Long-term spread of Argentine ant (Hymenoptera: Formicidae) European supercolonies on three Mediterranean islands

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Abstract

The Argentine ant is an invasive species that has spread all over the world and is organized in several supercolonies. While there are many studies about factors promoting the expansion of the species, little is known about the factors affecting the variation in spread among the different supercolonies. We examined the environmental and spatial variables affecting the invasion of the Argentine ant on three islands of the Mediterranean Sea (Corsica, Ibiza, and Formentera) and in the three European supercolonies that inhabit them (Main European, Corsican, and Catalonian). We used data from two sampling periods, nine years apart in the case of Corsica and 12 years in the case of Ibiza and Formentera, coupled with historical data of first detection dates and locations on islands of Southwestern Europe. Along the coast of the three islands, we sampled each beach to detect the presence of the Argentine ant and used aggression assays to identify the supercolony they belonged to. The Argentine ant expanded its range on all three islands. Although the three supercolonies maintained their same locations and expanded to new locations, the highest expansion for the Main Supercolony was on Ibiza and Formentera and for the Corsican Supercolony on Corsica. Interestingly, the Argentine ant did not dominate at all our study sites. On one third of the beaches of Ibiza and Formentera, it co-occurred with native ant species even after 12 years. Human presence affected the likeliness of a beach to be invaded on Ibiza and Formentera. On Corsica, beaches that had already been invaded before our study or were invaded during our study were the ones with lower distance to already invaded beaches, suggesting the importance of secondary introductions in the local expansion of the Argentine ant. Our findings help to understand the dynamics of invasions of the Argentine ant and its different supercolonies. Long-term studies at many invaded sites are of great importance in order to obtain general patterns of the spread of this global invader.

Key words: *Linepithema humile*, biological invasions, supercolonies, biotic resistance, invasion pathways.

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Introduction

Biological invasions are one of the major threats to native communities, leading to a loss of biodiversity (Cox 1999, Simberloff & al. 2013, Bellard & al. 2016, Blackburn & al. 2019). Humans have facilitated the establishment of species into new areas across geographical barriers, like the case of islands (Williamson 1996). Islands are characterized by low species richness and less complex food webs, but have higher rates of endemism due to their isolation (Pimm 1996, Naughton & al. 2019). These characteristics make them very vulnerable to invasions (Elton 1958, Bellard & al. 2017), which can even result in the loss of species even before their discovery (Lees & Pimm 2005). The number of native species on island communities is predicted by the theory of island biogeography (Macarthur & Wilson 1967), where isolation and island size influence diversity. Although these two factors could reduce the probability of invasive species reaching islands, human movements such as international trade, industry, or tourism facilitate their arrival (Courchamp & al. 2017, Seebens & al. 2017). Knowing what other factors influence the establishment and expansion of introduced species on islands is vital to work on the preservation of these fragile and valuable ecosystems.

Several ant species are considered among the world's worst alien species (Lowe & al. 2000). The success of species like the Argentine ant (*Linepithema humile* (Mayr,

1868)) has been attributed to life-history traits that make it a very efficient invader. For example, unicoloniality, a social organization where nestmates do not show aggression among nests that can be thousands of kilometers apart (Giraud & al. 2002), may confer an ecological advantage because intraspecific aggression is absent at the scale of the whole population. Unicoloniality in the Argentine ant leads to the appearance of different supercolonies around the world, with workers showing inter-specific aggression among supercolonies (Vogel & al. 2010). Vogel & al. (2010) described at least 15 supercolonies around the world. The largest supercolony is the so-called European Main Supercolony (hereafter Main Supercolony), which ranges over 6 000 km in Southwestern Europe (Giraud & al. 2002) and has spread all over the world, forming the largest cooperative unit ever recorded (Van Wilgenburg & al. 2010). In Europe, three different mutually aggressive supercolonies are known. Besides the Main Supercolony, the Catalonian Supercolony occurs mainly over the East coast of the Iberian Peninsula and the Balearic Islands (Gomez & Espadaler 2005) and has been recently detected in North France and Southwest Spain (Charrier & al. 2020, for Nantes, France; X. Espadaler & E. Angulo, unpubl. for Coria del Río, Spain). The Corsican Supercolony is present on Corsica and the South coast of France (Blight & al. 2010b, 2012, Berville & al. 2013).

Through the intensification of human activities, the Argentine ant has successfully spread into many areas with Mediterranean and sub-tropical climates (Suarez & al. 2001). It prefers moist habitats with mild temperatures and with dense or patchy vegetation as these help to provide these conditions (Hartley & al. 2006, Angulo & al. 2011, Roura-Pascual & al. 2011, Castro-Cobo & al. 2019). As most invasive ants, its nesting site plasticity allows them to invade human constructions (Lee 2002), like settlements or boats docks (Carpintero & al. 2003, Rizali & al. 2010), where it can find a stable climate and a constant source of food and water. These abiotic requirements, together with ports of entries as the main invasion pathway (Corin & al. 2007, Bertelsmeier & al. 2017), shape its distribution and expansion along coastal areas in Southwestern Europe (Espadaler & Gomez 2003, Gomez & Espadaler 2006, Blight & al. 2009, Wetterer & al. 2009).

As it has small workers and a high number of queens in nests, small propagules can be transported unnoticed by humans. Thus, in places with high rates of human activity, like touristic areas on islands, the Argentine ant can be easily transported and established if it finds suitable conditions. Locally, Argentine ant populations progress an average of 150 m / year at the invasion front by budding (Suarez & al. 2001, Hakala & al. 2019). Their spread often follows human disturbance such as roads and trails, however, even carrion dispersed by raptors has been documented as a dispersal mode for this invader (Castro-Cobo & al. 2019).

Supercolony identity may influence the expansion of the Argentine ant, and there is evidence that the Main Supercolony spreads faster than others (Van Wilgenburg & al. 2010, Vogel & al. 2010). However, there is no clear information about which factors cause differential expansion among supercolonies. Factors including genetic drift resulting from bottlenecks, new selective pressures (Tsutsui & al. 2000, Giraud & al. 2002), high aggressiveness, and high diet breadth have been discussed (Blight & al. 2012, 2017, Seko & al. 2021). However, differential expansion of the Main Supercolony could also be related to its invasion history (Wetterer & al. 2009) including secondary introductions, which are common in invasive ants (Bertelesmeier & al. 2017, 2018). In addition, other factors related to environmental suitability could explain differences in patterns of spread.

Long-term studies that keep track of the dynamics of populations of invasive species are needed to fully understand factors affecting their spread. As Zenni & Nuñez (2013) proposed, long-term monitoring studies of populations are a good method to identify invasion failures. They allow observation of the extent of the impacts of the invader (Jeschke & al. 2014) and have been used by several authors to analyze dynamics of invasive species (e.g., Nuñez & Medley 2011, Morris & al. 2013, Dyer & al. 2017, Ramirez & al. 2018). Invasive ant populations can expand over time, but they can also fluctuate, decline, or even collapse (Cooling & al. 2012, Lester & Gruber 2016, Tartally & al. 2016). Long-term studies on the Argentine ant have shown that depending on the locality, its populations can spread over decades (Menke & Holway 2020), provoking enduring ecological impacts (Menke & al. 2018) or collapse (Lester & Gruber 2016). Thus, the analysis of factors driving population progress or disappearance could provide relevant information to understand limitations to the invasion process.

