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REVIEW

Exotic Ants (Hymenoptera, Formicidae) Invading Mediterranean Europe: a Brief Summary over About 200 Years of Documented Introductions

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Abstract

Exotic ants have emerged as a relevant topic worldwide because of their remarkable impacts on native ecosystems and human activities. A first regional overview is given on the dozens of exotic ant species recorded in Mediterranean Europe since the end of the 19th century. About 40 exotic ant species, belonging to 17 genera and originating from 5 different biogeographical realms, are currently believed to be established in this region. The genera *Nylanderia* and *Tetramorium* are those hosting the larger proportion of species, while the Afrotropical realm is the prevalent source of taxa. According to the available data, France, Greece, Italy and Spain all host a high number of exotic species, which has increased at a dramatic rate during the last decades. On the other hand, Mediterranean countries on the Eastern part of the Adriatic Sea appear to be almost empty of exotic ants, perhaps due to both a lesser number of introductions and a lack of targeted investigations. Neighboring countries of the region do not necessarily have more species in common than those geographically distant. Very little is known on the intra-Mediterranean or intra-Palearctic introduction processes which probably occurred prior to the 19th century and on their influence on the current species distribution. The vast majority of the species that are currently established in the region are either restricted to indoor habitats or outdoor anthropogenic habitats, fewer of them were able to colonize semi-natural or natural habitats and very few are recognized as serious pests.

Introduction

Introduction of exotic species is a global problem affecting human activities and whole natural ecosystems. Exotic ants represent only a very tiny fraction of global ant diversity (McGlynn, 1999), and most of them tend not to spread outside the human-modified habitats where they first arrive (Holway et al., 2002). Nonetheless, many others have a significant ecological impact and may become invasive, even outside anthropogenic habitats, sparking serious concern and attention from researchers worldwide (Holway et al., 2002; Lach et al., 2010). Five ant species are considered among one hundred worst alien species in the world, representing almost one third of the terrestrial invertebrates of the list produced by Lowe et al. (2000). Eradication of these species may unfortunately prove to be extremely difficult to achieve if populations are well-established (Holway et al., 2002; Hoffmann et al., 2011; Hoffmann et al., 2016).

In Europe, alien terrestrial invertebrates represent one of the most numerous groups of organisms introduced, and are mostly represented by insects (Roques et al., 2009). An exponential increase of the number of established species is currently being witnessed, and it is expected to continue in relation to globalization and expanding commerce (Roques et al., 2009). Climatic conditions made it so that only very few exotic ant species have become established outside heated buildings in Central and Northern Europe (Seifert, 2018). On the contrary, Mediterranean Europe has seen dozens of

exotic ant species establishing during the last 200 years in non-heated and even undisturbed natural ecosystems. The Mediterranean basin was recognized as one of the twenty-five biodiversity hotspots worldwide (Myers et al., 2000), and it is host to a rich ant fauna (Borowiec, 2014). Its invasion by the exotic Argentine ant, *Linepithema humile* (Mayr, 1868), one of the worst invasive aliens in the world according to Lowe et al. (2000), attracted alone dozens of studies, making *L. humile* the single most-studied ant species of the entire region (e.g. Giraud et al., 2002; Espadaler & Gómez, 2003; Gómez et al., 2003; Rey & Espadaler, 2004; Blancafort & Gómez, 2005; 2006; Carpintero et al., 2005; 2014; Jacquiery et al., 2005; Oliveras et al., 2005a; 2005b; Wetterer & Wetterer, 2006; Abril et al., 2007; 2010; 2013; Carpintero & Reyes-López, 2008; Blight et al., 2009; 2010; 2012; Roura Pascual et al., 2009a; 2009b; 2010; Pons et al., 2010; Estany-Tigerström et al., 2010; Abril & Gómez, 2011; Angulo et al., 2011; Diaz et al., 2014; Centorame et al., 2017; Queiroz & Alvez, 2018). Displacement of native ants and significant changes in the native ant communities are among the most commonly documented consequences of ant invasions, but in many cases notable effects have been also reported in regard to other invertebrates, vertebrates and plants (Holldöbler & Wilson, 1990; Holway et al., 2002; Lach et al., 2010).

