

Body size structure of soil fauna along geographic and temporal gradients of precipitation in grasslands



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ABSTRACT

Precipitation is a global driver of animal abundance and diversity in terrestrial ecosystems, but we know little on how it influences the body size structure of invertebrate communities, particularly soil fauna. It is unclear whether aridity limits the abundance of large-bodied soil invertebrates, and whether temporal precipitation changes can induce local shifts. The potential role of trophic identity in modulating such relationships is also unexplored. Here we investigate the community-weighted mean body mass of soil nematodes, globally widespread invertebrates, in a two-year manipulative experiment with experimental drought and increased rainfall, conducted in three North American grassland ecosystems ranging from arid to semiarid and mesic conditions. We predict that community-weighted mean increases along with precipitation, and that long-term aridity prevents body size shifts in response to within-site temporal changes in precipitation. Nematode community-weighted mean mass increased from arid to mesic conditions. Altered precipitation within sites had much weaker effects, and none detectable in the arid site. When analysing community-weighted mean mass separately by feeding group, only plant-feeding nematodes responded positively to rainfall addition in semiarid and mesic conditions, as well as to ambient interannual differences consistently across sites, presumably due to a tighter ecological linkage with primary production. Our findings point to aridity as an environmental filter against large-bodied soil nematodes, with limited potential for community body size shifts in response to extremely dry or wet years. However, the different responses of plant-feeding taxa from other functional groups indicate potential mismatches between morphologically similar taxa in multitrophic invertebrate communities.

1. Introduction

Understanding how communities vary along environmental conditions is a fundamental goal of ecology and a prerequisite to predict ecosystems' responses to global change (Fukami and Wardle, 2005; Laliberté et al., 2017). Some of the most glaring knowledge gaps pertain to functional traits in invertebrate communities (Wong et al., 2018), particularly soil fauna (Eisenhauer et al., 2017), despite considerable progress for certain groups (Ulrich and Fiera, 2010; Mathieu, 2018).

This applies even to fundamental traits such as body size, which in turn regulates many other traits and overall ecosystem functioning (Woodward et al., 2005).

While the relationship between soil invertebrate body size and temperature has been studied in a wide range of systems and taxa (Makkonen et al., 2011; Lindo, 2015; Knox et al., 2017), the relationship of precipitation and body size has not been explored as thoroughly. Precipitation is the main global driver of productivity across terrestrial ecosystems (Knapp et al., 2008), and influences abundance, biomass,

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and diversity of soil fauna (Freckman et al., 1979; Caruso et al., 2019). That it may also explain geographic patterns of animal size has not escaped notice (e.g. Remmert, 1981), but this has been rarely tested at the community level in epigeous invertebrates (Brandl et al., 2009), let alone belowground. Similarly, how local temporal variation in precipitation (e.g. droughts vs wet years) affects soil animal abundance and taxonomic composition is well-studied (Blankinship et al., 2011; Landesman et al., 2011; Sylvain et al., 2014; Turnbull and Lindo, 2015; Torode et al., 2016; Cesarz et al., 2017), but the effects on morpho-functional traits are less explored (Lindo et al., 2012). This limits our ability to predict how soil communities will respond to shifts in precipitation and moisture – which are important aspects of anthropogenic climate change (Collins et al., 2013).

Soil nematodes are the most abundant terrestrial invertebrates globally (van den Hoogen et al., 2019). Although even the largest species are almost invisible without a microscope, they span orders of magnitude of body mass (Andriuzzi and Wall, 2018), and vary considerably in feeding ecology (Yeates et al., 1993) and life history traits (Ferris, 2010). Water availability is known to influence their abundance and taxonomic composition (Nielsen et al., 2014), but the effects on body size are not clear, despite a plausible two-fold mechanistic basis. Firstly, water availability controls productivity and therefore energy available to the soil food web, e.g. with fewer resources in arid conditions (Johnson et al., 2011; Torode et al., 2016). Soil nematode communities are especially skewed toward small body sizes where resources are limiting (Verschoor et al., 2001; Mulder, 2010; Andriuzzi and Wall, 2018), as observed in other animals too (Chen and Wise, 1999; Mulder and Elser, 2009; O’Gorman et al., 2017). Therefore, precipitation may control nematode body size by regulating resource availability. Secondly, direct physical effects may take place (Landesman et al., 2011), especially considering that active nematodes require water films or water-filled pores (Wallace, 1968; Demeure et al., 1979). All else being equal, a dry soil has less habitable space for large-bodied nematodes than a moister soil. In short, we expect high water availability to promote large-bodied soil nematodes. Since most soil nematode communities include several feeding groups (Yeates et al., 1993), they are well-suited for testing whether trophic identity modulates such responses.

