

Decadal ecosystem response to an anomalous melt season in a polar desert in Antarctica

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Amplified climate change in polar regions is significantly altering regional ecosystems, yet there are few long-term records documenting these responses. The McMurdo Dry Valleys (MDV) cold desert ecosystem is the largest ice-free area of Antarctica, comprising soils, glaciers, meltwater streams and permanently ice-covered lakes. Multi-decadal records indicate that the MDV exhibited a distinct ecosystem response to an uncharacteristic austral summer and ensuing climatic shift. A decadal summer cooling phase ended in 2002 with intense glacial melt ('flood year')—a step-change in water availability triggering distinct changes in the ecosystem. Before 2002, the ecosystem exhibited synchronous behaviour: declining stream flow, decreasing lake levels, thickening lake ice cover, decreasing primary production in lakes and streams, and diminishing soil secondary production. Since 2002, summer air temperatures and solar flux have been relatively consistent, leading to lake level rise, lake ice thinning and elevated stream flow. Biological responses varied; one stream cyanobacterial mat type immediately increased production, but another stream mat type, soil invertebrates and lake primary productivity responded asynchronously a few years after 2002. This ecosystem response to a climatic anomaly demonstrates differential biological community responses to substantial perturbations, and the mediation of biological responses to climate change by changes in physical ecosystem properties.

Polar regions are experiencing amplified climate changes, such as warming in the Arctic¹, and rising sea-surface temperature and ice melt along the Antarctic Peninsula, which are associated with profound responses in terrestrial and marine food webs and ecosystem functioning^{2–6}, although there are few long-term records of polar ecosystem response⁷. Recent studies demonstrate that West Antarctica is among the most rapidly warming locations on Earth^{8,9} (+0.12 and +0.47 °C per decade from 1957 to 2006 and from 1957 to 2011, respectively). In contrast, East Antarctica has exhibited no warming trend over the period of time for which meteorological records are available^{10,11}. The McMurdo Dry Valleys (MDV) on the western edge of the Ross Sea (Fig. 1) experienced a period of cooling from 1987 to 2000, observed both in mean annual and austral summer air temperatures (−0.7 and −1.2 °C per decade, respectively)¹², accompanied by an increase in seasonally averaged solar flux (+8.1 W m^{−2} per decade) and a decrease in average wind speed (−0.23 m s^{−1} per decade)⁵ from September to May.

Changes in polar climate elicit strong responses from local ecosystems, whose resident biota are adapted to climate conditions that have been metastable for at least the past few thousand years¹³. The MDV host relatively simple food webs dominated by prokaryotic and eukaryotic microorganisms and invertebrate species. During the 1987–2000 cooling period, the aquatic and terrestrial habitats in the MDV experienced synchronous decreases in glacial meltwater

generation, stream flow, lake levels, lake primary production and soil nematode populations, and increases in lake ice thickness⁷. These parallel trends indicate that the MDV ecosystem was sensitive to declining summer air temperature throughout this period.

This trend of cooling summer air temperature and synchronous ecosystem trajectory of change ended abruptly during the 2001–2002 austral summer (the flood year). The high mean summer air temperature of that season coincided with one of the highest observed mean summer solar fluxes (Fig. 2a), generating the greatest amount of glacial meltwater since 1969 (Supplementary Fig. 1). Here, we evaluate the ecosystem responses to this flood event during a subsequent more stable climate state that followed, compared with responses observed during the cooling phase before 2002. We use a significant zero crossings (SiZer) analysis^{14,15} to identify significant changes in ecosystem drivers and associated ecosystem responses over three decades of data collection¹⁶, and sequential linear regressions to determine if significant temporal trends occurred in the time series.

Results

Analysis of mean summer air temperatures since 1987 reveals that a break in this record occurred in 2002, and the best fit to the observed data was represented by a statistically significant decreasing linear regression (−1.1 °C per decade; $P=0.05$) for the period 1986–2001

