



Cross-taxon analysis in the highly threatened Mediterranean dunes reveals consistent diversity patterns in butterfly and plant communities

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Abstract

Butterflies and plant species are widely used as model systems in biodiversity and conservation research. However, little is known about spatial patterns of butterfly diversity linked to plant communities across coastal dune ecotones. We explored the relation between butterfly and vegetation diversity in a Mediterranean protected dune system in Central Italy. We sampled butterfly and plant communities on shifting and fixed dunes and investigated their distribution patterns by diversity indexes and Species Abundance Diversity models (SADs). We also computed species beta-diversity and analyzed the relation between butterfly communities and vegetation by correlation analyses. Cross-taxon congruence in species richness, composition and abundance was assessed using Mantel correlation tests. Both butterfly and plant diversity were higher on the fixed dunes than on the shifting dunes. In both communities, SADs were adequately described by the geometric series model, which is typical of harsh environments with simple communities dominated by few species. Among both butterflies and plants, we identified species found only on either the shifting or the fixed dunes. Correlation between plant and butterfly diversity was higher for entomophilous plant species than for the more abundant anemophilous ones. Our results indicate that both plant and butterfly communities respond to the sea-inland environmental gradient, forming distinct communities with specialized taxa. Our findings also provide evidence of the importance of butterfly-plant relations for preserving biological diversity and ecosystem functioning in Mediterranean coastal areas.

Keywords Biodiversity monitoring · Coastal ecosystems · Italy · Lepidoptera · LTER · Vascular plants

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Introduction

Placed at the interface between the terrestrial and marine realms, coastal dunes are extremely heterogeneous and dynamic landscapes (Schlacher et al. 2007; Acosta et al. 2009; Bazzichetto et al. 2016) that perform many essential ecosystem services, ranging from storm protection to recreational activities (Millennium Ecosystem Assessment 2005; Everard et al. 2010; Drius et al. 2019). Coastal ecosystems are at the same time under severe pressures worldwide, because of a number of anthropogenic factors, including urban, agricultural and afforestation spread, industrial and harbour development, coastal erosion and climate change (Hesp and Martínez 2007; Schlacher et al. 2007; Defeo et al. 2009; Malavasi et al. 2018; Fattorini 2021). Human activities in European coasts have steeply increased during the 20th century (Cori 1999) with sand dunes losing approximately 25% of their extent in half a century (Pessoa and Lidon 2013). Currently, about 80% of Mediterranean coastal dunes have been damaged or destroyed in Europe (Schlacher et al. 2007; Fattorini 2021). The need for urgent measures to counteract the ongoing processes of coastal alteration and loss led the European Union to include the coastal dunes in the Habitat Directive (hereafter, HD; European Council Directive 92/43/EEC) as ecosystems of conservation interest. Furthermore, the unsatisfactory (bad or inadequate) conservation status of coastal habitats in Italy (Genovesi et al. 2014) had urged the Italian Government to include the few fragments of coastal landscapes that are still in relatively well conditions within the European Natura 2000 network of sites of European importance. With approximately 26,000 sites that cover approximately 18% of the European territory, Natura 2000 is the largest network of protected areas in the world (Maiorano et al. 2015). For the Natura 2000 sites, management and monitoring plans focusing on target species and habitats are mandatory (European Council Directive 92/43/EEC).

A great effort has been devoted for monitoring diversity of Italian coastal sites for both plant (Acosta et al. 2009; Drius et al. 2016; Malavasi et al. 2016) and animal (Berardo et al. 2015; Fattorini et al. 2017) communities. Yet, studies focusing on community organization along the seashore-inland gradients for multiple taxonomic groups are limited (Kühl et al. 2020). In particular, despite the prominent role of butterflies (Lepidoptera, Papilionoidea) as model organisms in ecological research (Dennis 2020), little is known about butterfly diversity in relation with plant species and habitat variability across the seashore-inland environmental gradient (Fantinato et al. 2018).

Butterflies are a useful taxonomic group for biodiversity and ecosystem monitoring (Warren et al. 2021; Naik et al. 2022) and for conservation studies (Narayana et al. 2017). Previous research in temperate landscapes underlined the usefulness of butterflies as indicator species because of tight relations between vegetation characteristics and the distribution of these insects. For example, the horizontal and vertical structure of vegetation determines the presence of a variety of microclimatic conditions, while the presence of plants with different life cycles (perennial or annual), as well as flowering and vegetative periods, provide butterflies with a variety of feeding resources and sites for egg deposition (Davies and Asner 2014). Furthermore, each vegetation type, with its specific plant assemblages, can fulfil various facets of butterfly ecological niches, including microclimatic, breeding, and spatial requirements (Dennis 2010). Plant structural tissues (e.g., leaves, leaf buds and stems) provide butterfly larvae with food and protection, and plant reproductive organs offer food (nectar and pollen) for the adults, hereby ensuring a steady supply of resources throughout

the butterfly life cycles (Siemann et al. 1998; Romeis et al. 2005; Wäckers et al. 2007). Given the influence of vegetation on butterfly diversity (Aguirre-Gutiérrez et al. 2017), enhancing our understanding of butterfly diversity patterns in relation to the distribution of vegetation is of paramount importance to understand the factors that drive butterfly community structure and inform conservation actions. Mediterranean dune ecosystems, shaped by the interplay of the sea-inland environmental gradients and human impacts, are ideal systems for in-depth research into butterfly/plant diversity patterns. This research, necessary for enhancing our current knowledge of dune ecology, may offer important indications for the conservation of these valuable and endangered ecosystems (Schlacher et al. 2007; Fattorini 2021).

