

Article

Exploring Temporal Trends of Plant Invasion in Mediterranean Coastal Dunes

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Abstract: Alien plants represent a significant threat to species diversity and composition in natural habitats. Nevertheless, little is known about the dynamic of the invasion process and how its effects on native species change over time. In this study, we explored vegetation changes that occurred in invaded coastal dune habitats over the last 10–15 years (2005–2020), particularly addressing impacts on alien and diagnostic species. To monitor temporal trends, we used data resulting from a revisitation study. After detecting overall changes in alien species occurrence and cover over time, 127 total plots were grouped into plots experiencing colonization, loss, or persistence of alien species. For these three categories, we compared historical and resurveyed plots to quantify changes in native species composition (using the Jaccard dissimilarity index) and to measure variations in diagnostic species cover. The number of alien species doubled over time (from 6 to 12) and two species, *Yucca gloriosa* and *Agave americana*, strongly increased their cover (+5.3% and +11.4%, respectively). Furthermore, plots newly invaded appeared to record the greatest changes in both native and diagnostic species. Our results suggest the need for regular monitoring actions to better understand invasion processes over time and to implement effective management strategies in invaded coastal dune habitats.

Keywords: alien plants; coastal dunes; temporal trends; invasion trends; diagnostic species; Mediterranean coast



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1. Introduction

Biological invasion is recognized as an important source of disturbance that threatens biodiversity conservation worldwide [1,2]. The introduction and spread of alien species are strongly connected with the presence of human activities [3,4]. As a matter of fact, the human-related weakening of biogeographic barriers to species dispersal and the acceleration of disturbances have promoted, over the last decades, a considerable expansion of alien species in natural ecosystems (e.g., higher numbers of species covering wider areas) [4,5]. Alien plants that have established self-sustained populations, overcoming abiotic and biotic barriers, can cause severe environmental changes [6–8] and also impact socio-economic assets with consistent economic losses [9].

Despite the increasing number of studies dealing with alien species [10], only a small portion has investigated the process of invasion over time. For the most part, these studies are focused on the short-term effects of invasion; they generally examine a period of one or two years, taking into account a casual moment of the invasion process [10,11]. However, understanding how alien plants perform and affect natural habitats through time is useful

to improve effective management strategies and early warning plans able to define the best time to implement contrast actions [12,13].

The analysis of plant invasion over longer periods has unveiled different ecological processes related to diverse dynamics and long-term effects. Previous studies have identified the years subsequent to the introduction of a new alien species as a fast-changing stage of the invasion process, often characterized by an evident decline in native species diversity [11,14,15]. At the same time, the persistence of the invader over the years can gradually produce important alterations in plant community composition and/or in abiotic conditions, leading to an irreversible detachment from the initial non-invaded natural state (e.g., dominance of alien species, increase in generalist species and in organic matter content) [16,17]. Nevertheless, in those cases in which alien species were no longer found over time, the recovery of native species was a difficult and often incomplete process [15,18]. On some occasions, rather than endorsing the return of native species, the alterations produced by the “lost” invader in natural ecosystems have offered new habitats suitable not only for new alien but also ruderal species [19,20].

Coastal dunes are among the most invaded habitats by alien species in Europe [21,22]. Furthermore, they are recognized as one of the most threatened ecosystems, at both global and European level, mainly due to human-related disturbances (e.g., urbanization, trampling, pollution) [23–26]. The control of alien species is of crucial importance because these ecosystems host highly specialized flora and fauna that provide essential benefits to society, e.g., coastal defense, groundwater storage, and water purification, but also recreation and mental well-being [27–29]. Several factors were proposed to explain the high invasibility of coastal dunes: the strong and diversified abiotic conditions that are reflected in the habitat heterogeneity, the severe anthropic pressure, and the intense propagule pressure [30–34]. Previous studies have documented a negative impact of plant invasion on coastal dune biodiversity, specifically on native and focal species [8,35,36], on soil properties [37–39], and also on functional diversity [40–43]. However, there are very few examples that considered invasion trends over extended periods in Mediterranean coastal dunes. In particular, Del Vecchio et al. [44] described an increase in the level of invasion and an alarming degree of biotic homogenization within a 60-year time span, and Sperandii et al. [45] reported, over a ≈ 15 -year period, different trends in alien plant richness and in the cover of an alien species (*Carpobrotus* sp.) linked to the presence of disturbance. These preliminary findings have suggested the necessity of further studies exploring the ecological process of plant invasion over time.

