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Alien plant invasions in Mediterranean habitats: an assessment for Sicily

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Abstract Levels of plant invasions in different habitat types were assessed in several regional studies, but few of them were from the Mediterranean. Here we compare the levels of vascular plant invasion across habitats and plant communities of Sicily. We used a large dataset of plant species presences/absences in vegetation plots to analyze the invasion patterns across habitats considering biogeography, life form and phenology of alien plants. Vegetation plots were classified based on the EUNIS classification of European habitats. The invasiveness of each species was expressed in terms of its absolute and percentage frequency. Representation of different life forms and phenological patterns was compared between alien and native species. The fidelity of alien species to individual habitats was calculated using the *phi* coefficient. Our analysis shows that annual and woody species are the most represented life forms in the alien flora of Sicily and that alien species tend to have a longer flowering period than the native species. The investigated habitats differed strongly in their level of invasion by alien species, ranging from 0 to 15.6% of aliens of all species recorded. Most of the habitats were colonized by very few alien species or completely lacked them, except for sandy coasts, naturally-disturbed riverbeds, and synanthropic habitats. It must be noted, however, that the number of alien species occurring in a given habitat does not relate to the severity of the impact of invasion in that habitat. Some habitats are invaded by few (or single) species, which attain a high cover, transforming the whole ecosystem. The habitat-based approach proved to be suitable for evaluating the habitat specificity and frequency of alien species at a regional scale, improving the capacity for risk assessment in different ecological contexts.

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Introduction

Some authors have considered Mediterranean ecosystems less prone to invasion than temperate ecosystems

as a result of the long history of interactions between the environment and humans (Di Castri 1989; Quézel et al. 1990) and summer-drought stress, which prevents the establishment of non-adapted plants (Garcia-Serrano et al. 2009). This is consistent with recent syntheses that show generally lower numbers of alien species in the Mediterranean than in temperate Europe, based on national inventories of alien floras (Lambdon et al. 2008b), Atlas Florae Europaeae grid maps (Ronk et al. 2017) or standardized plot sampling of corresponding habitats in the Mediterranean and temperate cities (Kalusová et al. 2019). However, recent studies suggest that disturbance (Dimitrakopoulos et al. 2017), human population density (Malavasi et al. 2014), habitat fragmentation (Tomaselli et al. 2012), climate change (Gritti et al. 2005), global trade (Hulme 2004), and ornamental horticulture (Pretto et al. 2012) may lead to an accelerating trend of biological invasions also in the Mediterranean region (Sanz-Elorza 2006; Celesti-Grapow et al. 2010; Celesti-Grapow and Ricotta 2021), mainly by plant species arriving from climatically similar regions of the world (Cao Pinna et al. 2021).

Mediterranean islands also seem to be less invaded than areas of continental Europe, as indicated by qualitative observations of their flora (Dal Cin D'Agata et al. 2009; Podda et al. 2010; Puddu et al. 2016). However, islands tend to be more prone to invasions than mainland regions (Lonsdale 1999), and this pattern was also observed in the Mediterranean (Gimeno et al. 2006; Celesti-Grapow et al. 2016). The reasons include a higher probability of the occurrence of unsaturated communities, a lower competitive ability of native species (Hulme 2004) and more intense human pressure, notably in summer along the coast, in lowlands and riparian habitats (Hulme et al. 2008). Also, the exposure of Mediterranean islands to biological invasions may have accelerated in recent years as it happened elsewhere. For instance, Camarda et al. (2016) report on the naturalization of 72 new alien plant species never observed before in Sardinia. The distance from the mainland, size and shape of the Mediterranean islands can influence their vulnerability to alien plant invasion (Domina and Mazzola 2011). Still, some studies (Vilà et al. 2010, 2011) suggest that biological invasions in Mediterranean insular ecosystems are no exception to the general rule that levels of invasion are context-dependent and habitat-specific (Traveset et al. 2008).

The term "habitat" originates from a species-specific concept (Kirk et al., 2018), but it is frequently used to designate an integral unit comprising ecological functions and species assemblages (Morrison and Mathewson 2015), as it happens in the EUNIS habitat classification adopted in the European nature conservation policies (Rodwell et al. 2018). In this sense, the invasiveness of an alien species is determined not only by its habitat preferences but also by context-specific processes and interactions between biotic communities and their invaders (Lambrinos 2002; Evangelista et al. 2008; Crosti et al. 2016).

Regional studies comparing the levels of plant invasion across Mediterranean habitats and plant communities are uncommon, most of them performed on the Iberian Peninsula (Vilà et al. 2007; Chytrý et al. 2008; González-Moreno et al. 2014). Therefore, we extend this approach eastwards to test whether the patterns documented previously have a more general validity across the Mediterranean Basin.

We focus on Sicily, the largest Mediterranean island. Due to its long-lasting human history and central location in the Mediterranean Basin, Sicily represents an ideal study area to explore alien plant invasions patterns. Although Sicily's alien vascular flora is well known (Galasso et al. 2018a, b, c), the frequency and abundance of alien species within habitat types have never been assessed.

Since vegetation cover is a primary attribute in EUNIS habitat identification (Gigante et al. 2016; Rodwell et al. 2018) and vegetation plots offer a good measure of species percentage frequencies in different habitats (Guarino et al. 2018), we used vegetation-plot data from Sicily to answer the following questions: (1) What is the affinity of alien species to specific habitats at a fine-scale? (2) Which biogeographical regions contributed the most frequent alien vascular plants to Sicily and the study habitats? (3) Which are the most frequent life forms of the alien vascular plants in Sicily and in the study habitats? (4) Are there any differences in the flowering time of alien and native plants?

Methods

Study area

Sicily and its offshore islets are recognized as one of the biodiversity hotspots in the Mediterranean Basin

(Médail and Quézel 1999). Sharp topographic (Catalano 2004), edaphic (Fierotti 1997) and climatic (Bazan et al. 2015) contrasts make this island one of the most environmentally heterogeneous Mediterranean territories. The diversity of the Sicilian flora and vegetation is due to the complex geomorphology of the island (Carbone et al. 2018) and its palaeogeographic history, making Sicily an excellent example of the full range of common Mediterranean vegetation types (Guarino and Pasta 2017).

