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Plant species richness does not attenuate responses of soil microbial and nematode communities to a flood event

Daniela Wagner [a], Nico Eisenhauer [a, b, c, *], Simone Cesarz [a, b, c]

[a] Institute of Ecology, Friedrich-Schiller-University Jena, Dornburger Str. 159, 07749 Jena, Germany
[b] German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[c] Institute of Biology, University Leipzig, Johannisallee 21, 04103 Leipzig, Germany

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ABSTRACT

Human activities are causing climatic changes and alter the composition and biodiversity of ecosystems. Climate change has been and will be increasing the frequency and severity of extreme climate events and natural disasters like floods in many ecosystems. Therefore, it is important to investigate the effects of disturbances on ecosystems and identify potential stabilizing features of ecological communities. In this study, soil microbial and nematode communities were investigated in a grassland biodiversity experiment after a natural flood to investigate if plant diversity is able to attenuate or reinforce the magnitude of effects of the disturbance on soil food webs. In addition to community analyses of soil microorganisms and nematodes, the stability indices proportional resilience, proportional recovery, and proportional resistance were calculated. Generally, soil microbial biomass decreased significantly due to the flood with the strongest reduction in gram-negative bacteria, while gram-positive bacteria were less affected by flooding. Fungal biomass increased significantly three months after the flood compared to few days before the flood, reflecting elevated availability of dead plant biomass in response to the flood. Similar to the soil microbial community, nematode community structure changed considerably due to the flood by favoring colonizers (in the broadest sense r-strategists; c–p 1, 2 nematodes), particularly so at high plant diversity. None of the soil microbial community stability indices and few of the nematode stability indices were significantly affected by plant diversity, indicating limited potential of plant diversity to buffer soil food webs against flooding disturbance. However, plant diversity destabilized colonizer populations, while persister populations (in the broadest sense K-strategists; c–p 4 nematodes) were stabilized, suggesting that plant diversity can stabilize and destabilize populations depending on the ecology of the focal taxa. The present study shows that changes in plant diversity and subsequent alterations in resource availability may significantly modify the compositional shifts of soil food webs in response to disturbances.

1. Introduction

Human activities change environmental conditions globally and thereby alter the composition of ecological communities. One aspect of changing environmental conditions is the increased frequency and severity of extreme weather events, such as droughts and heavy precipitation events causing floods (IPCC, 2007; Kerr, 2007; Trenberth, 2011). As ecosystems are increasingly affected by environmental change, ecologists have been looking for ecosystem properties stabilizing communities and functions against disturbances and environmental fluctuations (McCann, 2000; Ives and Carpenter, 2007; Hautier et al., 2014; Wright et al., 2015).

Plant diversity is one such ecosystem property, which has been argued to stabilize (e.g., Tilman and Downing, 1994; Hautier et al., 2014) or destabilize community functions (e.g., Pfisterer and Schmid, 2002; Wright et al., 2015). Stabilizing effects mostly have been attributed to the dissimilarity of species' responses to environmental fluctuations ("insurance hypothesis"; Lehman and Tilman, 2000; McCann, 2000; Tilman et al., 2006; Yachi and Loreau, 1999) and the asynchrony of different species (De Mazancourt et al., 2013; Hautier et al., 2014). On the other hand, destabilizing effects were explained by elevated biomass

* Corresponding author. German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.
E-mail address: nico.eisenhauer@idiv.de (N. Eisenhauer).

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production at high biodiversity making those communities more responsive to alterations in resource availability (Pfisterer and Schmid, 2002; Wright et al., 2015). While empirical evidence and theoretical models mostly are based on plant diversity–primary productivity relationships, little is known about plant diversity effects on the stability of soil food webs (Milcu et al., 2010). In theory, more stable abiotic conditions and higher and more consistent plant-derived organic inputs to the soil at high plant diversity could potentially stabilize soil food webs (Milcu et al., 2010). On the other hand, however, stronger plant biomass responses to pulse perturbations at high plant diversity (Wright et al., 2015) may also cause decreased stability of soil food webs. Here, we test these conflicting hypotheses by exploring soil microbial community and nematode community responses to a severe natural flooding event in a grassland plant diversity experiment. This 200-year flood event in Central Europe developed due to heavy precipitation and led to severe floods in seven countries (Blöschl et al., 2013).

Floods lead to rapid changes in soil conditions and can cause the loss of existing biomass (Williamson and Wardle, 2007), reductions in soil nutrient availability, reduced mineralization and decomposition of dead organic material, limited soil gas diffusion, and inhibited absorption of oxygen into the soil (Schuur and Matson, 2001). As a consequence, anaerobic conditions develop fast in flooded soils (Visser and Voesenek, 2005), soil chemistry changes (Unger et al., 2010), and toxic substances for plants can accumulate in the soil (Schuur and Matson, 2001), which all might have significant effects on the composition of soil food webs.

