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The response of arctic Carabidae (Coleoptera) to climate change based on the fossil record of the Quaternary Period

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The response of Carabidae, based on ^{14}C-dated fossil assemblages, was to track climate change through dispersal and differential survival. Isolation of populations of arctic Carabidae caused by Quaternary climatic oscillations did not lead to enhanced rates of extinction and speciation, as it did in the mammals. Regional extinction of populations occurred as dispersing individuals encountered barriers such as ice sheets. Variation in mtDNA haplotype diversity in the arctic-alpine species *Amara alpina* (Payk.) in North America demonstrates the importance of climate change, glaciation, and extirpation in determining genetic variation. The future response of Carabidae to climate change will probably be similar to that of the past with the exception that species extinction is expected to be higher because of the additional fragmentation of habitats caused by human activities.

1. Introduction

While there is a consensus that the concentration of greenhouse gases in the atmosphere has increased over preindustrial levels, there is no agreement on what the effect of this change will be. Whether global warming will result is uncertain, although many atmospheric scientists believe it may already have begun (Kerr 1995). During this time of uncertainty we have every reason to be concerned. The Intergovernmental Panel on Climate Change (IPCC) estimated that during the next 100 years global temperature will rise between 1.5 and 4.5°C, with 2.5°C being the best estimate (Houghton *et al*. 1992). How increases in global average temperature will translate into regional climate change is proving especially difficult to model. For northern latitudes, it is considered very probable that sea ice and snow cover will be reduced, and that winters will be warmer (Barron 1995).

What is the response of Carabidae to climate change? Shifts in the geographic distribution of Carabidae during the last century in the Netherlands have been attributed to the greater frequency of warmer and wetter summers in the last few decades (Hengeveld 1985). On the other hand, similar shifts in geographic range in western Europe have been attributed to intensification of agriculture and to changes in land use (Turin & Den Boer 1988, Desender *et al*. 1994). These competing hypotheses indicate the general problem of separating out climatic effects from human effects in biological data from this century.

Abundant fossils, preserved in bog, marsh, and lake deposits, provide an unambiguous record that the ancestors of existing species survived the climatic changes of the Quaternary Period. The fossils are well-preserved three dimensional pieces of chitin that are easily removed from unconsolidated sediments by wet sieving and kerosene flotation (Elias 1994). Radiocarbon ages (^{14}C yr BP) are assigned to the fossils either by dating organic matter in the associated sediments or by direct dating of the chitin using accelerator mass spectroscopy (AMS dating). The relative accuracy with which fossil assemblages can be dated makes them especially useful for examining questions about climate change.

In this paper, the potential evolutionary and ecological response of Carabidae to climate change is interpreted from their late Tertiary and Quaternary fossil record (for bibliographies see Buckland & Coope 1991, Elias 1994). The Quaternary, in particular, was a time of repeated climatic change during which ice sheets covered northern Europe and North America on several occasions. The fossil record of this time of environmental instability is examined in terms of three questions: 1) Did climate change result in changes in geographic distributions? 2) Did climate change result in speciation? 3) Did climate change result in extinction?

2. The response of Carabidae to climate change in the fossil record

2.1. Changes in geographic range of species

There is abundant fossil evidence to demonstrate that shifts in geographic range occur as a result of climate change. Incremental tracking of climate occurs as individuals disperse. The end result is often referred to as migration, but this is a poor term better reserved for seasonal rather than long term changes in distribution. Long ago, it was reported that arctic Carabidae, such as *Diacheila polita* (Fald.), colonised the British Isles during glaciations (Coope 1962). Presumably, these species were able to disperse into the British Isles from mainland Europe at times when the climate was cold and when sea levels were lower in the English Channel. Certainly, arctic species inhabited the Vosges region of northeastern France and other regions of mainland Europe during the last two glacial intervals (Ponel 1995). One of the most spectacular range expansions associated with the last glaciation in Europe is the occurrence of *Amara alpina* (Payk.) in northeastern Italy at 18 870 yr BP (Foddai & Minelli 1994). Presently, this arctic species occurs no further south in Europe than alpine habitats in the mountains of Scandinavia and Scotland.

