

The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem

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Abstract. Climate change is occurring globally, with wide ranging impacts on organisms and ecosystems alike. While most studies focus on increases in mean temperatures and changes in precipitation, there is growing evidence that an increase in extreme events may be particularly important to altering ecosystem structure and function. During extreme events organisms encounter environmental conditions well beyond the range normally experienced. Such conditions may cause rapid changes in community composition and ecosystem states. We present the impact of an extreme pulse event (a flood) on soil communities in an Antarctic polar desert. Taylor Valley, McMurdo Dry Valleys, is dominated by large expanses of dry, saline soils. During the austral summer, melting of glaciers, snow patches and subsurface ice supplies water to ephemeral streams and wetlands. We show how the activation of a non-annual ephemeral stream, Wormherder Creek, and the associated wetland during an exceptional high-flow event alters soil properties and communities. The flow of water increased soil water availability and decreased salinity within the wetted zone compared with the surrounding dry soils. We propose that periodic leaching of salts from flooding reduces soil osmotic stress to levels that are more favorable for soil organisms, improving the habitat suitability, which has a strong positive effect on soil animal abundance and diversity. Moreover, we found that communities differentiated along a soil moisture gradient and that overland water flow created greater connectivity within the landscape, and is expected to promote soil faunal dispersal. Thus, floods can ‘precondition’ soils to support belowground communities by creating conditions below or above key environmental thresholds. We conclude that pulse events can have significant long-term impacts on soil habitat suitability, and knowledge of pulse events is essential for understanding the present distribution and functioning of communities in soil ecosystems.

Key words: Antarctica; ecosystem connectivity; extreme events; floods; Nematoda; polar desert; pulse events; Rotifera; soil fauna; Tardigrada.

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INTRODUCTION

Global surface air temperatures increased by 0.6°C during the 20th century (and 0.74°C between 1906 and 2005), and are predicted to increase a further 1.1–6.4°C by the end of the 21st century (IPCC 2007). Precipitation regimes are expected to change in concert with the predicted temperature changes but are more difficult to forecast (IPCC 2007). Considering the strong link between climate and living organisms, it is not surprising that such changes have already had an impact on communities as well as ecosystems across the globe. There are many examples of climate change impacts on organisms' behavior and phenology, including earlier bud burst, altered time of flowering (mainly earlier), range shifts (generally poleward or toward higher elevations), and asynchrony between predator and prey as well as insects and their plant hosts (i.e., due to unequal shifts in emergence from hibernation, peak abundances or biomass, etc.), and in some cases species extinctions (e.g., Walther et al. 2002). At larger scales, there is clear evidence of significant shifts in vegetation type and composition, particularly at high altitude and latitudes, often with unpredictable consequences for ecosystem function and potential cascading feedbacks to climate change (e.g., Wookey et al. 2009).

The number of studies that manipulate temperature and precipitation rates and/or patterns have increased rapidly over the last few decades in an effort to investigate the potential impacts of the predicted climate changes. However, the methods used to experimentally simulate such climate changes are often poor proxies for changes observed in and predicted for natural systems (Bokhorst et al. 2011). Moreover, as the recent meta-analyses of Blankinship et al. (2011) and Wu et al. (2011) show, the results of such climate change manipulations can be idiosyncratic, and the outcome often depends on local climate, ecosystem type and the type of organisms being studied (i.e., soil biota and plants in Blankinship et al. (2011) and Wu et al. (2011), respectively). For instance, increases in temperature and precipitation generally stimulate plant growth and ecosystem carbon (C) flux, while decreases in precipitation have the opposite effect (Wu et al. 2011). Similarly, increasing rates

of precipitation generally have a positive influence on soil biota in boreal, coniferous and deciduous forests but not in grassland, heath or tundra ecosystems (Blankinship et al. 2011). However, increasing temperatures generally have a negative influence on soil biota (measured as biomass or density) in drier sites and a positive influence in wetter sites, although the effect is taxon-dependent (Blankinship et al. 2011).

There are, however, other aspects of the predicted climate changes that may have a far greater impact than changes in mean annual temperature and precipitation. It has been predicted that the frequency of extreme events, such as high or low temperature, drought or heavy rainfall, and severe storms, is likely to accompany the increases in temperature and changed precipitation patterns (IPCC 2007). Sarewitz and Pielke (2001) defined an extreme event as an occurrence 'that, relative to some class of related occurrences, are either notable, rare, unique, profound, or otherwise significant in terms of their impacts, effects, or outcomes'. However, what we consider to be an extreme climatic event may not necessarily result in an extreme ecological response (Arnone et al. 2011, Jentsch et al. 2011, Smith 2011b). Hence, Smith (2011a) suggested that a true extreme climatic event should be defined as 'an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or functioning well outside the bounds of what is considered typical or normal variability'. We follow the latter definition throughout this article.

There is increasing evidence that extreme events may have disproportionately large impacts on Earth's communities and ecosystems (Jentsch and Beierkuhnlein 2008; Smith 2011b). Extended periods and greater magnitudes of drought and increased temperatures have, for example, been linked to widespread increased tree mortality observed across the globe since 1970 (Allen et al. 2010). Some other commonly encountered effects of extreme events include reduced above- and belowground productivity, altered species compensation, reduced reproductive success and altered phenology, although the realized impact of such events depends on current conditions and timing of the event (Jentsch et al. 2007). The

effects of extreme events can have great and long lasting impacts on ecosystems, despite the short temporal scale at which they exert their influences on organisms and ecosystems (Barrett et al. 2008, Smith 2011a). Extreme events even have the capacity to push ecosystems from one stable state to another stable state, and recovery to the initial state may not take place even after conditions returns to normal as exemplified by Allen and Breshears (1998).

Our knowledge about how extreme events influence communities and ecosystems, and in particular how this may affect ecosystem services and, through this, human well-being, is still limited (Jentsch and Beierkuhnlein 2008) and complicated by the complex interactions between ecological thresholds and feedbacks discontinuous in time and space (Peters et al. 2004). However, some ecosystems show characteristics that make it easier to identify and quantify climate change responses, and we may be able to utilize the responses observed in such systems to explore the underlying mechanisms responsible for the observed patterns. Such knowledge could help prediction of responses in other ecosystem types. In particular, ‘simple’ (in terms of species richness) communities such as those found in desert ecosystems can provide valuable insight because (1) community and ecosystem responses to climate changes are easier to observe in ecosystems with species poor communities (Wall 2007), and (2) climate changes may have a disproportionately high impact on species poor ecosystems as there appears to be less redundancy in these systems (e.g., Nielsen et al. 2011a).

