regular and important variations in the distribution of the principal dominant species on Floreana Island have an impact on general distribution and abundance of other species. Our hypothesis of a dynamic system with regular migrations is supported by the observation of similarities among nearby sampling stations in ant composition. This is not surprising for an environment that has suffered regularly and recently numerous alien species introductions. Random human-mediated introduction of species across the disturbed area logically diminishes the eventual emergence of structured ant assemblages.

Confrontation tests in Chapter 3 revealed a very low level of aggression for the fire ant *S. geminata*. We conclude that its ability in monopolizing a huge amount of food resources and in breaking the discovery-dominance trade-off is principally due to its numerical advantage. Holway and Case (2001) put forward identical asset for the dominance of the invasive Argentine ant *Linepithema humile* in its introduced range. At the opposite the behavior of *M. destructor* at food baits when confronted with other species was highly agonistic. This strong demonstration of aggression is inevitably correlated with a drastic reduction of resources acquisition since workers involved in fights are no more available for foraging. Thus we made the assumption that the cost of such a behavior in terms of worker losses decreases its ability to spread on Floreana where the rate of encounters with competitors is consequent. Moreover Eow et al. (2004) showed for *M. destructor* a smaller intrinsic colony growth rate than for *M. floricola* and *M. pharaonis,* meaning that workers are not so easily replaced.

From a functional point of view

We defined in the introduction the notions of tramp and invasive species. Tramp species share a series of life history traits such as monomorphism, small size of worker, high polygyny and reproduction by budding that facilitate their human-mediated transfer to new areas and maximizes their establishment and spread abilities. Invasive species are those with a clear negative impact on recipient ecosystems. Let's consider Floreana introduced ant fauna from this point of view.

S. geminata and its congeneric *S. invicta* are the only described invasive ant species in the world that do not fit with the definition of tramps. Their workers are polymorphic, they form monogynous as well as polygynous societies (see Adams et al. 1976) and they are able to disperse by nuptial flight. Most of all, they are never human commensals as tramp species commonly living in houses. Their absence from human structures and their relatively large workers size make them species less susceptible to be inadvertently transported. In comparison to *W. auropunctata* currently present on 12 islands of Galápagos, *S. geminata* is present on only five islands. The time and mode of introduction of *S. geminata* is unclear but probably anterior to the arrival of most other exotic ants. It was already present in Galápagos in early census (Emery 1893). Some argue that it might have arrived a very long time ago by natural means and thus be considered as native. Its ability to spread rapidly on Floreana over short periods suggests dispersal by nuptial flights. The observation of alate sexuals supports this assumption (pers obs). Dispersal by nuptial flight gives access to distant areas and subsequent reproduction by budding increase rapidly local nest density.

At the opposite, a majority of tramp species are not invasive. But most of them have a high ability to reach new areas and to disperse in their new range. They are not only easily transported by human activity but their opportunist behavior, at least in Galápagos, allows them to establish almost everywhere. The impact of such species on recipient biota is largely unknown. Since they may form relatively populous communities and since they are principally ground-foraging, one may ask what impact they have on the ground-dwelling fauna as competitors and/or predators. Scientific publications highlight exclusively the often spectacular impact of invasive dominant species. As mention by Causton et al. (2006) little is known about the status of Galápagos introduced insects and their effects on the biota. They describe six species as invasive out of the 463 listed alien insects, among which *S. geminata* and *W. auropunctata*. But they emphasize that the ecological impacts of the remaining species are unknown. This is true in particular for the opportunist tramp species.

Among worldwide known transferred species, *W. aurpunctata* is an exception. It distinguishes itself of all other transferred tramp and/or invasive species by its super-dominance behavior. In several invaded area around the world, it is known to reach dramatically high densities and exclude all other ant species (Clark et al. 1982, see Wetterer and Porter 2003 for references). The current extent of the territory occupied by *W. auropunctata* on Floreana is too important to consider an eventual eradication by man as it was successfully conducted on Marchena, a northern Galápagos island. It shares typical attributes of tramp species but it is less opportunist in regard to habitat at least on Floreana. Indeed, it seems fortunately confined to the moist areas. Its incursions outside of this humid environment occur exclusively during heavy rainfalls caused by the El Niño events (Silberglied 1982; Lubin 1985) and remain temporary. According to Floreana inhabitants, *W. auropunctata* is regularly noticed in houses when they bring back fruits and vegetables from the upper part. However it is not observed as established around habitations. Since the village is situated in the arid part, this support our assumption of a certain ecological requirement in regard to humidity conditions for this species.

