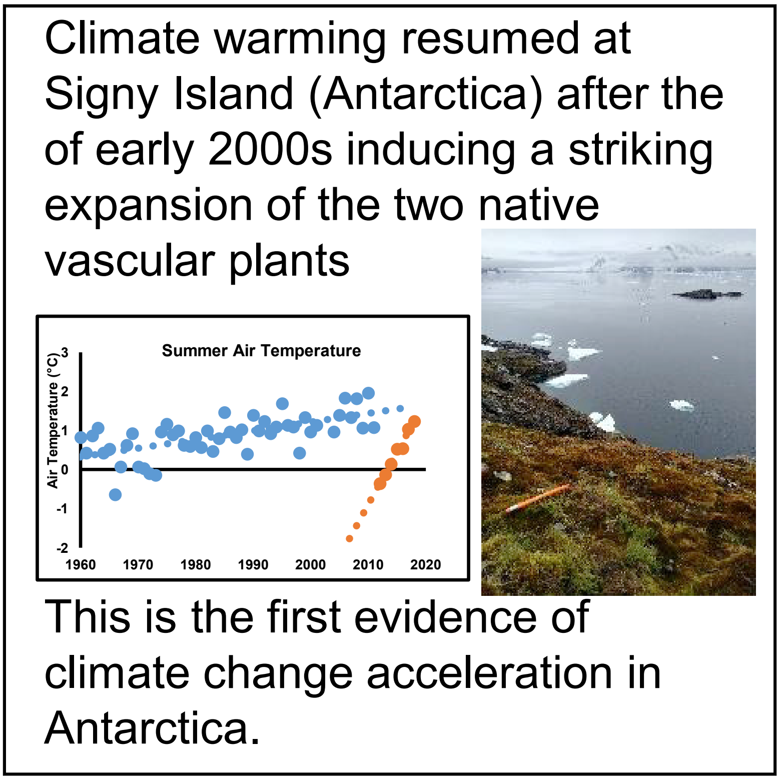
Report

Current Biology

Acceleration of climate warming and plant dynamics in Antarctica

Graphical abstract


Climate warming resumed at Signy Island (Antarctica) after the of early 2000s inducing a striking expansion of the two native vascular plants

This is the first evidence of climate change acceleration in Antarctica.

Authors

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In brief

Cannone et al. show a striking expansion of the two native Antarctic vascular plants in the last decade (2009–2018) at Signy Island (Antarctica), where a strong summer warming resumed after the pulse strong cooling event occurred in 2012. They provide the first evidence for accelerated ecosystem responses to climate warming in Antarctica.

Highlights

- At Signy Island a strong summer warming resumed after the pulse cooling in 2012
- The two native Antarctic vascular plants expanded strikingly at Signy Island in 2009–2018
- We show evidence of plant dynamics accelerated by climate warming in Antarctica

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Report

Acceleration of climate warming and plant dynamics in Antarctica

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SUMMARY

The strong air temperature warming between the 1950s and 2016 in the Antarctic Peninsula region[1] exceeded the global average warming[2,3] with evident impacts on terrestrial ecosystems and the two native Antarctic vascular plants *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl.[4–10] Subsequently, a short but intense cooling occurred from the Antarctic Peninsula to the South Orkney Islands (1999–2016),[1,11–13] impacting terrestrial ecosystems, with reduced lichen growth[14] and no further expansion of *D. antarctica* in the Argentine Islands.[5] The strong warming trend is predicted to resume[15] with expansion of ice-free areas and continued impacts on the abiotic and biotic components of terrestrial ecosystems including the ingression of non-native species[3,8,16,17] as recently recorded at Signy Island (South Orkney Islands).[18–20] In this study we document acceleration in the expansion of *D. antarctica* and *C. quitensis* in the last decade (2009–2018) at Signy Island, where the air temperature warming trend resumed in summer after 2012. We hypothesize that the striking expansion of these plants is mainly triggered by summer air warming and release from the limitation of fur seal disturbance. We also hypothesize that the "pulse" climatic event of the strong air cooling detected in 2012 did not appear to influence the vegetation community dynamics on this island. This is the first evidence in Antarctica for accelerated ecosystem responses to climate warming, confirming similar observations in the Northern Hemisphere. Our findings support the hypothesis that future warming will trigger significant changes in these fragile Antarctic ecosystems.

RESULTS

Climate warming resumed with accelerated trends after the 2012 cooling

The mean annual air temperature (MAAT) at Signy Island showed an increasing trend between 1960 and 2011 of +0.02°C per year, followed by four colder years and a subsequent sharp increase (+0.25°C per year), giving a net increase of ca. +1°C over the period 1960–2018 (Figure 1A).

Considering seasonal data, summer air temperature also exhibited a clear trend, with an increase between 1960 and 2011 of ca. 1.2°C, followed in 2012 by the second coldest summer of the entire period (mean of −0.35°C) and then a period of strong and consistent warming of 0.9°C in 7 years (Figure 1B). At decadal scale, MAAT showed a statistically significant increasing trend between the 1960s and 2010s, with a rate of +0.156°C per decade ($R^2 = 0.83$, $p = 0.015$), despite a slight decrease being observed in the last decade (Figure S1A). Total annual precipitation (MAP) was relatively constant in the period 1960–1997 (mean ≈ 660 mm/year) (Figure S1B), then showed much larger values in the decade 1998–2007 (mean ≈ 1,440 mm/year) followed by a large decrease in the following decade (mean ≈ 960 mm/year), with a statistically significant decreasing trend in the period 1998–2018 ($\beta = -39.9$; $R^2 = 0.43$; $p < 0.01$) (Figure S1B). Summer precipitation was characterized by a statistically significant increasing trend between 1960 and 2011 ($\beta = 5.43$; $R^2 = 0.43$; $p < 0.01$) (Figure S1C).

Exploring the relationships between the climatic parameters and the circulation features, the Antarctic Oscillation Index (AAO) did not show statistically significant relationships with either air temperature or precipitation between 1979 (when this index became available) and 2011, as well as in the period 2012–2018. The Southern Oscillation Index (SOI) also showed no statistically significant relationships with air temperature or precipitation in the period 1960–2011, although there was a significant relationship with autumn air temperatures in the period 2012–2018 ($p = 0.03$; $R^2 = 0.62$).

Despite the limited available data, it is notable that, in 2018–2019, data obtained at an elevation of ca. 100 m on the eastern coast of Signy Island were characterized by 200 mm less rainfall than on the western side of the island and that, on the latter, the rate of rain increase with elevation was 5.1 mm per m altitude gained.

