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Subordinate plant species moderate drought effects on earthworm communities in grasslands

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Loss of plant diversity resulting from forecasted drought events is likely to alter soil functioning and affect earthworm communities. Plant-soil interactions are expected to play an important role in mediating climate change effects on soil decomposers. In this study, we test above-belowground linkages after drought by focusing on the effects of subordinate plant species on earthworm communities. Using a combination of subordinate species removal and experimental drought, we show that subordinate species, when present, increased in biomass after drought and induced an increase in total earthworm biomass. These effects were thought to be associated with the maintenance of food quantity and quality (e.g. nitrogen-rich litter) in relation to subordinate species. In support to this hypothesis, we found a positive correlation between the abundance of juvenile earthworms and plant community biomass hence litter quantity, and between the total biomass of earthworms and the abundance of subordinate species. Anecic earthworms were the most benefited by the presence of subordinate species under drought, especially *Lumbricus terrestris*, which was significantly correlated to the biomass of the nitrogen-rich subordinate species *Veronica chamaedrys*. Results of a multiple factor analysis (MFA) also highlighted positive associations between earthworm and subordinate species, independently of the drought treatment. Our study highlights how climate change, in this case reduced summer rainfall, can influence plant functional groups, with cascading effects on earthworms. It is therefore crucial, considering forecasted climate change, to understand these processes in order to better predict ecosystem responses and to adapt grassland management.

1. Introduction

Anthropogenic environmental perturbations threaten both the diversity and functioning of ecosystems (Butchart et al., 2010). Many perturbations, such as climate and land-use change, are occurring simultaneously with uncertainties regarding their combined effects (Thébault et al., 2014). Indeed, grasslands have been increasingly transformed over the past decades, particularly by changes in agricultural practices (intensification or abandonment) (Buttler et al., 2012), altered disturbance regimes, and plant invasion with consequent losses of plant diversity (Manning et al., 2015). Simultaneously, extended periods of drought are expected to increase both in frequency and severity over the next few decades, especially in central and Southern Europe (Christensen et al., 2007). Loss of plant diversity resulting from forecasted drought events is likely to alter soil functioning and related ecosystem services, but this threat remains rarely explored (Vogel et al., 2012;

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Mariotte et al., 2013a). A few studies have focused mostly on plant productivity as a response variable to biodiversity loss (Zaller and Arnone, 1999a) and drought (Zaller and Arnone, 1999b), while soil processes and the diversity, abundance and functions of soil communities have been largely ignored (Milcu et al., 2010; Johnson et al., 2011; Thakur et al., 2015). Nevertheless, evidence is growing that drought impacts soil communities and the processes they drive (Zaller and Arnone, 1999b; Smith, 2011). Important ecosystem functions, such as litter decomposition and nutrient cycling, are governed by soil detritivores, among them dung flies and earthworms, which are also likely to be affected by global change (Eisenhauer et al., 2012).

Earthworms contribute significantly to soil porosity and fertility (Shipitalo and Le Bayon, 2004; Amossé et al., 2015) through bioturbation (e.g. mixing litter and soil) and egestion of nutrient-rich casts that can improve plant productivity (Zaller and Arnone, 1999b,c; Milcu et al., 2008; Eisenhauer et al., 2009). The abundance and biomass of earthworms are principally determined by sufficiently high levels of soil moisture (Perreault and Whalen, 2006) and by the availability (Abbott and Parker, 1981; Amossé et al., 2015) and quality of food (Lüscher et al., 2015). The productivity, composition and diversity of plant communities determine food quantity (e.g. litter and exudates) and quality (e.g. nitrogen-rich litter), therefore greatly influencing earthworm communities (Milcu et al., 2006, 2008; Partsch et al., 2006; Eisenhauer et al., 2010). Consequently, drought perturbations are expected to impact on earthworms both directly, by decreasing soil moisture and indirectly, by reducing food quantity and quality through changes in the plant community biomass and composition.

