Perspectives on Beetles and Climate Change

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ABSTRACT

The response of beetles to climate change during the Quaternary Period is reviewed for the purpose of evaluating their future response to global warming. Beetles responded to Quaternary climatic changes mostly by dispersal, which ultimately led to large scale changes in geographic distribution. Fragmentation and isolation of populations associated with climate change did not result in either higher rates of speciation or extinction, although local extinctions occurred when dispersal routes were blocked by barriers. Studies from archeological and late Holocene sites indicate that the fragmentation of the natural landscape by human activities had as great an impact on the local diversity of beetle populations as did climate change. Habitat reduction and fragmentation continues today and is making species increasingly vulnerable to extinction. The major difference between the future and past responses of beetles to climate change is that extinction rates are expected to be much higher, independent of whether the causes of climate change are natural or anthropogenic. The question of determining whether global warming has natural or anthropogenic causes is important because of the ethical implications of extinction.

INTRODUCTION

J. B. S. Haldane, the legendary British evolutionary biologist, is attributed with one of the most famous quips in biology. When asked what he could infer about the creator from his biological studies, he is said to have replied "an inordinate fondness for beetles." Whether or not Haldane actually made this irreverent response is open to question (Gould, 1995). What is not in question is the diversity of beetles implied in Haldane's witticism. In Haldane's day estimates for the numbers of beetle species were in the tens of thousands. Currently, the estimates range between 1.25 and 7.5 million species (Hammond, 1992; Erwin, 1997; Stork, 1997). Beetles are the most diverse group of organisms on Earth, accounting for about 20% of all species (Erwin, 1997).

Coleoptera (sheathed-wings) or beetles are an order within the class Insecta that occur in most freshwater and terrestrial habitats, including those of remote islands. Beetles are ubiquitous, occurring in the wettest rain forests and in the most arid deserts. There are species with physiologies adapted to survive periodic below freezing temperatures of high arctic summers. There are even species adapted to the littoral zone, where they survive daily tidal inundation by burrowing in sand. Antarctica is the only continent today that does not have an indigenous beetle fauna. A few species have been reported from the Antarctic Peninsula but all of them were probably introduced by humans. Beetles were present in the interior of Antarctica,

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climate change to ultracold and ultraxeric conditions (Ashworth et al., 1997).

Most beetles are small organisms, ranging in length from 0.25 mm to several centimeters. Average length is estimated to be in the range of 4-5 mm (Crowson, 1981). Small size has ensured that their activities mostly go unnoticed. The sheer numbers of species, however, makes them important members of all terrestrial and freshwater ecosystems. Because of their abundance, beetles are important food items for numerous species of reptiles, birds, small mammals and fish. Beetles are also important agricultural and forestry pests, with numerous species being injurious to crops, trees, and stored products (Patterson et al., 1999). Their most important beneficial roles, as pollinators and as recyclers of nutrients, are activities which ensure the health of ecosystems.

Several of the world's leading biologists believe an extinction crisis faces the Earth that has the potential to match or exceed the mass extinctions at the close of the Permian and Cretaceous Periods. The biggest problem facing beetles is the destruction of natural habitat by human activities. It is a sad commentary that for undescribed species the chance of extinction is greater than the chance of being described (Stork, 1997). The threat of extinction is most acute in tropical regions, but problems exist for beetle species in all densely populated areas.

Record keeping is so inadequate that even in more affluent nations it is difficult to assess the number of species that have become extinct during the last century. In the United Kingdom, 64 of about 4000 species of beetles have not been collected for more than 100 years and are assumed to be locally extinct (extirpated). In addition, there are perhaps the same number not categorized as 'extinct' but which have not been found for several decades (Hyman and Parsons, 1992; 1994). The locally extinct species are of various ecological types, but the majority are either wetland or forest-floor species. Populations of some of these species survive in isolated patches of old growth forests in Europe, but several others have not been collected in many years and are suspected of being extinct throughout their entire geographic ranges (P. M. Hammond, British Museum of Natural History, London, personal communication, 2000).

In North America, there is insufficient data to make a similar assessment of the status of the entire beetle fauna. Data that are available for the Cicindelidae, or tiger beetles[1] , suggest that 19% of tiger beetle species are in a vulnerable to critically imperiled condition (Stein et al, 2000). The tiger beetles are just one of more than 100 families of beetles in North America, and their vulnerability to extinction is probably typical. Most beetle diversity is now concentrated in isolated patches. Even in the absence of climate change, natural habitats will shrink and beetles will become extinct as the world's population, now at more than six billion, grows at a rate of about one billion people a decade.

How will climate change impact an already stressed biota? Lovejoy (1997) wrote that human activity has created an obstacle course for the dispersal of biodiversity and that climate change, even a natural one, could precipitate one of the greatest biotic crises of all time. Is the situation really as bad as Lovejoy paints it or is he indulging in hyperbole? How can we assess the response of beetles to future climate change? Insect collections provide information that the geographic ranges of some species have changed during the last century. Separating out cause

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[1]The tigers beetles are placed in the tribe Cicindelini, family Carabidae, by some taxonomists

and effect from this type of data, however, has proved to be very difficult (Ashworth, 1996; 1997). Experimental physiological data have also been used to predict the future response of species (Patterson et al. 1999). These data, however, are only available for a few beetle species that are of economic significance. In this paper, the response of beetles to Quaternary climatic changes and to human activities is examined for the purpose of speculating on how beetles will respond to future climate change.