In this study, we analyzed factors affecting the spread of Argentine ants and their ability to dominate native ant communities, specifically differentiating between the three different supercolonies present along the Southwestern Mediterranean coast. We selected three islands: Corsica, where the Corsican and Main Supercolonies are present, and Ibiza and Formentera (the Pityusic Islands), where the Catalonian and the Main Supercolonies are present. We used a temporal approach, recording the spread of the invasion between two time points eight and 12 years apart: We compared the invasion status along islands' coast – on Corsica 1999 with 2007 and on the Pityusic Islands 2004 with 2016. First, all the beaches along the coast were visited in order to record presence and relative abundance of the Argentine ant. Then, we obtained spatial factors related to human-driven dispersal and environmental factors related to habitat characteristics to test whether these factors affected the invasion process in terms of: (i) presence of the Argentine ant (current distribution of invaded beaches), (ii) ability of the Argentine ant to dominate native ant communities, (iii) progress of the invasion (i.e., the invasion of new beaches) through time, and (iv) differences among the three supercolonies. We hypothesized that probability of being invaded by the Argentine ant

would be predicted by disturbance by humans, availability of dense vegetation (due to its preference for moist habitats with mild temperatures; Hartley & al. 2006, Menke & al. 2007), and proximity to already invaded areas. We also predicted that the greater spread of the Main Supercolony over the two smaller ones is rather a consequence of its invasion history than due to variation in environmental variables. We tested this last prediction using historical data on first detection dates and locations of the Argentine ant invasion for 19 islands in Southwestern Europe.

Material and methods

Study area: Fieldwork was carried out on three Mediterranean islands: Corsica, Ibiza and Formentera (Fig. 1). Ibiza and Formentera are two Spanish islands that belong to the Balearic archipelago, located in the East of the Iberian Peninsula. Corsica is a French island located halfway between the Italian and the French coast.

The islands are characterized by a Mediterranean-like climate with mean annual temperatures around 15 - 17 °C (Morey & Ruiz-Perez 2008, Mouillot & al. 2008). Ibiza and Formentera consist of a mixture of arid areas with woodlands of *Pinus halepensis* (Miller, 1768) and *Juniperus phoenicea* L., 1753 or mixed formations of both (Morey & Ruiz-Perez 2008). Corsica's coastal vegetation consists of *Erica arborea* L. as the main native species with introduced *Quercus ilex* L. and *Pinus halepensis* (Reille 1992). Human population increases in summer months due to tourism on the three islands. In August, the daily number of tourists on Corsica can reach more than 430,000, twice the number of inhabitants. The total number of tourists per year is around 7.7 million, and reached 8.2 million in 2017 (Genovese-Bolleyn & al. 2018). In 2018, the number of tourists on Ibiza and Formentera was more than three million (Agència D'estratègia Turística De Les Illes Balears 2018).

Sampling Argentine ant populations and supercolonies: Three supercolonies of Argentine ants are present on the following islands: the Catalonian (Ibiza and Formentera), the Corsican (Corsica) and the Main Supercolonies (all islands). Ibiza and Formentera were first sampled in 2004 by Gomez & Espadaler (2005), when the whole accessible coastline of the islands was examined to locate populations of Argentine ants. All the locations were visited at times of the day that Argentine ants have maximum activity and only when meteorological conditions where adequate (e.g., avoiding rainy days). The ants were sampled by visual searching for at least 30 minutes in suitable parts of the beach, including car parks, streets or avenues, vegetation (natural or artificial), buildings, and other human constructions. When the invader was found, one-on-one aggression tests were performed with workers from both the Main and the Catalonian Supercolonies to determine the identity of the local population. Five replicates for each of the two combinations were carried out. When no aggression was recorded, the local population was assigned to the supercolony of its opponent (Gomez & Espadaler 2005).
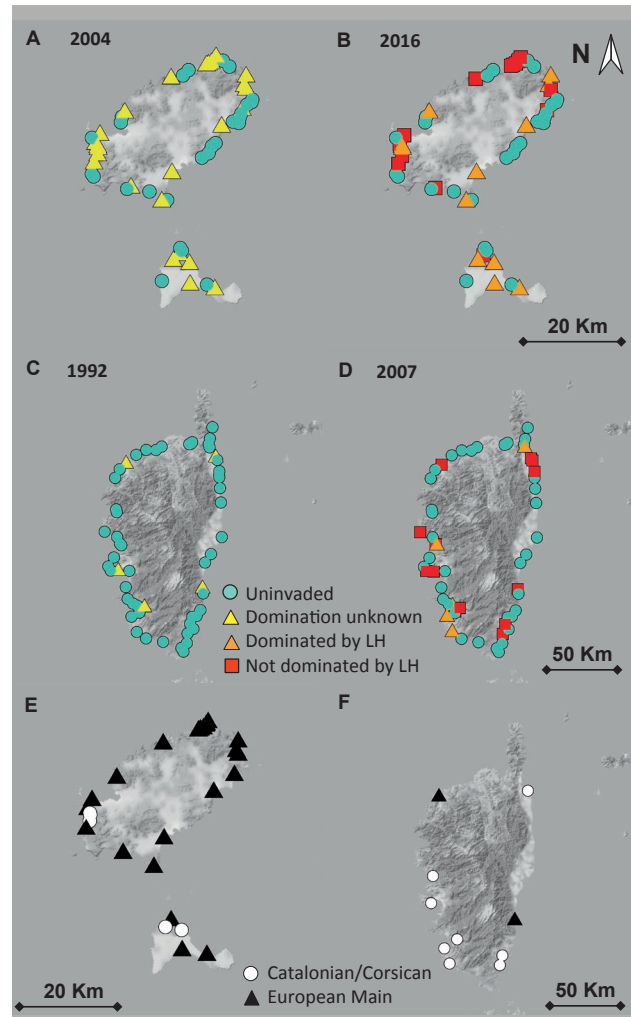

Fig. 1: Invasion of the Argentine ant on the three Mediterranean Islands. Invasion status of sampled beaches on Ibiza and Formentera in 2004 (A) and 2016 (B) and on Corsica in 1992 (C) and 2007 (D). Argentine ant supercolonies are shown on Ibiza and Formentera in 2016 (E) and on Corsica in 2007 (F).

Sampling on Ibiza and Formentera was repeated in August and September of 2016 to check the expansion of the invasion of the supercolonies. A total of 56 beaches were surveyed. In addition to recording the presence / absence of the Argentine ant, native ant species that were observed were recorded. Native species were identified to genus or species level by SCC (Castro-Cobo & al. 2019).

Corsica was sampled in 2007 and 2008 by Blight & al. (2009) from June to September. Due to the size of the island, which is considerably larger than the other two, it was not possible to conduct a comprehensive sampling of the coast. A total of 59 beaches were surveyed. At each site, the ground was inspected, searching under stones or dead wood during a 20 minutes scan. During the scan, several observations were made, separated by at least five meters, recording not only the number of observations with Argentine ants but also the number of observations with native ants. On long beaches, more than one site was sampled. Information about the identity of the supercolony was

Islands

Ibiza-Formentera | Corsica

Invasion status (first sampling):

Yes: Invaded
No: Uninvaded

Invasion status (last sampling):

Yes: Invaded — 28 — 19
No: Uninvaded — 28 — 40

Domination by the Argentine ant

Yes: Dominated — 16 — 14
No: Not dominated — 12 — 5

Argentine ant supercolonies:

