REVIEW ARTICLE

Investigating plant–pollinator relationships in the Aegean: the approaches of the project POL-AEGIS
(The pollinators of the Aegean archipelago: diversity and threats)

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Summary

Worldwide, there is a well-documented crisis for bees and other pollinators which represent a fundamental biotic capital for wild life conservation, ecosystem function, and crop production. Among all pollinators of the world, bees (Hymenoptera: Apoidea) constitute the major group in species number and importance, followed by hover flies (Diptera: Syrphidae). The Aegean constitutes one of the world’s hotspots for wild bee and other pollinator diversity including flies (mainly hover flies and bee flies), beetles, and butterflies. Despite this advantage, our present knowledge on Greek pollinators is poor, due to a lack of focused and systematic research, absence of relevant taxonomic keys, and a general lack of taxonomic experts in the country. As a result, assessments of pollinator loss cannot be carried out and the causes for the potential pollinator loss in the country remain unknown. Consequently, the desperately needed National Red Data list for pollinators cannot be compiled. This new research (2012–2015) aims to contribute to the knowledge of the pollinator diversity in Greece, the threats pollinators face, as well as the impacts these threats may have on pollination services. The research is conducted in the Aegean archipelago on >20 islands and several mainland sites in Greece and Turkey. Prime goals are: i. the assessment of bee and hover fly diversity (species, genetic); ii. their pollination services; and iii. the effects of climate change, grazing, intensive bee-keeping, fires, electromagnetic radiation on bee diversity and ecology, as well as on plant–pollinator networks. At the same time, this research contributes to the taxonomic capital in Greece and the Eastern Mediterranean, focusing on the creation of the first identification keys for pollinators, the training of new scientists, as well as the enrichment and further development of the Melissotheque of the Aegean, a permanent reference collection of insect pollinators established at the University of the Aegean.
Investigando relaciones planta - polinizador en el Egeo: los enfoques del proyecto POL-AEGIS (Los polinizadores del archipiélago Egeo: diversidad y amenazas)

Resumen

En todo el mundo hay una crisis bien documentada para las abejas y otros polinizadores los cuales representan un capital biótico fundamental para la conservación de la vida silvestre, la función de los ecosistemas, y la producción de cultivos. Entre todos los polinizadores del mundo, las abejas (Hymenoptera: Apoidea) constituyen el grupo principal en cuanto al número de especies y su importancia, seguido por los sírfidos (Diptera: Syrphidae). El Egeo constituye uno de los puntos importantes de diversidad de abejas silvestres y otros polinizadores del mundo, incluyendo moscas (principalmente sírfidos y bomblídios), escarabajos y mariposas. A pesar de esta ventaja, los conocimientos actuales sobre los polinizadores griegos son reducidos, debido a la falta de una investigación focalizada y sistemática, la ausencia de claves taxonómicas pertinentes, y una falta general de expertos en taxonomía en el país. Como resultado, no se pueden llevar a cabo evaluaciones de la pérdida de polinizadores y las causas de la pérdida potencial de polinizadores en el país siguen siendo desconocidas. En consecuencia, la imperiosamente necesitaba Lista Roja de datos para polinizadores no se puede compilar. Esta nueva investigación (2012-2015) tiene como objetivo contribuir al conocimiento de la diversidad de polinizadores en Grecia, enfrentarse a las amenazas para los polinizadores, así como investigar el impacto que estos amenazas pueden tener sobre los servicios de polinización. La investigación se llevará a cabo en el archipiélago del mar Egeo en más de 20 islas y en varios sitios del continente en Grecia y Turquía. Los principales objetivos son: i. la evaluación de la diversidad de abejas y sírfidos (especies, genética); ii. sus servicios de polinización, y iii. los efectos del cambio climático, el pastoreo, la apicultura intensiva, los incendios y las radiaciones electromagnéticas sobre la diversidad de abejas y la ecología, así como en las redes planta-polinizador. Al mismo tiempo, esta investigación contribuirá a la taxonomía en Grecia y el Mediterráneo Oriental, centrándose en primer lugar en la creación de las claves de identificación para polinizadores, la formación de nuevos científicos, así como en el enriquecimiento y el desarrollo de la Melisoteca del Egeo, una colección de referencia permanente de los insectos polinizadores establecidos en la Universidad del Egeo.