We investigated the body size structure of soil nematode communities in three grassland ecosystems differing in mean annual precipitation (MAP), under ambient and manipulated rainfall for 2 years at each site (Table 1). This work is part of a wider project on primary productivity, soil nematodes, and root herbivory responses to precipitation (Franco et al., 2019). The sites were chosen to represent contrasting points along a >1000 km aridity gradient in the Great Plains of North America. We analysed the community weighted mean (CWM) mass of nematodes at genus level. CWM gives a measure of trait composition unbiased by differences in abundance: two samples with exactly the same taxa in the same proportions will have identical CWM, regardless of differences in number of individuals. Well-established in plant ecology (Lavelle et al., 2008), CWM analyses have been successfully used to investigate animal body size shifts across habitats and climates (Merckx et al., 2018; Tiede et al., 2018). In soil invertebrates, CWM and complementary techniques have been used mostly to investigate land use and environmental gradient (Liu et al., 2015; Andriuzzi et al., 2017; Sechi et al., 2017; Andriuzzi and Wall, 2018), but never, to our knowledge, in relation to precipitation.

The following rationale guided our hypotheses. First, as discussed above our theoretical expectation is that aridity – whether by constraining habitable space, food resources, or both – is a limiting factor to large-bodied nematodes; therefore, higher precipitation should enable higher CWM mass. Second, ecological theory suggests a hierarchy in the source of variation, with regional differences in MAP having stronger effects than the local effects of rainfall manipulation (Sala et al., 2012). Third, previous studies showed that transient water availability shifts in desert have weak or null effects on nematode abundance and ecological

Table 1

Characteristics of the study sites. Mean annual precipitation and long-term mean for growing-season precipitation from NOAA climate data of nearby localities (Las Cruces [New Mexico], Nunn [Colorado], and Manhattan [Kansas]). Rainfall in 2016 and 2017, years of the experiment, was measured in rain gauges installed adjacent to each precipitation manipulation site. Rainfall treatments differed between sites in order to achieve the same statistical level of change relative to long-term records, see main text for details. Soil characteristics refer to the top 10 cm and are from the USDA Soil Survey (accessible at <https://websoilsurvey.sc.egov.usda.gov>).

	Arid site	Semiarid site	Mesic site
Coordinates	32°33'N, 106°49'W	40°50'N, 104°45'W	39°40'N, 96°34'W
Ecosystem	Chihuahuan desert	Shortgrass steppe	Tallgrass prairie
Mean annual precipitation (mm)	245	321	835
Ambient 2016 precipitation (mm)	212	207	991
Ambient 2017 precipitation (mm)	290	291	726
Mean annual temperature (°C)	14.7	8.4	12.5
Ratio of annual precipitation to potential evapotranspiration	0.25	0.50	1.10
Long-term mean growing-season precipitation (mm)	105	204	428
Rainfall treatments (change relative to ambient)			
Large reduction	–80%	–70%	–60%
Moderate reduction	–50%	–40%	–30%
Moderate addition	+50%	+40%	+30%
Large addition	+80%	+70%	+60%
Soil texture class	Fine sandy loam	Fine sandy loam	Silty clay loam
Soil organic matter	<1%	1–1.6%	>3%
Dominant plant species	Black grama (<i>Bouteloua eriopoda</i> ; Torr.)	Blue grama (<i>B. gracilis</i> ; Willd. Ex. Kunth) Lag. Ex Griffiths)	Big bluestem (<i>Andropogon gerardii</i> ; Vitman) Little bluestem (<i>A. scoparius</i> ; (Michx.) Nash) Yellow indiagrass (<i>Sorghastrum nutans</i> ; (L.) Nash)

