



Focusing on the role of abiotic and biotic drivers on cross-taxon congruence

Erika Bazzato^{a,h,*}, Erik Lallai^a, Michele Caria^a, Enrico Schifani^b, Davide Cillo^c,
Cesare Ancona^d, Paolo Pantini^e, Simona Maccherini^{f,i}, Giovanni Bacaro^g, Michela Marignani^a

^a Department of Life and Environmental Sciences, University of Cagliari, Via Sant'Ignazio da Laconi, 13, 09123 Cagliari, Italy

^b Department of Chemistry, Life Sciences & Environmental Sustainability, University of Parma, Parco Area delle Scienze, 11/a, 43124 Parma, Italy

^c Via Zeffiro 8, 09126 Cagliari, Italy

^d Via Mascagni 3, 09020 Ussana, Italy

^e Museo Civico di Scienze Naturali "E. Caffi", Piazza Cittadella 10, 24129, Bergamo, Italy

^f Department of Life Sciences, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

^g Department of Life Sciences, University of Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy

^h Department of Agricultural Sciences, University of Sassari, Viale Italia 39, 07100 Sassari, Italy

ⁱ NBFC, National Biodiversity Future Center, Palermo 90133, Italy

ARTICLE INFO

Keywords:

Trees Outside Forests
Diversity patterns
Abiotic factors
Biotic factors
Biotic interactions
Ground-dwelling arthropods
Arthropods
Invertebrates
Coleoptera
Hymenoptera
Pseudoscorpiones
Araneae
Vascular plants

ABSTRACT

Diversity patterns can show congruence across taxonomic groups. Consistent diversity patterns allow the identification of indicator surrogates potentially representative of unobserved taxa or the broader biodiversity patterns. However, the effective use of biodiversity surrogates depends on underlying mechanisms driving the strength of the relationship among taxonomic groups. Here, we explored congruence patterns in community composition among taxa occupying different trophic levels, accounting for abiotic and biotic factors: vascular plants and six groups of ground-dwelling arthropods (pseudoscorpions, spiders, darkling beetles, rove beetles, ground beetles and ants) were chosen as potential indicator surrogates. We evaluated the cross-taxon relationships using Mantel test; subsequently, we investigated if these relationships could partially depend on abiotic drivers, using partial Mantel tests; then, we evaluated the partial contributions of abiotic and biotic drivers in explaining these relationships through a series of variation partitioning analyses. Our results showed that a consistent cross-taxon congruence pattern was evident across almost all group pairs: pseudoscorpions, spiders, ground beetles and vascular plants showed the largest number of significant correlations with other taxa. Environmental gradients resulted as drivers of cross-taxon congruence, shaping composition patterns. However, they were not the only ones. Biotic drivers account for part of cross-taxon congruence among vascular plants and arthropod predators (i.e., pseudoscorpions and spiders, but also ground beetles), as well as among taxa at high trophic levels. Almost all strictly predatory taxa, known as biological control agents, emerged as the best predictors of plant community composition even when the role of environmental factors was considered. Spiders/ants and spiders/ground beetles showed close relationships and congruent composition patterns, irrespective of environmental parameters. Relationships among taxa might be driven by several complex biotic interactions (e.g., non-trophic and trophic interactions, direct and indirect interactions). Bottom-up and top-down forces, consumptive and non-consumptive interactions may play a role in influencing the community composition of taxa and driving the observed relationships. Future studies should broaden knowledge about the role of these forces and interactions in determining the congruence across taxa. The multi-trophic perspective in cross-taxon studies can be promising for identifying biodiversity surrogates and their application in conservation planning.

1. Introduction

Understanding the main drivers of diversity patterns is a major challenge for ecologists to sustain conservation efforts and decision-

making (Duan et al., 2016; Myers et al., 2000; Schuldt et al., 2015; Westgate et al., 2014). This challenge is related to the relevant question whether species richness and composition show a concordance across taxonomic groups (Ramos et al., 2021; Toranza and Arim, 2010; Zara

* Corresponding author at: Department of Life and Environmental Sciences, University of Cagliari, Via Sant'Ignazio da Laconi, 13, 09123 Cagliari, Italy.
E-mail address: erika.bazzato@hotmail.it (E. Bazzato).

et al., 2021). This concordance, known as cross-taxon congruence, allows the identification of biodiversity surrogates and proxies that can act as representative indicators of unobserved taxa or the overall biodiversity of an area (Santi et al., 2010; Ware et al., 2018; Westgate et al., 2014). Monitoring or management actions based on these surrogates will benefit other co-occurring taxonomic groups or the broader biodiversity patterns, improving conservation outcomes (Hunter et al., 2016; Margules and Pressey, 2000; Westgate et al., 2017; 2014). However, the effective use of biodiversity surrogates depends on underlying mechanisms driving the congruence among taxonomic groups, which can vary depending on the considered spatial and temporal scale (Burrascano et al., 2018; Hess et al., 2006; Westgate et al., 2014, 2017). Congruence among taxonomic groups can result from common responses of diversity patterns to environmental conditions or biogeographic history and from the effects of one taxon on another taxon's diversity due to biotic interactions (Andersen et al., 2020; Duan et al., 2016; Gioria et al., 2011; Ramos et al., 2021; Sabatini et al., 2016; Toranza and Arim, 2010). For example, geographical parameters such as latitude and elevation cause different climatic conditions and shifts in biotic distributions, determining congruent patterns among taxa (Westgate et al., 2017; 2014). The large amount of evidence regarding the role of the climatic conditions as drivers of diversity patterns (Pech et al., 2017) lend support to congruent responses among taxa that were found by previous studies (Duan et al., 2016; Ramos et al., 2021; Toranza and Arim, 2010). Changes in diversity patterns are related to habitat heterogeneity (Costanza et al., 2011; Stein et al., 2014) or disturbance level (Rooney and Azeria, 2015), but their roles in cross-taxon congruence remain poorly explored by cross-taxon studies (Piano et al., 2020; Rooney and Azeria, 2015; Zara et al., 2021). Other authors argue that taxa can show independent responses to environmental drivers (Bagella et al., 2011; Beck et al., 2013; Guareschi et al., 2015), which in turn determined a weak congruence among taxa, or a lack of cross-taxon congruence (Bae et al., 2014; Heino et al., 2003; Heino, 2010; Lovell et al., 2007). These may be either because different taxa can respond differently to environmental variation or perceive abiotic factors at different spatial scales (Bagella et al., 2011; Heino, 2010). Consequently, there is no consensus on which taxa are consistent surrogates for each other across a broad range of environmental conditions and what processes drive these surrogacy relationships (Westgate et al., 2017; 2014). This inconsistency across taxa implies limitations on the usefulness of surrogacy approaches in biodiversity conservation (Gioria et al., 2011; Heino, 2010; Westgate et al., 2017; 2014). The issue becomes even more complicated when we consider the effects of one taxon on another taxon's diversity in cross-taxon studies. Biotic drivers can alter distributional ranges, individual reproductive or population growth rates (Early and Keith, 2019) and ultimately species and community responses to environmental factors (Brooker, 2006; Brooker and Callaghan, 1998; Callaway et al., 2002; Choler et al., 2001; Davis et al., 1998). The effects of one taxon on another taxon variation may not be independent of one another (Morris et al., 2007) and change as a function of the abiotic and biotic context (Rzanny et al., 2013; Rzanny and Voigt, 2012), varying in magnitude and direction (Chamberlain et al., 2014; Maron et al., 2014; Tylianakis et al., 2008; Wisz et al., 2013). On the other hand, biotic interactions may account for part of the congruence patterns between vascular plants and other taxa, such as arthropods (Sabatini et al., 2016), promoting or constraining their relationships (Duan et al., 2016; Morlon et al., 2014; Özkan et al., 2014).