Main — 23 — 2
Catalonian/Corsican — 5 — 8

Change of status of uninvaded beaches

Yes: Changed to invaded — 19 — 14
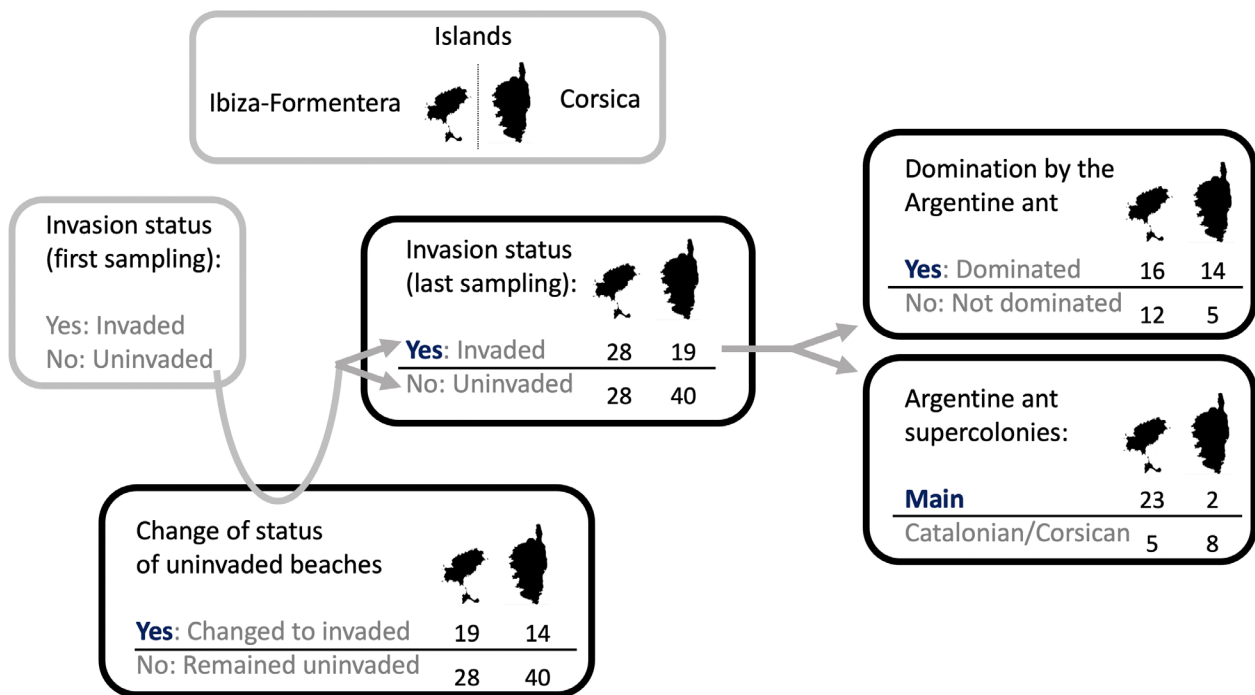No: Remained uninvaded — 28 — 40

Fig. 2: Number of beaches per island used in each of the analyses performed. Analyses represent: (i) invasion status (invaded vs. uninvaded), (ii) if the Argentine ant was dominant (e.g., did not co-exist with native ant species) at each location (dominant vs. not dominant), (iii) differences between supercolonies (Main vs. Catalonian or Corsican), and (iv) change of status (change from uninvaded to invaded vs. no change). Categories marked in bold are the ones modeled (models with binomial link distribution). In the change of status analysis, only 47 of 56 beaches were used on Ibiza and Formentera (the ones that were uninvaded in the first sampling).

extracted from Blight & al. (2012) for some of the sites. A previous sampling was made by Casevitz-Weulersse & Brun in 1999, although it was not as exhaustive as the one performed by Blight & al. (2009) in 2007 - 2008, but the information was extracted from the sampling points of this article for some of the analyses.

Categorization of the beaches: Beaches were categorized as invaded if they had Argentine ants when last sampled (2016 for Ibiza and Formentera, 2007 - 2008 for Corsica), and categorized as uninvaded if Argentine ants were not detected (Figs. 1 and 2). Invaded beaches were further categorized by the presence or absence of native ants together with the Argentine ant abundance, which was used as a measure of the ability of the Argentine ant to dominate invaded localities. The Argentine ant was considered to be dominant when it was the only species present and was at high abundance, and not dominant when at low abundance with native ants present. Because the sampling on the Balearic Islands was slightly different from the sampling on Corsica, the categorization was also different. On the Balearic Islands, a site dominated by the Argentine ant was assigned when it was the only species found on the beach and in large numbers, or if there was a maximum of three native species in very low numbers. When the Argentine ant co-occurred with more than three native species and was present in low numbers, the site was categorized as not dominated by the Argentine ant. Thus, a binary variable for dominated versus not dominated by the Argentine ant was established for each beach (Fig. 1).

In Corsica, the percentage of sampled points at each beach on which the Argentine ant was present was estimated. Thus, when a site was scored as invaded, an Argentine ant community domination index was calculated using the ratio between the number of Argentine ant observations that were separated by at least five meters and the total number of observations. When there were more than 70% of points with presence of Argentine ant, the beach was considered dominated by the Argentine ant, assigning also in this case a binary variable (Fig. 1).

On each island, information on where the three supercolonies were located was obtained (Fig. 1). On the Balearic Islands, the identity of the supercolony to which the Argentine ant belonged in both samplings was assessed with aggression assays (2004 and 2016). On Corsica, as information from aggression tests to identify the supercolony at each invaded site was not available, the information was extracted from literature. Blight & al. (2012) studied the supercolonies on Corsica, and 10 of their study sites coincided with those of this study, so the information for these localities were available.

Finally, information about newly invaded beaches on each island from the second survey (Fig. 1) was used to assess factors that could affect the invasion of new sites (Fig. 2). On Ibiza and Formentera, using the beaches that were uninvaded in 2004, comparisons were made between the ones that remained uninvaded in 2016 with the ones that changed their status to invaded in 2016. On Corsica,

information was again extracted from literature. Casewitz-Weulersse & Brun (1999) surveyed the island and published a list of the beaches that were invaded. This information was used to determine if the beaches invaded in 2008 were new invasions or if they had already been invaded in 1999.

Environmental and spatial variables affecting the invasion: To study the factors that can affect the expansion of the Argentine ant invasion on these islands, its ability to dominate invaded locations and the differences between supercolonies, the following environmental and spatial variables were measured: For the spatial variables, the distance to the nearest invaded beach was measured, as a potential invasion source, and to the closest building. The tool "Ruler" in Google Earth Pro (version 7.3.2.5776, Google Earth Pro 2019) was selected to calculate distances, taking the middle point of the beach coast as reference. To know which was the nearest invaded beach, the identity of the supercolony in the first sampling was taken into account when it was available. Details of which analysis used the variable "distance to the nearest invaded beach of the same supercolony" are evident in Table S1 (as digital supplementary material to this article, at the journal's web pages). The length of the beach was also measured with the tool "Add path" in Google Earth Pro, at three kilometers of eye view, to calculate the total length of the coastline.

