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Abstract

Invasive species are a major threat to biodiversity, likely a direct consequence of increasing globalization. Greece is situated on the crossroad between different continents, and has been invaded by several insect species in the past; nevertheless, a thorough investigation that would reveal and highlight the pathways and origins of insect species invasion has never been attempted. This study aims at filling this knowledge gap by providing a comprehensive review and in-depth analysis of the non-native entomofauna that has ever entered Greece. The role of neighbouring countries is likely significant, as is the unique features exhibited by each family, and these may help determine the progress of introduction (e.g. cryptic species, parthenogenetic reproduction, etc.). The flow of non-native species between Greece and its neighbouring countries over time shows some relationships with the historical course of turmoil in the region, highlighting for the first time a relation that has long been overlooked but nonetheless is of great economic importance.

Key words: terrestrial insects, invasive species, non-native species, Greece, Balkans, economic impact.

Introduction

Species adapt to changing environmental conditions by shifting their ranges, either by expanding into new territories or by retreating to remaining suitable areas (Huntley, 2007; Loarie *et al*., 2009; Pimm, 2009; Sahney *et al*., 2010; Pimm *et al*., 2014). Historically, species' natural movement affected primarily neighbouring areas that shared borders and therefore the impact on local biodiversity usually remained negligible, as non-native species were frequently detected promptly (Gillespie and Roderick, 2002; Gaston *et al*., 2003). This equilibrium has been distorted over the last few decades, as globalization and world-wide commodity movement have facilitated the rapid introduction of non-native species to the biota of easily-accessible and remote areas with consequences that scientists still struggle to measure (Hulme *et al*., 2008; Walther *et al*., 2009; Roques, 2010a; Keller *et al*., 2011; Seebens *et al*., 2017).

Although the effect of non-native species has long been universally recognized as negative (Pimentel *et al*., 2005; Vilá *et al*., 2009; Bradshaw *et al*., 2016; Early *et al*., 2016; Paini *et al*., 2016), little attention has been given to these species in Europe (Hulme *et al*., 2009; Kenis *et al*., 2009). Until the early 2000s, no comprehensive checklist of non-native terrestrial insects was available in any European country. To that end, the DAISIE project (Delivering Alien Invasive Species Inventories for Europe; http://www.europe-aliens.org/) was launched in February 2005 by the European Union. This project ran for three years, and by November 2008 more than 10.000 non-native species had been recorded, providing for the first time a thorough and detailed overview of the status of non-native species in Europe (Hulme and Roy, 2010). This database provides historical invasion data at the country level for all species introduced to Europe after 1700 (DAISIE, 2009). Terrestrial arthropods (mostly insects) comprised 23% of these species (Roques, 2010b). Concurrent with the DAISIE effort, several studies emerged focusing on invasive phytophagous insects that infest woody plants in Europe (e.g. Mattson *et al*., 2007, Kirkendall and Faccoli, 2010). More recently, the EASIN catalogue (European Alien Species Information Network; http://easin.jrc.ec.europa.eu/) provided year and country of a species' first record in Europe (Katsanevakis *et al*., 2015).

Historically, knowledge of non-native arthropod species in Europe was limited, as few countries had an official checklist of non-native arthropod species prior to DAISIE (e.g. Tomov *et al*., 2007). In Greece, terrestrial arthropods were largely neglected with the exception of occasional reports of new non-native species (e.g., Anagnou-Veroniki *et al*., 2008). As a result, the only checklists that presented insects of Greece involved predominantly the native entomofauna (Kailidis, 1991; Avtzis and Avtzis, 2001; Avtzis *et al*., 2013). Exploring the records of DAISIE and EASIN databases, our investigation provides the first comprehensive list of the non-native insect species of Greece and its neighbouring countries. Understanding that non-native species cannot (and should not) be handled only as raw numbers, we employed a region-wide analysis of the species that invaded Greece and its neighbouring countries in an attempt to better comprehend the impact that national borders exert on the occurrence and dispersal of non-native species.

