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Subordinate plant species moderate drought effects on earthworm communities in grasslands

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ABSTRACT

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 plot using a modified Braun-Blanquet index (1: cover less than 5%, 2a: 5–10%, 2b: 10–25%, 3: 25–50%, 4: 50–75%, 5: 75–100%). A total of 37 species were identified and classified in competitive hierarchical groups following Grime (1998) and according to a frequency–abundance curve (Mariotte et al., 2013c). A species was classified as dominant if its frequency exceeded 70% and its cumulative relative cover was greater than 12%. A species was classified as subordinate if its frequency was greater than 70% and its cumulative relative cover between 2 and 12% (Mariotte, 2014). This method resulted in the classification of eight dominant species: *Trifolium repens* L., *Cynosurus cristatus* L., *Festuca nigrescens* Lam., *Agrostis capillaris* L., *Carum carvi* L., *Ranunculus acris* ssp. *friesianus*, *Taraxacum officinale* agg., *Alchemilla monticola* Opiz, and five subordinate species: *Trifolium pratense* L. (*Tri.par*), *Achillea millefolium* L. (*Ach.mil*), *Leontodon autumnalis*/*hispidus* (*Leo.sp*), *Cerastium fontanum* ssp. *vulgare* (*Cer.fon*), and *Veronica chamaedrys* L (*Ver.cha*).

2.3. *Plant removal treatment*

The 20 most homogenous plots, according to the 2008 values on aboveground biomass records and species cover, were retained and a removal treatment was randomly applied to these plots: no removal (C) or removal of all subordinate species (S) – each treatment replicated with 10 plots. Subordinate species were removed between the last week of June and the first week of July 2009, and repeated in July 2010 and July 2011, with plants pulled out by hand in each S plot (*see* Mariotte et al., 2013a, 2015). In this site, community biomass production at the peak of the vegetation season (July) was 571 ± 52 g m^{-2} in 2009, 401 ± 43 in 2010 and 380 ± 32 in 2011 and the mean aboveground biomass removed in S plots (±1 SE) was 17 ± 3 g m^{-2} in 2009, 3 ± 1 in 2010, and 2 ± 1 in 2011. Care was taken not to disturb the soil more than necessary with pulling out only part of the root system. Based on the small amount of biomass removed, disturbance was assumed to be very low. In each plot, aboveground biomass was harvested twice at 3 cm above the ground, in early July and September, with individual subordinate species in C plots sorted and weighed separately. These harvests simulated the rotational cattle grazing as described above.

2.4. *Summer drought*

To simulate summer drought, we installed rainout shelters from 9 July to 6 September 2010. To control for potential artifacts due to shelter effects (Vogel et al., 2013), we established shelters for both control ($n = 10$) and drought plots ($n = 10$). Watering was then controlled manually during the 2-months drought simulation. After each natural rainfall, and within each treatment (10 no removal and 10 subordinates removal plots), half of the plots ($n = 5$) received an amount of water equivalent to the recorded precipitation (Bullet/La Frétaz, MeteoSwiss station of the study site), while the other half ($n = 5$) received no additional water. This resulted in four treatments (CW = control + watered, CD = control + drought, SW = subordinate species removal + watered, SD = subordinate species removal + drought), which were replicated five times each. During the experimental period, the amount of precipitation in the drought plots was reduced by 268 mm, representing 18% reduction of the mean summer precipitation. This resulted in a 67% average decrease in volumetric soil water content at 10 cm depth (*see also* Mariotte et al., 2013a).

2.5. *Earthworm community composition and biomass*

Earthworms were collected in each plot in September 2011, one year after the simulated summer drought perturbation, using the standard mustard extraction (Lawrence and Bowers, 2002) on a 1 m^2 surface with a corresponding depth of about 25 cm. Average soil depth (±1 SE) of the 20 plots was 30.5 ± 1.6 cm and we believe that most of the earthworms were successfully extracted from the soil. The “hand sorting” method ($20 \times 20 \times 20$ cm) was performed to guarantee that no earthworms remained in the soil. Earthworms were directly stored in ethanol 70% and identified at the species level in the laboratory (Bouché, 1972; Sims and Gerard, 1999; species names updated by; Blakemore, 2008). Dead fixed adults and juveniles were individually counted and weighed. Earthworms were also grouped within ecological categories: epigeics, endogeics, and anecics (Bouché, 1972).