QUATERNARY BEETLE FOSSILS

Quaternary beetle fossils consist mostly of disarticulated exoskeletons; setae and scales are frequently preserved, as are pigmented and structural colors (Figure 1). Fossils of sclerotized internal structures, such as the male genitalia, also occur as fossils.

Figure 1. A 14,000 cal yr BP (12,000 yr BP) old fossil beetle assemblage from Norwood, Minnesota (Ashworth et al., 1981). The fossils consist of a head, several pronota and elytra of 12 species of beetles in the families, Carabidae, Cicindelidae, Dytiscidae, Heteroceridae, Chrysomelidae and Curculionidae. Specimens with both structural (metallic appearance) and pigmented coloration are present in the petri dish.

For practical purposes, however, the parts most studied by paleoentomologists are heads, pronota (thoraces) and elytra (wing cases). Chitin is a nitrogenous polysaccharide that is insoluble in water, dilute acids and alkalis. It is stable in anoxic sedimentary environments but is broken down by bacteria during prolonged exposure to the atmosphere.

Fossils occur in unconsolidated sediments, mostly from shallow lacustrine, paludal and fluvial environments. Elias (1994) described the kerosene flotation method used to isolate the fossils, their preparation for study, and their identification. Fossil assemblages typically consist of hundreds of identifiable pieces. The age of fossil assemblages is based on ^{14}C dating, either directly by accelerator mass spectrometry (AMS dating) or indirectly by dating associated plant fossils. The dates in this paper are reported as calibrated ages (cal yr BP) based on a calibration of radiocarbon ages (Stuiver et al., 1998). Original radiocarbon dates are reported in parentheses (yr BP) following the calibrated dates.

THE FOSSIL RECORD AND THE RESPONSE OF BEETLES TO CLIMATE CHANGE

Speciation

Beetles are the most species-rich group of organisms on Earth and intuitively it would seem that they must evolve rapidly. Climatic changes, especially those resulting in the growth and melting of ice sheets, cause the fragmentation and isolation of biological populations. The conditions for reproductive isolation and allopatric speciation would seem to be optimal at times of climate change. Several hundred species of beetles have now been reported from a large number of

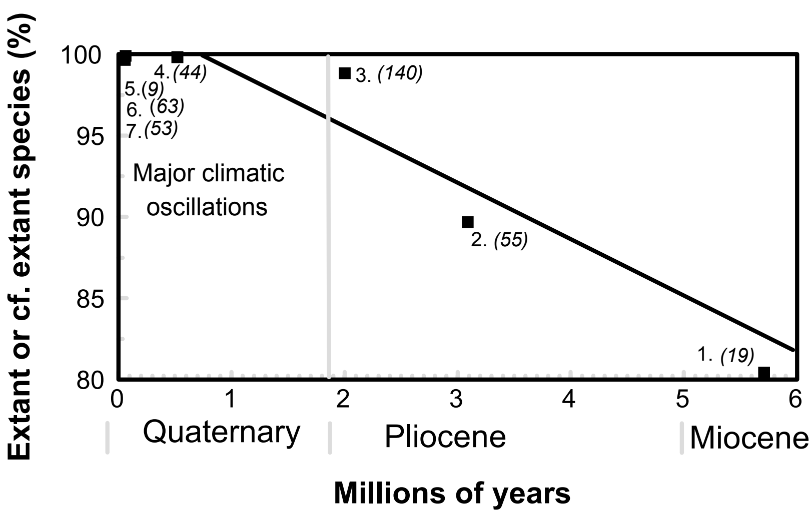

Figure 2. The percentage of extant or near (cf.) extant species of beetles in pre-late Wisconsinan fossil assemblages (numbers in parentheses refer to numbers of species). 1. Lava Camp, Alaska (Matthews, 1977); 2. Beaufort Formation sites (Matthews, 1977; Fyles et al, 1994); 3. Kap København Formation, Greenland (Böcher, 1995); 4. Cape Deceit, Alaska (Matthews, 1974); 5. Gastropod Silts, Minnesota, South Dakota (Garry et al. 1997); 6. Olympic Peninsula, Washington State (Cong and Ashworth, 1996); 7. Titusville, Pennsylvania (Cong et al., 1996).

studies of Pleistocene and Holocene fossil assemblages. References for these studies are listed in QBIB, a comprehensive electronic bibliography (Buckland et al., 1997). Several new species were described in the older literature but most of these have now been reassigned to extant species following taxonomic revisions. The Quaternary fossil record is unequivocally one of stasis not speciation (Figure 2).