Its central location made Sicily a major pathway of human migration and cultural, economic and ethnic crossroads. Although palaeontological and palaeogeographic data do not exclude the possibility of a Middle Pleistocene peopling (Sineo et al. 2015), the human presence in Sicily has been unequivocally continuous since 14,000 years ago (Mannino et al. 2012). During the long history of human habitation, plant assemblages have been shaped by human activity (Tinner et al. 2016). Many alien vascular plants were introduced, although the time and pathways of these introductions remain uncertain in most cases (Mazzola and Domina 2010). At present, Sicily has 4.97 million inhabitants, with a population density of 197 people/km^2. According to the second edition of the Flora of Italy (Pignatti et al. 2017–2019), the Sicilian vascular flora consists of 3012 species, 237 of which are alien species steadily naturalized on the island and 219 are casual aliens. About eighty new alien species have been recorded in Sicily in the last two decades (Galasso et al. 2018a, b). Although some species are represented in Sicily by different subspecies, varieties and forms, only species were considered in the present study.

Datasets

The vegetation plots from Sicily stored in the European Vegetation Archive (EVA; Chytrý et al. 2016) were used as source data for species occurrences and frequencies. In June 2020, data were retrieved from the following databases (database codes follow the Global Index of Vegetation-plot Databases; www.givd.info): Mediterranean Ammophiletea Database (EU-00–016; Marcenò and Jiménez-Alfaro 2017), CircumMed Pine Forest Database (EU-00–026; Bonari et al. 2019), European Weed Vegetation Database (EU-00–028; Küzmič et al. 2020), High Mediterranean Mountains Database (EU-00–029),

Vegetation Plot Database – Sapienza University of Rome (EU-IT-011; Agrillo et al. 2017), Iberian and Macaronesian Vegetation Information System (SIVIM, EU-00–004; Font et al. 2012) and VegItaly (EU-IT-001; Landucci et al. 2012).

Vegetation plots were classified using the classification expert system for EUNIS habitats (EUNIS-ESy version 2020–06-08; Chytrý et al. 2020). Habitat types within groups A (marine, in our case coastal saltmarshes), C (aquatic) and H (sparsely vegetated) were classified to the types accepted in the European Red List of Habitats (Janssen et al. 2016) because these groups of habitats were not yet subjected to the revision of the EUNIS system. Unclassified plots and those assigned to multiple habitats were discarded. Only habitats represented by at least 34 plots across the whole dataset were retained for data analysis. In some cases, similar habitats not reaching the minimum number of plots were merged. This happened in the case of the habitats C1+C2, N1B+N1G, S6+S72, S93+T14, T17+18 (see Online Resource 1 for the habitat codes).

The number of plots differed among individual regions within Sicily and habitats. This imbalance can bias the estimates of frequencies and relative alien species richness (Wagner et al. 2017). While we were unable to address the uneven number of plots per habitat, we tried to reduce the bias due to the uneven geographical distribution of the vegetation plots by dataset resampling. The group of plots belonging to each habitat was resampled geographically, retaining a maximum of five plots per habitat in each quadrat of a geographical grid of 2.0 longitudinal and 1.5 latitudinal minutes (approx. 3 km × 2.8 km in Sicily). The resampling procedure was not applied to the habitats containing less than 50 plots across the whole island.

Traits

Biogeographical status, life forms and months of flowering were retrieved from the electronic supplements of the Flora of Italy (Pignatti et al. 2017–2019). The origin and the status in Sicily of many archaeophytes (i.e. species presumably introduced to Italy before 1500 AD), particularly those related to wheat cultivation, is debated (Brullo and Guarino 2007). Therefore, we considered as alien species only the neophytes (i.e. species presumably introduced to Italy after 1500 AD), classified as such by Galasso, Banfi

and Bandini Mazzanti in Galasso et al. ([2018a](), [b](), [c]()). Archaeophytes were considered as native, with the only exception of those whose intentional introduction in Sicily is historically documented, as in the case of *Arundo donax, Avena sativa, Citrus limon, C. sinensis, Rhus coriaria* and *Triticum turgidum.*

Concerning the biogeographical status, we lumped into the "Mediterranean" all species recorded in the Flora of Italy as Pan-Mediterranean, Centro-Mediterranean, N-, NE-, NW-, E-, W-, SE-, SW- and S-Mediterranean; into the "Wide-Mediterranean" the species recorded as Eury-Mediterranean, Mediterranean-Saharian, Mediterranean-Macaronesian, Mediterranean-Turanian and Mediterranean-Pontic; into the "Subtropical" the species recorded as Saharo-Sindic, Pantropical and Palaeotropical. All the other biogeographical status were considered individually.

Only the following six life forms were considered: "Tree" (phanerophytes); "Shrub" (nano-phanerophytes and woody climbers); "Dwarf" (chamaephytes); "Herb" (hemicryptophytes and geophytes); "Hydrophyte" (helophytes and hydrophytes); "Annual" (therophytes). Some taxa were associated with more than one life-form. The complete list of alien species recorded in the dataset is reported in Online Resource 2.

Data analysis

The invasiveness of a given species was expressed as its absolute percentage frequency in the resampled dataset. The biogeographical status and the life forms were converted into dummy variables. We used the nonparametric Wilcoxon statistical test to compare the percentages of life-forms and phenology between alien and native species pools.

Following Catford et al. ([2012]()), we quantified the level of invasion as alien species richness and relative alien species richness. We defined these measures separately for the whole habitat and for vegetation plots belonging to the habitat. As individual habitats were represented by different numbers of plots, we calculated rarefaction with the "rarefy" function included in the vegan package 2.5-7 in R (Oksanen et al. [2020]()) and took estimated species numbers corresponding to 34 plots. We used four measures of the level of invasion: (1) alien species richness per

habitat (absolute number of alien species recorded across 34 plots belonging to the habitat), (2) relative alien species richness per habitat (number of alien species as a proportion of the number of all species recorded across 34 plots belonging to the habitat), (3) mean alien species richness per plot (absolute number of alien species recorded in a plot averaged across all the plots belonging to the habitat) and (4) mean relative alien species richness per plot (number of alien species as a proportion of all species recorded in a plot averaged across all the plots belonging to the habitat). For each habitat, life forms and biogeographical status were used as descriptors of the alien species pools.

