Soil Biology & Biochemistry xxx (2015) 1–15

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species

Q3

Q2

Kevin E. Mueller [a, *], Nico Eisenhauer [b, c, d], Peter B. Reich [d, e], Sarah E. Hobbie [f], Oliver A. Chadwick [g], Jon Chorover [h], Tomasz Dobies [i], Cynthia M. Hale [j], Andrzej M. Jagodziński [i, k], Izabela Kałucka [l], Marek Kasprowicz [m], Barbara Kieliszewska-Rokicka [n], Jerzy Modrzyński [o], Anna Rożen [p], Maciej Skorupski [i], Łukasz Sobczyk [p], Małgorzata Stasińska [q], Lidia K. Trocha [k], January Weiner [p], Anna Wierzbicka [i], Jacek Oleksyn [d, k]

[a] Rangeland Resources Research Unit, Agricultural Research Service, Fort Collins, CO, USA
[b] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[c] Institute of Biology, Leipzig University, Leipzig, Germany
[d] Department of Forest Resources, University of Minnesota, St. Paul, MN, USA
[e] Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, Australia
[f] Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN, USA
[g] Department of Geography, University of California, Santa Barbara, CA, USA
[h] Department of Soil, Water and Environmental Science, University of Arizona, Tucson, AZ, USA
[i] Department of Game Management and Forest Protection, Poznań University of Life Sciences, Poznań, Poland
[j] The Natural Resources Research Institute, University of Minnesota Duluth, Duluth, MN, USA
[k] Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland
[l] Department of Algology and Mycology, University of Łódź, Łódź, Poland
[m] Department of Plant Ecology and Environmental Protection, Adam Mickiewicz University, Poznań, Poland
[n] Institute of Environmental Biology, Kazimierz Wielki University, Bydgoszcz, Poland
[o] Department of Forest Sites and Ecology, Poznań University of Life Sciences, Poznań, Poland
[p] Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland
[q] Department of Botany and Nature Protection, University of Szczecin, Szczecin, Poland

A R T I C L E I N F O

Article history:
Received 6 May 2015
Received in revised form
5 October 2015
Accepted 13 October 2015
Available online xxx

Keywords:
Microarthropods
Mites
Nematodes
Beetles
Acidity
Nutrients

A B S T R A C T

Management of biodiversity and ecosystem services requires a better understanding of the factors that influence soil biodiversity. We characterized the species (or genera) richness of 10 taxonomic groups of invertebrate soil animals in replicated monocultures of 14 temperate tree species. The focal invertebrate groups ranged from microfauna to macrofauna: Lumbricidae, Nematoda, Oribatida, Gamasida, Opilionida, Araneida, Collembola, Formicidae, Carabidae, and Staphylinidae. Measurement of invertebrate richness and ancillary variables occurred ~34 years after the monocultures were planted. The richness within each taxonomic group was largely independent of richness of other groups; therefore a broad understanding of soil invertebrate diversity requires analyses that are integrated across many taxa. Using a regression-based approach and ~125 factors related to the abundance and diversity of resources, we identified a subset of predictors that were correlated with the richness of each invertebrate group and richness integrated across 9 of the groups (excluding earthworms). At least 50% of the variability in integrated richness and richness of each invertebrate group was explained by six or fewer predictors. The key predictors of soil invertebrate richness were light availability in the understory, the abundance of an epigeic earthworm species, the amount of phosphorus, nitrogen, and calcium in soil, soil acidity, and the diversity or mass of fungi, plant litter, and roots. The results are consistent with the hypothesis that resource abundance and diversity strongly regulate soil biodiversity, with increases in resources (up to a point) likely to increase the total diversity of soil invertebrates. However, the relationships between various resources and soil invertebrate diversity were taxon-specific. Similarly, diversity of all 10

* Corresponding author. 1701 Center Avenue, Fort Collins, CO 80526, USA. Tel.: +1 970 492 7126; fax: +1 970 492 7160.
E-mail address: kevin.e.mueller@gmail.com (K.E. Mueller).

http://dx.doi.org/10.1016/j.soilbio.2015.10.010

invertebrate taxa was not high beneath any of the 14 tree species. Thus, changes to tree species composition and resource availability in temperate forests will likely increase the richness of some soil invertebrates while decreasing the richness of others.

1. Introduction

Soils house a large proportion of species on Earth and soil biota, including invertebrate animals, contribute to ecosystem services via their key role in processes like decomposition and nutrient cycling (Anderson, 1975; Giller, 1996; Wardle, 2002; Decaëns, 2010). Yet, uncertainty regarding the fundamental controls of soil animal diversity makes it difficult to explain the enormous diversity of soil animals (Maraun et al., 2003) or predict how soil animal communities will change as the environment continues to change (Sylvain and Wall, 2011; Bardgett and van der Putten, 2014). Knowledge of soil animal diversity remains limited, to a great extent, because very few studies have simultaneously assessed diversity of many types of soil animals; this is due to the number and complexity of methods needed to study such cryptic organisms (Sylvain and Wall, 2011). Up to the present, even the more comprehensive surveys of soil organisms (e.g. van der Wal et al., 2009; Scherber et al., 2010; Postma-Blaauw et al., 2012) typically survey less than half of the taxonomic groups (families, orders, or classes) that represent common types of soil invertebrates (Bardgett and van der Putten, 2014). Since land management often occurs within local and regional scales, effective conservation of soil biodiversity and management of ecosystem services requires more information on the controls of soil biodiversity at those scales. More specifically, to maintain or increase soil biodiversity at these scales, land managers must have *quantitative* knowledge of how soil biodiversity is influenced by the ecological factors associated with management practices, including characteristics of vegetation, soil properties, and microclimatic conditions.

