STUDIA ECOLOGIAE ᴱᵀ BIOETHICAE

Biodiversity Gradients: Is Diversity Greater in the Tropics?

Gradienty bioróżnorodności – czy różnorodność jest większa w strefie tropikalnej?

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Abstract: This paper examines hypotheses explaining greater biodiversity in the tropics compared to regions located at higher latitudes. The results of studies of the biodiversity of different groups of organisms along latitudinal transects are presented to demonstrate the existence of latitudinal gradients of biodiversity. Hypotheses explaining the existence of regular gradients of biodiversity, i.e. such cha nges in biodiversity when it increases with approaching the equator: uneven distribution of the sizes of the tropics and temperate zones, the so-called middle domain effect, uneven latitudinal distribution of energy reaching the Earth's surface and other evolutionary and ecological hypotheses. Moreover, explanations for reverse gradients of biodiversity are discussed. Attention is drawn to the different nature of the conditions for these explanations and to the rather large gaps in data that could be useful to resolve these issues.

Keywords: biodiversity, latitudinal gradients of biodiversity, tropics, temperate zones, climate, species, ecosystems

Streszczenie: W artykule tym omówiono hipotezy wyjaśniające powody większej różnorodności biologicznej w tropikach w porównaniu z regionami położonymi na wyższych szerokościach geograficznych. Przedstawiono wyniki badań różnorodności biologicznej różnych grup organizmów wzdłuż południkowych transektów, aby wykazać istnienie południkowych gradientów różnorodności biologicznej. Omówiono hipotezy wyjaśniające istnienie normalnych gradientów różnorodności biologicznej, to jest takich zmian różnorodności biologicznej, gdy wzrasta ona w miarę zbliżania się do równika: nierówny podział wielkości obszarów tropików i stref umiarkowanych, tak zwany efekt środkowej domeny, nierówny południkowy rozkład energii docierającej do powierzchni Ziemi i inne ewolucyjno- ekologiczne hipotezy. Przedstawiono także wyjaśnienia odwróconych gradientów różnorodności biologicznej. Zwrócono uwagę na różny charakter natury tych wyjaśnień i na dość duże luki w danych, które mogłyby być przydatne do rozwiązania tych problemów.

Słowa kluczowe: różnorodność biologiczna, południkowe gradienty różnorodności biologicznej, tropiki, strefy umiarkowane, klimat, gatunki, ekosystemy

Introduction

Perhaps no other aspect of biodiversity has intrigued ecologists as much as the increasing biodiversity on the journey from the poles to the tropics. This phenomenon, described as the latitudinal gradient of diversity, has become the focal point of many considerations and studies. However, finding a possible cause of this phenomenon is a considerable challenge due to the growing number of hypotheses, their interconnections, and the difficulty of unequivocally undermining them.

The species richness of the tropics fascinated the first European naturalists who visited these regions in the 19th century. We can find traces of this in the writings left by Charles Darwin and Alexander von Humboldt, although, it can be assumed that the opinions of these first researchers were largely influenced by their fascination with the diversity of the nature of the tropics. Later preliminary observations indicated that biodiversity increases with decreasing latitude. However, there are certain groups of organisms that show the opposite trend: a decrease in species diversity towards the tropics. These other trends have been almost ignored in ecological and evolutionary literature. Identifying the reasons for this difference is also not easy.

Biodiversity studies at the level of entire ecosystems are difficult because they require the joint effort of many specialists. Therefore, it seems that such extensive information is not found in the literature on the subject. Usually, biodiversity studies concern only selected groups of organisms and cover areas that are more or less spatially limited.

There are two ways of testing hypotheses about greater biodiversity in the tropics. Comparisons of biodiversity can be made for regions of the Earth that are very differently located, but large enough for their parts located at different distances from the equator to be different, for example, in terms of climate. In such cases, biodiversity is analysed at selected points fairly freely scattered over the surface of the studied region.

However, such studies can be conducted in a more systematic way. The difference lies in a different way of selecting points on the world map at which diversity will be analysed. If the points at which biodiversity will be considered are located along the latitudinal lines from the North Pole to the equator and from the South Pole to the equator, then we can talk about searching for latitudinal gradients of biodiversity and formulate hypotheses assuming for example, that with decreasing latitude we will observe an increase in biodiversity. The results of biodiversity analyses conducted according to these two methods will be presented in this paper, although more emphasis will be placed on the analysis of biodiversity gradients, and the second of the presented research methods, i.e. the analysis of biodiversity on the scale of selected regions, will serve as a background for the analysis of its gradients.