In this context, the present work analyzed diversity patterns of butterflies and vascular plants in a well-preserved Mediterranean coastal dune system to specifically address the following questions: (a) Are alpha- and gamma-diversity patterns consistent for vascular plants and butterflies across different sectors of dune zonation? (b) Are their species abundance distribution patterns similarly shaped by coastal harsh environmental conditions (e.g., simple communities, dominated by few species able to survive)? (c) Does butterfly diversity vary seasonally? (d) Is the spatial variation in beta-diversity of butterflies correlated with the spatial variation in beta-diversity of plants? (e) Are butterfly diversity patterns associated with specific characteristics of the vascular plants occurring in different sectors of the dune zonation (e.g., plants with flowers potentially attractive for insect pollinators or with spikes)?

Methods

Study area

The study was conducted in the Natura 2000 site “Foce Trigno-Marina di Petacciato-IT7228221” (Molise Region), which is representative of the original ecological conditions of the Adriatic coast in Central Italy (Fig. 1). This coastal area is characterized by narrow belts of Holocene dunes with biotic conditions varying sharply from the sea to inland areas (Carranza et al. 2008; Drius et al. 2013). In this area, the landscape is represented by a natural, well preserved vegetation, from the annual communities that characterize the strandline zone of the beach to the Mediterranean maquis that can be found on the inland stabilized dunes (Acosta et al. 2009; Stanisci et al. 2014). Specifically, the vegetation occurring in this part of the Adriatic coast is well preserved (Drius et al. 2019) and includes the following habitats of European conservation concern (European Commission 2013): 1210-Annual vegetation of drift lines; 2110-Embryonic shifting dunes; 2120-Shifting dunes along the shoreline with *Calamagrostis arenaria*; 2130-Fixed coastal dunes with herbaceous vegetation (grey dunes) (Stanisci et al. 2014; Riviaccio et al. 2021); 2230-Malcolmietalia dune grassland; 2260-Cisto-Lavanduletalia dune sclerophyllous scrubs, and 2270-Wooded dunes with *Pinus pinaster* (partially invaded by *Acacia saligna*) (Tozzi et al. 2021; Marzialetti et al. 2021). Expanding urban areas and agricultural lands are present, however, on the adjacent coastal plains (Malavasi et al. 2013; Carranza et al. 2018). Because of its well-preserved conditions, and its inclusion in the Natura 2000 network, the study area has been

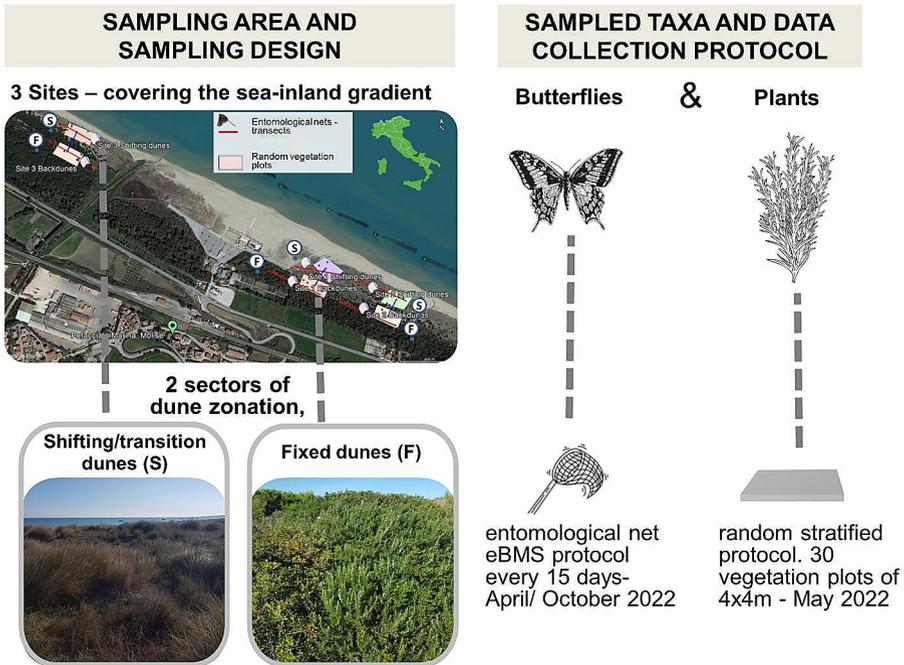


Fig. 1 Flowchart depicting the adopted sampling design for multi-taxon data collection carried out on the coastal site LTER IT20 (<http://www.lteritalia.it/?q=siti/foce-trigno-marina-di-petacciato-campobasso>; last visited 13/06/2024) along three sites including shifting dunes close to the seashore and fixed dunes on the inner coastal sectors. Butterflies were periodically recorded (every 15 days) with entomological nets following the European Butterfly Monitoring Scheme on dune sectors while vascular plants were sampled following a random stratified approach. Satellite imagine from Google Earth

also included as a node of the Long-Term Ecological Research (LTER) Network LTER IT20 (Stanisci et al. 2014; Capotondi et al. 2021).

Data collection

Butterflies and vascular plants were sampled in accordance with recommendations for data collection in LTER (Prisco et al. 2016). For LTER it is essential to use sampling procedures that can be reproduced over time in order to obtain comparable results (Muelbert et al. 2019). Thus, we adopted standardized sampling protocols which can be also easily reproduced in the future to monitor possible changes in multi-taxon diversity.