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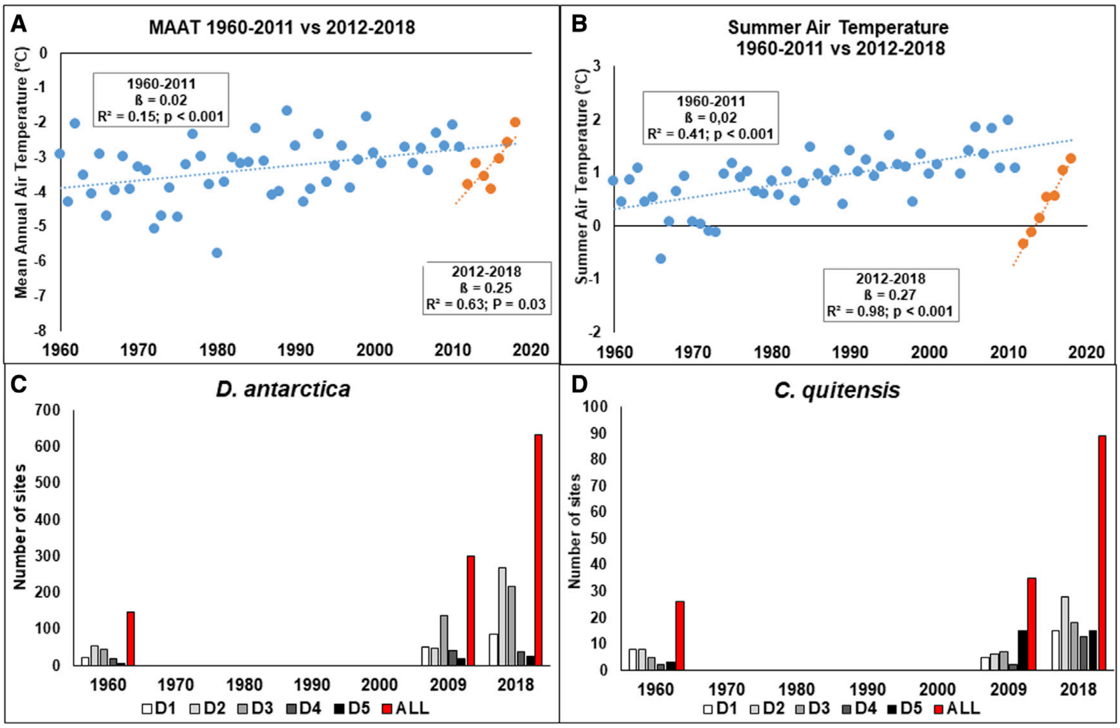

Figure 1. Climate warming resumed at Signy Island after the 2012 cooling and accelerated the expansion of *D. antarctica* and *C. quitensis*

Annual trends of (A) mean annual air temperature (MAAT, °C) and (B) summer air temperature (DJF, °C) comparing the periods 1960–2011 (blue dots) and 2012–2018 (orange dots), with reference to (C) the number of sites occupied by *D. antarctica* and (D) number of sites occupied by *C. quitensis*, separating the different population size classes (D1 to D5; Table 1, white to black bars) and showing the entire population (All, red bars) in 1960, 2009, and 2018. Regression equations show the statistically significant trends of MAAT and DJF. For more details, see Figure S1.

Acceleration of the expansion of *D. antarctica* and *C. quitensis* in response to resumed warming

In the almost six decades up to 2018, *D. antarctica* exhibited a very large increase in the number of sites of occurrence, which doubled between 1960 and 2009 and then again between 2009 and 2018 (Figure 1C). This population expansion was predominantly accounted for by individuals belonging to the small- and intermediate-size classes (Table 1; Figure 2). *Colobanthus quitensis* also showed a large expansion, even more so than *D. antarctica* in the last decade, involving both the number of sites of occurrence and their extent, with increased numbers of almost all size classes except the largest (Table 1; Figure 2).

The rate of decadal increase of these two species across the entire island exhibited a striking acceleration in the most recent decade, from +20.8% to +28.2% per decade (1960–2009 versus 2009–2018) for *D. antarctica*, and from +6.9% to +154.3% per decade over the same periods for *C. quitensis* (Table 1). The acceleration in rates of population expansion of both species was also apparent when the data were analyzed across the three selected elevation bands already adopted in the previous analysis (1960–2009)[7] (Figures 2, S2A, and S2B).

Distribution patterns of *D. antarctica* and *C. quitensis* in relation to topography and environmental gradients at Signy Island

In the last decade the overall distribution of *D. antarctica* across the island changed, shifting from a distribution dominated by sites of occurrence on the eastern side of the island (66% of the entire population before 2009) to a more balanced distribution between the eastern and western sides, with an increase of sites on the western side after 2009 from 33.7% to 46.6% (Figures 2A–2C; Table S1).

Colobanthus quitensis was already more abundant on the western side of the island (65.4% before 2009), with this dominance increasing further in the last decade (to 88.8% in 2018) (Figures 2D–2F; Table S1). Since the initiation of long-term monitoring, the distribution of both species in all surveys exhibited a consistent pattern in the northern versus southern part of the island, related to the smaller ice-free area available for colonization in the latter due to the presence of the island's small ice cap (Figure 2).

The distribution patterns of both species in relation to topography (elevation, slope, aspect) were similar to those observed during the previous surveys (2009 and 1960), with no evidence supporting significant upward migration for either species (Figures S3 and S4). Both species increased their abundance above 40 m a.s.l. (above sea level), but they remained predominantly below 80 m a.s.l., with the majority of *D. antarctica* present below 40 m a.s.l. and of *C. quitensis* below 80 m a.s.l. with a large expansion between 60 and 80 m a.s.l. in the last decade (Figures S3 and S4).