For the environmental variables, information about two main factors that could affect the Argentine ant invasion was extracted: vegetation types as a proxy for soil moisture and temperature (Menke & al. 2007, Angulo & al. 2011) and human constructions. Using a geographic information system (ArcGIS, version 10.5), the images for the year corresponding to the most recent sampling were selected, or if it was not available, the closest year with images. Then, a grid was created over each sampled point of 210 m², formed by pixels of 30 × 30 m², using the tool Create Fishnet. Thus, a square of 7 × 7 pixels per sample point was obtained that was exported to kml to work on Google Earth Pro. The square was centered on the shoreline of the beach to avoid losing information in coves with a "C" shape. Number of pixels of sea, beach, scarce vegetation (bushes or trees were isolated and separated from each other for at last five meters), dense vegetation (bushes or trees were together forming a continuum), human construction, and naked soil at each beach were counted to get a description of the surrounding habitat of the sampled areas (Fig. 3). When there was a mixture of categories in a pixel, the category selected was the one with higher representation in the pixel. As sea pixels did not provide any valuable information, they were removed from the final count. The other environmental variables were then calculated proportionally to the removal of sea pixels. Other factors that could be related to the Argentine ant survival (when was it first locally introduced into a beach) or to human intensity (number of visitors at the beach), such as the presence of a bar, a pier / port, the type of trail that leads to the area (road / path), or the main material forming the coast (sand / rocks), were also considered.
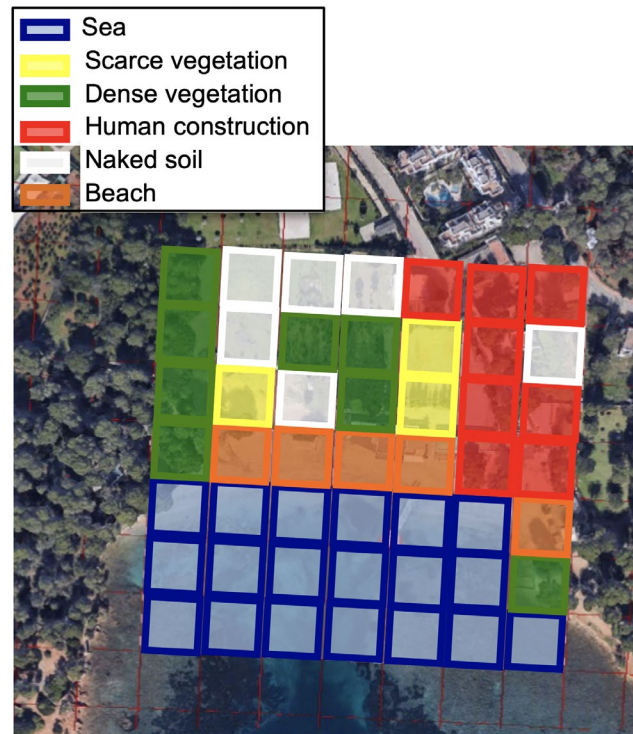

Fig. 3: Example of environmental variable measurement of a beach on Ibiza (Cala Pada). The cell used and the different categories to which each grid could be assigned are shown.

Data analysis: To reduce the number of environmental variables, a Principal Component Analysis (PCA) was conducted using the princomp function (stats package, R Core Team 2017). The principal components (herein, dimensions) were selected if they explained > 10% of the variance (Tab. 2). The contributions of the environmental variables to each dimension were obtained (Tab. 2), and finally the values of each selected dimension to each sampled location were extracted, and included in the analysis as independent variables.

To analyze what factors affected the invasion of the Argentine ant, four different generalized linear models were performed using the glm function (package stats, R Core Team 2015) for each of the island data sets: Ibiza and Formentera together, and Corsica. Dependent variables of the four models were: (i) the status of the invasion (if the beaches were invaded when last sampled or not); (ii) if the Argentine ant was considered dominant or not at each invaded location; (iii) which supercolony is the one present in the invasion (Main or Catalonian for Ibiza and Formentera, and Main and Corsican for Corsica); and (iv) the change of invasion status over time (the beach remained uninvaded or it changed its status to invaded).

Because the dependent variables analyzed were different for each analysis described below, sampling size was also different in each analysis (Fig. 2). When the dependent variable was the status of the invasion (invaded or uninvaded), data of the most recent sampling of all beaches that were invaded and uninvaded were used, that is, 56 for Ibiza and Formentera, and 59 for Corsica. When the

Tab. 1: Contribution of the variables included in the PCA to each one of the dimensions (D.1, D.2, and D.3) selected for each analysis on (A) Ibiza and Formentera and (B) Corsica. Contribution is represented by a percentage and the sign represents the direction of the relationship of each variable with the given dimension. White cells represent values lower than 1%. Lighter grey cells depict values between 1 and 30%. Darker grey cells represent values higher than 30%. Percentage of explained variance for each PC is given in the last row (% Variance).

(A)	Invasion			Dominance		Supercolony		Change of status		
IBI-FORM	D.1	D.2	D3	D.1	D.2	D.1	D.2	D.1	D.2	D.3
Bar										
Access										
Material										
Dock										
Beach	1 +		14 –					1 –		14 +
Dense veg.	**85 –**	13 –		77 –	23 +	77 –	23 +	77 +	18 –	2 +
Scarce veg.		16 +	70 +						18 +	**68 –**
Naked soil									2 +	
Construction	14 +	**70 –**	14 +	22 +	**74 +**	22 +	**74 +**	21 –	**61 –**	15 +
% Variance	**50**	31	11	**63**	27	**63**	27	**47**	32	13

(B)	Invasion			Dominance			Supercolony			Change of status		
CORSICA	D.1	D.2	D.3	D.1	D.2	D.3	D.1	D.2	D.3	D.1	D.2	D.3
Bar									1 +			
Access												
Material												
Dock									2 –			
Beach		69 –			15 –	14 –		8 –	**38 +**		71 –	7 –
Dense veg.	3 –	6 +	**78 –**	3 –	**78 +**	11 –	14 –	**76 +**	3 +	1 –		**70 +**
Scarce veg.	**51 –**	8 +	18 +	**69 –**		25 +	**53 –**	8 –	2 +	**50 –**	15 +	15 –
Naked soil				1 +		4 +			**44 –**	1 +		
Construction	**45 +**	16 +	4 –	26 +	6 –	**45 +**	**31 +**	7 +	10 +	**47 +**	14 +	7 –
% Variance	**50**	23	15	**53**	27	10	**56**	**26**	**11**	**49**	25	14

dependent variable was the Argentine ant domination of invaded locations (dominated or not dominated), data of the most recent sampling of beaches that were invaded were used, 28 for Ibiza and Formentera, and 19 for Corsica. When the dependent variable was the supercolony, data of the most recent sampling of beaches, for which the identity of the supercolony was known, were used (28 for Ibiza and Formentera, and 10 for Corsica). When the dependent variable was the change of invasion status over time (changed to invaded or not), data of the beaches that were uninvaded in the first sampling were used (both the ones that got invaded in the second sampling and the ones that remained uninvaded), 47 in the case of Ibiza and Formentera, and 54 in the case of Corsica (Fig. 2).

The four models had a binomial link distribution, and each model comprised as independent variables the previous spatial parameters and the selected components from the PCA (Tab. 1). For each model, the category that was modeled by the binomial distribution is marked in bold in Figure 2. The complete model was evaluated, except in the case of the analysis between supercolonies on Corsica. In this case, because the subset analyzed had a low sample size (Fig. 2), a forward stepwise regression was used.

All analyses were conducted in R (R Studio version 1.0.136, RStudio Team 2016), and the significance level cut off used was α = 0.05.

Historical analysis of supercolonies at first detection locations: To determine if historical precedence influenced expansion of the supercolonies, the locations where Argentine ants were first detected on each island were obtained from the literature and from personal observations. The identity of supercolonies at these sites was determined from sampling in this study and from the sampling of colleagues. Information for 19 islands including Corsica and all Balearic Islands was collected; some Atlantic Islands such as the Canary Islands, Madeira, and Azores were also included as information was available. As information for Corsica was complete and extensive, the history of invasion of the Argentine ant on this island since the first detection date was re-constructed.

Tab. 2: Effect of the environmental and spatial variables on different aspects of the Argentine ant's invasion process on (A) Ibiza and Formentera Islands and (B) Corsica. Environmental variables are represented by the selected dimensions in each PCA (Dim. 1, Dim. 2, Dim. 3) together with the length of the beach (Length), and the minimum distance to the closest invaded beach or building (Close inv. and Close buil., respectively). Analyses of the invasion process represent invasion status (invaded vs. uninvaded), dominance of Argentine ants at the location (dominant vs. not dominant), differences between supercolonies (Main vs. Catalonian or Corsican) and change of status (change from uninvaded to invaded vs. no change). s indicates the sign of the relationship. Significant relationships are marked in bold; significance level for all the analyses was α = 0.05.

