History of colonisation and updated distribution of the Monarch butterfly *Danaus plexippus* (Linnaeus, 1758) and its hostplants in mainland Portugal, Azores and Madeira

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Abstract. The first observations of the Monarch butterfly (*Danaus plexippus*) in Iberia date from 1886, although breeding records emerged almost a century later: 1960 in Spain, 1980s–1990s in Madeira and Azores, and 2003 in mainland Portugal. We reviewed the history of the colonisation of mainland and insular Portugal by the Monarch butterfly and its hostplants (*Gomphocarpus fruticosus*, *G. physocarpus* and *Asclepias curassavica*). We also compiled available historical and recent occurrence records as a basis for countrywide surveys of the butterfly and hostplants, to update their current distributions in Portugal. Locations for only a few of the older records represented newly rediscovered populations in the field, although recent occurrences were often confirmed. Hostplants were scarce and monarchs absent in northern and central mainland Portugal, but both were quite common in the southwest. In Madeira, hostplants were found in two locations, while monarchs were common and widespread. In the Azores, small hostplant patches were observed on four of seven surveyed islands, whereas monarchs were rare and restricted to two islands. Abandoned/semi-abandoned orange orchards represent the butterfly's stronghold in Portugal, with the species being increasingly scarce along rivers and road verges where hostplants are declining. Hostplant persistence is unstable, with many patches removed, while others have expanded or colonised new areas. Overall, hostplants appear to be declining, with implications for the persistence of monarch butterflies in the country.

Introduction

The Monarch butterfly and its worldwide expansion

The Monarch butterfly *Danaus plexippus* is one of the most charismatic butterfly species. This is largely because of the spectacular fall migration of its North American eastern population between southern Canada and Mexico (Urquhart and Urquhart 1978). Since the mid-19th century, the species has spread from its original North American range across the Pacific and Atlantic Oceans (Vane-Wright 1993; Zalucki and Clarke 2004), although genetics indicate a possible earlier expansion (Zhan et al. 2014). These authors suggested that southern USA or northern Mexico were the likely geographic origin of three independent dispersal events: (1) to Central and South America, Bermuda and Puerto Rico; (2) across the Pacific down to Australia and New Zealand; and (3) from Mesoamerica across the Atlantic to Portugal, and from there to Spain and Morocco. According to Pierce et al. (2014), the colonisation of the western Mediterranean must have occurred through multiple sporadic events involving few vagrant individuals.

The species became almost cosmopolitan after colonising up to 90 countries, islands or archipelagos worldwide (Fernández-Haeger et al. 2015; Nail et al. 2019), resulting in highly genetically differentiated populations globally. Throughout its new range outside of the Americas, the species became largely sedentary, though retaining some migratory behaviour in Australia (James and James 2019; Nail et al. 2019), and with medium-range dispersive movements out of its breeding grounds in Spain (Obregón et al. 2018). By becoming sedentary, monarchs lost some adaptive morphological traits of migratory populations, developing smaller forewings, lower wing loading, i.e., body mass/wing area (Altizer and Davis 2010; Li et al. 2016) and higher flight metabolic rates (Zhan et al. 2014).

Monarch colonisation of the Mediterranean and Macaronesia

Monarchs have long been sighted in non-breeding areas across Europe, from Great Britain (Kirby 1896; Emmet and Heath 1990) and Denmark (Toft 1980) to northern Spain (e.g., Fernández-Vidal 2002; Sabaté and Loaso 2004; Mortera and Pajuelo 2015). This has been interpreted as vagrancy from North America during particular meteorological conditions, such as strong winds across the Atlantic (Vanholder 1996; Asher et al. 2001). Monarchs are strong fliers known to use thermal soaring and gliding flight up to altitudes above 1200 m (Gibo 1981), so it is plausible that they travel long distances during cyclonic winds. This has also been suggested as an explanation for the colonisation of Australia from formerly well-established populations in the Pacific islands of Vanuatu and New Caledonia (Clarke and Zalucki 2004).

After the first sighting of a Monarch in Gibraltar in 1886 (Walker 1886a), the first breeding record from Iberia emerged in southern Spain in the late 1960s, after which records steadily increased in the region and the species became well established around the Strait of Gibraltar (Fernández-Haeger and Jordano Barbudo 2009). However, it may have settled in southern Spain long before being recorded by entomologists (Fernández-Haeger et al. 2011a). This, together with the fact that genetics revealed that monarchs established earlier on in Portugal (Zhan et al. 2014), does not support the speculation that their presence in Andalusia might have been the result of a deliberate introduction by British naturalists (Showler 2001). In Morocco, breeding records along the Atlantic coast and the Strait of Gibraltar increased from the end of the 20th century (Tarrier 2000; Tarrier and Delacre 2008; Fernández-Haeger et al. 2015). It is foreseeable that the species will expand its range along the Mediterranean coast of Spain and beyond, eventually colonising areas along the Mediterranean

coast of Europe (Sobrino et al. 2002; Zalucki et al. 2015; Obregón et al. 2018). In the archipelagos of Macaronesia, records of established populations date from much earlier on, namely from around 1880 in the Canary Islands (Wiemers 1995; Fernández-Haeger and Jordano Barbudo 2009).

Monarch hostplants in the Western Palearctic

Monarch butterfly larvae feed almost exclusively on asclepiads (Apocynaceae). Within the butterfly's original range in America, most hostplants belong to the genus *Asclepias*. Elsewhere, it relies mainly on alien Apocynaceae of the African genus *Gomphocarpus*, except for the cases of introduced *Asclepias curassavica*, which is native to Central America. The butterfly reportedly feeds mostly on *Gomphocarpus fruticosus* (e.g., Owen and Smith 1989; Wiemers 1995; Fernández-Haeger and Jordano Barbudo 2009; Nail et al. 2019) but also on *Gomphocarpus physocarpus* (Fernández-Haeger et al. 2010; James and James 2019). While the former has an extensive distribution from southern Arabia to Eastern and Southern Africa, *G. physocarpus* is mainly restricted to southern Africa (Goyder and Nicholas 2001). In Iberia and Macaronesia, Monarch larvae feed mainly on *G. fruticosus*, *G. physocarpus* and *A. curassavica* (Owen and Smith 1989; Fernández-Haeger et al. 2015), and exceptionally on the native *Cynanchum acutum* (Apocynaceae) in southern Spain (Gil-T 2006). In the Azores, larvae have also been observed feeding on *Gossypium arboreum*, Malvaceae (Neves et al. 2001).

