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Osmiine bees (Hymenoptera, Megachilidae, tribe Osmiini) of Europe: ecology, distribution, and conservation

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Osmiine bees (Hymenoptera, Megachilidae, tribe Osmiini) of Europe: ecology, distribution, and conservation

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Acknowledgements

Abstract

Bees are important pollinators in natural and agricultural ecosystems. Yet, increasing anthropogenic pressures threaten their populations. Following this decline, numerous projects, particularly in Europe, have been launched to understand and document these threats to which bees are exposed. As part of these projects, this Master's thesis aims, in the first place, to reassess the status of European osmiine bees (Megachilidae, tribe Osmiini) and update the first European IUCN Red List of bees. To conduct this re-assessment, data regarding their ecology and geographic distribution were gathered using literature data as well as private and public databases. The results highlighted a lesser uncertainty regarding the extinction risks of species compared to the first European Red List of bees as less than 8% of species lack enough scientific information to be assessed (Data Deficient species), compared to the previous 47%. This enabled us to demonstrate that the European osmiine bee species do not seem to be under significant threats, with over 73% of species being classified as Least Concern. We further gathered other traits related to the morphology (body size & hairiness), ecology (floral specialisation, nesting area, material, method & position) and geographic distribution (Extent Of Occurrence (EOO), Area Of Occupancy (AOO), Species Continentality Index (SCI) & Species Temperature Index (STI)) of the species to analyse their links to the status of conservation previously assigned. It has been found that only two traits, the EOO and STI, had a significant relationship with the IUCN Red List categories, with lower values of both traits being linked to a higher extinction risk. Finally, we used an ecological niche modelling approach to investigate the ecological suitability of this group based on environmental data and occurrence records of osmiine species across Europe. This demonstrates that the Mediterranean and Mountainous areas of Western Europe have highly suitable environmental conditions for European osmiine species. Consequently, effective conservation measures should be concentrated towards these areas. We further discuss the specific drivers occurring in these ecosystems and provide suggestions for future research with perspectives based on our findings.

Keywords: Pollinators, Red list, Decline, Conservation, ENM, trait, IUCN, Osmiini, *Chelostoma*, *Haetosmia, Heriades*, *Hofferia, Hoplitis*, *Osmia, Protosmia*, *Stenoheriades*

Résumé en français

Les abeilles sont des pollinisateurs importants dans les écosystèmes naturels et agricoles. Pourtant, des pressions anthropiques croissantes menacent leurs populations. Suite à ce déclin, de nombreux projets, notamment en Europe, ont été lancés pour comprendre et documenter ces menaces auxquelles les abeilles sont exposées. Dans le cadre de ces projets, ce mémoire vise, en premier lieu, à réévaluer le statut des Osmiini européennes (Megachilidae, tribu Osmiini) et à mettre à jour la première liste rouge européenne des abeilles de l'UICN. Pour mener à bien cette réévaluation, des données concernant leur écologie et leur distribution géographique ont été rassemblées en utilisant des données bibliographiques ainsi que des bases de données privées et publiques. Les résultats mettent en évidence une incertitude moindre concernant les risques d'extinction des espèces par rapport à la première liste rouge européenne des abeilles, puisque moins de 8 % des espèces ne disposent pas d'informations scientifiques suffisantes pour être évaluées (espèces à données insuffisantes), par rapport aux 47 % précédents. Cela nous a permis de démontrer que les espèces d'abeilles osmies européennes ne semblent pas menacées de manière significative, plus de 73 % des espèces étant classées dans la catégorie "préoccupation mineure". Nous avons également rassemblé d'autres traits liés à la morphologie (taille du corps et pilosité), à l'écologie (spécialisation florale, zone de nidification, matériel, méthode et position) et à la distribution géographique (la zone d'occurrence (EOO), la zone d'occupation (AOO), l'indice de continentalité spécifique (SCI) et l'indice de température spécifique (STI)) des espèces afin d'analyser leurs liens avec l'état de conservation précédemment assigné. Seuls deux traits, l'EOO et le STI, ont une relation significative avec les catégories de la Liste rouge de l'UICN, les valeurs les plus faibles de ces deux traits étant liées à un risque d'extinction plus élevé. Enfin, nous avons utilisé une approche de modélisation de niche écologique pour étudier l'adéquation écologique de ce groupe sur la base de données environnementales et de données d'occurrences d'espèces d'Osmiini à travers l'Europe. Cela démontre que les régions méditerranéennes et montagneuses d'Europe occidentale présentent des conditions environnementales très appropriées pour les espèces européennes d'Osmiini. Par conséquent, des mesures de conservation efficaces devraient être concentrées sur ces zones. Nous discutons en plus des facteurs spécifiques de déclin qui interviennent dans ces écosystèmes et proposons des suggestions pour les recherches futures, avec des perspectives basées sur nos résultats.

Mots-clés : Pollinisateurs, Liste rouge, Déclin, Conservation, ENM, trait, UICN, Osmiini, *Chelostoma*, *Haetosmia*, *Heriades*, *Hofferia*, *Hoplitis*, *Osmia*, *Protosmia*, *Stenoheriades*

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I.   Introduction

1. Bees: diversity, ecology and importance

Evolving from a group of predatory wasps, bees (Hymenoptera: Anthophila) appeared during the Cretaceous period (~ 125 ma), at the same time as the flowering plants (Angiosperms) (Almeida et al., 2023; Sann et al., 2018). This synchronicity allowed the two clades to co-evolve, leading to their respective radiation (Peris & Condamine, 2024; R. S. Peters et al., 2017). Nowadays, bees are distributed all over the globe (except Antarctica) (Michener, 2007) and include over 20,000 described species classified within seven families (i.e., Andrenidae, Apidae, Colletidae, Halictidae, Melittidae, Megachilidae and Stenotritidae) (Ascher & Pickering, 2020; Michez et al., 2019).

All of these bees go through several stages during their life cycle. Upon egg hatching (several days after the egg was laid), the larva feeds on nectar and pollen beforehand provisioned by the mother (Fig. 1A) or is taken care of by workers or a queen in the case of social bees (Michener, 2007). The larva grows into different larval stages before overwintering during the bad season (diapause) as a prepupae (the last larval stage), sometimes in a spun protective silk cocoon. In some cases (e.g., many Megachilidae), the individuals complete their whole development cycle before unfavourable conditions and therefore spend the bad season as an adult (Fig. 1B) (Antoine & Forrest, 2021; Sedivy & Dorn, 2014). After the diapause, the prepupae resume their development into a pupa (the stage between the larva and the adult) and finally emerge from the nest as a fully developed adult during spring or summer (Fig. 1C). The species whose development was achieved before overwintering will emerge as an adult as soon as the environmental conditions are favourable (Danforth et al., 2019; Michener, 2007). The males generally emerge several days before the females (protandry) and try mating with the females immediately as they come out of the nest (Fig. 1D) (Willmer & Stone, 2004). After mating, females of solitary species re-use or build a nest, provision it and lay eggs which will later hatch and develop into larvae (Fig. 1E-F) (Danforth, 2007; Michez et al., 2019). Regarding social species, only one female individual (the queen) lays eggs while other smaller and sterile individuals (the workers) supply the nest and take care of the larvae until the queen eventually dies and future potential queens replace it (Danforth, 2007; Radchenko & Pesenko, 1994). However, some species do not construct nests nor provision them but rather lay eggs within existing nests of other bees and will benefit from the provisions of their host (brood parasitic species) (Engel et al., 2020; Litman, 2019).
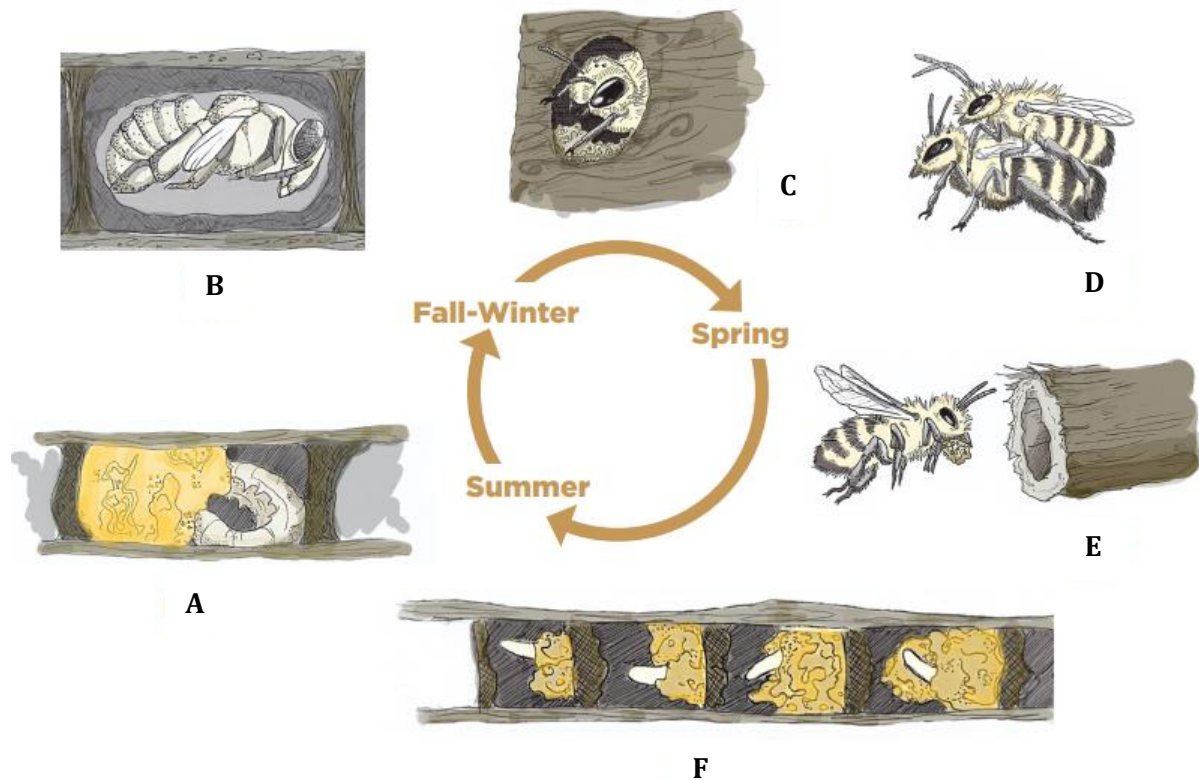
Figure 1. Example of the life cycle of a solitary bee nesting in preexisting cavities. A) Hatching of the larva which feeds on the provision during the summer. B) Overwintering, either as a prepupae or an adult, during the unfavourable season. C) Emergence from the nest during favourable conditions, in spring or summer. D) Mating between the male (top) and female (bottom). E) Nest construction within a preexisting cavity with materials to construct or provision the nest. F) The cavity is divided into several brood cells which are successively filled with pollen and nectar provisions, on top of which an egg is laid, before being sealed with diverse materials. Modified from Scott (2007).

During their entire life cycle, all bees therefore exclusively rely on plants, at least for nutrition. Whether at the larval or adult stage, most bees depend on pollen and nectar for protein and carbohydrate intakes, respectively (Danforth et al., 2019; Michener, 2007). Through this intimate relationship, bees indirectly contribute to the sexual reproduction of many flowering plants by foraging on flowers and facilitating pollination, i.e., the transfer of pollen grains from the male reproductive parts (stamen) to the female reproductive parts (pistil) of the flower (Ollerton, 2021). Pollination plays a key role in natural and agricultural ecosystems as roughly 90% of wild flowering plants (Ollerton et al., 2011) and ~70% of major world-cultivated crops (Klein et al., 2007) rely on animal vectors for their reproduction, with bees as principal pollinators (Khalifa et al., 2021; Winfree et al., 2011). Economically speaking, the ecosystemic service of insect crop pollination was estimated to exceed €150 billion per year worldwide (Gallai et al., 2009). Moreover, wild bees promote diverse wild plant communities making them keystone species for maintaining biodiversity and higher levels in the food web (Lundgren et al., 2015; Senapathi et al.,

2015). Besides these ecological and agricultural services, wild bee diversity is also part of the human cultural heritage (Matias et al., 2017), a cultural service inherently linked with human health and wellbeing (Clark et al., 2014).

Despite the unambiguous ecological importance of bees in natural and agricultural ecosystems, anthropogenic pressures increasingly affect their diversity and abundance through habitat loss and fragmentation, climate change, pollution and the introduction of alien (Bowler et al., 2020; Jaureguiberry et al., 2022). This induces a biotic loss that is reported globally in several groups (e.g., in birds (Rigal et al., 2023), amphibians (Luedtke et al., 2023) and corals (Eddy et al., 2021)) and that is even regarded as the sixth mass extinction by some authors (Barnosky et al., 2011; Cowie et al., 2022; Dirzo et al., 2014).

2. Wild bee decline

Insects, including wild pollinators, are no exception to the decrease in biodiversity (Hallmann et al., 2020; IPBES, 2016; Wagner, 2020). Their decline has been widely acknowledged with reports of decreasing bee diversity and abundance (Bartomeus et al., 2013; Biesmeijer et al., 2006; Ghisbain et al., 2024; Koh et al., 2016; Potts et al., 2010; Zattara & Aizen, 2021). The decline of bees is the consequence of several synergetic and mainly anthropogenic factors, namely, (i) habitat loss and fragmentation, (ii) climate change, (iii) agrochemical products, (iv) invasive alien species and (v) non-native pathogens (Danforth et al., 2019; Goulson et al., 2015; Michez et al., 2019).

(i) Land use changes, primarily through agricultural intensification but also increased wildfire and urbanisation, considerably impact bee communities and are believed to be the leading drivers of bee decline (Brown & Paxton, 2009; Danforth et al., 2019). Land use changes involve habitat loss, degradation and fragmentation of (semi-)natural habitats, which reduce the availability of floral resources and nesting sites (Goulson et al., 2015; Kline & Joshi, 2020). For instance, changes in agricultural management practices in Europe have considerably reshaped agricultural landscapes, drastically reducing the abundance of legume crops that once supported diverse communities of bumblebees (Rasmont et al., 2021). Concomitant phenomena are occurring in cities, where impervious surfaces are increasing, reducing habitat suitability and nesting sites and therefore the diversity and abundance of bees, particularly those nesting in the ground (Pereira et al., 2021).

(ii) Global warming impacts bee populations by inducing phenological changes and range shifts (Settele et al., 2016). Phenological shifts can lead to temporal mismatches between bloom time and the emergence of pollinators, reducing food availability and therefore

reduced fitness (Hegland et al., 2009; Schenk et al., 2018). Range shifts, often characterised by losses in warmer southern areas paired with a lack of gains in northern regions (Kerr et al., 2015; Settele et al., 2016), induce spatial mismatch and make populations more vulnerable to decline and extinction (Vanbergen & Initiative, 2013). Moreover, extreme climatic events such as droughts, floods and heat waves are also likely to increase in frequency and intensity with climate change (IPCC, 2023), impacting the reproduction (Martinet, Zambra, et al., 2021; Sales et al., 2018), immune system (Tobin et al., 2024), foraging behaviour and development of bees (Gérard et al., 2022). While most studies about bee decline have focused on bumblebees (see reasons in Ghisbain, 2021), a cold-adapted genus most likely to be more sensitive to this threat (Rasmont et al., 2015), some species of wild bees with similar traits could follow similar patterns (Bartomeus et al., 2013).

(iii)   Agrochemical products (including insecticides, herbicides and fungicides, among others) can be highly toxic compounds affecting the physiology and health of bees, both at the individual and community levels and at every life stage (Calatayud-Vernich et al., 2019; R. M. Johnson, 2015). Exposure to insecticides can cause lethal effects (Tosi et al., 2021), and sublethal effects by impacting food intake and bee activity (Azpiazu et al., 2019), larval development and mortality (Tomé et al., 2020; Wade et al., 2019) and colony growth (Crall et al., 2018) and by reducing the lifespan of individuals (Wu et al., 2023). Moreover, pesticides can decrease wild bee diversity directly or indirectly through the application of herbicides that reduces floral resources (Gabriel & Tscharntke, 2007; Woodcock et al., 2016).

(iv)   Invasive alien species are non-native species that are introduced intentionally or not and that rapidly expand their range from their area of introduction (Pyšek et al., 2020). They threaten ecosystems through predation and competition for nesting sites, resources and habitat with native species (Russo et al., 2021). For example, following the introduction and the expansion of *Osmia cornifrons* and *O. taurus* in America, six native *Osmia* species have seen their population decline significantly (~10% to 15% mean annual decline) due to niche overlapping and competition with the exotic species (LeCroy et al., 2020). Introduced species can also alter plant-pollinator interactions by disturbing native plant communities, which may reduce both bee abundance and diversity, especially the populations of specialist ones feeding on only one plant species (i.e., monolectic) or one genus/family of plant (i.e., oligolectic) (Dötterl & Vereecken, 2010; Stout & Morales, 2009; Vanbergen et al., 2017).

(v)   Bees suffer from a wide array of pathogens, including fungi, bacteria, protozoans and viruses (Potts et al., 2016). Although pathogens naturally occur in populations, human

activities can increase their transmission between species and lead to the emergence of new diseases for naïve populations (McMahon et al., 2018; Theodorou et al., 2016). Recent reports highlight several pathogen spillovers (i.e., transmission of a pathogen across and within species; Borremans et al., 2019) from managed pollinators to wild bee populations (Fleites-Ayil et al., 2023; Nanetti et al., 2021; Ravoet et al., 2014). It is for example the case of the deformed wing virus causing misshapen wings, neurological disorders and mortality or the sacbrood virus causing a high larval mortality rate, two honey bee pathogens that have spread to bumblebees and solitary bees (Fürst et al., 2014; Goulson & Hughes, 2015; Manley et al., 2015; Wei et al., 2022). These introduced diseases therefore represent a global threat to the pollinator communities (Brettell et al., 2021; Cameron et al., 2011).

All of the aforementioned drivers can interact with each other, concurrently or not, exacerbating the effect of one or several factors that previously weakened the population. The decline of wild bees is therefore not solely due to one particular threat but is rather a multi-faceted problem (Meeus et al., 2018; Yang et al., 2021). For instance, pesticides and heat stress can impair the performance of the immune system rendering bees more susceptible to pathogens (Grassl et al., 2018; L. Straub et al., 2022; Zhao et al., 2021). Nutritional stresses induced by habitat loss can also further impact these weakened bees by increasing the mortality rate following an infection (Brown et al., 2000) or following exposure to pesticides (Knauer et al., 2022).

The responses of bees to the different anthropogenic drivers are not uniform and are likely to vary between species due to differences in life-history traits (Cariveau & Winfree, 2015; Winfree, 2010). For example, the nesting biology, flight period, diet and sociality can modify the route of exposure and therefore the impacts of pesticides (Lundin et al., 2015; Raine & Rundlöf, 2024). Body size can also influence the extent of the impact, with smaller bee species being likely more resilient to increasing temperature (Pardee et al., 2022) while bigger ones may be more favoured in the context of habitat fragmentation due to a greater dispersal ability (Warzecha et al., 2016). Moreover, the loss of floral resources, either via habitat loss or invasive alien plants, has mitigated impacts depending on the diet of the species, with generalist ones being able to compensate with a broader range of host plants (i.e., polylectic) (Dötterl & Vereecken, 2010; Kline & Joshi, 2020).

3. European initiatives for bee conservation

The anthropogenic actions have important consequences on biodiversity, notably on pollinators. At the European scale, several projects aiming to stop and reverse biodiversity decline have been launched within the framework of the EU pollinator initiative (European Commission, 2021). In this context, the STEP project – Status and Trends of European Pollinators (Potts et al., 2015) - documented the magnitude of the pollinators decline, notably by developing the first European Red List of bees (Nieto et al., 2014). The Red List is a worldwide conservation and policy-making tool developed by the International Union for Conservation of Nature (IUCN). It can be used regionally or globally to classify and assess the extinction risk of species based on population trends and geographic distribution (IUCN, 2012a, 2012b). In the last European Red List of bees, Nieto and colleagues (2014) highlighted that around 9% of bee species were threatened but this result might be an underestimation as the extinction risk of $\sim 56\%$ of species was not evaluated due to a lack of scientific information (i.e., Data Deficient, "DD" species) (Fig. 2A). This results in high uncertainty as the number of threatened species could therefore vary between ~4% (none are threatened) and ~60% (all DD species are threatened). According to the authors, along with reports from other taxa, it is likely that more species would be assessed in a threatened category with more data availability (Caetano et al., 2022; Howard & Bickford, 2014; Nieto et al., 2014). To compensate for this lack of data and complement other knowledge gaps pointed out by a recent report (Potts et al., 2020), several European initiatives were developed such as ORBIT, Safeguard and PULSE, in which this Master's thesis is embedded. ORBIT (https://orbitproject.wordpress.com/about-the-project/) aims to develop resources for European bee inventory and taxonomy. Safeguard (https://www.safeguard.biozentrum.uni-wuerzburg.de/) aims to halt the decline of wild pollinators in Europe by investigating the factors driving their decline and their associated traits. Finally, the PULSE project (https://www.iucnredlist.org/) aims to develop and update the European IUCN Red List of Bees.
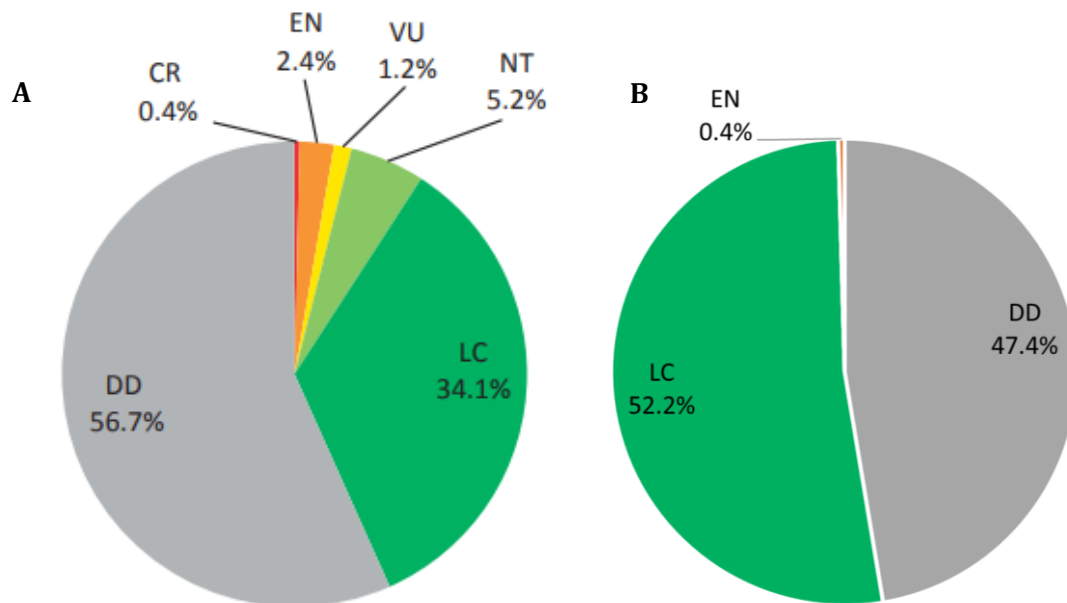
Figure 2. The status of all European bees (A) and European osmiine bees (B). *LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; DD: Data Deficient. Retrieved and based on Nieto et al. (2014).*

4. Osmiine bees

Among the species lacking the most information in the first Red List of European bees, 126 (108 DD and 18 unassessed species) were osmiine bees (Fig. 2B) (Nieto et al., 2014). This represents 51% of their current European diversity. Osmiine bees (tribe Osmiini Newman, 1834) (Fig. 3), commonly named the mason bees, are a monophyletic group of solitary and non-brood parasitic (with a few exceptions) bees within the Megachilidae family that includes over 1,100 species and 15 genera worldwide (Ascher & Pickering, 2020; Ungricht et al., 2008). They are present on virtually every continent except in Antarctica, Australia and South America (one exception, see Gonzalez & Griswold, 2011) and are especially diverse in xeric and Mediterranean climates (Müller, 2024; Praz et al., 2008). In Europe, the most recent checklist reported 246 osmiine species classified in eight genera: *Chelostoma* Latreille, 1809 (Fig. 3A), *Haetosmia* Popov, 1952 (Fig. 3B), *Heriades* Spinola, 1808 (Fig. 3C), *Hofferia* Tkalců, 1984, *Hoplitis* Klug, 1807 (Fig. 3D), *Osmia* Panzer, 1806 (Fig. 3E), *Protosmia* Ducke, 1900 (Fig. 3F) and *Stenoheriades* Tkalců, 1984 (Ghisbain, Rosa et al., 2023).
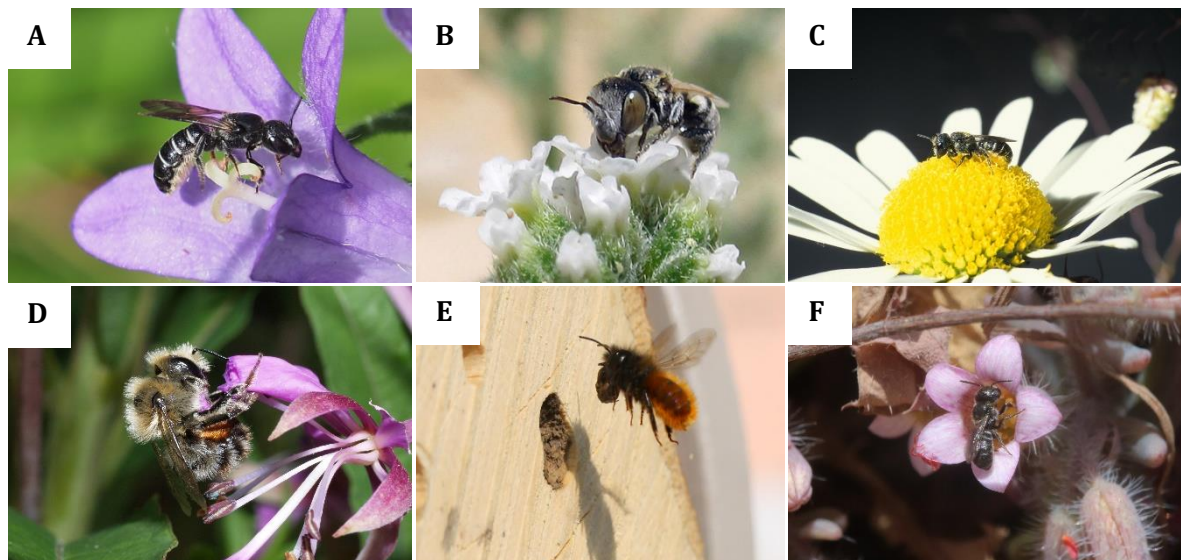
Figure 3. Illustrations of the diversity of European osmiine bees. A) Chelostoma rapunculi *collecting pollen on* Campanula sp*. (Campanulaceae) (Iyptala's Garden, 2022). B)* Haetosmia circumventa *on* Heliotropium sp*. (Boraginaceae) (Gotlieb et al., 2014). C)* Heriades truncorum *collecting pollen on an Asteraceae flower (Blink, n.d.). D)* Hoplitis villosa *cutting a petal of* Epilobium sp*. (Onagraceae) (terraincognita96, 2013). E)* Osmia cornuta *holding mud to close its nest (P. Straub, 2009). F)* Protosmia asensioi *on* Sedum sp*. (Crassulaceae) (Wood, 2022).*

These bees can be recognised by the presence of a ventral scopa on the female abdomen (which is characteristic of the Megachilidae family), long-tongued, the presence of an arolium between the simple claws of females, a long pterostigma (longer than wide) and two cubital cells (Engel, 2001; Michener, 2007; Michez et al., 2019) (Fig. 4).

Figure 4. Morphological characteristics of osmiine bees. A) Hoplitis onosmaevae *showing the ventral scopa (black arrow) and the long-tongued (blue arrow) (modified from Aubert et al., 2024). B) Claws of* Osmia sp*. with the arolium (arrow) in between. C) Wings of* Osmia sp*. showing the long pterostigma (black arrow) and the two cubital cells (blue arrows). B) and C) modified from Pauly (2015).*

The taxonomic diversity of osmiine bees also reflects a vast life-history trait diversity regarding their nesting biology and flower preferences, encompassing almost all of the variation seen in other bees (Fig. 5) (Cane et al., 2007; Praz et al., 2008). Osmiine bees most commonly nest within preexisting cavities which typically include hollow stems (Fig. 5A&C), rock cavities or crevices (Fig. 5G), old nests or holes left by other insects (Fig. 5D) and even in dead snail shells (Fig. 5E) (Gess & Gess, 2008; Westrich, 1989, 2019). Other species build nests directly on rock surfaces

(Fig. 5H), walls or small branches, underground (Fig. 5I), in stems or bark by excavating them (Müller et al., 2019, 2020; Sedivy, Dorn, & Müller, 2013). Most of these nests are divided into linear brood cells, each filled with pollen and nectar provisions on which a single egg is laid (Bosch et al., 2008). The cell is then sealed with diverse materials and this process is repeated until the cavity is filled and generally capped with a nest plug (Fig. 5B) (Danforth et al., 2019; Michener, 2007). The partitioned materials vary considerably between species but often include resin (Fig. 5B&C), small rocks (Fig. 5E), plant tissues (e.g., petals, leaves, etc.) (Fig. 5F&G) or mud (Fig. 5A), in combinations or not (Cane et al., 2007; Müller, 2024). Once the nest is completed, the larva consumes the reserves, completes its development before diapause (spent as an adult for most species) and emerges once environmental conditions are suitable (Fig. 1).
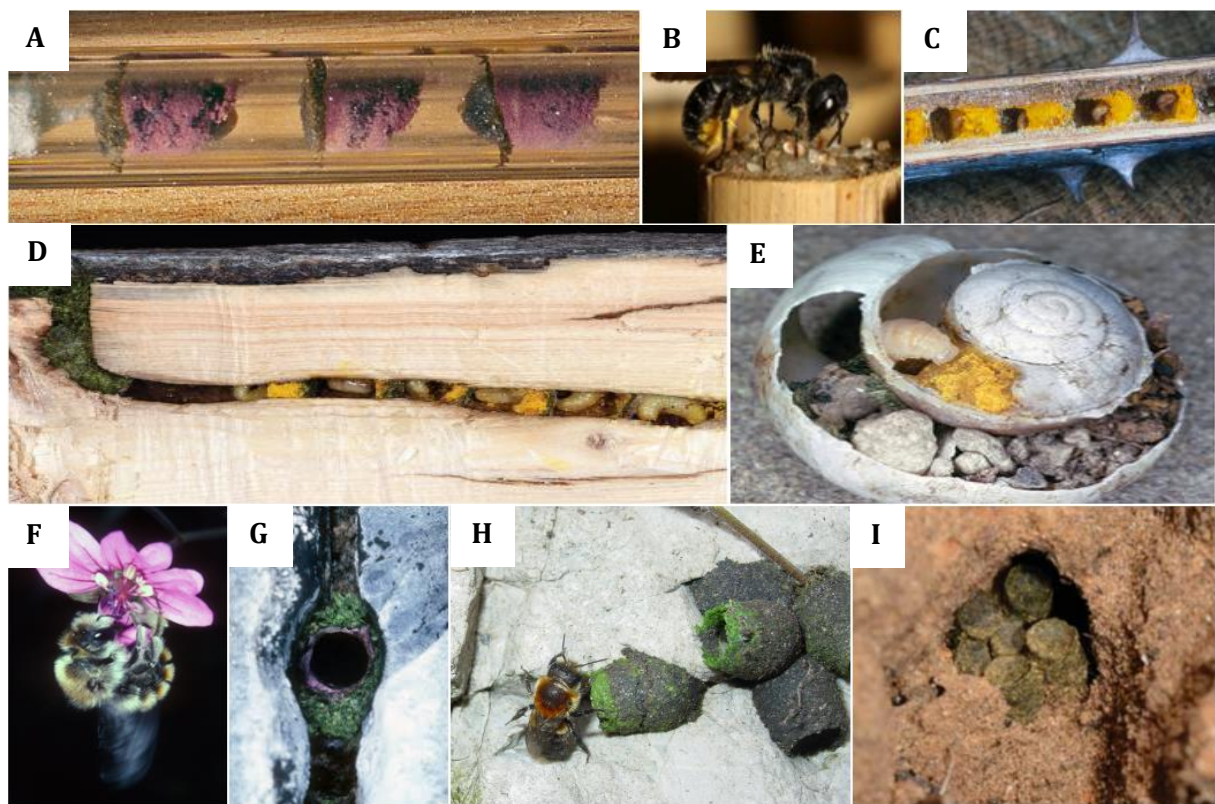

Figure 5. Examples of the diversity of nesting behaviour among osmiine bees. A) Nest of Chelostoma rapunculi *with brood cell partitions made of mud (Müller, 2015b). B)* Heriades truncorum *incorporating resin and pebbles into the nest plug. C) Nest of* H. truncorum *within a bramble stem; each cell is provisioned with pollen and partitioned using clear resin (Müller, 2024). D) Nest of* Hoplitis robusta *in a preexisting cavity in dead wood (Müller & Richter, 2018). E) Nest of* Osmia bicolor *in a snail shell (Müller et al., 2018). F)* Hoplitis dalmatica *cutting petals of* Geranium sp. *to (G) build its brood cells, also made of chewed leaves, in a stone fissure (Müller, 2024). H)* Osmia inermis *building free-standing brood cells attached to a stone using chewed leaves (Kunz, 2003). I) Nest of* Haetosmia vechti *in an excavated burrow (Gotlieb et al., 2014).*

Regarding flower choices, many osmiine bee species are oligolectic (Amiet et al., 2004; Sedivy et al., 2008; Westrich, 2019). In Central Europe, around 55% of species depend on one plant genus/family, most notably Asteraceae, Fabaceae and Boraginaceae (Müller et al., 1997). Many of

these specialist species have morphological adaptations to exploit pollen from their host plants (see below) (Gotlieb et al., 2014; Müller, 1996; Rightmyer et al., 2011). However, other species have much broader floral preferences, making their floral preferences as diverse as their nesting biology (Müller, 2022; Sedivy, Dorn, Widmer, et al., 2013).

4.1 Genus *Chelostoma* Latreille, 1809

Chelostoma species (Fig. 3A), also named the scissor bees, are small to medium-sized (~3.5 to ~9 mm, 14 mm for the biggest (*C. grande*)), slender and black osmiine bees and the sister group of every other Osmiini (Fig. 6) (Michener, 2007; Praz et al., 2008). They also display distinctive light stripes on their abdomen (Fig. 3A) (Michez et al., 2019). 54 species are currently recognised worldwide, with 45 species being in Eurasia, North Africa and the temperate part of the Arabian Peninsula (the Palearctic) and only nine species native to North America (Michez et al., 2019; Ungricht et al., 2008). The last IUCN Red List assessment reported 22 European species among which 11 were assessed Data Deficient (DD) and 11 Least Concern (LC) (Nieto et al., 2014). Since then, two more species were considered in the most recent European checklist, putting the total number of European species to 24 (Ghisbain, Rosa et al., 2023). Regarding their flight period, these bees are mainly active during spring or summer and have one generation per year (i.e., univoltine species) (Amiet et al., 2004; Grace, 2010).

Along with the majority of osmiine species, scissor bees nest within stems and cavities made by other insects. They partition their nests using a mixture of nectar and mud but can also integrate small rocks or sand into the brood cells or the nest plug (Fig. 5A) (Müller, 2024). A recent analysis of their host-plant association revealed that most species of this group are oligolectic, the most common plants on which they forage being Campanulaceae, Hydrophyllaceae and Ranunculaceae (Sedivy et al., 2008). In the Palearctic, only one species (*C. stefanii* under the name of *C. siciliae*) is currently known to be polylectic, feeding on both Ranunculaceae and Cistaceae (Müller, 2012).

4.2 Genus *Haetosmia* Popov, 1952

The genus *Haetosmia* (Fig. 3B) contains only six robust, small (~5 to 7 mm) and thermophilic species strongly associated with desertic and semi-desertic habitats of the Canary Islands to central Asia, via northern Africa and the Sahel region (Michener, 2007; Müller, 2024). Two species (*H. circumventa and H. vechti*) were assessed as DD by Nieto et al. (2014). However, the European record of *H. vechti* is most probably erroneous and the species is therefore no longer regarded as occurring in Europe by Ghisbain, Rosa et al. (2023).

The species of this genus have a white pilosity covering their body and the females also present, on their forelegs, long bristles covering their tibia and enlarged tarsi (Michez et al., 2019; D. S. Peters, 1974). These specialised bristles are likely used to dig sand during nest construction which consist of small chambers in which they build a small grouped pack of vertical brood cells made of sand, chewed leaves (of *Heliotropium* and *Centaurea*) and small rocks (Fig. 5I) (Gotlieb et al., 2014; Müller, 2024). Moreover, the females also exhibit spoon-like hairs on their proboscis which serve to exploit the narrow and tubular flowers of *Heliotropium* (Boraginaceae) to which they are exclusively associated, at least as pollen sources. Other flowers are also possibly exploited but only for nectar purposes (Gotlieb et al., 2014; D. S. Peters, 1974). The prolonged blooming periods of *Heliotropium* (Evenari et al., 1982; Feinbrun-Dothan, 1978) allow *Haetosmia* species to have at least two generations per year (i.e., bivoltine) or more (i.e., multivoltine), which is relatively uncommon among osmiine bees (Müller & Griswold, 2017).

4.3 Genus *Heriades* Spinola, 1808

Heriades (Fig. 3C) is a relatively common genus of small bees (~4 to 7mm) with a broad distribution, occurring on every continent except Oceania and Antarctica (Gonzalez & Griswold, 2011; Michez et al., 2019). They are distinguishable from other genera by the presence of a carina on the first segment of their metasoma (Michez et al., 2019). It is the third most diverse group of the tribe with around 140 described species worldwide (Ascher & Pickering, 2020). Six species were assessed in the European Red List of bees, three were DD and three were LC (Nieto et al., 2014). One species (*H. labiata*) is now not considered as occurring in Europe, bringing the total to five European species (Ghisbain, Rosa et al., 2023). These species are mainly univoltine bees that are active during summer (Michener, 2007; Westrich, 2019).

Heriades bees are also named the resin bees as they incorporate resin, along with sand or small rocks, in the nest plug and brood cells in their nest constructed in hollow or bramble stems and in insect galleries in old wood (Fig. 5B&C) (Müller, 2024; Rozen & Praz, 2016). The females of this genus are generally closely associated with Asteraceae on which they extract the pollen with their ventral scopa from the compound flower head (the capitula) by quickly raising and lowering their abdomen (tapping behaviour) while licking nectar at the same time (Amiet et al., 2004; Portman et al., 2019).

