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The Invasion and Colonization of the North Atlantic Islands: A Palaeoecological Solution to a Biogeographic Problem [and Discussion]

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The invasion and colonization of the North Atlantic islands: a palaeoecological solution to a biogeographic problem

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The North Atlantic islands, the Shetlands, Faeroes, Iceland and Greenland, have a flora and fauna with no truly endemic species. Their populations are dominated by Eurasian species, particularly conspicuous among which are the bulky flightless insects that should have found difficulty in reaching the islands after the retreat of the glaciers of the last ice age. The puzzling origin of this biota has been the subject of prolonged controversy. Most hypotheses have apparently insurmountable difficulties, largely because they are based on present-day observations augmented by presumed geological inferences for which there is very little hard supporting data. In recent years there has been a dramatic increase in our knowledge of the complexity of Quaternary events and also of the flora and fauna that lived along the southern margins of the ice sheets. It is suggested here that the islands lost almost all their biota at the height of the glacial periods and that they were invaded and colonized almost entirely from northwest Europe during the short phases at the end of the glacial periods, when fresh meltwater and ocean surface currents would have acted as potent aids to dispersal in the North Atlantic. It is suggested that the islands to the south of the major glacial influences, such as the Azores and Madeira, have endemic species because they were not subjected to the frequent exterminations and recolonizations that afflicted the islands further north. In testing this hypothesis, it has been possible to show that the carabid beetle faunas of the North Atlantic islands become more incomplete from east to west in terms of the potential numbers of species that each island could support, given its present-day climate and unimpeded access of invasion and colonization. This suggests a progressive loss of these earthbound insects as they were transported for increasing distances across a hostile ocean.

INTRODUCTION

The biogeographical history of the North Atlantic islands (the Shetlands, the Faeroes, Iceland and Greenland) has for long been a contentious subject, largely because each explanation offered seemed to be insuperably flawed. Taken as a whole, both the flora and fauna have a remarkably European aspect in spite of their intermediate position between the Old and New Worlds. As Lindroth (1957) pointed out, the boundary between the Palaearctic and Nearctic biotas is best placed at the Davis Strait, to the west of Greenland at what appears, at first sight, to be an insignificant barrier compared with the stretches of open ocean that separate the North Atlantic islands themselves.

This pattern of species distribution is all the more puzzling when it is compared with the atmospheric and ocean surface circulation of the present day. The dominant wind directions are from west to east, and although this does not preclude the possibility of aerial transport for occasional species from east to west, it is difficult to see why, if this was the principal means of dispersal, the faunas of all the islands should have such an overwhelming resemblance to that of Europe. Only amongst the readily airborne insects of the faunas of Greenland, and to a lesser extent of Iceland too, are there many Nearctic species present, no doubt the result of aerial invasions from the New World. On the other hand, the heavy, ground-dwelling Coleoptera, such as the weevils *Otiorhynchus nodosus* Mull. and *O. arcticus* F., ponderous animals that now have fused elytra which render them completely flightless, have a widespread distribution throughout the North Atlantic (see figure 1). Fossil evidence shows that these species have been flightless at least throughout the whole of the Upper Pleistocene, that is, for the last few hundreds of thousands of generations. For such species, aerial dispersal must have been well-nigh impossible because of their bulk and the prevalence of contrary winds.

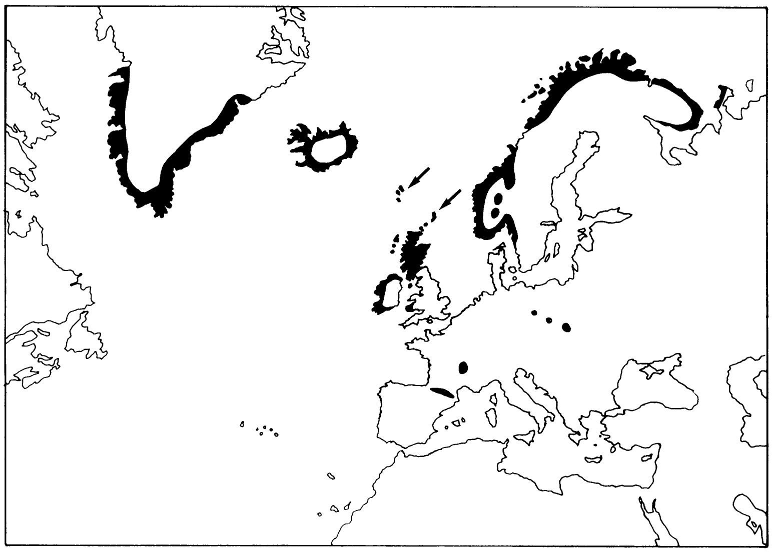

FIGURE 1. Modern geographical range of *Otiorhynchus arcticus* F., a heavy, flightless, soil-bound weevil with bisexual reproduction, which is therefore not easily spread. (Data from Lindroth 1957.)

Similarly, the present configuration of the North Atlantic surface currents provides little justification for invoking passive dispersal by this means as an important agent in the invasion of the islands. The familiar North Atlantic Drift, often referred to in Britain as the Gulf Stream, flows in a northeasterly direction along the west coast of Europe until it reaches a latitude of about 80° N, where it curls back to the southwest to flow down the east coast of Greenland. The survival prospects of any potential colonizer from Europe on such a protracted voyage would have been slim indeed, chiefly because the salinity of normal sea water causes lethal physiological desiccation. To this must be added the prevalence of hostile climatic conditions along the way. It is small wonder, therefore, that one of the few areas of general agreement among the biogeographers in the past has been that passive dispersal by ocean currents was an improbable means of transporting the flora and fauna to the islands.

For reasons such as those outlined above, the origin of the flora and fauna of the North Atlantic islands has remained enigmatic. Defenders of rival hypotheses have sometimes been reduced to supporting their cases with arguments of considerable vigour, for example in the compendium of papers on the origin of the North Atlantic biota edited by Löve & Löve (1963).

