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The naturalization of the almond Prunus dulcis in different ecological contexts in the Mediterranean: an underestimated process?

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Date 07/12/2021

Dear Editor,

We are pleased to submit the original research article entitled "**The naturalization of almond *Prunus dulcis* in different ecological contexts in the Mediterranean: an underestimated process?**", authored by Emilio Badalamenti, Rafael da Silveira Bueno, Giovanna Sala, Dario Cusimano, Tommaso La Mantia and Vincenzo Ilardi for consideration for publication in FLORA.

Although *Prunus dulcis* has been frequently listed in non-native floras all around the world, its naturalization process has been rarely investigated. Furthermore, to the best of our knowledge, the natural spread of *Prunus dulcis* in natural habitats has been never documented. We measured and characterized almond naturalization in four ecologically different sites, including two extensively managed prickly pear orchards, one pine reforestation and one natural area. We found interesting differences in the population structure and temporal dynamics of the naturalization process. We discuss our results based on the very limited current knowledge regarding almond naturalization, with a special focus in the Mediterranean. Almond is a species of global importance and its naturalization is expected to increase due to climate change, land-use changes, as well as the increased ability by *Prunus dulcis* to spread and invade new suitable sites. Finally, since the almond appears to be perfectly integrated within local plant communities in the natural habitat, the origin and meaning of this peculiar vegetation aspect deserve to be further deepened.

We confirm that this manuscript is original unpublished work and is not under consideration by any other journal and no data will be included in an article published or submitted elsewhere. All of the authors agree with submission to FLORA and will be updated on each step during the submission process by the corresponding author.

Thank you for your consideration of our manuscript.

Sincerely yours,

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Highlights

- The population structure and temporal dynamics of natural regeneration differed between habitats
- Almond densities were much higher under pine afforestations
- Almond naturalization is expected to increase due to climate change

The naturalization of the almond *Prunus dulcis* in different ecological contexts in the Mediterranean: an underestimated process?

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Abstract

Although *Prunus dulcis* is an archaeophyte frequently listed in non-native floras all around the world, its naturalization process has been rarely studied in the field. Moreover, this species has generally invaded synanthropic habitats. We assessed the density of natural regeneration of almond, biometric parameters (height and basal stem diameter), and the distribution in life stage classes in different ecological contexts in Sicily (Mediterranean Italy): one natural habitat (maquis), two prickly pear orchards, and one pine afforestation. We recorded 236 naturally regenerating almond individuals, with density ranging from 140 individuals per hectare in the prickly pear orchard 1 up to 2,400 individuals per hectare in the pine afforestation. There was no significant difference between the two prickly pear orchards. Despite the higher density, almond individuals presented the lowest height and basal stem diameter under pine afforestation. Reproductive individuals were dominant (67.8%), followed by pre-reproductive (22.1%), and juveniles (10.1%). Dendrochronological data indicates that individuals age ranged from 5 to 13 years old. Although the naturalization of the almond in Mediterranean contexts is not new, there is evidence of an increasing naturalization process in the last two decades. Most importantly, we found the almond thriving within a natural habitat in large areas covered by Mediterranean maquis. Since the almond appears to be perfectly integrated within local plant communities, the origin and meaning of this peculiar vegetation aspect deserve to be further deepened.

Keywords: archaeophyte; Mediterranean vegetation; natural regeneration; exotic tree species; seed dispersal

1. Introduction

One of the most intriguing and challenging issues in the naturalization process by some non-native plant species is the high unpredictability of its spatio-temporal dynamics (Kolar and Lodge 2001), as well as in the early identification of the most harmful invasive species (Fournier et al. 2019). This uncertainty is strongly tied to the many biotic, abiotic and anthropic factors involved, and to their inter-relations, which are inherently dynamic, as it is each factor alone (Caley et al. 2006, Pyšek et al. 2010, Aldorfová et al. 2020). However, many strides have been made in our understanding and predictive ability of the invasion process, as witnessed by the attempt of harmonizing under a systematic and comprehensive view of the most important hypotheses underlying the invasive success (Enders et al. 2020, Novoa et al. 2020). Particularly, resource availability, biotic interactions, propagule pressure and species' traits are reported to include the most significant theories (Enders et al. 2020). Such knowledge progress has been mostly achieved based on the studies and research addressed to the most widespread invasive plant species, bringing about large impacts on recipient ecosystems. Two relevant examples in that regard are *Ailanthus altissima* (Mill.) Swingle, *Robinia pseudoacacia* L. (Kowarik and Säumel 2007, Vítková et al. 2017). The situation is markedly different for plant taxa that are still not (or have rarely) naturalized elsewhere and which, therefore, have been much less studied. Furthermore, even introduced plants that remained confined to cultivation sites and/or utilization areas for many centuries may suddenly acquire the ability to escape into the wild and spread into novel ecosystems (Binggeli 2001, Kelly et al. 2021). Indeed, the duration of the lag phase, *i.e.* the time elapsed from the first signs of natural regeneration of non-native plant species up to the invasive and outbreak stage, can be very variable and different among different plant species (Aikio et al. 2010, Badalamenti et al. 2018, Aiello-Lammens 2020), and, above all, it is not predictable (Larkin 2012). For instance, two studies from USA and Australia found a common average lag time of about 46-47 years but the upper limit of the range well overcame 120 years in both works (Larkin 2012, Osunkoya et al. 2021). Understanding why this happens is of great importance both from an ecological perspective and for the management implications (Phillips et al. 2010). This could be the case for some archaeophytes, namely the plant taxa introduced before 1500 AD (Pyšek et al. 2004). An interesting example in Europe is the common walnut (*Juglans regia* L.), a tree species of very ancient introduction (Pollegioni et al. 2017), which has been increasingly reported as naturalized species in temperate and Mediterranean Europe only in the last decades (Lenda et al.

2018, Bueno et al. 2020a). Particularly, the abrupt change in walnut population has been put in relation to two promoting factors: the increasing land abandonment and the active seed dispersal by corvids, which allowed the establishment and spread in forest habitats (Lenda et al. 2012). This is not surprising as, rather than a single triggering factor, more commonly a set of factors may simultaneously act to determine relevant changes in the population of introduced species (Milbau and Stout 2008). Furthermore, a recent distribution model of the species would indicate a range contraction in the southern edge of the distribution range followed by a concomitant range expansion in the northern edge because of a warming climate (Paź-Dyderska et al. 2021).

