

INVITED REVIEW

Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems

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Abstract

Altered precipitation patterns resulting from climate change will have particularly significant consequences in water-limited ecosystems, such as arid to semi-arid ecosystems, where discontinuous inputs of water control biological processes. Given that these ecosystems cover more than a third of Earth's terrestrial surface, it is important to understand how they respond to such alterations. Altered water availability may impact both aboveground and belowground communities and the interactions between these, with potential impacts on ecosystem functioning; however, most studies to date have focused exclusively on vegetation responses to altered precipitation regimes. To synthesize our understanding of potential climate change impacts on dryland ecosystems, we present here a review of current literature that reports the effects of precipitation events and altered precipitation regimes on belowground biota and biogeochemical cycling. Increased precipitation generally increases microbial biomass and fungal:bacterial ratio. Few studies report responses to reduced precipitation but the effects likely counter those of increased precipitation. Altered precipitation regimes have also been found to alter microbial community composition but broader generalizations are difficult to make. Changes in event size and frequency influences invertebrate activity and density with cascading impacts on the soil food web, which will likely impact carbon and nutrient pools. The long-term implications for biogeochemical cycling are inconclusive but several studies suggest that increased aridity may cause decoupling of carbon and nutrient cycling. We propose a new conceptual framework that incorporates hierarchical biotic responses to individual precipitation events more explicitly, including moderation of microbial activity and biomass by invertebrate grazing, and use this framework to make some predictions on impacts of altered precipitation regimes in terms of event size and frequency as well as mean annual precipitation. While our understanding of dryland ecosystems is improving, there is still a great need for longer term *in situ* manipulations of precipitation regime to test our model.

Keywords: arid, biogeochemistry, climate change, dryland, microbes, nutrient dynamics, precipitation, semi-arid, soil fauna, soil respiration

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Introduction

More than a third of Earth's land surface area is classified as arid to semi-arid ecosystems (henceforth drylands), where the main constraint on biological activity is water availability (Noy-Meir, 1973; Stafford Smith & Morton, 1990; Collins *et al.*, 2008). In drylands, episodic precipitation events trigger a rapid pulse of biological activity, the size of which is moderated by the timing and magnitude of the event (Le Houerou, 1984; Gutierrez & Whitford, 1987; Schwinning & Sala, 2004; Sher *et al.*, 2004). Aboveground and belowground

communities interact to determine net biogeochemical fluxes; e.g., microbial mineralization makes nutrients available for plant uptake to determine retention vs. leaching. However, they differ in the spatial and temporal scales at which they function (Schwinning & Sala, 2004), with implication for ecosystem responses to precipitation events. While even minor precipitation events may trigger a microbial response (Huxman *et al.*, 2004; Potts *et al.*, 2006), many events are either too small, isolated in time, or decoupled from other resources such as nitrogen (N) and organic matter to stimulate a vascular plant response (Stafford Smith & Morton, 1990; but see Sala & Lauenroth, 1982 about the response of shallow-rooted plants to small events). Consequently, changes in the spatial and temporal availability of water could moderate biotic interactions, potentially causing trophic

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cascades and even ecosystem state changes. Given their extent, and that these ecosystems support a substantial proportion of the human population (Reynolds *et al.*, 2007), understanding potential climate change implications for dryland ecosystems is of great significance.

Global circulation models (GCMs) predict that the precipitation regimes in drylands will change during the 21st Century (e.g., IPCC, 2013). Dryland ecosystems are generally dominated by small rainfall events, but there is substantial variation in current precipitation regimes and projected changes among dryland ecosystems globally (Sala *et al.*, 1992; Golluscio *et al.*, 1998). For example, Australian drylands are dominated by many small events and a few large events (Stafford Smith & Morton, 1990) but the region is predicted to experience greater variability in precipitation and an increased frequency of extreme climatic events (Garnaut, 2008). Southwestern North America is predicted to become more arid over the next years-to-decades, with more intense, sporadic precipitation events delivering less water overall (Noy-Meir, 1973; Seager *et al.*, 2007; Christensen *et al.*, 2007), whereas other areas such as the Colorado Plateau may experience more frequent but smaller precipitation events (Zelikova *et al.*, 2012). Recently, precipitation in arid and semi-arid northern China has been increasingly delivered by highly variable heavy events (Liu *et al.*, 2005; Iwao & Takahashi, 2006), which is projected to continue to increase annual precipitation amounts (Min *et al.*, 2004; Zhang *et al.*, 2006; IPCC, 2013). Moreover, most GCMs predict an increased frequency of climate extremes, including more frequent and severe droughts and heavy precipitation events (Groisman & Knight, 2008; Karl *et al.*, 2008), which are likely to have disproportionately large impacts on ecosystems (Smith, 2011). Such alterations in precipitation patterns, including both amount of water and pattern of delivery, may have particularly significant consequences in vulnerable, water-limited dryland ecosystems (Austin *et al.*, 2004).

Much research has been conducted to determine how dryland ecosystems respond to increased and reduced precipitation, but most studies have largely focused on the response of plant communities. It is clear that plant communities generally respond to altered precipitation in terms of growth, resource use, and community composition, although responses vary among ecosystems and species. For example, drought decreases plant growth in some cases (Fay *et al.*, 2003; Heisler-White *et al.*, 2008; Hartmann & Niklaus, 2012), but not others (Kreyling *et al.*, 2008; Fay *et al.*, 2011; Jentsch *et al.*, 2011). Pulses, on the other hand, increase plant growth (Kreyling *et al.*, 2008; Notaro *et al.*, 2010) and extreme precipitation events can lead to plant community composition changes (e.g., Morecroft *et al.*, 2004).

By contrast, much less is known about the implications of altered precipitation regimes for belowground dryland communities and nutrient dynamics, though there is a growing body of literature that focuses on soil microbes (e.g., Clark *et al.*, 2009; Cregger *et al.*, 2012; Manzoni *et al.*, 2012). This is reflected in models of dryland processes, such as the Pulse-Reserve model (Reynolds *et al.*, 2004) and Threshold-Delay Nutrient Dynamics (TDND; Collins *et al.*, 2008) model that focus on the role of vegetation and microbes but do not account for the activities of soil fauna such as nematodes and microarthropods. These fauna influence microbial abundance, activity, and turnover (e.g., Griffiths, 1994; Cole *et al.*, 2004), and may be key in moderating microbial responses to altered climate (A'Bear *et al.*, 2012). For instance, a recent study showed that drought and increased temperature impact top-down effects of predatory soil invertebrates in an agricultural soil (Lang *et al.*, 2014). While many studies have shown impacts of altered precipitation regimes on soil biota in mesic ecosystems (e.g., reviewed by Borken & Matzner, 2009), results are ecosystem dependent (e.g., Stafford Smith & Morton, 1990), and relatively fewer studies have taken place in drylands than other ecosystems. Hence, there is a need to review published literature reporting impacts of altered precipitation regimes focusing on soil microbes, invertebrates, and the biogeochemical pools and fluxes for which they are responsible in dryland ecosystems to promote our understanding of climate change impacts and directing future research.