The species composition of plant communities is one ecological factor that impacts soil animal communities, likely because plant community composition shapes the diversity and abundance of resources available to soil animals (Sylvain and Wall, 2011). When comparing zones of influence beneath single plants, monocultures, and/or mixed-species communities, plant species often have divergent impacts on the diversity of soil animal communities; this "plant species identity" effect is often larger than effects of plant species richness (Wardle et al., 2003, 2006; De Deyn et al., 2004; Ball et al., 2009; Eissfeller et al., 2013b). Thus, as plant community composition shifts in response to global environmental changes (Iverson et al., 2008; Garbelotto and Pautasso, 2012) and management practices (Augusto et al., 2002; Fox et al., 2007), there will be corresponding impacts on the diversity of soil animals. Yet, the tremendous diversity of plant species also makes it difficult to widely estimate the impact of plant species and plant community composition on soil animal diversity. Given practical constraints on the number of plant species and communities that can be studied, a predictive framework of plant impacts on soil animal diversity must be based on studies that encompass a relatively small number of plant species. Development of such a predictive framework requires a better understanding of which ecological factors mediate the impact of plant species on soil animal diversity, including plant functional traits and various characteristics of plant communities and soils. Previous studies indicate that two general factors are most likely to mediate the effect of plants on soil animal diversity: resource availability and resource diversity (Hooper et al., 2000; Wardle, 2006). In this context, one must not only consider plant effects on metabolic resources, such as substrates for energy production and mineral nutrients, but also plant effects on other ecological factors that further shape soil habitats and niche space, including the presence and abundance of ecosystem engineers (Lavelle et al., 1997; Eisenhauer, 2010), microclimatic conditions, and general soil properties.

Theoretical and empirical studies support the idea that plant impacts on soil animal diversity will be determined by how plants affect the quantity and diversity of soil resources (Hooper et al., 2000). As the *quantity* of resources increases, the diversity of soil animals is expected to increase through at least intermediate levels of resource availability because of higher population densities and thus lower probability of local extinction (Bardgett, 2002). As resource availability increases to high levels, theory suggests that competitive exclusion could lead to declines in soil animal diversity; this could be exacerbated by constraints on niche differentiation among soil animals (Anderson, 1975; Maraun et al., 2003). However, a synthesis of available evidence suggests that competition does not have large impacts on many taxa of soil organisms, perhaps due to spatial or temporal niche differentiation (Wardle, 2002, 2006); but see (Giller, 1996; Decaëns, 2010). Several observational and experimental studies report a positive effect of resource availability on soil animal diversity (van der Wal et al., 2009; Mulder et al., 2012; Sayad et al., 2012). As the *diversity* of resources increases, diversity of soil animals is expected to rise due to enhanced opportunities for niche differentiation with respect to habitat use and sources of energy and nutrients (Anderson, 1978; Wardle, 2006; Coleman, 2008). Consistent with the hypothesis that resource diversity can mediate the impact of plant species on soil animal diversity, Eissfeller et al. (2013b) showed that oribatid mite diversity was higher beneath tree species that fostered development of more substantial organic horizons, perhaps because niche overlap was reduced by the increased depth, mass, and heterogeneity of the organic horizon.

Ecosystem engineers, such as earthworms, can influence diversity of other soil animals by regulating the availability, diversity, and spatial distribution of resources available to soil animals (Lavelle et al., 1997; Eisenhauer, 2010). Plants are expected to influence the presence and abundance of invertebrate ecosystem engineers, partly through variation of litter quantity and quality among plant species (Lavelle et al., 1997; Schwarz et al., 2015). Common garden experiments confirm this link; Reich et al. (2005) and Sayad et al. (2012) showed that variability of earthworm biomass across plantations of different tree species was positively correlated with the amount of calcium in leaf litter.

Similar to the role of ecosystem engineers, soil microclimate, and other general soil properties might regulate soil animal diversity in conjunction with plants through the links between these factors and soil resources or other niche dimensions. For example, soil pH is known to influence the relative abundance and diversity of soil bacteria and fungi (Mulder et al., 2005, 2009; Fierer et al., 2009) as well as the activity of soil enzymes (Sinsabaugh et al., 2008), which could cascade into bottom-up effects on soil animal diversity. Additionally, the metabolic activities of soil microbes and animals are sensitive to soil temperature, with potential