The history of *Prunus dulcis* (Mill.) D.A.Webb., subject to millennial cultivation in the Mediterranean basin, could follow a similar trajectory. The almond is a large-seeded tree species with a dry shell enclosing a single lipid-rich endocarp, probably originating from southwest Asia and the eastern Mediterranean (Zohary and Hopf 2000, Delplancke et al. 2013). The high nutritional value of its fruit and high commercial interest have favoured its large cultivation since thousands of years, greatly expanding its original distribution and exposing it to different environmental conditions (Zeinalabedini et al. 2010; Ladizinsky 1999). Although the almond has been frequently listed in alien floras all around the world (Randall 2017), its naturalization process has been rarely studied in the field (Homet-Gutierrez et al. 2015; Balaguer-Romano et al. 2021). Only recently, the active colonization of semi-arid areas previously afforested with *Pinus halepensis* Mill. and *Quercus ilex* L. has been documented and studied in south-eastern Spain (Homet-Gutierrez et al. 2015). Then, in similar ecological conditions, a relevant role for almond spread and establishment in new areas has been attributed to synzoochory, particularly the seed dispersal by rodents (*Apodemus* and *Rattus*) (Balaguer-Romano et al. 2021). Apart from these recent studies, however, no other information is available about the spatio-temporal pattern of the naturalization process of the almond in Europe and Italy. Then, more importantly, this non-native tree species has rarely (if ever) shown the ability to establish within natural habitats, interacting with local species and communities. Having observed a growing number of spontaneous nuclei of almond in Sicily, our first objective was characterize the natural regeneration, biometric parameters, and the distribution in life stage classes of almond wild populations occurring in different ecological contexts: Mediterranean maquis, prickly pear (*Opuntia ficus-indica* (L.) Mill.) orchard, and pine afforestation (mostly *Pinus halepensis*). We also carried out floristic and vegetation surveys in the Mediterranean maquis communities where the almond was fully established. To the best of our knowledge, it is the largest area (> 400 hectares) covered by almond wild populations within natural habitats known to date in Europe in its secondary range. Finally, to ensure the representativeness of this finding, and to assess how the almond as non-native tree species has been considered over time, we carried out a literaure search at European, national and regional level regarding its naturalization status.

2. Materials and methods

2.1 Study Sites

Almond naturalization was assessed in four study areas within three different ecological contexts in Sicily (Mediterranean Italy) (Figure 1, Table 1): a natural habitat (Mediterranean maquis), two prickly pear orchards and a pine afforestation (Figure 2).

The natural habitat is a maquis community, thriving on limestone rocky outcrops on the south-facing slopes of Pizzo Telegrafo (municipality of Caltabellotta, Province of Agrigento), at a mean altitude of 530 m a.s.l.. *E. dendroides* maquis formations, particularly widespread in the southern rocky slopes of the mountain complex of Monte Telegrafo, are among the few expressions of vegetation that can be defined of high naturalness in the overall district, together with the communities that colonizing screes and rocky cliffs. Here, favored by the carbonate nature of the rocks, which are intensely fractured, the phytocoenoses are particularly rich in endemisms and species with showy blooms such as *Lomelosia cretica* (L.) Greuter & Burdet, *Dianthus rupicola* Biv., *Anthemis cupaniana* Tod. ex Nyman, *Silene fruticosa* L., *Brassica villosa* Biv., *Euphorbia bivonae* Steud. and *Matthiola incana* (L.) R. Br.. At the edge of the breccias, instead, small nuclei of woody vegetation are preserved, characterized by the presence of a large population of *Celtis tournefortii* subsp. *asperrima* (Lojac.) Raimondo & Schicchi. Such plant communities, which always come into contact with each other, represent the only natural formations still present in the mountainous complex of Monte Telegrafo, due to their inaccessibility, which still host plant species and communities of high phytogeographic and conservation interest. On the contrary, vast areas of the upper altimetric belt of the mountain complex, once dominated by the evergreen holm oak forests, has been replaced by *Ampelodesmos mauritanicus* (Poir.) T.Durand & Schinz grasslands or *Phlomis fruticosa* garrigues, or by extensive reforestation interventions with the use of fast-growing pioneer species, mostly pines and eucalypts (Badalamenti et al. 2020). The climate is characterized by a mean annual temperature of 15 °C and mean annual rainfall of 700 mm (Drago 2005). Differently from the other study sites, the bioclimate here is upper meso-Mediterranean with lower sub-humid ombrotype (Bazan et al. 2015). The geological substrates mainly consist of calcareous megabreccias and marly debris, referred to the Mount Magaggiaro-Pizzo Telegrafo Unit (Di Stefano and Vitale 1992). The area lies within the Natura2000 Special Area of Conservation ITA 040006 “Complesso Monte Telegrafo e Rocca Ficuzza” and the Special Protection Area ITA 020048 “Monti Sicani, Rocca Busambra e Bosco della Ficuzza”.

The prickly pear orchard 1 (hereafter PP1) is located in Caltagirone (Province of Catania) at about 430 m a.s.l.. The orchard inter-rows are managed with mowing and tillage, whereas the prickly pear rows and their immediate surroundings are left unmanaged. Mean annual precipitation is 678 mm, mean annual temperature is 17 °C (Sicilian agro-meteorological information service: http://www.sias.regione.sicilia.it/), and the geological substrate is made up of sand and clays of marine environments grading up to transitional and continental deposits (Lentini and Carbone 2014). The bioclimate is upper thermo-Mediterranean with lower sub-humid ombrotype (Bazan et al. 2015). The surrounding areas are dominated by cultivated fields (including almond orchards), with remnants of natural vegetation occurring only in the least accessible areas such as ditches, field borders, or abandoned lands.

The prickly pear orchard 2 (PP2) is located in Roccapalumba (Province of Palermo), at 500 m a.s.l., in interior hilly areas dominated by clay soils and cultivated lands (wheat fields, olive groves and prickly pear orchards). The management practices are the same as for prickly pear 1. Mean annual precipitation is 561 mm, mean annual temperature 15.7 °C (Sicilian agro-meteorological information service: http://www.sias.regione.sicilia.it/) and the geological substrate is made up of yellowish graded quartzarenites and brown clay (Lentini and Carbone 2014). The bioclimate is upper meso-Mediterranean with upper dry ombrotype (Bazan et al. 2015). Although vineyards and almond orchards still occur in the surrounding areas, their presence has been constantly reduced in recent years as a result either of the replacement by more profitable tree crops or as a consequence of abandonment of cultivation. Particularly rare and confined are the residual aspects of natural woody vegetation, only consisting of downy oak (*Quercus virgiliana* (Ten.) Ten.) small nuclei, as well as of shrub vegetation occurring along ditches, field borders, valleys or uncultivated lands.