Only few studies have evaluated the effects of drought on earthworm communities (Zaller and Arnone, 1999b). Epigeic species living at the soil surface, such as *Lumbricus rubellus*, appear to be strongly affected by successive dry summers because these species live in the litter layer, without ability to move down the soil profile and escape desiccation (Eggleton et al., 2009). Drought resistance of cocoons seems to be an important strategy for the persistence of some epigeic earthworm species during summer drought perturbations (Holmstrup and Loeschcke, 2003). Endogeic earthworms, which make horizontal burrows through the soil, such as *Aporrectodea caliginosa*, are also very sensitive to drought conditions (Eggleton et al., 2009; Bayley et al., 2010). However, they are able to survive short periods of drought by burrowing to depths of 10–20 cm and forming an estivation chamber (Bayley et al., 2010; McDaniel et al., 2013), composed of mucus and gut content to protect against water loss. Similarly, some anecic earthworms, which make permanent vertical burrows in soil, can enter in a true diapause during a dry period and stay a few months in dormant stage (Jiménez and Decaëns, 2004). While these findings suggest a strong effect of drought on earthworm communities, the importance of the plant community composition in mediating these effects is still unclear.

Climate change effects on aboveground–belowground interactions have not been widely addressed, especially between plants and soil invertebrates (Zaller and Arnone, 1999a, 1999b, 1999c; Van der Putten et al., 2009; Johnson et al., 2011; Arnone et al., 2013). Van der Putten et al. (2009) suggested that plants should be assigned to functional groups to facilitate the search for general patterns in the effects of climate change on plant–soil interactions. For example, more than species richness *per se*, certain plant functional groups, such as legumes, were shown to be important drivers of earthworm abundance and community composition due to high nitrogen content of leaves and dead roots (Milcu et al., 2008; Eisenhauer et al., 2009). The same plant functional groups may be relevant for the resistance of grassland communities to drought (Vogel et al., 2012). In parallel, the recent 'subordinate insurance hypothesis' (Mariotte, 2014) suggests that highly diverse plant communities contain greater numbers of subordinate species (*sensu* Grime, 1998), which are more resistant than dominant species to climate change perturbations.

In calcareous grassland ecosystems, which are widely distributed over Europe, our previous work has shown that subordinate species increased in biomass and improved grassland productivity during drought (Mariotte et al., 2013a). Moreover, subordinate species possess distinct traits from dominant species (Mariotte et al., 2013b; Garbin et al., 2016), linked to resource conservation, such as enhanced leaf C and N contents (Grigulis et al., 2013; Ouédraogo et al., 2013; Mariotte, 2014), which greatly impact on soil microbial communities (Mariotte et al., 2013b). The litter of subordinate plant species might also influence earthworms, which are particularly dependent on nitrogen-rich litter, especially litter feeding species (Milcu et al., 2008; Eisenhauer et al., 2009; Fischer et al., 2014). By improving plant productivity and litter quality (i.e. high N content) under drought, subordinate species might also maintain high quantity and quality food for earthworms and potentially mediate drought effects on the earthworm community.

The objective of this study was to test above-belowground linkages between subordinate plant species and earthworm community size and structure in native calcareous grassland communities in the year after experimentally inducing drought. We manipulated plant community composition using a removal experiment of subordinate plant species, and soil moisture using rainout shelters in a multi-factorial design. Such experimental design allowed for disentangling the effects of drought and subordinate species on earthworm communities. After the drought perturbation, we examined the subordinates' removal effects on the earthworm community, characterized by total biomass of earthworms, the relative importance of ecological categories, species composition and the ratio of juveniles to adults. Since subordinate species are expected to produce high quality litter and improve plant productivity, we hypothesized that their absence would induce a reduction of earthworm biomass, through the decrease of food quantity and quality, especially under drought. Moreover, we investigated abundance patterns of single subordinate plant and earthworm species, expecting that earthworm species, which are naturally associated to some resistant subordinate species, would also show a better resistance to drought conditions.

2. Materials and methods

2.1. Site description

A field experiment was carried out in an extensively grazed, species-rich pasture (mean: 30 species per square meter) situated on a calcareous slope (30°; 1200 m a.s.l.) in the Swiss Jura Mountains (Agroscope Research Station, La Fretaz, western Switzerland, 6°34′30″ E, 46°50′50″ N). The soil was classified as Eutric Cambisol (World Reference Base for Soil Resources – IUSS Working Group WRB, 2006) and was no deeper than 40 cm. The climate in this region is suboceanic with a mean annual precipitation (±1 SE) of 1393 ± 64 mm and a mean summer precipitation of 325 ± 26 mm (MeteoSwiss station Bullet/La Fretaz, 1999–2008). The pasture was grazed by cattle following a rotational system from May to September.

2.2. Defining dominant and subordinate species

In June 2008, cattle were excluded in a 25 × 25 m area and 49 plots of 1.2 × 1.2 m were established at 1.6 m from each other. In July 2008, visual absolute plant cover was determined within each