European Journal of Soil Biology 82 (2017) 98–107

Contents lists available at ScienceDirect

European Journal of Soil Biology

journal homepage: http://www.elsevier.com/locate/ejsobi

Complex effects of precipitation and basal resources on the trophic ecology of soil oribatid mites: Implications for stable isotope analysis

Nereida Melguizo-Ruiz [a, b, *], Gerardo Jiménez-Navarro [a, b], Sarah L. Zieger [c], Mark Maraun [c], Stefan Scheu [c], Jordi Moya-Laraño [a]

[a] Estación Experimental de Zonas Áridas, Functional and Evolutionary Ecology, Consejo Superior de Investigaciones Científicas (CSIC), Carretera de Sacramento, s/n, La Cañada de San Urbano, 04120 Almería, Spain

[b] CIBIO/InBio-UE Research Center in Biodiversity and Genetic Resources, University of Évora, 7002-554, Évora, Portugal

[c] J.F. Blumenbach Institute of Zoology and Anthropology, Animal Ecology, Georg August University Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

ARTICLE INFO

Article history:
Received 7 November 2016
Received in revised form
6 February 2017
Accepted 22 August 2017
Available online 21 September 2017

Handling editor: Thibaud Decaens

Keywords:
Oribatida
Stable isotopes
Trophic ecology
Rainfall
Basal resources
Calibration

ABSTRACT

Given the relevant role played by soil organisms in fundamental ecosystem processes, current ecological research stresses the importance of understanding the trophic structure of soil communities in order to better predict the effects that global environmental change can have on the soil food web structure and dynamics. Using stable isotope analysis, we examined the trophic ecology of six soil oribatid mite species present in the leaf litter of beech forests which mainly differed in mean annual precipitation. We explored the relationship between animal and leaf litter signatures to determine which of the two approaches, conventional calibration or a novel solution we offer using statistical control (i.e., isotopic signature of the basal resource included as a covariate in the model), is more adequate to evaluate the trophic structure of soil communities across different sites, and investigated if the trophic niches of the species varied under two different precipitation regimes. The trophic position of some species varied with rainfall; the observed enrichment in ^{15}N in dry forests reflects trophic and spatial shifts probably resulting from changes in microbial activity and community composition. In addition, we find interactive effects between precipitation and the basal resource for some species and a lack of correlation between resource and oribatid mite stable isotope values for others. We discuss the pertinence of using conventional data calibration as it appears to mask relevant trends regarding the trophic ecology of oribatid mite species, and suggest using statistical control (a covariate approach) instead.

1. Introduction

Soil animals directly and indirectly affect nutrient availability in soils, e.g. by changing abiotic conditions and microbial activity, thereby altering plant growth [1–5] and ecosystem productivity [6,7]. In view of the current global diversity decline, understanding the trophic structure of soil communities is of crucial importance to estimate and anticipate the effects of global environmental change on the functioning of soil food webs and on terrestrial ecosystems in general [6,8–11].

Beech (*Fagus sylvatica*) forests of NW Spain are in the south-western most limit of the distribution for the species, where changes in temperature and precipitation patterns have been proposed to affect their decline in the last decades [12,13]. Regardless of the well-known linkage between precipitation and the functioning of terrestrial ecosystems [14,15], and the positive effects of precipitation on primary producers, consumers and decomposers [16,17] and references therein [15], little is known on the effects that altered precipitation can have on the functioning of the soil ecosystem (i.e., the consequences of altered rainfall patterns on the configuration of soil food webs, their trophic ecology, and their role in decomposition and nutrient turnover). Furthermore, water is one of the most indispensable resources which frequently becomes a limiting factor [18,19], but its role in structuring soil communities remains poorly known [20]. Soil moisture essentially drives microbial activity and biomass as well as invertebrate activity and their interactions with microorganisms [21–24]. Moreover, it has been proposed that precipitation alters ecosystem processes such as decomposition and nutrient cycling [20,25]. Indeed, water

* Corresponding author. CIBIO/InBio-UE Research Center in Biodiversity and Genetic Resources, University of Évora, 7002-554, Évora, Portugal.
E-mail address: nereidamelguizoruiz@gmail.com (N. Melguizo-Ruiz).

http://dx.doi.org/10.1016/j.ejsobi.2017.08.008
1164-5563/

availability determines species diversity and abundance in terrestrial ecosystems [26], and a strong correlation between rainfall and invertebrate abundance has been documented in beech forest soil food webs [27]. Water availability also drives the spatial distribution of taxonomic, functional and trophic groups of soil invertebrates [27–30]. Therefore, changes in precipitation and soil moisture are likely to strongly impact the structure and functioning of soil communities and their associated ecosystem processes [e.g. Refs. [31,32].

Oribatid mites (Oribatida) are often numerically the dominant group of arthropods in temperate forests soils, with densities ranging from 20,000 to 100,000 individuals per m^2 [33,34] and about 10,000 described species [35]. As they predominantly feed on decomposing plant material and fungi [36–38], but see Ref. [39], they represent a fundamental fraction of the decomposer community [38], although opportunistic predation and scavenging are probably underestimated. In beech forests of northern Spain, the abundance of oribatid mites comprises between 17 to 37% of the total abundance of soil arthropods (Melguizo-Ruiz, N. and Moya-Laraño, J. *unpublished data*). These mites are an ideal group to investigate the factors affecting the soil animal community structure, as their population dynamics have been shown to be influenced by both density-independent [40,41] as well as density-dependent factors [42,43]. The diversity of oribatid mite communities varies among habitats [44], although the soil predictors responsible for their variation in space are little understood. Moreover, while it has been assumed that oribatid mites are generalist feeders [45,46], recent studies have shown that their trophic niches differ markedly [38,47,48]. Also, although it has been proposed that the trophic position of oribatid mite species remains constant across different forests [38,49], spatial variability in trophic niche has been little explored thus far (but see Ref. [50]). Further, the actual food resources responsible for the observed niche constancy of oribatid mite species still remain little understood [11,38].

