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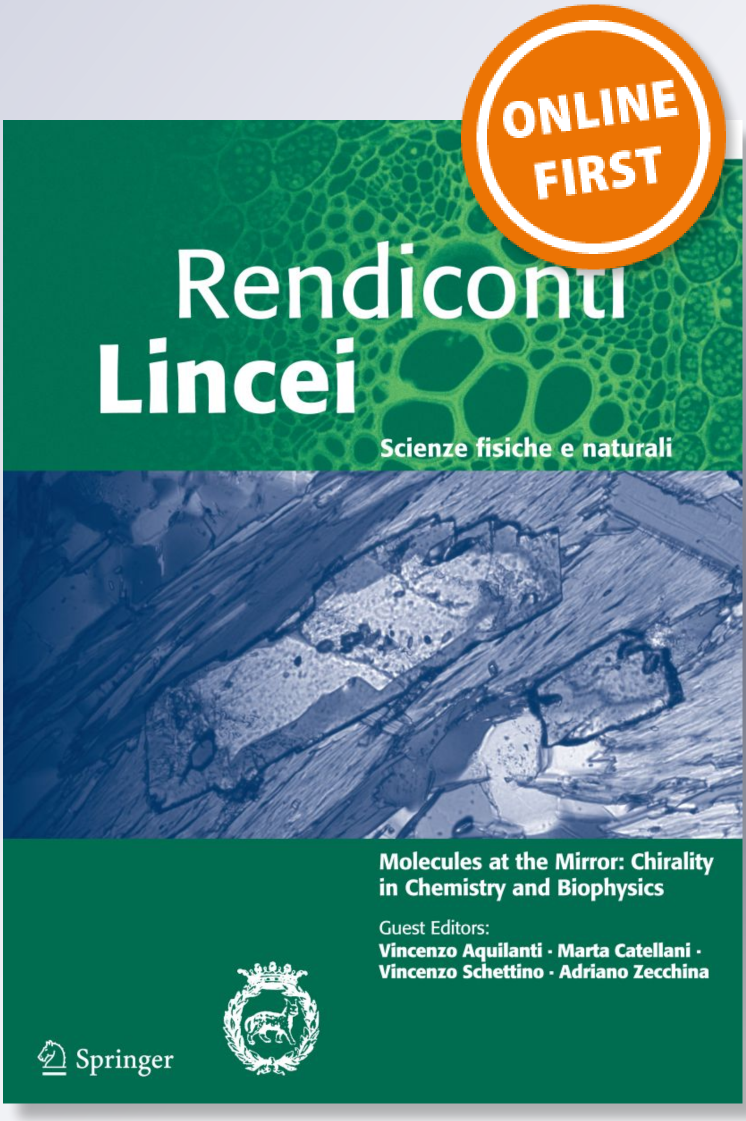

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Human disturbance, habitat degradation and niche shift: the case of the endemic *Calendula maritima* Guss. (W Sicily, Italy)

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Abstract *Calendula maritima* Guss. is a plant endemic to the coastline of W Sicily, whose distribution range experienced a dramatic shrinkage during the last centuries along with the degradation and fragmentation of the associated plant assemblages. According to that, it can represent an effective target species to test the response of coastal biota to anthropogenic disturbance. In order to better understand the niche width of *C. maritima*, the coastal plant communities in which it is still found have been investigated through vegetation relevés carried out on different size plots. Although the sea marigold has been considered as a pioneer species typical of shifting dunes, field investigations highlighted that it also occurs in different plant assemblages. Data concerning the smaller plots allowed the identification of three groups of relevés: one showing the highest number of trivial ruderal plants, another hosting some psammophilous species, and a third linked with rocky surfaces. These three groups do not cluster with the relevés issuing from literature, carried out some 40 years ago, that mostly focused on dune ecosystems. It is assumed that the strong floristic differences between these two different types of relevés may be linked with the destruction of shifting dunes occurred over the last decades, and which also caused the local extinction of many other plants related with this habitat. However, this could also reflect a lack of historical relevés concerning *C. maritima* populations growing on coastal rocky sites. Interestingly, a gradual expansion of the niche of *C. maritima* was highlighted, likely depending on the ability of the species to colonize new plant communities in response to increasing anthropogenic disturbance. Our results also confirm that hybridization with the contiguous congener species *Calendula fulgida* Raf. may represent a major threat for conservation of the remnant populations of *C. maritima*.

Keywords Coastal habitats · Extinction risk · Mediterranean islands · Taxonomic homogenization · Vegetation dynamics

1 Introduction

Coastal plant communities are among the most affected by human disturbance all over the world, being threatened with destruction, fragmentation, degradation and biological invasions (Lotze et al. 2006). Bierwagen (2007) pointed out that aggregated or continuous habitats are the most vulnerable to connectivity loss: thus, considering their peculiar geometry and location, coastal plant communities are intrinsically prone to disruption. Moreover, Schleicher et al. (2011) pointed out that also plants which are well adapted to tolerate anthropogenic disturbance may encounter dispersal problems when their populations are increasingly scattered and suitable habitats are more and more fragmented. These general considerations are still

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valid when applied to the specific case of the rocky and sandy shores of Trapani province (W Sicily), which host nearly 30 endemic, rare and/or endangered vascular plants (Raimondo et al. 2011). Among them, *Calendula maritima* Guss., the sea marigold, is a narrow endemic to Western Sicily and it is listed amongst the 50 most threatened plants of the Mediterranean islands (Troìa and Pasta 2005, 2006). Owing to that it could be considered a good target species to assess which is the response of endangered species to enduring coastal habitat perturbation.

