

Because trends and their statistical significance are random functions of time, an analysis of the time variation of detectability of flood-frequency change may be informative. Therefore, we generalized  $Z$  to  $Z(t)$ , where  $t$  is the hypothetical last year of available records, and evaluated  $Z(t)$  for the observations and the scenario experiments (Fig. 4). The observed flood trend  $Z(t)$  has been significantly (at 95% level, as evaluated from the control experiment) different from zero continuously since the flooding of the upper Mississippi River in 1993 and intermittently since 1972. Uninterrupted periods of statistically significant flood-frequency trends in scenarios 1 to 5 begin in years 2023, 2023, 1986, 2021 and 2006, respectively, and premonitory multidecadal periods of intermittent significance begin much earlier in scenarios 2 and 3 (1956 and 1937, respectively). Thus, the recent history of the observed trend index is generally consistent with the range of results from the scenario experiments.

Our detection of an increase in great-flood frequency and its attribution to radiatively induced climate change are tentative. The frequency of floods having return periods shorter than 100 yr did not increase significantly. Potentially significant effects of measurement non-stationarity are not easily assessed. The forced signal and unforced variability in the model contain errors of unknown magnitude. Absent from the model are forcings such as solar variability, volcanic activity, land-cover change<sup>9</sup>, and water-resource development<sup>10</sup>, and potential biospheric feedbacks such as CO<sub>2</sub>-induced stomatal closure<sup>11</sup> and water-stress-induced root extension<sup>12</sup>. Especially evident from our study are the needs for improvements in simulation of tropical hydroclimate and continued commitment to stream-gauging programmes worldwide. □

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## Antarctic climate cooling and terrestrial ecosystem response

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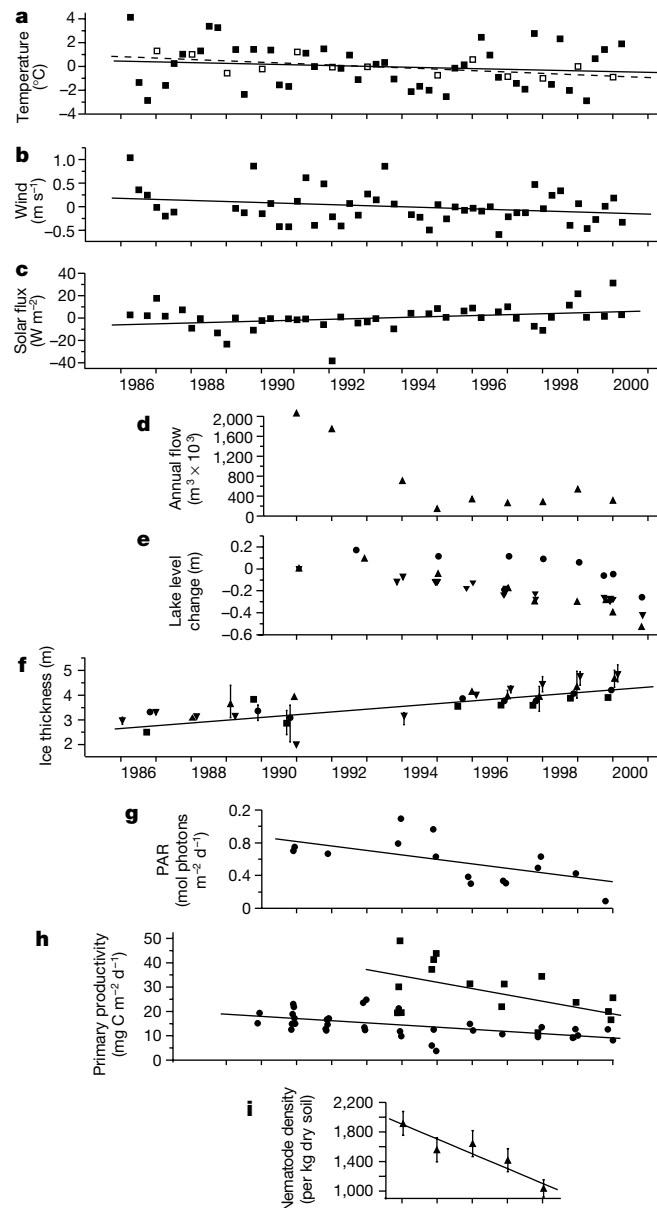
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The average air temperature at the Earth's surface has increased by 0.06 °C per decade during the 20th century<sup>1</sup>, and by 0.19 °C per decade from 1979 to 1998<sup>2</sup>. Climate models generally predict amplified warming in polar regions<sup>3,4</sup>, as observed in Antarctica's peninsula region over the second half of the 20th century<sup>5–9</sup>. Although previous reports suggest slight recent continental warming<sup>9,10</sup>, our spatial analysis of Antarctic meteorological data demonstrates a net cooling on the Antarctic continent between 1966 and 2000, particularly during summer and autumn. The McMurdo Dry Valleys have cooled by 0.7 °C per decade between 1986 and 2000, with similar pronounced seasonal trends. Summer cooling is particularly important to Antarctic terrestrial ecosystems that are poised at the interface of ice and water. Here we present data from the dry valleys representing evidence of rapid terrestrial ecosystem response to climate cooling in Antarctica, including decreased primary productivity of lakes (6–9% per year) and declining numbers of soil invertebrates (more than 10% per year). Continental Antarctic cooling, especially the seasonality of cooling, poses challenges to models of climate and ecosystem change.