The most remarkable example of stasis is from a fossil assemblage located near Kap København at latitude 82^o 30' N., Peary Land, northernmost Greenland. Presently, only two species of beetles survive the harsh polar desert conditions of Peary Land. The Kap København Formation was deposited about 2 million years ago (Late Pliocene) during a time when the climate in the Arctic was significantly warmer than at present. Preservation of chitin is excellent and 140 species of beetles have been identified from the deposits (Böcher, 1995). Böcher considered only two or three of the species to be extinct. The life histories of most arctic beetle species are either unknown or poorly documented. Even so, it is a reasonable assumption that the generation length of most of the Kap København species is about a year. This means that the genes of the living descendants of Kap København species have been shuffled about two million times during reproduction, with no observable morphological changes. Paradoxically, this remarkable record of stasis has been maintained during a time of repeated glaciations.

Beetles are ectotherms and are dependent on environmental temperatures during all phases of their life cycles. Life cycle processes affected by climate include lifespan duration, diapause, dispersal, mortality, and genetic adaptation (Patterson et al., 1999). Factors such as growth rates and timing of diapause vary within the geographic ranges of species (Butterfield, 1996; Butterfield and Coulson, 1997). For example, in North America and Europe the date of emergence of adults in northern populations is typically later in the summer than for southern populations. Intraspecific adaptations at the population level, to variations in climate and the amount of daylight, are ubiquitous. Subspecies resulting from these differences are considered as being intermediates in the formation of new species. If even a small percentage of these subspecies resulted in new species, then speciation in beetles should be commonplace. Why then have no new species of beetles been reported in the Quaternary fossil record? Is it possible that new species go undetected? Certainly, the fossil record represents only a small percentage of the fauna. Also, preservation favors certain ecological types, especially those of mesic habitats. Even so, a large number of species have been described as fossils and under representation does not explain why some percentage of those should not be new species. Some speciation may also go undetected because of the inability of paleoentomologists to separate new species from morphologically-similar ancestral species. In summary, it is possible that a low level of speciation goes undetected, but in the high latitudes of the northern hemisphere, fossil evidence suggests that there has been little speciation in the beetles during much of the Quaternary Period (Fig. 2).

Coope (1978) suggested that stasis might paradoxically be linked to the instability of environments during the Quaternary Period . He suggested that the migrations of species during times of climate change prevented populations from becoming genetically isolated long enough to evolve new species. Elias (1991) also used this mechanism to explain the absence of speciation in fossil assemblages from the Rocky Mountain region. Coope's hypothesis would imply that genetic variation between disjunct populations of living species of beetles should be relatively low and mostly of recent origin. This was not observed, however, in a study of the mitochondrial DNA of the North American ground beetle species *Amara alpina* Paykull (Reiss et al., 1999). *A. alpina* occurs in tundra and alpine habitats in four widely separated regions: Beringia, the Hudson Bay region, the northern and central Rocky Mountains, and the northern Appalachian Mountains. The genetic evidence indicates a large amount of divergence between Appalachian and Rocky Mountain populations, and indicates that these populations have been reproductively isolated for more than one glacial cycle, and possibly several (Reiss et al.,1999).

Vogler and DeSalle (1993) also detected a large amount of mitochondrial DNA variation in the tiger beetle species, *Cicindela dorsalis* Say, which has a geographic range in eastern North America. The species inhabits coastal sand dunes from New England to the Gulf Region. Parts of the species range in New England and New York State were glaciated, and the species must have colonized those areas during the Holocene. Throughout the remainder of the geographic range, eustatic changes in sea level associated with the growth and melting of ice sheets must have resulted in shifts in populations as dunes migrated in response to marine regression and transgression. Vogler and DeSalle identified 17 haplotypes, some representing ancient divergences, others more recent. The species is represented by four subspecies, two in the Gulf Region west of the Florida Panhandle, and two to the east on the Atlantic Coast. The subspecies are defined on the basis of external morphological characteristics. What is especially interesting is that haplotypes are shared between subspecies and generally the correlation between morphology and mitochondrial DNA is not especially strong. At least the major division in subspecies and haplotypes can be traced to the isolation of populations caused by the emergence of the Florida Panhandle during the Pliocene. Once again, this is strong evidence for long-term stasis at the species level.

Bennett (1997) offered an explanation of stasis as part of a hierarchy of evolutionary processes operating during the Quaternary Period. Natural selection, which operates on time scales of thousands of years, results in the accumulation of microevolutionary changes within species. In Bennett's hypothesis, climate changes driven by rhythmic orbital oscillations on 20,000 to 100,000 year frequencies (Milankovitch cycles) continually disrupt the accumulation of microevolutionary changes. The result is stasis of the type associated with the punctuated equilibria hypothesis (Eldredge and Gould, 1972). Eventually, populations become reproductively isolated and allopatric speciation occurs. The amount of time this takes, however, is measured in hundreds, not tens of thousands of years.

Most of the evidence for stasis in beetle species is based on studies of fossils from locations in Europe, North America and South America, which were either glaciated or on the margins of ice sheets. Stasis observations, however, are not confined to glaciated regions. Species identified from the La Brea asphalt deposits in California and packrat (*Neotoma*) middens from the deserts of the American Southwest and northern Mexico also indicate that stasis, not speciation, was the response of beetles to climate change (Elias and Van Devender, 1990; Elias,1992; Miller, 1997). Paleontological evidence supports stasis, but some caveats are necessary before I can conclude that speciation was globally insignificant during the Quaternary Period. The first is that no fossil assemblages have been examined from deposits in the species-rich tropical rain forests. The second is that no fossil assemblages have been examined from regions of high endemism, such as the Caucasus Mountains. It is possible that stasis is the norm but that there could also be speciation 'hotspots'.