Literature and herbarium data testify the ongoing reduction of the distribution range of *C. maritima*, whose outmost populations became extinct (e.g. San Vito Lo Capo, Monte Cofano, Favignana) or experienced a strong rarefaction (Isola Lunga) during the last two centuries (Fig. 1). Besides, recent field surveys, aiming at assessing the present risk level of remnant *C. maritima* populations, pointed out that the species is severely threatened with extinction due to habitat destruction and fragmentation, to the small size of many remnant populations, and to the ongoing introgression with *C. fulgida* Raf., another Sicilian endemic marigold. As concerns this latter issue, recent studies (Plume et al. 2015) pointed out that although the hybrids between the two species show a low reproductive fitness, nonetheless they are able to colonize the most disturbed habitats, where they may outcompete *C. maritima* within the next few decades. Notwithstanding the increasing interest on interactions among congeners, recent researches focusing on the comparison of species pairs sharing the same traits (see Lavergne et al. 2004; García-Serrano et al. 2007; Dostál 2011 and references therein) did not manage to explain why some of them are narrow endemics and others are invasive and/or have a wide distribution range and an even wider ecological niche (Landi and Chiarucci 2014). Congener species may avoid competition, thanks to trait divergence and indirect interactions (Beltrán et al. 2012); nonetheless, as introgression mechanisms may involve all the populations of narrow endemics, hybridization represents a serious threat for their survival (Rhymer and Simberloff 1996; Oberprieler et al. 2015).

The overview of the phytosociological literature on the perennial marigolds points out the wide ecological spectrum of the species complex. Four taxa, i.e. *C. fulgida*, *C. maritima*, *C. suffruticosa* subsp. *algarbiensis* and