2.6. *Statistical analysis*

All of the analyses were carried out with R version 3.1.2 (R Development Core Team, 2014). Treatment effects (removal: C/S, and drought: W/D) and their interactions on plant community biomass and earthworms (species, ecological categories, total biomass, number) were analyzed using two-ways ANOVAs followed by Tukey post hoc tests. Drought effects on subordinate species biomass were analyzed using one-way ANOVA. Earthworm species biomass data were square-root transformed to insure normality and homogeneity of variance, assessed by the Shapiro–Wilk test. The ratio of the number of juveniles to adult earthworms was calculated for each species in each plot to determine treatment effects on earthworm community age structure and stability. Ratios were then averaged per plot and analyzed (after log transformation) using linear mixed-effects models with ‘species’ nested in ‘plot’ as random factor.

Our experimental design allowed for testing the effects of subordinate species removal on earthworms communities but we were also interested in correlation between the abundance of subordinate species or plant community biomass and the earthworm community biomass and structure. In our field site, natural variation in subordinate species biomass and plant community biomass was relatively high between plots of the same treatment, which is likely to reduce statistical power of the ANOVA analysis. However, we used this plots' variability (*i.e.* gradient of productivity and subordinates biomass) to detect potential correlations between the abundance of earthworm and subordinate species, independently of the drought and removal treatment. We ran linear regressions between total earthworm biomass, juvenile:adults ratio, plant community biomass and subordinate species biomass. We also ran linear regressions between the biomass of each earthworm species (after square-root transformation) and each subordinate plant species (after square-root transformation) to test specific plant–earthworms interactions. To test the goodness-of-fit, statistical significance of linear regression was obtained from ANOVAs.

Additionally, a MFA was used here to link symmetrically the biomass of individual subordinate plant and earthworm species without assuming a priori any causal relationship and because it allows the simultaneous coupling of several groups or subsets of variables defined for the same plot (Borcard et al., 2011). A detailed description of this method is available in Bernier and Gillet (2012). We used a multiple factor analysis (MFA) (Escofier and Pagès, 1994; Borcard et al., 2011; Bernier and Gillet, 2012) that included a matrix of subordinate species biomass and a matrix of earthworm biomass for only the control plots (C plots without removal). The treatment (watered, drought) was added as a supplementary factor in a passive group (non constrained) and centroids of this factor were added in the MFA graph. RV-coefficients were used to test links between the biomass of subordinate plant species and earthworm species under drought. To assess the significant effects of drought on the association between individual subordinate plant species and earthworm species, we extracted each plot's coordinates on the five dimensions of the MFA that we constrained by the drought treatment using a redundancy analysis (RDA).

3. Results

3.1. Subordinate plant species removal and aboveground biomass production

Plant community biomass completely recovered, a year after the 2010 experimental drought simulation (Fig. 1A), as shown by a non-significant effect of drought ($F_{1,16} = 0.37$, $P = 0.55$) in the year after the drought treatment. By contrast, the removal of subordinate species (SW and SD) induced a significant decrease in plant community biomass (Fig. 1A, $F_{1,16} = 5.32$, $P = 0.03$). The biomass of all subordinate species collected in plots without removal (C plots) significantly increased in plots that received the drought treatment (Fig. 1B, $F_{1,8} = 6.29$, $P = 0.04$). Although not statistically significant, the mean biomass of some subordinate species, such as *A. millefolium* and *V. chamaedrys*, considerably increased in drought plots. Additional results of plant community and subordinate species resistance against the drought simulation are available in Mariotte et al. (2013b).

3.2. Earthworm community composition and biomass

Total earthworm biomass remained unaffected by the removal treatment of subordinate species in watered plots (CW and SW in Fig. 2A). By contrast, drought significantly increased the biomass of earthworms in plots where subordinate plant species were present (CD, removal × drought, $F_{1,16} = 12.75$, $P = 0.003$). The ratio of the number of juvenile:adult earthworms significantly decreased in plots where subordinate plant species were removed (Fig. 2B, $F_{1,16} = 4.78$, $P = 0.04$) and this was not affected by the drought ($F_{1,16} = 0.41$, $P = 0.53$).