Finally, the fidelity of alien species to a given habitat was determined by measuring the concentration of species occurrences in the vegetation plots assigned to that habitat, using the *phi* coefficient of association (Tichý and Chytrý [2006]()). Species with values of $phi \geq 0.3$ were reported as diagnostic of a given habitat in Online Resource 1. In the calculations, we assumed an equal number of plots per habitat. We disregarded those alien species whose concentration in the group was not significant at $p < 0.01$, based on Fisher's exact test (Tichý and Chytrý [2006]()).

Results

Alien flora

In total, 6366 vegetation plots were retrieved from EVA. After classification and resampling, the dataset comprised 3655 plots, 1601 species (corresponding to 53.1% of the whole Sicilian vascular flora) and 75,969 species occurrence records. There were 70 alien species recorded in the dataset. Considering that 15.1% of the whole Sicilian flora are alien species (Pignatti et al. [2017]()–2019), the proportion of alien species in our dataset was significantly lower, corresponding to 4.3% of the species recorded (Fig. [1]()a). The relative frequency of alien species across plots in the resampled dataset was 1.3% (Fig. [1]()b).

Oxalis pes-caprae was by far the commonest and most ubiquitous alien species in the dataset, with 302 occurrences in 13 different habitats (Table [1](); Online Resource (2), followed by *Xanthium orientale* and *Erigeron bonariensis.*
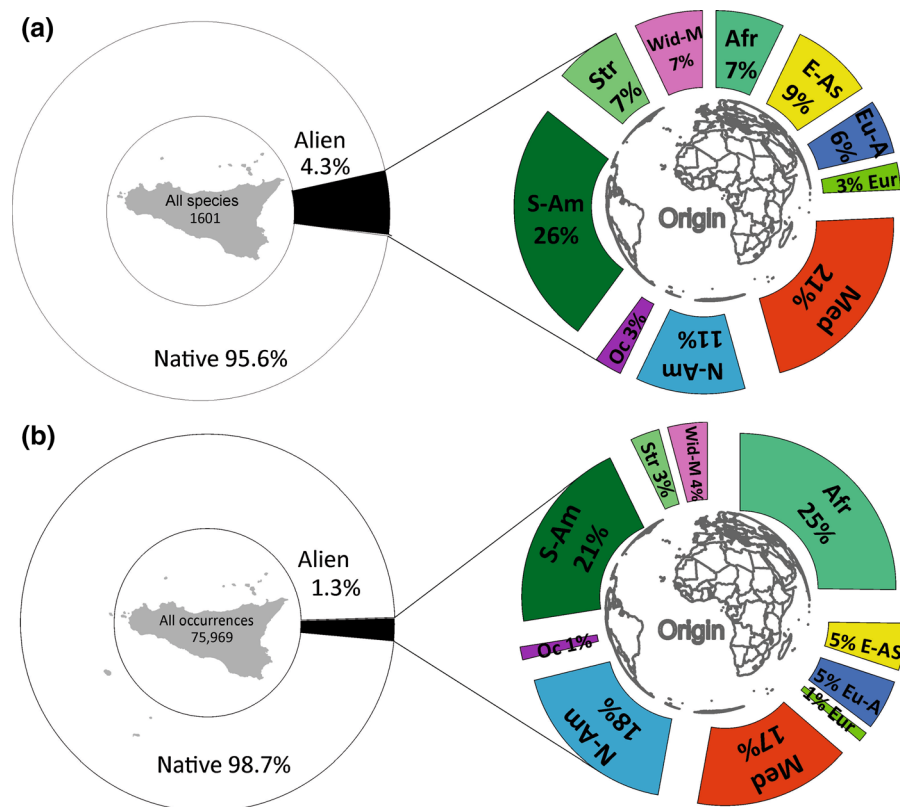
Fig. 1 a Percentage of alien species in the species pool and **b** relative frequency of alien species across plots in the resampled dataset, classified by their origin (standard error of the mean < 3%). Afr = African, E-As = East-Asian, Eu-A = Eurasian, Eur = European, Med = Mediterranean, N-Am = North-American, Oc = Oceanian, S-Am = South-American, Str = Subtropical, Wid-M = Wide-Mediterranean

Origin

Altogether, Mediterranean and wide-Mediterranean aliens were the most well-represented, accounting for 20 species and 21% of all occurrences (Fig. 1). However, the number of strictly Mediterranean aliens (15 species) was lower than that of the South American ones (18 species) and, if the relative frequencies of species across plots were considered, the most represented were African (25%), South American (21%), North American (18%) and Mediterranean (15%).

Life forms

In our dataset, 35 alien species were annuals, accounting for 50% of all alien species in the dataset (Online Resource 2). Compared to the life-forms of the native species pool (Fig. 2a), annuals, trees, shrubs, and dwarf shrubs were significantly over-represented and herbs significantly under-represented in the alien species pool. When the relative frequencies of species across plots were considered, alien annual and tree species were significantly more represented than the corresponding life forms of native species, whereas dwarf shrubs and herbs were significantly less represented (Fig. 2b).

The proportion of life forms in the alien pool differed (Fig. 3): South America and North America contributed mostly annual species, while most of the tree species came from Europe, East Asia and Oceania.

Phenology

Alien plant species had different patterns of flowering phenology than native species. The average curve of native species flowering time displays a more

Table 1 The alien species with absolute frequency ≥ 10 in the resampled dataset. Species are ordered by their occurrence frequency within the dataset, which is expressed both in the absolute number of occurrences (absolute frequency) and as a percentage of all plots in the dataset (percentage frequency)

Species	Origin	Life form	Absolute frequency	Percentage frequency	No. of EUNIS habitats (tot.)
Oxalis pes-caprae	African	Herb	224	6.1	13
Xanthium orientale	North American	Annual	97	2.7	6
Erigeron bonariensis	South American	Annual	62	1.7	4
Lycium intricatum	Mediterranean	Shrub	51	1.4	7
Symphyotrichum squamatum	South American	Annual	40	1.1	8
Rhus coriaria	Mediterranean	Shrub	31	0.8	5
Opuntia ficus-indica	North American	Shrub	30	0.8	5
Citrus sinensis	East Asian	Tree	23	0.6	3
Erigeron sumatrensis	South American	Annual	22	0.6	4
Veronica persica	Eurasian	Annual	21	0.6	3
Vicia faba	Mediterranean	Annual	19	0.5	2
Amaranthus retroflexus	North American	Annual	19	0.5	4
Galinsoga parviflora	South American	Annual	18	0.5	3
Asparagus officinalis	Wide-Mediterranean	Herb	17	0.5	2
Erigeron canadensis	North American	Annual	16	0.4	5
Arundo donax	Eurasian	Shrub, Herb	15	0.4	7
Citrus limon	East Asian	Tree	15	0.4	2
Dactyloctenium aegyptium	Subtropical	Annual	14	0.4	3
Sisymbrium orientale	Wide-Mediterranean	Annual	14	0.4	1
Amaranthus deflexus	South American	Annual	14	0.4	2
Acacia saligna	Oceanian	Shrub, Tree	11	0.3	4
Cichorium pumilum	Mediterranean	Annual	10	0.3	3
Megathyrsus bivonianus	Mediterranean	Herb	10	0.3	1
Cenchrus setaceus	Subtropical	Herb	10	0.3	1