The worldwide spread of the aforementioned hostplants was favoured by their invasiveness, likely associated with their self-compatible pollination ability (which in *G. physocarpus* seems to have been acquired during its expansion out of the native range), and with the capacity for fruiting through uniparental reproduction; invasiveness is further promoted by the observed potential for hybridisation in the case of the two *Gomphocarpus* species, through higher pollen yields and increased genetic variability (Ward et al. 2012). Moreover, the expansion and naturalisation of *G. fruticosus* in Europe and Macaronesia was probably favoured by its ancient exploitation as a textile plant (Quer 1762).

Objectives and rationale

Here, we review the history of colonisation of mainland Portugal, Azores and Madeira archipelagos, by the Monarch butterfly and its hostplants. Available historical and recent occurrence records were also compiled and used as the basis for countrywide surveys of the butterfly and hostplants, to update their distributions. Lastly, we investigated the trends in hostplant patch persistence, including the long-term persistence in old previously known locations (Palma and Bívar de Sousa 2003), and discussed their possible implications for the butterfly's populations.

Methods

Study area: – Mainland Portugal

The study comprehensively covered the localities with former records of the butterfly and its two main hostplants, *G. fruticosus* and *G. physocarpus*. This required surveying a large set of littoral and sublittoral lowland areas along the country's western and southern coasts. The study area belongs to two different Palearctic biogeographic domains (ETC 2006): the Eurosiberian, from the northern border with Spain south to the Aveiro marshlands, a temperate territory strongly influenced by the Atlantic Ocean; and the drier and warmer Mediterranean, encompassing all remaining southward coastal areas. The northern, central and Lisbon's coastal areas are heavily urbanised,

although in rural areas small property predominates. In contrast, along the southwestern coast, partially designated as a Natural Park, urban areas are smaller and scattered, and extensive farming in small to medium-sized rural property dominates, although intensive agriculture and greenhouses occupy the irrigated sectors of the coastal plateau. Along the southern coast of the Algarve, the coastline is heavily urbanised, touristic, and almost entirely bordered inland by farmland dedicated mainly to fruit production, especially oranges (LP, Pers. obs.).

Azores and Madeira

The original mesophytic vegetation of the mountainous volcanic islands of the Azores and Madeira was a laurel-type forest, with paleotropical or paleomediterranean affinities (Aguiar et al. 2008), denominated laurisilva. In the Azores, little remains of the original vegetation and the economy is centred on semi free-ranging dairy cattle. Madeira, on the other hand, still retains large extents of the original laurisilva, with small scale farming and villages mostly restricted to less rugged areas by the sea. As ruderal species, *Gomphocarpus* spp. occur predominantly in humanised areas such as fallow land, and in urban and suburban gardens and parks. Surveys targeted these areas, mostly in the low altitude periphery of the islands.

Compilation of historical and recent Monarch and hostplant occurrence records

We comprehensively reviewed the extant literature on monarch butterflies and their hostplants in mainland and insular Portugal, gathering reports of sightings and breeding activity for the butterfly, and introduction and naturalisation events for the hostplants.

These sources included museum herbaria, GBIF (2021) and online citizen science platforms (see below). We searched the herbarium Florae Lusitaniae of the University of Coimbra (1848–2015) and the Herbarium Lusitanicum of the University of Lisbon (1878–1886) for specimens of *G. fruticosus*. Data from Herbarium Lusitanicum were retained only if complementary to Florae Lusitaniae. Most of the older GBIF records corresponded to specimens held at Florae Lusitaniae. In the Azores and Madeira, owing to logistic and financial limitations, and to the fact that the main goal of the surveys was to collect Monarch specimens for a phylogenetic study, preliminary searches for data were more limited, and some repositories were not visited beforehand (e.g., Madeira's herbaria and museum entomological collections).

The following online citizen-science platforms were checked for recent occurrence records: (1) Biodiversity4all (https://www.biodiversity4all.org/); (2) Flora-on (https://flora-on.pt/) mostly for hostplant records (2017–2020); and (3) Observation.org (https://observation.org/) mostly for Monarch observations that were absent from the other platforms (2010–2017). Flora-on records proved to be largely redundant with those of Biodiversity4all. We also collected oral communications of researchers and amateur naturalists, and searched non-technical literature (e.g., Viana et al. 2009). For the Portuguese archipelagos, we further checked Neves et al. (2001) and the Azores Biodiversity Portal (http://azoresbioportal.uac.pt/) (Suppl. material 2).

Hostplant and Monarch field surveys: – Mainland Portugal

Surveys were conducted in 2016–18 and 2020–21. We assessed the persistence of hostplant patches in 53 (~77%) of 69 locations retrieved from the aforementioned sources, while also checking for the presence of the butterfly. Sixteen locations were not visited either because geographic references were vague or we presumed that the respective hostplant populations were very small

or had already disappeared, namely five records from the 19th century and eleven from the 20th and 21st centuries from urban areas in the centre and north of the country. Among the searched locations of older records (<1950) the plants were either absent or not found, with the exception of a 19th century record at Darque, Viana do Castelo.

Besides the previously reported locations, we systematically searched the areas where hostplant patches were more likely to be found due to their ecological requirements of water availability in summer, absence of frost and competitive vegetation induced by grazing, such as pasture fallow, under-managed or abandoned orange orchards, fences, stream banks, road verges and gardens in lowland coastal areas (Fernández-Haeger et al. 2010). Access to reported locations was made by car and on foot.

Almost half (56; ~41%) of the hostplant patches confirmed during the initial survey in 2016–18, which were mostly located within the butterfly's distribution range, were revisited in 2020–21 to verify their persistence and the butterfly's presence. Hostplant patches found only in the 2020–21 survey were visited only once (Suppl. material 2). Most of the few patches still unchecked in 2020 in the Lisbon, Setúbal and Beja districts were carefully checked in May 2021.