The pine afforestation patch (10 ha) is located about 1.5 km from prickly pear orchard 2, under analogous climatic and edaphic conditions (620 m a.s.l.), except for the geological substrate, which is made up of greenish and reddish silty clay with sandstones (Lentini and Carbone 2014). The dominant tree layer is exclusively composed of *Pinus halepensis*, planted around 45 years ago, and showing an average density of 400 plants ha^{-1} and average height of 7 m.

2.2 Sampling Design

Considering that the prickly pear orchards are regularly managed, we used different sampling designs in the three ecological contexts. Within the PP1 and PP2, we surveyed, respectively, 5 and 7 randomly selected rows, considering a minimum distance of three rows from each other. In each row, we surveyed 16 3x2 m rectangular plots under prickly pear individuals. The plots were established considering the main stem of each plant as the centroid. The longer axis was established along the row, while the smaller axis was directed to the inter-row, both remaining inside the non-managed surfaces. To reduce spatial autocorrelation, each plot was established two plants apart from each other (e.g. individual 1, 4, 7, etc..) and we added one 2x2 m square plot to reach 100 m^2 for each row (hereafter a plot), for a total surveyed area of 500 m^2 in prickly pear orchard 1 and 700 m^2 in prickly pear orchard 2. In the pine afforestation, we surveyed five 10x10 m plots (total 500 m^2), randomly distributed under the pine canopies but located at least 20 meters distant from the edges. In the natural area, due to its larger extension, we surveyed five 20x20 m plots (total 2,000 m^2) randomly distributed throughout the area covered by maquis. Furthermore, in the natural habitat, with the aim to understand the origin of this peculiar almond population, an in-site assessment of fruits' taste (either bitter or sweet) in seed-bearing almond plants was carried out.

2.3 Almond Population Assessment

Within each study site, we counted all almond individuals exceeding a minimum threshold of 10 cm in height and calculated the density ($N * 100\ m^{-2}$). This height threshold well represents established individuals, *i.e.* which survived the first critical seedling stage. For each almond individual detected, height (H, in cm) and basal stem diameter (BSD, in cm) were also measured. Then, based on height, BSD and the presence of flowers and/or fruits, we assigned the plants to three life stage classes: juvenile ($H < 100$ cm and $BSD < 0.5$ cm), pre-reproductive ($H < 200$ cm and $BSD < 2$ cm) and reproductive ($H > 200$ cm, $BSD > 2$ cm and presence of fruits or flowers). Furthermore, the occurrence of adult isolated almond plants or of almond orchards, in the sampling areas or their immediate surrounding (up to 150 m), was also registered.

2.4 Statistical Analysis

To test whether almond density, height and BSD of the individuals varied among habitats, we used a Generalized Linear Model (GLM) fitted to a negative binomial distribution with "log" link function. We selected such distribution once Poisson and quasi-Poisson models presented significant overdispersion and height and diameter did not follow a normal distribution (Shapiro-Wilk test $p < 0.001$). To make BSD integer values we multiplied all values by 10. Differences in life stage classes between study sites were tested by Likelihood Ratio Tests. Prickly pear orchard 1 was excluded from this analysis due to the lack of juvenile and pre-reproductive stages. All analysis were performed with R v3.6.1 with MASS package for the negative binomial GLM.

2.5 Floristic and vegetation surveys

Floristic and phytosociological surveys were carried out during spring 2021 within five 250-300 m^2-wide study plots in the southern slopes of Pizzo Telegrafo. The cover/dominance scale proposed by Braun-Blanquet (1932) was considered for each plant species. Classification of the vascular plants followed Pignatti et al. (2017) and hierarchical classification of the plant communities followed Guarino et al. (2017). Each plant species surveyed was included in one of the following groups: characteristic of Association *Oleo sylvestris-Euphorbietum dendroidis*, characteristic of Alliance *Oleo-Ceratonion* (Order *Pistacio-Rhamnetalia alaterni*, Class *Quercetea ilicis*), and other species belonging to other syntaxa.

2.6 Literature Search

To assess the naturalization status of the almond in Europe, Italy and Sicily, a thorough bibliographic search was carried out, also including historical bibliography and grey literature. Only documents reporting specific information about the naturalization status of *Prunus dulcis* were taken into account. With specific reference to Sicily, also personal observations were considered, with a special focus on nuclei clearly established without human intervention and composed of at least five individuals. Conversely, populations with a doubtful origin or partially composed of planted individuals were discarded.

Table 1. Main characteristics of the study areas. Sicilian Provinces: AG = Agrigento, CT = Catania, PA = Palermo.

Study site	Municipality (Province)	Altitude (m a.s.l.)	Mean temperature (°C)	Annual Precipitation (mm)	Bioclimate	Sampled area (m²)	Slope (%)	Geological substrate
Maquis	Caltabellotta (AG) 37°35'53.88"N, 13°11'10.54"E	530	15.0	700	Upper Mesomediterranean lower sub-humid ombrotype	2,000	20	Calcareous megabreccias and marly debris
Prickly pear orchard 1	Caltagirone (CT) 37°11'32.48"N, 14°33'25.40"E	427	17.0	678	Upper Thermomediterranean lower sub-humid ombrotype	500	< 10	Sand and clays of marine environments grading up to transitional and continental deposits
Prickly pear orchard 2	Roccapalumba (PA) 37°48'52.39"N, 13°39'26.34"E	455	15.7	561	Upper Mesomediterranean upper dry ombrotype	700	< 10	Yellowish graded quartzarenites and brown clay
Pine afforestation	Roccapalumba (PA) 37°48'27.64"N, 13°38'26.08"E	620	15.7	561	Upper Mesomediterranean upper dry ombrotype	500	10-15	Greenish and reddish silty clay with sandstones

