

PALEONTOLOGY

Extinction of austral diatoms in response to large-scale climate dynamics in Antarctica

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Despite evidence for microbial endemism, an understanding of the impact of geological and paleoclimate events on the evolution of regional protist communities remains elusive. Here, we provide insights into the biogeographical history of Antarctic freshwater diatoms, using lacustrine fossils from mid-Miocene and Quaternary Antarctica, and dovetail this dataset with a global inventory of modern freshwater diatom communities. We reveal the existence of a diverse mid-Miocene diatom flora bearing similarities with several former Gondwanan landmasses. Miocene cooling and Plio-Pleistocene glaciations triggered multiple extinction waves, resulting in the selective depauperation of this flora. Although extinction dominated, in situ speciation and new colonizations ultimately shaped the species-poor, yet highly adapted and largely endemic, modern Antarctic diatom flora. Our results provide a more holistic view on the scale of biodiversity turnover in Neogene and Pleistocene Antarctica than the fragmentary perspective offered by macrofossils and underscore the sensitivity of lacustrine microbiota to large-scale climate perturbations.

INTRODUCTION

Despite recent advances in microbial biogeography (1, 2), our understanding of the impact of tectonic and paleoclimatic events on the community assembly and evolution of regional microbiota remains limited. This is largely due to many microbial taxa being poorly preserved in the fossil record, hampering the documentation of changing distribution patterns through geological time, with foraminifera (3) and diatoms (4) being notable exceptions. More specifically, the siliceous frustules of diatoms allow (morpho)species-level identification and are generally well preserved in marine and lacustrine sediments (5). Rich fossil records of marine diatoms exist dating back as far as the Cretaceous (6). Examinations of these marine sedimentary records reveal strong linkages between diatom and climate evolution throughout the Neogene (7). In the Southern Ocean, planktonic diatoms have been affected by five major species-turnover episodes associated with cooling events over the past 15 million years (Ma) (4), underscoring the sensitivity of marine diatoms to major changes in global temperature (4, 7). However, the high dispersal abilities of marine diatoms and the continuous nature of ocean basins likely allow communities to track temperature changes and recover relatively rapidly from major climate perturbations (8), mitigating the risk of global extinction (9).

In contrast to marine diatoms, the long-term dynamics of their freshwater counterparts are not well understood, largely because of inherent differences between freshwater and marine environments and the species that inhabit them. Freshwater diatom populations are much smaller and less interconnected (10), and their habitats are generally ephemeral over geological time (11). Furthermore, freshwater diatoms speciate and go extinct at substantially faster rates than marine diatoms (12), suggesting that long-term turnover in community composition might be more pronounced in freshwater systems. Over time scales of several million years, freshwater diatoms are thought to have undergone a global biogeographical reorganization in response to the end of “greenhouse Earth” after the late Eocene about 34 Ma (13). The few available records of Miocene diatoms revealed the emergence of modern temperate planktonic freshwater diatom assemblages around the middle/late Miocene (14, 15), and late Miocene and Pliocene temperate diatom floras generally showed large similarities with present-day communities of the same regions (16, 17). This suggests that large-scale taxonomic turnover of freshwater diatom assemblages at the genus-level has been relatively limited in temperate regions since at least the Miocene. Nevertheless, comprehensive historical biogeographic studies of freshwater diatoms are still largely lacking, especially from high-latitude areas. Given that the polar regions have experienced some of the most marked environmental changes on Earth since the Miocene (18), fossil records from these areas are of critical interest to understand their impact on microbial taxa.

We analyzed fossil and recent lacustrine sediments spanning the Middle Miocene, Late Pleistocene, and Holocene to investigate long-term dynamics in the biogeographical structuring and diversity patterns of Antarctica’s freshwater diatom flora. Continental Antarctica experienced major climate shifts over the past 50 Ma, transitioning from a temperate/subpolar climate with much forest coverage toward a polar desert with almost full glaciation and no higher plant species (18). The Middle Miocene Climate Transition (MMCT), ca. 14 Ma, was one of the most important climate shifts driving this transition, both because of its rate and magnitude (19, 20), and resulted in the (regional) extinction of many tundra animals and plants in Antarctica (19). Further cooling during the Pliocene

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(ca. 3 Ma) marked the end of tundra vegetation in continental and maritime Antarctica (18). Cooling further intensified during the Pleistocene glacial/interglacial cycles (21), leading to the scattered distribution of geographically isolated ice-free regions. This geographic isolation, in combination with the selective survival of cold-adapted taxa, has been invoked to explain the existence of strong biogeographical patterns at different spatial scales and high levels of regional endemism in contemporary Antarctic lacustrine and terrestrial macrobiota (22). Similar patterns have recently been found in Antarctic diatoms (23). However, direct fossil evidence of the impact of past climatological and geological events on the evolution of Antarctic microbiota has proven elusive to date.

Here, we study the evolution of the diversity and composition of the Antarctic lacustrine diatom flora through time by analyzing fossil

and extant Antarctic diatom records from three main time slices: (i) the Middle Miocene (~15 to 14 Ma), representing the transition between the Middle Miocene Climate Optimum, a relatively warm phase (24), and the MMCT; (ii) the Pleistocene glacial-interglacial cycles (after 2.58 Ma), including the last major interglacial, the Eemian, i.e., Marine Isotope Stage (MIS) 5e [130 to 115 thousand years (ka)], and the Last Glacial Period (MIS 2 to 4), including the transition between the Eemian and the Last Glacial Period (MIS 5d-a) (~115 to 11.7 ka); and (iii) the present Holocene interglacial (from 11.7 ka), including recent material (Fig. 1). We dovetail this dataset with a comprehensive assessment of the contemporary freshwater diatom flora from the Northern and Southern hemispheres and a newly developed polar diatom database (Fig. 1), allowing us to examine the fossil and modern Antarctic diatom floras in a global context.