Here, we provide an overview of the published literature concerning the impacts of altered precipitation regime on soil properties, including microbial and invertebrate communities and their associated biogeochemical properties, in dryland ecosystems. We define drylands as systems with a mean annual precipitation (MAP) below 600 mm and where potential evapotranspiration exceeds precipitation as it is broadly accepted that such ecosystems are largely constrained by water (e.g., Noy-Meir, 1973; Austin *et al.*, 2004). This definition incorporates dryland ecosystems that differ in precipitation patterns, including arid deserts (both hot and cold), semi-arid shrublands and grasslands, and some Mediterranean ecosystems. We include an overview of observed belowground responses to single (artificial and natural) precipitation events as well as larger scale precipitation manipulations as this information provides an essential insight into biotic responses that can be used to make predictions about longer term responses. We limited our search to studies that had a significant belowground component as plant related responses to single precipitation events and altered precipitation regimes have been discussed in detail

elsewhere (e.g., Noy-Meir, 1973; Collins *et al.*, 2008). As such, this review is not exhaustive but rather meant to reflect the state of our understanding of belowground responses to precipitation regime in dryland ecosystems. Following the available literature, our discussion is focused mostly on microbial and invertebrate communities, and soil carbon (C) and N pools and fluxes. We discuss the results in the context of understanding how responses differ within and across ecosystems particularly with regard to MAP and current precipitation pattern (i.e., seasonality, event size, and frequency). From this, we developed a conceptual framework that expands the traditional pulse-reserve (Reynolds *et al.*, 2004) and TDND (Collins *et al.*, 2008) models for predicting potential impacts of altered precipitation regimes on soil communities and associated biogeochemical processes in dryland ecosystems, and use this to make predictions about the future state of dryland ecosystems under potential changes in precipitation regime. Finally, we outline key knowledge gaps that should be targeted in future experiments.

Belowground biotic responses to precipitation

Our review of the literature revealed only 20 journal articles that explicitly report on responses of microbial and/or invertebrate biomass and community composition to manipulation of precipitation under field conditions in drylands (Table S1). Of these, three investigated biotic responses to single artificial precipitation events, ten investigated responses to increased precipitation whereas only three investigated responses to both increased and decreased precipitation, and four investigated responses to altered frequency (more frequent, but smaller events).

Biotic responses to precipitation events

We found only a few studies that investigated the response of soil biota to precipitation events *in situ*. In a semi-arid steppe in Colorado, microbial biomass N increased rapidly after both a 10 and 20 mm pulse with greater responses observed in the larger event, suggesting that precipitation size moderated biotic responses (Dijkstra *et al.*, 2012). However, microbial biomass N peaked after 3 days and reverted to control levels within 10 days in both pulse sizes indicating that microbial responses to precipitation events are rapid but short-lived. In a Chihuahuan Desert shrubland, a precipitation event had no significant influence on the abundance of bacteria or protozoa for 8 days after wetting (Whitford *et al.*, 1981). The proportion of active nematodes, however, increased rapidly after the precipitation event, and as the soil moisture levels decreased

the proportion of inactive (anhydrobiotic) nematodes increased again. The activity of nematodes appeared to be limited below 5% soil water content. This suggests that only precipitation events that increase the soil water content beyond this threshold allow microbial grazing by nematodes (Whitford *et al.*, 1981). Another study similarly found that weekly 6 mm and monthly 25 mm precipitation events had no influence on nematode densities, but that irrigation induced activity in nematodes with the greatest response observed in the monthly event treatment (Freckman *et al.*, 1987). Increased grazing by invertebrates under a wetter climate or a climate where larger precipitation events become more prominent could have cascading impacts throughout the soil food web, and may explain why some studies have observed limited, or even negative, effects of precipitation on microbial biomass.

A few laboratory studies provide further insight into the biotic responses to water pulses. In an incubation study using soils from beneath two plant species in a semi-arid ecosystem in Rush Valley, Utah, microbial biomass was found to increase significantly after a 16-mm equivalent precipitation event (Saetre & Stark, 2005). Microbial biomass peaked after about 2 days and was possibly limited by available labile C content. Similarly, amoeba biomass increased after wetting and peaked at around 2–4 days postwetting. By contrast, protozoan biomass showed no significant response to the precipitation event, while nematode abundances decreased (Saetre & Stark, 2005). The decrease in nematode abundance appeared to be an unintentional effect of the experimental design, and this could have masked potential grazer effects on microbial biomass. Indeed, during a follow up study using less intrusive methods nematode abundances increased after a simulated precipitation event (Saetre & Stark, 2005). The 'activation' of soil invertebrate feeding should be explicitly incorporated into nutrient cycling models as grazing on microbes could significantly moderate microbial activity as well as biomass and through this nutrient cycling. This is supported by the finding of Jacobson & Jacobson (1998) who found limited cellulose decomposition in the Namib Desert takes place during dry periods and only rain events greater than 9 mm significantly increase rates of decomposition. The authors found that substrates were impacted by fungi, termites and tenebrionid beetle larvae (which were observed to feed on the litter/fungi on litter) after wetting (Jacobson & Jacobson, 1998).

Biotic responses to in situ precipitation manipulations

The most commonly reported soil biotic response to reduced or increased precipitation is microbial biomass.

Of the eleven papers that investigated microbial biomass the majority found that microbial biomass increased in response to increased precipitation (e.g., Illeris *et al.*, 2003; Liu *et al.*, 2009; Zhang *et al.*, 2013; Bell *et al.*, 2014), while three studies found no response (Bi *et al.*, 2012; Lai *et al.*, 2013; Cregger *et al.*, 2014) and two found variable context-dependent results (Cregger *et al.*, 2012; Sherman *et al.*, 2012). Only three of these papers reported responses to reduced precipitation but the results were idiosyncratic (Cregger *et al.*, 2012, 2014; Sherman *et al.*, 2012). Notably, these studies reported short-term responses to altered precipitation regime, and microbial community responses to decreased precipitation could take longer to manifest. It thus appears that an increase in precipitation is likely to stimulate microbial biomass. By extension it appears likely that increased aridity will have a negative effect on microbial biomass in the longer term, but this is yet to be confirmed experimentally.

Five studies investigated microbial community responses to altered precipitation regimes. Cregger *et al.* (2012) and Zhang *et al.* (2013) found no significant response of microbial community composition to increased precipitation. By contrast, Bell *et al.* (2014) and Sorensen *et al.* (2013) found that microbial community composition changed in response to increased precipitation, and that growing season irrigation had a positive effect on bacterial and fungal richness (Sorensen *et al.*, 2013). Moreover, two studies found that the fungi : bacteria (F : B) ratio increased in response to increased precipitation (Bi *et al.*, 2012; Bell *et al.*, 2014) further suggesting that microbial communities are likely to respond to altered precipitation regimes. Cregger *et al.* (2012) found no effect of increased precipitation on F : B ratio but did note that there was a positive relationship between F : B ratio and soil water content across all their treatment plots. The authors note that fungi may have been water limited in the drier plots. If this is the case, increased aridity may favor bacterial dominance. Moreover, the authors found that reduced precipitation caused a shift in fungal but not bacterial community composition (Cregger *et al.*, 2012). It is too early to draw any broad conclusions on the effect of altered precipitation regime on soil microbial community composition.

