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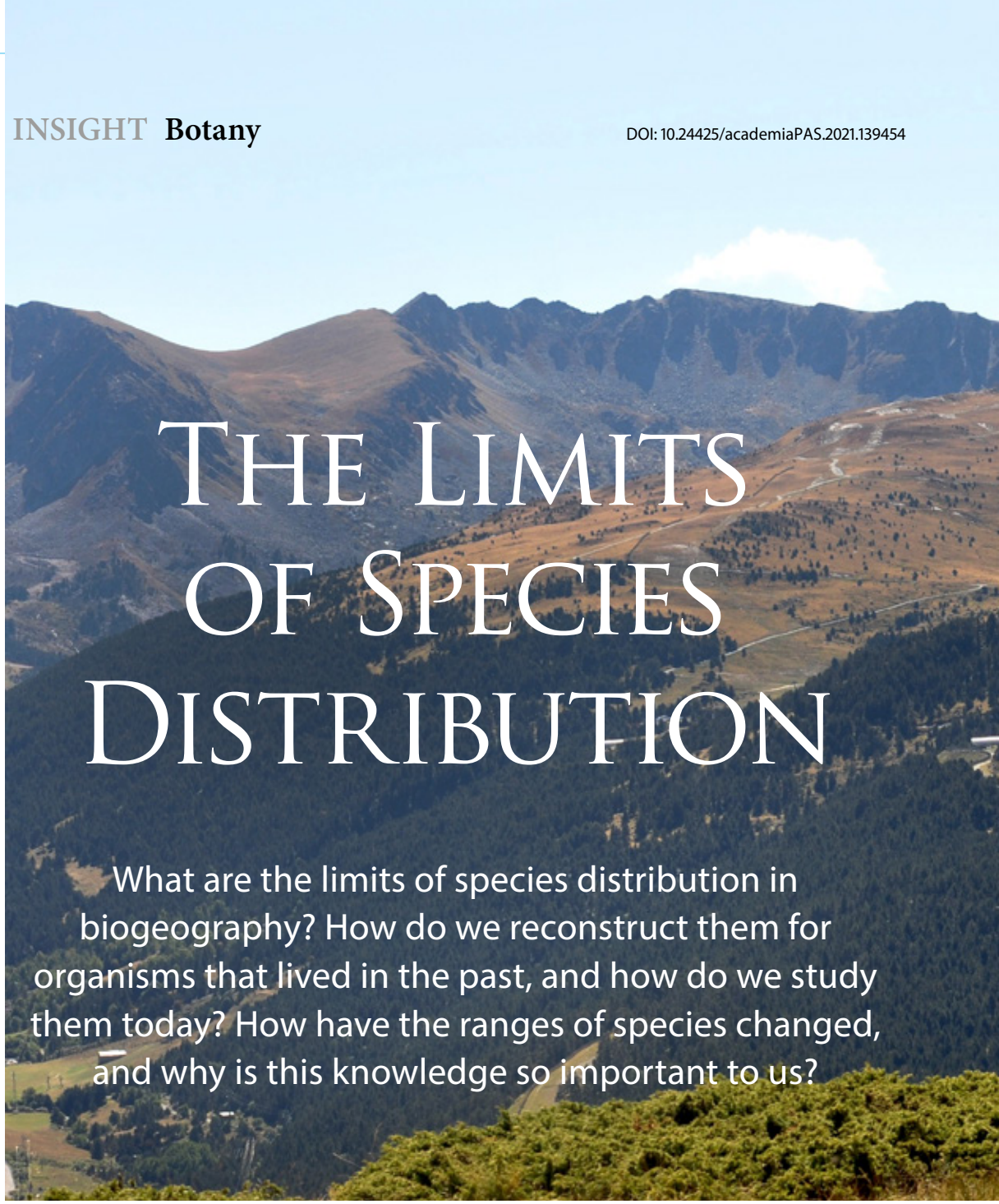

The Limits of Species Distribution

What are the limits of species distribution in biogeography? How do we reconstruct them for organisms that lived in the past, and how do we study them today? How have the ranges of species changed, and why is this knowledge so important to us?