Terrestrial ecosystem research in the Antarctic is restricted to a few ice-free areas of the coast, including the McMurdo Dry Valleys (77–78° S, 160–164° E). The dry valleys region is the largest ice-free area on the Antarctic continent. It is a cold desert, comprising a mosaic of perennially ice-covered lakes, ephemeral streams, arid soils, exposed bedrock, and alpine glaciers. Published historical weather observations in the dry valleys are limited<sup>11–14</sup>. Biological activity is microbially dominated and diversity is low. The largest animals are soil invertebrates, of which soil nematodes are the most widely distributed<sup>15</sup>.

Our 14-year, continuous automatic weather station record from the shore of Lake Hoare reveals that seasonally averaged surface air temperature has decreased by 0.7 °C per decade ( $P = 0.21$ ) from 1986 to 1999 (Fig. 1a). The temperature decrease is most pronounced in

the summer (December–February = 1.2 °C per decade,  $P = 0.02$ ) and autumn (March–May = 2.0 °C per decade,  $P = 0.11$ ). Winter (June–August) and spring (September–November) show smaller temperature increases (0.6 °C and 0.1 °C per decade,  $P = 0.62$  and 0.95, respectively). The dry valley cooling, and its seasonal pattern



**Figure 1** Meteorological and ecosystem changes in the McMurdo Dry Valleys, 1986–2000. **a**, Seasonally averaged air temperature over time at Lake Hoare station (full data set) with summer values highlighted (open squares). Trend lines are annual (solid line) and summer only (dashed lines). **b**, Seasonally averaged wind speed over time at Lake Hoare station. **c**, Seasonally averaged solar flux at Lake Hoare station (excluding winter, June–August). **d**, Total annual stream flow from eight streams in the Lake Fryxell basin. **e**, Lake level change in Lake Hoare (inverted triangles), Lake Fryxell (triangles), and Lake Bonney (circles). **f**, Lake ice thickness of west lobe Lake Bonney (squares), east lobe Lake Bonney (circles), Lake Fryxell (triangles), and Lake Hoare (inverted triangles). Ice thickness is measured from the water level to the bottom of the ice in holes drilled through the ice. The vertical bars indicate the range of measurements within a season. **g**, Mean monthly (November and December only) photosynthetically active radiation (PAR) 10 m below the surface of the ice in the east lobe of Lake Bonney. **h**, Depth-integrated primary productivity during November and December in east (circles and lower trend line) and west (squares and upper trend line) lobes of Lake Bonney. **i**, Total number of soil nematodes over time in experimental plots on the south shore of Lake Hoare.