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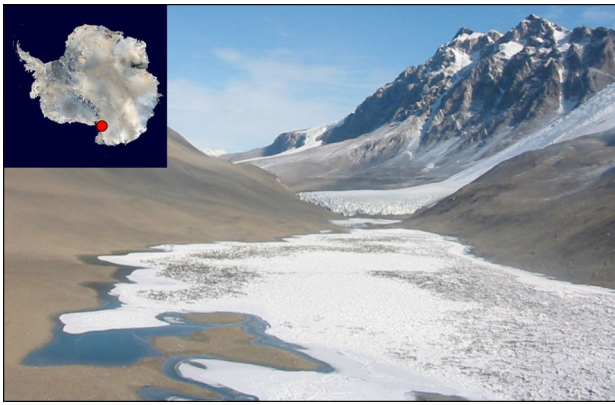


Fig. 1 | The MDV landscape (from authors' archive) with inset of location on the Antarctic continent (map image courtesy of NASA).

and no significant relationship for 2003–2013 ($+0.54^{\circ}\text{C}$ per decade; $P=0.25$) (Figs. 2a and 3a). The average mean (\pm s.d.) summer air temperatures during these periods were -4.2 (± 0.9) $^{\circ}\text{C}$ and -4.4 (± 0.5) $^{\circ}\text{C}$, respectively; thus the decadal cooling trend was followed by a decade of decreased variance in mean summer air temperatures. SiZer analyses also show two distinct periods in the record for mean summer (December–February; DJF) solar flux, increasing at a rate of 33.2 W m^{-2} per decade ($P=0.02$) from 1987 to 2001 with a mean (\pm s.d.) of 221.7 (± 21.8) W m^{-2} (Fig. 2a), followed by a period (2003–2013) with no significant temporal trend and a mean (\pm s.d.) of 234.4 (± 9.3) W m^{-2} . Of the 26 yr of record analysed here, the summer of 2001–2002 was the third warmest and had the sixth greatest solar flux (Supplementary Fig. 2). This summer was a pivot point when the summer climate shifted from the cooling period of decreasing summer air temperatures and increasing solar radiation to a period of consistently average annual summer air temperatures and high solar radiation (Fig. 3a,b).

Changes in summer climate prompted substantial responses in physical aspects of the ecosystem and, subsequently, biotic communities in streams, soils and lakes^{17,18}, the last of which are poised near the melting point of water in the austral summer. MDV streams transport meltwater from glaciers on the valley walls to lakes on the valley floor, while mobilizing solutes and sediment from stream channel weathering and erosion. Streams flow for 6–12 weeks per year and stream flow is dominated by glacial melt controlled by the surface energy balance. From 1991 to 2002, total stream flow observed in the Lake Fryxell basin (nine streams) decreased significantly ($-2.20 \times 10^9\text{ m}^3$ per decade; $P<0.01$; Fig. 2b), whereas no significant ($P>0.05$) trend in stream flow was observed after 2003, although two episodic high flow years occurred in 2009 and 2011. Mean total annual stream flow and variance (\pm s.d.) increased from 0.99×10^9 (± 0.90) m^3 for the period of 1991–2001 to 1.76×10^9 (± 1.09) m^3 for 2003–2011 ($P=0.05$).

Microbial mat communities of the MDV streams are dominated by cyanobacteria, persist in a freeze-dried state during winter and are strongly controlled by stream flow dynamics driven by seasonal climate¹⁹. In most streams, *Phormidium* spp.-dominated mats inhabit the main channel and *Nostoc* spp.-dominated mats inhabit most stream margins. Mat coverage ranges from abundant mats present throughout the channel to sparse mats in areas of stable substrate. These microbial mats also host diatom algae whose diversity is also largely controlled by stream flow dynamics; consistent-flowing streams host a greater proportion of cosmopolitan species, intermittent-flowing streams host a greater proportion of endemic species^{20,21}. In four streams with abundant mats, the biomass of *Nostoc*-dominated mats decreased from 1993 to 2003, the global minimum for the data set (-16.7 g m^{-2} per decade, $P=0.04$),

and increased from 2003 to 2011 ($+17.8\text{ g m}^{-2}$ per decade, $P=0.04$; Figs. 2c and 3c; no measurements were made in 2002). Biomass of *Phormidium*-dominated mats did not have significant trends before or after 2003, despite the indication of a decreasing trend before the flood year in the SiZer analyses (Fig. 3c). Microbial mat biomass is controlled in part by shear stresses from high flows, and the minimum biomass for the *Phormidium*-dominated mat time series was observed to occur in 2010, substantially lagging the flood year, although subsequent to one of the two most recently observed high flow years (Fig. 2b). These mats incurred an initial reduction and slow recovery to the flood event in 2002, and further reduction after another high flow year.

