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# Insight Mammalian Ecology



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# RODENT DILEMMAS

To flee somewhere far away and then return, or to stay put and wait things out? That was the dilemma faced by small mammals during the last glacial period. Some made it – but how did they survive, and where?

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uring the Vistulian glaciation (a period lasting from about 115,000 years ago to 11,700 years ago, named after the river Vistula in Poland), northern Europe was covered by an ice sheet. At that time the best conditions were found in places with temperatures and humidity levels that could sustain vegetation. For moderately sensitive species, that meant the south of the continent, including modern-day Spain and Portugal, Italy, and the Balkans. Cold-loving species were able survive in the harsher conditions much further up north, closer to the margins of the ice sheet. Those relatively hospitable areas did not have to be large: some were smaller pockets surrounded by more punishing conditions. As the ice sheet retreated, hardy survivors from those species that had braved the difficult conditions found themselves at an evolutionary advantage: they were the first to venture into newly available areas.

Paleontological data offers evidence of many plant and animal species surviving far north of the Mediterranean refugia (areas with more favorable conditions). Until recently that research was not well-coordinated between different disciplines. As a result, our understanding of those processes was patchy.

## Interdisciplinary insights

At first researchers believed that ice age refugia were located in the Mediterranean. However, the exact role played by those areas in the postglacial history of different species was unclear, and a long controversy

ensued. In fact, some scientists went so far as to reject the idea that the southern peninsulas (Iberian, Apennine, Balkan) might have played any particular role as starting points for postglacial species expansion. Instead, they believed that those southern areas were mostly home to endemic populations. They argued that species that found themselves capable of thriving in a moderate climate would have had no ecological need to migrate all the way south away from the ice sheet. After all, the conditions in the areas closer to the ice sheet would have still been perfectly tolerable. Such species would have been able to survive the glacial period north of the Mediterranean so long as they could find an area with a favorable set of climate and environmental conditions. That hypothesis now finds support in the data.

Thanks to a comprehensive interdisciplinary approach combining paleobotanic, paleozoological and paleoclimatic data with molecular evidence and advanced computer modelling to recreate the conditions during the Last Glacial Maximum, we now have a new understanding of the role and distribution of refugia in Europe's postglacial colonization. Fossil evidence has now been fleshed out with, and checked against, phylogenetic relationships. Combined with our understanding of the ecological needs of different species, our paleoclimatic and paleobotanic data has helped to reconstruct the distribution of plants and animals in the Pleistocene using complex mathematical models. This gives us a better idea of the developments in the Pleistocene, throwing a new light on past connections and modern-day distributions of often far-flung populations. The research suggests that species arriving from the Mediterranean after the retreat of the ice sheet were not alone in reclaiming Europe from the ice.

## Postglacial colonization

For instance, the role of the Carpathian refugium in the survival of different species is well-documented for the postglacial period. Many tree species found in



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Poland today survived the glacial period in that area. Sediments from the last glaciation in a number of locations in the Carpathian Mountains contain pollen of such common species as the Scots pine, the European spruce, the European larch, the warty birch, or the common hornbeam. Remains of many animals found in the same areas have been confirmed by molecular evidence to have been the ancestors of modern-day populations of wild boar, brown bears, gray wolves, red foxes, wildcats, European pine martens, badgers, beavers, European hares and mountain hares, as well as several species of small shrews and rodents, and some snail species.

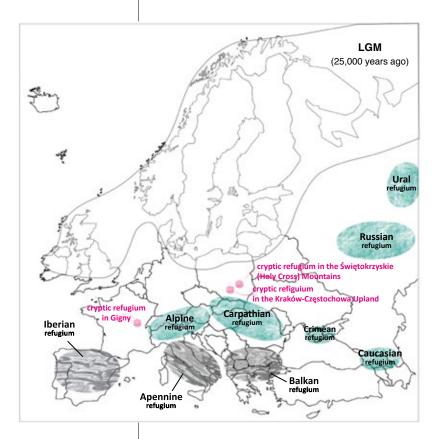
In addition to the Carpathian refugium, which covered a large geographical area, there was also a smaller Alpine refugium in the center of Europe. A number of other refugia scattered in the east across Eurasia (in places such as the Crimea, the Caucasus Mountains, the Ural Mountains, the East European Plain and Siberia) played a similar role, possibly triggering postglacial colonization of various zones in Europe, including areas in the south of the continent.