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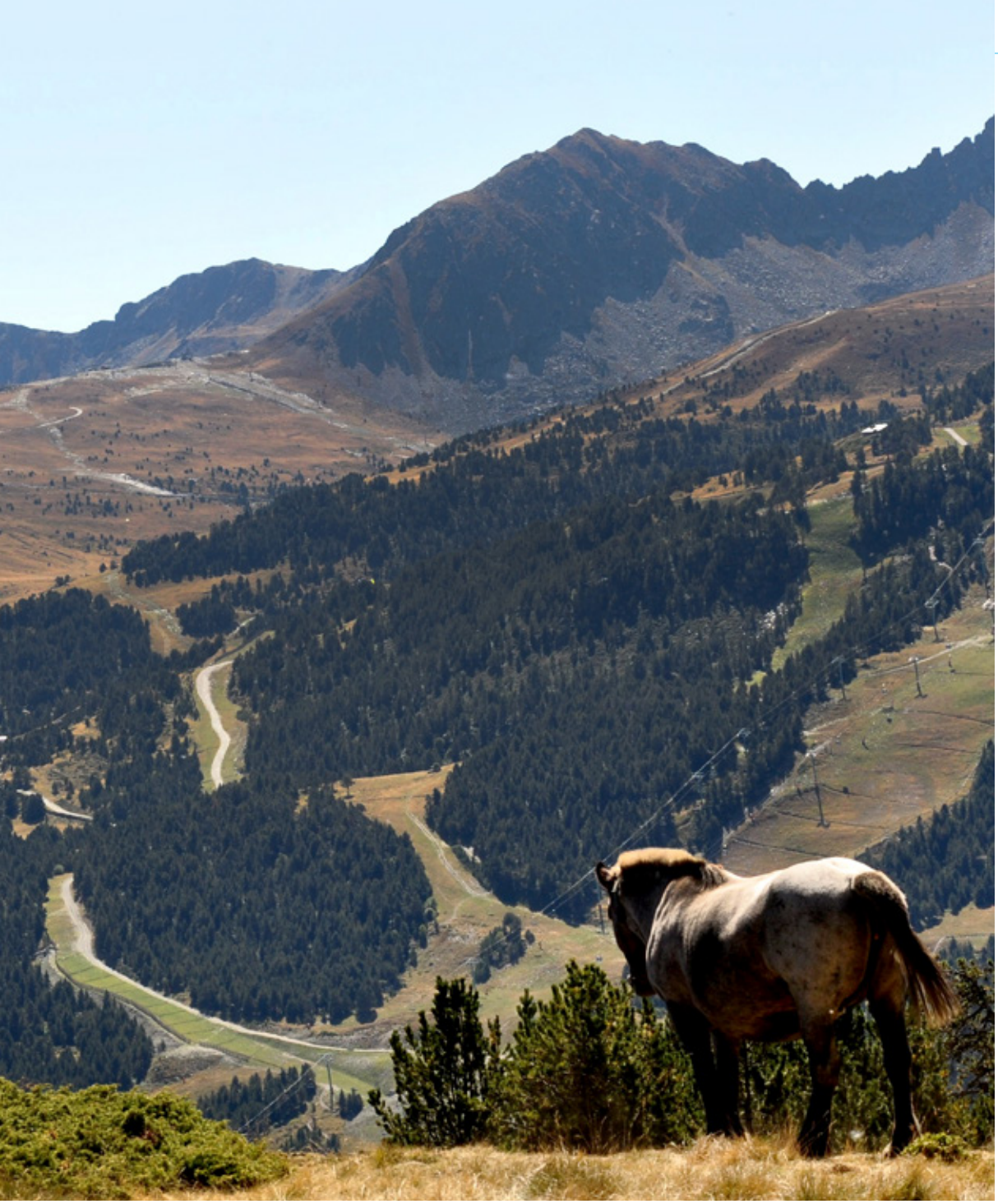
The concept of a "limit" (referred to as *limes* in Latin) is frequently used in biology. Among a wide variety of research aspects, the term "limit" is particularly central to biogeography, which studies spatial and spatiotemporal phenomena at various levels, ranging from the genetic scale, through the taxonomic (across the entire hierarchy of taxa – from species to genera, families, orders, and so on) and phytocoenotic (concerning plant communities) levels, all the way to the landscape scale. Local plant landscapes at higher levels of organization are expressed in regionally hierarchical plant formations that form the biomes of the entire Earth. All the categories of the organization of life on Earth occur or have occurred across specific time intervals and spatial zones, meaning that they have or have had specific geographic ranges and consequently range limits. The limits on the distribution of all categories of life and forms of its organization are not permanent in nature, but are subject to constant change, although it is generally rarely noticeable during the lifetime of one generation of researchers.