4.4 Genus *Hofferia* Tkalců, 1984

Hofferia bees are one of the least diverse genera of Osmiini with only two described species, *H. mauritanica* confined to northern Africa and *H. schmiedeknechti* in South-Eastern Europe and

South-Western Asia (Müller & Trunz, 2014). *Hofferia schmiedeknechti,* the only European species, was assessed LC in the last Red List assessment (Nieto et al., 2014)*.* They superficially resemble *Chelostoma* species as they have a black and elongated body but are relatively bigger (~8 to 10mm) and have a particularly long labrum (i.e., a cephalic piece covering the mouthparts) (Michener, 2007). These species are univoltine and active during summer (end of May to July) (Michez et al., 2019).

The nesting biology is only known for *H. schmiedeknechti* whose nests are in galleries dug by other insects in dead wood and in which a mixture of resin and pebbles are used to build the nest plug and the wall partitions of the brood cells (Müller & Trunz, 2014; Rozen & Praz, 2016; Tkalcǔ, 1984). Both species are oligolectic on Asteraceae flowers, more specifically within the subfamily Carduoideae (e.g., thistle, cornflower) (Müller & Trunz, 2014).

4.5 Genus *Hoplitis* Klug, 1807

The genus *Hoplitis* (Fig. 3D) is the most diverse clade within Osmiini with around 390 species currently recognised globally, hence showing greater morphological and biological variability compared to the species-poor genera of Osmiini (Ascher & Pickering, 2020). These bees occur worldwide (except in Oceania, South America and Antarctica) and are especially diverse in the Palearctic with more than 300 described species (Müller, 2024; Ungricht et al., 2008). In Europe, 100 species are currently recognised (Ghisbain, Rosa et al., 2023), among which 41 were assessed as LC, 50 as DD and 9 were not considered (Nieto et al., 2014). They generally range from 6 mm to 16 mm, with body shapes largely variable among species (robust, bulky, elongated or slim body) and are distinguished from other genera by having long parapsidal lines (i.e., long lines engraved at the margin of the dorsal part) (Michener, 2007). Moreover, they are univoltine species that mainly fly during summer (Michez et al., 2019).

The nesting biology of *Hoplitis* bees is diverse and reflects their taxonomic diversity. As most other Osmiini, *Hoplitis* nest in preexisting cavities but with a greater variety of substrates, including galleries in dead wood, unoccupied nests of other bees or wasps, snail shells, plant stems, rocks crevices or galls (Banaszak & Romasenko, 2001; Müller, 2014, 2015c; Müller & Mauss, 2016). They can also build brood cells freely on surfaces, between rocks (Fig. 5G), within vegetation or may excavate their burrows (e.g., in soil or stems) (Ivanov et al., 2023; Ivanov & Fateryga, 2018; Sedivy, Dorn, & Müller, 2013). Moreover, few species among the non-European subgenus *Bytinskia* are brood parasites, meaning that they do not construct nor provision their nests but lay eggs within nests of other bees (Litman et al., 2013; Sedivy, Dorn, & Müller, 2013). These diverse nesting behaviours come with a diverse use of nesting materials. Depending on the

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species, plant materials (e.g., petals, leaves, pith) (Fig. 5F&G), earth, sand, mud or small rocks can be used alone or in mixture to build the cell walls and nest plug or the whole brood cells in the case of free-standing nests (Banaszak & Romasenko, 2001; Müller, 2015a; Müller et al., 2017; Westrich, 1989). Only the use of resin seems to be rare as it has only been documented to be used by the North American species, *H. biscutellae* (Rust, 1980). Flower preferences are similarly diverse and a whole spectrum of floral specialisation, except monolecty, can be observed, from polylectic species (e.g., *H. robusta, H. zandeni*) to oligolectic ones (e.g., *H. maritima*) (Müller, 2016; Müller & Richter, 2018; Neff, 2009; Sedivy, Dorn, Widmer, et al., 2013). Several species have morphological adaptations specialised in the uptake of pollen from specific flowers. For example, some species have bristles on the legs (e.g., *H. flabellifera*) or the proboscis (e.g., *H. pici*) similar to the ones found in *Haetosmia* which are used to extract flower resources of Boraginaceae (e.g., *Anchusa*, *Heliotropium*) or Asparagaceae (e.g., *Muscari*) (Müller, 2006; Sedivy, Dorn, Widmer, et al., 2013; Warncke, 1991). Others (subgenus *Micreriades*) have bristles on their face that are curved at their tip which are used, in other taxa, to extract pollen from nototribic flowers, i.e., whose pollen is deposited on the dorsal part of the pollinators (e.g., Lamiaceae) (Müller, 1996, 2024; Thorp, 2000). Other species exploit their pollen host using behavioural aspects such as buzz pollination (shaking the flower to retrieve the pollen from anthers; e.g., *H. onosmaevae, H. holmboei*) but this behaviour remains an exception (Aubert et al., 2024; Pritchard & Vallejo-Marín, 2020; Sedivy, Dorn, Widmer, et al., 2013).

4.6 Genus *Osmia* Panzer, 1806

Osmia (Fig. 3E) is the second most species-rich genus of Osmiini with around 350 species described worldwide, most of them distributed in the Northern Hemisphere (Michener, 2007; Ungricht et al., 2008). Ghisbain, Rosa et al. (2023) reported 99 species in Europe, 96 were assessed in the last Red List assessment, including 36 DD species, 59 LC and one species (*O. maritima*) EN (Nieto et al., 2014). *Osmia* species are small to medium-sized bees (6 to 16 mm) with hairy and robust bodies that are generally black, sometimes with a shiny metallic cuticle (Westrich, 2019). They have short parapsidal lines and rounded axillae (paired tooth-like structures on both ends of the dorsal part of the bee) compared to other genera (Michez et al., 2019). Unlike *Hoplits* which are predominantly summer bees, many *Osmia* species are active earlier, in spring (Michez et al., 2019). Most of them are univoltine but some species (e.g., *O. caerulescens*) can be bivoltine in the southern part of their distribution (Amiet et al., 2004; Vicens et al., 1993).

The nesting biology of *Osmia* bees is variable and includes almost all the diversity seen in other taxa. It is largely similar to what is observed in *Hoplitis,* with roughly the same nesting site and material (with also only one North American species, *O. nemoris*, using resin; Rust & Clement

(1972)), except that they more frequently use preexisting cavities rather than excavating nests or building free-standing ones (Banaszak & Romasenko, 2001; Cane et al., 2007; Müller, 2020, 2024; Rozen et al., 2010). Other life-trait differences are that some species can excavate wood for nesting in the bark of the tree (*O. uncinata, O. nigriventris*) (Müller et al., 2019, 2020) and that snail shell nesting is more widespread (Fig. 5E) (Müller et al., 2018). Some species also display horn-like extensions on their face (e.g., *O. cornuta* (Fig. 3E), *O. bicornis, O. tricornis*) to smoothen the mud partition of their nest (Michez et al., 2019; Torchio, 1989). Regarding their flower preferences, all kinds of ranges are also found (except monolecty), from polylectic (e.g., *O. bischoffi, O. jason*) to oligolectic species   (*O. cerinthidis, O. apicata*) (Haider et al., 2014; Müller, 2022). Similar morphological adaptations described in other genera (i.e., specialised bristle on the proboscis or face) are also found among *Osmia* species (Cane, 2014; Frank & Tepedino, 1982; Prosi et al., 2016; Rightmyer et al., 2011).

Some species of this genus are also used in agriculture as managed pollinators (e.g., *O. lignaria* and *O. ribifloris* in North America, *O. cornifrons* in Asia and *O. cornuta* in Europe) (Bosch et al., 2008). These domesticated species can withstand unfavourable weather conditions (e.g., low T°, light rains, windy conditions) making them forage longer compared to honeybees (Vicens & Bosch, 2000). These managed pollinators are also early emerging and polylectic bees with a high floral constancy (i.e., visiting the same type of plants even with other available resources during one foraging trip) (Chittka et al., 1999; Cripps & Rust, 1989; Sedivy & Dorn, 2014). Moreover, they can be easily and massively reared in artificial nests (Benedek, 2008; Torchio & Asensio, 1985). These traits make them efficient and widely used crop pollinators, notably in early-blooming fruit trees (e.g., apples, cherries, pears, etc.) and berries crops and in greenhouses (Bosch et al., 2008; Bosch & Kemp, 2001). For example, *O. cornifrons* is used in more than 70% of apple crops in Japan (Batra, 1998; Sekita, 2001). In Europe, *O. cornuta* and *O. bicornis* are not only used in orchard crops but also for strawberries and Brassicaceae pollination where they can effectively enhance fruit quality (in *Fragaria* x *ananassa*) and seed yield (in *Brassica rapa*) (Herrmann et al., 2019; Krunic & Stanisavljevic, 2006; Ladurner et al., 2002).

4.7 Genus *Protosmia* Ducke, 1900

Protosmia (Fig. 3F) are small (~3.5 to ~9 mm) and univoltine bees that are phylogenetically close to *Heriades*, *Hofferia* and *Stenoheriades* (Fig. 6) (Michez et al., 2019; Praz et al., 2008). Just like *Chelostoma* species, they have a black cuticle with white strips on the side of their abdomen (Fig. 3F) but are relatively more robust (Michez et al., 2019). 31 species are currently recognised globally, almost all limited to the Palearctic region (only one species in North America and another one in Asia) (Griswold, 2013; Le Goff & Gonçalves, 2018; Ungricht et al., 2008). 13 species occur

in Europe (Ghisbain, Rosa et al., 2023) and 12 were assessed by Nieto and colleagues (2014), among which four were assessed LC and eight DD.

Based on the available literature information, they all nest within pre-established cavities whose nature depends on the species. Some nest in hollow stems or unoccupied nests in dead wood while others (mostly in the subgenus *Protosmia*) nest in snail shells, stone crevices or reuse old nests in the ground of other bees or wasps (Griswold, 1985; Michener, 2007; Müller, 2017). They partition and plug their nest using resin but some species can sometimes incorporate pebbles (e.g., *P. rubifloris*) (Chui et al., 2022; Griswold, 1986). All are polylectic species with some showing a preference for Fabaceae and Lamiaceae (Michez et al., 2019; Müller, 2017).

4.8 Genus *Stenoheriades* Tkalcŭ, 1984

Stenoheriades is a species-poor genus of Osmiini, sister group to the genus *Hofferia*, containing only 12 described species worldwide (Ascher & Pickering, 2020; Praz et al., 2008). They superficially resemble *Chelostoma* and *Hofferia* but females have long hairs on their mandible and part of their head (Michez et al., 2019). These small bees (~5 to 7 mm) are mainly distributed around the Mediterranean region (including the Arabian peninsula) in the Palearctic but their distribution can extend as far as South Africa (including Madagascar) (Michener, 2007; Ungricht et al., 2008). There are currently two recorded species in Europe (*S. coelostoma* and *S. maroccana*) (Ghisbain, Rosa et al., 2023) and only one (*S. coelostoma,* under the name of *S. hofferi*) was assessed and classified as DD in the European Red List of bees (Nieto et al., 2014). These species are univoltine and fly from May to July in Europe (Michez et al., 2019).

There is little information regarding the nesting biology of *Stenoheriades* bees but it appears that they use insect nests in dead wood as nesting sites. Moreover, these species likely use resin to partition their nest as they are closely related to *Heriades*, *Hofferia* and *Protosmia* (Fig. 6). All species appear to be oligolectic bees specialised on Asteraceae (Michez et al., 2019; Müller & Trunz, 2014).
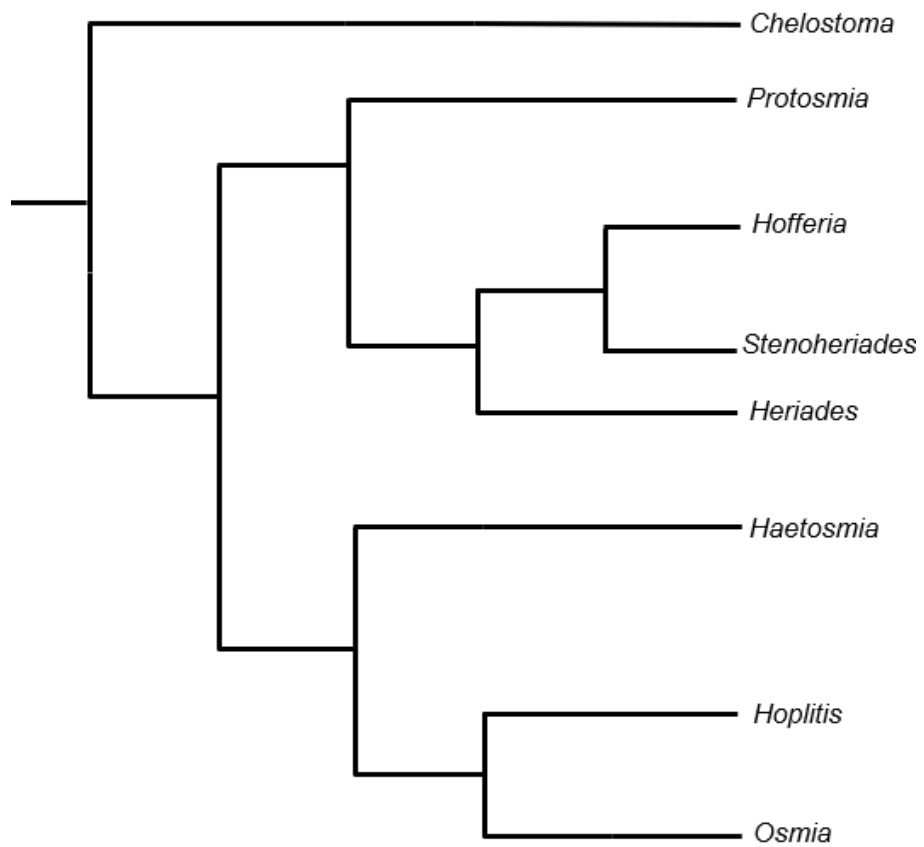
Figure 6. Simplified phylogeny of European Osmiini bees. *Modified from Praz et al. (2008).*

II.   Objective

This Master's thesis project is part of three European projects, namely ORBIT, Safeguard and Pulse. ORBIT (https://orbitproject.wordpress.com/about-the-project/) is a taxonomic and inventory project which develops resources and tools for wild bees. The objective of Safeguard (https://www.safeguard.biozentrum.uni-wuerzburg.de/) is to slow down the decline of wild pollinators. Finally, Pulse (https://www.iucnredlist.org/) aims to update the European Red List of Bees. In this context, this dissertation analyses the current threat and status of the osmiine bees (Hymenoptera, Megachilidae, tribe Osmiini) across Europe by examining their ecology, spatial distribution and extinction risk and the links between them.

The specific aims of my Master's thesis are:

(i)   Re-assess the status and trends of the osmiine bee fauna of Europe (246 species)

This first objective aims to reassess the first European Red List of 2014 by updating the current state of knowledge of the biology, geographic range and threat of species. This will provide an up-to-date and accurate view of the extinction risks of species and will allow us to coordinate and orientate action plans for pollinator conservation at the European level. It is expected to have a lower proportion of Data Deficient species and a higher proportion of Least Concern species compared to the first European Red List of bees due to the thermophilic feature of these bees.

(ii)   Analyse life-history traits linked to the status of conservation

This second objective aims to identify traits that can favour the resistance and resilience of osmiine species to global changes. By determining which traits are linked to the extinction risk, we can help predict future assessments of Data Deficient and Not Evaluated species. We hypothesise that species with lower EOO and AOO are more likely to be regarded as threatened as well as species being oligolectic.

(iii)   Predict the species range under various environmental variables

The third objective aims to model the ecological niche of osmiine across Europe using environmental variables for the present time. This will help understand the range of their suitable habitat given local environment variables, and their diversity hotspot and thus, focus on the important area in terms of conservation. Since Osmiini species in Europe have their highest species richness in Mediterranean countries, it is hypothesised that these areas represent highly suitable habitats. It is also possible that other areas such as the Mountainous ones appear as ecologically suitable as they have a lot of complex and heterogeneous habitats and some groups of Osmiini are restricted in these ecosystems.

III.   Materials and methods

1. Geographical and taxonomic scope

The geographic scope of this reassessment is the European mainland considered in the first IUCN Red List of bees (Fig. 7). This covers continental Europe which extends from Iceland in the west to the European parts of Russia in the east (delimited by the Urals). The European part of Turkey (Thrace) as well as all the Atlantic and Mediterranean Islands are also considered while the Caucasus region is excluded (Nieto et al., 2014). The species assessed in this report are all the bees in the Osmiini tribe occurring in Europe, following the latest European checklist of wild bees which includes 246 species (Ghisbain, Rosa et al., 2023). This represents 17 more species than considered in Nieto et al. (2014).
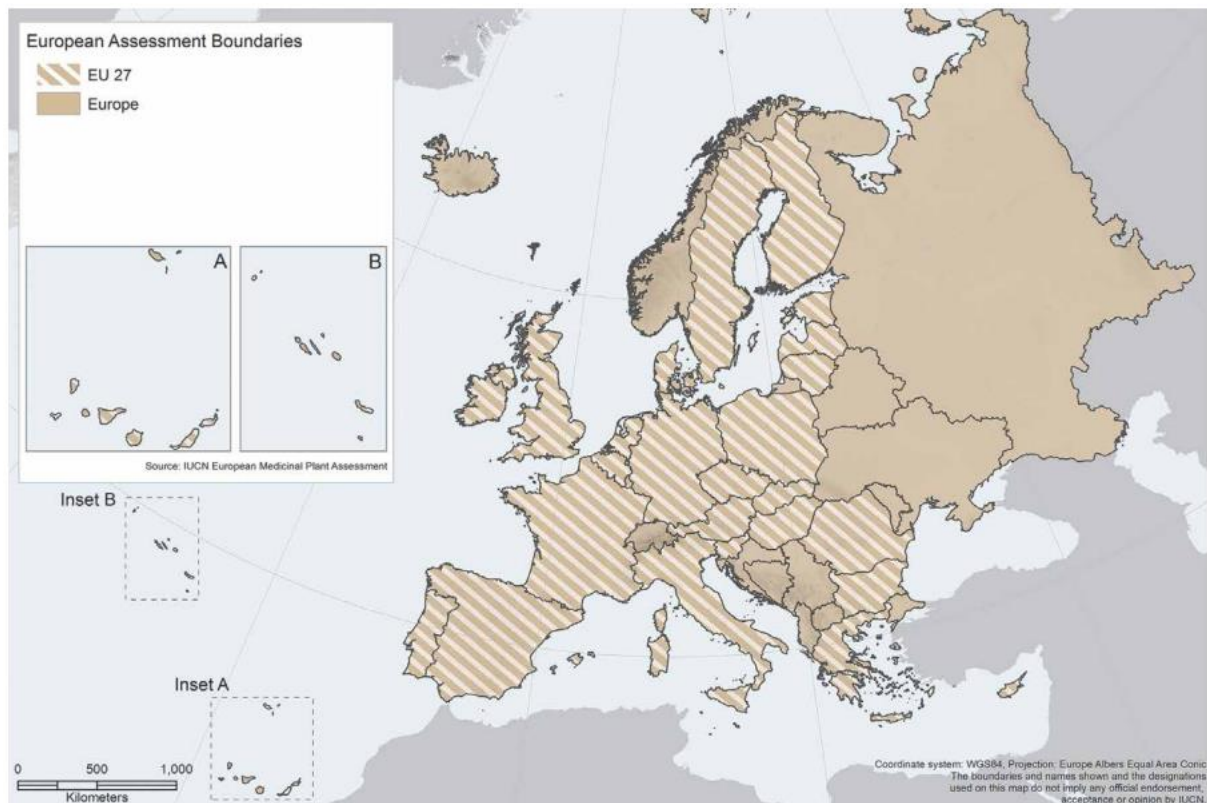
Figure 7. European boundaries used in the IUCN Red List assessment. Atlantic and Mediterranean islands as well as the European part of Turkey are considered while the Caucasus is excluded. The EU 27 level is not regarded in this report (Nieto et al., 2014).

2. IUCN Red List Assessments

To assess the species, we followed the protocol and methodology of the IUCN. Regionally, species can be classified into 11 categories (Fig. 8) based on five quantitatively set criteria based on population (size, trends and structure) and geographical range (App. 1) (IUCN, 2012a). For the

osmiine assessment, only criteria B (geographic range) and D (very small or restricted population) were used to define a threat category as data used for other criteria were lacking (i.e., population trends). If a species met any requirements of these criteria (and at least one or two supplementary conditions when it comes to criteria C and B, respectively; see Appendix 1), it was classified into one of the three threatened categories, i.e., Vulnerable (VU), Endangered (EN), Critically Endangered (CR), according to the conditions the species meet. If several categories were possible depending on one or other criterion, the taxon was classified in the highest threatened category possible. A species that did not meet the conditions for any of the criteria was classified as Least Concern (LC) but, if it nearly qualified for it or will probably meet any of these criteria soon, it was classified as Near Threatened (NT). If a species lacked enough scientific information to properly assess its extinction risk, it was classified as Data Deficient (DD). The Not Applicable (NA) category only concerns regional assessment and in this case, was applied to vagrant species or those having their natural range outside Europe (IUCN, 2012b). The reasons for a category change between the status of the first assessment and this work were also documented to distinguish species changing categories due to increasing or new threats (genuine change) or due to better knowledge about the species threat and ecology or taxonomic changes (non-genuine change).
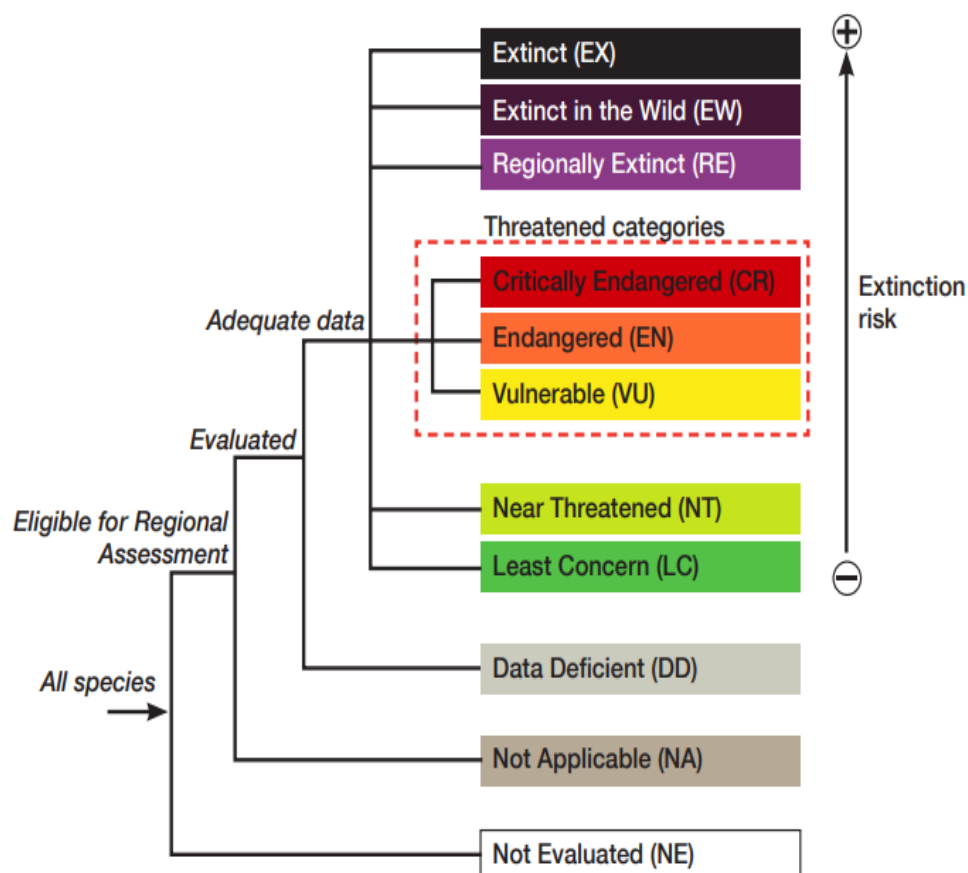
Figure 8. The IUCN Red List Categories at the regional scale. Retrieved from Nieto et al. (2014).

The required data and information that are used to assess a species are listed below:

- National and regional assessments
- Geographic Range
- Countries of occurrence
- Population information and trends
- Habitats and ecology requirements
- Species use and trade
- Threats and conservation measures
- Key references

These data were compiled and collected using relevant literature and expert-derived data to update the last pieces of information dating back to the last assessment of the European Red List of Bees (Nieto et al., 2014). These data were centralised using the Species Information Service (SIS), a platform used by the IUCN to house and manage information and assessments of species to publish it on the IUCN Red List (https://www.iucnredlist.org/assessment/sis).

The geographical data were also used to create a distribution map for each osmiine species. These distribution data are based on the previously gathered data from the first European Red List of bees (gathering more than 1,500,000 records) and were extended using published literature, open sources databases, museum collections and databases from expert databases taxonomists (App. 2). Over 5,300,000 occurrence records, and associated data if available (sex, collection date and localities, collecting method, collector, and determinator), were compiled into a single standardised database to which more than 270,000 records of European Osmiini were extracted. These distributional data were corrected (e.g., removing invalid characters, standardising the coordinates format, correcting species names, etc.) and georeferenced. Several batches of maps were then created and visually curated by experts to remove any doubtful points or those falling outside the known range of the species, but also potentially add any missing records until a consensus was reached. The validated maps (App. 3) were finally used to calculate the Extent Of Occurrence (EOO) and the Area Of Occupancy (AOO) using the 'red' package (v1.6.1; Cardoso, 2017). The EOO and AOO are two quantitative metrics for the criteria B used during the assessment of the species (Fig. 9). The EOO represents the area within the shortest imaginary boundaries containing all known occurrences of the taxon (Fig. 9B). The AOO represents the suitable area, within the EOO, that the taxon currently occupies and is measured using the total sum of the occupied cells (2x2 km) (Fig. 9C) (IUCN, 2012a).

An online workshop was finally held with national experts and IUCN members to review the gathered data and distribution maps to assign an IUCN Red List category for each osmiine species occurring in Europe.
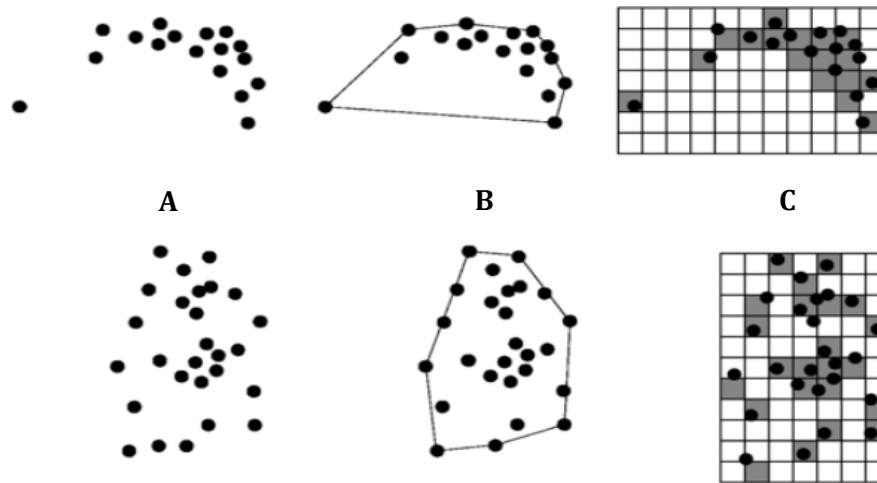
Figure 9. Examples showing the difference between the Extent Of Occurrence (EOO) and the Area Of Occupancy (AOO). *A) Spatial distribution of known occurrences of given species. B) The EOO, which is the area within the delimiting boundaries. C) The AOO, measured by the sum of the occupied cells (greyed cells). Modified from IUCN (2012b).*

3. Trait measurements

Data regarding life-history traits of species were gathered in the framework of the Safeguard project and are based on a previous private database of traits compiled by Stuart Roberts of the University of Reading. This database was further completed by compiling literature data and measurement on pinned specimens and extended by adding new traits (Tab. 1). 11 traits related to the morphology, ecology and spatial distribution of osmiine bee species were retained in this work. Other traits were not retained as they did not show enough variability among Osmiini. It is the case of sociality (all Osmiini are solitary), buzz pollination (only one species being able to buzz pollinate) and voltinism (only two species are not univoltine). All traits used, their description and associated bibliography are listed in Table 1.

The morphological traits that were considered are the hairiness index, which is an important trait modulating thermoregulation (Heinrich, 1993; May, 1979) and pollen collection (Stavert et al., 2016; Thorp, 2000), and the Inter-Tegular Distance (ITD) (Tab. 1), a proxy of the body size that can be used to estimate the foraging range (Greenleaf et al., 2007). Both traits were measured using a digital microscope (Keyence VHX-970F; ± 0.0001 mm) or a digital caliper (± 0.03 mm) for the ITD.

The **hairiness index** of an individual is obtained by multiplying its hair length by its hair density (Roquer-Beni et al., 2020). Three female specimens of a species were measured and their hairiness index was averaged to get the data for the species. To obtain hair length, five hairs of the dorsal part (mesoscutum) on each specimen were measured using the integrated measurement tool of the digital microscope. Hair density was measured on the same area by counting the hairs or their insertion point on the cuticle within two representative areas of 0.01 mm^2 (and then brought to mm^2). In the case where the hair length or density was not uniformly distributed across the mesoscutum, five more hairs or two more areas were re-measured in these distinctive areas. The hair length or density was then averaged and weighted according to the surface taken by these areas (Roquer-Beni et al., 2020). Regarding the **ITD**, it is a proxy of the body size and is measured on a minimum of five specimens per species, using the mean distance between the two tegulae, i.e., the insertion points of the wings (Cane, 1987). Only females were measured as they actively gather pollen and therefore play a more important role in pollination compared to males (Michener, 2007). Moreover, some ecological traits only concern females (i.e., nesting biology and floral specialisation).

Regarding ecological traits, data on **floral specialisation** (i.e., lecty) and **nesting biology** (nesting area, position, material and method) (Tab. 1) were compiled using published literature or online material that is based on expert opinion (mainly Müller, 2024). These two traits are widely used in trait studies as they can modify the route of exposure and therefore the impacts of pesticides and non-native pathogens (Lundin et al., 2015; Raine & Rundlöf, 2024; Williams et al., 2010). The lecty and the nesting biology can also modulate the response of the species to habitat loss and fragmentation (Bennett & Lovell, 2019; Williams et al., 2010).

Finally, the geographical traits include the **AOO**, used as it represents the suitable habitats occupied by the species, the **EOO,** representing the geographical range, (see above) and the **Species Continentality Index** (SCI) and **the Species Temperature Index** (STI), two traits representing the climatic niche of the species (Tab. 1). SCI and STI are derived from the occurrences and geographic distribution of a given species, gathered in the framework of the re-assessment of the European Red List of Bees (see point two: IUCN Red List assessment). These distribution data were mapped either into 1 km x 1 km or 50 km x 50 km UTM grid cells, depending on the sampling effort of the area (high or low respectively) (Rasmont et al., 2015). The climatic data (seasonality for SCI and temperature for STI) from each cell where a species occurs were extracted and then averaged to compute the SCI and STI. These measurements were finally weighted by the ratio of the number of occurrences of the species to the number of bee occurrences in the cell (Duchenne et al., 2020; O'Donnell & Ignizio, 2012).

Table 1. Summary of life-history traits used in this report. Traits marked with an asterisk (*) were not included in the original database of the University of Reading and were collected during this work. Other traits (ITD, Lecty, Nesting) were already compiled but were either completed or validated using new measures or literature sources.

Trait	Unit	Categories	Definitions	References
Hairiness index*	NA	NA	Quantitative measure of hair length and hair density	Roquer-Beni et al., 2020
Inter-Tegular Distance (ITD)	mm	NA	Proxy of the body size, measured using the mean distance between the tegulae	Cane, 1987
Lecty	NA	Oligolectic Polylectic	Floral specialisation based on the range of pollen collection of female bees **Oligolectic**: collect pollen from one plant family/genus **Polylectic**: collect pollen from more than one plant family	Cane & Sipes, 2006; Dötterl & Vereecken, 2010
Nesting area	NA	Snail shell Plant Rock Soil Variable	The area where the nest is constructed **Plant**: in stems, wood, gall **Rock**: in walls, on surfaces or cracks of stones **Soil:** in the ground **Variable**: within several categories	Protocol from the Safeguard project
Nesting material*	NA	Plant Mineral Plant/mineral Variable	The materials used to construct or partition the nest **Plant**: leaves, nectar, petals, resin, wood **Mineral**: mud, pebbles, sand, earth **Plant/mineral**: mixture of the two categories **Variable**: incorporate snail shells or insects cuticle in at least one of the aforementioned categories	Protocol from the Safeguard project
Nesting method	NA	Excavator Mason Renter Generalist	Method of nest construction **Excavator**: burrow its nest within a substrate **Mason**: build entirely its nests using loose materials **Renter**: construct its nests in a preestablished cavity **Generalist**: use several methods	Williams et al., 2010 Protocol from the Safeguard project
Nesting position	NA	Above ground Underground Variable	Position of the nest Variable is for species that can nest under and above ground	Protocol from the Safeguard project
Area Of Occupancy (AOO)*	Km^2	NA	The suitable area, within the EOO, that the taxon actually occupies	IUCN, 2012a, 2012b
Extent Of Occurrence (EOO)*	Km^2	NA	The area within the shortest imaginary boundaries containing all known occurrences of the taxon	IUCN, 2012a, 2012b

Species Continentality Index (SCI)*	NA	NA	Temperature seasonality, i.e., the variability of temperature that occurs throughout a species range	Duchenne et al., 2020; O'Donnell & Ignizio, 2012
Species Temperature Index (STI)*	°C	NA	The mean annual temperature to which a species is exposed throughout its range	Devictor et al., 2008; O'Donnell & Ignizio, 2012

4. Ecological niche modelling

4.1 Generalities and data acquisition

Ecological niche models (ENMs) are statistical tools used to predict species ecological niches across a given area based on both environmental and geographic data of a species (Elith & Leathwick, 2009). In this report, the spatial extent of the models is geographical Europe as defined by the IUCN Red List (see point 1: "Geographical and taxonomic scope"). The environmental data were retrieved from the Inter-Sectoral Impact Model Intercomparison Project phase 3 (ISIMIP3: https://www.isimip.org/protocol/3/) and comprised climatic (i.e., temperature, precipitation and relative humidity), land use (croplands, pastures, primary and secondary forest areas as well as primary and secondary non-forest areas) and human population data at a spatial resolution of 0.5° (55.5 km) from 2000 to 2019.

Regarding the presence records, they were retrieved from the aforementioned projects. These data were previously checked by expert taxonomists to remove any outliers and doubtful records falling either inside or outside the known range of species. Using the function clean_coordinates of the package 'CoordinateCleaner' (v.3.0.1; Zizka et al., 2019), we also excluded records whose coordinates were equal to zero, assigned to capital cities (within a radius of 10,000 m) and based imprecisely on centroids of countries and provinces (within a radius of 1,000 m) to avoid the spatial uncertainty of georeferenced records. We further retained species having a minimum of 30 unique occurrences (as suggested by Wisz et al., 2008) in the same grid size as the environmental data, i.e., 0.5° (55.5 km). This approach was implemented in similar recent studies which removed duplicate records to limit the effect of sampling bias and also to take into consideration the presence of the species rather than its density (Erazo et al., 2024; Ghisbain et al., 2024). While the temporal range of the occurrence data extends from 1800 to 2023, only the records with a collection date between 2000 and 2019 were retained to match the temporal range of the environmental data. Out of the 270,000 initial records, around 10,000 records from 66 species and four different genera (*Chelostoma, Heriades, Hoplitis* and *Osmia*) were retained (App. 4).

4.2   Boosted regression trees

A BRT approach using the 'dismo' package (v.1.3.14; Hijmans et al., 2023) was implemented to compute all the ecological niche modelling analyses. BRT is a machine learning method that builds an assemblage of sequential regression trees that are fitted iteratively by gradually focusing on observations that are poorly predicted by the current set of trees. This enhances the prediction probabilities of occurrence under a set of environmental conditions (Elith et al., 2008). This predictive probability is regarded as an ecological suitability measure, ranging from zero if the environmental conditions are not suitable to one if otherwise.

This approach was implemented using both presences and pseudo-absence records. The latter represents the range of environmental conditions across the modelled region (background environment; Guisan et al., 2017) and were randomly selected throughout the study area. These pseudo-absence points were sampled in grid cells where our target species has not been recorded and where at least one other species occurrence was recorded in the dataset. By doing so, we ensure to select background data in grid cells that have received at least some sampling effort for our taxonomic group of interest (Phillips et al., 2009). The number of selected pseudo-absences points was then equally weighted in accordance with the number of presence records (ratio 1:1) (Barbet-Massin et al., 2012). Only one presence record per grid cell was retained as only one occurrence is required to consider the species present. The same process was applied to pseudo-absence data.

Since spatial data are often autocorrelated, which could lead to model overfitting, a spatial cross-validation procedure was implemented based on the block generation of the 'blockCV' package (v.3.1-4; Valavi et al., 2019). Following this method, the dataset containing the presence and pseudo-absence data was divided into five spatial folds treating geographical units sharing analogous characteristics together. We trained models over similar parameters used in recent studies (see Erazo et al., 2024; Ghisbain et al., 2024). The BRT models were trained over ten replicates, using a tree complexity of five, a learning rate of 0.001, a step size of ten, an initial number of trees of 100 and a tolerance parameter of 0.001. The performance of the models was evaluated using the Area Under the receiver operating characteristic Curve (AUC), a value of 0.5 corresponds to random predictive performances of the model while a value of one corresponds to perfect accuracy.

5. Analytical framework

All analyses were performed using the R software (v. 4.3.0; R Core Team, 2023). The DD or NA species were removed from the analysis as their extinction risks are not defined. The other status were grouped into two categories: the LC category, containing all Least Concern species that are not threatened and a Red Listed category, "RL", containing all species being threatened or Near Threatened (NT) in the future. The links between each trait and the status of European osmiine bees were then assessed with Generalised Linear Models (GLM) with a binomial probability distribution using the 'glmmTMB' package (v. 1.1.9; Brooks et al., 2017). These tests were performed using a significance level of 5%. The package 'DHARMa' (v. 0.4.6; Hartig, 2022) was used to run the residual analysis and ensure that the application conditions were respected. Graphical representations were realised using the 'ggplot2' package (v. 3.5.1; Wickham, 2016).