Extinction

Similar conditions that favor allopatric speciation, also favor extinction. Certainly, the end of the Pleistocene Epoch was marked by a major extinction in North America of more than 40 species of large mammals, including mammoths (Martin and Klein, 1984). There were also several extinctions of large mammals in Europe (Yalden, 1999). Different hypotheses involving climatic and vegetational changes, and overkill by paleoindian hunters, have been proposed to explain the extinctions (Martin and Klein, 1984). The extinctions of large mammals in both North America and Europe were not accompanied by correspondingly large extinctions in the beetle fauna.

Only two species of dung beetles, *Copris pristinus* Pierce and *Onthophagous everestae* Pierce from the Rancho La Brea asphalt deposits, are reported as Quaternary extinctions (Miller et al., 1981). Climate change, the extinction of large herbivores, and the reduction in dung were all considered to be contributing factors to the extinctions. Miller (1997) considered it a possibility, however, that these species might still be living. He has reason to be cautious. In Europe, d'Orchymont (1927) described a pair of fossil elytra from glacial deposits in Germany as the extinct species *Helophorus wandereri* d'Orchymont. Subsequently, the species described as being extinct was discovered to be part of the extant fauna of Siberia, where it had been described as *H. obscurellus* Poppius. This synonymy is a reminder that beetle extinction is rare in the Quaternary fossil record.

Migration

Most beetles are highly mobile animals. Large numbers of species fly. Some are clumsy flyers and the distances they travel are small. Others, however, are strong fliers and capable of traveling tens or hundreds of kilometers in strong winds. The long-term response of beetle populations to climate change is referred to as migration. Migration used in this sense, however, is different than the seasonal movement from one area to another, but represents the long-term shift in geographic distributions resulting from dispersal and survival. The result has also been referred to as species tracking climate change, but at the level of species the process is more stochastic than deterministic (Figure 3).

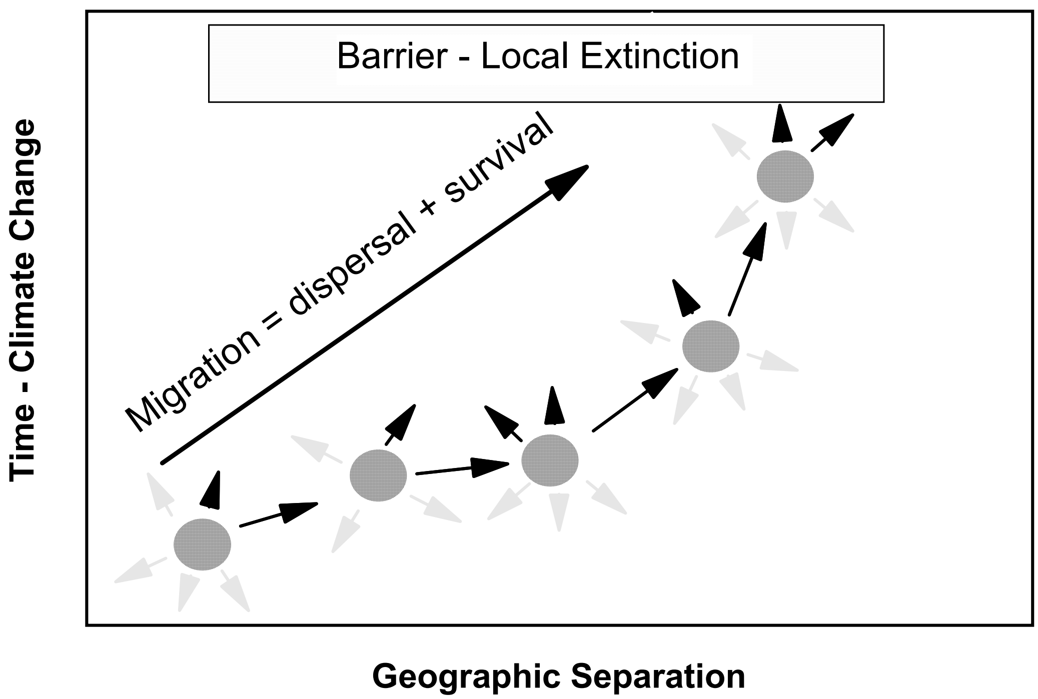

Figure 3. Schematic diagram representing the relationship between dispersal, survival and migration. As individuals disperse, some survive to reproduce the next generation (black arrows) and others die out (grey arrows). The geographic range shifts as the climate changes.