Vascular plants are considered good surrogates for several arthropod groups (Santi et al., 2010), such as spiders (Schoeman et al., 2020), ants (Zara et al., 2021), ground beetles (Duan et al., 2016; Uboni et al., 2019; Yanahan and Taylor, 2014) or other beetle families (e.g., dung beetles, darkling beetles; Schoeman et al., 2020). However, only few studies took into account abiotic and biotic drivers in plant-arthropod cross-taxon congruence focusing on lake (Andersen et al., 2020; Özkan et al., 2014) or terrestrial ecosystems (Barbato et al., 2019; Duan et al., 2016; Ramos et al., 2021). Some of these showed that a large proportion of the

congruence among phyto- and zooplankton or macroinvertebrate groups was independent of environmental control and consistent with the existence of biotic interactions across trophic levels, acting as driving factors of lake plankton (Andersen et al., 2020; Özkan et al., 2014). In contrast, studies in terrestrial ecosystems indicated that abiotic factors were stronger drivers of cross-taxon congruence than biotic interactions, considering plants and among arthropods orthoptera (Ramos et al., 2021), geometrid and arciid moths and ground beetles (Duan et al., 2016) or ground beetles and microarthropods (Barbato et al., 2019). Overall, there is contradictory evidence of whether the congruence of plants-arthropods reflects abiotic and biotic interactions (Heino, 2010; Özkan et al., 2014), especially considering that studies did not consider several potential surrogate taxa (Westgate et al., 2017; 2014). Therefore, more studies are needed to determine the underlying role of these factors in driving the congruence patterns, considering not only commonly studied taxa but also rarely investigated ones (Westgate et al., 2017; 2014). Studies of these poorly studied taxonomic groups could have considerable potential for identifying surrogates with important implications for biodiversity conservation (Westgate et al., 2017; 2014). This could be especially true in the case of plant-arthropod groups that constitute more than 80% of the world's described species (Stork, 2018), including taxon ascribable to different trophic levels (i.e., producers and several orders of consumers).

Here, we focused on the partial contributions of abiotic and biotic drivers in determining cross-taxon congruence in community composition, considering a rarely studied combination of taxa (Westgate et al., 2014): vascular plants and six groups of ground-dwelling arthropods (pseudoscorpions, spiders, darkling beetles, rove beetles, ground beetles and ants), covering different trophic levels (i.e., producers and several orders of consumers). We first hypothesized that congruence relationships exist between vascular plants and some commonly studied taxa (i.e., spiders, ground beetles and ants) and then that the other groups followed a similar pattern (Duan et al., 2016; Schoeman et al., 2020; Uboni et al., 2019; Zara et al., 2021). Furthermore, we expected that cross-taxon congruence in community composition could partially depend on abiotic drivers (Barbato et al., 2019; Duan et al., 2016; Ramos et al., 2021). To verify this expectation, we based our survey on a Mediterranean area with a large environmental variation over a short geographic distance in terms of climate, spatial-topography features and fragmentation degree (i.e., disturbance at landscape scale). Once the role of abiotic drivers in determining cross-taxon congruence was verified, we evaluated (i) the magnitude of the effect of each set of abiotic drivers on taxon variation, considering (ii) the strength and direction of the effect of biotic drivers on the community composition of each taxonomical group (i.e., the effect of each taxon on another taxon). The effect due to biotic interactions cannot be measured directly, but we expected that taxon variation could be explained by biotic drivers even when environmental factors were removed (Andersen et al., 2020; Duan et al., 2016; Toranza and Arim, 2010) due to the well-known consumer-resource relationships across taxa at different trophic levels (Turney and Buddle, 2016). Being the main group of primary producers and providing a great variety of structural habitats and resources, vascular plants regulate the community composition of organisms at different trophic levels (Ebeling et al., 2020; Langellotto and Denno, 2004; Schuldt et al., 2019) via non-trophic and trophic bottom-up effects (Castagneyrol and Jactel, 2012; Scherber et al., 2010; Schuldt et al., 2019; 2014). Ground-dwelling arthropods play key roles in the food chain as herbivores, predators, omnivores and decomposers, regulating the availability of resources and nutrient pool in the soil (Culliney, 2013; Samways and Samways, 1994; Schowalter, 2016). Feedback effects of taxa at higher trophic levels on plant composition are described, resulting in a top-down control by altering herbivore density, plant-herbivore interactions, and ultimately plant growth and reproduction (Moreira et al., 2016; Schuldt et al., 2017).

2. Materials and methods

2.1. Study area

This study was conducted on the Metropolitan City of Cagliari (the Southern coast of Sardinia, Italy), a medium-sized functional urban area (*sensu* Dijkstra et al., 2019) including seventeen municipalities at different conservation status (ILC, Pizzolotto and Brandmayr, 1996) and fragmentation degrees (see Palumbo et al., 2020). The study area extends over 18,000 ha showing a Mediterranean pluvioseasonal oceanic macrobioclimate, with strong euoceanic continentality, including four thermotypes (from lower thermo-Mediterranean to upper meso-Mediterranean) and five ombrotypes (from lower dry to lower humid) (Canu et al., 2015).

The study area is characterized by an environmental gradient that runs roughly in an east-south direction from natural areas, at higher altitudes, to urbanized zones at lower altitudes (see Bazzato et al., 2021a for further details): the NE sector is characterized by evergreen sclerophylls, dominated by *Quercus ilex* or *Quercus suber*, and other Mediterranean species (*Erica arborea*, *Arbutus unedo*, *Phyllirea latifolia*, *Myrtus communis* and *Juniperus oxycedrus*); the SW sector is dominated by high-shrub and pre-forest successions with wild olive and turbinata juniper shrublands (*Olea europaea* var. *sylvestris* with *Pistacia lentiscus*, *Juniperus turbinata* and *Euphorbia dendroides*), and near the coast, ponds and lagoons by halophilous and psammophilous communities (Bacchetta et al., 2009).

2.2. Sampling design

Using photo-interpretation of high resolution RGB orthophotos (pixel resolution of 20 cm; RAS, 2016), we identified and mapped all Small Woodlots Outside Forests present in the study area (Fig. 1). We

defined the Small Woodlots Outside Forests - SWOF (de Foresta et al., 2013; FAO, 2010) as the small patches with a size between 0.05 and 0.5 ha spread over all land-use types (see Bazzato et al., 2021a for further details).

To identify patches as homogeneous as possible, we classified the small patches according to the first hierarchical level of the regional land-use map (natural and semi-natural areas, NAT; agricultural areas, AGR; urban and artificial areas, URB; RAS, 2008), excluding those smaller than 0.1 ha (about 42%) and those embedded in a mixed land-use type (about 1.50%).

From a total of 201 detected small patches (64 in NAT, 70 in AGR, 67 in URB), we carried out a proportional stratified random sampling to select a total of 30 small patches (Table A.1 in Appendix A1). As in the urban and artificial areas (URB) category, most of the selected small patches were in private and inaccessible gardens, we sampled only eight small patches in URB, assigning the remaining sites (up to 30) to the other land-use types (11 sites in NAT and AGR). At each selected small patch, we used a transect line from the patch centroid to the farthest sides of patch boundaries to identify five plots of 1 m², with a unique identification (P1-P5), equally spaced along the longest axis (Table A.1. in Appendix A1; see Bazzato et al., 2022 for further details).

2.3. Data collection

2.3.1. Biotic data

In the field, biotic data were sampled in the same plots, adopting appropriate protocols for each selected taxonomic group. All the material was identified at the lowest possible taxonomic level (i.e., mainly species level). We recorded the presence of all trees, shrubs and herb layer species in the plots from April to August 2018. Hence, we visually estimated the abundance of each vascular plant species, measuring their coverage as the proportion of the area occupied by a species on the total