It is interesting that the problem of diversity gradients can be viewed from a variety of perspectives, not only from the biological one. There are studies showing that the diversity of cultures of human societies decreases as we move away from the equator (Collard and Foley 2002). However, it is not known whether in this case there is a connection with the postulated greater biological diversity of the tropics.

When writing this paper, the authors referred to the extremely helpful chapter titled "Why are the tropics so diverse?," which can be found in the book by Thomas Sherratt as well as to David Wilkinson's text titled "Big questions in ecology and evolution" (Sherratt and Wilkinson 2009), monographs: "Species diversity in space and time" by Michael L. Rosenzweig (Rosenzweig 1995), "Community ecology" by Peter J. Morin (Morin 1999) and "Scaling biodiversity" edited by David Storch, Pablo Marquet and James Brown (Storch et al. 2007).

2. Examples of Greater Tropical Biodiversity – Regular Diversity Gradients

In forests covering almost two million square kilometers in Thailand, Malaysia, the Philippines, Indonesia, and Indochina, there are about 35,000 species of flowering plants (Prance 1977). In one hectare of rainforest on the Atlantic coast of Bahia, Brazil, there are 450 species of trees (Thomas and Carvalho 1993). The plant diversity on one island off the coast of Puerto Rico, covered with relatively poor rainforest, consists of 214 species, whereas in the same area in the Cape Province in South Africa, there are only 138 species, and a similar number exist in the State of Victoria in southeastern Australia (Richards 1969). Proctor et al. (1983) studied the diversity of rainforests located in the immediate vicinity of the equator in Gunung Mulu National Park in Sarawak, Borneo, and found 223 species in one hectare of forest on alluvial soils, 214 species in a forest dominated by species from the Dipterocarpaceae family, 123 species in a heath forest, and 73 species in a forest on limestone. Oak-hornbeam forests in Poland in the same area may contain about 500 trees belonging to only a dozen or so species (Weiner 2020), and the number of tree species in the total area of the USA and Canada is 700 species (Wilson 1991).

Henderson et al. (1998) found 286 species of freshwater fish in a relatively small part of the Amazon floodplain. This is more species than in the whole of Europe, where about 215 species have been recorded (Maitland and Campbell 1992). Terborgh et al. (1990) counted the species of birds that breed in 97 ha of the floodplain forest of Amazonian Peru. There were 245 of them, and an additional 74 species were seasonal or migratory.

Rosenzweig (1995) makes a very strong case for the existence of distinct gradients in biodiversity, which indicate that the tropics are more species-rich than the temperate zones. He cites more detailed evidence from studies on a variety of plant and animal

groups: New and Old World plants (Gentry 1988), North and Central American bats (Rosenzweig 1992), North and Central American mammals (Sandlin and Rosenzweig (unpublished data)), snakes, frogs, and lizards (Arnold (1972) and Duellman (1990)), termites (Collins 1989), littoral fishes (Rhode 1992), and fossil foraminifera (Stehli et al. 1969). In all these cases, the sets are real gradients, since they span several dozen degrees of latitude. In the case of the abovementioned foraminifera, the material was from the last 70 million years, and the location of the rocks from which the samples were obtained was determined based on preserved traces of the magnetic orientation of the rocks. In angiosperms, the existence of similarly old (110 million years in this case) latitudinal diversity gradients can be found (Crane and Lidgard 1989).

Species diversity of birds with breeding grounds in Canada, the USA and Mexico increases equatorward (MacArthur and Wilson 1967). Attrill et al. (2001) compared species diversity data for invertebrates inhabiting the sediments from 20 estuaries from different regions of the world selected for similar salinity, similar sediment particle size and similar sediment sampling methods. They found a statistically significant relationship between diversity and latitude, with greater diversity at low latitudes. Gaston et al. (1995) analysed the diversity of reptile families on a global scale. The choice of the family level was dictated by the paucity of information on the diversity of this group of animals from the tropics, which are a less explored area. They showed that the highest diversity is characteristic of tropical America with a maximum in southern Mexico, and slightly smaller diversity in Nicaragua, southern Colombia, central Venezuela, and central Colombia. Similar geographic patterns of diversity are observed on different continents in the distribution of species from different groups and taxa (Tokeshi 2009; Gaston and Spicer 2004; Cox and Moore 2005). Analyses included the diversity of tree species on different

continents, freshwater fish in the world's rivers, marine bivalves, termites, and primates.