There are many examples of Quaternary climatic changes causing major shifts in geographic ranges of beetle species. In Europe, the ground beetle *Diacheila arctica* Gyllenhal inhabited the British Isles during the last glaciation. The species now has a distribution in northern Scandinavia and adjacent parts of Russia (Figure 4). At the onset of the last glaciation, individuals of *D. arctica* living in Arctic regions began to migrate southward. Some populations survived and colonized the British Isles from mainland Europe. Low sea level during the last glaciation exposed a corridor of land in the vicinity of the English Channel. Rapid warming at

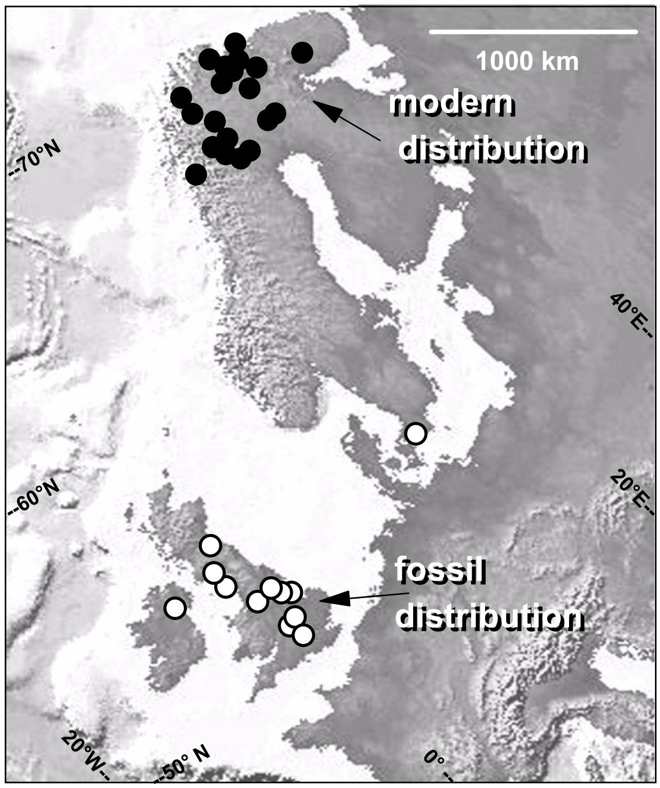

Figure 4. The modern (black dots) and late-glacial fossil distribution (white dots) of the subarctic ground beetle species *Diacheila arctica* (data for modern and fossil distributions from Buckland et al., 1997). The map is modified from Sterner,1996.

about 15,600 cal yr BP (13,000 yr BP) caused the local extinction of the species from lowland areas in the British Isles (Figure 5). The return to a cold climate during the Younger Dryas Stade resulted in the reappearance of the species in lowland areas. Whether or not it had become "extinct" in the British Isles and then recolonized from mainland Europe is unknown. Small populations could have survived in refugia in upland areas and colonized the lowlands as the climate cooled. Populations of the species inhabited the British Isles during the 1200 years of the Younger Dryas Stade, but in the rapid warming at 11,500 cal yr BP (10,000 yr BP) became locally extinct

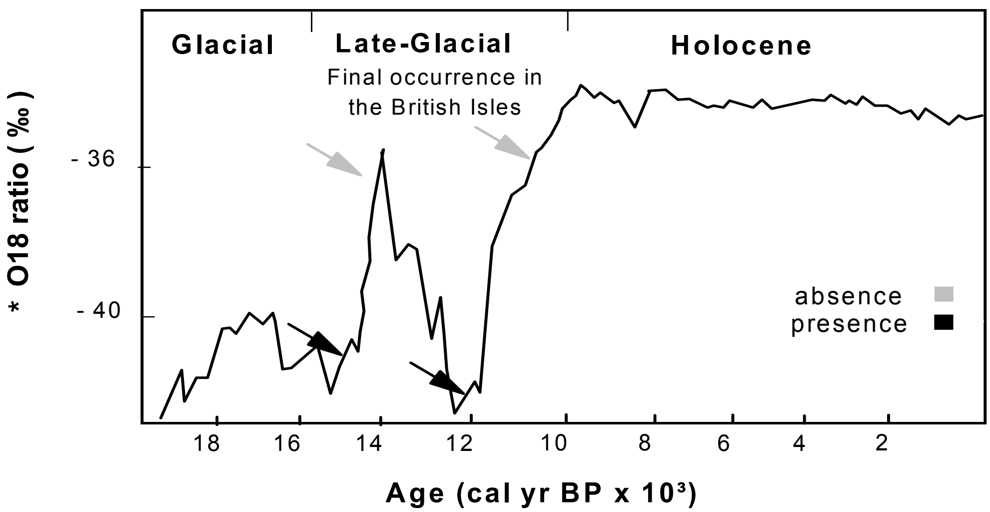

Figure 5. Rapid response of cold-adapted beetles to late-glacial climatic changes in the British Isles. Arctic species were extirpated when the climate changed from cold to warm. They reappeared when the climate cooled. Climatic warming at about 11,500 cal yr BP (10,000 yr BP), at the end of the Younger Dryas Stade, caused *Diacheila arctica* and other subarctic beetle species to become locally 'extinct' in the British Isles. Curve for * ^{18}O is based on the Greenland Ice Core Project (GRIP).