At the end of the last glaciation in Europe, between 13 000 and 10 000 yr BP, there was a series of climatic fluctuations (Coope 1977, Coope & Lemdahl 1995). At 13 000 yr BP the climate warmed rapidly. Cold-adapted species of Carabidae were replaced by warm-adapted species in a short time, probably a few decades at most. The climate change was so rapid that it caused a “disequilibrium” between the vegetation and beetles that lasted for about 1 000 years (Lowe *et al.* 1994). The expansion of birch forest in the British Isles was delayed, possibly because soil development was not keeping pace with the climatic change (Pennington 1986). By 11 000 yr BP, the climate had changed to colder conditions and arctic species once again colonised the British Isles. They persisted until 10 000 yr BP when they were rapidly replaced by temperate species. The difference in mean July temperatures between the peak warm and cold episodes is estimated to have been between 5 to 8°C. (Lowe *et al.* 1994). The response of the Carabidae to each climate change was extremely rapid. The most rapid changes appear to have occurred when temperate species replaced arctic species at 13 000 and 10 000 yr BP

Climate changes in geological time are often assumed to have occurred at rates too slow to be compared with the rapid change projected for greenhouse warming. Evidence from Greenland ice cores, however, suggests that the climate change at 10 000 yr BP was rapid by any standards, occurring within a period of 5–20 years (Taylor *et al.* 1993).

In North America, major changes in geographic distribution of Carabidae are also represented in the fossil record. Typical arctic species such as *Diacheila polita* , *Pterostichus caribou* Ball, *P. vermiculosus* (Mén.), *P. sublaevis* (J. Sahlb.), and several others, inhabited areas south of the Laurentide ice sheet in Iowa and Illinois between 21 500 and 14 500 yr BP (Schwert & Ashworth 1988, Schwert 1992). In North America, these species are presently restricted to the tundra of Alaska and Yukon Territory. To reach the mid-continental United States, arctic species dispersed southward in front of the Laurentide ice sheet

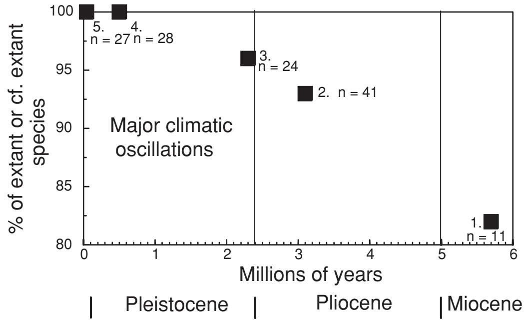

Fig. 1. The percentage of extant or near extant (cf.) species of Carabidae in fossil assemblages from North America and Greenland: — 1. Lava Camp, Alaska (Matthews 1979). — 2. Meighen Island, Northwest Territories (Matthews 1979). — 3. Kap København, Greenland (Böcher 1989). — 4. Cape Deceit, Alaska (Matthews 1974). — 5. Titusville, Pennsylvania (Cong *et al.* 1996).

and became isolated from ancestral populations which survived in unglaciated areas of Alaska and Yukon Territory (Schwert & Ashworth 1988).

2.2. Evolution

In order to survive in the mid-latitudes of Europe and North America, individuals of arctic species from northern and southern populations must have been adapted to different light regimes. Physiological adaptation, and therefore microevolutionary change, must have accompanied changes in geographic range. Intuitively, the isolation and fragmentation of populations that resulted from climate change and the growth of ice sheets should have favoured allopatric speciation. The evidence from the fossil record, however, is that northern species of Carabidae exhibited remarkable stasis through the last few million years (Fig. 1). Bousquet (1991) listed 946 species of carabidae from Canada and Alaska; 142 of these species have been described as fossils from deposits that predate the major climate change at the end of the last glaciation. The number of older fossil sites and the species described from them is small, but from the Miocene to the Mid-Pleistocene the representation of extant species increased from 82 to 100% (Fig. 1). Matthews (1979) reported that the majority of carabid species from the Miocene deposits on Meighen Island were extinct even though they were close to extant species. He now believes the majority of those species are within the range of variation of extant species (John Matthews, pers. comm. 1995).