Hypotheses for the origin of the North Atlantic biota

There are four main hypotheses that have been devised to explain how the North Atlantic islands came to be invaded and colonized by the species of plant and animal that are living there today. Although these explanations are not necessarily exclusive alternatives, they will be treated separately here because each presents its own unique suite of problems. They are: human introduction, land bridges, glacial survival, and glacial *tabula rasa* followed by colonization.

(*a*) *Human introduction*

This hypothesis would explain the colonization of the islands largely as a result of accidental introduction by man. The explanation has the attraction that, since people came to the islands almost entirely from northwest Europe (with the exception of the Inuit of northern Greenland), the European affinity of the flora and fauna would be nicely accounted for. There would be no difficulty in the presence of heavy flightless species, which could easily have been transported with animals and merchandise or even in ballast as suggested by Lindroth (1957). Furthermore, a curious feature of the North Atlantic biota is also explained by this hypothesis, namely the remarkable lack of the obligately cold-adapted species that clearly could find suitable habitats in the Faeroes, Iceland and Greenland. Such species would not be expected as inadvertent 'stowaways' taking advantage of human commerce.

There can be no doubt that many species of insect did reach the islands in this manner. Archaeological excavations, particularly in Iceland and Greenland (Buckland 1986), have shown the presence of numerous synanthropic species, some of which have subsequently died out. Thus Buckland reports that in Iceland there were originally three species of the dung beetle *Aphodius* (*A. lapponum* Gyll., *A. fimetarius* L. and *A.* cf. *prodromus* Brahm) brought in by man, but today only the first of these species survives. In Greenland, a suite of species dependent on western-style farming practice became extinct with the demise of the Norse Greenland settlement early in the sixteenth century. These introductions are obviously still going on at the present day, for new species are being recorded in contexts that leave little doubt that they are recently brought in by man. For instance, *Bembidion tetracolum* Duft. was recently reported from Reykjavik, and it has now been found in the hot spring area at Skagafjodur in the north of the island (P. C. Buckland, personal communication).

On the other hand, an increasing number of fossil insect assemblages are being recovered from deposits that pre-date the arrival of man in the islands; these show clearly that many species, including the flightless ones, had invaded the area without human intervention, thus supporting the views of Larsson (1959) that much of the non-synanthropic insect fauna could not be explained in this manner and some other mode of origin must be sought.

(*b*) *Land bridges*

This hypothesis was very popular in the earlier parts of this century, before the theory of plate tectonics became generally accepted. It was proposed that land masses, or preferably sequences of islands, once existed in the North Atlantic, across which species could migrate by 'island hopping'. These so-called land bridges have subsequently foundered or been flooded by a eustatic rise in sea level. The early basalt province whose rocks can be seen today in Greenland, Iceland, Faeroes and the northwest coasts of the British Isles was seen as the remnant of this hypothetical land connection. Although there can be little doubt that these basalt rocks were indeed once part of a single landmass, their present day disposition is a result of splitting by crustal formation along the mid-Atlantic rift, a process that can be seen today in the dramatically continued growth of Iceland by fissure eruptions of basalt along the same rift. This split, which ultimately became the Atlantic ocean, had begun in Cretaceous times and must have been an effective barrier to faunal dispersal since the mid-Tertiary, that is, for the past thirty million years. For insect species to owe their present day distribution to survival from some amphiatlantic early Tertiary biota would require an unacceptably long period of species constancy. Furthermore, the flora and fauna would have had to survive on the islands throughout the numerous glacial–interglacial cycles that can be shown to have had drastic effects on the biotas near the southern margins of the continental ice sheets on both sides of the Atlantic (Morgan *et al.* 1984; Coope 1977), at times leading to the development of barren polar desert.

(*c*) *Glacial survival*

Closely related to the land-bridge hypothesis is the belief that a major part of the biota survived the periods of glaciation *in situ* on the North Atlantic islands. This view is still remarkably popular among biogeographers working in this area today. However, it still begs the question of the mode of origin of the biota, namely by what means did the flora and fauna reach the islands before the glaciations? This used to be a relatively minor problem, because the glacial episodes were generally considered to have been few in number (traditionally there were four of them) and their duration was thought to have been short in comparison with the much longer interglacial periods when climates were much as we experience at the present day (Penck & Bruckner 1909). Survival was then a matter of enduring intense, but short, periods of harsh conditions.

With the great increase in our knowledge of Quaternary geology during the last two decades, both the terrestrial record and data from deep ocean cores point to the existence of a great many more glacial–interglacial cycles (Shackleton & Opdyke 1973, 1976), although it is not easy to give the exact number of them because the climatic oscillations are of varying magnitude and it becomes a matter of definition as to which of these we grant full interglacial or glacial status. What is more, the ocean-core data show clearly that the interglacial intervals were short when compared with the prolonged glacial periods. In round figures, the climate has been as warm as now for about 10% of the last half-million years; in other words, the 'normal' climatic mode is glacial rather than interglacial and the present day climate can, with some justification, be seen as unusual when set in this context. This revolution in Quaternary science has considerable ecological consequences; in this particular context, it casts very serious doubts on the possibility of the survival on the islands of temperate species throughout these numerous and prolonged glacial periods. The climatic conditions with which they would have had to contend were evidently much more hostile than were envisaged when this hypothesis was originally postulated.

Glacial survival has been, and to some extent still is, most popular in Iceland, probably because the presence of volcanic hot springs there has provided a convenient mechanism to account for the existence of relatively warm refuges in an overall harshly cold environment. It is geologically sound to believe that such hot springs must have been available in Iceland ever since the island originated in the Middle Tertiary. However, these springs are notoriously fickle in both their location and their duration, as may be seen by the fading intensity of the great Geyser in recent years. This capricious behaviour would have made unreliable refuge sites in which to survive the long periods of glaciation.