(A)	Invasion			Dominance			Supercolony			Change Status		
IBI-FORM	$\chi 2$	p	s	$\chi 2$	p	s	$\chi 2$	p	s	$\chi 2$	p	s
Dim. 1	**4.32**	**0.037**	+	3.50	0.061	+	1.47	0.226	+	3.34	0.068	-
Dim. 2	0.01	0.941	-	1.95	0.163	-	0.65	0.422	-	0.01	0.923	-
Dim. 3	1.38	0.241	-							1.02	0.314	+
Length	0.17	0.680	+	**11.54**	**<0.001**	-	0.765	0.382	+	0.29	0.591	-
Close inv.	1.92	0.165	-	1.25	0.264	+	2.479	0.115	+	0.08	0.776	+
Close buil.	0.08	0.774	-	0.02	0.898	-	0.315	0.575	-	0.19	0.661	+
(B)	Invasion			Dominance			Supercolony			Change Status		
CORSICA	$\chi 2$	p	s	$\chi 2$	p	s	$\chi 2$	p	s	$\chi 2$	p	s
Dim. 1	0.14	0.712	-	0.37	0.544	+	--	--	--	0.82	0.365	-
Dim. 2	0.26	0.613	-	0.25	0.617	+	--	--	--	0.15	0.697	-
Dim. 3	2.38	0.123	+	0.14	0.711	-	--	--	--	0.02	0.900	+
Length	0.05	0.816	-	0.02	0.875	+	--	--	--	0.10	0.755	+
Close inv.	**10.11**	**0.002**	-	0.31	0.577	+	--	--	--	**11.95**	**<0.001**	-
Close buil.	0.02	0.90	-	0.00	0.957	+	**4.40**	**0.036**	--	0.03	0.868	-

Results

In Ibiza and Formentera, the number of invaded zones tripled in 12 years, while on Corsica it quadrupled in nine years. We have no record of the identity of the supercolonies from the last survey on Corsica, but on Ibiza and Formentera, the Main Supercolony expanded the most. This was especially noticeable on Formentera: In 2004, there was only one location invaded, namely by the Catalonian Supercolony, while in 2016 the number of beaches with the Main Supercolony was higher than the number of beaches with the Catalonian Supercolony (Fig. 1). Furthermore, from 12 beaches invaded and not dominated by the Argentine ant on Ibiza and Formentera in 2016, four of them had already been invaded in 2004, meaning that in 14 years the Argentine ant was not able to completely displace the native ant community. Finally, we also observed that none of the invaded locations have become uninvaded through time.

Factors affecting the invasion (invaded versus uninvaded): For Ibiza and Formentera, we obtained three principal components that represented the environmental variables (Tab. 1A). The first dimension (70% variance explained) primarily accounted for the amount of dense vegetation (negative relationship) and, to a lesser extent, was positively related with the percentage of surface with human construction. Human construction was mostly represented in the second dimension (negative relationship) and, to a lesser extent, was positively related

with the amount of scarce vegetation and negatively with dense vegetation. Finally, the third dimension was represented by the amount of scarce vegetation (with a positive relationship) and, to a lesser extent, was positively related with the surface of human construction and negatively with the surface of the beach.

When we used these three environmental components, together with the spatial variables, to model the invasion status of the beaches on Ibiza and Formentera, we found that the only significant variable was the first dimension of the PCA ($\chi 2$ = 4.32, p = 0.037, N = 56, Tab. 2A); invaded beaches had a lower relative amount of dense vegetation than the uninvaded beaches, but a higher relative amount of human construction surface (Fig. 4A).

In Corsica, we obtained three principal components that accounted for the environmental variables (Tab. 1B). The first dimension (50% variance explained) represented the relative amount of human construction (positive relationship) and the relative amount of scarce vegetation (negative relationship). The second dimension accounted mostly for the relative amount of human construction (positively related). The third dimension accounted mostly for the relative amount of dense vegetation (positively related) and, to lesser extent, for the amount of scarce vegetation (negatively related).

When we modeled the invasion status of the beaches on Corsica, we found that the distance to the closest invaded area was the only variable that significantly increased the
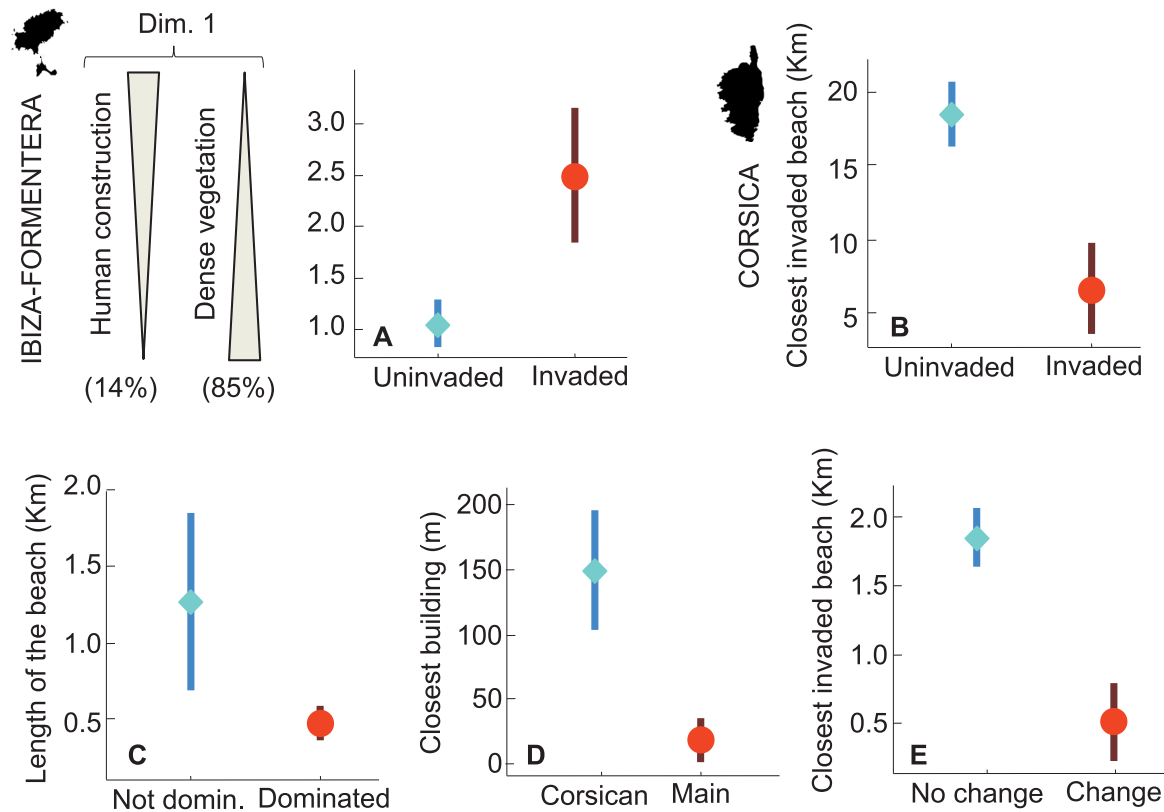
Fig. 4: Characteristics of beaches (average ± standard error) in relation to Argentine ant invasion. (A) Environmental dimension 1 for invaded (red circles) or uninvaded (light blue diamonds) beaches on Ibiza and Formentera; in the Y-axes appear the two variables that explain this dimension, their direction in the dimension and the percentage of variance explained in the dimension. (B) Minimum distance (km) to the closest invaded beach in the past (nine years before) for invaded (red circles) or uninvaded (light blue diamonds) beaches on Corsica. (C) Length of the beach (km) for Argentine ant dominated (red circles) and not dominated (light-blue diamonds) invaded beaches on Ibiza and Formentera. (D) Minimum distance (m) to the closest building among supercolonies on Corsica. (E) Minimum distance (km) to the closest invaded beach in the past for beaches that remained uninvaded (light blue diamonds) or that changed to invaded (red circles) in the second survey on Corsica.

likeliness of a beach to get invaded ($\chi2$ = 10.11, p = 0.002, N = 59, Tab. 2B). Thus, invaded beaches had significantly less distance to the nearest invaded beach in the previous survey (Fig. 4B).