Deschampsia antarctica showed evidence of increased colonization of younger terrains in the last decade. In the 1960 survey, the grass was mainly present on surfaces deglaciated

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Table 1. Number of sites, area, and percent change per decade of *D. antarctica* and *C. quitensis* showing their expansion in the period 1960–2009 and 2009–2018

Site size	Number of sites			Area (m^2)			Percent (%) change per decade	
	1960	2009	2018	1960	2009	2018	1960–2009	2009–2018
D. antarctica								
1 plant (D1)	21	52	85	0.21	0.52	0.85	29.6	63
2–20 plants (D2)	56	49	270	5.6	4.9	27	−2.6	451
>20 plants (D3)	45	139	217	22.5	69.5	108.5	41.8	56
<10 m^2 (D4)	19	41	38	95	205	190	23.3	−7
>1 m^2 (D5)	6	19	25	300	950	1250	43.4	32
Total	147	300	635	423.3	1230	1576	20.8	28.2
C. quitensis								
1 cushion (C1)	8	5	15	0.04	0.03	0.07	−7.6	200
2–10 cushions (C2)	8	6	28	0.16	0.1	0.6	−5	366
10–30 cushions (C3)	5	7	18	0.5	0.7	1.8	8	157
30–50 cushions (C4)	2	2	13	0.4	0.4	2.6	0	550
>50 cushions (C5)	3	15	15	1.1	5.6	5.6	80	0
Total	26	35	89	2.23	6.9	10.7	6.9	154

Number of sites and area (m^2) and their percent change (Δ %) across the entire study area in the periods 1960–2009 and 2009–2018 of *D. antarctica* and *C. quitensis* at Signy Island. Values are calculated based on field observations of the mean surface area (m^2) occupied by the distinct populations (1 individual ≅ 0.01 m^2 for *D. antarctica* and 0.005 m^2 for *C. quitensis* based on mean plant diameter measured in the field[7]). For more details, see Figures S1, S3, and S4.

before 6600 years before present (BP) while, since 2009, it has colonized terrains that became deglaciated after the end of the Little Ice Age (<LIA) (Figures 2A–2C). In contrast, *C. quitensis* continued to occur mainly on older surfaces, with only a slight increase in colonization of younger surfaces in the last decade (Figures 2D–2F).

In the last decade the impact of fur seal disturbance on both species decreased, becoming almost neglible. Before 2009, seal disturbance was greatest below 20 m a.s.l. although very clearly evident up to 60 m a.s.l. (Figures 2, S2A, and S2B; Table S2). The pattern of decreasing fur seal impact was very similar on both eastern and western sides of the island in the last decade (Table S2).

In 2018, both species were characterized by populations dominated by young individuals (Figure S1D), with a prevalence of virgin and young generative individuals (exceeding 70% of individuals for both species). No comparable data are available from previous surveys against which to compare these data.

Environmental drivers triggering the expansion of *D. antarctica* and *C. quitensis*

The redundancy analysis (RDA) was statistically significant ($p < 0.05$) and explained a very high proportion of the species-environment variance, as indicated by the high eigenvalues of the two axes (explaining 88.1% of the total variance) (Figure 3). The RDA confirmed that the distribution patterns of both species changed over time in a species-specific manner, comparing 1960–2009 and 2009–2018 (Figure 3). During the period 1960–2009, *D. antarctica* exhibited changes associated with the interaction between increasing air temperature and fur seal disturbance (in particular for the small- to medium-size populations, D1–D3), with expansion largely on the eastern side of the island (Figure 3). Over the same period, the dynamics of *C. quitensis* were also influenced by air temperature increase and animal disturbance, with expansion occurring on terrains with the oldest deglaciation (>6600 years BP) mainly located on the western side of the island (Figure 3).

During the last decade, both species expanded in response to air temperature warming and release from the limitation of animal disturbance. Populations of *D. antarctica* expanded on both sides of the island and toward higher elevations (consistent with its observed increase above 40 m a.s.l.) (Figures 3 and S3). Populations of the smaller size classes (D1 and D2) mainly expanded in lichen-dominated habitats, with those of larger size classes (D3–D5) increasing in moss vegetation and further expanding in previously colonized areas (Figure 3). *Colobanthus quitensis* was characterized by a clear expansion toward higher elevations (but mostly below first 80 m a.s.l.) (Figures 3 and S4) on the western side of the island, with a preference for habitat types characterized by the occurrence of mosses and/or the Antarctic vascular tundra rather than by lichens (Figure 3).

DISCUSSION

Accelerated plant dynamics

The data obtained in this study highlight that, over the last decade (2009–2018), there has been a striking acceleration in the dynamics of both vascular plant species at Signy Island, involving their capability to colonize new sites, as well as their areal expansion on the island (Table 1; Figure 2). Furthermore, the demographic data suggest that these populations will be able to expand further (Figure S1D). Such a trend of accelerated plant dynamics has not been detected previously in Antarctica, although it is in agreement with evidence reported in the Northern Hemisphere

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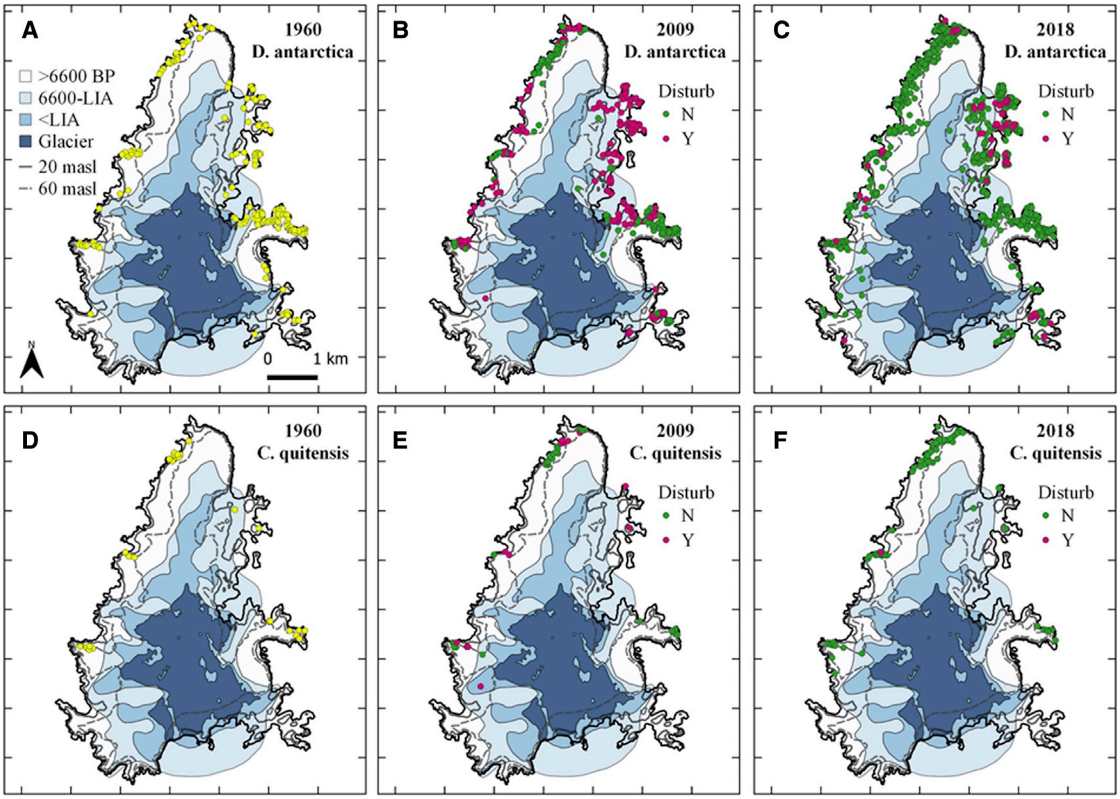