3. Examples of Reverse Diversity Gradients

There are quite numerous and clearly visible exceptions to the above-mentioned tendency (Kindlmann et al. 2007). An example of this can be those taxa whose occurrence is imited to high latitudes. Most of the 17 species of penguins can be found in the polar regions of the Southern Hemisphere (del Hoyo et al. 1992). In turn, species of albatrosses and petrels live mostly south of the Tropic of Capricorn, although some are endemic to areas north of the Tropic of Cancer (Chowne et al. 1998).

We also have results from studies conducted along latitudinal transects that show reverse patterns of diversity change. Cook (1969) found a significant decline in bird species diversity in deciduous forests of the eastern United States from New England to the southeastern United States. Valdovinos et al. (2003) studied shelf mollusks along the western coast of South America from northern Peru (10°S) to Cape Horn (55°S) in relation to shelf water temperature and surface area. The distribution of 629 species of Prosobranchia, Bivalvia, and Placophora was analysed, but only those occurring at depths of no more than 200 m. Their diversity was characterized by a clear reverse gradient, especially in the case of Prosobranchia, the most diverse group. However, the changes were not monotonous. Between 10°S and 40°S, bivalve diversity remained more or less constant at about 100 species, then increased rapidly to 300 species around Cape Horn. Statistical analysis showed that 59% of this variation was explained by the size of the shelf area.

The species diversity of aphids and the plants they use was also studied (Dixon et al. 1987). Data came from 23 countries. It turned out that aphid diversity reaches a maximum in the temperate zone and then declines in the tropics. A decline in diversity towards the tropics is also observed in one of the largest insect families,

the Ichneumonidae (Owen and Owen 1974). This is correlated with different, often opposite trends in different subfamilies (Janzen 1981; Gauld 1986). Subfamilies that are characterized by a diversity increase in the tropics are represented by generalist species with slow population growth. Subfamilies with lower diversity in the tropics mainly contain specialists characterized by the ability to grow their populations quickly. The structures of food webs of invertebrates, protozoa, and bacteria that inhabit the water-filled pitchers of the *Sarracenia purpurea* were also studied (Buckley et al. 2003). The results came from 39 natural populations of this species randomly selected from the USA. The species diversity of organisms living in the pitchers increased with latitude, and this was mainly due to an increase in the diversity of protozoa and bacteria; the diversity of invertebrates did not depend significantly on latitude. However, a significant decrease in the numbers of the top predator, the mosquito *Wyeomyia smithii*, was observed with increase of latitude.

Many other groups of organisms show their maximum diversity far from the tropics. This is also evident in soil organisms. For example, most earthworm species live in the temperate zone of the Northern Hemisphere (Phillips et al. 2019). The same phenomenon can be observed in many other soil invertebrates and their parasites (Cameron et al. 2018). Procter (1984) found that soil nematode species richness was higher in temperate zones, mainly because of the absence of predators. More detailed studies have shown that much depends on vegetation type (Boag and Yeates 1998): the highest diversity was found in temperate broadleaf forests, arable soils and grasslands in this zone, but tropical rainforests were more diverse than temperate coniferous forests, and the lowest soil nematode diversity was observed in polar regions. In contrast, in oribatid mites, there are no significant differences in diversity between the tropics and temperate zones (Maraun et al. 2007).

The problem of microbial diversity, which plays a key role in the cycling of matter in ecosystems, requires separate treatment. In the 1980s, Smith (1982) compiled information on the diversity of testate amoebas from various locations in the Antarctic and sub-Antarctic areas. It turned out that the Antarctic locations were characterized by lower diversity. Later studies, however, showed that in samples taken from islands located in the sub-Antarctic regions, the diversity of this group of organisms is comparable to the tropics (Vincke et al. 2004; 2006). Hilldebrand and Azovsky (2001) reviewed 179 studies of diatom diversity from various locations and found no dependence on latitude. On the other hand, studies of RNA in ribosomes of eukaryotic organisms from intertidal sediments of the Greenland coast have shown that this is the place with the highest diversity compared to all similar locations studied so far (Stoeck et al. 2007), which may suggest that the species diversity of this group of organisms reaches its maximum outside of the tropics. Other molecular studies, in which bacterial diversity was analysed in 98 soil samples taken from different locations in North and South America, do not indicate any dependence on latitude (Fierer and Jackson 2006). It turned out that soil pH is the only good predictor of bacterial diversity. There is no doubt, however, that the diversity of benthic foraminifera reaches its maximum in the tropics (Buzas et al. 2002).