The non-native entomofauna of Greece

We extracted the current distribution of all non-native insects known to have established in Greece from the DAISIE and EASIN databases covering every record from the 15th century until the December of 2014. Only species which are non-native to all of Europe (including the Canary Islands and Madeira) were included in the current investigation, excluding species whose native distribution included part of the European continent. Following the methodological approach employed by DAISIE, a proxy was used for the date of first arrival (the single temporal datapoint first obtained) as in many cases there was a delay (3-5 years) until the first report (Herard *et al*., 2006). A total of 266 non-native insect species were established in both continental Greece and the Greek islands (supplemental material table S1) whereas in the same time period, 1418 species were established in Europe (Roques *et al*., 2016). The vast majority (255 spp., 96%) were found on the Greek mainland with few non-native insect species (11 spp.) detected only on the Greek islands. Among the islands, most records were made in Crete, an unsurprising finding considering Crete is the largest and most populated island, with an active harbour that facilitates the transport of goods and tourists. The number of detected non-native species of Greece is significantly lower compared to some European Union countries (e.g. Italy, 700 species; France, 690 species) (Roques, 2010b). Nevertheless, when examining the correlation between the number of non-native species of a given country and its size, the colonization of Greece's mainland by non-native insects becomes comparable to the aforementioned countries, with Greece's mainland (131,957 km^2) being ca. 4.2 times smaller than continental France (551,500 km^2) and ca. 2.3 times smaller than continental Italy (301,337 km^2) ($r = 0.3621$, $P = 0.0384$; Roques, 2010b). Positive relationships exist between the number of non-native species and the total volume of merchandise imports of the country ($r = 0.875$; $P < 0.0001$), the density of the road network ($r = 0.7578$; $P = 0.0001$), and the size of the human population ($r = 0.5918$; $P = 0.0047$), underlining the influence of anthropogenic drivers in the expansion of non -native species (Roques, 2010b).

Taxonomy of non-native species

The non-native insect fauna of Greece includes 266 species from 78 families and 10 orders (Supplemental material table S2). The six most abundant families contained 104 species (about 40%), while the remaining 162 species were distributed among 72 families. This pattern was also consistent at the European level, where species numbers are unevenly distributed across the families (Roques, 2010b).

The number of native and non-native species per insect order in Greece was positively correlated ($r^2 = 0.4767$, $P = 0.0045$) (figure 1). Hemiptera contained the majority of non-native species (88 species, 33%), followed by Coleoptera (61 species, 23%) and Hymenoptera (58 species, 22%) (table 1). Six families contained more than 10 species each (Chrysomelidae, Aphididae, Coccidae, Diaspididae, Aphelinidae, Encyrtidae; table 1), comprising about 40% of the total non-native species of Greece.

In Europe as a whole (Roques, 2010b), non-native hemipteran species in Greece are proportionally far better represented (three times more) in non-native compared to the native entomofauna. This is also the case, but to a lesser extent, for Hymenoptera. Despite this commonality between these two orders, the reason for this trend is likely completely different. While most non-native hymenopteran species (37 species in total) have been intentionally introduced for biological control (e.g. the lepidopteran egg parasite, *Trichogramma pretiosum* Riley; the olive scale parasite, *Coccophagoides utilis* Doutt; and the whitefly parasite, *Eretmocerus eremicus* Rose et Zolnerowich), non-native hemipterans have almost exclusively been unintentionally introduced to new countries. Commonly introduced hemipterans, such as scales, aphids, and adelgids, are small, cryptic,