IV. Results

1. Status and threats of European osmiine bees

The reassessment of status among European osmiine bees reports 3.2% of threatened species (eight species of 246). Among these threatened species, 1.2% are EN (three of 246 species), 2.0% are VU (five of 246 species) and a further 3.3% of species are NT (eight of 246 species) (Fig. 10B). These species represent three genera of osmiine (*Chelostoma, Hoplitis* and *Osmia*) among the eight genera present in Europe and are all listed in Table 2. The only species assessed as EN in Nieto et al. (2014), *Osmia maritima*, is still assessed as EN in our results (Tab. 2). Other threatened and Near Threatened osmiine species were either DD (11 species), LC (three species) or Not Evaluated (one species) in the previous assessment and have seen their status changed following better knowledge of their distribution, ecology and threats (non-genuine).

The reasons for the decline of the threatened species are species-dependent with some being threatened by urban sprawl and tourism (*Hoplitis cypriaca*, *H. fulva* and *Osmia maritima*), while other, notably alpine (*Hoplitis saxialis,* restricted to high mountains of the Alps, Greece and Russia) and Nordic (*Osmia svenssoni,* occurring in the arctic part of Finland and Sweden) species, are threatened by global warming and also overgrazing. For others (*Hoplitis bicallosa, H. galichicae and H. holmboei*), the nature of the threats are not identified but were classified as endangered due to their small and restricted populations prone to extinction in a short period due to stochastic events. In addition to these endangered species, there are also Near Threatened species that do not currently fall under either of the IUCN threatened species criteria but may very well be in the near future. These species are globally under the same threats as the endangered species, i.e., global warming and overgrazing for the alpine species (*Chelostoma grande*, *Osmia alticola* and *O. steinmanni,* three species restricted to alpine meadows found in the high altitudes of the Alps) or habitat degradation (touristic development for *Osmia iberica* and *O. rutila,* two species occurring in sand dunes of Southern Iberia) and alteration (increased wildfire in the Canary Islands for *O. larochei*, a species occurring in pine forest of Gran Canaria) for more Mediterranean species.

The proportion of DD species compared to the first assessment decreased from 47.4% (109 of 229 species) to 7.3% (18 of 246 species). These DD species were either taxon with no occurrence records to calculate their EOO and AOO or taxon with poorly known distribution, ecology, habitats and population trends. Most of the previously assessed DD species were transferred into the LC category, which increased from 52.2% (119 of 229 species) to 73.6% (181 of 246 species) (Fig. 10). With the exception of one species (*Hoplitis fulva*), none of the previously assessed LC species changed category in this reassessment. Moreover, 12.6% of species (31 of 246 species) are now

classified as NA as their distribution range is marginal in Europe. The detailed criteria and the final IUCN Red List categories of all European osmiine bees are listed in Appendix 5.
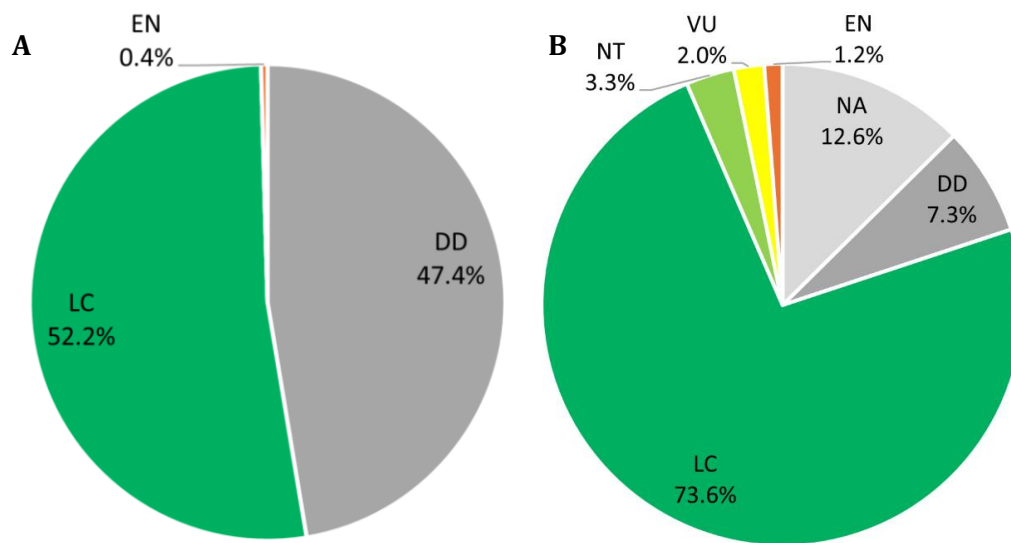
Figure 10. Status of conservation of European osmiine bee in 2014 (A) and 2024 (B). LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; DD: Data Deficient; NA: Not Applicable. Note that the total number of species differs between both assessments (229 in 2014, 246 in 2024 based on the updated checklist of (Ghisbain, Rosa et al., 2023)).

Table 2. Threatened and Near Threatened osmiine bee species at the European level. Status of 2014 are also listed for comparison (Nieto et al., 2014). DD: Data Deficient; LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered. One species, Hoplitis galichicae *, was not evaluated in the 2014 Red List as the species was not yet described.*

Species	IUCN Red List Category of 2014	Reassessment of the IUCN Red List Category
Hoplitis bicallosa	DD	EN
Hoplitis cypriaca	DD	EN
Osmia maritima	EN	EN
Hoplitis fulva	LC	VU
Hoplitis galichicae	Not considered	VU
Hoplitis holmboei	DD	VU
Hoplitis saxialis	DD	VU
Osmia svenssoni	DD	VU
Chelostoma grande	DD	NT
Hoplitis insularis	DD	NT
Osmia alticola	LC	NT

Osmia iberica	**DD**	**NT**	
Osmia larochei	**DD**	**NT**	
Osmia melanura	**LC**	**NT**	
Osmia rutila	**DD**	**NT**	
Osmia steinmanni	**DD**	**NT**	

2. Traits collection

The compilation and measurement of new traits in this work enabled us to complete the original database of Stuart Robert (University of Reading, UK) (Tab. 3). The hairiness index is the trait that has the most unmeasured species with around 65% of species missing data (159 out of 246 species). Other morphological (ITD) and ecological traits (nesting area, material, method and position) are more or less completed with around 50 to 60% of species with data. The traits having the highest coverage are the lecty and the geographical traits (EOO, AOO, SCI, STI) with only 11.8% (29 out of 246 species) and 5% (12 out of 246 species) of species missing data, respectively.

Table 3. Summary and proportion of each trait in the two respective databases. The original database of Stuart Robert contained 239 species while the one in this work contains 246 species. The proportion for the hairiness index only contains species with more than 3 measured specimens per species while the proportion for the ITD contains only species with five or more measures per species. Minimum and maximum values are given in brackets after the median values.

Trait	Data coverage in the original database	Data coverage in this work	Proportion in each category	Median (min-max)
Hairiness index	/	35.4%	/	114.67 (27.5 – 395.32)
Inter-Tegular Distance (ITD)	10%	56.1%	/	2.23 mm (0.91 mm – 3.92 mm)
Lecty	53.5%	88.2%	Oligolectic: 50% Polylectic: 38.2% NA: 11.7%	/
Nesting area	53.5%	55.3%	Plant: 10.1% Rock: 9.34% Snail shell: 9.75% Soil: 11.7% Variable: 14.2% NA: 44.7%	/
Nesting Material	/	50%	Mineral: 11.3% Plant: 19.5% Plant/mineral: 16.2% Variable: 2.84% NA: 50%	/

Nesting method	53.5%	67.5%	Excavator: 12.6% Generalist: 5.69% Mason: 1.22% Renter: 47.97% NA: 32.52%	/
Nesting position	53.5%	58.5%	Above ground: 41.05% Underground: 11.38% Variable: 6.1% NA: 41.46%	/
Extent Of Occurrence (EOO)	/	95.1%	/	407702 km^2 (15 km^2 – 10713049 km^2)
Area Of Occupancy (AOO)	/	95.1%	/	112 km^2 (4 km^2 - 40064 km^2)
Species Continentality Index (SCI)	/	95.1%	/	6.30 °C (2.38 °C – 11.31 °C)
Species Temperature Index (STI)	/	95.1%	/	14.04 °C (-1.15 °C - 20.78 °C)

3. Relationship between threat status and traits

Among all the tests performed, only two traits had a significant relationship with the IUCN Red List categories: the EOO and the STI. All *p*-values and associated metrics of these tests are listed in Appendix 6.

A significant difference was reported between the EOO values of threatened/Near Threatened species (RL category) and non-threatened species (LC category), with the LC species showing a significantly broader EOO than the RL species (GLM, χ^2 = 11.371, df = 1, *p*-value < 0.001) (Fig. 11). On the other hand, the AOO values were marginally significant with RL species having almost a significantly lower AOO (GLM, χ^2 = 3.3888, df = 1, *p*-value = 0.06564).
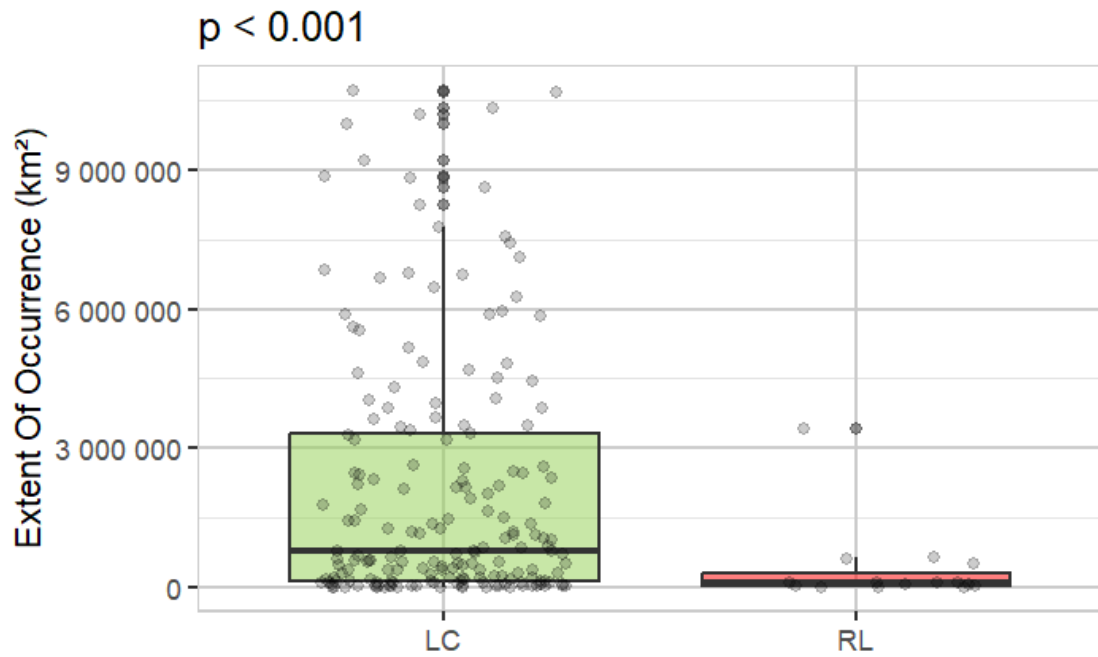
Figure 11. Values of the Extent Of Occurrence (EOO) in threatened/Near Threatened and non-threatened species. *LC: Least Concern; RL: Red Listed (including Near Threatened, Vulnerable and Endangered species). The p-value of the GLM is reported on the top left.*

Likewise, the STI values significantly differ between RL and LC species, the latter having a significatively greater STI than the RL species (GLM, χ^2 = 5.0671, df = 1, *p*-value = 0.02438) (Fig. 12).
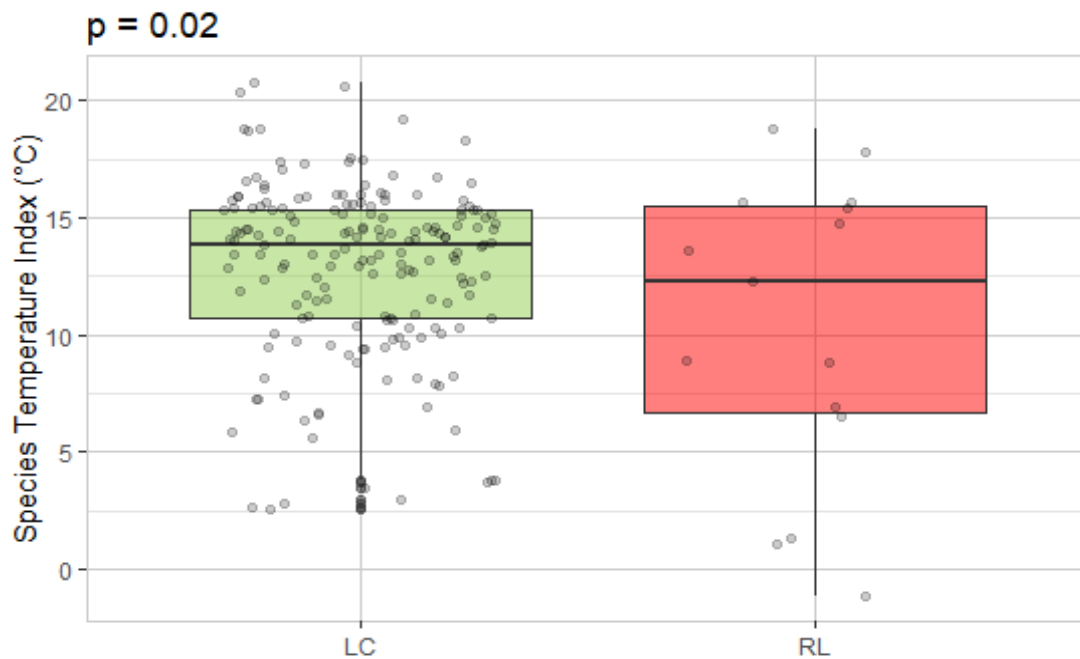
Figure 12. Values of the Species Temperature Index (STI) in threatened/Near Threatened and non-threatened species. *LC: Least Concern; RL: Red Listed (including Near Threatened, Vulnerable and Endangered species). The p-value of the GLM is reported on the top left.*

4. Ecological niche modelling

The median prediction performance of our 66 models of European osmiine species is shown in Figure 13. Under current environmental conditions, the models globally predict a south-to-north gradient characterised by decreasing ecological suitability. The area with the highest ecological suitability mainly comprised the Mediterranean basin in southern Europe, extending from the Iberian Peninsula (Portugal and Spain) to Greece (including Crete and Aegean Islands). It also includes Mediterranean islands such as the Baleares, Corsica, Sicilia, Sardinia and Cyprus and Atlantic ones such as Madeira and the Canary Islands. Other suitable environmental conditions are located in mountainous areas of western Europe such as the Alps, notably the French, Italian and Swiss parts, the Jura and the eastern part of the Massif Central. Moderate suitable conditions include some parts of inland Spain, especially in the north and also part of Eastern Europe, including the Balkans (excluding Greece which is more suitable), Ukraine and southern European Russia. Northernmost areas are predicted to have low suitability environmental conditions, especially in Scandinavian countries and northern European Russia.

Model performance, computed by the AUC, ranged from 0.585 (*Hoplitis anthocopoides*) to 0.941 (*Osmia dimidiata*). While some species were poorly modelled with AUC values barely above random predictions, the overall accuracy relatively was high with a median AUC value of 0.794. Mean AUC values, as well as the retained number of occurrences data for each species, are reported in Appendix 4.
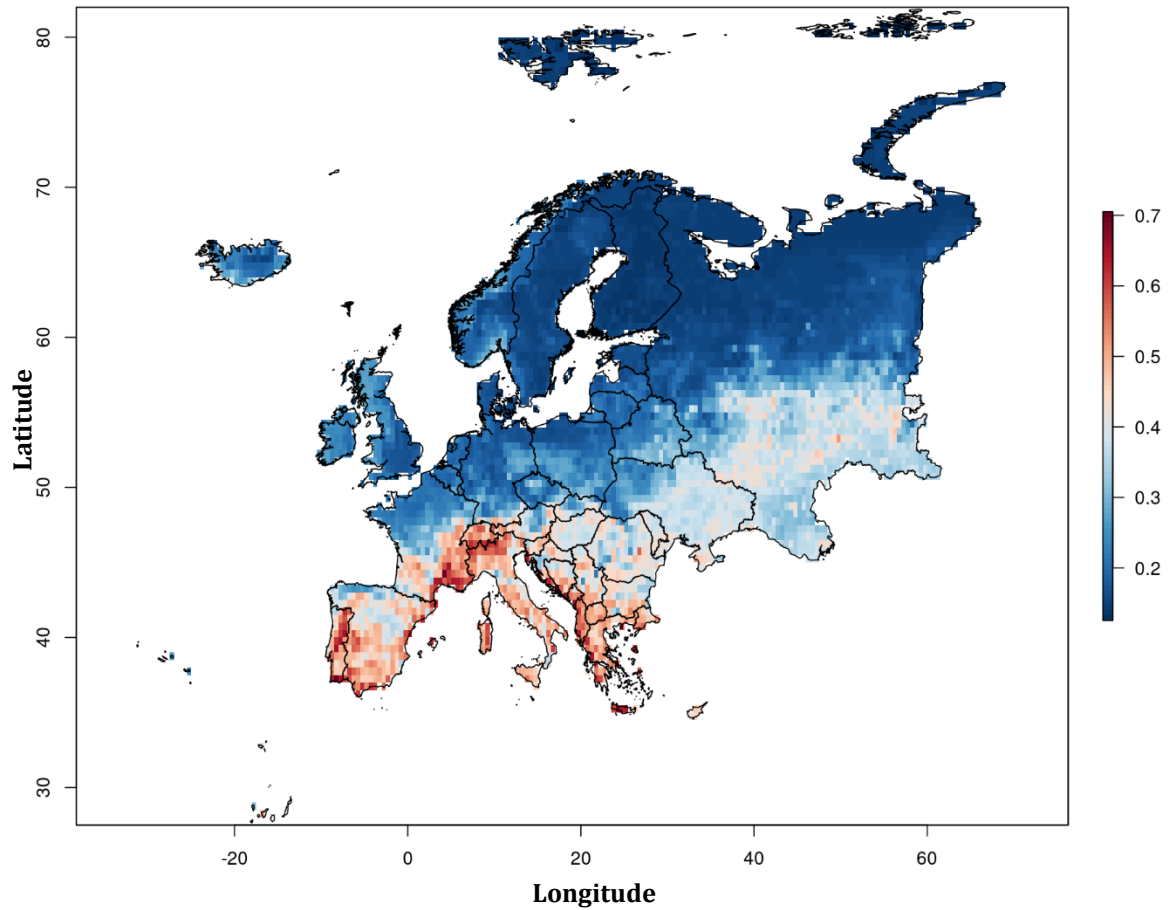
Figure 13. Ecological suitability map for 66 osmiine species in Europe. *Ecological suitability values are given by the coloured bar gradient and are computed using the median value of model performance over ten BRT model replicates. This value was estimated for the present time (2000-2019) based on environmental data obtained through ISIMIP3 and 9963 unique occurrence data for 66 European species of Osmiini.*

V.   Discussion
1. Red List reassessment of European osmiine bees
1.1   Status and threats

The results of this study highlight a much lesser uncertainty regarding the threat status of European osmiine bee species compared to Nieto et al. (2014). Although the extinction risks of 7.3% of species (DD species) remain undefined, 80.1% of species had adequate data to be properly assessed. More research needs to be carried out to define a more adequate category for the remaining DD species (18 of 246 species) but overall, the conservation status in Europe for the Osmiini seems to be not critical with over 73% of LC species. Osmiine bees represent, for most, thermophilic species that appear to benefit from climate change. For example, several species (e.g., *Heriades rubicola*, *Hoplitis anthocopoides*, *Osmia cornuta*) were reported to expand their range in the northernmost countries of their distribution following global warming (Cross & Notton, 2017; Högmo, 2019; Holmström, 2014; Saure & Wagner, 2018). Expanding its range in response to climate change is documented in other pollinators (e.g., butterflies; carpenter bees) and may be linked to milder winters lowering larval mortality (Banaszak et al., 2019; Crozier, 2003, 2004). There are also a lot of stem nesting species among osmiine species which may implement new populations in distant places due to global trade as seen in North America (Cane, 2003). If not expanding, species can also remain stable and retain their initial distribution due to better heat tolerance and plasticity (Ghisbain et al., 2021).

While being classified in the LC category does imply lower risks of extinction compared to threatened species, it does not exclude taxa declining locally. However, such species do not meet the requirements of the IUCN criteria for a threatened category nor decline sufficiently fast to be classified in the NT category at the moment. For example, *Osmia nigriventris*, *O. pilicornis* and *O. uncinata,* three boreo-alpine and cold-adapted species classified as LC, have declining populations over their range due to habitat alteration and climate change slowly reducing the suitability of their habitat, but this is still unquantified (Müller et al., 2019, 2020; Prosi et al., 2016). Another example is the 55 species (out of the 246 European species) being classified into one of the threatened categories in at least one national Red List, 17 of them are even classified as Regionally Extinct (RE) in these lists while being considered LC at the European level (Drossart et al., 2019; Falk, 1991; Głowaciński et al., 2002; Hejda et al., 2017; Hyvärinen et al., 2019; Kålås et al., 2010; Müller & Praz, 2024; Radchenko, 2009; Reemer, 2018; SLU Artdatabanken, 2020; Soon, 2020; Westrich et al., 2011; Wraber et al., 2002). This apparent mismatch between regional and national assessments might be explained by the differences in pressure experienced by local populations.

Smaller and localised populations are typically considered during national assessments and are more likely to highlight the effects of local threats compared to larger populations considered at a European scale (Herrera, 2019). Some species might also be at the limit of their range, with small and vulnerable populations being regarded as threatened in some countries. This issue of LC species that could slowly and locally decline was highlighted by a recent study modelling the projected decline of European bumblebees that demonstrated that several LC species are projected to decline due to global warming and land-use change (Ghisbain et al., 2024). This emphasises the potential underestimation of the IUCN Red List method to accurately capture the actual decline of population trends of some LC species.

While localised decline is concerning, it is also important to acknowledge the threatened species facing significant decline over their entire range. The results highlighted that eight species (eight of 246; 3.2%) were threatened at the European level, mainly due to climate change, overgrazing and habitat loss. To our knowledge, only one threatened and one Near Threatened species currently occur within a protected area. *Osmia iberica* occurs in two protected sites in Portugal while *Osmia maritima* occurs in three protected sites across Sweden and Norway. The latter had benefited from a national action plan in Sweden that recommended several conservation measures such as (i) restoration of coastal dunes where the species occurs, (ii) research to improve knowledge on its biology and distribution and (iii) public communication for awareness (Cederberg et al., 2010). Although this species is still assessed as EN in this work, positive population trends were observed at some rehabilitated sites and conservation efforts must continue (Bergquist & Erlandsson, 2019). This set an example of effective conservation measures whose protocol could be used to protect species inhabiting similar habitats or be the basis for future action plans for other threatened species.

Compared to the first Red List assessment, the number of threatened species increased from one to eight. Adding the NT species adds up to sixteen species. It is not possible to affirm that growing threats are affecting the population trends of these species as all of them were transferred into a threatened or NT category following a better overall knowledge about the species ('non-genuine changes' following the nomenclature of the IUCN; IUCN, 2012a). This highlights the importance of compiling sufficient knowledge on the ecology and distribution of species as the latter may incorrectly be referred to as not threatened because of a lack of information.

1.2 Comparison with other bees and pollinators

Regarding the status of all European bees, about 9% are NA (198 of 2096 species), 19% are DD (393 of 2096 species), 55.5% are LC (1162 of 2096 species), 8% are NT (166 of 2096 species) and 8.5% are threatened (177 of 2096 species) (unpublished data). In comparison, the status of European Osmiini is less worrying overall with 20% more LC species and 5% less threatened species. However, the overall situation of European bees displays mixed responses in different groups. For example, species with similar ecologies to Osmiini (solitary, thermophilic and cavity-nesting bees) such as yellow-faced bees (Colletidae: *Hylaeus*) and the leaf-cutting bees (Megachilidae: *Megachile*) have similar extinction risks with respectively 5.5% (5 of 88 species) and 5.2% (4 of 76 species) of threatened bees. On the other hand, cold-adapted species such as the bumblebees (Apidae: *Bombus*) show greater extinction risks with more than 20% of threatened species (15 of 67 species) and a further 20% NT species (14 of 67 species) (unpublished data). This difference in the assessment of different groups likely resides in their respective ecology and life-history traits (as discussed below) (Cariveau & Winfree, 2015; Winfree, 2010), with bumblebees showing, for most species, an overall population decline due to their sensitivity to heat and land-use changes (Ghisbain et al., 2024; Goulson et al., 2008; Kerr et al., 2015; Rasmont et al., 2015).

Some other pollinators across Europe show similar extinction risks, with 10.7% of saproxylic beetles (Coleoptera) and 9% of butterflies (Lepidoptera: Hesperiidae, Riodinidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae) being in a threatened category (Nieto & Alexander, 2010; Van Swaay et al., 2010). However, the hoverflies (Diptera: Syrphidae) are much more sensitive to anthropogenic drivers with 37.2% of species being in a threatened category (Vujić et al., 2022). The worrying situation of hoverflies can be compared to the situation of bumblebees (Apidae: *Bombus*) where 20% of species are threatened. Likewise, many threatened hoverflies occur in mountainous areas (the Alps and Rhodopes Mountains) that are increasingly under threat due to overgrazing and climate change.

While some of the threats regarding these groups are rather specific to their ecology (e.g., logging and wood harvesting for saproxylic beetles), other threats such as climate change, agricultural intensification and urbanisation or development of tourism often come up in the top five causes of decline. This highlights the widespread impact of these threats that drive the decline of several groups of pollinators, not only bees.

2. Relationship between threat status and traits

2.1 Geographical traits

Out of the different tests performed, only two geographical traits had values that significantly differed between the conservation status of osmiine bees in Europe: the Extent of Occurrence (EOO) (Fig. 9) and the Species Temperature Index (STI) (Fig. 10).

The EOO values of LC species are significantly greater than the ones of RL species. Having a greater EOO is therefore linked with a lower probability of extinction risks. Even if the assignment of a threatened category is based, among others, on EOO and thus a relationship was expected, the species still needs proof of declines or a fragmented population to be assessed as endangered using this trait. For example, several species having a low EOO (e.g., *Chelostoma aegaeicum*, *Hoplitis cadiza*, *Osmia jason*, *Protosmia maroccana*) were still assessed as LC. Moreover, this shows a trend in this tribe of bees demonstrating that, overall, species having a lower EOO have higher extinction risks of species. If species with a lower EOO are more likely to be threatened, it is because populations with a smaller geographic range are more sensitive to local and stochastic threats that might strongly impact the population, without other populations being able to mitigate the impact at a global scale (Işik, 2011; Ovaskainen & Meerson, 2010). Likewise, we expected a significant relationship between the AOO of threatened/Near Threatened and not-threatened species but the test was only marginally significant. The reason might be that the AOO is more sensitive to sampling bias than the EOO is and fails to capture the habitat that the taxon actually occupies (Marsh et al., 2023). The EOO is the area within boundaries that contains all known occurrences of the species and therefore is more likely to take into account under-sampled sites that may be occupied by the taxon while the AOO, which is calculated based on the grid cells actually occupied by the species, does not. This may result in lower differences between the AOO of threatened/Near Threatened and not-threatened species which explains the non-significant result of the test, despite the higher risks linked to smaller and localised populations.

Regarding the STI, species with a greater STI are significantly less likely to be classified as threatened than species with a lower STI. Although several Mediterranean species with high STI were classified into a threatened category, the significant trend is that a lower STI is linked to greater extinction risks as it predominantly concerns alpine or arctic species with a narrower climatic niche. Several of these species have very low STI (e.g., -1.15°C for *Osmia svenssoni* and 1.30°C for *O. alticola*) matching values of bumblebee species highly affected by global warming as modelled by Rasmont et al. (2015). Several LC species also have low STI values (e.g., 2.55°C for *Osmia nigriventris*, 2.67°C for *O. laticeps*, 2.82°C for *Hoplitis robusta*) and could be threatened in

the future by climate change as highlighted by our result. The SCI values were also expected to be significant between LC and RL species with higher values being associated with greater extinction risks as they can be influenced by more intense extreme climatic events such as heat waves or drought (EPA, 2021; Walsh et al., 2020). Although these events are already reported to impact some species (Martinet, Dellicour, et al., 2021; Rasmont & Iserbyt, 2012; Vilchez-Russell & Rafferty, 2024), it may be possible that they are not sufficiently marked to cause an observable decline within a higher taxonomic group of species. Moreover, the SCI is calculated throughout an entire year and does not inform us whether the temperature seasonality was higher during an active period of the bee or its larval development. Since either of the life stages responds differently to seasonality (Kingsolver et al., 2011), it could potentially mask any significant result if it affects a more resistant stage. An interesting complementary metric would be to specifically look at the seasonality during a specific life stage of the species to untangle the differential effect that it may have depending on the development stage of the species.

2.2 Morphological traits

The other tests did not highlight any significant links between the values of morphological traits and the categories of ecological traits of the threatened/Near Threatened and non-threatened species. This may be the result of mixed to contradictory effects of global changes that impact life-history traits in different ways at a continental scale. For example, larger species are favoured in fragmented areas as body size is linked to higher dispersal capacity (Warzecha et al., 2016). They also have a higher forage range compared to smaller bees and are therefore able to compensate for the lack of floral resources in patchy areas (Brasil et al., 2023; Greenleaf et al., 2007). However, small-bodied ones are more tolerant to increased temperature thanks to a greater surface-to-volume ratio which promotes better heat loss (Gardner et al., 2011). In response to increased temperature (in the context of global warming or even heat-islands in urbanised areas), small species are therefore favoured compared to bigger ones (D. J. Johnson & Stahlschmidt, 2020; Merckx et al., 2018; Pardee et al., 2022). It must be noted that around 45% of species lack data regarding their body size (Tab. 3). This lack of knowledge could also impair the results of this study.

Regarding hairiness, it plays an important role in several physiological and ecological functions of species. First, hairiness is important for thermoregulation as it creates an insulation layer which reduces heat loss (Heinrich, 1993; May, 1979). Some studies have demonstrated inter- and intraspecific hair length variation with longer hair being favoured in cooler climates and across altitudinal gradients (Peat et al., 2005; M. K. Peters et al., 2016). Hairiness could therefore be an important trait modulating response to climate change. It could also play an important role in

desiccation tolerance as another study on caterpillars demonstrated that hairless specimens lose more water than hairy ones (Casey & Hegel, 1981). This might indicate that species with lower hairiness index would be more sensitive to drought conditions, which are expected to be more frequent, longer and more intense in the future (Spinoni et al., 2018). Other studies suggest that hairiness could modulate pollen collection and its effectiveness (Stavert et al., 2016; Thorp, 2000) and also provide an effective barrier against predators and parasitic as shown in other insects (Lindstedt et al., 2008; Sugiura & Yamazaki, 2014). The interplay of these functions and how they vary in response to different global threats is relatively understudied, but might have contradictory effects as highlighted by the aforementioned examples and explains the non-significance of our results. Similarly to the ITD, the data coverage for the hairiness index is poor with around 75% of species lacking data (Tab. 3) and may influence the results.

2.3   Ecological traits

Likewise, the lecty category did not impact the assigned status, likely for the same reasons that one or another category is favoured depending on the context. Polylectic species are less impacted by the loss of floral resources induced by habitat fragmentation and alteration thanks to the higher plasticity of host plants (Dötterl & Vereecken, 2010; Kline & Joshi, 2020). Additionally, oligolectic species have higher infection risks to pathogens and might be more affected by this threat compared to polylectic ones (Ellner et al., 2020; Tiritelli et al., 2024). Although oligolectic species may also struggle more with competition with other pollinators (especially honey bees) (Martins, 2004), their specialisation may compensate for this impact by showing higher efficiency which outcompetes polylectic species (Dobson & Peng, 1997; Strickler, 1979). Besides, oligolectic species also better track the environmental cues predicting the availability of their host plants in drought conditions, which could be an advantageous trait in areas where it is expected to have more frequent and intensive droughts (Minckley et al., 2000, 2013). Furthermore, many European osmiine species are specialised foragers of Asteraceae (43 out of 123 oligolectic species), which is a diverse and cosmopolitan family of plants. Therefore, these bees are potentially less impacted by the loss of floral resources.

Finally, none of the traits regarding the nesting biology (nesting area, material, method, position) were significantly linked to extinction risks in our analysis. Several studies have demonstrated the impact of pesticide exposure in the case of ground-nesting bees. Pesticides are highly persistent chemical compounds in the soil (Bhandari et al., 2020) which represents a consequential exposure route to ground-nesting bees. By the nature of the nest, these species are highly exposed to contaminated soil during their larval development and also as active adults by digging in the soil. Even if the bee is a cavity nester above ground, they can still be subjected to

harmful residues as many species handle some kind of derived ground material (e.g., soil, earth, sand) to build the nest (Sgolastra et al., 2019), which is especially widespread among osmiine bee species (Müller, 2024). This is corroborated by a recent study that demonstrated impaired development and reduced adult longevity of the cavity-nesting bee *Osmia lignaria* following exposure to contaminated soil (Anderson & Harmon-Threatt, 2019). Pesticides are not only restrained to soils as they can be volatile compounds (Ferrari et al., 2003), and therefore, it is likely that the usage of other nesting materials (e.g., leaves, resin, petals) may also lead to some kind of exposure but this remains largely unexplored (Raine & Rundlöf, 2024). Although ground-nesting bees seem to be more thoroughly exposed to pesticides, they may be favoured in the context of climate change. For example, the soil may keep the nest relatively moist and provide an isolation layer protecting it from increasing temperature (Harmon-Threatt, 2020). Another consequence of climate change hypothesised by Harmon-Threatt (2020) is that species using certain plant materials may suffer from a lesser availability of these materials due to temporal mismatches, but that remains to be investigated. Habitat alteration also impacts nesting traits but once again, differently depending on the context. For instance, urbanised areas contain a lot of impervious surfaces, which decreases the availability of nesting sites for ground-nesting species while favouring cavity-nesting species and more opportunistic ones (Bennett & Lovell, 2019; Ghisbain et al., 2021). In contrast, cavity-nesting species are negatively impacted by recent wildfires and intensive agriculture where nesting sites are generally removed from the environment (Williams et al., 2010). However, data regarding the nesting biology of European osmiine species is still sparse (between 40 to 50% are lacking depending on the nesting trait), with some categories being poorly represented (Tab. 3), which may affect our results.

Overall, the relationship between traits and the risks of extinction depends on many factors and the interplay between each of them. Although a trait can influence the response of a bee to a particular threat, it becomes less accentuated when looked at globally with the action of each of the drivers of decline. The response of a species therefore depends on the most impacting threat occurring locally. At a continental level (herein Europe), several drivers occur on different populations of the same species and may mask a global trend which explains the non-significance of those tests. Nevertheless, we found two significant relationships between trait values of the different IUCN Red List categories. These traits either represent major and more global indicators of decline (EOO) or are more strongly affected by one ubiquitous threat, i.e., climate change (STI).

3. Ecological niche modelling

3.1 Ecological suitability

Our results show that the areas with the highest ecological suitability are the Mediterranean basin and mountainous areas of central Europe, which can be seen as their ecological optimum (Fig. 11). This follows the conclusion of recent studies corroborating a general pattern of distribution seen in bees, with xeric zones such as the Mediterranean countries being particularly diverse (Leclercq et al., 2023; Orr et al., 2021; Reverté et al., 2023). These regions represent dry and warm climates hosting high diversity, presumably because nectar and pollen loss is higher in humid environments due to their perishable nature and fungal attacks (Michener, 1979, 2007). In Europe, some of these southern areas also acted as refugia during the Pleistocene glaciations (Lecocq et al., 2013). Moreover, the biogeographic history of osmiine bees shows that this tribe has a Palaearctic origin with many exchanges with the North American continent, with both continents harbouring Mediterranean areas suitable to this group (Praz et al., 2008).

Mountainous ecosystems represent ecologically suitable areas because of their numerous heterogeneous environments and climates hosting high diversity and endemism (Körner, 2004; Testolin et al., 2021). Because of the rain shadow effect (i.e., reduced precipitation in areas behind mountain ranges), some alpine areas have a somewhat arid climate similar to the Mediterranean (Magnes et al., 2021; Stockham et al., 2018). This effect typically occurs in the inner alpine valleys, which therefore host several Mediterranean bee species that extend their distribution in central Europe (Praz et al., 2023; Steinmann, 2002). On the other hand, high peaks and northern flanks of mountains (e.g., Jura) have relatively colder climates hosting many cold-adapted bees such as the several lineages of osmiine bee (e.g., subgenera *Melanosmia* and *Formicapis*) that are alpine or boreo-alpine species (Müller, 2024; Praz et al., 2023).

3.2 Main threats

Since both mountainous and Mediterranean areas in Europe display highly suitable environmental conditions representing their ecological optimum and hotspot areas, they should be prioritised areas in terms of osmiine bee conservation. Yet, these areas are increasingly threatened by (i) climate change, (ii) touristic development and (iii) overgrazing.

(i)   Climate change is possibly the most ubiquitous threat to both ecosystems. It already impacts several cold-adapted European osmiine species (e.g., *Chelostoma grande, Hoplitis saxialis, Osmia alticola, O. svenssoni, O. steinmanni*) and is expected to further threaten alpine but also thermophilic species, both in mountain and xeric ecosystems.

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These regions are already impacted by increasing temperatures and extreme climatic events (e.g., droughts, heat waves) and are expected to intensify in Europe. This dramatically reshapes their natural habitat and distribution as highlighted by the decline of some bumblebee species inhabiting alpine regions (Ghisbain et al., 2024; Rasmont et al., 2015) but also by the expected range contractions in the Aegean Islands of Greece (Kougioumoutzis et al., 2022). Temperature warming and droughts also increase the frequency of wildfires in the Mediterranean countries (Dupuy et al., 2020; Moriondo et al., 2006). Although fires are part of the natural cycle of these ecosystems, a too-high frequency of these events may cause a shift in plant communities (Rodrigo et al., 2004) and also lead to reduced bee diversity (Potts et al., 2003), which already impacts *Osmia larochei* in the Canary Islands (C. Ruiz Carreira, pers. comm. 2024).

