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LEPIDOPTERA AND VASCULAR PLANTS DIVERSITY ACROSS DUNE ZONATION: INSIGHTS FROM THE CENTRAL ADRIATIC COAST IN ITALY

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ABSTRACT

Coastal dune systems represent dynamic and transitional ecosystems located at the narrow interface between terrestrial and marine environments. These habitats are of high conservation value, hosting highly specialized flora and fauna, delivering key ecosystem services, and facing intense human pressures. Due to their ecological relevance, the need of effective indicators of biodiversity and conservation status within dune systems are highlighted by several international environmental regulations. Although a considerable body of research has addressed plant communities and specialized fauna inhabiting coastal dunes, there remains a significant knowledge gap concerning how community organization varies along the seashore-inland gradient across multiple taxonomic groups. In particular, despite the well-recognized role of butterflies and moths as bioindicators in ecological research and their sensitivity to environmental changes little is known about their diversity in relation to vascular plant composition and habitat heterogeneity along the coastal environmental mosaic.

This PhD thesis aimed to enhance current knowledge on the diversity, structure and ecological characteristics of Lepidoptera and vascular plants communities across the environmental gradients of Mediterranean coastal dune ecosystems. Focusing on both diurnal and nocturnal Lepidopterans, the study explored their taxonomic and functional responses to dune zonation and vegetation composition within a well-preserved Natura 2000 site on the Adriatic coast. By investigating how butterfly and moth assemblages vary in relation with plant communities across dune zonation and by exploring cross taxon relations the research provides novel insights into plant–insect interactions at community level and contributes to informing effective biodiversity conservation strategies in these fragile and highly dynamic coastal landscapes.

The research was carried out inside the Natura 2000 site Foce Trigno-Marina di Petacciato (IT7228221), included in the Long-Term Ecological Research network (LTER IT20). Lepidoptera and vegetation communities were sampled along three transects perpendicular to the seashore and following the environmental gradient from the driftline to the backdunes, according LTER protocol. In two different sectors of zonation (the shifting dune and the fixed dune), butterflies were sampled following the European Butterfly Monitoring Scheme (eBMS), every 15 days (from April to October 2022) and moths were sampled using light traps equipped with UV LEDs every 15 days (December 2021 - November 2022). Vegetation data were collected following a random stratified protocol on 4x4m plots distributed in the two sectors of zonation.

After an accurate identification and redaction of a faunistic list of recorded lepidopterans, we investigated for the sampled fauna and flora the community structure and function by sectors (shifting dunes and fixed dunes) and compared species taxonomic diversity (e.g. richness, equipartition/dominance, turnover, species abundance distribution) and assessed the congruence between lepidopterans and plant diversity. We also explored the patterns of covariance between moth and plant ecological traits across dune zonation.

The research revealed a remarkable richness of Lepidoptera species and constituted a substantial expansion of the known assemblage on coastal dunes of the region. Besides providing valuable insights into the lepidopterofauna for an eLTER site and site of special conservation interest for the Molise Region in Italy, it identified consistent and significant associations between butterflies/moths and vascular plant communities diversity and structure with a notable proportion of habitat-specific species, shaped by combined influence of abiotic filters and biotic interactions.

The exclusive presence in shifting dunes of *Mythimna riparia* (Rambur, 1829), *Eucrostes indigenata* (de Villers, 1789) and other oligophagous species feeding on herbaceous vegetation, including forbs and graminoids (e.g., Poaceae), highlights the relation of moth communities and plant species distribution due to the nutritional niche. On the other hand, species as *Zebeeba falsalis* (Herrich-Schäffer, 1839), *Eupithecia dodoneata* (Guenée, 1858); *Lycia hirtaria* (Clerck, 1759) feeding on Mediterranean maquis species, exclusively occurs on fixed dunes, confirming a similar relationship. The research also identifies the peculiar habitat requirements of butterflies, geometrid and noctuoid moths in dune systems underscoring Lepidoptera as effective bioindicators for monitoring habitat integrity also in coastal dune ecosystems. The study emphasizes the importance of preserving intact dune systems not only for plant communities, but also for maintaining biodiversity and ecological functionality for the fauna, and offers important ecological insights that can guide the definition of conservation priorities in these fragile and highly vulnerable coastal environments.

Keywords Biodiversity conservation, Butterflies, Coastal ecosystems, Cross-taxon analysis, Dune vegetation, Functional traits, Mediterranean Basin, Moths, Natura 2000, European LTER.

INTRODUCTION

Coastal dunes systems represent transitional ecosystems of considerable conservation importance, located along the narrow interface between terrestrial and marine environments. Coastal dunes are highly dynamic systems shaped by harsh abiotic constraints and subject to frequent climatic and geomorphological disturbances (Acosta et al., 2009; Maun, 2009). Across the globe, coastal dunes are exposed to the same major types of environmental stress, including winds and salt spray, high temperatures, drought, substrate mobility and the presence of highly permeable and shallow sandy soils, (Barbour et al., 1985; Rozema et al., 1985; Hesp, 1991). Sand dunes function as natural barriers against waves and windy storms (McLachlan, 2001; Šilc et al., 2017). These systems comprise approximately the 20% of the world's coasts (Davidson-Arnott, 2010) and are crucial for biodiversity and human health, guaranteeing fundamental services (Millennium Ecosystem Assessment, 2005) with significant socio-economic impacts (Everard et al., 2010, Millennium Ecosystem Assessment, 2005).

These environments display marked ecological gradients resulting from these abiotic conditions that allow for the establishment of a typical spatial arrangement of plant community along a seashore-to-inland gradient, a pattern typically described as "dune zonation'' in plant ecology. This zonation reflects underlying soil-related constraints, including variations in salinity, moisture and nutrient availability (Acosta, 2021). It is widely recognized that the stability of coastal areas depends on the integrity of the ecomorphodynamic interactions between psammophilous plants encountered along the sea-inland gradient and sand (Maun, 2008). Plant cover acts as a physical barrier that traps and retains sediment, thereby contributing to dune formation and morphology while also enhancing their long-term stability and (Wolfe & Nickling, 1993; Acosta et al., 2007; Yousef Lalimi et al., 2017; Malavasi et al., 2021).

Accordingly, distinct vegetation zones can be identified along the seashore to inland coastal gradient, each characterized by specific plant assemblages: upper beach, embryo dunes, shifting dunes, and fixed dunes. The upper beach, embryo and shifting dunes being in close proximity to the shoreline, are subject to intense environmental stress. In contrast, fixed dunes are progressively sheltered from these abiotic stressors, resulting in more stable ecological conditions (Carboni et al., 2009; Fenu et al., 2012; Ruocco et al., 2014; Tozzi et al., 2021). Vegetation plays a fundamental role in shaping dune morphology by stabilizing sand and reducing its mobility. Particularly, shifting dunes constitute a highly selective habitat influenced by extreme maritime conditions (Clark, 1977; Sykes &

Wilson, 1991). Only a limited set of specialized vascular plants thrive here, exhibiting morphological and physiological features deep root systems and reduced leaf surfaces, adaptations crucial for minimizing water loss and ensuring survival under such harsh environmental conditions (Walker & Zinnert, 2022). This zone is also characterized by nutrient cycling and ecological responses to frequent disturbances (Cruz et al., 2023; Faucon et al., 2017). Successively along the zonation gradient moving inland from the shoreline, fixed dune plant communities tend to establish more permanent populations. As vegetation becomes progressively less exposed to harsh conditions derived to maritime influence, such as salt spray, strong winds, and sand burial, plant species exhibit a corresponding decline in stress tolerant strategies to these factors (Wiedemann & Pickart, 2004).

Associated with such environmental gradient and highly specialized biodiversity, coastal dune habitats offer a wide range of vital benefits to human society (MA, 2005; Drius et al., 2019). These benefits include the provision of ecosystem services (ES) with direct economic value, such as freshwater reserves stored within dune systems (Van Dijk, 1989), as well as essential regulating functions like water filtration and shoreline protection (Rhymes et al., 2015), coastal defense, nutrient cycling whose value is often reflected through the cost of human-made alternatives (Doody, 2013). In addition to these tangible services, coastal dunes offer important cultural ecosystem services, serving as spaces for tourism and recreational activities (Everard et al., 2010; Arkema et al., 2013; Drius et al., 2016; Durán & Moore, 2013; Feagin et al., 2015). They are frequently appreciated not only for their scenic and recreational appeal but also as natural refuges that foster a sense of solitude, contributing to psychological well-being (Everard et al., 2010). Beyond these widely acknowledged benefits, coastal dunes also deliver less commonly recognized services, including their role in buffering against wind and airborne particles and their contribution to local and global climate regulation (Drius et al., 2016). Moreover, due to the pronounced ecological gradient from sea to land, dunes support highly specialized biological communities. These habitats host unique assemblages of flora and fauna, sharing limited overlap with other terrestrial ecosystems (Acosta et al., 2009; Martínez et al., 2004). In terms of insect fauna, coastal dunes provide a reservoir of species that are very specialized to the extreme conditions of these environments. Coleoptera constitute by far the largest group in terms of both number of species and individuals; rigid and hardy teguments are an excellent preadaptation for successfully surviving in these hostile terrestrial environments (Fattorini et al., 2017). In

addition, other order of insects well represented are Hymenoptera, Neuroptera, Orthoptera, Neuroptera, Diptera, Hemiptera and Ortroptera (Audisio, 2012; Fattorini et al., 2021). Lepidoptera are reported to be less abundant than in other habitats, but well represented with thermophilous and xerophilic species in the different dune sectors. Among butterflies, the two most characteristic species are *Gegenes pumilio* and *G. nostrodamus*, which are related to grasses. Among moths, although there are few species exclusive to the dunes, they are frequented by many species, including migrant ones. One of the typical dune moths is the noctuid *Brithys crini*, whose larvae feed on *Pancratium maritimum* (Audisio, 2012; Fattorini et al., 2021).

The biodiversity inherent to dune vegetation not only holds intrinsic value (the so-called "existence value of biodiversity"; e.g., Drius et al., 2016; Stanisci et al., 2014), but also plays a crucial functional role in sustaining other ecosystem services, both directly, such as in erosion control, aerosol buffering, and recreational use (Martínez et al., 2004), and indirectly, by influencing climate regulation (Drius et al., 2016).

Despite their ecological and social importance, these habitats face severe vulnerability due to increasing anthropogenic pressures. Worldwide, and especially within the Mediterranean basin, coastal ecosystems are considered among the most threatened natural environments (Kutiel et al., 2000). Over recent decades, these areas have experienced significant biodiversity loss and structural simplification of habitats (Dolan and Walker, 2006), largely driven by escalating anthropogenic pressures (Curr et al., 2000; Brown et al., 2013), but coastal erosion and tourism are predominant (Iannantuono et al., 2004).

Based to the 4th Report under article 17 of the EU Habitats Directive 92/43/EEC (EEC 1992), in Italy, 88 % of coastal sand dunes ecosystems are in a bad conservation status, while the remaining 12 % is in inadequate conditions, and the trend is deteriorating for almost 70 % of them (Prisco et al., 2020). This alarming degradation affects particularly habitats like the "Shifting dunes with *Ammophila arenaria*," fundamental for dune formation and coastal erosion protection (La Bella et al., 2024). Along the Adriatic coast of Italy, multiple studies have highlighted that anthropogenic pressure alters both the structure and species composition of dune plant communities in several sites (Acosta et al., 2007, 2009; Carboni et al., 2009; Carranza et al., 2008; Stanisci et al., 2014).

As a result, many of the ecosystems are considered highly threatened and have been included within protected areas, such as Sites of Community Importance (SCIs) under the Natura 2000 Network, and the European Long-Term Ecosystems Research network

(eLTER). Their protection is primarily due to the coexistence of priority habitats and species of Community Importance as defined by the EU Habitats Directive (92/43/EEC). The Italian LTER network, which has been part of the European eLTER initiative since 2007, constitutes a structured and collaborative framework for long-term ecosystem observation. With over 300 sites across the country, it provides critical ecological data on terrestrial, freshwater, and marine systems. By promoting the harmonization of survey monitoring protocols of bio-ecological data, the network enhances data comparability across Europe, strengthens cooperation among institutions and stakeholders, and contributes to knowledge sharing, training, and integration in support of conservation efforts (Bertoni, 2012; Stoll et al., 2014). A protected site must satisfy two mains: representativeness, as it should represent the full variety of biodiversity, and persistence, as it should promote the long-term survival of biodiversity (Margules & Pressey, 2000).

Although many studies have focused on the analysis of plant communities (Acosta et al., 2009; Drius et al., 2016; Malavasi et al., 2016) and the specialized fauna hosted coastal dunes systems (Berardo et al., 2015; Fattorini et al., 2017; Villalobos Perna et al., 2024), little is known regarding community organization along the seashore-inland gradients for multiple taxonomic groups (Kühl et al., 2020; Rasino et al., 2024).

In particular, despite the prominent role of butterflies (Lepidoptera, Papilionoidea) or moths as important bioindicator in ecological research (Berg et al., 2013; New, 2004; Summerville et al. 2004; Luque et al., 2011; Uhl et al., 2016), and group sensitive to environmental change (Choi & Chun, 2009; Coulthard et al., 2019), little is known about butterfly and moths diversity in relation with vascular plant species and habitat variability across the seashore-inland environmental mosaic (Fantinato et al., 2018). This order of insect has ecologically important roles, as herbivores and as a prey for other insects, birds and bats (Vaughan 1997; van Klink et al., 2015; Enkhtur et al., 2017), and contributing significantly to pollination visiting flowers in order to take profit from their nectar (Krenn, 2010; Singh et al., 2022). As herbivores, larvae often display marked trophic specialization, relying on specific host plants, while adults typically remain within their native environments, highlighting their pronounced habitat fidelity (Wäckers et al., 2007; Lees & Zilli, 2019). Vegetation structure generates diverse microclimatic niches, while plant species with differing phenological stages offer lepidopterans a broad array of nutritional resources and oviposition sites (Dennis, 2004). Moreover, each plant community, through its unique species composition, supports distinct aspects of

lepidopteran ecological needs, encompassing thermal buffering, protection, reproductive substrates, and spatial heterogeneity (Dennis, 2010).

Biodiversity can be assessed across multiple spatial scales: α-diversity (alpha) refers to local level, β-diversity (beta) captures the turnover in species composition among communities and γ-diversity (gamma) to regional diversity (Whittaker, 1960, 1972; Cardoso et al., 2014). Conservation strategies that focus solely on identifying areas with high species richness (α-diversity) may overlook critical components of regional biodiversity. As emphasized by Socolar et al. (2016), effective conservation planning should adopt the principle of complementarity, placing emphasis on the selection of sites that, despite potentially lower richness, contribute unique species to the overall regional pool, thus recognizing the importance of β-diversity. Notably, the presence of areas with high species richness does not necessarily indicate the presence of taxa of conservation concern (Orme et al., 2005), whereas species-poor areas may host rare or threatened species of high conservation value (Harper et al., 2022). In addition, a cross-study congruence analysis is a promising approach for exploring diversity covariation patterns between two different biological groups (Rooney & Azeria 2015; Marignani et al., 2020). This strategy is particularly valuable in the context of biodiversity monitoring and conservation planning as it can help identify surrogate taxa or indicator groups. Statistical tools such as Mantel tests and Pearson correlation analyses are commonly employed to assess the strength and significance of these cross-taxon relationships, quantifying the correlation between community dissimilarity matrices derived from different taxa.

High cross-taxon congruence, defined by the spatial covariation in diversity and/or community composition patterns can provide insight into shared environmental drivers or biotic interactions (Rooney & Azeria, 2015). However, the degree of congruence often depends on the type of ecological data considered, such as presence/absence or abundance-based measures (Santi et al., 2016). Beyond their predictive utility, these methods provide insights into the underlying community assembly processes, helping to determine whether observed congruence reflects shared responses to environmental gradients and biotic interactions (Marignani et al., 2020; Zara et al., 2021). In this context, cross-taxon congruence not only improves monitoring efficiency, but also contributes to a more integrative understanding of ecosystem structure and function. Finally, exploring the relationships between moths and plant communities, considering both taxonomic composition and functional traits, offers a promising avenue for uncovering the ecological processes governing community assembly. Trait-based approaches, which enrich

traditional species-level analyses, have shown particular efficacy in identifying the environmental filters influencing species distributions along ecological gradients (Díaz & Cabido, 2001; Walker & Zinnert, 2022; Di Biase & Fattorini, 2025). Integrating functional trait analyses with novel ecological indicators, such as Disturbance Indicator Values (DI) and Ecological Indicator Values for Europe (EIVE) for plants and Life History Traits (LHT) for moths, offers a promising approach for exploring these dynamics (Potocký et al., 2018; Seifert et al., 2022; Dengler et al., 2023; Midolo et al., 2023).

The high vulnerability of biodiversity and increasing anthropogenic pressures on coastal dune mosaics, across multiple levels of biological organization (e.g., species, populations, communities, ecosystems), underscore the critical need for continuous monitoring and regular updates on their conservation status. Such monitoring efforts are claimed by several European regulations and directives (e.g., Habitat Directive 92/43/EEC, 1992) essential to support the design and implementation of effective management strategies aimed at safeguarding these unique habitats. Concurrently, identifying the key biotic and abiotic drivers shaping biodiversity patterns is crucial to developing targeted conservation interventions.

The present PhD research, is aimed investigate the biodiversity of diurnal and nocturnal Lepidoptera, and assessing their association with the characteristic dune zonation and specialized vegetation in Mediterranean coastal dune ecosystems. The study was conducted in a representative well preserved dune system inside a protected coastal Natura 2000 site Foce Trigno-Marina di Petacciato (IT7228221) (Molise Region), that is also a node of the European LTER network (IT20; https://deims.org/1835cda2-b56d-400a-b413-ab5c74086dc5) (Stanisci et al., 2014). This area represents a valuable biodiversity observatory, offering a representative model system for studying ecological processes and plant–insect interactions in Mediterranean coastal dune ecosystems.

The present research, seeks to contribute to a more comprehensive understanding of the ecological filters and interactions of these fragile habitats offering new insights supporting effective biodiversity conservation strategies. To achieve this, the research was guided by the following questions: (i) how do Lepidoptera respond to the abiotic environmental gradient of coastal dunes (dune zonation) in terms of taxonomic diversity and ecological traits? and, (ii) to what extent are these patterns influenced by the biotic gradient given by the composition and functional traits of the associated vegetation? Furthermore, the study explores how such responses vary across different lepidopteran

groups, contrasting diurnal and nocturnal assemblages, and examining variation within taxonomic levels such as families and superfamilies of nocturnal moths. It is hypothesized that Lepidoptera exhibit spatially and temporally heterogeneous patterns of habitat use across the dune mosaic. By investigating the relationships between vegetation composition, dune zonation, and both the taxonomic and functional dimensions of moth diversity, this research provide valuable ecological insights that can inform the identification of conservation priorities within these fragile and highly vulnerable coastal landscapes.

This PhD thesis is structured into 4 main chapters and one of miscellaneous research carried out during the PhD thesis:

In **Chapter 1** we present the faunistic list of both diurnal and nocturnal Lepidoptera sampled in the "Foce Trigno–Marina di Petacciato" Natura 2000 site (Molise, Central Italy, Adriatic coast), a protected coastal area that is also part of the European LTER network. The study identified 18 butterfly species and 205 moth species, with 48 taxa reported for the first time in the Molise region. A notable proportion of species were habitat-specific, though overall diversity patterns between shifting and fixed dunes were comparable. The resulting faunistic list serves as an essential reference for regional biodiversity assessments and conservation planning in Mediterranean coastal dune ecosystems.

In **Chapter 2** we focused on butterfly-plant associations across shifting and fixed dunes using diversity indices, Species Abundance Distribution (SAD) models, beta-diversity analyses, and cross-taxon correlation. The results show that both butterflies and plants exhibit higher diversity on fixed dunes compared to shifting dunes and both assemblages follow a geometric SAD pattern, reflecting simplified communities shaped by environmental stress. Species turnover across dune zones reveals the presence of habitat-specific taxa. Overall, the study highlights that both plant and butterfly communities respond to the shore-inland environmental gradient, forming distinct communities shaped by the combined influence of abiotic filters and biotic interactions. The observed spatial variation in species richness and composition underscores the need for conservation strategies that consider the entire dune zonation and its role in sustaining biodiversity and at broader scales.

In **Chapter 3** we analyzed diversity patterns of moth family Geometridae and vascular plants a well-preserved Mediterranean coastal dune system on the Adriatic coast of central Italy. Moth and plant communities were surveys in two different dune sectors in three replicates: the shifting dunes and the fixed dunes. Moths were collected using traps equipped with UV LEDs. Vegetation surveys were conducted using plots with a stratified random protocol. For both taxa, we investigated differences between dune sectors in species richness, species abundance distribution, and trait characteristics. To assess variation and covariation within and between moth and plant traits, we applied a Two-block Partial Least Squares (2B-PLS) analysis. Finally, we assessed the congruence between moths and plants between sectors. Differences in plant ecological features and moth ecological traits between the two dune zones highlights the close interplay between environmental gradients and plant community structure. Our findings identify the peculiar habitat requirements of geometrid moths, with cycles closely tied to plant communities, suggests that they may represent valuable indicators in ecosystem functioning.

In **Chapter 4** we focused on Noctuoidea, the largest superfamily of Lepidoptera for investigates their diversity and functional composition along the coastal dune zonation. The assemblage of noctuoid moths hosted by eLTER IT20 site is rich in species and our trait-based analyses revealed clear ecological covariation between dune zones, with fixed dunes supporting larger, trophic-generalist moths associated with woody plants, and shifting dunes hosted smaller and multivoltine species linked to herbaceous and disturbance-adapted plant communities. This chapter offer improve our understanding of how lepidopteran assemblages respond to environmental and disturbance conditions.

Chapter 1 - Lepidoptera of the 'Foce Trigno–Marina di Petacciato' Natura 2000 site, a European LTER area in Central Italy

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Lepidoptera of the 'Foce Trigno–Marina di Petacciato' Natura 2000 site, a European LTER area in Central Italy

Abstract

We present a faunistic list of both diurnal and nocturnal Lepidoptera sampled in the "Foce Trigno–Marina di Petacciato" Natura 2000 site (Molise, Central Italy, Adriatic coast), a protected coastal area that is also part of the European Long-Term Ecosystem Research (eLTER) network. Sampling was conducted over one year in both shifting and fixed dunes. UV light traps were used to collect moths, while butterflies were surveyed following the European Butterfly Monitoring Scheme. We identified 18 species of butterflies belonging to five families (Papilionidae, Hesperiidae, Pieridae, Lycaenidae, and Nymphalidae) and 205 species of moths belonging to 17 families (Tineidae, Alucitidae, Pterophoridae, Tortricidae, Coleophoridae, Cossidae, Yponomeutidae, Pyralidae, Crambidae, Drepanidae, Sphingidae, Lasiocampidae, Geometridae, Notodontidae, Erebidae, Nolidae and Noctuidae). 48 species are new records for the Molise region. Forty-three species (19%) were exclusive to the shifting dunes and 69 species (31%) were exclusive to the fixed dunes. 156 species were recorded in the shifting dunes and 180 in the fixed dunes. Although there were minor variations in species richness between the two zones for some groups, there was no consistent or statistically significant pattern across all families. Thus, the two zones support comparable levels of butterfly and moth diversity at the family level, although some weak trends may warrant further investigation. The resulting list, albeit likely not exhaustive, can serve as a valuable resource for entomologists, ecologists, conservation biologists, and environmental managers in biodiversity monitoring and the conservation of the study area and Mediterranean dune ecosystems more broadly.

Keywords: biodiversity conservation, butterflies, moths, dunes, Rhopalocera, Heterocera, Mediterranean ecosystems

Introduction

Coastal dune landscapes are highly dynamic and ecologically valuable mosaics (Acosta et al. 2009). They are shaped by strong environmental gradients, that give rise to high diversity of habitats, and specialized flora and fauna assemblages. Coastal dunes represent dynamic ecological interface between marine and terrestrial realms (Schlacher et al. 2007; Bazzichetto et al. 2016; Torca et al. 2019). Anthropogenic pressures such as urbanization, tourism and climate change have led to a severe decline in dune habitat quality (Hesp & Martínez 2007; Defeo et al. 2009; Malavasi et al. 2018; Fattorini 2021), highlighting the urgent need for comprehensive biodiversity documentation and monitoring. Despite their importance for biodiversity conservation and ecosystem functioning (Drius et al. 2016; Malavasi et al. 2016), the insect communities of Mediterranean coastal dunes remain poorly studied and underrepresented in ecological research (Fattorini 2021).

Lepidoptera (butterflies and moths) represent one of the most diverse and ecologically important insect orders (Scoble 1992; Boggs et al. 2003; New 2013; Dennis 2020). They fulfill numerous essential roles in ecosystems including herbivory (primary consumers), prey for birds and bats (food for secondary consumers), pollination (essential mutualists), acting as indicators of ecosystem health and environmental change (Summerville & Crist 2004; Truxa & Fiedler 2012; Singh et al. 2022). Due to their specialized association with larval host plants and their sensitivity to microhabitat availability and conditions, Lepidoptera may reflect plant community composition and integrity, thus being potentially useful indicators of environmental quality (Uhl et al. 2015; Rasino et al. 2024).

The Italian butterfly fauna is generally very well known (Balletto et al., 2023), whereas knowledge of moths remains comparatively more limited (Infusino et al. 2017a). The lepidopteran fauna of the Molise region (Central Italy) has been the subject of few dedicated faunistic investigations. Relevant contributions include the work by Sciarretta & Zilli (1998) and Sciarretta & Parenzan (1998), which provided the first structured records of noctuid, bombycid, and sphingid moths from the region, and the study by Sciarretta & Raineri (2001), which expanded the known diversity of geometrids through focused sampling in selected habitats, including coastal dune systems. Butterfly diversity in the region has been documented through a faunistic overview (Sciarretta & Parenzan 2001), but fine species distribution remains still poorly documented (see, for example, the relatively small number of records included in Balletto et al. 2006). In general,

available information provide scattered species records and research documenting site-specific assemblages – essential to understand the structure and temporal dynamics of local lepidopteran communities – remains largely insufficient. Micro-moths include the most critical groups, as they have received little attention and remain poorly studied to date. Among these, some information regarding Tortricidae and Pterophoridae is provided by Trematerra (1987, 2003) and Trematerra et al. (2006).

Despite its very small extent (about 35 km), the Molise coast still preserves sites of high conservation interest (Acosta et al. 2009). Documenting the lepidopteran diversity of such sites is of paramount importance to improve our faunal knowledge on a regional scale and to obtain a benchmark for future research. To this end we performed an annual systematic sampling in the dune system of a costal Nature 2000 site (Foce Trigno-Marina di Petacciato) which is also part of the European Long-Term Ecosystem Research network. By using an integrative approach covering the entire order Lepidoptera, we were able to compile a list of both butterfly and moth species present in this protected area and to investigate their association with dune zonation

Materials and methods

Study area

The study was conducted in the dune system of the Natura 2000 site Foce Trigno-Marina di Petacciato (IT7228221). This protected area is located on the coast of the Molise region and is included in the European Long-Term Ecosystem Research network (LTER IT20; https://deims.org/1835cda2-b56d-400a-b413-ab5c74086dc5) (Stanisci et al. 2014; Capotondi et al. 2021) (Fig. 1A.B). The coastal area under study is characterized by narrow belts of Holocene dunes, where biotic conditions change markedly from the shoreline toward the inland sectors (Carranza et al. 2008; Drius et al. 2013). Vegetation in this stretch of the Adriatic coast is notably well conserved (Drius et al. 2019), hosting a variety of dune habitats recognized as being of high conservation value at the European level (European Commission 2013): 1210-Annual vegetation of drift lines; 2110-Embryonic shifting dunes; 2120-Shifting dunes along the shoreline with *Calamagrostis*

arenaria; 2130-Grey dunes with herbaceous vegetation (Stanisci et al. 2014; Rivieccio 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).

