



HAL
open science

Antarctica as an evolutionary arena during the Cenozoic global cooling

Fabien L. Condamine, Gael J. Kergoat

► To cite this version:

Fabien L. Condamine, Gael J. Kergoat. Antarctica as an evolutionary arena during the Cenozoic global cooling. *Proceedings of the National Academy of Sciences of the United States of America*, 2021, 118 (27), pp.e2108886118. 10.1073/pnas.2108886118 . hal-03367498

HAL Id: hal-03367498

<https://hal.science/hal-03367498>

Submitted on 15 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 ***Title***

2 **Antarctica as an evolutionary arena during the Cenozoic global cooling**

3

4 ***Authors***

5 Fabien L. Condamine^{a,1}

6 Gael J. Kergoat^b

7

8 ***Affiliations***

9 ^aCNRS, UMR 5554 Institut des Sciences de l'Evolution de Montpellier (Université de
10 Montpellier), 34095 Montpellier, France

11 ^bCBGP, INRAE, CIRAD, IRD, Institut Agro, Univ. Montpellier, Montpellier, France

12

13 ¹ Email: fabien.condamine@gmail.com

14

15 Author contributions: F.L.C. and G.J.K. wrote the paper.

16 The author declares no competing interest.

17

18 It is striking to observe that species richness is not evenly distributed across the surface of the
19 planet. Current species diversity indeed decreases toward the poles, with Antarctica for
20 instance being depauperate compared to tropical regions. This ubiquitous pattern has long
21 attracted the attention of naturalists and more recently of evolutionary biologists and
22 paleontologists to understand why species diversity peaks at the equator. But it remains
23 poorly understood how polar biodiversity originated and diversified. Antarctica is currently
24 defined as three large biogeographic regions: the Maritime Antarctic, the sub-Antarctic and
25 the Continental Antarctic. The Maritime Antarctic region is largely separated from the rest of
26 the world's oceans due to the Antarctic Circumpolar Current (ACC), differences in
27 temperature along the Antarctic Polar Front (APF), and the presence of a deep sea
28 surrounding the Antarctic shelf (1). The sub-Antarctic region consists of dozens of islands
29 contained within the APF, generally characterized by the presence of tundra (absent from the
30 Continental Antarctic) and fellfield habitats. As for the Continental Antarctic region, it is
31 mostly uninhabitable, with less than 0.5% of its surface being ice-free. A long-standing idea
32 is that biodiversity in Antarctica is low, and only constituted of old and poorly diversified
33 lineages. In *PNAS*, a new study (2) – relying on both micro and macroevolutionary
34 approaches – challenges this idea and shows that terrestrial life can thrive there.

35

36 ***Diversity and diversification in Antarctica***

37 Our understanding of the origin and evolution of Antarctic biodiversity has greatly improved
38 in recent years, thanks in part to studies revealing high levels of cryptic diversity, especially
39 for marine organisms for which species diversity is often underestimated (3). Several
40 molecular studies also show evidence for recent colonization and high *in situ* diversification,
41 thus challenging the view that Antarctica is an inhospitable frozen region where groups
42 cannot adapt, thrive and successfully diversify (1). Interestingly, elevated speciation rates
43 have been recovered in marine organisms through estimations of divergence times coupled
44 with diversification analyses in several groups (Fig. 1), such as marine fishes (4,5) or
45 ophiuroids (6). Unexpectedly, these studies found higher diversification rates in Antarctica
46 than in tropical regions in the last 10 million years (5,6). Despite its isolation, Antarctica has
47 also been shown to act as an evolutionary source of marine biodiversity (7), as evidenced by
48 the inference of multiple out-of-Antarctica biogeographic patterns during the Cenozoic (8,9).
49 For terrestrial (including freshwater) organisms however, only a few groups are currently
50 adapted to the extreme conditions of the sub-Antarctic and Continental Antarctic (1) and
51 there had been no evidence supporting the hypothesis that sustained episodes of

52 diversification could have occurred for them since the onset of the global cooling of
53 Antarctica *ca.* 34 million years ago (Ma). The study of Baird *et al.* (2) elegantly questions the
54 paradigm related to the diversification of terrestrial organisms in Antarctica and reveals that
55 the sub-Antarctic region acted as a dynamic evolutionary arena for a beetle lineage during
56 major cooling episodes and glacial cycles, spurring a significant radiation that parallels some
57 of the adaptive radiations experienced by marine lineages (*e.g.* 10).