Predictions

At first sight, the endemic carpenter ant *C. macilentus* seems able to face competition with introduced species, thanks to its interference competition ability and to its adaptation to dry and harsh environment present on most surface of Galápagos Archipelago. We are missing data to extend this assumption to its congeneric *C. planus*. But since they share the same habitat its status is probably similar.

At the community level, the results we got do not allow us to build detailed predictions on the evolution of species spread and future patterns for Floreana Island. However, it appears that most tramps occupy relatively large areas. This let us suppose that they completed successfully the “spread” and “integration” stages that follow “arrival” and “establishment” (see Vermeij 1996; Williamson & Fitter 1996a; Kolar & Lodge 2001; Sakai et al. 2001; Heger & Trepl 2003).

Our data don't allow us to determine if Floreana is saturated of if ant density still has an increase potential. However, Baroni-Urbani in a paper on ant ecology (1979) argues that ant's ability to disperse and to spread is so high that most ant communities are probably not far from their saturation level. This is not incompatible with important variability in the qualitative composition of an assemblage. It is likely that arid environment can support less abundance, and probably less diversity. In average one pitfall trap laid for seven days collected 49 ants in the humid area and 25 in the arid one.

Concerning *M. destructor*, predictions are not evident. It is currently present at large density only in the village and around the garbage dump one km above, with a pattern almost identical then the one reported by Pezzatti et al. (1998). However, the detection of some workers in the agricultural area in 2000 (P. Licango, pers. comm.) indicates that it would be very risky to exclude a future spread of this species.

Conclusions and perspectives

Categorization of introduced species as invasive or tramp should be use carefully when trying to edict general trends. We observed an important variability of behavior and preferences among the 12 tramp species present on Floreana or between the two invasive fire ants. This implies that each species presents its own characteristics that make it different of other ones, even if classified in the same functional group. In particular, we lack data on the biology of most transferred species such as climatic requirements, food preferences, foraging behavior, social structure of introduced populations and intrinsic characteristic of societies (growing rate, number of individuals, reproductive strategy). The problematic of introduced ant species, their potential invasiveness and their possible impact on recipient biota has to be considered separately for each ant species.

Several authors (Parker et al. 1999; Kolar and Lodge 2001) pointed out that we generally lack information on the impact of introduced species on ecosystems. It is not known to which extend a common tramp species negatively alters an ecosystem. Ants probably disrupt arthropod community by competing for territory and food resource or as direct predators. As many of them feed on honeydew they may also threat plants by tending homopteran. Actually, the most insidious consequence subsequent to introduced species on Floreana is probably the slow but ineluctable erosion of the original biodiversity.

A first step to assess potential impact of ants on arthropod abundance and diversity would be to conduct parallel monitoring on infested and non-infested islands. This was done for *W.*

auropunctata (Lubin 1984) but has to be extended more generally to introduced ants. Similarly, to evaluate the impact on endemic ant species such as *Camponotus* spp., we might compare their range across ecological conditions in both invaded and non-invaded areas.

Floreana has to face similar pest management problems than the three other inhabited islands. The SICGAL inspection and quarantine program set up in 1999 by the Ministry of Agriculture of Ecuador is poorly applied for the moment. Boats traveling from and to other inhabited islands and transporting construction material and food supply reach the village about twice a week. This probably primary arrival spot for invaders is strongly connected to the above cultivated area since food and agricultural products are carried up and downhill daily. Thus it is likely that this agricultural area of nearly 300 ha situated in the upper central part of Floreana is a secondary introduction spot functioning as a regularly supplied reservoir of introduced ant species.

Once widely established, ant species are very hard to control. For this reason, efforts should be concentrated on prevention and early eradication. This view is largely supported by scientists working in management programs (see Causton et al. 2006). Control program should be applied for species like *M. destructor* whose potential invasiveness is hardly predictable and current spread still limited. This would be good for two reasons: firstly it would avoid its spread on Floreana and secondly if eradication is possible it will prevent other islands to be infested by this species currently present only on two islands in Galápagos.

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