In order to confirm whether monarchs were present outside of the previously known range in the south of the country (Palma and Bívar de Sousa 2003), the two largest populations of *G. fruticosus* identified in central (Carnaxide, Lisbon metropolitan area, over 1000 plants) and northern Portugal (Darque, near Viana do Castelo, several hundred plants) were thoroughly examined: Carnaxide was visited four times between August and October 2018, and Darque in August 2018. Larger patches in eastern Algarve were also revisited several times to confirm the absence of the butterfly.

The areas where the butterfly's presence was previously reported (Palma and Bívar de Sousa 2003) were surveyed by car at <40 km/h, carefully searching for hostplants and/or flying monarchs along 992 km of paved and unpaved secondary roads. This was done across ~350 km^2 of the southwest littoral belt and ~650 km^2 of the western coastal Algarve, including the river valleys of the adjacent foothills. The same was carried out along ~280 km in central and eastern coastal Algarve, throughout ~350 km^2. This survey was carried out in September-December 2017, September-October 2018, and July-October 2020. At each patch detected, we recorded the hostplant species, geographic coordinates and overall features regarding patch geometry and density (i.e., sparse or dense, linear or compact), as well as habitat type (i.e., riverbank, pasture fallow, field fence, road verge). Additionally, we recorded the number of hostplants per patch, counting the individuals in patches with up to ~50 plants, while visually estimating the number in patches with more than 50 plants. This involved counting the plants in a small fraction of the patch, and then extrapolating to the entire patch. Apparent threats, such as mechanical clearing, pasture conversion, competition by natural vegetation, were also recorded.

In addition, patches of Lantana (*Lantana camara*), an ornamental alien plant widespread on chalet walls and in gardens, and along road verges throughout the Algarve, were systematically watched for flying monarchs while driving. Because of its high nectar yield and sugar content (Torres and Galetto 2014; Carrión-Tacuri et al. 2014) this flowering plant strongly attracts butterflies, monarchs included (Fernández-Haeger and Jordano Barbudo 2009). Indeed, wherever monarchs and lantanas were present, the butterflies were often seen feeding from the flowers (LP, Pers. obs.).

Azores and Madeira

In the Azores, the islands of Terceira, São Jorge, Pico, Faial, Flores and Corvo were surveyed once in August 2018. São Miguel Island could not be visited in August due to logistic limitations, so it was surveyed in October 2018. Field work focused on localities with previous butterfly and

hostplant occurrence data, as well as on areas with higher probability of finding both, such as public parks, private urban gardens and yards, and abandoned farms.

Madeira Island was surveyed in September 2018. The work was carried out in public parks and gardens in urban and suburban areas, where hostplants, and hence the butterflies, were more likely to be found. Localities along the coastline and some surroundings were visited, although most of the effort was spent in the capital, Funchal. Logistic constraints prevented surveys on the island of Porto Santo and on the Desertas and Selvagens Islets. Furthermore, there was no information about the presence of monarchs or hostplants on the islets, and presumably no suitable habitat.

Results

Historical background of the Monarch and hostplants in Portugal

In mainland Portugal, Cruz and Gonçalves (1973) reported monarch sightings between 1932 and 1968 in the north of the country, which they attributed to vagrancy from the Azores, Madeira or the Canary Islands. Breeding was only confirmed in 2003 and 2004 in the Algarve (Palma and Bívar de Sousa 2003; Simonson 2004), although Simonson had reported Monarch sightings in the region since 1998. It is highly likely though that the species became established in the region much earlier on, as suggested by Obregón et al. (2018) and inferred from genetics, which showed that monarchs settled in Portugal earlier than in Spain (Zhan et al. 2014), i.e., before the 1960s. Curiously, its breeding was overlooked (Schmitt 2001) and attributed to immigration from North America or Macaronesia (Maravalhas 2003).

In the Azores, Godman (1870) and Walker (1886b) mentioned first sightings in 1864 on the islands of Terceira and Flores, followed by a number of irregular sightings (Neves et al. 2001). Cruz and Gonçalves (1973) considered the species rare but already established in the archipelago, while Neves et al. (2001) raised doubts about its breeding, suggesting that the records might only indicate vagrancy. The authors reported first breeding on the island of Faial in 1994, although the species was likely present there earlier, and on several other islands in 1999 and 2000 (see Suppl. material 1 for a summary of historical details).

In Madeira, monarchs appeared to be absent in Walker's time (Walker 1886b). According to Aguiar and Karsholt (2006), the Monarch was observed periodically in Madeira since 1889, but only became established in 1980. Cruz and Gonçalves (1973) considered the monarch very rare in Madeira but occasionally very common in Porto Santo. Indeed, Pereira (1989) reported large numbers of monarchs observed in Porto Santo for the first time in 1955. Swash and Askew (1982) also mentioned irregular and infrequent sightings of the Monarch in Madeira, and Jones et al. (1987), although mentioning the species' presence, made no reference to breeding. At the same time, however, Bívar de Sousa (1985) reported that the species was already breeding and frequently observed, and according to Meyer (1993), mostly along the island's southern shore.

Showler (2001) and Gardiner (2003) speculated about a possible introduction of monarchs and *A. curassavica* in Madeira, by a couple of British naturalists during the 1960–1970s, who had allegedly done the same in Andalusia. However, milkweeds were reportedly introduced much earlier in the island (Vieira 2002). It also seems unlikely that such a release of monarchs alone would have led to their colonisation of the archipelago, as they were already repeatedly observed in Madeira since the late 19th century and in Porto Santo since 1955 (see above). It thus seems much more likely that they became established following several natural colonisation events as defended by Pierce et al. (2014) concerning the Western Mediterranean.