In this context, the present work analyzed temporal trends of invasion in invaded coastal dune ecosystems of Central Italy over the last 10–15 years, exploring modifications in the occurrences and cover of alien and habitat diagnostic species and in native species composition. To evaluate changes occurring over time, we used data resulting from a revisitation study. Resurveys of historical vegetation plots serve in fact as an efficient tool in the evaluation of medium to long-term alterations in biodiversity and community composition [46,47]. Specifically, in this study we aim to:

- detect changes affecting the occurrence and cover of alien species in invaded coastal dune habitats over the last 10–15 years (from 2005–2008 to 2017–2020);
- analyze different invasion trends through vegetation plots that experienced colonization, loss, or persistence of alien species, with particular emphasis on the impacts alien species may exert on native and diagnostic species.

2. Materials and Methods

The study was carried out on Mediterranean coastal dunes along the Tyrrhenian and Adriatic coasts (Lazio and Molise region, Central Italy). The study area is characterized by a Mediterranean climate and consists of low sandy Holocene dunes that generally occupy a narrow strip along the seashore [48,49]. Coastal dune systems, in well-preserved condition, present a characteristic vegetation zonation influenced by a steep sea-inland ecological gradient with a wide diversification of habitats, from annual communities on

sand beach driftlines to Mediterranean shrubs further inland. However, the littoral in Central Italy has been intensely modified by severe disturbances related to human activities (e.g., urbanization, tourist exploitation, trampling), which have deeply affected the presence of natural communities [50].

2.1. Data Selection

Data were gathered from “RanVegDunes”, an Italian database collecting standardized, georeferenced, and randomly sampled vegetation plots carried out in coastal dune environments and continuously updated [51]. Vegetation was recorded using a square plot of 2 m × 2 m. For each plot, the presence of all vascular species was reported and their cover was estimated using a percentage scale. We extracted a set of 127 vegetation plots (Figure 1), originally sampled between 2005 and 2008 (hereafter T₀) and resurveyed between 2017 and 2020 (hereafter T₁); therefore, after a period of 10–15 years. The position of the plots was relocated using a GPS unit on which the geographic coordinates of the historical data were stored. The 127 selected plots included at least one alien species, present either at the time of the original survey (T₀) or during the resurvey (T₁). Alien species identification conformed to Galasso et al. [52] and only species classified as neophyte (introduced after the year 1500 AD) were considered. Furthermore, according to the European Nature Information System (EUNIS) [53,54], the selected plots were representative of four different EUNIS habitats: N12 (sand beach driftlines), N14 (shifting coastal dunes), N16 (dune grassland), and N1B (coastal dune scrubs).