3. Results

3.1 Almond Population Assessment

In the four study sites, we recorded a total of 236 individuals, having a mean height of 2.05 ± 1.11 m (maximum height 6.5 m), and a mean BSD of 4.07 ± 3.3 cm, ranging from 0.2 cm up to 16 cm (Table 2). Almond density ranged from 140 individuals per hectare in PP1 up to 2,400 individuals per hectare in the pine afforestation, and it was significantly higher in *Pinus* afforestation (GLM $p < 0.001$), while PP1 presented lower densities and PP2 higher densities than maquis, albeit being not statistically significant (Table 3). On the contrary, almond individuals under pine afforestation presented the lowest height and BSD (GLM $p < 0.001$), and individuals in PP1 presented higher heights than the other sites (Table 3). The reproductive stage was dominant (67.8%, n = 160), followed by pre-reproductive stage (22.1%, n = 52) and juveniles (10.1%, n = 24) (Table 2). Habitats differed in life stage classes abundance (Likelihood Ratio = 42.11, df = 6, $p < 0.001$, n = 236; Table 2). All sampled plots had at least one reproductive almond individual, while 45.5% had pre-reproductive and 31.9% had juveniles. Since the almond individuals were randomly distributed inside the plots, and height and diameter were highly correlated (Spearman 0.87, $p < 0.001$), we can rule out that they were planted or pruned, consequently been originated by natural regeneration from seeds. Based on the information given by the landowners, in both prickly pear orchards the oldest almond individuals were 15 years old, and the three individuals analyzed in the PP2 were 5 years old (BSD = 3.5 cm), 11 years (BSD = 4.5 cm) and 13 years (BSD = 11 cm), corroborating their information. Finally, no adult almond tree or almond orchard was found in a radius of 150 meters from the study sites.

Table 2. Mean density, height and basal stem diameter (± SD), and percentage of spontaneous almond individuals in each life stage.

Study site	Density (N * 100 m^{-2})	Height (cm)	Basal stem diameter (cm)	Juvenile (%)	Pre-reproductive (%)	Reproductive (%)
Maquis	3.2 ± 1.64	246 ± 111	6.6 ± 3.49	3.1	6.2	90.8
Prickly pear orchard 1	1.4 ± 0.89	435 ± 150	7.2 ± 4.3	0	0	100
Prickly pear orchard 2	5.7 ± 2.98	248 ± 93	5.2 ± 2.8	5.0	12.5	82.5
Pine afforestation	24.8 ± 8.76	170 ± 83	2.2 ± 1.7	16.1	34.7	49.2

Table 3. Summary of the negative binomial (log link) GLM with the comparison of almond density, height and basal diameter between the four study sites. Maquis is included in the intercept. PP1 = Prickly pear orchard 1, PP2 = Prickly pear orchard 2.

Study site	Density (N * 100 m^{-2})				Height (m)				Diameter (cm)			
	Estimate	SE	z	p	Estimate	SE	z	p	Estimate	SE	z	p
Intercept	1.16	0.27	4.34	< 0.001	5.51	0.06	88.50	< 0.001	6.50	0.09	73.58	< 0.001
Pine	2.05	0.30	6.85	< 0.001	-0.43	0.08	-5.55	< 0.001	-1.11	0.11	-10.20	< 0.001
PP1	-0.83	0.47	-1.75	0.081	0.57	0.20	2.87	0.004	0.09	0.28	0.31	0.758
PP2	0.58	0.32	1.80	0.089	0.01	0.10	0.07	0.946	-0.24	0.14	-1.68	0.093

3.2 Floristic surveys

Species richness ranged from 18 to 35 plant taxa in all study plots, whilst the plant taxa characteristic of Alliance *Oleo-Ceratonion* accounted for 21-38% of all species (Table 4). The vegetation surveyed can be considered as a variant of the typical aspect of Mediterranean maquis physiognomized by *Euphorbia dendroides* L. and *Olea europaea* var. *sylvestris* (Mill.) Lehr (the plant association *Oleo-Euphorbietum dendroidis* Trinajstic 1975), within which *Prunus dulcis* is well established, reaching significant values of abundance-dominance (Figure 3). We deem that the plant community in which the almond has been detected could be framed into the phytosociological sub-association *Pistacio terebinthi-Celtidetum aetnensis phlomidetosum fruticosae* Gianguzzi, Cusimano and Romano 2014 (Gianguzzi et al. 2014a), which has been described in the most xeric screes on south-facing slopes of Pizzo Telegrafo, under the same environmental conditions. Moreover, the differential plant taxon of the sub-association, *Phlomis fruticosa* L., is particularly abundant in the study area, as well as many of the species most frequently listed in the phytosociological relevés (Marcenò et al. 2002; Gianguzzi et al. 2014a, 2016), like *Euphorbia dendroides*, *Smilax aspera* L., *Clematis cirrhosa* L. and *Asparagus acutifolius* L. Particularly, the site is markedly shaped by the massive presence of *Phlomis fruticosa*, a species with an eastern-Mediterranean centre of gravitation, which in Sicily is located in the central-eastern sector, with rather rare and fragmentary distribution (Fanelli et al. 2015, Gianguzzi et al. 2016).

Table 4 – Synthesis of phytosociological surveys carried out within the natural habitat where the almond occurs. Locality: Pizzo Telegrafo, Sicani Mts., Sicily.

Parameter	Relevé number				
	1	2	3	4	5
Geographical coordinates	37°35'51.48"N, 13°11'14.42"E	37°35'53.69"N, 13°11'12.04"E	37°35'53.56"N, 13°11'9.41"E	37°35'47.26"N, 13°11'41.99"E	37°35'46.22"N, 13°11'39.83"E
Area (m^2)	250	300	250	300	300
Altitude (m a.s.l.)	497	526	538	436	434
Aspect	S	S	S	W	W
Inclination (°)	5	45	45	5	5
Lithology	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous
Outcropping rocks/stones cover (%)	50	40-50	40-50	50	40
Total vegetation cover (%)	85-90	90	90	95	100
Woody layer cover (%)	50	40-50	40-50	50	40
Woody layer height (m)	85-90	90	90	95	100
Shrub layer/understory cover (%)	80	80	75	85	90
Shrub layer height (m)	1.5-2.0	2.5-3.0	2.5-3.0	1.5-2.0	1.5-2.0
Herb layer cover (%)	80-90	60-70	60-70	70-80	70-80
Herb layer height (m)	1.0-1.5	1.0-1.5	1.0-1.5	1.0-1.5	1.0-1.5
Species richness (N)	**33**	**25**	**19**	**21**	**18**
Characteristic of Association *Oleo sylvestris-Euphorbietum dendroidis* (including *Prunus dulcis*)	**3**	**3**	**3**	**3**	**3**
Characteristic of Alliance *Oleo-Ceratonion*, Order *Pistacio-Rhamnetalia alaterni*, Class *Quercetea ilicis*	**7**	**10**	**7**	**8**	**6**
Other species	**23**	**12**	**9**	**10**	**9**

3.3 The Almond Population in the Maquis Community

The almond population is composed of individuals belonging to different age classes, indicating a not recent naturalization process. In this area, the almond behaves as a typical pioneer tree species. Indeed, the species does not reach great longevity and rarely exceeds the size of a small tree 5-6 m high and with 30 cm in basal diameter. On the contrary, the almond individuals experience a short juvenile period, and 4-6 years old plants with basal diameters of only 2-3 cm already begin to fructify, while reaching full maturity, at an estimated age of

40-60 years, they undergo rapid senescence and aging processes until death. For what concerns fruits' taste, we found that almost all the mature trees (n = 28) had bitter fruits, accounting for 96% of total surveyed plants. Finally, as widely observed throughout Sicily, spontaneous nuclei of almond are also commonly found on road slopes and at the edges of crops, where it coexists with native woody species such as *Crataegus monogyna* Jacq., *Pyrus spinosa* Forssk., *Rubus ulmifolius* Schott, *Rosa canina* L., *R. sempervirens* L. and *Clematis cirrhosa*.