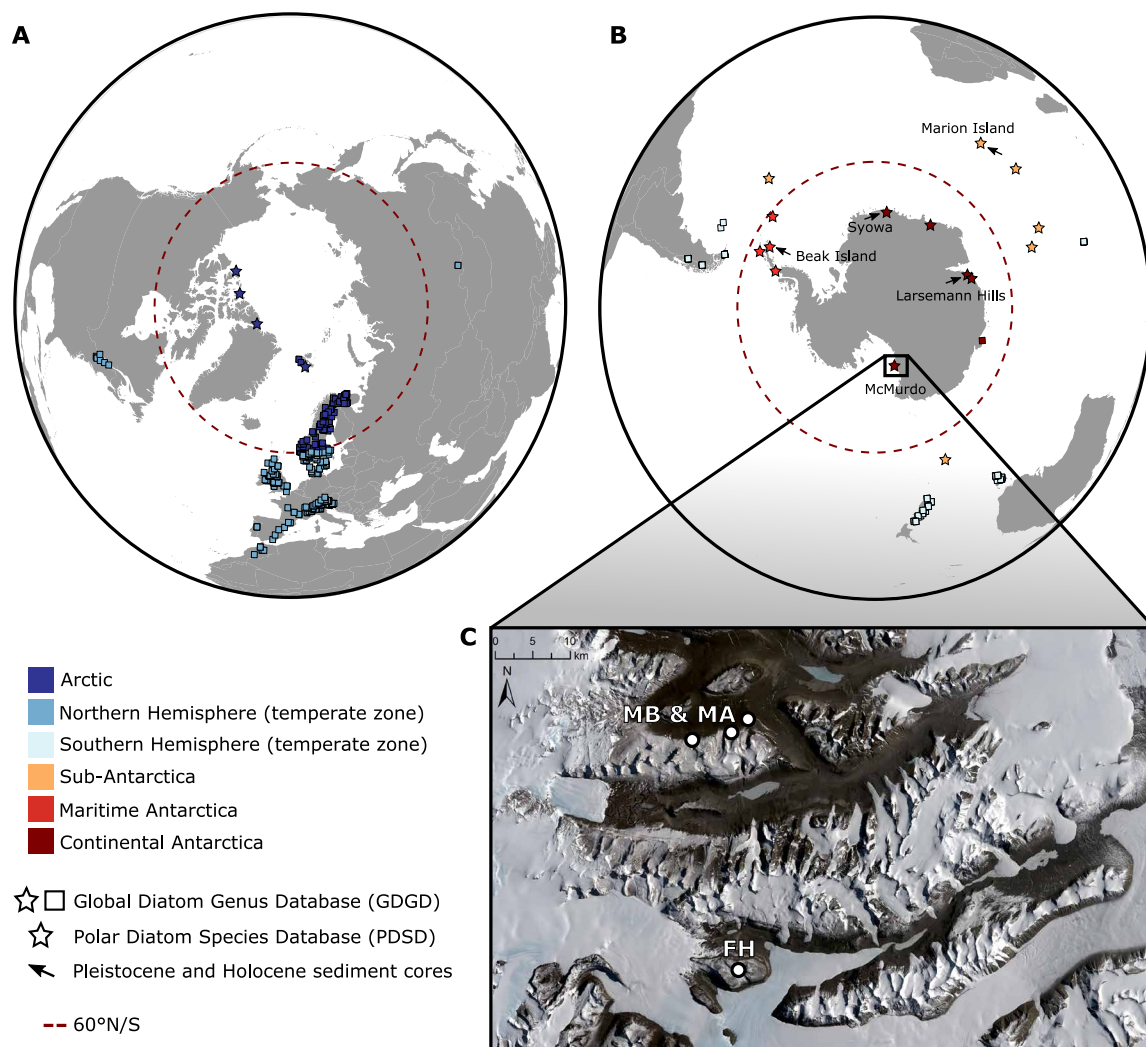


Fig. 1. Maps showing the sampling locations of modern and fossil material. Sampling locations of recent samples and Pleistocene and Holocene (sub)fossil lacustrine diatom communities in the Northern (A) and Southern (B) Hemisphere. Sampling locations are colored by their geographic location, distinguishing six major biogeographical zones. Sample locations for contemporary communities belonging to the Global Diatom Genus Database (GDGD) are indicated with squares and stars, and those belonging to the Polar Diatom Species Database (PDS) are indicated with stars. Sampling locations for (sub)fossil sediments that belong to the PDS are indicated with arrows. Sampling locations may include multiple water bodies. A full list of sample numbers per location is given in tables S5 and S6. (C) Satellite image showing the location of the fossil Miocene diatom deposits in the McMurdo Dry Valley sector (Transantarctic Mountains), with indication of the sampling localities in Mount Boreas (MB), Mount Aeolus (MA), and the Friis Hills (FH). Image (C) represents a Landsat 8 image, courtesy of U.S. Geological Survey, taken on 17 December 2019.

RESULTS

Miocene lacustrine deposits from continental Antarctica

Our data on the Miocene Antarctic diatom flora represent the first comprehensive well-dated Neogene diatom deposit from the Southern Hemisphere, yielding unique insights into the evolution of diatom assemblages in temperate and polar austral regions. These data are based on material originating from four sampling locations in the McMurdo Dry Valleys, including the Mount Boreas, Mount Aeolus, and Friis Hills fossil deposits, which date to ~15 to 14 Ma (Fig. 1) (19, 25). We identified a total of 212 diatom species belonging to 49 genera in the Miocene samples (tables S1 and S2). These identifications were based on a full literature search covering Quaternary and Neogene sediments from both hemispheres (see Supplementary Reference list).

A freshwater origin is supported for all fossil localities, as the observed diatom floras represented typical lacustrine communities (figs. S1 and S2). This confirms previous observations that the Mount Boreas and Friis Hills sediments contained obligate freshwater fossils, including plants and ostracods (19, 26). The fossil localities showed notable similarities in diatom community composition (figs. S3, A and C, and tables S1 and S2). In general, the observed Miocene diatom floras indicated that all investigated paleolakes were oligotrophic and permanently or seasonally ice-free water bodies that were likely several meters deep but with well-developed littoral habitats including moss-dominated substrates. The samples likely incorporated several millennia of lake evolution during which the lakes experienced alterations in pH, water depth, and microhabitat diversity (19). This resulted in substantial changes in the taxonomic composition of their diatom floras (fig. S3C), thus providing an integrative snapshot of the Miocene diatom flora in this part of the Antarctic continent. In addition, the Friis Hills supported a higher diversity of diatom taxa compared to Mount Boreas/Aeolus (fig. S3B) and is also compositionally distinct from Mount Boreas/Aeolus (fig. S4), despite a high overlap in species- and genus-level composition. This is suggestive of potential differences in habitat type and/or climate. This observation is in line with earlier work of the general geochronology of the area and reconstruction of mean summer temperatures via fossil macrobiota, which suggests that the Friis Hills locality might represent an older and warmer lake system than the Mount Boreas and Mount Aeolus paleolakes (19, 27). A detailed overview of the ecology of the Miocene paleolakes inferred from the diatom flora is given in Supplementary Text.

Miocene Antarctica shows similarities with modern Arctic and temperate lakes

To investigate the structural affinity of the Miocene flora with modern diatom communities across the planet, we incorporated the Miocene samples in the Global Diatom Genus Database (GDGD; Figs. 1 and 2) (28). The GDGD contains >1500 genus-level records of temperate and polar freshwater diatom communities representing 87 genera from both hemispheres and maintains full taxonomic consistency using a coarse-grained taxonomic level (see Materials and Methods for details). With 49 diatom genera (40 when using the same taxonomic resolution as the GDGD; see Materials and Methods for details), the genus-level diatom diversity was substantially higher during the Miocene than at present in both maritime (32) and continental (21) Antarctica and comparable to modern sub-Antarctic islands (46) (Fig. 2B and fig. S5). Genus-level diversity is higher in the contemporary Arctic and temperate regions in both hemispheres

compared to the Miocene, but this is most likely due to the low number of samples of Miocene Antarctica, as also suggested by the genus-accumulation curve (fig. S5). Four as yet undescribed and probably extinct genera were also detected in the Miocene material, all of which show very distinct morphologies, which to date have never been observed in other diatom genera (figs. S1, F and G, S2D).

Canonical Analysis of Principal Coordinates (CAP) of the GDGD revealed that the Miocene flora is differentiated from the contemporary continental Antarctic flora but shows a strong affinity with diatom communities from temperate zones of the Southern Hemisphere, as well as those of the Arctic and sub-Antarctic regions (Fig. 2A). Many of the genera observed in the Miocene material are currently absent from or represented only by a limited number of species in continental and maritime Antarctica (Figs. 2B and 3B and figs. S2C and S6). This includes diatoms belonging to the orders Eunotiales and Cymbellales (fig. S2, F and H), which are highly diverse in modern Arctic and temperate lakes (Fig. 3B and fig. S6) (29, 30). The dominance of small Fragilariales in the Miocene, such as *Staurosira* and *Staurosirella* (fig. S2G), is also typical of present-day alpine and Arctic lakes (31), whereas they are almost entirely absent from continental Antarctica today (Fig. 3B). Nevertheless, several of the genera that dominate the modern continental Antarctic flora were already present in the Miocene, including *Pinnularia*, *Humidophila*, and *Muelleria* (Fig. 3B and fig. S2, A and E).

Austral elements in Miocene continental Antarctica

We found representatives of the freshwater diatom genera *Veigaludwigia* (Fig. 4, A and B) and *Eunophora* (Fig. 4, A and D, and fig. S7) in the Miocene material. Today, these genera are restricted to Australia, New Zealand, and (*Veigaludwigia* only) southern South America and the Falklands (Fig. 4A and table S3) (32, 33). The presence of representatives of *Veigaludwigia* and *Eunophora* in the Miocene deposits provides strong evidence for the existence of typical (historical) austral distribution patterns in diatoms, with occurrences in several former Gondwanan landmasses. Slight morphological differences with modern *Eunophora* suggest that the fossil taxon might represent an ancestral form of this genus (see Supplementary Text for more details). This notion is corroborated by the age of the *Eunophora* fossil falling well within the estimated range for the origin of the genus as based on a molecular time-calibrated phylogeny (34). Note that this observation does not imply an Antarctic origin, as the ancestral morphology might have originated elsewhere and reached Antarctica through dispersal. In addition to *Veigaludwigia* and *Eunophora*, a third as yet undescribed endemic *Amphora* species, previously referred to as *Amphora tasmanica nomen nudum* (Fig. 4, A and C) (35), also appears to represent an austral element. The Miocene *Amphora* fossils are virtually identical to extant populations only occurring in Tasmania and New Zealand (Fig. 4, A and C, and table S3). Austral elements were detected in 10 of the 24 Miocene samples during the counts and in an additional three samples when scanning the slides for extra taxa after counting but never reached abundances >1%.