Keywords: wild bees, hover flies, ecological and genetic diversity, pollination networks, pollination services, fires, grazing, honey bee competition, climate change, Aegean islands, Merodon

Introduction

Pollination is a key ecosystem service that is essential for the world’s agricultural production (Klein et al., 2007; Ricketts et al., 2008) and for the reproduction and evolution of wild plants and their pollinator partners (Burd, 1994; Aguilar et al., 2006). Consequently, pollination is a valuable resource supporting the world economy (Gallai et al., 2009), and an invaluable resource for wildlife and ecosystem conservation (Ashman et al., 2004; Knight et al., 2005).

On a global scale, pollination services are provided by populations of both managed and wild animal pollinators, the majority of which are insects. Within insect pollinators, the most prominent groups, taxonomically and functionally, and in order of importance, are bees (Hymenoptera: Apoidea), hover flies – also called flower flies (Diptera: Syrphidae), and bee flies (Diptera: Bombyliidae). Situated on the overlapping zone of three major biogeographic regions, the Mediterranean supports a large part of the global bee diversity, constituting one of the world centres of bee speciation (Michener, 1979; O’Toole and Raw, 1991).

The diversity and effectiveness of pollinators are influenced by a series of environmental changes that have been seriously aggravated during the last decades. Using historical time-series, pollinator loss has been documented for the UK and The Netherlands, where the level of decline is associated with a reduction in flowering plant diversity (Biesmeijer et al., 2006). Thus, the maintenance of pollinator diversity has been of increasing global concern. Habitat fragmentation and loss, excessive land use (e.g. grazing) and land use change (e.g. urbanization, wild fires), pesticide use, various pathogens and parasites, biological invasions, climate change, and the Colony Collapse Disorder phenomenon are the most likely causes leading to this decline in pollinator diversity (Petanidou and Ellis, 1996; Memmott et al., 2007; Anderson and East, 2008; Hegland et al., 2009; Winfree et al., 2009; Bromenshenk et al., 2010; Potts et al., 2010a). In addition, in areas with intense apicultural activity, such as the Aegean (Potts et al., 2010b), honey bees may outcompete wild bees (Shavit et al., 2009) and possibly reduce their diversity.

As a result of the above, the decline of pollinator diversity is seen today by international organizations and governments as a daunting threat to the planet, having a similar far-reaching impact, as climate change, chemical waste deposit and biological invasions (Committee on the status of pollinators in North America, 2007; Convention on Biological Diversity, 2008).
Although many regional and national programmes are realised, our knowledge on pollinator diversity and temporal population dynamics and external threats remains very limited. Moreover, little is known about the services pollinators provide, both from the quantitative (visitation rate) and the qualitative (efficiency) points of view (Ashman et al., 2004; Dauber et al., 2010).

Greece has been recognised as an important hotspot for bee diversity, but it is possibly the only country in Europe, for which bees and other pollinators have not been extensively recorded (Buchmann and Nabhan, 1996; Matheson et al., 1996; Michener, 2000). Reasons could be their disproportionately large diversity vis-à-vis the limited number of researchers, the absence of a taxonomic culture and expertise – professionals or amateurs, and even the fear of insects. Thus, while Greece boasts one of the most diverse insect pollinator faunas in the world, the deficit of taxonomic knowledge is immense. Yet, apart from the lack of taxonomic (Linnean shortfall) and ecological knowledge (species richness and abundance), Greece also suffers from knowledge on the biogeography (Wallacean shortfall) of pollinators.

So far, the largest Greek pollinator study has been carried out in Dafni, Attica, encompassing 665 pollinator species, of which 262 were bees, 50 hover flies and 47 bee flies (Petanidou, 1991; Petanidou and Ellis, 1993; Petanidou and Vokou, 1993; Petanidou and Potts, 2006; Petanidou et al., 2011). In the past few years a sizeable amount of material has been collected on the island of Lesvos (c. 550 species of bees, >100 species of hover flies, and >65 species of bee flies: Potts et al., 2006; Vuić et al., 2007; García-Gras, 2008; Stähls et al., 2009; Nielsen et al., 2011; Radenković et al., 2011; Tscheulin et al., 2011). Most of the collected and identified entomological material of Lesvos is kept in the Melissotheque of the Aegean, a permanent reference collection of bees and other insect pollinators from the Aegean, currently unique in Greece, that is established at the University of the Aegean, in Mytilene (http://www2.aegean.gr/lab_biogeography-ecology/). Despite the above efforts, to date there is no official pollinator species list available in Greece, whereas a large number of new species continue to be recorded in the region (Petanidou, 1991; Vuić et al., 2007; Stähls et al., 2009; Radenković et al., 2011).