group composition (Freckman et al., 1987; Sylvain et al., 2014; Van-degehuchte et al., 2015). This is consistent with observations that moisture pulses may be insufficient to cross the biological response threshold in desert conditions, that is, strong rainfall events are required to trigger biological responses in arid-adapted organisms (Schwinning and Sala, 2004). Therefore, we expect stronger responses in semiarid than truly arid conditions. The effect of additional rainfall should then plateau moving to mesic conditions, where natural conditions of soil moisture are unlikely to pose constraints to nematodes. Lastly, we expect fungal-feeding nematodes to be the least responsive to rainfall because they are mostly small-sized, whereas we expect strong responses in omnivore-predators, because large-bodied and disturbance sensitive genera are particularly represented in this group (Ferris, 2010). With this rationale, we tested the following hypotheses. (1) Greater mean annual precipitation is linked to large-bodied nematode genera. Therefore, we predict CWM body mass to increase with MAP, that is in the order Arid < Semiarid < Mesic site. (2) Similarly, CWM mass is positively linked to transient changes in precipitation within-site, but long-term conditions buffer the effect. In particular, we predict that the response to within-site precipitation change is stronger in the Semiarid site than in the Arid site, and negligible in the Mesic site. (3) CWM body mass patterns within trophic levels differ from those of the total community, with the weakest changes in fungal-feeders and the strongest in omnivore-predators.

2. Materials and methods

2.1. Site description and experimental design

We collected samples in 2016 and 2017 from three grassland sites in North America (Table 1) differing in MAP. The Arid site is the Jornada Basin LTER, the Semiarid site is the Semiarid Grasslands Research Center of Colorado (formerly Shortgrass Steppe LTER), and the Mesic site is the Konza Prairie LTER. In each ecosystem, the two sampling years were markedly different in the amount of rainfall: 2016 was drier than 2017 in sites Arid and Semiarid, the opposite in Mesic (Table 1). In each site we established five rainfall treatments: an ambient control, moderate and large reductions, and moderate and large additions. Each treatment had $n = 8$ local replicates, resulting in a total of 120 plots. We randomly allocated treatments to plots 12.5 m² in size, spaced >5 m apart, in areas with the typical vegetation of their ecosystem. The rainfall reduction plots had rainout shelters that intercepted the desired proportion of incoming rainfall and drained it into temporary storage tanks. From these, through a solar-powered pumping system the target amount of water was automatically transferred to the addition plots (Gherardi and Sala, 2013). The corresponding non-ambient plots differed between sites in the absolute amount of rainfall added or reduced (Table 1), because the goal was to have the same statistical deviation from the ecosystem-specific historic record (see Knapp et al. (2017a) for a rationale). In particular, the moderate and large reduction corresponded to, respectively, the 1st and 10th percentiles, and the moderate and large additions to the 90th and 99th percentiles, of the long-term means.

2.2. Sample collection and nematode data

We sampled at the end of the growing season (September) in 2016 and 2017. In each plot, we took a composite sample of four subsamples below the dominant vegetation type using a 2.5 cm wide corer to 10 cm depth. The soil samples were bagged in coolers for transportation to Colorado State University, where they were stored at 4 °C. Within 2 days from sampling, nematodes were extracted from 100 g aliquots of each sample using Baermann funnels, collected in water over 3 days, and stored at 4 °C. Within 5 days of extraction, we counted nematodes using an inverted microscope (Olympus CKX41×, 200× magnification), fixed them in 5% formalin for preservation, and identified them to genera (Bongers, 1994; Mai et al., 1996). Separate aliquots from the samples were used to measure gravimetric soil water content (w/w) after oven-drying for 72 h at 105 °C, so that nematode counts could be converted as individuals kg⁻¹ dry soil. Nematode genera were allocated to feeding groups (Yeates et al., 1993): bacterial-feeders, fungal-feeders, plant-feeders, and omnivore-predators.