In summary, there is currently no convincing evidence that there are any clear geographical patterns of species diversity in microorganisms – both prokaryotic and eukaryotic. However, it should be emphasized that we do not have evidence that such patterns do not exist. Sherratt and Wilkinson (2009) point out that the possible reasons for this state of affairs may be the lack of research on microbial diversity and the unsystematic way of selecting sampling sites. The results have very often been obtained based on a small number of samples collected. A separate problem

is the way of determining the species affiliation of microorganisms. If there is a lack of clearly visible morphological diagnostic characters, researchers have at their disposal increasingly used molecular methods or earlier developed methods such as growth of bacterial cultures under laboratory conditions, lipid analysis or direct microscopic observation.

It also seems that the clarity of regular latitudinal gradients of biodiversity depends on the body mass of the organisms studied – they become more visible in larger organisms (Hilldebrand 2004). Most of the organisms analysed by this author are multicellular organisms. All the microorganisms were eukaryotes originating from just three groups: foraminifera with a maximum diversity in the tropics, and diatoms and ciliates, which were not characterized by regular diversity gradients.

It is worth noting that geographic patterns of diversity may differ between the Northern and Southern Hemispheres. Along the Atlantic coast of Europe, macrophyte floras show a regular pattern of diversity changes (van den Hoek 1975), but in the Southern Hemisphere, along the western coast of South America between 10°S and 55°S, the diversity of macrophytes increases with increasing latitude (Santelices 1980). Hemispheric differences may also consist of different degrees of distinctness of gradients of the same nature. For example, New World birds and many mammalian families show a more rapid decline in diversity with distance from the equator in the Northern Hemisphere than in the Southern Hemisphere. Similarly, although in the Northern Hemisphere the diversity of marine species appears to decline with latitude, studies (although few so far) indicate that the Southern Hemisphere is characterized by a high diversity of this group of organisms even in polar regions. For example, during studies of the deep-sea fauna around the Antarctic Peninsula, 674 species of isopod crustaceans were found, 586 of which were previously unknown (Brand et al. 2007).

4. Historical Conditioning of Diversity Gradients

4.1. Different time scales

Although when searching for latitudinal gradients of biodiversity we most often consider the current presence of species at different locations along these gradients, we should not forget about the influence of history on the presence or absence of species in the place we are studying.

Therefore, when considering the geography of biodiversity, current biodiversity should be viewed in the long term. The physical conditions in which we record biodiversity only show its current form. Changes in time that have an impact on it have taken place on three scales of different lengths. On the geological time scale, there have been very significant continental migrations. Those parts of the land that are currently in the tropics could have long ago been in the polar regions of the Earth and vice versa, and additionally, could have been in a very different configuration with the neighbouring lands. We have geological and paleontological evidence for this (Dzik 2003). We also have the evolutionary and ecological time scales. Each species has a longer or shorter evolutionary history behind it. Species may differ in their susceptibility to speciation, which may be the result of their internal characteristics, but may also be the result of the conditions in which they evolved. Therefore, the number of species is the result of speciation, but also of species extinction and dispersion, which should already be considered on an ecological time scale. Because of this the fact that a species is present in a certain place does not mean that it originated there and remained in its original location; it could have evolved somewhere else and later migrated to that place. On the other hand, the absence of a species in a certain place does not necessarily mean that it was never there, because it could have been there but over time migrated to another place.

4.2. Climate changes

There is paleontological evidence to show that in Earth's geological past, the tropical region of the Northern Hemisphere extended much farther north than it does today (Beerling 2007). We are currently living in a geological ice age that followed an era of global warming, meaning that the tropical climate region has narrowed significantly in geological time. This clearly visible trend over the past few million years has contributed to the extinction of evolutionarily older groups of organisms from higher latitudes. When the results of this extinction are linked with the fact that, as paleontological data show, the average age of orders and families of many groups of organisms (for example, sponges and corals) decreases with decreasing latitude, we can conclude that there is a higher rate of speciation in tropical regions (Jablonski et al. 2006; Mittelbach et al. 2007).

The rate of speciation in the tropics could have been faster because the organisms living there had shorter life cycles and therefore more opportunities for speciation. The higher temperature increases the speed of biochemical reactions, which could have increased the rate of mutation. In the tropics, we can also observe more different types of ecological interactions between species, the number of which is very often greater (thus, these interactions can be more powerful). In this way, on the basis of the evolutionarily shaped advantage of biological diversity in the tropics in specific geological conditions, we will observe its further increase in this region, supported and reinforced by ecological factors and processes.