Very few studies have investigated the effects of increased or reduced precipitation on soil invertebrates in dryland ecosystems. In a polar desert in Taylor Valley, McMurdo Dry Valleys, Antarctica, a snow fence increased soil moisture levels (1 to 5–9%) to cause a 45% decline in abundance of the dominant invertebrate, *Scottinema lindsayae*, a nematode typically found in dry soil, but a 4-fold increase in the nematode *Eudorylaimus* sp., a species that is associated with more moist soils

within the region (Ayres *et al.*, 2010). In another study, annual water additions at three sites in Taylor Valley had no direct impacts on nematode abundances, but a flood event increased the mortality of the dominant species, *S. lindsayae*, at one of the sites (Simmons *et al.*, 2009) suggesting that polar desert nematode communities are sensitive to altered soil moisture content. Similarly, our knowledge of invertebrate community and density responses to longer term increases or reductions in precipitation in hot dryland soils is limited. One year of irrigation had no effect on the total number of soil dwelling nematodes in a Chihuahuan Desert shrubland, but there was a significant increase in plant parasitic nematode density possibly reflecting increased root biomass (Freckman *et al.*, 1987). Moreover, the contribution of trophic groups toward total biomass differed between treatments with bacterial feeders contributing more, and omnivore predators less, toward total biomass with increasing water amendments, respectively (Freckman *et al.*, 1987). A recent paper combining a natural precipitation gradient with precipitation manipulations similarly found that nematode trophic groups respond differently to changes in soil moisture content (Sylvain *et al.*, 2014). Hence, there is some evidence that increased precipitation may influence soil invertebrate activity and community composition in ways that could have cascading impacts on soil food web structure.

Biotic responses to altered precipitation frequency

An important aspect of changes in precipitation regimes is that some drylands are predicted to shift toward more frequent, but smaller, events while other drylands are predicted to see less frequent, but larger, precipitation events. Given the hierarchical response of microbes, invertebrates and vegetation, such altered regimes are likely to impact ecosystem properties and functioning. However, few studies have investigated the effects of altered event frequency and magnitude on soil biota and processes under field conditions. One notable exception is a paper by Zelikova *et al.* (2012) in which the authors investigated the effect of more precipitation events (2 mm) over three growing seasons on biological crusts and soil processes in a cool dryland grassland on the Upper Colorado Plateau, UT. Increased frequency of small events had a strong negative effect on moss cover and bacterial and fungal biomass, but had a positive effect on cyanobacterial cover (Zelikova *et al.*, 2012). Similarly, negative effects of increased frequency of small water pulses on biocrusts was found in a 2-year study in a cold dryland on the Colorado Plateau near Moab, UT (Johnson *et al.*, 2012) and in an incubation study using biocrusts collected in

a similar ecosystem (Belnap *et al.*, 2004). In essence, respiration by cyanobacteria, lichen and mosses is initiated rapidly at very low soil moisture content levels, while enzymes involved in photosynthesis require longer time to become activated. For cyanobacteria, the compensation point for C, i.e., C lost through respiration being equal to C gained through photosynthesis, is reached after approximately 30 min. If the biocrusts repeatedly dry out before the compensation point has been reached they will eventually deplete their C reserves (Johnson *et al.*, 2012). The loss of N-fixing by biocrust associated cyanobacteria could have significant implications for dryland functioning by limiting N availability (Johnson *et al.*, 2012). An increase in small precipitation events could have similar detrimental effects on C balances of plants more broadly.

Only one study has investigated the effect of altered frequency on soil fauna abundances under field conditions. 2 years of increased frequency of small (2 mm) precipitation events during the growing season increased the abundance of amoebae and the relative abundance of microphytophagous prostigmatids, but had no effect on the total abundance of microarthropods or nematodes in the Colorado Plateau desert (Darby *et al.*, 2011). The authors concluded that soil fauna are more resistant to climate change than the biological crusts. However, their results indicate that different taxa will respond to different event sizes with potential implications for food web structure, which could have broader impacts on ecosystem functioning in the longer term.

Responses of soil C and N dynamics to altered precipitation

CO₂ efflux

Soil moisture has a well-documented influence on fluxes of CO₂ through processes such as photosynthesis and respiration. Therefore, changes in precipitation pulse size or frequency can alter soil moisture to influence CO₂ fluxes. Soil respiration (R_s) is one of the most commonly measured soil biological properties in studies of altered precipitation. Of the publications yielded by our search, 50 report a measure of soil C efflux (Table S2). The studies range in geographic location, with half coming from semi-arid climates, one-third from arid drylands, and the remaining ~20% from dry Mediterranean climates. Studies were heavily weighted toward western North America (42%) and Inner Mongolia and other areas of China (38%), but we also found reports from the Mediterranean region of Europe and the Middle East (14%), as well as a small number from Greenland and Africa. Our summary focuses on

increased precipitation, given that only six studies simulated a decrease in precipitation.

These studies show that, similar to the findings of earlier reviews a decade prior (Austin *et al.*, 2004; Huxman *et al.*, 2004), R_s typically quickly increases after precipitation pulses, even within an hour, resulting from water-driven increases in microbial biomass and activity including mineralization of cytoplasmic solutes (Fierer & Schimel, 2003; Inglima *et al.*, 2009), degradation of dead cells (Blazewicz *et al.*, 2014), root respiration following enhanced photosynthesis, and degassing of soil pore space CO₂ (reviewed by Huxman *et al.*, 2004; Borken & Matzner, 2009). This pulse of CO₂ flux can account for faster C-cycling and a loss of C, often a net loss if it is greater than photosynthetic uptake where plants are present. However, these pulses of increased R_s are often short-lived. When CO₂ efflux was measured on an hourly or daily scale after wetting, almost half of the papers report that R_s returned to prewetting levels within 2 days, and over two-thirds report recovery within a week (e.g., McCrackin *et al.*, 2008; Chen *et al.*, 2009; Munson *et al.*, 2010; Zhang *et al.*, 2010; Thomas *et al.*, 2011). Many studies, ranging from arid to semi-arid to Mediterranean climates (80 mm to 560 mm MAP) report that the size of the R_s pulse (e.g., Cable & Huxman, 2004; Xu *et al.*, 2004; Talmon *et al.*, 2011; Thomey *et al.*, 2011; Su *et al.*, 2012) and the time it takes to return to background levels (Chen *et al.*, 2008; Munson *et al.*, 2010; Song *et al.*, 2012; Su *et al.*, 2012) is positively related to the size of the precipitation pulse. However, precipitation-induced increases in R_s may be resource-limited in some circumstances, in which case increasing storm sizes will not influence CO₂ flux. For example, several studies report resource limitation of pulses due to low organic matter in the soil (Sponseller, 2007; Casals *et al.*, 2009; Chen *et al.*, 2009). Notably, all three of these study sites receive >300 mm MAP, and it is possible that at these wetter sites more frequent wetting and drying is limiting the pool of available organic matter (Borken & Matzner, 2009). In addition, time since last precipitation event was an important factor determining the response to precipitation treatment. When it was tested, there were greater respiration fluxes after rain if it had been a longer time between precipitation events (e.g., Sponseller, 2007; Jenerette *et al.*, 2008; Yan *et al.*, 2009; Bowling *et al.*, 2011; Coe *et al.*, 2012; Cable *et al.*, 2013). However, these studies all have >200 mm MAP, and time since last wetting was not important in one dryland site, which the authors attribute to the fact that the site is always rather dry regardless of time since last precipitation (<200 mm MAP; Ma *et al.*, 2012; Su *et al.*, 2013). Overall, research suggests that alterations in the amount of precipitation will influence soil CO₂ flux.