Water pulses are important to organisms in many ecosystems, but particularly in the arid and semi-arid ecosystems. Organisms inhabiting desert ecosystems are generally well-adapted to the lack of water and most can survive extended periods without any available water (Crawford 1981, Wharton 2002). Once water becomes available, plants and animals respond immediately to take advantage of the improved conditions (Huxman et al. 2004, Schwinning and Sala 2004). These pulses of water can however be of such a magnitude as to be considered extreme climatic events (floods) that have large-scale impacts on above- and belowground communities (*sensu* Smith 2011a). Considering the large proportion of water limited ecosystems world-

wide (‘drylands’ cover more than 40% of Earth’s land surface area and this estimate does not include the polar deserts; Millennium Ecosystem Assessment 2005) a change in water availability through floods may have large-scale impacts. While a flood could be seen as a large-scale disturbance in many types of environments through the removal of biomass and substrate, the positive effects associated with such a pulse of water delivered in otherwise water limited systems may outweigh the negative effects.

In the polar deserts of Antarctica, moist soils are most often associated with the shorelines of consistent water bodies such as lakes and streams (Gooseff et al. 2011), though some water tracks (zero-order seeps of water along hillslopes) that emerge primarily from melting snow patches also occur (Levy et al. 2011). In the McMurdo Dry Valleys (MDVs) annual stream flow is relatively predictable and limited to a few months during the austral summer due to very low annual temperatures. However, in the summer of 2001–02, an extreme climatic event in the form of exceptionally high temperatures (daily average temperature $>2^{\circ}\text{C}$ above the 10 year mean; Barrett et al. 2008), resulted in a dramatic increase in the availability of water across the landscape beyond the established stream channels (including the formation of isolated melts and wetlands; Barrett et al. 2008). As well as a substantial, long-term impact on soil moistures throughout Taylor Valley, MDVs (Barrett et al. 2008), this event had long lasting impacts on soil chemistry and was linked to changes in soil community composition and species abundances (Wall 2007, Simmons et al. 2009).

Here we build on the observations made by Wall (2007) and Simmons et al. (2009) and report the impacts of a new high flow event, which occurred in the summer of 2008–09, on soil communities within Wormherder Creek (WHC) and the associated wetland (henceforth the WHC watershed). While the 2001–02 flood event was mainly driven by high temperatures, the flood event in 2008–09 was associated with more moderate temperatures (degree days above freezing for surface air temperatures at Lake Bonney, Taylor Valley was 99.5 in 2001–02 and 52.5 in 2008–09 compared with a long-term average of 42.6 for 1993–94 to 2009–10; Nielsen

et al., *unpublished data*) and high solar radiation (McKnight et al., *unpublished data*). Our results show that (1) biotic and abiotic responses to the flood were evident immediately after the flood as well as in the following non-flood year, (2) the flow of water through the soil may ‘pre-condition’ the soils for successful colonization by soil fauna, and (3) the extent of wetting influences community composition. The study area will continue to be monitored by the McMurdo Long-Term Ecological Research program to follow the development of soil communities in response to an expected increase in the frequency of high-flow events.

METHODS

Sampling area

The study area is located in Taylor Valley ($77^{\circ}42' S$, $162^{\circ}18' E$), MDVs, continental East Antarctica. The landscape is a polar desert with average annual temperatures of c. $-17.5^{\circ}C$ and very limited precipitation (<100 mm; Fountain et al. 1999). Most of the soils are therefore extremely dry, and often highly saline, with significant impacts on the distribution of soil fauna (e.g., Powers et al. 1998, Courtright et al. 2001, Poage et al. 2008), and the soil faunal communities are generally limited to a few species of nematodes, tardigrades and rotifers (Freckman and Virginia 1997, Adams et al. 2006). The MDVs saw a general climate cooling trend in the last part of the 20th century but this trend was interrupted by discrete warming events similar in magnitude to ones that occurred sporadically during the previous half century (Bomblies et al. 2001, Doran et al. 2002, Lyons et al. 2005). These infrequent warm summer events lead to significant increases in water flow through snow and glacial melt and the reactivation of non-annual ephemeral streams, such as WHC that drains into Lake Bonney (Wall 2007, Barrett et al. 2008, Simmons et al. 2009). As mentioned above, WHC was last activated in the summer of 2008–09, and before that in 2001–02, and these events had a substantial impact on the water availability within the WHC watershed (Fig. 1).

During the high-flow event in 2008–09, we recorded the extent of the ‘wetted zone’, i.e., the soils that were visibly influenced by the run-off (Fig. 2). We then established 39 permanent

sampling points within the wetted zone (henceforth ‘in-flow’ samples) to explore the distribution of soil fauna in relation to the hydrological patterns during the high-flow event (McKnight et al., *unpublished data*). In the 2009–10 field season, we established 3 transects spanning the watershed and measured how the previous year’s high-flow event influenced soils by comparing soils within the wetted area to the soils outside the flow (i.e., compared ‘wet’ and ‘dry’ soils). All transects were arranged approximately perpendicular to the slope of the hill with transect 1 (T1) at the highest elevation (~105 m a.s.l.) and transect 3 (T3) at the lowest elevation (~55 m a.s.l.). Fifty-one permanent sampling points were marked along the transects depending on local topography (T1 = 19 sampling points; T2 = 17 sampling points; T3 = 15 sampling points). We collected the highest number of samples near the boundary between the ‘dry’ and the ‘wet’ zone (25 m interval) and less within and outside the wetted area (50 m interval; Fig. 2). Samples were labeled ‘dry’ if they were collected outside the wetted area, and ‘wet’ if they were collected inside the wetted area. However, three samples located inside the wetted zone on T1 (9 to 11) were situated on a small mound and did not get wet during the flood. These were subsequently labeled as ‘dry’. ‘Dry’ therefore included samples 1–5, 9–11 and 16–19 on T1; samples 1–6 and 15–17 on T2; and samples 1–5 and 12–15 on T3. ‘Wet’ samples include the remaining samples along the transects and the 39 in-flow samples. Thus, there were 29 and 61 ‘dry’ and ‘wet’ samples, respectively. The 90 sampling points (39 in-flow and 51 along transects) have been permanently marked to allow monitoring in the years to come.