Butterfly and moth data were collected in three sites (Figure 1B) through fortnightly sampling campaigns conducted for one year. In each site, data were collected from two zones: the shifting/transition dune (EU Habitats 2120 and 2230), morphologically characterized by the presence of a consolidating sandy substrate and dominated by herbaceous vegetation, and the fixed dune (EU Habitat 2260), characterized by more stable substrates, where a relatively high number of woody species occur (Fig. 1C).

Sampling methods

Butterfly sampling was conducted following the European Butterfly Monitoring Scheme (eBMS; Pollard & Yates 1993). At each study site, surveys were carried out along two georeferenced 200 m transects, oriented parallel to the shoreline: one located in the shifting dune and the other in the fixed dune. Transects were walked every 15 days from late April to early October 2022, between 09:00 and 16:00, under favorable weather conditions (i.e., absence of rain and strong winds). In total, 54 sampling sessions were completed – corresponding to nine sampling campaigns across three sites and two zones (shifting and fixed dunes).

Nocturnal species were collected using UV LED light traps (Infusino et al. 2017b). During each sampling session, three light traps were active for one night every 15 days at three different points in the same dune zone, then moved to the other zone. Light traps were settled fortnightly from November 2021 to December 2022. Sampling nights have been chosen during weather conditions favorable to moth activity, i.e., temperature near or higher than the mean of the period, no or low wind, no or light rain, one week before or after the new moon occurrence (Lenco et al. 2020). Since the shifting and fixed zones of the dune occupy a strip several tens of meters wide, a black panel was placed on the side of the trap facing the adjacent dune zone, to prevent the light from attracting individuals from there. Collected moths were subsequently anesthetized using cotton swabs soaked in ethyl acetate and placed in containers for transport to the laboratory for

preparation and identification. Specimens were then prepared and deposited in the entomological collection of the Department of Agriculture, Environment, and Food Sciences at the University of Molise (Campobasso, Italy).

Species identification and taxonomy

Species identification was primarily based on the wing patterns. In cases where external morphology alone did not allow reliable identification, genitalia were extracted and examined. Butterfly and moth taxonomy followed Balletto et al. (2014) and Rennwald et al. (2023), respectively.

Statistical Analyses

To compare patterns of species richness between shifting and fixed dunes, we employed two complementary statistical approaches. A paired samples Wilcoxon test was used to assess differences in species richness per family between the two zones. Effect size (*r*) for the Wilcoxon test was calculated as the *Z* statistic divided by the square root of the sample size *N* to aid interpretation of biological relevance:

$$r = \frac{Z}{\sqrt{N}}.$$

Additionally, a chi-square test of independence was applied to evaluate the association between lepidopteran families and zones, with Cramér's V used to estimate effect size:

$$V = \sqrt{\frac{\chi^2/N}{\min(k-1,\ r-1)}},$$

where *k* is the number of columns, and *r* is the number of rows. β-diversity was calculated to quantify species turnover between the two zones, both the Dice–Sørensen (β_{sor}) and Simpson indices (β_{sim}) were calculated (see Baselga, 2010; Lenco et al. 2020):

$$\beta_{sor} = \frac{b + c}{2a + b + c}$$

$$\beta_{sor} = \frac{\min(b,c)}{a + \min(b+c)},$$

where *a* is the number of species common to both zones, *b* is the number of species that occur in the first zone but not in the second and *c* is the number of species that occur in the second zone but not in the first.



Fig. 1 - Study area. A. Location of the study area ('Foce Trigno-Marina di Petacciato' Natura 2000 site). B. Sampling sites, including shifting and fixed dune zones. C. Zones sampled: shifting (i) and fixed (ii) dunes.

Results

The following list includes all species recorded during the sampling period. Families are listed in systematic order according to Balletto et al., 2024, while genera and species within them follow alphabetical order. For each species, the sector (S: Shifting dunes; F: Fixed dunes) and the date of observation/collection are reported. Species marked with an asterisk (*) are new records for the Molise Region.

Family Tineidae

Monopis neglecta (Šumpich & Liška, 2011) *
Records. F: 30 Apr 2022.
Morophaga morellus (Duponchel, 1838) *
Records. S: 27 May 2022; F: 5 Sep 2022.

Family Alucitidae

Alucita grammodactyla (Zeller, 1841) *
Records. S: 10 May 2022; 28 Jun 2022; 29 Jun 2022; 9 Jul 2022; F: 27 Jun 2022; 25 Jul 2022; 27 Sep 2022.
Alucita palodactyla (Zeller, 1847) *
Records. S: 29 Apr 2022; 10 May 2022; 26 Jul 2022; F: 10 Jul 2022.

Family Pterophoridae
Emmelina monodactyla (Linnaeus, 1758)
Records. S: 29 Jun 2022; 6 Sep 2022; F: 27 Jun 2022; 25 Jul 2022; 24 Nov 2022.
Stenoptilia pterodactyla (Linnaeus, 1761)
Records. S: 10 May 2022.

Family Tortricidae
Aethes williana (Brahm, 1791)
Records. S: 10 May 2022; 26 Jul 2022; 5 Aug 2022; 30 Aug 2022.
Agapeta hamana (Linnaeus, 1758)
Records. S: 28 Jun 2022.
Bactra venosana (Zeller, 1847)
Records. S: 10 May 2022; 4 Oct 2022; F: 9 May 2022.
Clepsis consimilana (Hübner, 1817)
Records. F: 9 May 2022; 26 May 2022; 6 Jun 2022; 27 Jun 2022.
Cnephasia pasiuana (Hübner, 1799)
Records. F: 26 May 2022.
Cnephasia stephensiana (Doubleday, 1849)
Records. S: 27 May 2022.
Cochylis sannitica (Trematerra, 1995)
Records. F: 10 Jul 2022.
Diceratura roseofasciana (Mann, 1855)
Records. F: 10 Jul 2022.
Epinotia thapsiana (Zeller, 1847)
Records. S: 6 Sep 2022; F: 29 Aug 2022; 5 Sep 2022.
Piniphila bifasciana (Haworth, 1811)
Records. S: 27 May 2022; F: 26 May 2022.

Family Coleophoridae
Coleophora ditella (Zeller, 1849) *
Records. S: 10 May 2022; F: 26 May 2022.
Coleophora vulnerariae (Zeller, 1839) *
Records. F: 30 Jun 2022.

Family Cossidae
Parahypopta caestrum (Hübner, [1808])
Records. S: 27 May 2022; 9 Jul 2022; 27 Jun 2022; 28 Jun 2022); F: 06 Jun 2022; 27 Jun 2022.
Phragmataecia castaneae (Hübner, [1790])
Records. S: 27 May 2022; 28 Jun 2022; F: 26 May 2022.

Family Yponomeutidae

Yponomeuta rorrella (Hübner, 1796) *

Records. S: 5 Aug 2022; F: 27 Jun 2022; 25 Jul 2022.

Family Papilionidae

Papilio machaon (Linnaeus, 1758)

Records. S: 10 Jul 2022; F: 10 Jul 2022; 20 Jul 2022.

Family Hesperiidae

Gegenes nostrodamus (Fabricius, 1793*)*

Records. S: 6 Sep 2022.

Thymelicus sylvestris (Poda, 1761*)*

Records. F: 27 May 2022; 7 Jun 2022.

Family Pieridae

Colias crocea (Geoffroy, 1785)

Records. S: 29 Sep 2022; F: 27 May 2022.

Pieris rapae (Linnaeus, 1758)

Records. S: 10 Jul 2022; F: 30 Apr 2022; 7 Jun 2022; 10 Jul 2022; 27 Jul 2022; 29 Sep 2022.

Pontia edusa (Fabricius, 1777)

Records. S: 7 Jun 2022; 10 Jul 2022; F: 30 Apr 2022; 27 May 2022; 7 Jun 2022; 29 Sep 2022;

Family Lycaenidae

Aricia agestis (Denis & Schiffermüller, 1775)

Records. S: 29 Sep 2022; F: 29 Sep 2022.

Leptotes pirithous (Linnaeus, 1767)

Records. S: 5 Oct 2022; 29 Sep 2022; F: 29 Sep 2022.

Lycaena phlaeas (Linnaeus, 1761)

Records. F: 27 Jul 2022.

Polyommatus bellargus (Rottemburg, 1775)

Records. S: 7 Jun 2022; 29 Sep 2022; 5 Oct 2022; F: 29 Sep 2022; 5 Oct 2022.

Polyommatus icarus (Rottemburg, 1775)

Records. S: 30 Aug 2022; F: 27 Jul 2022; 30 Aug 2022.

Family Nymphalidae

Coenonympha pamphilus (Linnaeus,1758)

Records. F: 30 Apr 2022; 5 May 2022.

Hipparchia semele (Linnaeus,1758)

Records. F: 29 Apr 2022.

Lasiommata megera (Linnaeus,1767)

Records. F: 30 Apr 2022; 7 Jun 2022; 27 Jul 2022; 29 Sep 2022.

Maniola jurtina (Linnaeus,1758)

Records. F: 5 May 2022.

Melanargia galathea (Linnaeus,1758)

Records. S: 7 Jun 2022.

Pyronia cecilia (Vallantin, 1894)
Records. S: 10 Jul 2022; F: 10 Jul 2022; 27 Jul 2022, 30 Aug 2022; 6 Sep 2022.
Vanessa atalanta (Linnaeus, 1758)
Records. F: 27 May 2022.

Family Pyralidae
Acrobasis legatea (Haworth, 1811) *
Records. S: 28 Sep 2022; F: 6 Jun 2022.
Acrobasis suavella (Zincken, 1818) *
Records. S: 29 Apr 2022; F: 30 Apr 2022.
Carda furcatella (Herrich-Schäffer, 1849) *
Records. S: 10 May 2022; 27 May 2022; F: 9 May 2022; 26 May 2022.
Dioryctria mendacella (Staudinger, 1859) *
Records. F: 26 May 2022; 25 Jul 2022; 4 Aug 2022.
Dioryctria pineae (Staudinger, 1859) *
Records. S: 30 Aug 2022.
Ematheudes punctella (Treitschke, 1833) *
Records. S: 28 Jun 2022.
Endotricha flammealis (Denis & Schiffermüller, 1775) *
Records. S: 5 Aug 2022; F: 10 Jul 2022; 25 Jul 2022; 5 Sep 2022.
Etiella zinckenella (Treitschke, 1832) *
Records. S: 28 Jun 2022; F: 27 Jun 2022; 10 Jul 2022; 4 Aug 2 2022.
Gymnancyla canella (Denis & Schiffermüller, 1775) *
Records. S: 5 Aug 2022; 30 Aug 2022; F: 5 Sep 2022.
Hypsopygia costalis (Fabricius, 1775) *
Records. S: 5 Aug 2022; F: 27 Sep 2022; 3 Oct 2022.
Hypsopygia incarnatalis (Zeller, 1847) *
Records. S: 9 Jul 2022.
Hypsopygia rubidalis (Denis & Schiffermüller, 1775) *
Records. F: 27 Jun 2022.
Laodamia faecella (Zeller, 1839) *
Records. S: 30 Aug 2022.
Melathrix coenulentella (Zeller, 1846) *
Records. S: 10 May 2022; 7 Jun 2022; 28 Jun 2022; 9 Jul 2022; 30 Aug 2022; 6 Sep 2022; F: 6 Jun 2022; 27 Jun 2022; 10 Jul 2022; 29 Aug 2022; 5 Sep 2022.
Myelois circumvoluta (Fourcroy, 1785) *
Records. F: 27 Jun 2022.
Polyocha venosa (Zeller, 1847) *
Records. S: 9 Jul 2022; 5 Aug 2022; F: 4 Aug 2022; 3 Oct 2022.
Psorosa dahliella (Treitschke, 1832) *
Records. S: 6 Sep 2022; F: 4 Aug 2022.

Family Crambidae
Achyra nudalis (Hübner, 1796) *
Records. S: 6 Sep 2022; F: 29 Aug 2022.
Agriphila geniculea (Haworth, 1811) *

Records. F: 27 Sep 2022.

Agriphila straminella (Denis & Schiffermüller, 1775) *

Records. F: 5 Sep 2022.

Aporodes floralis (Hübner, 1809) *

Records. S: 5 Aug 2022.

Dolicharthria punctalis (Denis & Schiffermüller, 1775) *

Records. S: 28 Sep 2022; F: 10 Jul 2022; Sep 2022.

Euchromius bellus (Hübner, 1796) *

Records. S: 28 Jun 2022; 30 Aug 2022; F: 27 June 2022; 10 Jul 2022; 25 Jul 2022; 4 Aug 2022; 5 Sep 2022.

Eudonia truncicolella (Stainton, 1849) *

Records. S: 26 Mar 2022; 2 Nov 2022; 26 Nov 2022; F: 24 Oct 2022; 1 Nov 2022.

Evergestis isatidalis (Duponchel, 1833) *

Records. S: 26 Nov 2022; F: 24 Oct 2022; 1 Nov 2022; 24 Nov 2022.

Evergestis politalis (Denis & Schiffermüller, 1775) *

Records. S: 5 Aug 2022; F: 3 Oct 2022.

Hydriris ornatalis (Duponchel, 1832) *

Records. F: 3 Oct 2022.

Mecyna asinalis (Hübner, 1819) *

Records. F: 24 Oct 2022.

Metasia ophialis (Treitschke, 1829) *

Records. S: 28 Jun 2022.

Nomophila noctuella (Denis & Schiffermüller, 1775) *

Records. S: 28 Sep 2022; 4 Oct 2022; F: 27 Jun 2022; 10 Jul 2022; 4 Aug 2022; 5 Sep 2022; 27 Sep 2022; 3 Oct 2022.

Palpita vitrealis (Rossi, 1794)

Records. S: 26 Jul 2022; 6 Sep 2022; F: 3 Oct 2022; 24 Oct 2022.

Paracorsia repandalis (Denis & Schiffermüller, 1775) *

Records. S: 29 Apr 2022; 27 May 2022; F: 26 May 2022.

Pediasia contaminella (Hübner, 1796) *

Records. S: 30 Aug 2022.

Platytes alpinella (Hübner, 1813) *

Records. S: 6 Sep 2022; F: 5 Sep 2022.

Pyrausta aurata (Scopoli, 1763) *

Records. F: 27 Sep 2022.

Pyrausta nanalis (Christoph, 1888) *

Records. S: 5 Aug 2022.

Schoenobius gigantella (Denis & Schiffermüller, 1775) *

Records. S: 6 Sep 2022.

Sitochroa palealis (Denis & Schiffermüller, 1775) *

Records. F: 25 Jun 2022.

Tegostoma comparalis (Hübner, 1796) *

Records. S: 30 Aug 2022.

Family Drepanidae

Watsonalla uncinula (Borkhausen, 1790)

Records. S: 27 Jun 2022; 25 Jul 2022; 5 Aug 2022; 27 Sep 2022; 24 Oct 2022; F: 4 Aug 2022; 3 Oct 2022.

Family Sphingidae

Agrius convolvuli (Linnaeus, 1758)

Records. S: 28 Sep 2022.

Hyles euphorbiae (Linnaeus, 1758)

Records. S: 22 Feb 2022; 13 Apr 2022; 10 May 2022; 27 May 2022; 7 Jun 2022; 29 Jun 2022; 9 Jul 2022; 26 Jul 2022; 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; 28 Sep 2022; 4 Oct 2022; F: 09 May 2022; 30 Jun 2022; 29 Aug 2022; 5 Sep 2022; 24 Oct 2022.

Hyles livornica (Esper, 1780)

Records. S: 10 May 2022; 27 May 2022; 28 Jun 2022; F: 26 May 2022.

Laothoe populi (Linnaeus, 1758)

Records. S: 10 May 2022; F: 27 Jun 2022.

Family Lasiocampidae

Lasiocampa quercus (Linnaeus, 1758)

Records. S: 6 Sep 2022.

Lasiocampa trifolii (Denis & Schiffermüller, 1775)

Records. S: 28 Sep 2022; F: 27 Sep 2022.

Pachypasa otus (Drury, 1773) *

Records. S: 5 Aug 2022.

Family Geometridae

Agriopis leucophaearia (Denis & Schiffermüller, 1775)

Records. F: 10 Feb 2022.

Ascotis selenaria (Denis & Schiffermüller, 1775)

Records. S: 28 Jun 2022; F: 27 Jun 2022; 25 Jul 2022; 10 Jul 2022; 4 Aug 2022.

Aspitates ochrearia (Rossi, 1794)

Records. S: 28 Sep 2022; F: 12 Apr 2022.

Chiasmia aestimaria (Hübner, 1809)

Records. F: 5 Sep 2022.

Colotois pennaria (Linnaeus, 1761)

Records. F: 1 Nov 2022; 24 Nov 2022.

Crocallis elinguaria (Linnaeus, 1758)

Records. F: 3 Oct 2022.

Cyclophora puppillaria (Hübner, 1799)

Records. F: 27 June 2022; 30 June 2022; 4 Aug 2022; 3 Oct 2022; 24 Oct 2022.

Eucrostes indigenata (de Villers, 1789)

Records. S: 27 May 2022; 28 June 2022; 26 July 2022; 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; F: 27 Jun 2022; 25 Jul 2022; 4 Aug 2022; 29 Aug 2022; 5 Sep 2022; 3 Oct 2022.

Eupithecia centaureata (Denis & Schiffermüller, 1775)

Records. S: 30 Aug 2022; 6 Sep 2022; F: 25 June 2022; 29 Jul 2022; 5 Sep 2022; 27 Sep 2022.

Eupithecia dodoneata (Guenée, 1858)

Records. F: 30 Apr 2022.

Gerinia honoraria ([Denis & Schiffermüller], 1775)
Records. F: 27 Sep 2022; 3 Oct 2022; 24 Nov 2022.
Horisme tersata (Denis & Schiffermüller, 1775)
Records. S: 28 June 2022; F: 9 May 2022.
Idaea aversata (Linnaeus, 1758)
Records. F: 5 Sep 2022.
Idaea consanguinaria (Lederer, 1853)
Records. S: 28 Jun 2022.
Idaea degeneraria (Hübner, 1799)
Records. S: 10 May 2022; 27 May 2022; 5 Aug 2022; 30 Aug 2022; 28 Sep 2022; F: 26 May 2022; 30 Jun 2022; 5 Sep 2022.
Idaea elongaria (Rambur, 1833)
Records. S: 6 Sep 2022; F: 29 Aug 2022.
Idaea filicata (Hübner, 1799)
Records. S: 27 May 2022; 5 Aug 2022; F: 30 Apr 2022; 26 May 2022; 25 Jul 2022.
Idaea mediaria (Hübner, 1819)
Records. S: 7 Jun 2022.
Idaea obsoletaria (Rambur, 1833)
Records. S: 10 May 2022; 27 May 2022; 28 Jun 2022; 26 Jul 2022; F: 26 May 2022; 25 Jul 2022.
Idaea rubraria (Staudinger, 1901)
Records. F: 4 Aug 2022.
Idaea seriata (Schrank, 1802)
Records. F: 4 Aug 2022.
Idaea subsericeata (Haworth, 1809)
Records. F: 29 Aug 2022.
Idaea rusticata (Denis & Schiffermüller, 1775)
Records. S: 28 Jun 2022; 5 Aug 2022; 6 Sep 2022; F: 29 Aug 2022; 5 Sep 2022; 3 Oct 2022.
Larentia clavaria (Haworth, 1809)
Records. S: 29 Jun 2022; 2 Nov 2022.
Ligdia adustata (Denis & Schiffermüller, 1775)
Records. S: 28 Jun 2022; F: 27 Jun 2022; 10 Jul 2022.
Lycia florentina (Stefanelli, 1882) (Figure 2C)
Records. S: 13 Jun 2022.
Lycia hirtaria (Clerck, 1759)
Records. F: 25 Mar 2022.
Menophra abruptaria (Thunberg, 1792)
Records. F: 30 Dec 2021.
Opisthograptis luteolata (Linnaeus, 1758)
Records. F: 3 Oct 2022.
Pennithera firmata (Hübner, 1822)
Records. F: 24 Oct 2022.
Peribatodes rhomboidaria (Denis & Schiffermüller, 1775)
Records. S: 28 Sep 2022; F: 26 May 2022; 27 Jun 2022; 10 Jul 2022; 5 Sep 2022; 27 Sep 2022; 3 Oct 2022; 24 Oct 2022.

Peribatodes umbraria (Hübner, 1809)
Records. S: 27 May 2022; F: 3 Oct 2022.
Rhodometra sacraria (Linnaeus, 1767)
Records. S: 6 Sep 2022; 4 Oct 2022; 25 Oct 2022; 2 Nov 2022; F: 4 Aug 2022; 24 Oct 2022.
Scopula (Calothysanis) imitaria (Hübner, 1799)
Records. F: 4 Aug 2022.
Scopula (Calothysanis) marginepunctata (Goeze, 1781)
Records. S: 10 May 2022; 29 Jun 2022; 5 Aug 2022; 28 Sep 2022; 25 Oct 2022; F: 30 Apr 2022; 27 Sep 2022; 24 Oct 2022.
Scopula (Calothysanis) minorata (Boisduval, 1833)
Records. F: 3 Oct 2022.
Scopula (Scopula) ornata (Scopoli, 1763)
Records. S: 30 Aug 2022.
Synopsia sociaria (Hübner, 1799)
Records. S: 27 May 2022; F: 26 May 2022.
Thalera fimbrialis (Scopoli, 1763)
Records. S: 28 Jun 2022; F: 27 Jun 2022.

Family Notodontidae
Thaumetopoea pityocampa (Denis & Schiffermüller, 1775)
Records. S: 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; F: 4 Aug 2022; 29 Aug 2022.

Family Erebidae
Arctia villica (Linnaeus, 1758)
Records. S: 29 Apr 2022.
Catocala dilecta (Hübner, 1808)
Records. S: 28 Sep 2022.
Catocala elocata (Esper, 1787)
Records. S: 28 Sep 2022.
Catocala nymphagoga (Esper, 1787)
Records. F: 27 Jun 2022.
Clytie illunaris (Hübner, 1813)
Records. S: 9 Jul 2022; F: 26 May 2022; 27 Jun 2022; 10 Jul 2022.
Cymbalophora pudica (Esper, 1785)
Records. S: 6 Sep 2022; 28 Sep 2022; 4 Oct 2022; F: 27 Sep 2022; 03 Oct 2022.
Diaphora mendica (Clerck, 1759)
Records. S: 29 Apr 2022; F: 30 Apr 2022.
Dysauxes famula (Freyer, 1836)
Records. S: 5 Aug 2022; 30 Aug 2022; 4 Oct 2022; F: 27 Jun 2022; 10 Jul 2022; 25 Jul 2022; 4 Aug 2022; 5 Sep 2022; 27 Sep 2022; 03 Oct 2022; 24 Oct 2022.
Dysgonia algira (Linnaeus, 1767)
Records. S: 30 Aug 2022; 6 Sep 2022; F: 27 Jun 2022; 10 Jul 2022.
Eilema caniola (Hübner, 1808)
Records. S: 27 May 2022; 28 Jun 2022; 9 Jul 2022; 30 Jul 2022; 28 Sep 2022; 4 Oct 2022; 25 Oct 2022; F: 26 May 2022; 27 Jun 2022; 04 Aug 2022; 5 Sep 2022; 27 Sep 2022; 03 Oct 2022; 24 Oct 2022.

Eublemma purpurina (Denis & Schiffermüller, 1775)
Records. S: 6 Sep 2022; 4 Oct 2022.
Euplagia quadripunctaria (Poda, 1761)
Records. S: 26 Jul 2022; F: 30 Apr 2022; 10 Jul 2022.
Hypena lividalis (Hübner, 1796)
Records. F: 29 Aug 2022; 24 Oct 2022.
Lithosia quadra (Linnaeus, 1758)
Records. F: 4 Aug 2022
Nodaria nodosalis (Herrich-Schäffer, 1851) *
Records. F: 3 Oct 2022; 1 Nov 2022.
Phragmatobia fuliginosa (Linnaeus, 1758)
Records. S: 28 Jun 2022; 26 Jul 2022; 28 Sep 2022; F: 30 Apr 2022; 9 May 2022;27 Sep 2022.
Prodotis stolida (Fabricius, 1775)
Records. S: 10 May 2022; 30 Aug 2022; 6 Sep 2022; 28 Sep 2022; F: 25 Jul 2022.
Zebeeba falsalis (Herrich-Schäffer, 1839)
Records. F: 26 May 2022; 27 Jun 2022; 10 Jul 2022; 29 Aug 2022; 5 Sep 2022; 27 Sep 2022.

Family Nolidae
Nola chlamitulalis (Hübner, 1813)
Records. S: 29 Apr 2022; 10 May 2022; 26 Jul 2022; F: 9 May 2022; 29 Aug 2022.

Family Noctuidae
Acontia lucida (Hufnagel, 1767)
Records. S: 5 Aug 2022; 28 Jun 2022.
Acontia trabealis (Scopoli, 1763)
Records. S: 28 Jun 2022; 26 Jul 2022; 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; F: 27 Jun 2022; 29 Aug 2022.
Acronicta rumicis (Linnaeus, 1758)
Records. F: 10 Jul 2022.
Agrochola lota (Clerck, 1759)
Records. F: 24 Nov 2022.
Agrochola lychnidis (Denis & Schiffermüller, 1775)
Records. F: 1 Nov 2022; 24 Nov 2022.
Agrotis catalaunensis (Millière, 1873)
Records. F: 30 Apr 2022; 3 Oct 2022.
Agrotis exclamationis (Linnaeus, 1758)
Records. S: 5 Aug 2022; F: 4 Aug 2022.
Agrotis ipsilon (Hufnagel, 1766)
Records. F: 27 Jun 2022; 4 Aug 2022; 3 Oct 2022.
Agrotis puta (Hubner, 1803)
Records. S: 13 Apr 2022; 28 Sep 2022; 4 Oct 2022; F: 12 Apr 2022; 30 Apr 2022; 27 Sep 2022; 3 Oct 2022.
Agrotis segetum (Denis & Schiffermüller, 1775)
Records. S: 9 Jul 2022; F: 27 Jun 2022; 10 Dec 2021.