Such special pleading on behalf of Icelandic refuges can not be applied to the Faeroe Islands, where there are no hot springs at the present time and where it is unlikely that there were any in the relevant past. Furthermore these islands were overwhelmed by an all-embracing ice cap at the height of the last glaciation and presumably by similar ones during each of the earlier glaciations, yet the Faeroes have a larger present day insect fauna than Iceland in spite of their very much smaller area of suitable habitat.

Although glacial survival in Iceland can not be completely excluded, there is a curious absence from its fauna, and from the faunas of all the Islands, of the obligately cold-adapted species that would have been expected to be among the likely survivors in glacial refuges, surrounded as they must have been by extensive ice sheets on land and pack-ice over the adjacent ocean. These cold-adapted species are important members of both the Eurasian and North American arctic insect faunas. There are today plenty of suitable habitats for such species on the more northerly of the islands, where there is ample relief to provide truly alpine environments. The absence of these species is thus not due to the lack of acceptable niches at the present day. This aspect of the insect fauna has been recognized for many years as difficult to reconcile with the glacial survival hypothesis.

Considerable support was given to the glacial survival hypothesis by the occurrence in Fennoscandia of species of both plants and animals that do not occur today outside this region and which were therefore thought to have survived the glaciations in refuges on the Norwegian coast. These refuges could have been increased in area by eustatic falls in sea level for which there was abundant geological evidence. Many of these presumed survivors have bimodal distributions: a southern area in the Norwegian mountains and another further north. For many species these two areas are not linked and the distribution is disjunct. It was possible to infer separate glacial refuges from which these two groups emerged after the retreat of the ice; being cold-adapted, they withdrew up into the mountains as the climate became warmer (Lindroth 1969, 1970, 1972). Elegant though these interpretations were, they have been gradually eroded by the discovery (from subfossil evidence), that many of the critical species were much more widespread during the closing stages of the last glaciation in the British Isles and across Europe south of the retreating ice margin, from where they have subsequently died out. The present-day ranges of these species are unreliable indicators of their recent history; many of them could have followed up the retreating ice, invading and colonizing the newly exposed landscape.

Almost every alleged insect 'hibernator' has now been found as a subfossil, with the exception of the small carabid beetle *Bembidion grapei* Gyll., which is common in the Fennoscandian fauna (and in Iceland and Greenland too). Lindroth (1979) believed, on the basis of both its geographical distribution and its wing dimorphism, that this species was a classic glacial survivor. He showed that populations of this species in western Fennoscandia have a higher proportion of brachypterous individuals than populations to the east and south in Sweden and Finland. Since this morph appears to be genetically dominant, it follows that 'longwinged individuals are homozygous recessives at this allele and are thus unable (except by recurrent mutation) by mutual cross breeding to produce short winged offspring' (Lindroth 1979). Thus populations with a preponderance of the brachypterous form were believed to have been derived from old centres, retaining to the present day this ghost of the characteristics that their ancestors acquired while isolated in their glacial refuges on the Norwegian coast. Conversely, the macropterous populations of the present day represent colonizers, flying in from the south-east, whose ancestors had not been through the restrictive ordeals of the glacial refuges. As pointed out by Lindroth, the period (or periods) during which the glacial refuges existed cannot be determined on biological factors alone. It is possible that these patterns of wing dimorphism may merely reflect refuges from the short, but intense, return of glacial conditions towards the close of the Last Glaciation (between 11000 and 10000 years ago) known as the 'Younger Dryas' period (Coope 1969).

Lindroth's attractive hypothesis is, however, not without its problems. Wing dimorphism may not be as simple as he imagined (see Hengeveld 1986) and it may well be that adaptation to present-day conditions so overprints the picture as to mask any historical significance it may have once possessed (Pearson 1964). Yet in spite of these reservations, no subfossil remains of *Bembidion grapei* have yet been found in deposits that were laid down near to the margins of the ice sheets, as we would expect if this species was a common member of the glacial fauna following up the retreating glaciers. Its absence is not for want of looking or because we cannot recognise it when it occurs as a fossil; it therefore seems to be genuinely absent from the west European fauna of late glacial times. The biogeographic history of this species remains enigmatic but should be amenable to solution when more is known about its fossil occurrences. (The late Carl Lindroth used to refer to this species as 'my darling *grapei* – the last standard bearer of the refugia'.)

In summary, the case against long-term survival of much of the biota of the North Atlantic Islands throughout the numerous glacial–interglacial cycles has been considerably weakened by the new insights into the complexities of Quaternary climatic oscillations. Furthermore, present-day geographical distributions can now be shown, from subfossil evidence, to be an inadequate guide to past biogeographic history, as many species can be shown to have changed their ranges on a large scale even within the timespan of the latest glacial–interglacial cycle. Finally, the glacial survival hypothesis does not provide a solution to the problem of the original invasion and colonization of the islands.

(*d*) *Glacial tabula rasa, followed by colonization*

In this hypothesis, glacial events are considered to have been so severe that during these periods almost all plants and animals were exterminated in the North Atlantic islands and from much of northwest Europe. Modern reconstructions of the ice limits of the last glacial maximum show that Fennoscandia was totally inundated at this time (Boulton *et al.* 1985) and as far south as the Netherlands extensive polar deserts fringed the ice margins (Zagwijn 1974). In England there are suitable deposits for the preservation of pollen that date from this time, but they are completely sterile; this sterility suggests that similarly barren conditions occurred there. In Britain and the adjacent continent, the climate was so severe that ice wedges developed in lowland areas (Shotton 1976; Morgan 1971). These are thermal contraction cracks, which form when the soil has cooled to below −15 °C to −20 °C during the winter (French 1976). Average annual temperatures must have been at or below −6 °C (Péwé 1966). It is not surprising, therefore, that only the most hardy species could have survived these hostile conditions along the southern margins of the glaciers, and that at times the flora and fauna seem to have succumbed completely. If such climatic conditions can be extrapolated to the North Atlantic islands, it is inevitable that from time to time an effective *tabula rasa* must have existed on all of the islands.

