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Spatial Patterns and Scales of Collembola Taxonomic and Functional Diversity in Urban Parks

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Abstract: Anthropogenic pressures can affect the distribution of species and elicit the appearance of spatial patterns that provide insights into the species' responses to environmental filtering, mediated by their functional traits. Due to the functional redundancy in ecological communities, the spatial variations of species and functional traits can occur at different scales, but little is known on this topic, especially for soil arthropods with limited dispersion capabilities and highly dependent on environmental characteristics. The present research aims at shedding light on the spatial ecology of both the taxonomic and functional biodiversity of collembolan communities colonizing urban parks, adopted as model taxa for their functional traits, diversity and sensitivity to environmental drivers. To this end, the spatial patterns and scales of collembolan communities from 8 parks in Naples (Italy) and 14 in Montpellier (France) were investigated through an approach based on Moran eigenvector maps, modified to allow for evaluating the community spatial connectivity and the scales underpinning the spatial variation of each species and functional trait. The obtained findings demonstrate a limited spatial connectivity of collembolan communities in terms of both taxonomic and functional diversity, with mostly species-specific micro-scale variations that may be shaped by environmental constraints.

Keywords: springtails; spatial structure; Moran eigenvector maps; fourth corner analysis

1. Introduction

The sustainable development of urban ecosystems pivots on networks of green infrastructures that allow preserving key ecosystem processes in otherwise constructed environments [1]. The provision of suitable habitats for flora and fauna, the regulation of organic matter and biogeochemical cycles, the climate mitigation and the environmental remediation are just some of the showcase processes supported by semi-natural environments in urban ecosystems [2,3]. At landscape scale, the interaction between these areas and the surrounding environment can be analyzed within the classical framework of island biogeography [4–6], with the urban tissue representing a hostile matrix that surrounds patches of habitat suitable for most of the flora and fauna. Urban parks represent most of these patches, with characteristics shaped by their size, topology, management and interaction with the surrounding matrix. Even in large parks, with limited protrusion of the urban tissue within their borders, management can have pervasive effects on their capability to act as biodiversity reservoirs. For example, complex canopies are able to

host richer communities and counteract biotic homogenization [7–9]. Conversely, canopy simplification or reduction and the realization of passageways or fences can constrain the movements and dispersal of organisms. Management-induced fragmentation within urban parks has dramatic effects, especially on organisms with small body size and limited movements, which are common traits within soil communities [10]. The perceived spatial scale is what exacerbates the effects of management on these organisms that may not only act at small temporal scale, but also develop into temporal legacies exerting their effects through decades or centuries. A clear example is the demonstrated effect of park history or age on several taxa, including enchytraeids, nematodes and springtails [11–14].

On a theoretical level, environmental drivers may exert different effects on community taxonomic and functional diversities, as well as on their spatial variations. However, in spite of the well-documented effects on the taxonomic diversity, those on the functional diversity are comparatively less studied, especially in the case of soil fauna [15]. In this context, even fewer studies tackle the issue from a spatial perspective, investigating the connectivity of communities and their scales of spatial variation.

The present research aims at shedding light on these topics through a comparative analysis of the spatial patterns and scales of the taxonomic and functional biodiversity of soil collembolan communities of urban parks, and the evaluation of the main drivers underpinning these patterns. The diversity in functional traits expressed by this group, with large variations in body size, feeding strategies, colonized environments, speed of movements or dispersal, as well as their sensitivity to environmental drivers, make Collembola exceptional models for such purposes. Under the community convergence hypothesis [16], the study focuses in parallel on two urban systems, in southern Italy and southern France, in order to strengthen the comparative analysis by stressing the differential responses of species vs. functional assemblages to the geographical distance.

2. Materials and Methods

2.1. Study Area and Sampling Design

The study was carried out in 8 urban parks of Naples (40°50′ N; 14°15′ E, Italy) and 14 of Montpellier (43°36′ N; 03°52′ E, France), two cities lying on the coast of the western Mediterranean Sea and characterized by similar climate, but ~900 Km apart from each other (great circle distance).