Agrotis trux (Hubner, 1824)
Records. S: 30 Aug 2022; 28 Sep 2022; 4 Oct 2022; F: 4 Aug 2022; 29 Aug 2022; 5 Sep 2022; 27 Sep 2022; 3 Oct 2022; 24 Oct 2022.
Allophyes corsica (Spuler, 1905)
Records. F: 1 Nov 2022; 24 Nov 2022.
Ammoconia senex (Geyer, 1828)
Records. F: 24 Oct 2022; 1 Nov 2022.
Amphipyra pyramidea (Linnaeus, 1758)
Records. F: 29 Aug 2022; 27 Sep 2022.
Amphipyra tragopoginis (Clerck, 1759)
Records. S: 28 Jun 2022; 28 Sep 2022.
Anarta trifolii (Hufnagel, 1766)
Records. S: 6 Sep 2022; 28 Sep 2022.
Aporophyla nigra (Haworth, 1809)
Records. S: 27 May 2022; 25 Oct 2022; 2 Nov 2022; F: 24 Oct 2022; 1 Nov 2022.
Athetis hospes (Freyer, 1831)
Records. S: 26 Jul 2022.
Autographa gamma (Linnaeus, 1758)
Records. S: 26 Mar 2022; 29 Apr 2022; F: 12 Apr 2022; 24 Oct 2022.
Caradrina clavipalpis (Scopoli, 1763)
Records. S: 29 Jun 2022; 30 Aug 2022; 6 Sep 2022; 28 Sep 2022; 2 Nov 2022; F: 30 Apr 2022; 9 May 2022; 27 Jun 2022.; 10 Jul 2022; 5 Sep 2022; 27 Sep 2022; 3 Oct 2022; 24 Oct 2022.
Caradrina flavirena (Guenée, 1852)
Records. F: 10 Jul 2022; 5 Sep 2022.
Cerastis faceta (Treitschke, 1835)
Records. S: 13 Apr 2022.
Conistra rubiginosa (Scopoli, 1763)
Records. S: 26 Mar 2022; F: 25 Mar 2022.
Craniophora ligustri (Denis & Schiffermüller, 1775)
Records. F: 27 Sep 2022.
Cryphia algae (Fabricius, 1775)
Records. S: 5 Aug 2022; F: 27 Jun 2022; 10 Jul 2022; 25 Jul 2022; 4 Aug 2022.
Cryphia ochsi (Boursin, 1940)
Records. S: 5 Aug 2022; F: 10 Jul 2022; 25 Jul 2022; 4 Aug 2022; 29 Aug 2022.
Cucullia santolinae (Rambur, 1834)
Records. S: 26 Mar 2022; F: 23 Feb 2022; 25 Mar 2022.
Cucullia thapsiphaga (Treitschke, 1826)
Records. S: 13 Apr 2022; 10 May 2022; F: 9 May 2022.
Cucullia verbasci (Linnaeus, 1758)
Records. S: 26 Mar 2022.
Dryobota labecula (Esper, 1788) *
Records. F: 24 Nov 2022.
Egira conspicillaris (Linnaeus, 1758)
Records. F: 25 Mar 2022.
Eupsilia transversa (Hufnagel, 1766)
Records. F: 1 Nov 2022.

Euxoa eruta (Hübner, 1817)
Records. F: 27 Jun 2022.
Euxoa seliginis (Duponchel, 1837)
Records. S: 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; 28 Sep 2022; 4 Oct 2022; F: 5 Sep 2022; 27 Sep 2022; 3 Oct 2022.
Hada plebeja (Linnaeus, 1761)
Records. S: 29 Apr 2022; F: 26 May 2022.
Hadena perplexa (Denis & Schiffermüller, 1775)
Records. S: 13 Apr 2022; 29 Apr 2022; 28 Jun 2022; F: 12 Apr 2022; 30 Apr 2022.
Hadena silenes (Hübner, 1822)
Records. S: 29 Apr 2022; F: 12 Apr 2022; 30 Apr 2022.
Helicoverpa armigera (Hubner, 1808)
Records. S: 30 Aug 2022; 28 Sep 2022.
Heliothis nubigera (Herrich-Schäffer, 1851)
Records. S: 29 Apr 2022; 27 May 2022.
Heliothis peltigera (Denis & Schiffermüller, 1775)
Records. S: 27 May 2022; 7 Jun 2022.
Hoplodrina ambigua (Denis & Schiffermüller, 1775)
Records. S: 28 Sep 2022; F: 5 Sep 2022; 27 Sep 2022; 3 Oct 2022.
Hoplodrina blanda (Denis & Schiffermüller, 1775)
Records. S: 29 Apr 2022.
Lacanobia oleracea (Linnaeus, 1758)
Records. S: 28 Sep 2022; F: 27 Jun 2022; 3 Oct 2022.
Lasionycta calberlai (Staudinger, 1883)
Records. S: 30 Aug 2022.
Leucania loreyi (Duponchel, 1827)
Records. S: 10 Dec 2021; F: 27 Sep 2022.
Leucania punctosa (Treitschke, 1825)
Records. S: 2 Nov 2022.
Leucania putrescens (Hubner, 1824)
Records. S: 6 Sep 2022; 28 Sep 2022; 4 Oct 2022; F: 29 Aug 2022; 5 Sep 2022; 27 Sep 2022; 3 Oct 2022; 24 Oct 2022.
Luperina dumerilii (Duponchel, 1826)
Records. S: 28 Sep 2022; 4 Oct 2022; F: 27 Sep 2022; 3 Oct 2022.
Lygephila craccae (Denis & Schiffermüller, 1775)
Records. S: 28 Jun 2022; F: 27 Jun 2022.
Meganephria bimaculosa (Linnaeus, 1767)
Records. F: 24 Oct 2022.
Mesapamea secalis (Linnaeus, 1758)
Records. F: 27 Jun 2022.
Mniotype solieri (Boisduval, 1840)
Records. F: 3 Oct 2022; 24 Oct 2022; 1 Nov 2022.
Mythimna albipuncta (Denis & Schiffermüller, 1775)
Records. S: 29 Apr 2022; 28 Jun 2022; 28 Sep 2022; 4 Oct 2022; F: 30 Apr 2022; 6 Jun 2022; 27 Jun 2022; 27 Sep 2022.
Mythimna l-album (Linnaeus, 1767)

Records. S: 5 Aug 2022; F: 10 Jun 2022; 3 Oct 2022.

Mythimna riparia (Boisduval, 1829)

Records. S: 27 May 2022; 4 Oct 2022.

Mythimna sicula (Treitschke, 1835)

Records. S: 29 Apr 2022; 10 May 2022; 5 Aug 2022; 30 Aug 2022; F: 27 Jun 2022; 29 Aug 2022.

Mythimna unipuncta (Haworth, 1809)

Records. F: 27 Sep 2022; 10 Dec 2021.

Mythimna vitellina (Hübner, 1808)

Records. S: 27 May 2022; 29 Apr 2022; 28 Sep 2022; 25 Oct 2022; F: 30 Apr 2022; 4 Aug 2022.

Noctua comes (Hübner, 1813)

Records. S: 28 Jun 2022; 26 Jul 2022; 30 Aug 2022; 6 Sep 2022; 28 Sep 2022; F: 26 May 2022; 27 Jun 2022; 29 Aug 2022; 27 Sep 2022; 3 Oct 2022; 24 Oct 2022.

Noctua janthe (Borkhausen, 1792)

Records. S: 28 Jun 2022; 9 Jul 2022; 5 Aug 2022; 30 Aug 2022; F: 27 Jun 2022; 25 Jul 2022; 04 Aug 2022; 29 Aug 2022; 27 Sep 2022; 3 Oct 2022.

Noctua janthina (Denis & Schiffermüller, 1775)

Records. S: 28 Jun 2022; 5 Aug 2022; 30 Aug 2022; F: 10 Jun 2022; 27 Jun 2022; 25 Jul 2022; 4 Aug 2022.

Noctua pronuba (Linnaeus, 1758)

Records. S: 7 Jun 2022; 28 Jun 2022; 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; 28 Sep 2022; 4 Oct 2022; 25 Oct 2022; F: 9 May 2022; 27 Jun 2022; 25 Jul 2022; 4 Aug 2022; 5 Sep 2022; 27 Sep 2022; 3 Oct 2022; 24 Oct 2022; 1 Nov 2022.

Noctua tirrenica (Biebinger, Speidel & Hanigk, 1983)

Records. S: 9 Jul 2022; 28 Sep 2022; F: 27 Jun 2022; 27 Sep 2022; 3 Oct 2022.

Odice suava (Hübner, 1813)

Records. F: 27 Jun 2022.

Omphalophana antirrhinii (Hübner, 1803)

Records. S: 10 May 2022.

Orthosia gothica (Linnaeus, 1758)

Records. S: 26 Mar 2022.

Parascotia nisseni (Turati, 1905)

Records. S: 27 May 2022; F: 26 May 2022.

Phlogophora meticulosa (Linnaeus, 1758)

Records. F: 30 Apr 2022.

Polyphaenis viridis (Villers, 1789)

Records. F: 27 Jun 2022; 10 Jul 2022.

Rhizedra lutosa (Hübner, 1803)

Records. S: 25 Oct 2022; 2 Nov 2022; F: 24 Nov2022.

Sesamia nonagrioides (Lefèbvre, 1827)

Records. S: 27 May 2022; F: 26 May 2022.

Spodoptera exigua (Hübner, 1808)

Records. S: 28 Sep 2022; 25 Oct 2022; 2 Nov 2022; F: 3 Oct 2022; 24 Oct 2022.

Spudaea ruticilla (Esper, 1791)

Records. S: 22 Feb 2022; 26 Mar 2022; F: 25 Mar 2022.

Stilbia faillae (Püngeler, 1918)

Records. F: 3 Oct 2022.

Sunira circellaris (Hufnagel, 1766)

Records. F: 24 Oct 2022.

Trigonophora flammea (Esper, 1785)

Records. S: 6 Sep 2022; 28 Sep 2022; F: 27 Sep 2022; 24 Oct 2022; 1 Nov 2022.

Tyta luctuosa (Denis & Schiffermüller, 1775)

Records. S: 9 Jul 2022; 26 Jul 2022; 5 Aug 2022; 30 Aug 2022; 6 Sep 2022; F: 27 Jun 2022.

Xestia xanthographa (Denis & Schiffermüller, 1775)

Records. S: 28 Sep 2022; F: 27 Sep 2022.

Overall, during the sampling campaign, a total of 223 species were identified: 18 species of butterflies belonging to 5 families (Papilionidae, Hesperiidae, Pieridae, Lycaenidae, and Nymphalidae) and 205 species of moths belonging to 17 families (Tineidae, Alucitidae, Pterophoridae, Tortricidae, Coleophoridae, Cossidae, Yponomeutidae, Pyralidae, Crambidae, Drepanidae, Sphingidae, Lasiocampidae, Geometridae, Notodontidae, Erebidae, Nolidae and Noctuidae). Among butterflies, the richest families were Nymphalidae (7 species), Lycaenidae (5 species) and Pieridae (3 species). Among the moths, the most species-rich families were Noctuidae (78 species) and Geometridae (39 species) followed by Crambidae (22). These families also had the highest number of genera (Table 1). Finally, 48 species of moths are new for the Molise fauna: 2 Tineidae, 2, Alucitidae, 2 Coleophoridae, 1 Yponomeutidae, 17 Pyralidae, 21 Crambidae, 1 Lasiocampidae, 1 Erebidae and 1 Noctuidae (Table 1).

To compare species richness per family between the two zones (shifting and fixed dunes, Fig. 2), two complementary statistical approaches were applied. A Wilcoxon rank test indicated no significant difference in species richness per family between shifting and fixed dunes ($W = 55.5$, $p = 0.181$). The effect size was small to moderate ($r = 0.29$), suggesting a potential ecological trend despite the lack of statistical significance. Additionally, a chi-square test of independence was used to assess the association between butterfly/moth family and zone. The test revealed no significant association ($\chi^2 = 5.83$, $df = 21$, $p = 0.9995$), and the corresponding effect size was small (Cramér's $V = 0.13$), indicating that the distribution of species richness across families was similar between the two zones. In total, 43 species (19%) were exclusive to the shifting dunes and 67 species (30%) were exclusive to the fixed dunes, whereas 113 species (51%) were found in both zones. β-diversity measures indicate a moderate spatial turnover in species composition ($\beta_{sor} = 0.325$, $\beta_{sim} = 0.276$).

Table 1. Number of genera and species of Lepidoptera found at the 'Foce Trigno-Marina di Petacciato' Natura 2000 site.

Family	**Number of genera**	**Number of species**	**Number of species new to Molise**
Tineidae	2	2	2
Alucitidae	1	2	2
Pterophoridae	2	2	
Tortricidae	9	10	
Coleophoridae	1	2	2
Cossidae	2	2	
Yponomeutidae	1	1	1
Papilionidae	1	1	
Hesperiidae	2	2	
Pieridae	3	3	
Lycaenidae	4	5	
Nymphalidae	7	7	
Pyralidae	13	17	17
Crambidae	19	22	21
Drepanidae	1	1	
Sphingidae	3	4	
Lasiocampidae	2	3	1
Geometridae	23	39	
Notodontidae	1	1	
Erebidae	16	18	1
Nolidae	1	1	
Noctuidae	51	78	1

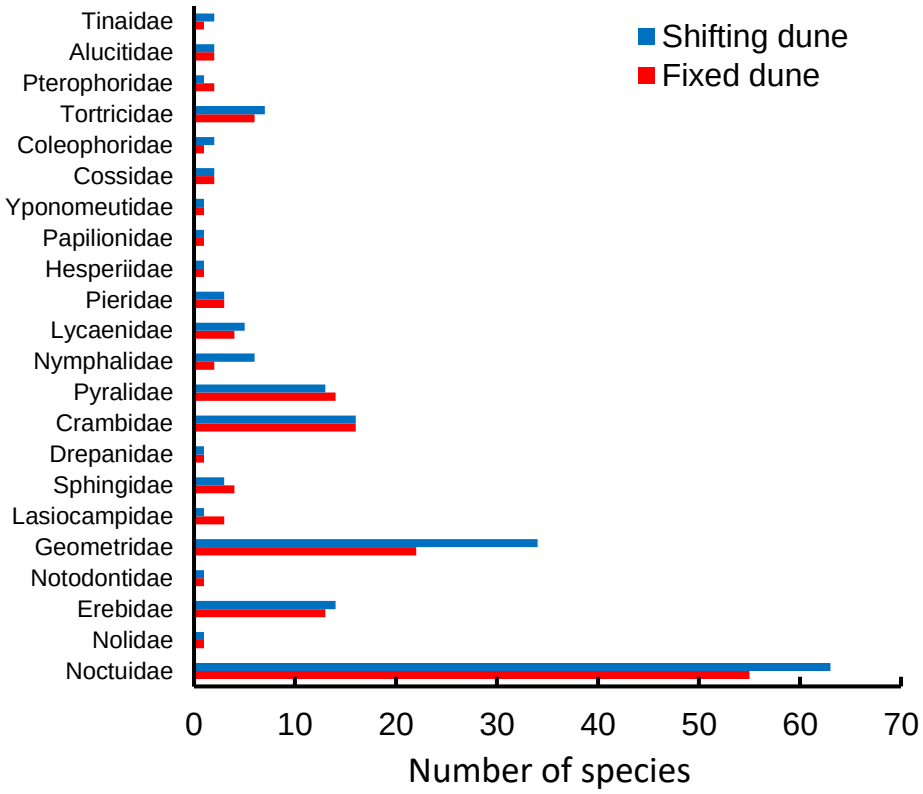


Fig. 2 - Number of species reported for each family in shifting (blue) and fixed (red) dunes at the 'Foce Trigno-Marina di Petacciato' Natura 2000 site.

Discussion

Faunistic knowledge is an important prerequisite to assess biodiversity loss and monitor changes in species communities (Páll-Gergely et al. 2024). Conservation strategies must be based on a solid foundation of knowledge about species distribution and abundance, their habitat requirements, and the pressures they face. The availability of insect inventories in protected areas is therefore of paramount importance, especially in poorly explored regions (Fattorini et al. 2012, 2024). The present paper provides valuable insights into the lepidopterofauna of a site of special conservation interest and a largely unexplored Italian region. In fact, Molise remains one of the least known regions in Italy in terms of insect fauna, including Lepidoptera. In particular, numerous families of Microlepidoptera have received little to no attention, as confirmed by the many species of Pyralidae and Crambidae that are cited here for the first time for the Molise Region.

Most of available data on the Lepidoptera of Molise regard Macrolepidoptera families, with various faunistic surveys (Sciarretta & Zilli 1998, Sciarretta & Parenzan 1998, Sciarretta & Parenzan 2001, Sciarretta & Raineri 2001), which included the same locality sampled in the present study. Nevertheless, our study recorded 84 additional species of Noctuoidea, 29 species of Geometridae, 3 species of Lasiocampidae, 2 species of Sphingidae, and 1 species of Drepanidae, substantially expanding the known assemblage for this eLTER site. Of special interest is the presence in the study area of *Gegenes nostrodamus* (a rare butterfly recognized as an indicator of well-preserved dune ecosystems; Rasino et al. 2024) and *Euplagia quadripunctaria* (a species included in the Annexes II and IV of the EU Habitats Directive).

The two zones of the study site showed similar values of species richness (156 species in the shifting dunes and 180 in the fixed dunes). While there are minor variations in species richness between the two zones for some groups – such as higher richness in certain families like Geometridae in the fixed dunes – there is no consistent or statistically significant pattern across all families. Thus, the two zones support comparable levels of butterfly and moth diversity at the family level, although some weak trends may warrant further investigation. In particular, the presence of many species exclusive to either one of the two zones suggest the presence of well distinct communities. The distribution of butterfly and moth species across all dune habitats highlights the critical importance of conserving the integrity of the entire dune system.

Conclusion

This lepidopteran list presented in this study results from a full annual cycle of standardized sampling in both shifting and fixed dunes, offering valuable temporal and spatial insights into the lepidopteran assemblages of a coastal system of high conservation value. This list, albeit likely not exhaustive, can serve as a valuable resource for entomologists, ecologists, conservation biologists, and environmental managers to: (1) compare the structure and composition of butterfly and moth communities across different Mediterranean coastal systems; (2) analyze temporal variations in lepidopteran communities, potentially linked to climate change or land-use dynamics; (3) support long-term monitoring programs (e.g., under the eLTER initiative); and (4) contribute to landscape and functional ecology studies, particularly in dune ecosystems where plant-insect relationships are tightly structured along environmental gradients.

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Chapter 2 - Cross-taxon analysis in the highly threatened Mediterranean dunes reveals consistent diversity patterns in butterfly and plant communities

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ORIGINAL RESEARCH

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 loosing 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; Rivieccio 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

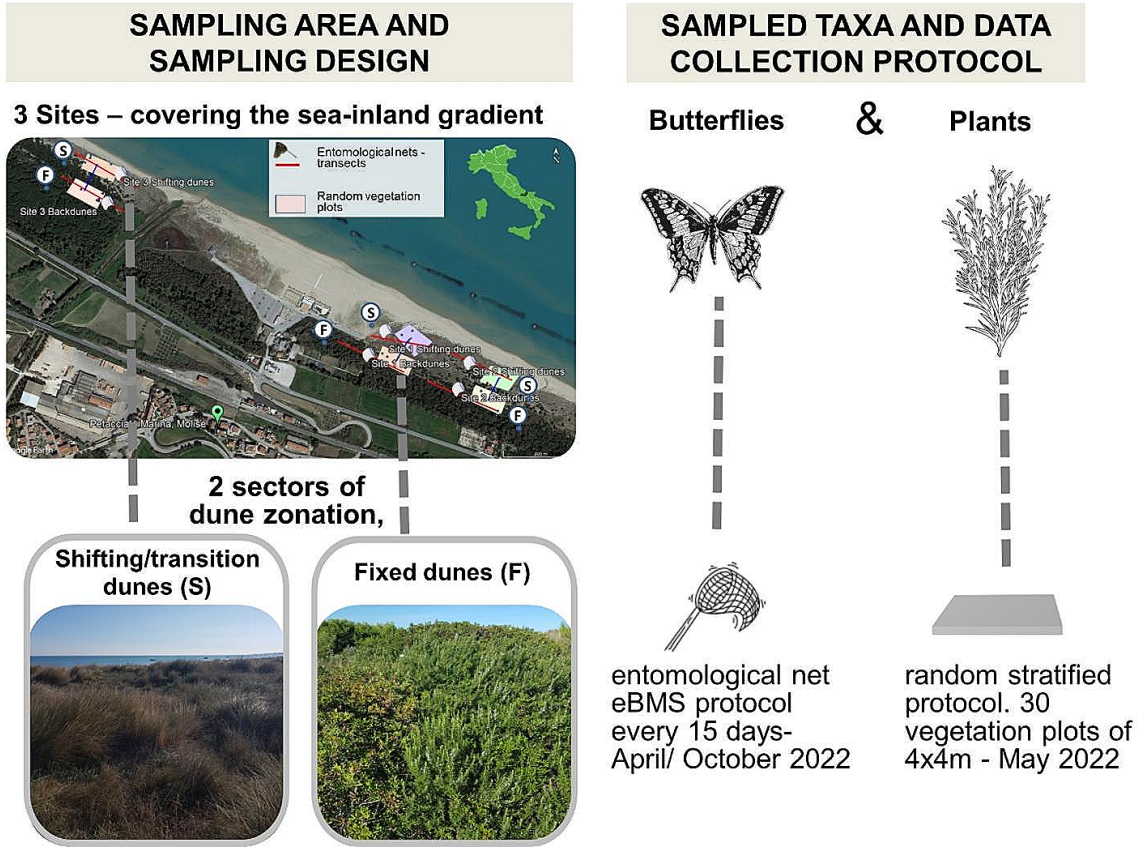


Fig. 1 Flowchart depicting the adopted sampling design for multi-taxon data collection carried out on the coastal site LTER IT20 (http://www.lteritalia.it/?q=siti/foce-trigno-marina-di-petacciato-campobasso; last visited 13/06/2024) along three sites including shifting dunes close to the seashore and 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-inland 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 Balletto et al. (2014). Information on host plants and ecological preferences were based on Balletto and Kudrna (1985), Villa et al. (2009) and Balletto 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 ${}^{q}D$ (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 × 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 where 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

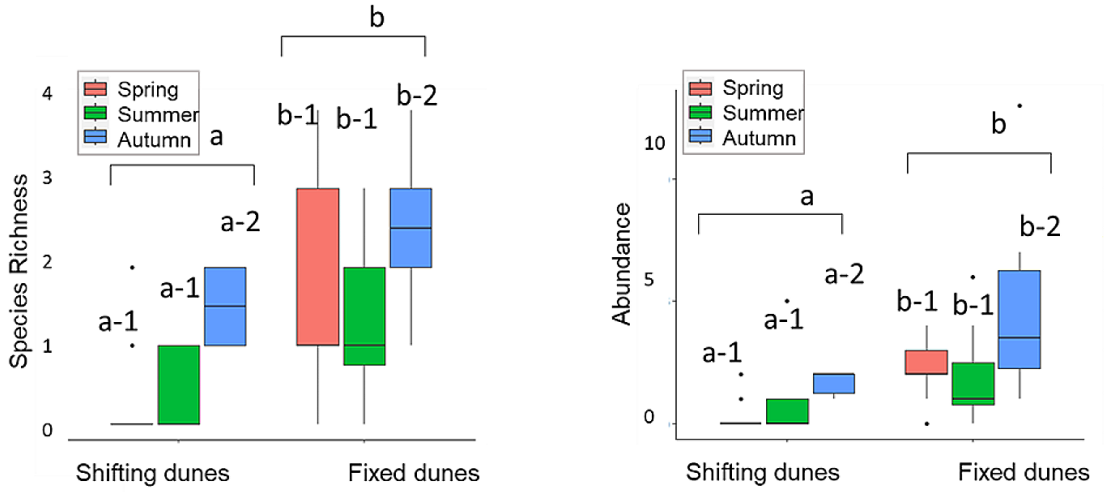


Fig. 2 Boxplots comparing butterfly species richness (Hill number with $q=0$) (left) and abundance (number of counted individuals) (right) in shifting/transition dunes and fixed dunes in different seasons (spring, summer, and autumn). Alphanumeric codes indicate significant differences ($p<0.05$) between 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}**

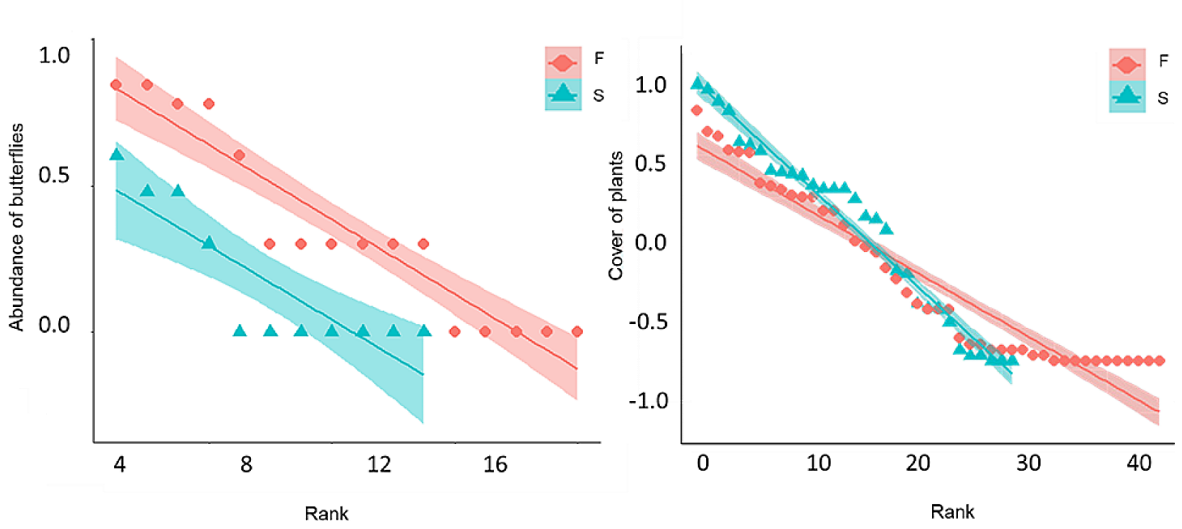


Fig. 3 Rank abundance curves for butterflies (left) and vascular plants (right) in shifting/transition dunes (S- green) and fixed dunes (F- pink) in the analyzed dune system. Species are ranked from the most to the least abundant (x-axis). Species cover and abundances are $\log_{10}$-transformed (y-axis). 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 nostrodamus* 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 form the seashore 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 nostrodamus*, 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. nostrodamus* is declining (Balletto et al. 2015). The presence in the study area of *G. nostrodamus* 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*; SI4). 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 costal habitats of European concern (Stanisci et al. 2014; Rivieccio et al. 2021), thus underlying the conservation importance of the study system. The butterfly community of the shifting/transitional 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 form 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 nostrodamus* 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 us the sea-inland stress gradient) and biotic interactions (e.g., variation, herbivory and symbiosis) as well as their seasonal varaition. 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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Chapter 3 - Linking taxonomic diversity and ecological traits of geometrid moths and plants in coastal dunes: insights from a Mediterranean LTER site

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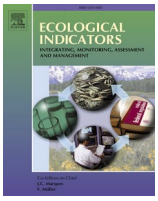
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Original Articles

Linking taxonomic diversity and ecological traits of geometrid moths and plants in coastal dunes: Insights from a Mediterranean LTER site

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ABSTRACT

Geometrid moths are widely regarded as effective bioindicators due to their sensitivity to changes in local plant communities, their preference for woody habitats and their limited dispersal capabilities. We analyzed geometrid moths and vascular plants diversity patterns inside a monitoring site that is a node of the European Long-Term Ecosystem Research network (eLTER IT20), placed on the central Italy Adriatic dune coast including a well-preserved Mediterranean system. Moth and plant communities were sampled in two distinct dune zones (the shifting dunes and the fixed dunes) in three replicates. Geometrids were collected using traps equipped with UV LEDs. Vegetation surveys were conducted using plots with a stratified random design. For both geometrids and plants, we investigated differences between dune zones in species richness, species abundance distribution and trait characteristics. To assess variation and covariation within and between geometrid and plant traits, we applied a Two-block Partial Least Squares (2B-PLS) analysis. Finally, we assessed the congruence between geometrids and plants in species composition and abundance variations between zones. The two groups responded in similar ways to the dune zonation. Trait associations identified through 2B-PLS revealed a distinct ecological differentiation driven by dune zonation, with coordinated trait patterns between moths and plants. Significant cross-taxon correlations in community similarity were found when species abundance patterns were considered. Our findings emphasize the importance of preserving diverse dune zones as distinct habitats that support unique geometrid moth communities and their potential role as bioindicators of coastal habitat conservation status.