The Central American *A. curassavica* was brought to the Iberian Peninsula in the 16th century by Spanish travellers, and *G. fruticosus* is known from coastal areas of Iberia since the 18th century, probably introduced by the Portuguese in the Azores, Madeira and mainland Portugal during the early 17th century from their former southern African colonies (Fernández-Haeger et al. 2015). In mainland Portugal, *G. fruticosus* has been recognised as naturalised since 1902 (Almeida and Freitas 2006) and is now commonly found along Mediterranean-type streams in the south of the country (Aguiar et al. 2007). *G. physocarpus* was only reported from Portugal in 2000 (Almeida and Freitas 2006) and from southern Spain (Fernández-Haeger et al. 2010; Fernández-Haeger et al. 2011a). Similarly, *A. curassavica* was quite recently (1999) reported as naturalised in mainland Portugal. The species is scarcely represented in herbaria and infrequently reported in GBIF and citizen-science platforms, reflecting its overall rareness, including within private gardens (Pers. obs.). According to Vieira (2002), *G. fruticosus* and *A. curassavica* were introduced long ago in the archipelago of Madeira for ornamental purposes. The first was introduced during the late 18th century (Menezes 1922) and the second was already present on the island in the late 19th century (Walker 1886b), both having become naturalised in uncultivated and fallow land. In Madeira, *G. physocarpus* also became naturalised in uncultivated areas and fallows, although it was only introduced in parks and gardens in the late 1970s. In the Azores, *G. fruticosus* was already reported by Godman (1870) as an occasional escape from gardens.

Hostplant distribution, abundance and persistence in mainland Portugal

In total, we compiled 136 locations for *Gomphocarpus* spp. across mainland Portugal (Suppl. material 2). These included the locations retrieved from the aforementioned sources as well as those newly found during fieldwork, of which 123 (89%) were visited. The great majority were located in western and central lowland Algarve (Faro district) and the sublittoral area of Odemira County (Beja district) (Fig. 1). Most of the remaining sites were distributed along the country's west coast, primarily around Lisbon and Setúbal districts (24), and the rest (11) in the coastal areas of the northern districts of Aveiro, Porto and Braga.

Gomphocarpus fruticosus was found from Minho region in the northwest to the Algarve in the south. In western Algarve (Fig. 1F), the plant was found across the sublittoral farmland and the south-flowing rivers crossing the area, in two types of habitats: 1) along river and stream banks and near road verges, from the Monchique foothills down to their lower reaches near the Atlantic; and 2) throughout the fruit growing area in the sublittoral lowlands, primarily within or at the edge of orange orchards. East of Messines, the plant is more localized, and is very rare in central-eastern Algarve. The plant was also found in a sublittoral tributary of the Mira River that flows westwards to the adjacent southwest coast.

Further north, between the Mira and Tejo Rivers, there were reports of *G. fruticosus* from six locations; three of four recent locations were visited, with the remaining two dating from the late 19th century. The species was not found in any of the three locations, suggesting that it might have disappeared from most if not the whole region. *G. fruticosus* was reported from eight locations in the Lisbon area, six of which were visited (Fig. 1E). Of these, we found it in three very small patches and two larger stands on the outskirts of Carnaxide, Oeiras County, one with ~250 plants and another with over 1000 plants. Further north, the plant was previously reported from six, mostly old, locations in the Santarém, Coimbra and Castelo Branco districts, but was absent in the three we could visit. North of the river Douro there is a large stand of hundreds of plants within