Most studies focus on altering precipitation during only the rainy and/or growing season (e.g., monsoon season or winter rainy season). Less than one-fifth of the studies yielded by our search report year-round or multi-season manipulation of precipitation (Cable *et al.*, 2008; Jenerette *et al.*, 2008; Talmon *et al.*, 2011; Jenerette & Chatterjee, 2012) or year-round observations of natural precipitation (Xu *et al.*, 2004; Grünzweig *et al.*, 2009; Barron-Gafford *et al.*, 2011; Bowling *et al.*, 2011; Carbone *et al.*, 2011). This is understandable given the magnitude of a study involving rainout shelters or water addition treatments remaining in place year-round for multiple years. However, multi-season studies show that responses to altered precipitation differ with season. During seasons with low soil activity, e.g., dry or cold seasons, responses to precipitation manipulations or natural pulses are smaller (Grünzweig *et al.*, 2009; Bowling *et al.*, 2011; Coe *et al.*, 2012; Jenerette & Chatterjee, 2012; Sherman *et al.*, 2012) or may even be negative (e.g., in one cold desert; Christiansen *et al.*, 2012). Season can also influence time since last wetting, for example when comparing monsoon vs. dry season precipitation (Barron-Gafford *et al.*, 2011; Carbone *et al.*, 2011). In addition, even among those studies that only manipulate precipitation during one season, many report that wetted treatments are more temperature sensitive (e.g., Liu *et al.*, 2008; Zhang *et al.*, 2010; Bowling *et al.*, 2011; Thomas *et al.*, 2011; Vargas *et al.*, 2012) and that soil temperature determines the size of the CO₂ flux response to wetting (Chatterjee & Jenerette, 2011), suggesting that seasonal fluctuations in temperature would play an important role in determining responses to altered precipitation.

One-third of the studies reporting soil CO₂ efflux compared plant and interplant spaces. Of those, most report that the response to altered precipitation is greater under plants than in interplant spaces (Sponseller, 2007; McCrackin *et al.*, 2008; Jin *et al.*, 2009; Barron-Gafford *et al.*, 2011; Jenerette & Chatterjee, 2012; Song *et al.*, 2012; Su *et al.*, 2013). In these circumstances, it appears that resource availability (e.g., soil organic matter and nutrient availability) will influence an ecosystem's response to altered precipitation. For example, N deposition influenced interplant respiration (McCrackin *et al.*, 2008), C addition influenced soil respiration (Xiao *et al.*, 2007), and shading-induced decreases in plant C inputs to soil influenced responses to pulses (Yan *et al.*, 2011). However, sometimes there is no great difference in response (Cable *et al.*, 2008; Bowling *et al.*, 2011; Talmon *et al.*, 2011). Talmon *et al.* (2011) suggest that perhaps plant roots and soil microbes are more robust than is commonly assumed, because they are adapted to high variability in precipitation. The sites where vegetation influences CO₂ efflux range from 80 to

600 mm MAP, and the sites where there is no effect of vegetation range from 60 to 200 mm MAP, so it does not appear that climate is directly responsible for the idiosyncratic responses. Moreover, it appears that the influence of precipitation pulses on CO₂ flux is vegetation specific, causing the comparative response of plant and interplant spaces to differ even within the same ecosystem. Within the Sonoran Desert, McCrackin *et al.* (2008) reported a different response of CO₂ flux from beneath creosote vs. interplant spaces, but Cable *et al.* (2008) reported no difference in the response of soils beneath grass vs. interplant space. This may be because creosote offers a more favorable microclimate for a larger microbial community that grass would not be able to provide, or because the recalcitrance of creosote litter offers a longer lasting resource for the microbial community. A larger pool of recalcitrant litter may for example lead to an increase in fungal biomass associated with litter decomposition processes. Given the fact that plant species differ in litter quality, belowground inputs, shading, etc. it is quite likely that the response of the soil community will differ by plant species, but this is not robustly tested in individual experiments.

Several studies report the existence of thresholds, above and below which the pulse have different effects (*sensu* Schwinning & Sala, 2004). Chen *et al.* (2009) observed a threshold between 10 and 25 mm pulse sizes, below which the response was largely heterotrophic and above which autotrophs are triggered and influence respiration. Other studies show a difference in timing between autotrophic and heterotrophic respiration, possibly due to the greater depths of water infiltration required to stimulate root activity in comparison to litter and soil microbial activity (Carbone *et al.*, 2011). Some studies observe that the influence of increasing pulse sizes on soil respiration reaches an asymptote, perhaps due to substrate limitation, and above this threshold pulses have little consequences for CO₂ flux (Sponseller, 2007; Chen *et al.*, 2009) or cause a decrease in R_s (Yan *et al.*, 2010). Coe *et al.* (2012) observed a threshold in desiccation length between 5 and 10 days, above which a pulse event results in a C deficit.

The summary provided above focuses on short-term effects, and may not be representative of longer term impacts on CO₂ efflux. Very few studies report CO₂ flux annually over the duration of a long-term study. Using studies reporting results from long-term manipulations in the Chihuahuan Desert (Thomey *et al.*, 2011; Vargas *et al.*, 2012), Inner Mongolia (Liu *et al.*, 2009), and Israel (Talmon *et al.*, 2011; Sherman *et al.*, 2012), we find that repeated measurements from individual studies do not suggest a predictable change in soil CO₂ flux over time under altered precipitation regimes. Vargas

et al. (2012) and Thomey *et al.* (2011) report that both altered amount and frequency of precipitation result in an increased effect size on both CO₂ flux and its temperature sensitivity during the second year, which is reset by fire in the third year to increase again in the fourth year. However, the other studies (Liu *et al.*, 2009; Talmon *et al.*, 2011; Sherman *et al.*, 2012) report variable effect sizes over the duration of their study, with no increasing effect size over subsequent years, suggesting that annual variability in seasonal weather had a greater influence than MAP.