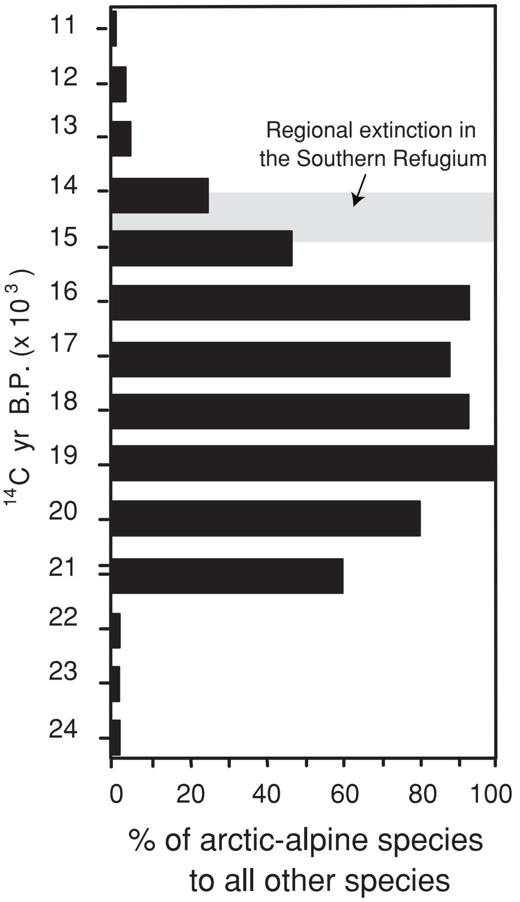

Fig. 2. The percentage of arctic-alpine to all other species of Carabidae in fossil assemblages from the mid-continental United States at the end of the last glaciation (Schwert 1992).

Coope (1978) speculated that "stirring" of gene pools caused by movement of populations and environmental instability was a possible cause of the stasis. His explanation involves genetic variation being maintained at low levels by outbreeding. Geographic variation, however, has been detected in the mitochondrial DNA (mtDNA) of the arctic species *Amara alpina*, suggesting that isolation of populations resulted in genetic differentiation. Regional extinction or extirpation of populations (see below) may have periodically caused reduction in genetic variation but what role, if any, this played in maintaining stasis is unknown.