Currently, records of exotic species in Mediterranean Europe come from a large number of different published studies, including only very few updated syntheses at national level (Salata et al., 2017; Blatrix et al., 2018). No comprehensive look at the exotic ants issue at regional or continental levels has ever been taken, while the same was done in case of organisms whose ecological impacts have been much less documented (e.g. Nentwig, 2015).

Materials and methods

A 'practical' definition of Mediterranean Europe was given: the sum the European territories of all the countries of the Mediterranean region (see Myers et al., 2000 for the region geographic definition), excluding the microstates (e.g. San Marino), was considered (Fig 1). Following this definition, Albania, Bosnia and Herzegovina, Croatia, France, Greece, Italy, Montenegro, Portugal, Slovenia, Spain and Turkey are the nations whose territories are included at least in part.

These territories are not entirely characterized by a Mediterranean climate, especially in the case of France, whose vast majority is not. However, since the non-Mediterranean areas are usually not witnessing significant exotic ant invasion processes, the European territories of these nations are simplistically considered in their entirety instead of being divided in Mediterranean and non-Mediterranean areas. Moreover, in order to facilitate the distinction of exotic from native species, especially in regard to the intra-Mediterranean exotics, all the Mediterranean islands that belong to these countries were excluded with the exceptions of the very large Corsica, Crete, Sardinia and Sicily. The hundreds of smaller islands of the Mediterranean basin are in fact mostly little-known from a myrmecological standpoint, and only very few were studied with particular regard to the exotic species (e.g. the Balearic Islands by Gómez & Espadaler, 2006).

The existing published studies which contain data on exotic ant species in these areas were the main source of data for this study, particularly those which published the first records of certain taxa for a geographic area (Nylander, 1856; Emery, 1869; Korlević, 1886; Mantero, 1908; Forel, 1911; Emery, 1916; Marchal, 1917; Bondroit, 1918; Paoli, 1920; Santschi, 1925; Zimmerman, 1934; Frisque, 1935; Donisthorpe, 1950; Schmitz, 1950; Ceballos, 1956; Bernard, 1968; Espadaler, 1979; Süss, 1979; Acosta & Martinez, 1983; Agosti & Collingwood, 1987; Bolton, 1987; Ortiz & Tinaut, 1987; Kugler, 1988; Poldi et al., 1995; Collingwood & Prince, 1998; Espadaler, 1999; Bračko, 2000; Espadaler & Collingwood, 2000; Seifert, 2000; Espadaler & Espejo, 2002; Seifert, 2003; Reyes & Espadaler, 2005; Aktaç & Kiran, 2006; Galkowski, 2008; Jucker et al., 2008; Reyes-López et al., 2008; Ugelvik et al., 2008; Boieiro et al., 2009; Casevitz-Weulersse & Galkowski, 2009; Legakis, 2011; Borowiec & Salata, 2012; Obregón Romero & Reyes López, 2012; Sanchez-Garcia & Espadaler, 2015; Espadaler & Pradera, 2016; Salata et al., 2017; Blatrix et al., 2018; Espadaler et al., 2018; Schifani & Alicata, 2018). Exotic ant species that quickly vanish from the areas where they are introduced are unlikely to have any significant impact on native ecosystems. Therefore, only most likely established species were considered in this study. The eventual other published records of the same species after its first discovery in a region, as well as regional and national checklists, were consulted in order to determine if each species was to be considered probably still established or not, and which kind of habitats it had occupied. Whenever no published indication could be found to confirm the surviving of an introduced population, the latter was considered extinct if