The number of EUNIS habitats in which the species was recorded is reported in the last column; for the whole list, see Online Resource 2

pronounced and earlier peak than the curve of alien species (Fig. 4). The flowering time of alien species is more prolonged than that of native species, with considerable prevalence in July and August.

Aliens in habitats

The investigated habitats differed strongly in their level of invasion by alien species, both of Mediterranean and non-Mediterranean origin (Fig. 5). The number of alien species ranged from 0 to 20, representing up to 16.7% of the total number of species recorded in each habitat. Similarly, the mean number of alien species per plot scored up to 17.2% of

the plot species list. The man-made habitats (habitats V1–V39) were the richest in alien species, with an average percentage frequency of 5.7%. However, this figure ranged from 0.6% in the case of the dry perennial anthropogenic herbaceous vegetation (V38) to 16.7% in the case of the commensal annual vegetation of crops (V37). The vegetation of coastal saltmarshes (A25d), sandy coasts (N14–N1G), perennial dry grasslands (R1E) and riparian thickets (S93+T14) was quite prone to colonization by alien species.

In contrast, some habitats were alien-free, such as Mediterranean temporary ponds (C16b), standing and running waters (C1 + C2), helophyte beds (Q5), volcanic fields (H61), rocky grasslands (R14),
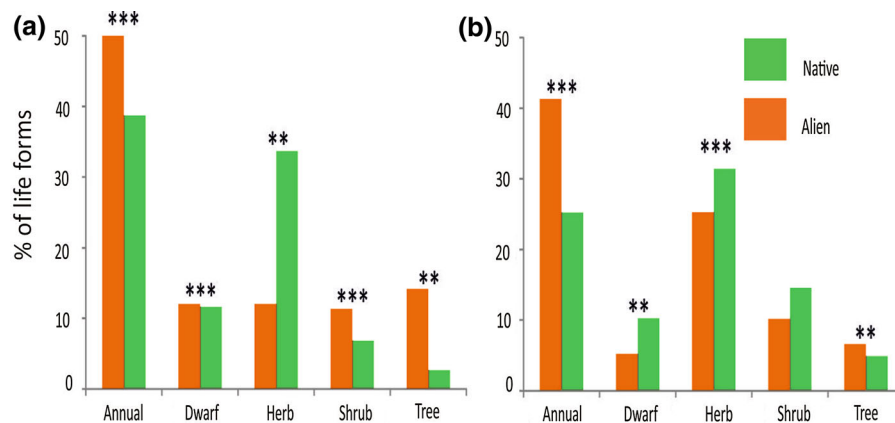
Fig. 2 **a** Percentage of life forms in alien and native species pools and **b** their relative frequency across plots in the resampled dataset. Asterisks indicate significant differences (Wilcoxon test, ** $p \leq 0.01$, *** $p \leq 0.001$). (standard error of the mean < 1.2%)
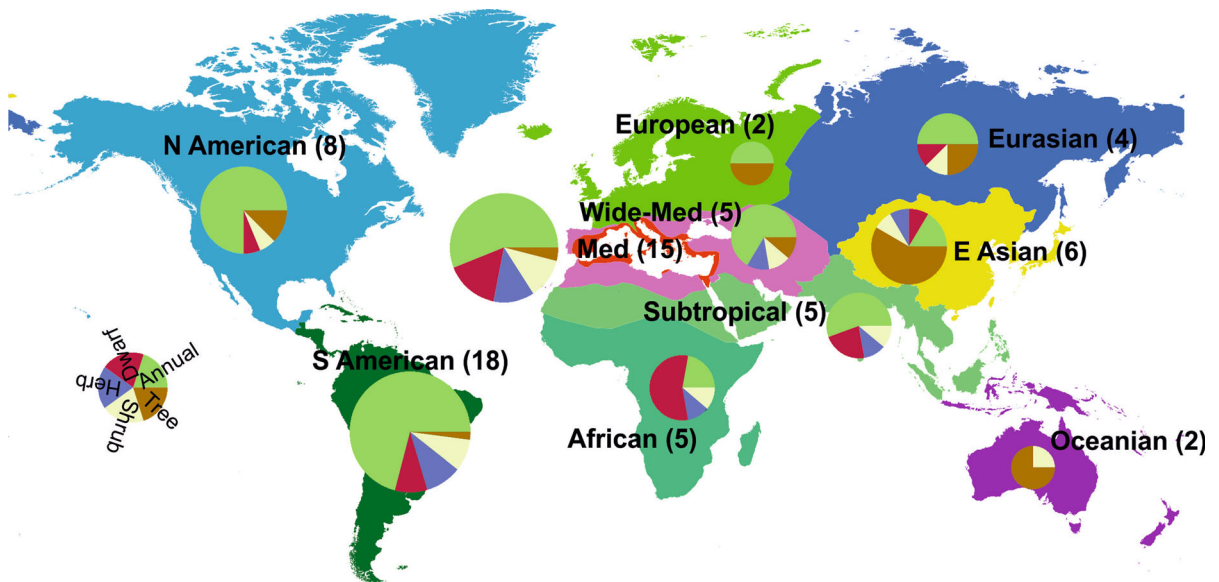

Fig. 3 Origin of alien plants in the Sicilian vegetation. The numbers of species coming from each individual region are reported in brackets. Pie size is related to the number of species contributed by each region. Pie sectors indicate the percentage frequency of the life forms of alien species from a given biogeographic region in the dataset (note that some species are represented by more than one life form)

rangelands (R1D), nutrient-poor annual dry grasslands (R1R), mountain grasslands (R4), hedgehog-heaths (S74), beech forests (T17+T18), poplar and birch forests (T1D), black pine forests (T37) and Mediterranean thermophilous deciduous forests (T1A). Also, the vegetation of coastal cliffs (N32), annual communities of shallow soils (R1F), thermomediterranean arid scrub (S54), garrigue and phrygana (S6 + S72) and lowland pine forests (T3A) were almost totally free from alien species.