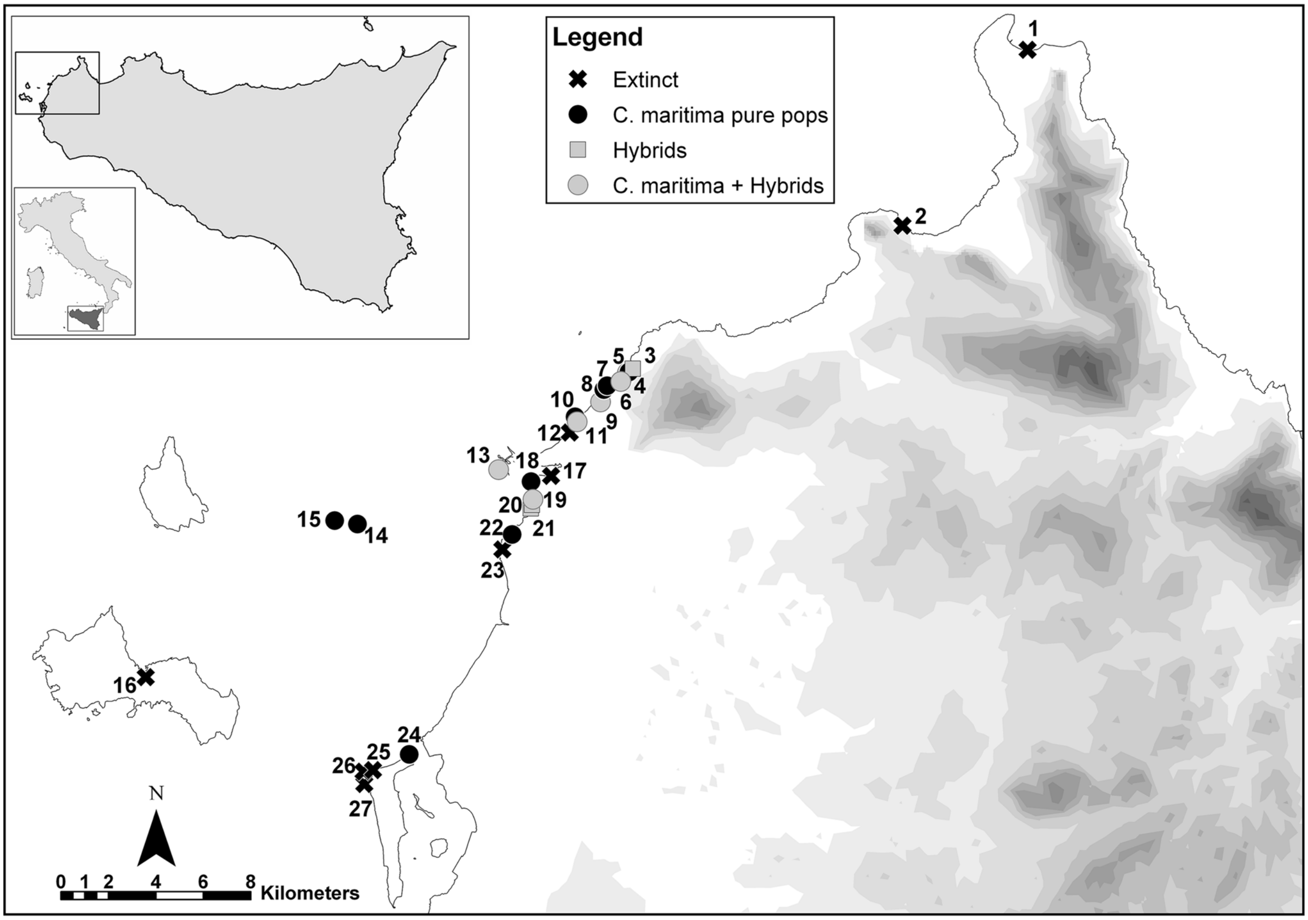

Fig. 1 Distribution range of all the extinct and extant populations of *C. maritima* Guss.

C. suffruticosa subsp. *lusitanica*, may occur in 4–6 different habitats, living not only within the plant communities typical to sandy and rocky coastlines but also taking part in the early stages of climatophilous vegetation series such as grasslands and shrubberies. According to the earliest published vegetation data including *C. maritima* (Frei 1937; Perrone 1964; Brullo and Di Martino 1974), this species was considered strongly linked to sand shores. This opinion was also followed by Brullo et al. (2001): describing the new association *Elytrigio athericae–Calenduletum maritimae* from Isola Lunga, these authors stated that the sea marigold is typical to the perennial vegetation of the shifting dunes, referred to the phytosociological class *Ammophiletea*.

With regards to that, to better understand if the *C. maritima* really experienced a niche shift or its ecological requirements were poorly studied in the past, in this paper we investigated through vegetation relevés the characteristics of all coastal plant communities hosting the target species. Moreover, we also tried to assess whether and to which extent the co-occurrence of hybrid marigolds could interfere with its present abundance cover in the aim to evaluate if introgression might hamper the survival of *C. maritima* in the medium and long term.

2 Materials and methods

2.1 Data sources and input procedures

Field surveys were carried out to identify remnant populations. A total of 145 phytosociological relevés (Braun-Blanquet 1932) including *C. maritima* was stored by means of TURBOVEG software (Hennekens and Schaminée 2001). Among them, 27 were issued from literature (Frei 1937; Perrone 1964; Brullo and Di Martino 1974) or unpublished surveys carried out between 2006 and 2011 by several colleagues (see acknowledgements), and had an area between 10 and 70 m^2; the remaining 118 relevés were carried out in the field by S. Pasta during spring 2012. To better understand the overall niche of *C. maritima,* we decided to make two series of relevés on plots with a different size: the smaller ones (104 relevés, size 1–4 m^2) were centered on single *C. maritima* nuclei in order to check the plants which really co-occur with the sea marigold; the larger ones (14 relevés, size 20–50 m^2) were considered to be more representative of the general context at landscape level.

A total of 111 infrageneric taxa were included in the data set (see online Appendix 1); their nomenclatural treatment follows Conti et al. (2005), with the exception of *C. maritima* Guss. and *C. fulgida* Raf., here reported as species instead of being treated as subspecies of *C. suffruticosa* Vahl, like many other authors (e.g. Nora et al. 2013) do, too.

2.2 Spatial ordination and classification

Vegetation data were imported in Juice 7.0 software (Tichý 2002). Subsequently, a modified Twinspan classification (Roleček et al. 2009) was run for the smaller and the larger plots (size plots A and B, respectively) alike to assess the optimal number of clusters identified according to classification crispness (Botta-Dukát et al. 2005). The two size plots were analyzed separately with the aim to verify any similarity between and among the identified groups of the same and the different size order.

Furthermore, a NMDS ordination was carried out through square root transformation. Downweighting of the rare taxa was performed through R Vegan package (Oksanen et al. 2009). The distance between the relevé groups was also performed through U Mann–Whitney analysis by using Sørensen similarity; once again the data were transformed as square root and all available distances were taken into account.

Diagnostic plants of each group were determined using the φ coefficient, which indicates the fidelity of a given taxon to a particular group (Sokal and Rohlf 1995; Chytrý et al. 2002). Only taxa with a φ coefficient higher than 0.30 and a probability of the observed pattern of occurrence under random expectation lower than 0.01 (Fisher's exact test) were considered to be diagnostic for each group. Constant taxa were defined as those with a frequency >30% within the vegetation unit. Dominant plants were defined as those occurring in at least 10% of all the relevés of a vegetation unit with a cover value >25% (Landucci et al. 2013).

To investigate the taxonomic diversity within the groups of relevés, the α-diversity value of each group was calculated as mean species richness by plot, while β-diversity was evaluated through the Sørensen index (number of iterations: 100; method: bootstrap; data transformation: square root). All the analyses were implemented by means of Juice 7.0.