A total of ten earthworm taxa were recorded including *Allolobophora chlorotica chlorotica* (*All.chl.chl*), *A. caliginosa caliginosa* (*Apo.cal.cal*), *A. caliginosa nocturna* (*Apo.cal.noc*), *Aporrectodea longa longa* (*Apo.lon.lon*), *Aporrectodea rosea* (*Apo.ros*), *Lumbricus castaneus* (*Lum.cas*), *Lumbricus friendi* (*Lum.fri*), *L. rubellus* (*Lum.rub*), *Lumbricus terrestris* (*Lum.ter*), and *Octolasium cyaneum* (*Oct.cya*) (Table 1). The earthworm community in control plots (no removal and watered) consisted of an average of 31 individuals per square meter and was composed of 72% of anecics, 24% of endogeics, and 4% of epigeics. The number of earthworms was not significantly affected by the removal of subordinate species and drought and only earthworm biomass is shown in this study. The biomass of earthworms was significantly affected by the interaction removal × drought ($P = 0.003$), and this principally was due to changes in *L. terrestris* biomass. The removal treatment of subordinate plant species only had a significant effect on the biomass of *L. terrestris* in drought plots (removal × drought, $P = 0.02$). Indeed, after the drought, the biomass of the anecic species *L. terrestris* was considerably greater in plots where subordinate plant species were present, while its biomass remained the same in plots where subordinate plant species were removed. The biomass of *A. caliginosa nocturna* followed the same pattern (3-fold increase in C plots) while the biomass of *A. longa longa* decreased after the drought ($P = 0.015$) independently of the subordinates' removal. Overall, epigeics and endogeics were not affected by the treatments but significant effects were observed for some of the species. The biomass of *A. rosea* ($P = 0.09$) decreased after the drought while the biomass of *A. caliginosa caliginosa* significantly increased ($P = 0.003$, Table 1). Although not significant, mean biomass of *A. chlorotica chlorotica* and *L. castaneus* followed the same pattern as *L. terrestris*.

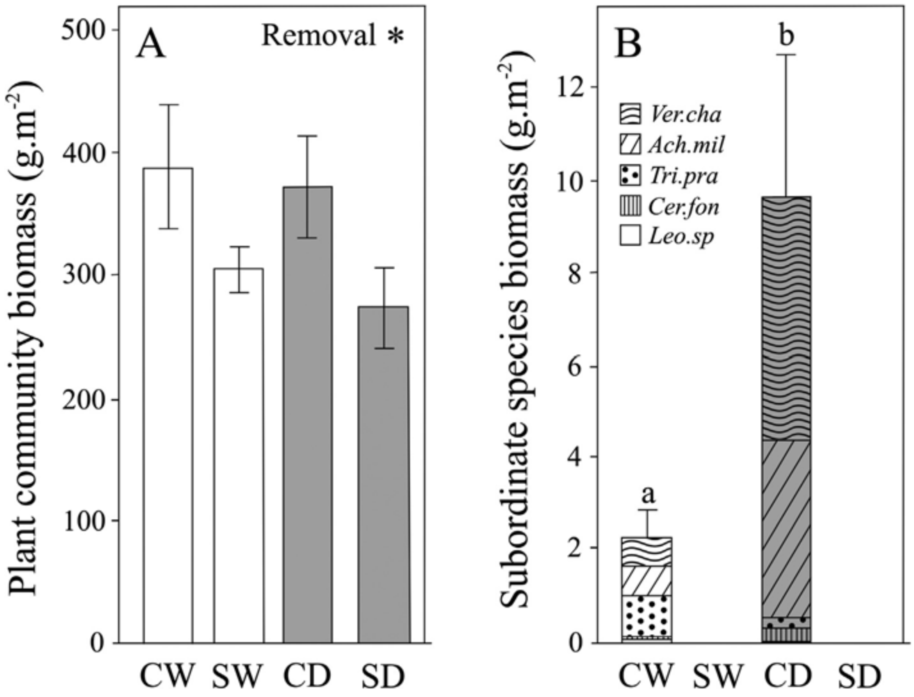

Fig. 1. (A) Mean plant community aboveground biomass production (g m^{-2}) and (B) mean aboveground biomass production of subordinate plant species (g m^{-2}, C plots only) including the proportion of the five different subordinate species measured one year after imposition of the drought treatment following the removal of subordinate plant species (C: control, no removal; S: subordinate plant species removed) and drought (W: watered, white bars; D: drought, grey bars). Each bar represents the mean ± 1 SE of each treatment ($n = 5$) and bars with different letters are significantly different ($P < 0.05$, Tukey's HSD test). For species names, refer to species abbreviations listed in the 'Materials and methods' section.