Sampling was carried out in three sites (replicates, Fig. 1), each encompassing the sea-land environmental gradient, which was divided into two zones: the “shifting/transition dunes” and the “fixed dunes”. Shifting/transition dunes are located near the sea, exposed to salt spray and wind, and are morphologically characterized by the presence of a consolidating sandy substrate contributing to shelter the innermost habitats. Fixed dune habitats, located further from the seashore, are less exposed to environmental stress and are characterized by more stable substrates, with incipient soils (Acosta et al. 2009; Bazzichetto et al. 2016).

Following the European Butterfly Monitoring Scheme - eBMS (Pollard and Yates 1993), in each site butterflies were sampled on shifting/transition dunes and on fixed dunes along georeferenced transects of 200 m parallel to the shoreline (Fig. 1). All transects were walked, under suitable climatic conditions (no rain and strong wind), every 15 days from the end of April to the beginning of October 2022, between 9 am and 4 pm, counting butterflies seen within an imaginary box 5 m wide, 5 m high, and 5 m ahead of the observer. This led to a total of 54 butterfly recording sessions (9 sampling campaigns per 3 sites per 2 sectors). Three of the 9 sampling campaigns were carried out in spring (April–May), 4 in summer (June–August) and 2 in autumn (September–October). Butterfly taxonomy followed Balleto et al. (2014). Information on host plants and ecological preferences were based on Balleto and Kudrna (1985), Villa et al. (2009) and Balleto et al. (2023).

In each site, also vascular plants were sampled following a random stratified protocol, with the dune zones (shifting/transition dunes and fixed dunes) as strata. Five 4 m × 4 m random plots for each zone and site (for a total of 30 plots) were sampled during spring (May 2022). All vascular plant species occurring in each plot were identified and their relative cover recorded using the Braun-Blanquet scale (Braun-Blanquet 1964; Westhoff and Van Der Maarel 1978). For further quantitative analysis, we rescaled the original Braun-Blanquet cover values for each species on the percentage cover scale (Tichý et al. 2020). Plant taxonomy followed Pignatti et al. (2017–2019). For each plant, the presence of flowers potentially attractive for insect pollinators (Wäckers et al. 2007) was also recorded. We considered as potentially attractive all flowers that can provide nectar to butterflies among flowering plants recorded in the field during 7 moth surveys. Each species was assigned to a Raunkiaer life form using Pignatti et al. (2017–2019). Despite some criticism (Sarmiento and Monasterio 1983), Raunkiaer (1905) life forms are the most accepted and used classification system (Klimeš 2003; Leuschner and Ellenberg 2017), because they are easy to use and represent a good surrogate of life strategies adopted by plants to deal with adverse environmental conditions (Acosta et al. 2003; Di Biase et al. 2021).

Statistical analyses

Butterfly alpha-diversity was evaluated using Hill numbers qD (Chao and Jost 2012; Chao et al. 2020; Chiu and Chao 2020). Hill numbers combine information on species richness, species rarity and species dominance, and being all expressed in the same units (i.e., effective number of species) are directly comparable (Chao et al. 2014; Chiu and Chao 2020). In Hill numbers, the diversity order q determines the measure's sensitivity to a species' relative abundance. Although q can assume any value, values larger than 3 or 4 are rarely used, because the resulting Hill numbers change very little, whereas values below 0 are not used, as the Hill numbers would be dominated by the abundances of rare species and have poor statistical sampling properties (Chiu and Chao 2020). Most commonly, Hill numbers for species richness ($q=0$), Shannon diversity in its exponential form ($q=1$; in fact, the limit case, as the Hill number is undefined for $q=1$) and Simpson diversity ($q=2$) are used (Chao and Jost 2012; Chao et al. 2014; Chao et al. 2020). Therefore, we used these three Hill numbers as butterfly diversity indices calculated for each site (three transect-strips placed perpendicularly to the seashore), dune zonation sector (shifting/transition dunes vs. fixed dunes), and season (spring, summer, autumn). The same indices were also calculated for vascular plants, for each unique combination of zone, transect and site. Hill numbers were

calculated using the iNEXT R package (Hsieh et al. 2016). In all cases, we used empirical values of Hill numbers.

We evaluated the variation between zones and seasons in butterfly Hill numbers using Linear Mixed Models (LMMs) and in abundance (number of counted individuals) using Generalized Linear Mixed Models (GLMM), with sites and transects as random factor (Response Variable~Zonation \times Season +(1|Site: Zonation)). A similar approach was used to evaluate differences in plant cover and diversity between zones (Response Variable~Zonation + (1|Site)). For analysis of abundance, we assumed a Poisson error distribution for butterflies, whereas the Gaussian distribution was used for the analyses dealing with plant cover and Hill numbers. Analyses were performed in RStudio version 4.1.0 (R CoreTeam 2021) using the R packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). We also compared overall butterfly species richness (gamma-diversity) by seasons (spring, summer and autumn), by computing species richness accumulation through sample-based rarefaction curves using abundance data with iNEXT (Hsieh et al. 2016).