Naples is an historical city and current megalopolis mainly lying on Andosols [17], characterized by an uninterrupted urban tissue, whereas Montpellier is a recently expanded city mainly lying on Calcisols [17]. According to the Köppen climate classification, both sites are classified as Csa (hot climate with drought summer). In Naples, mean temperatures range from 9.7 °C in winter to 25.7 °C in summer, with a mean annual temperature of 17.4 °C, and the annual precipitation is ~865 mm (http://www.meteo.unina.it/clima-di-napoli; accessed on 19 November 2021). In Montpellier, mean temperatures range from 5.9 °C in winter to 22.3 °C in summer, with a mean annual temperature of 13.9 °C, and the annual precipitation is ~745 mm (https://fr.climate-data.org/location/1126/; accessed on 19 November 2021). Woody habitats within the parks are dominated by *Quercus ilex* L. and, to a lesser extent, by *Quercus petrea* (Matt.) Lielb., *Platanus occidentalis* L. and *Pinus pinaster* Aiton. Brushwood layer, when present, is mostly represented by *Laurus nobilis* L., *Nerium oleander* L. and *Ruscus aculeatus* L.

Soil sampling, microarthropod extraction, Collembola species identification and counting, as well as the determination of environmental parameters and their coding are extensively reported in Milano et al. [13,14] and briefly reported hereafter.

Soil samplings were collected [18] after litter removal (if present) from four different plots (one sample per plot), either under canopy or from open spaces. Samples were then stored at 4 °C until microarthropod extraction, using a Macfaiden apparatus [19] and the following identification and counting of Collembola specimens.

In order to describe the environment experienced by Collembola, several descriptors of either park or sample properties, summarized in Table S1, were adopted. In particular,

the age since park opening to the public (very old, old, young), previous land use (forest, wilderness, tuff quarry, agricultural land), elevation and urban density, where employed at the park level, coupled to characteristics of the site where samples were collected: presence of canopy, brushwood and litter; soil chemical and physical properties. The latter encompassed dissolved organic carbon and C/N ratio, as proxies of quantity and quality of trophic resources, and pH and bulk density as general descriptors of soil characteristics. The determination of soil properties was performed on the soil cores after microarthropod extraction and oven drying, according to the protocols described in Milano et al. [13,14]. Species that were observed in more than 2% of the samples, reported in Table 1, were adopted for all the spatial analyses.

Table 1. Species of Collembola observed in urban parks of Naples (N), Montpellier (M) or both the cities (B), grouped according to the family they belong to and with indication of the identifying label.

Isotomidae			Entomobryidae		
Cryptopygus thermophilus Axelson	C_the	B	*Lepidocyrtus cyaneus* Tullberg	L_cya	M
Desoria tigrina Nicolet	D_tig	N	*Lepidocyrtus lanuginosus* Gmelin	L_lan	B
Folsomia penicula Bagnall	F_pen	N	*Lepidocyrtus lignorum* Fabricius	L_lig	N
Folsomia quadrioculata Tullberg	F_qua	N	*Pseudosinella alba* Packard	P_alb	M
Folsomia sexoculata Tullberg	F_sex	N	*Pseudosinella immaculata* Lie-Pettersen	P_imm	B
Folsomia similis Bagnall	F_sim	M			
Folsomides parvulus Stach	F_par	B			
Isotomiella minor Schaeffer	I_min	B			
Isotomodes templetoni Bagnall	I_tem	N			
Isotomurus maculatus Schaeffer	I_mac	N			
Parisotoma notabilis Schaeffer	P_not	B			
Proctostephanus stuckeni Borner	P_stu	M			
Proisotoma minuta Tullberg	P_min	B			
Hypogastruridae			Tullbergiidae		
Ceratophysella gibbosa Bagnall	C_gib	B	*Paratullbergia callipygos* Borner	P_cal	M
Schoettella ununguiculata Tullberg	S_unu	M	*Paratullbergia caroli* Luciañez, Ruiz & Simon	P_car	N
Willemia denisi Mills	W_den	M	*Paratullbergia macdougalli* Bagnall	P_mac	M
Sminthuridae			Onychiuridae		
Sminthurinus elegans Fitch	S_ele	N	*Protaphorura armata* Tullberg	P_arm	N
Sminthurus viridis Linnaeus	S_vir	N	*Protaphorura aurantiaca* Ridley	P_aur	B
Neanuridae			Brachystomellidae		
Lathriopyga longiseta Caroli	L_lon	N	*Brachystomella parvula* Schaeffer	B_par	N