58

59 ***Shifting biomes as potential evolutionary arenas***

60 Despite its scarcity, the Antarctic Eocene fossil record shows that terrestrial life was once
61 rich, as exemplified by the presence of *Nothofagus* forests, frogs (11), and diverse birds and
62 mammals (*e.g.* 12). All these groups progressively went extinct in Antarctica due to the major
63 global cooling that began at the Eocene-Oligocene boundary (13), coinciding with the
64 opening of the Drake Passage and the associated intensification of the ACC. Drastic
65 environmental changes led to massive ecosystem turnover, precipitating the downfall of
66 angiosperm communities and of their associated fauna. Further major cooling events
67 occurred during the middle and late Miocene climate transition (*ca.* 14 Ma and 7 Ma,
68 respectively), increasing the dominance of fellfield terrestrial habitats (even in the sub-
69 Antarctic region), and leading to the disappearance of tundra habitat from continental
70 Antarctica (14) and to the growth of ice sheets (13). Since then, it was thought the continent
71 and surrounding islands have been depauperate of life, or only contain a few relict lineages.
72 This seems true for most terrestrial groups such as snails (only one autochthonous species has
73 been observed), or in most insect lineages that are only represented by one (*e.g.* Hemiptera,
74 Hymenoptera) or a handful of species (*e.g.* Diptera, Lepidoptera).

75

76 However, this is not the case for the insect group studied by Baird *et al.* (2), the Ectemnorhini
77 weevils (Coleoptera: Curculionidae). This group consists of 36 known species, all of which
78 are distributed in the sub-Antarctic region, along the APF in the Kerguelen Province (*i.e.*,
79 Crozet, Kerguelen, Prince Edward Islands, and Heard Island & McDonald Islands
80 archipelagos). All species are flightless and present several unusual life-history traits, with
81 one clade exhibiting unique algae- and moss-feeding specialization ('cryptogam feeders'
82 *Bothrometopus* clade) and even including a so-called 'marine' species (*Palirhoeus eatoni*)
83 strikingly adapted to the supralittoral zone. Using a combination of phylogenomics (515
84 genes; fossil-calibrated tree of 12 Ectemnorhini species and 87 outgroups) and phylogenetics
85 (a five-gene phylogeny of Ectemnorhini including two-thirds of known species), Baird *et al.*

86 (2) inferred that this clade colonized the sub-Antarctic islands between 55 and 38 Ma
87 (Eocene) from Africa, likely through the Crozet Archipelago. Such a journey would have
88 involved a long-distance dispersal, which may seem unfeasible for these flightless insects.
89 Yet, throughout their evolutionary history, these weevils have repeatedly colonized the sub-
90 Antarctic islands, especially in the last 10 Myrs, despite these islands being isolated by
91 >1,000 km of ocean in the ACC. Even more surprising is that a single species, *Palirhoeus*
92 *eatoni*, is also distributed across several of these islands, thus testifying to the ability of these
93 weevils to cross oceanic barriers. With knowledge on weevil resilience to dehydration and
94 starvation, Baird *et al.* (2) propose the hypothesis that bird-mediated dispersal can explain the
95 biogeographic pattern and the numerous intra-island dispersal events. Indeed, Antarctic
96 seabirds regularly fly hundreds of kilometers in a single day when migrating between sub-
97 Antarctic islands, and it is likely that invertebrates can attach to their feathers and then
98 disperse with their carrier.

99

100 Importantly, Baird *et al.* (2) found evidence that the weevil clade is diversifying faster today
101 than at its origin (especially in the last 5 Myrs), which goes against the general trend of
102 diversification slowdown after origination (15). Consistent with the inferred increase in
103 speciation rates, additional phylogeographic analyses focusing on *Palirhoeus eatoni*
104 (population structure analysis based on 5,859 SNPs) also indicated that this lineage is in the
105 process of incipient speciation, supporting the hypothesis that the clade is currently
106 expanding. Using multiple diversification approaches, Baird *et al.* (2) inferred that speciation
107 rates correlate with trends in global cooling, such that weevils diversified faster when climate
108 cooled and when fellfield habitats became dominant. They postulate that changes in Antarctic
109 conditions likely promoted their diversification on novel polar niches, in relation for instance
110 with adaptation to cryptogams and better freezing tolerance in association with flightlessness.
111 This diversification pattern parallels the specific adaptations observed in Antarctic fishes
112 (4,10) and penguins (16), which also led to successful recent radiations.

113

114 ***Implications***

115 The study of Baird *et al.* (2) calls for re-evaluation of the paradigm on the origin and
116 evolution of species diversity in Antarctica during the Cenozoic. For the first time it is
117 demonstrated that diversification of Antarctic terrestrial organisms may mirror those of
118 marine organisms. This unveiling calls for more studies in other terrestrial groups, especially
119 for those that potentially house high levels of cryptic biodiversity such as springtails (17) or

120 tardigrades (18). This study on weevils should encourage further studies to infer dated
121 phylogenies for Antarctic groups, as it is of paramount importance to determine their mode
122 and tempo of diversification and assess whether there are similar trends in relation with
123 known paleoenvironmental changes (Fig. 1). Studying these Antarctic groups can also bring
124 light on the evolution of the latitudinal diversity gradient, in particular to understand why
125 some regions are species-poor compared to others, but show high *in situ* diversification.