Figure 2. Location of the sites where *D. antarctica* and *C. quitensis* expanded at Signy Island since 1960

Distribution of *D. antarctica* and *C. quitensis* in 1960 (yellow dots) (A and D), 2009 (B and E), and 2018 (C and F) (green and magenta dots) in relation with the patterns of Holocene deglaciation and glacier boundaries and indicating the occurrence (magenta dots) or absence (green dots) of marine vertebrate disturbance in 2009 and 2018. Legend: dark blue, glacier boundaries as recorded in 2016; blue, glacier boundaries during the Little Ice Age; pale blue, terrains deglaciated between 6600 years BP and the Little Ice Age; white, terrains deglaciated before 6600 years BP. For more details, see Figures S1–S4.

involving at least two of the four biotic indicators (phenology, distribution, composition, and dynamics) identified by Walther et al.[21] as responses to climate change. A strong increase in plant species richness has been reported on mountain summits across Europe in response to climate warming[22] (with a 5-fold increase in 2007–2016 compared with 1957–1966). Similarly, advances in plant phenology have been reported in response to climate warming in North America and Europe, with more intensive impacts at higher latitudes above 60° N.[23] In Antarctica, several studies have reported biotic and abiotic responses to increasing air temperatures in both terrestrial and marine ecosystems,[10,24] but none have reported an acceleration, in particular following the short and strong cooling that occurred in the early 2000s.

We also hypothesize that the accelerated population expansion of *D. antarctica* and *C. quitensis* could result from a combination of climate warming and the recently reduced impacts of animal disturbance. This hypothesis is compatible with observations in the Northern Hemisphere, in particular in Europe, where land use change correlates with vegetation change but, as here, the primary driver of these responses was climate warming.[20,22,25]

Impacts of accelerated warming versus pulse events in Antarctica

Our data are consistent with the acceleration of plant dynamics at Signy Island occurring in response to long-term air temperature warming, which exhibited an accelerated trend after the particularly cold summer of 2012. It also indicates and that the cold “pulse” event of 2012 did not impact vascular plant dynamics over the long term. These data highlight the different sensitivity of the Antarctic vegetation to climatic pulse events. Indeed, the same cooling event resulted in a clear negative impact on lichens in the South Shetland Islands.[15]

Other pulse events have previously been reported in Antarctica, with various impacts on the different components of terrestrial ecosystems. In the Victoria Land Dry Valleys in continental Antarctica, a warming pulse event that occurred during the 2001/02 summer triggered permafrost melt, resulting in widespread flooding with erosive and/or depositional processes in the Dry Valleys. This event had persistent negative impacts on the soil nematode fauna and on lake ecosystems, affecting their chemistry and phytoplankton floristic composition.[26–29] However, simulated pulse events increasing precipitation (using snow or water additions) without surface disturbance (flooding, erosion, etc.) performed across five degrees of latitude in Victoria Land did not induce changes in soil chemistry, suggesting that such events may trigger persistent changes only when associated with geomorphological disturbance.[30] Therefore, even slight but consistent air warming may be more effective in producing persistent

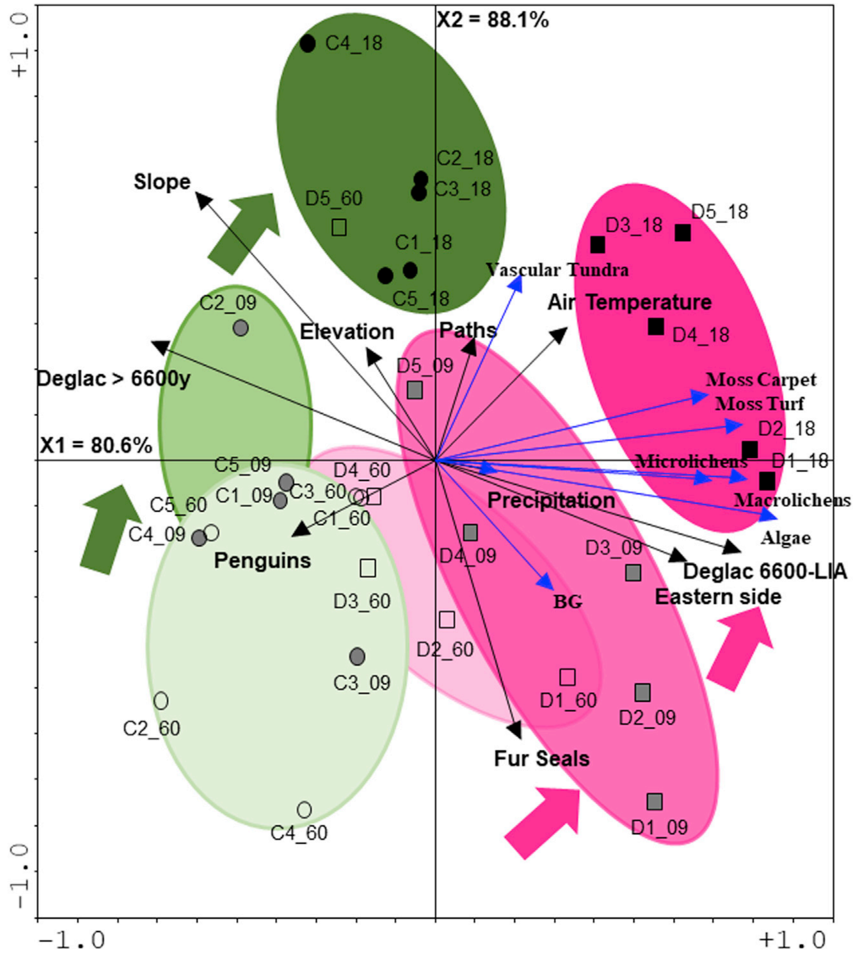

Figure 3. Multivariate analysis showing the environmental drivers triggering the expansion of *D. antarctica* and *C. quitensis*