2.3 Ecological interpretation of species cover patterns

When plant communities are difficult to interpret due to intense habitat disturbance, ascribing each co-occurring species to a single phytosociological class may help to assess the ecological niche of a given target species, like *C. maritima* in our study. To evaluate the meaning of any cover differences, all the taxa were a priori ascribed to a single phytosociological class according to Rivas-Martínez et al. (1999), Biondi et al. (2012), Mucina (2016), and the authors' peer opinion (see online Appendix 1). Four classes, i.e. *Ammophiletea* (=vegetation of white and grey coastal sand dunes), *Crithmo-Staticetea* (=chasmophytic coastal vegetation under salt-spray influence), *Cakiletea maritimae* (=strandline-dwelling, short-lived nitrophilous vegetation) and *Papaveretea rhoeadis* (=annual, herb-rich ruderal and segetal communities) were the most represented, while other classes such as *Lygeo Stipetea* (=Mediterranean steppes, pseudo-steppes and perennial grasslands), *Saginetea maritimae* (=dwarf pioneer vegetation populating loamy and sandy soils in habitats under salt-spray influence), *Stipo-Trachynietea distachyae* (=Mediterranean terrestrial plant communities dominated by annual low-grown herbs), etc. (see online Appendix 1) counted very few taxa and were not considered in further analyses. Moreover, we compared the estimated mean cover values of all taxa corresponding to both group series using transformation standards for each plot. Cover estimates among groups were compared with the non-parametric Kruskal–Wallis test. The cover values of both *C. maritima* and *C. maritima* × *C. fulgida* hybrids, which are rather safe and easy to recognize, were considered separately in order to avoid biases during data elaboration.

Moreover, we searched for clues on the ecology of the nearest relatives of *C. maritima*, the so-called "*suffruticosa-incana*" species complex (Nora et al. 2013), by consulting the available phytosociological literature (Brullo and Signorello 1989; Ladero et al. 1991; Brullo et al. 1998; Costa et al. 1998, 2000, 2001, 2004, 2005, 2011; Rivas-Martínez et al. 1999; Capelo et al. 2000; Pinto-Gomes et al. 2007).

3 Results

3.1 Floristic composition of the plant assemblages

Modified Twinspan analysis allowed splitting the 1–4 m^2-wide plots into 3 groups. The maximum dissimilarity (0.632) was found between group *A1* and groups *A2*–*A3* (Fig. 2). The analysis of the >10 m^2 relevés allowed the identification of two main groups (*B1* and *B2*), with a dissimilarity of 0.636. NMDS ordination shows a clear separation between the identified groups *A1*, *A2* and *A3*, all of which largely overlap with group *B2*. Group *A1* appears to be rather marginal, while group *B1* (with plots mostly corresponding to the relevés carried out more than 40 years ago) is clearly isolated. The Mann–Whitney U analysis (Table 1), used to detect the similarity between the relevé groups, confirms the results of the ordination: group *B2* is similar to group *A2* (percentage difference = 27.81, *p* value <0.001) and to group *A3* (percentage difference = 35.87, *p* value <0.001), while it is rather different from group *A1* (percentage difference = 58.83, *p* value <0.001). Once again, group *B1* seems to be different from all the other groups (Table 1; Fig. 2). Among the groups with a surface comprised between 1 and 4 m^2, groups *A2* and *A3* are the most similar and appear to be quite different from group *A1*. Table 2 provides an overview of the diagnostic, constant and dominant plants of each detected plot group. Several plants which are exclusive to group *A1*, such as *Euphorbia peplus, Oxalis pes-caprae* and *Thapsia garganica* subsp. *garganica* are typical to ruderal communities. Group *A2* includes several psammophilous plants, such as *Cakile maritima*, *Centaurea sphaerocephala*, *Matthiola tricuspidata* and *Pancratium maritimum*, together with many ruderal plants (*Anisantha* spp., *Cynodon dactylon*, *Echium plantagineum*, and *Scolymus hispanicus*). In group *A3* several salt-tolerant taxa linked to rocky shores (e.g. *Daucus carota* subsp. *drepanensis* and *Hyoseris taurina*) are intermingled with some ruderal and nitrophilous plants typical to disturbed places. The two nitrophilous and

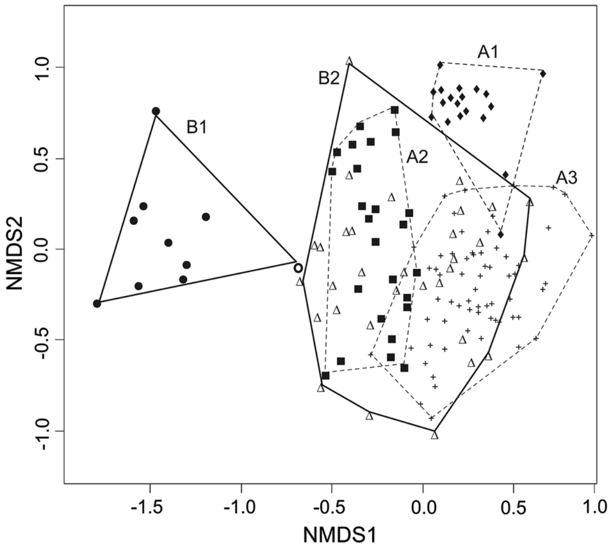

Fig. 2 NMDS plot (first and second axis) of the vegetation relevés considered in this study. The *broken lines* bound the five groups identified by TWINSPAN; the *continuous lines* refer to the plots whose surface is >10 m^2, the *dashed ones* the 1–4 m^2-wide ones. As for Group B1, the *full circles* correspond to 9 relevés done before 1974, the only *empty one* refers to a relevé carried out after 1974