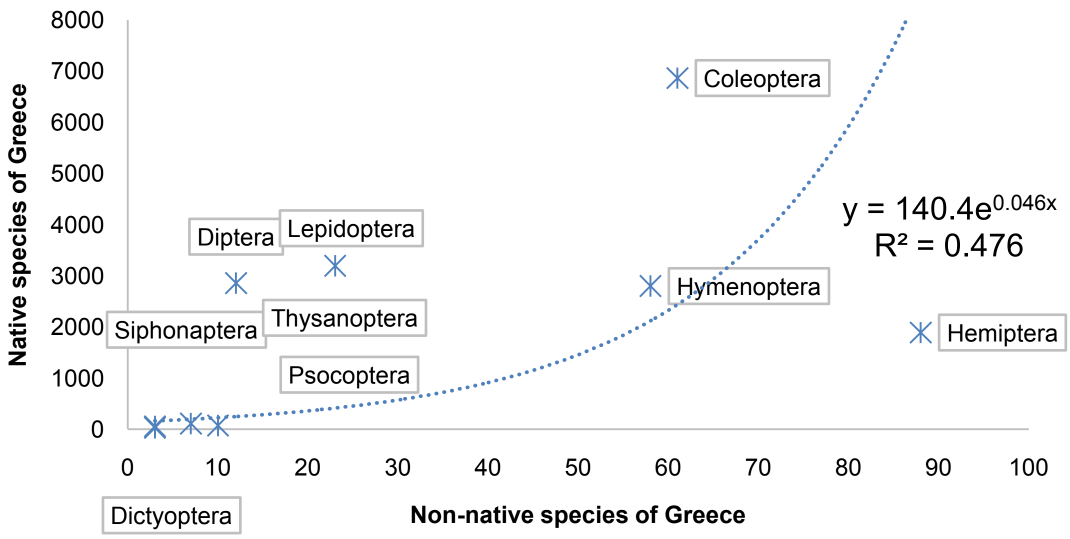

Figure 1. Scatterplot of the number of native and non-native species in Greece.

Table 1. Number of the non-native species of Greece per order and family.

Order Family	Species
Diptera	
Agromyzidae	2
Braulidae	1
Cecidomyiidae	3
Culicidae	2
Drosophilidae	2
Muscidae	1
Sphaeroceridae	1
Coleoptera	
Anobiidae	5
Anthicidae	2
Apionidae	1
Bostrichidae	2
Carabidae	1
Cerambycidae	3
Chrysomelidae	12
Ciidae	1
Coccinellidae	6
Cryptophagidae	2
Dryophthoridae	1
Hydrophilidae	2
Laemophloeidae	3
Latridiidae	2
Lyctidae	1
Nitidulidae	8
Silvanidae	1
Staphylinidae	2
Tenebrionidae	6
Hymenoptera	
Aphelinidae	18
Agaonidae	1
Braconidae	4
Ceraphronidae	1
Chalcididae	1
Cynipidae	1
Encyrtidae	11
Eulophidae	4
Eurytomidae	1
Formicidae	7
Figitidae	1
Pteromalidae	3
Siricidae	1
Tenthredinidae	1
Trichogrammatidae	3
Dictyoptera	
Blatellidae	1
Blattidae	2
Hemiptera	
Aleyrodidae	3
Anthocoridae	1
Aphididae	34
Coccidae	10
Coreidae	1
Diaspididae	19
Eriococcidae	2
Flatidae	1
Margarodidae	1
Miridae	2
Pentatomidae	1
Phylloxeridae	1
Pseudococcidae	6
Psyllidae	2
Reduviidae	2
Tingidae	2
Lepidoptera	
Arctiidae	1
Castniidae	1
Gelechiidae	4
Gracillariidae	3
Noctuidae	1
Nymphalidae	1
Pyralidae + Crambidae	8
Tineidae	2
Tortricidae	1
Yponomeutidae	1
Phthiraptera	
Linognathidae	1
Psocoptera	
Ectopsocidae	2
Liposcelididae	4
Psyllipsocidae	1
Trogiidae	3
Siphonaptera	
Ceratophyllidae	2
Pulicidae	1
Thysanoptera	
Phlaeothripidae	2
Thripidae	5

and extremely difficult to detect (e.g. Roques, 2010b). These insects usually arrive in a new country as an accidental side effect of global trade, and may have extremely ecologically or economically detrimental impacts on the local environment [e.g. the jumping plant louse, *Acizzia jamatonica* (Kuwayama); and the citrus flatid planthopper, *Metcalfa pruinosa* (Say)]. On the contrary, taxa that were more frequently intercepted (e.g. Cerambycidae, Curculionidae: Scolytinae) had little contribution to the established entomofauna (Kenis *et al*., 2007), possibly related with the ease of prompt detection. Nevertheless, despite the ease of detection, Chrysomelidae and Bruchidae contain several major agricultural and seed pests that have caused severe damage in several crops [e.g. *Leptinotarsa decemlineata* (Say), *Diabrotica virgifera* LeConte, *Callosobruchus* spp.] (Jolivet and Verma, 2002).

The orders Coleoptera, Lepidoptera and Diptera contribute slightly less to the non-native entomofauna compared to their proportion in the native fauna. This outcome could be possibly attributed to slight differences in the establishment patterns among insect orders (e.g. voltinism), as it has already been suggested (Roques *et al*., 2009). The least diverse order in our study is Diptera, with 1.7 species per family (12 species in 7 families), whereas this ratio is tripled in Hemiptera (5.5 species/family), with 88 species clustered in only 16 families. Siphonaptera, Dictyoptera and Phthiraptera cannot be directly compared with the other orders, as the number of families and species detected is low (table 1).