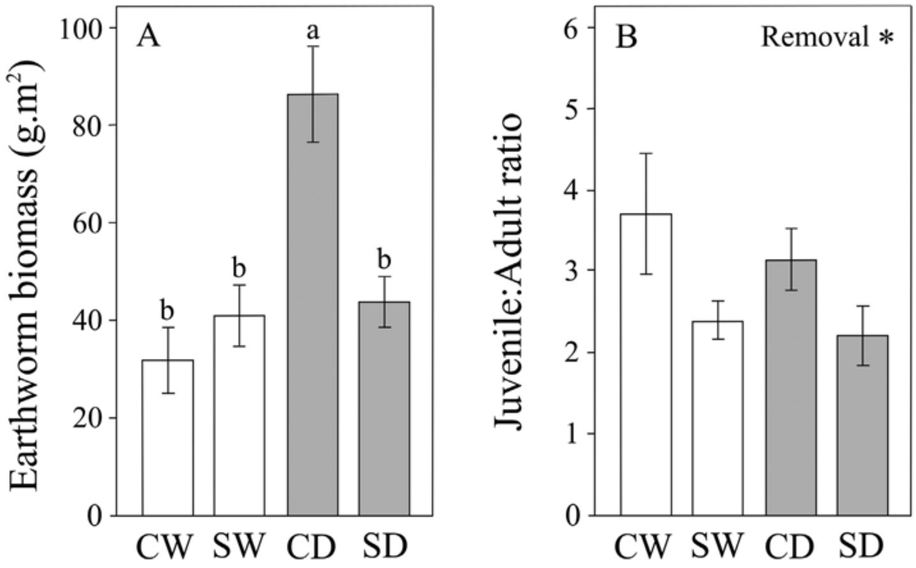

Fig. 2. (A) Total biomass and (B) ratio of the number of Juvenile:Adult earthworms as affected by the removal of subordinate plant species (C: control, no removal; S: subordinate plant species removed) and drought imposed in 2010 (W: watered, white bars; D: drought, grey bars).

Table 1
Mean earthworm biomass per species (g m^{-2} ± 1 SE) and ecological categories (epigeic, endogeic, and anecic earthworms) in control (C) plots and in plots where subordinate plant species had been removed (S plots) in watered and drought plots. Table of F- and P-values for the effects subordinate plant species removal, drought, and the interaction between removal and drought on the biomass of different earthworm species. Number of earthworms is not shown as not significantly affected by the removal of subordinate plant species and drought.

Earthworms functional groups and species	Watered		Drought		Drought		Removal		Interaction	
	Control − C	Removal − S	Control − C	Removal − S	$F_{1,16}$	*P*	$F_{1,16}$	*P*	$F_{1,16}$	*P*
Epigeics	1.25 ± 0.42	4.13 ± 2.98	2.98 ± 0.96	1.75 ± 0.44	0.04	0.842	0.27	0.608	1.65	0.217
Lumbricus castaneus	0.64 ± 0.26	0.69 ± 0.15	2.39 ± 1.04	0.64 ± 0.13	2.43	0.139	2.43	0.139	2.69	0.121
Lumbricus friendi	0.21 ± 0.21	0.45 ± 0.45	0.52 ± 0.32	0.82 ± 0.37	0.94	0.347	0.63	0.440	0.01	0.930
Lumbricus rubellus	0.40 ± 0.33	2.99 ± 2.99	0.07 ± 0.07	0.29 ± 0.13	1.01	0.330	0.87	0.364	0.62	0.443
Endogeics	7.60 ± 2.56	13.65 ± 5.91	17.03 ± 6.26	15.42 ± 4.73	1.16	0.298	0.22	0.648	0.53	0.476
Allolobophora chlorotica chlorotica	0.22 ± 0.13	3.07 ± 1.82	5.67 ± 3.26	3.14 ± 2.58	1.48	0.242	0.02	0.943	1.40	0.254
Aporrectodea caliginosa caliginosa	2.30 ± 1.36	1.60 ± 0.73	10.30 ± 3.46	11.03 ± 3.13	12.59	**0.003**	0.00	0.990	0.08	0.775
Aporrectodea rosea	5.08 ± 3.19	2.45 ± 0.90	0.90 ± 0.80	1.04 ± 0.98	3.15	*0.090*	0.07	0.795	0.08	0.780
Octolasion cyaneum	0	6.53 ± 5.70	0.16 ± 0.16	0.21 ± 0.21	1.16	0.297	1.32	0.266	1.29	0.273
Anecics	22.91 ± 6.06	23.22 ± 1.10	66.41 ± 14.33	26.63 ± 8.54	6.39	**0.022**	4.69	**0.045**	5.95	**0.026**
Aporrectodea caliginosa nocturna	9.03 ± 6.48	11.57 ± 2.33	26.20 ± 11.80	18.33 ± 6.80	2.46	0.137	0.12	0.732	0.47	0.505
Aporrectodea longa longa	6.48 ± 3.62	1.85 ± 1.16	0	0.49 ± 0.49	7.29	**0.015**	0.86	0.369	2.48	0.135
Lumbricus terrestris	7.40 ± 1.80	9.80 ± 1.60	40.21 ± 13.53	7.81 ± 2.17	4.91	**0.041**	4.65	**0.046**	6.26	**0.024**
Total	31.75 ± 6.84	41.01 ± 6.31	86.41 ± 9.85	43.81 ± 5.24	15.64	**0.001**	5.27	**0.036**	12.75	**0.003**