Miocene Antarctica was home to a diverse and unique freshwater diatom flora

We developed the Polar Diatom Species Database (PDSD; Figs. 1, 3, and 5) to provide insights into patterns of species-level diatom diversity in Antarctica. The PDSD contains >600 taxonomically verified species-level records from extant diatom communities in

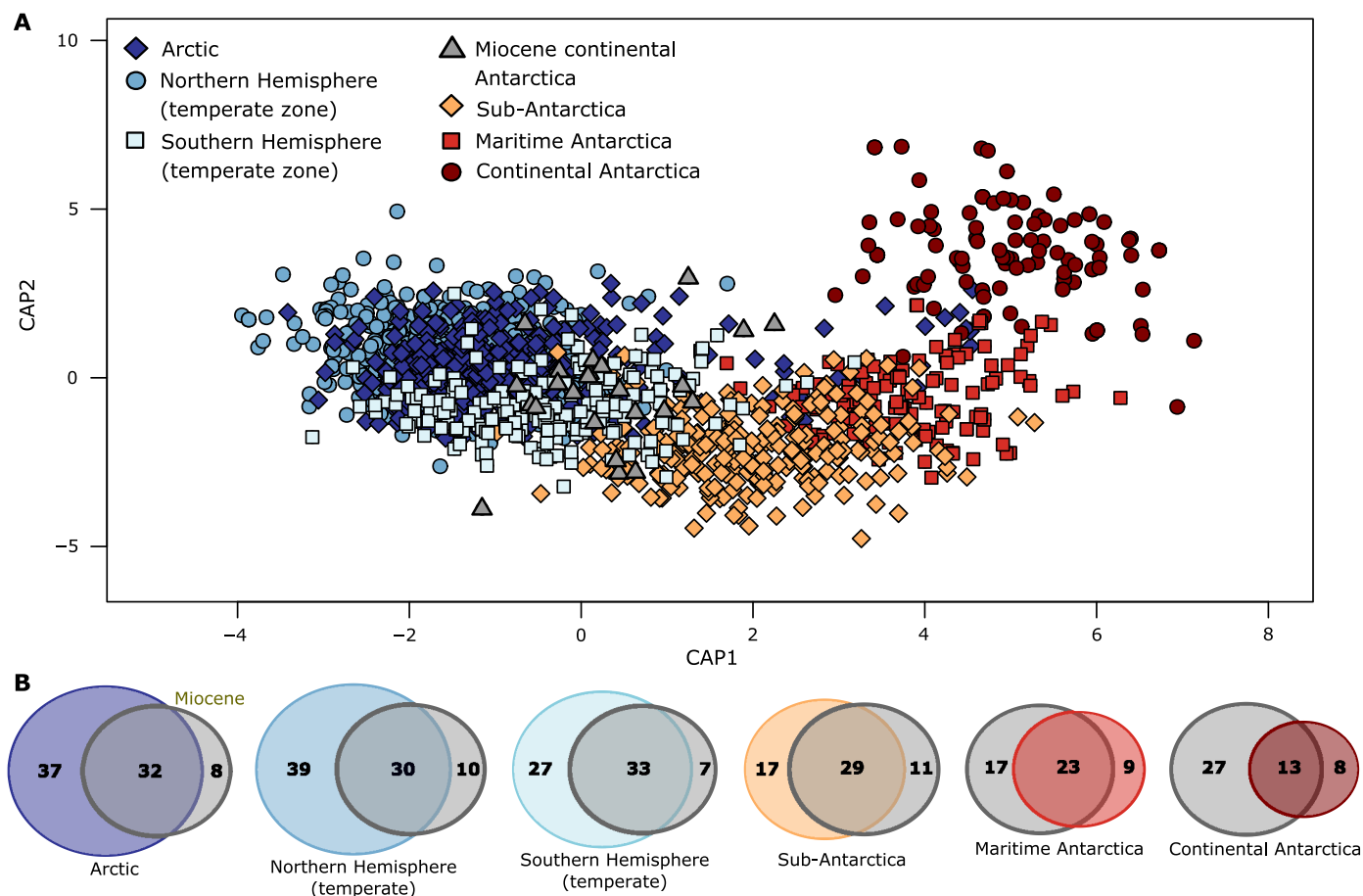


Fig. 2. Genus-level diversity and composition of freshwater diatom communities on a global scale. The figures are based on the GDGD. **(A)** CAP showing the Miocene samples and the six major biogeographic regions indicated in Fig. 1. **(B)** Venn diagrams showing the number of unique and shared genera between the Miocene samples and the six major biogeographical zones of Fig. 1. For the Miocene data, genera encountered outside the counts were included in the Venn diagrams to partially account for the lower sample coverage of Miocene Antarctica. Note that although 49 genera were distinguished in the Miocene continental Antarctic diatom flora, this number was reduced to 40 following the lumping of several genera to allow for taxonomic consistent incorporation in the GDGD (see Materials and Methods and table S7).

the High Arctic and Antarctica. With a total of 212 species, the diversity of the Miocene flora is well above that currently observed in continental (59) and maritime Antarctica (161), comparable to contemporary regional diversity in sub-Antarctica (284) but lower than the High Arctic (370) (Fig. 3). In our entire Antarctic dataset, 417 contemporary species were detected. Note that our species-richness estimates are based on an almost complete sampling of contemporary Antarctic diatom diversity (Fig. 3A and fig. S5) (23), providing robust estimates for comparison. Our High Arctic data were limited to 143 samples from the Canadian Arctic (29) and Svalbard (30), as other publicly available databases of the Arctic could not be integrated because of their lack of taxonomic consistency. Although this underestimates the true freshwater Arctic diatom species richness, which could be >1000 species (36), it is already clear from our data that Arctic diatom species richness vastly exceeds that of modern continental and maritime Antarctica.

The vast majority of diatoms observed in the Miocene assemblages are unknown to science. Only six Miocene diatom taxa could be assigned to the common modern diatom species complexes of *Achnanthes minutissimum*, *Encyonema silesiacum*, and *Pinnularia borealis*. Three further taxa somewhat resembled present-day

(sub-)Antarctic endemics (fig. S2E): *Achnanthes australexiguum*, *Pinnularia australomicrostaurum*, and *Stauroneis latistauros*. The vast majority of species in the Miocene material therefore represents most likely new, yet undescribed, species, as they showed unique combinations of morphological features not observed in either extant or Quaternary and Neogene communities from around the world. Consequently, the Miocene flora shows little overlap with modern polar floras (Fig. 5B).

Non-analog freshwater diatom communities in Pleistocene Antarctica

To better understand the turnover of the Antarctic diatom flora through time, we investigated a series of Late Pleistocene paleorecords from continental Antarctica dating back to the previous interglacial (the Eemian, MIS 5e) and the Last Glacial Period (MIS 2 to 4). The latter also included samples from the transition between the Eemian and the Last Glacial Period (MIS 5d-a). We integrated these records in the PDSD. We also included several sediment cores spanning the middle-to-late Holocene from sub-, maritime, and continental Antarctica. Our analysis showed that per-sample diversity levels in continental Antarctic lakes had decreased markedly by the