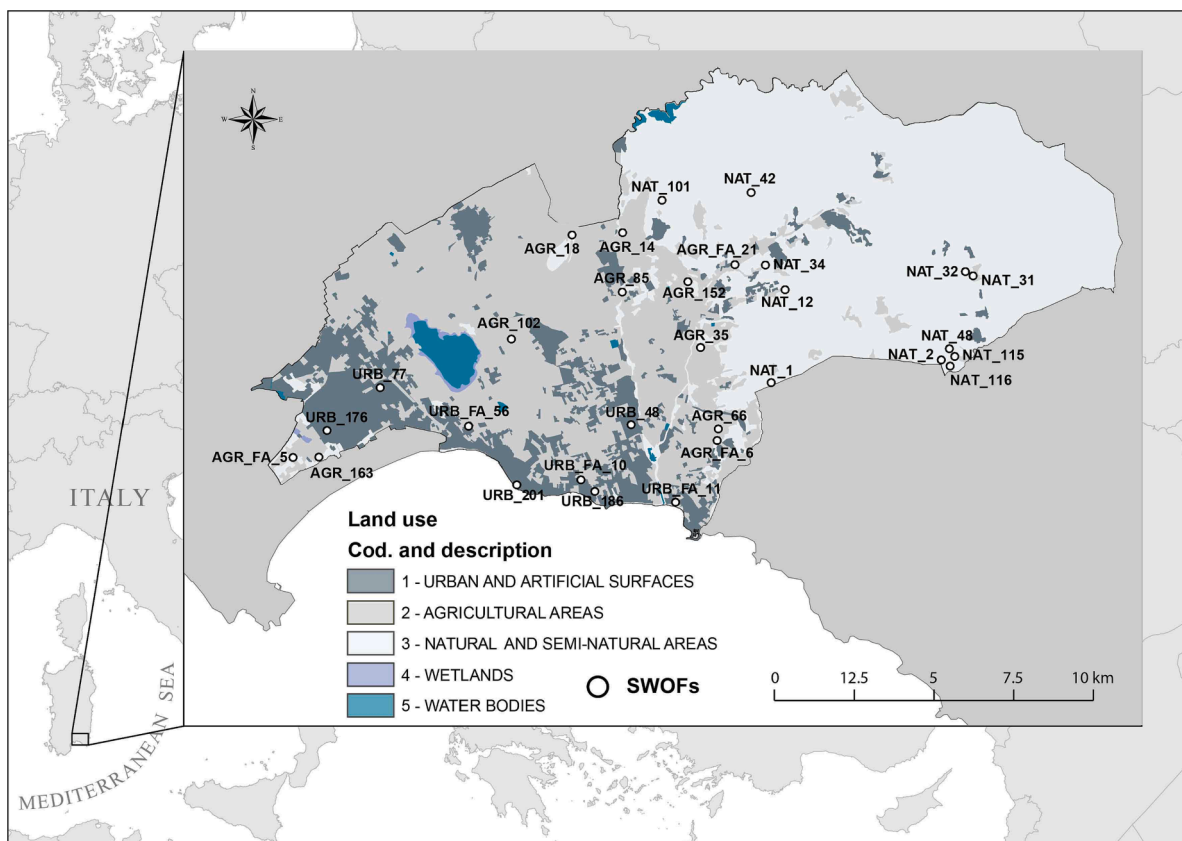


Fig. 1. Study area located in the Metropolitan City of Cagliari (Sardinia, Southern Italy).

surface of plot (i.e., 1 m²) in percentage.

Ground-dwelling arthropods were collected by means of pitfall traps. Pitfall traps are considered a standard, cost-effective and reliable method for sampling mobile, surface-dwelling arthropods (Skvarla et al., 2014; Yi et al., 2012). Following Brandmayr et al. (2005), traps were made by small plastic vessels, 9 cm in diameter and 11 cm deep, with a small hole near the top to allow the drainage of rainwater. We placed five pitfall traps per transect line, each of which was in the centre of the plot. Each trap was filled with wine-vinegar saturated by sodium chloride as preservation method. Ground-dwelling arthropods were collected for a year (from April 2018 to May 2019) to catch the highest biological activity of each group. The traps were emptied every 30–40 days; thus, nine trap-emptying made up a year-sample. Since some traps were found overturned or tampered, 101 out of the 1350 placed traps (5 traps for each of the 30 small patches, for 9 sampling periods and sampling sessions) were not included in the analysis. Arthropod specimens were deposited in the Zoological research Museum Alexander Koenig (ZFMK; Bonn, Germany) and in the Museo Civico di Scienze Naturali “E. Caffi” (MSNB; Bergamo, Italy).

Because arthropods are hyper-diverse taxa (Mestre et al., 2013) with a broad range of feeding habits (Table 1), we deemed six different groups (pseudoscorpions, spiders, darkling beetles, rove beetles, ground beetles and ants) following the higher taxonomic ranks - basically order level - but with further distinctions in beetle families to distinguish strictly predatory taxa from detritivores or other ones feeding on multiple food resources (Potapov et al., 2022).

2.3.2. Biotic data aggregation

To produce comparable data sets, all data collected at plot or trap level were aggregated to transect level, obtaining a total of 30 sampling units (i.e., the number of the 30 considered small patches). We used the sum as the aggregation method across the five plots and five traps, respectively, for vascular plants and ground-dwelling arthropods. For each ground-dwelling species, abundances collected by 1249 active traps were also pooled over time (9 periods) to optimize the catch and overcome occasional trap losses (Kotze et al., 2011). Hence, we represented each taxonomic group as a site-by-species matrix (i.e., the community composition) containing the abundance of a given species in a given sampling unit. For all the analyses we used the community composition data aggregated to transect level (i.e., 30 sampling units).

2.3.3. Abiotic environmental drivers

We considered three distinct sets of abiotic environmental drivers at the patch level: (i) spatial-topographic factors, (ii) bioclimatic variables, (iii) and landscape metrics (Table 2). Abiotic environmental variables were obtained by ArcGIS 10.2.1 (Esri, 2014).

The spatial-topographic set includes 8 features (i.e., geographic coordinate, elevation, inclination, exposition and distance to the coast,

river, lake and lagoon; Table 2). Geographic coordinates, expressed as angular units (degrees) in the WGS84 geographic coordinate system (EPSG 4326), were recorded through a global positioning system (GPS) instrument. We used the Digital Terrain Model (DTM, pixel resolution of 10 m; RAS, 2017) to derive elevation values and data of inclination and exposition (ranging from 10° to 332°) by the aspect-slope function. We also calculated three spatial distances from the centroid of each patch to the nearest coastline (coastal distance), to the nearest river (river distance), and the nearest artificial or natural lake and lagoon (lake distance).

The bioclimatic variables set consisted of 19 biologically meaningful climate variables related to temperature (BIO01-BIO07 and BIO10-BIO11), precipitation (BIO12-BIO17) and both temperature and precipitation (BIO08-BIO09 and BIO18-BIO19). We extracted bioclimatic variables from a high-resolution dataset (pixel resolution of 40 m; Bazzato et al., 2021b) specifically developed for the island of Sardinia (Italy) based on high-quality meteorological data of the regional climatic database of the Weather and Climate Department (ARPA Sardegna).

The landscape metrics set consisted of 17 metrics at the landscape level (McGarigal et al., 2002; Table 2) that describe the fragmentation degree (i.e., disturbance at landscape scale) by quantifying the compositional and configurational features of the surrounding landscape of each patch. Landscape metrics were calculated within a 500 m buffer distance of each patch centroid, using the regional land-use map at the third hierarchical level of detail (3-level Corine Land Cover, scale 1:25.000; RAS, 2008) and Patch Analyst extension (Elkie et al., 1999; Rempel et al., 2012).

2.4. Statistical analyses

We adopted a multiphase approach to evaluate (i) the cross-taxon relationships with (Mantel tests) and (ii) without (partial Mantel tests) considering abiotic factors, and (iii) the partial contributions of abiotic and biotic drivers in explaining taxon variation (Fig. 2, from left to right). All analyses were carried out in the R Language for Statistical Computing (R core Team, 2020).

2.4.1. Cross-taxon congruence patterns

In the first phase, raw community composition data were square-root transformed before computing the Bray-Curtis dissimilarity. In the following steps, we used Bray-Curtis dissimilarity to perform (i) Mantel test and (ii) partial Mantel test for each pair of taxa, using the Spearman rank correlation (Legendre and Legendre, 2012).

Mantel tests allowed us to perform a pairwise correlation analysis among taxa and determine the degree of cross-taxon congruence in community composition. Such Mantel relationships may derive from (i) a similar response to environmental conditions, (ii) biotic interactions,

Table 1
Overview of arthropod taxa sampled and their predominant and non-predominant feeding habits.

Common name	Taxon	Predominant feeding habit	Details on predominant and non-predominant feeding habits	Reference
Pseudoscorpions	Arachnida, Pseudoscorpiones	Predators	Generalist predators	(Liebke et al., 2021; Potapov et al., 2022)
Spiders	Arachnida, Araneae	Predators	Generalist predators, specialist predators (myrmecophages, araneophages, lepidopterophages, termitophages, dipterophages, and crustaceophages), and opportunistic predators	(Cardoso et al., 2011; Pekár et al., 2012; Potapov et al., 2022)
Darkling beetles	Insecta, Coleoptera, Tenebrionidae	Decomposer	Generalist detritivores, and saprophages	(Cheli et al., 2013; Fattorini et al., 2020)
Rove beetles	Insecta, Coleoptera, Staphylinidae	Predators	Generalist predators and specialist predators (myrmecophages), but including also saprophages, phytophages, mycophages, coprophages, and necrophages	(Méndez-Rojas et al., 2021; Potapov et al., 2022)
Ground beetles	Insecta, Coleoptera, Carabidae	Predators	Generalist predators and specialist predators (aphidophages, helicophages, myrmecophages), but including also omnivores, granivores	(Bennewicz and Barczak, 2020; Kotze et al., 2011)
Ants	Insecta, Hymenoptera, Formicidae	Omnivores	Omnivores, but including also generalist and specialist predators, scavengers, herbivores, and granivores	(Potapov et al., 2022)

Table 2

Description of the three sets of abiotic environmental drivers: spatial-topographic factors, bioclimatic variables and landscape metrics.