Table 1 Mann–Whitney *U* test comparison among groups implemented in Juice software

	Z				
	A1	*A2*	*A3*	*B1*	*B2*
% Dissimilarity					
A1	–	17.57	35.49	16.15	18.14
A2	69.19	–	25.43	18.31	9.62
A3	76.29	49.44	–	35.72	20.68
B1	99.95	93.66	99.15	–	19.81
B2	58.83	27.81	35.87	82.05	–

For all analysis *p* value is <0.001

Table 2 Diagnostic, constant and dominant plants of the vegetation groups *A1* to *B2*

Plot area (m^2)	1–4			>10	
Group	*A1*	*A2*	*A3*	*B1*	*B2*
Nr of relevés	18	24	62	10	31
α-Diversity	9.1 ± 2.19	9.45 ± 2.58	7.30 ± 1.97	10.00 ± 5.19	12.09 ± 3.75
β-Diversity	0.36 ± 0.037	0.50 ± 0.026	0.58 ± 0.017	0.49 ± 0.083	0.63 ± 0.025
Diagnostic taxa	*Allium commutatum* 0.85, *Calendula* hybr. 0.62, *Galium verrucosum* subsp. *halophilum* 0.58, *Thapsia garganica* subsp. *garganica* 0.55, *Euphorbia peplus* 0.50, *Oxalis pes-caprae* 0.47, *Malva arborea* 0.30	*Anisantha madritensis* 0.45, *Cakile maritima* 0.43, *Cynodon dactylon* 0.41, *Centaurea sphaerocephala* 0.38, *Anisantha sterilis* 0.38, *Echium plantagineum* 0.36, *Beta macrocarpa* 0.35, *Pancratium maritimum* 0.33	*Hyoseris taurina* 0.38, *Euphorbia pinea* 0.35	*Elytrigia juncea* subsp. *mediterranea* 0.67, *Cakile maritima* 0.67, *Euphorbia paralias* 0.65, *Spartina versicolor* 0.65, *Anthemis maritima* 0.57, *Eryngium maritimum* 0.57	*Sonchus oleraceus* 0.64, *Malva arborea* 0.47, *Daucus carota* subsp. *drepanensis* 0.45, *Hyoseris taurina* 0.43, *Plantago macrorhiza* 0.40
Constant taxa	*Calendula maritima 100, Sonchus oleraceus 89, Cynodon dactylon 56, Reichardia picroides 33*	*Calendula maritima 100, Lotus cytisoides 58, Malva arborea 54, Sonchus oleraceus 54, Matthiola tricuspidata 46, Calendula* hybr. *33, Scolymus hispanicus 33*	*Calendula maritima 100, Sonchus oleraceus 63, Malva arborea 58, Beta macrocarpa 50, Daucus carota* subsp. *drepanensis 48, Reichardia picroides 32*	*Calendula maritima 90, Sporobolus pungens 80, Matthiola tricuspidata 60*	*Calendula maritima 97, Lotus cytisoides 48, Matthiola tricuspidata 48, Beta maritima 45, Lotus creticus 42, Reichardia picroides 42, Echium plantagineum 35, Centaurea sphaerocephala 32, Crithmum maritimum 32, Sporobolus pungens 32*
Dominant taxa	*Calendula* hybr., *Malva arborea*	*Calendula maritima, Centaurea sphaerocephala*	*Calendula maritima, Malva arborea*	*Elytrigia juncea* subsp. *mediterranea, Sporobolus pungens, Pancratium maritimum*	*Calendula maritima*

Calendula hybr. plants with clear morphological evidences of breeding between *C. maritima* and *C. fulgida*

The number of diagnostic taxa corresponds to φ value (ranging from 0 to 1), that of constant taxa is the relative frequency (from 1 to 100)

synanthropic species *Malva arborea* and *Sonchus oleraceus* are common within all the three detected groups.

Concerning the larger plots, the most representative species recorded in the Group *B2* are salt-tolerant plants linked to rocky substrata, like *Crithmum maritimum*, *Daucus carota* subsp. *drepanensis*, *Hyoseris taurina*, *Lotus cytisoides*, *Plantago macrorrhiza*. However, several psammophilous species, such as *Centaurea sphaerocephala*, *Lotus creticus*, *Matthiola tricuspidata* and *Sporobolus pungens*, are also common. Group *B1* is characterized by few species strictly linked to sandy shores (e.g. *Cakile maritima* and *Matthiola tricuspidata*) and shifting dunes, such as *Elytrigia juncea* subsp. *mediterranea*, *Eryngium maritimum*, *Euphorbia paralias*, *Pancratium maritimum*, *Spartina versicolor*, *Sporobolus pungens*, etc.