The closed-basin, ice-covered lakes of the MDV integrate changes in climate and the ecosystem processes that occur in their associated watersheds. Lake levels and associated volumes are maintained by a balance of inflowing glacial melt, ablation of ice covers and evaporation of open moats that form along the lake perimeter during the austral summer (Fig. 1). Perennial ice covers thickened from 1987 to 2001 on the east lobe of Lake Bonney (ELB; 0.89 m per decade, $P<0.01$) and the west lobe of Lake Bonney (WLB; 0.85 m per decade, $P<0.01$; Figs. 2d and 3d), and began to thin significantly in the flood year of 2002 (ELB: -1.20 m per decade, $P<0.01$; WLB: -0.61 m per decade, $P<0.01$; Figs. 2d and 3d). The level of Lake Bonney, which lacks stream outflow, declined from 1987 to 2001 (-0.33 m per decade, $P=0.01$) and then began to rise in the flood year of 2002 ($+2.38\text{ m}$ per decade, $P<0.01$; Figs. 2e and 3e). Underwater PAR (photosynthetically active radiation) varies due to changing lake ice thickness and optical properties of the ice covers, especially sediment content of the ice. Before 2003, underwater PAR decreased ($-6.73\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ per decade, $P=0.01$) in ELB, although no trend was observed after 2003, and no trends were observed in WLB (Figs. 2f and 3f). Primary productivity rates (PPR) in ELB and WLB decreased significantly through the cooling period ($-5.7\text{ mg C m}^{-2}\text{ d}^{-1}$ per decade, $P=0.01$; $-20.81\text{ mg C m}^{-2}\text{ d}^{-1}$ per decade, $P<0.01$, respectively; Figs. 2g and 3g). Following the flood year (2002), when a more stable climate prevailed, PPR increased significantly in WLB ($+15.3\text{ mg C m}^{-2}\text{ d}^{-1}$ per decade; $P<0.01$; Fig. 2g) but showed no significant trend in ELB.

Populations of the bacterivorous soil nematode *Scottinema lindsayae* decreased at rates in excess of 10% yr^{-1} during the cooling trend⁷. This decline has been attributed to cooling temperatures, given the sensitivity of *Scottinema* populations to temperature²². Populations of *Scottinema* decreased through 2005 (at a rate of -820 individuals per kg dry soil per decade; $P=0.02$), although the global minimum of the time series lagged the flood year, occurring in 2005. After 2002, there is no significant temporal trend in populations (Figs. 2h and 3h), possibly because of shifts in nematode community structure accompanying greater water availability following the flood in 2002. In contrast, populations of a subordinate nematode species, *Eudorylaimus* sp. (omnivore preferring wetter habitats²³), exhibited no significant piecewise linear trend prior to or after the flood year (Fig. 3h), but breakpoint analyses (Fig. 3h) indicate a positive trend through the middle of the record, when soil water content peaked following the flood event of 2002²⁴. A significant linear trend occurs over the entire period of record for *Eudorylaimus* (13.8 individuals per kg dry soil per decade; $P=0.02$; Fig. 3h, trend not shown), probably indicating a strong response to soil moisture conditions. The strongest period of increase of *Eudorylaimus* occurs shortly after the time of the flood year (Fig. 2h).

Discussion

The flood year was a pivot point for the physical state of the MDV ecosystem (for example, ice volume, melt, stream flow, lake level, ice thickness and so on), which serves as an important driver of biological community structure and its functioning. These physical states act as intermediaries between climate and biologically mediated