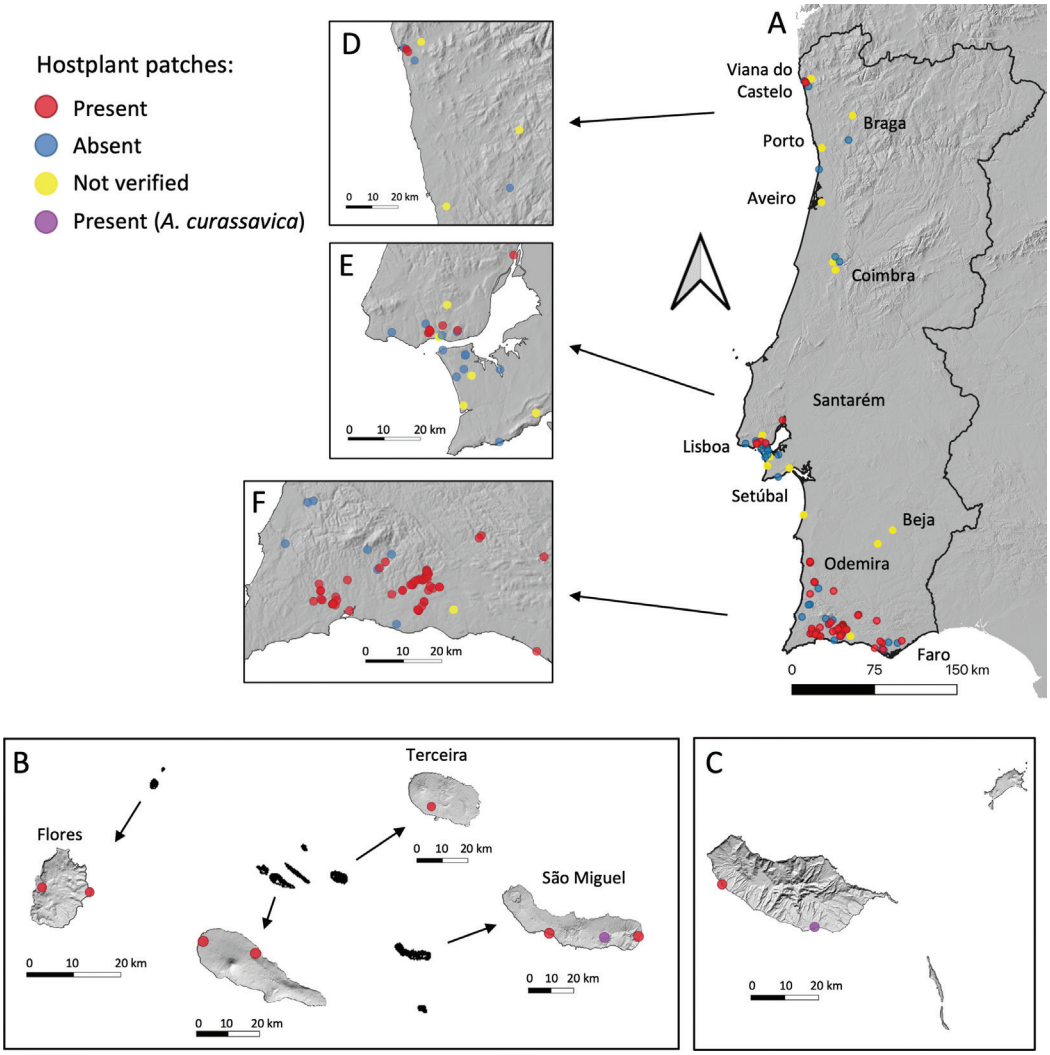

Figure 1. Distribution of the Monarch's hostplants in **A.** Mainland Portugal; **B.** Azores; and **C.** Madeira. Inserts show the detailed distribution of *Gomphocarpus* spp. **D.** In the northwest; **E.** Lisbon region and **F.** Western Algarve.

an abandoned periurban estate near Viana do Castelo (Fig. 1D). Remarkably, the first record of the species in the area dates back to 1886 (Suppl. material 1). Three of the four other locations, from the 1960s, were visited; the plant was found in only one, with 4–5 individuals remaining in a village (Fig. 1D).

Gomphocarpus physocarpus is much scarcer than *G. fruticosus* and has a dissimilar distribution. In western Algarve, the plant was found in only six stands across the orange growing area. The stands typically consisted of one to 30 and exceptionally up to 80 plants, either pure or mixed with *G. fruticosus* and morphologically apparent hybrids in variable proportions. In central-eastern Algarve, *G. physocarpus* is even rarer and occurs in very small patches, with only six former

locations known and few plants in general, mostly restricted to private gardens and backyards. A naturalised stand of ~20 plants is probably the largest one currently remaining in the region. Near the southwest coast, hundreds of individuals were known in 2017 among greenhouses and fallow ground of an intensive farm near Odemira. However, they were reduced to four plants in 2020 after land was cleared due to shifts in production.

Further north, the species is slightly more widespread though still rare (15 locations), occurring mostly in small sparsely distributed patches in urban and suburban areas of the coastal districts of Setúbal, Lisbon, Aveiro, Porto and Braga (Fig. 1D, E). Most of these records are recent (2017–2020), which is why we could only check four of them within the study timeframe. The species was not found in any. Still, in the town of Aveiro, we were able to trace back the fate of a relatively large patch of *G. physocarpus* in an abandoned yard, as photos were posted on iNaturalist in February 2016 (https://www.inaturalist.org/photos/2996383). Using Google Earth, we verified that a storehouse was built in its place and the plants were eradicated between 2016 and 2018. Interestingly, Monarch observations from that same neighbourhood and vicinity were repeatedly posted in Observation.org from October 2013 to January 2017. Although we thoroughly surveyed the area in July 2018, we found neither hostplant nor butterfly, which were possibly eliminated with the conversion of the yard.

Throughout the western Algarve and along the southwest coast, a large number of patches, mainly of *G. fruticosus* but also of *G. physocarpus*, disappeared or were strongly reduced between 2017 and 2020. This was mostly due to clearing for agriculture and pasture, but also due to removal of roadside vegetation and in a few cases to competition with native vegetation. This reduction was observed in 8 of 11 (~73%) of the patches revisited in the southwest coastal area and 32 of 63 (~48%) revisited in the Algarve. Conversely, a marked expansion was seen in five patches during the same period, especially in abandoned orange orchards, while resprouting was often observed in cleared stands, indicating strong metapopulation dynamics in both species.

Monarch distribution in mainland Portugal

The monarch's presence was confirmed in the majority of the patches surveyed in the western Algarve and the Mira valley (Fig. 2; Suppl. material 4). In the latter, monarchs were very abundant in 2017 when the plants were counted by the thousands, but less so during the 2020 survey after ~2/3 of the patches were almost entirely cleared for renewed cattle pasture. Still, in two remaining clusters with ~50 plants each, there were 30 and 71 individual Monarch sightings. At the time, monarchs were also present in the large patch of *G. physocarpus* further inland near Odemira, but were absent in July 2020 after the plants were cleared (see above).

Monarch populations were also formerly known between the Mira and western Algarve, especially along the Seixe valley where the species was first observed breeding in Portugal (Palma and Bívar de Sousa 2003). Several large extant patches of *G. fruticosus* along the river floodplain in 2003–2005, as well as the previously widespread and abundant monarchs, almost totally vanished due to land conversion back to cattle pasture. After the disappearance of these formerly large Monarch populations of the Seixe valley, and apparently of other small populations reported from the southwest coastal plateau (P. Canha, Pers. comm.), the Monarch population of the Mira became very isolated in relation to western Algarve. If the hostplants continue to be extensively removed there, this northernmost Monarch population may disappear.

