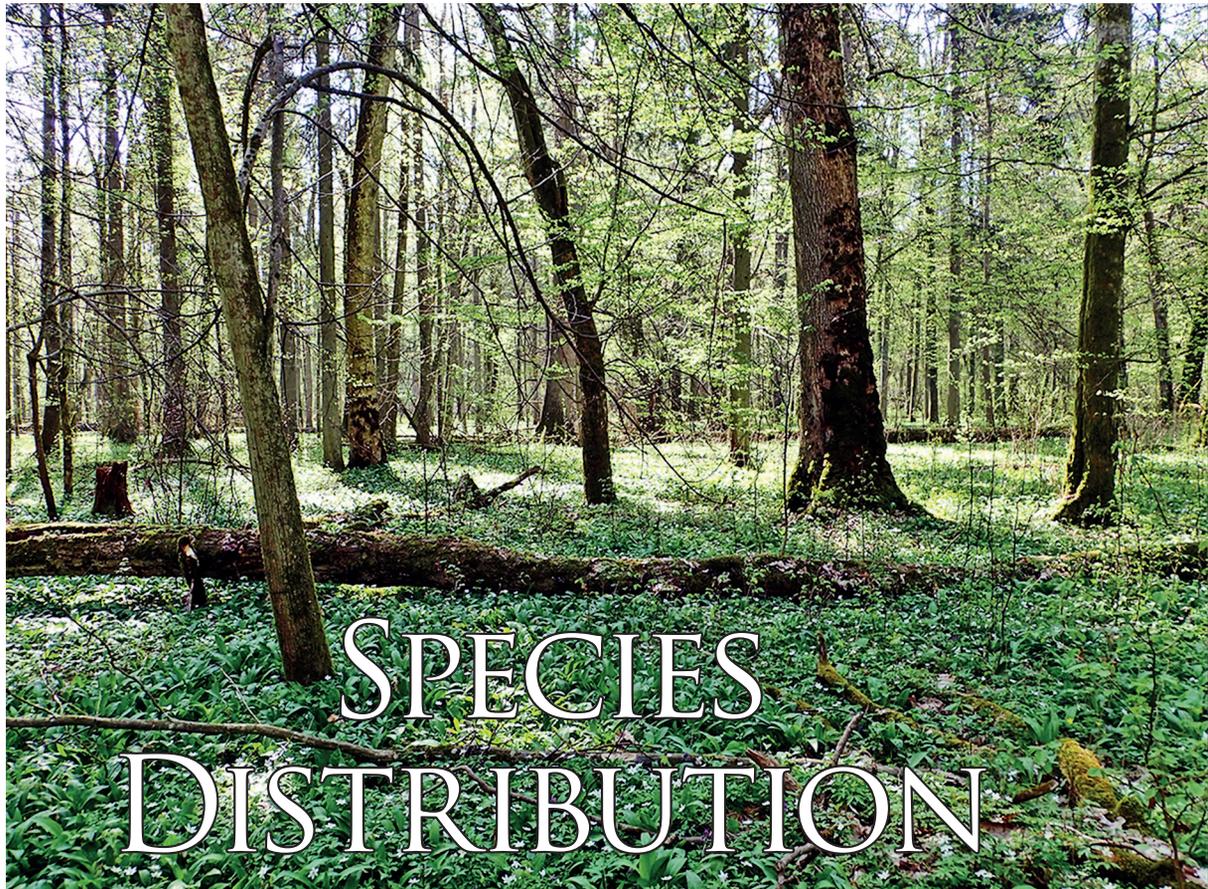




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How can we best describe the living space of given species? Are geographical criteria sufficient, or do we need more dimensions to specify an ecological niche? What can we learn from such analyses?