(that is, dominated by summer and autumn), reflects longer term continental Antarctic cooling between 1966 and 2000 (Fig. 2 and Table 1). Owing to the exclusion of dry valley records in Fig. 2, compatibility with the dry valley data increases the validity of the analysis. Moreover, Fig. 2 is consistent with maps of individual station trends during 1976–2000 presented in the Intergovernmental Panel on Climate Change (IPCC) report<sup>1</sup>. We focus here on the Lake Hoare record because it is the longest dry valley record, but seven other dry valley floor stations show similar trends<sup>16</sup>.

The seasonally averaged wind speed decreased by 0.23 m s<sup>-1</sup> per decade ( $P = 0.07$ ) at Lake Hoare from 1986 to 1999 (Fig. 1b), and is significantly correlated with the seasonally averaged temperature decrease ( $P < 0.01$ ). Furthermore, both easterly on-shore coastal (dominant in the summer) and westerly katabatic (dominant in winter, spring and autumn) wind speeds are significantly correlated ( $P < 0.01$ ) with temperature. Annual temperatures at individual dry valley sites are strongly controlled by exposure to wind; the dry adiabatic lapse rate and distance to the coast are of secondary importance<sup>16</sup>. Our results suggest that estimating long-term temperature change in coastal Antarctica requires an understanding of the synoptic controls on surface wind variability, which at present are incompletely understood<sup>17,18</sup>.

Seasonally averaged (excluding June–August) solar radiation has increased from 1986 to 1999 by 8.1 W m<sup>-2</sup> per decade ( $P = 0.05$ ; Fig. 1c). Radiation during non-winter months decreased with increasing wind speed during this period ( $P = 0.08$ ). The inverse relationship between wind speed and radiation is highly significant for spring and autumn ( $P < 0.01$ ). Radiation decreases significantly with easterly wind speed during the summer ( $P = 0.02$ ), and with westerly wind speed during the spring ( $P = 0.03$ ). Observers in the field routinely noted cloudiness during high wind events. Together, these results indicate that increased solar radiation in the dry valleys is related to decreased wind and associated cloudiness over time.

Changes in dry valley moisture indices (relative humidity and precipitation) are inconclusive because of measurement uncertainties. Snow accumulation (precipitation minus evaporation) on two local valley glaciers showed no clear trend between the summers of 1993–94 and 1999–2000. We infer from the increased clear-sky conditions that cloudiness decreased from 1986 to 1999. Soil moisture decreased from 2.2% (by weight) to 1.4% between 1993 and 1999 in an elevational transect in Taylor Valley.

The McMurdo Dry Valley environment has long been viewed as sensitive to low amplitude climatic shifts<sup>19–21</sup>. Local hydrology is dependent on small changes in summer temperature and solar radiation, which can melt glacier ice and provide liquid runoff to soils, streams and lakes. From 1969 to 2000, all discharge observations were made in dry valley streams between 10 November and 24 March, but typically most flow occurs in December and January. All streams are fed largely by glacial melt, with minor inputs coming from seasonal snow banks. Storage of stream water occurs in hyporheic zones: moist soil areas adjacent to and beneath the streams<sup>22</sup>. The discharge from the eight principal inflow streams in the Lake Fryxell basin since 1990–91 (except 1992–93 when field measurements were not made) decreased nonlinearly by an average rate of  $1.8 \times 10^5 \text{ m}^3 \text{ yr}^{-1}$  (Fig. 1d). Total annual stream flow in these streams increased by 41,000 m<sup>3</sup> per degree-day above freezing at the

**Table 1** Proportions of Antarctica warming and cooling (1966–2000)

Period	Antarctica	Antarctica without the Antarctic Peninsula
Annual	+41.4%, -58.3%	+33.8%, -65.9%
Winter (June–Aug.)	+62.5%, -37.3%	+56.3%, -43.4%
Spring (Sept.–Nov.)	+54.1%, -45.7%	+49.4%, -50.4%
Summer (Dec.–Feb.)	+31.7%, -67.4%	+22.8%, -76.3%
Autumn (Mar.–May)	+12.6%, -87.4%	+0.3%, -99.7%

Plus signs indicate the proportions warming; minus signs indicate the proportions cooling. The Antarctic Peninsula is defined as the area north of 80° S and east of 80° W.