Predictor set	Variable name	Variable description	Type of variable	
Spatial-topographic factors	X	x geographic coordinate (degrees)	Spatial variable	
	Y	y geographic coordinate (degrees)	Spatial variable	
	Z	elevation (m)	Topographic variable	
	Inclination	inclination (degrees)	Topographic variable	
	Exposition	exposition (degrees)	Topographic variable	
	Coast_dist	Distance from the coast (m)	Spatial variable	
	River_dist	Distance from the river (m)	Spatial variable	
	Lake_dist	Distance from the lake and lagoon (m)	Spatial variable	
	Bioclimatic variables	BIO01	Annual Mean Temperature (°C)	Temperature-related variable
		BIO02	Mean Diurnal Range (Mean of monthly (max temp - min temp)) (degrees Celsius, °C)	Temperature-related variable
BIO03		Isothermality (BIO2/BIO7) (x 100)	Temperature-related variable	
BIO04		Temperature Seasonality (standard deviation × 100)	Temperature-related variable	
BIO05		Maximum Temperature of Warmest Month (°C)	Temperature-related variable	
BIO06		Minimum Temperature of Coldest Month (°C)	Temperature-related variable	
BIO07		Temperature Annual Range (BIO5-BIO6) (°C)	Temperature-related variable	
BIO08		Mean Temperature of Wettest Quarter (°C)	Temperature-related and rainfall-related variable	
BIO09		Mean Temperature of Driest Quarter (°C)	Temperature-related and rainfall-related variable	
BIO10		Mean Temperature of Warmest Quarter (°C)	Temperature-related variable	
BIO11		Mean Temperature of Coldest Quarter (°C)	Temperature-related variable	
BIO12		Annual Precipitation (mm)	Rainfall-related variable	
BIO13		Precipitation of Wettest Month (mm)	Rainfall-related variable	
BIO14		Precipitation of Driest Month (mm)	Rainfall-related variable	
BIO15		Precipitation Seasonality (Coefficient of Variation)	Rainfall-related variable	
BIO16		Precipitation of Wettest Quarter (mm)	Rainfall-related variable	
BIO17		Precipitation of Driest Quarter (mm)	Rainfall-related variable	
BIO18		Precipitation of Warmest Quarter (mm)	Temperature-related and rainfall-related variable	
BIO19		Precipitation of Coldest Quarter (mm)	Temperature-related and rainfall-related variable	
Landscape metrics	SDI	Shannon's Diversity Index	Diversity Metric	
	SEI	Shannon's Evenness Index	Diversity Metric	
	AWMSI	Area Weighted Mean Shape Index	Shape Metric	
	MSI	Mean Shape Index	Shape Metric	
	MPAR	Mean Perimeter-Area Ratio	Shape Metric	
	MPFD	Mean Patch Fractal Dimension	Shape Metric	
	AWMPFD	Area Weighted Mean Patch Fractal Dimension	Shape Metric	

Table 2 (continued)

Predictor set	Variable name	Variable description	Type of variable
	TE	Total Edge	Edge Metric
	ED	Edge Density	Edge Metric
	MPE	Mean Patch Edge	Edge Metric
	MPS	Mean Patch Size	Patch Density & Size Metric
	NumP	No. of Patches	Patch Density & Size Metric
	MedPS	Median Patch Size	Patch Density & Size Metric
	PSCoV	Patch Size Coefficient of Variance	Patch Density & Size Metric
	PSSD	Patch Size Standard Deviation	Patch Density & Size Metric
	TLA	Total Landscape Area	Area Metric
	CA	Class Area	Area Metric

or (iii) chance (i.e., spurious relationships) (Cushman et al., 2013; Cushman and Landguth, 2010; Perner and Voigt, 2007; Rzanny and Voigt, 2012). Since the simple Mantel tests could indicate the presence of cross-taxon congruence in community composition without considering if relationships were direct or indirect mediated through abiotic factors (Rzanny and Voigt, 2012), we tested if this concordance remained consistent after removing the conditional effect of environmental drivers using partial Mantel tests. The Euclidean environmental distance matrix was obtained with all predictors (i.e., retained PCs of each abiotic environmental set, see below). The advantage of this test is the possibility to detect the direct or pure relationship between taxa (Legendre and Fortin, 2010), by controlling for the effect of environmental variables (Guillot and Rousset, 2013).

Given the hierarchically stratified sampling design adopted (i.e. each land-use strata encompassed more than one small patch), both tests were computed in the whole study area, constraining 999 permutations at the land-use level, using the argument 'strata' in the *mantel* and *mantel.partial* functions of the *vegan* package (Oksanen et al., 2019). Since sites within a land-use stratum are expected to be more similar to each other, this permutation method returns a conservative estimate of the result significance (Oksanen et al., 2019).

2.4.2. Role of abiotic and biotic drivers

Raw community composition data were Hellinger-transformed before analyses, as this transformation is appropriate for zero-inflated data (Legendre and Gallagher, 2001; Peres-Neto et al., 2006). Then, we performed a series of principal component analyses (PCA) to simplify the complexity of high-dimensional abiotic and biotic data and reduce the multicollinearity while retaining most of the variance of the data (i.e., dominant patterns) (Borcard et al., 2011; Lever et al., 2017). We computed a PCA for (i) each abiotic environmental set, scaled to zero mean and unit variance (Borcard et al., 2011), and for (ii) each of the seven taxonomic groups based on Hellinger-transformed community data, using the *rda* function in the *vegan* package (Oksanen et al., 2019). For each PCA, we applied a broken-stick model through the *PCAsignificance* function of the *BiodiversityR* package (Kindt and Coe, 2005) to evaluate the number of principal components (PCs; see Fig. A.1 and Fig. A.5 in Appendix A1) to retain for interpretation, i.e., the number of PCs with eigenvalues exceeding the expected value generated by a random distribution (Legendre and Legendre, 2012). Next, we examined the retained PCs comparing (i) scaling 1 with a circle of equilibrium contribution (i.e., variable or species that have vectors outside of the equilibrium circle and make a higher contribution than average to the ordination graph) to scaling 2 of the PCA space (Figs. A.2-A.4 and Figs. A.6-A.18 in Appendix A1), as well as (ii) component loadings of individual variables (Tables A.2-A.4 in Appendix A1) or species (Tables A.5-A.11 in Appendix A1) and axes (i.e. the standardized correlation; Legendre and Legendre, 2012). Hence, the scores of each