3.3. Relationships between subordinate plant species and earthworm species

Since the subordinates' removal significantly reduced total earthworm, juvenile:adults ratio and plant community biomass, we sought for potential correlation between plants and earthworms. We found a positive correlation between earthworm biomass and the biomass of subordinate species (Fig. 3A) and between the relative abundance of juvenile earthworms and plant community biomass (Fig. 3B). Plant community biomass was also positively correlated with the abundance of subordinate species ($F_{1,18} = 5.84$, $P = 0.03$, $R^2 = 0.20$). The multiple factor analysis (MFA) principally highlighted the associations between subordinate plant species and earthworm species (Fig. 4, *see* groups representation). Dim 1 and Dim 2 accounted for 54.9% and 24.2% of the explained variance, respectively. RV-coefficients of the MFA were 0.6 between earthworms and subordinate species ($P = 0.02$), 0.5 between earthworms and drought, and 0.3 between subordinate plant species and drought. The RDA performed on the plots' coordinates of the MFA and constrained by drought ($P = 0.01$) also shows that some associations between earthworm and subordinate plant species were stronger in drought or watered plots with Dim 1 associated to the drought treatment (*see* Supplementary material 1). We found positive associations between the abundance of *A. millefolium* and *A. caliginosa caliginosa* and *L. friendi* independently of the drought treatment. *T. pratense* was more associated with the drought sensitive *A. longa longa* (*see* Table 1). By contrast, the association between *V. chamaedrys* and *L. terrestris* seemed stronger in drought plots (Fig. 4). Linear regressions between subordinate plant species and earthworms species abundance confirmed significant correlations between *A. millefolium* and both *A. caliginosa caliginosa* ($F_{1,8} = 5.64$, $P = 0.04$, $R^2 = 0.34$) and *L. friendi* ($F_{1,8} = 6.07$, $P = 0.04$, $R^2 = 0.57$) and between *V. chamaedrys* and *L. terrestris* ($F_{1,8} = 10.57$, $P = 0.01$, $R^2 = 0.52$).

4. Discussion

Our study highlights how climate change, in this case reduced summer rainfall, can interact with plant functional groups to affect soil ecosystem engineers (e.g. primary consumers) in calcareous mountain grasslands. The presence of subordinate species induced