We compared butterfly and plant species abundance distribution (SAD) patterns between dune zones by using rank abundance curves (May 1975; Magurran 1988; Hayek and Buzas 2010), with data from different sites and seasons merged. For this purpose, SADs were modeled using the geometric series, which mathematically expresses the niche pre-emption model, in which the sizes of the niche hypervolumes (measured by species abundances) are sequentially pre-empted by the most abundant to the least abundant species (Giller 1984; Fattorini 2005; McGill et al. 2007). Communities living in harsh environments and early successional stages typically follow the niche pre-emption model, which is the reference model for communities composed of few species and with high dominance (Fattorini 2005). To fit the rank abundance plots, we adopted the method based on the use of Ordinary Least Squares (OLS) regressions described by Fattorini (2005). This approach is based on the fact that, if species are ranked from the most to the least abundant, and abundances are logarithmically transformed, a geometrical series exactly follows a strength line, which can be fitted using an OLS regression. With this approach, the coefficient of determination R^2 can be used as a goodness-of-fit measure, and differences between slopes can be assessed by analysis of covariance (ANCOVA). In the niche pre-emption model, the fixed proportion of used resource is given by the niche pre-emption parameter k , because the first (most abundant) species in the sequence occupies a fraction k of resource hypervolume, the second species a fraction k of hypervolume not occupied by the first, and so on. The niche pre-emption parameter k was calculated following He and Tang (2008). The same approach was used to test for differences between seasons, by accumulating data from different zones, transects and sites. All these analyses were carried out in RStudio version 4.1.0 (R CoreTeam 2021).

We also computed species beta-diversity (for vascular plant and butterfly communities) between shifting/transition dunes and fixed dunes using Whittaker index (Whittaker 1960):

$$b_w = \frac{S}{\bar{\alpha}} - 1,$$

where S is the total number of species and $\bar{\alpha}$ is the average number of species.

Butterfly and plant habitat preferences were evaluated as the percentage of abundance/cover of each species in the two zones.

We analyzed the influence of vegetation on butterfly communities by correlation analyses. Specifically, we used the Pearson correlation coefficient to test if butterfly abundance and richness at transect level were positively influenced by the following vegetation characteristics: number of overall plant species, cover of plant species with flowers potentially attractive for insect pollinators, and cover of anemophilous species. As the number of sampling events for butterflies and plants were different, correlation analyses were performed by using values of richness and abundances averaged across the sampling events. Cross-taxon congruence in variation in beta-diversity between sites was assessed using Mantel correlation tests. For both butterflies and plants, we calculated distances (beta-diversity) between sites using Dice-Sørensen distances (for presence-absence data) and Bray-Curtis distances (to take into account abundances) (Baselga 2010, 2013). Then, plant and butterfly matrices of distances were correlated with Mantel test (Pearson's correlation) with 1000 permutations. The use of the cross-taxon approach can explain patterns of interaction between different biological groups and their application in conservation studies can be important to inform management measures (Rooney and Azeria 2015; Marignani et al. 2020). All these analyses were carried out in RStudio version 4.1.0 (R CoreTeam 2021).

Results

Overall, we recorded 18 butterfly species and 71 vascular plant species (SI3; SI4). Most species belonged to the family Nymphalidae (7 species), followed by Lycaenidae (5 species) and last Pieridae (3 species). The most common plant families were Poaceae (17 species, 24% of the sampled flora), Asteraceae (11 species, 15%) and Fabaceae (6 species, 8%). Fixed dunes showed higher values of butterfly abundance and species richness, especially in autumn (Fig. 2; Table 1), while no significant differences were found using Shannon and Simpson diversity (SI2b). We found no significant differences in plant cover and diversity between fixed and shifting/transition dunes (SI1; SI2a).

Rarefaction curves showed differences in diversity values across dune zonation sectors and seasons. Although curves did not reach clear plateaus, comparison of species richness

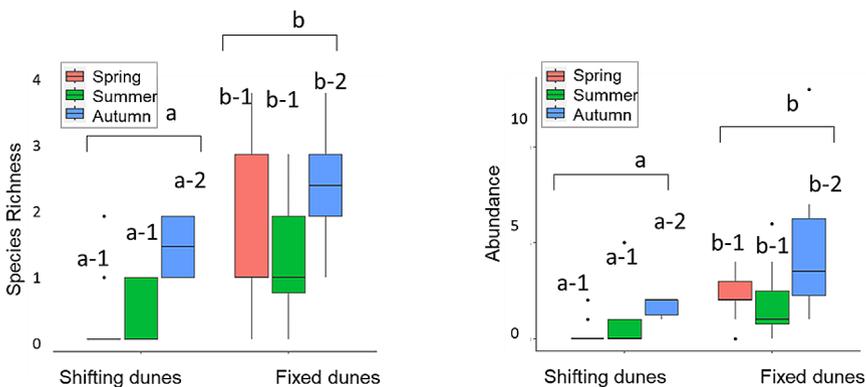


Fig. 2 Boxplots comparing butterfly species richness (Hill number with $q=0$) (left) and abundance (number of counted individuals) (right) in shifting/transition dunes and fixed dunes in different seasons (spring, summer, and autumn). Alphanumeric codes indicate significant differences ($p < 0.05$) between zones (letters a-b) and seasons (numbers 1,2) detected by linear mixed models and generalized linear mixed models

Table 1 Generalized linear mixed models for the influence of zonation (shifting/transition dunes and fixed dunes) and season (spring, summer, autumn) on the butterfly community species richness and abundance (number of observations). SE=standard error, p =probability. Significant effects ($p < 0.05$) are shown in bold

	Estimate	SE	P
Species Richness			
Intercept	0.593	0.280	0.04
Fixed dunes	1.037	0.280	4.98 e⁻⁴
Autumn	0.889	0.383	0.002
Abundance			
Intercept	-0.507	0.280	0.070
Fixed dunes	1.232	0.284	6.76e⁻⁴
Autumn	0.916	0.258	3.87e⁻⁴