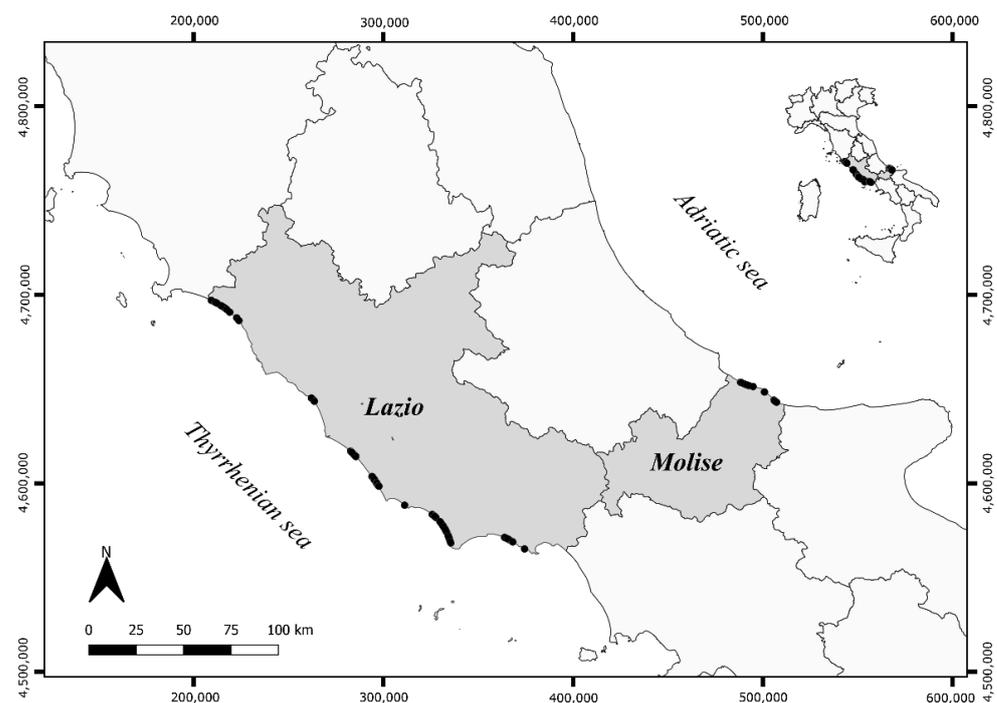


Figure 1. Study area along with sampling plots (reference system WGS84 33N, epsg: 32633).

2.2. Overall Trends in Alien Species

To evaluate vegetation changes in invaded plots over time, we selected (for the two time-points separately) only those plots that presented at least one alien species. Through the above selection, we obtained a subset of 87 invaded plots at T₀ and 91 at T₁ (Figure 2). On this subset, we calculated the total number of alien species, as well as the total number of occurrences and the mean cover of the whole set of alien species for both time periods. For each alien species, we also calculated the occurrence frequency at T₀ and T₁ (Table S1). Additionally, in order to compare the proportional cover of each invader with

respect to the total cover of the whole set of aliens, we used rank-abundance curves for the two time-points (R package “BiodiversityR”) [55].

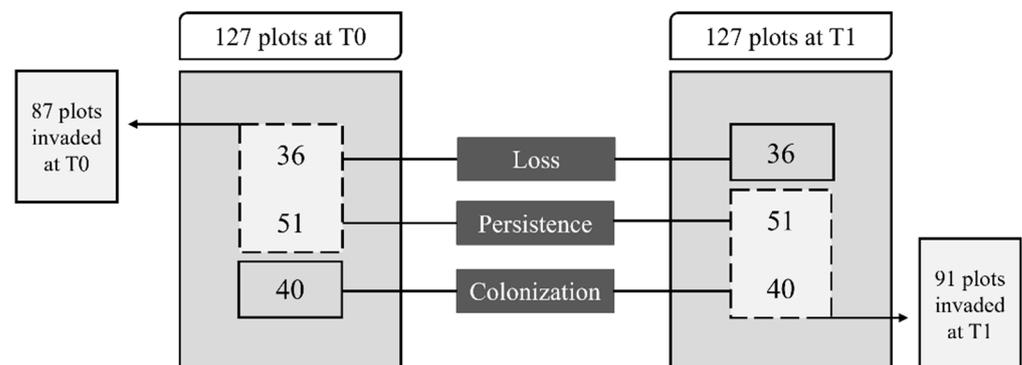


Figure 2. Scheme of the analyzed plots including plot grouping. The 127 plots selected from the database at T_0 and revisited at T_1 were divided into three categories based on the loss, persistence, and colonization of alien species. Invaded plots at T_0 (87) and T_1 (91) are delimited by a dotted line inside the main boxes.