Concerning the >10 m^2 relevés, the α-diversity was higher in those included in group *B2* (12.09 ± 3.75) and the same pattern was observed also for the β-diversity (Table 2). As for the relevés with a surface comprised between 1 and 4 m^2, the α-diversity was higher in Group *A2* (9.45 ± 2.58), while *β*-diversity decreased from group *A3* (0.58 ± 0.017), to groups *A2* (0.50 ± 0.026) and *A1* (0.36 ± 0.037) (Table 2).

3.2 Plant cover and inter-specific competition

The five identified groups showed significant differences in terms of cover rate performed by the plants referred to different phytosociological classes (Table 3). More in detail, the plants referred to *Ammophiletea* (dune habitats), show a significant decrease from group B1 (mean cover

Table 3 Non-parametric Kruskal–Wallis test

	A1	*A2*	*A3*	*B1*	*B2*	χ^2
Phytosociological classes						
Ammophiletea	1.16 (±3.07)	12.25 (±13.36)	0.79 (±1.97)	47.90 (±19.63)	12.40 (±18.90)	66.03
Cakiletea maritimae	0.70 (±1.32)	7.40 (±11.06)	0.83 (±1.38)	7.60 (±7.38)	7.40 (±11.06)	36.05
Crithmo-Staticetea	6.66 (±5.87)	2.29 (±3.40)	8.24 (±9.65)	1.30 (±2.40)	13.60 (±14.91)	34.40
Papaveretea rhoeadis	24.70 (±17.80)	20.37 (±18.61)	22.37 (±18.05)	2.30 (±4.11)	17.60 (±14.86)	24.20
Investigated species						
Calendula maritima	6.66 (±15.50)	21.70 (±22.06)	38.80 (±22.18)	2.10 (±0.87)	25.50 (±23.41)	64.65
Hybrids of *Calendula*	19.40 (±16.30)	1.29 (±2.77)	0.05 (±0.38)	0.00 (±0.00)	2.30(±1.21)	74.49

Differences among Groups *A1*, *A2*, *A3*, *B1* and *B2* in terms of cover performed by the investigated species referred to different phytosociological classes

Numbers represent the percentage cover and the standard deviation; for all analyses p value <0.001

47.90%) to Group *A3* (mean cover 0.79%) where salt-tolerant plants of rocky shores and some ruderals and nitrophilous species abound. Similar trends were observed for the taxa ascribed to *Cakiletea maritimae*, with characteristic species dropping from 7.60% in group *B1* to 0.70% in group *A1*. Groups *A1* and *A3* are dominated by ruderal plants typical to the class *Papaveretea rhoeadis* (mean cover 24.70 and 22.37% for Groups *A1* and *A3*, respectively). The taxa ascribed to the class *Crithmo-Staticetea* (salt-tolerant plants of rocky substrata and psammophilous plants) have a significantly lower cover in group *B1* than in group *B2*. The cover rate of *C. maritima* within the different groups varies significantly (Table 3). The highest abundance value of sea marigold was recorded in habitats where salt-tolerant, psammophilous and ruderal species thrive (groups *A2*, *A3* and *B2*). *Calendula* hybrids also show a significant variation in cover patterns. However, they largely prevail in the plots dominated by ruderals (group *A1*, cover 19.40%), while being totally or almost absent in the communities referred to groups *B1*, *A2* and *A3*, respectively.

4 Discussion

4.1 Ecological meaning of plant assemblages

For the >10 m^2 plots, NMDS analysis allowed the identification of two groups (*B1* and *B2*), the former including all the assemblages linked to sandy shorelines, the latter litho-halophilous ones. Among the clusters identified within the smaller-sized plots, groups *A2* and *A3* overlap with group *B2*, whilst group *A1* appears to be quite different and linked to the most degraded ecosystems, where the ruderal nitrophilous taxa perform a much higher cover rate with respect to psammophilous and litho-halophilous plants. Group *A2* includes the remnant psammophilous assemblages, while Group *A3* mainly consists of lithophilous salt-tolerant communities. The frequency and the co-occurrence of many ruderal nitrophilous plants within groups *A1–A3* (Table 2) suggest that anthropogenic disturbance caused a strong taxonomic homogenization of all local plant communities, a common pattern both in urban (McKinney 2006) and in natural areas (Keith et al. 2009). Overall, the data reported in Tables 2 and 3 emphasize the high impact of human disturbance, outlining the important increase of ruderals that have been able to colonize and even to invade both psammophilous and litho-halophilous communities.

Unexpectedly, our recent relevés pointed out that *C. maritima* occupies a wider ecological niche than previously assumed. In fact, according to their floristic composition, the three groups of relevés *A1*, *A2* and *A3* (Fig. 2) may be referred to at least three different phytosociological classes. Many of the populations located along the coasts of Sicily grow within ruderal assemblages which should be referred to *Papaveretea rhoeadis*. Moreover, these populations still host many psammophilous taxa typical to *Ammophiletea* or share many lithophilous salt-tolerant plants included within *Crithmo-Staticetea*.