1. Introduction

Coastal sand dunes are ecosystems of high conservation importance (Martínez and Psuty, 2004; Feola et al., 2011) that provide essential ecosystem services (Drius et al., 2019). Coastal dunes are among the most threatened landscapes in Europe, facing severe pressures from urbanization, tourism, invasive alien species and coastal erosion (Carranza et al., 2018; Fantinato, 2019; Fattorini, 2021; Janssen et al., 2016; Malavasi et al., 2018). In Italy, 88 % of coastal sand dune habitats are classified as being in poor conservation status, while the remaining 12 % are considered to be in inadequate condition (Prisco et al., 2020). Improving the conservation and management of coastal dunes in Europe, and in Italy in particular, is therefore urgently needed. To this end, evaluating the integrity of plant and animal communities in these vulnerable habitats is of paramount importance.

The conservation status of vulnerable habitats is frequently assessed by monitoring the presence and abundance of key indicator organisms (Cardoso et al., 2013; Santoro et al., 2012). In particular, the analysis of local plant communities, complemented by selected animal species of special conservation interest (Díaz et al., 2001; Berardo et al., 2015; Villalobos Perna et al., 2024), may play a vital role in assessing ecosystem integrity. Since lepidopterans are highly sensitive to pollution and habitat disturbances, responding to such pressures with noticeable shifts in species composition, abundance and diversity, butterflies (Berg

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et al., 2013; Rasino et al., 2024) and moths (Fiedler et al., 2007; Luque et al., 2011; Uhl et al., 2022) are good candidates as bioindicators for assessing the impact of anthropogenic factors on terrestrial ecosystems. In particular, moths are key invertebrates for ecosystem functioning in many terrestrial environments, contributing significantly to pollination and herbivory, and act as reliable indicators of environmental change (Truxa and Fiedler, 2012a; Uhl et al., 2016, 2022; Mangels et al., 2017; Singh et al., 2022). Larvae of moths frequently exhibit specialized feeding niches, and adults tend to remain within their native habitats, denoting strong habitat specificity (Wäckers, Romeis and van Rijn 2007; Lees and Zilli, 2019). Among moth families, Geometridae exhibit a marked preference for woody habitats, although many species also thrive in open environments such as grasslands, thus being potential bioindicators in different ecosystems (An et al., 2013; Bodner et al., 2010; Toko et al., 2023). In particular, Geometridae are considered valuable bioindicators due to their relatively low dispersal capacity and high sensitivity to changes in local plant communities, habitat integrity, and environmental disturbance (Usher and Keiller, 1998; Kitching et al., 2000; Hausmann, 2002; Bodner et al., 2010; An et al., 2013; Toko et al., 2023). Numerous studies across tropical and temperate forests have shown strong correlations between geometrid moth and plant community composition, with significant shifts in species richness and taxonomic structure along disturbance gradients (Beck et al., 2002; Axmacher et al., 2004; An et al., 2013). In addition, the family is globally distributed and, after the Erebidae, constitutes the second most species-rich family in the order Lepidoptera, with approximately 24,000 described species worldwide (Mitter et al., 2017; Rajaei et al., 2022). Geometrid caterpillars display a wide range of dietary needs, from monophagy to polyphagy, and utilize a wide spectrum of resource types, including forbs, shrubs, trees, lianas, leaf litter, and lichens. Due to their diverse life history traits and morphological adaptations, this moth family may represent an ideal model for investigating ecological patterns related to trophic interactions and species distribution dynamics (Beck et al., 2017; Holm et al., 2019).

Given this background, the study of the relationships between geometrid moth and plant communities, taking into account both taxonomic and trait characteristics, can provide valuable understanding into the ecological processes that shape these communities and important knowledge to inform conservation actions. Trait-based analyses, which complement traditional species-based approaches, have been proven particularly effective for identifying factors driving species distributions along environmental gradients (Díaz and Cabido, 2001; Uhl et al., 2016; Walker and Zinnert, 2022; Di Biase et al., 2023; Di Biase and Fattorini, 2025). Although moth-vegetation relationships have been studied in several ecosystems worldwide (Fiedler et al., 2007; Luque et al., 2011; Scalercio et al., 2007; Infusino and Scalercio, 2018), these interactions remain poorly understood in Mediterranean coastal dune environments.

The present research aims to provide new insights into the taxonomic and ecological trait diversity patterns of geometrid moths and vascular plants, as well as their interactions across the zonation ranging from the sea towards inland dunes along a Mediterranean coast. Environmental gradients in coastal landscape mosaics, such as nutrient availability, moisture levels and disturbance intensity, strongly shape the distribution patterns and functional strategies of both plant and animal communities (García-Mora et al., 1999; Acosta et al., 2009; Malavasi et al., 2016; Torca et al., 2019; Keddy, 2017; Berardo et al., 2015; Fattorini et al., 2017), leading to characteristic zonations.

In the shifting dune zone, near the drift-line, pioneer plant species highly adapted to extreme coastal conditions dominate. These species exhibit functional traits that allow them to thrive under conditions of frequent disturbance, high salinity, and intense coastal winds (McGuirk et al., 2022). These grasses are dune-building species whose deep root systems and morphological adaptations significantly enhance sand stabilization and reduce erosion (García-Mora et al., 1999; Drius et al., 2016; La Bella et al., 2023). In contrast, fixed dunes, characterized by more stable environmental conditions, support a greater diversity of life forms (Prisco et al., 2016). Here, dominant plant species include chamaephytes and phanerophytes, which have traits adapted to environments characterized by increased plant cover and resource availability (La Bella et al., 2024). This vegetation zonation is expected to influence animal communities, particularly among phytophagous insects that depend closely on plant communities. Understanding how these insect communities respond to dune zonation is essential for assessing habitat quality and guiding conservation. Due to their larval host specificity, limited dispersal, and sensitivity to habitat structure and disturbance, geometrid moths are especially suited for this purpose.

In this context, the present study addresses the following issues: (a) Are the α-, γ- and β-diversity patterns of geometrid moths and plants consistent across different zones on coastal dunes? (b) How does plant community functioning (e.g., plant Ecological Indicators Values) and moths (e.g., moth life history traits) vary along the dune zonation? (c) How does cross-taxon congruence between moth and plant communities differ along the dune gradient?

2. Material and methods

2.1. Study area

The study was conducted on a representative stretch of the Mediterranean coastline along the Adriatic coast of Central-Southern Italy in the Molise Region (Fig. 1A) (Carranza et al., 2008). This area is part of the Natura 2000 network (Foce Trigno-Marina di Petacciato – IT7228221) and is included in the ecological monitoring system called European Long-Term Ecosystem Research network (eLTER IT20; https://deims.org/1835cda2-b56d-400a-b413-ab5c74086dc5) (Stanisci et al., 2014). The coastal mosaic consists of narrow belts (less than 100 m deep) of recent dunes, where environmental (biotic and abiotic) conditions change markedly across a gradient that ranges from the seashore to the inland sectors (Carranza et al., 2008; Drius et al., 2013). The coastal mosaic is characterized by well-preserved natural vegetation, including the strandline with annual plant communities and the stabilized inland dunes with Mediterranean maquis (Tozzi et al., 2021; Drius et al., 2019). The dune vegetation follows a characteristic succession pattern, progressing from shifting/transition dunes to stabilized dunes, often followed by pine woodlands, which are typically of anthropogenic origin (Carranza et al., 2008).

2.2. Data collection

Geometrid moth and plant communities were sampled on three sites, each serving as a replicate. Within each site, moth collection and vegetation surveys were conducted in two distinct zones characteristic of the dune zonation: the shifting/transition dunes, located near the seashore, and the fixed dunes found in the inner zones. To prevent interference between light traps used to sample moths (see below), sites were spaced apart as follows: 300 m between Sites 1 and 2, 1,600 m between Sites 1 and 3, and 1,900 m between Sites 2 and 3 (Fig. 1B and C). Within each site, the distance between the two sampled dune zones was 25 m, reflecting their natural spacing in the studied system, characterized by intact but low and narrow dunes (Acosta et al., 2003, Drius et al., 2013).

2.3. Lepidoptera

Geometrid moths were sampled using light traps equipped with UV LEDs. The LED traps consisted of a 2.5-meter-long ultraviolet strip containing 150 LEDs (emission peak: 398 nm; beam angle per LED: 120°; 12 V; ~15 W). The strip was mounted on a cylindrical PVC support, with four transparent plexiglass plates arranged radially around it. This structure was positioned above a container fitted with a large funnel, featuring a lower opening approximately 5 cm in diameter. Traps were

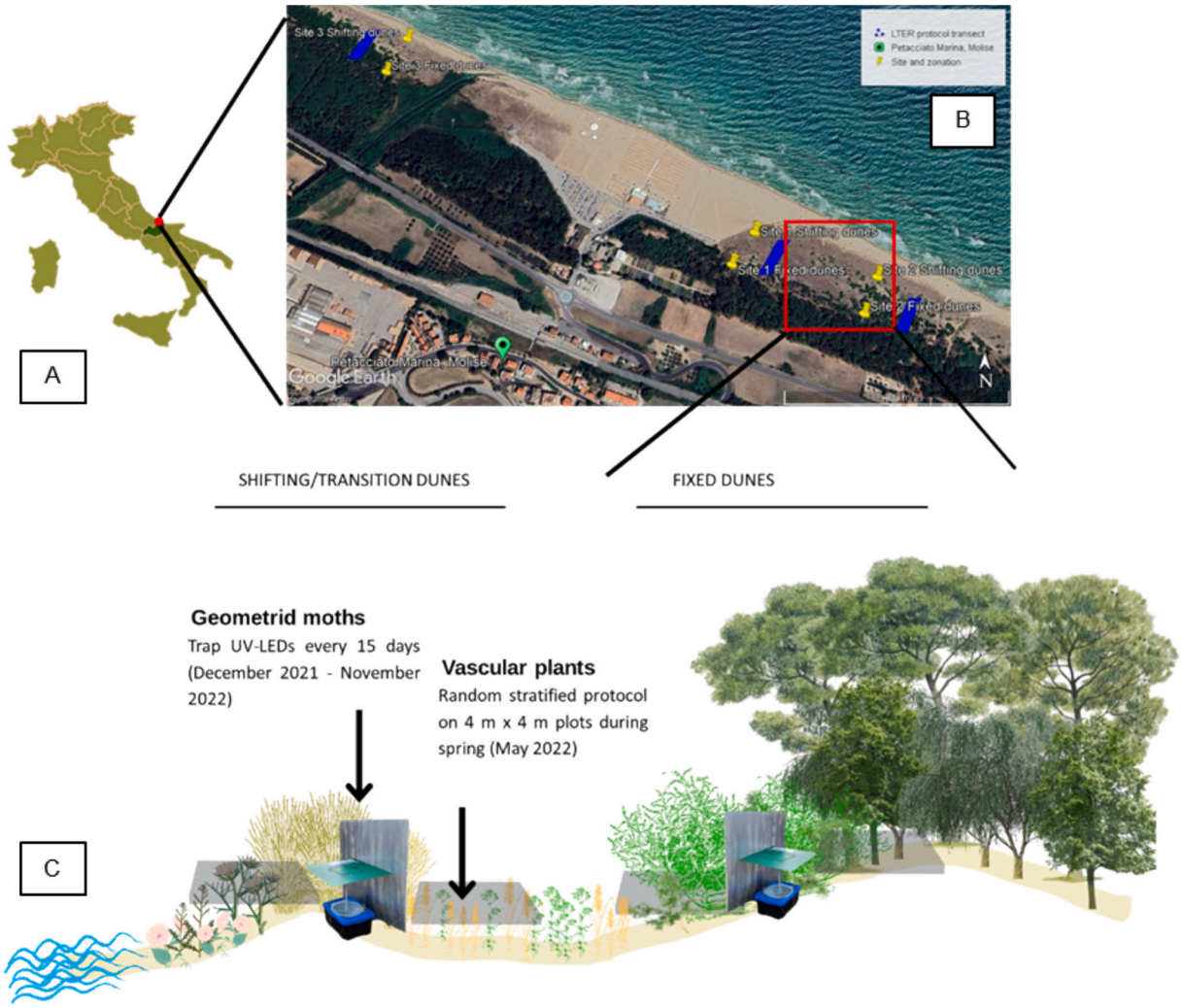


Fig. 1. Study area. (A) Location of the study area (LTER coastal site IT20 – https://deims.org/1835cda2-b56d-400a-b413-ab5c74086dc5) on the Italian Adriatic coast. (B) Distribution of sampling sites (blue strips) and dune zone (yellow pins). (C) Schematic representation of the multi-taxon sampling design implemented on transects including shifting dunes and fixed dunes. Geometrid moths were sampled every 15 days with UV-LED traps, while for plants we adopted a random stratified protocol implemented on spring. QGIS Geographic Information System (Version 3.34). Open Source Geospatial Foundation Project. Map Data: Google, ©2024 Airbus. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

placed at ground level and were powered by a portable lead-acid battery (Infusino et al., 2017). In each site, sampling was done on two successive nights every 15 days for one year (December 2021 – November 2022) during nights favorable to moth activity (i.e., in the absence of wind and rain and during the new moon phase). On the first night, traps were placed in the shifting/transition dunes, while on the second night they were positioned in the fixed dunes (Fig. 1C). Loosely arranged egg cartons were put in the collecting bucket to provide resting places for the captured individuals. In all sampling sessions, to avoid attracting specimens from adjacent areas, an opaque plastic panel was placed on the side of the trap facing the other zone of the dune (Fig. 1C). Although there is some variability depending on the moth group and the specific characteristics of the trap model used, light traps typically attract moths from within 30 m, and often within 10 m (Baker and Sadovy, 1978; Truxa and Fiedler, 2012b; Merckx and Slade, 2014), which is below the distance between traps adopted in our study. Ethyl acetate, contained in a 250 mL bottle inside the collecting bucket, was used as a killing agent. Species identification was performed in the laboratory using a reference collection of the General and Applied Entomology Laboratory at the Department of Agricultural, Environmental and Food Sciences, University of Molise, Italy. When necessary, genitalia were examined to distinguish cryptic species. Although light traps collected a broad spectrum of moths which are currently under study, in the present paper we focused exclusively on Geometridae because, unlike Noctuoidea or Rhopalocera, which have been used in previous dune studies (e.g., Favilli, 2018; Zilli et al., 2014), geometrid moths remain largely unexplored in these ecosystems. Our targeted approach thus addresses a significant knowledge gap and lays the groundwork for future comparative studies involving other moth groups, including Noctuoidea and microlepidopterans. Nomenclature of geometrid moths follows Rajaei et al., (2022; https://geometroidea.smns-bw.org/geometridae/Catalogue/). Data are given in Supplementary Material, Table S1.

2.4. Ecological traits for moths

To explore how different geometrid moth communities are structured along the coastal zonation we categorized all species according with their ecological and life history traits extracted from literature (Hausmann, 2001; Mironov, 2003; Hausmann, 2004; Macek et al., 2007, 2008, 2012; Leraut, 2009; Hausmann and Viidalepp, 2012; Skou and Sihvonen, 2015; Potocký et al., 2018; Müller et al., 2019; Seifert et al., 2022a, 2022b). Following Potocký et al. (2018) we included among traits also species distribution extent types as they may convey important ecological information. Missing information on traits was imputed

using the status known for allied species (i.e., species of the same genus or tribe). A total of 17 traits were tabulated (see Supplementary Material, Table S2 and Table S3).

2.5. Vascular plants

Vegetation was sampled in spring (May 2022) using 4 m × 4 m plots following a stratified random design. Within each site, five plots were randomly placed in the shifting and five in the fixed zones of the dunes, resulting in a total of 30 plots. For each plot, vascular plant species name and cover were recorded conforming the Braun-Blanquet scale (Braun-Blanquet, 1964; Westhoff and Van Der Maarel, 1978). For the analyses, the original Braun-Blanquet cover values were then converted to a percentage cover scale (Tichý et al., 2020). Data are given in Supplementary Material, Table S4.

Plant taxonomy and Raunkiær life forms conformed Pignatti et al. (2017-2019) (see Supplementary Material, Table S5). Even if some authors suggest some weakness on Raunkiær classification (Sarmiento and Monasterio 1983), we adopted this system as it remains widely accepted, it is effective to gather plant species into classes based on similarity of function and structure and, because of its easy utilization as a surrogate of plant life strategies in response to the ecological context (Acosta et al., 2003; Klimeš, 2003; Leuschner and Ellenberg, 2017; Di Biase et al., 2021a).

2.6. Ecological characteristics and level of disturbance of vascular plant community

To analyze how different plant communities are structured along the coastal zonation we categorized all vascular plants according to their ecological and disturbance adaptations. We used the Ecological Indicator Values for Europe (EIVE) (Dengler et al., 2023) to express species preferences for temperature (EIVE T), nitrogen (EIVE N), soil reaction (EIVE R), soil moisture (EIVE M) and light (EIVE L). These indicators, which are a particular version of Ellenberg's indicator values (Di Biase et al., 2023), range from 0 to 10, with lower values corresponding, for example, to sciophilous or cold-tolerant species, and higher values indicating heliophilous and thermophilous species. To evaluate the ability of plant communities to withstand disturbance, we assigned each plant species in each plot to the corresponding Disturbance Indicator (DI) values (Midolo et al., 2023). These indicators reflect species tolerance to: (a) aboveground biomass removal due to grazing, ranging from 0 (no biomass loss) to 1 (complete plant cover loss); (b) soil disturbance, quantified as the proportional increase in bare ground caused by furrowing or soil turning, on a scale from 0 to 1; (c) the severity of herb layer disturbance, measured as the proportion of aboveground biomass removed (0 to 1); (d) the frequency of disturbance events at the community level, expressed as the $\log_{10}$ mean inverse of return time in centuries; and (e) the tolerance to mowing, represented by the $\log_{10}$ mean inverse of mowing event return time in centuries. Finally, we assigned numerical values to growth forms as follows: herbs = 1, shrubs = 2, trees = 3. Data are given in Supplementary Material, Table S6.

2.7. Statistical analyses

We used a binomial test to assess if the number of geometrid species exclusive of woody plants was significantly different from the number of obligate herb feeders. We used a Chi-square test to assess if the proportion of different trophic categories (polyphagous, monophagous, oligophagous) deviated from a uniform distribution. Similarly, a contingency table was used to assess if the proportion of Raunkiær categories differed between the two zones.

Spatial and temporal variations in geometrid moth α-diversity were investigated using Hill numbers ${}^{q}D$ (Chao and Jost, 2012; Chao et al., 2014, 2020; Chiu and Chao, 2020). We considered Hill numbers for $q = 0$ (which corresponds to species richness), $q = 1$ (in fact, the limit case, which corresponds to Shannon diversity in its exponential form) and $q = 2$ (which corresponds to Simpson diversity). To express moth diversity separately for each sampling session, we adopted these three Hill numbers, defined by a unique combination of dune zone (shifting and fixed), season (spring, summer, autumn), and site. Because only two species were captured in winter, this season was excluded from the analysis. The same Hill numbers were also calculated for vascular plants, considering each unique combination of dune zone and site.

We used Linear Mixed Models (LMMs, assuming a Gaussian distribution) to investigate variations in geometrid moth Hill numbers and a Generalized Linear Mixed Model (GLMM, assuming a Poisson distribution) for variations in moth abundance. For both models, we considered sites as a random factor (Response Variable ~ Zonation × Season + (1|Site: Zonation)). In the same way, we compared the diversity and the cover of plants across zones (Response Variable ~ Zonation + (1|Site)). We also compared overall geometrid moth species richness (γ-diversity) by seasons (spring, summer and autumn), by computing species richness accumulation through sample-based rarefaction/extrapolation curves (Hsieh et al., 2016).

We compared the patterns of species abundance distribution (SAD) between dune zones using rank-abundance curves for geometrid moths and plants (May, 1975; Magurran, 1988; Fattorini, 2010; Hayek and Buzas, 2010). For SAD calculation, the sites data and the seasons data were pooled. SADs were modeled using the geometric series, a mathematical representation of the niche pre-emption model. This model postulates that niche hypervolumes (quantified by species abundances) are sequentially pre-empted by species, starting from the most to the least abundant (Giller, 1984; Fattorini, 2005; McGill et al., 2007). This model is particularly effective in describing communities with few species and high dominance, as commonly observed in environments characterized by harsh conditions and in early successional stages (Fattorini, 2005). We adopted the method based on Ordinary Least Squares (OLS) regressions to fit the rank-abundance plots (see for details Fattorini, 2005). Geometrical series precisely follows a straight line on the species-rank curve based on log transformed abundances. This line, fitted by OLS regression and the coefficient of determination R^2, express the similarity of SAD and a geometric series. Moreover, with this approach, it is possible to test differences between slopes through analysis of covariance (ANCOVA). The same approach was used for plants, where abundance was expressed as relative cover (see Moradi et al., 2025). We applied this approach to test differences in SADs between zones and seasons. For the inter-season comparison, data from different sites and zones were pooled and Tukey post hoc tests were applied for pairwise comparisons.

Habitat preferences of geometrid moths and plants were assessed by calculating the percentage of abundance (moths) and cover (plants) in each dune zone (shifting/transition dunes vs fixed dunes) with z-tests.

To explore patterns of covariance between geometrid moth and plant ecological traits, we calculated a Community-Weighted Mean (CWM) for each trait. The CWM is calculated as the sum of trait values of the species in a community, weighted by their relative abundance:

$$CWM = \sum_{i=1}^{S} p_i x_i$$

where S is the total number of species, p_i is the relative abundance (weight) of species i and x_i is the trait value of species i, allowing the identification of the prevailing trait values within a community (see Di Biase et al., 2021; Di Biase and Fattorini, 2025 for a discussion). In CWM calculation data from plots of the same zone were pooled (i.e., all shifting dune plots and all fixed dune plots from replicates 1, 2, and 3). To examine relationships between plant and moth traits across dune zones, we applied a Two-Block Partial Least Squares (2B-PLS) analysis. This method is particularly suitable for datasets with small sample sizes and highly correlated variables (Barker and Rayens, 2003; Carrascal et al., 2009) and has frequently been used in ecological research (Innangi et al., 2017, 2018, 2019). To optimize the 2B-PLS analysis

while balancing the number of sites and variables, we applied a two-step selection process. First, we excluded traits exhibiting near-zero variance, as they would not contribute to multivariate differentiation. Second, to reduce multicollinearity, we calculated the Variance Inflation Factor (VIF) for remaining traits and excluded cases with VIF values greater than 5 (see James et al., 2017; Naimi et al., 2014). From the collinear traits, we retained those considered to be the most ecologically meaningful, based on previous studies and biological relevance. This approach ensured a statistically robust and ecologically interpretable analysis. For instance, we retained wingspan, which is a good proxy for adult dispersal ability (Sekar, 2012), host plant use (Lindström et al.,1994; Cizek et al., 2006; Seifert et al., 2022b). Concerning plants, we retained the growth forms, which depict plant structural characteristics that provide moths with trophic, spatial and reproductive niches, as well as local microclimatic conditions (Davies and Asner, 2014). The retained variables along with the rationale and related references are reported in Table 1. The 2B-PLS constructs pairs of linear combinations from each set of variables (plant and geometrid moth traits) to maximize the covariation between these two groups (Rohlf and Corti, 2000). The covariance structure between the two trait matrices was visualized using scatterplots of the first 2B-PLS axis, with the *x*-axis representing moth traits and the *y*-axis representing plant traits. This visualization clearly identifies direct or inverse relationships both within and between trait sets.

To assess the cross-taxon congruence in β-diversity between sites we used Mantel correlation tests. For both geometrid moth and plant communities, we calculated pairwise dissimilarity distances using both the Dice-Sørensen index (which only considers presence-absence data) and the Bray-Curtis index (which considers abundances) (Baselga, 2010, 2013). Correlations between moth and plant distance matrices were assessed by Mantel tests using Spearman's correlation coefficients with 1,000 permutations. These cross-taxon comparisons provide valuable insights into potential interactions and co-structuring between geometrid moth and plant communities.

We used R version 4.1.0 (R Core Team, 2021) and the R packages iNEXT (Hsieh et al., 2016), lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), plsdepot (Bertrand and Sanchez, 2023) and ggplot2 (Wickham, 2016) for data analysis.

Table 1
Ecological traits for geometrid moths and plants recorded in a Mediterranean coastal area (LTER coastal site IT20) used for a 2B-PLS analysis.

Moth traits	Type of trait	Rationale
Wingspan	Continuous (mm)	Proxy for adult dispersal ability (Sekar, 2012) and plant use (Lindström et al.,1994; Cizek et al., 2006; Seifert et al., 2022b) with higher values indicating higher dispersal capability and plant use potential.
Voltinism	Continuous. Mean number of generations per year	Higher values indicate higher generalism (Dapporto and Dennis, 2013) and higher development speed (WallisDeVries, 2014).
Migration behavior	Binary (0/1)	Species are distinguished in migratory (1) or not (0). Migratory species have larger habitat extents.
Plants traits	**Categories**	**Rationale**
Indicator value "EIVE M''	Continuous, from 0 to 10	Describes the species' optimal positioning along a soil moisture gradient (Dengler et al., 2023).
Growth form	Ordinal value, 1: herbs; 2: shrubs; 3: trees	Plant structure provides moths with feeding resources and egg-laying sites, also shaping local microclimatic conditions (Davies and Asner, 2014).

3. Results

3.1. General patterns of species and traits. γ-diversity

At the study area level (γ-diversity) we recorded 39 species of Geometridae, belonging to 4 subfamilies and 23 genera (Supplementary Material, Table S1). The most common subfamily was Sterrhinae (44 % of the species), followed by Ennominae (38 %), Larentiinae (13 %) and Geometrinae (5 %). *Idaea* was the richest genus, with 9 collected species. Concerning the host plant types, the proportion of geometrid moths exclusive of woody plants (54 %) was similar to that of obligate herb feeders (46 %) (binomial test, $p = 0.749$). Regarding the trophic range, 64 % of recorded species were polyphagous, while 23 % were monophagous and 13 % were oligophagous. These proportions deviated significantly from a uniform distribution (Chi-square test: $\chi^2 = 17.231$, df = 2, $p < 0.001$). Four species (*Cyclophora puppillaria, Rodometra sacraria, Scopula minorata* and *Scopula imitaria*) are known to have migratory behavior.

In the same sample sites, we recorded 71 species of vascular plants (Supplementary Material, Table S4). The plant families with higher number of species were Poaceae (24 % of the sampled taxa), Asteraceae (15 %) and Fabaceae (8 %). 36 plant species were recorded in the shifting dunes, and of these, the 50 % are therophytes, 19 % geophytes, 14 % hemicryptophytes, 14 % chamaephytes and less than 3 % phanerophytes (Supplementary Material, Table S5). The fixed dunes, are also rich in therophytes (42 %) and hemicryptophytes (16 %), and also host a good number of woody and perennial species, as revealed by a 22 % of phanerophytes, 15 % of geophytes and 5 % of chamaephytes (Supplementary Material, Table S5). Although the overall difference in life form composition between the dune zones was not statistically significant ($\chi^2 = 8.01$, df = 4, $p = 0.09$), adjusted residuals indicate a potential overrepresentation of phanerophytes in the fixed dunes and a corresponding underrepresentation in the shifting dunes (adjusted residuals = ±2.54, Benjamini-Hochberg corrected *p*-value $p = 0.056$). These patterns indicate a possible trend in vegetation structure, with woody plants (phanerophytes) being more associated with stabilized, late-successional habitats.

3.2. Alpha and beta diversity. Species abundance distribution patterns

As regards α-diversity, Shannon index ($q = 1$) of geometrid moths did not differ significantly between the two dune zones (shifting/transition dunes near the seashore and fixed dunes inland), while the effect of summer approached significance (Table 2). No significant differences were found for Simpson diversity ($q = 2$), while species richness ($q = 0$) showed some seasonal variation (Supplementary Material, Table S7). Plant species cover and diversity did not varied significantly between the dune zones.