Nitrogen pools and fluxes

Nitrogen dynamics will also respond to altered precipitation, either through biotic (e.g., altered microbial, faunal, and plant N transformations) or abiotic (e.g., leaching; reviewed by Austin *et al.*, 2004) mechanisms. Fewer studies have investigated N pools and fluxes than CO₂ dynamics, with only 20 studies yielded by our search (Table S3). Most studies were conducted in semi-arid regions (80%), with only three studies from arid drylands and two from a Mediterranean climate. Again, studies were heavily weighted toward western North America (47%), with a few studies each from Inner Mongolia and Patagonia, and only one study each from Greenland, Israel, Africa, and Eastern Europe. Only two of the studies report year-round manipulations of precipitation, with more than two-thirds of the studies focusing on summer manipulations, and only four studies simulate decreased precipitation.

These studies show that water pulses can stimulate biological transformations of N, including microbial N uptake, gross N mineralization, ammonification, and nitrification (e.g., Schaeffer & Evans, 2005; Yahdjian & Sala, 2010; Dijkstra *et al.*, 2012; Zhou *et al.*, 2013), though one Arctic study showed a decrease in microbial and total organic N (Schaeffer *et al.*, 2013). Pulse size influences N process responses but results are idiosyncratic. For example, in one study a larger pulse resulted in a greater stimulation of N uptake, mineralization and nitrification (Dijkstra *et al.*, 2012), but in another case smaller, more frequent pulses stimulated ammonification and nitrification greater than less frequent, larger pulses (Yahdjian & Sala, 2010). Many studies report microbial responses that outlast the water pulse, still noticeable even after soil moisture has returned to background levels. However, this is not always the case, as some studies that report the duration of the response after the pulse show that N processes returned to background levels within 4–10 days (Hartley & Schlesinger, 2000; Schaeffer & Evans, 2005; Liu *et al.*, 2008; Dijkstra *et al.*, 2012). The TDND assumes that microbes respond to smaller pulses than

plants because small events only infiltrate soils at shallow depths, and that microbial responses will outlast plant responses. However, this was not the case in a short-grass steppe ecosystem (Dijkstra *et al.*, 2012). In addition, it is possible that over the course of longer term measurement periods, differences caused by water treatments may disappear. This may explain why several studies find no differences in N mineralization over precipitation gradients (Yahdjian *et al.*, 2006; McCulley *et al.*, 2009; Yahdjian & Sala, 2010) while other studies do (Delgado-Baquerizo *et al.*, 2013).

Precipitation regime can also influence gaseous losses of N from the soil. Pulses have been shown to increase NO and N₂O fluxes (Hartley & Schlesinger, 2000; Yahdjian & Sala, 2010; Chen *et al.*, 2013) although no effect on N₂O flux was observed in a semi-arid grassland in Inner Mongolia (Liu *et al.*, 2008). Drought has also been shown to increase denitrification (Evans & Burke, 2013) although the effects of precipitation may be reduced at lower temperatures (Horváth *et al.*, 2010; Chen *et al.*, 2013). By contrast, precipitation does not appear to increase ammonia volatilization when measured (Yahdjian *et al.*, 2006; Yahdjian & Sala, 2010; Schaeffer *et al.*, 2013).

Mineral nitrogen may also be lost by leaching, and NO₃[−] leaching is often stimulated by pulse events (Yahdjian & Sala, 2010; Schaeffer *et al.*, 2013). By contrast, NH₄⁺ leaching is not influenced as greatly by pulses (Yahdjian & Sala, 2010). Leaching may result in gross N loss (Dijkstra *et al.*, 2012), but the timing of altered precipitation can influence whether mineral N is lost or gained (Sorensen *et al.*, 2013), with drier sites being more susceptible to N loss (McCulley *et al.*, 2009). Alternatively, drought can increase inorganic N accumulation in soil, persisting beyond the drought treatments (Augustine & McNaughton, 2004; Evans & Burke, 2013; Cregger *et al.*, 2014).

The stimulation or inhibition of N processes caused by pulses or droughts will have a net influence on soil N pools, which are more frequently measured in studies than the processes themselves, particularly mineral NO₃[−] and NH₄⁺ pools. Most often extractable NO₃[−] decreases after precipitation events (Yahdjian *et al.*, 2006; Yahdjian & Sala, 2010; Dijkstra *et al.*, 2012; Bell *et al.*, 2014), though there are also reports of no net change in NO₃[−] pools (Schaeffer & Evans, 2005; Wang *et al.*, 2014). Soil extractable NH₄⁺ pools have been reported to decrease (Hartley & Schlesinger, 2000; Sætre & Stark, 2005; Sorensen *et al.*, 2013; Zhou *et al.*, 2013), increase (Schaeffer & Evans, 2005; Bell *et al.*, 2014), or remain the same (Yahdjian *et al.*, 2006; Evans & Burke, 2013) with added water. Such changes in soil mineral pools will influence nutrient availability for plants, but the large amount of variability in net

changes in mineral pools makes it difficult to predict the consequences of altered precipitation for nutrient availability.

While the influence of plant presence is often explored in studies of R_s , plant and interplant spaces are only compared in three studies measuring N dynamics (15% of the studies), with each study measuring a different N metric. One study in Israel found no major differences between the two on total soluble N (Sherman *et al.*, 2012) and another in Utah found no difference in gaseous N losses (Schaeffer & Evans, 2005). Only one study from the Chihuahuan Desert in New Mexico shows a differing response between under- and between shrub soils, with greater NO emissions under plant canopies (Hartley & Schlesinger, 2000).

Compared to R_s , much less is certain about how altered precipitation patterns will influence N processes. The large variability in N responses to precipitation cannot be explained by site MAP or the % change in precipitation used in the experimental treatment. Fewer studies have been conducted, with much more bias toward semi-arid ecosystems. Results to date are idiosyncratic, and potential factors such as seasonality, spatial heterogeneity (e.g., plant vs. interplant), and varying pulse size and frequency are not well explored.

Discussion

There has been an increase in studies that incorporate belowground responses to altered precipitation regimes in dryland ecosystems over the past decade, but there are substantial knowledge gaps that need to be addressed before we can fully understand climate change implications for dryland ecosystems. Our synthesis of current knowledge of biotic and biogeochemical responses to natural or simulated precipitation events and altered precipitation regimes does, however, allow us to elaborate on observed patterns and make some predictions about the potential impacts of climate change on dryland ecosystems. We start by describing how ecosystems respond to single precipitation events and then extrapolate to longer term responses to changes in precipitation amounts and regimes.