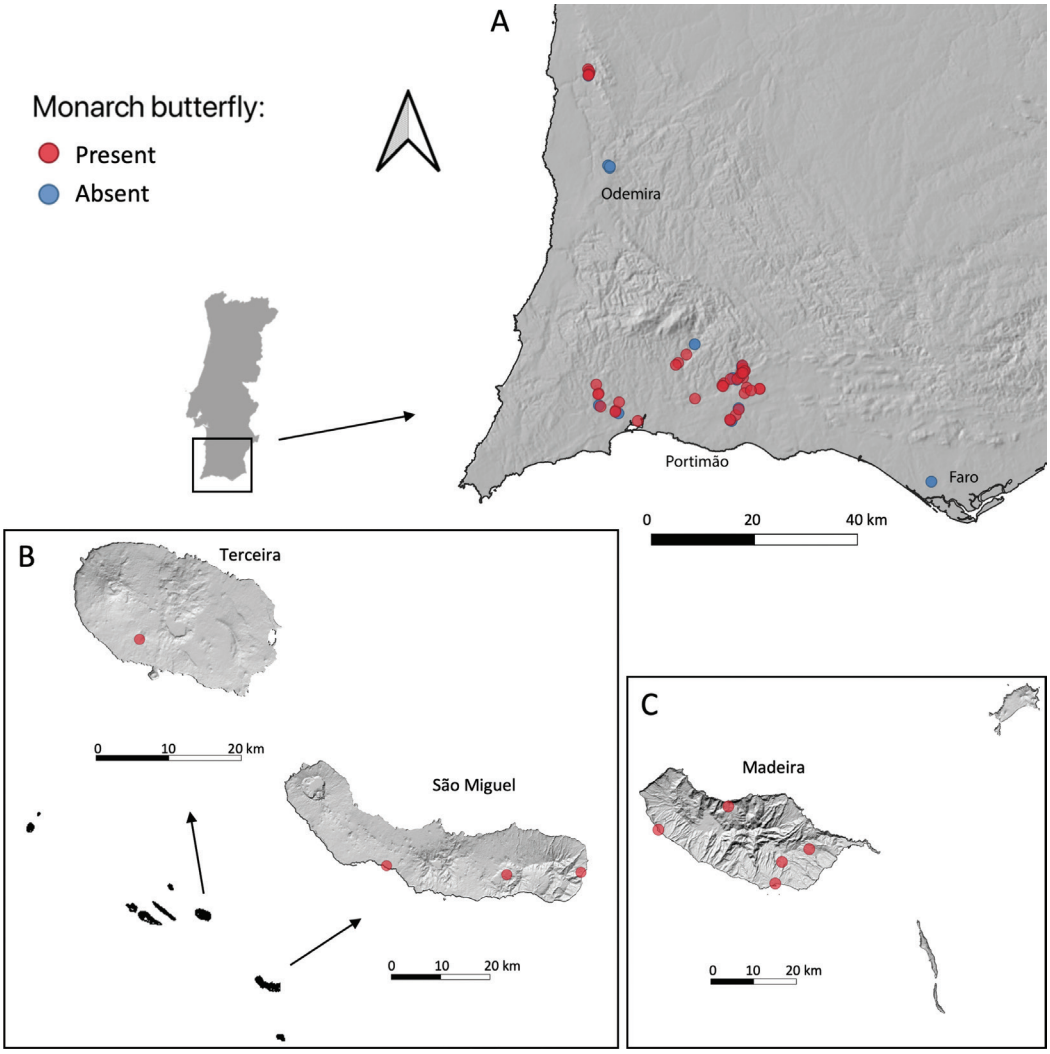

Figure 2. Distribution of Monarch butterfly in **A.** Mainland Portugal; **B.** Azores; and **C.** Madeira.

In central-eastern Algarve, we have repeatedly surveyed the largest extant patch (~20 plants) of *G. physocarpus* for the butterfly since 2018, but have not detected its presence. Furthermore, the only medium-sized patch of *G. fruticosus* (23 plants) known in the region was also lengthily inspected in mid-October 2020, with no adult butterflies or larvae observed. Until at least 2016, monarchs could be observed in small numbers in central-eastern Algarve, but became accidental at most, probably vagrants from the west. It thus appears that monarchs have not been breeding in central-eastern Algarve for some years (Fig. 2A).

Monarchs and hostplants in the Azores and Madeira

The most likely locations for hostplant and Monarch occurrence on the islands of Terceira, S. Jorge, Pico, Faial, Flores, Corvo, and S. Miguel, such as abandoned farms, public parks, private

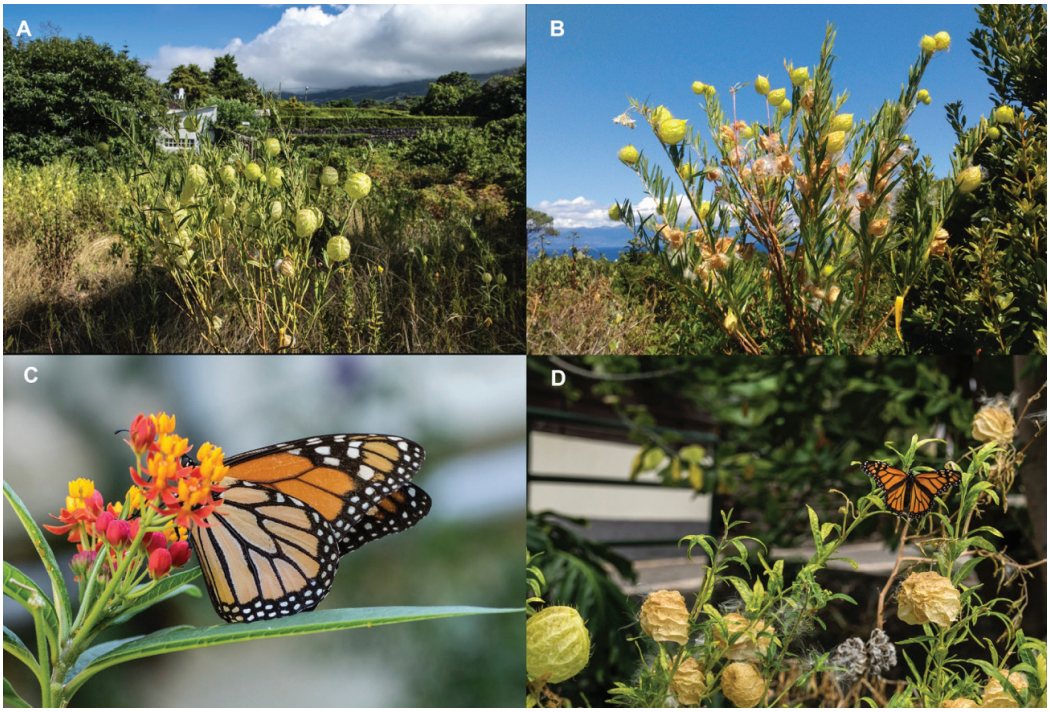

Figure 3. Photographs of the Monarch butterfly and its host plants. **A.** *G. physocarpus* on Pico island; **B.** *G. fruticosus* on Pico island; **C.** A Monarch butterfly feeding on *A. curassavica* on Madeira island; **D.** A monarch resting on *G. physocarpus* at Jardim do Mar, Madeira.