4. Discussion

In this study, we found evidence that the almond is actively spreading in different ecological contexts in Sicily (Mediterranean basin), also including a natural habitat. While our study has confirmed a high colonization potential in pine afforestation (Buono 2013, Homet-Gutiérrez et al. 2015), we also added two novel ecological contexts of almond spread. More importantly, we found from literature search that the naturalization events of the almond in Europe are currently restricted to small areas and synanthropic contexts, such as roadsides, ex-cultivated areas, afforestation withdrawn from management, abandoned places, arid hills, ruderal habitats and hedges (Blanca et al. 1998, Essl & Rabitsch 2002, Homet-Gutiérrez et al. 2015). Complementarily, very few studies have found the almond spreading in natural habitats, such as in the Kashmir Himalaya (India) (Khuroo et al. 2010), and in the Monegros Desert in Spain (Sanz-Elorza et al. 2010). However, no quantitative assessment has been made hitherto in those ecological contexts, leaving the strong suspicion the naturalization process is not as advanced as in our natural site. Conversely, the observation of the almond in the Mediterranean maquis here reported describes a natural process affecting an entire mountain complex over several hundred hectares. The lack of information and/or description of wild populations of *Prunus dulcis* within natural habitats would suggest a rare event, limited research or both. Whatever the reason, this is the largest area (> 400 hectares) of natural regeneration of the almond in natural habitats known to date in its European secondary range.

4.1 The naturalization of the almond in different ecological contexts

The density of natural regeneration of the almond ranged from 140 up to 2,400 individuals per hectare, thus indicating the ability to thrive in different ecological conditions. The distribution in life stage classes allowed us to get indirect information about the temporal dynamics of the naturalization process of the almond in the study areas. One interesting finding is the large between-site variation. Within prickly pear orchard 1, only reproductive individuals occurred, suggesting that the process could have started earlier there, while in prickly pear orchard 2 and maquis, just a few juveniles were recorded, suggesting a past burst of natural regeneration now showing signs of recruitment limitation regardless the reproductive individuals' density. In comparison, Homet-Gutiérrez et al. (2015) found a higher density of juveniles and a lower density of reproductive individuals, a pattern more similar to that found in the pine afforestation in our study, where the overall density of spontaneous individuals was significantly higher than in the other study sites, with a higher number of juveniles and pre-reproductive individuals. Moreover, as the almond individuals were lower and smaller there, we hypothesized that the almond establishment could be more recent in the afforestation. The first barrier that a plant needs to overcome to colonize new sites is seed dispersal (Richardson et al. 2000, La Mantia et al. 2019). The relatively large size of the fruit, the lack of fleshy pulp and the hard woody endocarp confine the almond to the dispersal by seed predators, namely corvids, woodpeckers and rodents, as in other nut species such as walnuts and oaks (Homet-Gutiérrez et al. 2015, Gómez et al. 2019, Martínez-Baroja et al. 2019, Bueno et al. 2020a). In our study sites, there are no large woodpeckers, but corvids such as *Corvus cornix* (hooded crow) and *Pica pica* (magpie) have been often observed inside all the study areas, as well as flying from and to nearby vegetation patches. Moreover, an increase in these bird populations has been registered in the last decades (Cairone et al. 2020), and it is known that these demographic shifts may play a relevant role in the establishment success of Mediterranean woody plants (La Mantia & Bueno 2016). Since rodents seed dispersal is generally spatially constrained (Pons and Pausas 2007, Martínez-Baroja et al. 2019, Balaguer-Romano et al. 2021), and considering the lack of adult almond individuals in the immediate surroundings (150 m) of the study sites, we hypothesized that the main trigger for almond colonization could have been corvids. Moreover, as corvids prefer to cache seeds in afforestations (Gomez 2003, Purves et al. 2007), this preferential behaviour could explain the higher almond density found under the pine afforestation in our study. Then, along with the increasing number of reproductive individuals, higher local seed dispersal is expected. In this regard, rodents such as rats (*Rattus* spp.) and woodmouse (*Apodemus sylvaticus* L.) were reported to be important almond seed dispersers (Homet-Gutiérrez et al. 2015, Vander Wall 2001), and were found to play a relevant role in fostering germination, seedling emergence and establishment in Mediterranean areas (Balaguer-Romano et al. 2021). They may be acting at small spatial scales, hoarding the seeds produced by reproductive individuals as well as promoting secondary dispersal of seed arriving from outside (Homet-Gutiérrez et al. 2015).

Environmental constraints and herbivory could have played a key role in shaping and driving the observed patterns. Poor soils and severe drought can cause seedling mortality, but the almond may grow well in harsher conditions than those found in our sites (Roldan-Fajardo et al. 1982, Camposeo et al. 2011, Sanz-Elorza et al. 2010, Homet-Gutiérrez et al. 2015). Indeed, herbivory, especially by ungulates, has been detected as the main bottleneck for almonds recruitment in semiarid Mediterranean habitats (Homet-Gutiérrez et al. 2015). In both prickly pear orchards and the pine afforestation, the access to domestic or wild large herbivores is very restricted, while in the maquis, domestic animals (goats, cows and sheep) may eventually browse. Then, although rabbit faeces were observed in all sites, in the afforestation rabbits have no shelter, because pine individuals are quite high (mean height of 7 m) and without lower branches, resulting in an open understory. Thus, based on previous studies and considering our sites' characteristics, we believe that the higher densities found under the pine afforestation could be due to a combination of favourable canopy cover, open understory and lower herbivores pressure, particularly by rabbits and sheep.