Feeding behaviour and habitat selection of non-native species

Over half of the non-native insect species of Greece are phytophagous, and within a feeding guild certain taxa tend to be more common (table 2). For example, parasitic species are almost predominantly Hymenoptera, with only few species of Coleoptera and Diptera sharing the same behaviour. Non-native Diptera are mostly phytophagous, with *Obolodiplosis robiniae* (Haldeman) being the most recent addition to this list (Duso and Skuhrava, 2003). Beetles are mostly detritivorous and phytophagous, with few being predators (e.g. the Harlequin ladybug that is commonly employed against aphids) (Majerus *et al*., 2006). One of the most iconic and interesting examples of phytophagous beetles is the red palm weevil, *Rhynchophorus ferrugineus* (Olivier). As Roques (2010a) has shown, its introduction to Greece coincided with the 2004 Olympic Games, which were held in Athens, when palm trees already colonized by the weevil (but unknown to the workers) were imported in large numbers from other European Union countries. Shortly thereafter, the red palm weevil successfully colonized the entire Eastern Mediterranean basin (Kontodimas *et al*., 2006), posing a deadly threat to the endangered and endemic date palm (*Phoenix theophrasti* Greuter) in Crete.

In compliance with the classification of habitats made by the European Nature Information System (EUNIS) level 1 (Davies *et al*., 2004) that has already been used in several different studies (DAISIE, 2009; Pyšek *et al*., 2010) and adapted to the needs of DAISIE database (Lopez-Vaamonde *et al*., 2010a), non-native insect species occurring in Greece were assigned to the following habitat categories: urban settlements; greenhouse settlements; building and houses; parks and gardens; agricultural and horticultural lands; inland without vegetation; woodlands and forests; heathland, scrub, and tundra habitats; grassland and tall forb habitats; wetlands and riparian habitats; coastal habitats. Non-native species show a strong affinity for human-influenced habitats, such as greenhouses, parks and gardens, urban areas, nurseries/horticultural areas, and agricultural lands (figure 2). Altogether, human-influenced habitats host

Table 2. Feeding behaviour of the non-native insect species of Greece.

Order	Phytophagous	Detrivorous	Parasitic	Unknown
Diptera	8	1	3	0
Coleoptera	28	28	11	2
Dictyoptera	0	3	0	0
Hemiptera	84	0	4	0
Hymenoptera	6	0	52	0
Lepidoptera	16	7	0	0
Phthiraptera	0	0	1	0
Psocoptera	0	10	0	0
Siphonaptera	0	0	3	0
Thysanoptera	7	0	0	0
Total	149	49	74	2

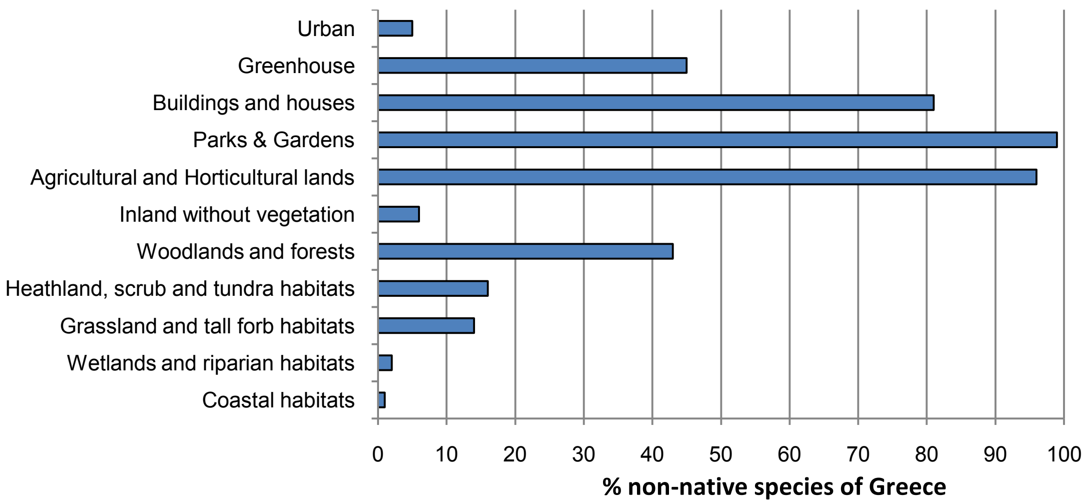

Figure 2. Main habitats colonized by non-native species of Greece.