2.3. Colonization, Loss, or Persistence of Alien Species

In order to explore different trends of invasion, we divided the original dataset (127 plots) into three categories: alien “colonization” ($n = 40$), indicating plots that did not present alien species at T_0 but were invaded at T_1 , alien “loss” ($n = 36$), indicating plots invaded at T_0 that no longer displayed the presence of alien species at T_1 , and alien “persistence” ($n = 51$), characterized by plots invaded at T_0 and T_1 (Figure 2). Cover values for each species were rescaled between 0 and 1, dividing each value by the maximum cover of each reference plot. The relative cover for the whole set of alien species was then calculated for each plot by summing up the relative cover values of all the alien species [45]. To verify significant cover changes in the whole set of alien species between T_0 and T_1 , we performed a paired t -test (note that this was possible only for the category “persistence”).

Furthermore, we used a beta-diversity index to investigate temporal variation in non-alien (i.e., native) species composition. First, cover values of native species were converted into presence–absence data, then pairwise dissimilarity values between plots (T_0 vs. T_1) were computed employing the Jaccard index of dissimilarity (β_{jacc}), using equation:

$$\beta_{\text{jacc}} = \frac{b + c}{a + b + c} \quad (1)$$

where a is the number of species recorded at both T_0 and T_1 , b is the number of species recorded only at T_0 , and c is the number of species recorded only at T_1 . Values of the index range from 0 to 1. Values equal to 0 indicate a null dissimilarity (paired plots with the same species composition), whereas values equal to 1 indicate a complete dissimilarity (plots that do not share any species) [56,57]. This analysis was done using R package “adespatial” [58]. Subsequently, differences in Jaccard values in the three categories were tested using the Kruskal–Wallis rank-based non-parametric test.

2.4. Changes in Diagnostic Species Cover

We further analyzed temporal changes in diagnostic species—those species with occurrences concentrated in a particular habitat that play a crucial role in supporting the structure and functions of their reference habitat [49,53]. Diagnostic species were identified following Chytrý et al. [53], resulting in 34 species attributable to the four EUNIS habitats mentioned above. Using the same approach implemented for alien species, the relative cover for the whole set of diagnostic species was calculated for each plot by summing up the relative cover values of all diagnostic species occurring in that plot. To explore the presence of significant changes in diagnostic species cover between T_0 and T_1 in the

different categories (colonization, loss, and persistence), a Wilcoxon–Pratt signed rank test for paired samples was performed. This was done using R package “coin” [59].

Finally, to find out changes in single species cover over time, Wilcoxon–Pratt signed rank test for paired samples was also performed for each diagnostic species, separately analyzing plots that experienced colonization, loss, or persistence of alien species. For this analysis, plots were further divided into herbaceous habitats (sand beach driftlines, shifting coastal dunes, dune grassland) and woody habitats (coastal dune scrubs).

3. Results

3.1. Overall Trends in Alien Species

Overall, 12 alien species were detected (Table S1). Eight of them are classified as invasive (species occurring in self-maintaining populations capable of spreading over a large area without human intervention), while four are referred to as naturalized at national level [52]. Nine species were originally from America (*Agave americana*, *Amorpha fruticosa*, *Cenchrus incertus*, *Erigeron canadensis*, *Oenothera gr. biennis*, *Opuntia ficus-indica*, *Spartina versicolor*, *Xanthium orientale subsp. italicum*, and *Yucca gloriosa*), two from Africa (*Carpobrotus sp.* and *Drosanthemum floribundum*), and only one from Asia (*Pittosporum tobira*). Note that for *Carpobrotus acinaciformis* and *Carpobrotus edulis*, clonal South African succulents, unresolved issues in the taxonomy of the species should still be defined [60,61]; therefore, in the present study, even if our results could slightly vary, they will be considered as a single taxon, namely *Carpobrotus sp.*

All the six alien species recorded in the historical plots (*Carpobrotus sp.*, *Agave americana*, *Pittosporum tobira*, *Oenothera gr biennis*, *Xanthium orientale subsp. italicum*, and *Erigeron canadensis*) were still present during the resurvey; however, the number of alien species doubled in the revisited plots (from 6 up to 12 species). The newly recorded alien species were: *Amorpha fruticosa*, *Cenchrus incertus*, *Drosanthemum floribundum*, *Opuntia ficus-indica*, *Spartina versicolor*, and *Yucca gloriosa*. At the same time, the total number of alien species occurrences and the mean alien cover were found to be quite stable through time (Table 1).

