PERSPECTIVES: PALEOECOLOGY

The Refugial Debate

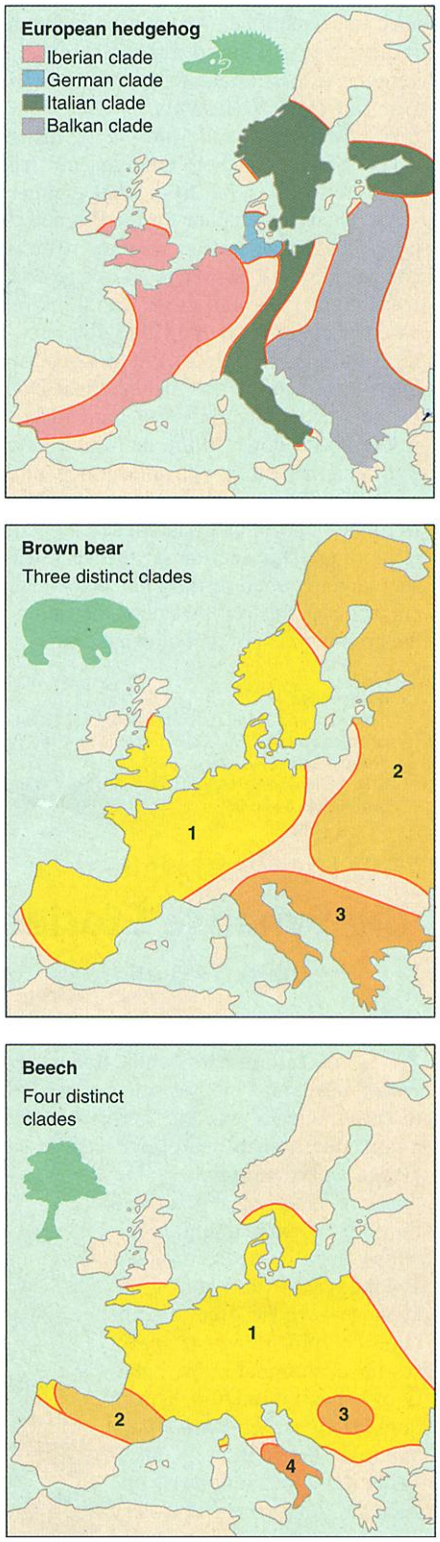
K. J. Willis and R. J. Whittaker

Glacial conditions on Earth have prevailed for approximately 80% of the past 2 million years. Biologists have long debated the fate of temperate fauna and flora during these glacial periods and the part played by cold-stage isolation of plant and animal species in determining current patterns of biodiversity. Biogeographers coined the term "refugia" to describe the localities where temperate fauna and flora existed during full-glacial conditions. However, the precise locations of refugia and their impact on the present-day distribution and diversity of species is still under investigation.

Past researches into full-glacial refugia have fallen into two camps: those dealing with refugia in the tropics and those dealing with refugia in higher, "temperate" latitudes, just beyond the ice-permafrost boundary. Most of the work on refugia in temperate latitudes has centered on seeking isolated pockets where plants and animals survived (*1*). The focus in tropical regions, in contrast, has been the investigation of how refugia behaved as "species pumps," that is, the extent to which isolation in refugia led to the development of new species (speciation). This line of research was stimulated 30 years ago by Haffer (*2*). He suggested that patterns of unique species or lineages—for example, birds that are unique to a particular area (avifaunal endemicity)—were the product of full-glacial isolation in refugial pockets of the Amazonian rain forest. Isolation in refugia has now become a well-established theory to explain high levels of endemicity in many tropical regions. In the tropics, therefore, refugia have been seen primarily as regions that promote long-term biodiversity, whereas in higher latitude locations they have, on the whole, been viewed as areas protecting biodiversity, but playing a passive rather than an active role.