more than 75% of the non-native entomofauna of Greece, most of which occur in multiple habitats. A similar affinity of non-native species has been observed even within Europe as a whole (Roques *et al*., 2009; Lopez-Vaamonde *et al*., 2010b).

Origin and temporal trends of the non-native species in Greece

Though more than 75% of the non-native entomofauna species in Greece originate from Asia, Australasia, and North America, the five most common insect orders do not originate from all regions evenly (table 3). While most Diptera have arrived from North America (42%), Asia is the most common origin of Coleoptera (28%), Lepidoptera (26%), Hymenoptera (29%), and Hemiptera (36%), a possible side-effect of the increased trade occurring in the last decades between European and Asian countries. In fact, certain countries are more likely to export products harbouring non-native species than others (Brenton-Rule *et al*., 2016); this is likely related to a country's regulatory emphasis on exports. With 246 first records of invading species but also based on related investigations (Jucker and Lupi, 2011), Italy, being an important commercial and touristic hub in the Mediterranean Sea, seems to be the main entry country of non-native species in Europe. For Greece in particular, 73 non-native insect species were first detected in Italy (27.4%), rendering Italy the most common origin of non-native species for Greece (table 4).

In the first half of the 20th century, Europe was ravaged by two world wars (1914-1918 and 1939-1945); consequently, careful recording of non-native species was a very low (probably non-existent) priority. In addition, the general condition of the continent did not particularly favour the strengthening of transnational interactions, and this may have affected the non-native species records. In the period that followed (1950-1974), but even more so after the 1990s, the number of non-native insect species recorded in Europe has shown a remarkable increase - one that could be linked with the combined effects of the political and socioeconomic changes in Eastern Europe, the release of the internal borders within the enlarged European Union, and the continuous increase in trade of ornamental plants (Roques *et al*., 2016). Weaker regulatory authority by exporting countries and an increase in trade of ornamental plant material have been shown to increase the likelihood of non-native species introductions (Liebhold *et al*., 2012; Brenton-Rule *et al*., 2016). For Greece, the trend is similar, though at a lower scale, as the country

Table 3. Origin of the non-native species of Greece.

Family	Non-native species	Africa	Asia	Australasia	North America	South America	Tropical	Cryptogenic
Diptera	12	2	2	0	5	1	0	2
Coleoptera	61	10	17	8	4	7	3	12
Dictyoptera	3	2	0	0	0	0	0	1
Hemiptera	88	7	32	4	21	7	8	9
Hymenoptera	58	16	17	3	12	3	1	6
Lepidoptera	23	3	6	2	1	3	1	7
Phthiraptera	1	0	0	0	0	0	0	1
Psocoptera	10	0	0	0	0	0	0	10
Siphonaptera	3	1	1	0	0	0	0	1
Thysanoptera	7	2	1	1	1	1	0	1
Total	266	43	76	18	44	22	13	50

Table 4. Countries from where the non-native species of Greece originate.

Family	Total	Albania	Austria	Belgium	Bulgaria	Croatia	Czech Rep.	Cyprus	France	Germany	Great Britain	Greece	Hungary	Iceland	Italy	Lithuania	Malta	Netherlands	Poland	Portugal	Romania	Russia	Serbia	Slovenia	Spain	Sweden	Swiss	Unknown
Diptera	12	2							3		1				2			1							1			2
Coleoptera	61			1	4	1	10		11	3	2	2		1	11	1				4	1		1		3			5
Dictyoptera	3						1			1					1													
Hemiptera	88								17	2	13	7	1		29			1		4		1			3		1	9
Hymenoptera	58		1		1		4	1	7	2	1	3	1	5	23				1	3					3			2
Lepidoptera	23									6	3		1		4		1			1				1	6			
Phthiraptera	1																											1
Psocoptera	10								2	3	2				1							1						1
Siphonaptera	3														2											1		
Thysanoptera	7		1					1	1	1		2						1										
Total	266	2	2	1	5	1	15	2	41	18	22	14	3	6	73	1	1	3	1	12	1	2	1	1	16	1	1	20

has actively participated not only in both world wars, but also in regional hostilities that preceded in the beginning of the 20th century (1912-1913: Balkan Wars). As a result, the trend in non-native insect species detection is low (0.92 species per year) until 1949, but accelerates during the last quarter of the 20th century when the rate is doubled (2.5 species per year).