4.2 The almond as non-native tree species in Europe, Italy and Sicily

In Europe, the almond would seem to be able to escape from cultivation for a long time, being considered as "*frequently naturalized in the Mediterranean region*" in "Flora Europaea" (Tutin et al. 1968). For instance, the first record in Portugal dates back to the end of the nineteenth century (de Almeida and Freitas 2006). However, until about 25 years ago, the almond was still regarded as "*occasionally naturalized*" throughout Europe (Heywood and Zohary 1995). In fact, its naturalization status is uncertain or unknown in many European countries (Kurto 2009), and the knowledge about its naturalization process (invaded sites, spatio-temporal dynamics, ecc.) is scarce (Avanzato and Vassallo 2006). In the last few years, *Prunus dulcis* has established in different European countries. The preference for Mediterranean-climate areas is witnessed by its naturalization in Albania (Barina et al. 2014), Bosnia and Herzegovina (Maslo 2014), Cyprus (Hadjikyriakou and Hadjisterkotis 2002), Greece (Arianoutsou et al. 2010), Malta (Mifsud 2010), Portugal (de Almeida and Freitas 2006) and Spain (Blanca et al. 1998). Interestingly, the almond has also established in much cooler regions at higher latitudes: Austria (Essl & Rabitsch 2002), Finland (Kurtto et al. 2019), Slovakia (Medvecká et al. 2012), Switzerland (Wittenberg 2005) and Aosta Valley in Italy (Alpine region), where the species has shown preference for the warmer valleys (Bovio 2014).

The consideration of *Prunus dulcis* as non-native plant species is not linearly changed over time in Italy (Saccardo 1909, Celesti-Grapow et al. 2009). Indeed, the species does not seem to have followed the typical trajectory of alien species along the continuum introduction-naturalization-invasion. This irregular trend reveals the difficulty to deal with taxa with ancient introduction (i.e. archaeophytes) or with a doubtful origin. The almond has been included among naturalized non-native taxa since the beginning of the last century (Saccardo 1909, Beguinot & Mazza 1916). Saccardo (1909) even considered it as fully naturalized. However, the subsequent national flora did not confirm this statement (Fiori 1923/1925), treating the almond as "*sometimes naturalized*". In fact, the ability of the almond to spread outside cultivation in Italy has been repeatedly questioned and it was also estimated to be lower than that of congeneric species. In the most important and comprehensive checklist of Italian exotic flora of the last century (Viegi et al. 1974), including all the national literature reporting specific information about naturalized plants, only four references were referred to *Prunus dulcis*, whilst, for instance, more than twenty references concerned both *Prunus cerasus* (the sour cherry) and *Prunus persica* (the peach). Such a trend has been confirmed in the two subsequent national floras (Pignatti 1982, Pignatti et al. 2017), where the almond was considered only rarely naturalized. The two more recent updates of non-native flora of Italy have confirmed the uncertainties around the almond. Celesti-Grapow et al. (2009) included *Prunus dulcis* among the doubtful alien taxa, to which an invasive status could not be assigned due to limited knowledge. However, something in the ecological behavior of the species could have changed in the last decade as the species has been increasingly reported in regional records (Bovio 2014, Camarda et al. 2016, Laface et al. 2020), sometimes showing the ability to entry within semi-natural and natural habitats such as Mediterranean afforestations and open maquis (Buono 2013). Accordingly, the almond is currently a naturalized archaeophyte in Italy, where it is found growing wild in all regions (Galasso et al. 2018, Laface et al. 2020): as casual in 17 regions, including Sicily, and naturalized only in three regions (Galasso et al. 2018).

Two wild almond species are present in Sicily: *Prunus dulcis*, cultivated since historical times, and *Prunus webbii* (Spach) Vierh, widespread in eastern Sicily (Marcenò et al. 1995b, Minissale et al. 2008) and with few stations in western areas (Scuderi and Pasta 2009). Sicily plays a major role in the almond production in Italy, with about 15,000 ha of almond orchards and accounting for more than 65% of national production (Sottile et al. 2014). The observation of spontaneous almond individuals is neither new in Sicily nor being recent in time. Gussone (1842) reported the occurrence of *Prunus dulcis* in calcareous rocky cliffs close to the sea. Bianca (1871) early formulated the hypothesis that almond was spontaneous on the basis of the observations made on some naturalised plants and the morphology of different plant organs, apart from providing the description of many fruits of plants considered as wild. Then, more than a century ago, Lojacono-Pojero (1908) observed the almond on rocky habitats on Mount Pellegrino, in Palermo province. However, despite being widely cultivated in the island, we did not find more recent records of naturalization events and, in effect, *Prunus dulcis* has never been studied as a typical non-native species so that knowledge of its spatio-temporal dynamics is very limited. However, the growing number of spontaneous nuclei and self-sown individuals observed in the last few years suggests a steep increase in the naturalization process. Indeed, the almond was observed growing wild in Sicily in more than 25 different sites in different ecological contexts: abandoned lands, previously cultivated areas (olive groves, prickly pear orchards, ecc.), roadsides and rocky outcrops sometimes covered by Mediterranean maquis (*Oleo-euphorbietum*) aspects (for instance at Castello di Baida, Castellammare del Golfo, TP). However, differently from other *Prunus* spp., the almond is not contributing to natural regeneration and expansion of woody vegetation in other areas (Bueno et al. 2020b). In most of the observed nuclei, many young individuals were present, suggesting a recent process of seedling recruitment and establishment. Such observation appears to be corroborated by the maximum age (13 years old) of the almond trees in the prickly pear orchard 2, and is consistent with the information gathered in prickly pear orchard 1 (Michele Russo, pers. observ.) and in pine afforestation (Andrea Cairone, pers. observ.), where the natural regeneration of the almond has not started before than 10-15 years ago. The observation of many spontaneous nuclei, including a large population in a natural habitat covering large areas, where it characterizes some peculiar aspects of Mediterranean vegetation, demonstrates the full naturalization of *Prunus dulcis* in Sicily. Despite all this growing body of evidence, in Sicily this tree is still considered among casual non-native plant species (Galasso et al. 2018), which "*rely on repeated introductions for their persistence*" (Pyšek et al. 2004). This fact underlines a strong underestimation of this widespread natural process.