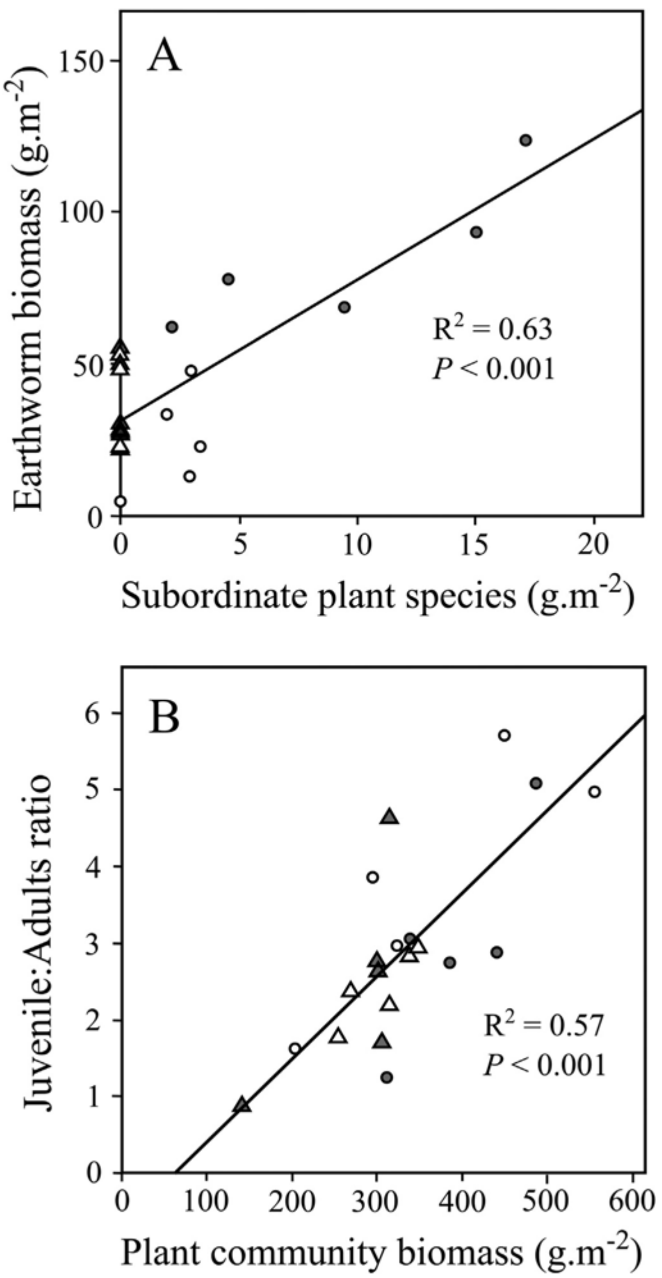

Fig. 3. Simple linear regressions using all 20 experimental plots between (A) the total biomass of earthworms and the biomass of subordinate plant species and between (B) the relative abundance of juveniles and plant community biomass. Control plots (treatment C) are depicted as circles and subordinate plant removal plots (S) as triangles. Filled symbols depict plots exposed to drought (treatment D) using rainout shelter in 2010 and open symbols depict plots receiving water to match natural precipitation (W).

a full recovery of plant community biomass in the year after the drought (Fig. 1, *see also* Mariotte et al., 2013b), and the removal of subordinate species led to a 20% decrease in aboveground biomass production. These results clearly demonstrate that subordinate plant species play a large role in maintaining plant productivity (i.e. ecosystem function) and resistance to drought (Mariotte et al., 2015). Others have also found a similar relationship with warming (Ouédraogo et al., 2013) and elevated CO_2 (Stinson and Bazzaz, 2006). Earthworm taxonomic richness was relatively high (10 taxa) at our field site, based on those previously recorded in European grassland sites (ranging between 5 and 9 taxa; Zaller and Arnone, 1997; Zaller and Arnone, 1999a, 1999b; Plum and Filser, 2005; Eisenhauer et al., 2009; Arnone et al., 2013). The relative abundance of juvenile earthworms was higher in plots where subordinate species were present (Fig. 2B), and also increased with increasing plant community biomass (Fig. 3B) led by subordinate species. Juvenile earthworms have been shown to be more susceptible to food limitation than conspecific adults, reflecting their higher energy requirements (Curry et al., 1995). By maintaining plant productivity, subordinate species presumably provided sufficient quantities of litter for the development and growth of juvenile earthworms, which can directly impact on earthworm population growth. Surprisingly, subordinate species, when present, increased in biomass after drought (4-fold compared to control) and led to an increase in total earthworm biomass (3-fold compared to control).