126

127 Even if Antarctica and the surrounding islands are isolated and inhospitable for humans, they
128 are not spared from human-driven threats and their regional biodiversity remains poorly
129 protected (19). If most groups follow a similar diversification pattern to Ectemnorhini
130 weevils in relation to climate cooling, they may be highly vulnerable to global warming. The
131 Antarctic ice cap is indeed melting at unprecedented rates (20), which may destabilize the
132 ecosystem relied upon by this regional pool of species that may currently be in the process of
133 diversifying.

134

135 **ACKNOWLEDGMENTS**

136 We thank J. L. Abbate for comments and suggestions.

137

138 **REFERENCES**

- 139 1. P. Convey, *et al.*, Antarctic terrestrial life – challenging the history of the frozen
140 continent? *Biol. Rev.* **83**, 103-117 (2008).
- 141 2. H. P. Baird *et al.*, Fifty million years of beetle evolution along the Antarctic Polar
142 Front. *Proc. Natl. Acad. Sci. USA* **XXX**, XXXX-XXXX (2021).
- 143 3. M. L. Verheye, T. Backeljau, C. d’Udekem d’Acoz, Looking beneath the tip of the
144 iceberg: diversification of the genus *Epimeria* on the Antarctic shelf (Crustacea,
145 Amphipoda). *Polar Biol.* **39**, 925-945 (2016).
- 146 4. T. J. Near *et al.*, Ancient climate change, antifreeze, and the evolutionary
147 diversification of Antarctic fishes. *Proc. Natl. Acad. Sci. USA* **109**, 3434-3439 (2012).
- 148 5. D. L. Rabosky *et al.*, An inverse latitudinal gradient in speciation rate for marine
149 fishes. *Nature* **559**, 392-395 (2018).
- 150 6. T. D. O’Hara, A. F. Hugall, S. N. C. Woolley, G. Bribiesca-Contreras, N. J. Bax,
151 Contrasting processes drive ophiuroid phylodiversity across shallow and deep
152 seafloors. *Nature* **565**, 636-639 (2019).

- 153 7. A. Dornburg, S. Federman, A. D. Lamb, C. D. Jones, T. J. Near, Cradles and
154 museums of Antarctic teleost biodiversity. *Nat. Ecol. Evol.* **1**, 1379-1384 (2017).
- 155 8. K. Göbbeler, A. Klussmann-Kolb, Out of Antarctica? – New insights into the
156 phylogeny and biogeography of the Pleurobranchomorpha (Mollusca, Gastropoda).
157 *Mol. Phylogenet. Evol.* **55**, 996-1007 (2010).
- 158 9. L. Dietz, J. S. Dömel, F. Leese, A. R. Mahon, C. Mayer. Phylogenomics of the
159 longitarsal Colossendeidae: the evolutionary history of an Antarctic sea spider
160 radiation. *Mol. Phylogenet. Evol.* **136**, 206-214 (2019).
- 161 10. S. Rutschmann *et al.*, Parallel ecological diversification in Antarctic notothenioid
162 fishes as evidence for adaptive radiation. *Mol. Ecol.* **20**, 4707-4721 (2011).
- 163 11. T. Mörs, M. Reguero, D. Vasilyan, First fossil frog from Antarctica: implications for
164 Eocene high latitude climate conditions and Gondwanan cosmopolitanism of
165 *Australobatrachia*. *Sci. Rep.* **10**, 5051 (2020).
- 166 12. S. N. Davis *et al.*, New mammalian and avian records from the late Eocene La Meseta
167 and Submeseta formations of Seymour Island, Antarctica. *PeerJ* **8**, e8268 (2020).
- 168 13. T. Westerhold *et al.*, An astronomically dated record of Earth’s climate and its
169 predictability over the last 66 million years. *Science* **369**, 1383-1388 (2020).
- 170 14. A. R. Lewis *et al.*, Mid-Miocene cooling and the extinction of tundra in continental
171 Antarctica. *Proc. Natl. Acad. Sci. USA* **105**, 10676-10680 (2008).
- 172 15. H. Morlon, M. D. Potts, J. B. Plotkin, Inferring the dynamics of diversification: a
173 coalescent approach. *PLoS Biol.*, **8**, e1000493 (2010).
- 174 16. Vianna *et al.*, Genome-wide analyses reveal drivers of penguin diversification. *Proc.*
175 *Natl. Acad. Sci. USA* **117**, 22303-22310 (2020).
- 176 17. Carapelli *et al.*, Evidence for cryptic diversity in the “Pan-Antarctic” springtail
177 *Friesea antarctica* and the description of two new species. *Insects* **11**, 141 (2020).
- 178 18. A. Velasco-Castrillón *et al.*, Mitochondrial DNA analyses reveal widespread
179 tardigrade diversity in Antarctica. *Invertebr. Syst.* **29**, 578-590 (2015).
- 180 19. H. S. Wauchope, J. D. Shaw, A. Terauds, A snapshot of biodiversity protection in
181 Antarctica. *Nat. Commun.* **10**, 946 (2019).
- 182 20. P. Convey, S. L. Peck, Antarctic environmental change and biological responses. *Sci.*
183 *Adv.* **11**, eaaz0888 (2021).
- 184