Rarefaction/extrapolation curves showed that the two zones had similar values of geometrid moth species richness (γ-diversity), with largely overlapping confidence limits both for the pooled data and for

Table 2
Results of a Linear Mixed Model assessing the influence of the dune zones (shifting vs fixed) and of the seasons (spring, summer, autumn) on the diversity of geometrid moths (exponential version of Shannon index) in a Mediterranean coastal area (LTER coastal site IT20). SE = standard error; *p* = probability. Bold reports significant results.

	Estimate	SE	*p*
Shannon			
Intercept	0.675	0.173	0.000236***
Zonation Shifting dunes	−0.463	0.286	0.110
Season Spring	−0.088	0.265	0.739
Season Summer	**0.428**	**0.233**	**0.070**
Zonation Shifting dunes: Season Spring	0.379	0.403	0.350
Zonation Shifting dunes: Season Summer	0.302	0.366	0.412

the three seasons separately (Supplementary Material; Fig. S1 and Fig. S2). However, it interesting to notice that the curve for autumn increased less abruptly in comparison with the curves for summer and spring. Overall, these curves suggest that the observed γ-diversity of geometrid moths at the study area level was adequately sampled.

Geometrid moths and vascular plants species abundance distribution patterns resulted adequately modeled by the geometric series in both zones (Fig. 2).

Geometrid moth rank-abundance regression lines showed slightly significantly different slopes between the two zones (ANCOVA: $F_{1,65} = 4.099$, $p = 0.047$) and significantly different intercepts (ANCOVA: $F_{1,66} = 41.71$, $p < 0.0001$). Additionally, geometrid moth rank-abundance regressions showed significantly different slopes between seasons (Fig. 3; ANCOVA: $F_{2,61} = 21.73$, $p < 0.0001$). No significant differences in regression slopes were registered between autumn and spring (Tukey test, $p = 0.089$), as the regression line for summer had a significantly lower slope in comparison with those of the autumn ($p < 0.001$) and spring ($p < 0.001$). The slope for the regression curve for plants of the shifting dunes resulted significantly higher when compared with the fixed dunes regression curves (ANCOVA: $F_{1,72} = 56.125$, $p < 0.00001$).

We recorded a high geometrid moth species turnover between zones (β-diversity), with many taxa predominantly or exclusively associated with one of the two zones (Fig. 4). Five geometrid moth species (*Idaea consanguinaria*, *Idaea mediaria*, *Larentia clavaria*, *Lycia florentina* and *Scopula ornata*) were found only in the shifting/transition dunes, while 16 species (*Agriopis leucophaearia, Gerinia honoraria, Chiasmia aestimaria, Crocallis elinguaria Eupithecia dodoneata, Idaea subsericeata, Idaea aversata, Idaea rubraria, Idaea seriata, Lycia hirtaria, Menophora abruptaria, Opisthograptis luteolata, Pennithera firmata, Scopula imitaria, Scopula minorata* and *Aspitates ochrearia*) were exclusively observed on the fixed dunes. The proportion of exclusive species (16.7 % vs 41.0 %) differed significantly between the two zones (z-test: $z = -2.180$, $p = 0.029$).

Similarly, we recorded a high plant species β-diversity between the two zones, with 43.2 % of species recorded exclusively in the shifting dunes and 78 % restricted to the fixed dunes, respectively (z-test: $z = -3.209$, $p = 0.001$) (Supplementary Material, Fig. S3). The exclusive or prevalent plants of shifting dunes included numerous Poaceae therophytes and geophytes (e.g., *Calamagrostis arenaria*, *Festuca fasciculata, Thinopyrum junceum* and *Anisantha madritensis*), low Fabaceae chamaephytes (e.g., *Medicago marina* and *Lotus cytisoides*) and Asteraceae geophyte (e.g., *Sonchus bulbosus*). On the other hand, plants occurring exclusively in the fixed dune zones were predominately phanerophytes (e.g., *Salvia rosmarinus*, *Asparagus acutifolius*, *Acacia saligna*, *Phillyrea angustifolia* and *Pistacia lentiscus*).

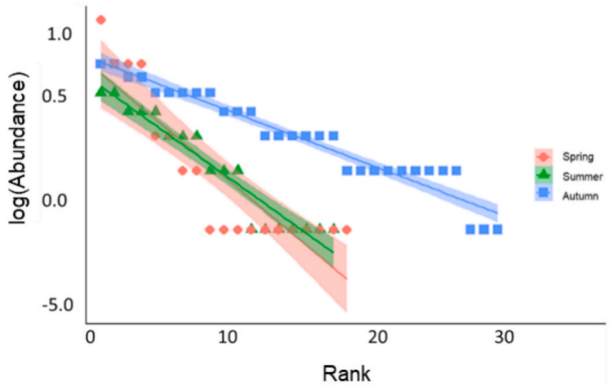


Fig. 3. Rank-abundance plots depicting species abundance distributions of geometrid moths in different seasons (spring, summer and autumn) in a Mediterranean dune system (LTER coastal site IT20). x-axis report species ranked from the most to the least abundant as *y*-axis the species abundances (number of individuals) $\log_{10}$-transformed. The regression equations for moths across seasons are: spring: $y = -0.050x + 0.783$, $R^2 = 0.922$, $p < 0.0001$; summer: $y = -0.027x + 0.883$, $R^2 = 0.934$, $p = 0.0001$; autumn: $y = -0.058x + 0.854$, $R^2 = 0.766$, $p < 0.0001$.

The presence of several plant species that are diagnostic of the presence of habitats of conservation concern in Europe (according with the Habitat Directive – HD), underscores the conservation value and the complexity of this dune. The protected area encompasses seven distinct HD habitats, including: 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 on shifting and mobile dunes (EC-2230), *Cisto-Lavanduletalia* dune sclerophyllous scrubs (EC-2260), and Wooded dunes with *Pinus pinaster* (EC-2270) (Supplementary Material, Table S5).

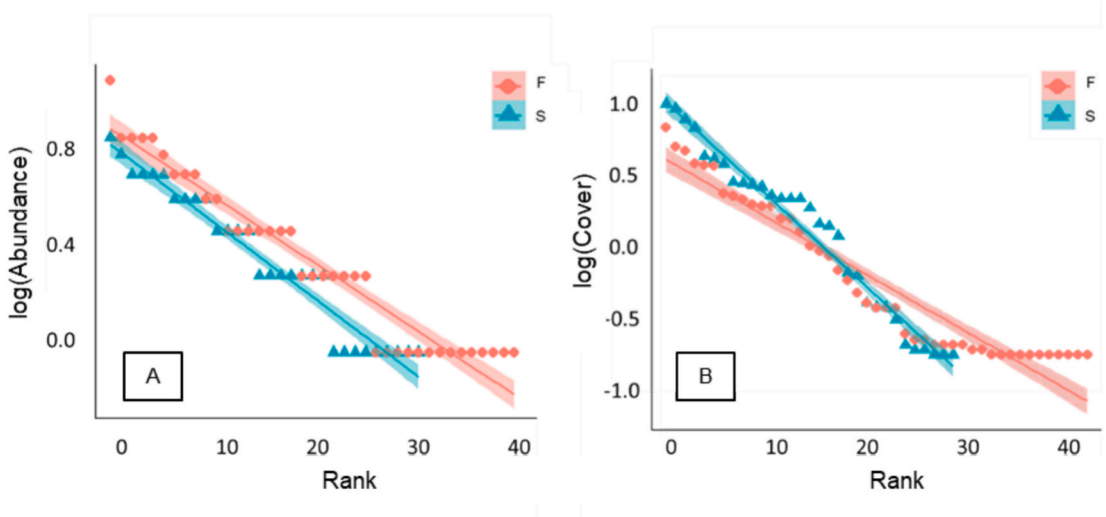


Fig. 2. Rank-abundance plots depicting the species abundance distributions (SADs) of (A) geometrid moth and (B) vascular plant communities in shifting (blue) and fixed (pink) dunes in a Mediterranean coastal area (LTER coastal site IT20). The *x*-axis report the species, ranked from the most to the least abundant. The *y*-axis report the $\log_{10}$-transformed species abundances (number of individuals). The equations of regression for moths are: shifting dunes: $y = -0.032x + 0.850$, $R^2 = 0.950$, $p < 0.0001$; fixed dunes: $y = 0.028x + 0.909$, $R^2 = 0.933$, $p < 0.0001$. The equations of regression for plants are: shifting dunes: $y = 0.057x + 0.980$, $R^2 = 0.969$, $p < 0.0001$; fixed dunes: $y = -0.035x + 0.591$, $R^2 = 0.919$, $p < 0.0001$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

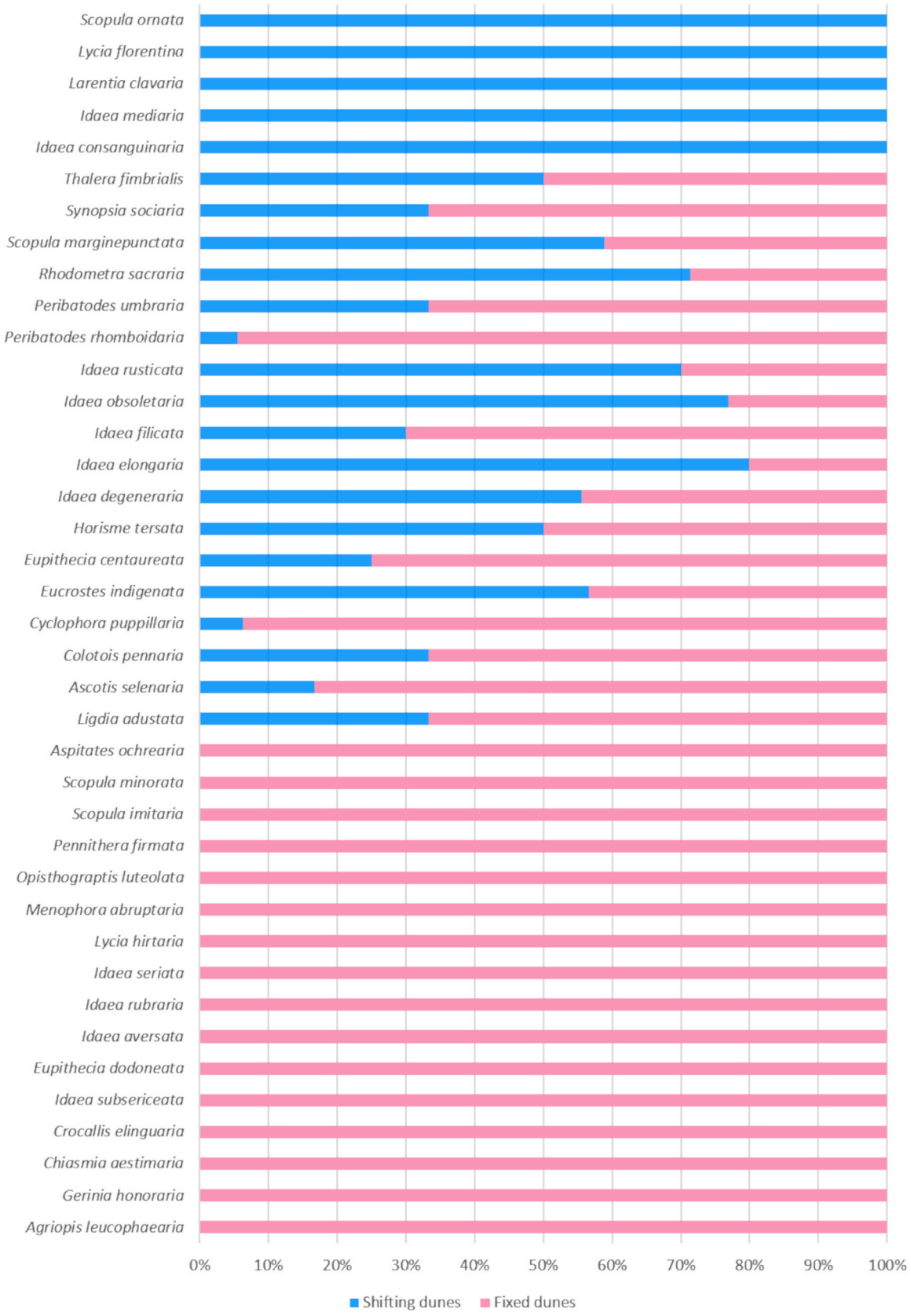


Fig. 4. Abundance distribution of geometrid moth species (% of collected individuals) in dune zones (blue = shifting dunes, pink = fixed dunes) in a Mediterranean coast (LTER coastal site IT20). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

3.3. Plant–moth trait relationships across dunes zones

The 2B-PLS analysis (Fig. 5) highlighted a clear differentiation between the dune zones, emphasizing a strong covariance between geometrid moth and plant ecological traits in response to dune zonation. Fixed dunes (upper-right quadrant in the plot) were characterized by geometrid moths with larger wingspans, migration behaviors and moderate voltinism. These moth traits align closely with plant communities in fixed dunes, which display higher proportions of woody life forms (e.g., chamaephytes and phanerophytes). Conversely, shifting/transition dunes (bottom-left quadrant in the plot) showed plant communities with preferences for soils with moderate humidity (EIVE M). The trait associations revealed by 2B-PLS thus indicated clear ecological differences shaped by dune zonation, highlighting joined trait co-structuring between plant and geometrid moth communities along the environmental gradient.

3.4. Cross-taxon analysis

The cross-taxon correlation resulted significant for species abundances (Mantel test, $r_s = 0.708$, $p = 0.026$). By contrast, Mantel test based on presence/absence data revealed a lack of significant correlation between plant and moth species composition ($r_s = 0.199$, $p = 0.230$).

4. Discussion

In the present study, we analyzed geometrid moth communities in a Mediterranean coastal dune system along the Adriatic coast (Central Italy), focusing on diversity patterns between dune zones (shifting dunes vs fixed dunes) and their functional relationships with vascular plants. Our findings revealed significant associations between geometrid moth and vascular plant communities, both shaped by dune ecological zonation.

4.1. General patterns of species and traits. γ-diversity

The species richness of geometrid moths on the analyzed coast (γ-diversity) is moderately low, as expected for a stressful system, with 39 ascertained species. However, this value represents about 6 % of the entire Italian fauna (around 650 species, Lepiforum e. V.: https://lepiforum.org/wiki/taxonomy/Geometroidea/Geometridae?view=0&regions=it-all), a proportion virtually identical to the that of the butterflies recorded in the same area and period (18 species, Rasino et al., 2024; 6.2 % of the entire Italian fauna, 290 species; Balletto et al., 2023). With reference to a previous study conducted by Sciarretta and Raineri (2001)

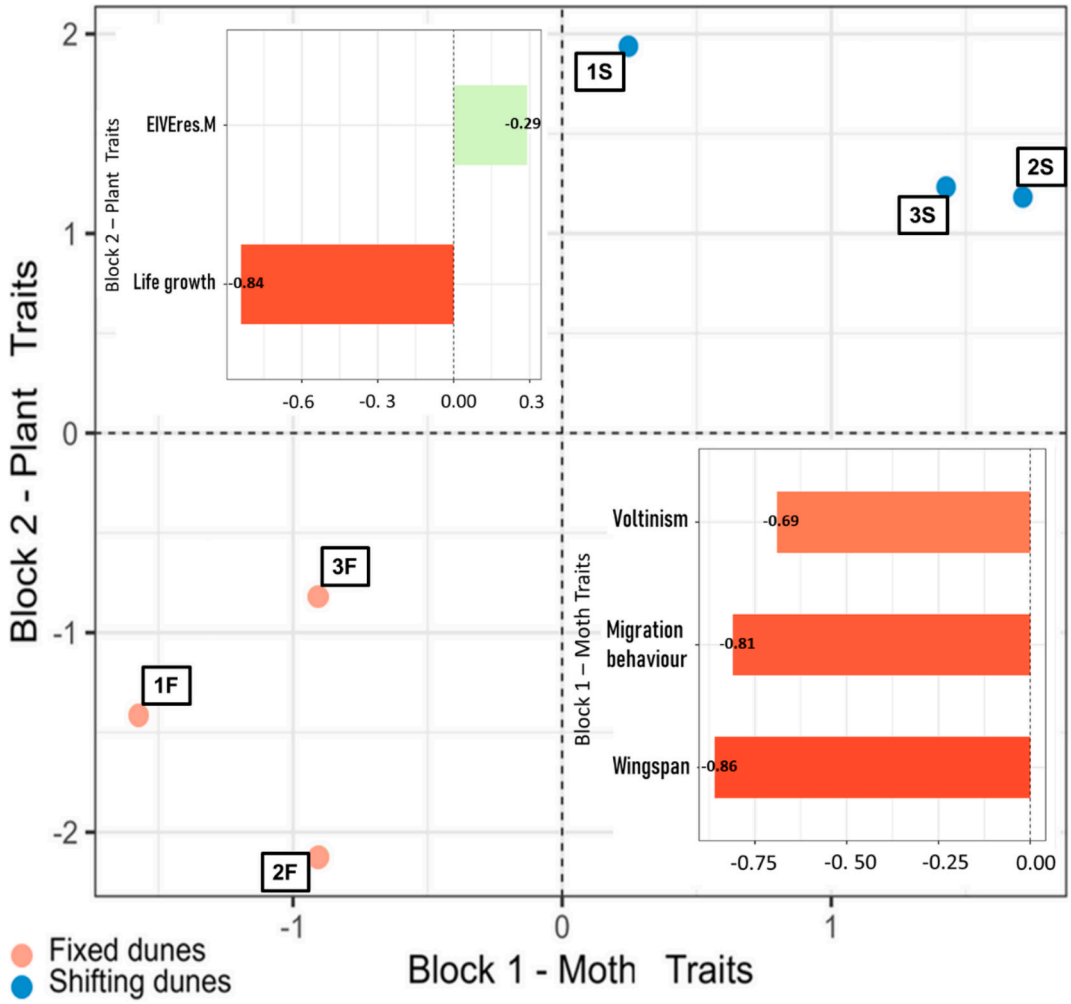


Fig. 5. Scatterplot for the first axis of a Two-Block Partial Least Squares analysis for geometrid moth and plant traits in a Mediterranean dune system (LTER coastal site IT20). Points are mean moth CWM values on Block 1 and mean plant CWM values on Block 2. Replicates (1, 2, 3) are reported in pink for the fixed dunes (F) and in blue for the shifting/transition dunes (S). The insets show the correlation of traits of moths (Block 1) and plants (Block 2) with the two zones (in green, relation with shifting/transition dunes; in red, relations with fixed dunes: color intensity proportional to correlation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

on the geometrid moths of the Molise Region for the same habitat, the present study led to the discovery of 29 additional species, increasing the number of geometrid moth species known for this LTER site to 48 species.

Geometridae are predominantly associated with woody habitats (Usher and Keiller, 1998; Kitching et al., 2000; Hausmann, 2002), which is reflected by our findings, where most species were found to depend on woody plants as their primary hosts. Additionally, the high proportion of polyphagous species suggests an adaptive strategy that enhances survival and ecological success in unstable environments. This dietary flexibility may help the persistence of geometrid moth populations in Mediterranean dune ecosystems, where environmental conditions and plant communities fluctuate across both space and time (Biondi et al., 2009; de Francesco et al., 2023; Bernabé-Ruiz et al., 2024).

The plant diversity recorded in the study system (γ-diversity) is typical of similar dune systems and the composition of major taxonomic groups aligns with that recorded in previous studies in Central Italy (Acosta et al., 2009; Prisco et al., 2020). Many of the recorded species are also diagnostic of the presence of habitats of conservation concern in Europe (Stanisci et al., 2014; Rivieccio et al., 2021), highlighting the conservation significance of the study coastal system. Regarding vegetation structure (life and growth forms) and ecology (EIVEs and Disturbance Indicators), our data suggest a relatively good conservation status of the investigated dunes (Innangi et al., 2025). Our findings are also consistent with the general observation that in the shifting dunes plant communities are primarily composed of a few monocot species from the Poaceae family, whereas fixed dunes are dominated by woody dicots with high cover (Drius et al., 2016). The shifting dune zone is a highly selective environment, favoring therophytes and hemicryptophytes, which possess physiological and morphological adaptations to withstand high salinity, severe drought, and an unstable substrate (Acosta et al., 2003; Prisco et al., 2016; Bazzichetto et al., 2016). In the study system, therophytes which predominate in lowland Mediterranean areas with thermo-xeric climates (Di Biase et al., 2021) were particularly numerous, accounting for 50 % of the vascular flora in shifting dunes and about 42 % on the fixed dunes. These species thrive in spring and summer, but persist as seeds in winter when sea storms erode established vegetation. A certain preponderance of phanerophytes on the fixed dunes is consistent with the fact that in this zone exposure to maritime winds, salt fog and sand burial is reduced (Tozzi et al., 2021, Feola et al., 2011). Overall, the dune system is a harsh environment for both plants and geometrid moths, only those species from the regional Italian lowland species that can withstand multiple stressors such as salt spray, strong winds and intense insolation during summer are able to establish.

4.2. Alpha and beta diversity. Species abundance distribution patterns

Similar patterns of α- and β-diversity of geometrid moth and plant communities were registered. However, differently from studies conducted along other environmental gradients (Babin-Fenske and Anand, 2011; Truxa and Fiedler, 2012a), we found no association between moth α-diversity and dune zonation, except when accounting for seasonal variability. Our results also differ from butterfly patterns reported for the same study system, where α-diversity was higher on fixed dunes (Rasino et al., 2024). The lack of distinct zonation in geometrid α-diversity is likely related to the nocturnal habits of these moths, which reduce exposure to sea-to-inland stressors, such as thermal extremes and other harsh environmental conditions that are particularly severe in Mediterranean coastal areas. Nonetheless, we also acknowledge that the close spatial proximity of our light traps may have allowed for some cross-attraction, particularly among mobile species, potentially leading to overlap in species records across zones. While our trap setup minimized this risk through the use of opaque barriers and known attraction distance thresholds, we cannot fully exclude the influence of occasional vagrants. These factors, combined with the relatively low γ-diversity and strong environmental filtering typical of coastal dune ecosystems, may contribute to the absence of strong α-diversity patterns across the zonation gradient.

Notable seasonal variation in geometrid moth diversity was observed in species richness ($q = 0$), but not in other diversity indices ($q = 1$ and $q = 2$). Seasonal differences in geometrid moth diversity may largely be determined by variations in the timing of adult emergence, overwintering stage, and voltinism (see Seifert et al., 2023), all traits influenced by the availability and palatability of host plant resources (Niemelä et al., 1982). In particular, deciduous and annual plants offer higher nutritional quality in the beginning of the early season, declining as leaves mature and age (Kause et al., 2001; Barton et al., 2019; Seifert et al., 2023). Leaf maturation is often accompanied by changes in plant secondary chemistry, including the production of anti-herbivore metabolites (Prinsloo and Nogemane, 2018; Barton et al., 2019). The observed increase of geometrid moth richness during spring and summer corresponds with the vegetative period of coastal ecosystems, while the lower richness registered in winter coincides with the die-off of annual plants (Bricca et al., 2023). This temporal pattern suggests a synchronization of moth communities with the phenology of the transition dune vegetation, which provides abundant food sources for both larvae and adult pollinators during spring and summer seasons (Biondi et al., 2009; Singh et al., 2022; de Francesco et al., 2022). However, these patterns may be influenced by rare species, some of which may represent vagrants rather than resident populations (Dennis and Fattorini, 2025). As such, these results should be interpreted with caution and considered preliminary. Future work incorporating additional years of sampling and independent validation of species residency status will be important to clarify the ecological significance of these seasonal trends.

The observed plant diversity in the two zones, including species richness and abundance, is consistent with values reported in the literature for other Mediterranean dune ecosystems (e.g. Martínez and Psuty, 2004; Feola et al., 2011), with lower values near the seashore (La Bella et al.,2024; Torca et al., 2019).

The observed high β-diversity of geometrid moth communities highlights a strong association of certain species with specific dune zones (shifting dunes and fixed dunes), and is also likely determined by the ecological relationships between larval stage and vegetation characteristics. However, the presence of several species represented by very few individuals (e.g., singletons) may have influenced these patterns. Such rare species can influence measures of species turnover and exclusivity between zones, potentially exaggerating the true ecological differentiation. Therefore, caution is warranted when interpreting β-diversity patterns, and further sampling or repeated surveys may help distinguish between genuine ecological associations and artefacts of sampling rarity.

Consistent with findings from other environmental gradients (Usher and Keiller, 1998; Kitching et al., 2000), the fixed dunes, which offer more stable and moderate conditions, host a higher number of exclusive geometrid moths compared to the harsher environment of the shifting dunes. On the fixed dunes, the most abundant geometrid moth species were *Cyclophora puppillaria* and *Peribatodes rhomboidaria*, both associated with woody species. Additionally, in this zone, we observed the exclusive presence of geometrid moth species preferentially feeding on woody plants (e.g., *Eupithecia dodoneata; Lycia hirtaria*), which is consistent with a higher presence of phanerophytes. This is consistent with the vegetation characteristics of this zone. In general, it is known that woody, multi-strata vegetation is particularly important for Lepidoptera (Dover et al., 1997; Clausen et al., 2001), as it provides cooler, shaded and less windy conditions compared to open habitats. As vegetation on fixed dune zone includes well-developed vertical strata, with shrubs and trees able to provide moths with a variety of spatial niches, this zone can allow the presence of a larger number of exclusive moth species. In particular, the more complex vegetation structure in this zone may be particularly favorable to more specialized species, as it may offer numerous resting and mating sites in a less harsh environment,

compared to the shifting dunes. On the shifting dunes, we observed a prevalence of geometrid moths that feed on herbaceous vegetation, including forbs and graminoids (e.g., *Poaceae*), such as the exclusive presence of two *Idaea* species (*I. mediaria* and *I. consanguinaria*). Although several *Idaea* species may partially utilize dry or senescent plant material, their trophic associations typically involve herbaceous or graminoid vegetation (e.g., Hausmann, 2004; King and Viejo Montesinos, 2010). This corresponds well with the vegetation structure of the shifting dunes, where grasses such as *Calamagrostis arenaria* (Poaceae) dominate. Notably, *C. arenaria* retains large amounts of dead leaves attached to the plant, which contribute substantially to the standing biomass and provide important microhabitats and feeding resources in arid dune systems (Huiskes, 1979; White et al., 2024). It has been observed that in unmanaged dunes non-living biomass can exceed living biomass by more than 50 %, further underscoring its ecological relevance (White et al., 2024). This furtherly underlies the importance of *Idaea* species as herb-associated moths in this particular context. However, the most abundant geometrid moth species in this zone was *Eucrostes indigenata*, which is primarily associated with another herbaceous plant, *Euphorbia paralias* (Euphorbiaceae). Although shifting dunes can provide a suitable environment for these species, the peculiar conditions of this zone act as a strong environmental filter that predominantly supports species which are not host-specific, but feed on widely available resources and can survive the dry and hot Mediterranean summer conditions.

The geometric series model correctly described the species abundance distribution (SAD) for both geometrid moths and plants. This distribution pattern is characteristic of simple communities dominated by a low number of species adapted to thrive under challenging ecological conditions (Giller, 1984; McGill et al., 2007; Fattorini, 2010). Similar patterns have been reported for other insects in Mediterranean dune ecosystems (Fattorini and Carpaneto, 2001; Fattorini et al., 2016, 2017; Rasino et al., 2024). Geometrid moth SADs of the shifting and fixed dunes differed slightly, with the intercept for the fixed dune slightly higher. This indicates that the harsh conditions of moving/transiting dunes curtail the abundance of geometrid moths, still maintaining the community organization compared to the fixed dunes. Plant SADs of the two dune zones exhibited distinct slopes, with the shifting dunes revealing a steeper slope, which suggest a more dominated community structure, aligning with the harsher environmental conditions that characterize this habitat.