Redundancy analysis showing the changes in distribution of *D. antarctica* (squares named D) and *C. quitensis* (dots named C) separating the different population size classes (as in Table 1; from D1 to D5 for *D. antarctica*; from C1 to C5 for *C. quitensis*) between surveys in 1960 (white squares/dots: D1_60 to D5_60; C1_60 to C5_60), 2009 (pale gray squares/dots: D1_09 to D5_09; C1_09 to C5_09), and 2018 (black squares/dots: D1_18 to D5_18; C1_18 to C5_18) in relation with air temperature, total precipitation, deglaciation age of terrains, topography (elevation, slope), occurrence of fur seals, penguins, footpaths, location on the eastern or western side of the island (black arrows), and as co-variables, habitat preference for colonization (vascular tundra, moss carpet, moss turf, macrolichens, microlichens, algae, barren ground [BG]) (blue arrows). The changes are represented by green clusters (1960, pale green; 2009, intermediate green; 2018, dark green) and arrows for *C. quitensis*, and by magenta clusters (1960, pale magenta; 2009, intermediate magenta; 2018, full magenta) and arrows for *D. antarctica*. For more details, see Figures S3 and S4.

impacts on the fragile ecosystems of continental Antarctica, as observed in Victoria Land, where only one decade of air warming resulted in detectable changes in soil chemistry and the associated moss and lichen vegetation.[30] Pulse events observed in the Windmill Islands, East Antarctica, led to decreases in moss health and community composition in response to regional drying and colder summers, followed by recovery in subsequent years.[31] Taken in combination, these studies emphasize the different sensitivity of the main components of Antarctic terrestrial ecosystems (vascular plants, mosses, lichens, soils, and soil fauna) to pulse events relative to long-term climatic change in the different Antarctic biogeographical regions.

Species-specific responses to climate warming and pulse events

The changes observed in the abundance and distribution patterns of the two vascular plants on Signy Island, providing one the longest records of vegetation distribution and their changes in Antarctica, emphasize that the stronger warming trend observed in the last decade (in particular during the summer) confirmed their responsiveness to warming. Species-specific responses were also apparent, confirming the suggestions of previous physiological studies and manipulation experiments. Laboratory studies have reported a broad temperature range for photosynthesis for both species, with somewhat higher optimal canopy temperatures for *C. quitensis* (19°C) than *D. antarctica* (13°C).[32,33] The stronger response to warming of *C. quitensis* observed here is consistent with its higher optimum temperature and capability to perform photosynthesis over a wider temperature range than *D. antarctica*, although the latter has a higher photosynthetic capacity.[32,34]

Simulated *in situ* warming experiments have confirmed greater responsiveness of *C. quitensis* than *D. antarctica*, with enhanced photosynthetic assimilation, higher leaf carbon gain and plant growth in the former, and no anatomical or physiological adjustments in the latter.[35,36] These features suggest that future warming would improve vegetative growth of these species due to greater biomass allocation to leaf-area production.[37,38] Moreover, warming could also improve seed production and pollen quality and increase sexual reproduction, in particular in *D. antarctica*.[39–41] However, it has also been hypothesized that excessive warming (in particular associated with water deficit) could decrease the efficiency in response of *D. antarctica*.[42] The stronger response to warming of *C. quitensis* in the last decade could be underlain by greater capability to exploit temperature increases through plastic adjustments promoting local scale population expansions in response to global change.[38]

The lack of negative impacts of the strong pulse cooling event in 2012 on both species could be explained by their ability to perform photosynthesis at low ambient temperatures (with a rate of ca. 30% of their maximum photosynthetic rate at 0°C).[32] During the cooling event in 2012, the mean summer air temperature was only slightly below 0°C (Figure 1), while typical

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daily variation at this location would mean that low positive temperatures would be commonly experienced,[43] especially within the plant canopy.

In conclusion, we report the first evidence in Antarctica for accelerated ecosystem responses to climate warming, confirming similar observations in the Northern Hemisphere. Sustained climate warming had a stronger influence than did a major cold pulse event on plant dynamics, with a striking acceleration in the rate of population increase of both native vascular plants, *D. antarctica* and *C. quitensis*, documented in the last decade on Signy Island.

Strong regional climate warming is forecast to resume in the Antarctic Peninsula and Scotia Arc region in the remainder of the twenty-first century. If this follows the "worst case" business as usual scenario (RCP 8.5),[44] as at present, Earth's climate by as soon as 2030 could resemble warmer periods such as those recorded during the mid-Pliocene.[17] Such climate warming may benefit some and possibly many native Antarctic terrestrial species and communities in isolation, but will also lead to increased risks from non-native species establishment.[3,8,16,17] These may outcompete native species and trigger irreversible biodiversity loss and changes to these fragile and unique ecosystems.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.01.074.

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AUTHOR CONTRIBUTIONS

N.C. conceived the project and led the manuscript preparation; F.M. performed the field survey; N.C., M.G., and F.M. performed the analyses; and all authors contributed to data interpretation and developing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Jones, M.E., Bromwich, D.H., Nicolas, J.P., Carrasco, J., Plavcova, E., Zou, X., and Wang, S.H. (2019). Sixty years of widespread warming in the southern middle and high latitudes (1957–2016). J. Clim. *32*, 6875–6898.
2. J. Turner, ed. (2009). Antarctic Climate Change and the Environment (Scientific Committee on Antarctic Research), p. 526.
3. Siegert, M., Atkinson, A., Banwell, A., Brandon, M., Convey, P., Davies, B., Downie, R., Edwards, T., Hubbard, B., Marshall, G., et al. (2019). The Antarctic Peninsula under a 1.5°C global warming scenario. Front. Environ. Sci. *7*, 102.
4. Fowbert, J.A., and Smith, R.I.L. (1994). Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. Arct. Alp. Res. *26*, 290–296.
5. Parnikoza, I., Convey, P., Dykyy, I., Trokhymets, V., Milinevsky, G., Tyschenko, O., Inozemtseva, D., and Kozeretska, I. (2009). Current status of the Antarctic herb tundra formation in the central Argentine Islands. Glob. Change Biol. *15*, 1685–1693.
6. Torres-Mellado, G.A., Jana, R., and Casanova-Katny, M.A. (2011). Antarctic hairgrass expansion in the South Shetland archipelago and Antarctic Peninsula revisited. Polar Biol. *34*, 1679–1688.
7. Cannone, N., Guglielmin, M., Convey, P., Worland, M.R., and Favero Longo, S.E. (2016). Vascular plant changes in extreme environments: effects of multiple drivers. Clim. Change *134*, 651–665.
8. Convey, P., and Peck, L.S. (2019). Antarctic environmental change and biological responses. Sci. Adv. *5*, z0888.
9. Smith, R.I.L. (1994). Vascular plants as bioindicators of regional warming in Antarctica. Oecologia *99*, 322–328.
10. Amesbury, M.J., Roland, T.P., Royles, J., Hodgson, D.A., Convey, P., Griffiths, H., and Charman, D.J. (2017). Widespread biological response to rapid warming on the Antarctic Peninsula. Curr. Biol. *27*, 1616–1622.e2.
11. Turner, J., Lu, H., White, I., King, J.C., Phillips, T., Hosking, J.S., Bracegirdle, T.J., Marshall, G.J., Mulvaney, R., and Deb, P. (2016). Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. Nature *535*, 411–415.
12. Gonzalez, S., and Fortuny, D. (2018). How robust are the Antarctic Peninsula trends? Antarct. Sci. *30*, 322–328.
13. Oliva, M., Navarro, F., Hrbáček, F., Hernández, A., Nývlt, D., Pereira, P., Ruiz-Fernández, J., and Trigo, R. (2017). Recent regional climate cooling on the Antarctic Peninsula and associated impacts on the cryosphere. Sci. Total Environ. *580*, 210–223.
14. Sancho, L.G., Pintado, A., Navarro, F., Ramos, M., De Pablo, M.A., Blanquer, J.M., Raggio, J., Valladares, F., and Green, T.G.A. (2017). Recent warming and cooling in the Antarctic Peninsula region has rapid and large effects on lichen vegetation. Sci. Rep. *7*, 5689.
15. Bracegirdle, T.J., Colleoni, F., Abram, N.J., Bertler, N.A.N., Dixon, D.A., England, M., Favier, V., Fogwill, C.J., Fyfe, J.C., Goodwin, I., et al. (2019). Back to the future: using long-term observational and paleo-proxy reconstructions to improve model projections of Antarctic climate. Geosci. *9*, 255.
16. Lee, J.R., Raymond, B., Bracegirdle, T.J., Chadès, I., Fuller, R.A., Shaw, J.D., and Terauds, A. (2017). Climate change drives expansion of Antarctic ice-free habitat. Nature *547*, 49–54.