2.2. Species Traits

Collembola species traits were obtained from the Betsi online database (http://betsi.cesab.org/; accessed on 16 September 2021) for soil invertebrates [20], integrated with information from various dichotomous keys [21–27], coded according to the Betsi rules. Each species was described by morphological proxies of life-form *sensu* Gisin [28]: body length, shape, pigmentation, presence of visual organs, scales, postantennal organ (PAO) and length of the furca. The set of functional traits adopted aimed at including different aspects of the species' ecological niches that may be directly or indirectly related to their spatial distribution. Indeed, whereas body length is an overall proxy of food resource use, traits such as body shape, the presence of pigmentation for camouflage or as a means of protection against excessive light and the presence of organs for sensing the environment such as ocelli or PAO are directly related to the habitat preferences [29]. In terms of movements, instead, the length of the furca is directly involved in dispersion and predation evasion, to which the presence of scales also contributes [30].

In order to limit the dimensionality of the functional traits dataset and compress the information into few informative variables, the traits were coded as in Table 2 and

transformed into dummy variables (presence–absence) according to Podani [31]. In the case of multilevel variables (body and furca lengths), each level defined a new presence–absence variable. Traits were then employed in calculating the community weighted mean (CWM) as a measure of functional composition of communities in each soil sample [32].

Table 2. Functional traits and the relative coding adopted in the present research, together with the rationale behind trait choice.

Trait	Coding	Rationale
Body length	Short (<1.5 mm)	Food resource use
	Medium (1.5–3.0 mm)	
	Long (>3.0 mm)	
Body shape	Spherical	Habitat preference
	Cylindrical	
Furca	Absent/Vestigial	Movement/dispersion
	Short	
	Long	
Pigmentation	Present	Habitat preference
	Absent	
Eyes	Present	Habitat preference
	Absent	
PAO	Present	Habitat preference
	Absent	
Scales	Present	Predation avoidance
	Absent	

2.3. Data Analysis

The spatial analysis relied on the algorithm described in Bellino and coworkers [33], allowing investigation of the spatial organization and scales of variation of each species or trait within communities. In particular, 88 spatial weighting matrices (SWMs) were defined according to 4 connectivity diagrams with varying degrees of connectedness (Delaunay triangulation, Gabriel's graph, minimum spanning tree and relative neighbors graph) and 22 weighting schemes. The schemes comprised linear, concave and convex functions, the second and third with varying exponential parameters in the set η = {0, 0.1, 0.2, ... , 1.0}. The selection of the SWMs describing the spatial organization of communities and CWMs in Naples and Montpellier relied on the definition of least absolute shrinkage and selection operator (LASSO) models relating each species or trait to the Moran eigenvector maps (MEM) derived through eigen analysis of each SWM. The models relative to the species and the CWMs will be hereafter referred to as S-models and T-models, respectively. The active set of the models was chosen based on the Akaike information criterion (AIC) profile. The AICs relative to the active sets of the LASSO models were then ranked and aggregated by calculating the mean rank, and the SWM identified by the lowest mean rank was chosen as the consensus SWM, describing the spatial patterns of either species or CWMs. The MEMs derived from the consensus SWM associated to non-zero LASSO coefficients were considered the spatial scales describing the spatial variations of each species and functional trait.

As a means to detect the presence of relationships between the number of MEMs and the spatial distribution of species, i.e., the hypothesis of common species being described by more spatial scales, the Spearman correlation between the number of parks in which species in Naples and Montpellier were observed and the number of their associated MEMs was adopted.

Finally, in order to evaluate the effects of environmental drivers on the spatial scales of species and traits, an approach based on fourth corner analysis was adopted. In particular, the analysis was carried out using either species or CWMs as the community elements, the MEMs associated to each species and CWM as functional traits, and the descriptors of

park/sample characteristics as environmental variables. A permutational approach was adopted in deriving P-values, which were adjusted using a false discovery rate criterion.

All the analyses were carried out within the R 4.0.5 [34] programming environment, using the core functions employed in Bellino et al. [33] and the function "fourthcorner" from the ade4 package [35].

3. Results

The mean rank of each SWM based on either the species or the CWMs in Naples and Montpellier is shown in Figure 1. Overall, the mean ranks show a consistent trend of decreasing values associated to concave weighting schemes and high η, with a progressive reduction in their differentiation among topologies. The consensus SWM, always weighted according to a concave function, has different topologies and η: relative neighbor graph with η = 0.9 and Gabriel's graph with η = 1.0 in the case of the S-models for Naples and Montpellier, respectively, and Gabriel's graph with η = 0.2 and Delaunay triangulation with η = 1.0 in the case of the T-models. The MEMs derived from the consensus SWMs are shown in Figure 2. Approximately half of the species and all the CWMs in both Naples and Montpellier are associated to non-zero LASSO coefficients, i.e., have non-random spatial patterns that, in addition, are described by several MEMs spanning wide ranges of scales. The number of MEMs describing species' spatial variations (Figure 2) does not depend on species distribution, since no relationship (for $\alpha = 0.05$) between the number of parks in which species were observed and number of MEMs describing their variations was found. Species with random spatial patterns belong to a few genera: *Brachystomella*, *Desoria*, *Lathriopyga*, *Lepidocyrtus*, *Sminthurinus*, *Sminthurus*, *Willemia*, as well as *Folsomia* and *Isotomurus*. In the latter two cases, however, the genus comprises also species with spatial variations described by several MEMs. The few species that occur in both Naples and Montpellier tend to have spatial variations described by similar scales (albeit with the limitations in comparing scales derived from different SWMs) or to exhibit random spatial variations in both locations. Fourth corner analysis indicates that none of the environmental drivers was significant (for $\alpha = 0.05$) in explaining the spatial variations of species and CWMs in Naples and Montpellier.
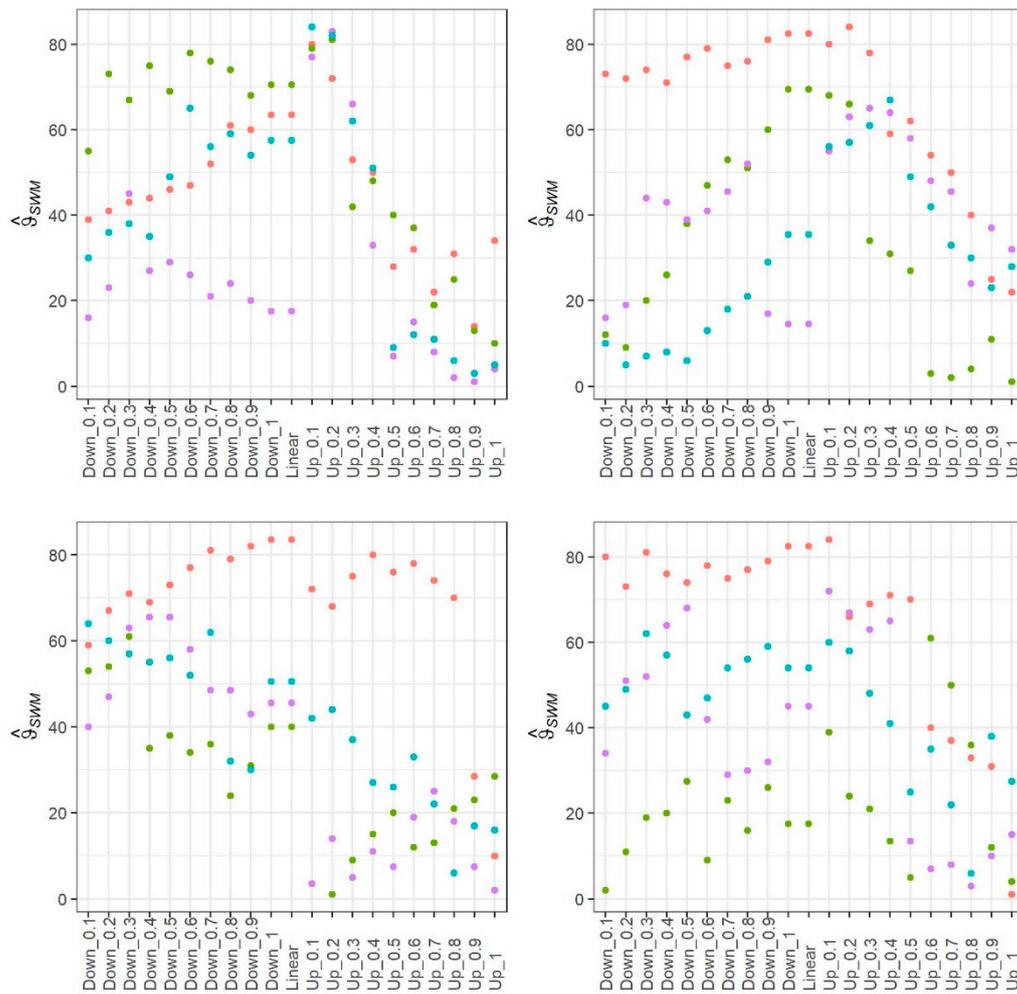
Figure 1. Mean ranks ($\hat{\vartheta}_{SWM}$) relative to each SWM for the S-models (**upper** panels) and the T-models (**lower** panels) in Naples (**left** panels) and Montpellier (**right** panels). Mean ranks are coded in different colors according to the connectivity topology (red: Delaunay triangulation, green: Gabriel's graph, cyan: minimum spanning tree, violet: relative neighbour graph) and are ordered according to the weighting schemes, reported on the x-axis along with their exponential parameter (η). The SWM scoring the lowest mean rank for each model was adopted as the SWM describing the spatial pattern of Collembola communities (for the S-models) and CWMs (for the T-models).

Figure 2. Heatmaps of the LASSO coefficients associated to the MEMs deriving from the consensus SWMs for the S-models (**upper** panels) and the T-models (**lower** panels) in Naples (**left** panels) and Montpellier (**right** panels). MEMs are ordered from the largest to the finest scale. The number of colored squares for each column indicates the number of MEMs describing species or trait spatial variations. Labels on the x-axes are coded according to Tables 1 and 2.

4. Discussion

Overall, the patterns observed in the ranking of SWMs and in the choice of MEMs from the consensus SWMs, as well as the lack of relationships between MEMs and potential environmental drivers, provide clear insights into the spatial ecology of Collembola and of their functional traits. In terms of spatial patterns, species abundances and CWMs exhibit mostly small-scale variations, with limited spatial connectivity. Indeed, on the one hand, the degree of connectedness has little effect on the choice of SWMs in both S- and T-models, as indicated by the reduced differentiation among the mean ranks of SWMs based on different topologies. On the other hand, the generally high η of the concave weighting functions indicates that the abundance of species or the values of the CWMs change abruptly in space, actually removing (weighting down to zero) edges even in highly connected topologies. Taken together, these results suggest that collembolan communities could exhibit either random spatial structures or spatial structures at scales lower than the ones investigated in the present study, with patterns that disappear at larger spatial scales.

These deductions are in line with the fourth corner analysis, indicating that none among elevation, land use, park age, urban density, presence of litter, brushwood, or canopy cover, soil origin, C/N ratio, pH or bulk density explain the spatial variations of species and CWMs. Indeed, such an occurrence would be a direct consequence of a mismatch between the spatial scales at which the environmental parameters were measured and the scales of their variations that are relevant in determining Collembola spatial patterns. In other words, the spatial variations in environmental characteristics may structure collembolan communities at scales coherent with the perceived spatial scales of most of the species, but not at larger ones [36,37]. Such a hypothesis is confirmed by several studies on the drivers of diversity in edaphic communities, indicating either the presence of stochastic spatial distribution in the absence of environmental gradients [38] or micro-scale spatial structures shaped by both environmental filtering and species interactions [39–42].

An additional explanation for the independence of spatial patterns from environmental drivers refers, instead, to the effects of adaptation and amplitude of species' ecological niches, which may actually decouple their distribution from environmental constraints. In this context, with wide variations in environmental parameters within and between parks/cities [13,14], the distribution of species can be considered a proxy of their ecological niche amplitude. A notable example of widely distributed species among the investigated parks is *Cryptopygus thermophilus*, which, unsurprisingly, colonizes a wide variety of environments worldwide [43,44]. Other species observed in both Naples and Montpellier are *Isotomiella minor*, *Ceratophysella gibbosa*, *Protaphorura aurantiaca*, *Parisotoma notabilis*, *Proisotoma minuta*, *Lepidocyrtus lanuginosus*, *Pseudosinella immaculata* and *Folsomides parvulus*. Interestingly, in spite of their wide distribution, these species encompass taxa with different patterns of spatial scales, from species characterized by both large- and small-scale variations, such as *C. thermophilus* or *P. minuta*, to species without clear spatial structure, such as *L. lanuginosus*. On the one hand, the lack of correlation between the number of significant MEMs and the number of parks where species were observed guarantees MEMs' independence from species spatial distribution, and thus their ability to unbiasedly model species's spatial structure. On the other hand, it is remarkable that species tend to show similar spatial structure, or the lack thereof, in both Naples and Montpellier, with patterns that are congruent with their taxonomy. For example, and considering all the observed species, those belonging to the Isotomidae family, with few exceptions, are all spatially structured, whereas those belonging to other families, such as Sminthuridae and Entomobryidae, are not. The appearance of spatial structure and the scales at which it appears seem thus to be species-specific rather than environment-driven characteristics [45]. In other words, the spatial patterns of Collembola, in terms of the scales describing their spatial variations, appear to be primarily determined by intrinsic factors, such as functional traits affecting the perceived spatial scale [36] and the dispersion or adaptability to different environments [37]. Species' adoption of different dispersion strategies, such as wind transport or active locomotion [46], also supports this hypothesis, since species

morphology or behavior may directly affect the efficiency of different dispersion processes. As a corollary for this explanation, the environment plays a minor role, likely contributing to shape species distribution at micro-scale only [36,40,42]—a conclusion in agreement with the deductions derived from the fourth corner analysis.

Overall, Collembola spatial patterns appear thus at micro-scale, where they are likely affected by environmental constraints, with scales of variation defined by species characteristics. In this respect, we supposed that CWMs would exhibit spatial patterns with higher connectivity and variations at larger scales than species, as for the expected behavior of functional diversity vs. taxonomic diversity according to the community convergence hypothesis [16]. However, the deduced scenario for species' spatial variations holds true for the spatial patterns and scales of the functional traits, with mostly abrupt changes in CWM values from site to site and scales independent from the analyzed environmental parameters. In terms of scales, the functional traits investigated vary, with few exceptions, not only at large, but also at local scales, an occurrence that may be explained by the peculiar environment where the collembolan communities were studied. Indeed, urban parks are intrinsically more spatially heterogeneous than natural areas, with dramatic changes in the environment even at very fine scales, which may reflect the changes of not only the species composition of communities, but also their functional traits. One notable exception corroborating such a hypothesis is the pigmentation, which varies at large to medium scales, as expected from the scales of variation in the canopy cover or other means of shading modifying the light environment to which species are subjected, that affect this functional trait [47].

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