Lake Fryxell meteorological station ( $P < 0.01$ ).

Lake levels rose at an average rate of  $16 \text{ cm yr}^{-1}$  between 1903 and approximately 1990, and lake ice thinned before 1986<sup>19,21</sup>. Our data show that lake levels receded (Fig. 1e) in response to cooler summers and decreased stream flow since 1990. Cooler, quiescent conditions in summer reduce sublimation loss from lakes, but not enough to compensate for the decreased stream flow. The thickness of lake ice has increased since 1986 by an average of  $11 \text{ cm yr}^{-1}$  ( $P < 0.01$ ) in response to the lower temperatures (Fig. 1f).

We believe that climate cooling has significantly impacted ecosystem properties in the McMurdo Dry Valleys. The climate-induced increase in lake ice thickness has reduced underwater irradiance during November–December in the east lobe of Lake Bonney by  $0.055 \text{ mol photons m}^{-2} \text{ d}^{-1}$  ( $P = 0.01$ ) since 1990 (Fig. 1g). Because phytoplankton primary production in the dry valley lakes is limited by light<sup>23</sup>, we suggest that this decrease in irradiance has affected the rate of primary production in the lakes (Fig. 1h). Depth-integrated primary production in the east and west lobes of Lake Bonney has decreased by  $0.88$  ( $P < 0.01$ ) and  $2.6$  ( $P = 0.03$ )  $\text{mg C m}^{-2} \text{ d}^{-1}$  annually, amounting to a 6% and 9% decrease per year, respectively. Recent data on the carbon biogeochemistry of Lake Bonney show that contemporary photosynthesis to respiration ratios are less than unity<sup>24</sup>. The inferred climate-induced reduction in primary production will exacerbate this situation producing a system that may act as a  $\text{CO}_2$  source and eventually become depleted in organic carbon stores. Reduced nutrient loading associated with decreasing stream flows is not the cause of the noted reduction in primary production, as a large portion of the nutrient supply for phytoplankton growth arises from internal vertical diffusion<sup>24</sup>.

Soil invertebrate communities showed changes in diversity and abundance from 1993 to 1998. The abundance of tardigrades and nematodes, including the dominant nematode species *Scottinema lindsayae*, declined in an elevational transect<sup>29</sup>, and across all treatments (moisture, temperature, and carbon) in a climate

manipulation experiment by 200 individuals ( $>10\%$ ) per year ( $P = 0.01$ , Fig. 1i). Given the low diversity and long generation times of these invertebrates, these declines in population represent important shifts in the diversity, life cycles, trophic relationships and functioning of dry valley soils<sup>25</sup>.

We have shown a 14-yr Antarctic dry valley meteorological record and 35-yr continental temperature compilation that indicate an annual cooling trend during recent time over much of the continent of Antarctica, outside of the peninsula. Although other studies (for example, ref. 10) have cited a trend of continental warming in Antarctica, the trends are sensitive to the period analysed and to the distribution of stations. The warming reported in ref. 10 occurs almost entirely from 1958 to 1978, but not thereafter. As the shorter term dry valley data are for the period subsequent to the primary warming, the trends deduced in the different studies are not incompatible. Moreover, the large-scale cooling reported here results from an approach designed to avoid over-weighting of station-dense regions (for example, the peninsula) in the evaluation of overall trends. In the dry valleys, the cooling trend is significantly correlated with decreased winds and increased clear-sky conditions over the period of record. These changes are indicative of the strong influence that winds (mostly onshore during the summer and katabatic during other seasons) have on the dry valley climate. We propose that prolonged summer cooling will diminish aquatic and soil biological assemblages throughout the valleys, and possibly in other terrestrial Antarctic ecosystems. Winter temperatures are well below the threshold for liquid water production and can fluctuate significantly with minimal direct hydrological or ecological impact. Summer temperatures are the critical driver of Antarctic terrestrial ecosystems, and our data are the first, to our knowledge, to highlight the cascade of ecological consequences that result from the recent summer cooling. □