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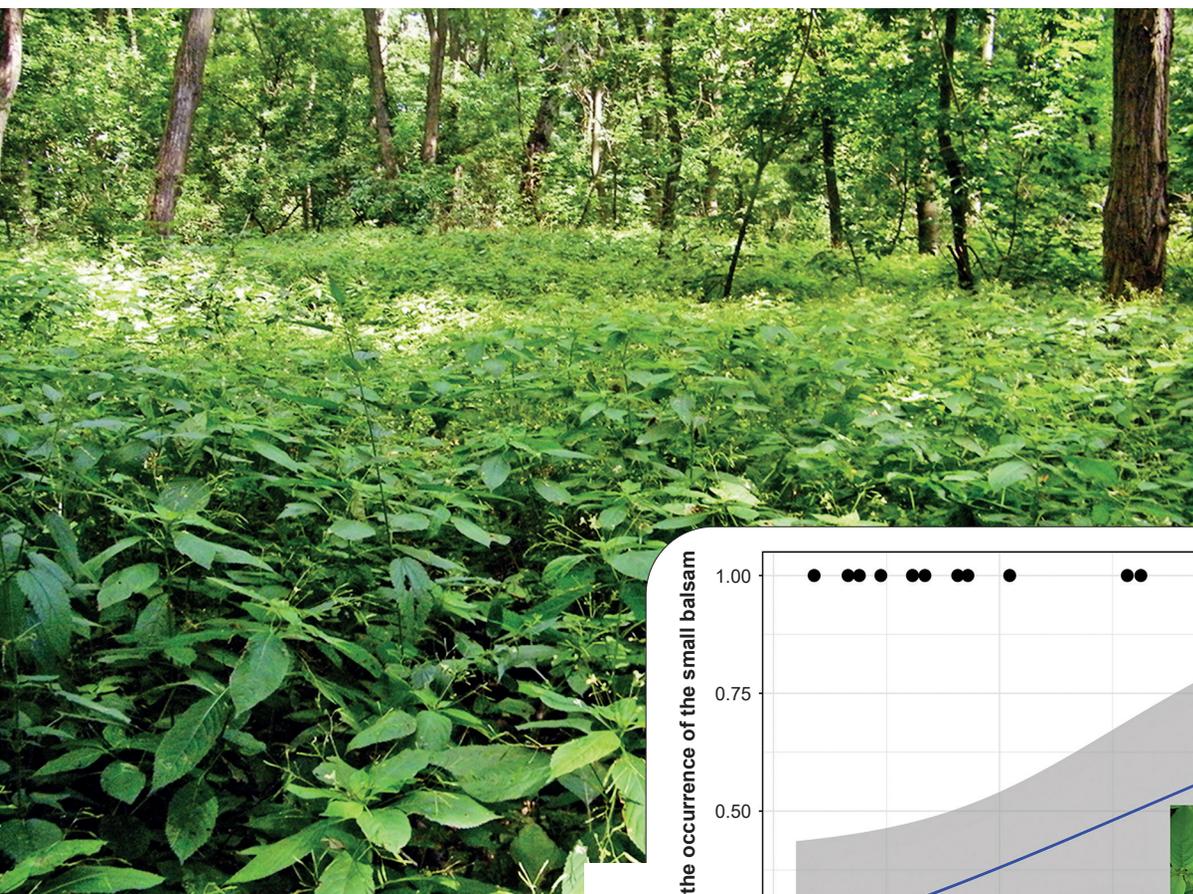
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Animals, including humans, have always intuitively identified places where they may encounter representatives of particular species that interest them. No matter whether they were looking for edible fruits or for shelter from predators, knowledge of the conditions conducive to the presence of the appropriate species was an essential part of the art of survival. As humans transitioned from a nomadic to a settled lifestyle, these skills allowed them not only to find sources of food, but also to successfully culti-

vate plants. Such knowledge, passed down from generation to generation, allowed farmers, hunters, and gatherers to draw conclusions as to the factors that the occurrence of living organisms depends on. This intuitive understanding of nature continues to allow us to choose good berry-picking spots in the forest or the ideal temperature for getting yeast dough to rise.

The minimum

Knowledge about the distribution of organisms slowly came to be accumulated in the scientific field of ecology. When studying the use of fertilizers in crop production, Carl Sprengel discovered that plant growth is limited by the one particular nutrient that is present in the soil in the least-sufficient quantity, even with an abundance of all other nutrients. This rule, published in 1841 by Justus von Liebig, became known as

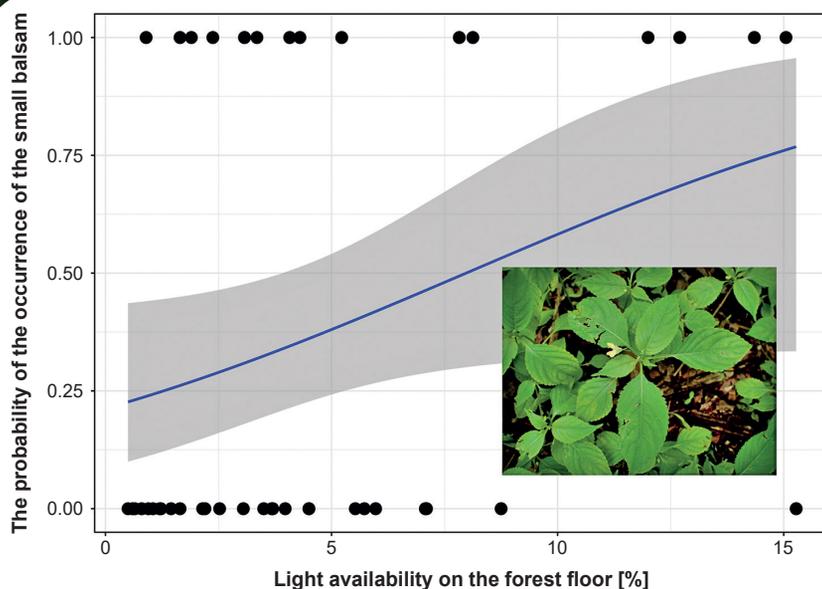


MARCIN K. DYDEBSKI (2)