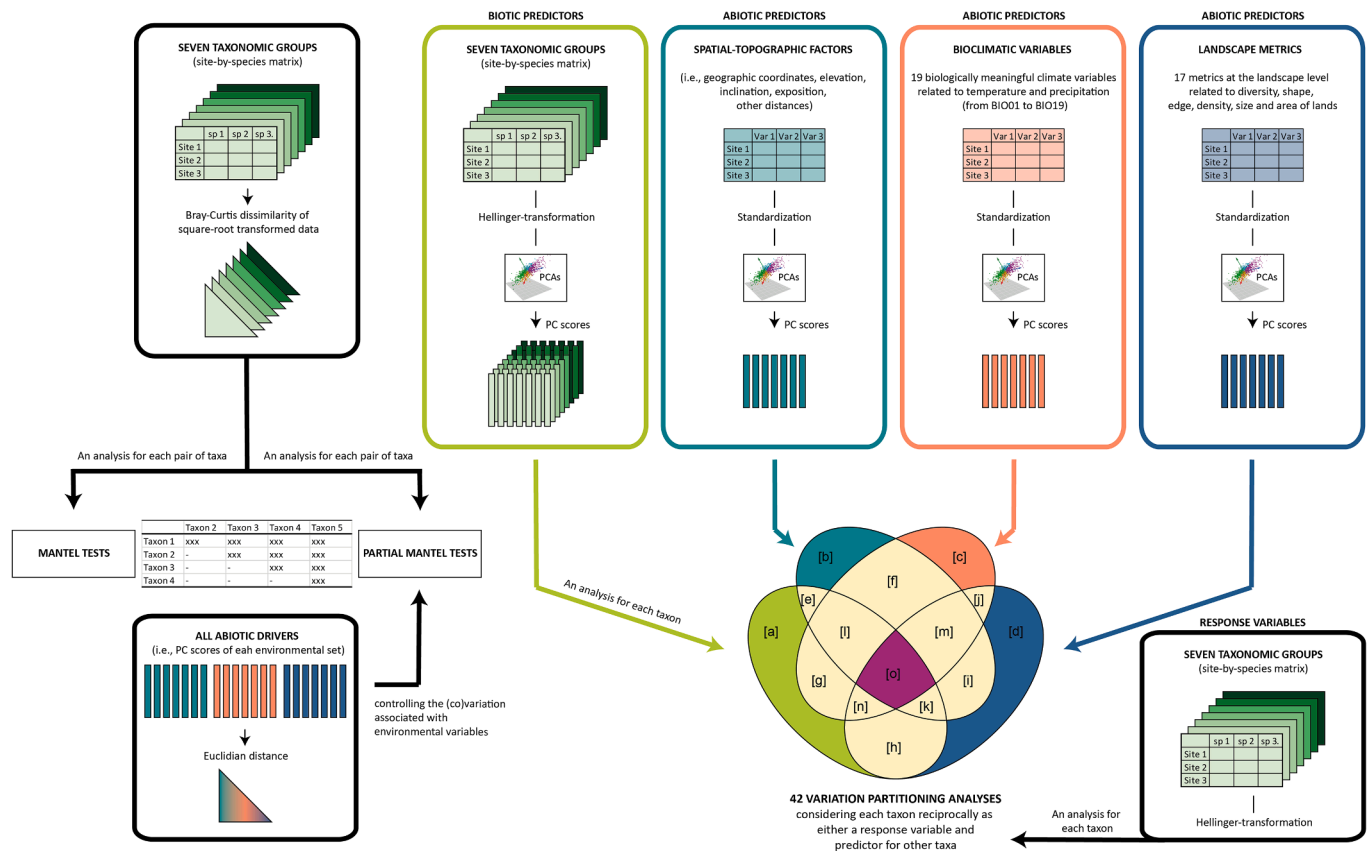


Fig. 2. Overview of multiphase approach adopted for the analysis and derivation of response variables and predictors (i.e., scores of the principal component analysis, PCA). Site-by-species matrices of each taxonomic group contain species abundance data. (Left) We evaluated cross-taxon relationships with (Mantel tests) and without (partial Mantel tests) considering abiotic factors. (Right). Variation partitioning was used to evaluate the partial contributions of abiotic and biotic drivers in explaining taxon variation.

retained PC (Fig. A.1 and Fig. A.5 in Appendix A1) were interpreted (see paragraph A.2.1 for abiotic drivers and paragraph A.2.2 for biotic ones in Appendix A1), extracted and used as explanatory variables in a series of variation partitioning analysis: scores of the 2 PCs for spatial-topographic and bioclimatic variables; scores of the 3 PCs for landscape metrics; scores of the 2 PCs for pseudoscorpions; scores of the 4 PCs for spiders, darkling beetles and vascular plants; scores of the 6 PCs for ground beetles and ants; scores of the 7 PCs for rove beetles.

As a final step, we performed a total of 42 variation partitioning analyses (Borcard et al., 1992) using Hellinger-transformed community data of each group as response variable, PC scores as predictors, and adjusted R^2 statistics (Legendre and Legendre, 2012; Peres-Neto et al., 2006) in the *vegan* package (Oksanen et al., 2019). These analyses were used to appraise (i) the magnitude of the effect of each set of abiotic drivers on taxon variation and (ii) the strength and direction of the effect of biotic drivers on the community composition (i.e., the effect of each taxon on another taxon), considering each taxon reciprocally as either a response variable or predictor for other taxa (Halpern et al., 2006; Rzanny et al., 2013). For each taxon community set as response variable, the approach allowed us to distinguish the degree of variance explained by the [a] pure effect of another taxonomic group, [b] pure effect of spatial-topographic factors, [c] pure effect of bioclimatic variables, [d] pure effect of landscape metrics, [e + f + g + h + i + j + k + l + m + n] partial shared effect of two/three predictor sets, [o] total shared effect of all predictors, [p] unexplained variation. We tested the significance of each fraction by ANOVA like permutation test for redundancy analysis (RDA), constraining 999 permutations within the land-use level (Peres-Neto et al., 2006).

3. Results

We recorded a total of 330 species of vascular plants and 66,412 specimens of ground-dwelling arthropods grouped into the six taxonomic groups: 390 individuals belonging to 13 species of pseudoscorpions; 2,821 spiders assigned to 106 species; 1,084 darkling beetles of 22 species; 7,215 rove beetles of 55 species; 2,777 ground beetles assigned to 38 species; and 52,125 ants identified to 35 species.

3.1. Cross-taxon congruence patterns

Mantel tests among all pairs of seven taxa identified 17 significant positive correlations out of 21 pairwise comparisons (Table 3). All taxonomic groups had significant correlations with more than half other taxa (≥ 3): pseudoscorpions and vascular plants had the highest number of significant correlations, followed by spiders, darkling beetles, ground beetles and ants.

After removing the conditional effect of environmental factors on taxa congruence using partial Mantel tests, 13 out of 21 pairwise correlations appeared still significant (Table 4). Pseudoscorpions, spiders, ground beetles and vascular plants maintained the largest number of significant correlations with other taxa; rove and darkling beetles and ants remained correlated with a low number of other taxa (Table 4).

3.2. Role of abiotic and biotic drivers

Results of 42 variation partitioning analyses showed that although part of the variability in the communities remained unexplained (min = 62.72%, max = 96.92%), the explanatory capacity of predictor variables

Table 3

Correlation coefficients between taxonomic groups (pseudoscorpions (Pseudoscorpiones), spiders (Araneae), darkling beetles (Tenebrionidae), rove beetles (Staphylinidae), ground beetles (Carabidae), ants (Formicidae), and vascular plants), calculated by using Mantel Test (Spearman rank correlation). Significance codes: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$.

	Araneae	Tenebrionidae	Staphylinidae	Carabidae	Formicidae	Vascular plants
Pseudoscorpiones	0.32**	0.18*	0.19**	0.32**	0.33**	0.42***
Araneae	–	0.31**	0.20	0.43**	0.50***	0.61***
Tenebrionidae	–	–	0.01	0.31***	0.22*	0.36***
Staphylinidae	–	–	–	0.09	0.26*	0.28*
Carabidae	–	–	–	–	0.23	0.37**
Formicidae	–	–	–	–	–	0.53***

Table 4

Correlation coefficients between taxonomic groups (pseudoscorpions (Pseudoscorpiones), spiders (Araneae), darkling beetles (Tenebrionidae), rove beetles (Staphylinidae), ground beetles (Carabidae), ants (Formicidae), and vascular plants) calculated by using Partial Mantel Test (Spearman rank correlation) accounting for the conditional effect of abiotic environmental drivers. Significance codes: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$.

	Araneae	Tenebrionidae	Staphylinidae	Carabidae	Formicidae	Vascular plants
Pseudoscorpiones	0.25*	0.12	0.12*	0.29*	0.28*	0.36***
Araneae	–	0.21**	0.06	0.39**	0.42**	0.49***
Tenebrionidae	–	–	–0.08	0.27***	0.14	0.27**
Staphylinidae	–	–	–	0.03	0.18	0.15
Carabidae	–	–	–	–	0.18	0.32**
Formicidae	–	–	–	–	–	0.44**

was generally high in most analyses (medium adjusted $R^2 = 22.74\%$; fraction [abcdefghijklmno] in Appendix A2). The relative importance of each predictor for structuring taxa communities differed markedly (Fig. 3).

Darkling beetles and vascular plants were able to explain a large and significant degree of variance in pseudoscorpion communities (8.35%, 10.42%, respectively; fraction [a] in Appendix A2); a considerable and significant degree of variance was also explained by climate variables (6.67%, fraction [c] in Appendix A2) and landscape metrics (6.34%; fraction [d] in Appendix A2) when darkling beetles and vascular plants were considered as predictors, respectively. Variation in the spider communities were significantly explained by ground beetles and ants (9.21% and 9.02%, respectively; fraction [a] in Appendix A2), spatial-topographic (min = 2.98% and max = 5.77%; fraction [b] in Appendix A2) and climate variables (min = 4.62%, max = 8.60%; fraction [c] in Appendix A2), which assume a major role when pseudoscorpions, darkling and rove beetles and vascular plants were set as predictors. In darkling beetles, only ants explained a significant degree of variance (11.71%; fraction [a] in Appendix A2), followed by spatial-topographic factors when pseudoscorpions and vascular plants were set as predictors (6.28% and 6.16%, respectively; fraction [b] in Appendix A2). When the ant communities were considered as response variables, most of the significant variation were attributed to the pure effect of another taxonomic group (spiders, and darkling beetles; 10.88% and 7.50%, respectively; fraction [a] in Appendix A2) and the pure effect of spatial-topographic factors (min = 5.55% and max = 5.61%; fraction [b] in Appendix A2). The pure effect of environmental predictors (spatial-topographic and climate variables, landscape metrics) was not significant for ground beetles and vascular plants: most of the variation in these two groups were attributed to the pure effect of another taxonomic group. Spiders (9.16%; fraction [a] in Appendix A2) and vascular plants (7.90%; fraction [a] in Appendix A2) appeared as the strongest predictors, explaining the greatest and significant proportion of variation in ground beetle communities. Pseudoscorpions, spiders and ground beetles were important predictors of the variation of vascular plants (4.33%, 5.24%, 7.90%, respectively; fraction [a] in Appendix A2).