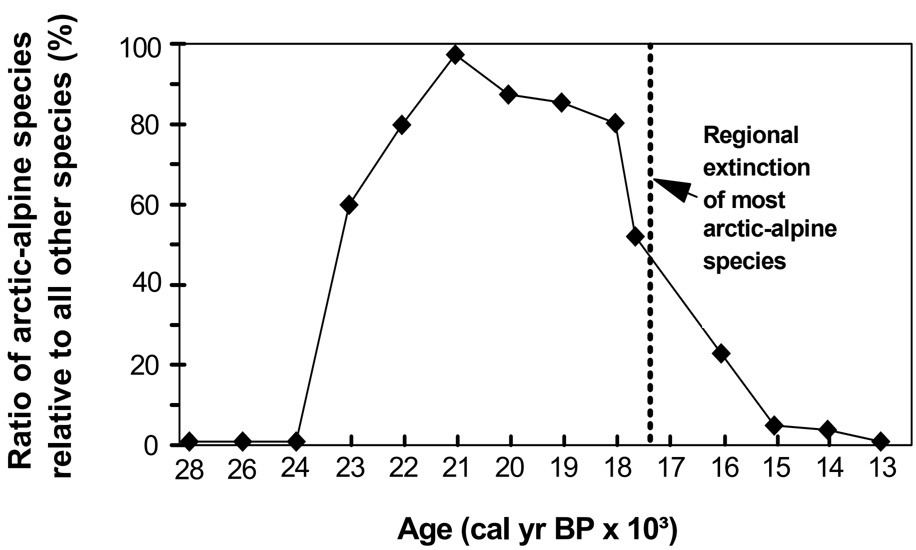

Figure 6. The appearance and disappearance of subarctic and arctic beetle species in fossil sites located along the southern margin of the Laurentide ice sheet from Iowa to New York State. The more cold-adapted species became 'extinct' along the margin of the ice sheet at about 17,400 cal yr BP (14,500 yr BP) as the climate warmed (Morgan, 1987; Schwert and Ashworth, 1988; Schwert, 1992; Ashworth and Willenbring, 1998).

In eastern and central North America, arctic beetle species replaced boreal forest species along the southern margin of the Laurentide ice sheet at about 25,500 cal yr BP (21,500 yr BP) (Figure 6). Colonization was probably from populations that dispersed southward in front of the growing Laurentide ice sheet and from populations that dispersed westward and eastward from montane refugia in the Appalachian and Rocky mountains, respectively. This 'glacial' fauna, dominated by tundra species, inhabited the ice margin until about 17,400 cal yr BP (14,500 yr BP) (Morgan, 1987; Schwert, 1992; Ashworth, 1996).

Mean July temperature along the ice margin is estimated to have been10-12^{o} C lower than at present. Warming, in combination with the ice sheet acting as a barrier to northward dispersal caused the extirpation of tundra species in the mid-latitudes at about 17,400 cal yr BP (14,500 yr BP) (Schwert and Ashworth, 1988). The ice marginal fauna, until 14,700 cal yr BP (12,500 yr BP) was characteristic of open terrain but warmer climatic conditions than had existed earlier. By 14,700 cal yr BP (12,500 yr BP), this fauna was replaced by a boreal forest fauna.

In southern South America, several fossil beetle assemblages have been studied from lowland sites (Hoganson and Ashworth, 1992; Hoganson et al. 1989; Ashworth and Hoganson, 1993). From about 28,000 cal yr BP (24,000 yr BP) until between 18,000 and 17,000 cal yr BP (15,000 to 14,000 yr BP) the beetle fauna consisted of only a small number of species, mostly from

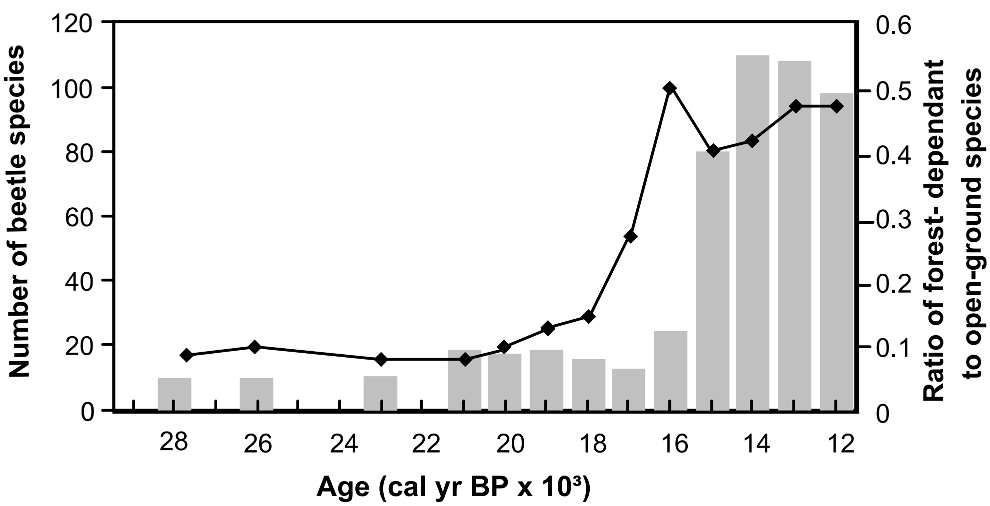

Figure 7. Rapid replacement of open ground species by forest species as the climate warmed at the end of the last glaciation in southern Chile between 18,000 - 17,000 cal yr BP (15,000 to 14,000 yr BP) (Hoganson et al.,1989; Hoganson and Ashworth, 1992; A. C. Ashworth, unpublished data).

open, wet habitats (Figure 7). Species of an earlier forest fauna had been extirpated as the climate cooled. The survivors of the extirpation were joined by species from habitats at or above treeline in the Cordillera de la Costa and the Cordillera de los Andes. These species were able to survive in the lowlands because of colder climatic conditions. Based on the occurrence of high-elevation species at low elevations, the mean January temperature is estimated to have been 4-5^{o} C lower than present. The glacial fauna is very different than the species-rich forest fauna that started to replace it at about 17,000 cal yr BP (14,000 yr BP) (Ashworth and Hoganson, 1993).