The spring and summer aspect of the undergrowth in an oak-hornbeam forest – an example of the separation of ecological niches increasing forest biodiversity

“Liebig’s law of the minimum,” and the factor whose short supply limits the growth of organisms was called a “limiting factor.” Examples include the scarcity of heat, light, or nitrogen in the soil as well as repetitive disruptions, such as plowing, river flooding, and fires. For this reason, species typical of later stages of succession will not appear in places subject to frequent disruptions.

Advances in research into the ecology of individual organisms showed that not only the scarcity of a specific factor, but also an excess of it can be detrimental to species. In 1911, Victor Ernest Shelford found that for each species, it was possible to identify certain minimum, maximum, and optimum factors, as a set of conditions determining its occurrence. For example, both too high and too low temperatures reduce photosynthetic efficiency of plants, thus determining the range of a given species. Similarly, too little salt in seawater limits the ability of saltwater fish to live in lakes. The space between the minimum and the maximum is therefore called an “ecological niche” with respect to a specific factor. In other words, a given species will not be found in places where certain factors fall below or above specific values. Obviously, the scale of tolerance of different factors will vary depending on the species. For example, the Scots pine is tolerant of considerable soil moisture, whereas the Norway

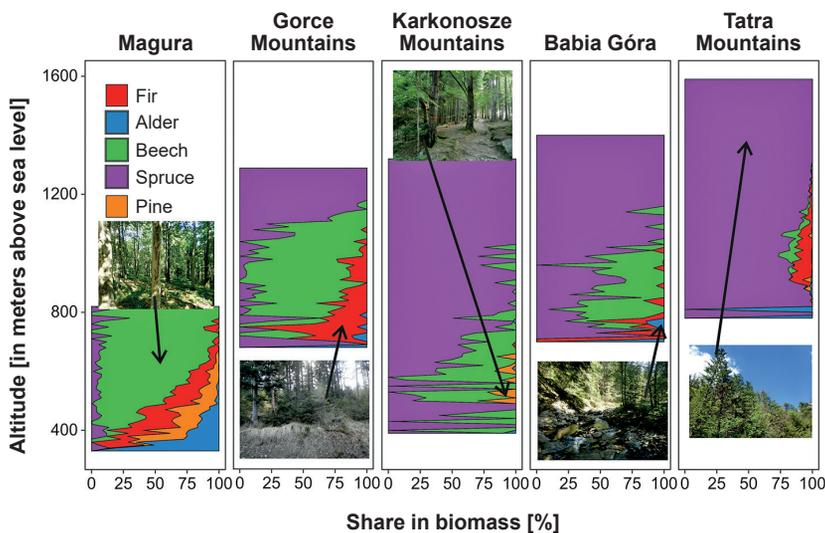


spruce is tolerant of higher moisture. At the same time, the pine requires more light, while the spruce can grow in semi-shade.

Various aspects

More generally, the ecological requirements of many species can be described as a large set of variables of this kind. Factors important for plant growth include the availability of water, nitrogen, and light, as well as air temperature, which regulates the rate of photosynthesis, and the soil pH, which regulates the uptake of nutrients. Other significant factors include interactions with other organisms: competition for resources, support received through symbiotic relationships, the presence of pathogens and predators. These factors determine how likely we are to find a particular species living in a given location. Based on differences in niche width, we can distinguish groups of vegetation

An analysis of the ecological niche of the small balsam – the probability of the occurrence of the species grows with the availability of light on the forest floor



frost and the scarcity of nutrients in the soil can gain an edge over their more vulnerable competitors. This means that such species are driven into separate ecological niches. Also, species with different ecological niches can co-occur in a single patch of vegetation: the wood sorrel *Oxalis acetosella*, which thrives in shade and has shallow roots, can grow in the heavy shade cast by the canopy of a beech forest. Other examples include alder carrs, where some plants are found on drier tufts and others in wetter depressions. Species that require different levels of moisture do not compete with each other, creating systems characterized by a high level of functional diversity. On the other hand, in meadows of *Molinia* moor grasses (partially cultivated, mowed irregularly once a year or even less often), their main component is more likely to be found in places with a high diversity of the ecological niches of the co-occurring species, whereas the common hedgenettle *Betonica officinalis* prefers places characterized by a lower level of diversity.