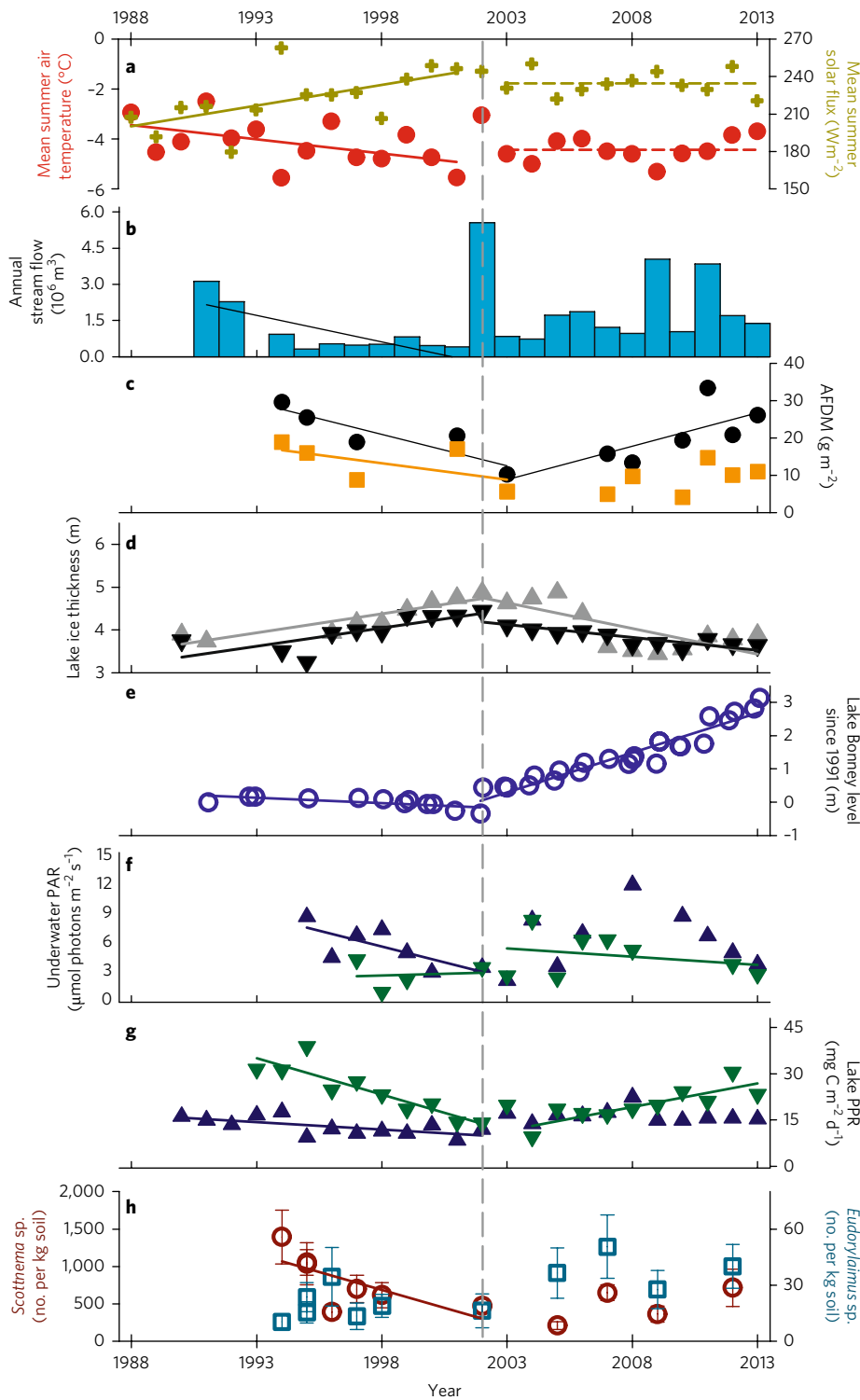


Fig. 2 | Climate and ecosystem metrics for the MDV. Trend lines are shown (colour-coded to the data provided). Climate data measured at the Lake Hoare meteorological station. **a**, Mean summer (DJF) air temperature and short-wave radiation. **b**, Annual volumes of stream flow observed on nine streams in the Lake Fryxell basin. **c**, Stream cyanobacterial mat ash-free dry mass (AFDM) of orange (*Phormidium*-dominated) and black (*Nostoc*-dominated) mats for permanent transects on four streams (Bowles, Canada, Green and Von Guerard) in the Lake Fryxell basin (error bars represent standard deviations of many samples collected for each season). **d**, Lake ice thickness for the ELB (grey) and WLB (black; mean of 3 manual measurements), as measured in November and December. **e**, Lake levels from 1991 (manually surveyed from reference benchmarks). **f**, Underwater PAR (measured at 10 m depth, mean for December of each year) for ELB and WLB. **g**, Primary productivity measurements in the ELB and WLB. **h**, *Scottinema* (red) and *Eudorylaimus* (blue) nematode abundances (error bars represent standard error of replicate samples) measured at long-term monitoring sites in Taylor Valley. Linear regressions are shown for periods up to and after the flood year (2002), unless no observation was made in 2002, in which case we used the next observation (that is, 2003). Where no trend lines are given, no significant regressions were present.