Anecic earthworms constituted 72% of earthworm functional groups and were the most affected by the increase of subordinate plant biomass after drought (Table 1). In particular, *L. terrestris* biomass increased five-fold and *A. caliginosa nocturna* biomass increased three-fold in plots with subordinate plant species. As primarily litter feeding species, both are particularly dependent on litter quantity (Eisenhauer et al., 2009) and quality, principally nitrogen-rich litter (Milcu et al., 2008; Fischer et al., 2014; Lüscher et al., 2015). In addition to the maintenance of a high quantity of litter material through higher plant community biomass production, the increases of subordinate plant species following drought may also have improved litter quality through an increased amount of N-rich litter of subordinate plant species. For example, two of the subordinate species, which highly increased in biomass under drought, *A. millefolium* and *V. chamaedrys*, possess high leaf N content (respectively 2.4% and 2.5%, measured from this experiment). Our results showing significant positive correlations between the biomass of *A. millefolium* and *A. caliginosa nocturna,* and between the biomass of *V. chamaedrys* and *L. terrestris*, highlight also significant species-specific above-belowground interactions. Interestingly, most of the associations between subordinate and earthworm species occurred independently of the drought treatment, showing that subordinate-earthworm associations are not as tightly linked to drought as expected. Only the association between *L. terrestris* and *V. chamaedrys* was stronger in drought plots (Fig. 4). Nevertheless, due to the better drought-resistance of subordinate species, these subordinate-earthworm associations are likely to moderate drought effects on earthworm communities. *A. longa longa* was the only anecic earthworm species negatively affected by drought, but it also was the species that showed no correlations with beneficial subordinate plant species under drought.

Endogeic and epigeic earthworms were less abundant, representing only 24% and 4% of the total earthworm biomass, respectively. Overall, both ecological groups were not affected after drought and did not suffer from the removal of subordinate species. However, at the species level, two endogeic species, *A. caliginosa caliginosa* and *A. rosea,* were significantly affected after drought. The biomass of *A. caliginosa caliginosa* increased after the drought while it decreased for *A. rosea*. *A. rosea* has a low assimilation efficiency (Edwards and Bohlen, 1996) and forms estivation chambers close to the soil surface (average depth: 6 cm; Gerard, 1967), which do not allow this species to survive extended drought periods. By contrast, *A. caliginosa caliginosa* has been shown to be very resistant to dehydration and can survive the rapid loss of as much as 60% of the body water (Roots, 1956). Moreover, this species survives drought by forming estivation chambers (McDaniel et al., 2013) deeper in the soil (10–20 cm) and by increasing its body fluid osmolality to maintain its water content (Bayley et al., 2010).

Our data showing a stimulation of community earthworm biomass when subordinate species were present, especially after