The change in the beetle fauna is first marked by an increase in the ratio of forest to open ground species and later by an increase in the total number of species (Figure 7). The last fossil occurrence of the most characteristic beetle of the glacial fauna, the weevil *Germainiellus dentipennis* Germain occurs at about 15,450 cal yr BP (12,800 yr BP). By 15,100 cal yr BP (12,500 yr BP), several species of the forest fauna had recolonized the deglaciated terrain. The fauna at this time is inferred to have had a diversity similar to that of the present day.

Human activities

The response of beetles to human activity has been inferred from the study of beetles in archeological sites, especially from the British Isles (Buckland and Dinnin, 1993; Osborne, 1997; Whitehouse, 1997; Dinnin and Sadler, 1999). Forest clearance by Neolithic to Bronze Age peoples during the period from about 5700 to 2800 cal yr BP (5000 to 2700 yr BP) resulted in the extirpation of 35 species. A further six species of beetles were extirpated between the Roman and Medieval periods (Dinnan and Sadler, 1999). The species most affected were those of old- growth forests, especially those associated with dead pine logs (Whitehouse, 1997). Aquatic species were also reduced in numbers. The decline in woodland and aquatic species was accompanied by an increased representation of grassland and dung-feeding species that exploited the newly created pastures. A small amount of climatic change may have played a role in the extirpation of species but habitat fragmentation resulting from human activities is believed to be largely responsible.

Europeans colonized Iowa during the mid-nineteenth century. The forest patches were cut down and the prairie was ploughed. Ground beetle species declined and dung beetles increased, as they had following the Neolithic forest clearance in the British Isles. The most spectacular change, however, was in the aquatic environment. This is documented by fossiliferous sediments deposited in the floodplain of Roberts Creek. Before colonization, the stream was rich in elmid beetles, indicating clear running water. After colonization, elmids essentially disappeared, indicating turbid water, presumably caused by increased runoff (Baker et al., 1993). The perturbation of the beetle fauna by farming practices in mid-Holocene Britain and those in the nineteenth century North America have striking parallels. In both places, the changes to the beetle fauna are as great as those resulting from climatic change.

THE RESPONSE OF BEETLES TO GLOBAL WARMING

Meteorological records indicate that the Earth has warmed during the last century. The present warming trend started in 1970, with several of the warmest years being recorded during the last decade. The oceans have have also warmed. A temperature increase during the last 40 years has been detected in the Pacific, Indian, and Atlantic oceans to a depth of 3000 m, with the largest amount of warming, 0.3^{o} C, in the upper 300 m (Levitus et al., 2000).

Effects attributed to global warming have also been reported from both polar regions. On the Antarctic Peninsula, a temperature increase of 2.5^{o} C during the last 40 years is associated with the rapid disintegration of the northern Larsen and Wilkins Ice Shelves and the formation of huge icebergs (Drinkwater, 1999). On March 23, 2000, the National Ice Center reported the detection of what may be the largest iceberg (B-15) ever detected. The iceberg, recently calved from the Ross Ice Shelf, is 292 km long and 37 km wide. In the Arctic region, warming has resulted in the reduction of sea ice and that, in turn, is linked to a population decline in polar bears (Stirling, 2000).

Mann et al. (1998) analyzed high-resolution proxy climate records for the last six centuries. Their data clearly show an increase in temperature during the last century. They reported that variations in solar radiation and volcanic aerosols were the main causes of climatic variation before the last century. During the last century, however, they attributed at least part of the climatic forcing to the build-up of greenhouse gases.

Beetles have survived times of past climatic change because of their small size, population dynamics, and their ability to disperse. In the future, beetles will undoubtedly respond to climate change by dispersal, but it is less certain whether this will ensure their survival. The geographic ranges of some species will expand and others will contract. Undoubtedly, beetles will adapt genetically to differences in diurnal and seasonal temperatures and to day length. The relationship between genetic variation and morphological variation at the subspecific level is poorly understood but it seems probable that genetic isolation on the scale of decades and centuries will not lead to speciation.