This extrapolation could well be criticized on the grounds that the Atlantic Ocean should have exerted a moderating influence on the climate of those times just as it does at the present day. In fact no such moderating influence appears to have existed during the protracted glacial periods. Elegant research by the CLIMAP team, principally by Ruddiman & McIntyre (1976, 1981; Ruddiman *et al.* 1977; McIntyre *et al.* 1976) have mapped the palaeotemperatures of the surface of the North Atlantic for various periods in the recent past. By studying fossil planktonic Foraminifera recovered from the deep ocean cores and comparing their past occurrences with their present-day thermal tolerances, they have been able to demonstrate that, during the periods of glaciation, polar water covered all of the North Atlantic down to a latitude of about 42° N (the latitude of central Portugal) where a polar front occurred, separating arctic water to the north from warmer water to the south. During the summer, sea surface temperatures north of this line were below 10 °C; during the winter, most of this area was ice-covered. Thus, at this time, there was no North Atlantic Drift to transport masses of relatively warm water northwards into the Norwegian Sea; the warm water circulated from west to east along the southern margin of the polar front where there was a steep thermal gradient. This front took up a similar position during each of the glacial periods so that 'the North Atlantic is divided roughly into two parts – a dynamic area to the north of approximately lat. 42° N and a relatively stable area from lat. 43° N to the Equator. The northern part undergoes temperature changes between glacial and interglacial modes of as much as 18 °C in some areas, whereas in the southern part the variation seldom exceeds 3 °C' (McIntyre *et al.* 1976). From this work it appears that the North Atlantic Ocean is the most variable of all the world's oceans in terms of its surface temperature changes between glacial and interglacial periods. This evidence shows that, far from being a moderating influence, the glacial North Atlantic Ocean would have contributed to the hostility of the climate of the islands at these times. However, although a glacial *tabula rasa* now seems inescapable for the North Atlantic islands, the questions still remain: what was the source of their present-day flora and fauna, and by what means did the species reach the islands?

A MODERN SYNTHESIS

(*a*) *The source of the present biota*

The answer to the first of these questions may well lie in the Quaternary fossil record. In the last few decades the development of Quaternary entomology, the study of subfossil remains of insects that lived during the glacial and interglacial periods, has greatly augmented the vast array of Quaternary botanical data that has been amassed for more than half a century. It can now be shown that almost all the species of Coleoptera of the present-day faunas of the islands were present in western Europe towards the close of the last glaciation though in many cases they are now extinct there (Coope & Brophy 1972; Coope & Joachim 1980). In contrast, the Coleoptera that lived in western Europe during earlier phases of the last glaciation include many characteristic species that are *not* found today in the islands. Some of these are today exclusively arctic species and their absence cannot be attributed to the unsuitability of present-day habitats. It seems most likely that, at the height of the Last Glaciation, northwest Europe lost almost all its Coleoptera and many species did not return when the climate started to ameliorate, because of historical accidents of space and time. These species were not available in western Europe when the opportunity for invasion and colonization of the North Atlantic islands presented itself. The fossil evidence thus shows that the Coleoptera of the islands today *could* have come from that part of western Europe that lay to the south of the waning ice sheets towards the end of the Last Glaciation. (Coope 1970, 1979).

At this stage in the argument, it should be pointed out that the fossil record puts special emphasis on the Coleoptera, because the robustness of their exoskeletons makes for excellent preservation and the fossils are often complicated enough to permit specific identification. Furthermore, many of them are heavy-bodied and some are entirely flightless. If such species could have been transported to the islands, then other components of the flora and fauna could have gone the same way. Thus the Coleoptera should be viewed as indicators of what was available for export from western Europe at a particular time. Furthermore they provide constraints on the modes of transport that would be appropriate for their transference across hundreds of kilometres of open ocean to these remote islands. Wind dispersal by itself seems inadequate for the heavy flightless species and in any case the prevailing wind direction is from west to east. Ocean currents, as they are disposed today, provide a very circuitous route via the Arctic and there are the serious physiological problems associated with salinity that would have made such a route impossible. It would seem that all transport mechanisms based on the present-day patterns of wind or ocean currents present insuperable difficulties and reconstructions of past circulatory patterns were based on inadequate information; indeed, these problems were the major reason why hypotheses of glacial survival themselves survived in the face of fierce geological opposition. There appeared to be no other option.

(*b*) *The polar front*

To answer the question of how the flora and fauna was transported from western Europe to the North Atlantic islands, it is necessary to return again to the ocean core data and in particular to the changes in circulation patterns in the North Atlantic towards the closing stages of the last glaciation. Associated with these ocean current changes, there were large-scale alterations in the terrestrial flora and fauna of the nearby continents, which, because of their timing and intensity, appear to be causally related to the shifts in the surface water masses of the west coast of Europe.

Once again it is the position of the polar front that is crucial to the argument. At the height of the glaciation at about 18000 years ago, it lay approximately along latitude 42° N, and remained close to that position until about 14000 years ago (figure 2). The circulation pattern then underwent a dramatic change. In the eastern North Atlantic the polar front moved very rapidly northwards so that by about 13000 years ago (figure 3) it was situated to the north of the islands and a flush of warm ocean water was directed up the west coast of Europe, with summer surface temperatures rising by about 7 °C (Ruddiman *et al.* 1977). At the same time both the flora and fauna showed clear evidence of climatic amelioration on land: the Coleoptera provide independent evidence for a rise in mean July temperatures of about 7 °C (Coope & Brophy 1972). Apparently associated with the disappearance of the sea ice, there was an even greater increase in the winter temperatures at this time, of about 20 °C (Atkinson *et al.* 1986). This climatic warming saw the total extermination of the old arctic beetle fauna from the lowlands of western Europe and its replacement by a thoroughly temperate assemblage, certainly as far north as southern Scotland (Bishop & Coope 1977). By this time, the ice sheets had apparently retreated from Britain as indicated by radiocarbon dates of around 13000 years ago from the basal sediments in ice-gouged lakes in the Scottish Highlands (Sissons & Walker 1974). However, extensive glaciers remained covering most of Fennoscandia