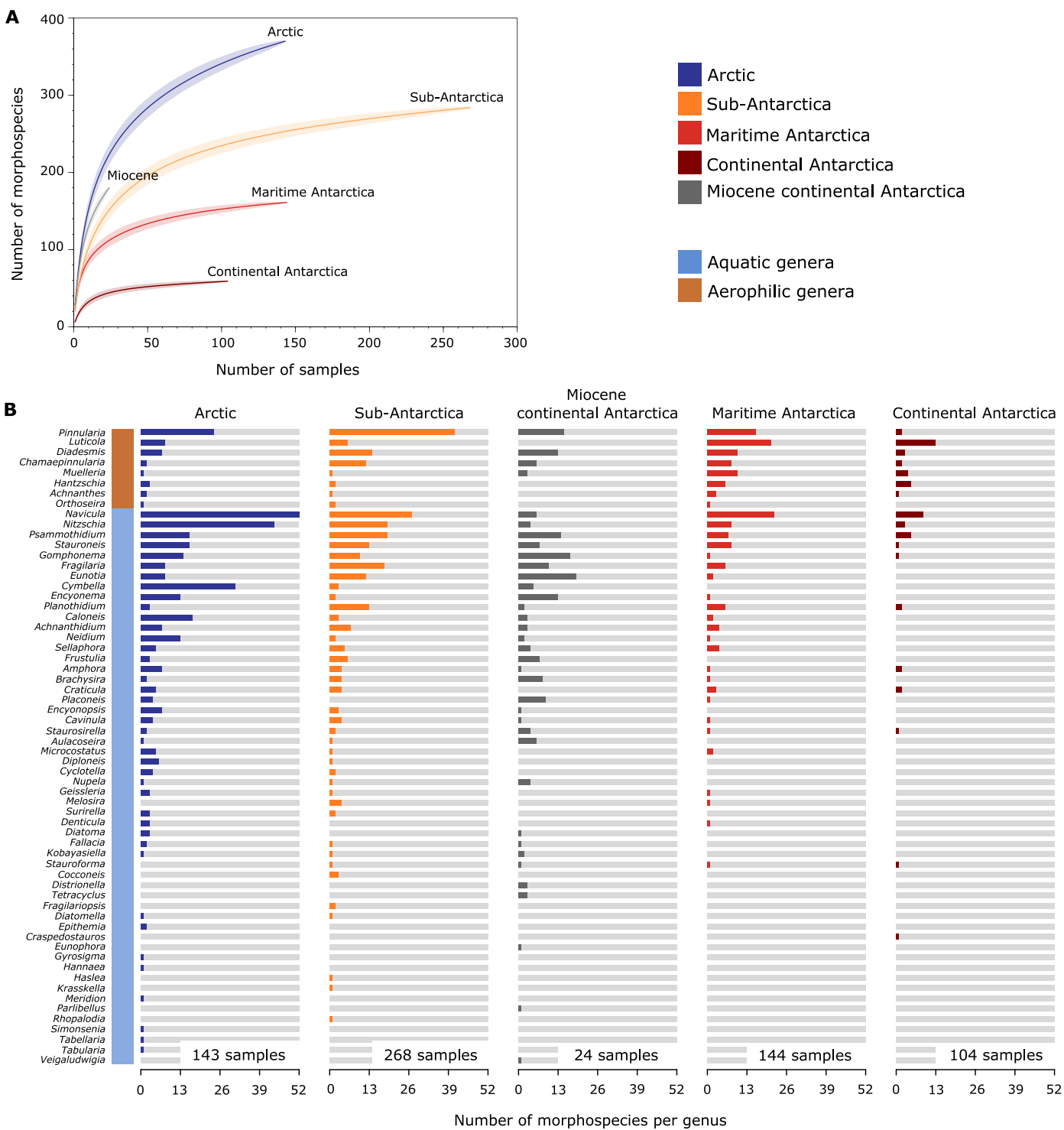


Fig. 3. Species-level diversity and community composition of polar freshwater diatom floras. The figures are based on the PSD. **(A)** Sample-based interpolation (rarefaction) of the diatom morphospecies richness in the polar regions. The transparent areas indicate the 95% confidence interval. Morphospecies that were only detected after counting 400 valves were not included in the analysis. **(B)** Bar plots showing the number of morphospecies per genus in different geographic regions. A distinction is made between genera that contain predominantly aerophilic taxa and those mostly containing obligate aquatic taxa. Within each habitat type, genera are ordered from highest richness to lowest richness over all sets together. The genera represent a coarse-grained taxonomic level, following the classification in the GDGD (see Materials and Methods and table S7). For example, the genera *Staurosira* and *Humidophila* are respectively embedded within *Fragilaria* and *Diademsis*. Morphospecies that were only detected after counting 400 valves were included for the Miocene samples in (B) to partially account for the lower sample coverage in the Miocene dataset. Taxa belonging to the unknown genera detected in the Miocene material were not included.

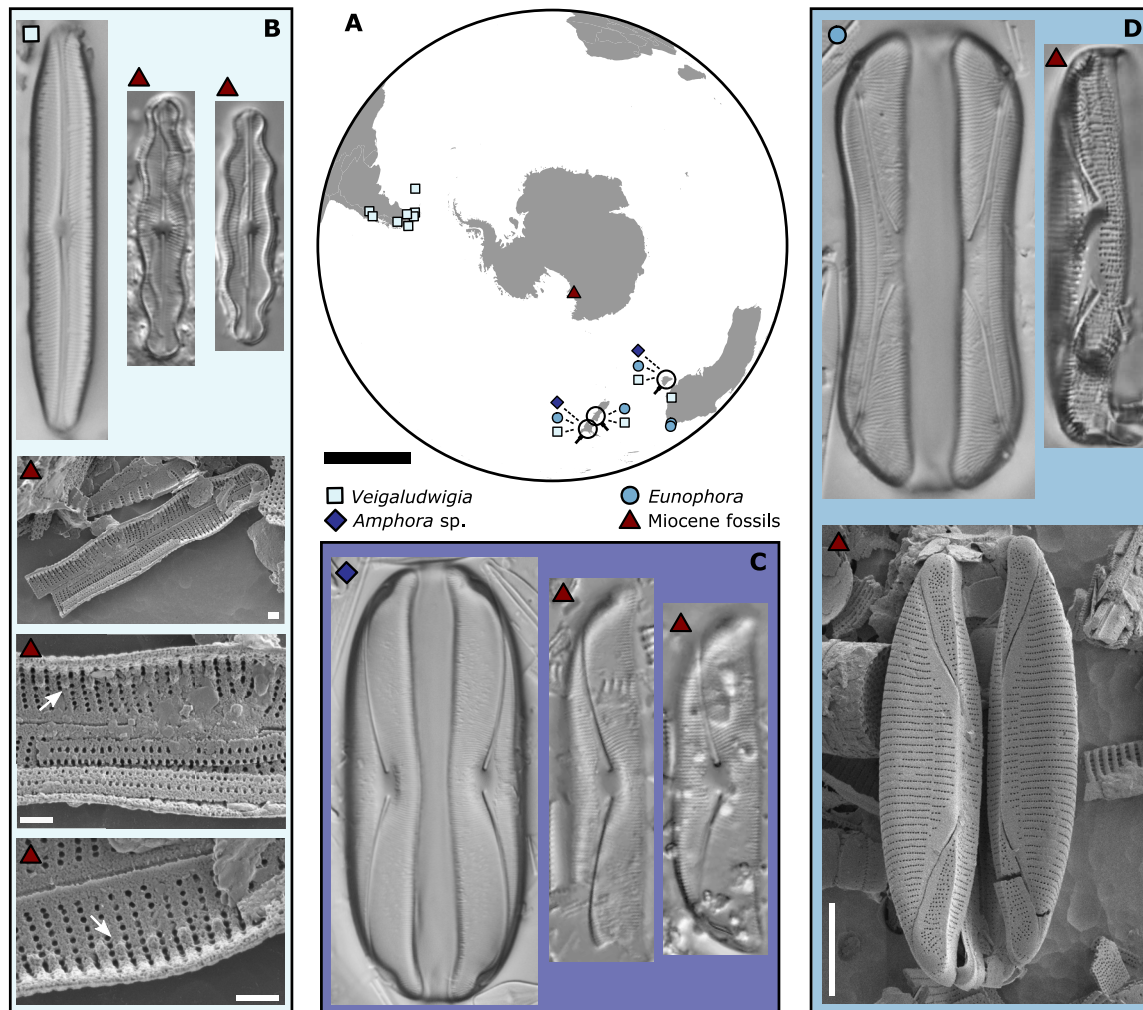


Fig. 4. Austral elements in Miocene continental Antarctica, showing affinities between Antarctica and other former Gondwanan landmasses. (A) Contemporary geographic distributions of three austral elements: *Amphora* sp. [*Amphora tasmanica* nomen nudum in (35)], *Eunophora*, and *Veigaludwigia*. Table S3 lists all the studies that were consulted to determine the extant distributions of the three austral elements. (B) Light microscopy (LM) and scanning electron microscopy (SEM) micrographs of contemporary and Miocene *Veigaludwigia*. The white arrows indicate the presence of the internal spines, a unique diagnostic feature for the genus *Veigaludwigia*. (C) LM micrographs of contemporary and Miocene *Amphora* sp. (D) LM and SEM micrographs of contemporary and Miocene *Eunophora*. All contemporary pictures were taken from a sample from Arthur Tarn in Tasmania (Australia) (see table S3). Black scale bar, 10 μm (A) (for all LM micrographs). White scale bars, 1 μm (B) (SEM) and 10 μm (D) (SEM).