Origin

The alien species with a Mediterranean origin were significantly ($p < 0.05$) underrepresented in man-made habitats (V1–V39), riparian thickets (S93 + T14), herbaceous vegetation of coastal dunes (N12–N16) and saltmarshes (A25d). In contrast, they were significantly overrepresented ($p \leq 0.01$) in the Mediterranean perennial dry grasslands (R1E), coastal cliffs (N32) and coastal dune thickets (N1B+N1G).

Fig. 4 Flowering phenology of alien and native species pools. Asterisks indicate significant differences (Wilcoxon test, **$p \leq .01$; ***$p \leq .001$)
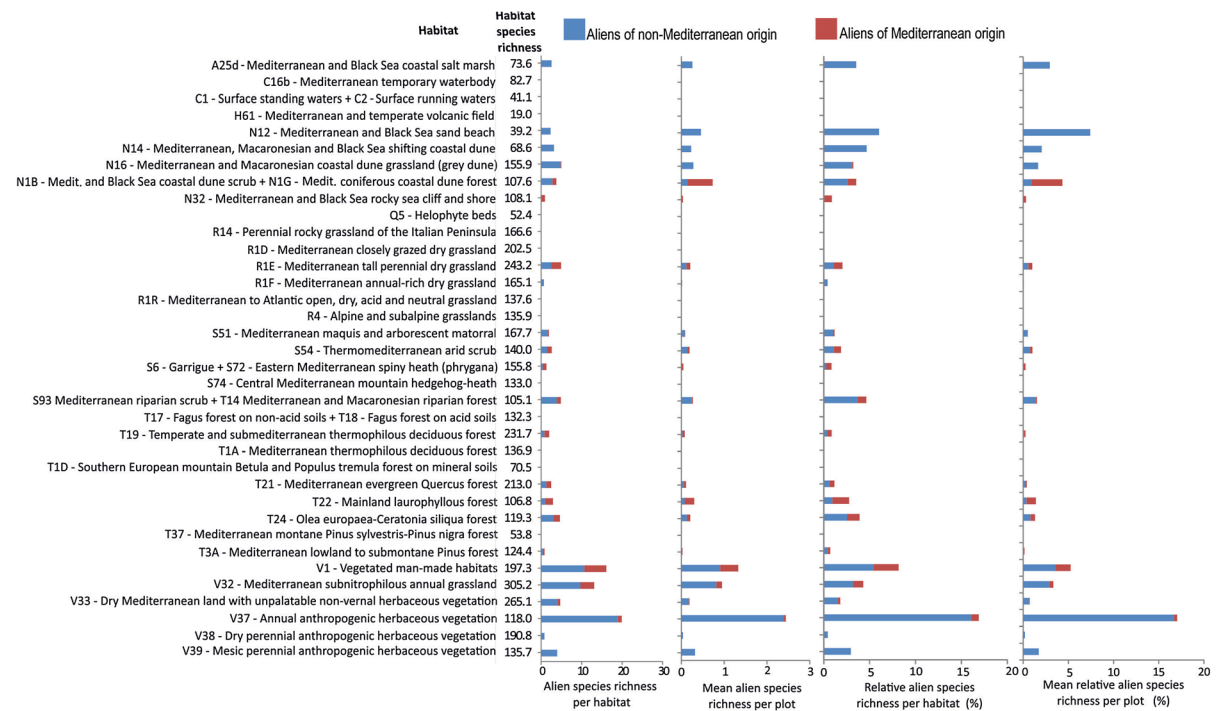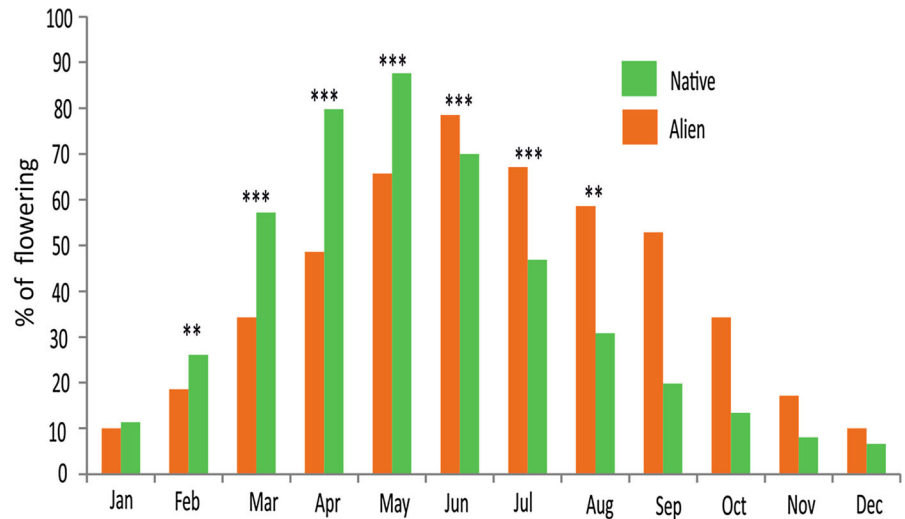

Fig. 5 Alien species richness per habitat type calculated by rarefaction for 34 plots and four different measure of the level of invasion (alien species richness per habitat, mean alien species richness per plot, relative alien species richness per habitat and mean relative alien species richness per plot)

The South American species were represented in 11 different habitats, but they were significantly ($p < 0.01$) prevalent only in man-made habitats (V1–V37), with 15 species recorded, 12 of which were exclusive.

The pattern of the North American species is comparable to that of the South American ones because they were recorded in 13 habitats. However, only three species were strongly related to man-made habitats (V1–V37). The rest of the species were related

to sandy coasts (particularly N12 and N1B) and Mediterranean arid scrub (S54).

Despite accounting for only five species, the African species were represented in 12 different habitats, with a strong affinity to coastal sand dunes (N14 and N16) and man-made habitats (V1 and V32).

The European species were the least well-represented in the alien species pool (2 species and 0.9% of all occurrences) and mostly related to *Quercus pubescens* woods (T19). The Eurasian species (4 species) were mainly related to riparian thickets (S93+T14).