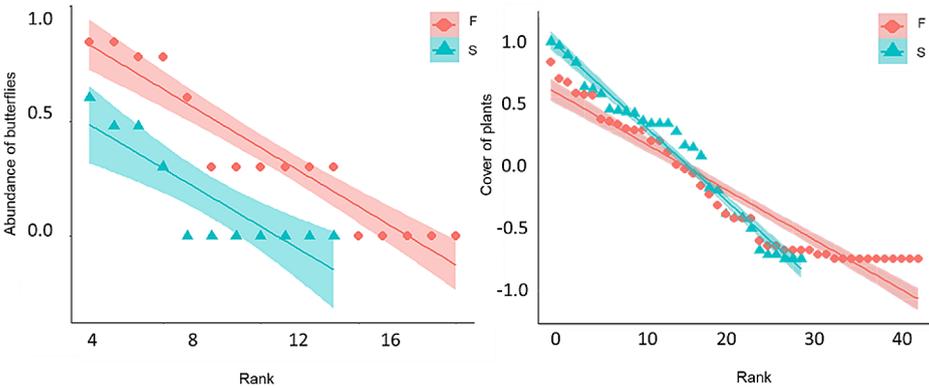


Fig. 3 Rank abundance curves for butterflies (left) and vascular plants (right) in shifting/transition dunes (S- green) and fixed dunes (F- pink) in the analyzed dune system. Species are ranked from the most to the least abundant (x-axis). Species cover and abundances are \log_{10} -transformed (y-axis). Regression equations for butterflies are as follows: shifting/transition dunes: $y = -0.063x + 0.548$, $R^2 = 0.739$, $p < 0.0001$; fixed dunes: $y = -0.064x + 0.896$, $R^2 = 0.897$, $p < 0.0001$. Regression equations for plants are as follows: shifting/transition dunes: $y = -0.057x + 0.980$, $R^2 = 0.969$, $p < 0.0001$; fixed dunes: $y = -0.035x + 0.591$, $R^2 = 0.919$, $p < 0.0001$

at a standardized level of abundance indicated lower richness values on the shifting dunes in comparison to the fixed dunes. However, it should be noted that the rarefaction curve for spring grows less abruptly than those of summer and autumn. (SI6, SI7, SI8).

SADs of both butterflies and vascular plants were adequately modeled by the geometric series in both zones (Fig. 3). However, while the slopes of the curves of the two zones were similar in butterfly SADs (ANCOVA: $F_{1,23} = 0.003$, $p = 0.958$), the slope for the plant community of the shifting/transition dunes was significantly higher than that of the fixed dunes (ANCOVA: $F_{1,72} = 56.125$, $p < 0.00001$). Butterfly SADs did not change their slopes across seasons (Fig. SI5; ANCOVA: $F_{1,21} = 0.663$, $p = 0.526$). The niche pre-emption parameter k for butterflies was $k = 0.149$ on the shifting/transition dunes and $k = 0.165$ on the fixed dunes. Regarding the value of k for different seasons, we obtained $k = 0.159$ for spring, $k = 0.226$ for summer, and $k = 0.248$ for autumn.

We observed a strong vegetation zonation across the sea-inland gradient with a high turnover of plant species ($b_w = 0.56$), whereas turnover in butterfly composition was more moderate ($b_w = 0.33$).

Butterfly distribution reflected dune zonation, with two species only found on the shifting/transition dunes (*Gegenes nostradamus* and *Melanargia galathea*) and seven species exclusive to the woody dune vegetation (*Coenonympha pamphilus*, *Hipparchia semele*, *Lasiommata megera*, *Lycaena phlaeas*, *Maniola jurtina*, *Thymelicus sylvestris* and *Vanessa atalanta*). The other 9 species (*Aricia agestis*, *Colias crocea*, *Leptotes pirithous*, *Papilio machaon*, *Pieris rapae*, *Polyommatus bellargus*, *Polyommatus icarus*, *Pontia edusa* and *Pyronia cecilia*) occurred in both habitats, although with different frequencies. Some of these species present in both dune zones show migratory behaviors (*Pieris rapae*, *Colias crocea* and *Vanessa atalanta*) (Fig. 4; SI4).

Species distribution of plants between the two zones showed that 23% of the species were exclusively found on the shifting/transition dunes, and 49% on the fixed dunes, respectively (Fig. 4). The species exclusively found on the shifting/transition dunes included several Poaceae (e.g., *Festuca fasciculata*, *Calamagrostis arenaria*, *Anisantha madritensis* and *Thinopyrum junceum*), some Fabaceae with flowers potentially attractive for insect pollinators (e.g., *Lotus cytisoides* and *Medicago marina*) and Asteraceae (*Sonchus bulbosus*),