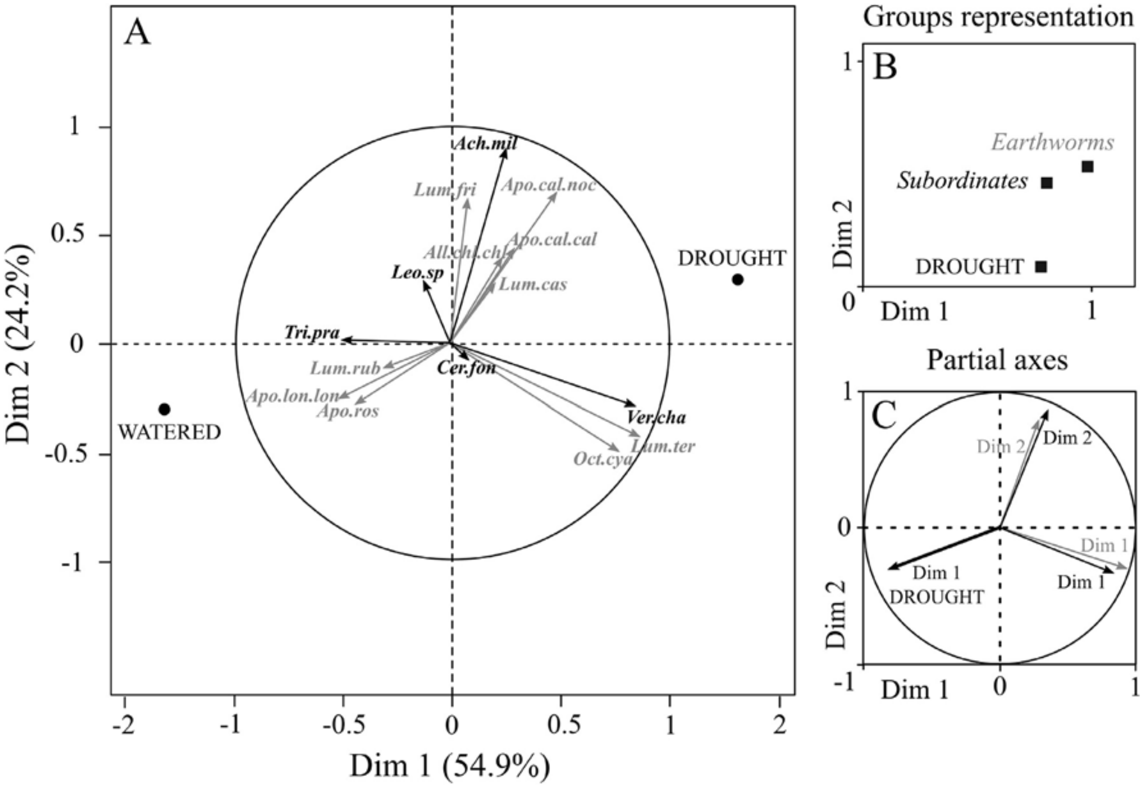

Fig. 4. (A) Multiple factor analysis (MFA) representing the biomass of subordinate plant species (black) and earthworm species (grey) one year after the experimental summer drought. Axis 1 (related to drought treatment) and axis 2 account for 54.9% and 24.2% of the explained variance, respectively. The graphs of groups representation (B) and partial axes (C) highlight the proximity of subordinate species and earthworms within the scatter plot (subordinates in black and earthworms in grey). For species names, refer to species abbreviations listed in the 'Materials and methods' section.

drought, suggest that these species had a disproportional stimulatory effect. This disproportionate effect may have derived from subordinate plant species traits that enhance resource conservation (e.g. high N content) and improve litter quality that benefit earthworms (Lüscher et al., 2015). Previous results in the frame of the same experiment also showed that these same traits enable subordinate plants to induce an increase in fungal biomass under drought (Mariotte et al., 2015; *see also*; De Vries et al., 2012; Grigulis et al., 2013). Subordinate species have also been shown as highly colonized by AM fungi (Mariotte et al., 2013b), which might explain their better resistance to drought (Mariotte et al., 2015). Since soil fungi are considered as an important food source for earthworms (Bonkowski et al., 2000; Curry and Schmidt, 2007), it is likely that positive effects led by subordinate species on fungal abundance also benefited earthworms under drought.

Positive effects of subordinate plant species on very few earthworm species and only one functional group can feed back to multiple ecosystem functions, such as litter decomposition (Gomez-Brandon et al., 2012) and nutrient cycling (Zaller and Arnone, 1999c; Van Groenigen et al., 2014). For example, both Ernst et al. (2009) and Gómez-Brandón et al. (2012) showed that earthworms increased litter decomposition, directly through feeding activity, and indirectly by increasing microbial activity. Earlier, it has been shown that the presence of subordinate plant species improves litter decomposition during and after the drought at the studied field site (Mariotte et al., 2015, *see* Supplementary material 2), which is likely related to interactions between subordinate plant species and anecic earthworms. Interestingly, in a similar calcareous grassland, Zaller and Arnone (1999c) found higher tiller and ramet production of subordinate plants when located near large surface casts deposited by anecic species, indicating that earthworms might in turn benefit subordinate species. Anecic earthworms might also benefit some subordinate plant species by the selective consumption of its seeds and subsequent deposition in their nutrient-rich surface casts. Earthworms produce large amounts of casts, which in grasslands range between 1.5 and 4.5 kg per square meter annually (Zaller and Arnone, 1997). For example, the anecic earthworm species *L. terrestris* produces abundant casts at the soil surface (Marhan and Scheu, 2005), which is likely to increase nutrient availability for plants (Le Bayon and Binet, 2006; Van Groenigen et al., 2014). Drought reduces soil nitrogen availability and mineralization (Dijkstra et al., 2015), but we suggest that the increase in earthworm abundance, led by subordinate plant species after drought, moderated these effects, thus partially explaining the full recovery of plant community biomass.

Together the findings of our experiment underline for the first time the important role of subordinate plant species in influencing earthworm community composition and biomass after drought. By supplying high quality and quantity food, respectively through resource conservation traits and increased community aboveground biomass, subordinate species moderated drought effects on earthworm communities. The fact that subordinate plant species effects were felt primarily by the large anecic earthworms suggests a strong plant-earthworm feedback which may impart resilience of ecosystem functions in case of global change factors such as drought, but may also disrupt normal ecosystem functioning and resultant ecosystem services in case of environmental perturbations that impact either subordinate plants or anecic earthworms. This experiment provides a strong example of the importance of quantitatively understanding plant and soil invertebrate interactions and their response to climate change and emphasizes the need for future studies to examine the underlying mechanisms of subordinate species effects on earthworm communities.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.01.020.

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