Soil fauna and chemistry

We collected samples for extraction of soil fauna and chemistry at the 39 in-flow sampling points within the wetted zone in January 2009 (at the end of the 2008–09 summer season), and at all 90 sampling points in January 2010 (at the end of the 2009–10 summer season one year later). Samples were collected with a sterile scoop to about 10 cm depth and transferred into a sterile Whirlpack (~1 kg soil per sampling point), homogenized gently and stored in ice chests during transport to the Crary lab at McMurdo Station. Once the samples arrived in the lab, they

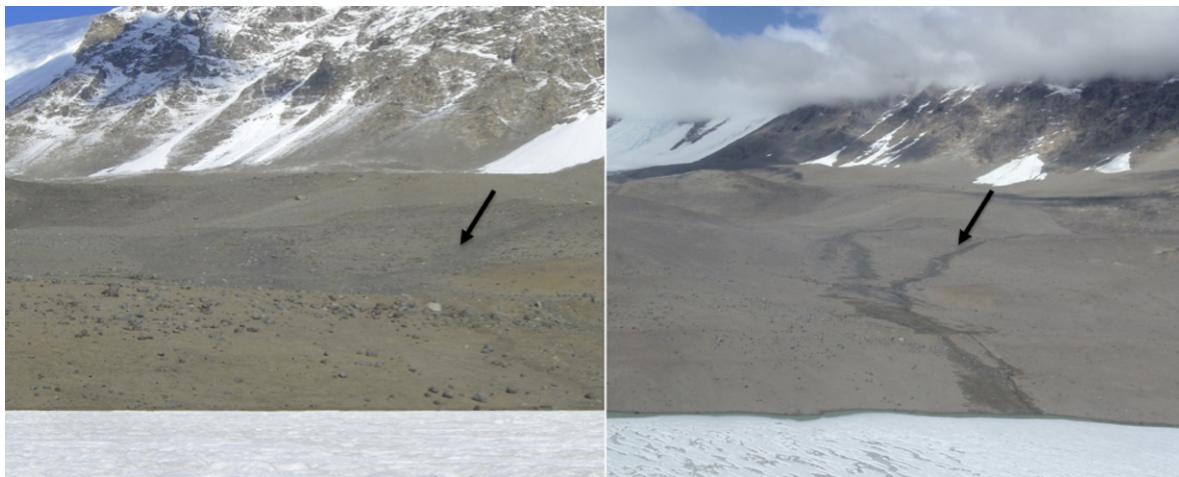


Fig. 1. View of Wormherder Creek during a normal year (left) and during the high-flow event in 2008–09 (right). Notice the extended wetted area during the high-flow event. The main branch of Wormherder Creek is denoted by an arrow in each photo.

were stored at +4°C until processed. Soil fauna were extracted within two days of sampling from approximately 100 g wet soil using a standard sugar centrifugation method (Freckman et al. 1977). All nematodes were identified to species level and classified as male, female or juvenile for both living and dead individuals, and live rotifers and tardigrades were counted. Counts were transformed to individuals per kg dry soil.

Soil moisture was estimated by drying approximately 50 grams of soil at 105°C for 24 hrs and calculated as the percentage of dry soil (i.e., % dry weight). Sub-samples for soil chemistry were frozen at -20°C, shipped to Dartmouth College and kept frozen until analyses were performed. pH was measured using a 2:1 water : soil dilution with a standard pH electrode (VWR 8015 pH meter) (Barrett et al. 2004). Electrical conductivity (EC) was measured using an Orion 160 EC meter on a 5:1 DI water : soil dilution by weight and reported as $\mu\text{S}/\text{cm}$. Measurements were calibrated by measuring the conductivity of a standard solution of 0.01 M KCl and correcting values for the influence of solution temperature (Barrett et al. 2004).

For measurements of extractable phosphate (PO_4^3- -P), 10 ± 0.5 g soil was extracted in 50 ml 0.5 M NaHCO_3 at pH 8.5. The samples were decanted into centrifuge tubes and spun at $27,216 \times g$ for 10 min. The supernatant was poured into a Nalgene bottle, through a 0.45 μm

nylon filter to remove remaining sediment where necessary, and 3 ml of 6 N HCl was added to each sample. The samples were allowed to degas prior to being frozen until run on a Lachat Autoanalyzer (Barrett et al. 2007). For extractable inorganic N ($\text{NO}_3^- + \text{NO}_2^-$ -N and NH_4^+ -N), 20 ± 0.5 g soil was extracted in 50 ml 2 M KCl, and then decanted into centrifuge tubes and spun 10 min at $27,216 \times g$. The supernatant was poured into a Nalgene bottle, again through a 0.45 μm filter where necessary, and frozen until run on a Lachat Autoanalyzer (Barrett et al. 2007).

Data analysis

A standard curve estimation procedure was used to explore the relationship between abundance of live individuals of each nematode species, as well as rotifer and tardigrade abundance, and environmental variables for all 2010 (post-flood) samples. Differences in soil chemistry and soil faunal abundances between 'dry' and 'wet' samples were investigated using ANOVAs.