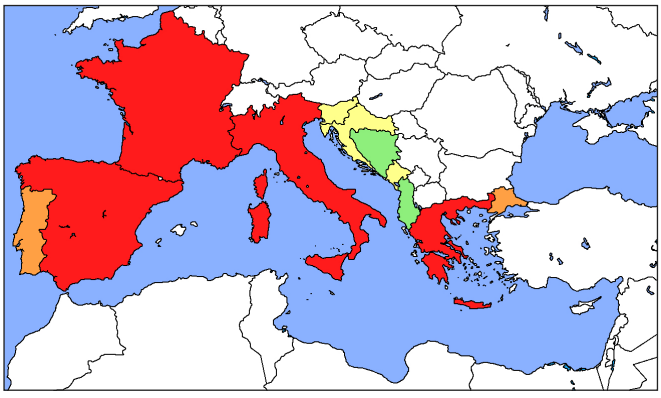

Fig 1. Map of the Mediterranean region. The areas not considered in this study are left blank. Areas hosting no exotic ant species are marked in green, areas hosting a single exotic ant species are marked in yellow, areas hosting 4-7 exotic ant species are marked in orange, the remaining countries, hosting 14-21 exotic ant species, are marked in red.

more than 15 years had passed without further records after the first, otherwise it was considered established unless published information explicitly suggested differently. Finally, species only recorded at their very first arrival sites (e.g. most of those recorded by Jucker et al., 2008) were not counted, as these introductions are mostly extremely temporary. Antmaps (Janicki et al., 2016) was also often consulted.

Results and Discussion

A total of 40 different species, belonging to 17 genera and four subfamilies, originating from five biogeographical realms, were found to be currently considered to be present as exotic in Mediterranean Europe and recorded since the second half of the 19th century. The prevalent genera are *Nylanderia* Emery, 1906 and *Tetramorium* Mayr, 1855 with 5 species each. The count also includes three provisionally unnamed morphospecies whose identity still needs to be ascertained (*Brachymyrmex* sp. from France and *Nylanderia* spp. from Italy – see Blatrix et al., 2018; Schifani & Alicata, 2018) and a dubious identification (*Tetramorium* cf. *simillimum* (Smith, F., 1851) from France – see Blatrix et al., 2018).

Four relatively well-studied countries (France, Greece, Italy and Spain) are characterized by four relatively rich lists of exotic species (Table 1, Fig 1), and similar incremental trends across the decades (Fig 2). Although some of the more recently introduced species may not manage to establish durable populations (thus lowering the '2000' peaks in Fig 2), the vast majority of them are already known as very successful tramp species across other regions of the world (see Antmaps). France is distinguished among the four countries by its comparatively smaller number of exotic species established outdoor (only about 27% of the list, while 73% to 90% in the others), most-likely due to the fact that only a very small part of its territory belongs to the Mediterranean climatic region. In these four countries, the exotic species number represent approximately around 4.5-7.5% of the entire myrmecofauna present. The Afrotropical realm is always the most important source of species, while the rest of the species origins are mostly divided between the Palearctic, Indomalayan and Neotropical realms (Fig 3). Such pattern is significantly different compared to the one at a global scale (McGlynn, 1999). It is important to note that many of these species are currently widespread across the globe due to human introductions, so that they may have easily been introduced to Europe from areas outside their native range. Five exotic species are actually shared by these four countries (*Hypoponera punctatissima* (Roger, 1859), *Linepithema humile*, *Monomorium pharaonis* (Linnaeus, 1758), *Paratrechina longicornis* (Latreille, 1802), *Tetramorium bicarinatum* (Nylander, 1846)), while four others are present in only three of them (*Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, 1990, *Nylanderia jaegerskioeldi* (Mayr, 1904), *Pheidole indica* Mayr, 1879, *Strumigenys membranifera* Emery, 1869). In Greece, the presence of *L. neglectus* was initially supposed to be incorrectly recorded due to misidentification with the native *L. turcicus* Santschi, 1921 (Borowiec & Salata, 2012). Later, the same authors reported to have collected material of both species (Borowiec & Salata, 2013; Salata & Borowiec, 2018) and the situation remained unresolved as the two may be conspecific (Borowiec & Salata, 2017a). In any case, *L. neglectus* was listed as a non-exotic species in Greece lately (Salata et al., 2017; Salata & Borowiec, 2018).