4.3 The almond population in the Mediterranean maquis

In Sicily, Mediterranean maquis is frequently linked to coastal environments, placing itself between the coastal halophilous communities and the thermoxerophilous forest formations dominated by evergreen oaks (cork oak and holm oak) or deciduous (*Quercus virgiliana*) (Brullo et al. 2008). The plant communities physiognomized by *Euphorbia dendroides* represent the only aspect of Mediterranean maquis also capable of thriving in inner areas of the Sicilian territory as this species, indifferent to the geolithological substrate, has colonized all the semi-rocky environments from sea level up to about 1000 m of altitude, *i.e.* the substrates not suitable, due to extreme edaphoclimatic conditions, to host oak species (Brullo et al. 2008). In the mountainous complex under investigation, these are phytocoenoses of high phytogeographical interest that strongly shap the plant landscape, particularly the southern slopes, geomorphologically more rough and climatically more xeric. Furthermore, the most extensive and significant expressions of woody vegetation are found in the same areas, which include the microwoods of *Celtis tournefortii* subsp. *asperrima* (Gianguzzi et al. 2014a). The almond is right established within the most advanced and preserved forest aspects of the local edapho-xerophilous series (Gianguzzi et al. 2014a), where, moreover, non-native species are completely missing, further underlining a reduced anthropic influence.

Furthermore, in the natural habitat, the almond appears to be perfectly integrated within local plant communities, proving the ability to co-exist with native species, as well as generating an alternative food source for native fauna (Homet-Gutiérrez et al. 2015). What surprises the most is that the almond has never been reported, not even as a minor component of plant communities, in any of the many vegetation surveys carried out in the overall floristic district just in the last decades (Marcenò et al. 1995a; Marcenò et al. 2002; Marino 2009; Gianguzzi et al. 2014a, Gianguzzi et al. 2016,). One of the most likely reasons for this missing is that these studies were mostly addressed to study *Celtis tournefortii* subsp. *asperrima*, a Sicilian endemic species which forms nuclei of woody vegetation of relict significance and high conservation value. Indeed, it is considered a threatened taxon of Sicilian flora, which calls for strict protection measures (Schicchi & Marino 2011). The most abundant population of this valuable tree species is just found on the southern slopes of Pizzo Telegrafo (Gianguzzi et al. 2014b). Furthermore, interviews with local farmers and breeders have confirmed the presence of the almond in the area in historical times, dating back to at least the two previous generations, i.e. about 60-80 years ago. Then, our observations in the last 20 years have verified nor an increase or a reduction in almond population, which, conversely, showed a stable trend suggesting the absence of replacement processes of native flora as well as the perfect adaptation to local climate and harsh edaphic conditions and highly selective of calcareous lithosols of Mount Telegrafo. Also based on this evidence, we think that there are circumstances to hypothesize that the population of *Prunus dulcis* object of study might be a relict station, as well as certainly with the meaning of relict formations are those characterized by *C. tournefortii* occurring on the screes and debris of the same reliefs within which *Prunus dulcis* is perfectly established (Schicchi & Marino 2011). Indeed, according to Gianguzzi et al. (2014b), such aspects of woody vegetation have a "*clear relictual and residual significance*" and are linked to "*pioneer vegetation series typical of screes of carbonate nature*". Indeed, it is a habitat of difficult practicability and is conservative like that of rocky cliffs. For this reason, it hosts the most preserved aspects of natural vegetation occurring in these mountains, where human presence is witnessed since the Mesolithic, and the progressive deforestation processes led to the complete removal of original woodlands (Marcenò et al. 2002, Gianguzzi et al. 2016). Paleobotanic studies, archaeological information, as well as genetic analyses, will be needed if we are to clarify the origin of this peculiar almond population. Interestingly, even the most recent research about the genetic structure and diversity of the almond has hypothesized that relict populations from disjoint ecological stations could contribute to explain the overall genetic diversity within the species (Delplancke et al. 2013).

5. Conclusions

The almond is a tree species historically and widely cultivated in Europe, especially in southern regions, for its edible fruits. Indeed, anecdotal evidence and old literature have shown that its ability to reproduce naturally is neither new nor recent in time. However, on the one side, we found from literature search that a growing number of naturalization events have been observed in the last decades in many European countries, including Italy and Sicily as well. This trend is worth to be further studied with the aim to detect possible changes in the affected habitats or species, or in the distribution range (e.g. a northward latitudinal shift due to climate change effects). On the other side, in Europe, the natural regeneration of the almond in the field has been little studied and the occurrence in natural habitats has been rarely (if ever) observed. Conversely, we report here the largest almond population occurring in natural habitats known to date in Europe in its secondary range, spread over 400 hectares in Mediterranean maquis communities. Furthermore, the presence of the almond in this large area dates back to at least 70-80 years ago, and no demographic variation in the population has been observed in the last two decades. In conclusion, our study expands the current knowledge regarding almond naturalization in the Mediterranean basin, indicating the increasing ability of establishment and spread in afforestations and agricultural fields. At the same time, the meaning and origin of the very large areas of Mediterranean maquis where the almond nuclei are definitely established deserve further research, including genetic analyses.

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Authors' contributions

EB, RSB, TLM and VI conceived the study and established methodology, EB, RSB, GS, DC, TLM and VI collected data, GS analysed dendrochronological data, RSB performed the statistical analysis, EB, RSB, TLM and VI wrote the manuscript. All authors read and approved the final manuscript

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Figure captions

Figure 1. Localization of the study areas in Sicily (from left to right): Mediterranean maquis (Caltabellotta, Province of Agrigento), pine afforestation (Roccapalumba, Province of Palermo), prickly pear orchard 2 (Roccapalumba, Province of Palermo), prickly pear orchard 1 (Caltagirone, Province of Catania).

Figure 2. Images of natural regenerating almonds within maquis (A), pine afforestation (B), prickly pear orchard 1 and 2 (C and D).

Figure 3. A general (on the left) and detailed (on the right) picture showing the characteristic Mediterranean maquis aspects with *Prunus dulcis*, *Olea europaea* var. *sylvestris* and *Euphorbia dendroides*, in the southwestern slopes of Monte Gargalufo (777.5 m a.s.l.).