We used non-metric multidimensional scaling (NMDS) to investigate the relationship between community composition and environmental variables using only the samples where soil fauna occurred. This approach is based on the assumption that soil fauna are limited to certain samples due to thresholds (i.e., soil moisture over a certain value, and salinity under a certain value etc.) rather than gradients, and including all

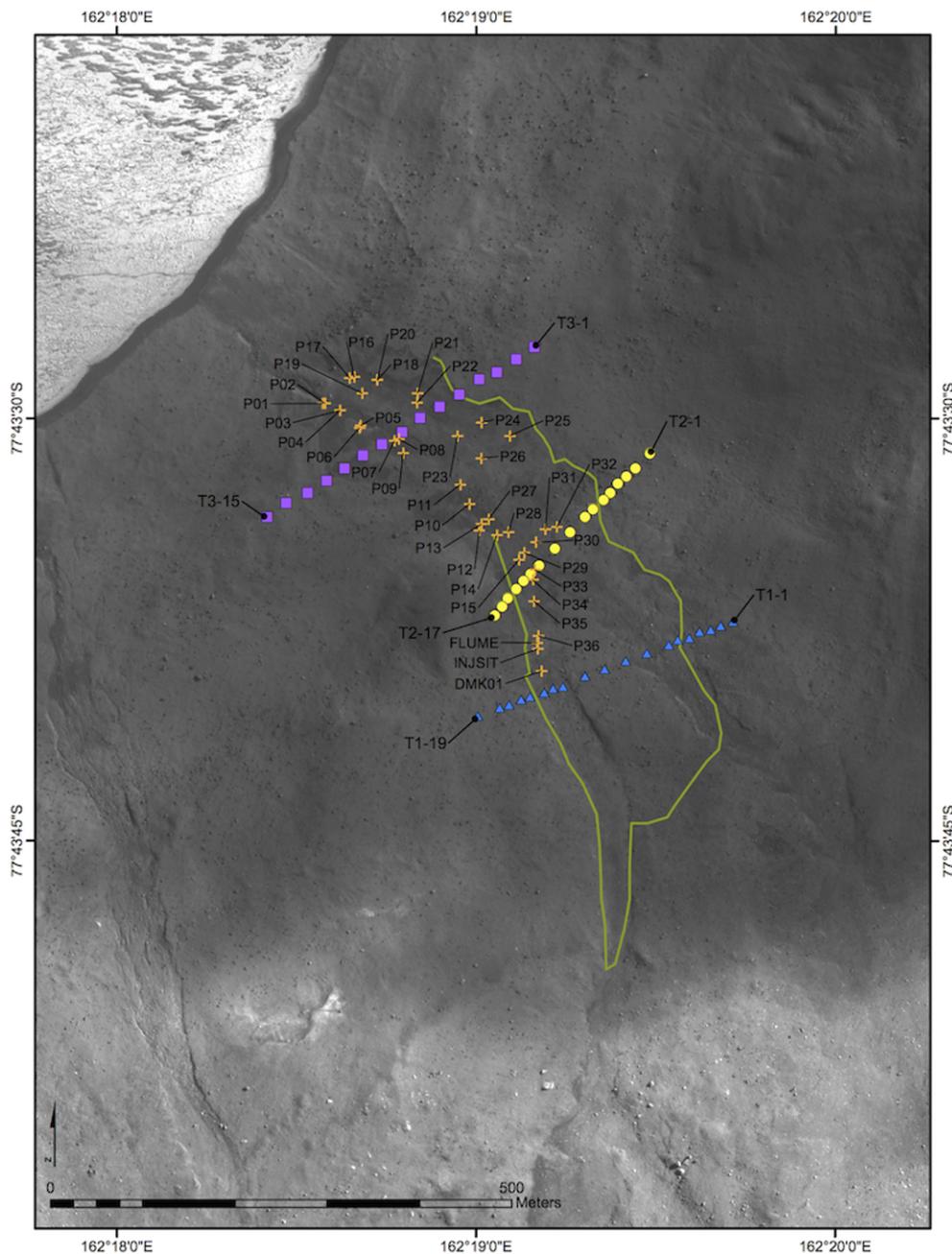


Fig. 2. Wormherder Creek watershed with sampling points and outline of the wetted area as it occurred in 2008–09. The green line represents the extent of the wetted zone. The orange crosses indicate the 39 (in-flow) sampling points established during the 2008–09 field season within the wetted zone (P01–P36; Flume; Injsit = tracer injection site; DMK-01 = background reference). The blue triangles, yellow circles and pink squares represent transect 1, 2 and 3, respectively, that were established in 2009–10. Transect 1 is located furthest uphill and transect 3 is downslope. Water flows into Lake Bonney (ice covered), which is visible in the upper left hand corner. Map compiled by Spencer Niebuhr, Antarctic Geospatial Information Center. Imagery ©DigitalGlobe, Inc.; provided by NGA Commercial Imagery Program.

Table 1. Mean \pm SE of soil properties and abundance of soil fauna measured as live individuals per kg dry soil ($\log x + 1$ transformed) in wet and dry soils within the Wormherder Creek watershed in January 2010 (in-flow and transect data combined). Superscript letters indicate significant differences between wet and dry samples.

Variable	Wet	Dry
<i>n</i>	61	29
Soil chemistry		
pH	8.9 ^A \pm 0.1	8.6 ^B \pm 0.1
Conductivity ($\mu\text{S cm}^{-1}$)	183 ^A \pm 54	1735 ^B \pm 394
PO_4 ($\mu\text{g g soil}^{-1}$)	0.44 ^A \pm 0.03	2.41 ^B \pm 1.36
$\text{NO}_2 + \text{NO}_3$ ($\mu\text{g g soil}^{-1}$)	1.75 ^A \pm 0.8	14.0 ^B \pm 4.3
NH_4 ($\mu\text{g g soil}^{-1}$)	0.11 \pm 0.01	0.18 \pm 0.05
Soil moisture (%)	2.96 ^A \pm 0.4	1.02 ^B \pm 0.16
Fauna ($\log x + 1$)		
<i>Scottnema lindsayae</i>	1.88 ^A \pm 0.11	0.55 ^B \pm 0.18
<i>Eudorylaimus</i> spp.	1.27 ^A \pm 0.10	0.13 ^B \pm 0.07
<i>Plectus murrayi</i>	0.31 ^A \pm 0.10	0.00 ^B \pm 0.00
Tardigrades	0.90 ^A \pm 0.12	0.08 ^B \pm 0.08
Rotifers	0.31 ^A \pm 0.09	0.00 ^B \pm 0.00

samples would impair the strength and ecological relevance of the analysis. Chi-squared tests of threshold values obtained by visual inspection of the curve estimations supported this notion (data not shown). Threshold values were set as the value that best represented the main proportion of samples with individuals of the species in question. It should be noted that several variables might preclude certain taxa simultaneously. Finally we compared soil chemistry and soil faunal abundance of the 39 samples collected within the wetted zone between the two field seasons using paired *t*-tests to determine interannual variation in these variables.