Vertical distribution of trees in five mountain national parks in Poland illustrates the spatial separation of ecological niches

characterized by species with a narrow range of requirements. Vegetation is usually formed by a group of species highly tolerant of environmental factors that may be found in a wide range of ecosystems, enriched by species typical of a particular system. We can therefore observe how plants form groups along major gradients of change in species composition. For example, a detrended correspondence analysis (DCA) performed for various forest types shows a smooth transition from coniferous forests through acidophilous oak forests to oak-hornbeam forests. The left part of the graph groups the positions of species typical of poor habitats, the central part shows forest species with a wide ecological scale, and the right part shows species typical of deciduous forests growing on fertile soils.

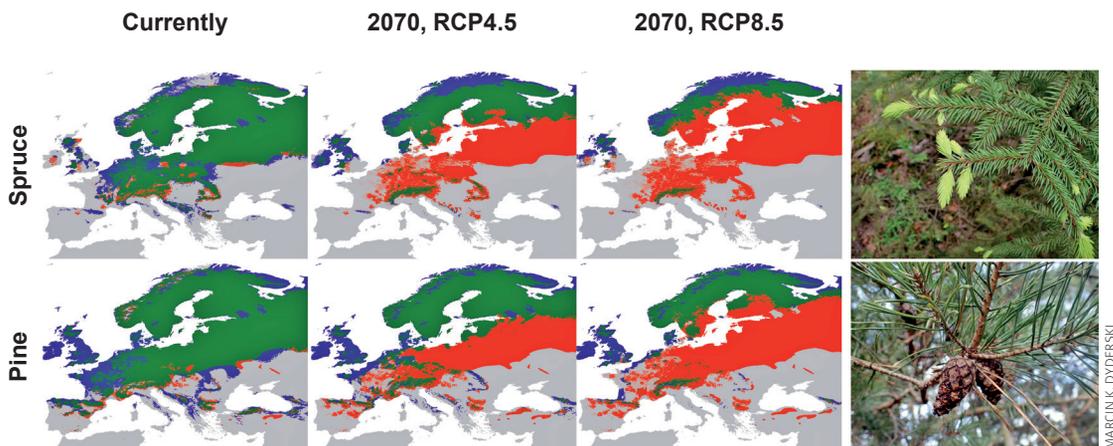
Modern ecological studies analyze multiple factors of this type, which determine the distribution of species that interest us. This multidimensional approach explains, for instance, the presence of altitudinal zones of vegetation in the mountains. At lower elevations, there is considerable competition for light. At higher elevations, however, species with higher tolerance of

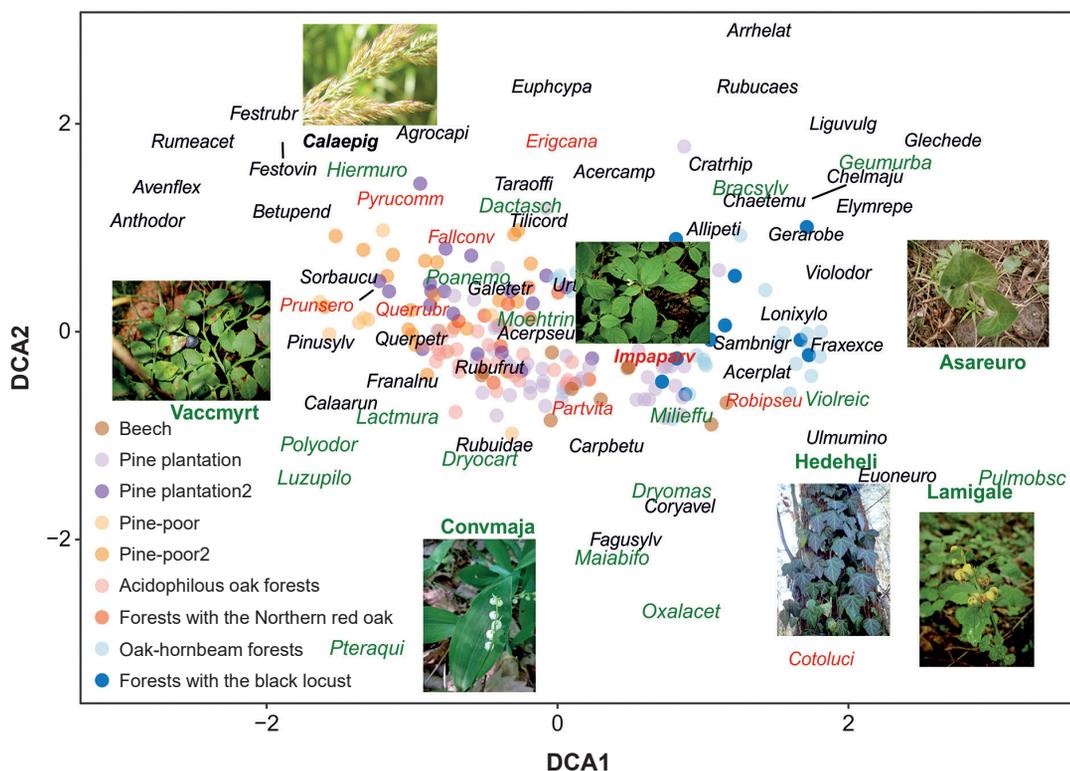
Niche diversity may also be linked to the seasonal dynamics of vegetation: spring-flowering plants of the genera *Anemones*, *Corydalis*, and *Hepatica* may appear before trees develop leaves and significantly reduce the amount of light reaching the forest floor.