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17. Chown, S.L., and Brooks, C.M. (2019). The state and future of Antarctic environments in a global context. Annu. Rev. Environ. Resour. *44*, 1–30.
18. Favero-Longo, S.E., Worland, M.R., Convey, P., Smith, R.I.L., Piervittori, R., Guglielmin, M., and Cannone, N. (2012). Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, Maritime Antarctic. Antarct. Sci. *24*, 323–336.
19. Cannone, N., Dalle Fratte, M., Convey, P., Worland, M.R., and Guglielmin, M. (2017). Ecology of moss banks on Signy Island (maritime Antarctic). Bot. J. Linn. *184*, 518–533.
20. Malfasi, F., Convey, P., Zaccara, S., and Cannone, N. (2020). Establishment and eradication of an alien plant species in Antarctica: Poa annua at Signy Island. Biodivers. Conserv. *29*, 173–186.
21. Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. Nature *416*, 389–395.
22. Steinbauer, M.J., Grytnes, J.A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., et al. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. Nature *556*, 231–234.
23. Park, H., Jeong, S., and Peñuelas, J. (2020). Accelerated rate of vegetation green-up related to warming at northern high latitudes. Glob. Change Biol. *26*, 6190–6202.
24. Gutt, J., Isla, E., Xavier, J.C., Adams, B.J., Ahn, I.Y., Cheng, C.C., Colesie, C., Cummings, V.J., di Prisco, G., Griffiths, H., et al. (2021). Antarctic ecosystems in transition - life between stresses and opportunities. Biol. Rev. Camb. Philos. Soc. *96*, 798–821.
25. Piccinelli, S., Brusa, G., and Cannone, N. (2020). Climate warming accelerates forest encroachment triggered by land use change: a case study in the Italian Prealps (Triangolo Lariano, Italy). Catena *195*, 104870.
26. Barrett, J.E., Virginia, R.A., Wall, D.H., Doran, P.T., Fountain, A.G., Welch, K.A., and Lyons, W.B. (2008). Persistent effects of a discrete warming event on a polar desert ecosystem. Glob. Change Biol. *14*, 2249–2261.
27. Ball, B.A., Barrett, J.E., Gooseff, M.N., Virginia, R.A., and Wall, D.H. (2011). Implications of meltwater pulse events for soil biology and biogeochemical cycling in a polar desert. Polar Res. *30*, 14555.
28. Balks, M.R., and O'Neill, T.A. (2016). Soil and permafrost in the Ross Sea region of Antarctica: stable or dynamic? Cuad. de Investig. Geog. *42*, 415–434.
29. Gooseff, M.N., Barrett, J.E., Adams, B.J., Doran, P.T., Fountain, A.G., Lyons, W.B., McKnight, D.M., Priscu, J.C., Sokol, E.R., Takacs-Vesbach, C., et al. (2017). Decadal ecosystem response to an anomalous melt season in a polar desert in Antarctica. Nat. Ecol. Evol. *1*, 1334–1338.
30. Cannone, N., Guglielmin, M., Malfasi, F., Hubberten, H.W., and Wagner, D. (2021). Rapid soil and vegetation changes at regional scale in continental Antarctica. Geoderma *394*, 115017.
31. Robinson, S.A., King, D.H., Bramley-Alves, J., Waterman, M.J., Ashcroft, M.B., Wasley, J., Turnbull, J.D., Miller, R.E., Ryan-Colton, E., Benny, T., et al. (2018). Rapid change in East Antarctic terrestrial vegetation in response to regional drying. Nat. Clim. Chang. *8*, 879–884.
32. Edwards, J.A., and Smith, R.I.L. (1988). Photosynthesis and respiration of *Colobanthus quitensis* and *Deschampsia antarctica* from the maritime Antarctica. Br. Antarct. Surv. Bull. *81*, 43–63.
33. Montiel, P., Smith, A., and Keiller, D. (1999). Photosynthetic responses of selected Antarctic plants to solar radiation in the southern maritime Antarctic. Polar Res. *18*, 229–235.
34. Xiong, F.S., Ruhland, C.T., and Day, T.A. (1999). Photosynthetic temperature response of the Antarctic vascular plants *Colobanthus quitensis* and *Deschampsia antarctica*. Physiol. Plant *106*, 276–286.
35. Torres-Díaz, C., Gallardo-Cerda, J., Lavin, P., Oses, R., Carrasco-Urra, F., Atala, C., Acuña-Rodríguez, I.S., Convey, P., and Molina-Montenegro, M.A. (2016). Biological interactions and simulated climate change modulates the ecophysiological performance of *Colobanthus quitensis* in the Antarctic ecosystem. PLoS ONE *11*, e0164844.
36. Sáez, P.L., Cavieres, L.A., Galmés, J., Gil-Pelegrín, E., Peguero-Pina, J.J., Sancho-Knapik, D., Vivas, M., Sanhueza, C., Ramírez, C.F., Rivera, B.K., et al. (2018). In situ warming in the Antarctic: effects on growth and photosynthesis in Antarctic vascular plants. New Phytol. *218*, 1406–1418.
37. Cavieres, L.A., Saez, P., Sanhueza, C., Sierra-Almeida, A., Rabert, C., Corcuera, L.J., Alberdi, M., and Bravo, L.A. (2016). Ecophysiological traits of Antarctic vascular plants: their importance in the responses to climate change. Plant Ecol. *217*, 343–358.
38. Acuña-Rodríguez, I.S., Torres-Díaz, C., Hereme, R., and Molina-Montenegro, M.A. (2017). Asymmetric responses to simulated global warming by populations of *Colobanthus quitensis* along a latitudinal gradient. PeerJ *5*, e3718.
39. Convey, P. (1996). Reproduction of Antarctic flowering plants. Antarct. Sci. *8*, 127–134.
40. Day, T.A., Ruhland, C.T., Grobe, C.W., and Xiong, F. (1999). Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. Oecologia *119*, 24–35.
41. Yudakova, O.I., Tyrnov, V.S., Kunakh, V.A., Kozeretskaya, I.A., and Parnikoza, I.Y. (2016). Adaptation of the seed reproduction system to conditions of maritime Antarctic in *Deschampsia antarctica* E. Ontogenez *47*, 170–180.
42. Sáez, P.L., Rivera, B.K., Ramírez, C.F., Vallejos, V., Cavieres, L.A., Corcuera, L.J., and Bravo, L.A. (2019). Effects of temperature and water availability on light energy utilization in photosynthetic processes of *Deschampsia antarctica*. Physiol. Plant *165*, 511–523.
43. Convey, P., Coulson, S.J., Worland, M.R., and Sjöblom, A. (2018). The importance of understanding annual and shorter term temperature patterns and variation in the upper layers of polar soils for terrestrial biota. Polar Biol. *41*, 1587–1605.
44. IPCC (2014). Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge University Press).
45. Ter Braak, C.J.F., and Šmilauer, P. (1998). CANOCO. Reference Manual and User's Guide to CANOCO for Windows. Software for Canonical Community Ordination, Version 4 (Centre for Biometry).
46. Royles, J., Ogée, J., Wingate, L., Hodgson, D.A., Convey, P., and Griffiths, H. (2012). Carbon isotope evidence for recent climate-related enhancement of CO_2 assimilation and peat accumulation rates in Antarctica. Glob. Change Biol. *18*, 3112–3124.
47. Tarca, G., Guglielmin, M., Convey, P., Worland, M.R., and Cannone, N. (2022). Small-scale spatial–temporal variability in snow cover and relationships with vegetation and climate in maritime Antarctica. Catena *208*, 105739.
48. Smith, R.I.L. (1993). Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In Antarctic Ecosystems: Ecological Change and Conservation, K.L. Kerry, and G. Hempell, eds. (Springer), pp. 32–50.
49. Cannone, N., Ellis-Evans, J.C., Strachan, R., and Guglielmin, M. (2006). Interactions between climate, vegetation and active layer in maritime Antarctica. Ant. Sci. *18*, 323–333.
50. Guglielmin, M., Ellis Evans, C.J., and Cannone, N. (2008). Active layer thermal regime under different vegetation conditions in permafrost areas. A case study at Signy Island (Maritime Antarctica). Geoderma *144*, 73–85.
51. Guglielmin, M., Worland, M.R., and Cannone, N. (2012). Spatial and temporal variability of ground surface temperature and active layer thickness at the margin of maritime Antarctica, Signy Island. Geomorphology *155*, 20–33.
52. Smith, R.I.L. (1972). Vegetation of the South Orkney Islands with particular reference to Signy Island. Sci. Rep. Br. Antarct. Surv. *68*, 1–124.