4. Discussion

4.1. Cross-taxon congruence patterns

As we hypothesized, congruence relationships exist between several investigated taxa, indicating that some of these were representative of each other, even when the environmental drivers were removed: pseudoscorpions, spiders, ground beetles and vascular plants showed the largest number of significant correlations with other taxa. These results were in contrast with previous findings that reported a generally poor congruence among taxa (Filgueiras et al., 2019; Harry et al., 2019; Larrieu et al., 2018; Oberprieler et al., 2020; van Schalkwyk et al., 2019). However, studies of cross-taxon congruence rarely give consistent results due to the spatial and temporal scale dependence of different types of organisms (Burrascano et al., 2018; Westgate et al., 2017; 2014), analytic approach (Gioria et al., 2011) and the identity of factors driving the congruence (Santi et al., 2016; Westgate et al., 2014). Thus, from a theoretical perspective, a better understanding of determinants of community composition may improve the application of indicator surrogates in conservation planning (Gjerde et al., 2007; Margules and Pressey, 2000; Sætersdal and Gjerde, 2011) by identifying drivers of consistency in biodiversity congruence (Westgate et al., 2014).

4.2. Role of abiotic drivers

Altitudinal variation commonly reflects a wide range of environmental factors, such as precipitation, air humidity, barometric pressure, airborne particles, and water–energy balance (Fischer et al., 2011; Lomolino, 2001; Vetaas et al., 2019). In our study area, spatial-topographic factors describe the decreasing of altitude, longitude, coastal distance, lake and lagoon distance from the northeast to the southwest sector of the study area (Bazzato et al., 2021a). Topography and altitude can play a role for the community variation of spiders, darkling beetles, and ants (Crist and Wiens, 1996; Fattorini, 2014; Fattorini et al., 2020; Kaspari et al., 2000; Sattler et al., 2010), influencing diversity patterns of various animal groups in a variety of contexts (Lomolino, 2001; Peters et al., 2016; Stevens, 1992) and determining the congruence across taxa (Barbato et al., 2019; Duan et al., 2016; Ramos et al., 2021). Accordingly, we found that parameters associated with the spatial-topographic variation exerted an influence on the community composition of spiders, darkling beetles and ants.

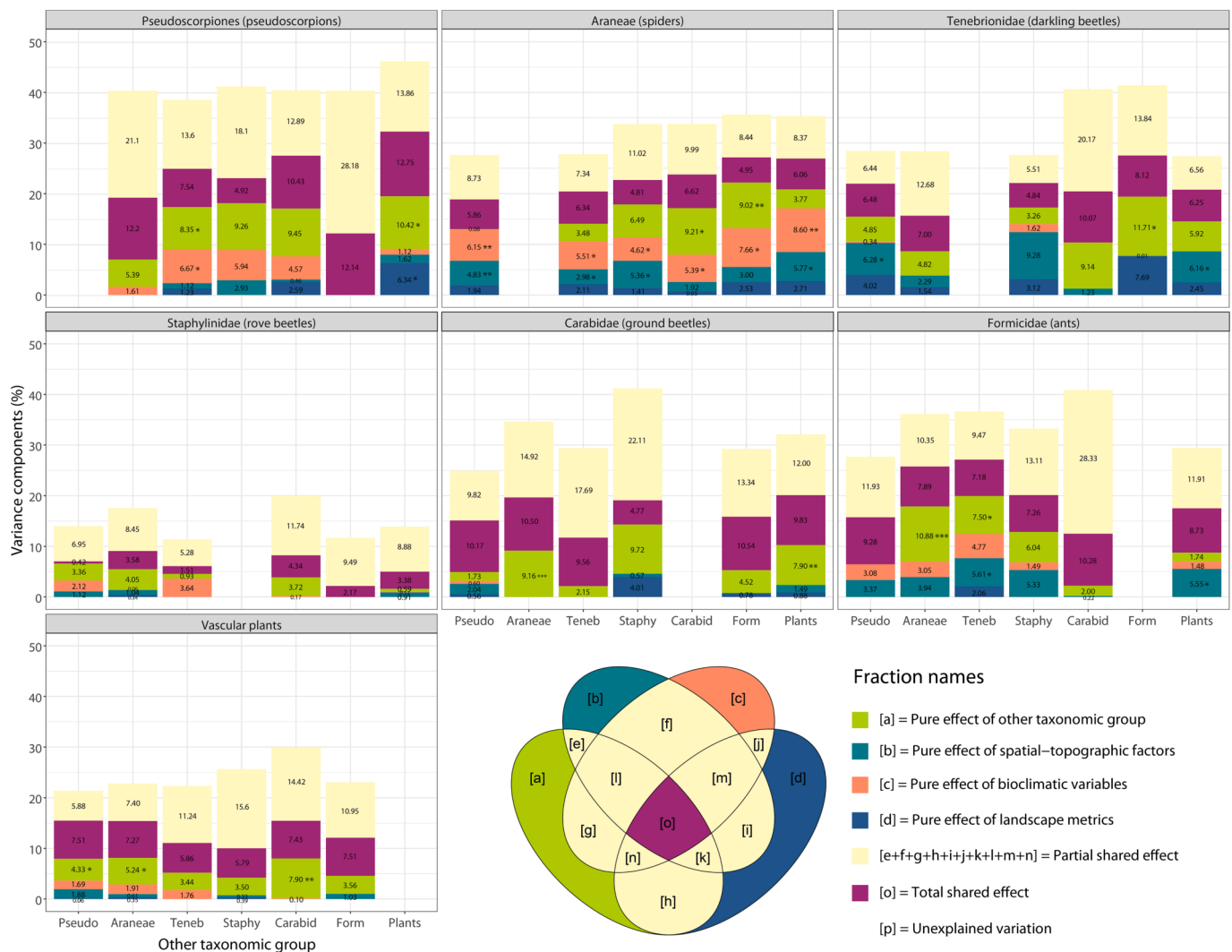


Fig. 3. Partitioning of variation in community composition of each taxonomic group recorded along the environmental gradient. Response variables (Hellinger-transformed community data) are shown in the multi-panel plot: pseudoscorpions (Pseudoscorpiones), spiders (Araneae), darkling beetles (Tenebrionidae), rove beetles (Staphylinidae), ground beetles (Carabidae), ants (Formicidae), and vascular plants. Colours within each bar chart category show the unexplained variation and pure or combined effect of predictors (scores of principal component analyses): another taxonomic group, spatial-topographic factors, bioclimate variables, and landscape metrics. On the bottom, Venn’s diagram shows the name of each fraction: [a] pure effect of another taxonomic group, [b] pure effect of spatial-topographic factors, [c] pure effect of bioclimatic variables, [d] pure effect of landscape metrics, [e + f + g + h + i + j + k + l + m + n] partial shared effects of two/three set of factors, [o] total shared effect of all predictor sets, [p] unexplained variation. In the chart, fractions with negative values of adjusted R^2 were interpreted as zeros and were not shown in the diagram. Significance codes: (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$.

Congruence among taxa could not persist by removing environmental drivers when groups respond similarly to the same environmental variables (Axmacher et al., 2009; Barbato et al., 2019; Duan et al., 2016; Hawkins and Porter, 2003; Toranza and Arim, 2010). In our study, only the congruence among pseudoscorpions/darkling beetles, darkling beetles/ants, rove beetles/ants, and rove beetles/plants disappeared once the environmental drivers were removed. However, communities of pseudoscorpions/darkling beetles, rove beetles/ants and rove beetles/plants did not show common or shared responses to the same set of abiotic drivers, suggesting the existence of spurious relationships between taxa (Cushman et al., 2013; Cushman and Landguth, 2010; Perner and Voigt, 2007). Pseudoscorpions and darkling beetles reacted distinctly different to the tested parameters: climate (Adis and Mahnert, 1993; Battistola et al., 2017; Jiménez-Hernández et al., 2020; Villarreal et al., 2019) and landscape variables influenced pseudoscorpion communities while spatial-topographic factors significantly explained the community composition of darkling beetles.