The Oceanian species (2 species) were strongly related to coastal grey dunes (N16, N1B). The Subtropical species (5 species) were most related to the beach driftline (N12) and perennial dry grasslands (R1E).

Life forms

The proportion of life forms in the alien species pool differed among habitat types (Fig. 6): annuals were most related to man-made habitats (V1–V37) and coastal sandy vegetation (N12, N14); trees to riparian

thickets (S93 + T14); shrubs to coastal dune scrub and forests (N1B+N1G) and *Olea-Ceratonia* forests (T24); herbs to perennial dry grasslands (R1E), laurophyllous forests (T22) and man-made habitats (V1, V32); dwarf shrubs to coastal dunes (N14, N16), perennial dry grasslands (R1E) and evergreen shrublands (S51, S54).

Discussion

Our results show that the distribution and frequency of alien species vary across Sicilian habitat types and are not correlated with the native species pools (Fig. 5). Rejmánek (1989) suggested that plant communities in mesic environments seem to be more prone to biological invasions than those in xeric environments. However, in contrast with this 'mesic hypothesis', the percentage frequency of alien species in the natural habitats of Sicily did not show significant differences between the habitats exposed to a prolonged and intense summer drought and those where microclimatic and edaphic conditions buffer the summer drought stress. Absence or infrequent occurrence of
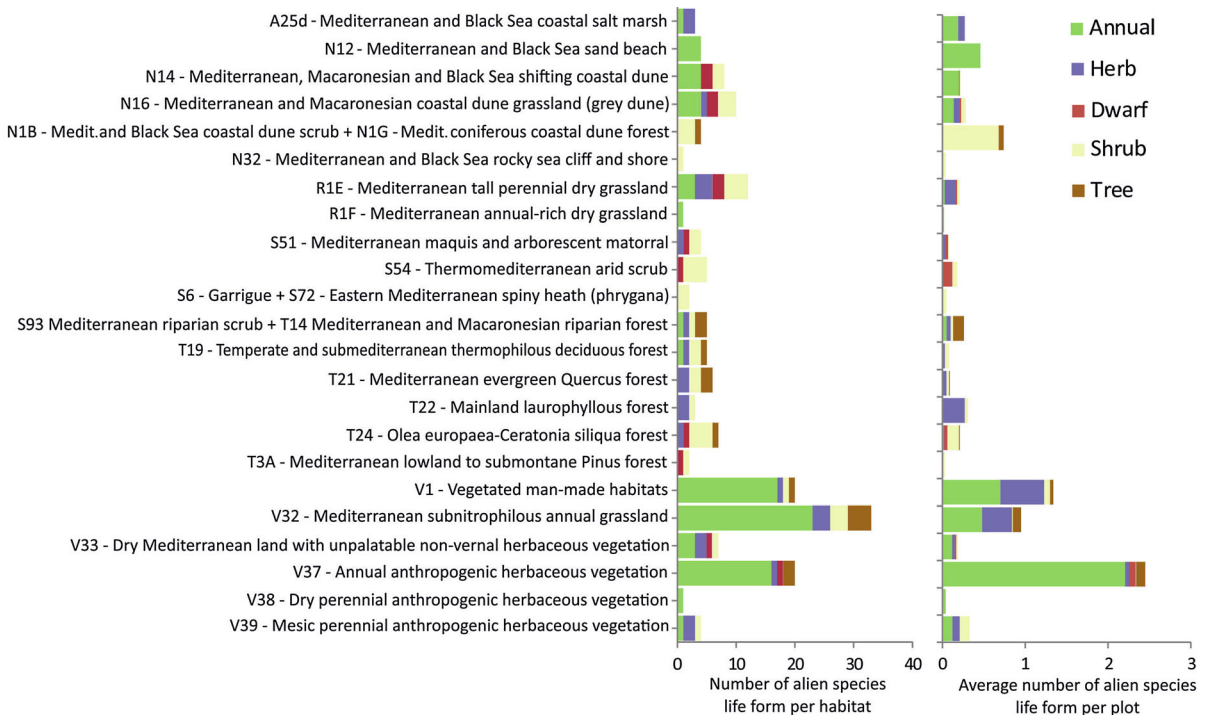

Fig. 6 Life forms of alien species per habitat type. The absolute number of aliens in the species pool, the percentage of aliens in the species pool and the mean number of aliens per plot are shown (only the habitats with at least one alien species are included)

alien species (occurrence frequency < 2%; Fig. 5) were found not only in dry habitats with nutrient-poor soils but also in mesic and very wet habitats. Similarly, the scarcity of alien species pertained not only to the typical Mediterranean evergreen forests but also to mesophilous deciduous forests and shrublands of Sicily. It must be noted, however, that the number of alien species occurring in a given habitat does not relate to the severity of the invasion in that habitat. Some habitats are invaded by few (or single) species, which attain a high cover, transforming the whole ecosystem.

Not surprisingly, highly conservative and stable habitats with constantly low levels of nutrient availability, such as coastal cliffs (N32) and rocky grasslands (R14), were characterized by the absence or low proportions of alien species (compare Cao Pinna et al. 2021), although some of these can be highly invasive, e.g. *Opuntia* spp. and *Cenchrus setaceus*. More unexpected is the observation that low proportions of alien species were also recorded in habitats that in temperate ecosystems are more prone to plant invasions, such as the thermophilous deciduous forests (T19, T1A) and even in disturbed habitats, such as the closely grazed dry grasslands (R1D) and the dry-mesic perennial anthropogenic vegetation (V38–V39). There are different possible explanations of these unexpected patterns that are partially different from what was observed in the corresponding habitats of the temperate zone (Chytrý et al. 2008). In the case of the thermophilous deciduous forests (Guarino et al. 2015) and beech forests (Brullo et al. 1999), Sicily represented a refuge area during the coldest phases of the Pleistocene (Guarino and Pasta 2018). At present, the persistence of plant communities typical of temperate or submediterranean ecosystems in isolated areas on the Sicilian mountains could make the arrival and establishment of alien species more difficult.