In February 2018, we retrieved mean fresh body mass of the nematode genera occurring in the samples from the “Nemaplex” database (developed and maintained by Howard Ferris, University of California, http://nemaplex.ucdavis.edu/Ecology/nematode_weights.htm). Combining body size (μg) with nematode abundance, the CWM mass in all samples was calculated using R package FD (Laliberté and Legendre, 2010). CWM is calculated as the sum of average trait values of taxa occurring in the community weighted by their relative abundance (Laliberté and Legendre, 2010). An increase in CWM mass indicates a community shift to larger sizes. CWMs were calculated for the total community and also in each feeding group, namely bacterial-feeders, fungal-feeders, plant-feeders, and omnivore-predators. A caveat of our data is that the body size values from the “Nemaplex” database mostly refer to fully-grown adult females, which are usually outnumbered by juveniles and subadults, leading to overestimates of individual and community biomass (Andriuzzi and Wall, 2018). We also recognise that these data necessarily leave out intraspecific size variation, which may also reveal notable ecological responses (Knox et al., 2017). Nonetheless, the available data are suited to our goal of assessing whether higher

water availability promotes larger-bodied species in nematode communities. See Table S1 for a full list of the genera and their body mass reference values.

2.3. Statistical analyses

We tested responses of CWM mass of soil nematodes in mixed-effect models with R package nlme. In accordance with our hypotheses and broad study objectives, we started by testing the regional effects of long-term precipitation (i.e. MAP) in combination with the local effects of short-term precipitation manipulations (i.e. amount of rainfall received by plots), both as continuous variables. We used MAP, rainfall and their interaction as fixed effects, and plot identity as random effect (to account for the non-independence of samples collected from the same plot in the two years). This regression approach reflects our gradient design and is statistically powerful (Cottingham et al., 2005; Kreyling et al., 2018). Then, to specifically address our first hypothesis, we tested the effects of MAP alone, using a random effect with plot identity nested in rainfall treatment (to account for the variation related to treatment without specifically testing for it). To detect potential non-monotonic responses, we also fit alternative models with site as a three-level factor (arid, semiarid, mesic) rather than a continuous variable. To disentangle the potential effect of MAP from the effect of the experimental manipulation, we also fitted these models using ambient precipitation only (control plots). To test hypothesis 2, we analysed each site separately in mixed-effect models with within-site precipitation as fixed effect and plot identity as random effect; again, we also tested models with a factorial fixed effect (the five treatment levels). To complement the analyses on within-site precipitation change, we also tested for the difference between the two study years in each site; we interpreted such results with particular caution because (i) two years do not constitute a reasonable time series, and (ii) there are likely legacy effects of past years' precipitation. Finally, to test hypothesis 3 we performed all the above analyses on the CWM mass values also separately for each feeding group.

We assessed effects with Wald F-tests, and extracted means and standard errors (SE) with the associated p-values using the summary() function. In models with the five treatments as factor levels, we performed post-hoc comparisons of means with Tukey tests (R package lsmeans (R Core Team, 2014)). Variance explained by fixed effects, the marginal R² (Nakagawa and Schielzeth, 2013), was calculated with R package MuMIn (Bartoń, 2017). Statistical assumptions of homogeneity and normality were checked by graphical inspection of the model residuals. These were often heteroskedastic due to differences in variance between sites and/or rainfall levels, which we corrected using an appropriate variance-covariance structure (R argument varIdent). Subsequent inspection of the residuals validated the improved models.

3. Results

3.1. Whole-community patterns

Overall, CWM mass was linked to long-term water availability ($F_{1,114} = 112.58$, $p < 0.0001$), increasing according to MAP as predicted ($p < 0.0001$, $R^2 = 0.79$). The three sites were clearly differentiated (Fig. 1), with CWM mass increasing in the expected order Arid < Semiarid < Mesic (marginal $R^2 = 0.75$, pairwise comparisons $p < 0.0001$). The pattern was apparent also in the control plots alone, but statistical support for the difference between sites Semiarid and Mesic was less clear ($p = 0.052$).