Table 1. Number of invaded plots and alien species, total number of alien species occurrences, and mean alien cover recorded at T₀ and T₁.

	T ₀	T ₁
Invaded plots	87	91
Number of alien species	6	12
Total alien occurrences	98	110
Mean alien cover (%)	25.06	23.46

The most frequent species over time were *Carpobrotus sp.*, *Agave americana*, and *Xanthium orientale subsp. italicum* (Table S1). In particular, *Carpobrotus sp.* presented the highest values of both occurrence and cover at T₀ and T₁. Rank-abundance curves displayed remarkable changes in *Agave americana* (3.9–15.3%) and *Yucca gloriosa* cover (0–5.3%) and an opposite trend in *Carpobrotus sp.* cover (89.2–69.5%) (Figure 3). The recent expansion of *Yucca gloriosa* is noteworthy; whereas it was not recorded in the historical survey, it appeared as the third most abundant alien species in the resurvey (Figure 3).

3.2. Colonization, Loss, or Persistence of Alien Species

The comparison between the paired plots evidenced a statistically significant difference in the relative cover for the whole set of alien species in the “persistence” category; moreover, this category exhibited the highest values of mean alien cover both at T₀ and T₁ (Table 2).

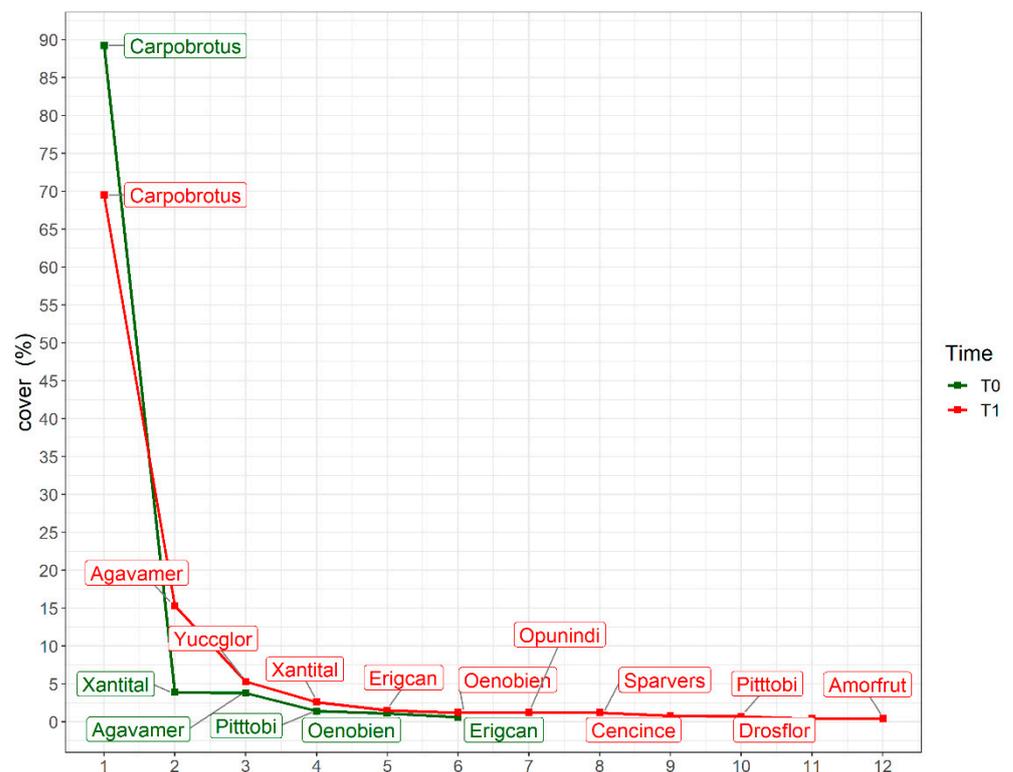


Figure 3. Rank-abundance curves for both time-points (T_0 and T_1) representing the percentage cover of each alien species with respect to the total cover of the whole set of aliens at T_0 and T_1 . *Agavamer*, *Agave americana*; *Amorfrut*, *Amorpha fruticosa*; *Carpobrotus*, *Carpobrotus* sp.; *Cencince*, *Cenchrus incertus*; *Drosflor*, *Drosanthemum floribundum*; *Erigcan*, *Erigeron canadensis*; *Oenobien*, *Oenothera gr biennis*; *Opunindi*, *Opuntia ficus-indica*; *Pitttobi*, *Pittosporum tobira*; *Sparvers*, *Spartina versicolor*; *Xantital*, *Xanthium orientale subsp. italicum*; *Yuccglor*, *Yucca gloriosa*.