The Sørensen–Dice coefficient was used in order to compare the list of these four species-rich countries (Table 2). Very different results were obtained if the comparison was made between all the exotic species of each country, only between those species that managed to establish outdoor or only between those able to colonize non-urban habitats. In any case, the coefficient values that were obtained do not show any strong biogeographic pattern of colonization: neighboring countries do not necessarily show a higher degree of similarity than geographically more distant countries do, suggesting that species often spread through multiple introduction events.

Portugal, whose fauna is usually regarded as relatively much less explored than that of neighboring Spain (Boieiro et al., 2009; Borowiec & Salata, 2017b) hosts a total of seven exotic species, all shared with Spain with the exception of *Strumigenys silvestrii* Emery, 1906. The exotic ant fauna of Turkish Thrace (Kiran & Karaman, 2012), a relatively small region, only counts three species, all shared with neighboring Greece, with the exception of *N. vividula*, which is probably absent from Greece according to Salata et al., 2017. Only *M. pharaonis*, long regarded as the most ubiquitous household ant in the world (Wetterer, 2010), is known in Croatia (Bračko, 2006), Montenegro (Karaman, 2011) and Slovenia (Bračko, 2007).

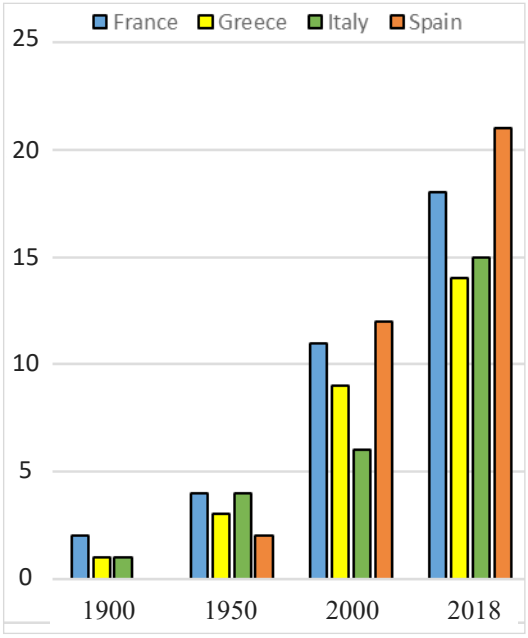

Fig 2. Number of exotic ant species known in France (Corsica, mainland), Greece (Crete, mainland, Peloponnese), Italy (mainland, Sardinia, Sicily) and Spain (mainland) since the beginning of the 1900th century.

Table 1. Exotic ant species established or seemingly established in France (Corsica, mainland), Greece (Crete, mainland, Peloponnese), Italy (mainland, Sardinia, Sicily) and Spain (mainland). The first confirmed record of the species in each country is presented on the right of the species name. Species that have been found outdoors are marked in yellow, species that have also colonized areas outside urban contexts are marked in red.