No clear relationship with within-site precipitation is apparent when the effect of MAP is accounted for ($p \geq 0.1$). Once MAP is removed, although a positive relationship of within-site precipitation with CWM mass does emerge across sites ($F_{1,118} = 37.42$, $p < 0.0001$), the explanatory power remains very limited (only 7% of variance explained). Splitting the analysis by site, no linear change in CWM along within-site

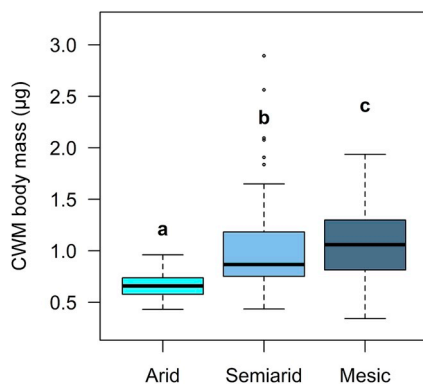


Fig. 1. Nematode CWM body mass in the three grassland sites (black lines are the medians, boxes delimit the second and third quartiles, and the whiskers 1.7 times the interquartile range, with points above being outliers). The different letters indicate that pairwise differences were statistically clear ($p < 0.05$). Restricting the comparison to the control plots gave a similar pattern, although the gap between sites Semiarid and Mesic was reduced.

precipitation was observed, as well as no clear pairwise treatment differences (Tukey tests, all comparisons $p > 0.1$). Comparing the two study years site-by-site revealed that CWM mass was greater in 2017 than in 2016 in the Semiarid site only ($F_{1,39} = 22.99$, $p < 0.0001$, $R^2 = 0.65$, Fig. S1).

3.2. Feeding group-specific patterns

CWM mass values calculated separately by feeding group revealed similarities as well as discrepancies with the whole community. In bacterial-feeders, CWM mass did not vary monotonically with MAP ($F_{1,114} = 0.66$, $p = 0.4$) and within-site precipitation change had no statistically supported effects regardless of the MAP level. Overall, bacterial-feeder CWM mass (Fig. 2a) was clearly lower in Semiarid than Mesic ($p = 0.02$) whereas in Arid tended to overlap with both ($p = 0.06$ and 0.07 , respectively). In the control plots, all three sites overlapped extensively ($p > 0.1$).

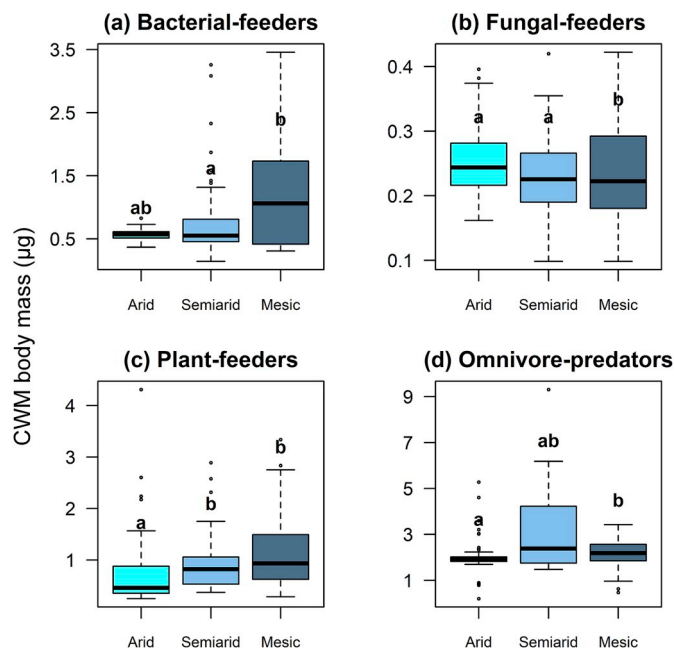


Fig. 2. CWM body mass in each feeding group across the three grassland sites. Different letters indicate clear statistical support for pairwise difference ($p < 0.05$).

In fungal-feeders, the effect of within-site precipitation change depended on MAP (interaction, $F_{1,116} = 9.69$, $p = 0.002$, Fig. 3a), switching from neutral in Arid and Semiarid ($p > 0.1$) to negative in Mesic ($p < 0.0001$, marginal $R^2 = 0.40$). Fungal-feeder CWM mass varied differently to the rest of the community (Fig. 2b), being smaller in Mesic than either Arid ($p < 0.0001$) or Semiarid ($p < 0.001$), although the latter difference was not as clear if only the control plots were analysed ($p = 0.07$).