Data were $\log(x + 1)$ transformed when necessary. Curve estimations, ANOVAs and paired *t*-tests were performed using PASW v.18 (IBM, Chicago, Illinois, USA) and the NMDS based on Bray-Curtis dissimilarities was performed in R (R Development Core Team 2009) using the package *vegan*, and the relationship with environmental variables was explored using the function *envfit*.

RESULTS

The flow pattern in the WHC watershed has a dramatic impact on local soil chemistry. As expected, the in-flow soil samples collected during the high-flow event in January 2009 were

considerably wetter than those collected from the same sampling points in January 2010 (11.19% \pm 0.69 SE and 3.75% \pm 0.56 SE dry weight for 2009 and 2010 samples, respectively; $t_{38} = 9.169$, $p < 0.001$) reflecting the change in water availability within the wetted zone between the two seasons. However, the samples collected in January 2010 also showed lower pH values ($t_{38} = 3.410$, $p < 0.01$) and $\text{PO}_4\text{-P}$ ($t_{38} = 6.463$, $p < 0.001$), and an increase in $\text{NH}_4\text{-N}$ ($t_{37} = -9.314$, $p < 0.001$). Moreover, there was also a small albeit significant drop in the abundance of *S. lindsayae* ($t_{38} = 2.530$, $p < 0.05$) as well as *Eudorylaimus* spp. ($t_{38} = 3.687$, $p < 0.01$) between January 2009 and January 2010 within the in-flow samples.

Despite the change in soil biogeochemistry between seasons, the impact of the high-flow event in 2009 was still evident in 2010. Of the 90 samples collected in January 2010, those collected within the wetted zone ('wet', $n = 61$) were significantly moister and less saline (lower EC), and had lower concentrations of $\text{PO}_4\text{-P}$ and $\text{NO}_3 + \text{NO}_2\text{-N}$ and higher pH values than those collected outside the wetted zone ('dry', $n = 29$; Table 1). Similarly, we observed a substantial difference in soil communities between dry and wet soils. Wet soil had significantly higher densities of *Scottnema lindsayae*, *Eudorylaimus* spp. and tardigrades than dry soil, and *Plectus murrayi* and rotifers were not observed outside the wetted zone at all (Table 1, Fig. 3).

When we explored the relationships between soil fauna and environmental variables using the in-flow and transect samples collected in the 2009–10 field season, it appeared that the abundance of all faunal groups was most closely related to soil moisture (data not shown). However, the explanatory value was always low, and on closer inspection of the graphs, it is apparent that thresholds rather than gradients limit most groups (Fig. 4). *S. lindsayae*, *Eudorylaimus* spp. and tardigrades appear to be limited by high salinity in particular, and each taxon only occurred in one sample with EC above $\sim 330 \mu\text{S/cm}$ (Fig. 4). *P. murrayi* and rotifers appeared more restricted by soil moisture. Rotifers did not occur in any, and *P. murrayi* only occurred in two samples with soil moisture contents below c. 2.9% (a rather arbitrary value considering the large fluctuation in soil moistures between dry and wet years). Although chi-square tests suggest that the above mentioned