In fact, despite the recognized importance by previous cross-taxon

studies (Barbato et al., 2019; Duan et al., 2016; Ramos et al., 2021), the significant explanatory value of spatial-topographic factors for the variation of communities underpinned inter-taxon congruence only across darkling beetles and ants, which reacted to this set of variables showing a common response. On the contrary, the decrease in mean temperature and the increase in precipitation appeared to govern the community composition of pseudoscorpions and spiders without determining their reciprocal concordance and their associations with other taxa. Similarly, the variation of spatial-topography, climate and landscape variables did not drive the congruence of ground beetles and vascular plants with the other groups, which remained associated even when environmental parameters were removed.

4.3. Role of biotic drivers

Plant-animal relationships can result from two non-exclusive mechanisms, such as common responses to similar environmental factors or biogeographic history and the effects of one taxon on another taxon’s

diversity due to biotic interactions (Duan et al., 2016; Gioria et al., 2011; Ramos et al., 2021; Sabatini et al., 2016; Toranza and Arim, 2010). In our study, the persistence of a significant association among taxa, after considering environmental conditions, can suggest that biotic interactions could be considered as an explanation of cross-taxon congruence in community composition (Duan et al., 2016; Toranza and Arim, 2010).

Biotic interactions, including both non-trophic and trophic interactions, direct and indirect interactions, may promote or constrain cross-taxon congruence (Duan et al., 2016; Morlon et al., 2014; Özkan et al., 2014). Vascular plants - as the main group of primary producers - regulate the diversity and community composition of organisms at higher trophic levels, both belowground and aboveground, via bottom-up effects (Castagneyrol and Jactel, 2012; Scherber et al., 2010; Schuldt et al., 2019; 2014). Non-trophic bottom-up effects might occur through plant structure-mediated modifications (Birkhofer et al., 2008; Schuldt et al., 2017), such as changes in microclimate conditions and abiotic properties that can influence the community composition of arthropod predators (Langellotto and Denno, 2004; Mupepele et al., 2014; Podgajski et al., 2013). In our study, the biotic links between vascular plants and arthropod predators (i.e., pseudoscorpions and spiders, but also ground beetles) could be partly sustained by such non-trophic effects. However, these could have less value on spiders, as indicated by the poor degree of variance attributed to the pure effect of primary producers. Rather, our results point to the intriguing hypothesis that plant-mediated bottom-up forces may assume a role in structuring the pseudoscorpion communities, explaining why this predator group was much more influenced by vascular plant composition than by other environmental parameters. Although bottom-up effects of plants on pseudoscorpions are mainly unknown (but see Liebke et al., 2021) and need further investigation, plant-mediated controls on leaf litter accumulation can affect the microclimate (i.e., temperature and humidity conditions) in the litter layer, determining changes in arthropod communities (Hartshorn, 2021; Ottermanns et al., 2011), including pseudoscorpions (Aguiar et al., 2006; Dennis et al., 2001; Jiménez-Hernández et al., 2020). Previous studies also found an influence of thin litter layers and canopy openness on pseudoscorpion density, pointing to the usefulness of this arthropod group as sensitive bioindicators (Liebke et al., 2021).

Additionally, the relationships between plants and arthropods can even involve a trophic component (Schuldt et al., 2017) because plants supply food sources for herbivores and attract prey for larval or adult predators (Birkhofer et al., 2008; Diehl et al., 2012; Gardarin et al., 2018). This could be especially true for ground beetles, a chiefly predatory insect taxon with some omnivorous and granivorous species (Kromp, 1999). All trophic groups of recorded ground beetles (i.e., predators, omnivores, and granivores) could have benefited from resources provided or mediated by plant communities (Diehl et al., 2012; Honek et al., 2013; Sasakawa, 2010). Since we found an influence of plant communities on ground beetles, not related to environmental parameters, our results suggest biotic links between plants and ground beetles, supporting the significant congruence in their composition patterns and the findings of previous studies (Corcos et al., 2021; Duan et al., 2016).

On the other hand, arthropod predators can trigger significant cascading effects proceeding down through herbivores to the producer trophic level (Halaj and Wise, 2001; Moran et al., 1996), altering herbivore density, plant-herbivore interactions, and ultimately plant growth and reproduction (Moreira et al., 2016). Coherently, our study does not rule out the possibility of these top-down effects of arthropods on plant community composition: almost all strictly predatory taxa (i.e., pseudoscorpions, spiders, but also ground beetles) emerged as the best predictors of plant community composition irrespective of environmental factors, driving the observed cross-taxon relationships. Top-down effects are known for arthropod predators such as spiders (Birkhofer et al., 2016; Sanders and Platner, 2006) but also well applied

to ground beetles, for which the biological control of herbivore populations and insect pests, with benefits for plants, is described (De Heij and Willenborg, 2020). In our study spider assemblages were characterized by the coexistence of dominant species with different foraging strategies and abilities to obtain prey (Cardoso et al., 2011; Michalko and Pekár, 2016): they include strict ant-eating specialists (e.g., *Zodariion* spp.) that possess effective prey-capture tactics (i.e., bite-and-release, a single bite followed by a release of prey) (Traxler, 2016), hunters (e.g., ground hunters, ambush hunters, and other hunters) that are more effective in capturing epigeal prey, but also web-builders (e.g., sheet-web weavers) that are able to capture flying or arboreal arthropods (Cardoso et al., 2011; Potapov et al., 2022). Spider species with different foraging strategies may show great prey variability and exploit different resources in different proportions (Michalko and Pekár, 2016; Uetz et al., 1999): our findings may also suggest the efficiency of this predator group in suppressing a broad spectrum of prey with potential significant implications for biological control and plant community composition (Michalko et al., 2019). Similarly, ground beetle assemblages can vary considerably in their trophic structures or strategies (Bennewicz and Barczak, 2020), including zoophagous species (generalists or specialists, e.g., helicophages as in the case of the genus *Licinus*, and some species belonging to the genus *Carabus*), haemizoophagous species that feed on animals and seeds (e.g., *Harpalus*, *Zabrus*, *Amara*), and granivorous species (e.g., belonging to the genus *Acinopus*, *Carterus*, *Ditomis*) (Brandmayr et al., 2005; Chatenet, 2005). Both these genera were represented in our research, including so-called seed predators (*Harpalus*, *Amara*) mentioned as weed seed bank regulators (Bohan et al., 2011), thanks to their capacity of reducing weed seedling emergence (White et al., 2007). These findings support previous evidences for the major ecological functions that this taxon provides in ecosystems (Bennewicz and Barczak, 2020; but see De Heij and Willenborg, 2020) and the existence of a promising biological control role of ground beetle communities.

Taxa within the same trophic level can also interact with each other via consumptive interactions (e.g., predation, intraguild predation, or cannibalism) or non-consumptive interactions (e.g., anti-predator behaviour or interference phenomena) (Losey and Denno, 1998; Michalko et al., 2019; Schmitz, 2007; Snyder, 2019), respectively, with direct and indirect effects on their assemblages (Moran et al., 1996). Spiders exhibit key functions as dominant predators in most terrestrial food webs (Potapov et al., 2022), and consumptive or non-consumptive interactions among spiders/ants (Schuldt and Staab, 2015) and spiders/ground beetles (De Heij and Willenborg, 2020) are likely to be reflected in significant associations between groups (Vleminckx et al., 2019). Interestingly, our study confirms as these taxa (i.e., spiders and ants, but also spiders and ground beetles) showed close relationships and congruent composition patterns, irrespective of environmental factors. Consistent with other cross-taxon studies (Schuldt and Staab, 2015; Vleminckx et al., 2019), we observed that spiders and ants were affected by each other. While experimental manipulations are needed to verify the causality of the observed relationships (Schuldt and Staab, 2015), both the intraguild predation and the intraguild competition may have played a key role in shaping their communities. For example, the association between spiders and ants may result from the dominance of different ant-eating species (*Zodariion elegans*, *Z. pseudonigriceps*, *Z. pusio*) in the spider assemblages that can influence the community of ant prey (Traxler, 2016), or it may reflect the intraguild competition occurring between these taxa (Schuldt and Staab, 2015; Vleminckx et al., 2019), which both comprise diverse predators. The dominant species of ant assemblages observed in our study are all characterized by an omnivorous lifestyle, including a variable predatory component in almost all of them (*Aphaenogaster ichnusa*, *Camponotus aethiops*, *Lasius niger*, *Linepithema humile*, *Myrmica spinosior*, *Tapinoma magnum*, *Tetramorium semilaeve*) (see Seifert, 2018). In the case of spiders/ground beetles, the reciprocal interaction could be explained by considering differences in competitive ability for the use of resources and the differences in

predation susceptibility that can determine assemblages with more similar and related taxa (Magura et al. 2018).