Species	Croatia	France	Greece	Italy	Montenegro	Portugal	Slovenia	Spain	Turkish Thrace
Aphaenogaster splendida (Roger, 1859)			Roger, 1859						
Brachymyrmex sp.		Blatrix et al., 2018							
Brachymyrmex patagonicus Mayr, 1868								Espadaler & Pradera, 2016	
Camponotus atriceps (Smith, F., 1858)				Jucker et al., 2008					
Cardiocondyla emeryi Forel, 1881								Reyes-López et al., 2008	
Cardiocondyla mauritanica Forel, 1890			Seifert, 2003			Seifert, 2003		Ortiz & Tinaut, 1987	
Cardiocondyla obscurior Wheeler, W.M., 1929								Sanchez-Garcia & Espadaler, 2015	
Hypoponera eduardi (Forel, 1894)			Borowiec & Salata, 2012						Agosti & Collingwood, 1987
Hypoponera ergatandria (Forel, 1893)		Bernard, 1968							
Hypoponera punctatissima (Roger, 1859)		Bernard, 1968	Agosti & Collingwood, 1987	Emery, 1916		Collingwood & Prince, 1998		Ceballos, 1956	
Lasius neglectus Van Loon, Boomsma & Andrasfalvy, 1990		Seifert, 2000		Poldi et al., 1995				Espadaler, 1999	
Lepisiota syriaca (André, 1881)			Stitz, 1928						
Linepithema humile (Mayr, 1868)		Marchal, 1917	Bernard, 1968	Paoli, 1920		Schmitz, 1950		Frisque, 1935	
Monomorium bicolor Emery, 1877			Agosti & Collingwood, 1987						
Monomorium carbonarium (Smith, F., 1858)		Galkowski, 2008				Collingwood & Prince, 1998		Espadaler & Collingwood, 2000	
Monomorium monomorium Bolton, 1987			Forel, 1911						
Monomorium pharaonis (Linnaeus, 1758)	Korlevic, 1886	Nylander, 1856	Bolton, 1987	Mantero, 1908	Zimmermann, 1934	Collingwood & Prince, 1998	Bračko, 2000	Santschi, 1925	Aktaç & Kiran, 2006
Nylanderia jaegerskioeldi (Mayr, 1904)			Borowiec & Salata, 2012	Schifani & Alicata, 2018		Obregón Romero & Reyes López, 2012		Espadaler & Collingwood, 2000	
Nylanderia vividula (Nylander, 1846)		Bernard, 1968						Espadaler & Collingwood, 2000	Donisthorpe, 1950
Nylanderia sp. 1				Schifani & Alicata, 2018					
Nylanderia sp. 2				Schifani & Alicata, 2018					

Table 1. Exotic ant species established or seemingly established in France (Corsica, mainland), Greece (Crete, mainland, Peloponnese), Italy (mainland, Sardinia, Sicily) and Spain (mainland). The first confirmed record of the species in each country is presented on the right of the species name. Species that have been found outdoors are marked in yellow, species that have also colonized areas outside urban contexts are marked in red. (Continuation)

Species	Croatia	France	Greece	Italy	Montenegro	Portugal	Slovenia	Spain	Turkish Thrace
Paratrechina longicornis (Latreille, 1802)		Nylander, 1856	Kugler, 1988	Süss, 1979				Espadaler & Collingwood, 2000	
Pheidole anastasii (Emery, 1896)		Bernard, 1968							
Pheidole bilimeki Mayr, 1870		Casevitz-Weulersse & Galkowski, 2009							
Pheidole indica Mayr, 1879			Legakis, 2011	Schifani & Alicata, 2018				Acosta & Martinez, 1983	
Pheidole megacephala (Fabricius, 1793)		Bernard, 1968						Espadaler & Pradera, 2016	
Plagiolepis alluaudi Emery, 1894		Blatrix et al., 2018							
Strumigenys membranifera Emery, 1869			Agosti & Collingwood, 1987	Emery, 1869				Espadaler, 1979	
Strumigenys silvestrii Emery, 1906						Boieiro et al., 2009			
Tapinoma melanocephalum (Fabricius, 1793)		Casevitz-Weulersse & Galkowski, 2009						Espadaler & Espejo, 2002	
Technomyrmex difficilis Forel, 1892		Blatrix et al., 2018							
Technomyrmex pallipes (Smith, F., 1876)				Jucker et al., 2008					
Technomyrmex vitiensis Mann, 1921		Blatrix et al., 2018							
Temnothorax longispinosum (Roger, 1863)								Espadaler & Collingwood, 2000	
Tetramorium bicarinatum (Nylander, 1846)		Bondroit, 1918	Salata et al., 2017	Jucker et al., 2008				Reyes & Espadaler, 2005	
Tetramorium caldarium (Roger, 1857)								Reyes & Espadaler, 2005	
Tetramorium lanuginosum Mayr, 1870				Schifani & Alicata, 2018				Reyes & Espadaler, 2005	
Tetramorium lucayanum Wheeler, W.M., 1905				Jucker et al., 2008					
Tetramorium cf. simillimum (Smith, F., 1851)		Bernard, 1968							
Wasmannia auropunctata (Roger, 1863)								Espadaler et al., 2018	

No exotic species is currently recorded in Albania and Bosnia and Herzegovina. Such condition of these countries, confirmed in the aforementioned relatively recent checklists, may partly be explained by a lack of targeted searches but may also be partly related to the recent history of the former Yugoslavia, and certainly requires further investigations.