Progress in determining trophic niches of soil animal species and progress in understanding the high diversity and complexity of soil animal communities [51] is closely associated with the use of relatively novel methodologies, such as fatty acid analysis [52–55], molecular gut content analysis [56–59] or stable isotope analysis [38,48,60]. Among these methods, the analysis of natural variations in stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) is the most commonly used technique providing an integrative view of the trophic position of consumers in the long term and insights into the trophic structure of soil animal food webs [48,60–62]. Generally, consumers are enriched in ^{15}N by on average 3.4 δ units relative to their food source [63–66]. In contrast, fractionation of ^{13}C is lower, averaging ~0.4 δ units per trophic level [65,66], and therefore is of little use to determine the trophic structure of communities [67], but allows to trace the resources of consumers that differ in delta ^{13}C values [68,69].

Despite the major step forward that stable isotope analysis has entailed for disentangling the structure of soil food webs, there are still open challenges to this approach. In particular, when comparing food webs across different habitats one of the most critical issues is the calibration of stable isotope signatures [65,66,70,71]. The need for calibration usually arises because $\delta^{15}N$ and $\delta^{13}C$ values of basal resources vary significantly between habitats and ecosystems, resulting in correlated variations in $\delta^{15}N$ and $\delta^{13}C$ values of consumers [65,72,73]. However, results may differ across studies and organisms. For instance, a recent study showed how $\delta^{15}N$ values of soil macrofauna can be predicted based on the $\delta^{15}N$ values of plant litter, while this was not the case for $\delta^{13}C$ values [74]. In terrestrial ecosystems and especially in soil food webs, leaf litter, fine roots or primary decomposers have been used to calibrate stable isotope signatures of soil animal species and this has been shown to effectively reduce variations in stable isotope ratios of soil animals between habitats [49,50]. However, in spite of the potential to control for basal resources using calibration, spatial variability in the activity and diversity of fungi and bacteria, which could differently affect the signature linking roots or litter to the decomposer animal community, has been little considered. In fact, given the scarcity of studies focusing on the spatial variation of soil microbial communities (but see Ref. [75]), further research is needed to substantiate previous findings and to explore the factors responsible for spatial variation in stable isotope ratios of soil animal species (whether these are directly affected by microbiota as foraging resources or indirectly via abiotic factors, such as humidity and rainfall).

However, conventional calibration may actually not be appropriate if it does not fit the purpose (e.g., comparison of animal signatures across environments accurately controlling for variability of basal resources among these environments). We here propose a fresh and alternative view on how to control for variation in basal resources by using statistical control (aka partial effects) in multiple regression and its extension to General and Generalized Linear Models [76–79]. The relevance of this approach lays on the fact that the environment is made statistically constant (i.e., variability is controlled for by the so-called covariates), to test hypotheses about target predictors even though the habitat may show strong variation in its original gathered data. For the purpose of controlling variability in basal resources, including the signature of the basal resources as an additional (accompanying) covariate in the model ensures that one tests for the remaining predictors as if the basal resources were all the same among replicates, and most importantly, as if the basal resources had an identical constant effect on the dependent variable (e.g., the animal signatures). Notice that such an approach would always fit the purpose of controlling the variability of isotopic signatures in basal resources regardless of how much variation there is.

The overall objective of this study was to investigate the variation in the trophic structure of the decomposer community in forest systems under two different precipitation regimes by focusing on oribatid mites, as this group has been studied most intensively, as well as to show the usefulness of using statistical control when compared to conventional calibration. First, to elucidate changes in trophic niches with soil moisture, we tested if the isotopic signatures of the oribatid mite species varied with precipitation, by analyzing the $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios of six abundant oribatid mite species and leaf litter of eight beech forests in NW Spain, which mainly differed in mean annual precipitation or MAP (four of them were drier with MAP ranging between 1000 and 1200 mm/year, and the other four were wetter, with MAP ranging between 1400 and 1500 mm/year). Previous studies have found a negative correlation between plant and soil $\delta^{15}N$ values and MAP (e.g., Ref. [80]), meaning that the leaf litter of rainier sites will be depleted, while the drier ones will be enriched in the heavier N isotope. Moreover, in forests with lower MAP, the surface leaf litter layers may dry up more often and may have relatively lower nutrient availability and different species of microorganisms, better adapted to dry conditions, and therefore the trophic niches of oribatid mites can potentially track such changes in microbial communities. Further, many soil animals – especially smaller ones that are more sensitive to desiccation – tend to avoid drier surface horizons, and prefer moister and more profound layers [81]. Downground migration has been proposed to be a survival strategy under lowered soil moisture conditions during dry periods, and several invertebrates with different body sizes, including collembolans [82], or enchytraeids [83], have been shown to take refuge in wetter areas such as deeper leaf litter layers or moist woody structures