5. Conclusion

By considering both abiotic and biotic drivers, our findings suggest that the congruence among organisms occupying different trophic levels was not driven by a single driver. We observed that environmental factors (e.g., latitudinal, altitudinal, climate variables) (Toranza and Arim, 2010; Warman et al., 2004) were drivers of cross-taxon congruence, but they were not the only ones (Kraft et al., 2015; Magura et al., 2018): biotic drivers exerted a significant influence on community composition, revealing that they account for part of cross-taxon congruence among the investigated taxa (Kissling et al., 2007; Toranza and Arim, 2010). In fact, abiotic and biotic filtering can act together to determine the congruence among groups, shaping composition patterns (Stein et al., 2014): environmental factors might represent the first filter for the presence of species and communities, but species and communities adapted to a certain environmental condition could be further filtered out by biotic interactions (Duan et al., 2016; Magura et al., 2018). Thus, both drivers should be incorporated in cross-taxon studies, especially at a fine spatial scale (Toranza and Arim, 2010), where the role of biotic interactions in determining congruence patterns can be prominent (Duan et al., 2016). Our study highlighted that several not mutually exclusive biotic interactions (e.g., non-trophic and trophic interactions, direct and indirect interactions) may have played a role in shaping the community composition of taxa, likely driving the observed relationships. These biotic interactions can provide an opportunity for experimental research on cross-taxon congruence studies under variable ecological contexts. Future studies will help us understand what regulates these complex interactions and how they may evolve, affecting diversity patterns and driving the congruence across taxa. The knowledge of the main drivers of cross-taxon congruence integrating the multi-trophic perspective can be promising for the identification of biodiversity surrogates and for providing indications for their application in conservation planning.

CRedit authorship contribution statement

Erika Bazzato: Conceptualization, Methodology, Software, Validation, Formal analysis, Resources, Data curation, Writing – Original Draft, Writing – review & editing, Visualization. **Erik Lallai:** Investigation, Data curation. **Michele Caria:** Investigation, Data curation. **Enrico Schifani:** Investigation, Data curation, Writing – review & editing. **Davide Cillo:** Investigation. **Cesare Ancona:** Investigation. **Paolo Pantini:** Investigation, Data curation, Resources. **Simona Maccherini:** Conceptualization, Methodology, Validation, Writing – review & editing. **Giovanni Bacaro:** Conceptualization, Methodology, Validation, Writing – review & editing. **Michela Marignani:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition

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.

Data availability

Data will be made available on request.

Acknowledgements

We are very grateful to Giulio Gardini and Jan Matějček, respectively, for the identification of pseudoscorpions and rove beetles. We

also thank Leonardo Rosati for supporting and confirming the identification of plant species. Our gratitude also goes to Dr. Dirk Ahrens of the Zoological research Museum Alexander Koenig (ZFMK, Bonn, Germany), and the director Marco Valle and all the staff of the Museo Civico di Scienze Naturali “E. Caffi” (Bergamo, Italy) for their hospitality and for placing their equipment at our disposal. We also thank Federico Alamanni, Francesca Ganga, Elisa Serra, and Andrea Ambus, who kindly helped with the fieldwork or laboratory activities. We gratefully thank the project ‘ALIEM’ (ALIEM Apostrophe, CUP No.: G17H03000130001), co-financed by the Interreg Italy-France Maritime 2014-2020 programme, for funding a research grant to EB. This work was supported by Regional Adaptation Strategy to Climate Change (SRACC) of Sardinia (CUP No.: F25F20000380002).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110323>.

References

- Adis, Mahnert, 1993. Vertical distribution and abundance of pseudoscorpions (Arachnida) in the soil of two different neotropical primary forests during the dry and rainy seasons. *Mem. Queensl. Mus.* 33, 431–440.
- Aguiar, N.O., Gualberto, T.L., Franklin, E., 2006. A medium-spatial scale distribution pattern of Pseudoscorpionida (Arachnida) in a gradient of topography (altitude and inclination), soil factors, and litter in a central Amazonia forest reserve, Brazil. *Braz. J. Biol.* 66, 791–802. <https://doi.org/10.1590/S1519-69842006000500004>.
- Andersen, T., Hessen, D.O., Häll, J.P., Khomich, M., Kyle, M., Lindholm, M., Rasconi, S., Skjelbred, B., Thrane, J.-E., Walseng, B., 2020. Congruence, but no cascade—Pelagic biodiversity across three trophic levels in Nordic lakes. *Ecol. Evol.* 10, 8153–8165. <https://doi.org/10.1002/ece3.6514>.
- Axmacher, J.C., Brehm, G., Hemp, A., Tünte, H., Lyaruu, H.V.M., Müller-Hohenstein, K., Fiedler, K., 2009. Determinants of diversity in afro-tropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *J. Biogeogr.* 36, 337–349. <https://doi.org/10.1111/j.1365-2699.2008.01997.x>.
- Bacchetta, G., Bagella, S., Biondi, E., Farris, E., Filigheddu, R., Mossa, L., 2009. Vegetazione forestale e serie di vegetazione della Sardegna (con rappresentazione cartografica alla scala 1:350.000). *Fitosociologia* 46, 3–82.
- Bae, M.-J., Li, F., Kwon, Y.-S., Chung, N., Choi, H., Hwang, S.-J., Park, Y.-S., 2014. Concordance of diatom, macroinvertebrate and fish assemblages in streams at nested spatial scales: implications for ecological integrity. *Ecol. Ind.* 47, 89–101. <https://doi.org/10.1016/j.ecolind.2014.07.030>.
- Bagella, S., Gascón, S., Caria, M.C., Sala, J., Boix, D., 2011. Cross-taxon congruence in Mediterranean temporary wetlands: vascular plants, crustaceans, and coleopterans. *Community Ecol.* 12, 40–50. <https://doi.org/10.1556/ComEc.12.2011.1.6>.
- Barbato, D., Perini, C., Mocali, S., Bacaro, G., Tordoni, E., Maccherini, S., Marchi, M., Cantiani, P., De Meo, I., Bianchetto, E., Landi, S., Bruschini, S., Bettini, G., Gardin, L., Salerni, E., 2019. Teamwork makes the dream work: disentangling cross-taxon congruence across soil biota in black pine plantations. *Sci. Total Environ.* 656, 659–669. <https://doi.org/10.1016/j.scitotenv.2018.11.320>.
- Battirolo, L.D., Rosado-Neto, G.H., Batistella, D.A., Mahnert, V., Brescovit, A.D., Marques, M.I., 2017. Vertical and time distribution of Pseudoscorpiones (Arthropoda: Arachnida) in a floodplain forest in the Brazilian Pantanal. *Rev. Biol. Trop.* 65, 445–459. <https://doi.org/10.15517/rbt.v65i2.24134>.
- Bazzato, E., Lallai, E., Serra, E., Melis, M.T., Marignani, M., 2021a. Key role of small woodlots outside forest in a Mediterranean fragmented landscape. *For. Ecol. Manag.* 496, 119389. <https://doi.org/10.1016/j.foreco.2021.119389>.
- Bazzato, E., Rosati, L., Canu, S., Fiori, M., Farris, E., Marignani, M., 2021b. High spatial resolution bioclimatic variables to support ecological modelling in a Mediterranean biodiversity hotspot. *Ecol. Modell.* 441, 109354. <https://doi.org/10.1016/j.ecolmodel.2020.109354>.
- Bazzato, E., Lallai, E., Caria, M., Schifani, E., Cillo, D., Ancona, C., Alamanni, F., Pantini, P., Maccherini, S., Bacaro, G., Marignani, M., 2022. Land-use intensification reduces multi-taxa diversity patterns of Small Woodlots Outside Forests in a Mediterranean area. *Agric. Ecosyst. Environ.* 340, 108149. <https://doi.org/10.1016/j.agee.2022.108149>.
- Beck, J., Pffiffer, L., Ballesteros-Mejia, L., Blick, T., Luka, H., Ferrier, S., 2013. Revisiting the indicator problem: can three epigeal arthropod taxa inform each other's biodiversity? *Divers. Distrib.* 19 (7), 688–699.
- Bennewicz, J., Barczak, T., 2020. Ground beetles (Carabidae) of field margin habitats. *Biologia* 75, 1631–1641. <https://doi.org/10.2478/s11756-020-00424-y>.
- Birkhofer, K., Wise, D.H., Scheu, S., 2008. Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. *Oikos* 117, 494–500. <https://doi.org/10.1111/j.0030-1299.2008.16361.x>.
- Birkhofer, K., Arvidsson, F., Ehlers, D., Mader, V.L., Bengtsson, J., Smith, H.G., 2016. Organic farming affects the biological control of hemipteran pests and yields in spring barley independent of landscape complexity. *Landscape Ecol.* 31, 567–579. <https://doi.org/10.1007/s10980-015-0263-8>.