In tropical regions, isolated refuges can also form, preserving the diversity of tropical fauna and flora during ice ages even when diversity around them is reduced by falling temperatures. The geographic isolation of refuges favoured increased allopatric speciation in tropical regions when biodiversity had completely disappeared at higher latitudes during ice ages (Haffer 1969).

Gaston and Blackburn (1996) have drawn attention to the possibility of a dual view of the tropics. They can be seen as a "cradle" where species originate, or as a "museum" where species accumulate (Stebbins 1974). To choose between these two points of view, one must answer the question whether the higher biodiversity in the tropics is due to a higher rate of speciation or a low rate of species extinction? The aforementioned authors compared the average age of avifauna in different latitudes using DNA analysis. They found that for birds, equatorial areas are more of a "museum" than a "cradle." The average age of taxa is the highest in the tropics and decreases towards both poles (particularly rapidly in the Northern Hemisphere). It can therefore be assumed that the tropics are characterized by a low rate of species extinction. However, more recent studies of other groups of organisms suggest that the tropics act both as a cradle where rapid speciation occurs and as a museum where extinction rates are low (Jablonski et al. 2006; Marshall 2006).

4.3. Ecological niche conservatism

Let us assume that, for whatever reason, there is an initial asymmetry in the distribution of species along the latitudinal gradient. For example, more species started their history in the tropics because they cover a larger area, or they had more favourable conditions for speciation there, which seems very likely. As a result, relatively few species will be able to migrate to the temperate zone, for example because they lack adaptations to survive the winter. It therefore seems likely that if a species originated in the tropics, it will tend to remain there, accentuating or even reinforcing the initial asymmetry between regions (Wiens and Graham 2005).

5. Explanations of Regular Diversity Gradients

5.1. Importance of land area

The tropics appear to cover a larger area of the globe than other regions (Rosenzweig 1995). This is more evident on globes than on flat maps, because the Mercator projection used for the latter greatly distorts the proportions of the areas, making the areas around the tropics proportionally larger. The tropical regions of the Northern and Southern Hemispheres meet at the equator, which doubles the continuous area occupied by the tropics, while the temperate and polar zones of the two hemispheres remain mutually isolated. Thus, in accordance with statements known from island biogeography (MacArthur and Wilson 1963; 1967), greater species diversity can be expected in the tropics. The larger area of the tropics also allows for the maintenance of larger populations, which should protect the species living there from extinction. A larger area means that this environment may also be characterized by increased heterogeneity, and may be divided into sub-areas, each large enough to support a large population, and contain more geographic barriers, which will favour higher rates of speciation.

Opponents take a different view of the above arguments (Mittelbach et al. 2007). More species in the tropics may mean fewer individuals representing each of them, potentially increasing the threat of extinction in the long term. If species with larger ranges dominate the tropics (see below: mid-domain effect), this may mean that these species are more tolerant to different environmental conditions, making speciation less likely. It should also be remembered that the tropics are a very diverse region, with uninhabited deserts, so taking into account the total area occupied by this zone may be misleading.

5.2. Mid-domain effect

A hypothesis called the mid-domain effect in the literature assumes that the gradient of biodiversity with a maximum occurring in the tropics is the result of geometric constraints faced by species inhabiting a given area (Colwell and Lees 2000). We should observe such an effect in the case of any area that is limited on all sides. Let us imagine that species with different,

randomly selected but small sizes of their ranges are scattered at random in such an area. The spatial distribution of such species will be more or less variable in this area. There is no reason to expect any gradient in any direction that can be distinguished in the area under consideration. The situation is different for species with large ranges, comparable to the size of the area, although not necessarily as large as the area itself. In order to fit into the available area, these will have to be in such a place that the centres of their ranges coincide with the centre of the area they occupy. If we additionally assume that a higher density of a population occurs in the middle of its range, then we get a clearly visible increase in the number of species near the centre of the area considered.

The above model works for a two-dimensional area as well as for a one-dimensional case. In both cases, we can observe the presence of biodiversity gradients. Imagine a line stretching from the Mediterranean Sea, or from the southern edge of the Sahara for species that cannot tolerate a lack of water, to South Africa. Then the equator falls in the middle of such a line, and the centres of the ranges of species that fill the area of tropical Africa would be located on the equator.