The economic impact of ecological invasions

Besides the well-documented ecological impact of invasive species, the economic damage caused by pests invading new territories has also received much attention (Kenis and Branco, 2010; Kovacs *et al*., 2010; Paini *et al*., 2016). For Greece, a country experiencing an economic crisis since 2009, the additive impact of pest invasions together with the cost of pesticide control (Pimentel *et al*., 2005) further threaten any attempted financial recovery. For example, the introduction of the western corn rootworm beetle, *Diabrotica virgifera virgifera* LeConte (Coleoptera Chrysomelidae), in Europe has resulted in severe (up to 30%) losses in maize production (Sivcev and Tomasev, 2002). A very conservative estimate (using an average yield loss of 10%) of the potential pecuniary losses in a selection of countries could be up to 147 million €/ year (Baufeld and Enzian, 2005), while in Baden-Württemberg alone, about 20 million € would accumulate over a decade because of *D. virgifera virgifera* is present (Baufeld and Enzian, 2005). Predictive models forecast an economic impact of about 500 million €/ year in Europe (http://www.europe-aliens.org/pdf/Diabrotica_virgifera%20virgifera.pdf), and, consequently, Greece is expected to face respective damages in its annual production of 1.700 tons of maize. A similar impression comes from the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), that has been impacting tomato production for a decade. A pest risk analysis conducted by the Netherlands Food and Consumer Product Safety Authority in 2013 showed the direct economic consequences for Netherlands' tomato sector alone ranged from 5 to 25 million €/ year, while the cost for control and management of the pest amounts to about 4 million €/ year, in the worst-case scenario. In Greece, *T. absoluta* has been detected in several locations, indicating multiple introductions (Roditakis *et al*., 2010), and is now present in at least 10% of the greenhouse crops, potentially increasing the cost of cultivation by 1729-2470 €/ hectare (http://www.agrotypos.gr/index.asp?mod=articles&id=97172).

Non-native species of the southern Balkans

A constant exchange of organisms - including natural dispersal and human-aided movements - occurs among neighbouring countries, and this is reflected in the number of shared species (Supplemental material table S2). For example, Albania (56%) and Bulgaria (48%) have almost half of their non-native species in common with Greece. Former Yugoslavic Republic of Macedonia (FYROM) and Cyprus demonstrate a greater percentage (78% and 73%, respectively) of common species that nonetheless should be examined in context with the sampling effort of these countries. Closely examining the timeline of introduction events, it appears that Greece often acts as an intermediate country, with species arriving from Bulgaria, Albania, and FYROM, which are later transported to Cyprus. For example, the psyllid *A. jamatonica* that infests *Albizia julibrissin* Durazz. (Fabaceae Mimosoideae) was first detected in Italy in 2001 (Alma *et al*., 2002), and in the years that followed, rapidly expanded its range in Slovenia and Croatia (Seljak, 2003; Šimala *et al*., 2006), Serbia (Vétek *et al*., 2009), and finally appeared in Bulgaria in 2009 (Vétek and Rédei, 2009); in Greece, *A. jamatonica* was recorded two years later (Lauterer *et al*., 2011). The opposite direction of exchange seems to exist between Greece and Cyprus, as the example of the red palm weevil supports, as it was detected in Cyprus two years after Greece (Kontodimas *et al*., 2006).

Non-native insect species move throughout Greece and its neighbouring countries, and this rate seems to keep up with the events that defined the history of the region. The accelerating rate of common non-native species that emerged on the onset of the 20th century gradually declined as these countries entered a period of intense hostility (1925-1949). Even after 1950, as the general condition in Europe became more stable, the rate of shared non-native species continued to decline. This trend could be attributed to each country's different political regimes that may not have favoured commercial exchange among neighbouring countries. However, as the political affairs steadily improved and equilibrated, countries increased transnational interactions, something that is also evident from the peak that common non-native species experience (figure 3). Even though the most recent period (2000-2014) is shorter and thus the results cannot be directly compared to the previous periods, the trend therein seems to decline, a possible consequence of the intensification of surveys against the expansion of quarantine pests, which are now employed almost by every country.