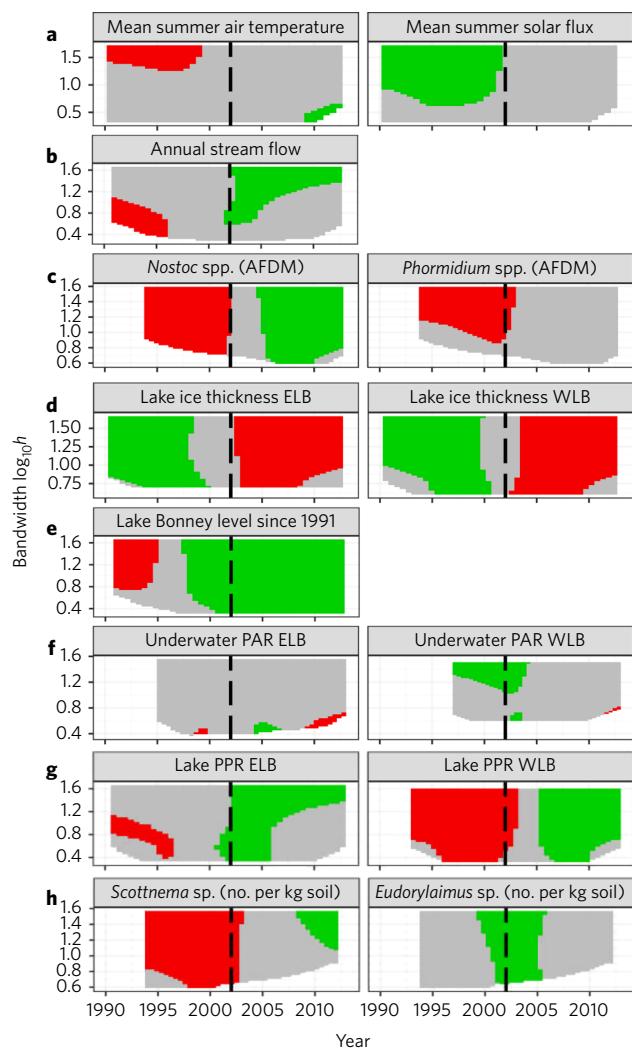


Fig. 3 | Heat maps from SiZer breakpoint analyses for time series data sets for physical and biological variables in Taylor Valley (that is, Fig. 2). **a–h**, Heat maps include data from: the meteorological station in Lake Hoare basin (**a**); total stream discharge into Lake Fryxell (**b**); standing biomass (AFDM) for black and orange mats in streams flowing into Lake Fryxell (**c**); lake ice thickness (**d**); lake level change for Lake Bonney (**e**); underwater PAR in the ELB and WLB (**f**); PPR in the ELB and WLB (**g**); and abundances of live nematodes, *Scottinema* and *Eudorylaimus* (**h**). The y-axis represents the bandwidth (smoothing window) used in the SiZer analysis. Green indicates a significantly (95% CI) positive change over time, red indicates a significantly negative change over time and grey indicates no significant temporal trend. The dashed line indicates the flood year in 2002. Lake levels are measured twice during most austral summers and often show an increase from November (before stream flow starts) to January (while stream flow is occurring), and a drop during the winter months. Hence, the SiZer analyses seem to pick up on this shorter timescale dynamic by indicating a change in trajectory prior to 2002.

ecosystem response²⁵. The flood year should have been a pivotal year for several biotic components of the ecosystem as well, if they are tightly controlled by physical conditions of their habitats. The biological responses to the flood and new summer climate regime varied. *Nostoc* spp. biomass in streams responded immediately, with an incipient increase continuing through the current decade. However, several biological aspects lagged behind the climate shift. For example, lake PPR in WLB reached a minimum two seasons