## Methods

### Dry valley ecosystem parameters

All dry valley meteorological data were collected using Campbell Scientific data loggers. The network consists of four stations in Taylor Valley, two in Wright Valley, and one in Victoria Valley. Precise station locations can be found in ref. 26. Four other stations on glacier surfaces in Taylor Valley are not discussed in this paper. Air temperature was collected at 3 m from the ground using a fenwall-type thermistor in a shielded Campbell Scientific model 207 probe. We calculated all temperature data from raw voltages using a Steinhart–Hart equation. Wind speed was measured at 3 m above the ground using a Met One model 014A wind speed sensor and model 024A wind direction sensor, up to 1993, and an R.M. Young model 05103 wind speed and direction sensor thereafter. Since 1993, we replaced all wind monitors once for recalibration. Solar flux was measured using Li-Cor model LI-200 pyranometers, which have a maximum stated uncertainty of  $\pm 5\%$ , and were recalibrated against an Eppley pyranometer every 2 yr. These pyranometers do not measure the ultraviolet range absorbed by ozone. Relative humidity was measured at all stations using Phys-Chem humidity transducers in Campbell Scientific 207 probes. Calibration drift in these transducers is significant, thereby possibly obscuring any long-term trends. We measured stream flow using pressure transducers in flumes. We calibrated rating curves frequently during the melt season.

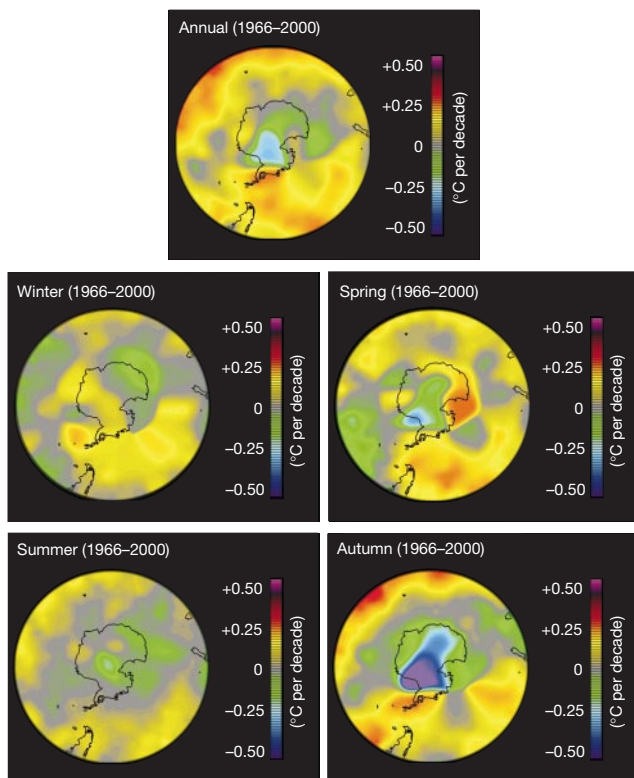
Soil moisture was determined gravimetrically (48 h at  $105^\circ\text{C}$ ) from 50-g soil samples that were collected in polyethylene bags in the field. On each sampling date, soil moisture was determined for 51 soil samples collected from  $10 \times 10 \text{ m}$  grids established at 83, 121 and 188 m elevation near the south shore of Lake Hoare, Taylor Valley. See ref. 27 for further details on the transect.

Irradiance in the water column of the Taylor Valley lakes was measured with a Li-Cor model 193 spherical quantum (400–700 nm) sensor moored 10 m beneath the surface of the permanent lake ice. The data were logged with a Campbell 21x data logger at 20-min intervals throughout the year. Primary productivity in lakes was measured using the  $^{14}\text{C}$  method, outlined in ref. 22, during 24-h *in situ* incubations.