4.3. Plant–moth trait relationships across dunes zones

The 2B-PLS analysis revealed correlations between geometrid moth and plant functional traits, highlighting distinct patterns associated with dune zonation (shifting dunes vs fixed dunes). Geometrid moth communities in the fixed dunes were characterized by larger wingspans and a high incidence of migratory behavior. This pattern may reflect differences in geometrid moth ecological niche requirements. Fixed dunes are typically dominated by shrublands, comprising woody plant species, primarily chamaephytes and phanerophytes. In terms of trophic niches, woody vegetation provides relatively stable and reliable food resources capable of supporting larger-bodied moth species (Lindström et al., 1994; Seifert et al., 2023; Seifert et al., 2025). In Mediterranean systems, migratory and mesophilous species tend to spend the daytime in woody vegetation, which provides important shelter from predators and aridity stress (Scalercio et al., 2007). In addition, this zone was characterized by a certain prevalence of multivoltinism. The habitat stability and plant diversity mentioned above could provide favorable food resources and micro-habitats for longer periods of the year (as, for example, the presence of flowering plants not only in spring but also in autumn during blooms of the rosemary garrigue; Katerinopoulos et al., 2005), allowing some generalist moths to develop multiple annual generations. The high incidence of woody life forms in the fixed dunes reflects an adaptation to more stable environments with lower levels of disturbance (Torca et al., 2019). Compared to shifting dunes, the vegetation on the fixed dune zone experiences less directly exposure to harsh maritime conditions such as salt spray and strong winds (Wiedemann and Pickart 2004; Tozzi et al., 2021). The reduced intensity of these stressors facilitates greater ecosystem stability, supporting plant species adapted to moderately stable soils with fewer resource constraints.

In contrast, on the shifting dunes, geometrid moths had smaller sizes. This pattern may stem from the prevalence of small-bodied Sterrhinae species in this sector, suggesting a relationship between host plant community structure and moth size (Lindström et al.,1994; Seifert et al., 2022b; 2023). The plant communities are characterized by a moderated association with indicator values for soil moisture (EIVE M). These plants typically exhibit deep root systems and a reduced leaf surface area, crucial adaptations for counteract water loss in this environment (Walker and Zinnert, 2022). The geometrid species found in this zone are ecologically flexible and capable of exploiting resistant host plants, reflecting a strong environmental filtering effect. These characteristics of geometrid moth and vascular plants are crucial for survival in the harsh Mediterranean summer conditions typical of shifting dunes.

4.4. Cross-taxon analysis

Our results indicate a strong relationship between geometrid moth and plant β-diversity when considering abundances, whereas the relationship is weak when based solely on species presence/absence. This cross-taxon pattern suggests that, likely due to the limited number of species recorded, abundance variations exert a more pronounced influence on β-diversity than differences in species composition alone. Interestingly, similar trends have also been documented on butterfly-plant correlations (Rasino et al., 2024), suggesting the potential role of species abundance in structuring beta diversity patterns across taxa along environmental stress gradients.

The observed distribution of geometrid species across the entire ecological dune zonation further emphasizes the importance of preserving intact dune systems not only for plant communities (Acosta et al., 2009; Drius et al., 2013), but also for maintaining regional biodiversity and ecological functionality for the fauna (e.g., Berardo et al., 2015; Fattorini et al., 2017).

4.5. Potential role of geometrid moths as ecological indicators in dune systems

We found that geometrid moth community composition and ecological traits mirrored habitat-specific environmental conditions, such as zonation gradients, but also respond to plant resource availability. The more stable conditions of fixed dunes support geometrid moth communities characterized by larger size and resource specialization, closely associated with plant communities comprising woody, stress-tolerant species adapted to moderate environmental stability. Conversely, the shifting dune environment, characterized by harsher conditions and dynamic disturbance regimes, promotes specialized adaptations in plants but a high degree of generalism in moths.

Based on their exclusive or strongly predominant presence in a specific dune zone, as well as their ecological and trophic characteristics, several geometrid moth species such as those mentioned above for each zone (e.g., *C. puppillaria*, *P. rhomboidaria*, *E. dodoneata; L. hirtaria* for fixed dunes and *I. mediaria*, *I. consanguinaria*, *E. indigenata* for shifting dunes; see section 4.2) may serve as potential ecological indicators. Our study suggests that in this context valuable indicators can be identified by a combination of factors, such as: the (i) exclusive or predominant occurrence in one dune zone (shifting vs. fixed), (ii) documented host plant associations that reflect the vegetation characteristics of the respective zone, and (iii) peculiar ecological traits, such as wing size and habitat affinity. This integrative approach may allow the identification of geometrid moth species as ecological indicators for shifting and fixed dune environments. Species restricted to the fixed dunes have larger

wingspans, show more migratory behavior and are typically associated with woody plant hosts and more stable habitats, thus reflecting the structure and composition of that zone. Conversely, species exclusive to the shifting dunes are generally associated with open, herbaceous vegetation and harsher environmental conditions.

4.6. Limits and future directions

Although our light traps collected a broader range of moth taxa (including many noctuoids and microlepidopterans), the present study focused exclusively on Geometridae – a family recognized for its strong bioindicator potential due to its sensitivity to vegetation structure, habitat integrity and environmental disturbance. This targeted approach also addressed a gap in current knowledge, as geometrid moth communities remain understudied in coastal dune ecosystems. Importantly, Geometridae differ substantially from other moth groups, such as Noctuoidea and microlepidopterans, in life history traits, habitat preferences, dispersal abilities, and ecological roles. Combining these taxonomically and ecologically diverse groups in a single analysis could obscure meaningful patterns and reduce interpretability. Therefore, limiting the scope to Geometridae allowed for a taxonomically coherent dataset and clearer ecological inference. We also emphasize that this study serves as a first step in identifying ecological indicator species within coastal dunes using Geometridae. However, one limitation to consider is the potential influence of rare species (e.g., singletons) on observed patterns of β-diversity. These low-abundance species may inflate estimates of species turnover between dune zones and could exaggerate the ecological distinctiveness of assemblages. Future research with increased temporal replication or targeted sampling could help distinguish between true ecological patterns and artefacts related to sampling rarity.

Looking ahead, future studies should incorporate additional moth groups (e.g., Noctuoidea and microlepidopterans) to refine and validate indicator selection across the entire dune gradient. Expanding the taxonomic scope will also allow for broader cross-taxon comparisons and help assess the generality of observed ecological patterns, ultimately strengthening the applicability of moths as bioindicators in dynamic dune landscapes.

5. Conclusions

Our study provides key insights into the community structure of geometrid moths inhabiting a Mediterranean dune system in relationship with the vegetation. By focusing on Geometridae, a moth family largely unexplored in these habitats, we addressed an important knowledge gap enhancing both: our understanding of moth–vegetation interactions and establishing a foundation for future comparative research involving other Lepidoptera groups, such as Noctuoidea and microlepidopterans. These findings open new perspectives for the use of moths as ecological indicators in dynamic Mediterranean dune ecosystems. The fixed dunes, characterized by a complex vegetation with a variety of woody plant species, supports a greater number of exclusive geometrid moth species compared to the shifting dunes, providing them cooler, sheltered and diverse habitats. Differences in plant ecological functioning (Ecological Indicator Values, EIVs) and geometrid moth ecological traits between the two dune zones highlights the close interplay between environmental gradients and moth and plant community structure. In addition, this study highlighted the potential role of EIVs and ecological traits in investigating how environmental gradients shape geometrid moth and plant communities. Moth and plant β-diversity patterns resulted strongly correlated when considering abundance data, emphasizing the importance of considering species abundances rather than presence/absence alone in investigating community response to habitat structure. This observation also aligns with ecological patterns observed in other lepidopteran-plant interactions (Rasino et al., 2024), reinforcing the value of integrating traits and abundance metrics in ecological studies.

The peculiar habitat requirements of geometrid moths, with cycles closely tied to plant communities, suggests that they may represent valuable ecological indicators of alterations in ecosystem functioning, caused, for instance, by trampling or intensive beach cleaning. These attributes, coupled with the fact that their populations can be efficiently sampled using standardized light trapping methods, make geometrid moths valuable tools for monitoring the ecological integrity of Mediterranean coastal dunes. Since geometrid moths are especially abundant in spring and summer when tourist pressure on coastal dunes is at its peak conservation measures are urgently needed to mitigate anthropogenic disturbance. Key actions should include the installation of wooden boardwalks to prevent trampling on sensitive vegetation, as well as the use of rope-and-post barriers to clearly demarcate dune habitats and restrict access to the most fragile zones (Tozzi et al., 2022). Additionally, regulating beach cleaning practices and reducing light pollution during peaks of moth activity are essential to preserve both plant and moth communities.

The relationships between ecological traits of flora and fauna shown by geometrid moth and vascular plant assemblages in the study system, underscores the need for conservation strategies able to incorporate local-scale variability and encompass the overall dune seashore-inland gradient. Such an integrated approach is essential for preserving biodiversity and maintaining ecological functioning across broader spatial scales.

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CRediT authorship contribution statement

Micaela del Valle Rasino: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michele Innangi:** Writing – review & editing, Visualization, Validation, Software, Investigation, Formal analysis, Data curation, Conceptualization. **Mirko Di Febbraro:** Software, Formal analysis, Conceptualization. **Simone Fattorini:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Formal analysis, Data curation, Conceptualization. **Andrea Sciarretta:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization. **Angela Stanisci:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Investigation, Conceptualization. **Maria Laura Carranza:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113975.

Data availability

Data will be made available on request.

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Chapter 4 - Taxonomic and functional diversity of noctuoid moths in a Mediterranean coastal area: Implications for dune conservation in a Long-Term Ecological Research eLTER Site

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Taxonomic and Functional Diversity of Noctuoid Moths in a Mediterranean Coastal Area: Implications for Dune Conservation in a Long Term Ecological Research eLTER Site

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Keywords:	conservation, cross-taxon analysis, dune mosaic, ecological traits, Lepidoptera, vascular plants
Abstract:	Coastal dunes are highly vulnerable ecosystems that require adequate bioindicators for effective biodiversity monitoring. Although moths are recognized as good bioindicators in many contexts, their diversity patterns in these habitats remain understudied. This research examines the taxonomic and functional diversity of noctuoid moths in a well-preserved, protected dune system in Central Italy (Adriatic coast). Specifically, the study aimed at investigating how vegetation composition, and hence dune zonation, influences noctuoid diversity and traits. Moth sampling was carried out on an annual basis using UV LED traps in both shifting and fixed dune zones. Vegetation surveys were conducted in spring using 4 m × 4 m plots. We compared noctuoid species richness, species abundance distribution patterns, and trait attributes between the two dune zones in relation to vegetation characteristics. We also evaluated the congruence in species composition and abundance between dune zones for both moths and plants. Sampled noctuoids included 98 species (78 Noctuidae, 18 Erebidae, one Nolidae and one Notodontidae). The presence of habitat-exclusive species underscores the influence of both abiotic and biotic filtering processes in shaping noctuoid assemblages along the seashore-inland gradient. Trait-based analyses and diversity patterns showed clear ecological links between noctuoid assemblages and dune zones. This congruence supports the use of noctuoid moths as effective bioindicators and stresses the need to conserve the entire dune system as an integrated ecological unit.

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Taxonomic and Functional Diversity of Noctuoid Moths in a Mediterranean Coastal Area: Implications for Dune Conservation in a Long Term Ecological Research eLTER Site

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Running title: Noctuoid diversity on an LTER dune

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For Review Only

Abstract Coastal dunes are highly vulnerable ecosystems that require adequate bioindicators for effective biodiversity monitoring. Although moths are recognized as good bioindicators in many contexts, their diversity patterns in these habitats remain understudied. This research examines the taxonomic and functional diversity of noctuoid moths in a well-preserved, protected dune system in Central Italy (Adriatic coast). Specifically, the study aimed at investigating how vegetation composition, and hence dune zonation, influences noctuoid diversity and traits. Moth sampling was carried out on an annual basis using UV LED traps in both shifting and fixed dune zones. Vegetation surveys were conducted in spring using 4 m × 4 m plots. We compared noctuoid species richness, species abundance distribution patterns, and trait attributes between the two dune zones in relation to vegetation characteristics. We also evaluated the congruence in species composition and abundance between dune zones for both moths and plants. Sampled noctuoids included 98 species (78 Noctuidae, 18 Erebidae, one Nolidae and one Notodontidae). The presence of habitat-exclusive species underscores the influence of both abiotic and biotic filtering processes in shaping noctuoid assemblages along the seashore-inland gradient. Trait-based analyses and diversity patterns showed clear ecological links between noctuoid assemblages and dune zones. This congruence supports the use of noctuoid moths as effective bioindicators and stresses the need to conserve the entire dune system as an integrated ecological unit.

Key words: conservation; cross-taxon analysis; dune mosaic; ecological traits;·Lepidoptera; vascular plants

For Review Only

Introduction

Coastal dunes are dynamic systems, characterized by steep environmental gradients over relatively small spatial scales (e.g., Acosta et al., 2003; Martínez & Psuty, 2004, Malavasi et al., 2021) and are at the same time particularly vulnerable to anthropogenic pressures (Schlacher et al., 2007). Consequently, most sandy coastal vegetation types in Europe are habitats of conservation concern under the EU Habitats Directive (EEC 2013) and several dune-associated animal species are listed as imperiled (Fattorini, 2021). These transitional and dynamic systems provide a valuable context for investigating the responses of threatened individual taxa and assemblages along environmental and disturbance gradients (Berardo et al., 2015; Fattorini et al., 2016; Rasino et al., 2024).

Among faunal groups that are largely influenced by vegetation characteristics, lepidopterans hold a prominent position. Lepidopterans have distinct life cycles closely linked to plant communities during both larval and adult stages and occupy key positions in trophic networks as both plant consumers and prey for higher trophic levels (Enkhtur et al., 2017; van Klink et al., 2015; Dennis, 2020), being therefore particularly sensitive to vegetation characteristics and their alterations (Rákosy et al., 2011). In particular, cross-taxon congruence between lepidopteran and plant assemblages provides a valuable framework for understanding community assembly processes and improving biodiversity monitoring strategies (Rooney & Azeria, 2015; Marignani et al., 2020; Piccini et al., 2024). Despite growing interest in the biodiversity and functioning of coastal ecosystems, the relationship between lepidopteran assemblages and vegetation types across coastal dune zonation remains largely unexplored. A recent study on the butterflies of a Mediterranean coastal area evidenced distinct spatial patterns and strong responses of species diversity to coastal dune zonation, highlighting strong habitat filtering effects

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mediated by abiotic factors, resource availability and vegetation diversity and structure (Rasino et al., 2024), thus showing their potential in evaluating and monitoring dune conservation status. While butterflies are largely recognized as an important target in insect conservation (Dennis, 2010; Fattorini et al., 2023), moths are more rarely investigated, although the two groups may provide different and complementary information (Rákosy et al., 2011). In this paper, we focused on the diversity and conservation of a moth group (Noctuoidea) in the same Mediterranean coastal area where the aforementioned study on the butterfly community (Rasino et al., 2024) was conducted.

Noctuoidea are the largest superfamily of Lepidoptera, including more than 42,000 known species worldwide (Van Nieukerken et al., 2011; Zahiri et al., 2011). This group encompasses a wide ecological spectrum, including both generalist and specialist herbivores, taxa with varying mobility capacities, and species adapted to environments ranging from xeric to mesophilous conditions (Betzholtz et al., 2011; Pérez-Guerrero et al., 2011). Incorporating noctuoids into the study of Mediterranean coastal dune ecosystems may offer the potential to improve our understanding of how lepidopteran assemblages track environmental gradients and disturbance stress. Their ecological diversity makes them particularly suitable for comparative analysis with diurnal lepidopterans potentially enriching assessments of habitat filtering and functional community structure.

The present work investigates the diversity and functional composition of noctuoid moths in a protected Adriatic site of high conservation importance to enhance our understanding of how noctuoid assemblages respond to the environmental and structural gradients characteristic of coastal dunes. Specifically, it addresses the following

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questions: (a) Do patterns of α- and β-diversity in noctuoids vary significantly between coastal dune zones (i.e. shifting and stabilized dunes)? (b) How do plant and noctuoid traits vary between zones? (c) To what extent does cross-taxon congruence between noctuoid and plant assemblages vary along the coastal environmental gradient?

By examining the links between vegetation composition, dune zonation, and noctuoid diversity and traits, this study may offer scientific support to the identification of conservation priorities in these fragile and highly vulnerable landscapes.

Material and Methods

Study area

The study was conducted in the Natura 2000 site "Foce Trigno-Marina di Petacciato-IT7228221" (Molise Region, Adriatic coast, Central Italy), a protected area included in the European Long Term Ecological Research (LTER) Network (LTER IT20) (Stanisci et al., 2014; Capotondi et al., 2021; Fig. 1). This dune system is characterized by a well-defined zonation driven by abiotic stressors (Stanisci et al., 2014). Noctuoid moths and vascular plants were surveyed following LTER data collection guidelines (Prisco et al., 2016). Noctuoids and plants were sampled in three sites, each serving as a replicate. Within each site, noctuoid collection and vegetation surveys were conducted in two distinct zones characteristic of the sea-to-inland dune zonation: the shifting dunes, located near the seashore, and the fixed dunes found in the inner sectors. The shifting dunes are subject to strong environmental stressors, while the fixed dunes are less exposed to abiotic perturbations (Acosta et al., 2009; Bazzichetto et al., 2016). To avoid interference between the light traps used for moth sampling (see below), the study sites were

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positioned at the following distances: 300 m between Sites 1 and 2, 1,600 m between Sites 1 and 3, and 1,900 m between Sites 2 and 3 (Fig. 1). At each site, the two sampled dune zones were separated by at least 25 m, corresponding to their natural distribution within the system, which features intact yet low and narrow dunes (Acosta et al., 2003; Drius et al., 2013). Although there is some variability depending on the moth group and the specific characteristics of the trap model used, light traps typically attract moths from within 30 m, and often within 10 m (Baker & Sadovy, 1978; Truxa & Fiedler, 2012; Merckx & Slade, 2014), which is below the distance between traps adopted in our study.

Data collection

Noctuoids were sampled using light traps with UV LEDs. The LED traps consisted of a 2.5-m-long ultraviolet strip containing 150 LEDs (emission peak: 398 nm; beam angle per LED: 120°; 12 volts; ~15 W). The strip was mounted on a cylindrical PVC support, with four transparent plexiglass plates arranged radially around it. This structure was positioned above a container fitted with a large funnel, featuring a lower opening approximately 5 cm in diameter. Traps were placed at ground level and were powered by a portable lead-acid battery (Infusino et al., 2017). Traps operated during favorable conditions for moth activity. Sampling was carried out over a full annual cycle (December 2021 – November 2022), with each site visited every 15 days. On the first night of each sampling session, traps were placed in one zone; on the second night, they were relocated to the other zone. Each trap was equipped with loosely arranged egg cartons inside the collection bucket to provide shelter for captured individuals. To prevent interference from the adjacent zone, an opaque plastic panel was placed on the side of the trap facing the other zone. Ethyl acetate was used as a killing agent. All specimens were identified to the

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143 species in the laboratory using the reference collection of the General and Applied
144 Entomology Laboratory at the Department of Agricultural, Environmental and Food
145 Sciences, University of Molise. This sometimes required genitalia dissection. Taxonomy
146 followed Rennwald et al. (2023). Data are given in Table S1.

147 To investigate how noctuoid assemblages are structured across coastal zonation
148 and are related with vegetation we considered four ecological traits using literature
149 information (Macek et al., 2007, 2008, 2012; Potocky et al., 2018; Table 1; full data are
150 given in Table S1)..

151 Vegetation sampling was conducted in spring (May 2022) using 4 m × 4 m plots,
152 following a stratified random design. Within each site, five plots were randomly
153 positioned in the shifting dune zone and five plots in the fixed dune zone, resulting in a
154 total of 30 plots. All vascular plant species within each plot were identified, and their
155 relative cover was assessed using the Braun-Blanquet scale (Braun-Blanquet, 1964;
156 Westhoff & Van Der Maarel, 1978). For subsequent analyses, the original Braun-
157 Blanquet scores were converted into percentage cover values following the method of
158 Tichý et al. (2020). Each species was assigned to a Raunkiær life form following Pignatti
159 et al. (2017-2019). The Raunkiær system was adopted for its simplicity of application and
160 its effectiveness as a proxy for plant life strategies in response to environmental
161 conditions (Acosta et al., 2003; Di Biase et al., 2021a). Data are given in Table S2.
162 To analyze how different plant assemblages are structured along the coastal zonation
163 and the relationship with noctuoid assemblages we categorized all vascular plants
164 according to their ecological preferences and disturbance adaptations. We used
165 Ecological Indicator Values for Europe (EIVE) (Dengler et al., 2023) to express species
166 preferences for temperature (EIVE T), nitrogen availability (EIVE N). These indicators,

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which are a particular version of Ellenberg's indicator values (Di Biase et al. 2023), range from 0 (very low) to 10 (very high). Temperature and nitrogen preferences vary markedly along the dune zonation and EIVE values are good indicators for species turnover in response to environmental gradients occurring from the seashore to inland (Acosta et al., 2003; Malavasi et al., 2021). Additionally, to evaluate plant ability to withstand disturbance and adaptation to the dynamic conditions of coastal dunes (Innangi et al., 2025), we assigned Disturbance Frequency and Soil Disturbance Indicator values to each species (Midolo et al., 2023). These indicators quantify a species' ecological optimum along a disturbance gradient and its capacity to thrive in environments characterized by increased bare ground resulting from physical disturbances. Data are given in Table S2. In our context, such disturbances can be attributed to both natural dune dynamics (Bazzichetto et al., 2020; Innangi et al., 2025) and anthropogenic pressures, such as trampling (Malavasi et al., 2016, 2021). Finally, we assigned numerical values to plant growth forms (e.g., herbs = 1, shrubs = 2, trees = 3), which are known to vary along the seashore–inland gradient (Acosta et al. 2003; Acosta et al. 2009). These growth forms also play a key role in providing trophic resources and refuge habitats for lepidopterans (Rasino et al., 2024).

Statistical analysis

Spatial and temporal variations in α-diversity were investigated using Hill numbers ${}^{q}D$ (Chao & Jost, 2012; Chiu & Chao, 2014; Chao et al., 2020). Hill numbers integrate species richness, rarity and dominance into a single metric expressed as the effective number of species, allowing direct comparisons across diversity orders (Chao et al., 2014; Chiu & Chao, 2014). The sensitivity of Hill numbers to species abundances increases with increasing q: in particular, with $q = 0$, which corresponds to species richness, the

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contribution of rare species is emphasized; with q = 1, which corresponds to the exponential version of Shannon diversity, species are weighted in proportion to their abundances; with q = 2, which corresponds to the Simpson diversity, the contribution of the most abundant species is emphasized (Chao & Jost, 2012; Chao et al., 2020). We used these three Hill numbers to express noctuoid diversity separately for each sampling session, defined by a unique combination of dune zone (shifting dunes and fixed dunes), season (spring, summer, autumn), and site. Because winter sampling captured few species, this sampling session was excluded from analyses dealing with temporal patterns.

We used Linear Mixed Models (LMMs, assuming a Gaussian distribution) to investigate variations in moth Hill numbers and a Generalized Linear Mixed Model (GLMMs, assuming a Poisson distribution) for variations in moth abundance. In both cases, sites were considered as a random factor (Response Variable ~ Zonation × Season + (1|Site: Zonation)). A similar approach was applied to compare plant cover and diversity across zones (Response Variable ~ Zonation + (1|Site)).

Habitat preferences of noctuoids were assessed by comparing the percentage of moth abundance in the two dune zones with a z-test.

Noctuoid and plant species abundance distribution (SAD) patterns were compared between dune zones using rank-abundance curves (May, 1975; Fattorini, 2010; Hayek & Buzas, 2010; Dennis & Fattorini, 2025). In these analyses, data from different sites and seasons were pooled. To fit the rank-abundance plots, we adopted the method based on Ordinary Least Squares (OLS) regressions described by Fattorini (2005). When species are ranked from the most to the least abundant and abundances are logarithmically transformed, a geometric series precisely follows a straight line. This line can be therefore

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fitted using an OLS regression and the coefficient of determination R^2 will express how well the geometric series described the SAD. Moreover, with this approach, it is possible to test differences between slopes through analysis of covariance (ANCOVA). We applied this approach to test differences in noctuoid SADs between zones and seasons. The same approach was used for plants, where abundance was expressed as relative cover (see Moradi et al., 2025).

To explore patterns of covariance between noctuoid and plant ecological traits, we calculated a Community Weighted Mean (CWM) for each trait. The CWM is calculated as the sum of trait values of the species in an assemblage, weighted by their relative abundance (see Di Biase et al., 2021b and Di Biase & Fattorini, 2025 for a discussion). In CWM calculation, data from plots of the same zone were pooled (i.e., all shifting dune plots and all fixed dune plots from replicates 1, 2, and 3). To examine relationships between plant and noctuoid traits across dune zones, we applied a Two-Block Partial Least Squares (2B-PLS) analysis, a technique that constructs pairs of linear combinations from each set of variables (plant and moth traits) to maximize the covariation between these two groups (Rohlf & Corti, 2000). The covariance structure between the two trait matrices was visualized using scatterplots of the first 2B-PLS axis, with the *x*-axis representing moth traits and the *y*-axis representing plant traits. This visualization clearly identifies direct or indirect relationships both within and between trait sets.

Mantel tests (Pearson's correlation) with 9999 permutations were performed to evaluate the correlation between noctuoid and vascular plant β-diversity patterns. Analyses were based on dissimilarity matrices derived from Sørensen-Dice distances for

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presence/absence data and Bray–Curtis distances for abundance data (Baselga, 2010, 2013).

Results

We collected 98 species of moths belonging to the families Noctuidae (78 species), Erebidae (18 species), Nolidae (1 species) and Notodontidae (1 species) (see Table S1), including species typical of littoral sandy ecosystems (e.g., *Agrotis catalaunensis* (Millière, 1873), *Euxoa seliginis* (Duponchel, 1837) and *Hadena silenes* (Hübner, 1822)), Mediterranean maquis (e.g., *Catocala nymphagoga* (Esper, 1787) and *Zebeeba falsalis* (Herrich-Schäffer, 1839)),open xeric habitats (e.g., *Acontia trabealis* (Scopoli, 1763), *Cucullia santolinae* (Rambur, 1834), *Cucullia thapsiphaga* (Treitschke, 1826), *Omphalophana antirrhinii* (Hübner, 1803) and *Spudaea ruticilla* (Esper, 1791)) and mesophilic woodlands (e.g., *Ammoconia senex* (Geyer, 1828) and *Cryphia algae* (Fabricius, 1775)). Finally, a few euryecious and polyphagous species are reported to be common crop pests (Zhang 1994) (e.g., *Agrotis exclamationis* (Linnaeus, 1758), *Agrotis segetum* (Denis & Schiffermüller, 1775), *Autographa gamma* (Linnaeus, 1758) and *Helicoverpa armigera* (Hubner, 1808)). It should be noted the presence of *Euplagia quadripunctaria* (Poda, 1761), a species of conservation concern in Europe and included in Annexes II and IV of the Habitats Directive. The most abundant species in the shifting dune was *E. seliginis* (Noctuidae), with 108 individuals, whereas the most abundant species in the fixed dune were *Noctua pronuba* (Linnaeus, 1758) (Noctuidae), with 143 individuals, *Eilema caniola* (Hübner, [1808]) (Erebidae), with 51 individuals, and *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775) (Notodontidae), with 44 individuals.