The same hypothesis could explain the latitudinal gradients of biodiversity in South America, because the land areas there are similarly located relative to the equator. In Southeast Asia and Australia, however, the situation is different: large land areas are located on one side of the equator, so the assumptions of this model seem to be very simplistic.

There are some reservations about the validity of the arguments put forward by the mid-domain hypothesis. No species arises with a precisely defined range, but rather its geometric form is subject to many ecological influences of varying intensity. Moreover, many species have discontinuous ranges. We also usually have some difficulty in precisely defining the geometry of species'

range boundaries. It is currently accepted that the mid-domain effect may have some power to explain latitudinal gradients in biodiversity, but for those areas where the equator runs through their midpoint and for species with large ranges. It should also be mentioned that recent tests of this hypothesis have yielded rather unsatisfactory results (Currie and Kerr 2008).

5.3. Energy abundance hypothesis

Studies that use very large databases of geographical locations of species (although sometimes these refer to higher taxonomic units) show strong dependence of biodiversity on climate (Clarke 2007; Currie 2007). These comparisons were made on the scale of large regions and mainly concerned the level of primary producers, for example vascular or flowering plants, and sometimes other groups of organisms. The characteristic of climate is usually temperature or, more often, temperature and water availability.

The tropical region receives more solar energy per unit area than the temperate and polar zones. This means not only a greater flux of energy reaching the Earth's surface, but also higher average temperatures in the tropics. As a result, this leads to higher primary production in the tropics, of course where water shortages do not limit it. This probably means a greater number of organisms taking advantage of this abundant primary production. However, this does not automatically have to be associated with greater biodiversity, since one can imagine a single hypothetical species of primary consumers represented by a huge number of individuals, which dominated the ecosystems of tropical regions. However, taking into account the mechanisms mentioned earlier, which may promote a higher rate of speciation in the tropics, it is reasonable to assume that higher primary production will enhance these processes and promote greater biodiversity in the tropics (Pianka 1966).

In addition, the above mechanism may be aided by the fact that the tropics, compared

to regions located further north or south, are not only warmer, but they also have more stable climatic conditions throughout the year; solar energy is more evenly distributed there over time, and the growing season lasts longer or there are no winter breaks at all there, unlike in temperate regions of the Earth. Food for primary consumers is available for longer. This may encourage the development of food specialization of species living in the tropics, which consequently weakens competition between them and leads to an increase in the biological diversity of the tropics.

Currie and Paquin (1987) and Currie (1991) conducted studies in the tropics on the species diversity of trees and vertebrates such as amphibians, reptiles and birds, comparing the results with those for North America. All these groups showed a regular geographical pattern of species diversity. The number of tree species was well correlated with evapotranspiration and with all the factors influencing it – latitude and insolation, and less strongly with humidity and precipitation. Thus, the better the physical conditions for primary production, the more tree species. Evapotranspiration was also a factor strongly correlated with the species diversity of the terrestrial vertebrates studied.

Temperature affects the speed of biochemical reactions, which can increase the frequency of mutations and, consequently, the likelihood of the emergence of features that allow the exploitation of available ecological niches. At higher temperatures, especially in the absence of clear seasonal changes, organisms grow and mature faster, and generations last shorter. A high and constant ambient temperature guarantees cold-blooded organisms a continuous, high metabolism. In a warmer climate, a warm-blooded organism can devote more energy to other purposes. This enables the evolution of a greater variety of life strategies, or this made possible the evolution of energy-costly adaptations. However, warm-blooded organisms have to bear high costs of thermoregulation. The climate in the tropics not only accelerates the process of evolution and speciation but also creates much greater opportunities for natural selection to influence biodiversity compared to colder climates and those characterized by more pronounced seasonality (Weiner 2020).

5.4. Other ecological hypotheses

The range of a species increases with distance from the equator (Rapoport 1982). The explanation for this so-called Rapoport rule refers to climatic conditions. In temperate latitudes, climate conditions are more variable than in the relatively stable thermal environment in the tropics. Species from the temperate climate zone had to develop a wide range of adaptations to live in an environment with variable conditions. This allowed species from the temperate zone to extend their range into diversified areas, in other climate zones. Rapoport's rule is also true for the elevation gradient. It follows that where species have a larger range, i.e. in zones further from the equator, fewer of them can "fit" into an area of the same size as in the tropics.