For nematode analysis, soil samples were collected with pre-sterilized plastic scoops and placed in sterile polyethylene Whirl-Pak bags. All soils were transported in insulated coolers to the McMurdo station laboratory facilities, where they were immediately stored at  $4^\circ\text{C}$ . Nematodes, tardigrades, and rotifers were extracted from the soils within 48 h using standard sugar centrifugation procedures, modified to keep the soils and all extraction materials at a constant cold temperature. Extracted nematodes were identified to genus level. All nematode counts were adjusted for soil moisture to give number of nematodes per kilogram of dry soil.

### Continental temperature trends

Continental temperature trend maps were computed from the gridded University of East



**Figure 2** Annual and seasonal Antarctic surface temperature trends ( $^\circ\text{C per decade}$ ) between 1966 and 2000 calculated from the University of East Anglia Climate Research Unit's  $5^\circ \times 5^\circ$  HadCRUT data set<sup>28</sup>.

Anglia HadCRUT temperature data set, based on land station and ship reports<sup>28</sup>. The trends for each 5° × 5° grid cell were evaluated by a least-squares fit for the period 1965–2000. The gridded trend values were then smoothed spatially using a Cressman analysis, which effectively determines a pixel value as a weighted sum of contributions from surrounding grid points for which data are available. Weights vary as the inverse fourth power of the distance from the pixel in question. The radius of influence is 500 pixels, or approximately one-quarter the maximum width of the image.

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# DNA reveals high dispersal synchronizing the population dynamics of Canada lynx

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Population dynamics of Canada lynx (*Lynx canadensis*) have been of interest to ecologists for nearly sixty years<sup>1–4</sup>. Two competing hypotheses concerning lynx population dynamics and large-scale spatial synchrony are currently debated. The first suggests that dispersal is substantial among lynx populations<sup>5</sup>, and the second proposes that lynx at the periphery of their range exist in small, isolated patches that maintain cycle synchrony via correlation with extrinsic environmental factors<sup>2</sup>. Resolving the nature of lynx population dynamics and dispersal is important both to ecological theory and to the conservation of threatened lynx populations: the lack of knowledge about connectivity between populations at the southern periphery of the lynx's geographic range delayed their legal listing in the United States<sup>6</sup>. We test these competing hypotheses using microsatellite DNA markers and lynx samples from 17 collection sites in the core and periphery of the lynx's geographic range. Here we show high gene flow despite separation by distances greater than 3,100 km, supporting the dispersal hypothesis. We therefore suggest that management actions in the contiguous United States should focus on maintaining connectivity with the core of the lynx's geographic range.

Trapping records show that twentieth-century lynx population dynamics in parts of North America exhibit patterns of lagged synchrony, with irruptions occurring in the centre of the continent 2–3 years before they occur at the periphery of the range<sup>5</sup>. One potential mechanism for this phenomenon is a travelling wave of lynx emanating from the centre of the continent, which synchronizes the lynx populations<sup>4</sup>. If this 'dispersal hypothesis' is correct, then populations at the periphery of their range should be highly influenced by lynx periodically diffusing outwards from the core.

Alternatively, lynx populations at the periphery of their geographic range may be self-sustaining, and largely isolated<sup>7</sup>. Under this 'peripheral isolation hypothesis' there would be few dispersers and the number of dispersers would decline exponentially with distance, leading to lower connectivity at the edge of the geographic range<sup>3</sup>. To support the peripheral isolation hypothesis there are weak correlations between lynx irruptions in Alberta and British Columbia and lynx abundance indices in some southern, peripheral populations, as well as the patchy nature of lynx habitat in southern Canada, Montana, and Washington<sup>5,7</sup>. If populations are relatively isolated, synchrony between peripheral lynx populations could be generated by exogenous density-independent events such as weather<sup>2</sup> (that is, the Moran effect<sup>8</sup>).

We used nine microsatellite loci to estimate gene flow among lynx populations (see Methods). We analysed lynx samples from 17 collection sites in the periphery and core of the lynx's geographic range (Fig. 1). If the dispersal hypothesis is correct, gene flow should be high among populations, including central Canadian populations and the populations on the periphery of the geographic range. Alternatively, if the peripheral isolation hypothesis is correct, then gene flow should be low between peripheral lynx populations and