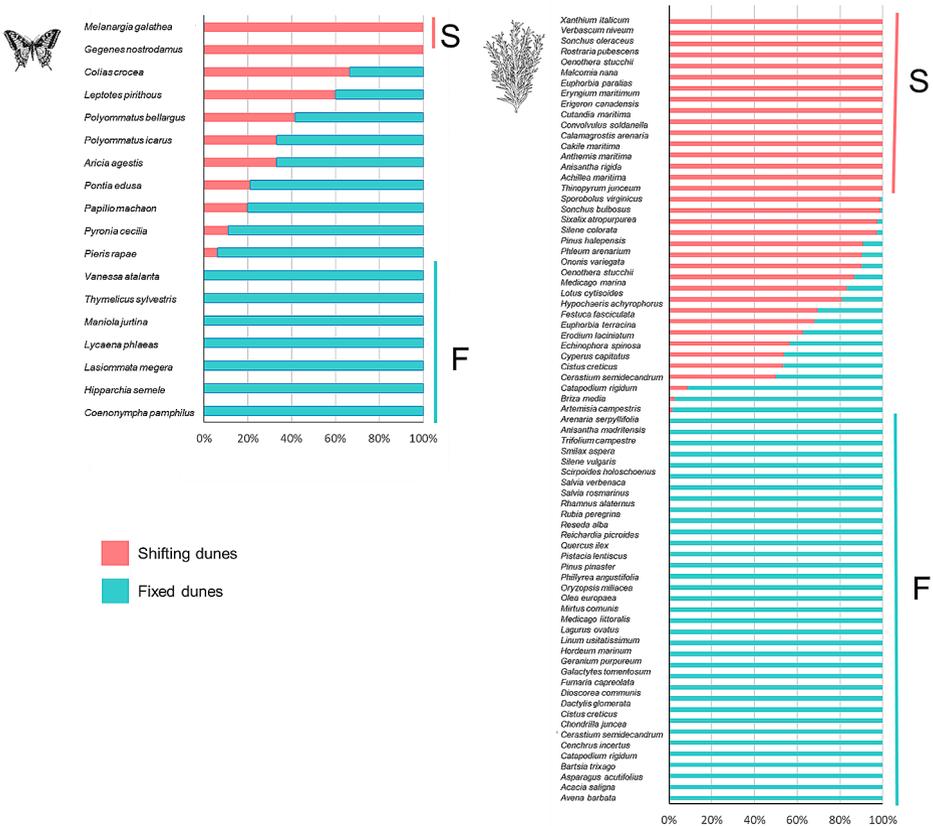


Fig. 4 Abundance distribution of butterfly (left, % of collected individuals) and plant (right, % of cover) species in dune sectors (S=shifting/transition dunes and F=fixed dunes) of the analyzed Mediterranean coast

whereas those exclusively found on the fixed dunes were mostly entomophilous species (e.g., the Lamiaceae *Salvia rosmarinus*, the Asparagaceae *Asparagus acutifolius* and the Fabaceae *Acacia saligna*) and a few potentially useable by pollinators (e.g., the Oleaceae *Phyllirea angustifolia* and the Anacardiaceae *Pistacia lentiscus*). Out of the 36 plant species growing on the shifting/transition dunes, 50% are therophytes, followed by geophytes (19%) and hemicryptophytes (14%). Fixed dunes, even if rich in therophytes (38%) and hemicryptophytes (18%), also hosted several perennial woody plants with a good amount of phanerophytes (22%) and chamaephytes (5%) (SI3). Based on available information on host species (SI4), out of 17 butterfly species for which host plants occurred in the study system, about 65% can use therophytes, and about 24% hemicryptophytes.

The presence of a high number of species indicated as diagnostic for habitats of European concern by the Habitat Directive (SI3) highlights the occurrence of seven different habitats forming a complex dune mosaic zonation, including the following HD habitats: Annual vegetation of drift lines (EC-1210), Embryonic shifting dunes (EC-2110), Shifting dunes along the shoreline with *Calamagrostis arenaria* (EC-2120), Fixed coastal dunes with herbaceous vegetation (grey dunes) (EC-2130), Malcolmietalia dune grassland (EC-2230) on shifting and mobile dunes, Cisto-Lavanduletalia dune sclerophyllous scrubs (EC-2260) and Wooded dunes with *Pinus pinaster* (EC- 2270) (SI3).

Correlation analysis showed a weak relation between butterfly and vascular plant species richness ($r=0.655$; $p=0.15$). Butterfly richness was however positively correlated with the number of dicots with flowers ($r=0.794$; $p=0.058$) and negatively with monocots with spikes ($r = -0.835$; $p=0.038$). Results of Mantel tests indicated a weak correlation in beta-diversity values between plants and butterflies when only species identity was used ($r=0.309$; $p=0.170$), whereas a relatively high cross-taxon correlation was found when abundances were considered ($r=0.402$; $p=0.06$).

Discussion

Mediterranean coastal dunes represent dynamic environmental ecotones (Acosta et al. 2009; Berardo et al. 2015; Fattorini et al. 2017). Because of their conservation importance, dune biotas have attracted increasingly attention (Acosta et al. 2003; Berardo et al. 2015; Fattorini et al. 2017). Yet, few works have investigated cross-taxon micro-habitat distribution patterns simultaneously involving plant and animal communities (Fantinato et al. 2018).

In this research we found that butterfly and plant communities showed similar alpha- and gamma-diversity patterns. Consistently with previous observations in other Mediterranean coasts (Balletto and Toso 1982; Scalercio 2001; Sciarretta and Parenzan 2001; Favilli 2018), butterfly communities in our study system included few species. As for other animal groups (Fattorini et al. 2016, 2017), the low butterfly diversity found on the shifting/transitional dunes is a consequence of the severe halophilic and xerothermic conditions, which are important environmental filters for most insects (Sykes and Wilson 1991; Fattorini et al. 2017; Fantinato et al. 2018). We also found that both butterfly richness and abundance were higher on the fixed dunes than on the shifting dunes, and this difference was accentuated in autumn during blooms of the rosemary garrigue (*Salvia rosmarinus*) (see Katerinopoulos et al. 2005). Indeed, butterfly communities resulted shaped by the seasonality (as shown by accumulation curves and GLMMs) with higher diversity (richness) during the grow-

ing season (summer and secondarily autumn) (see Depetris et al. 2023). We also recorded low species richness in spring, and such low values may be related with the particularly adverse climatic conditions (hot and dry spring) registered during the year 2022. Similarly, we observed low alpha-diversity of vascular plants, with increasing values from the sea-shore to the inland sectors corresponding to the environmental gradient extending from the sea to inland areas (Acosta et al. 2009; Bazzichetto et al. 2016).