(ii)   Mediterranean areas are further threatened by the development of tourism. This threat impacts several species mainly occurring in the Mediterranean basin such as *Osmia iberica*, *O. rutila* and *Hoplitis cypriaca*. According to Plan Bleu (2022), more than 500 million international arrivals are forecast for the Mediterranean basin in 2030. This results in highly detrimental urban development and coastal management in many southern countries of Europe (e.g., roughly 80% of coastal habitat along the French, Italian and Spain Mediterranean coast have been destroyed) (Drius et al., 2019; Van Der Meulen & Salman, 1996). The Mediterranean is not the only region to be confronted with this problem as other countries further north may be impacted by infrastructure development as well. In Sweden, the *Osmia maritima* population has seen its numbers decrease (now estimated to be less than 50 female individuals) following the construction of a harbour and a golf course destroying its coastal dunes habitats (B. Cederberg, pers. comm. 2014; Cederberg et al., 2010). This species is also threatened by other factors such as eutrophication and overgrazing. Similar situations are occurring for the population of the coastal dunes of Norway (Kålås et al., 2010) and the species has already disappeared in the Netherlands (Reemer, 2018).

(iii)   Even though a limited grazing regime can be beneficial for alpine grassland and Mediterranean shrubland by avoiding shrub and tree development which could ultimately turn into forest (Chauchard et al., 2007), intensive grazing can, on the contrary, lead to overall land degradation. The repeating grazing and stamping from live stocks erode the soil and decrease flower coverage which can result in barren soil impairing the re-generativity of plant communities (Klug et al., 2002; Skoulikidis, 2021; Wiesmair et al., 2017). It also alters plant density and diversity which indirectly affects the survival of pollinators by decreasing the availability of floral resources, nesting sites and material availability (Potts et al., 2009). These effects negatively impact bee

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communities as observed in some European osmiine bee species such as *Chelostoma grande* and *Hoplitis saxialis* (C. Praz, pers. comm. 2024; M. Aubert & J. Devalez, pers. comm. 2024). Some authors even designated grazing as one of the most serious threats in the Mediterranean region (Petanidou & Ellis, 1996).

VI. Conclusion and perspectives

Compared to the first European Red List of bees, the knowledge regarding the threats of European osmiine bees is in a much better state. New gathered data enabled us to lower the proportion of Data Deficient species from almost 50% to ~7%. This allowed a more accurate assessment of their status which globally indicates a low extinction risk with almost 75% of Least Concern species. However, these results must be taken cautiously as some species do not have favourable population trends. The statistical analysis indicated that only two traits, namely the Extent Of Occurrence (EOO) and the Species Temperature Index (STI), are relevant indicators of the assigned IUCN Red List category, with lower EOO and STI values associated with higher extinction risks. The morphological and ecological traits were not significantly associated with the conservation status of our species, likely due to the mixed responses of the traits to the various threats at a continental scale. Ecological niche modelling (ENM) further pointed out the importance of the Mediterranean and mountainous areas in terms of ecological suitability for European Osmiini species and highlighted the importance of conservation of such fragile ecosystems that are increasingly threatened by anthropogenic actions.

Although this work provides insightful resources regarding the decline of European osmiine species, further research and conservation efforts must be undertaken to fully grasp the problem of wild bee decline in Europe. For example, continuing to update the European Red List of bees would enable tracking changes in threat regime through time with a Red List index used to monitor changes in the biodiversity state (https://www.iucnredlist.org/assessment/red-list-index). For this purpose, it is also important to keep monitoring the populations of wild bees as well as improving the knowledge about their threats, ecology and geography so that conservation plans are as effective and appropriate as possible. Furthermore, the IUCN Red List assesses the relative extinction risk of a species but is not a tool to set conservation priorities. The latter also depends on socio-economic, cultural and political factors which further research could investigate. It is also important to take into account local factors, notably to set national conservation action, which may lead to threatened status that is different from the continental situation. One of the last steps following this work would be to implement concrete conservation plans, for example through legal protection of the species, habitat restoration and public awareness, to halt their decline.

To further assess species whose status is still undetermined or is yet to be evaluated, some geographical traits (EOO and STI) could be used to explore and estimate the extinction risks of these species. Furthermore, even if the study of the ecological and morphological traits has proven

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its limitation at a continental scale, further research focusing on local and national scales could use these traits to gain a mechanistic explanation of the decline of a taxon and its local cause. We also highlighted the lack of data for certain traits (body size, hairiness and nesting biology) that are essential for the survival of the species. We therefore suggest that more research and data collection should be conducted to implement this knowledge gap.

Regarding ENM, the representativity of the model could be improved as only 66 European osmiine bee species were modelled. Gathering more data for unrepresented species but also in under-sampled areas may unravel other ecologically suitable areas that are important to preserve, not only for European osmiine species but also for other wild bees as this follows the general pattern of bee diversity. This is also a crucial step that goes hand in hand with an accurate assessment of species. Finally, ENM has been widely used to assess changes in ecological suitability through time using environmental data representing several global change scenarios. This approach could be used to further assess each species based on another criteria of the IUCN Red List looking at a projected population size reduction (criteria A3).

Overall, this work sets the basis for the conservation of the Osmiini in Europe and provides directions for future research. With reports demonstrating that these important pollinators are potentially under higher threats than previously reported, it is our responsibility to take action to halt this global decline to set a better and sustainable future.

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Appendices

Appendix 1. The criteria (A-E) used to evaluate the Threatened category of a taxon. Retrieved from IUCN (2012b).

A. Population size reduction. Population reduction (measured over the longer of 10 years or 3 generations) based on any of A1 to A4			
	Critically Endangered	**Endangered**	**Vulnerable**
A1	≥ 90%	≥ 70%	≥ 50%
A2, A3 & A4	≥ 80%	≥ 50%	≥ 30%

A1 Population reduction observed, estimated, inferred, or suspected in the past where the causes of the reduction are clearly reversible AND understood AND have ceased. **A2** Population reduction observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood OR may not be reversible. **A3** Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) [(a) cannot be used for A3]. **A4** An observed, estimated, inferred, projected or suspected population reduction where the time period must include both the past and the future (up to a max. of 100 years in future), and where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.	*based on any of the following:* **(a)** direct observation *[except A3]* **(b)** an index of abundance appropriate to the taxon **(c)** a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality **(d)** actual or potential levels of exploitation **(e)** effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.

B. Geographic range in the form of either B1 (extent of occurrence) AND/OR B2 (area of occupancy)			
	Critically Endangered	**Endangered**	**Vulnerable**
B1. Extent of occurrence (EOO)	< 100 km²	< 5,000 km²	< 20,000 km²
B2. Area of occupancy (AOO)	< 10 km²	< 500 km²	< 2,000 km²
AND at least 2 of the following 3 conditions:			
(a) Severely fragmented **OR** Number of locations	= 1	≤ 5	≤ 10
(b) Continuing decline observed, estimated, inferred or projected in any of: **(i)** extent of occurrence; **(ii)** area of occupancy; **(iii)** area, extent and/or quality of habitat; **(iv)** number of locations or subpopulations; **(v)** number of mature individuals			
(c) Extreme fluctuations in any of: **(i)** extent of occurrence; **(ii)** area of occupancy; **(iii)** number of locations or subpopulations; **(iv)** number of mature individuals			

C. Small population size and decline			
	Critically Endangered	**Endangered**	**Vulnerable**
Number of mature individuals	< 250	< 2,500	< 10,000
AND at least one of C1 or C2			
C1. An observed, estimated or projected continuing decline of at least (up to a max. of 100 years in future):	25% in 3 years or 1 generation (whichever is longer)	20% in 5 years or 2 generations (whichever is longer)	10% in 10 years or 3 generations (whichever is longer)
C2. An observed, estimated, projected or inferred continuing decline AND at least 1 of the following 3 conditions:			
(a) **(i)** Number of mature individuals in each subpopulation	≤ 50	≤ 250	≤ 1,000
(ii) % of mature individuals in one subpopulation =	90–100%	95–100%	100%
(b) Extreme fluctuations in the number of mature individuals			

D. Very small or restricted population			
	Critically Endangered	**Endangered**	**Vulnerable**
D. Number of mature individuals	< 50	< 250	**D1.** < 1,000
D2. *Only applies to the VU category* Restricted area of occupancy or number of locations with a plausible future threat that could drive the taxon to CR or EX in a very short time.	-	-	**D2.** typically: AOO < 20 km² or number of locations ≤ 5

E. Quantitative Analysis			
	Critically Endangered	**Endangered**	**Vulnerable**
Indicating the probability of extinction in the wild to be:	≥ 50% in 10 years or 3 generations, whichever is longer (100 years max.)	≥ 20% in 20 years or 5 generations, whichever is longer (100 years max.)	≥ 10% in 100 years

Appendix 2. Lists of databases used to gather the occurrence records (at the date of August 2023).
The "ULB_STEP_PLUS" database was the one used for the first assessment of European bees. The row data represent the data before cleaning process.

Database names	Data providers	Row data
ULB_STEP_PLUS	N.J. Vereeken	1,543,382
Andrenidae_BDFGM	P. Rasmont	603,861
Switzerlands_GBIF	C. Praz	449,827
Netherlands_EIS	M. Reemer	359,970
SAPOLL_BDFGM	P. Rasmont	321,038
Sweden_Artportalen	L. Petterss	299,921
Halictidae_BDFGM	S. Flaminio	245,716
Finland_GBIF	J. Paukkunen	196,879
Estonia_UniversityOfTartu	V. Soon	138,743
Megachilidae_BDFGM	P. Rasmont	133,114
Norway_GBIF	F. Ødegaard	129,901
Finland_LUOMUS	J. Paukkunen	102,216
Anthophorinae_BDFGM	P. Rasmont	90,836
Estonia_GBIF	V. Soon	80,966
Iberia_IgnasiBartoumeus	I. Bartomeus	74,746
Finland_AmateurEntomologist	J. Paukkunen	66,365
Nomada_JanSmit	J. Smit	51,090
Bees_JakubStraka	J. Straka	44,889
Melittidae_BDFGM	P. Rasmont	25,028
France_JeroenSchepe	J. Scheper	17,563
Andrena_ThomasJamesWood	T. J. Wood	15,923
Austria_Zobodat	E. Ockermueller	14,865
Osmiini_AndreasMuller	A. Muller	14,215
Eucera_StephanRisch	S. Risch	11,512
Boshommel_DavidKleijn	D. Kleijn	11,228
Cuckoobees_PetrBogusch	P. Bogusch	11,182
Luxemburg_GBIF	L. C. Salazar	11,032
Russia_literature	L. Fedorova	10,535
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SURMZ_Sapienza	M. Mei	7,593
CzechRepublic_PetrBogusch	P. Bogusch	6,924
Hylaeus_SergeGadoum	S. Gadoum	6,630
GrandiCollection	L. Lenzi, F. Glostra	5,617
Belgium_WilliamFiordaliso	W. Fiordaliso	5,152
Serbia_SonjaStojnic	S. M. Stojnic	4,302
Austria_NHMW_DominiqueZimmermann	D. Zimmermann	3,520
BalearicIslands_JoanDiazCalafat	J. D. Calafat	3,467
Lithuania_EduardasBudrys	E. Budrys	3,339
Italy_MarcoSelis	M. Selis	1,996
Netherlands_DavidKleijn	D. Kleijn	1,932
KobeJanssen	K. Janssen	1,819
Anthidiini_MaxKasparek	M. Kasparek	1,044
Portugal_HugoGaspar	H. Gaspar	977
Halictus_Ebmer	S. Flaminio	912
Bosnia_AdiVesnic	A. Vesnic	744
Romania_ImreDemeter	I. Demeter	664
Italy_SimoneFlaminio	S. Flaminio	587