urban gardens and yards, were carefully surveyed. Hostplant species were only found on four islands, from west to east: Flores (a group of 10–20 *G. fruticosus*, and a solitary plant at a second site); Pico (abundant *G. physocarpus* and *G. fruticosus* in five closely located patches, Fig. 3A, B); Terceira (10–20 *G. physocarpus*); and S. Miguel, where patches of *G. physocarpus* and *A. curassavica* were found at three sites (Fig. 1B). Monarch butterflies were observed at three locations in S. Miguel and one location in Terceira (Fig. 2B). From the latter, additional information was provided by a local collaborator (N. Cabeceiras, Pers. comm.). The Monarch therefore seems to be relatively rare and localized in the Azores, and apparently with an irregular presence, as it appeared to be absent from the islands of Pico and Faial, where its occurrence was previously reported. Occasional oral records also pointed to yearly irregularity of Monarch occurrence. In Madeira, hostplants (Fig. 1C) were found in Funchal (*A. curassavica*, Fig. 3C) and in Jardim do Mar (*G. physocarpus*), along with butterfly imagos, larvae, pupae or eggs (Fig. 3D). Monarchs were also observed at several other locations in the Funchal area, and at six others in the SW, E and N of the island (Fig. 2C), associated with urban green areas and vegetation bordering streams, e.g. in Machico.

Discussion

We provide a review of the history of colonisation of mainland Portugal and of the Azores and Madeira archipelagos by the Monarch butterfly and its main hostplants. We have also conducted the

first countrywide surveys of both butterfly and hostplants to update their distributions in Portugal. Although the surveys in the Azores and Madeira were not systematic, they are the first extensive surveys of the Monarch and its hostplants in the archipelagos, representing a notable advance in our understanding of these species' distributions in both regions.

We found that, despite the extensive though patchy distribution of the hostplants along the coastal areas of mainland Portugal, Monarch butterflies are currently restricted to the western Algarve and more locally along the southwest coast. The Monarch's absence further north may be the result of limiting environmental factors, (e.g. climate), since potential food resources for the larvae exist, in a few cases made up of large stands of hundreds and more plants. Conversely, towards central and eastern Algarve the butterfly seems to have lost ground during the last 15 years.

Historical and current distribution of the Monarch's hostplants: – Mainland Portugal

The Monarch's hostplants are sparsely represented in museum collections, and exclusively comprise specimens of *G. fruticosus*. Those from the late 19th and early 20th centuries present in classical herbaria comprise only six locations, widely scattered from the extreme north of the country to the Lisbon area and southwestern coastal areas. This may indicate that the plant has long been widespread in the country, yet with a different distribution to the current one. However, it is not possible to judge whether it was previously common or quite localized, as past field survey conditions were incomparable to present ones. The notable exception is near Viana do Castelo, where the species was collected in 1886 (Herbarium Lusitanicum, Lisbon University) and a large population of *G. fruticosus* still exists. Only six records of this plant species from the 1900s could be found, mostly in herbaria, of which five were checked in the field. Only a small group of plants was found in one northern location.

In contrast with *G. fruticosus*, we did not find historical records of *G. physocarpus* in herbaria or elsewhere, and all records date from 2003 to 2021. This is in line with its first occurrence record in Portugal in 2000 (Almeida and Freitas 2006). Due to its scarcity in herbaria and citizen-science platforms, *A. curassavica* was intentionally not surveyed, but its rarity could be opportunistically confirmed on the ground. This rarity contrasts with the situation in Andalucía, southern Spain, where this plant is common in some areas and used as a hostplant by Monarch larvae (Fernández-Haeger and Jordano Barbudo 2009).

As expected from their ecological requirements (Fernández-Haeger et al. 2011a), the two *Gomphocarpus* species range along the country's littoral and sublittoral belt, mostly in lowland areas, but are patchy everywhere (Fig. 1). Although these species are present from north to south, their abundance is uneven, with both species concentrated in the western Algarve where the patches are generally small to medium-sized (Suppl. material 3), but common. Together with the Mira valley, this appears to be the area with the best ecological conditions for *G. fruticosus* in the south of the country. It is increasingly rare and localized towards the north and east of Portugal, occurring in small to very small patches (<25 plants). In central/eastern Algarve the species is largely replaced by *G. physocarpus*, which appears to better tolerate drier conditions.

The general disappearance of both *Gomphocarpus* species from most of the historical and many of the recent locations to the north of Lisbon and its environs (Fig. 1E), with remnant patches being generally very small, is probably due to the large urban expansion in these

regions. The large populations of *G. fruticosus* near Viana do Castelo and Carnaxide are the only exceptions, due to being located in an abandoned rural estate and a track or fallow rural land, respectively.

Azores and Madeira

Data on the distribution and abundance of the Monarch's hostplants in the Azores and Madeira are very scarce. Apart from the oldest references to their introduction and naturalisation (Godman 1870; Menezes 1922; Vieira 2002), there is only one specimen of *G. fruticosus* in the Coimbra herbarium, collected in Funchal in the late 19th century. More recent and detailed articles about the Monarch in the Azores and Madeira (Cruz and Gonçalves 1973; Neves et al. 2001) are also not very informative about the current distribution of its hostplants in the archipelagos. Likewise, citizen-science platforms only provide a few records of the two *Gomphocarpus* species and none of *A. curassavica*, and only the Azores Biodiversity Portal provides more detailed data on the distribution of *G. fruticosus* in these islands.

Hostplant patch persistence

The second survey (2020–2021) revealed that 48–73% of hostplant patches had disappeared since the initial survey (2016–2018). The strong extinction/recolonisation dynamics are certainly related to the ruderal nature of the plants and in the case of *G. fruticosus*, to the fact that the species is linked to the cycle of cattle grazing. Field preparation and cattle grazing contribute to the elimination of potential native competitors, such as *Rubus ulmifolius* and *Scirpus holoschoenus* that tend to replace the hostplant, but during subsequent fallow *G. fruticosus* quickly colonises the area (Fernández-Haeger et al. 2010; Fernández-Haeger et al. 2011b). Yet, when fields are converted to pasture, the plants are once more mechanically eliminated. Likewise, the periodical clearing of road edges for traffic security also contributes to their recurrent removal. On the other hand, urban expansion likely strongly affected most of the historical hostplant locations in north and central Portugal, unlike further south, where this happens much less often because the plants seldom occur within urban areas.