On the other hand, we should avow the difference between the sets of historical and recent phytosociological plots may be partially due to their different spatial position rather than to true vegetation change over time (Chytrý et al. 2014; Jiménez-Alfaro et al. 2014). Taking into account this assumption two divergent, or even complementary, hypotheses may explain the observed patterns: (1) *C. maritima* only survived where it was able to escape from disappearing dunes to new human-made communities or to neighboring litho-halophilous assemblages since many sandy shores have been completely destroyed by urbanization, reduced by coastal erosion, and/or degraded and fragmented by human pressure linked to seasonal recreational activities (Bertacchi et al. 2016); (2) the sea marigold

Table 4 Overview on the synecology of seven perennial marigolds of the "*incana-suffruticosa*" species complex

Taxon	Phytosociological classes														
	C–S	SF	P–S	A	OR	C–U	QI	PR	C–P	P–RI	TR	AT	L–S	SG–AC	S–TD
C. maritima Guss.[1]	X	(X)		X				(X)							
C. suffruticosa Vahl subsp. *algarbiensis* (Boiss.) Nyman	X			X	(X)	(X)			X						X
C. fulgida Raf.[1]								(X)	X		X	(X)	(X)		
C. suffruticosa Vahl subsp. *lusitanica* (Boiss.) Ohle							(X)		X	X		X		(X)	
C. suffruticosa Vahl subsp. *maderensis* (DC.) Govaerts			X												
C. suffruticosa Vahl subsp. *suffruticosa*	X											X			
C. suffruticosa Vahl subsp. *tomentosa* (Ball) Murb.									X						

In brackets occasional presence. The following abbreviations refer to different phytosociological classes, whose nomenclature follows Mucina (2016): *A Ammophiletea* Br.-Bl. & R. Tx. ex Westhoff et al. 1946, *AT Asplenieta trichomanis* (Br.-Bl. in Meier & Br.-Bl. 1934) Oberd. 1977, *C-P Cymbalario-Parietarietea diffusae* Oberd. 1969, *C-S Crithmo-Staticetea* Br.-Bl. in Br.-Bl. et al. 1952, *C-U Calluno-Ulicetea* Br.-Bl. & Tx. ex Klika & Hadač 1944, *L-S Lygeo sparti-Stipetea tenacissimae* Rivas-Martínez 1978, *OR Ononido-Rosmarinetea* Br.-Bl. in A. Bolòs y Vayreda 1950, *P-S Pegano harmalae-Salsoletea vermiculatae* Br.-Bl. & O. de Bolòs 1958, *QI Quercetea ilicis* Br.-Bl. ex A. Bolòs y Vayreda & O. Bolòs in A. Bolòs & Vayreda 1950, *SF Salicornietea fruticosae* Br.-Bl. & Tx. ex A. Bolòs y Vayreda & O. de Bolòs in A. Bolòs y Vayreda 1950, *PR Papaveretea rhoeadis* Brullo et al. 2001, *S-TD Stipo-Trachynietea distachyae* S. Brullo in Brullo et al. 2001, *P-RI Phagnalo saxatilis-Rumicetea indurati* (Rivas Goday & Esteve 1972) Rivas-Martínez et al. 1973, *SG-AC Stipo giganteae-Agrostietea castellanae* Rivas-Martínez et al. 1999, *TR Thlaspietea rotundifolii* Br.-Bl. 1948

[1] Nora et al. (2013) treat *Calendula fulgida* and *C. maritima* as subspecies of *C. suffruticosa* Vahl.

has always been adapted to also live on coastal rock outcrops and/or on nutrient-rich soils and areas prone to frequent natural disturbance, but these habitats were neglected by researchers in the past. It is worth emphasizing that group *B1*, which includes only the relevés carried out on well preserved shifting dune communities before the 1980s, is very distinct with respect to all the assemblages where *C. maritima* occurs at present. Indeed, it seems unlikely that the sea marigold was able to perform such a wide niche shift within a few decades. Although the first hypothesis is based on concrete evidences, the second one cannot be discarded at all or, in any events, is complementary to the former one.

The wide ecological spectrum shown by several perennial marigolds of the '*incana-suffruticosa*' complex (Table 4) appears to support our hypotheses. Moreover, the abiotic characteristics of the localities which hosted the extinct populations of *C. maritima* suggest that the sea marigold may have occupied a larger niche also in the past. For example, the rocky coasts near Monte Cofano, where the sea marigold used to live in the past, have never had any sand dunes but small gravelly shores. According to the historical description made by Boccone (1697), the islet of Ronciglio, now incorporated in the southern docks of the port of Trapani, had soil described as "negro, misto di ghiara, terra, alghe, e marciumi di mare" (=brown, made of a mixture of gravel, ground, seaweeds and rotten marine sediments) and further records from the seventeenth and eighteenth centuries also make reference to sea marigolds growing "in glareosis et arenosis maritimis" (=on maritime gravels and sands; Gussone 1843–1844; Ponzo 1905; Béguinot 1924). *C. maritima* was also common on the sandy shores and in the "*Salicornietum*" (perennial chenopod scrub communities referred to *Salicornietea fruticosae*) along the W, NW and N coast of Isola Lunga (Perrone 1964; Di Martino and Perrone 1970), where nowadays the only remnant population takes part in a lithophilous assemblage which should be ascribed to *Crithmo-Staticetea*.