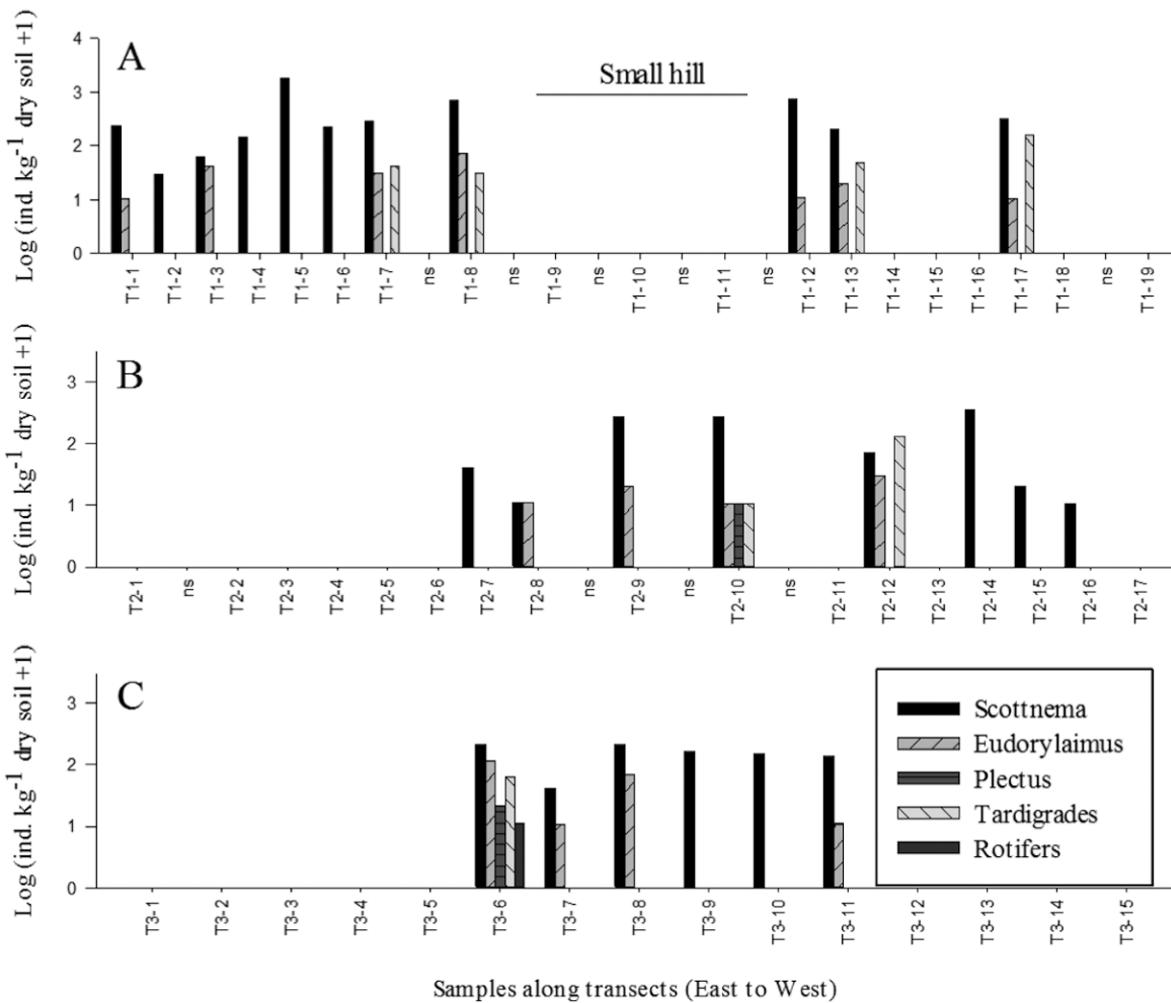


Fig. 3. Occurrence and abundance (individuals kg^{-1} dry soil) of live nematodes, rotifers and tardigrades along the three transects in January 2010. Transect 1 and 2 are presented in 25 m increments while transect 3 is presented in 50 m increments. Notice the presence of a small mound on transect 1 (i.e., samples T1-9 to T1-11). These samples did not get wet during the high-flow event.

threshold values are statistically significant for all groups (*S. lindsayae*, *Eudorylaimus* spp., *P. murrayi* and rotifers: $p < 0.001$; Tardigrades: $p < 0.01$) it needs to be noted that several environmental factors change simultaneously and that different groups may be responding singly, or to combinations of these variables. For example, *P. murrayi* and rotifer occurrence is best predicted using soil moisture values. Yet, if salinity had been high, which it is unlikely to be in moist soils in this particular watershed, such conditions would undoubtedly also have excluded their presence.

Considering the clear evidence of these threshold values, we excluded samples that did not

contain any animals from our NMDS analysis to obtain the most ecologically relevant view of the influence of environmental gradients on soil faunal communities within the watershed. The NMDS was performed on 63 samples and showed that overall community composition of soil fauna was significantly related to soil moisture content and $\text{NO}_2 + \text{NO}_3\text{-N}$ concentrations (Fig. 5). However, soil moisture alone could explain almost 54% of the variation in abundance of the different groups between the samples. The NMDS suggested that *S. lindsayae* dominates at low soil moistures, while *P. murrayi* and rotifers become more dominant at the highest soil moistures.

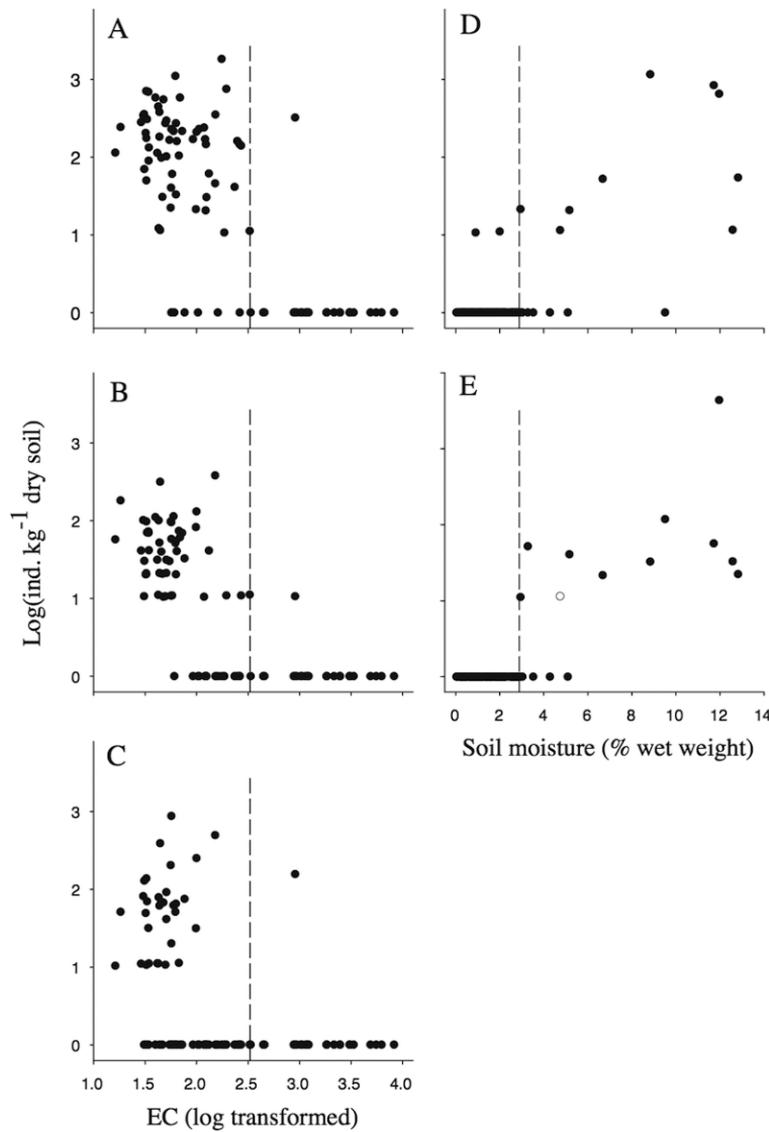


Fig. 4. Abundance of live *S. lindsayae* (A), *Eudorylaimus* spp. (B) and tardigrades (C) plotted against electrical conductivity (EC) and the abundance of *P. murrayi* (D) and rotifers (E) plotted against soil moisture content (using samples collected in January 2010 only for all groups). The relationship between faunal abundances and EC are not significant, but notice that soil fauna are limited to samples with relatively low EC (only 1 sample with an EC above $\sim 330 \mu\text{S}/\text{cm}$ has live individuals). There is a significant albeit weak relationship between the abundance of *P. murrayi* and rotifers with soil moisture ($p < 0.05$ for both). However, rotifers are not found in samples with soil moistures $<2.9\%$ and *P. murrayi* are only found in two such samples. This indicates the existence of threshold values for all faunal groups within the system. Visually estimated thresholds for EC and soil moisture are indicated by the stippled lines for each of the biotic groups.