We also found a high overall beta-diversity between the two habitats, which is consistent with the strict association of certain species with specific zones of the dunes, because of their response to steep variations in environmental parameters along the ecotone, from the sea shore to the inland part of the coast (e.g., Isermann 2005; Kuiters et al. 2009). Some butterflies were sampled exclusively on the shifting/transition dunes and others on the fixed dunes respectively. It is interesting to notice the presence of *Gegenes nostradamus*, a rare and xerothermophilous species of high conservation concern, which is typically associated with well-preserved environments (Sciarretta and Parenzan 2001; Fattorini 2021) and which in the study area occurs in the mosaic of habitats of conservation concern present on the shifting/transition dunes (EC-2110: Embryonic shifting dunes; EC-2120: Shifting dunes along the shoreline with *Calamagrostis arenaria*; and EC-2230: Malcolmietalia dune grassland). The Italian population of *G. nostradamus* is declining (Balletto et al. 2015). The presence in the study area of *G. nostradamus* testifies the importance of Natura 2000 sites as reservoirs and shelter of biodiversity (Maiorano et al. 2015; Drius et al. 2016; Pellissier et al. 2020). On the other hand, on stabilized dunes, where no typical taxa of Mediterranean maquis were found, some sciophilous species were detected (e.g., *Maniola jurtina*, *Lycaena phlaeas*; S14). This can probably be due to the fact that in the inner dunes often covered by woody vegetation, the structural complexity of plants creates ideal microclimatic conditions for adult species of butterflies that do not tolerate high sunlight and wind (Dover et al. 1997). Concerning plant communities, shifting/transition dunes vegetation is dominated by few monocots of the Poaceae family (*Festuca fasciculata*, *Calamagrostis arenaria*, *Thinopyrum junceum*, *Anisantha madritensis*), while fixed dunes are characterized by high cover of woody dicots (e.g., *Salvia rosmarinus*, *Acacia saligna*, *Pistacia lentiscus*, *Phillyrea angustifolia*). These dominant species are also among those listed as diagnostic for the identification of coastal habitats of European concern (Stanisci et al. 2014; Riviuccio et al. 2021), thus underlying the conservation importance of the study system. The butterfly community of the shifting/transition dunes is dominated by two abundant species that represent together more than 40% of the total butterfly abundance in this habitat (*Polyommatus bellargus*: 24%; *Pontia edusa*: 19%). This hyperdominance of just two species is consistent with previous research showing that shifting dunes are dominated by few species able to cope with the high levels of environmental stress that characterize this habitat (Sykes and Wilson 1991; Fattorini et al. 2017; Fantinato et al. 2018). Fixed dunes, being more distant from the seashore and covered by woody vegetation that curtails the effects of high temperatures and winds (Audisio 2002), are dominated by two very generalist species (*Pontia edusa*, 21%; *Pieris rapae*, 21%), but also host sciophilous species because of the presence of woody habitats of European concern (EC-2260: Cisto-Lavanduletalia dune sclerophyllous scrubs) that assure milder microclimatic conditions (Dover et al. 1997). This is consistent with previous observations on the presence of several lepidopterans in back dunes woods (EC-2270: *Pinus pinaster* and *Pinus halepensis*), where adult butterflies find refuge from intense solar radiation and high temperatures (Altini et al. 2017; Favilli 2018).

Furthermore, the high cover of dicots with flowers that can be used by butterflies, combined with the presence of woody species, increases the architectural complexity of the vegetation, which probably influences positively insect communities (Rudgers and Whitney 2006). Concerning plant communities, on the shifting/transition dunes, characterized by a very selective environment influenced by the proximity to the sea, the dominant vascular plants are therophytes and hemicryptophytes with specific morphological and physiological adaptations to the presence of high salt concentration, severe drought, and unstable substrate (Acosta et al. 2003; Bazzichetto et al. 2016). We found that the dune zone near the drift line was very rich in therophytes, which are a predominant group in lowland Mediterranean areas with thermo-xeric climatic conditions, being particularly adapted to habitats characterized by pronounced seasonality (Di Biase et al. 2021). These species accounted for 50% of the vascular flora on the shifting/transitional dunes, being able to thrive during spring and summer months, and surviving as seeds during winter, when the sea-storms remove established plants. Geophytes (the second most represented life form category) and hemicryptophytes dominated the upper sectors of the shifting dunes, and the latter occurred also in the small depressions among shifting dunes, where they play an incipient role in sand stabilization. These particular life forms are well adapted to survive, growth and reproduce under relatively harsh conditions, also playing a pivotal role as dune builders (Prisco et al. 2012). Notice that these groups, and in particular the therophytes, are those mostly used as host species by butterflies for which information on feeding preferences for larvae was available. In contrast, on stabilized dunes, where the exposure to maritime winds, salt spray and sand burial is reduced, the plant community was characterized by a relatively high number of woody species (phanerophytes and chamaephytes), which, however, seem to have a secondary role as host species for butterflies. This stresses the importance of vegetation of shifting dunes for conservation of the butterfly community of this habitat.