Pleistocene (Fig. 5A). Throughout the Eemian, these diversity levels remained higher compared to more recent periods, after which levels further decreased during the Last Glacial Period (Fig. 5A). This is confirmed by species accumulation curves of lakes from the Larsemann Hills in continental Antarctica (fig. S8), which experienced pronounced species impoverishment throughout the Last Glacial Period. Moreover, while the Eemian flora from continental Antarctica consisted entirely of extant diatom taxa, it represents a non-analog community due to the presence of diatoms that today are confined to sub-Antarctica and the northern tip of the Antarctic Peninsula (Fig. 5B and fig. S9), e.g., *Humidophila crozetikerguelensis* and *Gomphonema maritimo-antarcticum*. This demonstrates the localized extinction of certain taxa from continental Antarctica during Late Pleistocene glaciation.

Long-term stability and impoverishment of Holocene Antarctic diatom floras

The Antarctic sediment cores incorporated in the PDS indicated that their Holocene diatom assemblages remained stable throughout the Holocene and fit directly into their respective biogeographic provinces as recognized in Antarctica today (Fig. 5B and fig. S9). In addition, Holocene diversity levels never recovered to those of the previous interglacial (fig. S8). Because aquatic diatom genera are potentially more susceptible to environmental stress, for example, as experienced during climate extremes, than their aerophilic counterparts (37–39), we also investigated the link between habitat preference of diatom genera and species-level diversity (Fig. 3B). Whereas aquatic diatom genera almost exclusively inhabit submerged environments such as the littoral zones of lakes, ponds, and rivers or

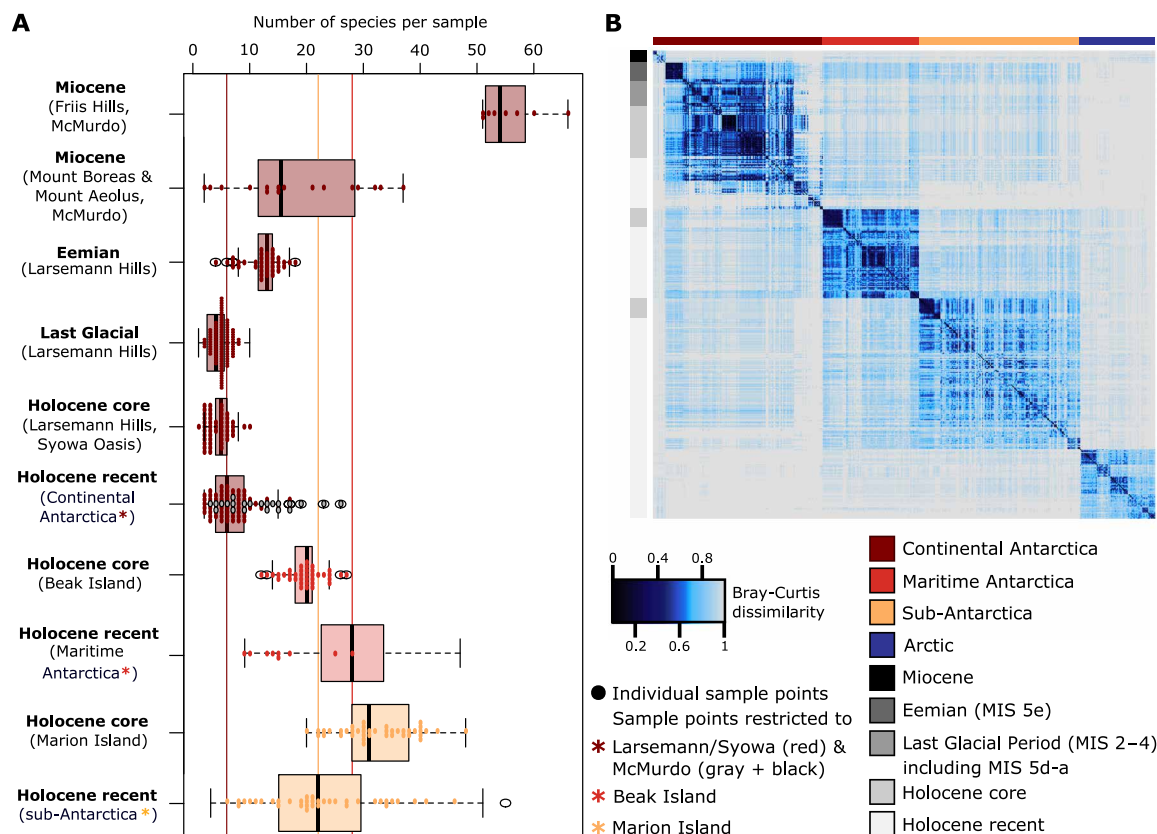


Fig. 5. Species-level richness of Antarctic freshwater diatom biomes through space and time. (A) Number of morphospecies per sample for different time periods in the Antarctic region. Species encountered outside the counts were not included. Per-sample diversity is visualized with box plots and individual sample points. For the recent Holocene material, box plots give the diversity of all available samples from the respective region, whereas individual sample points highlight the per-sample diversity from areas for which fossil data are available. Solid colored vertical lines indicate the median present-day diversity in the three main Antarctic regions. (B) Heatmap of the PDS matrix with indication of fossil and recent samples (vertical gray-shaded bars) from the three main regions in Antarctica and the High Arctic (horizontal colored bars).

have a (tycho)planktonic existence in the water column, aerophilic diatoms usually thrive in terrestrial environments such as moist and dry soils and mosses. Our analysis revealed that throughout the Holocene, lakes in continental Antarctica, and, to a lesser extent, maritime Antarctica, were dominated by species belonging to predominantly aerophilic genera. By contrast, samples from sub-Antarctica, Miocene Antarctica, and the High Arctic showed a more balanced flora, i.e., the flora from these regions included many representatives from predominantly aquatic genera with only trace occurrences of aerophilic taxa (Fig. 3B). Similarly, the Miocene flora also showed a much more balanced species composition (Fig. 3B), indicating that the shift to aerophilic species happened after the onset of the MMCT.

DISCUSSION

Lacustrine paleosediments of pre-Pleistocene origin are notoriously difficult to find, especially in Antarctica, where extensive glaciation hampers preservation. Our comprehensive analysis in which Antarctic fossil assemblages are considered with explicit comparison to contemporary floras provides a detailed view of the long-term evolution of the freshwater diatom floras of Antarctica. This includes the first fossil evidence for an austral distribution in protists, with

some genera being present in Miocene Antarctica, and the former Gondwanan landmasses of South America, Australia, and New Zealand. The discovery on the Antarctic continent of diatom taxa now found only in the temperate Southern Hemisphere strongly suggests the existence of an ancient origin of contemporary biogeographic patterns in diatoms.