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Cyprus_AndroullaVarnava	A. Varnava	513
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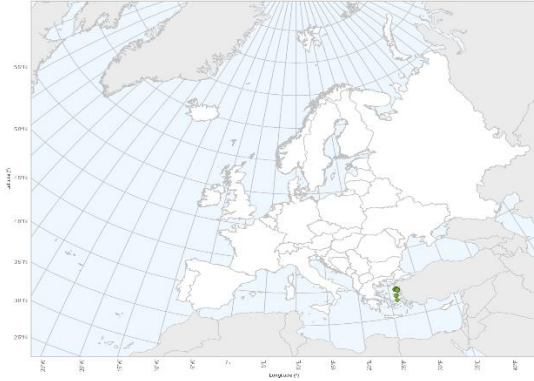
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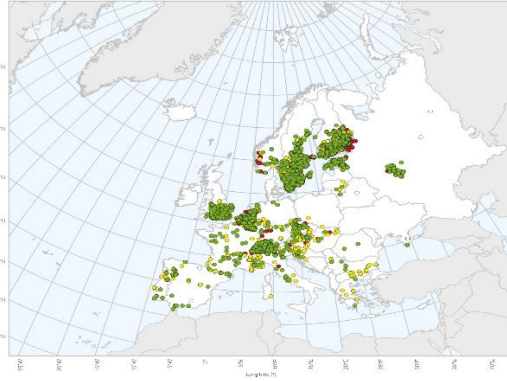
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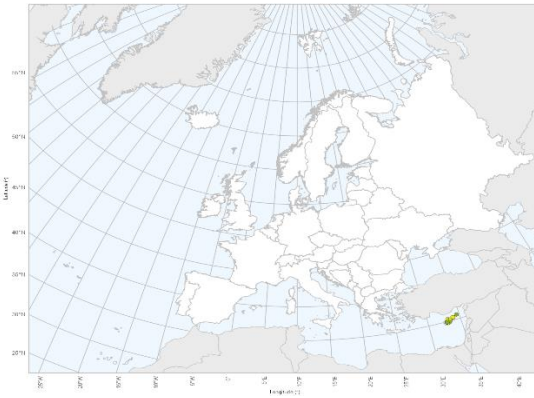
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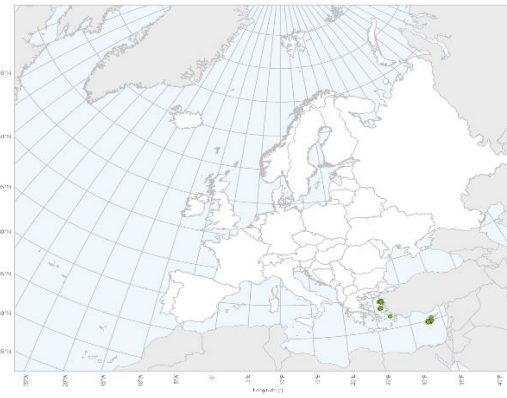
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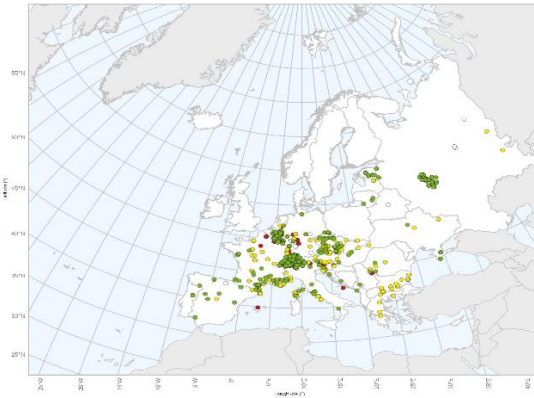
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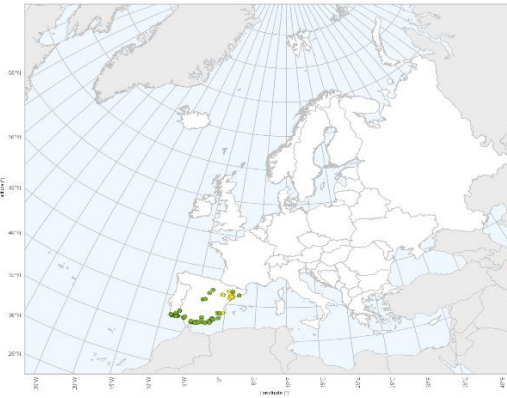
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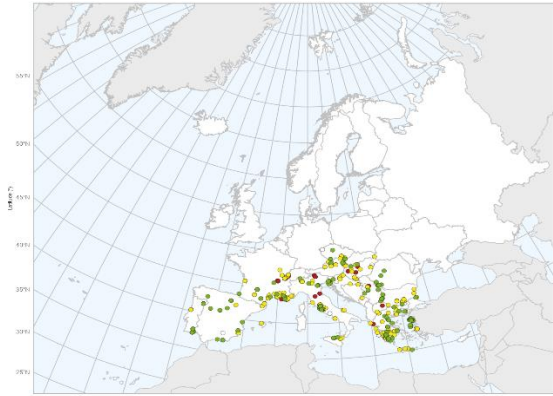
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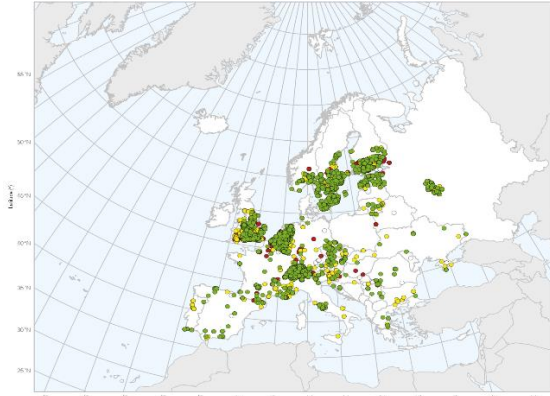
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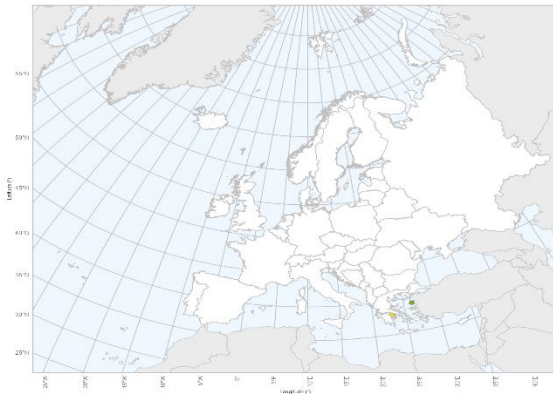
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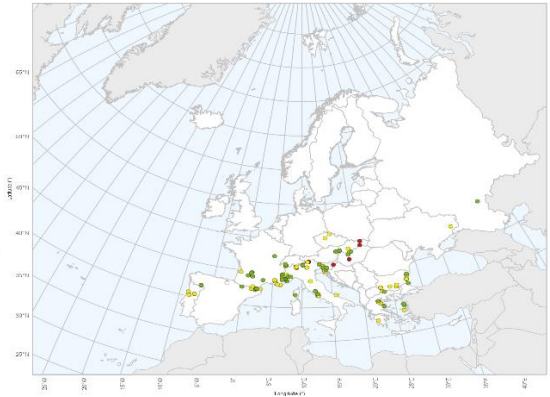
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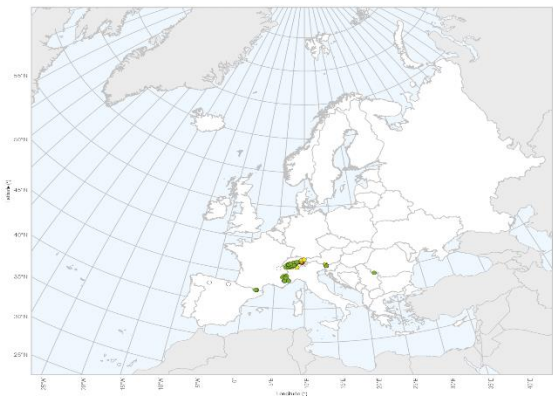
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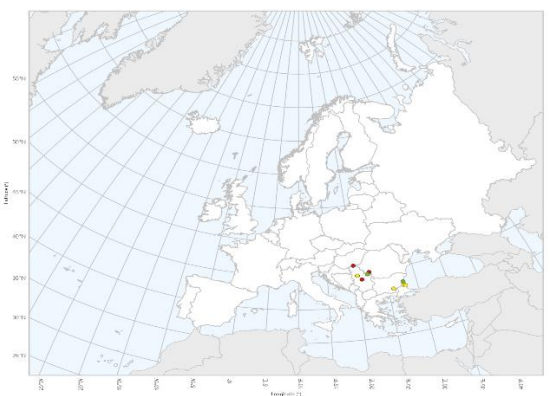
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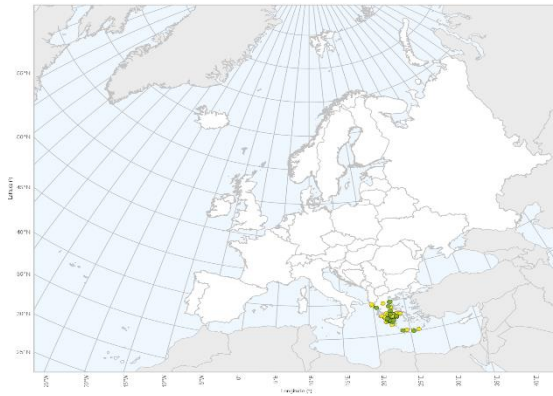
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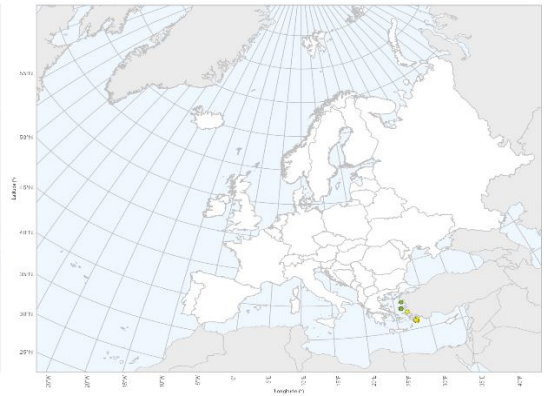
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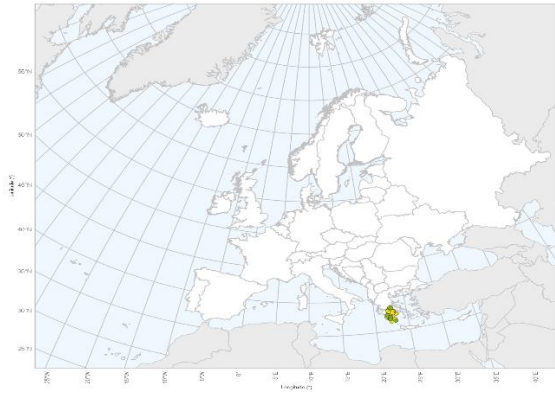
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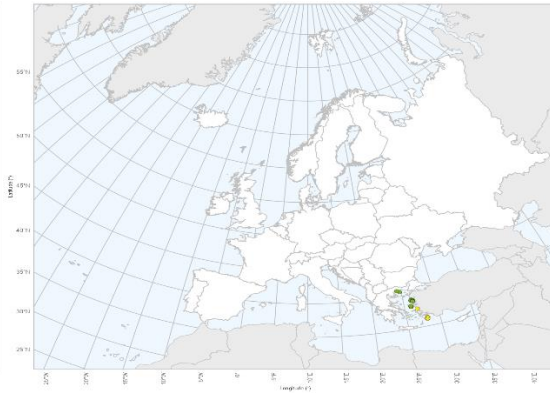
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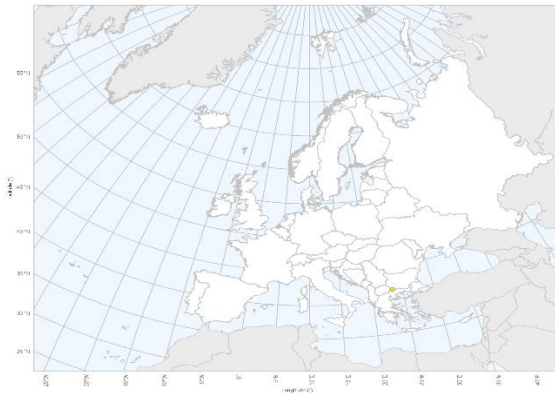
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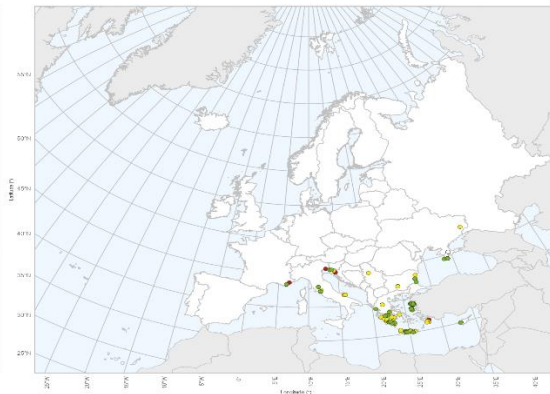
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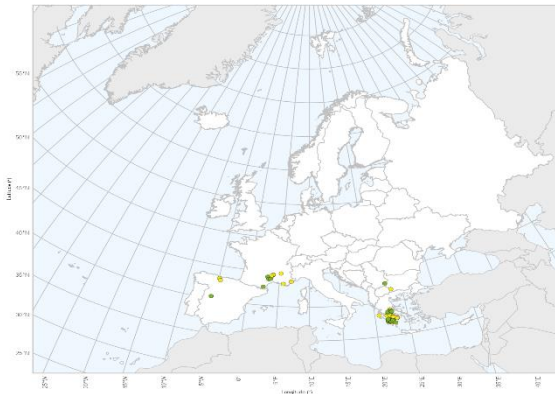
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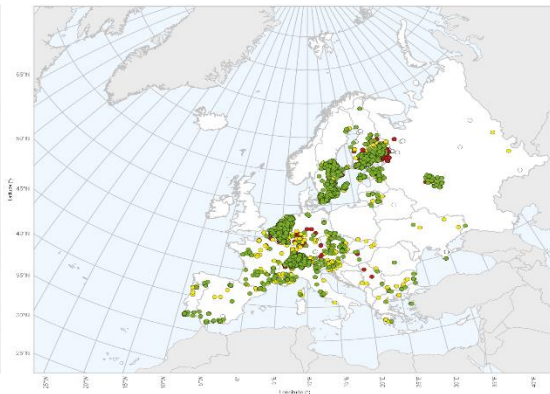
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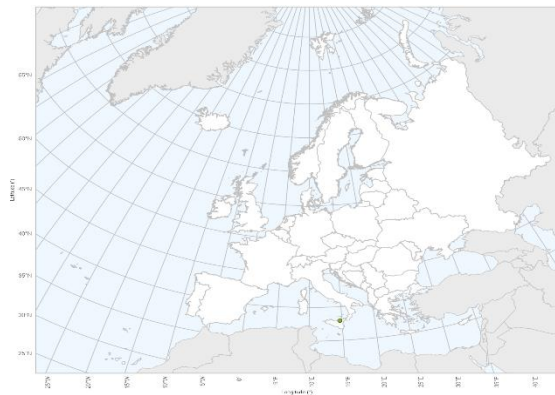
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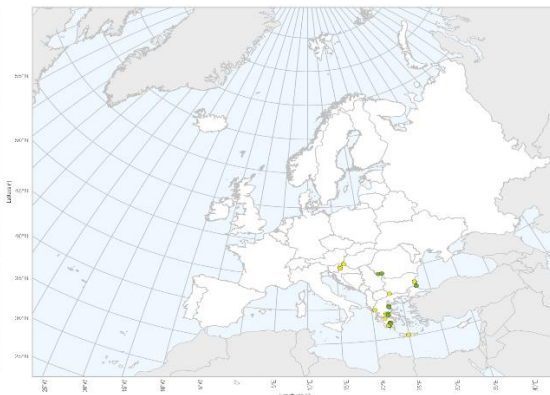
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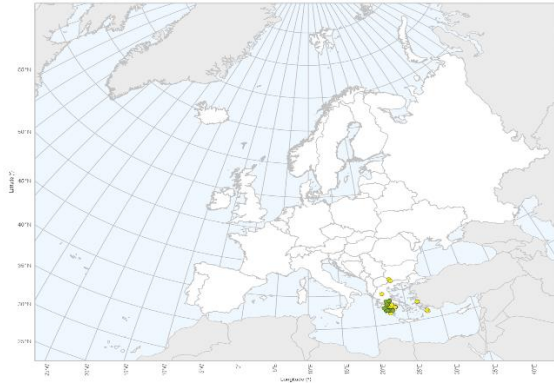
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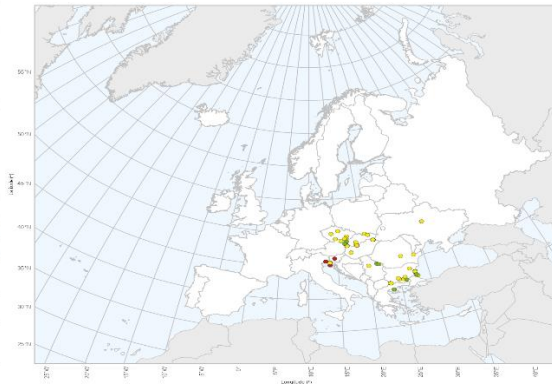
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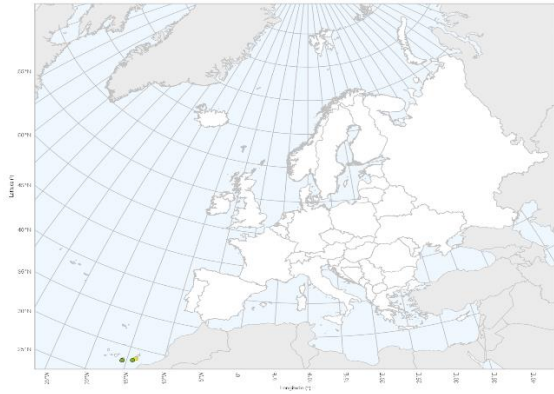
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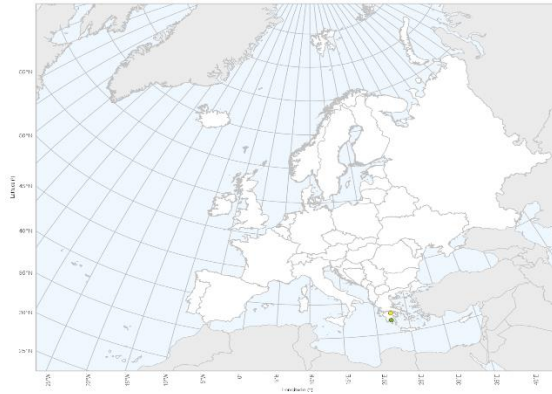
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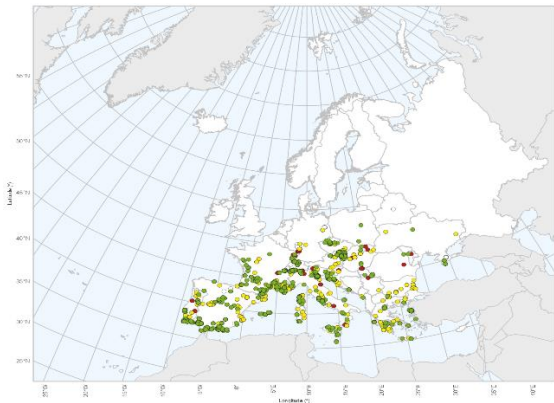
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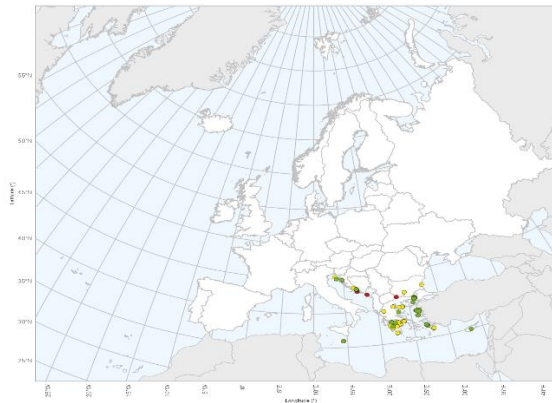
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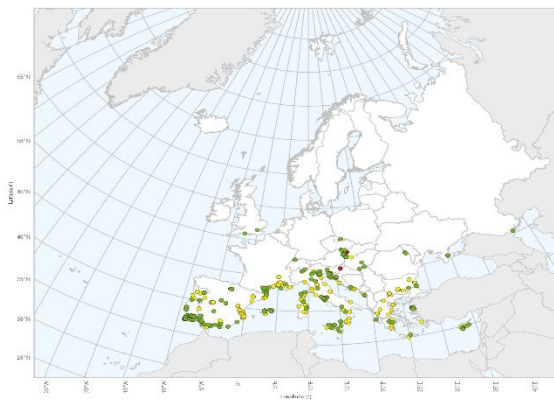
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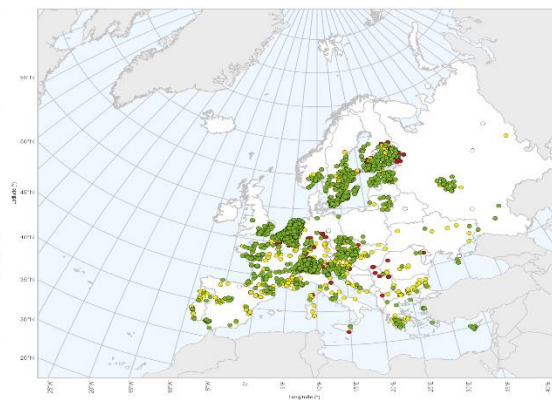
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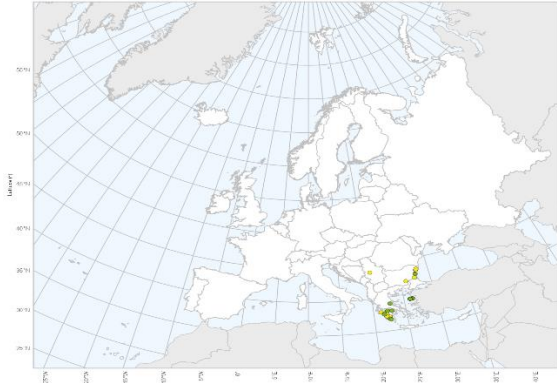
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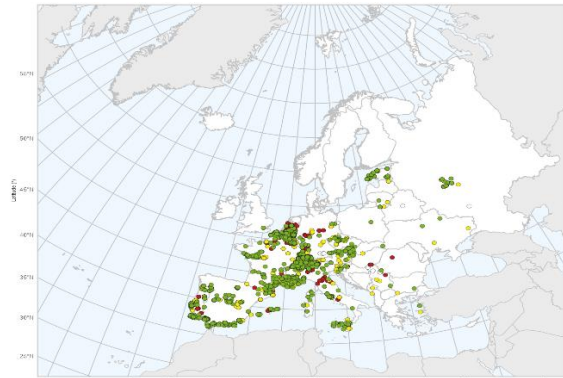
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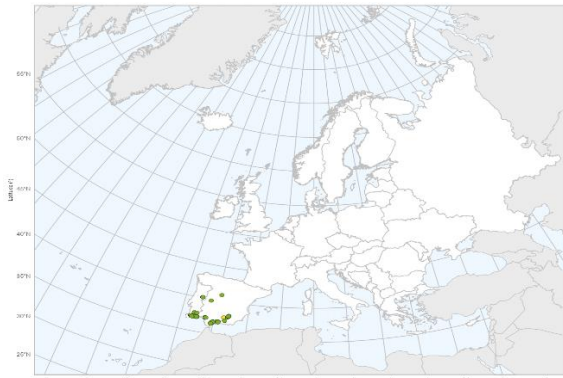
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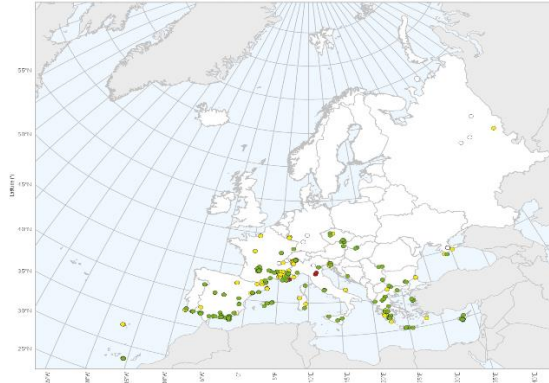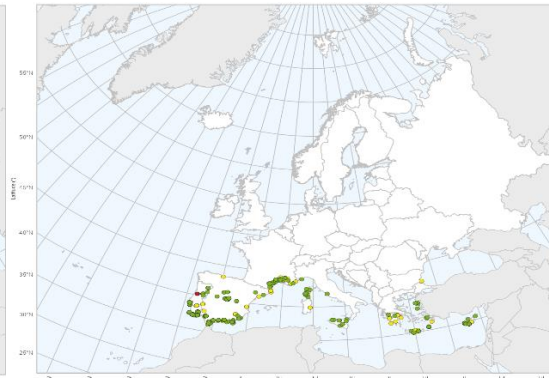
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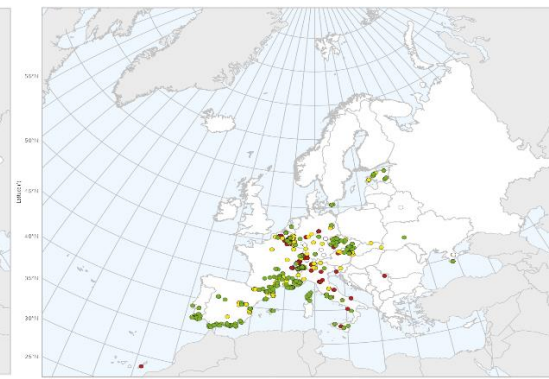
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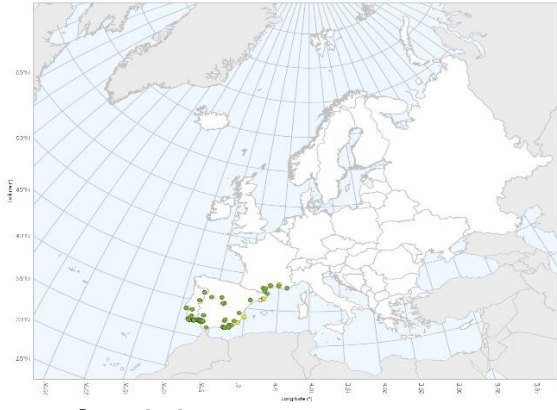
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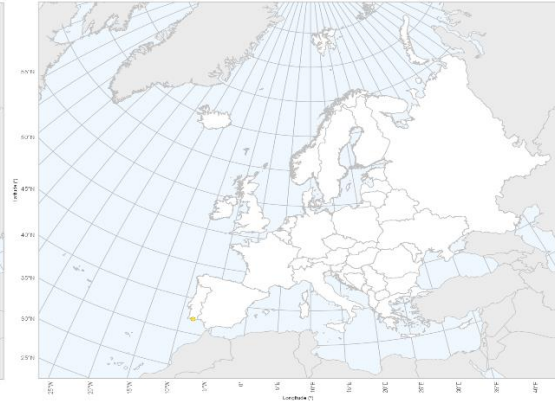
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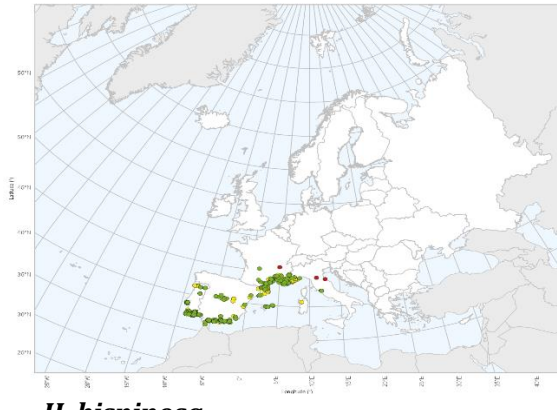
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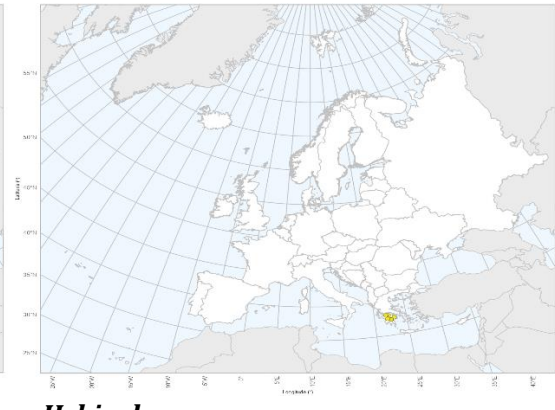
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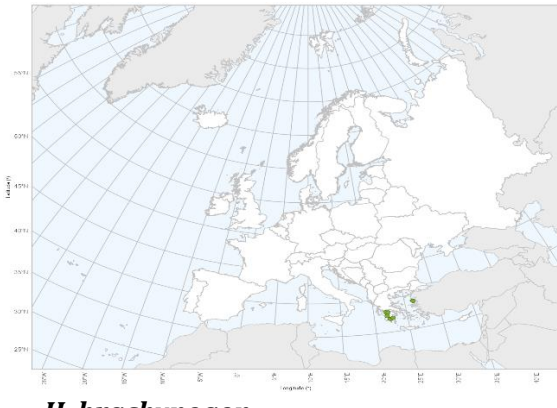
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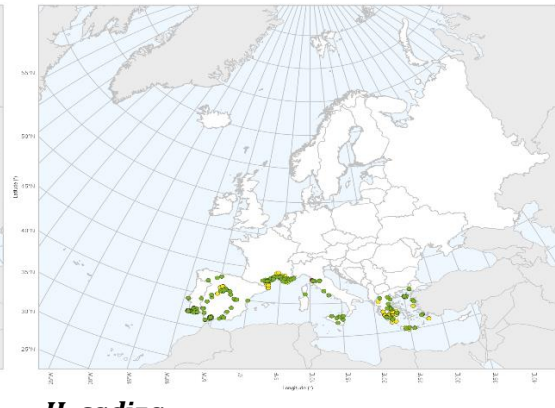
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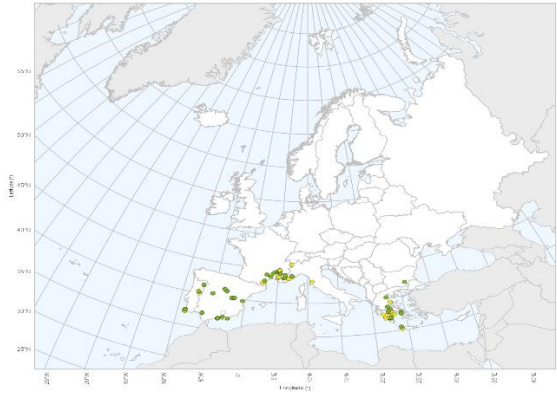
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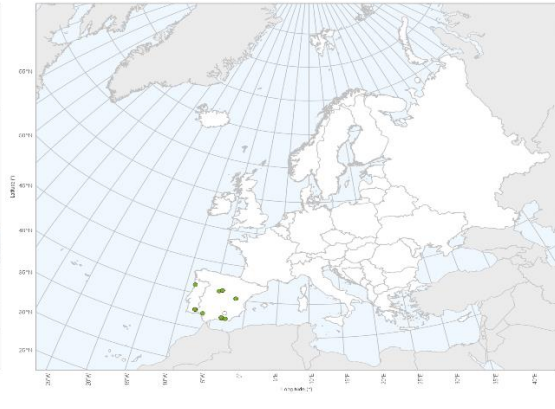
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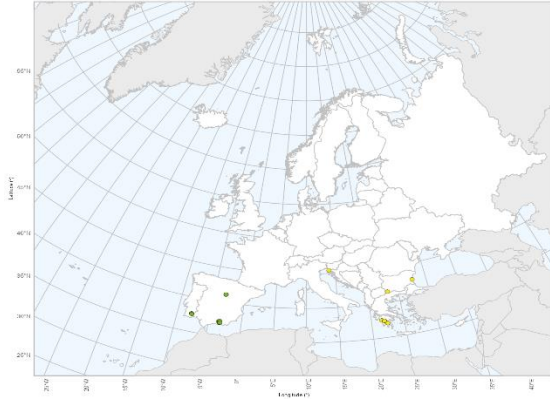
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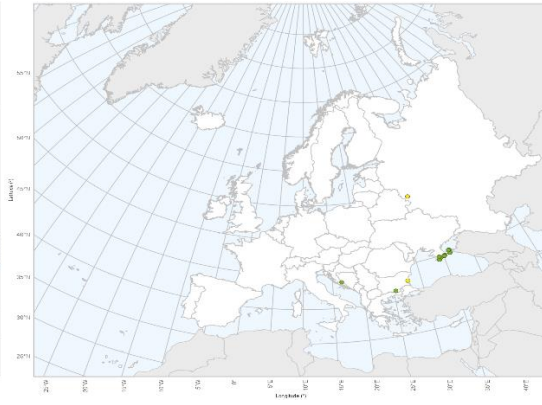
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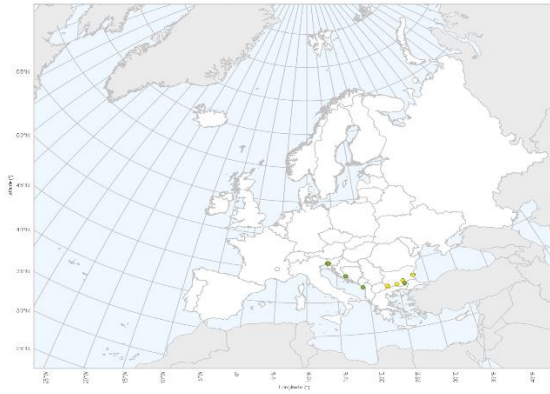
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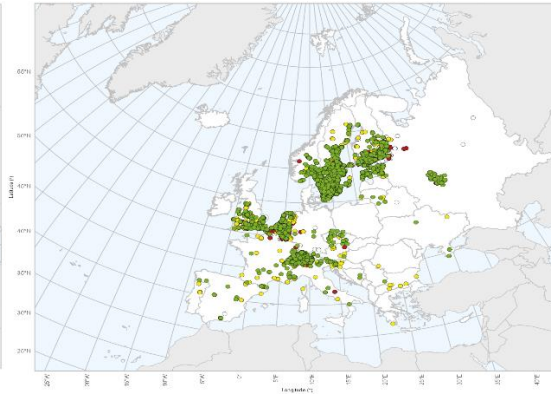
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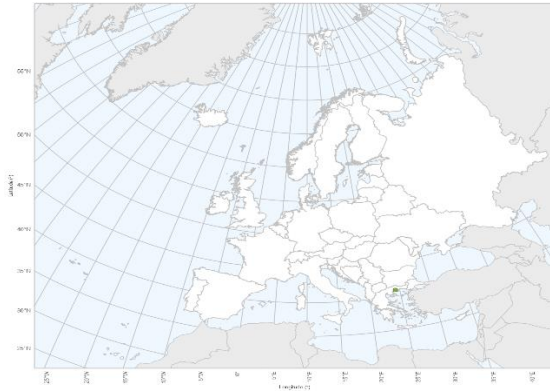
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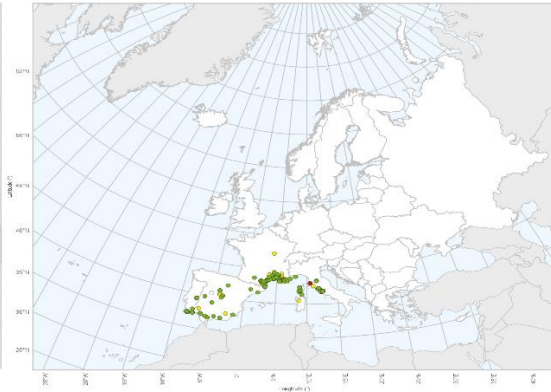
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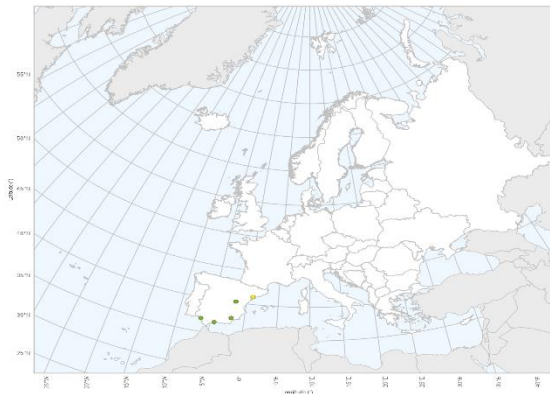
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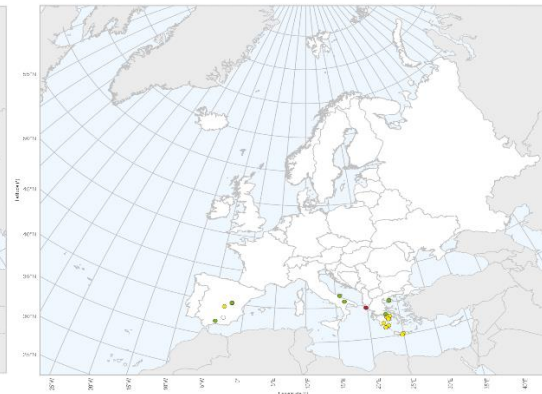
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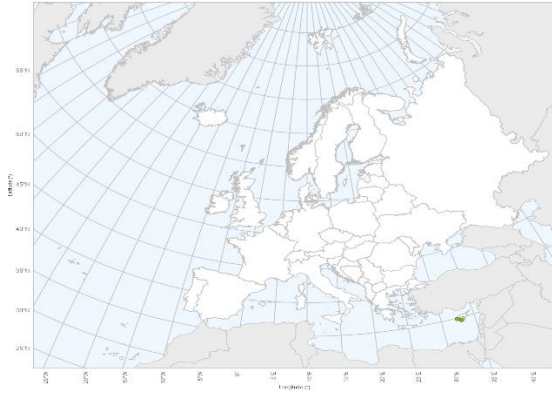
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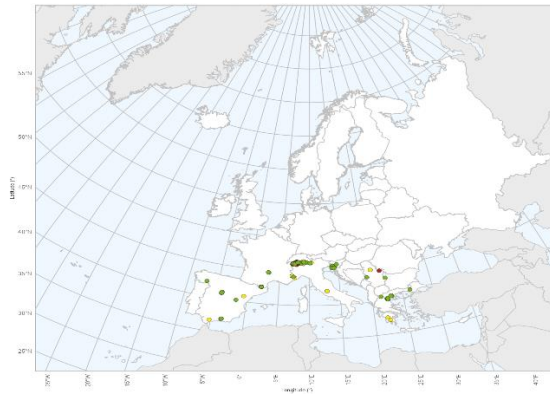
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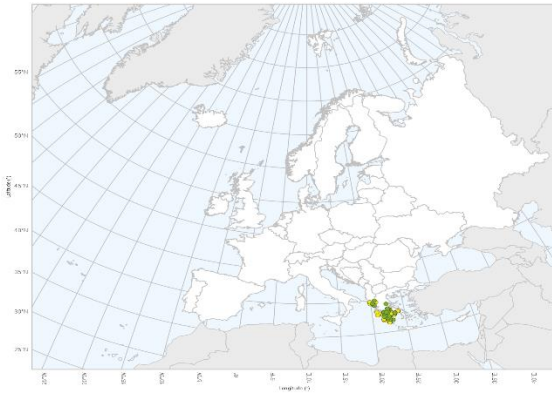
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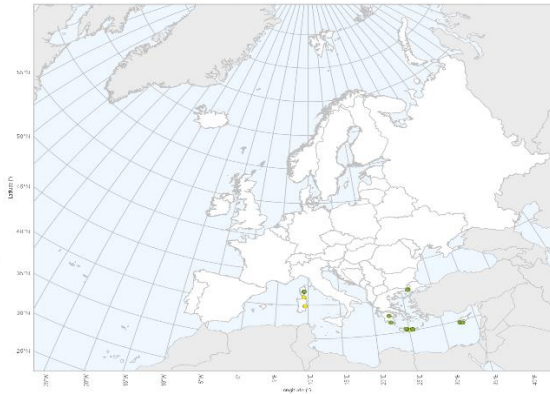
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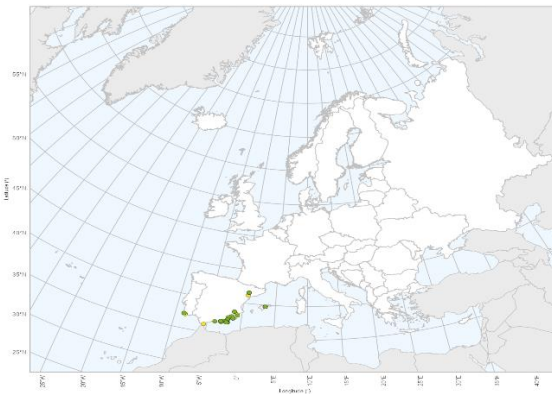
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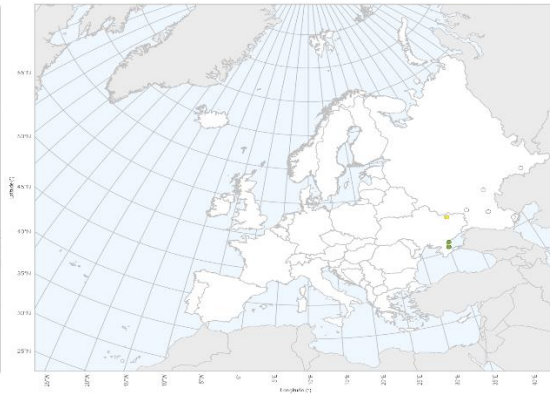
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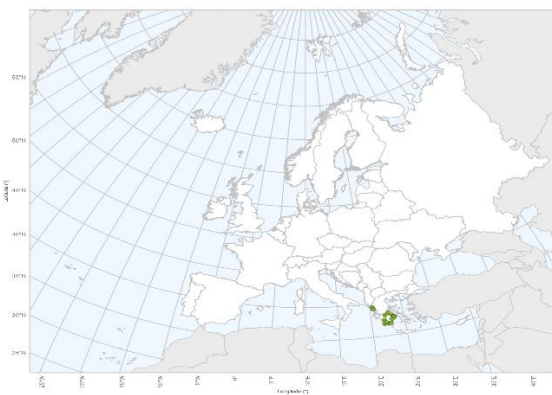
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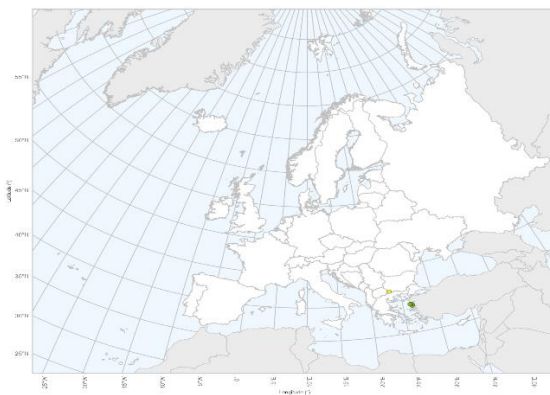
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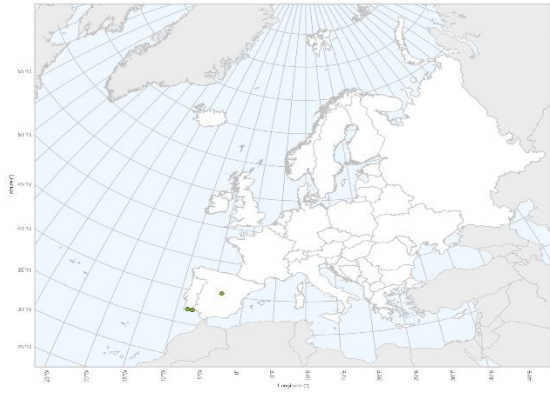
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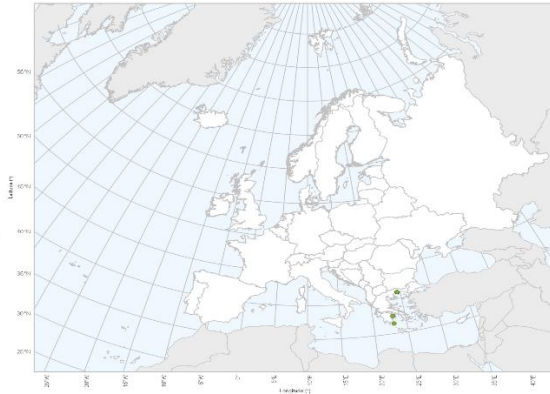
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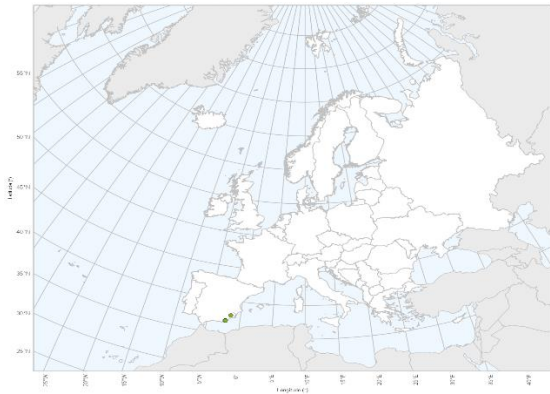
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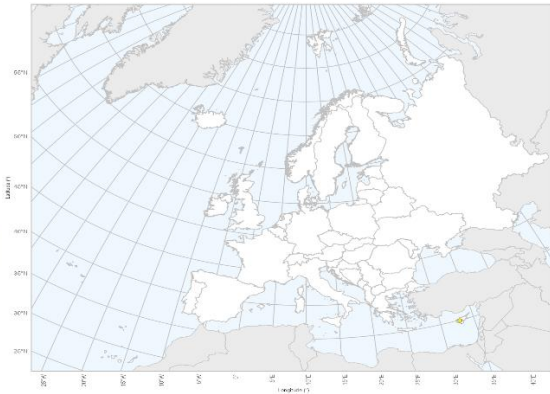
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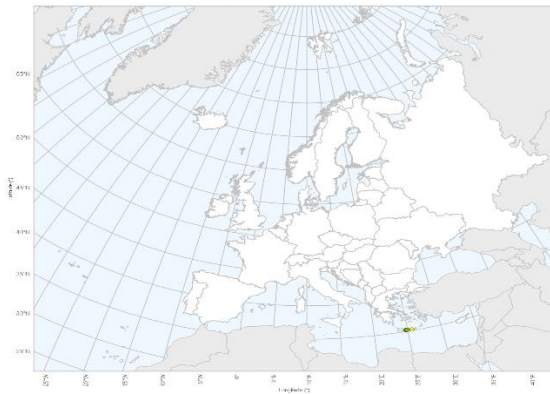
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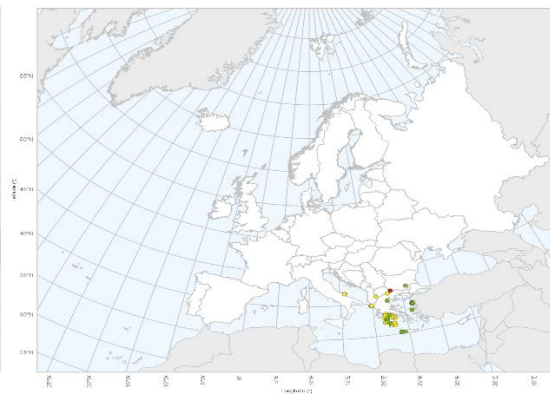
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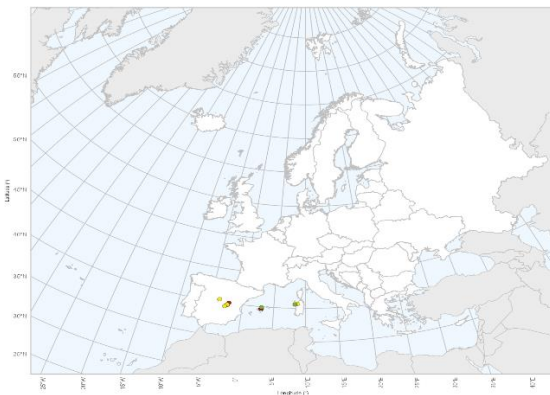
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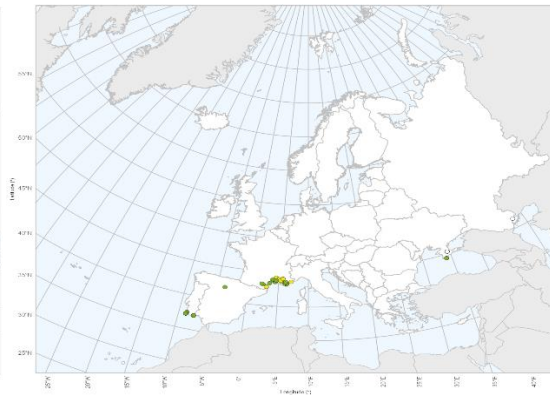
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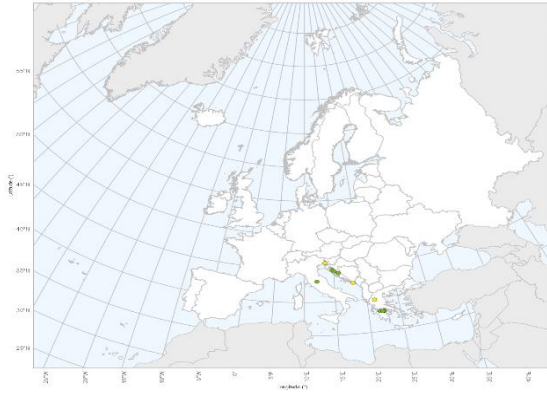
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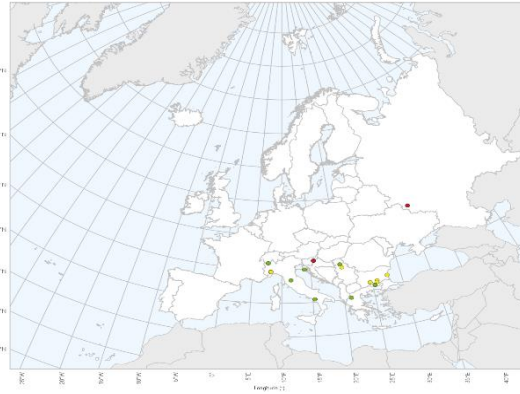
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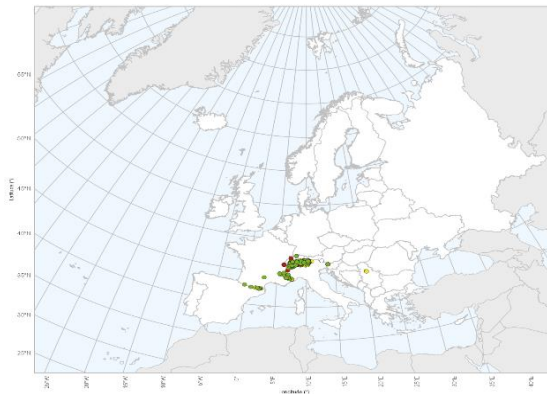
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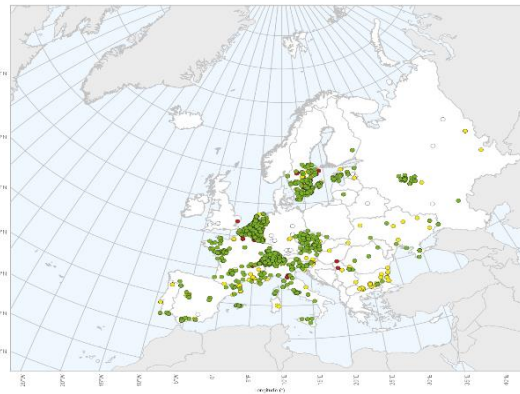
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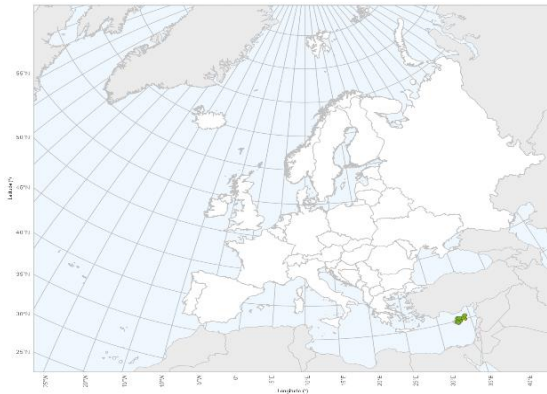
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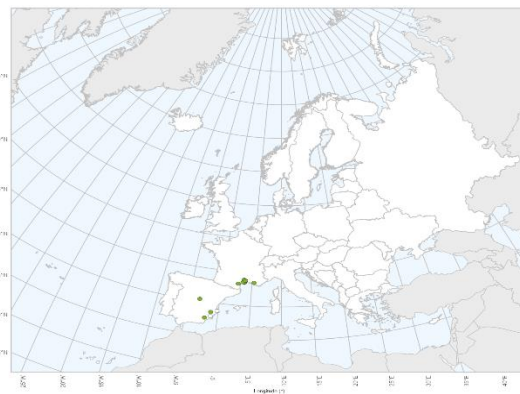
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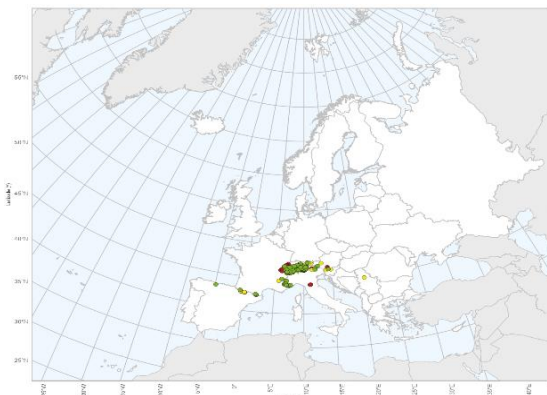
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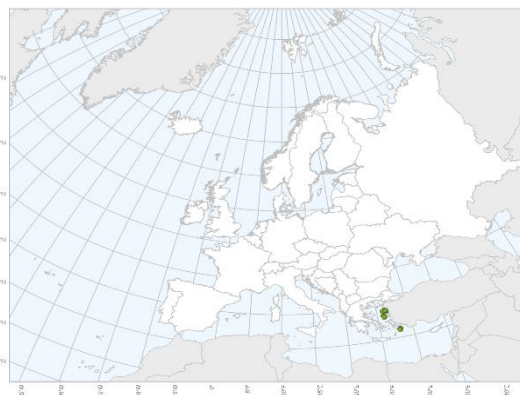
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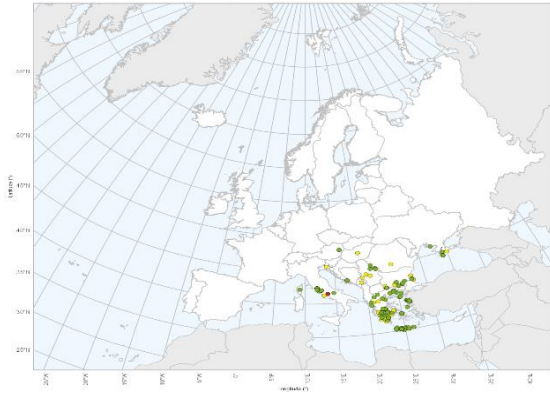
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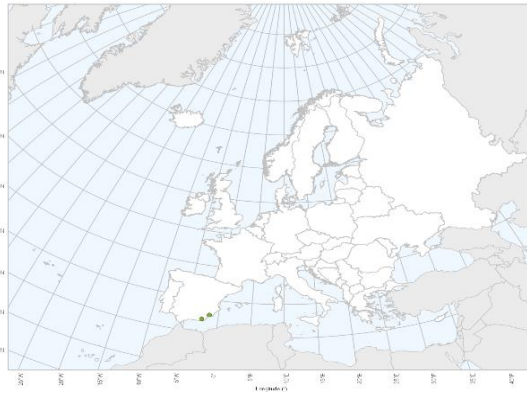
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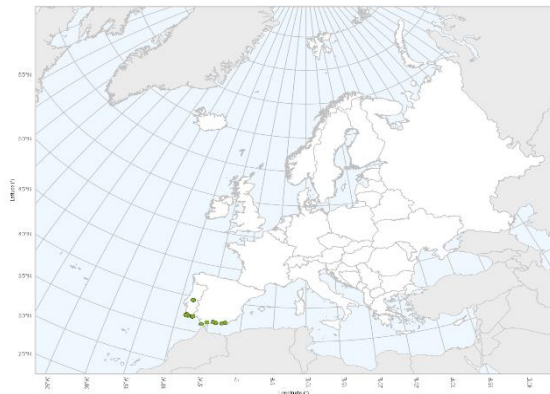
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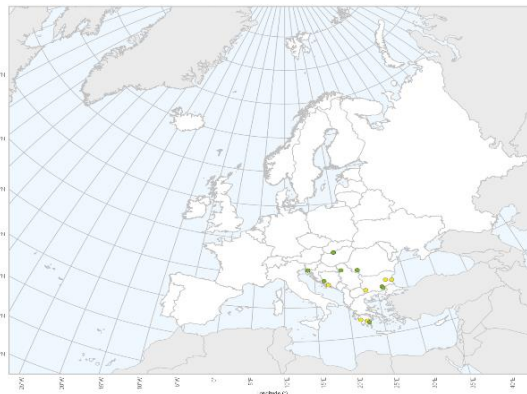
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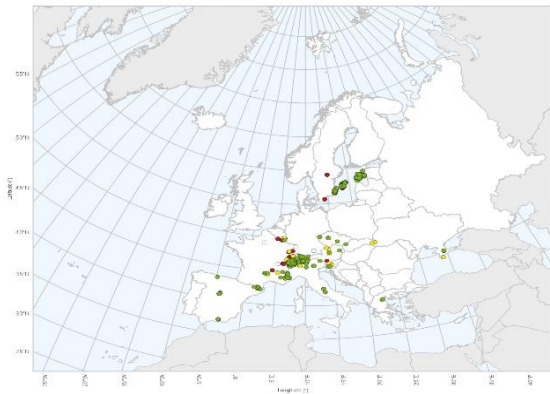
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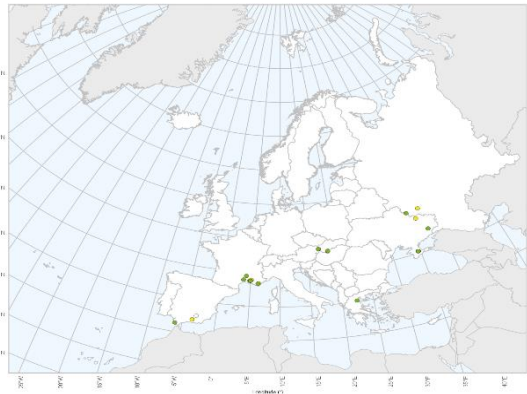
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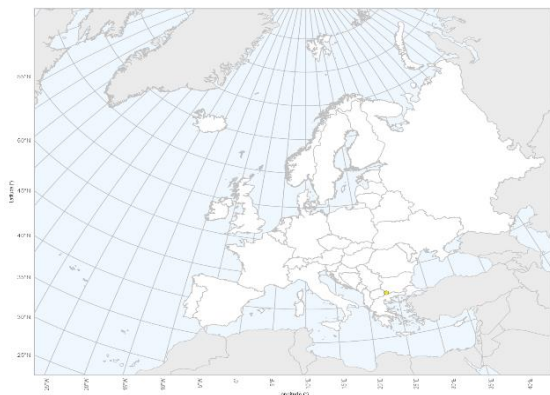
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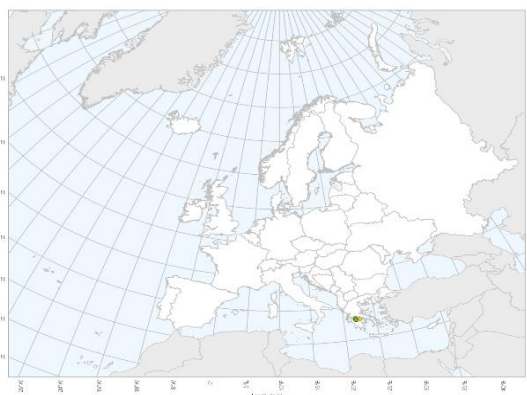
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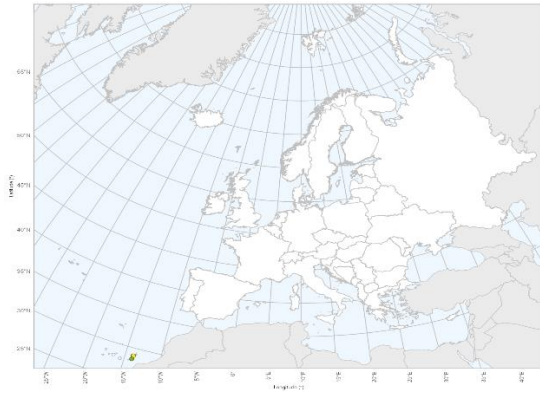
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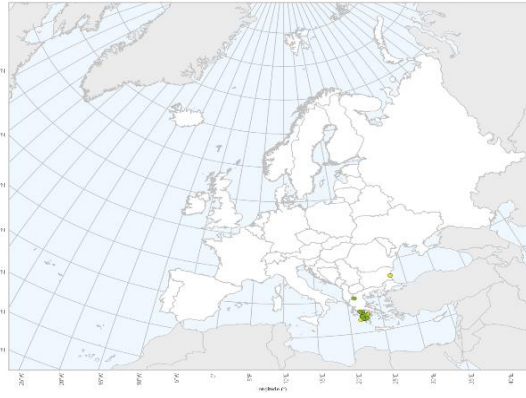
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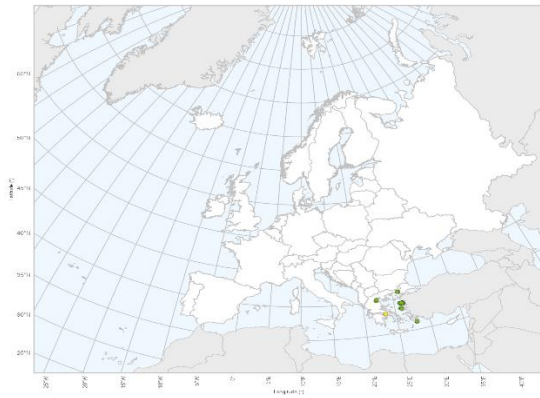
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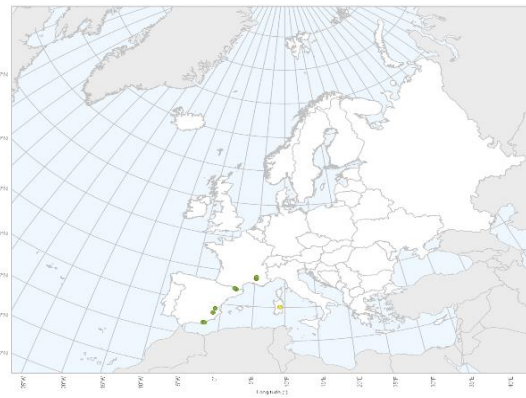
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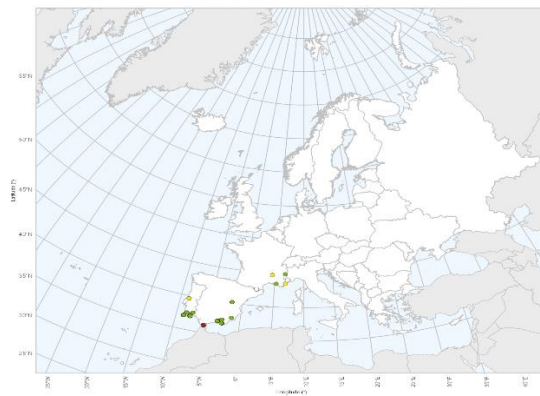
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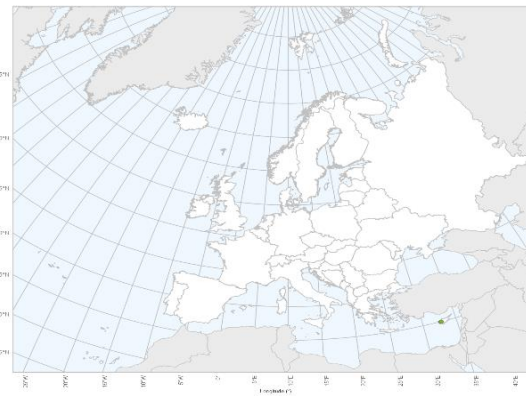
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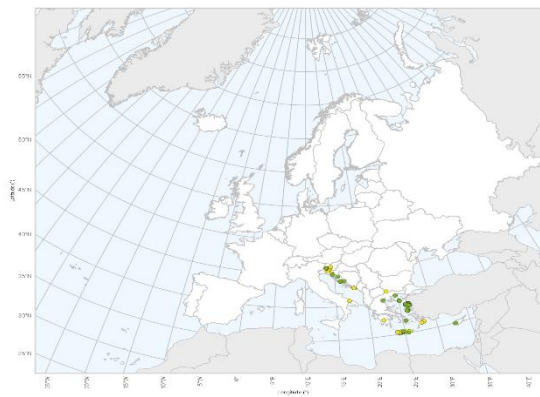
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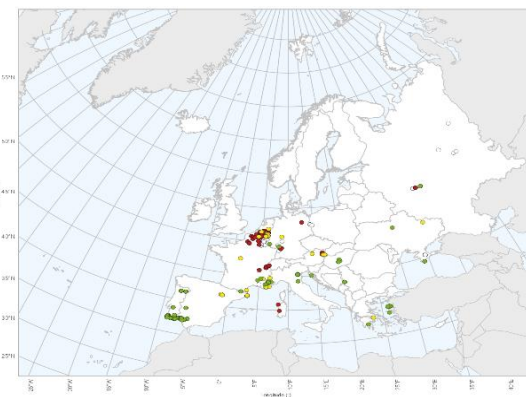
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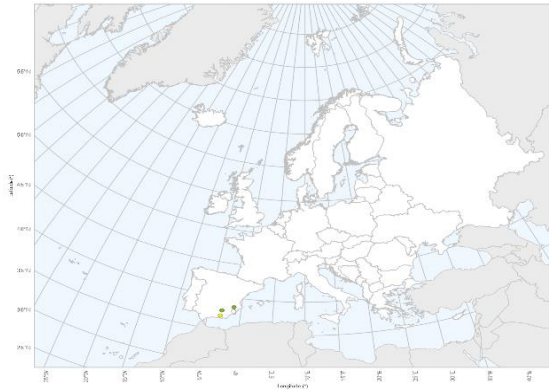
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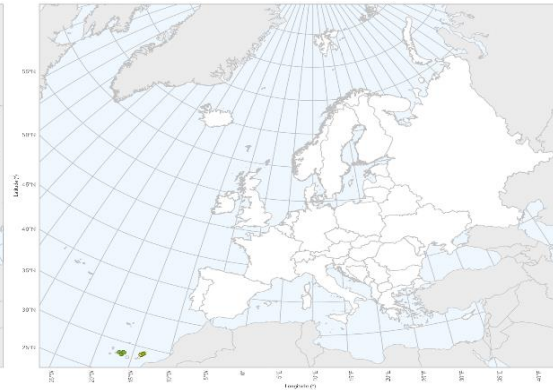
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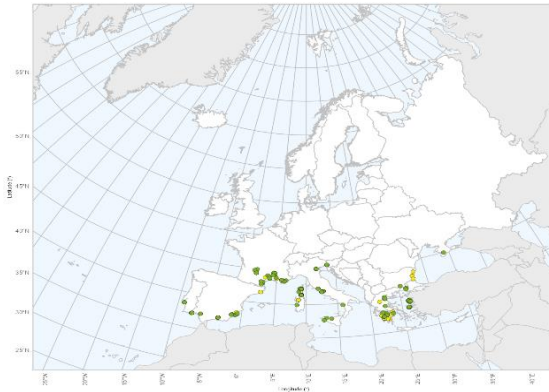
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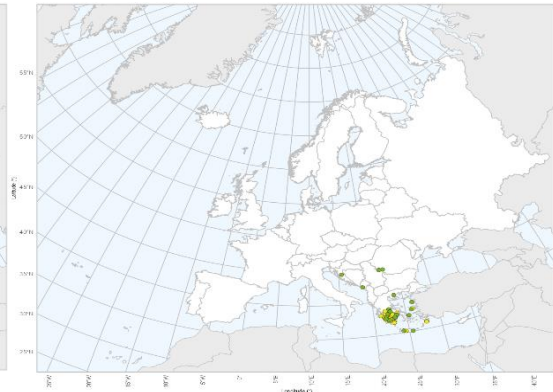
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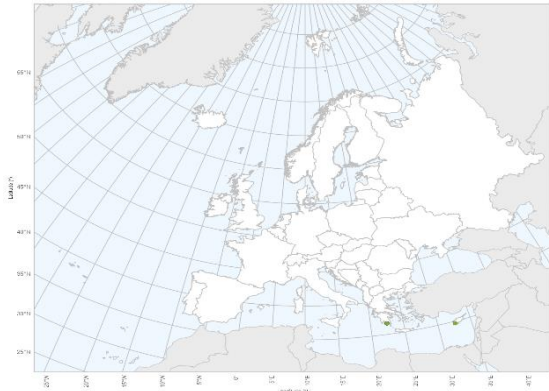
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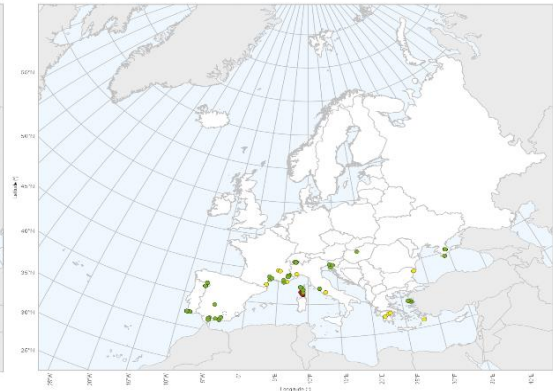
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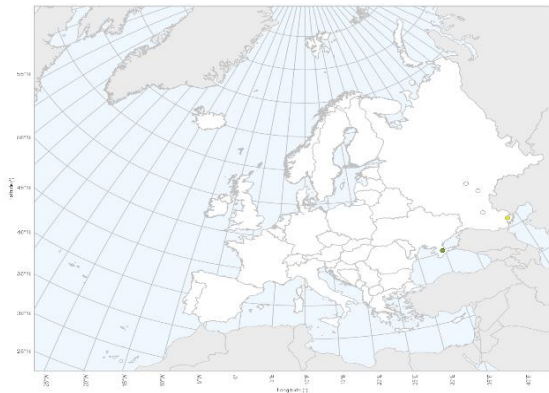
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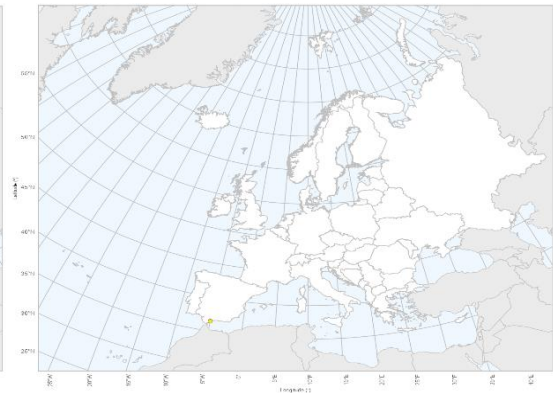
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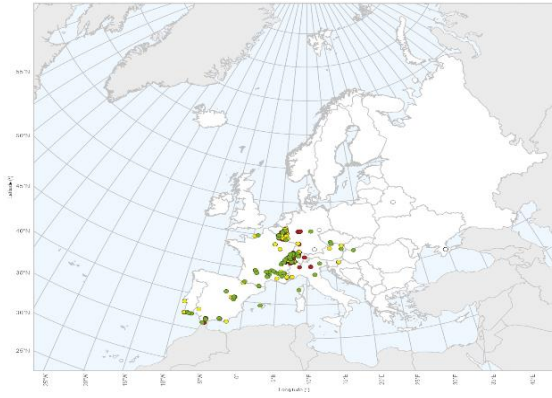
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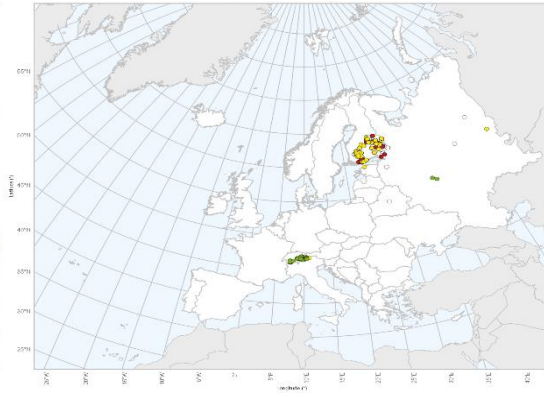
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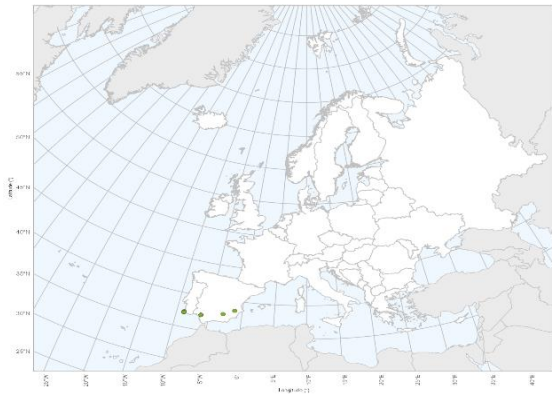
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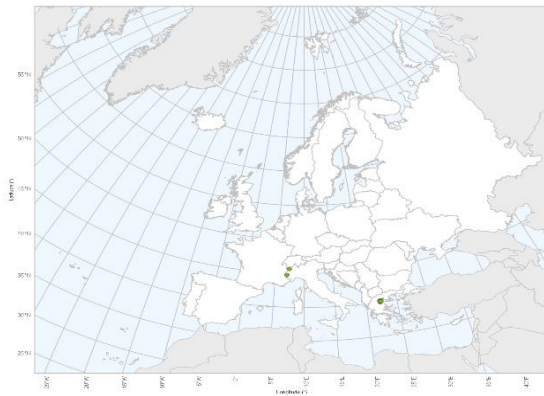
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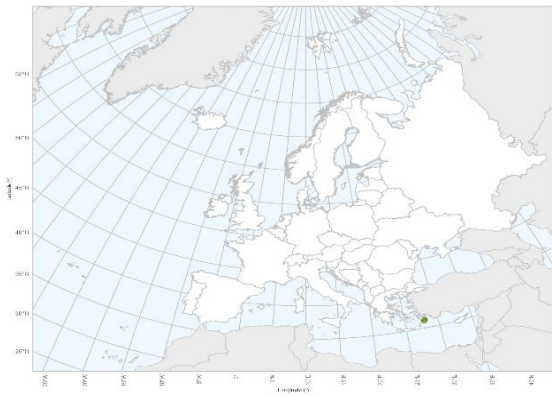
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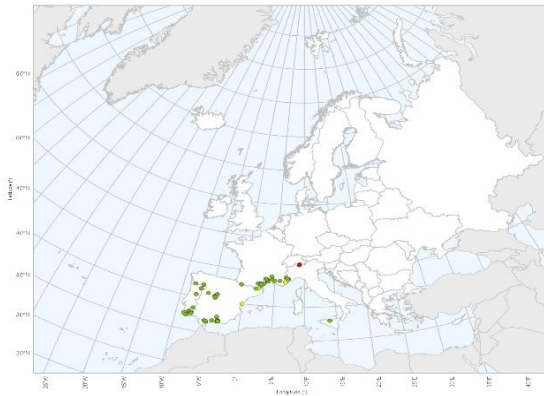
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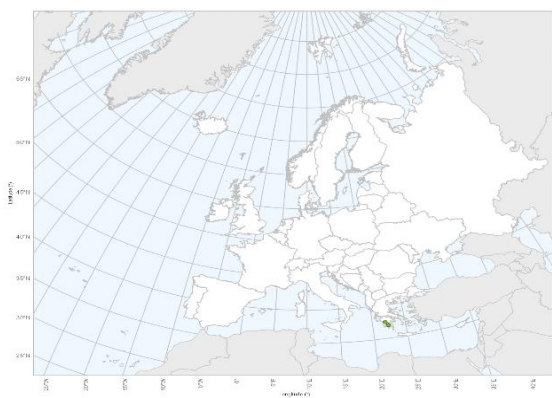
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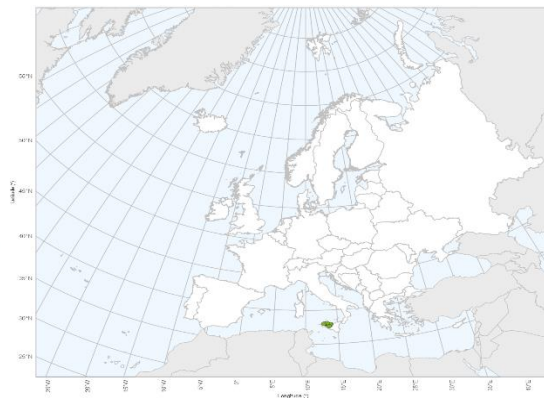
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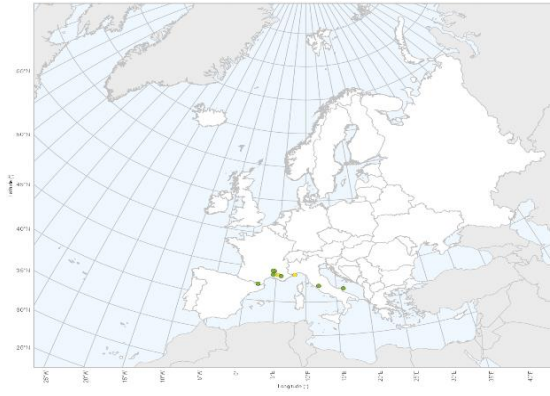
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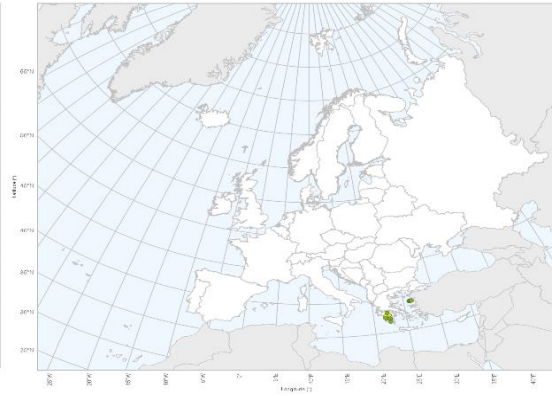
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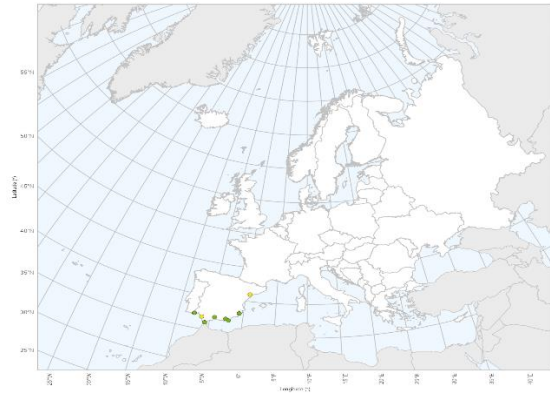
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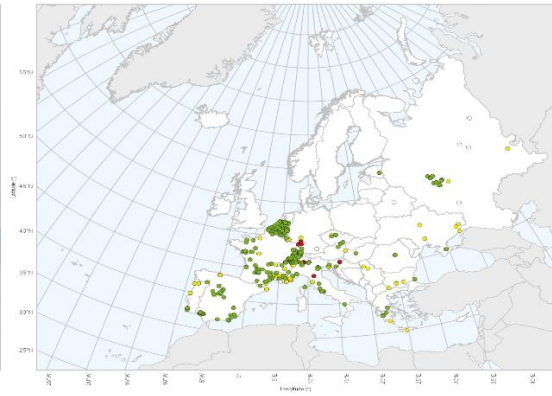
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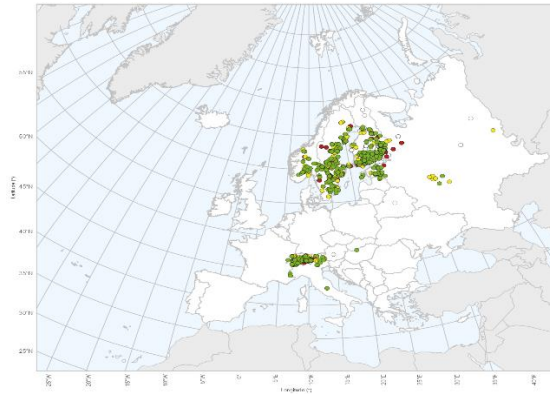
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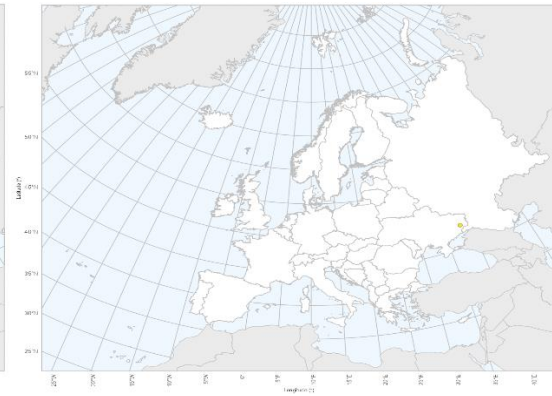
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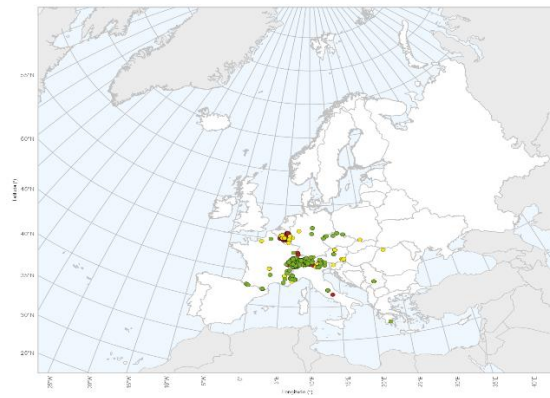
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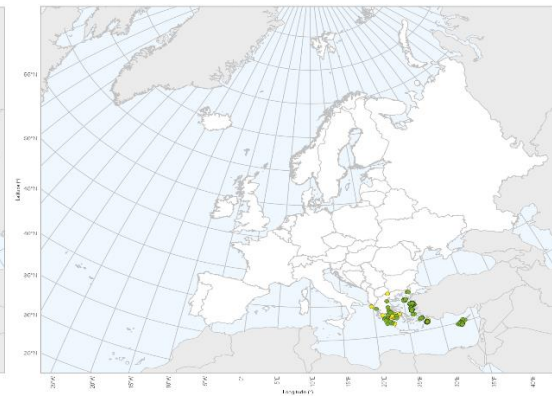