Table 2. Mean relative cover of the whole set of alien and diagnostic species at T_0 and T_1 in the three categories considered. The mean delta between T_1 and T_0 and the general trend for alien (t -test, * p -value < 0.05) and diagnostic (Wilcoxon–Pratt signed rank test, * p -value < 0.05) species are also reported.

	Category	Mean Relative Cover (T_0)	Mean Relative Cover (T_1)	Δ Cover	Trend
Alien	Colonization	-	0.19	0.19	↑
	Loss	0.22	-	-0.22	↓
	Persistence	0.36	0.24	-0.12	↓*
Diagnostic	Colonization	0.812	0.644	-0.168	↓*
	Loss	0.631	0.803	0.172	↑*
	Persistence	0.532	0.581	0.049	↑

Furthermore, Jaccard values of dissimilarity unveiled that native species composition experienced substantial changes over time and significant differences were recorded across the three categories (Kruskal–Wallis, $p < 0.005$). The plots showing the highest dissimilarity values were those recently colonized by alien species (mean = 0.78; “colonization” category in Figure 4).

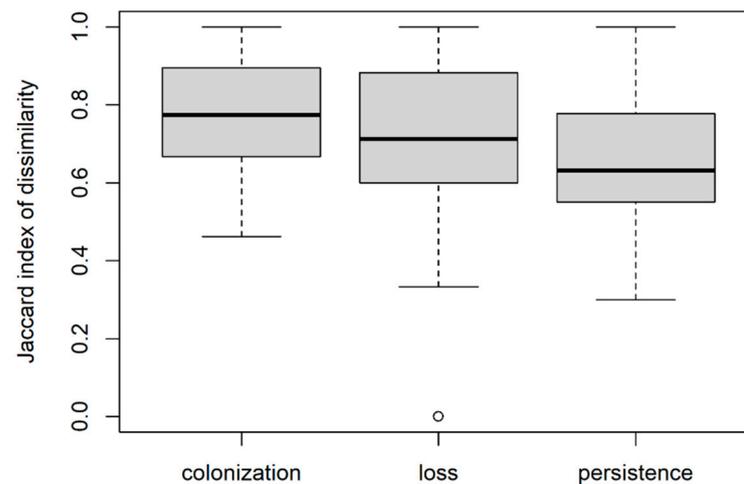


Figure 4. Boxplot showing values of the Jaccard index of dissimilarity in plots that experienced colonization, loss, and persistence of alien species. Alien species were excluded from the computation.

3.3. Changes in Diagnostic Species Cover

In the last 10–15 years, the relative cover of the whole set of diagnostic species has undergone different modifications. Significant temporal changes were recorded for plots experiencing both colonization and loss of alien species. In particular, the category “colonization” exhibited a decrease and, on the contrary, the category “loss” reported an increase in the relative cover of the whole set of diagnostic species (Table 2).

