Soil Biology & Biochemistry xxx (2015) 1–13

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Review paper

Q4 How tree diversity affects soil fauna diversity: A review

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A R T I C L E I N F O

Article history:
Received 19 May 2015
Received in revised form
23 November 2015
Accepted 26 November 2015
Available online xxx

Keywords:
Microarthropods
Earthworms
Collembola
Springtail
Oribatid mites
Mixed stands

A B S T R A C T

In the context of sustainable forest management and climate change, increasing tree richness has been proposed as a possible strategy to reach both ecological and productivity goals. This review focuses on the effects of mixed stands and increasing tree richness on soil fauna in temperate forests. Effects on earthworm and microarthropod (Collembola and Oribatid Mites) species diversity and abundance and community structure are examined, and clues to the main factors affecting soil communities in these stands are proposed.

Our statistical analyses showed no evidence of any general trend for the effect of mixture either on earthworm or microarthropod diversity or on their abundance. Indeed, positive, negative and non-significant effects have all been reported. Nevertheless, the majority of the studies did find that increased tree richness or the introduction of broad-leaves had a positive effect. In addition, our review shows that soil organism abundance and diversity can be strongly affected by the presence of certain tree species and that the soil organism community structure is, in most cases, significantly affected by an increase in tree richness or by a mixing effect. Litter features appear to be important drivers of soil fauna community composition, while mixture effect seems to have less impact on soil biota. Soil fauna are directly affected by the physical characteristics (microhabitats) and chemical composition (resource quality) of the litter specific to each tree species. Soil communities are then indirectly affected by the subsequent humus characteristics. We conclude our review with some guidelines for forest management and further research.

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http://dx.doi.org/10.1016/j.soilbio.2015.11.024
0038-0717/© 2015 Published by Elsevier Ltd.

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1. Introduction

Soil biota plays an essential role in ecosystem functioning, especially in biogeochemical cycles (Petersen and Luxton, 1982; Hattenschwiler, 2005) with feedback on plant diversity, abundance, succession (Kardol et al., 2006; Bardgett and Van der Putten, 2014) and productivity (Chapman et al., 1988). Spatial patterns of soil biodiversity are shaped by a hierarchy of environmental factors, population processes and disturbances operating at different spatial and temporal scales (Wu et al., 2011; Bardgett and Van der Putten, 2014). At the landscape scale, Vanbergen et al. (2007) showed that habitat heterogeneity affects soil diversity regardless of taxon. Furthermore, at the local scale, soil fauna diversity and/or activity are controlled by both top-down (Ponette, 2010; Cesco et al., 2012) and bottom-up processes (Hattenschwiler and Gasser, 2005). However, correlations between diversity of aboveground and belowground organisms can be either positive, negative or non-significant – both locally and across larger biogeographical scales (Hooper et al., 2000). For forest ecosystems, it is known that management practices which influence stand composition, for example, can also affect soil fauna diversity and functioning (Farska et al., 2014) through both direct (litter quality) and indirect effects (microhabitats, environmental factors such as pH, radiation, soil humidity). For example, conversion from deciduous to coniferous stands affects soil communities through acidification and a modification of humus characteristics (Ponge and Prat, 1982; Zaitsev et al., 2014). Other rarely investigated factors related to specific tree traits like root morphology, root nutrient content (Lang and Polle, 2011) or root exudates may vary after conversion and therefore impact soil biota belowground.

In Europe, forested area consisting of a single tree species has decreased annually over the last 15 years, and today about 70 percent of European forests are dominated by two or more tree species (San-Miguel-Ayanz et al., 2011). Such stands are hereafter referred to as “mixed stands”, as opposed to “single-species stands” (also called “pure stands” or “monocultures”) such as spruce plantations. Mixed stands are composed of at least two species with the main species representing at least 80% of the total basal area, and with the basal area of the secondary species less than that of any one of the main species alone. Forest managers have been showing increased interest in mixed forest stands thanks to their better resistance to certain biotic disturbances (Jactel and Brockerhoff, 2007), their suspected better resilience to drought (Merlin et al., 2015), and, in many cases, their higher productivity compared to pure stands (Kelty and Larson, 1992; Pretzsch et al., 2010; Vallet and Perot, 2011). Mixed stands are also likely to host greater species diversity for plants and aboveground animals. The main studies to date on the effects of mixed stands on forest biodiversity have focused on vascular plants (Scherer-Lorenzen et al., 2005; Barbier et al., 2008; Cavard et al., 2011), but very few can be found on animals. There is limited evidence that mixed forest stands host a greater α-diversity of plants and animals. Indeed, aboveground diversity in mixed stands is rarely greater in terms of abundance and equitability than the diversity found in at least one of the pure stands (Cavard et al., 2011). In addition, tree species composition has also been described as a factor affecting plant diversity but only after canopy tree age and canopy stratification, (Gao et al., 2014). Diversity among canopy trees promotes the emergence of different microhabitats that can shelter different species (Cavard et al., 2011) and the identity of the tree in the mixture appears more important than diversity per se (Jactel and Brockerhoff, 2007; Cavard et al., 2011). Finally, literature on plants and above-ground animals reveal any species that was exclusively associated with mixed stands.