Several published reviews describe, and present models that try to explain, biotic and biogeochemical responses to precipitation events in dryland ecosystems (e.g., Reynolds *et al.*, 2004; Collins *et al.*, 2008). While these models explain a significant proportion of the variation in responses to pulse events, the data presented in this review suggest that the models need to more fully incorporate biotic responses to precipitation and implications for biogeochemical cycling and C and nutrient pools. Specifically, we argue that hierarchical biotic response thresholds (*sensu* Schwinning & Sala,

2004) and the effects of 'activation' of invertebrates need to be incorporated more explicitly in the models. We propose a modified conceptual framework (Fig. 1) that builds on the ideas presented in earlier work (e.g., Reynolds *et al.*, 2004; Collins *et al.*, 2008). Our proposed framework indicates that biotic responses to precipitation events are moderated by the amount of rain received (which in turn influence depth of infiltration), antecedent soil moisture content and temperature (or

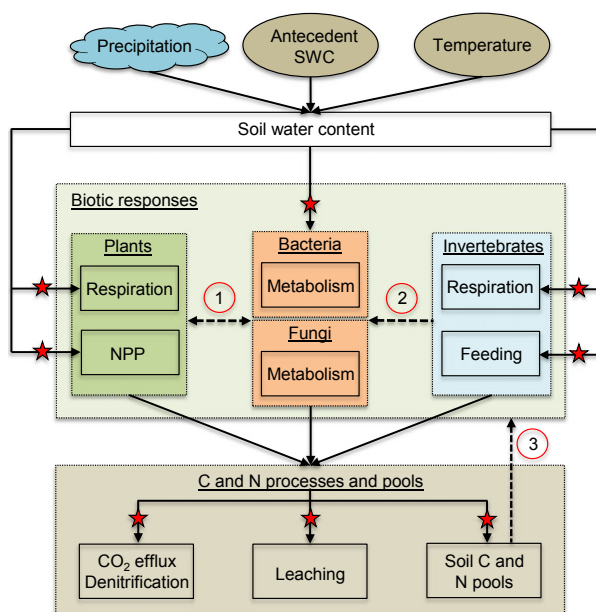


Fig. 1 Simplified overview of the effects of precipitation events on dryland ecosystems. Precipitation events stimulate the vegetation and biota, which in turn impact biogeochemical cycling and through this, ecosystem level pools of C and nutrients. Overall, the main effect of precipitation events is moderated by the amount of rain received and depth of infiltration, antecedent soil moisture content (including legacy effects) and temperature (or season). Historical precipitation regime is likely to influence biotic responses but this is not explicitly outlined. Altered precipitation regimes are predicted to change both the amount of rain received in a given pulse event as well as the time between rainfall to influence antecedent soil moisture. Responses of different organisms are induced by different event sizes (hierarchical thresholds; Fig. 2) and less water is required to induce respiration or metabolism in both plants and biota than is required for production of new biomass. These 'hierarchical thresholds' indicated by the red stars have implications for short- and long-term responses. Biotic responses, and biogeochemical cycling, are moreover moderated by interactions between plants, microbes and invertebrates as indicated by the dashed lines: 1) competition for nutrients between microbes and autotrophs; mutualistic and symbiotic effects; 2) grazing by invertebrates impact microbial activity and/or microbial biomass; and 3) indicates that biotic responses may be limited by resource availability.

season) mostly through changes in soil moisture content. All of these factors are expected to change under altered precipitation regimes. Moreover, historical precipitation regime influences how local communities respond to precipitation events (Fierer *et al.*, 2003; Evans & Wallenstein, 2012) and responses may be dampened due to resource limitation (Stafford Smith & Morton, 1990). It follows that precipitation events induce greater biotic responses when they have large impacts on soil moisture content, for example, when antecedent soil moisture is low (as after prolonged drought conditions) or during the growing season when soil moisture is most limiting, provided that the biota are not C or nutrient limited. However, biotic responses are controlled by a series of hierarchical thresholds (Fig. 2), and plants and biota generally start respiring, metabolizing or photosynthesizing (in the case of autotrophs) before they start to produce new biomass, with implications for their long-term persistence. Ultimately, the effect on biogeochemical cycling, and through this pools of C and nutrients, is governed by the degree to which plants, microbes, and invertebrates respond as well as by interactions among these biotic groups. It is important to recognize that invertebrates grazing on microbes impact both microbial activity and biomass. While prolonged periods of moist to wet conditions may be required to induce reproduction of invertebrates, even smaller events may activate feeding by at least part of the invertebrate community (e.g., Whitford *et al.*, 1981; Saetre & Stark, 2005) with potential impacts on the microbial communities. The importance of soil invertebrates in nutrient cycling is, however, likely to be proportional to the degree of wetting. Hence, the release of nutrients through invertebrate grazing activities would coincide with periods in

which plants and microbes are actively taking up nutrients.

To further define the role of hierarchical thresholds to event size in this model, we use this framework to illustrate the expected effects of different 'ecologically relevant' precipitation event sizes in dryland ecosystems (Fig. 3). A small precipitation event will have a limited impact on soil moisture content and only affect the soil surface, but may stimulate short-term microbial activity and respiration by invertebrates and shallow-rooted plants. The threshold for a net gain of photosynthetically derived C is generally not reached and autotrophs experience a loss of biomass C. Similarly, invertebrates may be respiring but unable to feed with negative effects on their C balance (Fig. 3a). A medium precipitation event will have a marked effect on soil moisture, infiltrating to greater depths, and will activate microbes, induce plant respiration as well as primary production and feeding activities by invertebrates. There will be significant interactions between biota and potential impacts on ecosystem C and nutrient pools (Fig. 3b). Lastly, a large precipitation event will similarly greatly impact soil moisture content throughout the soil profile and induce a 'full' biotic response but may lead to leaching (or run-off during storms) of C and nutrients (Fig. 3c).

This conceptual framework for impacts of single events can be used to predict longer term impacts of altered precipitation regimes when combined with knowledge from field studies manipulating precipitation regimes (Fig. 4). Our review suggests that increased precipitation will generally stimulate below-ground biomass, particularly at arid sites where water availability is the main limiting factor (Fig. 4, x-axis). By extension decreased precipitation may reduce below-ground biomass due to increased water limitation, but there are surprisingly few studies to support this hypothesis, and there is evidence that this may not occur if ecosystems are already water limited (e.g., Co-trufo *et al.*, 2011). Furthermore, both reduced and increased precipitation may lead to changes in community composition as different functional groups show varying responses to changes in soil moisture (Darby *et al.*, 2011; Cregger *et al.*, 2012; McHugh *et al.*, 2014; Sylvain *et al.*, 2014). Increased aridity may also have significant impacts on nutrient availability by reducing biological breakdown of organic matter and potentially lead to a decoupling of C, N and P cycling (Delgado-Baquerizo *et al.*, 2013; Evans & Burke, 2013). Changes in seasonal distribution of precipitation could have significant impacts mirroring those of long-term increases or decreases in MAP particularly if occurring during the growing season (e.g., Grünzweig *et al.*, 2009; Bowling *et al.*, 2011; Coe *et al.*, 2012; Sherman *et al.*, 2012).