The threats pollinators face amplify further the need for action. At the European level initiatives aim at understanding the multiple stressors pollinators face, together with the magnitude these stressors have had on the diversity of pollinators and their services (STEP project: http://www.step-project.net/; Potts et al., 2011). Such evaluations, however, are difficult to effectuate in Greece, as species checklists and time series data on pollinator populations are lacking. To date no study has yet looked at the status of pollinators in Greece, and with the commonly acknowledged threats and accelerated loss due to local and global environmental changes (climatic, land use etc.), knowledge on the pollinator diversity of Greece is more needed than ever, if not imperative.

The project POL-AEGIS (The POLlinators of the AEGean Archipelago: Diversity and Threats) constitutes a pioneer effort to fill the abovementioned gaps of knowledge. Focusing on a wide range of the Aegean archipelago, from January 2012 to September 2015, the project aims at (i) assessing pollinator diversity (ecological, genetic), (ii) investigating the drivers of pollinator diversity loss and, (iii) contributing towards resolution of the Linnean shortfall in Greece. The outreach of a successful achievement of the above will boost pollination studies, facilitate the compilation of a Red Data list of pollinators, promote bee-friendly land management, and give guidelines for a better use of pollinators for crop production in Greece.

Research approach and expected results
A conceptual framework of the project work topics is illustrated in Fig. 1. The project consists of 10 work topics of which seven concern pure research. The remaining three work topics include enhancement of the taxonomic human capital in Greece, dissemination of the results, and project coordination. Below we give a short description of the rationale, main targets and expected results for all topics except coordination.

**Fig 1.** Overview of the project’s research plan and work topics (WT).

**Topic 1: Assessment of pollinator diversity in the Aegean**
This part of the project aims to fill the knowledge gaps regarding the pollinator diversity and to confront the lack of taxonomic resources in the country by focussing on: (i) a systematic collection of pollinators on a geographic scale that is unprecedented; (ii) a systematic classification of collected insects with a collaboration with the most experienced pollinator taxonomists in Europe; (iii) the enhancement of human resources in pollinator taxonomy in Greece and Europe, by involving young researchers; and (iv) the enrichment of the Melissotheque of the Aegean insect reference collection.
is certainly related to the high diversity of bulbous plants (et al., 2007; Ståhls et al., 2009; Radenković et al., 2011).

As most hover flies, species of the genus Merodon are strong flyers. Therefore, they would be expected to show less pronounced phylogeographical structure than found for tenebrionid beetles by Papadopoulou et al. (2009). On the other hand, by being strictly dependent on geophyte bulbs (e.g. Liliaceae, Amaryllidaceae), we assume immature stages of Merodon to be limited by the geographical distribution of their host plants (Hurkmans, 1993). Based on our preliminary results on the genetic diversity of Merodon spp. in two Eastern Aegean islands (Ståhls et al., 2009), we hypothesize that larval feeding ecology is a strong predictor of phylogeography and that hover flies thus divert from the aforementioned general pattern.

This part of the project aims at detecting the spatial patterns of genetic variability and estimate the phylogeographic propensity of Merodon in the Eastern Mediterranean. Specimens of co-distributed species will be collected on several islands and particularly across the mid-Aegean trench, as well as on the Greek and Turkish mainlands (Fig. 2). MtDNA COI barcode sequences will be used for construction of haplotype networks exploring the phylogeographic signature of focal Merodon species following Ståhls et al. (2009).