In the case of rangelands and perennial anthropogenic vegetation, a possible explanation is that having lumped the archaeophytes with native species in our dataset, the long-lasting occurrence of archaeophytes in centuries-old cultural landscapes became undetectable. It could be that archaeophytes saturated the empty niches created by disturbance, thus leaving little space for neophytes in these ancient man-made habitats. Moreover, the long-lasting pastoral activities led to nutrient depletion and soil impoverishment, which may hinder the alien species establishment in

the Mediterranean rangelands (Ambarlı et al. 2018; Guarino et al. 2020). Additional evidence that low nutrient content can reduce the incidence of invasive plants is provided by intentional nitrogen impoverishment carried out by restoration practitioners in grassland systems of temperate Europe (Török et al. 2014). Conversely, nutrient addition (Burke and Grime 1996) and fluctuating nutrient availability (Davis et al. 2000) can facilitate the alien plant invasion in (semi-)natural grasslands.

As far as coastal dunes are concerned, although the number of aliens in the regional species pool is substantial, their frequency in vegetation plots from the Mediterranean Region tends to be lower than along the Atlantic and Black Sea coasts (Campos et al. 2004; Giulio et al. 2020). In accordance with previous studies (Acosta et al. 2006), our results confirm that the most frequent alien species on coastal sands are: (1) fast-growing annuals with prolific seed sets, such as *Dactyloctenium aegyptium* and *Xanthium orientale*, which mainly occur on beach driftlines (N12), and (2) clonal perennial succulent species, such as *Carpobrotus edulis* and *C. acinaciformis*, mostly related to sand dunes (N14 and N16). In coastal dune scrub (N1B), the proportion of woody species, such as *Acacia saligna* and *Eucalyptus camaldulensis*, frequently also planted for dune fixation, increases as well.

In contrast to coastal sandy habitats, Mediterranean saltmarshes (A2.5d) could be less prone to alien plant invasion than those on the other European coasts due to the higher mean salinity of the Mediterranean Sea and sharply contrasting salt concentration between dry and wet seasons, which requires specific morphological and physiological adaptations (Rogel et al. 2000; Pennings et al. 2005). Similarly, the trophic and thermic seasonal fluctuations of the Mediterranean (temporary) inland waterbodies (C1.6b, C1 + C2) could be the reason for the minor incidence of alien species compared to temperate Europe, even though this might not apply to artificial waterbodies (Naselli Flores and Marrone 2019).

As expected, the highest proportion of alien vascular plants was detected in periodically disturbed habitats with intermittent increases in nutrient availability (Davis et al. 2000; Chytrý et al. 2008; Viciani et al. 2020). This is particularly the case of the anthropogenic annual vegetation (V1–V37), which was by far the richest both in the number and occurrences of alien species, with the maximum

values in the weed vegetation of irrigated summer crops (V37).

Origin

Because of the strong environmental filtering by the Mediterranean summer drought, highly successful species in the alien species pool of Sicily did not include those originating from Eurasian or European temperate regions. Also, invasions in plant communities with seasonally oscillating water availability can be dependent on different water relations and resource-use dynamics of invasive vs native species in response to water deficits (Caplan and Yeakley 2010; Funk 2013). The alien species with a Mediterranean origin were not particularly invasive in the studied habitats, as their morpho-physiological adaptations and resource-use efficiency have evolved in environmental conditions similar to those of native species (Galán Díaz et al. 2021). Instead, the subtropical region of the Old World provided several successful species, most of them highly specialized, being widespread in the Sicilian beach driftlines and gravelly riverbeds (*Dactyloctenium aegyptium*) and perennial dry grasslands (*Boerhavia repens* and *Cenchrus setaceus*). In particular, the alien *Cenchrus setaceus* can replace the native *Hyparrhenia hirta* in the dominance of perennial grasslands at stony sites near the coast (D'Amico and Gianguzzi 2006; Pasta et al. 2010).

The recurrence of African species in many different habitats is due to *Oxalis pes-caprae*, which was the most frequent alien in our dataset. The affinity of the African species to coastal dunes is due to *Carpobrotus acinaciformis, C. edulis* and *Solanum linneanum*. The original habitat of these species are coastal sands and rocky grasslands of the Cape Region (Goldblatt and Manning 2000), and they colonized sites with ecological conditions similar to those of their ancestral niche all over the Mediterranean-climate regions in the world (Santoro et al. 2011).

South America gave an important contribution to the Sicilian weeds because *Amaranthus deflexus, A. muricatus, A. viridis, Datura stramonium, Erigeron bonariensis, E. sumatrensis,* and *Galinsoga parviflora* are some of the most common and typical species in the weed vegetation of hoed crops, with optimum in the late summer-fall season, on sandy or loamy soils (Brullo et al. 2007). However, the present study revealed also the affinity of *Symphyotrichum squamatum* and *Paspalum dilatatum* to coastal saltmarshes of Sicily.

North American also contributed to the Sicilian weed flora, including *Amaranthus blitoides*, *A. retroflexus* and *Erigeron canadensis*. In contrast, *Xanthium orientale* became very common at coastal sites, particularly on beach driftlines and in the proximity of river mouths (riparian vegetation was its second-most preferential habitat in Sicily, after beach driftlines). However, the most significant North American species in the alien flora of Sicily is *Opuntia ficus-indica*, which became one of the most common and typical elements on the warm and dry slopes and in rocky habitats of the Sicilian landscapes, both inland and near the coast (Lo Verde and La Mantia 2011).

Oceania provided only two species to the studied alien species pool: *Acacia saligna* and *Eucalyptus camaldulensis*. Both have been favoured by deliberate plantations on coastal grey dunes since the first half of the twentieth century, threatening many autochthonous woody species typical of coastal grey dunes, such as *Juniperus macrocarpa, Ephedra fragilis, E. distachya* and *Retama raetam* subsp. *gussonei* (Minissale and Sciandrello 2013; Sciandrello et al. 2015).

Life forms

Annuals were largely prevailing in the alien species pool of Sicily because they can adapt very well to the combined effect of seasonal drought and disturbance related to multiple land-use patterns (Goldblatt 1978; Guarino 2006). The ubiquity of annual alien species is also related to the large extent of agricultural areas in Sicily (Brullo and Guarino 2007).