Conclusions and future directions

The global impact of non-native species is estimated to be at least 66 million €/year, and increasing human populations and international trade will only cause this figure to increase (Bradshaw *et al*., 2016). And, while there is a nearly universal acceptance of the negative consequences of non-native species, there are still significant challenges to managing this issue, particularly on a landscape, ecosystem, or continental level.

Given the limited information available for some insect taxa - especially those without any measurable economic impact - and the absence of taxonomists in many areas - it is likely that the non-native entomofauna having colonized Greece and its neighbouring countries is still underestimated. Further, although the recent political stability seems to have reduced the rate at which species move among countries in this region, the con-

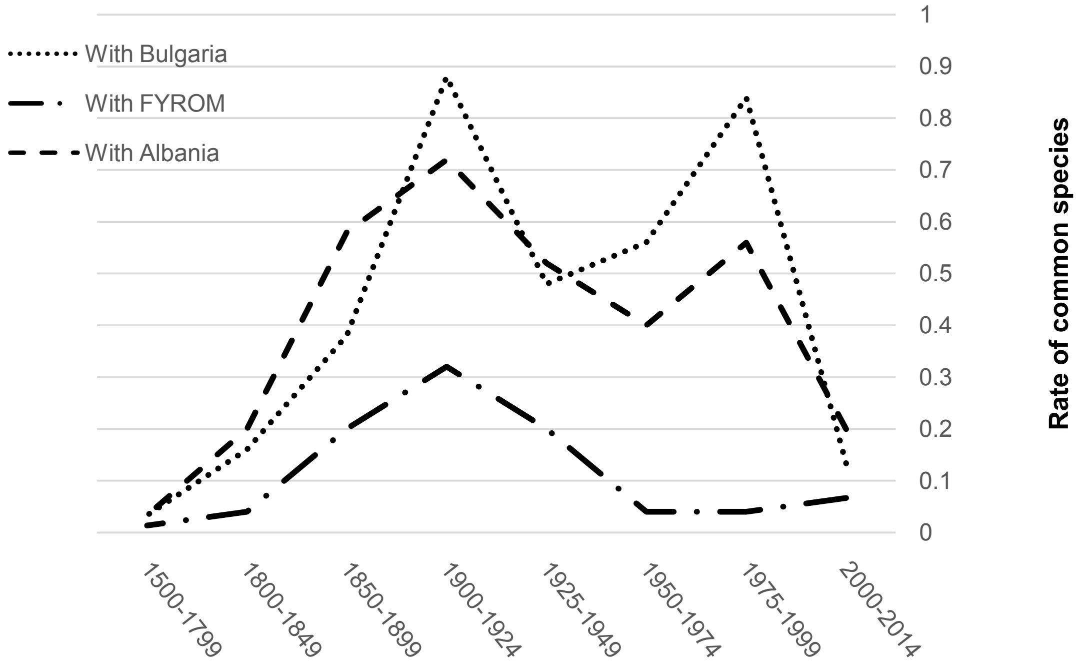

Figure 3. Rate of non-native species of Greece over time, shared with the three neighbouring countries of the Balkan peninsula.

stantly increasing worldwide trade (Hulme, 2009) and inconsistent inspection regimes at country borders (Bacon *et al*., 2012) remain major factors in the introduction of non-native species.

Certain countries (e.g. USA and Canada) have invested heavily in non-native species detection and management, while others (e.g. Greece) have not had the political stability to allocate an equivalent amount of resources to this issue. Further, in some areas of the world (e.g. parts of war-torn Africa) measuring the impact of non-native species is likely non-existent for obvious socioeconomic reasons. As a result, we now live in a world with varying levels of non-native species knowledge due to a multitude of factors. We do not know what an "appropriate" amount of emphasis or resources is toward this issue, nor do we know what factors most greatly impact the introduction of non-native species. Certainly international trade volume and common partners would be a factor, as would climate or ecoregion. A thorough evaluation of these factors, for countries in different socioeconomic or political stability levels, would be an excellent next step in the global management issue of non-native species.

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