**Topic 3: Impacts of climate change on pollinator diversity, structure of plant–pollinator interaction networks, and nectar secretion**

Climate change can impact pollination in several ways. First, it may change the composition of flora and fauna, with local extinctions of natives and invasion by alien species (Parmesan, 2006; Hegland et al., 2009; Schweiger et al., 2010). Second, it may impact individual phenologies of interacting species, thereby impeding their interaction, because of a temporal mismatch such as between flowering and pollinator activity (Petanidou and Ellis, 1996; Harrison, 2000; Kevan, 2001; Wall et al., 2003; Memmott et al., 2007; Schweiger et al., 2008; Hegland et al., 2009; Schweiger et al., 2010). In general, with global warming the flowering periods seem to start earlier and last longer (Roy and Sparks, 2003; Menzel et al., 2006). It has been shown, that during the last century, the onset of flowering periods of plants and activity periods of insect pollinators have shifted an average of four days per Celsius degree increase (Memmott et al., 2007). However, the specific mechanisms behind these phenomena differ and so do the responses (Visser and Both, 2005; Both et al., 2009).

Third, it may influence the distribution of species of plants and pollinators in space. Such changes have been recorded for both plants (Lenoir et al., 2008) and pollinators (Wilson et al., 2007). An
important question is how this will impact plant–pollinator networks, e.g., their species and link composition, structural organization, and further the reproduction of plants and animals.

Finally, climate change may influence the availability of floral rewards such as nectar to pollinators, since it alters the availability of water (Willmer and Corbet, 1981; Petanidou and Smets, 1996), which in return can decrease pollinator foraging efficiency (Goulov et al., 1999). Petanidou and Smets (1996) showed that the floral nectar secretion of *Thymus capitatus* (L.) Hoffmanns. & Link, a widespread and characteristic plant of the Mediterranean, is significantly reduced at relatively high temperatures (> 32.5°C). It is expected that annual plants, which constitute the majority in the Mediterranean, may suffer more severe reduction in nectar secretion at high temperatures, and thus hypothesised that the overall nectar reward offered to pollinators will be considerably reduced with climate change.

Topic 3 aims at estimating the effect of climatic factors on the diversity of pollinators and the structure of plant–pollinator networks (i.e., made up of interacting plant and pollinator communities within a defined area and time period), as well as on the floral rewards (nectar and pollen) offered to pollinators. The data will be collected in the field (particularly, on islands with different climatic profiles shown in Fig. 2) and in climate chambers under controlled conditions. We expect that this approach will produce results that will give a prospective description of the future under different climate change scenarios and allow us to forecast the impact of climate change on pollinator diversity and pollination networks, highlighting possible local extinction threats. In the case of temporal mismatches between plants and their pollinators we expect a disruption of the pollination network, which will be compared with already studied networks of the region and various null models (Petanidou et al., 2008; Schweiger et al., 2008; Kallimanis et al., 2009).

**Topic 4: Impacts of honey bee competition on the diversity, foraging efficiency and reproduction of wild bees, as well as pollination services to wild plants**

The honey bee (*Apis mellifera* L.) is one of approximately 20,000 species of bees in the world, which are specialised in exploiting floral rewards. As opposed to honey bees and a few other bee species that are colony-forming social bees, the majority of the bees of the world are solitary. For example, out of the approximately 1100 species of bees that are estimated to occur in Greece, only the honey bee and bumble bees are considered true eusocial species, while the remaining bees are solitary, with a few species of Halictidae showing intermediate levels of sociality (e.g. semisocial or communal sensu Michener, 2000).

Of all 33 European countries, Greece has the highest density of honey bee hives, and is the only EU country in which beekeeping is increasing (De la Rua et al., 2009; Potts et al., 2010b). Honey bees can outcompete solitary bees because of their high numbers and foraging efficiency as documented recently in Israel (Shavit et al., 2009). So far no study has addressed the question whether solitary bee diversity is affected by potential competition from honey bees.

Topic 4 aims to examine if and to what extent intensive beekeeping in Greece causes competition to wild bees and to highlight potential impacts. In particular, it aims at investigating the effect of hive density on the foraging efficiency and reproduction of wild bees, as well as on their diversity and pollination effectiveness. Data about species diversity, pollination services, and reproductive rate of wild bees will be collected in up to 10 Cycladic islands, differing significantly in bee hive density (Papas, 2008; Fig. 2).

**Topic 5: Impacts of livestock grazing on pollinator diversity, pollination services, and plant–pollinator network structure**

Plant–pollinator interactions represent ecosystem functions that are influenced considerably by the extent, intensity and type of grazing (Carvell, 2002; Krueß and Tscharntke, 2002; Sjödin, 2007). Consequently, grazing constitutes a regulating factor in the structure and dynamics of pollinator communities (Potts et al., 2003b; Navarro et al., 2006), further influencing pollination services.