4.2 Community dynamics and diversity

Although the plant communities dominated by *C. maritima* or by hybrid marigolds are similar from a floristic point of view, group A1 seems to include the most disturbed plots, as suggested by the highest cover rates performed by ruderal species. Interestingly, group *A1* is also the one dominated by the hybrid *C. maritima* × *C. fulgida*. This pattern is consistent with the higher disturbance tolerance reported for hybrids (Ellstrand and Schierenbeck 2000; Vilà et al. 2000). In fact, it seems difficult to disentangle the effects of anthropogenic disturbance, plant invasion processes and resource availability. However, *C. maritima* appears to prevail in more resource-limited and less disturbed areas.

A lively debate is going on about the somewhat antagonistic role of disturbance and stress factors on shaping species composition, structure and dynamics of sandy shore plant communities (Wilson and Sykes 1999; Forey et al. 2008; Macedo et al. 2010; Ciccarelli 2015). As concerns our study case, the high number of ruderal and nitrophilous plants that are shared among the groups *A1*, *A2* and *A3* suggests that these plant communities are unsteady either because they are still recovering after the invasion of ruderal taxa or because the frequency of local disturbance and the severity of stress factors continue to favor in turn R- and S-strategists (sensu Grime 2006).

Biotic homogenization, i.e. increasing similarity among communities over time, depends on changes in species composition which may come from both extinction and immigration (Olden et al. 2004; Keith et al. 2009). Both these counteracting processes may have occurred within our plots. As groups *B1* and *B2* include relevés carried out in different years, a comparison between them provides some clues about the ongoing evolution of the habitats hosting *C. maritima*. The higher values of both α- and β-diversity recorded in Group *B2* plots suggest that the latter is more dynamic. Group *B1* includes relevés that were carried out on less disturbed patches of psammophilous communities (now disappeared) that were more homogeneous, species poor and conservative. Therefore, the recorded increase of species richness could be mostly due to the recent income (and/or the ongoing intense turnover) of many ruderal and widespread plants. In the meantime several psammophilous plants became rare and experienced a decrease in terms of cover rate or even disappeared, as a consequence of the destruction and the degradation of local dune ecosystems during the last decades, as recorded elsewhere along Sicilian shores (Sciandrello et al. 2015).

4.3 Conservation measures in the light of an emergent 'widened' niche

The apparently widened niche issuing from our study could affect/resize the policy of conservation measures suggested for *C. maritima*, and have some important consequences on the urgent prioritization suggested for all the target species included for instance in the IUCN 'Top 50' list concerning the most threatened plants growing on the Mediterranean islands (Troìa and Pasta 2006). On the other side, *C. maritima* could be seen as one of the victims of the contradictions laying behind conservation initiatives (Guarino and Pignatti 2010; Guarino et al. 2015): although most of its remnant populations fall within recently established nature reserves, the protection measures alone appear to be unable to preserve the species integrity, because its ecological plasticity and the ongoing breeding processes with *C. fulgida* remained so far unexplored and underestimated.

5 Conclusions

This study provides a quantitative measure of a pattern already observed by other researchers recently coping with *C. maritima* (Grammatico and Fici 2008; Plume et al. 2015). As a mater of fact, the ecological niche of the sea marigold is larger than expected, as this species is able to colonize a wide spectrum of habitats, taking part in rather diverse plant communities and performing higher cover rates when compared with the values recorded on shifting dunes half a century ago. However, well-documented studies recently showed that typical psammophilous plants, such as *Anthemis maritima*, are also able to colonize shingle beaches and sea cliffs (Spanò et al. 2013), while typical chasmophilous salt-tolerant species, like *Crithmum maritimum*, can also live on sandy dunes as well (Ben Amor et al. 2005). In some other cases, habitat selection seems to have driven the evolution of coastal plants: this is the case of *Hyoseris lucida* L., whose type subspecies is typical of sands, while subsp. *taurina* (Pamp.) Peruzzi & Vangelisti only occurs on rocky cliffs (Peruzzi and Vangelisti 2010).

As most part of the life traits of C. *maritima* (i.e. small size, high fecundity, wide dispersal spectrum, eurytopy, tolerance of human disturbance, etc.) are typical of 'winners' (cfr. McKinney and Lockwood 1999) and remind those of alien invasive plants, the recent extinction of nearly all the outermost populations of *C. maritima* from potentially suitable sites is an irrefutable fact which still needs to be explained.

Borrowing the terminology of McKinney (2006), the sea marigold appears to act as an 'urban adapter', but this could not be enough to face 'urban exploiters' such as *C. maritima* × *C. fulgida*, which takes advantage from new ecotones like many other hybrids (Vilà et al. 2000; Ellstrand and Schierenbeck 2000). Therefore, only regular monitoring through permanent plots may allow evaluating whether and to which extent *C. maritima* and *C. fulgida* compete. Floristic and ecological comparisons between these plots will permit understanding if the areas currently dominated by *C. maritima* × *C. fulgida* correspond to the natural evolution of those dominated by *C. maritima*. If so, hybrids may be able to gradually outcompete 'pure' *C. maritima* stands. Hence, the concerns raised by Plume et al. (2015) are legitimate and, what is even worse, any forecast of the speed of species substitution could be underestimated due to the lack of knowledge on the real composition of the local soil seed bank.

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