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53. Waluda, C.M., Gregory, S., and Dunn, M.J. (2010). Long-term variability in the abundance of Antarctic fur seals Arctocephalus gazella at Signy Island, South Orkneys. Polar Biol. *33*, 305–312.
54. Smith, R.I.L. (1988). Destruction of Antarctic terrestrial ecosystems by a rapidly increasing fur seal population. Biol. Conserv. *45*, 55–72.
55. Favero-Longo, S.E., Cannone, N., Worland, M.R., Convey, P., Piervittori, R., and Guglielmin, M. (2011). Changes in lichen diversity and community structure with fur seal population increase on Signy Island, South Orkney Islands. Antarct. Sci. *23*, 65–77.
56. Edwards, J.A. (1972). Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: distribution, ecology and vegetative performance on Signy Island. Br. Antarct. Surv. Bull. *28*, 11–28.
57. Kozeretska, I.A., Parnikoza, I.Y., Mustafa, O., Tyschenko, O.V., Korsun, S.G., and Convey, P. (2010). Development of Antarctic herb tundra vegetation near Arctowski station, King George Island. Polar Sci. *3*, 254–261.
58. Smith, R.I.L. (1996). Terrestrial and freshwater biotic components of the western Antarctic Peninsula. Foundations for ecological research west of the Antarctic Peninsula. Antarct. Res. Ser. *70*, 15–59.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data on Deschampsia antarctica and Colobanthus quitensis stored in Figshare	This paper	https://doi.org/10.6084/m9.figshare.18282695
Software and algorithms		
REDUNDANCY ANALYSIS	Ter Braak and Šmilauer[45]	http://www.canoco.com
Statistica version 10	Statsoft	https://www.statistica.com

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact Nicoletta Cannone (nicoletta.cannone@uninsubria.it)

Materials availability

This study did not generate new unique reagents

Data and code availability

- The datasets generated during the current study have been stored in figshare https://doi.org/10.6084/m9.figshare.18282695
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Plants

The two native Antarctic vascular plants *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. were analyzed in this study. We did not collect plant samples for our survey.

METHOD DETAILS

Study Area

Signy Island (60°43′S, 45°38′W) is located in the South Orkney Islands (Maritime Antarctic) and is characterized by a cold oceanic climate, with mean annual air temperature of −3.5°C and annual precipitation ranging from 350 to 700 mm, primarily as summer rain.[46] During the period 1981-2010 the mean annual air temperature recorded at Orcadas (the closest World Meteorological Observation (WMO) weather station providing a long-term record) was −3.1 ± 0.7°C and the mean summer temperature was +1.1 ± 0.5°C^2. The only available snow cover data for Signy Island were obtained from a grid of 15 × 20 m close to the island's research station monitored for about a decade since 2009.[47] This dataset indicated very high spatial variability in snow cover, reflecting mainly the microtopography and wind direction but also the underlying vegetation type. Mean snow cover between 2009 and 2017 ranged between 3.9 and 25.3 cm, while maximum values were between 27 and 85 cm.