Extinction of an ancient diatom flora

Our study demonstrates that the modern lacustrine diatom flora of continental Antarctica is strongly influenced by extinction events since the MMCT, both at the genus- and species-level. The Miocene diatom flora is characteristic of a warmer-than-present climate, as it shares many genera with contemporary lacustrine floras from sub-polar and temperate regions, including (sub-)alpine sites, while remaining compositionally distinct from any present-day assemblages from continental Antarctica. This is in line with the finding that during the Middle Miocene, the McMurdo Dry Valley sector was home to a diverse set of aquatic macrobiota that became extinct in the region after the MMCT (19, 26, 27). Using modern autecologies of some of the macrofossils in the Mount Boreas core, it was suggested that the mean summer temperature of the site was approximately 5°C during the Middle Miocene, whereas presently, it is −12°C (19). This cooling of the Antarctic continent occurred in a stepwise manner over

the past 14 Ma, suggesting that extinction likewise pulsed in distinct waves tied to the cold climate extremes in the Middle Miocene and Plio-Pleistocene. Stepwise turnover of Antarctic biota over this time scale has been shown previously for marine diatoms (4) and is also evident in macrofloristic records (18). In particular, the impact of the MMCT was substantial: in about 220,000 years' time, temperatures dropped at least 8°C in the McMurdo Dry Valley sector (19). This coincided with a 6° to 7°C drop in sea surface temperatures in the Southern Ocean (20), suggesting the MMCT substantially affected the entire Antarctic region. A cooling event of this rate and magnitude would almost certainly be responsible for a regional mass extinction of freshwater microbiota, including diatoms, in tandem with the extinction of Antarctica's tundra animals and plants (19). This is further evidenced by the observation that McMurdo Dry Valley sediments directly postdating the MMCT do not contain any fossils (19). Nevertheless, a subset of the Miocene diatom flora likely survived the MMCT, either directly in the McMurdo Dry Valley sector or in other parts of the continent. This is evidenced by the observation of three fossil diatom species with direct affinities to present-day Antarctic endemic forms.

The Pleistocene Antarctic paleorecords examined here revealed direct evidence for a stepwise impoverishment of Antarctica's diatom flora over shorter time scales, characterized by local extinctions during the Late Pleistocene. The diatom assemblages of the previous and relatively warm interglacial, the Eemian, were characterized by extant morphospecies yet represent non-analog communities, which contained species that are today confined to sub-Antarctica and the Antarctic Peninsula. The Eemian flora is thus witness to local extinctions among the continental Antarctic diatom flora that likely occurred during the last glaciation. Furthermore, our data indicate that Holocene Antarctic floras have been remarkably stable, as they fit into their respective biogeographic provinces recognized in Antarctica today, and these floras were present immediately after deglaciation. This suggests that most, if not all, diatom taxa present in these cores survived the Last Glacial Maxima in situ in glacial refugia and do not represent new colonizations during the Holocene (40, 41).

Dissimilarities between Antarctica and the Arctic and the role of in situ speciation

The observations of an impoverished diatom flora in Antarctica are in notable contrast with the relatively diverse High Arctic (36) and this despite being at similar latitudes. This contrast is likely the result of differences in climate and geological history between the polar regions. Specifically, the Arctic is well connected by landmasses in the Northern Hemisphere, which allows for north-south migrations during glacial/interglacial cycles. For example, direct terrestrial connections with lower latitudes must have allowed for stepwise short-distance dispersal, which is expected to be more effective for survival than long-distance dispersal over large maritime barriers. In that sense, migration of freshwater diatom species in the Arctic has likely been facilitated by both aeolian pathways and animal vectors (42). This includes the Arctic's avian fauna, which is far richer than in Antarctica. This lack of strong dispersal barriers in the Arctic likely prevented a substantial loss of genetic diversity during the ice ages or earlier cooling events by allowing southward migrations of cold-adapted species and subsequent recolonization of the Arctic (43) in addition to in situ survival in glacial refugia (44). As a consequence, many macroorganisms have a circumarctic distribution

(45), and the existence of a circumarctic diatom flora has been suggested (30, 46).

By contrast, Antarctica is meteorologically and oceanographically isolated from neighboring continents, effectively hampering large-scale latitudinal reorganizations of biota during climate extremes (47, 48). As a consequence, Antarctica's macrobiota have long been known to be highly impoverished with respect to species richness, retaining distinct biogeographic "islands" between individual ice-free regions (22, 49). This impoverishment of Antarctica's macrofauna must have further reduced potential dispersal pathways for microbiota, which currently probably rely predominantly on aeolian dispersal in the area. It was recently shown that biological regionalism also exists in present-day Antarctic diatom communities, which show high levels of endemism, particularly in continental Antarctica (up to 64%) (23). Our data suggest that stepwise cooling during the Neogene and Quaternary incrementally culled species richness without comparable replenishment by new colonization or diversification events, resulting in the decline of species richness in Antarctica through time. Nevertheless, colonizations, and in situ speciation of colonizers and ancient elements that survived the progressive cooling and glaciation of the region since the Middle Miocene, must have played a major role in shaping the high levels of endemism in Antarctica today. Specifically, repeated glacial-interglacial cycles in the Antarctic region might have acted as a species pump, causing repeated range shifts and isolation of diatom populations in glacial refugia followed by vicariant speciation. Even during the less extreme interglacial periods, suitable habitats for diatoms in continental Antarctica were few and very far between, hampering effective gene flow between populations. Together, these processes likely resulted in both the high number of endemic diatom taxa prevalent in the area today and the modern biogeographical distributions observed in the Antarctic diatom biome (23).

A shift from an aquatic to aerophilic diatom flora

Since the Miocene, the Antarctic freshwater diatom flora underwent a marked change regarding the type of composing species, from one dominated by aquatic taxa to one with a disproportionately high representation of aerophilic taxa. This observation is most likely related to a decrease in lacustrine habitat availability as a response to the MMCT (19) or more recent Plio-Pleistocene cooling. The MMCT most likely substantially decreased the number of ice-free lakes in Antarctica, and the few lakes that escaped glacial overriding during the Pleistocene glacial maxima were probably permanently covered with lake ice (50), precluding the survival of many obligate aquatic biota, including diatoms (19). By contrast, aerophilic diatom taxa are much better adapted to tolerate extreme freezing (37) and desiccation events (38) and possibly also oxygenation, high conductivities, and ultraviolet radiation (39) and are thus more likely to survive extreme cooling and the associated loss of aquatic habitats. Open niche space created by the decimation of many obligate aquatic diatoms, in combination with novel polar niches, most likely benefited the local colonization and subsequent diversification of aerophilic taxa in aquatic habitats since the MMCT (23). Widespread habitat restructuring and new ecological opportunities since the MMCT have been found to drive diversification in both terrestrial (51) and marine (52) Antarctic macrobiota specialized in extreme polar environments.

Two aerophilic genera that today are prime components of the continental and maritime Antarctic diatom flora, i.e., *Hantzschia*

and *Luticola*, are entirely absent from the Miocene samples (Fig. 3B), whereas other predominantly aerophilic genera that presently dominate continental Antarctic habitats (e.g., *Pinnularia*, *Humidophila*, and *Muelleria*) were found in the Miocene material. Although *Hantzschia* and *Luticola* might have been present in other locations in Miocene Antarctica, this observation could also suggest post-Miocene colonization and/or diversification of aerophilic diatom taxa. Molecular phylogenies of the terrestrial diatom species complex *P. borealis* are indicative of multiple colonization events of the Antarctic region over the past 20 Ma, including at least two such colonizations in the past 5 Ma, as well as regional speciation in the sub- and maritime Antarctic region over the past ~6 Ma (2). The extreme levels of endemism in modern Antarctic *Luticola* also confirm the idea of local diversification, although the timing remains an open question (53).

Link between Antarctica and other Gondwanan landmasses

A major find in our study is the biogeographic link between diatom floras in Antarctica and other Gondwanan landmasses. This includes both general similarities in genus-level community assembly and distinct austral elements such as *Eunophora*, *Veigaludwigia*, and *A. tasmanica*. Such a link has previously been demonstrated for several biota, including mites, tardigrades, and angiosperms (54–56), but had not yet been demonstrated for protists, which are generally assumed to be less dispersal limited than macrobiota because of their small size and huge population sizes. Although many of these connections were originally ascribed to vicariant speciation after breakup of Gondwana, it is becoming increasingly clear that long-distance dispersal, or a combination of both, played a major role in shaping of modern Gondwanan species distributions (54, 57). Although the exact drivers responsible for the geographic distributions of the austral elements in our data remain unknown, their fossil and modern occurrences demonstrate that Antarctica's microbial flora shares a common history with its neighboring continents.