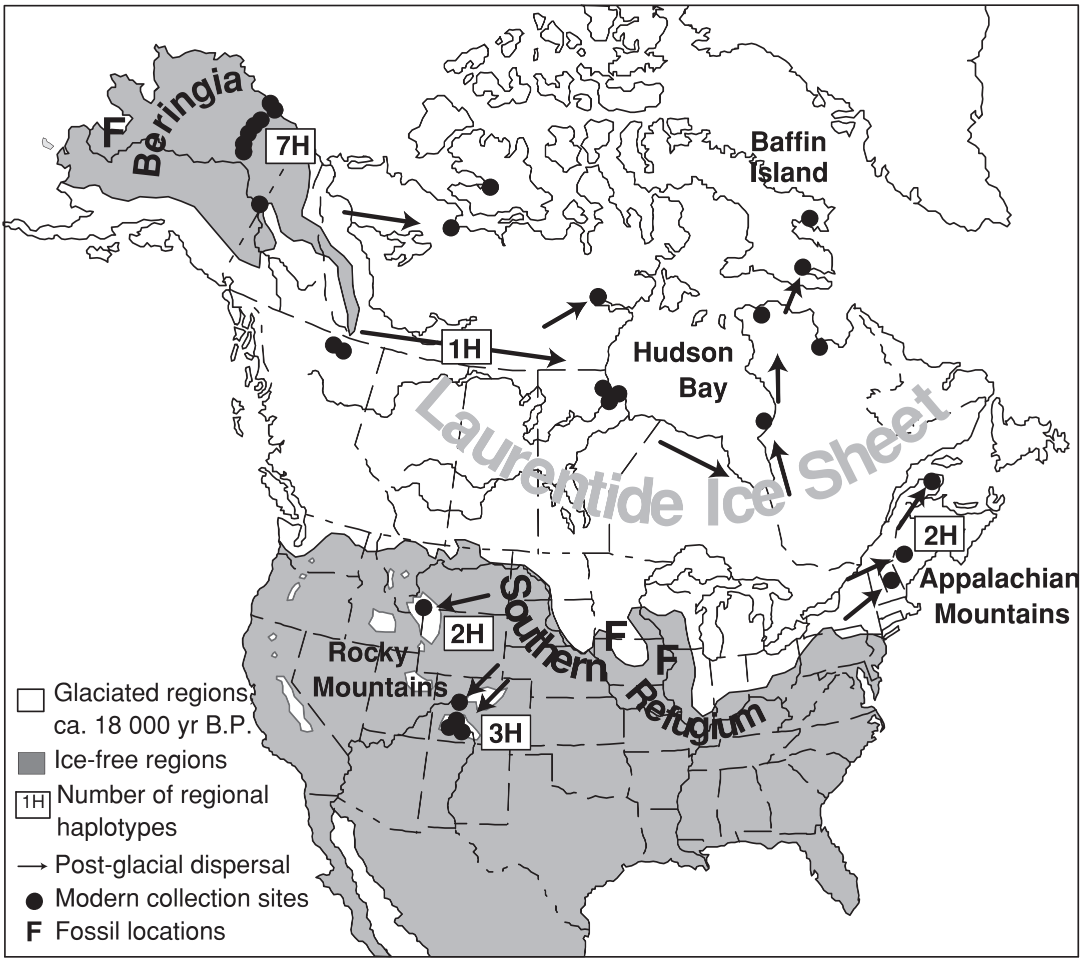

Fig. 3. The distribution of haplotypes of *Amara alpina* (Payk.) and postglacial dispersal pathways for arctic-alpine species of Carabidae (Schwert & Ashworth 1988, Reiss, Ashworth & Schwert, ms. in prep.).

2.3. Extinction

The demise of the mammoth and numerous other Pleistocene mammals has produced the expectation that extinction is a major outcome of climate change. The fossil record for beetles does not support that conclusion. There are no known extinctions of Carabidae, and the only records of extinction of beetles during the Pleistocene are for two species of Scarabaeidae, *Copris pristinus* and *Onthophagus everestae*, both from the La Brea tar pits in California (Miller 1983).

Species extinction of Carabidae was not a factor during Pleistocene climatic changes. Regional extinction or extirpation of populations occupying areas of thousands of km^2, however, may have been a significant factor in shaping genetic variation. In the midcontinental United States, few arctic species occur in fossil assemblages that postdate 14 500 yr BP (Fig. 2). One of the few exceptions is the occurrence of *Diacheila polita* in Pennsylvania at 12 080 yr BP (Barnosky *et al*. 1988). To explain the disappearance of arctic species from habitats on the margins of the ice sheet, it was proposed that climatic warming, without significant change in the areal shape of the Laurentide ice sheet, caused their extinction (Schwert & Ashworth 1988) (Fig. 3). Populations that were marginal to high terrain, in both the Rocky Mountains and the northern Appalachian Mountains, survived by dispersing to higher elevations. Only where the mountains were highest and would support alpine vegetation did these species survive the warmer climates of the Holocene. Some populations, such as *Diacheila polita* in Pennsylvania, may have been able to survive in hilly regions after the main regional extinction at 14 500 yr BP but eventually were extirpated as the climate warmed.

3. The effects of Quaternary climate change on the existing fauna

A major consequence of regional extinction in the Southern Refugium (see Fig. 3) was that postglacial colonisation of the central and eastern Arctic was from Beringia, with species dispersing eastward as the Laurentide Ice sheet melted (Schwert & Ashworth 1988). A corollary of this hypothesis is that populations of arctic Carabidae have been isolated from one another for different amounts of time, i.e. 1) populations in Beringia have been isolated from populations in the mid-latitudes of North America for at least 80 000 years, the length of time since the beginning of the last glaciation; 2) populations in the Rocky Mountains have been isolated from populations in the Appalachian Mountains for at least 14 500 years, dating from the time of regional extinction in the Southern Refugium; and 3) populations on individual mountain summits in the northern Appalachian and Rocky Mountains have been isolated from each other since alpine communities reached their present elevational distributions, about 10 000 years ago.