after the flood (2004), probably due to sediment loading during the high flows and channel cutting of 2002²⁶. Once the sediment settled, PPR increased in response to enhanced nutrient loading during the flood year. Biomass of *Phormidium* spp. stream mats changed their temporal trend in 2007, after a lag of five years. *Scottinema* populations in the soils shifted from mortality-driven population dynamics during the cooling phase, when the low temperatures limited reproduction and development, to slowly expanding populations following the flood year. *Eudorylaimus* sp. populations responded positively to the higher soil water availability of the flood year and the carryover of this moisture into subsequent summers²⁴. The asynchronous responses of these biota (lake phytoplankton, stream cyanobacteria and microalgae, and nematodes) to the climate shift contrast with the more consistent trends exhibited during the cooling phase and suggest that the influence of the flood year forced MDV biotic communities out of a trajectory driven by declining energy, nutrient availability and population. Such lagged ecosystem responses to climate change experiments are not uncommon²⁷ and may be linked to differences in population turnover times and growth rates, relative to physical drivers^{28,29}. However, the biological aspects of the ecosystem continue to respond to the changing physical aspects of the ecosystem that are directly influenced by climate. Climate change impacts on ecosystems are not related to shifts in air temperature alone (Supplementary Fig. 2). Coincident changes in solar flux, for example, alter physical states of the ecosystem, which in turn influence communities within ecosystems. Thus, the biological responses to climate changes can be buffered or amplified by alteration of the physical states of the ecosystem. In this case, the prolonged impact of the flood year resulted in a direct change in the temporal trajectories of both physical and biological aspects of the MDV ecosystem.

The terrestrial ecosystem responses to climate change observed in the MDV, together with the marine ecosystem responses to ocean warming on the Antarctic Peninsula^{2,11}, point to significant transformations of Antarctic ecosystems occurring now and expected to amplify in the coming decades. Our results lead us to contend that it may be the abrupt, short-lived events and perturbations that occur in response to climate changes that cause long-term changes to physical and biological aspects of polar ecosystems.

Methods

All temporal trends described in the paper and shown in Fig. 2 were quantified and assessed for significance using an ANOVA process, as completed with Systat Software (Systat Software, San Jose, CA, USA).

We used a significant zero crossings (SiZer) analysis, available as the SiZer package for R, to identify thresholds in each time series data set^{14,15}. This method provides a quantitative, non-parametric approach to identify when the sign of a slope in a time series shifts. We used this method to fit a locally weighted polynomial regression (LWPR) to smooth data trends over time. For each data set, we used the 95% confidence interval (CI) of the first derivative of the fitted LWPR model to identify when the slope of the smoother was significantly positive, significantly negative, or not significantly different from 0. Using this method, we explored trends in the first derivative of LWPR models using smoothing bandwidths that ranged from narrow (overfitting the data; short timescales) to wide (simple linear regression including timescales up to the point that all data in the data set are considered). By exploring a range of bandwidths, we were able to assess the robustness of identified thresholds. In each of the time series, we identified when a response variable was significantly decreasing over time (shaded red in heat maps), increasing over time (green in heat maps), or was stable (grey in heat maps).

Where significant breaks in trends were indicated from the SiZer analyses, we identified a local maximum or minimum value in the time series data and used that to define the break between two groups of data—pre- and post-impact. We then conducted linear regressions within those groups to determine whether trends were significant ($P < 0.05$, matching ref.¹³). Only significant trends are noted in Fig. 2.

Data availability. Field sampling, sample analysis and other protocols are available from the McMurdo Long-term Ecological Research (LTER) online database, <http://mcmilter.org>. The data sets analysed during the current study are available in the McMurdo LTER repository, also available at <http://mcmilter.org>.