Geographic patterns of current Monarch occupancy in mainland Portugal

Prior to reports of Monarch breeding activity in southwest Portugal (Palma and Bívar de Sousa 2003; Simonson 2004), knowledge about the species in the country was scarce and vague. Only then were sightings of the species reported more frequently in the south of the country, in the Algarve region in particular. The large number of Monarch sightings in hostplant patches in western Algarve may be explained by the profusion of *Gomphocarpus* occurrence and the relative closeness between patches (Figs 1F, 2), especially in abandoned or semi-abandoned orange orchards and along road verges of the Silves-Messines area. In contrast, outside of the orange growing area towards the W-NW, unoccupied patches become more recurrent. This might occur because the patches located along the banks and road verges of the southerly flowing river valleys of the Monchique Mountain, are fewer and farther apart. To the east and the north of the core area of western Algarve, with the exception of the Mira valley, monarchs are absent and seemingly unable to recolonise isolated patches (Fig. 2). This contrasts with observations ~15 years ago, when despite the rareness and small size of most plant patches, monarchs were observed with relative frequency and sometimes confirmed breeding. In short, the orange growing area is currently the chief stronghold of the Monarch butterfly in Portugal.

Although the majority of the previously reported locations were searched, some hostplant patches, especially smaller ones, may have gone undetected, as some might have been in closed estates. Also, some plant patches in peripheral areas of their known ranges were found at later stages of the study and could not be visited during the Monarch survey. Nevertheless, we are confident that both cases represent a small fraction of the extant hostplant populations, and do not significantly change their overall occurrence patterns.

Future research and conservation directions

Although this study is geographically comprehensive, it provides baseline information, and much remains to be investigated about the ecology and demography of the Monarch butterfly, namely its metapopulation structure and dynamics; hostplant dispersal, extinction and recolonisation dynamics and causal factors; as well as habitat suitability modelling of both monarchs and hostplants.

Although Monarch hostplants are allochthonous and potentially invasive, their colonisation by *Danaus plexippus* in Macaronesia and the Mediterranean was a natural process. These Monarch populations are probably genetically unique (Pierce et al. 2014), and therefore irreplaceable, thus deserving conservation concern. However, the high removal rate of the hostplants, even if other areas are being colonised or recolonised following agricultural abandonment, is worrying because it could lead to the rarefication or disappearance of the butterfly from a number of former locations. Although *Gomphocarpus* can be invasive, their indiscriminate control may hinder the Monarch's persistence (Fernández-Haeger et al. 2011b). In the case of Portugal, however, invasiveness remains at such a small scale that it should not be an impediment to the preservation of this charismatic butterfly.

Based on our study, we cannot assume that the observed clearance of hostplant patches will lead to a steady decline in hostplant availability. As in the case of the areas of the Mira and Seixe Rivers in the southwest, shifting productions or the conversion of fallows to traditional grazing, may rapidly reduce or even eliminate entire patches of *Gomphocarpus*, strongly affecting local Monarch populations. Moreover, small scale changes such as the gradual removal of plants from road verges and gardens, or their disappearance due to environmental factors (e.g. drought, competition from recovering native vegetation), could lead to the disappearance of the butterfly from large peripheral areas of its range in central-eastern Algarve, where hostplants were never abundant and have become increasingly rare. The accumulating cues for a possible and quick decline of the hostplants, and consequently of the butterfly, should thus be a matter of concern. However, given the long distance seed dispersal by wind that enables these plants to colonise remote favourable areas (Fernández-Haeger et al. 2010), and the strong flight ability driving the butterfly's metapopulation dynamics (Fernández-Haeger et al. 2011a), the observed trend should be viewed cautiously as the situation may change if conditions become more favourable.

Nevertheless, we recommend the adoption of practical solutions to avoid the potential disappearance of the Monarch butterfly due to rarefication of its hostplants. For instance, by assessing the viability of creating a network of sizeable hostplant micro-reserves across the butterfly's core range, in partnership with collaborative landowners. Due to the butterfly's appeal, these stable patches could be promoted as touristic add-on destinies, a sort of "open-air" butterfly gardens. A similar initiative was started in Andalucía, southern Spain ("Ruta de la Mariposa Monarca de Castellar de la Frontera, Cádiz", El Giroscopio Viajero 2020). Additionally, promoting *A. curassavica* as an ornamental in suitably watered private gardens would be another means to attract the monarchs. Altogether, these actions could help elude the instability of hostplant availability and promote the persistence of *Danaus plexippus* in the country.

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Supplementary material 1

Summary of occurrence and colonisation records of the monarch butterfly and its hostplants in the Iberian Peninsula

Authors: Luís Palma, Sasha Vasconcelos, Ana Filipa Palmeirim, Juan Pablo Cancela

Data type: Occurence records.

Link: https://doi.org/10.3897/nl.46.89665.suppl1

Supplementary material 2

Georeferenced hostplant patches and patch size

Authors: Luís Palma, Sasha Vasconcelos, Ana Filipa Palmeirim, Juan Pablo Cancela

Data type: Georeferenced data.

Link: https://doi.org/10.3897/nl.46.89665.suppl2

Supplementary material 3

Frequencies (%) of hostplant patch size classes arranged in geometric progression (2× ratio) (N patches = 78)

Authors: Luís Palma, Sasha Vasconcelos, Ana Filipa Palmeirim, Juan Pablo Cancela

Data type: figure.

Explanation note: This data was retrieved from Suppl. material 2.

Link: https://doi.org/10.3897/nl.46.89665.suppl3

Supplementary material 4

Georeferenced butterfly relative abundance records

Authors: Luís Palma, Sasha Vasconcelos, Ana Filipa Palmeirim, Juan Pablo Cancela

Data type: Georeferenced data.

Link: https://doi.org/10.3897/nl.46.89665.suppl4