185 **Fig. 1.** Cenozoic environmental changes and diversification patterns in Antarctica. Molecular
186 dated phylogenies (2,4,5,6,16) provide evidence of the timing of diversification in Antarctica
187 for marine (blue silhouettes) and terrestrial (black silhouettes) groups. One terrestrial clade
188 (Ectemnorhini weevils, 1) and one marine clade (Antarctic icefishes, 4) show increasing
189 diversification toward the present (yellow stars) potentially correlated to climate cooling.
190 Estimates of Antarctic endemics species for each group are provided on the right. The
191 Cenozoic climate curve indicates the main events of global cooling (13). Pli., Pliocene; P,
192 Pleistocene. Organism images credit (*Top to Bottom*): Phlyopic/Jonathan Lawley;
193 Phlyopic/Lily Hughes; Phlyopic/Mathilde Cordellier, licensed under CC BY-NC 3.0;
194 Phlyopic/Steven Traver; Phlyopic/Ernst Haeckel and T. Michael Keeseey; Phlyopic/JCGiron,
195 licensed under CC BY 3.0; F.C. and G.K.; Phlyopic/Kamil S. Jaron; Phlyopic/Fernando
196 Carezzano; and Phlyopic/Birgit Lang, licensed under CC BY 3.0.
197



ophiuroids

estimated origin in Antarctica



Eocene/Oligocene climate transition

middle Miocene climate transition

late Miocene climate transition



origin of the Antarctic clade

notothenioids



Antarctic species origin

penguins



cladocera

recent origin →



mosses

recent origin →



100+

100+

10

16

29

4

36

124

67

500+

estimated origin in Antarctica

chironomids

weevils



springtails



tardigrades



mites



present before the Gondwana break-up

cold temperate *Nothofagus* rainforests



→ to tundra *Nothofagus* assemblages → to tundra & fellfields

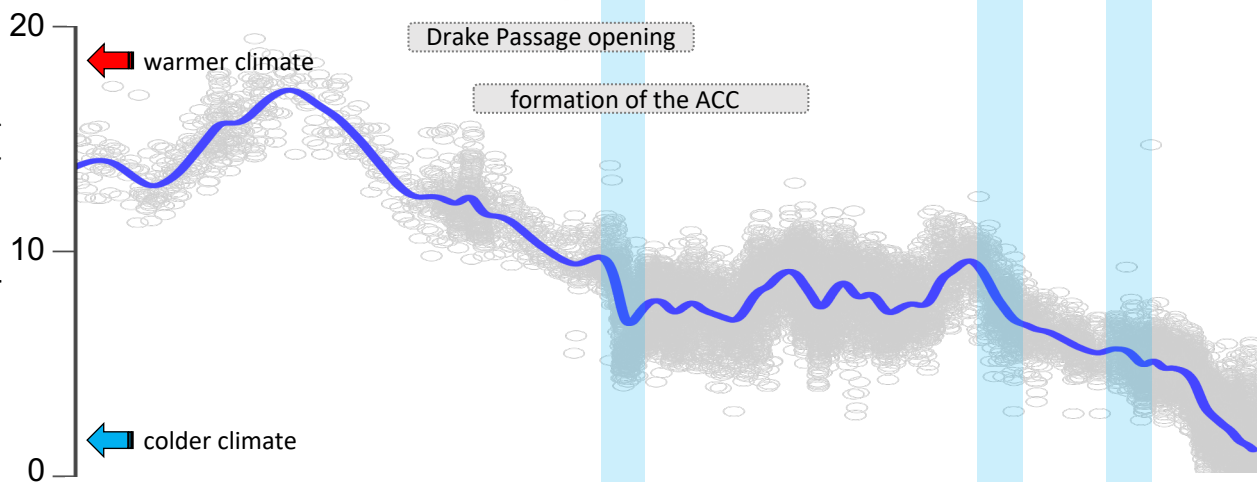


warmer climate

Drake Passage opening

formation of the ACC

colder climate



Paleocene

Eocene

Oligocene

Miocene

Pli. P.

60.0

50.0

40.0

30.0

20.0

10.0

0.0