DISCUSSION

In hot deserts, water pulses arise from rainfall events, whereas abnormally hot and sunny

summers lead to water pulses in the polar desert of the MDVs due to greater melt from glacier surfaces and potentially of sub-surface ice. This melt contributes to the activation of non-annual

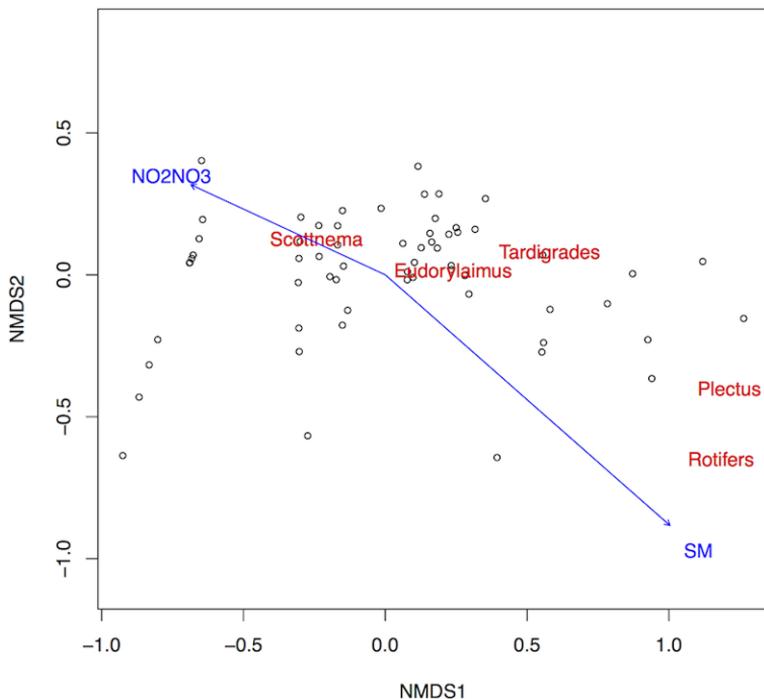


Fig. 5. Non-metric multidimensional scaling based on Bray-Curtis similarities of community composition in soil samples where soil fauna were present ($n = 63$) with the relationship with environmental factors overlain. Open dots represent samples and samples that are placed close to each other within the ordination space have more similar faunal communities than samples more distant to each other. The positioning of faunal group names indicates the relative dominance of faunal groups within the ordination space. Vectors indicate the relationship between environmental variables and community composition across the samples. Only variables that showed a significant relationship with community composition are presented (SM: $R^2 = 0.54$, $p < 0.001$; NO₂NO₃: $R^2 = 0.17$, $p < 0.01$). Stress = 0.1. Abbreviations: SM = soil moisture; NO₂NO₃ = NO₂ + NO₃-N.

ephemeral streams and wetlands, such as Wormherder Creek and its associated wetland (the WHC watershed), which has substantial impacts on soil moisture availability and salinity (Wall 2007, Simmons et al. 2009). These changes are likely to have a strong impact on the composition of belowground communities as high soil salinity appears to be a limiting factor for the presence of living soil fauna within the MDVs (Moorhead et al. 2003, Nkem et al. 2006a), and community composition has been related to soil moisture availability (Treonis et al. 1999, Poage et al. 2008, Ayres et al. 2010). The results presented here, and in Wall (2007) and Simmons et al. (2009), support this hypothesis.

Our results furthermore suggest that a pulse of water can ‘precondition’ soils for the successful colonization by soil fauna and lead to substantial alterations in belowground communities through

the leaching of salts as well as by increasing soil moisture availability. During the previous high-flow event, which occurred in 2001–02, a long-term experimental plot meant to represent a dry site became inundated (Wall 2007, Simmons et al. 2009). Although the flood interfered with the experimental treatments, this event allowed the authors to investigate the impact of these types of pulse events on belowground communities. Their results showed an increase in soil moisture and a decrease in salinity, and changes in the composition of belowground communities similar to those observed in this study (Wall 2007, Simmons et al. 2009). We found a similar soil biogeochemical response to the 2008–09 flood and conclude that, besides being wetter, soils subjected to a flood were considerably less saline, and had lower concentrations of PO₄-P and NO₂ + NO₃-N as well as slightly higher pH values,

than soil samples collected outside the area that was flooded. Together this accumulating information suggests that the flow of water through the soil within the watershed during these high-flow events leads to a significant leaching of salts and nutrients (Lyons et al. 2005, Barrett et al. 2008, Simmons et al. 2009). While the slight increase in pH value may impact on the microbial communities, which are known to be strongly influenced by pH-value (Lauber et al. 2009), it is unlikely to have a strong direct impact on the faunal communities. By contrast, the observed increase in soil water availability and the greatly reduced salinity will directly impact on the soil fauna communities (e.g., Freckman and Virginia 1997, Virginia and Wall 1999, Courtright et al. 2001). Accordingly, soil fauna abundances were significantly higher in soil samples collected within the wetted zone for all groups, and *P. murrayi* and rotifers were not found in dry soils at all. This suggests that salt concentrations need to get below a certain threshold value before successful colonization by soil fauna can take place.

While the threshold values for salinity presented here ($\sim 330 \mu\text{S cm}^{-1}$) are higher than those mentioned elsewhere ($\sim 200 \mu\text{S cm}^{-1}$ in Poage et al. 2008) it is important to note that such values will depend on the type of salts present in the soils. For example, Nkem et al. (2006a) showed that *S. lindsayae* and *P. antarcticus* are more sensitive to increased concentrations of nitrate salts than chloride or sulfates. It is interesting that the NMDS presented here suggests that higher abundances of soil fauna is also associated with lower concentrations of $\text{NO}_3 + \text{NO}_2\text{-N}$, a pattern that has been observed before (Poage et al. 2008). Yet, some groups (rotifers and *P. murrayi*) appeared to be further limited by a soil moisture threshold suggesting that species are likely to show idiosyncratic responses to water pulses depending on the impact on soil geochemistry.