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Regarding the vascular plants, we recorded 71 species (Table S2), with the most represented families being the Poaceae (17 species, 24% of the sampled flora), Asteraceae (11 species, 15%) and Fabaceae (6 species, 8%).

Noctuoid species richness and abundance were similar between the two zones (shifting dunes and fixed dunes), although seasonal variation was observed (Table 1; Fig. 1). No significant effect of zone or season was found for Shannon and Simpson diversity. No significant variation in plant species cover and diversity between the two zones was identified (Table S3).

Slopes of the noctuoid rank-abundance regression lines did not differ between the two zones (Fig. 2; ANCOVA: $F_{1,145} = 1.583$, $p = 0.210$). Additionally, noctuoid rank-abundance regressions showed significantly different slopes between seasons (Fig. 2; ANCOVA: $F_{2,82} = 71.59$, $p < 0.0001$). The slope for the plant regression of the shifting dunes was significantly higher than that of the fixed dunes (ANCOVA: $F_{1,72} = 56.125$, $p < 0.00001$; Figure S1).

Despite the total richness was relatively similar in the two zones (70 species in the shifting dunes and 79 species in in the fixed dunes), we found a rather high noctuoid β-diversity, with 19 moths sampled exclusively on the shifting dunes and 28 on the fixed dunes, respectively (Fig. 3). However, the proportion of exclusive species (27% vs 35%) did not differ significantly between the two zones (z-test: $z = -1{,}088$, $p = 0.276$).

The 2B-PLS analysis (Fig. 4) highlighted a clear differentiation between the two zones, emphasizing a strong covariance between noctuoid and plant ecological traits in response to dune zonation. Fixed dunes (upper-right quadrant) are characterized by noctuoids that have larger wingspans, use mainly chamaephytes and phanerophytes as

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host plants, and exhibit a generalist feeding strategy (high trophic range). Plant assemblages of the fixed dunes display higher values of woody life growth (e.g., shrubs and trees) and EIVE T. Conversely, shifting dunes (bottom-left quadrant) showed noctuoid assemblages displaying a moderate multivoltine behavior. Plant assemblages in this zone showed high values for disturbance frequency, soil disturbance values, and EIVE N. The trait associations revealed by 2B-PLS indicated clear ecological differences shaped by dune zonation, highlighting joined trait co-structuring between plant and moth assemblages along the environmental gradient.

Mantel tests showed a positive correlation between moth and plant β-diversity both for presence/absence ($r = 0.725$; $p = 0.004$) and abundance ($r = 0.867$; $p = 0.026$) data.

Discussion

In this study, we analyzed noctuoid assemblages in a Mediterranean dune system along the Adriatic coast (Central Italy), focusing on diversity patterns between dune zones (shifting dunes and fixed dunes) and functional relationships with dune vegetation. Our findings revealed significant associations between noctuoid and plant assemblages, both being shaped by dune ecological zonation.

The noctuoid assemblage revealed a remarkable level of species richness, with Noctuidae (the most numerous family) including 78 species. This richness is consistent with patterns observed in Mediterranean environments, where noctuids often represent a highly diverse moth family due to their wide range of ecological strategies and host plant

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associations (Scalercio et al., 2020; Mosconi et al., 2024). Among the species characteristic of coastal habitats, *Euxoa seliginis* was found to be particularly abundant in the study area, highlighting the conservation value of dune ecosystems as refugia for species that are increasingly rare or declining in disturbed ecosystems (Zilli et al., 2014). These results parallel those previously obtained for the butterflies of the same study area (Rasino et al. 2024), where the presence of *Gegenes nostrodamus* (Fabricius 1793), a localized and xerothermophilous species, highlights the high conservation value of this protected area.

Our results showed that the noctuoid assemblages exhibit distinct patterns of species richness and abundance across seasons, consistent with patterns previously documented for butterflies (Rasino et al., 2024). These seasonal fluctuations likely reflect phenological variability in moth life cycles (Niemela & Haukioja, 1982) and seasonal changes on coastal vegetation (Marzialetti et al., 2019; Bricca et al., 2023). Observed patterns of plant diversity are congruent with that recorded from other Mediterranean dune environments (e.g. Acosta et al., 2009; Martínez et al., 2004; Feola et al., 2011), with lower values near the seashore (La Bella et al., 2024; Torca et al., 2019).

Noctuoid species abundance diversity (SAD) patterns were adequately described by the geometric series model, as already found in the same area for butterflies (Rasino et al., 2024). This distribution pattern is typical of simplified assemblages dominated by a limited number of species well-adapted to harsh environmental conditions (Giller, 1984; McGill et al., 2007; Fattorini, 2010; Dennis & Fattorini, 2025). SADs did not reveal significant differences in noctuoid assemblage structure between dune zones, but differences emerged between seasons, with autumn period characterized by more

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dominated assemblages. Together, these patterns underline the role of seasonal dynamics but not zonation in shaping noctuoid assemblages.

The observed number of noctuoid species exclusive to one of the two zones (19 for the shifting dune and 28 for the fixed dune) highlights the ecological filtering exerted by environmental zonation. Although the proportion of exclusive species was not significantly different between the two zones, their identity suggests the presence of distinct ecological assemblages shaped by dune dynamics. These findings are consistent with a previous study showing strong compositional shifts in butterfly assemblages between zones (Rasino et al., 2024). In particular, the exclusive presence of *Mythimna riparia* (Rambur, 1829) and other oligophagous species feeding on Poaceae on the shifting dunes, and that of *Zebeeba falsalis*, a species that feeds on Mediterranean maquis plants (e.g. *Pistacia lentiscus* and *Asparragus acutifolius*), on the fixed dune, respectively, highlights the importance of moth trophic niche in shaping their microscale distribution. These findings underscore the ecological significance of maintaining the integrity of coastal dune zonation (Drius et al., 2013) to preserve the diversity and functional complexity of associated moth assemblages.

The 2B-PLS analysis revealed a clear ecological segregation between dune zones, driven by covariance traits in both noctuoid and plant assemblages. In the fixed dunes, noctuoid assemblages were composed of species with wider wingspans, broad trophic ranges, and larval associations with woody plant life growth. These moth traits mirrored the structural and ecological features of the fixed dunes plant assemblages, which were dominated by woody forms and species adapted to warm conditions (EIVE T). These life forms are typical of more stable environments and their temperature indicator values reflect the environmental conditions of the Mediterranean maquis, where plants are

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adapted to high photosynthetic activity (Innangi et al. 2025). Our findings support previous observations that larger moths are predominantly associated with woody vegetation (e.g., Lindström et al., 1994; Cizek et al., 2006; Seifert et al., 2023, 2025). Larger body size and broader trophic range in Noctuoidea of fixed dunes indicate greater migration capacity and colonization ability (Dapporto & Dennis, 2013). Smaller body size in shifting dunes is consistent with findings by Seifert et al. (2025) who reported that smaller body sizes, often associated with herbaceous plants, showed an evolutionary advantage by enabling multiple generations per year, thereby facilitating more rapid adaptation to fluctuating environmental conditions. In line with the above, shifting dune plant assemblages were characterized by adaptations to frequent disturbances, including soil disturbance. Moreover, plants of shifting dunes were characterized by high nitrogen levels (EIVE N), which is consistent with the organic matter inputs they receive from the shoreline (Brown & McLachlan, 1994; Martínez & Psuty, 2004) and the high coverage of the grass *Calamagrostis arenaria*, as its long-term biomass accumulation increases organic matter deposition (Jones et al., 2004). Overall, plants in shifting dunes are well adapted to unstable and highly dynamic environments (Angiolini et al., 2018) and the dominance of therophytes and geophytes supports Grime's (1979) hypothesis that disturbances favor annual species (Midolo et al., 2023).

Results of Mantel tests indicated a strong and significant association between moth and plant β-diversity patterns. The positive correlation based on presence/absence data suggests that the identity of moth species is closely linked to the types of vegetation present. In addition, the abundance-based correlation revealed that moth population sizes also respond strongly to vegetation structure. In the case of butterfly-plant correlations (Rasino et al., 2024) abundance variations exert a more pronounced influence on β-

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diversity than differences in species composition alone. These findings indicate that noctuoid moths strongly depend on local vegetation and support the idea that plant community composition and structural complexity act as a key biotic filter in shaping moth assemblages.

Conclusions

This study provided important insights into the relationship between noctuoid diversity and the environmental gradient characterizing Mediterranean coastal dune systems. Although species richness and abundance did not show differences between shifting and fixed dunes, clear seasonal fluctuations and distinct assemblage structures emerged, reflecting the dynamic temporal nature of these ecosystems. Moreover, the occurrence of species exclusive to one of the two zones highlights the role of both abiotic and biotic filtering processes in structuring moth assemblages along the seashore–inland gradient. These findings underscore the ecological significance of maintaining the integrity of coastal dune zonation to preserve the diversity of associated moth assemblages. Our trait-based analyses revealed clear ecological segregation between dune zones, with fixed dunes supporting larger moths associated with woody vegetation, and shifting dunes harboring smaller, multivoltine species linked to herbaceous and disturbance-adapted vegetation. Moreover, the high cross-taxon congruence between noctuoid and plant assemblages highlights the ecological interdependence of these taxa. This suggests a high potential for noctuoid moths as bioindicators and supports the integration of functional trait approaches in biodiversity monitoring and conservation planning. In sum, our findings contributed to a deeper understanding of how species interactions and

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environmental gradients shape biodiversity in coastal dune ecosystems. They emphasize the importance of preserving both biotic and abiotic heterogeneity in these vulnerable habitats and highlight the potential of cross-taxon, trait-based frameworks to inform ecological assessment and habitat management strategies.

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Disclosure

The authors declare that they have no conflicts of interest associated with this work.

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716 **Table 1** Ecological traits of noctuoid moths and plants recorded in a Mediterranean dune system ("Foce
717 Trigno–Marina di Petacciato" Natura 2000 site, Italy) along with measurement units and the rational.

Moth traits	Type of trait and description	Rationale
Wingspan	Continuous (mm).	Proxy for adult dispersal ability (Sekar, 2012) and plant use (Lindström et al., 1994; Cizek et al., 2006; Seifert et al., 2022b) with higher values indicating higher dispersal capability and plant use potential.
Voltinism	Continuous. Mean number of generations per year.	Higher values indicate higher generalism (Dapporto & Dennis, 2013) and higher development speed (WallisDeVries, 2014).
Trophic range	Ordinal, 1: monophagous (species feeding on <4 genera of one family); 2: oligophagous (on <3 genera from different families); 3: polyphagous (>3 plant families).	Higher values indicate wider larval trophic niche breadths.
Host plant form	Ordinal, 1: forbs, 2: grasses, 3: shrubs, 4: trees.	Describes how moths exploit the host plants and their spatiotemporal variability (e.g., reproductive and biomass phenology) and potential anti-herbivore defenses (Lindström et al., 1994; Altermatt, 2010; Seifert et al., 2022).
Plants traits	**Categories**	**Rationale**
Indicator value ''EIVE T''	Continuous, from 0 to 10.	Describes the species' optimal positioning along a temperature gradient (Dengler et al., 2023). Proxy for local microclimate, which can in turn influence insect species richness and composition (Buse et al., 2015).

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Indicator value ‘‘EIVE N’’	Continuous, from 0 to 10.	Describes the species’ optimal positioning along a nitrogen availability gradient (Dengler et al., 2023), with soil nutrient content shaping plant nutritional quality, which in turn affects herbivore food resources and ultimately insect diversity (Kurze et al., 2018).
Disturbance Frequency	Continuous, from 0 (no biomass loss) to 1 (complete plant cover loss).	Describes the species optimal positioning along a disturbance gradient (Midolo et al., 2023).
Soil Disturbance	Continuous, from 0 to 1.	Measured as the proportional increase in bare ground caused by furrowing or soil turning (Midolo et al., 2023).
Growth form	Ordinal: 1: herbs; 2: shrubs; 3: trees	Plant structure provides moths with feeding resources and egg-laying sites, also shaping local microclimatic conditions (Dennis, 2004).

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721 **Table 2** Results of Linear Mixed Model for the influence of zonation (fixed dunes vs shifting dunes) and
722 season (autumn, spring, summer,) on noctuoid species richness and abundance in a Mediterranean dune
723 system ("Foce Trigno–Marina di Petacciato" Natura 2000 site, Italy). SE = standard error; *p* = probability.
724 Significant effects are in bold.

	Estimate	**SE**	***p***
Intercept	8.867	1.001	$8.01e^{-14}$
Zonation Shifting dunes	-2.617	1.501	0.084836
Season Spring	**-5.867**	**1.469**	**0.000134**
Season Summer	-2.054	1.393	0.143919
Zonation Shifting dunes: Season Spring	3.083	2.100	0.145665
Zonation Shifting dunes: Season Summer	1.392	2.019	0.492256
Abundance			
Intercept	3.29402	0.10684	$< 2e^{-16}$
Zonation Shifting dunes	-0.16350	0.15484	0.290990
Season Spring	**-1.78482**	**0.13746**	**$< 2e^{-16}$**
Season Summer	**-0.41716**	**0.07681**	**$5.6e^{-08}$**
Zonation Shifting dunes: Season Spring	0.16029	0.19178	0.403254
Zonation Shifting dunes: Season Summer	**-0.48010**	**0.12562**	**0.000133**

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728 **Fig. 1** Study area and sampling design. (A) Geographical location of the study area ("Foce Trigno–Marina
729 di Petacciato" Natura 2000 site) on the Adriatic coast of central Italy and distribution of the three sampling
730 sites. Each site included both shifting and fixed dunes. (B) Schematic representation of the sampling design,
731 with five 4 m × 4 m vegetation plots surrounding a central UV LED light trap used for moth sampling.
732 Satellite imagine from Google Earth.

733

734 **Fig. 2** Rank-abundance plots depicting the species abundance distributions (SADs) of noctuoids for dune
735 zones (shifting dunes and fixed dunes) and seasons (spring, summer and autumn) in a Mediterranean dune
736 system ("Foce Trigno–Marina di Petacciato" Natura 2000 site, Italy). Species are ranked from the most to
737 the least abundant (x-axis). Species abundances (number of individuals) are $\log_{10}$-transformed (y-axis).
738 Regression equations for zones are: shifting dunes: $y = -0.021x + 1.295$, $R^2 = 0.889$, $p < 0.0001$; fixed dunes:
739 $y = -0.023x + 1.50$, $R^2 = 0.906$, $p < 0.0001$; regression equations for seasons are: spring: $y = -23.304x +$
740 27.743, $R^2 = 0.898$, $p < 0.0001$; summer: $y = -23.584x + 40.128$, $R^2 = 0.903$, $p = 0.0001$; autumn: $y = -$
741 $12.752x + 27.652$, $R^2 = 0.976$, $p < 0.0001$.

742

743 **Fig. 3.** Distribution of exclusive noctuoid species in dune zones (blue = shifting dunes, pink = fixed dunes) in a
744 Mediterranean dune system ("Foce Trigno–Marina di Petacciato" Natura 2000 site, Italy).

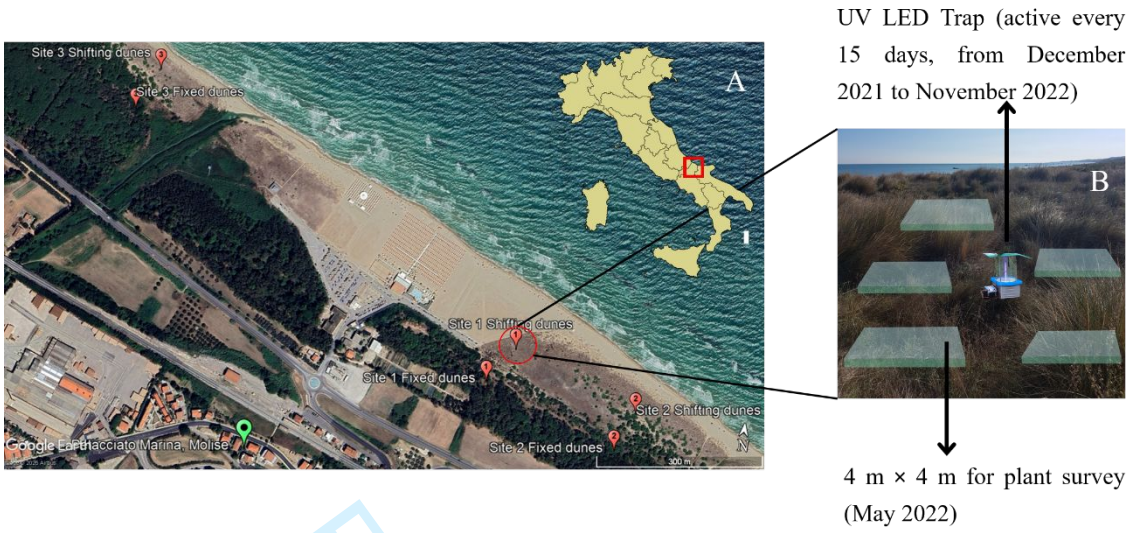
745

746 **Fig. 4** Scatterplot for the first axis of a Two-Block Partial Least Squares analysis for noctuoid moth and
747 plant traits in a Mediterranean dune system ("Foce Trigno–Marina di Petacciato" Natura 2000 site, Italy).
748 Points are mean moth CWM values on Block 1 and mean plant CWM values on Block 2. Replicates (1, 2,
749 3) are reported for the fixed (F) and shifting (S) dunes. The insets show the correlation of traits of moths
750 (Block 1) and plants (Block 2) with the two zones.

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754 **Fig. 1**

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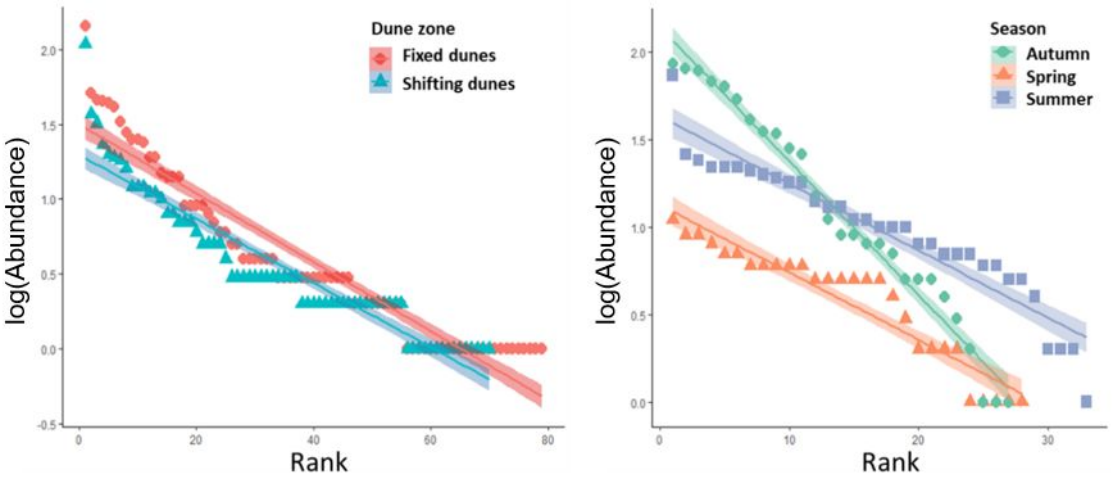
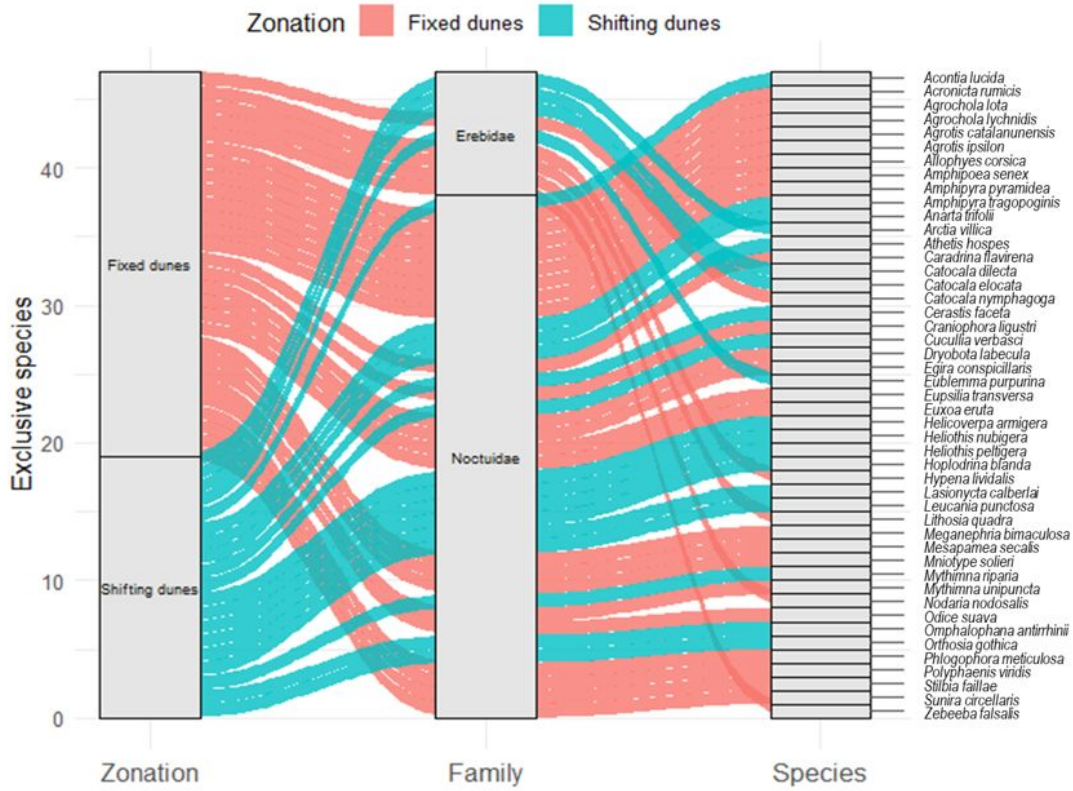


Fig. 2

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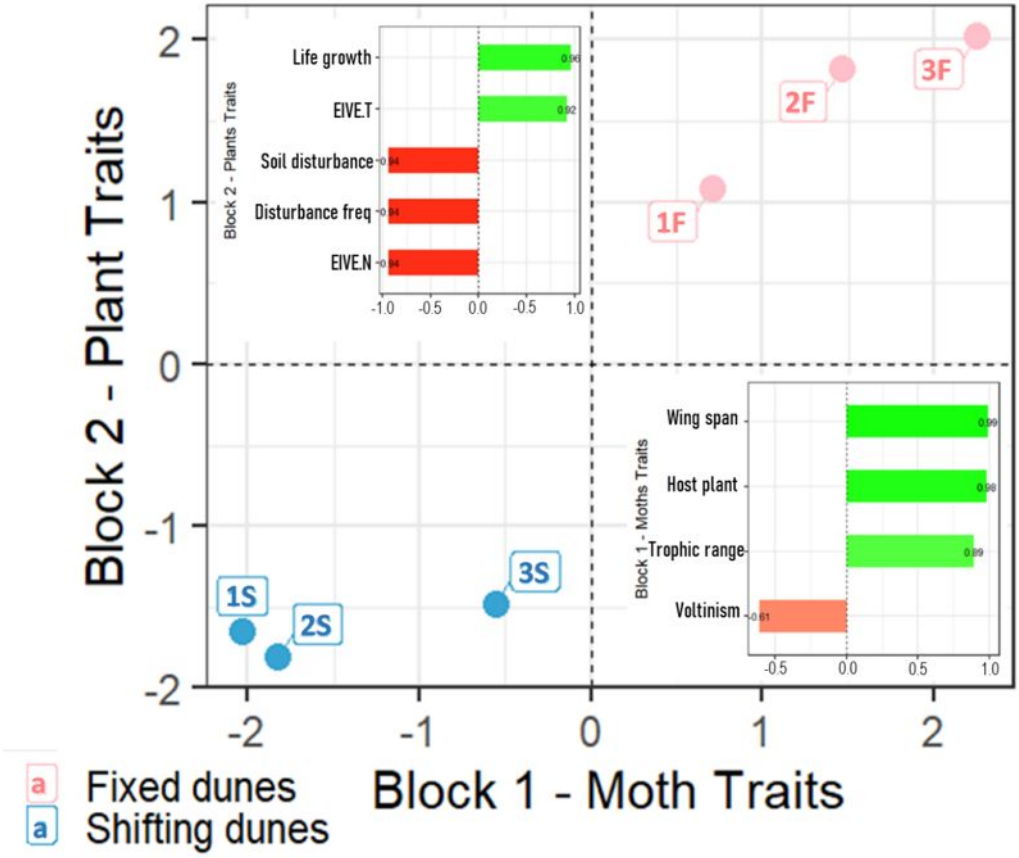


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762 **Fig. 3.**

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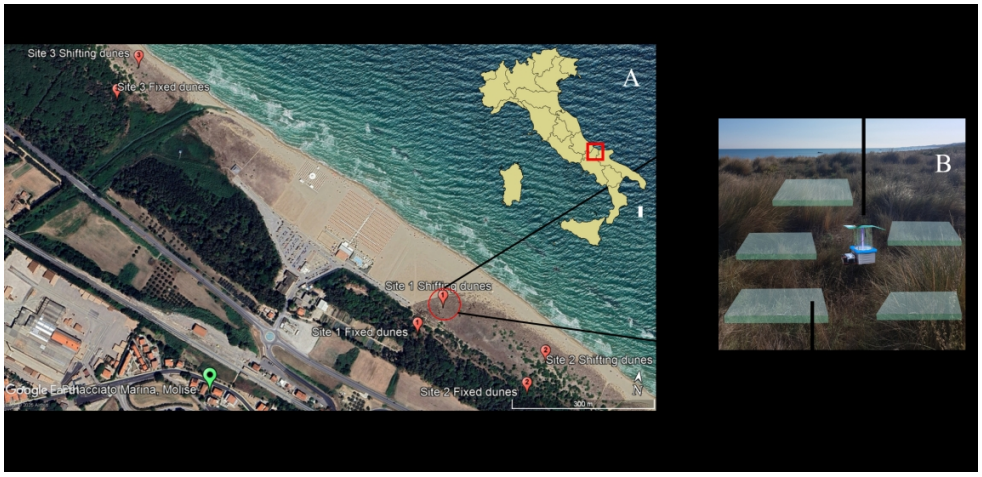