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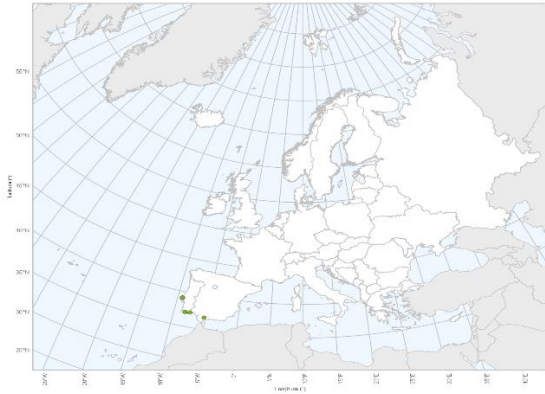
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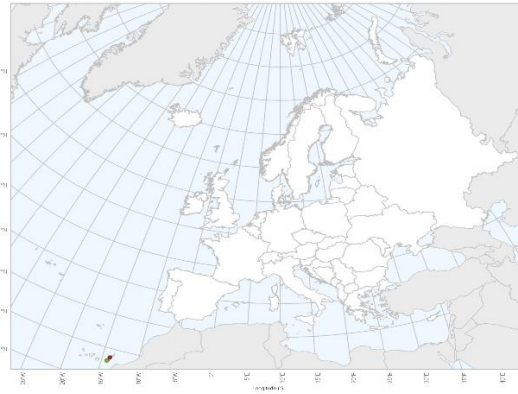
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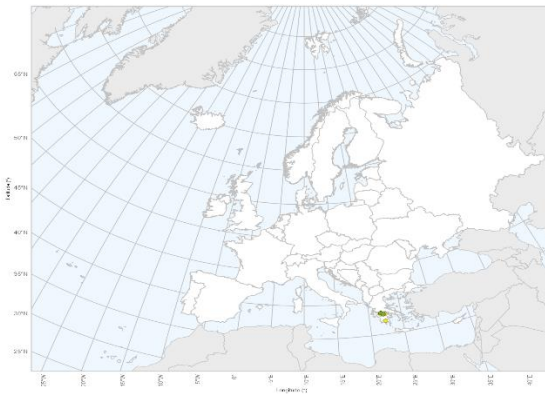
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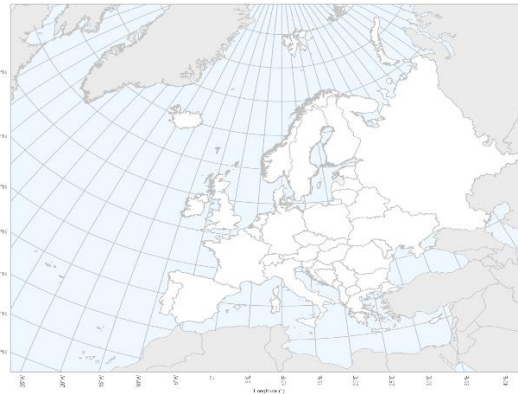
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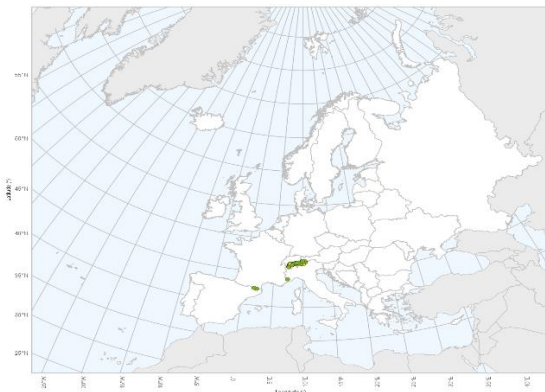
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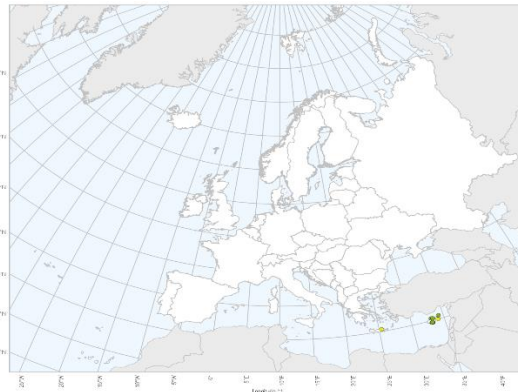
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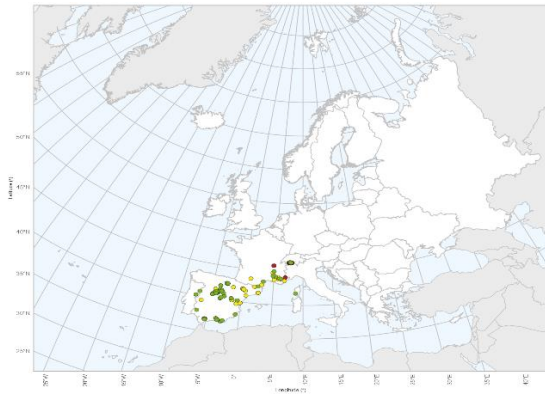
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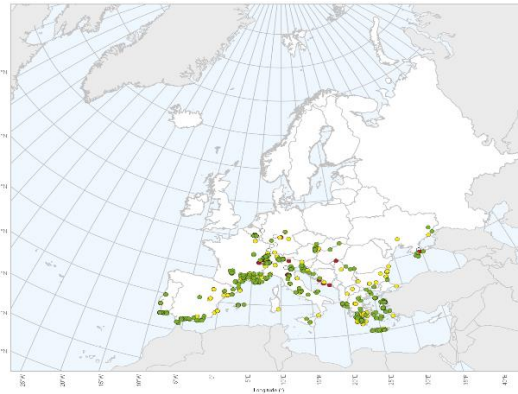
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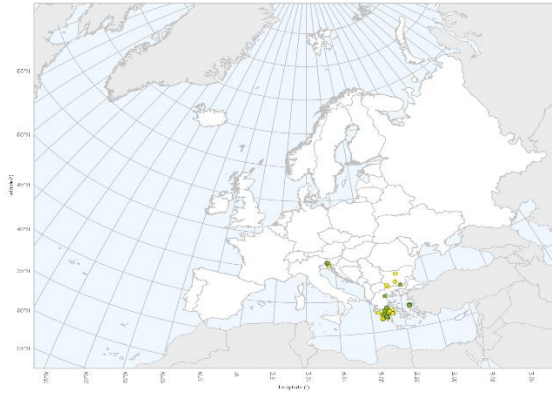
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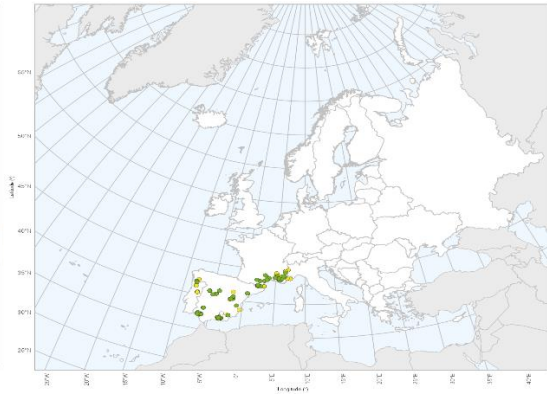
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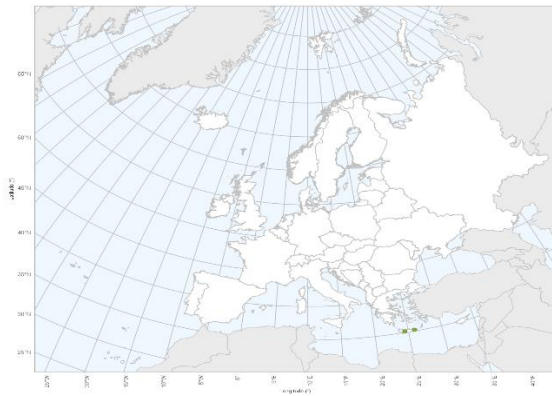
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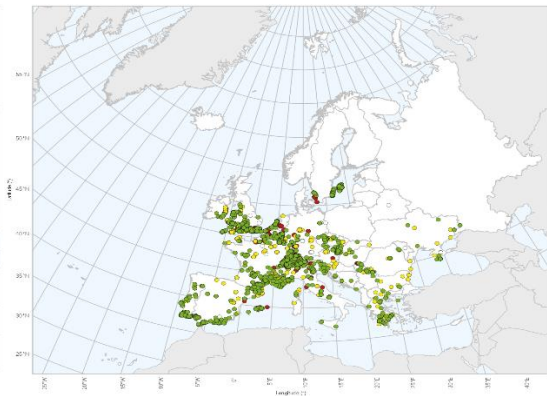
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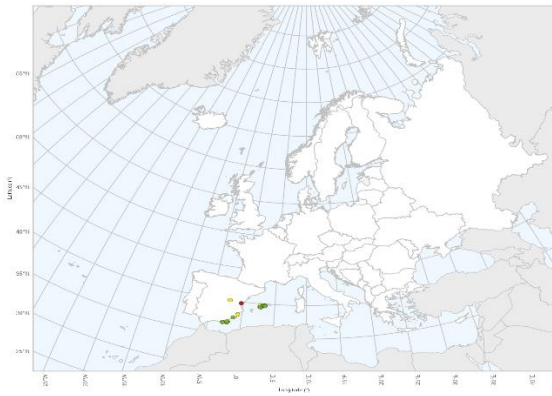
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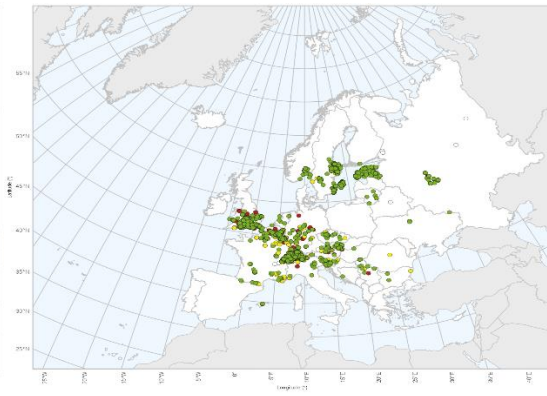
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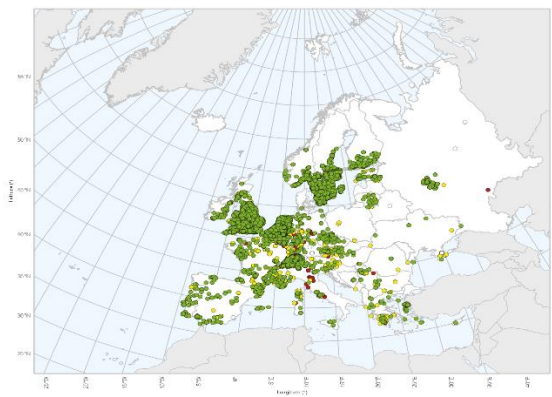
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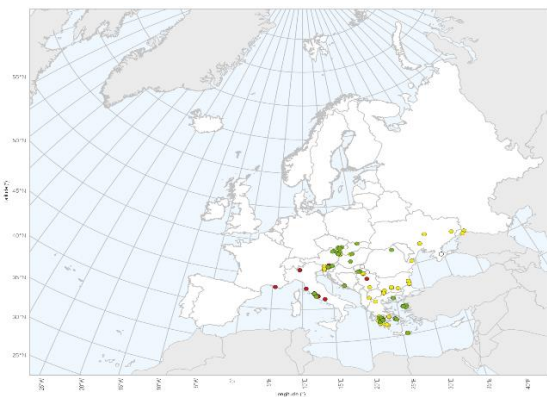
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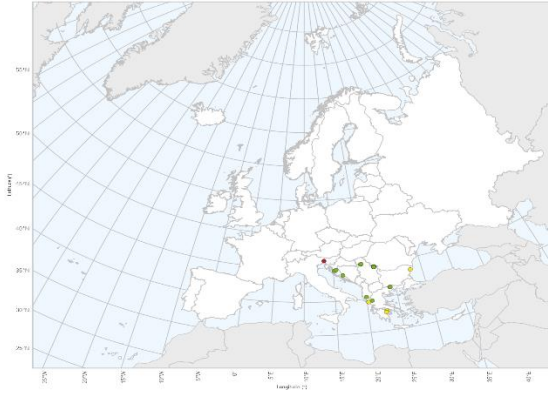
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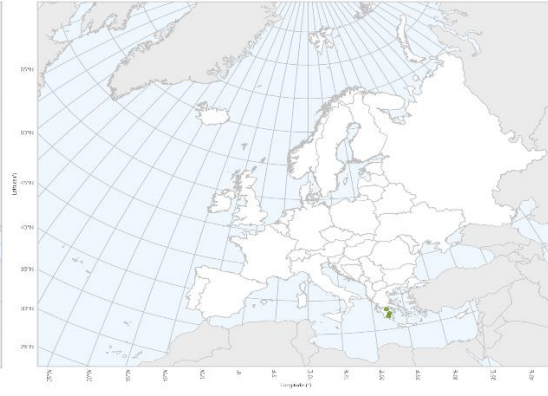
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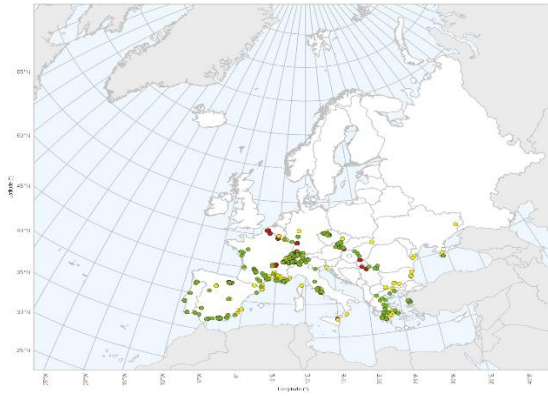
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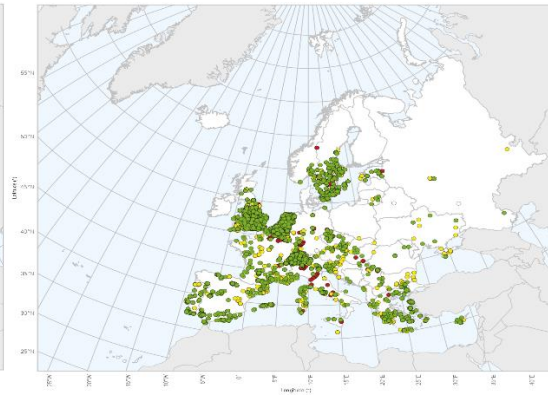
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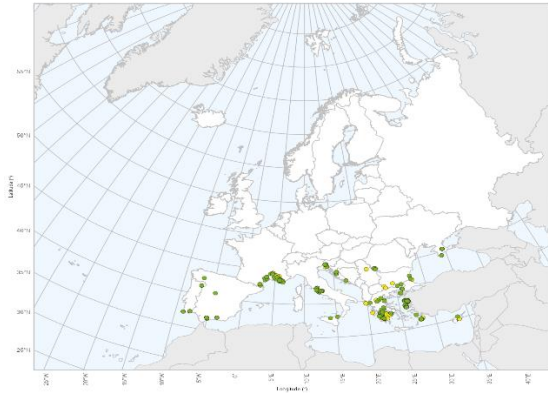
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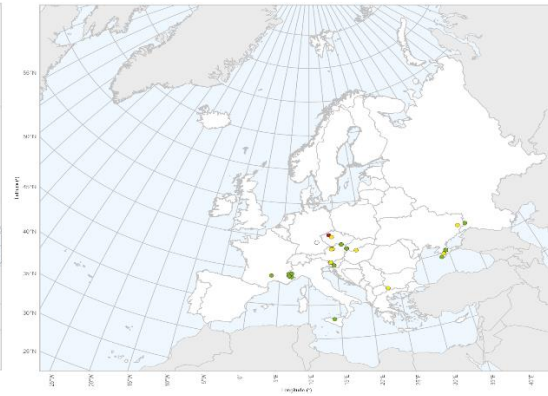
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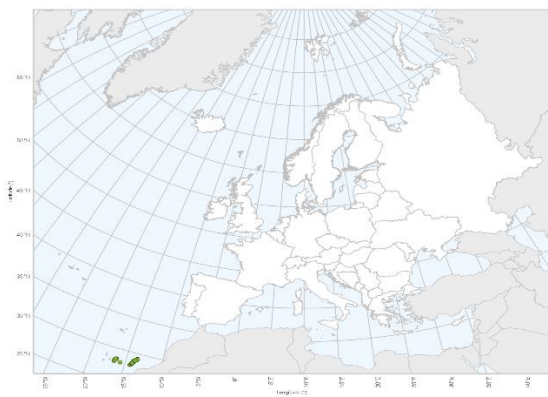
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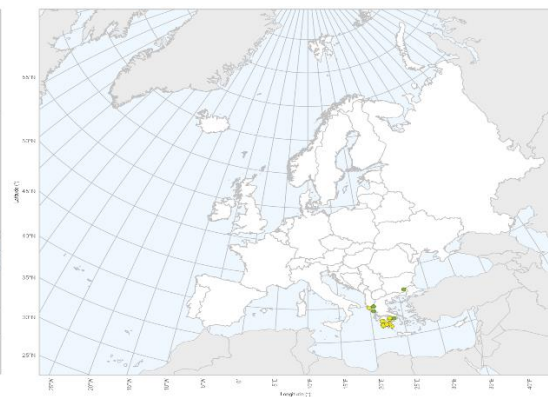
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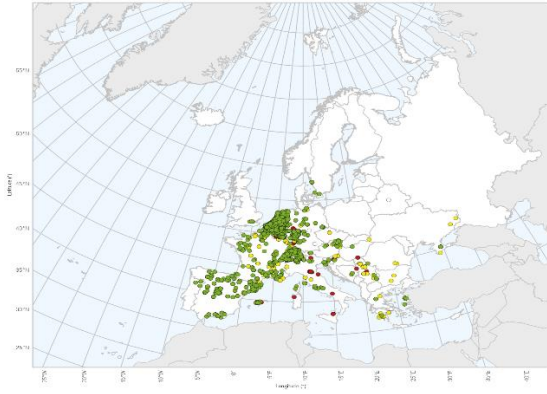
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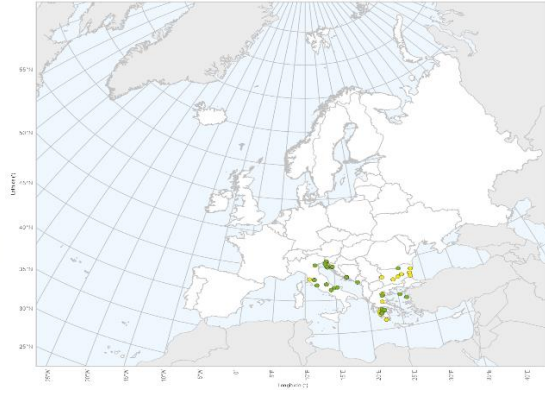
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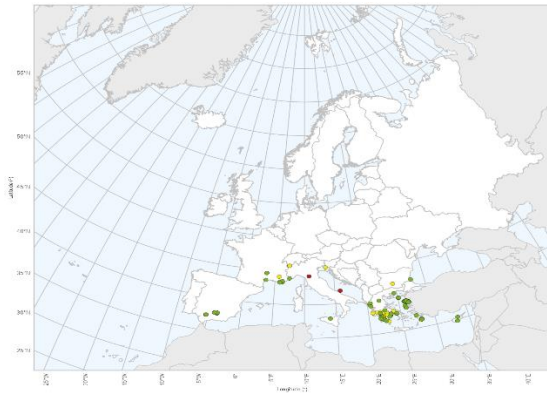
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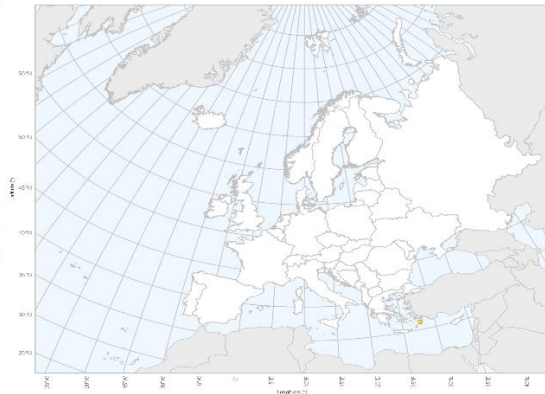
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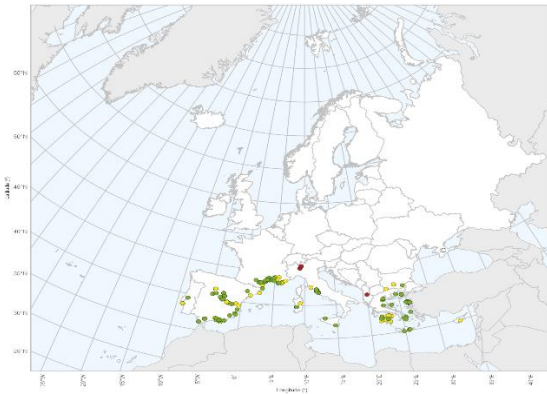
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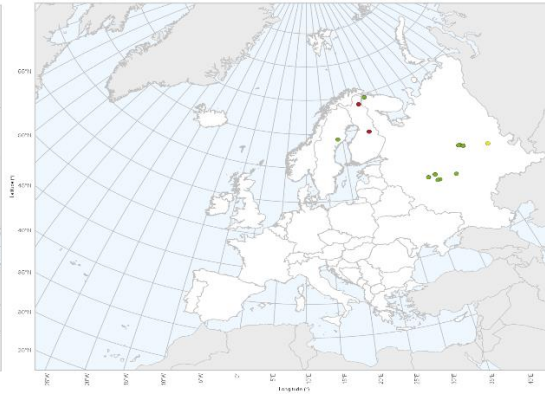
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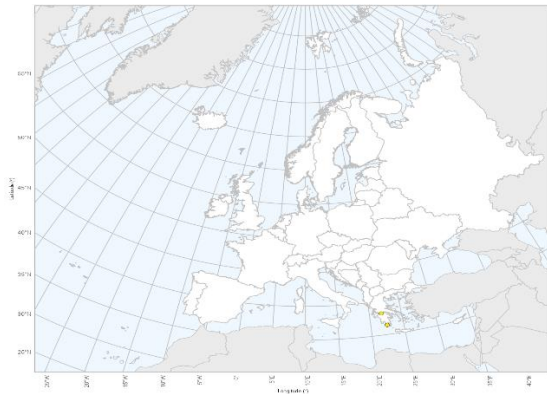
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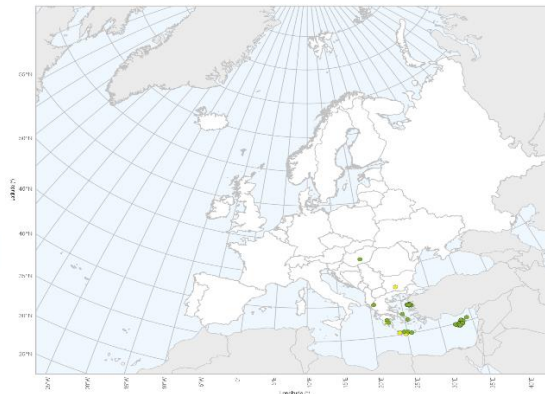
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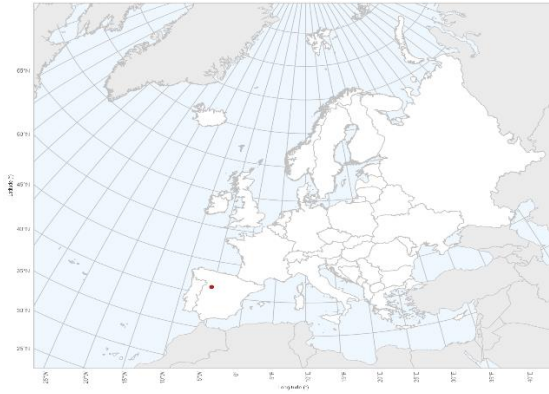
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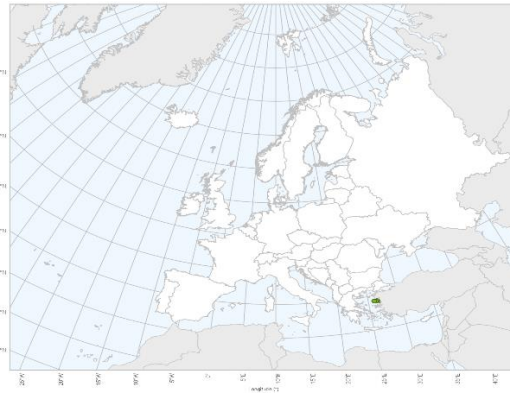
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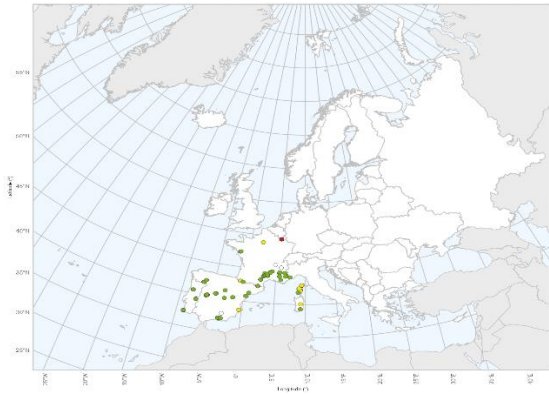
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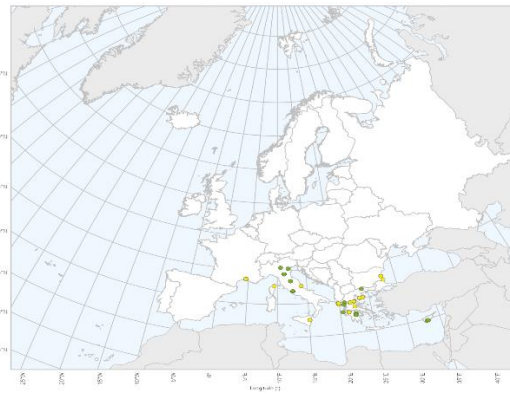
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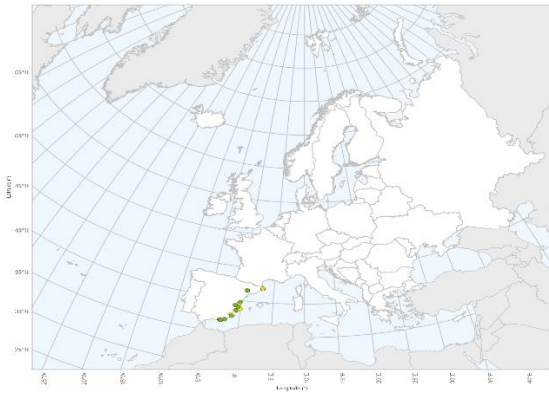
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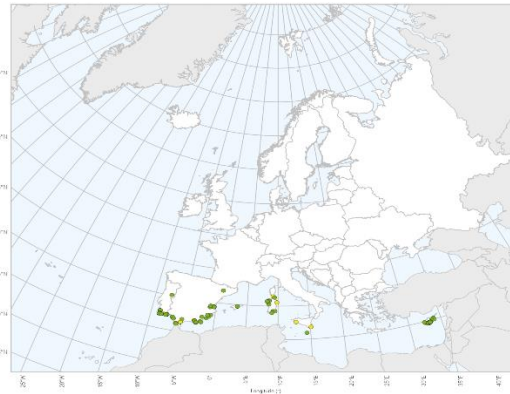
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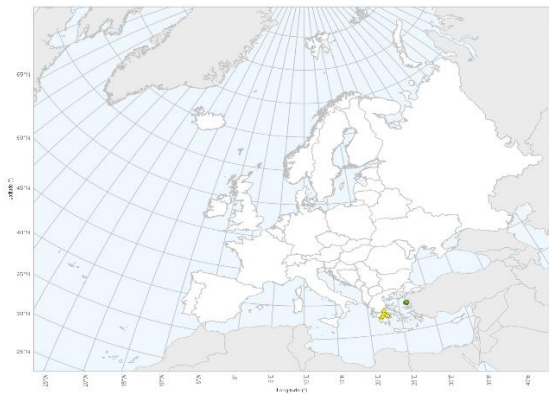
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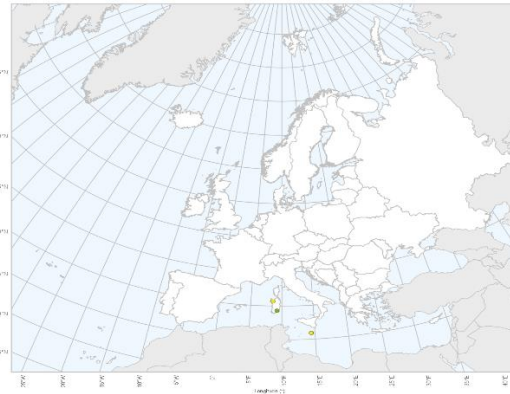
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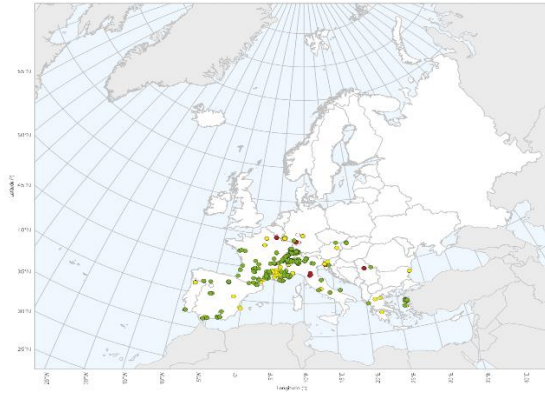
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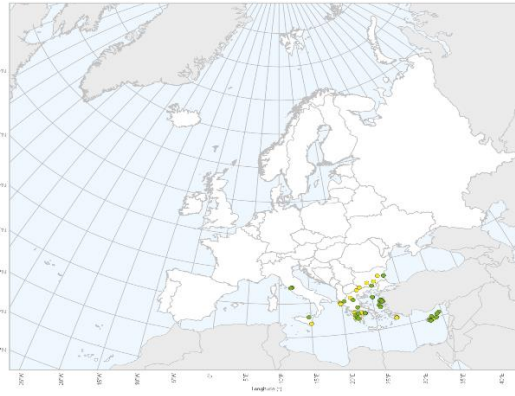
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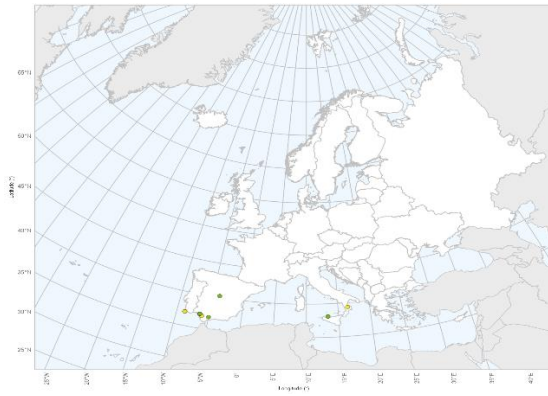
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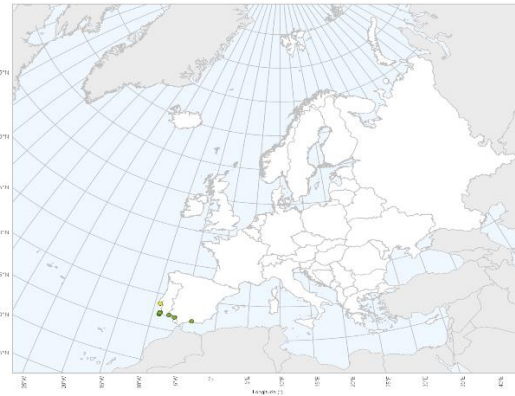
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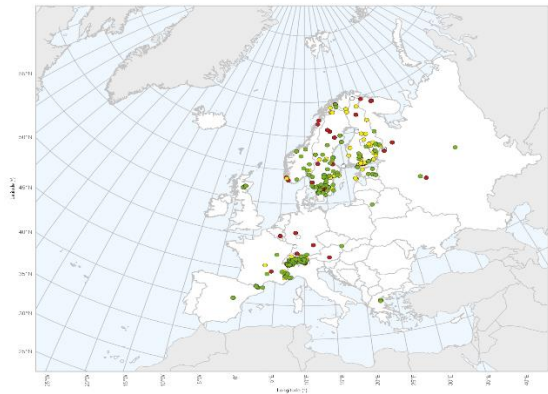
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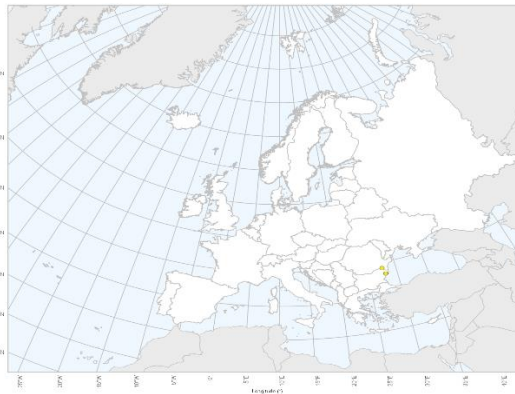
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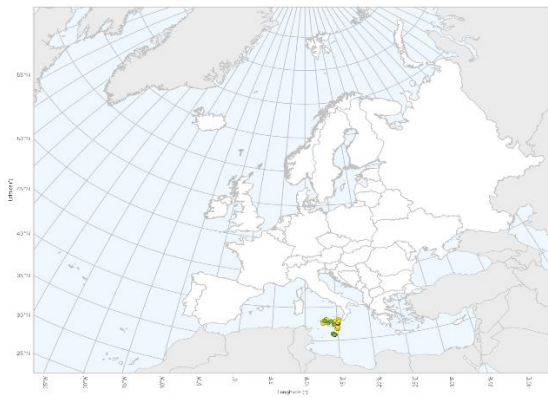
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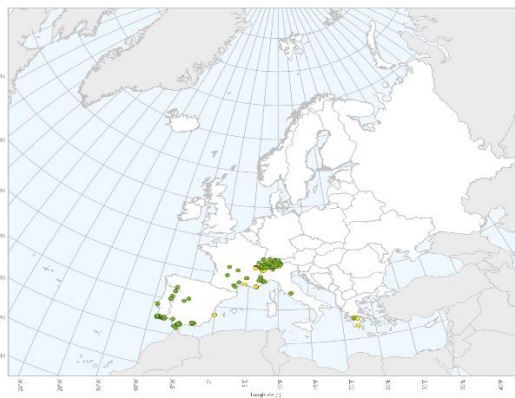
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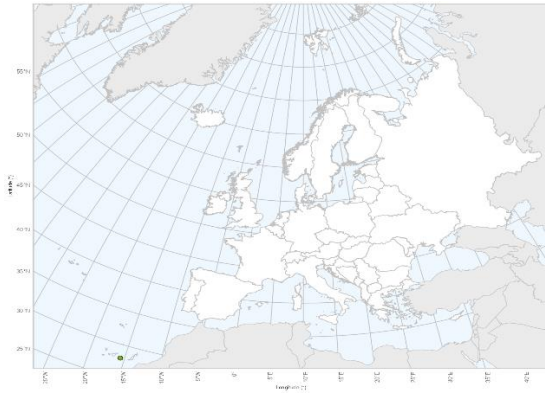
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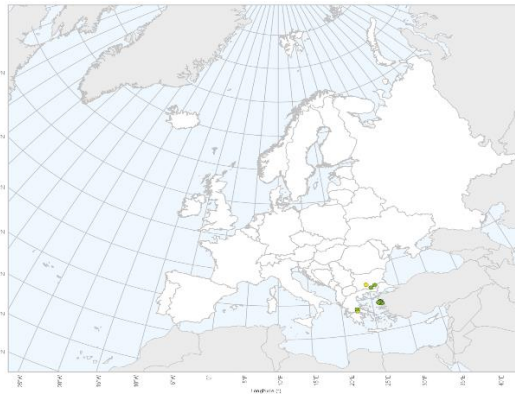
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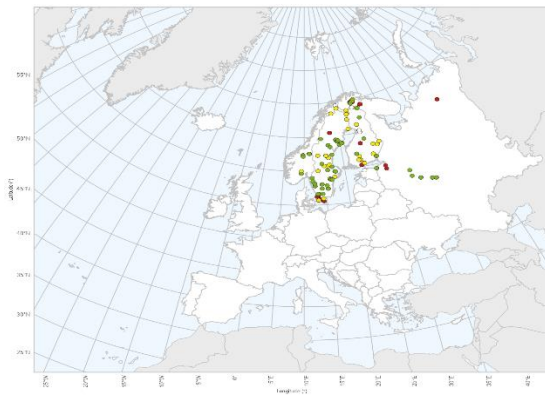
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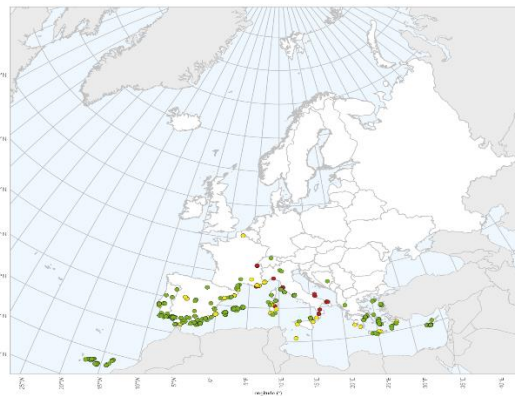
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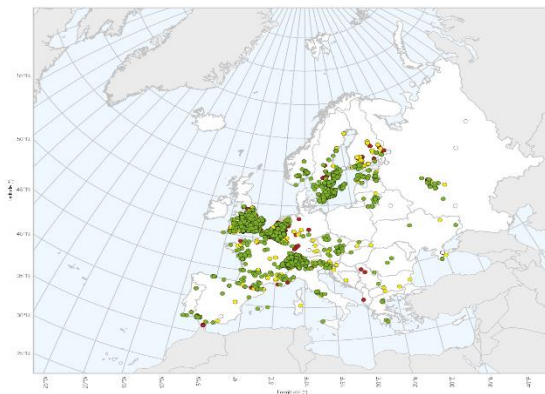
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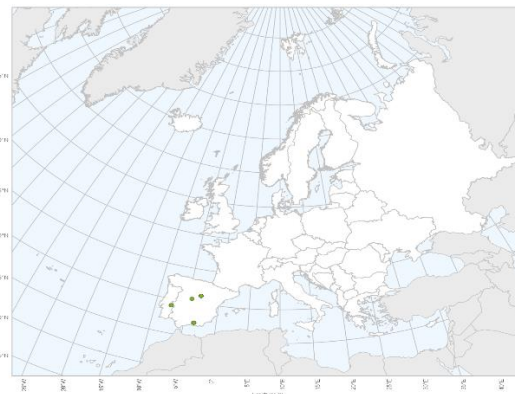
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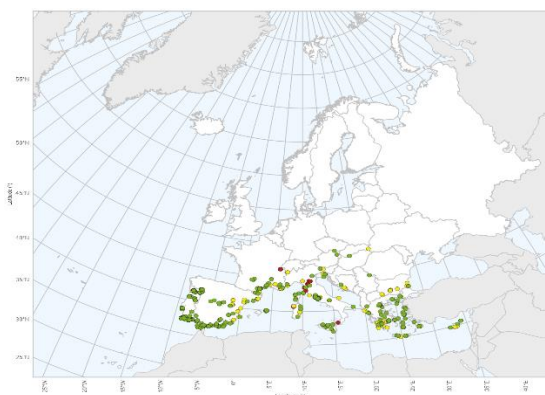
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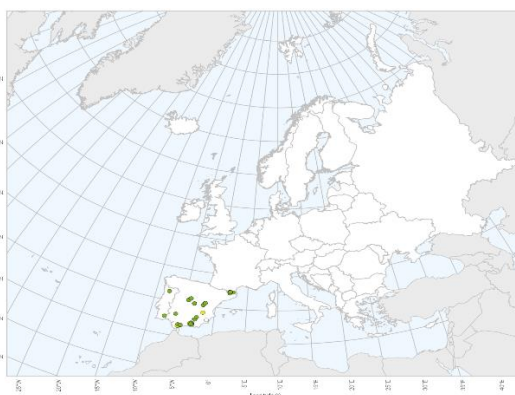
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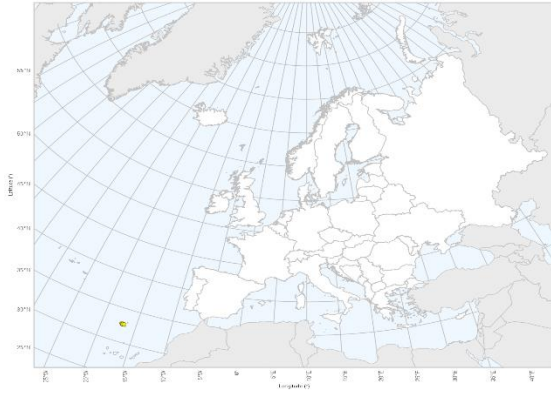
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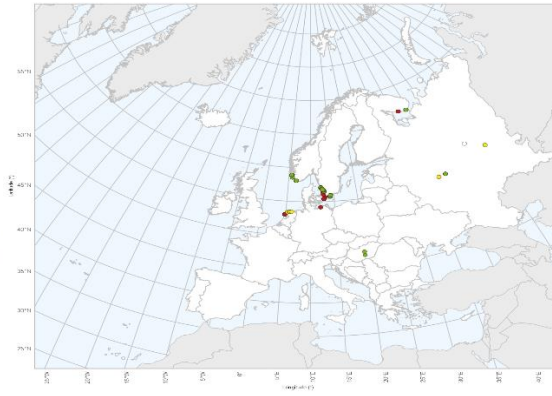
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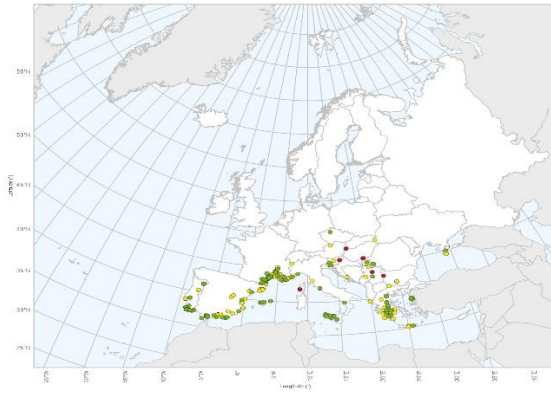
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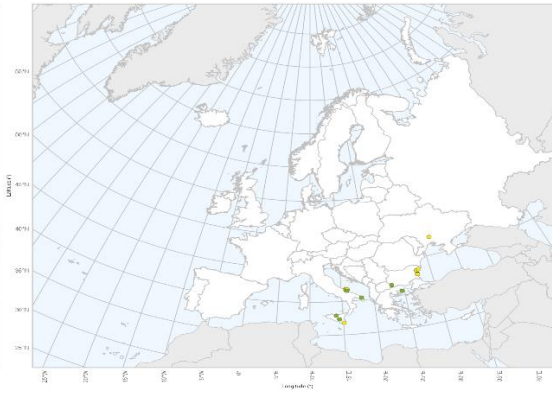
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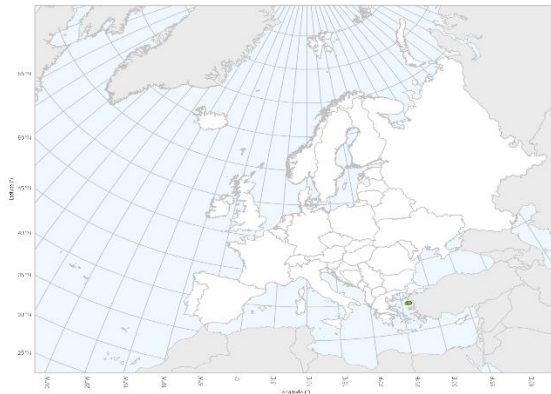
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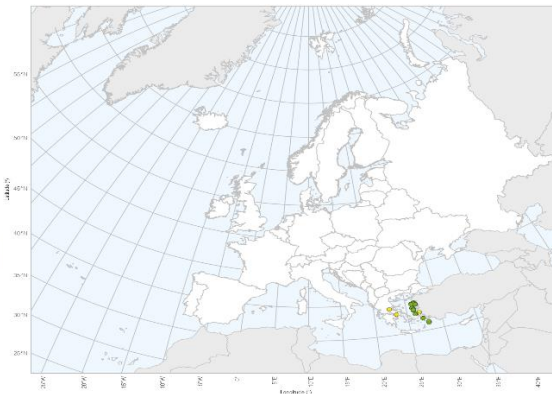
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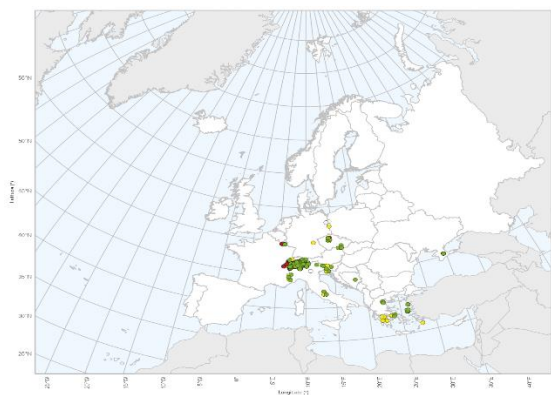
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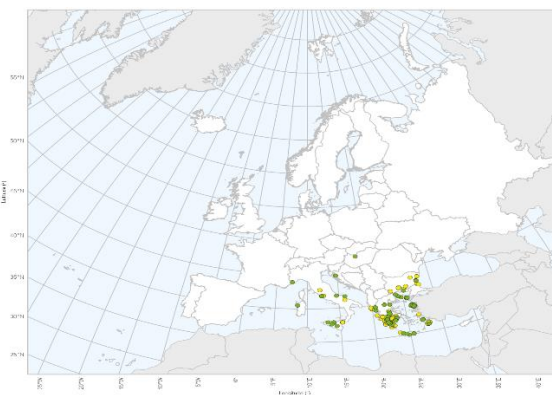
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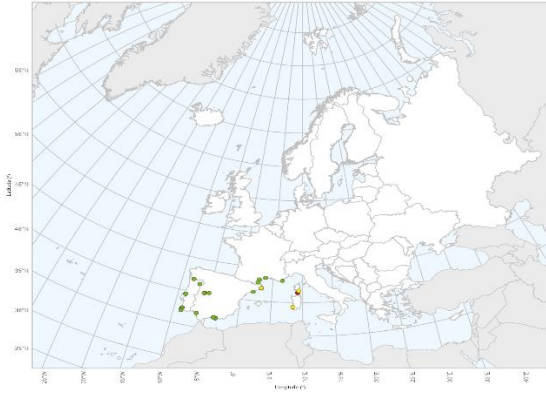
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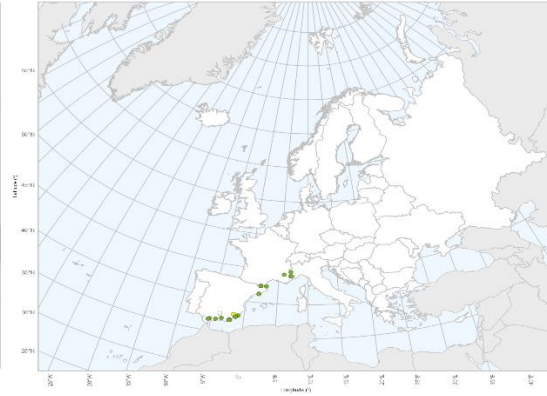
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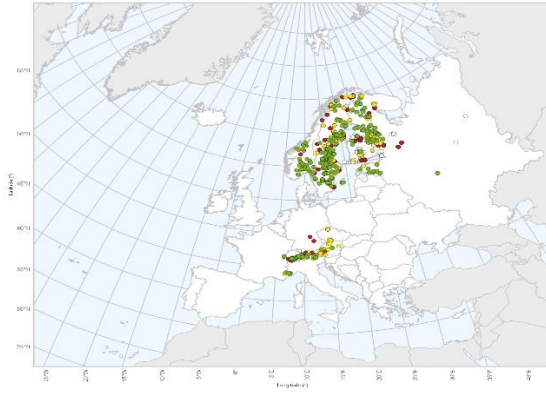
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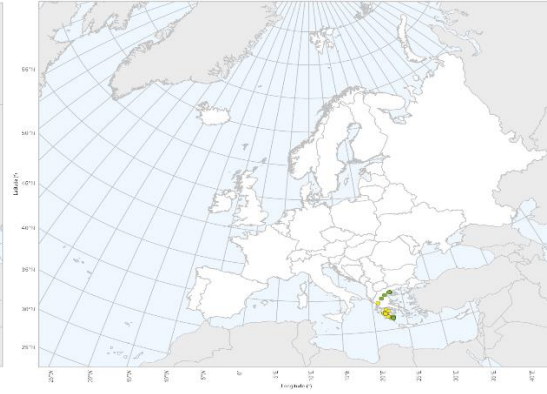
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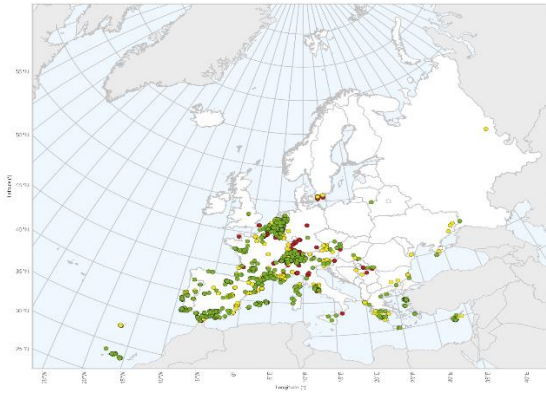
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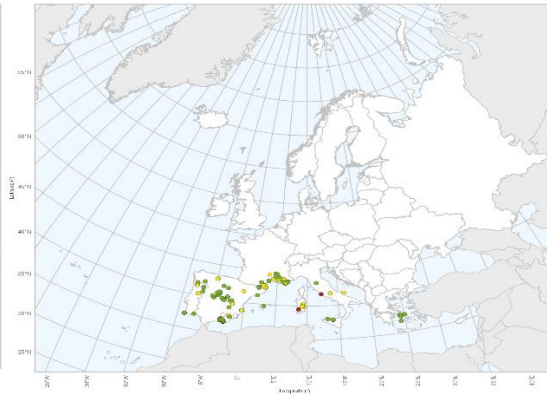
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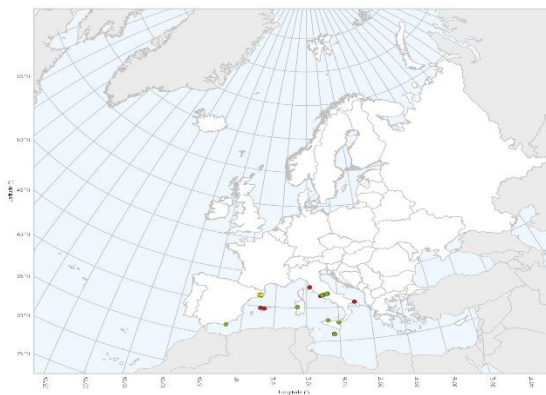
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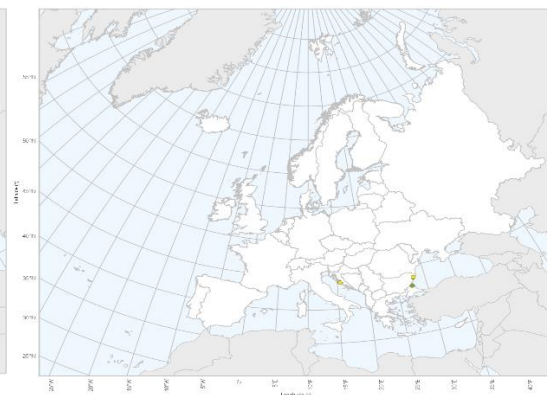
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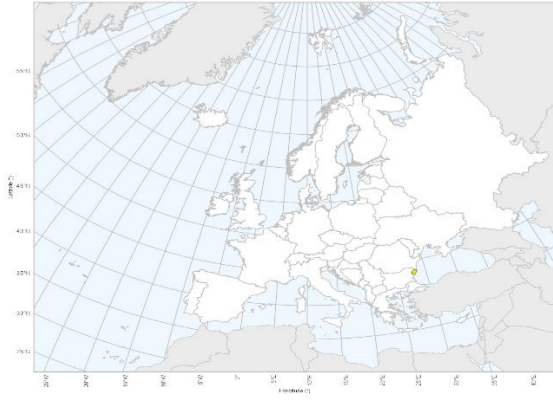
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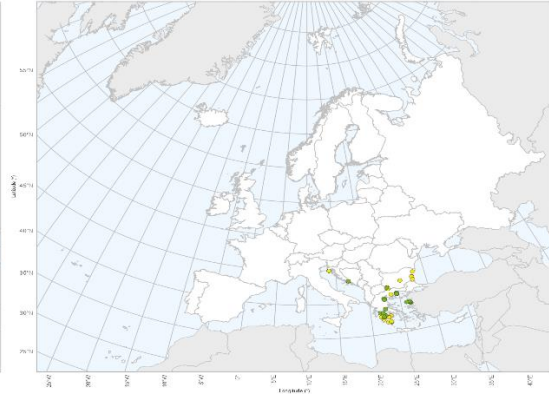
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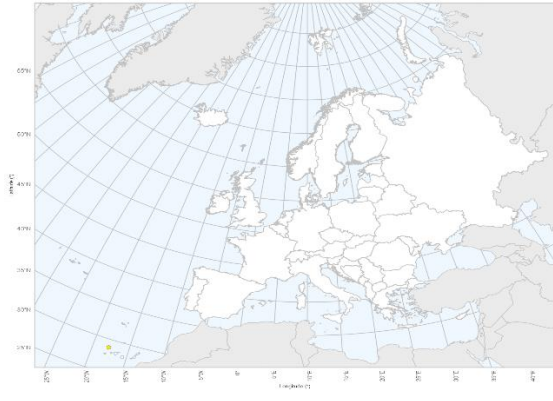
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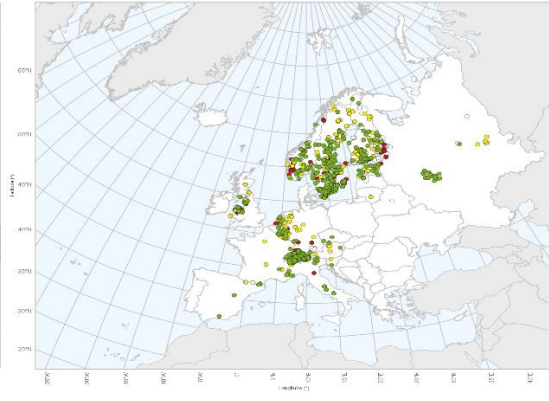
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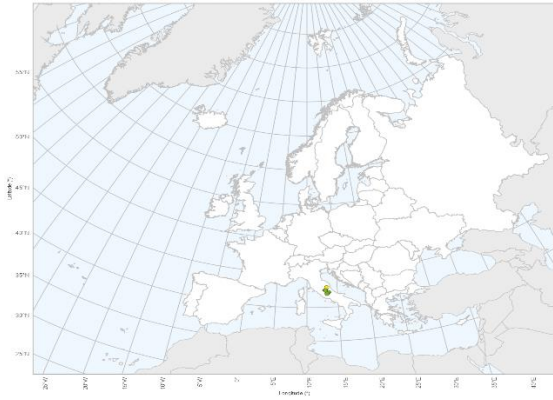
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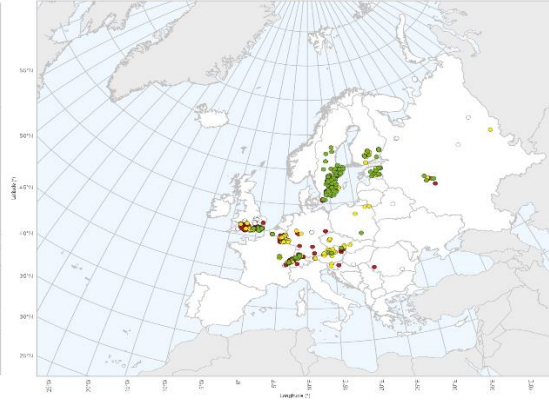
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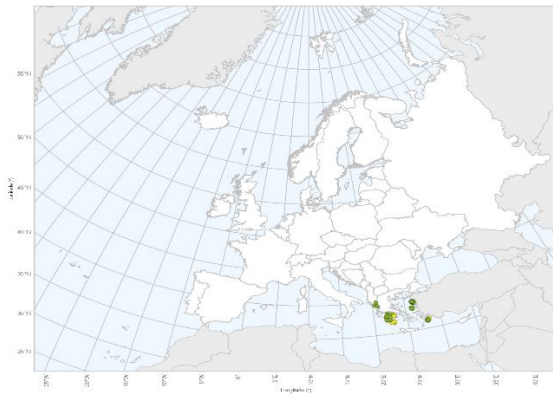
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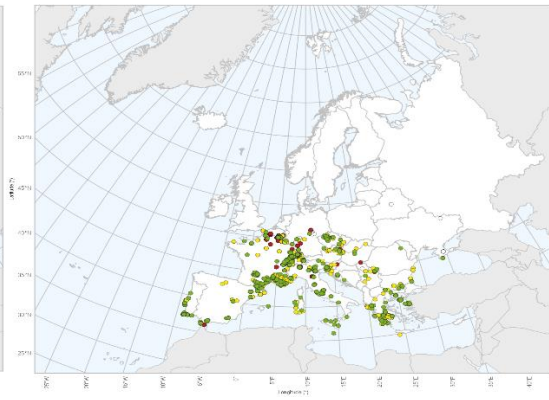
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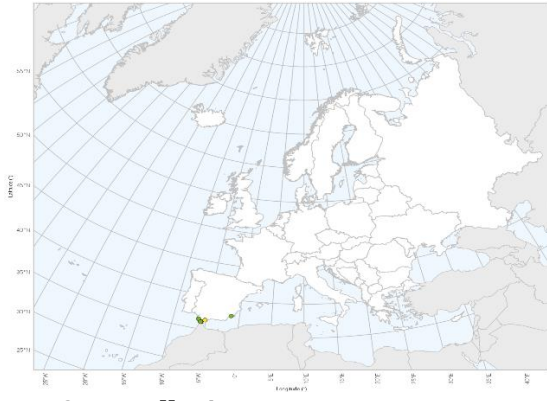
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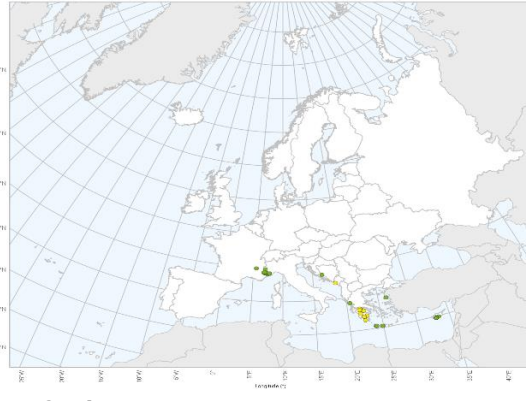
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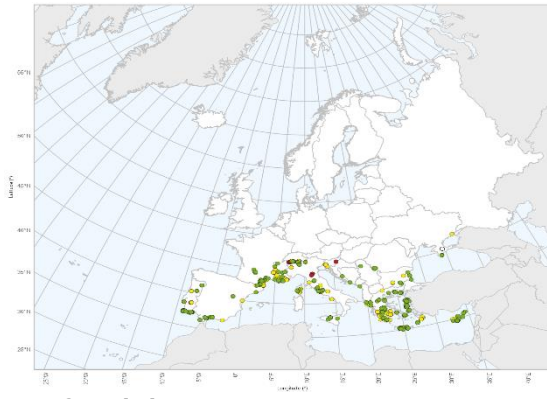
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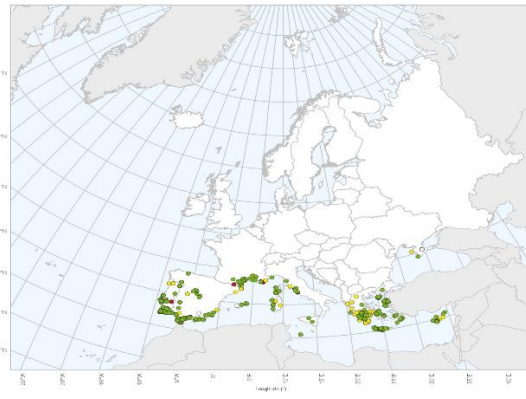
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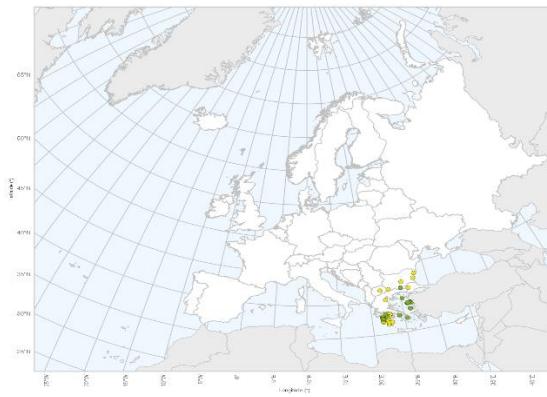
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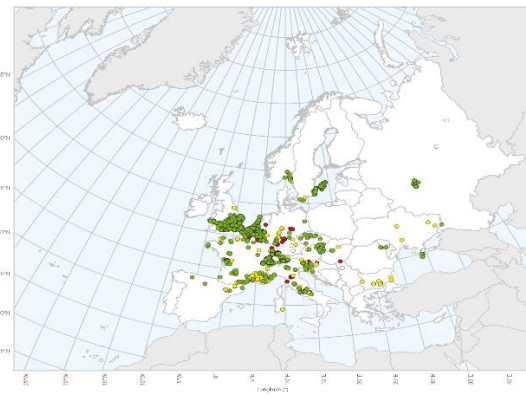
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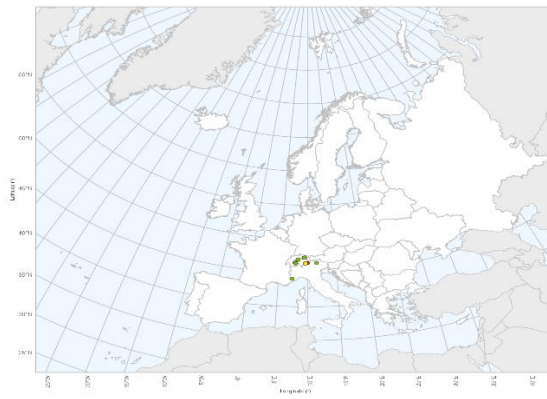
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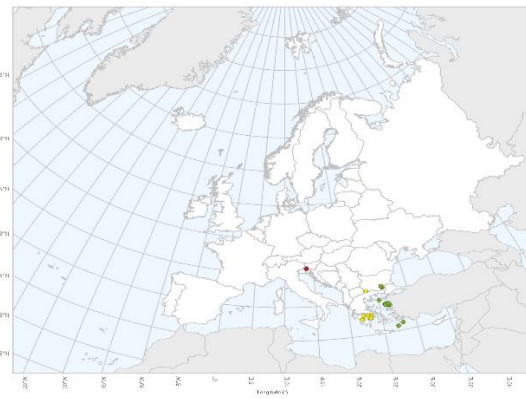
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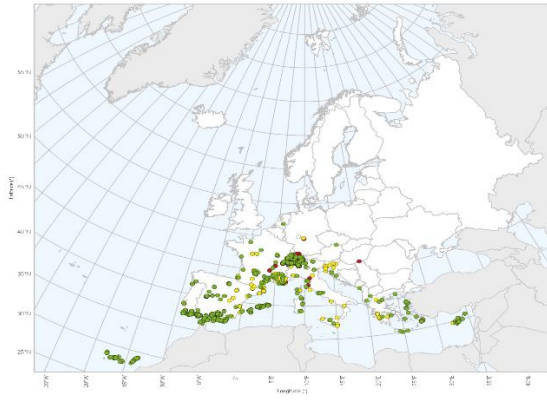
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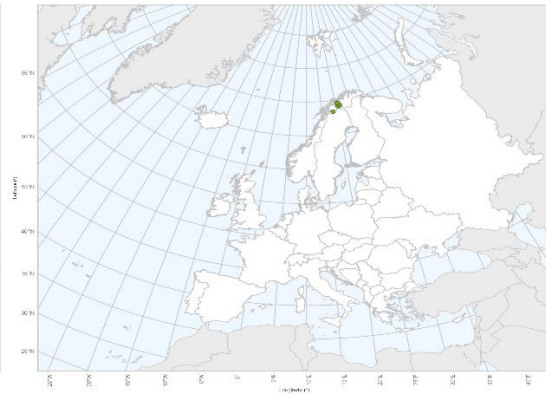
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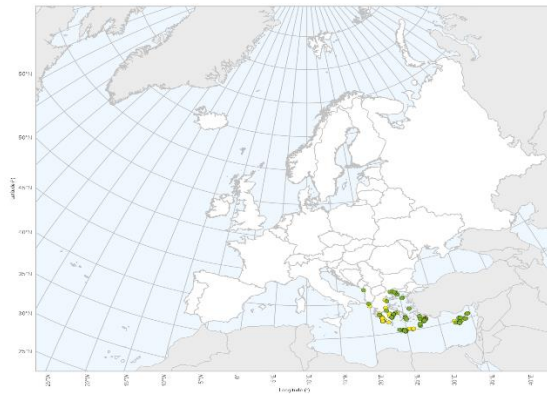
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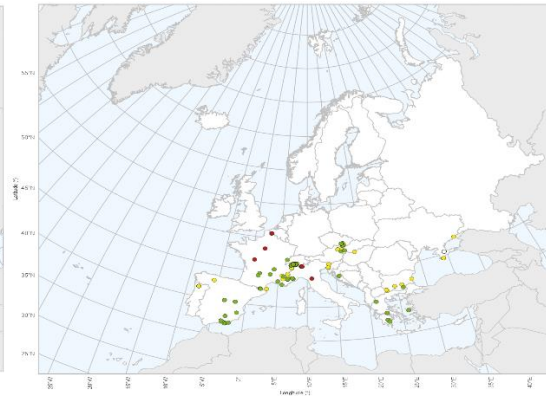
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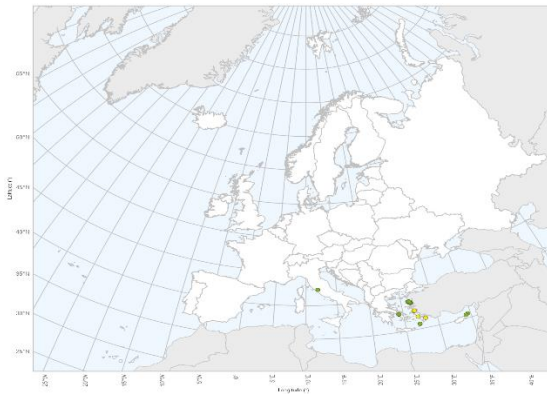
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O. uncicornis
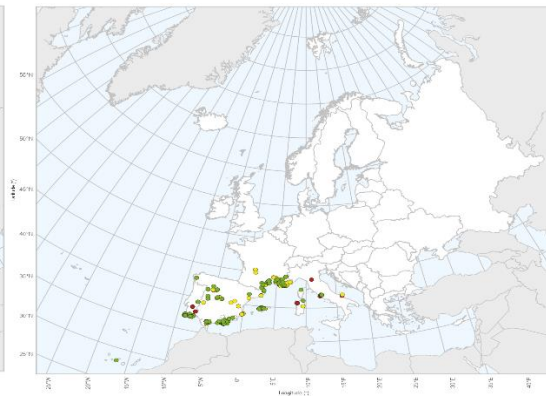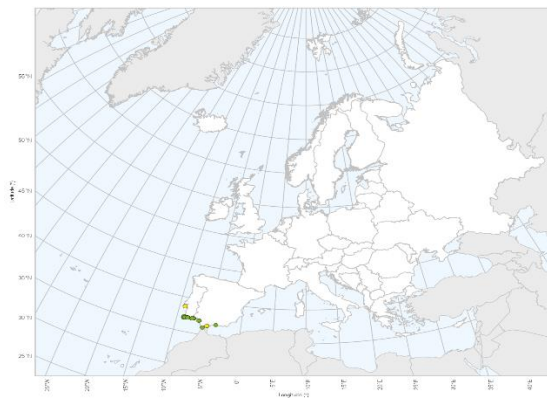
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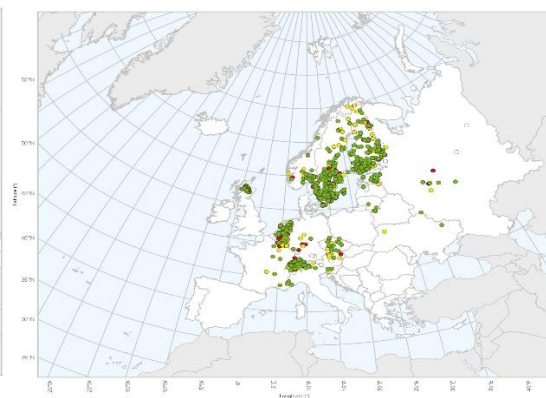
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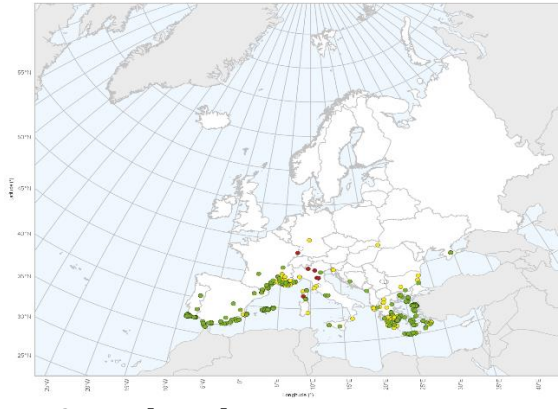
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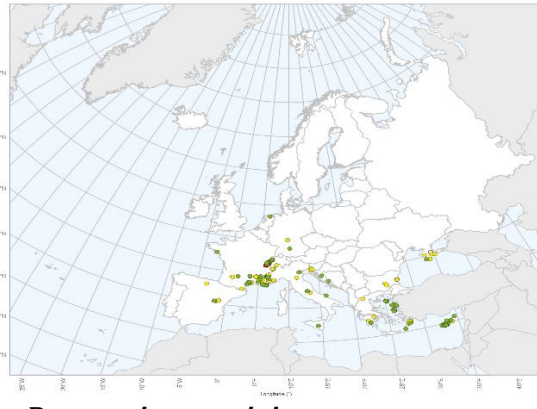
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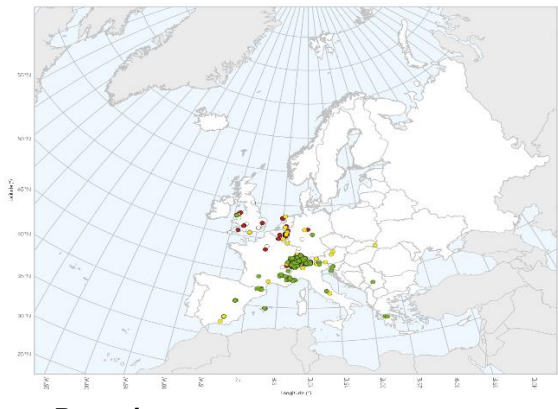
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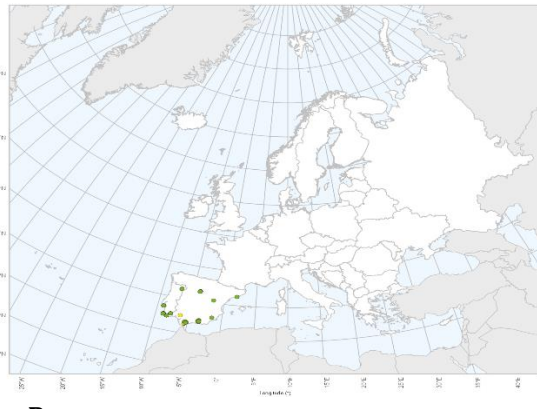
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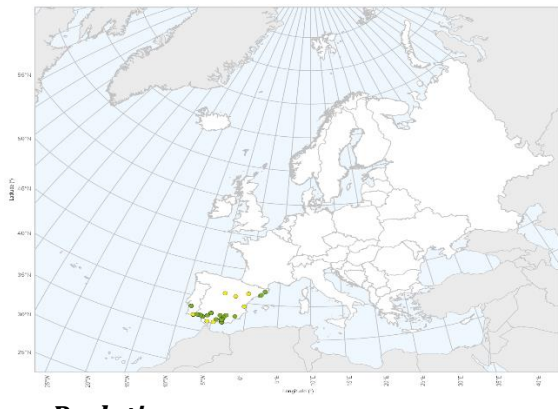
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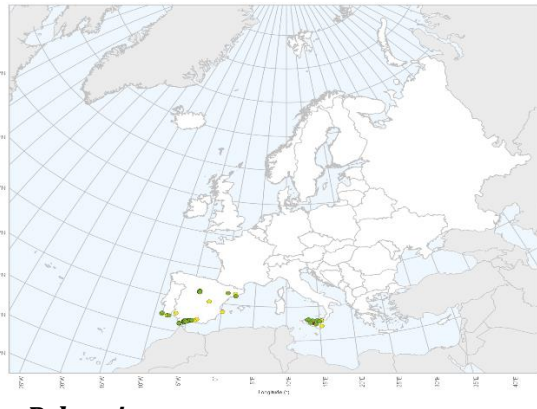
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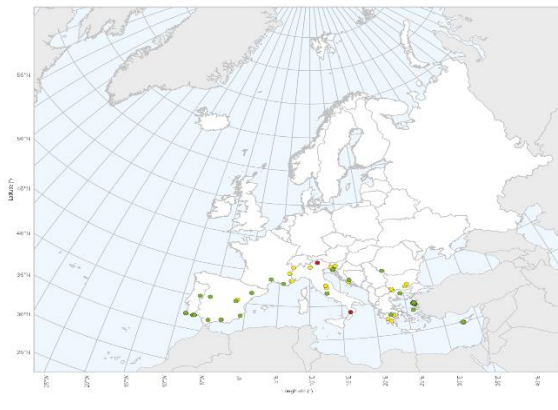
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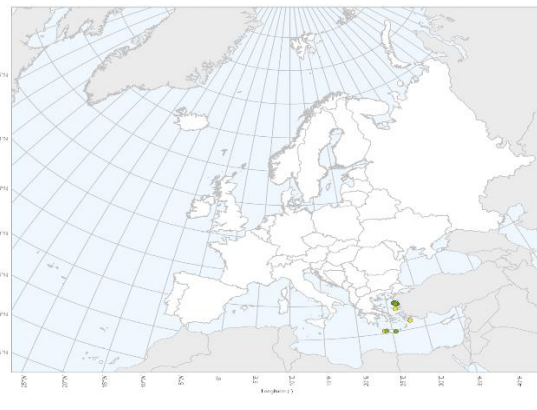
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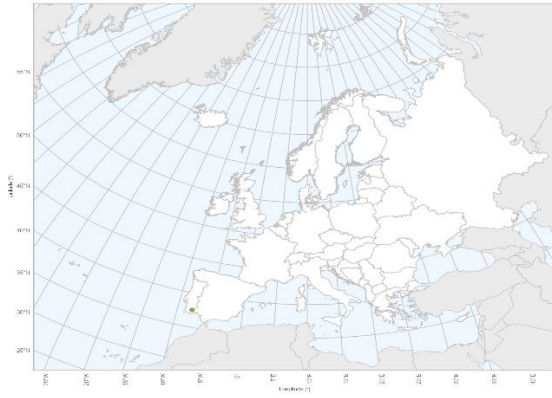
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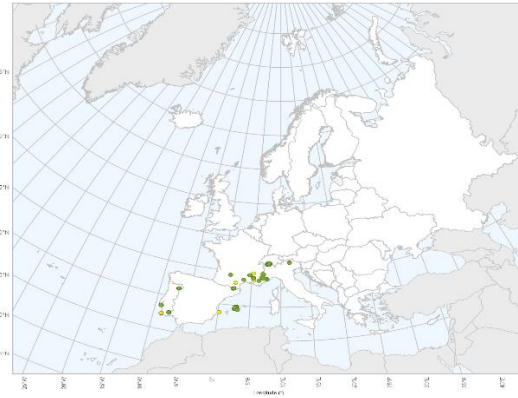
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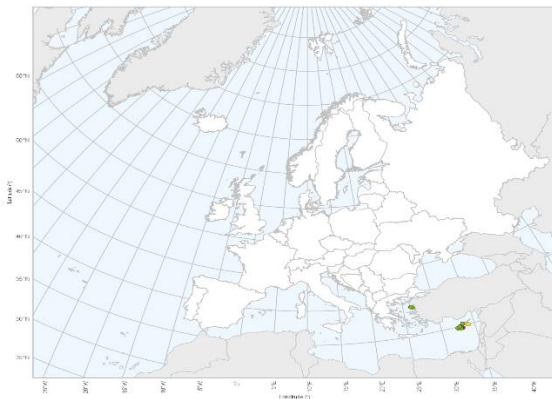
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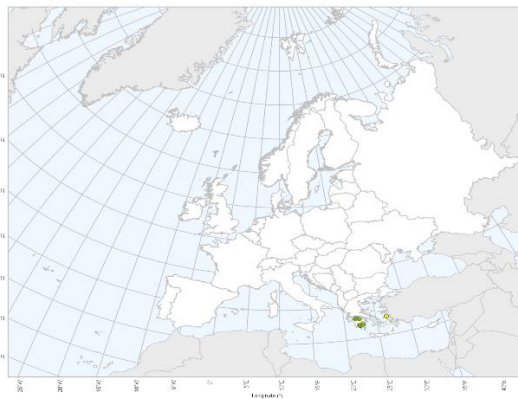
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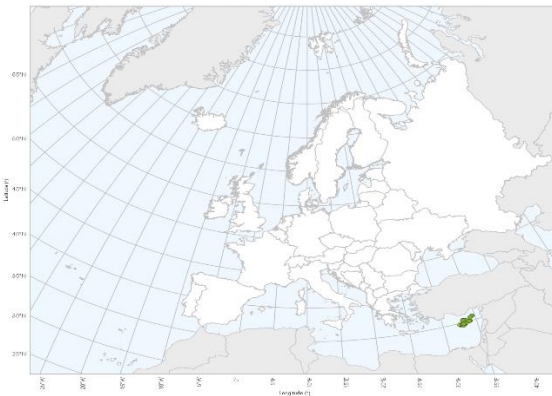
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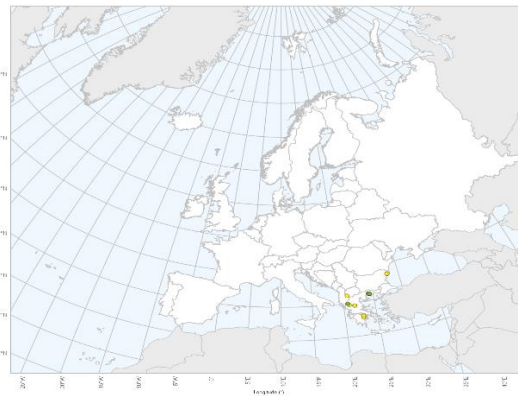
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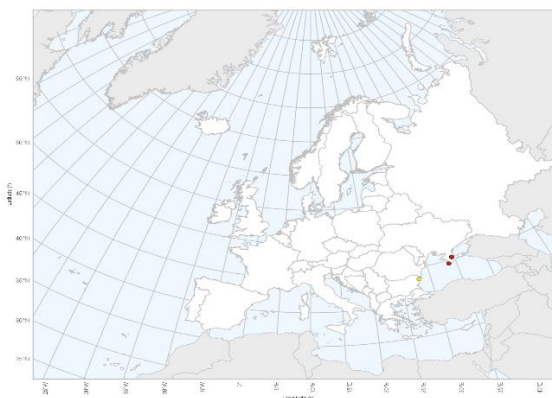
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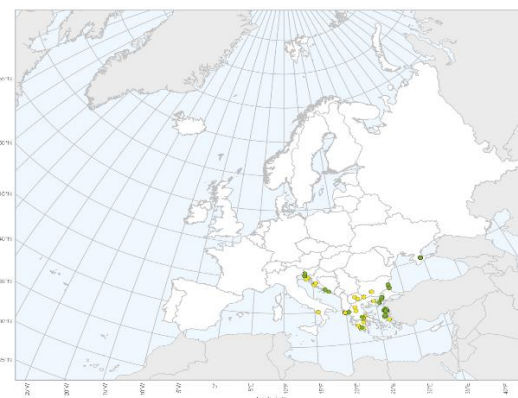
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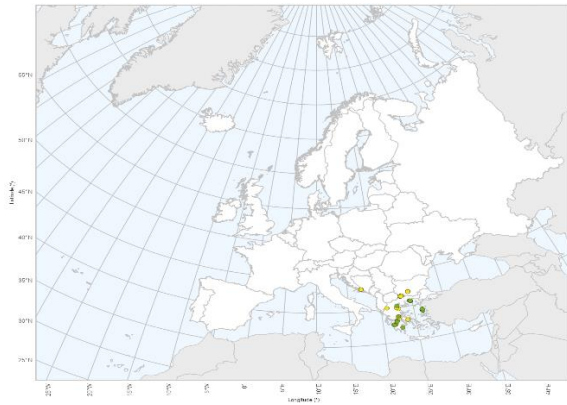
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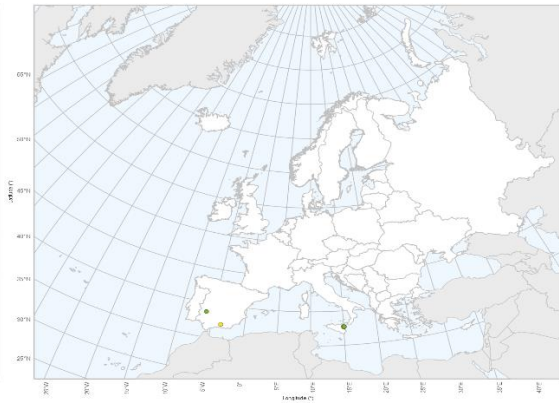
Appendix 4. List of the 66 modelled species with their number of unique occurrences data and mean AUC value. Only species with a minimum of 30 unique occurrence records were retained. AUC values were averaged across ten replicates for each species.