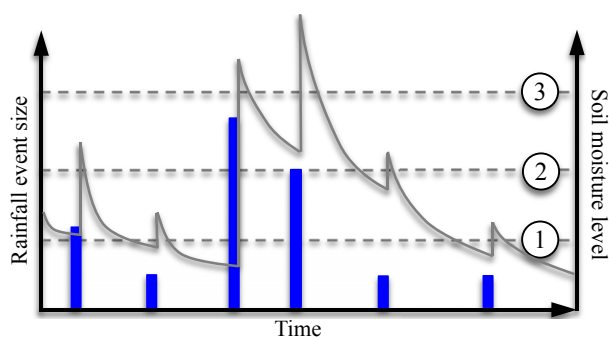


Fig. 2 Simplified representation of the theoretical relationship between precipitation event size, soil moisture, and biotic responses over time. Antecedent conditions moderate the effect of precipitation event size on soil moisture and biotic responses are governed by taxa specific soil moisture thresholds (hierarchical thresholds). The dashed lines represent hypothetical thresholds for: 1) microbes; 2) plants; and 3) soil invertebrates.

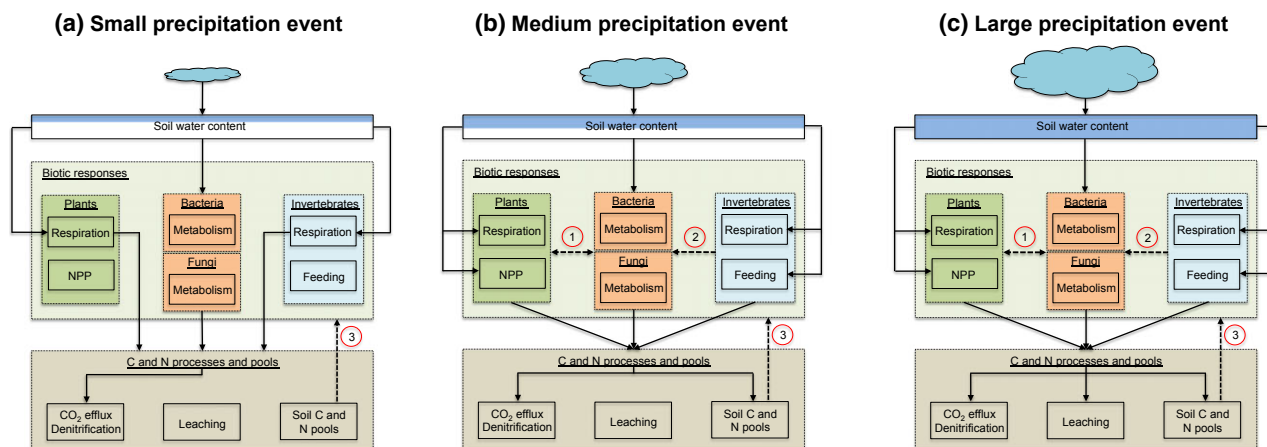


Fig. 3 A simplified cartoon illustrating the main effects of precipitation events of different sizes (in terms of 'ecological relevance') in dryland ecosystems not taking into account antecedent soil moisture or seasonal effects. (a) A small precipitation event will have limited impact on soil moisture contents and will only infiltrate the surface layer but may induce respiration by microbes, invertebrates and shallow-rooted plants which may lead to a loss of ecosystem C. (b) A medium precipitation event will have a marked effect on soil moisture and infiltrate to greater depths. Such events will activate microbial metabolism, induce plant respiration and primary production as well as grazing by invertebrates. There will be significant interactions between biota and potential impacts on ecosystem C and nutrient pools. (c) A large precipitation event will similarly greatly impact soil moisture, in this case throughout the soil profile, and induce a full biotic response but may lead to leaching (or run-off during storms) of C and nutrients. In each case lines indicate pathways that have been induced by the event. As outlined in Fig. 1 effect sizes will be influenced by historical precipitation regime. The dashed lines indicate: 1) interactions between plants and microbes including competition for nutrients, mutualistic and symbiotic effects; 2) that grazing by invertebrates impact microbial activity and/or microbial biomass; and 3) that biotic responses may be limited by resource availability.

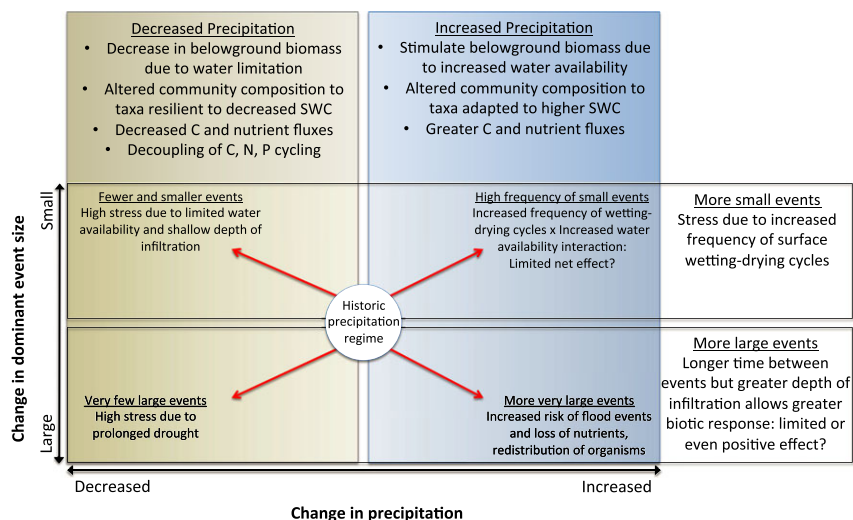


Fig. 4 Conceptual diagram illustrating the likely effects of altered precipitation regime in terms of changes in event size and frequency and mean annual precipitation on dryland ecosystem properties. Reduced precipitation is likely to increase physiological stress due to lower moisture availability with impacts on vegetation and biota alike and cause a decoupling of C and nutrient cycles. Similarly, a shift toward a regime dominated by many small events or a shift toward a regime dominated by a few large events is likely to cause increased physiological stress. A high frequency of small precipitation events may induce mortality and shifts in community composition through wetting-drying cycles while prolonged periods of drought may induce mortality due to dehydration in poorly adapted species. Simultaneous changes in event size, and frequency, and mean annual precipitation may interact to compound or alleviate impacts depending on current climatic conditions.

Shifts in the frequency and event size are also likely to have significant impacts on dryland ecosystems (Fig. 4, y-axis). Our framework suggests that a shift toward smaller event sizes may have a general negative effect on vegetation and soil microbial and invertebrate communities in dryland ecosystems (e.g., Johnson *et al.*, 2012; Zelikova *et al.*, 2012). As outlined earlier, respiration and photosynthesis are induced at different moisture levels, and repeated wetting without reaching the photosynthetic compensation point may lead to mortality of the autotroph. We recognize that this is difficult to model, given that the compensation point will differ among types of autotrophs, but the mechanism should be taken into account. Similarly, a series of water pulses that induce soil invertebrate activity without enough time to feed and compensate for biomass C lost through respiration may cause increased mortality. This is particularly relevant for organisms such as nematodes that enter anhydrobiosis during extended drought periods. As many dryland soil invertebrates are microbial grazers, a decrease in their densities due to the stress of the drying-wetting cycles could have cascading impacts on microbial biomass. A net gain in microbial biomass is, however, only likely where the positive effects of release from grazing outweighs that of the increased stress related to lower moisture availability. Impacts are likely to be greater in regions already dominated by small events such as Australian drylands (Stafford Smith & Morton, 1990) and the North American short-grass steppe (Sala & Lauenroth, 1982). These ecosystems already experience a high frequency of wetting events that only infiltrate the surface layers, and a decrease in average event size could negatively impact plant and biotic communities through increased stress associated with wetting-drying cycles. Moreover, the impacts of a shift toward smaller precipitation events is likely to be exacerbated if it is associated with a decrease in precipitation, whereas increased precipitation may ameliorate the effect of reduced event size due to an increase in event frequency if this allow greater retention of soil moisture.