In 1967, another hypothesis appeared that fits well into the above sequence of ecological-evolutionary arguments (Janzen 1967). It seems that mountains in the tropics may constitute a greater barrier to the dispersal of organisms than in more northern regions. However, this is not because mountain passes in the tropics are located higher, but because of physiological factors. In the tropics, species living in valleys adapted to live in higher temperatures have difficulty in overcoming the thermal barrier created by the higher parts of the mountains. In the temperate zone regions, this is probably easier for the organisms living there. The consequence of this phenomenon is greater geographical isolation of species living in the tropics, and consequently their faster rate of speciation.

The following arguments presented by Janzen (1970) and Connell (1978) provide evidence that an increase in biodiversity in a certain group of organisms can also

affect its increase in other groups ecologically related to the former. If we assume that the number of herbivores and plant parasites (in both cases, let them be insects) is greater in the tropics, which can be explained by greater primary production in these regions, then plants will "try" for their offspring to germinate further away from the parent plant, because they will not be subjected there to the pressure of species that "make life difficult" for the parents. As a result, this leads to greater spatial heterogeneity of plant communities in the tropics than in higher latitudes and, in turn, promotes an increase in biodiversity in the tropics.

Theoretical considerations suggest that interspecific competition may be the cause of greater species diversity at each trophic level, as natural selection promotes speciation, which leads to narrowing the width of ecological niches. At the same time, competitive exclusion of species with similar niches reduces the diversity of the community of competing species. In turn, greater diversity of predators and their more intensive interactions with prey in the tropics will lead to a situation in which a greater number of competitors will be able to co-occur (Morin 1999). This would be in accordance with the already classical concept postulated years ago in theoretical ecology, that the complexity of an ecological system is the cause of its stability (Elton 1958, May 1973). Observations of nature in the tropics show what the result of these contradictory tendencies may be. In the tropical forests of the Amazon, on the Venezuelan-Brazilian border, one hectare can contain 580 trees of 283 different species, and in the rainforest on the island of Borneo, trees of 1175 species grow on 52 hectares (Hubbell 2001). Disturbances such as hurricanes destroying forests or storms destroying coral reefs (Rhode 2005) may also explain the high diversity of species in the tropics, with relatively little differentiation in their ecological niches. For this reason, these ecosystems do not reach the species-poor equilibrium state postulated by classical theoretical ecology (May

and McLean 2007). Connell (1978) argues that most real ecosystems never reach equilibrium, and some high-intensity disturbances such as hurricanes and typhoons occur much more frequently in the tropics than in temperate zones.

Morin (1999) points out that if we assume that the tropics are the cradle of biological diversity, then species originating in the tropics, especially sedentary species with a relatively short history, may not have had time to spread to habitats located in temperate zones. This author uses the same argument to note that the process of competitive exclusion of species has not yet had time to proceed so far in the tropics as to reduce their diversity.

5.5. Human impact

The majority of the human population is located in the temperate zone (especially in the Northern Hemisphere). The vast majority of large, economically developed urban centres, characterized by increased human activity, are located outside of the tropics. Since human presence and activity most often adversely affect the environment and biodiversity, this may be the reason for greater biodiversity in the tropics, where humans have had lesser impact on nature.

6. Explanations of Reverse Diversity Gradients

It appears that some of the reverse diversity gradients can be explained by relatively simple physical and ecological factors. For example, the southern regions of North America are relatively dry and have low primary production (Hulbert and Haskell 2003). As a result, the species diversity of birds with breeding grounds in North America declines southward. In turn, the decline in the diversity of fauna inhabiting the pitchers of the *Sarracenia purpurea* can be attributed to an increase in the abundance of predators using this food source (Kneitel and Miller 2002; Buckley et al. 2003). In contrast, the reverse gradient observed in seaweeds from the Pacific coast of South America

results from the co-occurrence of species of different origins (Santelices 1980). This area is characterized by a high proportion of endemic species (over 32%) and an unevenly distributed share of tropical species (a share of several percent) and subantarctic species (their share is also over 30%) along the coast. The number of tropical species decreases towards the south, the number of subantarctic species increases, and the number of endemics is relatively constant along the entire coast.

