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.

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 organisms (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,b). 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

2.1. Sampling and data collection

We surveyed holm oak (*Quercus ilex* L.) stands in two Italian cities, Siena and Naples, in 2009 (Fig. S1. Supplementary information *a* and *b*). Holm oaks form typical urban woodland in Mediterranean countries and in many urban gardens and parks 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 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 m separating the road from the closest sampling site and an average distance of 100 m between adjacent sites in each city (Fig. 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 ($10 \times 10 \times 5$ 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.

2.2. 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 so 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 (Rota et al., 2014a), 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 enchytraeid 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