The rank abundance curves revealed that both butterfly and plant species abundance distribution (SAD) patterns were adequately modeled by the geometric series, a distribution pattern typical of simple communities, dominated by few species able to survive in harsh environmental conditions (Giller 1984; McGill et al. 2007) as already observed for other insects in Mediterranean dunes (Fattorini et al. 2016, 2017; Fattorini and Carpaneto 2001). Butterfly SADs for shifting/transitional and fixed dunes had virtually identical slopes, with a higher intercept for the fixed dune. This suggests that the harsher conditions of the shifting/transitional dunes reduce butterfly abundance, but do not alter their community organization. Plant SADs instead showed for the two zones very different slopes, with a steeper slope in the shifting/transitional dune, indicating a more dominated community, in accordance with the harsher conditions of this habitat. As regards the values of k of the geometric series, which indicate the sequential, constant proportion of the total number of butterfly individuals in the community, they appear in both habitats much lower ($k=0.15$ on the shifting/transitional dunes, and $k=0.17$ on the fixed dunes, respectively) compared to those of other insect communities, like tenebrionids ($k > 0.4$; Fattorini et al. 2016, 2017). This might be due to the higher mobility of butterflies, which allow them to maintain a more balanced SAD through immigration from adjacent environments.

Although we did not explicitly investigate butterfly-plant interactions, our results suggest that butterfly diversity patterns are associated with vegetation and specific characteristics of the vascular plants occurring in different sectors of the dune zonation (e.g., plants with flowers potentially attractive for insect pollinators or with spikes). For instance, larvae of

butterflies exclusively present on the shifting/transition dunes (*Gegenes nostradamus* and *Melanargia galathea*) feed on grass species that have been sampled in this dune sector (e.g., Poaceae species such as *Calamagrostis arenaria*, SI3 and SI4), while those only found on the fixed dunes (*Coenonympha pamphilus*, *Hipparchia semele*, *Lasiommata megera*, *Lycaena phlaeas*, *Maniola jurtina*, *Thymelicus sylvestris* and *Vanessa atalanta*) feed on several Poaceae species present in this habitat (e.g., *Festuca* spp., *Dactylis glomerata*, *Briza media*, *Phleum* sp., *Brachypodium* sp.) (SI3 and SI4, Fig. 4). Furthermore, the variability on species distribution across zonation suggests that inter-taxon interactions (e.g., herbivory, mutualism) play a pivotal role. Indeed, each butterfly species depends on the distribution of plant species offering trophic resources for both larvae (e.g., Poaceae and Fabaceae species) and adults (e.g., flowers with nectar) (Siemann et al. 1998; Romeis et al. 2005). In addition, plant species also provide butterflies with shelter against harsh weather conditions (e.g., well-structured perennial vegetation) (Wäckers et al. 2007).

We found a positive correlation between butterfly diversity and plants with flowers, which is most likely due to the pivotal role of floral resources during the adult phase of butterfly life cycles (Siemann et al. 1998; Romeis et al. 2005; Dennis 2020). By contrast, butterflies and monocots with spikes exhibited a negative relationship, possibly because these plants are typically anemophilous. This relationship, however, is only based on adult butterflies, and thus does not take into account the crucial role of Poaceae growing on shifting/transitional dunes as food resources for caterpillars. Because herbivory by larval stages and nectar feeding by adults are strictly interrelated phenomena (Wäckers et al. 2007), future directions should include further analyses of the multitrophic level interactions between butterflies and plants on the dune habitats. Since most butterflies are generalist nectarivores able to feed on ecologically widely distributed plant species (Fabaceae, Caryophyllaceae and some Asteraceae), this may facilitate the selection of egg-deposition sites (Grossmueller and Lederhouse 1987; Adler and Bronstein 2004) throughout the dune zonation. Thus, intact dunes provide important refuges for butterflies, key floral nectar resources for adults (also for migrating species) and essential habitat for larvae of very specialized species (see discussion on *G. nostradamus*). Given that butterflies serve as pollinators able to fly for long distances (Bloch et al. 2006), they may have a significant role in maintaining biodiversity in coastal areas and in ensuring fruit production in the adjacent orchards (e.g., peaches, almonds, apricots, vineyards) which are an important element of several coastal landscapes in the Mediterranean (Altini et al. 2017; Petrosillo et al. 2022). Although patterns of variation in beta-diversity between plants and butterflies show low correlation when only species identities were considered, we found a higher (marginally significant) correlation when abundances were considered, which indicates that, possibly due to the small number of species found in the study system, differences in abundances are more important than those in species composition, and that these patterns of variation in beta-diversity are similar between plants and butterflies.

The distribution of butterfly species through the whole ecological mosaic of coastal plain agroecosystems (Altini et al. 2017) underlays the importance of preserving the entire dune zonation (shifting/transition, fixed, and back dunes) within Natura 2000 sites to maintain regional biodiversity and ecological functionality (Drius et al. 2013). Furthermore, as the use of pesticides inside Natura 2000 sites is strictly regulated, and they are not used on dunes, these sites may constitute a crucial reservoir of pollinators supporting agricultural production in coastal plains (Isenring 2010; Maiorano et al. 2015; Pellissier et al. 2020).

Conclusions

This research provided new insights into the structure of plant and butterfly community patterns in coastal dune ecotones as a result of the interplay between abiotic filters (such as the sea-inland stress gradient) and biotic interactions (e.g., variation, herbivory and symbiosis) as well as their seasonal variation. Dune zonation supports a high plant diversity that offers important environments for many butterflies assuring them host plants for larval development and flowers for adult feeding. Multi-taxon variability in species richness (alpha-diversity) and composition (beta-diversity) across dune zonation highlights the importance of conservation programs that take into account local-scale variability and the entire dune zonation to preserve diversity and ecological functioning at broader scales, also including beneficial effects on agriculture through the services provided by insect pollinators for which well-preserved dunes represent important habitats. Our study also highlights the importance of Natura 2000 coastal sites as part of protected areas networks.

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Declarations

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