Factors affecting dominance in invaded locations: In Ibiza and Formentera, we obtained two principal components that represented the environmental variables (Tab. 1A). Similar to the factors explaining new populations, the first dimension (63% variance explained) accounted mostly for the relative amount of dense vegetation (negative relationship) and, to a lesser extent, it was positively related with the relative amount of human construction. The second component was represented mostly by the relative amount of human construction (negatively related), and, to a lesser extent, was positively related with the relative amount of dense vegetation.

When modeling dominance at a location for the Argentine ant on Ibiza and Formentera, we found that dominance was influenced negatively by only one variable: the length of the beach ($\chi2$ = 11.56, p < 0.001, N = 56). Argentine ants were more likely to be scored as dominant on short beaches than on large beaches (Fig. 4C).

In Corsica, we found three principal components representing the environmental variables (Tab. 1B). The first dimension (53% variance explained) was mainly represented by the relative amount of surface with scarce vegetation, with a negative relationship. The relative amount of human constructions and naked soil were represented to a lesser extent, with a positive relationship. The second dimension accounted mostly for the relative amount of dense vegetation (positively related), and, to a lesser extent, with the relative amount of beach (negatively related). The relative amount of human construction was the main variable represented in the third dimension (positive relationship), but, to a lesser extent, the relative amount of beach and dense vegetation surface (negatively related) and the relative amount of scarce vegetation (positively related) were also represented (Tab. 1B). None of these components or spatial variables predicted the dominance of areas by the Argentine ant on Corsica (Tab. 2B).

Factors affecting the spread of the three supercolonies: For Ibiza and Formentera, two principal components were selected to represent the environmental variables (Tab. 1A). The first dimension (63% of the vari-

Tab. 3: First detection dates (FDD) for the Argentine ant, locations, and supercolonies that were observed in the nearest locations, for some island archipelagos in South Western Europe. Supercolonies abbreviations are M for the Main, Ca for the Catalonian, and Co for the Corsican supercolonies. The nearest supercolony to the earliest record is in the column "Near", while other supercolonies of each island are in the column "Other" with the number of locations in parentheses (N). References for the earliest records on each island (Ref): [1]Ashmole & al. (1996), [2]Bernard (1956), [3]Chopard (1921), [4]Comín (1977), [5]Comín & Espadaler (1984), [6]Donisthorpe (1936), [7]Espadaler (2007), [8]Espadaler & Bernal (2003), [9]Gómez & Espadaler (2006), [10]Stitz (1917), [11]Wellenius (1949), [12]Wellenius (1955), [13]Wetterer & al. (2007), [14]Wetterer & Wetterer (2006), [15]Wheeler (1927), [16]Yarrow (1967). Date: month / year of assessment of supercolony identity; Author: authors or publications of the assessment: AT: A. Tucci; KG: K. Gómez; SCC: S. Castro-Cobo; VB: V. Bernal; XE: X. Espadaler. Multiple locations: [a]Puerto de la Luz, Las Palmas, Telde, Teror, San Lorenzo, Arucas, Galdar; [b]Airport, Cabeça da Ponta, Camacha, Campo de Baixo, Pico do Castelo, Ponto, Ponta da Conveira, Serra de Dentro, Serra de Fora, Vereda da Terra, Vila Baleira.

Archipelago / Island	Location	FDD	Ref	Supercolonies		Supercolony assessment	
				Near	Other (N)	Date	Author
Balearic Islands							
Mallorca	Soller Port	1956	2	M	M (44), Ca (4)	08 / 2013	AT (XE)
Menorca	Maó Port	1976	4	M	M (14)	10/ 2004	KG
Ibiza	Ibiza city	1976	5	M	M (8), Ca (3) M (20), Ca (3)	09 / 2004 09 / 2016	KG & XE SCC
Formentera	La Savina Port	2004	9	Ca	Ca (1) M (3), Ca (2)	09 / 2004 09/2016	KG & XE SCC
Corsica	Calvi	1959	2	M	M (2), Co (8)	2007-8	OB
Canary Islands		1909	15				
El Hierro	Valverde	1950	12	M	M (2)	12 / 2003	7
Lanzarote	Ye	1988	8	M	M (3)	08 / 2005	VB
Fuerteventura	Betancuria	1992	8				
Gomera	--	1927	15	M	M (2)	08 / 2004	XE
Teneriffe	La Orotava	1909	10	M	M (1)	04 / 2006	XE
Gran Canaria	Multiple[a]	1927	15	M	M (2)	12 / 2005	XE
Palma	Los Llanos, San Andrés	1927	15	M	M (2)	04 / 2006	XE
Madeira							
Madeira	Funchal	<1858	12	M	M (6)	2002	14
Porto Santo	Multiple[b]	2002	13	M	M (1)	2002	14
Deserta Grande		2003	13				
Azores							
no locality		<1921	3				
Terceira	Angra de Heroismo	1930	6	M	M (2)	2002	14
Sao Miguel	Punta Delgada, Furnas	1930	6	M	M (3)	2002	14
Flores	Calheta, Ribeira do Salto	1938	11				
Sao Jorge	--	1929	6				
Pico	Baía Cachorro	1987	1				
Santa Maria	Fonte do Mourato	1957	16				

ance explained) was represented by the relative amount of dense vegetation on the beach (negatively related) and, to a lesser extent, by the relative amount of human constructions (positively related). The second dimension explained the same two variables, but both with a positive relationship. Although the Main Supercolony has expanded more broadly on Ibiza and Formentera (from two to five beaches for the Catalonian Supercolony and from eight to 23 for the Main Supercolony, Fig. 1), there were no factors favoring differently their expansion (Tab. 2A).