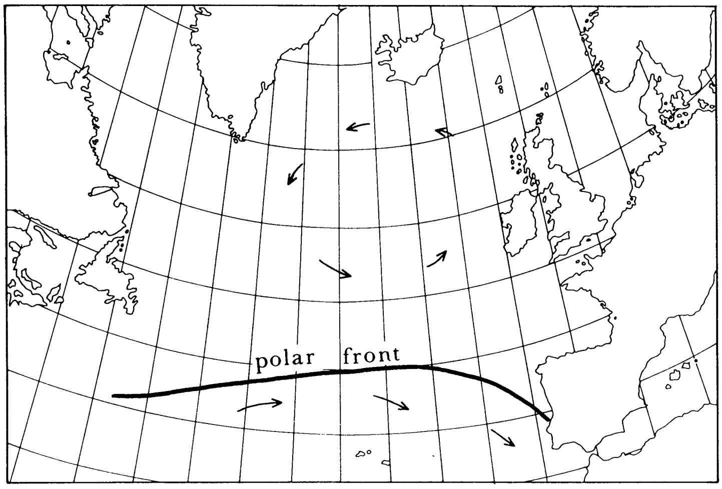

Figure 2. Position of the polar front in the North Atlantic at the time of the maximum glaciation (data from Ruddiman & McIntyre 1981). The arrows indicate surface current directions.

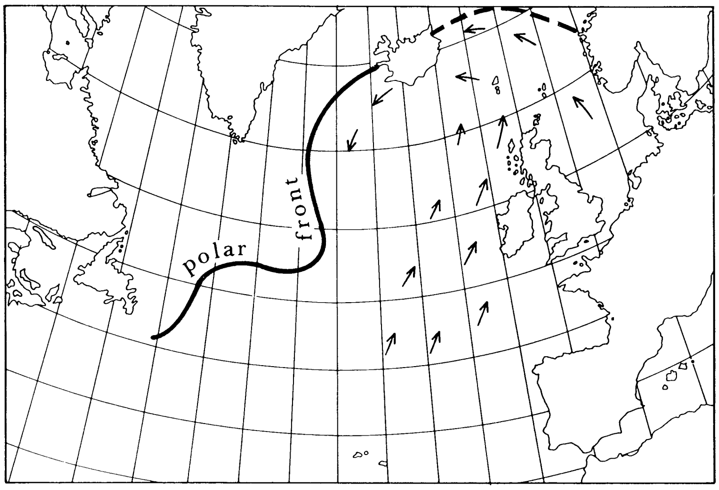

Figure 3. Position of the polar front in the North Atlantic during the first phase of deglaciation at 13000 years ago (data from Ruddiman & McIntyre 1981). The arrows indicate surface current directions.

at this time, but they were rapidly retreating so that the extreme south of Sweden and the coastal margins of Norway were bare of ice.

This general pattern of retreat was interrupted by a brief return to glacial conditions between 11000 and 10000 years ago, when the polar front moved southwards to latitude 50° N (figure 4). Associated with this reversal were corresponding changes on land. Almost all trees were lost from the landscape; the increase in herbaceous vegetation suggests that tundra-like conditions became prevalent over much of northwest Europe. At the same time there was a sudden increase in the cold-adapted Coleoptera, with many arctic species ranging down into southern England (Peake & Osborne 1971; Coope 1982) and Ireland (Coope *et al.* 1979). As the land became thinly vegetated there was much mass movement of sediment, triggered off by freezing and thawing; streams became overloaded with sediment and great expanses of sand

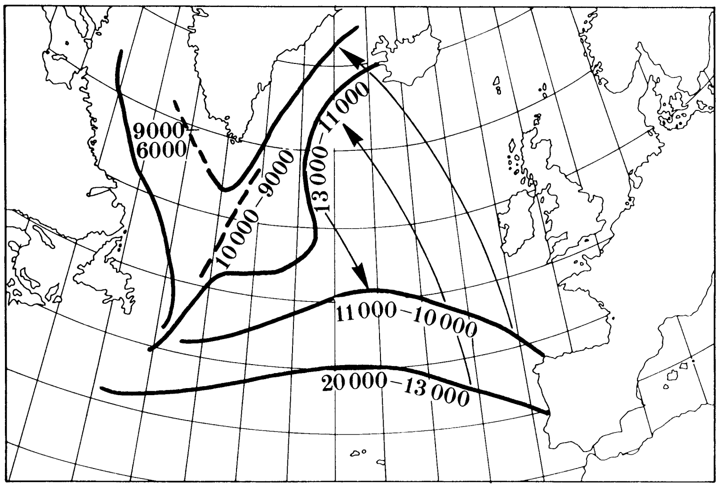

FIGURE 4. Retreat positions of the polar front in the North Atlantic from 20000 years ago to its position in the modern interglacial after 6000 years ago. The arrows indicate the direction of movement of the front as it oscillated during the closing phases of the last glaciation. These movements were not necessarily instantaneous, but occurred so quickly that the rates are hard to measure on a geological timescale (data from Ruddiman & McIntyre 1981)

and gravel were deposited along their valleys (Rose *et al.* 1980). Ice wedges developed in places on these gravel plains and have been found as far apart as the Isle of Man in the west (Joachim 1978) to the Netherlands in the east (Vandenberghe *et al.* 1986). This cold episode, usually referred to as the Younger Dryas period, has all the qualities of a microglaciation and was widespread in western Europe and, maybe, even further afield than this (Van der Hammen 1985). At this time the islands must have been isolated again by extensive sea ice, even during the summer, and the ocean was probably ice-bound at least as far as the southwest approaches to the British Isles.