The potential

The simplest way to determine ecological niches involves using species distribution models. They allow us to estimate the range of minimum, optimum, and maximum climate factors affecting the distribution of species. The simplest ones are called “climate envelope models” and assume a 95% range of variables (such as temperature and precipitation) in which a specific species occurs. Other approaches include generalized linear models and machine learning techniques. A model allows us to determine the conditions in which a given species could occur, as well as the probability of finding a species living in the optimum of its niche at a given point on the map.

An example of the use of climate niche modeling to predict threats related to climate change. The map shows the climate optimum area (green), the expected range expansion (blue), and the expected loss of the climate optimum (red). Scenarios being considered: RCP4.5 is the moderate scenario (a temperature increase of 1.0–2.6°C), and RCP8.5 is the pessimistic scenario (an increase of 2.6–4.8°C)





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A multidimensional analysis of the ecological niches of understory species in the Wielkopolski National Park. In this reduced ordination space (DCA – detrended correspondence analysis), the points represent the positions of the study plots, and the species name labels represent their relationships to the plots and other species.

The colors of the labels: green – forest species, red – alien species, black – other species. The labels of the species visualized in the photographs are in bold

Observations of the geographic ranges of species and their climate niches allow us to conclude that species do not occupy the entirety of the area that favors them. A 2004 study by Svenning & Skov showed that, on average, European tree species fill 38% of their climatically determined potential ranges. This means that their realized niche (the one they currently occupy) is smaller than their potential niche. For many plant species, the rate of migration from glacial refugia did not allow them to fully inhabit their ecological niche. For slowly migrating trees, therefore, it is crucially important that they can be spread by other organisms, such as birds and rodents. For example, the Eurasian jay is an important partner for oak trees – the bird picks up acorns and hides them even several hundred meters away from the source of the seeds. Another problem may be posed by the lack of mycorrhizal fungi or pollinating insects. For this reason, predictions made about changes in species distribution have to take these limitations into account.

The future

By determining the ecological niches of individual species, we can attempt to predict how they will be affected by changing conditions. Most soil conditions are determined by climate conditions. For this reason, in the broader spatial context (e.g. continental), we can assume that climate conditions are the main factor affecting the distribution of species. Climate studies allow us to use species distribution models and maps

of future climate conditions to predict changes in the potential climatic niches of specific species. This approach will first of all allow us to estimate if a given species stands a chance of surviving in the place of its occurrence in a specific climate change scenario. Consequently, we can estimate the degree of the threat faced by Europe's forests and adjust forest management to the changing conditions. We can also predict how far invasive species, especially those that cause ecological and economic damage, will be able to migrate. In this way, risk analyses can take into account the changing climate and facilitate better adjustments of conservation management. When making predictions, however, we should take into account the fact that the loss of the optimum for an invasive species (such as the giant hogweed) in Central Europe means that the climate conditions will not be favorable not only to that particular species but to many other species as well.

Projects carried out in recent years using species distribution models show that climate change will significantly alter the range of the climate optimum for many species. In the case of forest trees, the predicted changes will push the main forest-forming coniferous species in Central Europe outside their ecological optimum. Their retreat will significantly alter the functioning of forest ecosystems, as well as the possibility of their use in forest management. Also, many tree-dependent species will also have to retreat north to find favorable habitats. The forests as we know them will therefore undergo significant changes, depending on the extent of climate change. ■

Further reading:

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