To determine if genetic differentiation had resulted from populations being isolated for different amounts of time, a study of the molecular genetics of the arctic-alpine species *Amara alpina* was initiated. Restriction Fragment Length Polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA) was conducted on specimens from populations in Alaska, Hudson Bay, the mountains of northern British Columbia, the southern Rocky Mountains of Montana and Colorado, and the northern Appalachian Mountains of New Hampshire, Maine, and Quebec (Fig. 3). The details of this study are reported in an unpublished manuscript by Rebecca Reiss (New Mexico Institute of Mining and Technology), Donald Schwert and Allan Ashworth (North Dakota State University). In the following summary, predictions based on the Schwert-Ashworth (1988) hypothesis are compared to the results of the mtDNA study (Fig. 3).

— **Prediction 1**: there should be high genetic diversity in Beringia. Beringia was unglaciated and is the longest continually inhabited region in North America.
— The prediction is confirmed by 8 of the 15 haplotypes occuring in Alaskan and British Columbian populations.
— **Prediction 2**: there should be low genetic diversity in the Hudson Bay region as it was not deglaciated until about 6 000 yr BP.
— The prediction is confirmed by only 1 haplotype being represented in populations from the northwestern, southern, and eastern shores.
— **Prediction 3**: Hudson Bay populations were derived from Beringia.
— The prediction is supported by the Hudson Bay haplotype being shared by populations in the mountains of northwestern British Columbia on the southern margin of Beringia. The mountains in British Columbia were deglaciated several thousand years before Hudson Bay so it is probable that the founder populations of the shared haplotype came from the west.
— **Prediction 4**: isolated populations in the Rocky Mountains and also in the Appalachian Mountains should be closely related.
— The prediction is confirmed by the 3 haplotypes in Colorado differing by only a single restriction site from each other, the 2 haplotypes in Montana differing by a single restriction site, and the 2 haplotypes in Maine, New Hampshire, and Quebec, differing by only a single restriction site.
— **Prediction 5**: Rocky and Appalachian Mountain populations would have a closer genetic relationship to each other than to populations in Beringia and around Hudson Bay.
— The prediction is refuted by a five restriction site difference in the RFLP analysis between eastern and western populations. The molecular genetic evidence suggests that these populations have been isolated from one another for a period of time longer than the last glacial-interglacial cycle.

The good correlation between the results of the molecular genetic study and the predictions from paleontology and biogeography emphasise the importance of events such as climate change, glaciation, and regional extinction in helping to shape genetic diversity. The haplotype differences between populations of *Amara alpina* suggest that Beringia, the Rocky Mountains, and the northern Appalachians, acted as independent centers for the survival and dispersal of many arctic-alpine species during the last glacial-interglacial cycle. It now seems improbable that mixing of individuals from populations of *Amara alpina* occurred in the Southern Refugium during the last glaciation. This leads back to the question of stasis. How is morphological stasis maintained in genetically differentiated populations that are in isolation for long periods of time?

4. Conclusions

The Quaternary fossil record is an important resource for studying the response of Carabidae to climate change. Knowledge of past responses should be considered as management protocols for conservation are developed. Based on the fossil record, the following general comments are made about responses to future climate change.

1) The geographic range of species will change. Responses will be rapid and arctic Carabidae should be considered as primary indicator species for monitoring climate change.
2) Physiological adaptations will accompany the change in geographic distributions but are unlikely to lead to speciation.
3) Regional extinction of species will occur as dispersal is blocked by landscape barriers, such as large rivers and marine embayments. Many alpine populations will be extirpated as alpine habitats are reduced in size by the expansion of treeline forests.
4) Species extinction is unlikely to occur in arctic species. This conclusion does not extend to the Carabidae of more southerly latitudes. In the past, these species survived climate change by movement to suitable habitats. In landscapes fragmented by human activities, dispersal will be blocked by unsuitable habitats and and species extinctions are expected to occur.
5) Genetic variation detected in populations of *Amara alpina* is partly attributed to climate change and associated events. Little variation was detected in the mtDNA in populations from a large area around Hudson Bay. If the nuclear DNA parallels the mitochondrial DNA in low diversity, it is expected that these populations would be susceptible to regional extinction during a time of rapid climatic change. Conversely, because of high genetic diversity, populations in Beringia would not be as susceptible to regional extinction.

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