Figure1

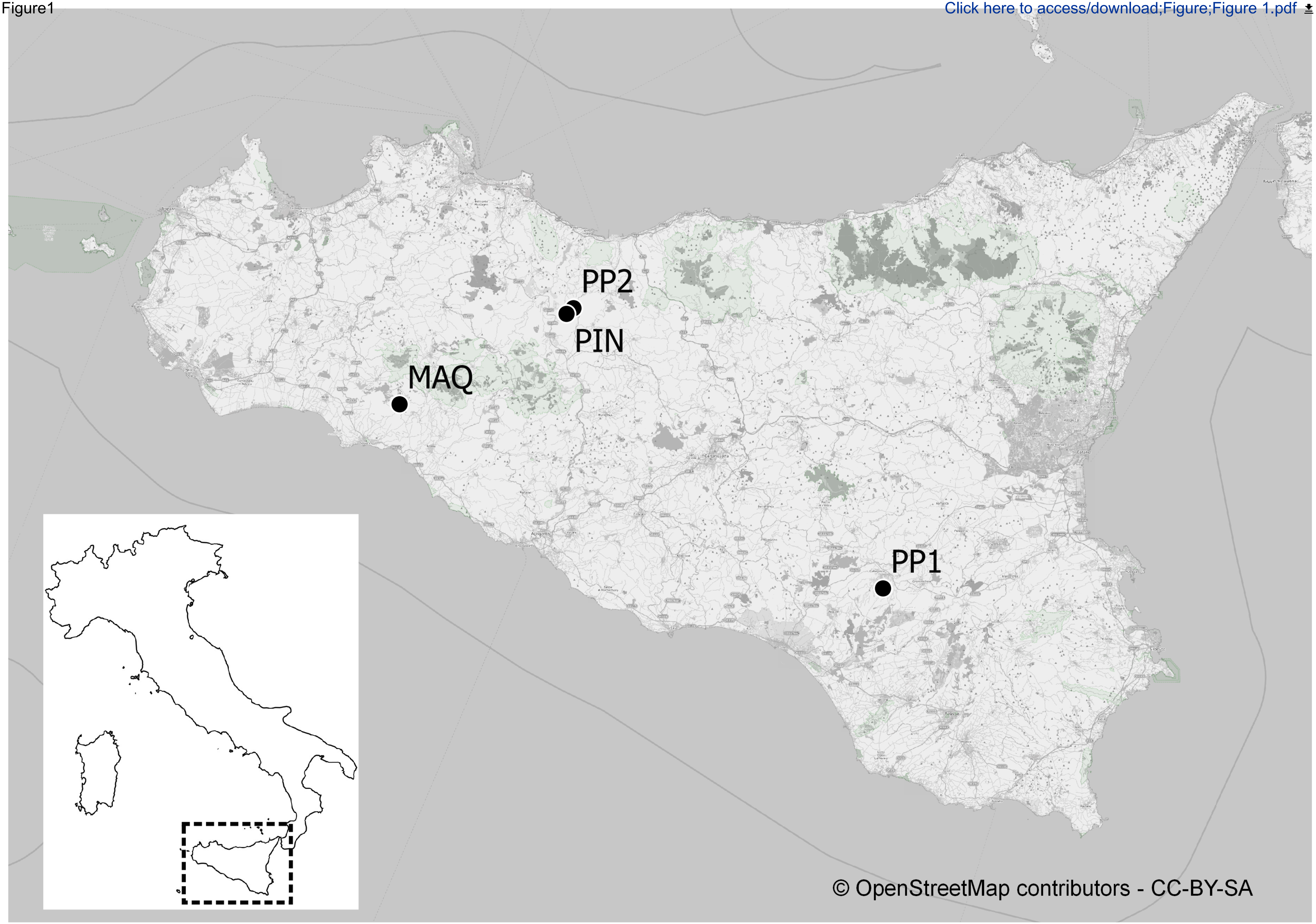

Figure2

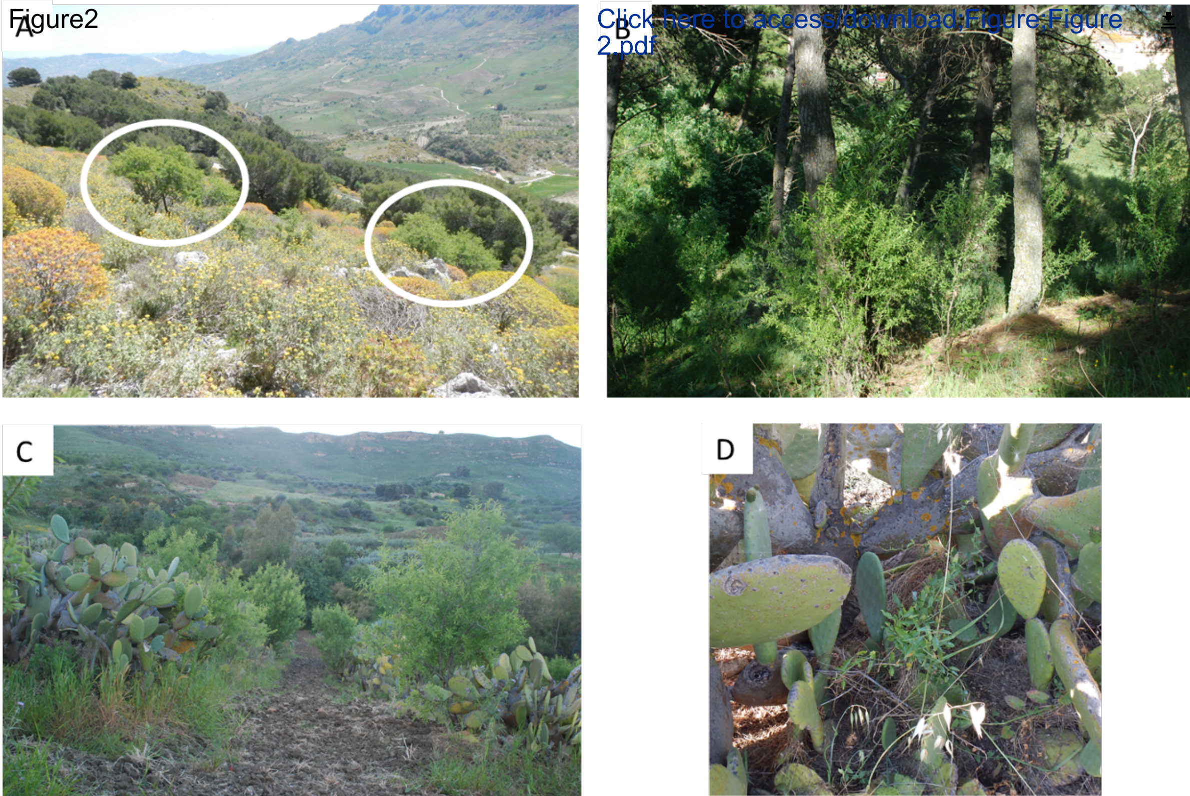

Figure3


Euphorbia
dendroides
Prunus dulcis
Olea europaea
var. sylvestris

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: