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Caruso, T., Migliorini, M., Rota, E., & Bargagli, R. (2017). Highly diverse urban soil communities: does stochasticity play a major role? *Applied Soil Ecology*, *110*, 73-78. https://doi.org/10.1016/j.apsoil.2016.10.012

Published in:
Applied Soil Ecology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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Highly diverse urban soil communities: does stochasticity play a major role?

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ABSTRACT

Urban soil biota can be surprisingly diverse and recent studies hypothesize that such biodiversity is partly due to stochastic community dynamics caused by fragmentation and high environmental variability, We aimed to quantify the relative effects of these factors on the community structure of soil oribatid mites inhabiting holm oak woodlands in two Mediterranean cities. We partitioned the community variation into fractions uniquely attributable to gradients in soil abiotic properties, pollution, microbiological properties, and spatial and temporal variation that could not be related to measured soil factors. As we found strong spatial structure at the local scales, a neutral model was fitted to test whether beta diversity patterns of relatively isolated communities were consistent with a purely stochastic assembly process. The overall diversity of the assemblage was remarkable: a total of 124 species were identified and rarefaction curves demonstrated that urban parks are as rich in species as their counterpart woodlands in suburban areas. The fraction of variation explainable in terms of soil properties, microbiology and pollution was statistically significant but surprisingly low. At the site scale, patterns of beta diversity (i.e. spatial turnover in species composition and relative abundances) were not significantly different from those predicted by neutral models. Stochastic models can parsimoniously predict background levels of urban soil biodiversity at local scales, while disturbance and environmental variation still play some significant but not major role at broader scales.

Keywords: soil biota, Oribatida, urban biodiversity, disturbance, stochasticity, beta diversity.

1. Introduction

As urban areas continue to expand and human population concentrates in these areas, ecologists are seeking to quantify the structure and functions of urban ecosystems (Grimm et al., 2008; Seto et al., 2012). Most biodiversity studies have focused on aboveground biodiversity (e.g. Cannon et al., 2005; Koh and Sodhi, 2004), but the bulk of terrestrial biodiversity is hidden in the soil (Bardgett and van der Putten, 2014). Some invertebrate groups can be very diverse in urban areas, where they can also vary much in time, including long term successional changes

and extinction processes (Bolger et al., 2000; Fattorini, 2011; Savage et al., 2015). Chronic levels of pollution, especially polycyclic aromatic hydrocarbon (PAHs), Pb and Cd, harsh climatic conditions, and physical disturbance further increase spatial and temporal variability of urban biota (Rota et al., 2013; Weigmann and Kratz, 1987). Especially at local scales, habitat fragmentation may amplify natural, demographic stochasticity in small and relatively isolated populations, while high variance in environmental variables and disturbance regime may contribute to environmental stochasticity. The overall emerging picture is that urban soil communities are regulated by a multitude of processes that may result in high levels of environmental variability and demographic stochasticity, but we are not aware of any study that has addressed this key point systematically through a combination of spatially explicit and quantitative modelling techniques. Also, comparisons of species richness and community structure along urban gradients have often been conducted without clarifying the relative contributions of different potential drivers (e.g., intrinsic spatial processes vs. spatially structured environmental gradients vs. the effects of biotic interactions).

To address these topics, we analysed the community structure of oribatid mites, one of the most diverse, abundant and important groups of soil fauna (Caruso et al., 2012; Maraun et al., 2011). We adopted a spatially explicit sampling design to account for patterns in community structure at multiple scales and measured several soil and microbiological properties that could potentially structure the mite assemblage (Rota et al., 2013, 2014a, 2014b). We partitioned the relative effects of spatial processes, gradients in soil chemistry, pollutants, and microbiological variables to identify the main drivers of community structure. As we found strong spatial structure at the site scale and sites are fairly disconnected in urban gardens and parks (i.e. fragmentation), we completed the analysis with a neutral model, so to test whether patterns of beta diversity were consistent with stochastic assembly processes and/or showed the signature of disturbance (Dornelas et al., 2006; Etienne, 2007; Maaß et al., 2014).

2. Material and Methods

(a) Sampling and data collection

We surveyed holm oak (*Quercus ilex* L.) stands in two Italian cities, Siena and Naples, in 2009 (Figure S1. Supplementary Information *a* and *b*). Holm oaks form typical urban woodland in Mediterranean countries and in many urban gardens and park are used as ornamental trees. In many habitats at these latitudes, the hot, dry summer climatic pattern forces drought-vulnerable soil animals to either adjust their life cycle timing or to migrate to deeper soil layers. The undisturbed floor of evergreen sclerophyllous forests, however, can provide some protection against harmful climate events through a multi-layered, organic topsoil compartment, offering to a diverse pedofauna moist microhabitats throughout the year. We sampled this habitat twice: in spring and autumn 2009. The two sampling points in time were selected to sample over a period of high biological activity and also to maximize the range of weather conditions, from spring rains at increasing temperature, to the summer drought, and then the first rains of the autumn. Water is in fact known to be a key factor regulating oribatid mites communities (Lindberg et al., 2002; Tsiafouli et al., 2005). In this way we aimed to obtain a comprehensive estimate of species richness. In each city, three urban sites were located at increasing distance from a heavily trafficked road in an attempt to capture a disturbance gradient related to vehicular pollution (e.g. metals, PAHs; see below), with 10 meters separating the road from the closest sampling site and an average distance of 100 meters between adjacent sites in each city (Figure S1). The control site was located in the outskirt of the city ("suburban"), in a location not impacted by vehicular traffic. The sites were selected trying to maximise the disturbance gradient but minimise possible differences in soil properties such as bulk density, organic matter, and ages of stands. In terms of age, all sites have been established for more than three decades but the control sites were also overall less disturbed in terms of trampling or tree management. Sites understory was consistent between all sites and by far dominated by species in the genera *Hedera* and *Ruscus* with some occasional presence of *Prunus*, *Lamium* and *Tradescantia species*

Ten samples (10 x 10 x 5 cm) were randomly collected in a 5 by 5 m plot within each site, with 5 samples collected in the spring and 5 in the autumn, for a total of 80 samples analysed in this study. Soil depth was capped at 5 cm as in urban plots 5 cm was the average depth of the organic horizon. The UTM position of each of the 80 samples was recorded to treat each sample

as a community replicate, which allowed an explicit analysis of the spatial dependence between replicates but also between sites and cities (Caruso et al., 2012; Maaß et al., 2014; see also below and details in Supplementary Information d). Key soil variables were however used in statistical analysis to control for between sites variability in underlying pedological and biotic (e.g. understory such as mosses) features. Specifically, soil samples were analyzed for texture, pH, organic matter, water holding capacity, consistence, elemental concentrations (Al, Cd, Cr, Cu, Fe, Ni, Pb, Zn; by ICP-EAS and GFAAS), Polycyclic Aromatic Hydrocarbons (PAHs, by GC-MSD), and the EDTA extractable fractions of Cu, Pb, Zn and Ca. Elements such as Pb and Cd, and PAHs were quantified to account for the pollution generated by the vehicular traffic. Ergosterol and PLFAs were analysed to estimate the biomass of fungi, bacteria and actinomycetes, while FDA-hydrolysis and β-glucosidase activities and the catabolic evenness (CE) were used to measure microbial community functioning). Details on the methods are given in Supplementary Information *c* and *d* and references therein). Oribatid mites were extracted using a modified Berlese-Tullgren apparatus and counted and identified to the species level using Weigmann (2006) and a number of specialised publications cited at the end of Table S1, in the Supplementary Materials.

(b) Statistical analysis and neutral model of beta diversity

Soil and microbiological data were analysed with Principal Component Analysis (PCA) to extract non-collinear predictors of oribatid mite community structure (Supplementary Information *d*). Here we used microbiological data as a predictor of oribatid mite community structure given that fungi and bacteria provide resources to many, although not all, species in this assemblage. However, oribatids, too, affect microbiota by consuming or interacting with it and we thus interpret microbiological properties as a generic correlate more than a factor regulating oribatid mites unidirectionally.

In order to work on ecologically meaningful distance metrics and ensure no inflation of the weights of rare species, we Hellinger-transformed community data before RDA and variance partitioning (Legendre and Gallagher, 2001): in fact RDA is based on PCA and thus Euclidean distance, and the Hellinger-transformation removes the issues caused by using Euclidean

distance as an ecological distance metrics. Accordingly, we used principal coordinate analysis (PCoA) of Hellinger-transformed data to illustrate patterns of community structure. We also used the well established Principal Coordinate analysis of Neighbour Matrices (PCNM; Borcard and Legendre, 2002) to account for spatial structure at multiple scales in the sampling design, which aims to capture spatial structure in the species assemblage. The method is applied to the sample distance matrix and produces a number of eigenvectors (PCNMs) that account for the spatial patterns solvable by the sampling design in terms of extent (span of the study area), interval (average distance between two samples) and grid (full details: Supplementary Information *d*). In PCNMs, we also included sampling time as a covariate so to statistically control for potential and confounding differences in species distribution between the two sampling times. Variance partitioning and permutational approaches were used to quantify and test the effects of each factor (space and time as PCNMs, soil, microbiology) while statistically controlling for the other factors. Oligochaetes, especially earthworms, have been hypothesised to affect the soil oribatid mite community structure by the mechanical perturbation they create with their borrowing activity, with the effect weaker in forests, where earthworms are usually not very abundant (Maraun et al., 2003). Accordingly, earthworms were present in very low abundance in our holm oak woodlands, especially when compared to enchytraeids. In two previous publications, we analysed the community structure of enchytraeids collected at the same sampling sites (Rota et al., 2014a, 2013). Here, we also tested the hypothesis that the oribatid mite and enchytreid assemblages might correlate due to the multitude of biotic interactions that link all animal taxa in complex soil food webs. To test this hypothesis robustly, we removed all the effects that spatial and environmental factors had on the variance of the oribatid mite and enchytraeid matrices and then correlated the residuals of the two soil animal groups matrices using a Mantel test.

Species richness was estimated using individual-based rarefaction curves (Gotelli and Colwell, 2001). There are many definitions of beta diversity but here we used the general one provided by Legendre and De Cáceres (2013), i.e. the total variance of the species by sample matrix, after Hellinger-transformation. When applied to properly transformed abundance data, this variance accounts for species turnover and changes in relative abundances from sample to sample. Given

the spatial patterns observed in the data, we calculated this type of beta diversity for each of the eight sites and then fitted a neutral model to the community structure of each site so to create a null distribution of beta diversity values under the assumption of neutrality (Maaß et al., 2014). The observed value can then be compared to the null distribution. The neutral model was fitted using a formula for multiple samples with a PARI/GP code (Etienne, 2007), and the PARI/GP function urn2.gp (Etienne, 2007) was used to simulate 4999 neutral communities (details in Supplementary Information *e*).

3. Results

A total of 34,228 individuals and 124 species of oribatid mites were found (Supplementary Information, Table S1) while sample species richness ranged from 17 to 47 species, with a median and a mean of 29 species. When controlling for the number of sampled individuals, the total site species richness of control woodlands was on average slightly higher than that of urban parks but overall confidence limits of rarefaction curves suggest that differences in some case were only marginally or just not statistically (Naples) significant (Figure 1).

All factors analysed in the study plus their shared variation (i.e. covariation) could account for 22% of community variance (Table 1), but the unique effects of abiotic soil properties (including the effects of pollutants such as PAHs, Pb and Cd), space (PCNMs) and microbiological gradients were low while all statistically significant at $p < 0.01$. An ordination plot (Figure 2) of individual samples clarifies these patterns: both in Siena and Naples, samples clearly clustered by sites, which implies spatial structure in the assemblages due to changes in species distribution from site to site. In Siena, differences between sites were clearer than in Naples (compare ellipsoid overlaps). Yet, both in Siena and Naples there were not clear directional effects of factors such as increasing distance from traffic road or a clear separation between control and urban sites.

Given the clear spatial structure observed at the site scale but not clear patterns between sites, we tested whether beta diversity within each site was compatible with purely stochastic dynamics. Results were consistent with a neutral model (Figure 3) of community dynamics, that is site assemblages have neither significantly higher nor significantly lower beta diversity than

expected under neutral assembly. We then removed all effects due to soil, microbiological properties and spatial and temporal autocorrelation for both the oribatid mites of this study and the enchytraeid assemblage investigated in the same sites in two other studies (Rota et al., 2014a, 2013). We used a mantel test to correlate the resulting residual variation in the oribatid mites and enchytraeids and obtained a correlation coefficient r = 0.16 and a p value <<0.05, suggesting a significant and robust link between the two assemblages.

4. Discussion

As recently observed in urban microbial communities (Ramirez et al., 2014), our results also show that, at local scales, urban oribatid mite communities can be as rich in species as their controls in suburban woodlands, which is surprising given the potential of urban conditions (pollution, physical disturbance) to negatively affect natural populations. Intriguingly, at the same scales patterns of beta-diversity did not differ across urban and control sites, and were consistent with a stochastic assembly process involving random population fluctuations and dispersal (Hubbell, 2001; Rosindell et al., 2012). Our results may at first seem difficult to explain: urban environments impose high levels of physical and chemical disturbance, which should strongly structure communities. Some qualitative observations on species autoecology (see table S1 for references) would actually suggest that the assemblage is structured towards a generalist oribatid mite composition: most of the collected species (e.g. *Aphelacarus acarinus, Sphaerochthonius splendidus, Mesoplophora michaeliana, Sellnickochthonius meridionalis, Phthiracarus boreosetosus, Licnodamaeus pulcherrimus, Tectocepheus sarekensis, T. velatus, Microppia minus, Oribatula tibialis, Chamobates subglobulus, Ceratozetes elongatissimus*) are typical of thermophilous woodlands and fairly ubiquitous, and some are known to have great adaptive capabilities and high reproductive rates. Also, and not surprisingly given the caonpy offered by holm oak, we found some mesophilous and muscicolous species such as *Carabodes* species, *Platyliodes scaliger*, *Belba corynopus*, *Rastellobata rastelligera*, *Quadroppia pseudocircumita*, *Suctobelba trigona*, *Parachipteria petiti*, and *Pergalumna myrmophila*.

The fact that at the site scale a neutral model fits the data well does not demonstrate that the mechanisms assumed by the model are the only ones responsible for community structure in

general (Clark, 2012; Rosindell et al., 2012). Actually, variation in soil physico-chemistry, pollution (e.g. PAHs) and microbiota have statistically significant effects that partially cause differences between sites. Also, when we removed all effects accounted for physico-chemistry, pollution (e.g. PAHs) and microbiota, we could still find a significant correlation with another animal assemblage (enchytraeids), which reasonably suggests a potential role for biotic interactions with other soil animal taxa. Still, all these effects, while statistically significant, accounted for very low variance, despite the high number and diversity of potential predictors measured in this study, including biotic factors.

In urban parks, sites such as a small flower bed, tree stands, or isolated allotments form an archipelago-like landscape for biological communities (Bolger et al., 2000; Savage et al., 2015), especially for small soil organisms with limited dispersal abilities (Ettema and Wardle, 2002). This habitat configuration creates metacommunities (Leibold et al., 2004), whose connectivity, species spatial turnover and diversity of species may, in the first instance, be simply approximated by random dispersal and drift dynamics (Rosindell et al., 2012). Especially at the site level, oribatid species populations may be modelled as stochastically fluctuating populations while their local diversity is in balance between immigration and extinctions: our results are consistent with this hypothesis in terms of beta diversity patterns. Some faunistic observations also seem to confirm the potential role of isolation and occasional colonization events in shaping the investigated urban assemblages. For example, in Naples we found species that are rare in the Italian peninsula, such as *Papillacarus pseudoaciculatus*, *Lopheremaeus laminipes*, *Microzetes castrii*, *Amerus troisii*, *Berniniell*a (*Hypogeoppia*) *hypogea*, *Oribatella brevicuspidis* and even *Siciliotricus siculus*, which was so far known only from Sicily. *Lopheremaeus hispanicus*, collected in Naples urban parks, is a species that was so far known only from Andalucia (Spain) and three populations in the genera *Thamnacarus*, *Protoribates* and *Xyphobates* probably belong to species new to science. These data support the idea that isolation and dispersal limitation can profoundly shape the structure of urban soil assemblages over time while results also suggest that community structure is also changing, in response to changes in environmental and biotic variables, including pollutants, although the effect of these variables is neither strong nor always clear.

Oribatid mites show that soil communities of urban areas can be highly rich and stochastic at local scales while partially controlled by environmental and biotic factors at larger scales. We propose that the source of local stochasticity is in the fragmentation and disturbance regimes typical of urban areas, and therefore, we interpret urban local soil communities as islands highly subjected to extinction and immigration processes. The isolation between those islands may increase beta diversity at some scale but can expose local population to extinction and communities to unpredictable dominance of a few opportunistic species, which may alter interactions between soil fauna and microbes and so soil functioning.

Acknowledgements

This research was supported by a grant from MIUR (PRIN -2007AH8KT8). TC was also supported by the project SENSE (EC FP7 - 631399 - SENSE).

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Table 1. RDA-based (after Hellinger transformation) variance partitioning of the several sources of variation in the oribatid mite community. Effects were divided into unique effects, tested while controlling for all others effects. The significance of shared effects cannot be tested (Legendre and Legendre, 1998). The total (22%) is the sum of unique (3+3+2) and shared (6+6+2) effects.

Source	Variance (%)	P-value
Unique Effect		
Soil properties (chemico-physical variables, pollutants)	3	<0.01
Microbiology	3	<0.01
Spatial factors + time (PCNMs)	2	<0.01
Shared (sensu Legendre and Legendre, 1998)		
Soil properties-Microbiology	6	n.t.
Soil properties-PCNMs	6	n.t.
PCNMs-Microbiology	2	n.t.
Total	22	

Figure captions

Figure 1. Individual-based rarefaction curves providing unbiased estimates of species richness in holm oak locations in urban parks (urban 1, 2, and 3) and suburban holm oak woodland (control) in Siena (a) and Naples (b). The grey shade areas represent confidence limits around the mean (solid line).

Figure 2. PCoA ordination of individual samples (empty circles) of the oribatid mite community from Siena (left panel) and Naples (right panel) urban parks. Samples were clustered by site using the function ordispider of the R package vegan. In each city, there were one control site (i.e. not impacted by vehicular traffic) and three urban plots at increasing distance from a traffic road: plot urban 1 was closer to the road, urban 3 was farther, and urban 2 was between urban 1 and 3. Ellipsoids around the site centroids are 95% confidence interval, which were drawn using the ordiellipse function of the R package vegan.

Figure 3. Histograms show the null distribution of simulated beta diversity values. Simulations were based on the estimate of neutral parameters from the species abundance distribution of the multiple samples collected in each site (six urban sites potentially impacted by a traffic road and 2 suburban sites taken as a control). The analysis was conducted within each urban site (6 sites) and control site (2 sites) and results were similar across all sites. Here we show the two control sites and two (one per city) out of 6 urban sites. The red line is the observed site beta diversity, defined as the total variance of the Hellinger transformed species matrix. The results show that observed site beta diversity lies always higher than the central tendency of the null distribution, but in no case it is significantly different from the null distribution (the red line falls well inside 95 % of the distribution).