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References

1. Polyakov, I. V. et al. Observationally based assessment of polar amplification of global warming. *Geophys. Res. Lett.* **29**, 24–25 (2002).
2. Schofield, O. et al. How do polar marine ecosystems respond to rapid climate change? *Science* **328**, 1520–1523 (2010).
3. Post, E. et al. Ecological dynamics across the Arctic associated with recent climate change. *Science* **325**, 1355–1358 (2009).
4. McClintock, J., Ducklow, H. & Fraser, W. Ecological responses to climate change on the Antarctic Peninsula. *Am. Sci.* **96**, 302–310 (2008).
5. Hinzman, L. D. et al. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Clim. Change* **72**, 251–298 (2005).
6. Jia, G. J., Epstein, H. E. & Walker, D. A. Greening of Arctic Alaska, 1981–2001. *Geophys. Res. Lett.* **30**, 2067 (2003).
7. Grebmeier, J. & Prisco, J. C. *Frontiers in Understanding Climate Change and Polar Ecosystems: Report of a Workshop* (National Academies Press, Washington DC, 2011).
8. Steig, E. J. et al. Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. *Nature* **457**, 459–62 (2009).
9. Bromwich, D. H. et al. Central West Antarctica among the most rapidly warming regions on Earth. *Nat. Geosci.* **6**, 139–145 (2013).
10. Chapman, W. L. & Walsh, J. E. A synthesis of Antarctic temperatures. *J. Clim.* **20**, 4096–4117 (2007).
11. Fountain, A. G. et al. The impact of a large-scale climate event on Antarctic ecosystem processes. *BioScience* **66**, 848–863 (2016).
12. Doran, P. T. et al. Antarctic climate cooling and terrestrial ecosystem response. *Nature* **415**, 517–520 (2002).
13. Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693 (2001).
14. Sondergerger, D. L., Wang, H., Clements, W. H. & Noon, B. R. Using SiZer to detect thresholds in ecological data. *Front. Ecol. Environ.* **7**, 190–195 (2009).
15. Clements, W. H., Vieira, N. K. M. & Sondergerger, D. L. Use of ecological thresholds to assess recovery in lotic ecosystems. *J. N. Am. Benthol. Soc.* **29**, 1017–1023 (2010).
16. Bestelmeyer, B. T. et al. Analysis of abrupt transitions in ecological systems. *Ecosphere* **2**, 1–26 (2011).
17. McKnight, D. M. et al. Dry Valley streams in Antarctica: ecosystems waiting for water. *BioScience* **49**, 985–995 (1999).
18. Fountain, A. G. et al. Physical controls on the Taylor Valley ecosystem. *BioScience* **49**, 961–971 (1999).
19. Kohler, T. J. et al. Life in the main channel: long-term hydrologic control of microbial mat abundance in McMurdo Dry Valley streams, Antarctica. *Ecosystems* **18**, 310–327 (2015).
20. Stanish, L. F., Nemergut, D. R. & McKnight, D. M. Hydrologic processes influence diatom community composition in Dry Valley streams. *J. N. Am. Benthol. Soc.* **30**, 1057–1073 (2011).
21. Esposito, R. M. M. et al. Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophys. Res. Lett.* **33**, 2–5 (2006).
22. Moorhead, D. L., Wall, D. H., Virginia, R. A. & Parsons, A. N. Distribution and life-cycle of *Scottinema lindsayae* (Nematoda) in Antarctic soils: a modeling analysis of temperature responses. *Polar Biol.* **25**, 118–125 (2002).
23. Wall, D. H. Biodiversity and ecosystem functioning in terrestrial habitats of Antarctica. *Antarct. Sci.* **17**, 523–531 (2005).
24. Barrett, J. E. et al. Persistent effects of a discrete warming event on a polar desert ecosystem. *Glob. Change Biol.* **14**, 2249–2261 (2008).
25. Obryk, M. et al. Responses of Antarctic marine and freshwater ecosystems to changing ice conditions. *BioScience* **66**, 864–879 (2016).
26. Foreman, C. M., Wolf, C. F. & Prisco, J. C. Impact of episodic warming events on the physical, chemical and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquat. Geochem.* **10**, 239–268 (2004).
27. Gherardi, L. A. & Sala, O. E. Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proc. Natl Acad. Sci. USA* **112**, 12735–12740 (2015).
28. Kohler, T. J., Chatfield, E., Gooseff, M. N., Barrett, J. E. & McKnight, D. M. Recovery of Antarctic stream epilithon from simulated scouring events. *Antarct. Sci.* **27**, 1–14 (2015).
29. Overhoff, A., Freckman, D. & Virginia, R. Life cycle of the microbivorous Antarctic Dry Valley nematode *Scottinema lindsayae* (Timm 1971). *Polar Biol.* **13**, 151–156 (1993).

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Author contributions

M.N.G., J.E.B., B.J.A., P.T.D., D.M.M., J.C.P., C.T.-V., R.A.V. and D.H.W. designed the experiments, field monitoring and analysis protocols, and analysed data; M.L.V. assembled and corrected long-term soil invertebrate data; E.R.S. performed SiZer analyses; M.N.G. wrote the paper, with substantial input from all authors; all authors assisted with fieldwork.

Competing interests

The authors declare no competing financial interests.

Additional information

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