Very few studies have focused on the diversity of soil fauna in mixed stands (Scheu, 2005; Wardle et al., 2006), despite the huge diversity belowground and the essential role soil fauna plays in ecosystem processes like organic matter decomposition, nutrient mineralisation regulation and plant productivity, among others. Specific among soil organisms, earthworms are recognised ecosystem engineers (Lavelle et al., 1997). They are a major component of the decomposer fauna in many forest ecosystems (Lavelle and Spain, 2001). Through soil bioturbation (e.g. burrowing, casting and mixing litter), they influence the physical and chemical characteristics of the first soil layers (generally the first 30 cm) (Edwards and Bohlen, 1996; Decaëns et al., 2001). This has important consequences in terms of plant productivity and plant community structure (Partsch et al., 2006; Eisenhauer et al., 2009). Besides earthworms, smaller organisms (i.e. mesofauna and microfauna) also play crucial roles in soil systems (Petersen and Luxton, 1982; Hopkins, 1997). For example, among the mesofauna, microarthropods (mainly Collembola and mites) accelerate by 10–20% organic matter decomposition rates (Hattenschwiler and Gasser, 2005), associated to increases in carbon and to nitrogen loss (Handa et al., 2014). By depositing their faecal pellets in the soil, these microarthropods form nutrient-rich patches (Petersen, 2000; Wickings and Grandy, 2011). Soil organisms also directly interact with vegetation through root herbivory or parasitism or through mutualism (mycorrhiza fungi) (Wardle et al., 2004). They also indirectly affect plant nutrition by transporting fungal propagules (Lussenhop, 1992) and by releasing nutrients when they graze on microflora (Verhoef and Brussaard, 1990; Filser, 2002). However, the effects of tree richness on soil meso- and macrofauna diversity have rarely been studied and several unanswered questions remain:

- To what extent do mixed stands affect soil communities and soil processes (such as decomposition processes, nutrient cycles, etc.)?
- Is there a relation between tree richness and soil fauna diversity?
- What are the implications of soil communities and functioning changes in terms of forest stand vulnerability to climatic and biotic hazards and in terms of tree productivity?

Establishing a relationship between tree richness and soil fauna diversity is far from obvious since the difference in species number magnitude between the two communities is considerable (Scheu, 2005). Therefore, our first hypothesis is that no relationship between tree richness and soil fauna diversity will be found (hypothesis 1). On the contrary, the factors affecting soil fauna diversity, abundance and distribution are numerous and correspond to the physical, biological and chemical environment. Mixed stands should therefore affect soil communities differently compared to monospecific stands (the “mixture effect”). We raised the following hypotheses concerning mixture effect on richness and abundance of soil organisms: hypothesis 2, an additive effect: mixed stands could harbour higher diversity than corresponding pure stands because all the given species coexist in the mix (this could be the case for broadleaves mixed with conifers, for example); hypothesis 3: mixed stands could harbour an intermediate diversity between the two pure stand types (the diversity of the mixed stand would not exceed the diversity of the best of the pure stands); hypothesis 4: mixed stands might not shelter “endemic species” since the mixture would not provide a new niche compared to the pure stands. Given that two communities can show a similar richness (number of species) but have very different compositions (species and/or functional groups composing the community), we assessed the mixture effect on soil

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Please cite this article in press as: Korboulewsky, N., et al., How tree diversity affects soil fauna diversity: A review, Soil Biology & Biochemistry (2015), http://dx.doi.org/10.1016/j.soilbio.2015.11.024

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