For other reverse gradients, more specific hypotheses are needed. Janzen and Pond (1975) and Janzen (1981) formulated the so-called resource fragmentation hypothesis to explain the reverse latitudinal gradient of diversity in Ichneumonidae. The larvae of these insects are parasitoids of the larvae of other insect species. This is usually associated with a high degree of specialization of the parasitoids. If the potential hosts of Ichneumonidae species are characterized by the regular diversity gradient, then their species diversity in the tropics will be high, which may make it difficult for specialist parasitoids to find a suitable host. Only parasitoid species with a low degree of specialization will be able to maintain viable populations. Populations of specialist species will become extinct, which will then lead to a decline in Ichneumonidae diversity in the tropics. This effect may be amplified by increased predation in the tropics (Pain 1966; Elton 1973), and it is likely that resource fragmentation (which parasitoids receive from their diverse hosts) will further impede speciation of specialist parasitoids (Shaw 1994).

The common host hypothesis is a certain elaboration of the earlier resource fragmentation hypothesis (Dixon 1987; Kindlmann 1988). It formulates more precisely the conditions that parasitoid species characterized by a reverse gradient of diversity should meet: it should be a specialist in terms of host selection, it should repeatedly and cyclically search for this host and do it in a random manner, and the search time

should be short, while the species diversity of the group to which the host species belongs should show a regular latitudinal gradient of diversity. Parasitoids with such features will be characterized by a reverse gradient of diversity – their diversity in the tropics will be lower. This will happen because, with a high diversity of hosts in the tropics, none of them will be common enough for parasitoids to encounter it.

Toxicity is more common among tropical plant species than in temperate zones (Levin 1976). This observation has led to the formulation of the so-called nasty host hypothesis. Insects such as aphids that directly use plant resources and consequently parasitoids of such insect species will have difficulty finding a safe food source. This may lead to a decline in the diversity of these insect groups (Gauld et al. 1992).

Conclusion: Are the Tropics More Diverse?

The problem addressed in this paper concerns the diversity of nature on a vast time and spatial scale. It would not be an exaggeration to say that it concerns the entire current diversity of nature on a global scale, as well as the entire evolutionary history of nature, which took place against the background of the geological history of the Earth. The biodiversity gradient is an attempt to find order in this variability. As one can see, it is difficult. After getting familiar with the available material on biodiversity gradients, we may have the impression that we know less than we did before. There is neither certainty that latitudinal gradients of diversity actually exist, nor (if we assume that they do) that we can clearly indicate a convincing hypothesis explaining their causes. This state of affairs is caused by a great many factors of different nature, intertwined and most often difficult to clearly indicate.

A separate and very important problem is the quality of available data on species diversity. These are compilations made very selectively in terms of where they come from and the group of organisms they concern.

According to Rosenzweig (1995), the data documented so far on the diversity of terrestrial ecosystems in the tropics are greatly underestimated. Most of what we know comes from the two lowest meters of ecosystems, which in fact reach up to 50 or even 60 meters. This is due to the fact that the upper levels of tropical forests are difficult for researchers to access. It is perhaps also significant that most research centres dealing with biodiversity are located in the Northern Hemisphere outside the tropics, and research in the tropics is an extraordinary event for them. Phillips et al. (2019) and Cameron et al. (2018) point to the huge disproportion in our knowledge of the diversity of soil organisms compared to organisms with an overground lifestyle and the lack of information from vast areas of Siberia, Canada, Central Africa and Central Asia. Most studies on the diversity of soil organisms have been conducted in Europe and the USA. Important elements that are missing in the considerations of diversity gradients are Siberian ecosystems (for example taiga) despite the fact that there is a rich literature on them. The results of studies conducted there (see for example: Pavlov (2006), Striganova (2009); Striganova and Poriadina (2005)) are not taken into account by western researchers of biodiversity gradients.

It should also be said, however, that there are existing premises which may lead to the conclusion that points to the existence of regular latitudinal gradients of biodiversity. The data concerning them cover a wider spectrum of species and environments. In turn, examples of reverse latitudinal gradients concern more specific situations. From the arguments presented in this paper in the form of facts and hypotheses, it follows that the most probable explanations for regular latitudinal gradients of biodiversity should be considered as follows: (1) the middle domain effect, (2) a larger and continuous area of the tropics, (3) more opportunities for speciation for various reasons, (4) warmer and less variable climatic conditions, and (5) a long and more stable geological history.

It is also worth noting that the arguments for regular and reverse gradients of biodiversity discussed above are of different quality. Each example of a reverse gradient of diversity finds its own explanation in the specific ecological and evolutionary situation in which the species described happened to live. On the other hand, explanations of regular gradients of diversity are general hypotheses, related of course to the specificity of life in the tropics, but general enough to be applied to very different species occupying different ecological niches. This may indicate the real existence of regular gradients of biodiversity, from which, as always in nature, there are exceptions.

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