The postglacial climatic amelioration must have been extremely rapid; by 9000 years ago the polar front had returned northwards once again to stand to the northwest of Iceland and the ocean circulation was similar to what it had been at 13000 years ago. The associated floral and faunal changes show that there was a return to temperate climatic conditions and the suite of arctic Coleoptera had disappeared completely from lowland Britain by this time (Osborne 1974; Bishop & Coope 1977).

(*c*) *The transport of biota to the islands*

It was during these terminal spasms of the Last Glaciation that two unusual circumstances conspired together to enable the ocean to ferry flora and fauna to the newly deglaciated North Atlantic islands.

The first of these unusual circumstances was the temporary arrangement of the ocean surface currents as they shifted from a glacial mode to an interglacial mode. While the polar front was situated to the south and much of the North Atlantic was ice covered for much of the year, there would be little opportunity for transport and certainly not for the temperate species that seem to have undertaken the journey. However, there were two suitable periods as the North Atlantic Drift current was becoming established, namely for the thousand years after 13000 and after 10000 years ago. At these times, relatively warm water flowed northwards along the west coast of Europe but turned westwards either just before entering the Norwegian Sea (in the first of these periods) or rather further north during the second period (Jansen *et al.* 1983). Any plants or animals set adrift on these currents would have a much shorter route to the islands than they would if they had to take the circuitous path of the present-day currents. During these periods the faunas of ice-free areas in western Europe were devoid of the obligately cold-adapted species; thus only temperate species were available for 'export'. Of these, only those capable of surviving the rigours of a cold journey, with sea surface temperatures similar to those of the present, would have reached the northern islands. Thus the absence of arctic Coleoptera from such apparently suitable islands as Iceland and Greenland may be accounted for by this hypothesis.

The second unusual circumstance was the presence of abundant glacial meltwater, and probably also icebergs and fragmented fjord ice, in the North Atlantic at these times. With the rapid retreat of the Fennoscandian ice sheets, a vast quantity of fresh water must have poured into the adjacent ocean. All the meltwater from Finland and Sweden debouched through the straits to the north of Doggerland and south of Norway and to this must be added the product of the melting of the Norwegian ice sheets. Much of this fresh water would have floated on the saline ocean water just as it does today off the ice margins in the Arctic or on the sea surface hundreds of kilometres from the mouths of major rivers. Because fresh water is no impediment to insect transport, these 'fresh water slicks' would have facilitated the dispersal of insects that had been inadvertently swept to sea. Fjord ice has been seen off the coast of Spitzbergen loaded with plant debris and presumably carrying insects as well. Such a mode of transport would have carried winged or flightless species alike and it accounts for the widespread distribution in the islands of heavy flightless species, such as *Otiorhynchus arcticus*, which were such a puzzle to past historical biogeographers. However, ice rafts of this sort would be precarious vehicles and most would have disintegrated long before reaching the islands.

For those fortunate survivors that were cast ashore there were hostile habitats on the recently glaciated islands, with sterile soils and few nutrients. Of these early pioneers, few would survive. They illustrate the difference between invaders and colonizers (or the old distinction between reach and grasp).

Since these unusual circumstances came together for only brief periods at the end of glacial periods, it follows that during fully interglacial periods the North Atlantic islands would have become biologically isolated as well as during the fully glacial periods. The only invasions would be either by airborne means or else by assisted passage with some other organism or on floating vegetation. In either case the number of species travelling in this way was probably minimal.

(*d*) *Mid-Atlantic islands*

In this context it is instructive to look at the biotas of the groups of islands that lie to the south of the latitude repeatedly taken up by the polar front during times of glaciation. These island groups have today a large number of species that are unique to each archipelago. Their faunas and floras have not been subjected to the repeated exterminations and recolonizations that were imposed on those of the North Atlantic islands by the comings and goings of the polar front. The Azores and Madeira probably developed their unique species over a relatively long period, though exactly how long this was must await the investigation of Quaternary fossils of these islands. The prolonged isolation of these islands, indicated by this high proportion of unique species, stands in marked contrast to the situation in the North Atlantic islands, discussed here, which have no species peculiar to themselves and whose floras and faunas behave just as if the islands were part of the Eurasian continent both in their specific composition and, from the meagre fossil evidence of their earlier faunas (Buckland 1986), in their response to the glacial–interglacial cycles. The explanation for this contrast between these two suites of islands resides in their respective recent geological histories rather than their present-day ecologies or their modern climates and oceanographic settings.

A TEST FOR THE *TABULA RASA* HYPOTHESIS

In all historical sciences where we seek explanations for events that have already happened, it is often difficult to conduct convincing tests in which the outcome of some definitive experiment is predicted. Explanations often take on the form of 'just so stories', the credibility of which rests with the preconceived stances of the listener and maybe even more on the skill of the story teller. However, in a limited sense, it is frequently possible to make predictions about future discoveries that we would expect if the explanation offered in the first place were valid. In practice it may be difficult to disentangle the actual order of discoveries in an investigation that is often far from the logical procedure portrayed in scientific papers; a view of the scientist's ways of working that has been succintly explored by Medawar (1972, 1986) on numerous occasions. However, the following test was run after the bulk of this paper was written and thus temporally, if not necessarily conceptually, it follows from what has been presented above. Its gratifying outcome was not, therefore, a retrospective rationalization of facts already taken into consideration in the initial formulation of the hypothesis.

In the course of a long programme investigating the climatic significance of Quaternary fossil insects, the interpretation has hinged on the present-day geographical distributions of the species and the changes induced in these ranges by the oscillations of ice age climates. In quantitative climatic assessments of fossil insect assemblages there has always been a problem arising from the fact that species may not have taken up their full potential range for a variety of historical reasons. Simple overlapping of geographical ranges to find the present locality in which most species could coexist, and thus the climate in which they could have lived, was frequently unsatisfactory.