The island's ice cap has shrunk rapidly in recent decades.[18] Three main deglaciation stages have been identified on the island.[18,19,48] The oldest stage occurred before 6600 y BP, followed by an intermediate stage that occurred between 6600 y BP and the Little Ice Age (LIA) and a youngest stage after the LIA. Ice-free ground is underlain by continuous permafrost, with an active layer depth ranging between 40 cm and 2 m.[49–51] Soils are mainly Gelisols and Fibristels.[51]

The vegetation includes two major formations: the Antarctic herb tundra formation (characterized by the occurrence of the two native vascular plants *D. antarctica* and *C. quitensis*), and the Antarctic non-vascular cryptogam tundra formation.[52] The latter covers most of the ice-free area of the island. Between 1960 and 2009 a rapid expansion of the two vascular plants was reported, interpreted as primarily a response to air warming.[7] However, heterogeneity in responses across an elevation gradient on the island for both species supported inference that the changes observed were also influenced by the interaction of multiple drivers, in particular climate warming and marine vertebrate disturbance.[7]

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Since around 1970, and particularly since the 1980s, the island has been impacted by a large increase in the number of resting and moulting male Antarctic fur seals (*Arctocephalus gazella* Peters 1875) that are present in summer due to recent rapid recovery of the species' main South Georgia breeding population following historical over-exploitation.[53] Fur seal disturbance has heavily impacted vegetation communities on the island.[54,55] The last detailed vegetation survey performed in 2009 allowed quantification of the patterns of fur seal impact on both vascular plants.[7]

Field survey

A detailed field survey of the distributions of the two vascular plants on Signy Island was carried out in January-March 2018, following the protocol previously described by Cannone et al.[7] and Edwards et al.[56] Each site where either species occurred was mapped with a resolution of 20–25 m, recording the size of the population following the classification proposed by Edwards et al.[56] The presence or absence of fur seal disturbance was also recorded on the basis of the visible plant health and that of the surrounding bryophyte communities (e.g., crushing/flattening, color changes due to urine deposition, etc), as well as of direct interaction with fur seals and/or penguins, and/or the occurrence of nearby footpaths.[7] In addition, the age structure and reproductive features of both species were also recorded as described by Kozeretska et al.[57] The following developmental stages were used to describe the population age profiles of the two species:[57] a) three pre-reproductive stages incluing juveniles (J), immature (Im), virgin (V); b) reproductive stages including young generative (G1), middle-aged generative (G2), old generative (G3), and subsenile plants (SS). To assess whether the current distribution of species was related to the colonization of preferred habitat types, the occurrence of the main sub-formations recognized by Smith[52,58] was recorded as follows: 1) alga sheet; 2) moss carpet; 3) moss turf; 4) foliose and fruticose lichens (macrolichens); 5) crustose lichens (microlichens); 6) vascular tundra. All data recorded in the survey were geo-referenced and included in a GIS system to which the data obtained in the surveys performed in 2009 and 1960 were also added. Therefore, for each survey year (1960, 2009, 2018) each colonized site was characterized in terms of elevation (m asl), slope (°) and aspect (divided into 8 sectors: N, NE, E, SE, S, SW, W, NW), using the most recent digital elevation model of Signy Island. The deglaciation age of the terrains as assessed by Cannone et al.[19] was recorded. GIS analyses were performed using ArcGIS 9.2.

QUANTIFICATION AND STATISTICAL ANALYSIS

Climatic data

As long-term climatic data since the mid-1990s are not available from Signy Island, the nearest automatic weather station (AWS) of the WMO providing a long-term data record was used in this study, from Orcadas AWS (Orcadas Station, Laurie Island, c. 50 km from Signy Island). The air temperature record of the Orcadas dataset is very closely correlated ($p < 0.01$, $R^2 = 0.98$) to the record available from Signy Island between the 1950s and mid-1990s.[7,46] The mean annual (MAAT) and seasonal (summer = December, January, February; Autumn = March, April, May; Winter = June, July, August; Spring = September, October, November) air temperatures (°C) and total annual precipitation (MAP) (mm) were computed as well as the total seasonal precipitation for the periods 1960-2009 and 2009-2018, as well as over the entire period 1960–2018. We also estimated the distribution pattern of precipitation with respect to altitude and slope on Signy Island for the single annual period (2018-2019). In particular, using four pluviometers located at different elevations (between 16 m asl and 150.5 m asl) and on the western and eastern coasts of Signy Island, we estimated the precipitation gradient on the opposing slopes of the island.

To explore potential links between the local climate of the island and general circulation features, we calculated the monthly Southern Oscillation Index (SOI) (measuring the variability of the El Niño–Southern Oscillation, ENSO), and the monthly mean Antarctic Oscillation index (AAO) (that corresponds to the Southern Annular Mode, SAM), using data obtained from the NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov/).

Data analyses

Air temperature, precipitation, SOI and AAO trends over time were assessed using linear regression in the package Statistica version 10.

The 2009 survey data indicated that the impact of fur seals was not homogeneous with respect to elevation, identifying three elevation bands with decreasing impacts (< 20 m; between 21 and 60 m; > 61 m).[6] Therefore, the occurrence data of *D. antarctica* and *C. quitensis* in the period 2009-2018 were analyzed both across the whole island and separately in the three elevation bands. For the data obtained in 2009 and 2018, we tested whether the disturbance exerted by fur seals showed specific distribution trends comparing the eastern and western sides of the island. We also tested whether consistent patterns could be identified for *D. antarctica* and *C. quitensis* occurrence on the two sides of the island over the entire study period (1960, 2009, 2018), as consistent differences were reported in a parallel study of the distribution of bank forming mosses on the island.[19] Finally, to assess whether there was any change in the dynamics of the two species, their rates of change were computed per decade.

To analyze the relationships between the dynamics of the two species (number of occupied sites for each population size for each year) with topography (elevation, slope), deglaciation age (> 6600 y BP; between 6600 y BP and LIA; post LIA), location on the eastern versus western side of the island, disturbance (fur seals, penguins, footpaths), climate [mean annual air temperature (°C), total annual precipitation (mm)] and, as co-variables, of colonized habitat, a multivariate analysis (redundancy analysis, RDA) was performed. The RDA (square-root transformation of species data, centered and standardized by species, performing the Monte Carlo permutation test on the first and all ordination axes) was performed using CANOCO 4.5.[45]