One of the surprises of the Quaternary fossil beetle record is that species extinction is not associated with climate change. On the face of it, this would appear to be good news for the future. The unexpectedly high numbers of species that were extirpated from the British Isles between the Neolithic and Medieval periods, however, is a clue that the rate of extinction may be significantly higher in the future than it was in the past. The reason is that natural habitats have become increasingly fragmented by human activities. Many species currently have very restricted geographic ranges and are more vulnerable now to extinction than they were during most of the Quaternary Period. One of the surprises of the Quaternary fossil beetle record is that species extinction is not associated with climate change. On the face of it, this would appear to be good news for the future. The unexpectedly high numbers of species that were extirpated from the British Isles between the Neolithic and Medieval periods, however, is a clue that the rate of extinction may be significantly higher in the future than it was in the past. The reason is that natural habitats have become increasingly fragmented by human activities. Many species currently have very restricted geographic ranges and are more vulnerable now to extinction than they were during most of the Quaternary Period.

Global warming potentially makes a bad situation even worse. For many species, dispersal will mean abandoning the security of patches of natural habitat for disturbed areas where they will probably be more vulnerable to predators, to disease, and to being poisoned by pesticide residues in soils and by chemicals ingested from genetically altered crops. Some individuals will make it to the next patch of natural habitat, but the analogy that humans have set up an obstacle course to dispersal is a good one (Lovejoy, 1997). The chances of dispersing beetles finding habitat in which they can survive have been reduced by human activities, and so extinction is more probable than it was in the past (Figure 8).

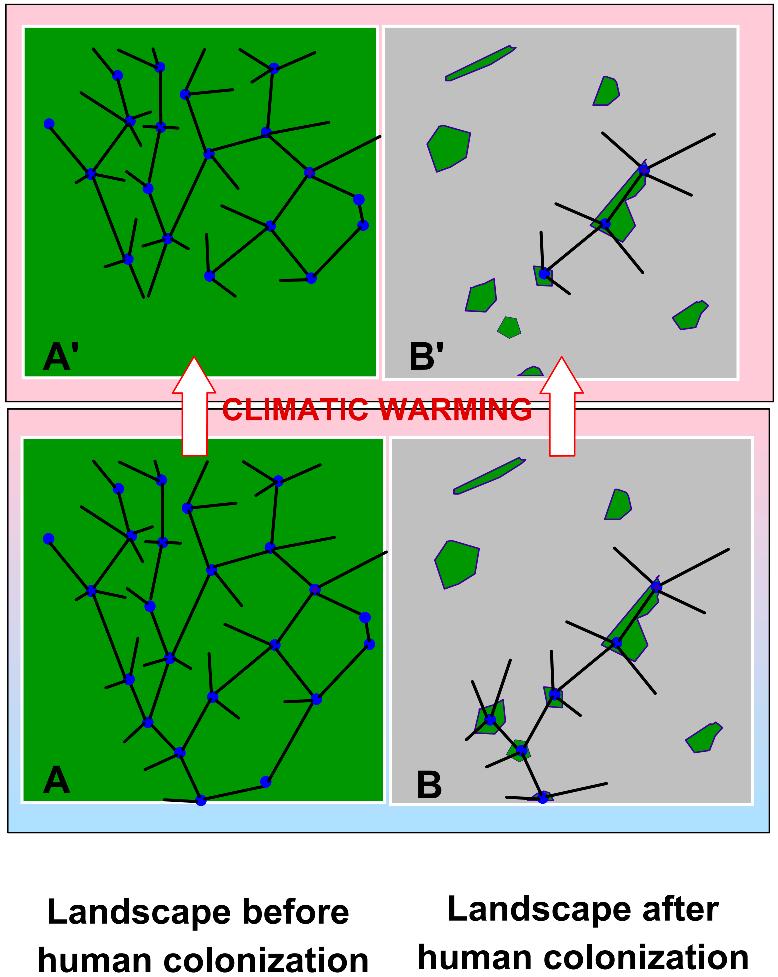

Figure 8. Schematic diagram representing a comparison in the effect of climatic warming on a beetle species before (A - A') and after (B - B') landscape modification by human activities. On the precolonization landscape some extirpation of populations occurs as the climate warms (A'). On the postcolonization landscape (B), the geographic distribution of the same species has been reduced because of fragmentation of the landscape. As the climate warms, the species not only is extirpated through part of its range that it would have been under natural conditions, but it is also extirpated from other parts of its range because the distances between habitat patches are beyond its dispersal capabilities (B'). The reduction in populations (from 19 to 3 populations) makes the species more vulnerable to extinction.

Increasingly, evidence suggests that the global temperature increase of the past century is real, and that it may be caused by human activities (Mann et al.,1998). With respect to this highly contentious and politicized issue, Overpeck et al. (1998) framed a series of questions, namely: How much warming has occurred due to anthropogenic increases in atmospheric trace-gas levels? How much warming will occur in the future? How fast will the climate warm? What other kinds of climatic change will be associated with future warming? Answers to these questions relating to the magnitude and speed of future climate change, and also to questions relating to regional effects, are needed in order to refine predictions concerning insects and health, pest management, and conservation.

Organisms will respond to global warming whether it is of natural or anthropogenic origin. To them, the scientific questions of cause are irrelevant. For human beings it is a different issue, and as much a philosophical as a scientific question. If at some point we determine beyond reasonable doubt that our activities are contributing to global warming, then we will have placed ourselves firmly on the horns of a moral dilemma. To continue on our current course will place us in the untenable situation of knowingly being the agents of extinction.

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