Species	Number of unique occurrences data	Mean AUC value
Chelostoma campanularum	457	0.748
Chelostoma distinctum	146	0.743
Chelostoma emarginatum	66	0.808
Chelostoma florisomne	438	0.733
Chelostoma foveolatum	36	0.871
Chelostoma rapunculi	395	0.624
Heriades crenulata	182	0.784
Heriades rubicola	101	0.772
Heriades truncorum	515	0.681
Hoplitis acuticornis	87	0.800
Hoplitis adunca	271	0.665
Hoplitis annulata	65	0.847
Hoplitis anthocopoides	103	0.585
Hoplitis benoisti	69	0.800
Hoplitis bisulca	74	0.868
Hoplitis claviventris	456	0.784
Hoplitis cristatula	35	0.902
Hoplitis lepeletieri	30	0.895
Hoplitis leucomelana	288	0.638
Hoplitis loti	35	0.890
Hoplitis manicata	53	0.806
Hoplitis mitis	60	0.809
Hoplitis perezi	53	0.817
Hoplitis ravouxi	42	0.69
Hoplitis stecki	32	0.885
Hoplitis tridentata	123	0.654

Hoplitis tuberculata	166	0.871
Hoplitis villosa	53	0.784
Hoplitis yermasoyiae	36	0.926
Osmia andrenoides	143	0.784
Osmia aurulenta	350	0.679
Osmia bicolor	248	0.766
Osmia bicornis	693	0.751
Osmia brevicornis	108	0.757
Osmia caerulescens	557	0.671
Osmia cephalotes	62	0.876
Osmia cornuta	224	0.697
Osmia cyanoxantha	37	0.897
Osmia dimidiata	44	0.941
Osmia ferruginea	31	0.862
Osmia gallarum	79	0.679
Osmia inermis	94	0.794
Osmia labialis	44	0.746
Osmia laticeps	37	0.659
Osmia latreillei	88	0.901
Osmia leaiana	372	0.711
Osmia ligurica	121	0.868
Osmia melanogaster	68	0.812
Osmia mustelina	43	0.809
Osmia nana	43	0.912
Osmia nigriventris	157	0.892
Osmia niveata	222	0.762
Osmia niveocincta	35	0.835
Osmia parietina	239	0.773
Osmia pilicornis	73	0.693
Osmia rufohirta	159	0.712
Osmia scutellaris	99	0.874
Osmia signata	109	0.854
Osmia spinulosa	211	0.737
Osmia submicans	158	0.779
Osmia sybarita	40	0.921
Osmia tricornis	46	0.890
Osmia uncinata	275	0.793
Osmia versicolor	99	0.873
Osmia viridana	42	0.671
Osmia xanthomelana	46	0.823