For Corsica, there were three principal components that accounted for the environmental variables (Tab. 1B).
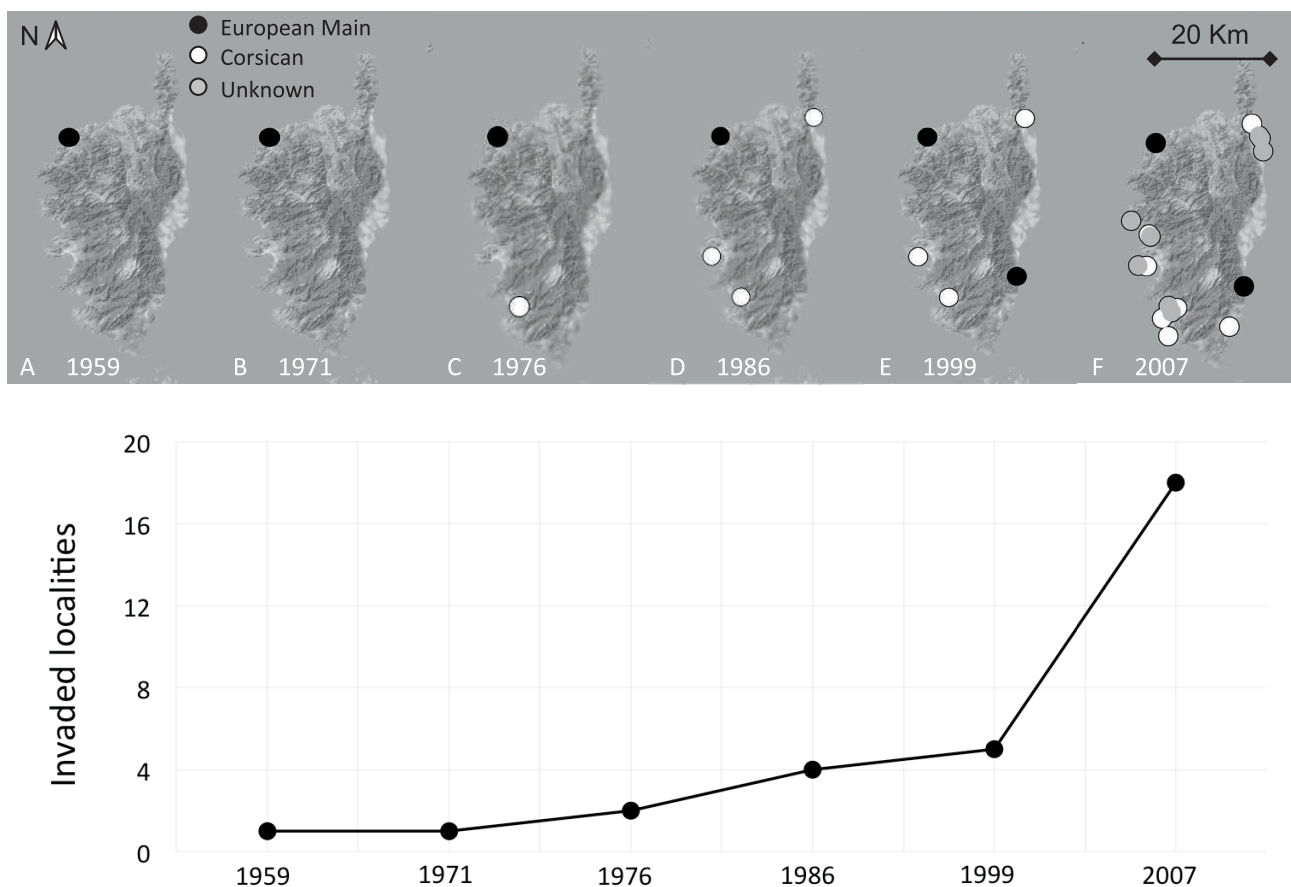
Fig. 5: Expansion of the Argentine ant on Corsica since its first detection and supercolonies that are present in our days: A 1959, B 1971, C 1976, D 1986, E 1999, and F 2007 - 2008. Data for (A) are from Bernard (1959); data for (B, C, and D) are from Casevitz-Weulersse (1989); data for (E) are from Casevitz-Weulersse & Brun (1999); and data for (F) are from Blight & al. (2009).

The first dimension (56% variance explained) accounted mostly for the relative amount of scarce vegetation (negative relationship) and of human construction (positive relationship), and, to a lesser extent, with the relative amount of dense vegetation (negatively related). The relative amount of dense vegetation was the main variable explaining the second dimension, with a positive relationship. The third dimension accounted mostly for the relative amount of beach and naked soil, both with a negative relationship, and, to a lesser extent, for the relative amount of human constructions (negatively related).

As the sampling size for this analysis was low (n = 10), we performed a forward stepwise regression. Distance to building was the only variable showing significant differences between the Main and the Corsican Supercolonies ($\chi2 = 4.40$, p = 0.036, N = 59; Tab. 2B). The negative sign in this case means that locations with buildings very close to the shore were more likely to be invaded by the Main Supercolony than by the Corsican Supercolony (Fig. 4D).

Factors affecting the change of status from uninvaded to invaded (change versus no change): As none of the locations invaded in the past appeared uninvaded when we sampled them the second time, the data used here only corresponded to beaches that were uninvaded during the first sampling (Tab. 1). On Ibiza

and Formentera, we obtained three principal components to represent the environmental variables (Tab. 1A). The first dimension (47% variance explained) represented the relative amount of dense vegetation (with a positive relationship) and, to a lesser extent, the relative amount of human construction (with a negative relationship). The relative amount of human construction was the main variable represented in the second dimension (positively related), and, to a lesser extent, the relative amount of dense and scarce vegetation (positively and negatively related, respectively). Finally, the third dimension was represented mostly by the relative amount of scarce vegetation (positive relationship) and, to a lesser extent, it was positively related with the relative amount of human construction and negatively with the relative amount of beach. When modeling the change of status on Ibiza and Formentera adding these environmental dimensions and the spatial variables, we found that none of the variables seemed to affect this process (Tab. 2A).

For Corsica, we obtained three principal components that accounted for the environmental variables (Tab. 1B). The first dimension (49% variance explained) accounted mostly for the relative amount of human construction (positive relationship) and scarce vegetation (negatively related). The second dimension was explained by the

relative amount of beach (negatively related), and, to a lesser extent, by the relative amount of scarce vegetation and human constructions (positively related). The last dimension was represented mainly by the relative amount of dense vegetation (positive relationship), and, to a lesser extent, by the relative amount of scarce vegetation (negative relationship). The model with these environmental dimensions and the spatial variables revealed that distance to an invaded beach in the past negatively affected the probability of suffering a change of status ($\chi2 = 11.95$, p < 0.001, N = 59; Tab. 3B). Uninvaded beaches that were closer to invaded beaches were more likely to be invaded (Fig. 4E).

Supercolonies at first detection locations: We assigned a supercolony identity for most of the studied islands, including all Balearic Islands and Corsica (Tab. 4). First assessments of supercolonies for each island were made between 2002 (Madeira and Azores) and 2013 (Mallorca). First detection dates of Argentine ant on these islands ranged from before 1858 on Madeira to 2004 on Formentera. Assuming supercolonies do not change temporally in a given location, as we have shown with the data of Ibiza and Formentera, we suggest that the Main Supercolony was probably the first introduced on all these groups of islands, except for Formentera (Tab. 3).

In Corsica, the first detected location with Argentine ant was Calvi in 1959 (BERNARD 1959), and the supercolony that was present in Calvi in 2007 - 2008 was the Main Supercolony. The first location with the Corsican Supercolony (assessed in 2007 - 2008) could correspond to Propriano, when the Argentine ant was first detected in 1976 (CASEVITZ-WEULERSSE 1989). From 1959 to the last sampling in 2007 - 2008 on Corsica (a time span of 48 years), the Corsican Supercolony seems to have expanded to more locations than the Main Supercolony (Fig. 5).

Discussion

We followed the invasion of the three European Argentine ant supercolonies on three Mediterranean islands for nine years (in the case of Corsica) and for 12 years (in the case of Ibiza and Formentera). Argentine ants have consistently expanded their range on the three islands, especially the Main Supercolony that expanded more than the Catalonian on Ibiza and Formentera (where 82% of the currently invaded beaches are colonized by the Main Supercolony), but less than the Corsican on Corsica (where only 20% of the currently invaded beaches are colonized by the Main Supercolony). All beaches that had been invaded at the time of the first sampling remained invaded. Moreover, more than half of the beaches where Argentine ants were not considered "dominant" in the first sampling remained this way; while still present 12 years later, the Argentine ant does not always become dominant in areas it invades. Environmental and spatial variables helped us to corroborate the importance of human presence for the invasion of the Argentine ant: The likeliness of a beach to be invaded on Ibiza and Formentera was negatively related with the amount of dense vegetation but positively related with the amount of human constructions in the area. Moreover, the Main Supercolony was more likely to spread to beaches when there was a building close by than the Corsican Supercolony. Finally, on Corsica, beaches that had already been invaded before our study or were invaded during our study were closer to previously invaded beaches, highlighting the importance of secondary introductions in the expansion of the Argentine ant.