No species were found to be considered exotic in any of the four large islands included in this study while at the same time being considered native in the respective country's mainland or vice-versa.

Some species seem to differ in their invasion success across different countries examined: the same species may be restricted to indoor habitats in a country, be present outdoor but only in anthropogenic habitats in another, and to be present in semi-natural or even natural-habitats in a third one. Such differences can be related to many factors, including environmental aspects and priority effects in the area where the species were introduced, genetic variability and consistence of the introduced population and time-related effects, since many invasion processes are known to be subject to a variety of lag phenomena (Crooks, 2005). While only a small portion of the exotic ants listed in Tab. 1 are considered significantly threatening to semi-natural and natural ecosystems in the Mediterranean basin (*Lasius neglectus* and *Linepithema humile* above all), some others have aroused different levels of concern in different countries. For example, *Tetramorium bicarinatum*, first recorded in the Mediterranean region by Bondroit (1918), is globally considered a low threat (Wetterer, 2009), and usually restricted to indoor areas. However, it has lately started to be reported in outdoor urban contexts in Spain (Reyes & Espadaler, 2005), Italy (Borowiec & Salata, 2015; Schifani & Alicata, 2018) and Greece (Salata et al., 2017). Moreover, in Greece it was also considered by Salata et al. (2017) among the three exotic species that displace native ants in the areas they occupy.

In general, the few species that successfully invaded large areas of outdoor habitats in all the countries considered in this study are mostly distributed in areas characterized by a strictly Mediterranean climate (e.g. Blatrix et al., 2018). A

Table 2. Sørensen-Dice coefficient between exotic ant species present in France – F (Corsica, mainland), Greece – G (Crete, mainland, Peloponnese), Italy – I (mainland, Sicily, Sardinia) and Spain – S (mainland) as defined in this study and listed in Table 1.

	All species	Species established outdoor	Species established outside urban habitats
F-G	31%	11%	0%
F-I	30%	37%	80%
F-S	46%	33%	60%
G-I	55%	54%	0%
G-S	51%	46%	13%
S-I	60%	60%	44%

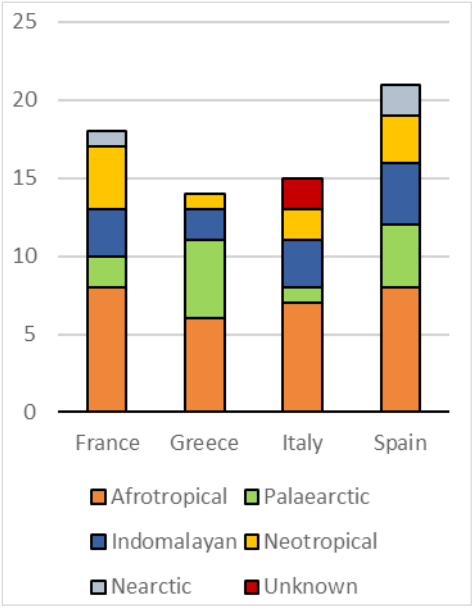

Fig 3. Geographic origin of the exotic ant species of France (Corsica, mainland), Greece (Crete, mainland, Peloponnese), Italy (mainland, Sardinia, Sicily) and Spain (mainland).

significant exception is that of *Monomorium carbonarium* (Smith, F., 1858), whose presence is mostly distributed along the Atlantic coast of France, while mostly along the Mediterranean in Iberia (Miravete et al., 2013).