Geographical phenomena are most fully depicted in the form of maps of geographical ranges of taxa or hierarchical phytosociological units (from plant communities to higher-level units: plant landscapes,



The upper forest limit formed by the *Pinus uncinata* forest, Pyrenees, the slopes of the Incles Valley (2010)

plant formations, and biomes). So far, the most comprehensive discussion of these issues in Poland can be found in Prof. Janusz B. Faliński's book *Kartografia geobotaniczna* [Geobotanical Cartography]. In Europe, Salvador Rivas-Martínez et al.'s *Bioclimatic Map of Europe* is particularly noteworthy. Most of the types of maps presented there also make use of the concept of the limits of distribution or ranges.

Historically, the earliest studies defining the areas of distribution of specific taxa were the works of ancient philosophers discussing plants, such as *Enquiry into Plants* by Theophrastus of Eresos, or later works, especially *Natural Histo*ry by Pliny the Elder. In these works, the geographic aspect is reduced to the identification of places where particular plants could be found in the world as it was known to the authors (the concept of species was not known at the time). This way of defining geographical ranges was retained for a very long time. In Poland, for example, the ranges of basic tree species were discussed (for example in Michał Szubert's 1827 *Opisanie drzew i krzewów leśnych Królestwa Polskiego* [Description of the Forest Trees and Shrubs of the Kingdom of Poland] and in the same author's subsequent study published in the first volumes of the Polish journal *Sylwan*. It was not until the nineteenth century that geographic phenomena related to living organisms began to be depicted on a larger scale in the form of maps, but it was the twentieth century that saw the development of the field. In other words, every species (also higher-level taxonomic units, namely genera, families, and orders), every formation, or every biome in nature is found in specific areas that have their own boundaries. In this view, we speak of the

Photo 1
Upper forest limit formed by *Cupressus sempervirens*, Lefka Ori, Crete (2009)

Photo 2
The upper limit of the distribution of *Pinus mugo*, Kamnik Alps, Slovenia (2008)

Photo 3
The upper limit of the distribution of *Pinus mugo*, Chochołowska Valley, Tatra Mountains (2011)

limits of the distribution of species or the limits of the geographical ranges of taxa, plant formations, and so on.

Until about the mid-twentieth century, geographical ranges were presented on maps using a line following along the extreme ends of the locality of each species. Areas of species distribution presented in this way, initially highly simplified due to the relative scarcity of data, were subsequently corrected and supplemented. Nowadays, maps of the distribution of living organisms are usually published in the form of cartograms with the use of a grid of squares. The length of their sides depends on the presented area, based on a geographical grid or a grid prepared specifically for the needs of the publication. Examples of such works include *Atlas Florae Europaeae*, published in Helsinki. In Poland, publications in this form include *Atlas rozmieszczenia roślin naczyniowych w Polsce* [Distribution Atlas of Vascular Plants in Poland], together with a supplement, edited by Prof. Adam Zając and Prof. Maria Zając.

The first range limits presented in the form of maps were primarily of economic importance, as they determined the expected areas of distribution of specific species (in the sense of goods to be exploited). Attempts were made to attribute those limits to environmental conditions, most often the climate and habitat-related ones. Thermal conditions determine the course of the most visible range limits found in nature, namely the upper limit of the forests in the mountains. Likewise, these can be easily used to explain the upper and lower limits of the distribution of particular species, especially plants. In the mountains, however, the vertical range limits for living organisms tend to blur, and we should rather talk about the upper forest limit as a zone wherein the individuals of the tree species forming it become lower and lower, forming increasingly dispersed clusters, until they are found in the form of single, shrubby specimens. Other range limits found in nature are even less clear-cut.