A within-site precipitation change \times MAP interaction ($F_{1,115} = 64.11$, $p < 0.0001$) was found also with plant-feeders (Fig. 3b), whose CWM mass was invariant across the experimental gradient in site Arid ($p = 0.61$), but increased with rainfall in Semiarid ($p < 0.001$, marginal $R^2 = 0.20$) and Mesic ($p < 0.001$, marginal $R^2 = 0.31$). Overall, plant-feeder CWM mass (Fig. 2c) was clearly lower in site Arid than Semiarid or Mesic (both $p < 0.0001$), whereas it overlapped substantially in the latter two ($p = 0.56$). This pattern was not a by-product of the manipulated rainfall plots, as it was observed also in the control plots alone. Plant-feeders were the only group in which CWM mass was clearly higher in the wetter year at all three sites (all three $p < 0.0001$), although the difference was statistically stronger in Arid ($R^2 = 0.92$) than in the other sites (Semiarid $R^2 = 0.17$, Mesic $R^2 = 0.16$).

CWM mass in omnivore-predators was interactively affected by within-site precipitation change and MAP ($F_{1,105} = 13.27$, $p < 0.0001$), with a positive effect of the former levelling off as the latter increases. However, this relationship can be hardly described as linear (marginal $R^2 = 0.08$ across sites). Rather, CWM mass increased with within-site precipitation in Semiarid ($p < 0.0001$, marginal $R^2 = 0.39$, Fig. 3c) but neither in Arid ($p = 0.57$) nor Mesic ($p = 0.48$). In terms of sites (Fig. 2d), omnivore-predator CWM mass was lower in Arid than Mesic ($p = 0.0001$), with Semiarid intermediate although more similar to the former ($p = 0.14$) than to the latter ($p = 0.07$). The patterns were observed also in the control plots alone.

4. Discussion

4.1. Soil nematode community-weighted mean body size and long-term water availability

As predicted, soil nematode CWM mass was positively linked to MAP, clearly increasing in the order Arid $<$ Semiarid $<$ Mesic site (Fig. 1). This supports our first hypothesis, and suggests that large-bodied soil nematodes benefit from higher long-term water availability, i.e. mesic conditions select for larger-bodied taxa. This could arise through a combination of two mechanisms, namely (i) more water-filled space in soil enabling larger nematodes to survive as a direct physical effect, and (ii) greater primary productivity and soil organic matter content at higher MAP providing more energy to support large consumers in the micro-food web. Both mechanisms are plausible: nematodes require water-filled habitat space in proportion to their size (Wallace, 1968), and greater resource inputs enable the soil food web to support more large-bodied soil nematodes (Verschoor et al., 2001; Andriuzzi and Wall, 2018). As studies on other animal communities have shown, resource availability may outweigh and even reverse direct effects of such a fundamental abiotic factor as temperature (O'Gorman et al., 2017; Kaspari and de Beurs, 2019), but, because higher mean annual precipitation usually enhances primary productivity (Sala et al., 1998), we expect the abiotic and resource-mediated effects of water availability to affect soil nematodes in tandem rather than antagonistically.

We are aware that other factors besides MAP could be invoked to explain our findings. For example, fine soil texture may contribute to select against particularly thick-bodied species (Hassink et al., 1993; Niklaus et al., 2003; Andriuzzi and Wall, 2018). However, our sites are similar in terms of texture (Table 1). On the other hand, they differ in temperature. Although precipitation is a stronger determinant of resource availability (Knapp et al., 2017b), thermal conditions may have