When analyzing cover changes for diagnostic species individually, herbaceous habitats (sand beach driftlines, shifting coastal dunes, and coastal dune grassland) revealed significant differences in newly invaded plots (“colonization”) (Table 3). In this category, *Salsola kali*, *Ammophila arenaria subsp. australis*, and *Sporobolus virginicus* significantly decreased their cover, while the annual *Cutandia maritima*, conversely, increased its cover. At the same time, in plots experiencing alien species loss, the annual *Silene canescens* significantly increased its cover and in plots characterized by alien species persistence, the perennial *Lotus cytisoides* displayed an increase in its cover over time (Table 3). In contrast to herbaceous habitats, woody habitats (coastal dune scrubs) did not display any significant differences in diagnostic species cover over time.

Table 3. Cover change of diagnostic species (Δ cover) in the different categories and corresponding p -value of the Wilcoxon–Pratt signed rank test. Only species that presented a significant difference over time are displayed.

Category	Species	p -Value	Δ Cover
Colonization	<i>Ammophila arenaria subsp. australis</i>	0.031	−7.1%
Colonization	<i>Cutandia maritima</i>	0.000	+4.3%
Colonization	<i>Salsola kali</i>	0.044	−5.8%
Colonization	<i>Sporobolus virginicus</i>	0.011	−4.9%
Loss	<i>Silene canescens</i>	0.011	+3.2%
Persistence	<i>Lotus cytisoides</i>	0.013	+4.8%

4. Discussion

During the time period considered (10–15 years), alien species displayed considerable changes in invaded coastal dune habitats. Moreover, different trends of invasion (alien colonization, loss, and persistence) were related to different impacts on native and diagnostic species.

First of all, the number of alien species has doubled over time, which highlights the continuous threat represented by the introduction and spread of new invaders in natural ecosystems [5]. It is important to note that the six species sampled in the historical plots

(*Carpobrotus* sp., *Agave americana*, *Pittosporum tobira*, *Oenothera gr biennis*, *Xanthium orientale subsp. italicum*, and *Erigeron canadensis*) were all retrieved during the resurvey, proving their successful introduction and self-sustaining capacity in coastal dune habitats. Six new invaders were identified during the resurvey and although their cover and occurrences were quite low (except for *Yucca gloriosa*), the possible expansion of these species represents a further risk for the future conservation of coastal ecosystems. In particular, four of these invaders are classified as invasive (*Amorpha fruticosa*, *Yucca gloriosa*, *Opuntia ficus-indica*, and *Cenchrus incertus*) and two as naturalized (*Spartina versicolor* and *Drosanthemum floribundum*). The majority of the species were introduced voluntarily, mainly for ornamental reasons or for preventing erosion [52]. All 12 species have already been recorded in previous studies at national level [62,63], and most of them also at continental level [64]; therefore, their presence during a revisitation study based on random plots confirms their ongoing expansion in these habitats.

Carpobrotus sp. is a fast-growing, mat-forming plant and proved to be the most frequent and abundant species at both time-points, which is not surprising as it is one of the most widespread aliens in Mediterranean coastal areas, especially on the Tyrrhenian coast [61,62]. Although its proportional cover appeared to decrease from T_0 to T_1 (−19.7% considering the whole set of alien species), the values remain undoubtedly the highest of all species recorded. Previous studies [45] observed a decline in *Carpobrotus* sp. in coastal dunes characterized by a high level of disturbance. Therefore, it is possible that, during the time period considered, the increasing level of disturbance affected both native and alien species, leading to a decrease in *Carpobrotus* sp. *Yucca gloriosa* and *Agave americana* distinctly increased their contribution to total alien cover over time (+5.3% and +11.4%, respectively). These species are perennial rhizomatous shrubs capable of withstanding the harsh climatic conditions of the dune ecosystems [62]. In particular, the recent and fast expansion observed in *Yucca gloriosa* appears alarming, as the species was not present during the original survey, and recent studies indicate that it is rapidly spreading in other Italian coastal areas [65].