All those findings paint a complicated picture of postglacial expansion, made even more complex in recent years by the abundance of paleozoological fossil evidence that points to potential smaller refugia locat-



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Distribution of glacial refugia during the period of Last Glacial Maximum. The southern (Mediterranean) refugia are marked in grey. The northern and eastern refugia are marked in green. The northern cryptic refugia are marked in pink (Jancewicz and Falkowska 2017, modified).

Further reading:

Futuyma & Kirkpatrick (2017) *Evolution*. 4th ed. Oxford University Press.

Jancewicz E., Falkowska E. (2017). Refugia lodowcowe w Europie: co wiemy o historii współczesnych gatunków roślin i zwierząt [Glacial Refugia in Europe: What We Know about the History of Modern Species of Plants and Animals]. *Sylwan*, 161 (12), 982—990. ed even further up north than the better known and documented ones discussed here. Such localities, called "microrefugia" or "northern cryptic refugia" in the literature, could form anywhere with a suitable set of environmental and climatic conditions for survival, and some were actually very close to the ice sheet. Those areas may have played a much bigger role in postglacial recolonization than the large Mediterranean refugia. They may have served as starting points for the expansion of small local populations of cold-loving species that survived the glaciation period and spread to create new populations, speeding up the colonization of areas now free of the retreating ice sheet.

## The economy of survival

Local species radiating from the small refugia would have been far more successful than species coming over long distances from the southern areas. That would have conferred an ecological advantage on boreal (cold-loving) species well adapted for living in very low temperatures. The climate during the Last Glacial Maximum in areas closer to the ice sheet would have been similar to that found in modern day Siberia or Yakutia, with harsh winters, low average temperatures and scant precipitation. The dominant biome included different types of tundra, mostly consisting of forest-tundra zones. In the summer, trapped water from melting permafrost created wetlands, leading to

the emergence of a mosaic of different environments including local ecological islands, with conditions of varying suitability for the subsistence of species. Only a small number of species with specific ecological adaptations would have been able to survive in those conditions.

The same applied to areas north of the 50th parallel, including areas in modern-day central and southern Poland located close to the perimeter of the ice sheet (which covered what is now northern Poland during the LGM). A small cryptic refugium for many modern-day mammalian species existed in the area during the last glacial period. Remains of several species of small vertebrates dating back to the last glacial period have been found in the Kraków-Częstochowa Upland and in the Świętokrzyskie Mountains, including those of root voles, small rodents similar to hamsters now living in different environments.

Genetic research on modern populations of root voles in eastern Poland has shown that voles from populations found in different geographical areas are to a degree genetically distinct. Some populations (including all populations in eastern Poland and some in north-eastern Poland) share ancestry with voles from isolated populations in Slovakia, Hungary and Holland, and probably stem from a shared ancestral population that had lived in the Carpathian refugium - as opposed to vole populations found in southern Poland (in the San Valley, and in the valley and basin of the River Tanew). By contrast, ancestors of voles found in the south of Poland (and of some voles from the region of Polesie and the valleys of the Nurzec and Narewka rivers) survived the most recent glaciation in small cryptic refugia located in the Kraków-Częstochowa Upland and in the Świętokrzyskie Mountains, which later became the base for their expansion northward. The harsh conditions kept the population small, and the genetic consequences are still observable in the modern vole populations.

Remains of root voles dating back to the last glacial period have also been found in cave sediments at Gigny near the French Alps (N 46°25'). However, the refugia located in southern Poland (in the Świętokrzyskie Mountains and the Kraków-Częstochowa Upland) were much closer to the margins of the ice sheet during the Last Glacial Maximum. To date, those two refugia are the only attested ones located this far north that provide molecular evidence of having sheltered mammalian populations whose descendants survive today.

Based on molecular evidence from multiple species, researchers now postulate that species with a lot of genetic variability may have a history of surviving the past glaciation in microrefugia or small northern cryptic refugia.

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