Given the relatively young estimated age, ca. 130 to 120 Ma (34), of the pennate diatom clade to which our austral elements belong, an ancient origin in Gondwana before continental separation is highly unlikely. However, the final breakup of Gondwana was delayed until the opening of the Tasman Gateway, ca. 33.5 Ma (58), which separated Australia from Antarctica, and the opening of the Drake Passage between South America and Antarctica, ca. 34 to 30 Ma (59). This indicates that direct land bridges between Antarctica and several neighboring landmasses existed until the Oligocene. It is an open question whether the common austral diatom flora predominantly originated before isolation of Antarctica, Australia, and South America or whether it was mostly shaped by long-distance dispersal between neighboring landmasses after the final isolation of Antarctica. In any case, substantial barriers to gene flow were likely present since the initiation of the Antarctic Circumpolar Current and its associated atmospheric fronts, which are known to act as dispersal barriers (47). Because the Antarctic Circumpolar Current formed in the late Eocene/early Oligocene after the isolation of Antarctica (58, 59), the Miocene Antarctic diatom flora may have evolved in relative isolation for an extended time period before the MMCT and possibly even before the Late Eocene (18). Alternatively, long-distance dispersal during the Oligocene and Early to Middle Miocene, even when infrequent, might have shaped the similarities between Miocene Antarctica and the neighboring continents. In this scenario, Miocene Antarctica might have served as stepping-stone

for long-distance dispersal between Australia, New Zealand, and South America before the MMCT.

It is possible that several other taxa from the Miocene flora represent distinct austral elements. We observed four undescribed, likely extinct, diatom genera. Despite an extensive literature search (see the Supplementary Reference list), we did not observe any of these unknown genera in other Neogene deposits, including the available records of the Southern Hemisphere. However, as Neogene diatom deposits from the Southern Hemisphere have only been rarely studied, it cannot be excluded that these unknown genera had wide austral distributions during the Miocene. Alternatively, these genera might represent unique lineages that evolved in Antarctica, underscoring the possibility of long-term evolution in isolation of Antarctica's diatom flora. Additional fossil freshwater diatom localities from former Gondwanan landmasses, ideally in combination with molecular phylogenetic data, are needed to fully investigate the long-term evolution of diatom floras in the polar and temperate Southern Hemisphere. These studies will also help understand where and when the identified austral elements in our study, i.e., *Eunophora*, *Veigaludwigia*, and *A. tasmanica*, initially evolved. Only few fossil occurrences are known for *Eunophora* (in New Zealand) and *Veigaludwigia* (in South America and New Zealand) (fig. S10 and table S3). Although no dating is available for these fossil records, they are indicative of long-term presence in the temperate regions of the Southern Hemisphere.

Integrating our findings on the long-term evolution of Antarctica's diatom flora

Combined, our data reveal a marked turnover in freshwater diatom diversity and community composition in response to the major climatic transitions during the Neogene and Quaternary. We demonstrate that the modern continental Antarctic diatom flora became established after the MMCT, once global temperatures decreased, and Antarctic glaciation reintensified. Antarctica's cooling climate, combined with its geographic isolation, caused stepwise and widespread, but selective, extinction among an ancient diatom flora that shared a common history with several former Gondwanan continents. Although there are multiple records of regional extinctions and species turnover of lacustrine diatoms in Quaternary paleorecords of the Northern (60) and Southern (61) Hemisphere, the scale of the extinction of diatoms in continental Antarctica since the mid-Miocene is, both at the species- and genus-level, beyond anything reported in the literature thus far. Although extinction likely dominated since the MMCT, colonizations and in situ diversification of ancient elements and new colonizers have been crucial for the evolution of the highly adapted and largely endemic, albeit species-poor, modern Antarctic diatom flora. Although molecular phylogenetic data on diatoms show direct evidence for both in situ diversification and colonizations since the MMCT (2), additional research is necessary to unravel the relative roles of both processes in shaping Antarctica's extant diatom flora.

In combination with molecular phylogenies, which showed that major climate events and habitat shifts can drive diversification in diatoms (2), our data highlight that large-scale climate and environmental change may have major evolutionary consequences for the diversity and richness of important clades of microorganisms such as the diatoms. Furthermore, we expect that the high degree of extinction and stepwise impoverishment experienced by Antarctic freshwater diatoms throughout the Neogene and Quaternary is mirrored

in many other biota that inhabit(ed) the area. This includes (micro) biota for which no fossil records are available. Fossil diatom assemblages offer the unique advantage of being able to study the overall biodiversity of an entire clade on morphospecies-level, rather than the more fragmentary view offered by macrofossil remains. Lacustrine diatoms thus allow gaining a more holistic view of the scale of overall biodiversity turnover in terrestrial Antarctica during the MMCT and later glaciations.

MATERIALS AND METHODS

Study design

This study analyzes the evolution of the diversity and composition of Antarctica's freshwater diatom flora through time by investigating fossil records from the Miocene, Pleistocene, and Holocene, as well as the contemporary Antarctic diatom flora. To achieve this, we designed two datasets of contemporary and fossil freshwater diatom communities from around the world. First, the GDGD provides a taxonomically curated and consistent dataset of contemporary diatom community composition on a global scale, using genus-level incidence data. Second, the PDSO similarly provides a taxonomically curated and consistent dataset of contemporary Antarctica and the High Arctic, using incidence data at morphospecies-level resolution. The PDSO also incorporates fossil Antarctic diatom assemblages from sediment cores spanning the Pleistocene and Holocene. Miocene fossil diatom material from continental Antarctica was incorporated in both the GDGD and PDSO. Together, these datasets provide >2000 records of fossil and contemporary diatom communities from around the world.

Miocene fossil material

We retrieved well-preserved Miocene diatom fossils of lacustrine paleosediments from several sampling locations in the McMurdo Dry Valleys (Transantarctic Mountains, continental Antarctica). A first set of samples were from near Mount Boreas in the Olympus Range in the western Dry Valleys (13 samples) (Fig. 1). These samples came from the east and west side of the paleolake Boreas. Seven of these samples form a complete continuous sequence. Previously, the Mount Boreas locality has been extensively described in (19), which also lists further sampling details. Three additional samples were taken at two different localities near Mount Aeolus, to the east of Mount Boreas (Fig. 1). Two of the Mount Aeolus samples originated from small moraine-dammed lake basins. All aforementioned samples date back to ca. 14.07 ± 0.05 Ma, the age of which is based on a dated ash layer (19). Another Miocene fossil locality is the Friis Hills adjacent to the Asgard Range in the southern Dry Valleys, from which eight samples were available (Fig. 1). The Friis Hills material originated from two short sediment cores, which correspond with the Friis Hills II lower drift zone (27). Recent dating of this drift zone indicated an age of ca. 15 to 14 Ma (25). All samples thus originated from the transition between the Middle Miocene Climate Optimum, a relatively warm phase during the Miocene, and the Middle Miocene Climate Transition (MMCT) (19, 25, 27). Further details on the samples can be found in table S4.

We prepared subsamples of the Miocene paleosediments for light microscopy (LM) following (62): We cleaned samples by adding 37% H_2O_2 and heating to 80°C for about 1 hour, after which we added KMnO_4 to complete the reaction, and we centrifuged the samples 3×10 min at 3700g. We dried cleaned diatom material on coverslips

and mounted it onto slides using Naphrax. In each sample, we counted and identified 400 diatom valves on random transects at $\times 1000$ magnification under oil immersion using an Olympus BX51 LM microscope equipped with differential interference contrast (Nomarski) optics. After counting, we scanned slides for additional taxa. For scanning electron microscopy (SEM), we filtered parts of the oxidized material through a $5\text{-}\mu\text{m}$ Isopore polycarbonate membrane filter (Merck Millipore). We sputter-coated the stubs with a gold-palladium layer of ~ 10 nm and studied them in a JEOL JSM-7100F SEM (Meise Botanic Garden, Belgium), and a ZEISS Ultra SEM microscope (Natural History Museum London, UK).

We identified diatom genera and morphospecies using LM and SEM micrographs using the complete available literature on Pleistocene, Pliocene, and Miocene fossil diatoms and contemporary diatoms (see Supplementary Reference list). LM figures of all taxa can be found on Mendeley Data (doi: 10.17632/2h88dnxb7w.1). The fossil floras were well preserved, allowing for the taxonomic identification of the composing taxa.