Aboveground and belowground subsystems are closely linked as plants provide organic material to the decomposer community, which form the basis of soil food webs and, in turn, delivers nutrients by breaking down plant-derived material (Wardle et al., 2004). Higher plant diversity is supposed to increase the diversity and quantity of available dead organic matter in soil resulting in more niches and often higher biomass and diversity of soil organisms (Laakso and Setala, 1999; Hooper et al., 2000, 2012; Porazinska et al., 2003; Balvanera et al., 2006; Cardinale et al., 2011). Accordingly, plants have great effects on the composition and functioning of soil communities (Diaz et al., 2004).

Plant diversity may be able to buffer negative effects of floods on soil food webs (Fig. 1a) by providing more niches for soil organisms to coexist (Hooper et al., 2000; Chung et al., 2007). According to the insurance hypothesis, a higher diversity of soil organisms in high plant diversity communities (Scherber et al., 2010; Eisenhauer et al., 2013; Lange et al., 2015) may then represent a greater variety of responses to flooding, which could provide higher stability at the community level. Further, different plants have different strategies to withstand flooding disturbances, e.g., by aerating the soil and thereby maintaining activity (Voesenek and Bailey-Serres, 2013).

In contrast to the potentially stabilizing mechanisms above, however, a recent study by Wright et al. (2015) on impacts of a flood disturbance in the same grassland plant diversity experiment where this study was performed showed that increasing plant species richness can decrease the stability of plant communities during a disturbance (Fig. 1b). This study showed that an increase in plant productivity due to increased water and resource availability at low flood severity led to decreased stability in high diversity plots due to strong biomass changes, and therefore to a negative diversity–stability relationship. In addition, plant productivity was reduced most at high plant diversity and high flood severity, also causing a negative diversity–stability relationship, because higher plant diversity communities had 'higher to fall' in terms of biomass production (Pfisterer and Schmid, 2002; Wright et al., 2015). This increased variability of resource inputs to the soil at high plant diversity may have specific and destabilizing effects on different groups of soil organisms.

In this study we focus on the responses of soil microbial and soil nematode communities to variations in plant diversity and to flooding. While soil microorganisms (mostly bacteria and fungi) represent the functional backbone of most processes in soil (Van Der Heijden et al., 2008), nematodes cover all major trophic consumer levels and are involved in the decomposition of dead organic material, in the regulation of microbial activities, and nutrient cycling because of their different feeding strategies (Bardgett et al., 1999; Cortet and Vaufléry, 1999). Depending on their food, nematodes are closely related to other soil fauna, bacteria, fungi, or plants (Yeates, 1979; Bongers and Bongers, 1998; Cortet and Vaufléry, 1999; Neher, 2001). Therefore, nematodes are common indicators of soil health and used in ecological studies to investigate the functional composition of soil communities (Cortet and Vaufléry, 1999).

Flooded soils are associated with anaerobic conditions reducing the microbial biomass and changing soil microbial community structure (Unger et al., 2009). Aerobic microorganisms are replaced by facultative anaerobes and then by strict anaerobes (Yoshida, 1978). Monounsaturated fatty acids (often assigned to gram-negative bacteria) and fungi often decline when oxygen is reduced, whereas branched fatty acids (often assigned to gram-positive bacteria) were found to occur more often in anaerobic conditions (Sundh et al., 1997; Bossio et al., 2006; Tian et al., 2013) highlighting different functional responses of the microbial community. Further, it was shown that gram-negative bacteria are associated with the plant rhizosphere, whereas gram-positive bacteria predominate in bulk soil (Söderberg et al., 2004). It thus is likely that gram-negative bacteria will reflect changes in plant performance.

Given that soil microbial and nematode communities are strongly associated with plant communities and plant community productivity, we hypothesized that (1) the stability of these communities will decrease with increasing plant species richness in response to flooding (Fig. 1b; Wright et al., 2015). (2) Soil microbial community composition will change most likely due to the lack of oxygen in soil and altered resource availability (Reddy and Patrick Jr., 1975; Schuur and Matson, 2001; Unger et al., 2009). (2a) Gram-negative bacteria and fungi will be particularly negatively affected by anaerobic soil conditions, because they usually are found in well-aerated soil layers (Fig. 1c; Fierer et al., 2003). (2b) Gram-positive bacteria will be less affected by anaerobic soil conditions, because they occur in higher densities in deeper soil layers, where less oxygen is available (Fig. 1c; Fierer et al., 2003; Unger et al., 2009). (3) Nematode community composition will change due to alterations in soil oxygen levels and resource availability in soil. (3a) C–p (colonizer–persister) 1 and 2 nematode species will be less negatively affected by flooding because they can form dauerlarvae (c–p 1), generally are tolerant to disturbances and pollutants, and can recolonize disturbed habitats very quickly (Fig. 1d; Bongers and Bongers, 1998). (3b) C–p 3, 4, and 5 nematodes should be more susceptible to flooding and decrease in densities, e.g., due to their permeable cuticle (Fig. 1d; Bongers and Bongers, 1998) and because they are less tolerant to disturbances (Bongers, 1990; Ettema and Bongers, 1993). (4) Flooding effects on soil resource availability should be more pronounced at high plant diversity, which will destabilize soil microbial and nematode communities reflected by an increase in c–p 1 and 2 nematodes and a decrease of gram-negative bacteria and c–p 3, 4, and 5 nematodes (Fig. 1c, d).