More specifically, grazing can: (i) alter the population density and diversity of entomophilous plants considerably (Vazquez and Simberloff, 2004; Chaideftou et al., 2011); and (ii) directly or indirectly change the abundance and availability of floral resources (Vulliamy, 2003; Ågren et al., 2006; Mayer et al., 2006). With respect to insect pollinators, grazing can: (i) influence the foraging behaviour of pollinators because of a change in floral rewards (Chittka et al., 1999; Vohland et al., 2005), or influence their movement when, for example, grazing alters the height of the vegetation (Goulson, 2000); (ii) influence the number of nesting sites available to ground-dwelling wild pollinators by causing an expansion of areas of bare soil, which are favoured nesting sites (Petanidou and Ellis, 1996; Potts et al., 2003a), or alter the availability of water, that is essential for nest construction (Gess and Gess, 1993; Vinson et al., 1993); (iii) directly influence the survival rate of pollinators by trampling of the grazing animals (Sjödin, 2007) or indirectly, by decreasing the extent of shelters in the vegetation (Potts et al., 2009); and (iv) increase the abundance of bees whereas the influence on their diversity remains unknown (Vulliamy et al., 2006).

This topic aims at investigating how the pollinator diversity and effectiveness, as well as the structure of plant–pollinator networks are influenced by various grazing intensities. It is expected that grazing pressure influences the pollinator diversity in accordance with the Intermediate Disturbance Hypothesis (Grime, 1973; Sousa, 1984; Malavasi et al., 2009), which may also apply for the structure of plant–pollinator networks. The study will lead to valuable knowledge on
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pollination services in Mediterranean regions with livestock. Furthermore, it will allow the recommendation of management practices of pasture land that benefits the diversity of plants and pollinators.

**Topic 6: Assessment of the post-fire restoration rate of pollinator diversity, plant–pollinator network structure, and pollination services after extended wild fires**

In the short term, wild fires are devastating to pollinator communities. Solitary bees are almost completely absent from burnt areas immediately after a fire because of (i) direct mortality from the fire, (ii) limited local food resources (nectar and pollen), but also because of (iii) their limited flight range, which initially impedes recolonisation (Ne’eman *et al.*, 2000). Large pollinators, which generally have more extensive flight ranges, are at an advantage at the initial stages of succession, because they can use the mosaic of burnt and unburnt patches in the post-fire region (Moretti *et al.*, 2006). The post-fire recovery of the diversity and the composition of main pollinators in Mediterranean ecosystems peaks during the first post-fire years and decreases in the later stages of post-fire succession (Petanidou and Ellis, 1996; Potts *et al.*, 2003a).

In the past decades, due to increased human activity, the intensity and extent of wild fires have reached unnatural dimensions. While we know that after some time interval the biodiversity in small burnt areas recovers (Petanidou and Ellis, 1996; Potts and Dafni, 2001; Potts *et al.*, 2003a, 2006), we do not know to what extent this happens in large burnt areas such as those created by the catastrophic wild fires in recent years (2008 to date). In addition, although both functional restoration and plant–pollinator networks are recognised as important analytical and managerial tools (Ehrenfeld and Toth, 1997; Forup *et al.*, 2008), so far no studies have addressed how biodiversity recovery translates into the functional restoration of plant–pollinator networks and pollinator effectiveness.

This topic aims at studying the impacts of fire on pollinator diversity and the provided pollination services, and on pollination networks. The focus upon food web restoration is novel in ecology (Memmott, 2009), and for the first time this tool will be applied in post-fire restoration ecology. The research will be carried out in areas that were heavily burnt in the last few years in Greece (Fig. 2). Potentially influential factors such as spatial extent of the burnt area, distance to unburnt areas, fire history, and landscape complexity and type are included in the study. The results are expected to lead to valuable input to post-fire management of burnt regions, aiming at the functional recovery of ecosystems and not merely the recovery of their structural components.