The analysis of native species composition in plots experiencing colonization, loss, or persistence of alien species also revealed important changes, especially in newly invaded plots (which displayed the greatest Jaccard dissimilarity values for native species). Previous studies reported that the impacts of the invader on natural plant communities can change through time, being more severe in the period following the introduction of an alien species and having a tendency to stabilize after several decades [11,16].

A particularly interesting result was that the relative cover of the whole set of diagnostic species displayed an inverse trend compared with that of alien species. During the last 10–15 years, diagnostic species significantly decreased their cover within newly invaded plots (“colonization”), but they increased their cover in plots where alien species were no longer found (“loss”). On one hand, this suggests the negative impact of alien species introduction on diagnostic species [35], while, on the other, it could represent a possible sign of recovery of the community once the disturbance linked to alien species has ceased [15,18]. At the same time, whereas a significant decrease in alien cover was detected in plots persistently invaded, we recorded no significant change in the cover of diagnostic species. In fact, the presence of alien species over extended periods can strongly impact natural communities due to changes in biotic and abiotic factors (such as soil acidification, litter deposition, and nitrogen content), which make the habitat no longer suitable for the development of its characteristic species [37–39].

The decrease in the cover of diagnostic species such as *Ammophila arenaria subsp. australis* (−7.1%), *Salsola kali* (−5.8%), and *Sporobolus virginicus* (−4.9%) in herbaceous plots experiencing alien “colonization” raises considerable environmental concern. All three species are important dune specialists and, in particular, *Ammophila arenaria subsp. australis* is a typical shifting dunes species that plays a key role in dune formation and stabilization. Furthermore, an opposite trend was recorded for two annual species, *Cutandia maritima* (“colonization”) and *Silene canescens* (“loss”), which increased their cover over time, and

also for the chamaephyte *Lotus cytisoides* (“persistence”). Changes in annual species can reflect a higher level of disturbance in comparison with the past; therefore, these data need to be evaluated with care. Nevertheless, these results confirm the high vulnerability of the first sector of the coastal dune zonation, which is also recognized as the most affected by biological invasion [35,45].

5. Conclusions

As coastal dunes are highly dynamic systems, revisitation studies allow the detection of significant temporal changes in their plant communities [45,49]. This study revealed an increase in the number of alien species, as well as different impacts on native and diagnostic species, related to diverse temporal trends of invasion. During the last 10–15 years, the greatest changes were recorded in newly invaded plots, which also featured a decrease in the cover of typical dune builders, such as *Ammophila arenaria subsp. australis*.

Overall, our results support the important role of alien plants in shaping the structure of invaded plant communities over time. Detailed knowledge of these complex processes can be very important in the management of these habitats and in the planning of effective conservation actions. Nevertheless, regular surveys are necessary to provide more detailed insights into the invasion processes acting in these fragile ecosystems.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/su132413946/s1>, Table S1: List of alien species recorded in alphabetical order. Each species is described by biological (class and growth form) and geographical (origin) features and their occurrence frequencies are recorded in invaded plots at T₀ and T₁. INV, invasive; NAT, naturalized; P, phanerophyte; Ch, chamaephyte; T, therophyte; H, hemicryptophyte; G, geophyte; surf, suffruticose; scap, scapose; bi, biennial; suc, succulente; rhz, rhizomatous.

Author Contributions: All authors contributed substantially to the work: S.C., A.T.R.A. and M.G.S. conceived the study; M.G.S. and S.C. collected resurveyed data; S.C., M.G.S. and L.C.P. analyzed the data; M.G.S., L.C.P. and F.M. reviewed the manuscript; A.T.R.A. and M.L.C. supervised the research. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Vegetation plots are archived in the database “RanVegDunes” accessible from the “European Vegetation Archive” (EVA) (<http://euroveg.org/eva-database>) (last accessed 10 December 2021).

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