If, however, the occurrence of a species is plotted, not on geographical coordinates, but on axes denoting variation in the thermal climate, the stacking of these ranges becomes much easier. This is illustrated by the occurrence of *Bembidion fumigatum* Duft., which has a ragged geographical range in Europe associated chiefly with saline habitats (figure 5). The distributional data are of varying adequacy and sometimes merely regional with no precise idea of the localities in which the species has been actually found. It is easy to appreciate the difficulty of stacking a series of maps of this sort. On the instigation of Tim Atkinson, of the Climatic Research Unit at the University of East Anglia, all the occurrences of our fossil species were plotted on coordinates showing the mean temperature of the warmest month against the difference between the mean temperatures of the coldest and the warmest months. In these two variables, many parameters of the thermal environments across Eurasia are subsumed. When the occurrence of *Bembidion fumigatum* is plotted on these coordinates, the distributional area condenses (figure 6) and becomes much more amenable to computer handling. A computer-based package was designed by means of this methodology, in which the climatic implications of Quaternary fossil coleoptera could be dealt with mathematically, thus obviating the necessity for subjective assessment of a mass of diffuse geographical data (Atkinson *et al.* 1986).

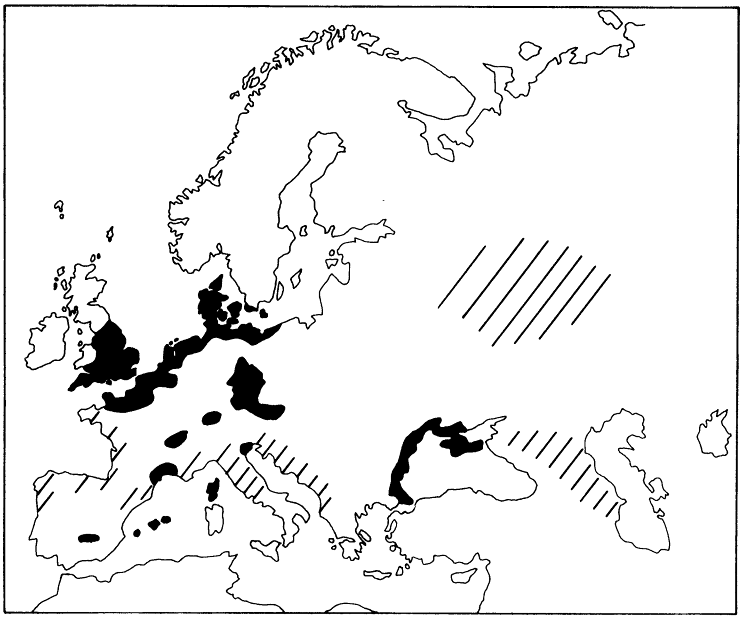

Figure 5. Modern European distribution of *Bembidion fumigatum* Duft. Black areas indicate firm data; diagonal lines indicate regional data only. The species also lives in suitable habitats in Siberia as far east as the Lena river.

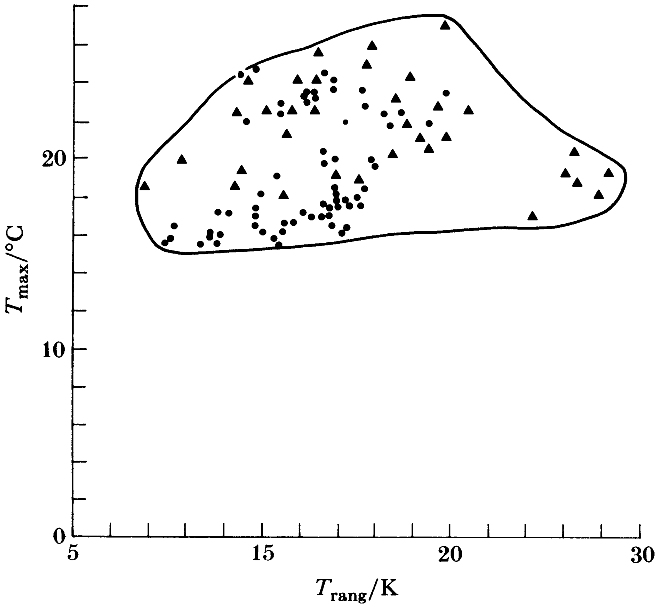

Figure 6. Climatic ranges of *Bembidion fumigatum* Duft. $T_{\max}$ is the mean temperature of the warmest month; T_{rang} is the difference between the mean temperatures of the warmest and coldest months in areas inhabited by the beetle. ●, A certain record; ▲, a possible record.

While working on this programme, my research assistant, David Perry, suggested that it should be possible to reverse the procedure and use the 'climatic range' of a species in a predictive sense; in other words, it ought to be possible to say what the potential range of a species might be. To test this idea we applied it to the carabid beetles from the North Atlantic islands.

The Carabidae were chosen for a number of reasons. They are robust animals and thus provide a good fossil record. Their geographical ranges and ecological preferences are fairly well known. Because they are either predators or general scavengers, they are little restricted by other ecological factors, such as the availability of a particular food plant, and their food requirements do not present complicated overlays to the picture. They are ground beetles and thus unlikely to have been extensively transported by air, and would have been among the species that we should expect to have been ferried across the ocean at the time of the melting of the glaciers.

In figure 7, the ovals circumscribe the thermal climate of the North Atlantic islands with respect to $T_{\max}$ (the mean temperature of the warmest month) and T_{rang} (the difference between the mean temperatures of the warmest and coldest months). The figures within each envelope show the actual numbers of carabid species present on each island and the percentage of the potential numbers of carabid species that each island could have had if there had been no impediment to their colonisation. It becomes immediately evident that there is a marked fall-off in this percentage from Shetland (96%), Faeroes (49%), Iceland (35%) to Greenland (17%). Although it has been known for a long time that the insect faunas of these islands diminish in their diversity in a northwesterly direction, this has usually been seen as a reflection of the northwesterly climatic deterioration. These percentage figures, however, make allowance for this climatic deterioration and show clearly that the climatic explanation is inadequate by itself. The only satisfactory view of these figures is that the faunas were derived from the east and that there were progressive losses in the transatlantic 'sweepstake'.