In addition, our results suggest that once the soil has been preconditioned, soil fauna can begin to colonize and establish viable populations, but eventually the communities will conform to environmental characteristics as species find their ‘optimal’ microhabitat based on niche differentiation mainly along a soil moisture gradient. The soil fauna groups found

within the MDVs are well known to show habitat preferences (e.g., Nielsen et al. 2011b) and the results from this study match those findings. The unusually inhospitable soil conditions outside the wetted area are highlighted by the very low occurrence of *S. lindsayae*. While this nematode is often found in the drier, saltier soils throughout the MDVs (Adams et al. 2007), it appears that the conditions of the soils outside the wetted zone in the WHC watershed are so harsh that even this species is unable to sustain viable populations.

The rate of community development will depend somewhat on the dispersal of soil fauna. Within the WHC watershed dispersal appears to be correlated with the connectivity to other landscape features that serve as sources of biota for colonization (McKnight et al., *unpublished data*). In particular, it appears that overland flow, but not subsurface lateral flow, can create connectivity within the watershed and enhance colonization through increased dispersal opportunities (McKnight et al., *unpublished data*). Similarly, there is evidence that as in other terrestrial ecosystems, soil fauna use water as a means of dispersal within the MDVs. For instance, collembolan population structures are related to ancient lake shorelines, which suggest that they disperse by flowing along the water edge (Nolan et al. 2006), and we have observed live individuals of most invertebrate groups in plankton net samples collected from streams in the MDVs (Simmons et al., *unpublished data*). Dispersal via overland flow may be important for the soil fauna within the MDV due to the greater chance of being transported to suitable habitat that receive water flow regularly. Yet, wind dispersal allows animals to colonize hot-spots of habitable soils throughout the landscape that are not connected by flowing water and may therefore be a main factor for colonization of otherwise unconnected habitable areas (Nkem et al. 2006b, Adams et al. 2007).

It appears that the observed flood events are accelerating ecosystem change from salt accumulation patterns associated with the colder, drier period (Doran et al. 2002) to a pre-cooling ecosystem state. Whether the positive effect the flood had on the belowground communities (i.e., favorable soil conditions supporting complex soil communities) is maintained will depend on the frequency and magnitude of water pulses within

the WHC watershed in the years to come. Some of the changes in soil chemistry and soil fauna abundances observed between the 2008–09 and 2009–10 summer seasons for the samples collected within the wetted zone indicate a change towards soils more similar to those outside the wetted area (i.e., a decrease in pH, lower abundances of *S. lindsayae* and *Eudorylaimus* spp.). This suggests that although the impacts of the flood were substantial and may be long lasting (at least one year), the system may return to the original state unless another flood occurs. In light of the predicted climate changes for Antarctica, i.e., increasing temperatures and more extreme events (Tebaldi et al. 2006, Steig et al. 2009, Turner et al. 2009), it is likely that WHC will be reactivated at greater frequencies and higher magnitudes over the 21st century, and we are likely to see the formation of more ephemeral wetlands like WHC throughout the MDVs (Gooseff et al. 2011). Indeed, another albeit smaller flood event occurred in 2010–11, which had total flows that reached magnitudes about half of the total flows of the 2001–02 event. In short, what we currently interpret as extreme climatic events may become the norm in the future of the MDVs. The impact of wetting events will however be highly dependent on the magnitude of wetting and flow patterns (Levy et al. 2011), and wetting events may have negative effects on lakes and low lying soils by increasing the input of salts (Lyons et al. 2005, Ball et al. 2011). Smaller scale wetting of soils, known as water tracks, is a common occurrence within the MDVs and can both increase and decrease local soil salinity depending on the amount of water carried in the tracks and local topography (Levy et al. 2011). While water tracks with relatively high flow of water can result in significant leaching from certain soils, and thus increase habitat suitability, this leaching may result in salts being deposited in soils at lower elevations with potential negative effects on communities in these soils (Levy et al. 2011). Furthermore, salt accumulation is likely to occur near the edges of the water tracks and where water accumulates leading to evaporative concentration and soils of low habitat suitability (Levy et al. 2011). However, high-flow events on steeper hill slopes, such as the one observed in the WHC watershed, will on average likely result

in an increase in habitat suitability for soil fauna and we expect to see an overall increase in soil community complexity throughout the region in otherwise present dry and salty soils.

Besides the results presented here and in other studies from the MDVs (e.g., Wall 2007, Barrett et al. 2008, Simmons et al. 2009), few studies have documented the impacts of extreme events on belowground communities but the potential for large scale impacts is indicated by several studies. For example, a recent study showed how larger rainfall events caused a great increase in soil erosion within a watershed in semi-arid Sub-Saharan Africa but also increased infiltration rates and recharged groundwater levels (Hrachowitz et al. 2011). This is likely to have a direct impact on soil communities through removal and/or redistribution of organic material and resources, but could also have indirect effects through vegetation responses considering the strong link between belowground communities and the vegetation aboveground (e.g., Wardle 2002, Bardgett 2005, Nielsen et al. 2010). Furthermore, extreme events may impact on belowground communities through aboveground responses. For example, there is growing evidence for large-scale drought and heat-induced tree mortality occurring in recent years across the globe (e.g., Breshears et al. 2005, Allen et al. 2010). Beyond the initial impact (i.e., the die-off of overstory trees), this can result in rapid changes in vegetation cover (Mueller et al. 2005) and can have cascading and long-lasting impacts on the understory vegetation and ecosystem functioning by increasing the near ground solar radiation (Royer et al. 2011). Such aboveground vegetation responses are likely to be reflected belowground.

Conclusion

As we show here, low diversity systems provide valuable insight into how ecosystems respond to climate changes. Through this study, we have obtained a holistic view of the factors that contribute most to the realized community response within a whole watershed. Such detailed description of mechanisms underlying the present belowground community composition at the watershed level is rare and often not possible to easily obtain in more complex systems below- or aboveground. In short, our results show how

multiple ecological mechanisms (e.g., environmental thresholds; niche differentiation along environmental gradients; dispersal limitations and connectivity) may act in concert to structure soil communities over time. Such evidence is highly valuable for understanding how communities in other systems are structured and how they may respond to environmental changes, as well as for predicting how other systems may respond to climate changes. Our results also highlight that knowledge of prior events is crucial to interpret the distributional patterns we observe today. If we had not observed the high-flow events in 2001–02 and 2008–09 and recorded the outline of the wetted zone, we could only speculate about the cause of the dramatic changes in soil chemistry observed within the watershed. Such information is most easily obtained through long term monitoring.

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