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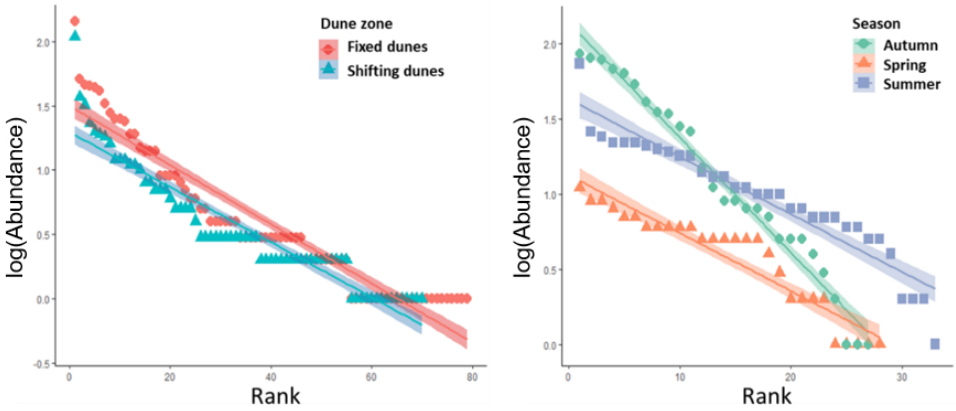
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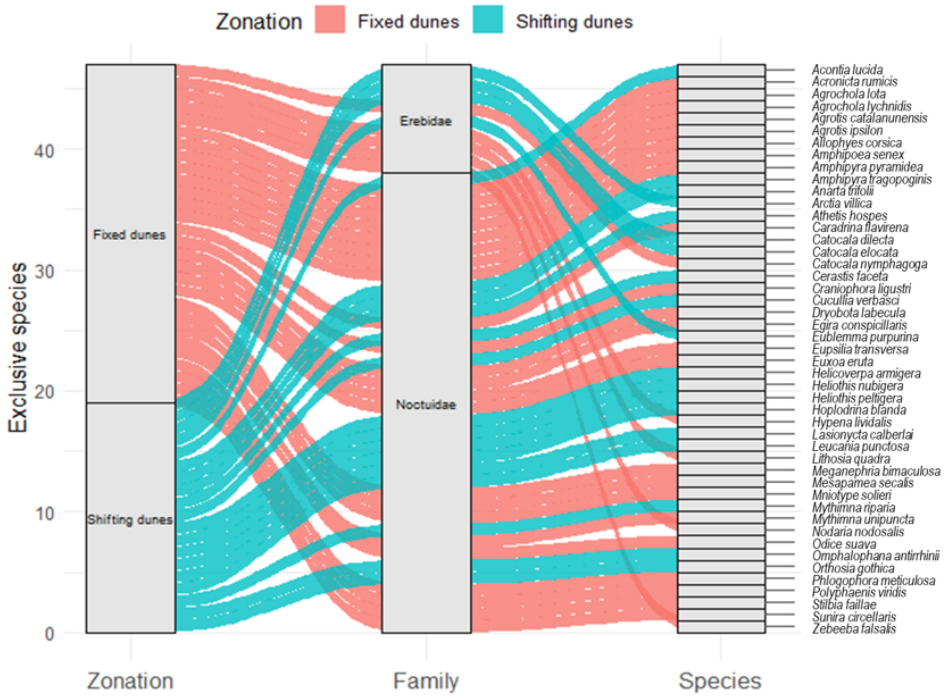
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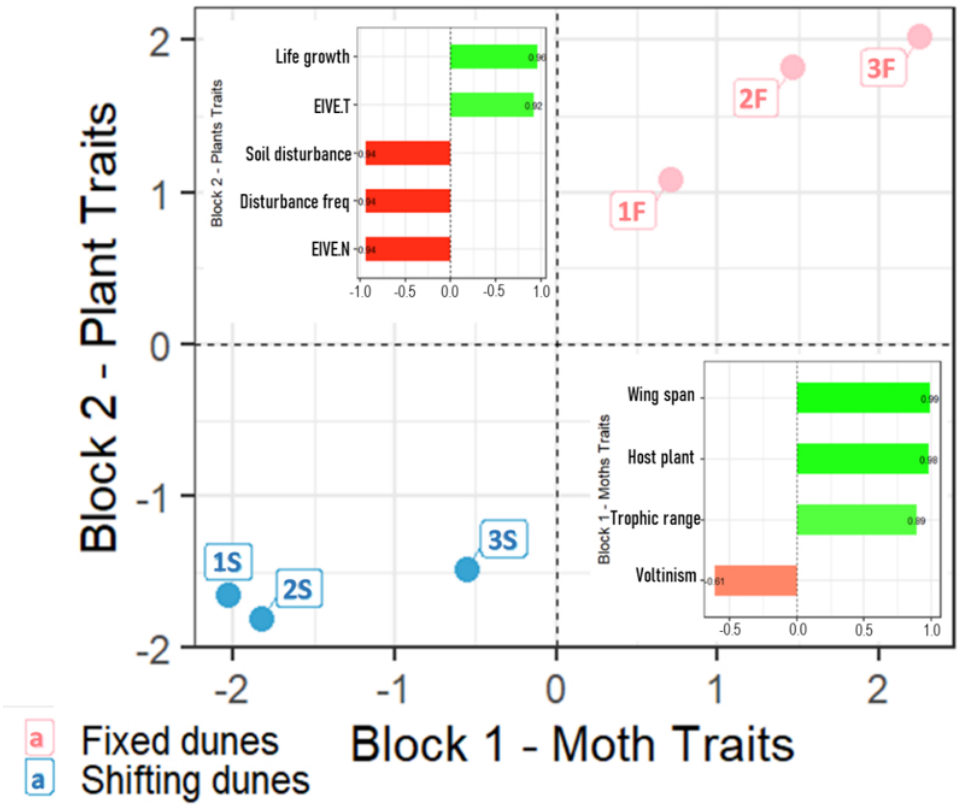
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MAIN FINDINGS

This PhD thesis contributed to the documentation and updating of the faunistic records of Lepidoptera associated with dune ecosystems in the coastal area of Molise Region (Italy). Also, it provided new insights into the ecological characteristics of Lepidoptera and vascular plants communities across coastal dune system, revealing consistent and significant associations between butterflies/moths and vascular plant communities, shaped by dune ecological zonation.

Additionally, the thesis sheds light on potential utilization of Lepidoptera, specifically Rhopalocera (butterflies), Geometridae and Noctuoidea (moths), as bioindicators for assessing the ecological quality of the coastal dune ecosystems. Ranging from larval stages that feed on specific host plants to adult stages that play a crucial role in pollination, their presence, absence, or variation in species composition and abundance can provide meaningful insights into ecosystem integrity.

Finally, the combined use of alpha-, beta-, and gamma-diversity metrics, functional trait analyses and cross-taxon correlations provided an effective analytical framework to reveal biodiversity patterns along coastal dune gradients. This integrative approach could potentially be applied to other taxonomic groups, such as different families of Lepidoptera or other phytophagous taxa.

Firstly, Lepidoptera recorded in a site of special conservation interest and still unexplored Italian region, are listed in the faunistic study, which encompassed a total of 223 species: 18 butterfly species from 5 families (Papilionidae, Hesperiidae, Pieridae, Lycaenidae, and Nymphalidae) and 205 moth species belonging to 17 families (Tineidae, Alucitidae, Pterophoridae, Tortricidae, Coleophoridae, Cossidae, Yponomeutidae, Pyralidae, Crambidae, Drepanidae, Sphingidae, Lasiocampidae, Geometridae, Notodontidae, Erebidae, Nolidae, and Noctuidae). Among the butterflies, the families with the greatest species richness were Nymphalidae with 7 species, followed by Lycaenidae with 5 species and Pieridae with 3 species. In the case of moths, the most diverse families were Noctuidae (78 species) and Geometridae (39 species), with Crambidae ranking third with 22 species. These families also exhibited the highest genera number. Notably, 48 moth species are new records for the Molise fauna: 2 Tineidae, 2 Alucitidae, 2 Coleophoridae, 1 Yponomeutidae, 17 Pyralidae, 21 Crambidae, 1 Lasiocampidae, 1 Erebidae and 1 Noctuidae. Although data on the Macrolepidoptera families of Molise collected in previous faunistic surveys (Sciarretta & Zilli 1998, Sciarretta & Parenzan 1998, Sciarretta

& Parenzan 2001, Sciarretta & Raineri 2001) included the same locality sampled in the present work, our study recorded 84 additional species of Noctuoidea, 29 species of Geometridae, 3 species of Lasiocampidae, 2 species of Sphingidae, and 1 species of Drepanidae, substantially expanding the known assemblage for this eLTER site. Species richness per family between the two dune zones (shifting and fixed dunes) showed no statistically significant difference. However, the size effect ranged from small to moderate, hinting at a possible ecological pattern despite the lack of statistical significance. Furthermore, the relationship between lepidopteran family and dune zone also exhibited no significant association, with a small effect size, indicating that the distribution of species richness among families was comparable across the two zones. The presence of many species exclusive to either one of the two zones suggest the presence of well distinct assemblages and highlights the critical importance of conserving the integrity of the entire dune mosaic. The lepidopteran list presented in this study offers valuable reference for researchers and environmental managers to compare the structure and composition of Lepidoptera communities across Mediterranean coastal systems, assess temporal dynamics linked to environmental change, support long-term monitoring (e.g., eLTER), and contribute to ecological studies in dune habitats **(Chapter 1).**

The second scientific study **(Chapter 2)** explored cross-taxon habitat distribution patterns of both butterfly and plant communities along the Mediterranean coastal dunes of central Adriatic coast. We found that butterfly and vascular plant communities exhibited comparable patterns of alpha-, beta-, and gamma-diversity. Both butterfly richness and abundance were greater in the fixed dunes than in the shifting dunes, particularly during autumn, coinciding with the blooms of the rosemary garrigue (*Salvia rosmarinus*) (see Katerinopoulos et al., 2005). In addition, butterfly assemblages were clearly shaped by seasonal dynamics, with the highest species richness recorded during the growing season, primarily in summer, followed by autumn (Depetris et al., 2023). Vascular plant communities showed similarly low alpha-diversity near the seashore, with diversity increasing progressively toward the inland sectors. This pattern, observed in similar studies, reflects the environmental gradient from the coast to the inland (Acosta et al. 2009; Bazzichetto et al. 2016). Among both butterflies and plants, we identified species exclusive to either the shifting or the fixed dunes. Notably, *Gegenes nostrodamus*, a localized xerothermophilous species of high conservation concern, was found in the shifting/transition dunes, where a mosaic of priority habitats take place (e.g., EC-2110,

EC-2120, EC-2230). Its presence underscores the biodiversity value of Natura 2000 sites, especially given its national decline. In contrast, fixed dunes hosted sciophilous species (e.g., *Maniola jurtina, Lycaena phlaeas*), likely favored by the microclimatic buffering provided by woody vegetation. Vegetation structure also differed markedly along sectors: Poaceae monocots (*Festuca fasciculata, Calamagrostis arenaria, Thinopyrum junceum, Anisantha madritensis*), dominated the shifting dunes, while fixed dunes featured high cover of diagnostic woody dicots (e.g., *Salvia rosmarinus, Pistacia lentiscus*), highlighting their conservation relevance. This dominant flora is also among those listed as diagnostic for the identification of costal habitats of European concern (Stanisci et al., 2014; Rivieccio et al., 2021), emphasized the conservation importance of the study system. In addition, species exclusive to the shifting dunes (e.g., *Gegenes nostrodamus, Melanargia galathea*) feed on grasses typical of this sector (e.g., *Calamagrostis arenaria*), while those restricted to the fixed dunes feed on several Poaceae found there (e.g., *Dactylis glomerata, Briza media, Brachypodium* sp.). These patterns suggested that trophic relationships, microhabitat preferences, and plant-provided resources for larvae and adults (Siemann et al., 1998; Romeis et al., 2005) shaped butterfly distribution across the dune gradient. The SADs of both communities' taxa were well described by the geometric series model, typical of simplified systems dominated by a few stress-tolerant species (Giller, 1984; McGill et al., 2007). Butterfly abundance distributions had similar slopes across habitats, though lower intercepts in shifting dunes suggest reduced abundance under harsher conditions without changes in community structure. In contrast, plant communities displayed steeper slopes in shifting dunes, indicating stronger dominance patterns. The correlation between plant and butterfly diversity was stronger for plant with flowers compared to the more abundant anemophilous ones. Given that most butterflies are generalist nectar feeders, with the capacity of utilizing widely distributed plant species such as Fabaceae, Caryophyllaceae, and certain Asteraceae, this likely facilitates oviposition across the dune zonation (Grossmueller & Lederhouse, 1987; Adler & Bronstein, 2004). Intact dune systems therefore act as critical refuges, offering both floral resources for adult butterflies and suitable larval habitats for more specialized taxa (e.g., *G. nostrodamus*). As long-distance pollinators (Bloch et al., 2006), butterflies may also contribute to the maintenance of biodiversity in coastal ecosystems and support fruit production in nearby agroecosystems which are integral to many Mediterranean landscapes (Altini et al., 2017; Petrosillo et al., 2022). Finally, although cross-taxon patterns between butterflies and plants showed a higher and significant correlation

emerged when abundances were considered, while evidenced a low correlation when only species identities were considered, suggesting that variation in abundance may better reflect shared ecological responses in this dune system. Our findings suggest that butterfly and plant communities are primarily shaped by the shore-inland environmental gradient, with biotic interactions playing secondary roles in defining distinct communities across dune zonation.

The third scientific contribution **(Chapter 3)** aimed to analyze geometrid moth communities in the same Mediterranean coastal dune system along the Adriatic coast, focusing on diversity patterns between dune zones (shifting dunes vs fixed dunes) and their functional relationships with vascular plants. The main results indicated significant associations between geometrid moth and vascular plant communities, both shaped by dune ecological zonation. Geometrid moths are largely linked to woody habitats, as confirmed by our findings showing most species feed on woody plants as primary hosts. The smaller wingspan observed in herb-feeding species likely reflects the dominance of small-bodied Sterrhinae in shifting dunes habitats, suggesting a connection between host plant structure and moth body size (Lindström et al.,1994; Seifert et al., 2022). Plant diversity in the study area is consistent with previous research on Central Italian dune systems regarding the composition of major taxonomic groups in Central Italy (Acosta et al., 2009; Prisco et al., 2020). Shifting dunes, characterized by hard environmental conditions, support mainly therophytes and hemicryptophytes adapted to selective stressors. Therophytes were particularly abundant, comprising 50% of species in shifting/transition dunes and 42% in fixed dunes. These annual plants dominate in spring and summer but persist as seeds during winter storms. In contrast, the fixed dunes showed a greater presence of phanerophytes, likely due to reduced exposure to wind, salt spray, and sand burial (Tozzi et al., 2021, Feola et al., 2011). Moth and vegetation displayed similar patterns of alpha, beta and gamma diversity. We did not find association between moth alpha diversity and dune sectors, except for seasonal variability. The absence of clear zonation in geometrid alpha diversity may stem from their nocturnal behavior, which limits exposure to harsh environmental gradients typical of Mediterranean dunes. Seasonal shifts in diversity appear linked to species life history traits, such as voltinism, and generation length, which depend on the quality and phenology of host plants (Niemelä & Haukioja, 1982), which supplies abundant resources for both larvae and adult pollinators during spring and summer (Biondi et al., 2009; Singh et al., 2022). The

proportion of exclusive species differed significantly across dune zones. As observed along other environmental gradients (Usher & Keiller, 1998; Kitching et al., 2000), the fixed dunes, characterized by more stable and buffered conditions, hosted more exclusive moth species than the harsher shifting dunes. Dominant species included *Cyclophora puppillaria* and *Peribatodes rhomboidaria*, both associated with woody plants. Other exclusive taxa, such as *Eupithecia dodoneata* and *Lycia hirtaria*, also feed on phanerophytes, which are more common in the fixed dunes. The structured vegetation of this zone, with shrubs and trees forming vertical strata, likely offers a greater diversity of microhabitats supporting Lepidoptera assemblages (Dover et al., 1997; Clausen et al., 2001). On the contrary, in the shifting dunes, moth communities were dominated by species feeding on herbaceous plants (e.g., Poaceae family). The most abundant were *Eucrostes indigenata*, primarily associated with *Euphorbia paralias*, and *Idaea* spp., which typically specialize on herbaceous hosts (Hausmann, 2004; King & Viejo Montesinos, 2010). The species abundance distributions (SADs) of both taxa followed a geometric pattern, reflecting the environmental harshness of dune systems, as seen in previous studies (Fattorini & Carpaneto, 2001; Fattorini et al., 2017; Rasino et al., 2024). Moth SADs showed similar structure between dune types, though abundance was lower in shifting dunes. In contrast, plant SADs differed more markedly, with steeper slopes in shifting dunes, indicating stronger dominance by a few species in more extreme conditions. The 2B-PLS analysis revealed clear correlations between moth and plant functional traits linked to dune zonation. In fixed dunes, geometrid moths showed larger wingspans and migratory behavior, reflecting their ecological niche in woody habitats dominated by chamaephytes and phanerophytes. These stable habitats provide reliable food and protection from predators and aridity (Scalercio et al., 2007), supporting larger-bodied and multivoltine moth species able to exploit extended flowering periods (e.g., rosemary blooms; Katerinopoulos et al., 2005). Lower disturbance and reduced maritime stress in fixed dunes enhance ecosystem stability, favoring plants adapted to moderately stable soils (Torca et al., 2019; Wiedemann & Pickart, 2004; Tozzi et al., 2021). In contrast, shifting dunes host smaller geometrid moths, while plant communities show moderate soil moisture indicator values (EIVE M). These plants often have deep roots and reduced leaf area, key adaptations to minimize water loss in this harsh environment (Walker & Zinnert, 2022). Different plant features and moth ecological traits between dune zones highlight the close link between environmental mosaics and plant community structure. This study underscores the usefulness of EIVs and functional traits to explore

how such gradients influence moth and plant communities. Moreover, cross-taxon patterns of moths and plants showed strong correlations when based on abundance data, stressing the importance of considering species abundances rather than mere presence/absence. Geometrid moths, with life cycles closely linked to plant communities, may represent useful bioindicators for changes at coastal habitats caused by disturbances like trampling or intensive beach cleaning. Because geometrid moths peak in spring and summer, coinciding with high tourist pressure on coastal dunes, urgent conservation actions are needed to reduce human impact on integrity of Mediterranean dune systems.

The fourth study **(Chapter 4)** focused on the diversity and functional composition of noctuoid moths along the coastal dune zonation and exploring the relationships between dune vegetation diversity. This study provides a scientific basis for the identification of conservation priorities in these highly threatened Mediterranean dunes. The study registered 98 species of moths from the families Noctuidae (78 species), Erebidae (18 species), Nolidae (1 species) and Notodontidae (1 species). The dominance of Noctuidae is consistent with trends in Mediterranean environments, where often represent the most diverse moth family due to their broad ecological strategies and varied host plant associations (Scalercio et al., 2020; Mosconi et al., 2024). A significant number of species are characteristic of specific habitats such as littoral sandy ecosystems, e.g., *Agrotis catalaunensis* (Millière, 1873) and *Euxoa segilinis* (Duponchel, 1837), underscoring the role of dune ecosystems as important refuges for species that are becoming rare or declining in more disturbed landscapes (Zilli et al., 2014; Rasino et al., 2024); and Mediterranean maquis, such as *Catocala nymphagoga* (Esper, 1787) and *Zebeeba falsalis* (Herrich-Schäffer, 1839), the latter very abundant. We found marked seasonal variation, consistent with patterns previously reported for butterflies and geometrid moths in similar Mediterranean systems (Rasino et al., 2024; 2025). SADs revealed clear differences in community structure across dune zones and seasons, emphasizing the combined influence of habitat zonation and seasonal dynamics on noctuoid moth assemblages. The high turnover observed between dune zones, including 19 exclusive species in shifting dunes and 28 in fixed dunes, underscores the ecological filtering imposed by environmental zonation. The presence of oligophagous species such as *Mythimna riparia* in shifting dunes, linked to genera *Calamagrostis* sp., and *Zebeeba falsalis* in fixed dunes, associated with Mediterranean maquis plants like *Pistacia lentiscus* and *Asparagus acutifolius*, illustrates how moth community composition closely follows the distribution of host

plants within nutritional niches. The 2B-PLS analysis showed a clear ecological segregation between dune zones, driven by covarying traits in moths and plants. In fixed dunes, noctuoid moths were generally larger, with broader trophic ranges, and associated with woody plants, reflecting the structure of the plant community, dominated by woody life growth and species adapted to warm conditions (EIVE T), typical of Mediterranean maquis (Innangi et al., 2025). These findings align with previous studies (Lindström et al., 1994; Seifert et al., 2023, 2025) and confirm that larger, generalist moths benefit from the structural complexity and stable resources of woody habitats, as also shown for geometrids in Chapter 3. In contrast, shifting dunes hosted smaller-body size noctuoid moths, similar to geometrids (see Chapter 3), exhibiting multivoltine life cycles. This agrees with Seifert et al., (2025), who reported that smaller moths associated with herbaceous plants can exploit rapid, multiple generations to cope with fluctuating environments. Shifting dune vegetation showed high nitrogen levels (EIVE N) and adaptations to frequent disturbance, including soil disturbance. Organic inputs from the shoreline (Brown & McLachlan 1994; Martínez & Psuty, 2004) and the biomass accumulation of *Calamagrostis arenaria* (Jones et al., 2004) likely enhance nitrogen availability. Finally, the strong congruence between moth and plant communities, reflected in both presence/absence and abundance-based correlations, underscores their ecological interdependence. This highlights the value of noctuoid moths as bioindicators and supports the use of functional trait approaches in biodiversity monitoring and conservation strategies. Our findings contribute to a deeper understanding of how species interactions and environmental gradients shape biodiversity in coastal dune landscapes.

FUTURE DEVELOPMENTS

The results of this PhD thesis provide a multi-taxon perspective on coastal dune biodiversity by integrating species inventories (Chapter 1), comparative diversity analyses of butterflies and vascular plants (Chapter 2), and diversity analyses and functional trait-based analyses studies on Geometridae and Noctuoidea (Chapters 3 and 4). Several future directions emerge from this research, pointing to both methodological refinement and applied conservation opportunities.

Studies across various European countries have documented a gradual decline in Lepidoptera populations, particularly moths, due to climate change, habitat loss, agricultural intensification, and pollution (Coulthard et al., 2019). For this reason, the creation of comprehensive species inventories is a critical step in identifying and protecting areas of high biodiversity value. Such data will not only inform conservation priorities but also guide future ecological monitoring and land management strategies.

In addition, this thesis highlights the potential of integrating entomological and botanical data to explore ecosystem functioning. In fact, the combined analysis of diverse taxa as vascular plants and Lepidoptera across chapters underscores the value of cross-taxon comparisons for detecting ecological patterns. Future work should reinforce this approach by incorporating a broader range of insect taxa (e.g., microlepidoptera, other pollinators or phytophagous) and expanding the use of functional traits. Traits related to dispersal, resource specialization, and stress tolerance can help clarify how environmental filtering shapes community assembly along dune gradients. Additionally, applying trait-based frameworks in other Mediterranean ecosystems would allow for meaningful comparisons across habitats.

A key priority for future research is to provide continuity to the long-term monitoring programs (LTMP) (Zucco & Scalercio, 2023). The richness and seasonal dynamics documented in all chapters point to the importance of continued monitoring of both flora and Lepidoptera. Long-term datasets are crucial for detecting trends related to climate change, land-use intensification, and phenological shifts. Monitoring programs should be designed to capture seasonal variation in community composition and abundance, particularly during spring and summer when anthropogenic pressures on dunes are highest.

The identification of habitat-specialist species (e.g., *Gegenes nostrodamus*, *Euxoa seliginis*) and distinct diversity patterns across dune zones has direct implications for conservation. As suggested in Chapters 2 to 4, indicator species and trait-based

assessments can guide the design of dune conservation priorities. Management strategies should include measures such as installing boardwalks (Tozzi et al., 2022), reducing trampling, minimizing light pollution, and planning beach cleaning during no sensitive periods for moths and plants.

The thesis presents a replicable model for studying biodiversity in the Mediterranean Basin. Extending this integrative methodology to other ecosystems could enhance regional conservation planning and contribute to a broader understanding of biodiversity drivers in fragmented and vulnerable landscapes.

This study is limited by its temporal scope, as sampling was restricted to a single year, preventing the assessment of interannual variability in moth and plant communities. Phenological shifts linked to climate fluctuations may have influenced the detection of certain species. Additionally, while environmental filtering was inferred through plant traits and habitat characteristics, no direct measurements of abiotic factors, such as soil salinity and temperature, were collected. Including such variables would enhance the mechanistic understanding of dune community assembly.

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LIST OF PAPERS

Scientific Articles

Rasino, M.D.V., Fattorini, S., Sciarretta, A., Colacci, M., Stanisci, A., & Carranza, M.L., (2024). Cross-taxon analysis in the highly threatened Mediterranean dunes reveals consistent diversity patterns in butterfly and plant communities. Biodiversity and Conservation, 33: 3643–3661. https://doi.org/10.1007/s10531-024-02914-w

Rasino, M.D.V., Innangi, M., Di Febbraro, M., Fattorini, S., Sciarretta, A., Stanisci, A., & Carranza, M.L. (2025). Linking taxonomic and functional diversity of moths and plants in coastal dunes: insights from a Mediterranean LTER site. Ecological Indicators. (Accepted with revisions)

Rasino, M.D.V., Colacci, M., Fattorini, S., Stanisci, A., Carranza, M.L., & Sciarretta, A. (2025). Lepidoptera of the 'Foce Trigno–Marina di Petacciato' Natura 2000 site, a European LTER area in Central Italy. Fragmenta Entomologica. (Submitted- Under Review)

Congress Abstracts

Rasino, M.D.V., Carranza, M.L., Fattorini, S., Stanisci, S., Innangi, M., Di Febbraro, M., & Sciarretta, A. (2025). The influence of zonation and habitat type on geometrid moth diversity in an Italian coastal dune ecosystem. XII International congress of Forum Herbulot. Abstract book, pp. 29.

Rasino, M.D.V., Fattorini, S., Sciarretta, A., Stanisci, A., & Carranza, M.L. (2024). Distribution patterns of moth assemblages (Lepidoptera Geometridae) of sandy coasts in the Italian Central Adriatic. XXXIII Congresso della Società Italiana di Ecologia "Misurare e prevedere il cambiamento per una gestione sostenibile degli Ecosistemi". Abstract book, pp. 120.

Rasino, M.D.V., Fattorini, S., Sciarretta, A., Stanisci, A., & Carranza, M.L. (2024). Exploring butterfly and plant communities along dune environmental gradients: a cross-taxon study in the central Adriatic coast. IncontrALI 2024 - quarto incontro nazionale dell'Associazione Lepidotterologica Italiana. Libro degli Abstract, pp.16.

Rasino, M.D.V., Fattorini, S., Sciarretta, A., Stanisci, A., & Carranza, M.L. (2024). Exploring diversity patterns of geometrid moths (Lepidoptera Geometridae) across

Adriatic coastal dune habitats. IncontrALI 2024 - quarto incontro nazionale dell'Associazione Lepidotterologica Italiana. Libro degli Abstract, pp.17.

Rasino, M.D.V., Sciarretta, A., Colacci, M., Fattorini, S., Stanisci, A., & Carranza, M.L. (2023). Butterfly diversity patterns across dune ecotones in the Adriatic coast. XXXII Congresso Annuale della Società Italiana di Ecologia "Sostenibilità ecologica: scienza, scenari e partecipazione. Libro degli Abstract, pp 170.

Rasino M.D.V., Sciarretta, A., Colacci, M., Fattorini, S., Stanisci, A., & Carranza, M.L. (2023). Mediterranean coastal landscapes and moth diversity: does dune zonation matter? XXXII Congresso Annuale della Società Italiana di Ecologia "Sostenibilità ecologica: scienza, scenari e partecipazione. Libro degli Abstract, pp 162.

Rasino, M.D.V., Sciarreta, A., Fattorini, S., Colacci, M., Stanisci, A., & Carranza, M.L. (2023). Diversity of diurnal lepidopterans and coastal dune vegetation: insights from shifting and backdunes of an Adriatic protected area (Italy). XXVII Congresso Nazionale Italiano di Entomologia. Libro degli abstract, pp. 99.

Rasino, M.D.V., Sciarretta, A., Colacci, M., Fattorini. S., Stanisci, A., & Carranza, M.L. (2023). The importance of coastal dune mosaics as reservoirs of moth diversity in central Italy (Molise). XXVII Congresso Nazionale Italiano di Entomologia. Libro degli abstract, pp. 100.

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