**Topic 7: Impacts of electromagnetic fields from telecommunication antennas on pollinator diversity**

The rapid growth of mobile telephony during the last decade has resulted in a pronounced increase of electromagnetic fields (EMFs) in the environment. The effects EMFs have on various organisms are the subject of on-going research, but they have been suspected to cause chronic problems in the physical defence of organisms and their reproductive ability, as well as locally reduce their distribution (Balmori, 2009). Studies show that the effects of EMFs vary. They were reported to have no effects in rats and mice (Sienkiewicz *et al.*, 2000; Cobb *et al.*, 2004; Dasdag *et al.*, 2004), but showed negative effects in birds (Doherty and Grubb, 1996) and insects (increased stress: Weisbrot *et al.*, 2003; reduction of fertility: Panagopoulos *et al.*, 2004; Atli and Unlu, 2006; induced honey bee worker piping: Favre, 2010). Additionally, EMFs may change the behaviour of dogs, cats and cows (Marks *et al.*, 1995; Löscher and Käs, 1998) and impact the nervous system of birds (Beason and Semm, 2002), mammals (Salford *et al.*, 2003) and amphibians (Balmori, 2006).

This topic aims at investigating if electromagnetic pollution affects the diversity of wild pollinators, especially bees and flies. Pollinator diversity will be assessed using pantraps from a number of telecommunication antennas and at different distances from each antenna, each sampling site corresponding to a known electromagnetic radiation. The building of a predictive model may include also other variables, e.g. flower cover.

**Topic 8: Addressing taxonomic and research deficit on pollinators in Greece**

To combat the current deficit of taxonomic knowledge in Greece, a strong programme in systematic education is paramount. In the framework of this topic we will focus specifically on training students in the field in sampling and identification of insects and plants, as well as in pollination ecology techniques. To improve the taxonomical expertise in Greece this project will: (i) organise three workshops to train young scientists in taxonomy (insects, mainly bees and hover flies; and plants), pollination ecology techniques, and data analysis (including network analysis); (ii) provide young researchers the opportunity to work with material collected during the project; (iii) support one collaborator to be trained in bee taxonomy in the US and get further training by a European expert.

**Topic 9: Result dissemination**

The taxonomical and functional diversity of pollinators is extrinsically and intrinsically related to many social functions. Therefore, an
The exploitation of the diversity. Last, and certainly not least, the established knowledge and conservation, restoration, and sustainable use of the pollinator Council, FAO, IUCN, CBD, UNEP, Council of Europe) regarding policy making at national and international level (e.g. European based. Finally, expert knowledge will contribute to recommendations monitoring and sustainable management of pollinator diversity can be constitute the first baseline database, on which future diachronic more synthetic view of biodiversity. At regional level, the results will improve crop quality, beekeepers to move towards a more balanced management based on the project's results will encourage farmers to

Conclusions

POL-AEGIS is a pioneer project both in its scientific approach and community outreach.

In its scientific approach, the project aims at undertaking the massive task of a systematic collection of pollinators from a very fragmented area at unprecedented scale, necessitating intense collaboration with several European taxonomical experts in bees and flies. Apart from various scientific results filling several gaps of the Linnean and Wallacean shortfalls in Greece and knowledge regarding drivers of pollinator loss at different spatial scales, the overall outcome will be a decisive step towards the creation of the Greek Red Data list for pollinators. Further on, it will enrich and develop essentially the Melissotheque of the Aegean as a taxonomic infrastructure of immense value in our efforts to understand the ecology and evolution in the Eastern Mediterranean, create the first taxonomic keys and atlas for important pollinator groups in Greece, and set up the first nucleus of human capital in bee and hover fly taxonomy in the country.

Many of the results of the project will be valuable to the society at several levels. At the local level, an application of bee-friendly management based on the project’s results will encourage farmers to improve crop quality, beekeepers to move towards a more balanced apiculture, and wildlife conservationists and land managers towards a more synthetic view of biodiversity. At regional level, the results will constitute the first baseline database, on which future diachronic monitoring and sustainable management of pollinator diversity can be based. Finally, expert knowledge will contribute to recommendations and policy making at national and international level (e.g. European Council, FAO, IUCN, CBD, UNEP, Council of Europe) regarding conservation, restoration, and sustainable use of the pollinator diversity. Last, and certainly not least, the established knowledge and the exploitation of the Melissotheque of the Aegean will aid environmental education at all levels and recipients (schools and education centres), creating a promising pool of bee aficionados and future taxonomists, which Greece is in dire need of.

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