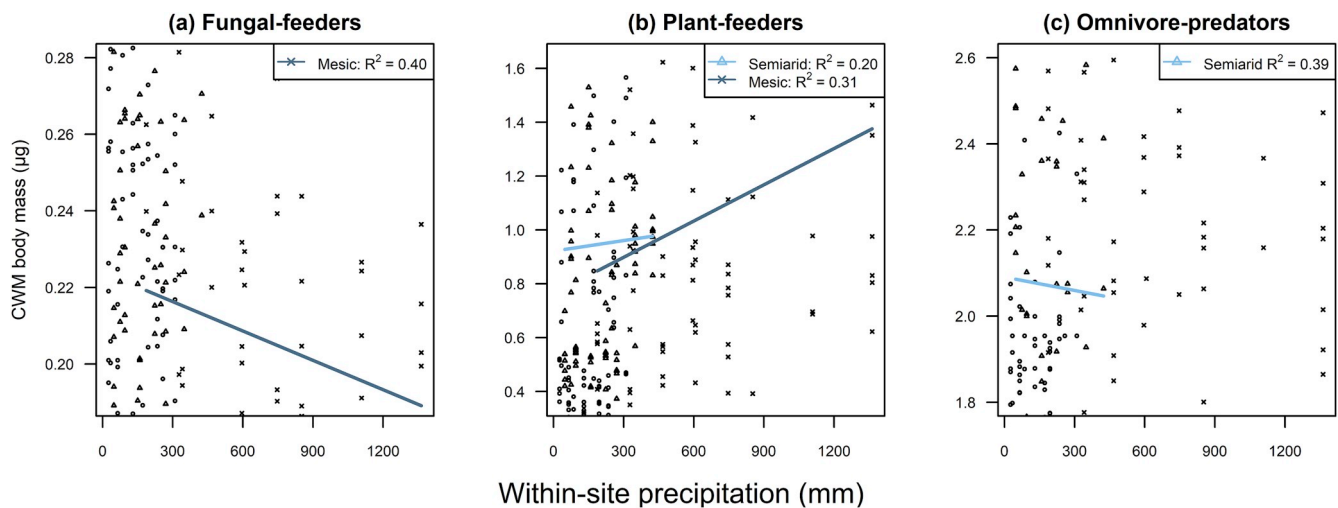


Fig. 3. Relationship between CWM body mass and within-site precipitation in three feeding groups, with statistically supported regression lines and their marginal R^2 , and different symbols by site (dots = Arid, triangles = Semi-arid, crosses = Mesic). Changes in precipitation through time within sites (x axis) resulted from a combination of variability between years and rainfall manipulation treatments. For visual clarity, points outside the interquartile range are not shown here.

shaped nematode body size via mechanisms other than resource availability. It is well-known that, due to fundamental physiological responses, warming generally causes downsizing in ectotherms (Gardner et al., 2011; but see Blanckenhorn and Demont, 2004). However, such association mostly consists of intraspecific variation, not necessarily community structure (our focus here). The two levels should not be confounded (Blackburn et al., 1999): knowing that individuals within a taxon tend to be smaller under given conditions does not imply that the community has more small-bodied taxa as well. Finally, body size shifts in response to temporal change are not the same as patterns along spatial gradients, and there is only a handful of examples that dominance of small-bodied invertebrates increases along natural warming gradients (Holmstrup et al., 2018; Robinson et al., 2018). Having said that, it is not implausible that the low CWM values in the Arid site were partly selected by the higher soil temperatures. Differences in plant species composition could also have played a role, for example through different root exudates and effects on resource availability.

4.2. Weak and context-dependent effects of temporal changes in precipitation

Investigating trait responses to temporal precipitation changes has important implications in the context of climate change. We expected the response to precipitation change to be weak in the Arid site, strong in the Semi-arid site, and null in the Mesic site. At the whole-community level, this was not confirmed. Our finding that body size varied more clearly between sites than according to the local experimental gradients mirrors results in terms of abundance (Franco et al., 2019). More broadly, it is consistent with the fact that primary productivity varies more between ecosystems of contrasting long-term water availability than as a result of temporal precipitation changes locally (Knapp et al., 2017b).

When analysing feeding groups separately (Fig. 3), some relationships of CWM mass with within-site precipitation change did emerge in Semi-arid and Mesic sites but not in the Arid site, in partial agreement with our predictions. Our interpretation is that water availability limitations at low MAP were so strong that neither two years of drought nor of high rainfall had sizeable effect on body size traits as already shaped by aridity. Note that some of the largest-bodied genera occurred also in the Arid site (e.g. *Xiphinema* sp.), but CWM mass would not have been biased due to their low abundance. Soil nematode abundance in arid grasslands is quite robust to rainfall fluctuations (Freckman et al., 1987; Sylvain et al., 2014; Vandegehuchte et al., 2015), and our results

indicate that their body size structure is even less responsive.