A shift toward larger events may similarly influence the biota but we find it unlikely to have as adverse effects as a shift toward more small events unless it is associated with a decrease in precipitation (Fig. 4). The depth of water infiltration is greater during large rainfall events and the soils are likely to remain moist for longer, which allows all organisms including microbes, soil invertebrates, and plants to take advantage of the improved conditions. Dependent on current conditions, a shift toward less frequent but larger events may allow increased net primary productivity and keep organisms active for longer as long as the event does not cause local flooding and associated loss of nutrients and soil

through surface run-off. The increased time between events that would be associated with such a regime shift may impact some organisms, but most dryland organisms are well adapted to periods of drought to survive these conditions. A shift toward larger events and reduced precipitation is likely to increase the risk of prolonged droughts with potential negative impacts on biotic communities. By contrast, a shift toward larger events and increased precipitation could have positive impacts on biotic communities but may increase the risk of heavy downpours. There is virtually no information about potential impacts of prolonged droughts or heavy precipitation events on dryland ecosystems. We hypothesize that the impacts of prolonged droughts will be greater in semi-arid than arid ecosystems, because in arid ecosystems the organisms already experience longer periods without available water and are likely better adapted to such conditions. Heavy downpours by contrast could lead to loss of nutrients, organic matter, and soil through leaching or overland flow (Yahdjian & Sala, 2010), but may also serve to redistribute organisms and nutrients within the landscape (e.g., Nielsen *et al.*, 2012). Longer term belowground responses may also be induced indirectly through changes in plant community structure (i.e., biomass, rooting depth etc.) and plant functional and species composition (Heisler-White *et al.*, 2008; Kreyling *et al.*, 2008; de Graaff *et al.*, 2014).

Future research directions

We have a fairly good understanding of vegetation responses to altered precipitation regimes but few studies incorporate belowground responses in terms of soil biota and biogeochemical cycling. Although still limited there is an increasing amount of data on microbial responses to altered precipitation regimes but few studies investigate the impacts on, and consequences of, the structure and activity of soil invertebrate communities. Moreover, observed belowground responses are often idiosyncratic and context dependent particularly with regard to N processes, microbial community and invertebrate responses to altered precipitation regimes. Importantly, these idiosyncrasies may be due to taxa specific responses to altered precipitation regimes and subsequent changes in biotic interactions. For example, increased activity of soil invertebrates may influence nutrient availability by disrupting the microbial community with potential consequences for plant growth and ecosystem processes. Furthermore, there is evidence that even when no microbial community responses are evident at the DNA level there may be responses at the rRNA level in seasonally dry ecosystems (Cruz-Martínez *et al.*, 2009; Barnard *et al.*, 2013;

Blazewicz *et al.*, 2014). Such changes indicate a potential for altered ecosystem functioning and should be investigated further. Hence, there is a great need for studies taking a more whole systems approach to quantifying effects of altered precipitation regimes in dryland ecosystems, and studies that quantify high-resolution changes in microbial and invertebrate activity and biomass with links to ecosystem functioning could be highly influential.

The effect of single precipitation events on soil CO₂ efflux has been fairly well studied, but longer term responses of C fluxes and pools to altered precipitation regimes are less well understood. Similarly, our understanding of N fluxes and pools to altered precipitation regimes is limited, while data on phosphorus (P) and other nutrients are virtually nonexistent, limited to a few studies that measure PO₄³⁻ pools or enzyme activity (e.g., Ochoa-Hueso *et al.*, 2014; Wang *et al.*, 2014). This is problematic as a recent global scale study indicated that increased aridity in drylands may lead to a decoupling of soil C, N, and P cycles as C and N availability is primarily controlled by biological processes such as decomposition, while P is more strongly influenced by geochemical processes (Delgado-Baquerizo *et al.*, 2013). Hence, there is a need for more long-term studies that explicitly investigate soil C and nutrient dynamics under altered precipitation regimes and link this to biotic responses from primary producers to top predators.

Finally, many of the published studies focus on ecosystems with mean annual precipitation in the range of 200 to 400 mm with less studies targeting the more extreme climates. Including a broader range of precipitation levels would allow us to determine whether ecosystem responses shift across a precipitation gradient. We stress that studies on altered precipitation regime impacts on dryland ecosystems (and elsewhere) should consider manipulating both the amount of precipitation (i.e., increased and decreased) as well as event size and frequency, seasonal shifts in rainfall distribution, and extreme events. Fewer than 20% of studies quantified the impacts of decreased precipitation, though it is predicted to occur in many locations, and there is a great need to study its impacts across a variety of these ecosystems. Efforts should also be made to diversify the regions studied, given that most of what is known comes from North American southwest and Inner Mongolia, with much still to be understood about other dryland ecosystems.

Conclusions

We have presented an overview of the current literature on impacts of precipitation events and altered

precipitation regimes on dryland soil biota and C and nutrient dynamics. We then used a conceptual diagram focusing on belowground responses to precipitation pulses to predict potential belowground responses to altered rainfall regime in terms of both amounts and event size and frequency. Overall, we demonstrate that altered precipitation patterns will significantly impact soil biology and associated biogeochemistry, though the precise outcome will be ecosystem dependent. The modified model we propose includes soil invertebrates and the hierarchical thresholds of response to aid in the prediction of outcomes for a given ecosystem and its characteristic community and historical precipitation regime. However, to make broad conclusions about the impact of altered precipitation on belowground ecosystems, there is a mandatory need for more long-term studies that (i) focus on decreased precipitation and altered frequency in addition to the impacts of increased pulses; (ii) focus on soil invertebrate responses to these manipulations; and (iii) cover a wider geographic area to even out current geographic biases. Some coordinated global efforts are underway, such as the International Drought Experiment (www.drought-net.org/), and more efforts should be geared toward this and other similar projects.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of literature reporting on the response of soil biotic communities to single precipitation events or altered precipitation regimes in arid and semi-arid ecosystems.

Table S2. Summary of results from the literature reporting the response of soil CO₂ efflux under natural and manipulated precipitation in arid and semi-arid ecosystems.

Table S3. Summary of results from the literature reporting the response of soil nutrient pools and fluxes under natural and manipulated precipitation in arid and semi-arid ecosystems.