Recent paleoecological and molecular evidence has increasingly led to the questioning of both of these paradigms. Ironically, it is becoming clear that full-glacial refugia may have had more influence on current patterns of biodiversity in temperate regions than in tropical zones. In Europe, for example, there are distinctive patterns of genetic variation and subdivision within present-day populations of grasshoppers, hedgehogs, oak trees, the common beech, black alder, the brown bear, newts, voles, silver fir, and house mice (*3*). The geographic patterns of these variations can be linked to isolation in various cold-stage refugia in the three southern peninsulas of Europe (Spain, southern Italy, and the Balkans; see the figure). They suggest that cold-stage isolation has left a recognizable imprint on present-day biodiversity. Whether the differences seen in present-day populations of European animals and plants herald the beginning of speciation for some groups is questionable. Many populations live in mixed zones where genetically distinct groups become intermingled. However, molecular analyses of the diversity of North American songbirds suggest that even if isolation during the cold stages of the Quaternary period (the last 1.8 million years) was not responsible for all of the initial speciation events (*4*), it was essential for the completion of speciation events inaugurated in earlier geological time (*5*). (For example, it has been proposed that glaciation in central North America caused the fragmentation of black-throated green warbler populations leading to the formation of three new species in western North America.) It is, therefore, not possible to rule out the emergence of new lineages that resulted from the genetic distinctions apparent in present-day European populations.

In tropical regions, however, the theory that full-glacial refugia account for current patterns of biodiversity—and, in particular, for apparent pockets of endemicity in regions such as the Amazon basin—is gradually disintegrating. This theory postulates that the aridity in full-glacial eras resulted in savanna replacing lowland tropical rain forest; consequently, lowland rain forest biota were restricted to small refugial belts in the mountains where conditions would have been wetter (*2*). Yet increasingly, paleoecological evidence suggests that this interpretation is incorrect. Recent pollen evidence from Amazon river sediments deposited on the ocean floor of the Atlantic (the Amazon deep-sea fan) provides a 50,000-year record of Amazon basin vegetation (*6*). The evidence clearly indicates that the lowland tropical forests were not extensively replaced by savanna vegetation during the glacial periods, but



The advantage of long holidays. Patterns of genetic variation in European populations of hedgehogs (*Erinaceus* species) (*3*), brown bears (*Ursos arctos*) (*11*), and beech trees (*Fagus sylvatica*) (*11*). In all three cases, isolation in southern European refugia during the cold-stages of the Quaternary period caused discernible genetic differences that are apparent in the present-day populations.

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rather that the forests dominated throughout (*7*). So, for low-latitude environments, isolation in refugia may not have occurred in the manner originally anticipated, if at all (*8*). Indeed, the emerging picture from the Neotropics—South America, the West Indies, and Central America, south of the Mexican plateau—as a whole is that the effectiveness of cold-stage aridity in rolling back rain forest has been greatly overestimated. For instance, a recent study of the genetic diversity among widely separated populations of the lowland canopy tree *Poulsenai armata* in Central America has demonstrated that they have greater within-population diversity than would be consistent with a postglacial expansion from distant South American refugia (*9*). Rather, the evidence points to a persistence of this and other lowland forest species in Central America during full-glacial periods.

The latest twist in the Amazonian refugial debate, however, is the suggestion (*10*) that a substantial part of the patterning of endemic species within lowland Amazonia is the product of rises in sea level of about 100 meters that took place during warm phases (that is, not during glacials) of the Quaternary and late Tertiary periods (10 to 2 million years ago). Such transgressions would have fragmented the region into two large islands and a series of smaller archipelagos, encouraging speciation through geographic isolation during warm stages rather than cold stages.

The picture now emerging depicts refugia as a crucial influence in shaping mid- and high-latitude biodiversity. However, this view is probably no longer valid for low-latitude tropical regions. For these zones, it would appear that the refugial hypothesis is far too simplistic (*8*). Clearly, a much more complex model is needed to explain the biotic patterns in these regions and, in particular, the pockets of endemicity for which full-glacial refugia were originally thought to be the cause (*2*).