Given the long history of human activities and commerce across the Mediterranean basin, many cases of old historical or pre-historical introductions have been detected for both animal and plant species. However, intra-Mediterranean or intra-Palearctic introductions of ants, usually much less obvious to detect than these of ants from other continents or latitudinal regions, actually represent a mostly unexplored topic. Some cryptic species belonging to the *Tapinoma nigerrimum* complex and the *Tetramorium caespitum* complex were only recently recognize as exotic in some or all of the countries in this study after the latest taxonomic advances (Seifert et al., 2017; Wagner et al., 2017). However, the time of their introduction is unknown and thus they were excluded from the present analysis. Another issue is that for a number of other Mediterranean species, there is no precise knowledge about where their native range ends and where the exotic range begins. For example, the status of *Cardiocondyla mauritanica* Forel, 1890 in Sicily is currently dubious (Schifani & Alicata, 2018): it is considered as an exotic species in Greece (Salata et al., 2017) and Spain (Reyes & Espadaler, 2005; Reyes-López et al., 2008), while as likely native to North Africa (Wetterer, 2012). In Sicily, it is found in both natural and anthropogenic habitats, and many species appear to be naturally present in both Sicily and North Africa (Alicata & Schifani, 2019). *Monomorium subopacum* (Smith, F., 1858) was considered as exotic in Greece by Salata et al. (2017), while it is usually considered native in the Mediterranean region, however it was removed in a more recent list by the same authors (Salata & Borowiec, 2018).

Aphaenogaster splendida (Roger, 1859) may be exotic at least in some parts of the Italian territory (Schifani & Alicata, 2018) and was only recently treated as an exotic species in Crete (Salata & Borowiec, 2018). Still, the definition of its native range remains unclear. Similarly, *Monomorium monomorium* Bolton, 1987 is considered as exotic in Greece (Salata & Borowiec, 2018) but it is usually considered native in Mediterranean Europe (e.g. Antmaps). *Hypoponera eduardi* is usually considered native to the Mediterranean, but it is regarded as exotic in Greece (Salata et al., 2017) and Turkey (Kiran & Karaman, 2012), although Lapeva-Gjonova and Kiran (2012) treat it as a rare species attributing conservation value to an area of Turkish Thrace. Another example can be provided by some forms related to *Lepisiota frauenfeldi* (Mayr, 1855), whose scattered distributions across the Mediterranean basin may suggest some of these populations are introduced, especially given the vast exotic range attained by *L. syriaca* (André, 1881) in Greece according to Salata et al. (2017) or the recent quick invasion of the Canary Islands by *L. frauenfeldi* cf. *kantarensis* (Forel, 1911) (Schifani et al., 2018). Molecular data may allow to shed light into this complex and mostly unexplored issue in the future, as in the case of *Anochetus ghilianii* Forel, 1915 in Southern Spain (Jowers et al., 2015).

Conclusions

The numerical increase of exotic ant species established in Mediterranean Europe during the last decades is impressive, and so is also the increasing rate at which they continue to be introduced. Nonetheless, other countries around the world are already dealing with much higher numbers of exotic species (e.g. Deyrup et al., 2000). The Balkan countries bordering the Adriatic Sea make an interesting exception in the region, which requires further investigation. It is impossible to predict which species are going to be successful invaders when they arrive, and the ongoing climate change further complicates this equation (Bertelsmeier et al., 2015). Moreover, existing data do not allow to attempt predictions on which species are going to be the next to be introduced in the region, especially that similarity between exotic ants assemblages is not always greater between neighboring countries. While our understanding of invasive ants has tremendously increased over the last decades, long-term effects and dynamics of the invasive populations are little-known since they are just starting to be observed (e.g. Tartally et al., 2016). Our knowledge also remains extremely scarce on those successful ants' introductions that have most likely occurred across the Mediterranean basin in historic and pre-historic times, and on their possible role in shaping the current faunas. The number of species which have caused serious damage and concerns in Mediterranean Europe remains relatively low for the time being. Still, the current situation is concerning for the equilibrium and management of natural and anthropogenic ecosystems in the future.

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