The relationships that we report between feeding groups and rainfall in the Semi-arid and Mesic sites could not have been predicted based on abundance data alone. In the Mesic site all feeding groups except predators declined in abundance as rainfall increased (Franco et al., 2019), but only the CWM mass of fungal-feeders also fell, and that of plant-feeders increased along the within-site precipitation gradient. These discrepancies show that functional shifts in community composition not captured by abundance data alone can be detected with trait CWM analyses (Gagic et al., 2015), and that shifts in abundance and community trait composition are not necessarily coupled.

4.3. Trophic position and community-weighted mean body size

Our hypothesis that CWM mass patterns differed by feeding groups was supported, although the results were more complex than expected. The most conspicuous discrepancy is that CWM mass of fungal-feeders was lowest in the Mesic site (Fig. 2), and increasing precipitation within this site resulted in further downsizing of these nematodes (Fig. 3). It is worth noting that this group has the fewest genera (6 across all sites) and the lowest CWM mass. We expected that fungal-feeders would be non-responsive given their generally small body size, which makes them presumably less likely to be directly affected by reduction of water-filled pore space. The negative response to precipitation in the Mesic site is difficult to explain based on our data, but top-down effects of predatory nematodes might have contributed (Franco et al., 2019). Another possibility is that the wetter conditions further promoted the bacterial against the fungal energy channel in the soil food web, depriving the larger fungivores of resources.

The pattern observed at the whole-community level was confirmed in plant-feeders and, partly, bacterial-feeders (Fig. 2). The CWM mass of omnivore-predators was highest in the Semi-arid site, particularly at the low end of the within-site precipitation gradient (Fig. 3), rather than in the Mesic site or at high precipitation. Body size shifts in nematode communities are often partly or largely ascribed to responses of omnivore-predators (Niklaus et al., 2003; Liu et al., 2015; Zhao et al., 2015), which include large and sensitive taxa, but in this study they did not determine the total pattern. While predators may be particularly important in driving body size shifts in animal communities (Chen and Wise, 1999; O'Gorman et al., 2017), in this study we found a stronger contribution of lower consumers. In fact, the strongest body size patterns in relation to MAP, as well as to within-site precipitation gradients, was that of plant-feeders. These were also the only group in which CWM

mass was higher in the wetter of the two years across sites, that is, 2017 in Arid and Semi-arid and 2016 in Mesic (Fig. S2). Although such interannual differences should be interpreted with caution (e.g. due to possible temporal legacies), they match the main results in suggesting that plant-feeding nematodes have a tighter ecological linkage to water availability than other soil nematodes, presumably due to the direct dependence on plant growth. This was not a foregone result, because other morpho-functional traits (e.g. stylet length, or whether the nematode is an endo- or an ectoparasite of roots) have the potential to offset the positive relationship between resource availability and body size in plant-feeding nematodes (Verschoor et al., 2001).

4.4. Implications and conclusions

In contrast to a large body of research on how invertebrate body size varies with temperature and latitude, the role of precipitation has been almost neglected. Besides pointing to gaps in fundamental ecology, this also limits our ability to inform experiments and models on how body size and related traits may shift under climate change, which is leading not only to warmer temperatures but also to alterations in rainfall and soil moisture. Here we contribute to address this timely knowledge gap by focusing on a globally important group of invertebrates, soil nematodes. In our study, higher precipitation is positively linked with large-bodied taxa in soil nematode communities, but MAP has greater effects than two years of rainfall manipulations, despite the latter including extremely dry and wet conditions. This suggests that community body size of soil fauna may be predicted based on long-term conditions of precipitation. However, discrepancies between feeding groups indicate that community-level data may obscure ecologically meaningful patterns, that is, morphologically similar taxa in multitrophic invertebrate communities may not respond to water availability in the same way. The total absence of temporal change of precipitation effects at low MAP suggests that the community size structure determined by long-term aridity is unlikely to undergo shifts under climate change unless there are lasting alterations.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.107638>.

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