Trees were also significantly over-represented in the alien species pool, both in terms of pool percentage and species frequency across plots. This is the result of extensive tree plantations in coastal sites (particularly with *Acacia saligna* and *Eucalyptus camaldulensis*), but also of reforestation for the consolidation of unstable slopes (particularly with *Ailanthus altissima, Eucalyptus camaldulensis*, *Pinus canariensis*, *P. radiata* and *Robinia pseudoacacia*) and of partly abandoned cultivation (in the case of *Citrus* spp., *Crataegus azarolus, Juglans regia, Malus domestica, Prunus domestica, P. dulcis* and *Pyrus communis*). The over-representation of trees, in terms of relative frequency and species richness, compared to the life

forms of the other alien species, was also reported by Wagner et al. (2017) in the European woodlands.

Phenology

Differences in the flowering phenology between alien and native species can be influenced by climatic conditions and photoperiod in the native distribution range (Godoy et al. 2009a, b), pollination strategy (Fontaine et al. 2006), different responses to disturbances (e.g. drought, cold, fire, see Rathcke and Lacey 1985) and biotic interactions with co-occurring plant species (Ollerton and Lack 1992; Elzinga et al. 2007). We detected different flowering phenology patterns between the groups of alien and native species. Flowering at a different time, i.e. avoiding competition for pollinators with co-occurring native species, could represent an advantage for alien species (Lambdon et al. 2008a; Sargent and Ackerly 2008). Some of the late-flowering alien species in the dataset (e.g. *Echinochloa colona* and *Setaria italica*) are related to irrigated summer crops (Lake and Leishman 2004; Lloret et al. 2005), or to the post-harvest weed vegetation of hoed crops, with an optimum in the late summer-fall season (e.g. *Amaranthus* spp., *Datura stramonium* and *Galinsoga parviflora*). Also, tropical bunchgrasses (*Cenchrus setaceus* and *Megathyrsus bivonianus*) invading dry grasslands and disturbed areas exhibit a later flowering than natives (Godoy et al. 2009a). Additionally, some annual species can have two generations per year in Sicily (e.g. *Erigeron* spp. and *Symphyotrichum squamatum*), one in early spring and one after the rain that marks the end of summer drought. Even if some of the recorded alien perennial species may take advantage from early (e.g. *Calendula officinalis* and *Oxalis pes-caprae*) or late (e.g. *Artemisia* spp., *Boerhavia repens* and *Ricinus communis*) flowering, the majority of them exhibits a long flowering season (*Carpobrotus* spp., *Lycium intricatum, Nicotiana glauca* and *Solanum linneanum*) in Sicily.

Previous studies have shown that alien species, particularly the invasive ones, generally display early flowering or long blooming periods (Goodwin et al. 1999; Lloret et al. 2005; Pyšek et al. 2009). However, our results reveal that there are many aliens blooming later than most of the native species, confirming previous observations from the Mediterranean Region

(Godoy et al. 2009a, b). The relatively mild winters in the Mediterranean offer more opportunities for fruit and seed development of late flowering alien species than the climates at more northern latitudes (Roche et al. 1997), even though longer and late flowering is also contributing to alien plant invasion success in central Europe (Küster et al. 2008).

Caveats

The vegetation plot data processed in this paper were sampled between 1955 and 2015, which does not allow to detect ongoing invasion processes. For instance, the recently observed trend towards naturalization and invasive behaviour by *Eucalyptus camaldulensis* in the pebbly riverbeds of Sicily (Badalamenti et al. 2018) remained undetected in our dataset.

Understanding the transition from non-invasive naturalized to invasive stage of the plant invasion process is important, particularly for those species that recently established in a new habitat. The presence/absence data, as used in our study, accurately portray the adaptability of a given species to different habitats and its relative frequency but they are less suitable for assessing the invasiveness of individual alien species. For example, *Cenchrus setaceus* is highly invasive in the ecological niche occupied by *Hyparrhenia hirta* (González-Rodríguez et al. 2010; Pasta et al. 2010). Since many *Hyparrhenia*-dominated dry grasslands still occur where *Cenchrus* has not yet arrived in Sicily, our data do not reflect the extent and severity of the ongoing invasion. If the scope is to analyse the invasiveness of individual alien species, the use of cover values and diachronic studies would be recommendable.

Last but not least, the vegetation plots of our dataset were collected for the purposes of phytosociological classification (Chytrý et al. 2016). Phytosociologists tend to avoid some habitat types, such as linear features and heterogeneous habitat mosaics, especially in anthropogenic ecosystems. These habitats host not-easy-to-classify vegetation with highly stochastic species composition, but they can be preferential habitats for some plant species, especially alien. Therefore, we cannot exclude that some alien species may have been underrepresented in our dataset.

Conclusions

Our results provide new evidence to already known general trends: (1) in small-scale vegetation plots, native and alien species richness are not related (Knops et al. 1997; Naeem et al. 2000; Hector et al. 2001; Landi et al. 2020), even if at regional scale native and alien species richness tends to be correlated (Levine and D'Antonio 1999; Levine 2000; Sax 2002; Stohlgren et al. 2003); (2) the most successful invasive species in Sicily come from climatically similar biomes (Cao Pinna et al. 2021) and tend to have an earlier, later or longer flowering period than native species (Pyšek et al. 2009; Godoy et al. 2009a, b); (3) man-made habitats harbour more alien species than any natural habitat type (Chytrý et al. 2005, 2009; Cadotte et al. 2006; Arianoutsou et al. 2010; Kalusová et al. 2017; Viciani et al. 2020); (4) naturally disturbed riverine habitats offer many temporarily vegetation-free areas to the establishment of alien species (Tickner et al. 2001; Richardson et al. 2007; Schnitzler et al. 2007; Liendo et al. 2016); (5) sandy coasts are also quite prone to colonization by alien species (Chytrý et al. 2008; Giulio et al. 2020). Except for these last three habitats, the investigated Sicilian habitats were colonized by very few alien species or completely lacking them, although lower proportions of alien species do not prevent some of these to exert the most severe environmental impacts, particularly in habitats with limited resources. Some of the alien species recorded in this study are still in a phase of rapid expansion. Three of these (*Acacia saligna*, *Ailanthus altissima* and *Cenchrus setaceus*) are listed in the EU Regulation 1143/2014 among the invasive species of European Union concern and possibly some more will be added in the near future, considering that many recent references (mentioned in the introduction to our study) suggest an accelerating trend of biological invasion in the Mediterranean Region.

The habitat-based approach adopted here is a suitable procedure to assess, at a regional scale, the level of invasion of different habitats (Pyšek and Chytrý 2014). Risk assessment, monitoring and management of alien plants can benefit greatly from information on the identity of receptor habitats.

Declarations

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