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# Antarctica as an evolutionary arena during the Cenozoic global cooling

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1 ***Title***

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

3

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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

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137

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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;  
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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

colonization of Antarctica

springtails

present before the Gondwana break-up

tardigrades

present before the Gondwana break-up

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

20

10

0

Paleocene

Eocene

Oligocene

Miocene

Pli. P.

60.0

50.0

40.0

30.0

20.0

10.0

0.0

Δ temperature (°C)