Human-linked dispersion patterns: Biological invasions on islands have been linked to human dispersal for centuries, particularly through commerce or tourism (e.g., COURCHAMP & al. 2017). This is especially true for invertebrates, such as beetles or ants (MARINI & al. 2011, BERTELSMEIER & al. 2018). Remote and inhabited islands with docks have higher rates of exotic species because they facilitate boat traffic (RIZALI & al. 2010, INOUE & al. 2013, MORIGUCHI & al. 2015). We did not find an association between Argentine ant invasion and the presence of small docks at beaches. This probably results from the fact that our study islands have main ports that dominate commercial and touristic maritime traffic.

Secondary introductions of invasive ants from primary ports of entry are common in both continental and island systems (INOUE & al. 2013, BERTELSMEIER & al. 2018). Our results corroborate this pattern on Corsica, the largest of the three studied islands, where both existing invaded beaches and newly invaded beaches were close to already invaded ones. In Japan, the cause of some of these jumps was permanent ship routes among ports or commercial exchanges between locations (INOUE & al. 2013). On Ibiza and Formentera, invaded beaches had less dense vegetation but more human construction than uninvaded beaches. Argentine ants can spread to natural areas (HOLWAY & al. 2002, MENKE & HOLWAY 2006, ANGULO & al. 2011), but its ability to dominate is closely related to the distance to the nearest urban area (MORIGUCHI & al. 2015, VONSHAK & GORDON 2015).

Argentine ant invasions – not always dominant: Although the Argentine ant is considered a very successful invader, our surveys suggest that it does not always dominate areas it invades. On almost half of the invaded beaches on Ibiza and Formentera and in one third on Corsica, the Argentine ant co-occurred with native species (Fig. 2). Beaches that were not dominated by the Argentine ant were characterized by a longer shoreline than beaches where it was dominant. Moreover, the Argentine ant has been co-occurring with the native community on four beaches for at least 12 years. This lack of dominance could be a consequence of a lack of suitable abiotic conditions (HOLWAY & al. 2002, MENKE & HOLWAY 2006). Although we do not have specific measures of temperature and moisture for these beaches, the shorelines of the islands seem to be very suitable habitats for the Argentine ant (GIRAUD & al. 2002, GOMEZ & ESPADALER 2005), and the beaches where it is not dominant are interspersed between those where it is dominant (Fig. 1). We suggest that abiotic factors, such as temperature or humidity, are therefore not a likely cause of the prolonged coexistence of the Argentine ant with native

species in these locations, although data is needed in order to corroborate this suggestion.

Biotic resistance could be another factor explaining coexistence of native ants with the Argentine ant (MARRAFFINI & GELLER 2015, HOWETH 2017) or the presence of certain co-dominant native species (HOBBS & HUENNEKE 1992, WARDLE 2001, KENNEDY & al. 2002, HENRIKSSON & al. 2015). For example, native ants from the *Tapinoma nigerrimum* group on Corsica can slow the spread of the Argentine ant (BLIGHT & al. 2010a), and traits like behavioral dominance or mass recruitment can be important in biotic resistance through competition for resources (CASTRO-COBO & al. 2021). Several dominant species that mass recruit have been able to resist the Argentine ant, including *Crematogaster scutellaris* (OLIVIER, 1792), *Lasius grandis* FOREL, 1909, *Pheidole pallidula* (NYLANDER, 1849), *Tetramorium forte* FOREL, 1904, or *Tapinoma* sp. (WAY & al. 1997, PAIVA & al. 1998, WALTERS & MACKAY 2005, WETTERER & al. 2006, MOTHAPO & WOSSLER 2014, BLIGHT & al. 2010a). More detailed studies are needed to determine if biotic resistance could explain the long-term coexistence between the Argentine ant and native ants on these islands.

The Argentine ant remained present on all the beaches where it had previously been detected. Collapses of Argentine ant populations have been observed in other regions, including New Zealand, California, and Madeira (LESTER & GRUBER 2016). Similarly, population declines have occurred with other invasive ants such as *Anoplolepis gracilipes* (F. SMITH, 1857) in Australia (COOLING & HOFFMANN 2015) and *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990 in several European countries (TARTALLY & al. 2016). Although they have not been observed at our study sites over a 12-year period, longer-term surveys are needed to determine population dynamics in this system if they occur.

Differential expansion of supercolonies: Although we did not expect to find differences between the supercolonies in terms of environmental factors affecting their presence, we found that on Corsica the Main Supercolony was linked to beaches with closer buildings to the shoreline. Similar to other invaded areas maintaining several different supercolonies, we observed that supercolonies on the three islands seem to be excluding each other (THOMAS & al. 2006, SUNAMURA & al. 2009). Ants from the Corsican and the Main Supercolonies can tolerate each other in a border zone with no aggression between them (BERVILLE & al. 2013). This may be driven by differences in personality traits that are correlated to ecological success of different supercolonies (BLIGHT & al. 2017).

The pattern of expansion of the Main Supercolony relative to the others is not well explained by its invasion history. On Corsica, the Corsican Supercolony has expanded more than the Main Supercolony since the introduction of the Argentine ant in Calvi in 1959 (BERNARD 1959). This was despite the fact that the Main Supercolony also occurs in Calvi, suggesting that it was the first introduced supercolony on the island. Conversely, the Main Supercolony expanded more than the Catalonian Supercolony on the two Balearic Islands. On Ibiza, the first detection of Argentine ants was in Ibiza city (COMÍN & ESPADALER 1984), where the Main Supercolony is located now. However, the Catalonian Supercolony was first detected on Formentera in 2004 in La Savina (GOMEZ & ESPADALER 2006). Although this location remains occupied by the Catalonian Supercolony, the Main Supercolony has occupied four more locations on Formentera while the Catalonian Supercolony has not expanded on this island. Thus, with the exception of Formentera, the Main Supercolony appears to have been the first to be introduced to the Mediterranean and Atlantic Islands examined. The greater rate of expansion of the Main Supercolony throughout this region is therefore likely a consequence of its invasion history of primary and secondary introductions.

Propagule pressure could be another factor affecting the expansion rate of the supercolonies. Given that Argentine ants only need a queen and as few as 10 workers to colonize a new area (HEE & al. 2000), the greater expansion of the Main Supercolony could be driven by its ability to produce new propagules. While we did not examine the role of propagule pressure in this study, SAGATA & LESTER (2009) found that propagule size has limited predictive power with species that display behavioral plasticity as the Argentine ant does. The Main Supercolony has also been described as more aggressive and active than other supercolonies (ABRIL & GOMEZ 2011, BLIGHT & al. 2017). This could result in it displacing other supercolonies over time, although we never observed substitutions between supercolonies over the years in this system.

Supercolonies are a subject of interest in evolutionary ecology because of uncertainty in their origin and their possible incompatibility with the kin selection theory (TSUTSUI & al. 2000, HELANTERÄ & al. 2009, HAKALA & al. 2019). Following the distribution of supercolonies over time can contribute meaningfully to the understanding of this paradox. Argentine ants continue to expand their range, and factors related to global change like climatic change, habitat loss, or globalization can speed up the process (BERTELSMEIER & al. 2015, 2016, 2017, 2018). We show that the Argentine ant's spread is influenced by the presence of human activity, directly and indirectly, through jump-events. Long-term monitoring is needed, together with broad networks of researchers working with this global invader, to determine general patterns of invasion of Argentine ant supercolonies on a global scale.

Acknowledgments

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