While modern geographic ranges are determined based on the documented distribution of specific organisms or plant associations or formations, attempts to reconstruct the boundaries of their ranges in the geologic past can only be based on an inherently much smaller amount of paleontological data and are consequently a lot more general in nature. One method characteristic of plants is the method of isopollen maps, first used by Prof. Władysław Szafer. When refined and significantly enriched in terms of the number of the pollen profiles being analyzed, such maps make it possible to follow changes in the likely limits of the distribution of species over time based on the share of their pollen deposited in Holocene sediments. For Poland, such maps were recently constructed by a team led by Magdalena Ralska-Jasiewicz, and even earlier maps, from the Eemian period, were developed by a team led by Mirosława Kupryjanowicz.

The range limits of plant species changed repeatedly, first during the Pliocene cooling (around 5,332,000–2,580,000 years ago), and then as a result of cyclical climate changes in the Pleistocene (from 2,580,000 years ago to the present). In Europe, many plant species reduced their ranges during the cooling

GLOSSARY

Plant formation – a unit of the classification of plants based on their physiognomy, such as a forest, a steppe, and a tundra. It can be approached taxonomically (in other words, in terms of species composition). In such situations, we speak of the **flora** of a specific region. In can also be described in phytocoenotical terms, or in terms of the occurrence of repeated combinations of species, forming plant communities – in such situations, we speak of **vegetation**. Plant formations of the same type have different species composition in different regions of the world and form plant communities specific to the region.

Biome – a spatial unit of the Earth with similar climate characteristics and access to solar energy, which results in (roughly) equal conditions for the assimilation of carbon dioxide by plants and the decomposition of dead organic matter. This leads to a similar amount of primary production within the biome. The plants within a biome have a specific physiognomy, although the species composition varies depending on the geographical region. Similarly, the animals found within the same biome may be different on different continents.

Pollen profile – the percentage composition of pollen species found in a vertical section cut through sedimentary rocks of various geological ages. Most commonly, these are peat or lake bottom sediments from the most recent postglacial period – the Holocene (roughly the past 10,000 years), but some of them may be older and come, for example, from the Eemian period (the previous interglacial period, lasting from 125,000 to 75,000 years ago). A pollen profile is presented graphically in a **pollen diagram**, which shows the percentage shares of the pollen of many plant species (or genera), most commonly trees. Numerous pollen profiles from the area of Europe or Poland make it possible to create maps showing lines that connect points with similar percentage shares of the pollen of a given species in different periods, which are called **isopollen maps**. They illustrate changes in likely species range limits in space and time in an optimal manner.

of climate, finding refuge on the southern edges of the continent. From there, they migrated north during the following warmings, which is very well illustrated using the example of the isopollen maps mentioned earlier. As a result of those migrations, tree populations found at the southern, rear occurrence edge in Europe have higher levels of genetic variation than those found at the northern edge. Moreover, many plant species did not reattain the potential climatic limit of their distribution in the Holocene, and their existing ecological niches are often a lot smaller than the potential climatic ecological niches.

The ongoing warming of the climate may – and certainly will – result in consecutive adjustments of the ranges of living organisms, which may reduce or extend their areas of distribution, not only potential but also actual ones, despite the growing degree of urbanization. Perhaps this is the perspective from which we should consider the sometimes-rapid expansion of geographic ranges by expansive species or the encroachment of rare and protected species on anthropogenic habitats. However, these are different issues that will require special study.

PHOTOS BY **ADAM BORATYŃSKI**

Photo 4
The upper forest limit formed by Picea abies and the lower limit of *Pinus mugo* on the south-eastern slopes above the Kocioł Łomniczki glacial cirque, Karkonosze Mountains (2008)

Photo 5
The upper forest limit formed by *Pinus heldreichii*, Olympus slopes, Greece (2010)

Photo 6
The transition of the *Pinus uncinata* forest into the subalpine zone, Pyrenees, Andorra (2007)

Photo 7
The transition of the *Abies cilicica – Cedrus libani* forest into a forestless area above the upper forest limit, Taurus Mountains, Turkey (2005)