In the context of this discussion meeting, there are interesting riders to these observations. The faunas of these islands can be shown to be more and more 'incomplete' in a westerly direction, as if ecosystems were becoming increasingly riddled with holes. Numerous questions arise. Does the invasibility potential of each island vary in proportion to this faunal incompleteness? I certainly have the subjective impression that some Icelandic Carabidae occupy a wider range of habitats there than the same species occupy in Britain. This is

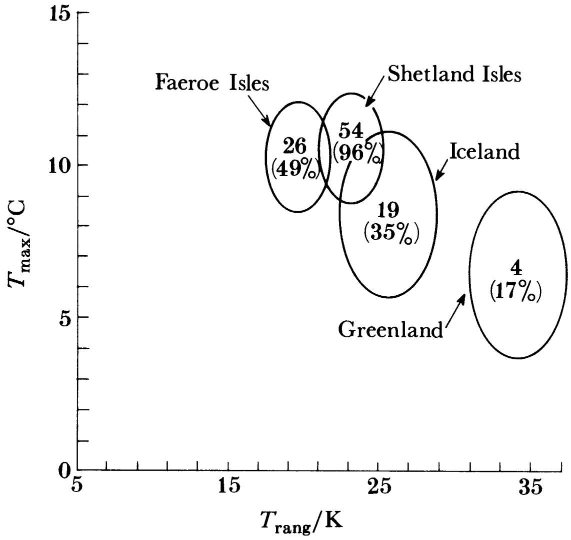

FIGURE 7. Diagram showing the present-day climatic ranges of the North Atlantic islands and the numbers of species of carabid beetle on each island. The numbers in brackets show the percentages of the modern fauna compared with the potential faunas for each island.

exemplified by *Nebria gyllenhali* Sch., which is much more ubiquitous in Iceland than in northern Britain. Would such species be dislodged easily from these marginal habitats if competitors were introduced from western Europe or by a complete outsider from elsewhere? Would the Shetland Islands be more difficult to colonize than, say, the Faeroe Islands, which have much the same climate but proportionately less of their potential fauna? Faced with the readiness with which insects become accidental stowaways of human traffic, these questions may not be purely academic.

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Discussion

P. D. MOORE (*King's College London, Strand, London WC2R 2LS, U.K.*). An assumption is made that since there is morphological stability there will be physiological stability in a taxon. Among plants, there is considerable evidence for physiological and therefore habitat diversification over the last 10000 years.

In *Armeria maritima* (thrift), for example, British populations have been restricted from a widespread distribution 10000 years ago to two major habitats today, namely maritime and alpine ones. These disjunct populations differ in their physiological but not their morphological characters; they are ecotypes. In Poland, the diversity of habitats in which the species is found is greater, including sandy roadside verges and *Sphagnum*-rich mines. Clearly this species has evolved and diversified physiologically over the last 10000 years, although its morphology is little changed.

This being so, is it not possible that some of the beetle species upon which climatic reconstructions are based have also changed in their physiology and therefore in their value as precise indicators of climate?

G. R. Coope. The assumption that physiological stability accompanies the demonstrable morphological constancy of many species during the Quaternary period is fundamental to all of our palaeoecological reconstructions. The test of all assumptions of this kind is the pragmatic one: does it work? In almost all cases the answer is that ecological sense results from using it and that the interpretations are internally consistent and match the inferences from associated geological data. Had physiological evolution been going on in a clandestine fashion under the cloak of morphological constancy, we would have expected a gradual distortion of this picture of ecological conformity with increasing geological age of our fossil biotas. In practice, this expectation is not borne out; species kept much the same company throughout the Quaternary as they do at the present day. Nevertheless there are a few species that persistently offend against ecological conformity, being found repeatedly in strange company in our fossil assemblages. It is tempting to see in these species some evidence of physiological evolution occurring without any morphological expression. However, there are other possible explanations for their non-conformist behaviour, namely, (1) our knowledge of the present day occurrences of the species may be incomplete; (2) some environments of the past may have no precise present-day analogue; (3) the gene pool at present available to the species may be more limited than in the past. Of these possibilities, I believe that the first is probably the most important.

With regard to the specific case of *Armeria maritima*, I do not see why the postglacial restriction of the geographic range of this species in Britain is evidence that 'this species has evolved and diversified physiologically over the last 10000 years'. If we look at the total distribution of this species today, it is clear that its occurrences in the British Isles do not fully reflect its ecological potential. The fossil record of this species throughout the Last Glaciation shows that this species was characteristic of a variety of open habitats, as it is in eastern Europe at the present time. Viewed in its entirety, there would seem to be no reason to believe that *A. maritima* has changed its environmental requirements during this period. I see no reason why the existence of local ecotypes is at all inconsistent with this interpretation.

A. Gibbs (*Australian National University, Canberra City, ACT* 2601, *Australia*). I am a little surprised that the species discussed did not migrate further into North America. And what explanation does Dr Coope give for still longer dispersions, for example of bi-polar species? There are species of byrrhid beetles with such a distribution. Has any search been made for remains in peats in the high Andes, as a possible migration route?

G. R. Coope. Considerable work has now been done in North America on the response of insect species to the glacial–interglacial cycles (see Morgan *et al.* (1984) for a review). The only work on Quaternary fossil insects in the Andes that I am aware of has been carried out in Chile by Ashworth & Hoganson (1983), but they deal with insect faunas of the final stages of the Last Glaciation only. I suspect that bi-polar distribution patterns are of much greater antiquity than this and that when dealing with insects at the family level (e.g. Byrrhidae) we should seek dispersion routes in the Tertiary when mountain chains and island arcs may well have provided means of access quite different from those of the present day.

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