References and Notes

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PERSPECTIVES: SURFACE SCIENCE

Catalysis on Oxide Surfaces

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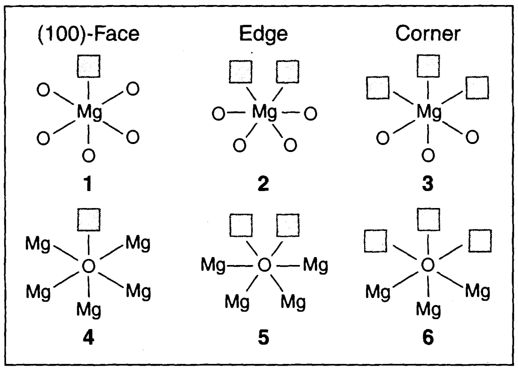
Free coordination sites play a major role in catalysis by metal complexes, because reactants may bind to these sites and become activated for catalytic conversion (*1*). Similar considerations apply to the surfaces of solid catalysts in general and of metal oxides in particular, because the surface atoms are characterized by a "ligand" sphere that differs from that in the bulk. The surface atoms generally have lower coordination numbers than those characteristic for the bulk: They are cus (*2*). Their coordination sphere may be completed by adsorbed molecules, and these may be activated for catalytic transformations, in close analogy to processes occurring on metal complexes. On page 1474 of this issue, Over *et al.* (*3*) succeed in verifying this concept coordinatively unsaturated sites (cus) on the atomic scale.

The coordination numbers of surface atoms in real catalysts may vary over wide ranges because different crystallographic faces, edges, steps, point defects, and dislocations may be exposed, resulting in an often substantial energetic heterogeneity (*4*). Oxide surfaces typically expose cus cations and cus oxygen anions, and chemisorption—adsorption involving chemical bond formation—frequently involves both simultaneously. For a specific catalytic transformation, certain geometric and energetic requirements must be fulfilled, so that frequently only a small percentage of all surface atoms may act as active sites.

The cus surface sites on real, high–surface area catalysts can only be characterized indirectly, with the use of probe molecules that can fill the free coordination sites. For example, the carbonyl infrared spectra of CO adsorbed on microcrystalline α-Cr_2O_3 (*5*, *6*) and on epitaxially grown chromium oxide films (*7*) show a complex pattern of bands of carbonyl surface complexes characterizing the heterogeneity of chromium sites.



Site-specific catalysis. Schematic representation of cus Mg^{2+} and cus O^{2-} ions on the surface of microcrystalline MgO. Sites on the (100) plane, on edges, and at corners are shown.

In another example, infrared spectroscopy has shown that methane is adsorbed on MgO in a C_{3v} symmetry at low temperature (*8*). Density-functional calculations (*8*) suggest that CH_4 does not bind to any of the cus Mg^{2+} sites **1** through **3** (see the figure), which have coordination numbers of 5, 4, and 3, respectively. Interaction with the cus O^{2-} sites **4** and **5** is also repulsive. A finite binding energy was found only for the three-coordinate cus O^{2-} corner site **6**, characterizing an H-bonding interaction of the type O ··· H–CH_3.

This last example clearly demonstrates that very specific geometric and energetic requirements must be fulfilled by the adsorption sites for methane. An interesting example of reactive chemisorption is the adsorption of CO on MgO. CO binds to the Mg species **1**, **2**, and **3** as suggested on the basis of the infrared spectra of adsorbed CO (*9*). The simultaneous formation of chemisorbed CO_2^- species coordinated to Mg^{2+} sites is indicative of the concerted action of cus Mg^{2+} and cus O^{2-} sites (cation-anion pairs) (*8*).

For a more detailed understanding of the nature and action of chemisorption and catalytically active sites, their structure and reactivity must be characterized directly on an atomic scale. Modern surface analysis techniques, including low-energy electron diffraction (LEED) and scanning tunneling microscopy (STM), permit this type of observation, provided that the substrate is sufficiently electrically conductive and crystallographically well-defined (*6*, *10*). Monocrystals of many oxides are available today, but their poor conductivity often prevents their investigation

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