Appendix 5. Red List status of European osmiine bees. Status of 2014 are also listed for comparison (Nieto et al., 2014). Synonymies used in 2014 are put between brackets. The IUCN Red List Criteria specifies which categories and subcategories were used to assess the threatened or Near Threatened category of the species. LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; DD: Data Deficient; NA: Not Applicable. Several species (marked as not considered) were not evaluated in the 2014 Red List as they were either not described or not listed in Europe yet.

Species	IUCN Red List Category of 2014	Reassessment of the IUCN Red List Category	IUCN Red List Criteria
Chelostoma aegaeicum	DD	LC	
Chelostoma campanularum	LC	LC	
Chelostoma comosum	Not considered	DD	
Chelostoma diodon	DD	LC	
Chelostoma distinctum	LC	LC	
Chelostoma edentulum	DD	LC	
Chelostoma emarginatum	LC	LC	
Chelostoma florisomne	LC	LC	
Chelostoma forcipatum	DD	NA	
Chelostoma foveolatum	LC	LC	
Chelostoma grande	DD	NT	B1b(iii)+2b(iii)
Chelostoma handlirschi	DD	DD	
Chelostoma hellenicum	DD	LC	
Chelostoma incognitum	DD	LC	
Chelostoma laticaudum	DD	LC	
Chelostoma longifacies	DD	LC	
Chelostoma lucens	LC	LC	
Chelostoma mocsaryi	LC	LC	
Chelostoma nasutum	LC	LC	
Chelostoma rapunculi	LC	LC	
Chelostoma stefanii	Not considered	LC	
Chelostoma styriacum	LC	LC	
Chelostoma transversum	DD	LC	
Chelostoma ventrale	LC	LC	
Haetosmia circumventa	DD	LC	
Heriades clavicornis	DD	NA	

Heriades crenulata	LC	LC	
Heriades punctulifera	DD	LC	
Heriades rubicola	LC	LC	
Heriades truncorum	LC	LC	
Hofferia schmiedeknechti	LC	LC	
Hoplitis acuticornis	LC	LC	
Hoplitis adunca	LC	LC	
Hoplitis agis	DD	NA	
Hoplitis albatera	DD	DD	
Hoplitis albiscopa	DD	LC	
Hoplitis anipuncta	DD	NA	
Hoplitis annulata	LC	LC	
Hoplitis antalyae	Not considered	LC	
Hoplitis anthocopoides	LC	LC	
Hoplitis antigae	DD	LC	
Hoplitis batyamae	DD	NA	
Hoplitis benoisti	LC	LC	
Hoplitis bicallosa	DD	EN	B1ab(ii)+2ab(ii)
Hoplitis bihamata	DD	LC	
Hoplitis bispinosa	DD	LC	
Hoplitis bisulca	LC	LC	
Hoplitis brachypogon	LC	LC	
Hoplitis cadiza	DD	LC	
Hoplitis campanularis	LC	LC	
Hoplitis carinata	LC	LC	
Hoplitis caucasicola	Not considered	DD	
Hoplitis ciliaris	LC	LC	
Hoplitis claviventris	LC	LC	
Hoplitis corcyraea	NE	DD	
Hoplitis cristatula	LC	LC	
Hoplitis curtula	DD	LC	
Hoplitis curvipes	LC	LC	
Hoplitis cypriaca	DD	EN	B2ab(iii)
Hoplitis dalmatica	LC	LC	
Hoplitis fabrei	DD	LC	
Hoplitis fasciculata	DD	LC	
Hoplitis fertoni	DD	LC	
Hoplitis fulva	LC	VU	B2ab(ii,iii)
Hoplitis galbula	DD	NA	
Hoplitis galichicae	Not considered	VU	D1
Hoplitis graeca	DD	LC	
Hoplitis grossepunctata	DD	NA	
Hoplitis grumi	DD	NA	

Hoplitis haemi	DD	DD	
Hoplitis hilbera	DD	DD	
Hoplitis holmboei	DD	VU	D1
Hoplitis idaensis	DD	NA	
Hoplitis illyrica	LC	LC	
Hoplitis insularis	DD	NT	B2b(ii,iii)
Hoplitis jakovlevi	LC	LC	
Hoplitis jheringii	LC	LC	
Hoplitis laevifrons	LC	LC	
Hoplitis lepeletieri	LC	LC	
Hoplitis leucomelana	LC	LC	
Hoplitis limassolica	DD	LC	
Hoplitis lithodorae	DD	LC	
Hoplitis loti	LC	LC	
Hoplitis lysholmi	DD	LC	
Hoplitis manicata	LC	LC	
Hoplitis manuelae	DD	DD	
Hoplitis marchali	LC	LC	
Hoplitis mazzuccoi	LC	LC	
Hoplitis mitis	LC	LC	
Hoplitis mocsaryi	LC	LC	
Hoplitis mollis	DD	NA	
Hoplitis monticola	DD	NA	
Hoplitis moricei	DD	LC	
Hoplitis nicolaei	DD	LC	
Hoplitis obtusa	DD	LC	
Hoplitis occidentalis	DD	LC	
Hoplitis ochraceicornis	LC	LC	
Hoplitis onychophora	Not considered	NA	
Hoplitis pallicornis	LC	LC	
Hoplitis papaveris	LC	LC	
Hoplitis parnesica	DD	DD	
Hoplitis peniculifera	DD	DD	
Hoplitis perambigua	Not considered	LC	
Hoplitis perezi	LC	LC	
Hoplitis pici	LC	LC	
Hoplitis pomarina	DD	DD	
Hoplitis praestans	LC	LC	
Hoplitis princeps	DD	LC	
Hoplitis pulchella	DD	NA	
Hoplitis quinquespinosa	LC	NA	
Hoplitis ravouxi	LC	LC	
Hoplitis robusta	LC	LC	
Hoplitis saundersi	LC	LC	
Hoplitis saxialis	DD	VU	B2ab(iii)

Hoplitis serainae	DD	NA	
Hoplitis stecki	Not considered	LC	
Hoplitis stellaris	DD	NA	
Hoplitis strymonia	DD	NA	
Hoplitis subbutea	DD	LC	
Hoplitis submanicata	DD	LC	
Hoplitis taurica	NE	DD	
Hoplitis tenuispina	DD	LC	
Hoplitis teucrii	Not considered	NA	
Hoplitis tigrina	DD	LC	
Hoplitis tkalcuella	DD	LC	
Hoplitis tridentata	LC	LC	
Hoplitis tuberculata	LC	LC	
Hoplitis turcestanica	Not considered	NA	
Hoplitis villosa	LC	LC	
Hoplitis yermasoyiae	LC	LC	
Hoplitis zaianorum	DD	LC	
Hoplitis zandeni	DD	LC	
Osmia aeruginosa	DD	NA	
Osmia alfkenii	DD	NA	
Osmia alticola	LC	NT	B2b(iii)
Osmia amathusica	DD	LC	
Osmia anceyi	LC	LC	
Osmia andrenoides	LC	LC	
Osmia apicata	LC	LC	
Osmia argyropyga	LC	LC	
Osmia ariadne	DD	DD	
Osmia aurulenta	LC	LC	
Osmia balearica	DD	LC	
Osmia bicolor	LC	LC	
Osmia bicornis	LC	LC	
Osmia bidentata	LC	LC	
Osmia bischoffi	LC	LC	
Osmia breviata	DD	DD	
Osmia brevicornis	LC	LC	
Osmia caerulescens	LC	LC	
Osmia cephalotes	LC	LC	
Osmia cerinthidis	LC	LC	
Osmia cinnabarina	DD	LC	
Osmia clypearis	LC	LC	
Osmia corniculata	DD	DD	
Osmia cornuta	LC	LC	
Osmia croatica	LC	LC	
Osmia cyanoxantha	LC	LC	
Osmia dilaticornis	DD	NA	

Osmia dimidiata	LC	LC	
Osmia disjuncta	Not considered	LC	
Osmia distinguenda	LC	NA	
Osmia dives	LC	LC	
Osmia dusmeti	DD	DD	
Osmia elegans	DD	LC	
Osmia emarginata	LC	LC	
Osmia erythrogastra	LC	LC	
Osmia fallax	DD	LC	
Osmia ferruginea	LC	LC	
Osmia forticornis	DD	NA	
Osmia frieseana	DD	NA	
Osmia gallarum	LC	LC	
Osmia hellados	DD	LC	
Osmia heteracantha	LC	LC	
Osmia iberica	DD	NT	B2b(iii)
Osmia inermis	LC	LC	
Osmia jason	LC	LC	
Osmia kohlii	DD	LC	
Osmia labialis	LC	LC	
Osmia larochei	DD	NT	B1ab(i,ii,iii)+2ab(i,ii,iii)
Osmia laticauda	DD	LC	
Osmia laticeps	LC	LC	
Osmia latreillei	LC	LC	
Osmia leaiana	LC	LC	
Osmia leucopyga	Not considered	LC	
Osmia ligurica	LC	LC	
Osmia lunata	LC	LC	
Osmia madeirensis	DD	LC	
Osmia maritima	EN	EN	B2ab(ii,iii,v)
Osmia melanogaster	LC	LC	
Osmia melanura	LC	NT	B2b(i,ii)
Osmia mirhiji	DD	NA	
Osmia moreensis	DD	LC	
Osmia mustelina	LC	LC	
Osmia nana	DD	LC	
Osmia nasoproducta	DD	LC	
Osmia nasuta	DD	LC	
Osmia nigriventris	LC	LC	
Osmia nigrohirta	DD	LC	
Osmia niveata	LC	LC	
Osmia niveocincta	DD	LC	
Osmia notata	LC	LC	
Osmia nuda	Not considered	NA	
Osmia olgae	DD	NA	

Osmia padri	DD	LC	
Osmia palmae	DD	DD	
Osmia parietina	LC	LC	
Osmia picena	DD	LC	
Osmia pilicornis	LC	LC	
Osmia pinguis	LC	NA	
Osmia rhodoensis	LC	LC	
Osmia rufohirta	LC	LC	
Osmia rutila	DD	NT	B2b(ii,iii)
Osmia saxicola	LC	LC	
Osmia scutellaris	LC	LC	
Osmia signata	LC	LC	
Osmia spinigera	DD	LC	
Osmia spinulosa	LC	LC	
Osmia steinmanni	DD	NT	B2b(iii)
Osmia subcornuta	LC	LC	
Osmia submicans	LC	LC	
Osmia svenssoni	DD	VU	B2ab(iii)
Osmia sybarita	LC	LC	
Osmia tergestensis	LC	LC	
Osmia teunisseni	DD	LC	
Osmia tricornis	LC	LC	
Osmia uncicornis	LC	LC	
Osmia uncinata	LC	LC	
Osmia versicolor	LC	LC	
Osmia viridana	LC	LC	
Osmia xanthomelana	LC	LC	
Protosmia asensioi	DD	LC	
Protosmia capitata	DD	LC	
Protosmia exenterata	LC	LC	
Protosmia glutinosa	LC	LC	
Protosmia longiceps	DD	LC	
Protosmia lusitanica	Not considered	DD	
Protosmia minutula	DD	LC	
Protosmia monstrosa	DD	LC	
Protosmia montana	DD	NA	
Protosmia paradoxa	DD	LC	
Protosmia sideritis	DD	LC	
Protosmia tauricola	LC	NA	
Protosmia tiflensis	LC	LC	
Stenoheriades coelostoma	DD (as *S. hofferi*)	LC	
Stenoheriades maroccana	Not considered	LC	

Appendix 6. Summary of tests performed (GLM) between status and traits. *Significant p-values under a significance threshold of 5% are in bold, and marginal ones are underlined. χ²= chi-square values; df = degree of freedom.*

Trait	χ^2	df	*p*-value
Inter-Tegular Distance (ITD)	0.0373	1	0.8469
Hairiness index	0.2712	1	0.6025
Nesting area	2.5104	4	0.6428
Nesting material	5.0355	3	0.1692
Nesting method	2.81	3	0.4219
Nesting position	3.2102	2	0.2009
Lecty	0.4625	1	0.4964
Extent Of Occurrence (EOO)	11.371	1	**0.000746**
Area Of Occupancy (AOO)	3.3888	1	<u>0.06564</u>
Species Continentality Index (SCI)	4e-04	1	0.9833
Species Temperature Index (STI)	5.0671	1	**0.02438**