GDGD and PDSO

We incorporated the Miocene flora into two databases covering contemporary diatom assemblages from around the world: the GDGD and PDSO. First, to allow for comparison of the Miocene database with the contemporary diatom flora on a global scale, we integrated the Miocene flora in the GDGD of (28) (Fig. 1 and table S5), with exclusion of samples from tropical regions. This database provides a genus-level taxonomically consistent dataset of diatom incidence data from >1500 freshwater bodies from (sub-)polar and temperate, including (sub-)alpine, sites in both hemispheres (Fig. 1 and table S5). In addition, we reduced the recent data of the PDSO (see below) to the genus-level and incorporated these into the GDGD, resulting in 1997 records (table S5). The GDGD was limited to contemporary datasets. Only few well-dated records on early Quaternary and Neogene freshwater diatom deposits are known, the vast majority of which deal with sediment records from the Northern Hemisphere. Although fossil diatomite deposits are known from several Southern Hemisphere localities (see Supplementary Reference list), no well-documented freshwater diatom records from the Southern Hemisphere of the early Pleistocene, Pliocene, or Miocene have been published in the literature. The few available studies did not completely analyze the fossil diatom floras but instead focused on selected taxa, showed limited micrographic documentation (which is essential for taxonomic comparison), and/or used outdated taxonomy (see Supplementary Reference list). As a result, a formal comparison of the Miocene Antarctic diatom flora with early Quaternary and Neogene floras from the neighboring continents was not possible.

Second, we assembled the species-level PDSO, which contains diatom incidence data of samples from the High Arctic and Antarctica (Fig. 1 and table S6). This database incorporates the (sub-)Antarctic freshwater diatom incidence data of (23), which constitutes a standardized and taxonomically consistent morphospecies-level dataset of the extant Antarctic diatom flora of >400 water bodies. We incorporated additional Antarctic data in our dataset, including from the McMurdo Dry Valleys and the sub-Antarctic Prince Edward Islands, as well as lakes with conductivity values >1.5 mS/cm originally excluded in (23). This resulted in a total of 516 modern Antarctic samples (table S6). All Antarctic samples originated from the main ice-free regions containing lakes in continental, maritime, and

sub-Antarctica (Fig. 1) and cover the full range of present-day lacustrine Antarctic lake ecosystems. We also incorporated lacustrine diatom counts from the High Arctic, amounting to a total of 143 samples (table S6). In addition, we included 276 records of Pleistocene and Holocene Antarctic lacustrine diatom assemblages in the PDSD (Fig. 1 and table S6). Continental Antarctic fossils originated from Syowa Oasis (West Ongul Land, Lützow-Holm Bay) and the Larsemann Hills (Prydz Bay). These sediment cores covered the last interglacial period before the Holocene (the Eemian, MIS 5e), the Last Glacial Period (MIS 2 to 4), and the Holocene. The set of samples of the Last Glacial Period also included samples covering the transition from the Eemian to the Last Glacial Period (MIS 5d-a). Maritime and sub-Antarctic samples originated from Beak Island and Marion Island, respectively, and span the mid-to-late Holocene. In total, the PDSD contains 959 records and is curated at a fine-grained taxonomic level, ensuring full taxonomic consistency across all samples. Last, there are more studies reporting on the diatom flora of the Arctic region (63), including many studies that were incorporated in the GDGD. However, these studies were not incorporated in the PDSD, as they used a predominantly coarse-grained taxonomy where different species are lumped together under one species name. These datasets thus did not match the fine-grained taxonomy standard of the PDSD and could therefore not be included in this dataset. The same is true for paleoecological studies of Holocene and Late Pleistocene diatom material from the Southern Hemisphere, including Antarctica. Incorporation of the Antarctic core material used in the PDSD was only possible after careful reanalysis of the core material to ensure full taxonomic consistency with the recent samples of the PDSD.

Apart from achieving taxonomic consistency between databases, curation was necessary to avoid issues with differences in taxonomic resolution between different studies, i.e., taxonomic “lumpers” versus “splitters” (64). Consequently, the GDGD largely follows the genus-level differentiation in (5) (a coarse-grained taxonomic level), instead of the more recent consensus that many previously species-rich diatom genera constitute of smaller distinct entities that merit genus-level differentiation. Table S7 lists which genera have been lumped in the GDGD to ensure full taxonomic consistency between all samples. The PDSD uses a fine-grained taxonomy, which was possible through taxonomic harmonization of existing datasets in combination with taxonomic revisions by the same taxonomic expert (23). Last, to avoid issues with spatial correlation between samples, only one modern sample per water body was retained in both the GDGD and PDSD, unless both a modern littoral and a deepwater sediment sample (top layer of a sediment core) were available, in which case both samples were included. The latter was done since littoral and deepwater samples represent fundamentally different habitats in lacustrine water bodies.

Data analysis

Data analysis was performed in R v4.0.2 (R Core Team, 2020), predominantly using the packages *vegan* (65), *BiodiversityR* (66), and *dendextend* (67). In the analyses, further outlined below, we distinguished between major biogeographical and climatological zones following (28): Antarctica, the Arctic (i.e., latitudes >60°N), and temperate and (sub)-alpine sites in the Northern and Southern Hemisphere (Fig. 1). Following (68), we further subdivided Antarctica in continental, maritime, and sub-Antarctica (Fig. 1). Unless otherwise indicated in the figure captions, the analyses of the Miocene samples

only included taxa encountered during the counts, whereas additional taxa detected afterward were not included. All R code and datasets can be found on Mendeley Data (doi: 10.17632/2h88dnxb7w.1).

To compare Miocene genus- and species-level richness with modern diatom floras, we performed a sample-based interpolation on both the GDGD and PDSD using *Vegan*'s *specaccum* function with 1000 permutations. In addition, we used Venn diagrams on the GDGD to detect the degree of overlap in genus-level community composition between the Miocene diatom flora and the major biogeographical regions outlined above (Fig. 1). Using the higher-order diatom classification in (69), we further calculated the number of genera per diatom order, while making a distinction between the major biogeographical regions (Fig. 1). This enabled the detection of differences in diatom richness between regions on a higher taxonomic level, which is reflective of fundamental differences in community composition. We further applied bar plots to visualize the number of species per genus in the Miocene and modern samples of the PDSD, making a distinction between aquatic and aerophilic genera, and different biogeographic regions. This allowed us to detect differences in the dominant habitat type of diatom floras in different polar regions. To this end, we first lumped the diatom genera in the PDSD to the same taxonomic resolution as the GDGD (table S7).

To evaluate the affinity of the Miocene Antarctic diatom flora with modern temperate and polar diatom floras from around the world, we visualized the variation in genus-level community composition in the GDGD via CAP, using 999 permutations and Bray-Curtis dissimilarity. To gain a more detailed view on the affinity of Miocene Antarctica with modern and (sub)fossil polar floras, we build a heatmap of the PDSD using Bray-Curtis dissimilarity.

To evaluate the affinity of the Antarctic core samples with modern samples from the same regions, we performed a Ward's hierarchical cluster analysis with Euclidian distances on the modern and Pleistocene/Holocene Antarctic samples of the PDSD. We repeated the Ward's hierarchical cluster analysis for the Miocene dataset, allowing the detection of affinities between the Miocene samples from different localities. The Miocene samples were not included in the first analysis because most diatom taxa identified in the Miocene material were not conspecific with more recent Antarctic samples. Last, we visualized species-level diversity per sample in the Miocene, Pleistocene, and Holocene Antarctic samples of the PDSD by means of bar plots and beeswarm plots, which allowed the detection of shifts in per sample species richness in Antarctica since the Miocene. The fact that, in all cases, ~400 diatom valves were counted per sample (with exception of James Ross Island, maritime Antarctica, for which 300 valves per sample were counted) ensured that per sample species richness could be compared between sites.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abh3233>

[View/request a protocol for this paper from Bio-protocol.](#)

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the literature study on Miocene diatom fossils and austral taxa. E.P. counted the Miocene diatom samples, analyzed the data, and wrote the paper. E.P. and B.V.d.V. prepared the figures. E.V. assisted with the data analysis. W.V., E.V., B.V.d.V., and K.S. assisted in writing the paper. All authors commented on the paper. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All datasets and R code generated in this study are available from Mendeley Data (doi: 10.17632/2h88dxb7w.1). The Mendeley Data repository also lists a series of figures outlining all Miocene diatom taxa identified in this study. All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

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